Effect of biotic interactions on the structure

of microphytobenthos

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Kiel 1999

DOI 10.3289 / IFM_BER_308

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1 Introduction

The benthic microalgae inhabiting the littoral of marine and brackish coastal areas have been taxonomically investigated since the beginning of the last century (Kützing 1844, Karsten 1899, Edsbagge 1966). Different communities were distinguished with respect to their substrate (Round 1972): "epilithon" denotes algae on hard substrates, "epiphyton" on other plants, "epipelon" consists of (mainly mobile) algae inhabiting fine sediments, and "epipsammon" of algae attached to sand grains. In freshwater research, the term periphyton (Aufwuchs) was widely applied for benthic algae, consisting of unicelluar and filamentous species. Within these communities, the establishment of phytosociological entities of taxa inhabiting the same vertical or horizontal microhabitat was attempted (e.g. Aleem 1950, Edsbagge 1966).

Despite this long history of research, the knowledge on forces structuring the microphytobenthic community remained poor, especially in comparison to the work done in phytoplankton. Only during the last two decades the research on benthic microalgae was intensified and extended to the ecology of these organisms (Admiraal 1984). It became obvious that benthic microalgae play an important role in the coastal environment in terms of primary production and biomass, often exceeding an annual production of 200 g C m^{-2} a^{-1} (Cadee 1980, Colijn & de Jonge 1984, Pinckney & Zingmark 1993). On tidal flats, the microphytobenthos consisting of diatoms and cyanobacteria tends to be the only benthic autotrophic community (Cadee & Hegeman 1974), but even in seagrass beds the edaphic algae may contribute >20% of the total benthic primary production (Daehnick et al. 1992).

The observation that the microphytobenthos is exposed to harsh abiotic conditions in tidal areas like the Dutch-German wadden sea led to intensive research on physical and chemical parameters affecting the growth and biomass of benthic microalgae. There was strong indication that benthic microalgae in the Wadden Sea were highly tolerant against changes in salinity (Admiraal 1977c), temperature (Admiraal 1977b, Admiraal & Peletier 1980), sulphide concentrations (Admiraal & Peletier 1979), or ammonia concentrations (Admiraal 1977a, Admiraal et al. 1987).

Generally, biotic interactions like facilitation, competition and grazing were considered less important (Admiraal et al. 1983, Admiraal 1984).

This view has been shifted. Studies investigating the effect of nutrient supply and enrichment revealed the occurrence of nutrient limitation for sand-inhabiting microflora and the effect of changed nutrient supply on biomass and community composition (Sundbäck & Snoeijs 1991, Pinckney et al. 1995). In laboratory experiments, Sommer (1996a) showed that changes in N:P:Si supply ratios led to changed dominance patterns of attached algae. These patterns were qualitatively similar to those known from phytoplankton studies. Freshwater experiments with artificial nutrient enrichment showed the response of the taxonomic composition, architectural structure, biomass and diversity of periphyton communities to changed nurient conditions (Pringle & Bowers 1984, Fairchild et al. 1985, Pringle 1987, 1990). Those experiments indicated the presence of nutrient competition, but an explicit test of the importance of competition is still missing and progress towards a conceptual model of community organization has been slow (McCormick 1996).

The effect of herbivory on microalgae was studied first in marine habitats (Castenholtz 1961, Nicotri 1977), but subsequent research has been more intensive since then in freshwater (Steinman et al. 1987, Hill & Knight 1987, Feminella & Resh 1991), leading to a consistent body of results on changes in biomass and structure of benthic microphytes due to herbivores (Steinman 1996). However, only few studies have investigated competition and grazing simultaneously, showing effects and interactions of both bottom-up and top-down processes (Neckles et al. 1993, Rosemond 1993). Facilitation was proposed to be a primary force of succession in periphyton (Blinn et al. 1980, Hoagland et al. 1982, Miller et al. 1987).

In the case of marine microphytobenthos, the knowledge on biotic interactions remained scarce. In contrast, several common patterns in microbenthic communities lack proper explanations. An example are repeated seasonal patterns with a distinct spring bloom, followed by a summer minimum of biomass and sometimes a second bloom in autumn (epipelon & epipsammon: Wasmund 1986, Underwood & Paterson 1993; epiphyton: Snoeijs 1994; artificial substrates: Kawamura & Hirano 1992). Ultimate factors for the described biomass decrease in summer have not been analyzed.

The lack of mechanistic understanding of the functioning of the marine littoral microflora is surprising, not only because of their contribution to primary production (see above), but also because benthic microalgae may provide information for applied and basic aspects of community ecology. On the one hand, coastal ecosystems are greatly influenced by human impact, e.g. by eutrophication (Cederwall & Elmgren 1990, Valiela et al. 1997), but the significance of these changes for benthic microalgae and their consumers is not established. A more thorough investigation could lead to the use of benthic microalgae as indicator organisms (for freshwater, see Lange-Bertalot 1978, 1979; Rott et al. 1998). On the other hand, benthic microalgae could serve as model organisms for ecological theory, because of their short generation times and their structural similarity to terrestrial vegetation. Phytoplankton studies have been very influential in ecology (Tilman 1977, Sommer 1983), but pelagic organisms live in a rather homogenous habitat compared to benthic and terrestrial vegetation (Huston & De Angelis 1994).

The main objectives of this study were:

- to investigate the effect of biotic interactions, especially nutrient competition and herbivory, on the biomass, species composition and diversity of benthic microalgae

- to evaluate the influence of increased nutrient supply (eutrophication) on these interactions

- to compare these results on coastal marine epilithon with concepts drawn from phytoplankton and freshwater periphyton.

These topics were analyzed experimentally *in situ* and in the laboratory. The field experiments were chosen to allow a high degree of realism and the employment of a natural species pool. Since the degree of control is lower *in situ* than in the laboratory, I conducted additional experiments on the stoichiometry of nutrient-limited benthic microalgae in the laboratory. The outline of this thesis is structured in different chapters, dealing with these different aims:

- Colonization experiments were conducted *in situ* to reveal patterns emerging during the initial development of the benthic microflora on newly established substrates. Data on species composition and diversity were obtained in order to

evaluate the suitability of the substrates and the experimental setup used for *in situ* enrichment experiments. Furthermore the experiments were designed to give insight into the analogy between terrestrial and microbenthic succession (Chapter 2).

- Laboratory experiments were conducted to investigate the use of biomass stoichiometry as an indicator of nutrient limitation in periphyton under different abiotic conditions (Chapter 3). The results of these experiments were used to evaluate the C:N:P ratios of natural microalgal assemblages.

- *In situ* experiments were performed to investigate the response of benthic microalgae to nutrient enrichment, in terms of biomass, species composition and diversity. The main objectives were to detect the pattern of nutrient limitation and the dependence of species composition on nutrient supply ratios, thus allowing to evaluate the importance of competition in marine periphyton (Chapter 4).

- The simultaneous influence of herbivores and nutrient enrichment on periphyton was analyzed in cage experiments, in which herbivores were excluded and nutrients added. Moreover, the spatial and temporal variability of top-down control and the impact of trophic cascades exerted by fishes were tested in these experiments (Chapter 5).

- The experimental results will be discussed in the general context of benthic ecology, resulting in a conceptual model of periphyton organization (Chapter 6).

- Background information will be given in separate appendices. These comprise a glossary and a list of abbreviations (Appendix 1), a species list of benthic microalgae (Appendix 2), data on herbivore abundances (Appendix 3) and a survey on literature data on benthic microalgal diversity (Appendix 4).

2 Colonization of artificial substrates

2.1 Introduction

Artificial substrates represent new and open space for benthic colonizers, and the colonization of these bare substrates reflects a primary succession, enhanced by the multitude of propagules of benthic micro- and macroorganisms suspended in the water column (McIntire & Overton 1971). The sequence of species on new substrates has rarely been in the focus of marine studies (but see MacLulich 1986). In freshwater ecosystems, it was shown that the colonization of new substrates by periphyton follows distinct patterns, which are similar to those in terrestrial habitats, generally increasing the complexity of physical structure in the system (Hudon & Bourget 1981, Hoagland et al. 1982).

In the following chapters, experiments on the effect of nutrients and herbivores on microphytes will be presented, most of which are *in situ* experiments employing artificial substrates (Chapters 4 and 5). In order to evaluate the results of these experimental manipulations, it is important to know the colonization process of benthic microalgae on these artificial substrates, the available species pool, and the abiotic and biotic environment of the experiments. These informations will be provided in this chapter. Furthermore, analogies to the colonization process in terrestrial (Connell & Slatyer 1977, Pickett & McDonnell 1989) and planktonic succession (Sommer et al. 1986) will be discussed.

The colonization of artificial substrates by benthic microalgae was analyzed on different time scales: days, weeks and months, using different types of substrates employed also in the enrichment experiments (Chapter 4). Specifically the following questions will be addressed: (i) Do the artificial substrates allow the attachment of benthic microalgae? (ii) Which amount of time is needed to establish a 'mature' epilithic biofilm after the exponential growth phase? (iii) Which replacement processes occur during the colonization process? (iv) Is there a trade-off between the colonization *versus* the competitive ability of microphytobenthic species?
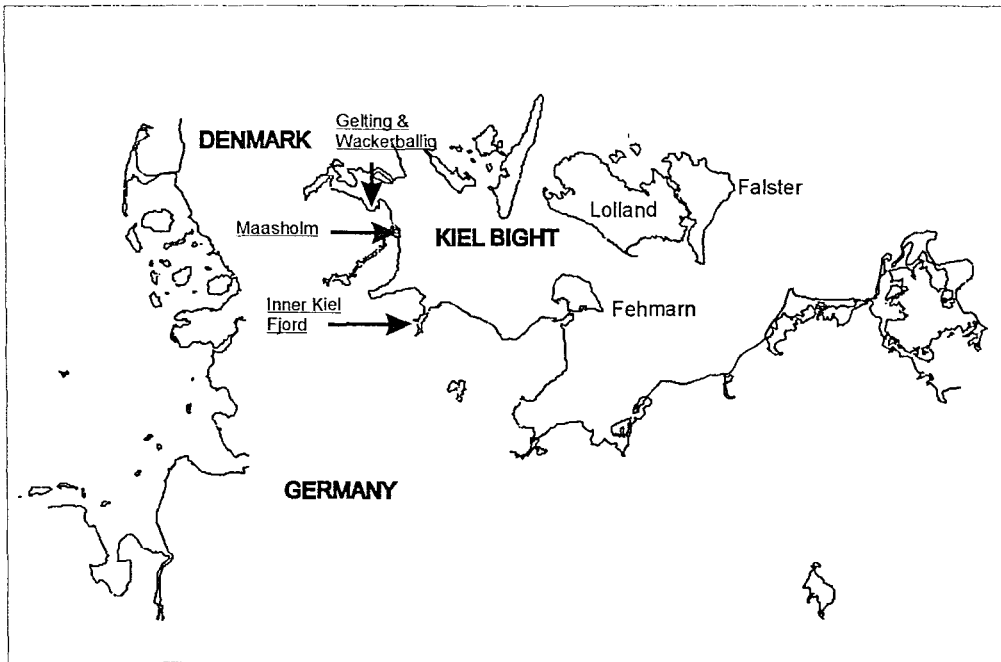
Fig. 2.1: Map of the Kiel Bight region showing experimental sites. In the Inner Kiel Fjord, colonization and enrichment experiments were conducted (Chapters 2 and 4). Grazing experiments were situated in Maasholm and Geltinger Noor/ Wackerballig (Chapter 5).
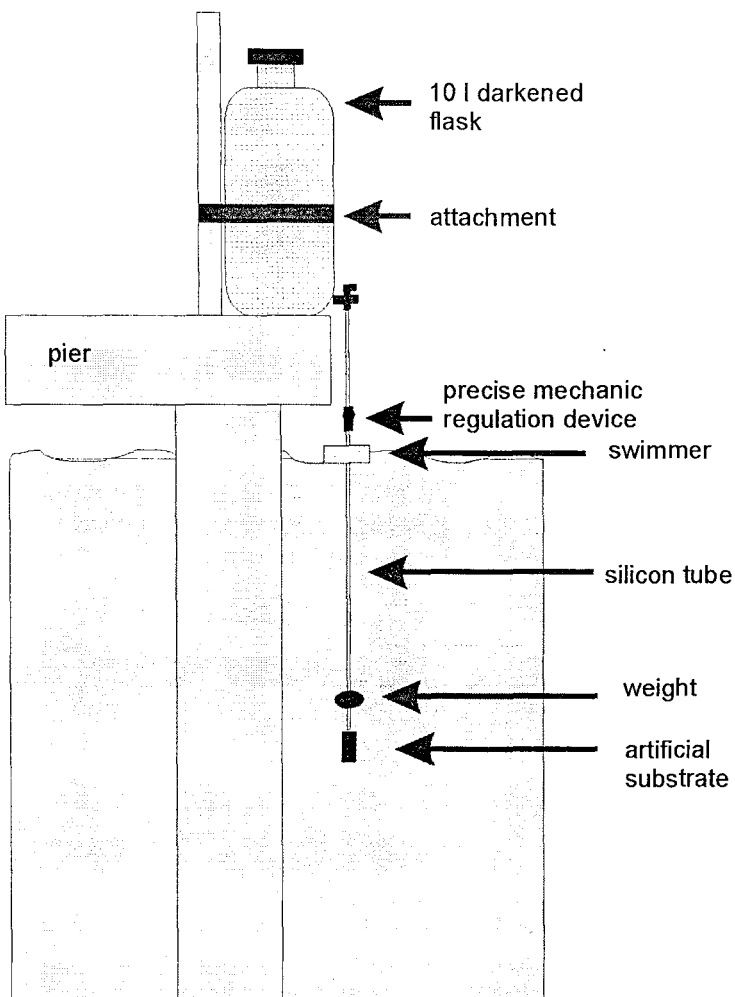
Fig. 2.2: Schematic diagram of one experimental unit, attached on the pier of the institute. One setup consisted of a 10 l darkened flask and an artificial substrate, connected with silicone tubes. For further details, see text.

2.2 Methods

2.2.1 Experimental setup

In situ experiments to investigate colonization patterns were conducted in the Kiel Fjord (Fig. 2.1) at the pier of the Institut für Meereskunde. Artificial substrates were suspended from the outermost, unused part of the pier to a mean depth of 1.5 m. Although the Western Baltic Sea is virtually non-tidal, wind-induced variations in water level occur. However, the artificial substrates remained at least 0.5 m below the water level.

Experiments with daily, weekly and monthly sampling intervals were performed (Table 2.1). The substrates for weekly and monthly sampled experiments consisted of kieselgur aquaria stones (50 x 25 x 25 mm³). The substrates for monthly aspects of colonization (in total 24 stones) were suspended in the water column in December 1996. Beginning with January 1997, two stones were collected in monthly intervals. For daily intervals, wood-substrates (25 x 15 x 15 mm³) were suspended in May 1998 and 3-4 substrates were harvested on each of 6 sampling dates.

Table 2.1: List of colonization experiments conducted in the Inner Kiel Fjord, giving information on names, duration, substrates, sampling procedure, and treatments.

experiment	time	substrate	sampling method	treatment
season 97	5 Dec 1996-9 Dec 1997	kieselgur	monthly intervals	none
autumn 96	26 Sep-12 Dec 1996	kieselgur	weekly intervals	+ 150 µM N + 10 µM P
spring 97	11 Feb-6 May 1997	kieselgur	weekly intervals	+ 150 µM N
summer 97	6 May-8 Jul 1997	kieselgur	weekly intervals	none
summer 98	25 May-3 Jun 1998	wood	daily intervals	none

For each of the three experiments with weekly sampling intervals, 12 experimental units were used. These experiments were designed to allow a direct comparison of colonization and enrichment experiments, for which only final harvest was analyzed (Chapter 4). Therefore, both experiments were performed with a similar setup. Darkened 10 l PE-flasks were installed on top of the pier of the institute in Kiel and filled with medium (Fig. 2.2). The medium was based on seawater from the

surrounding of the pier. This was filtered (0.2 µm cellulose-acetate filters) and enriched with different concentrations of nutrients. Nitrogen was added as $NaNO_3$, phosphate as KH_2PO_4. The concentrations of the other nutrients were not changed, i.e. remained at background levels (cf. Fig. 2.3). This liquid medium flowed through silicon tubes (inner diameter 4 mm) and trickled out through the artificial substrates. With a precise mechanic regulation device, which was invented for intravenous infusion (Angiokard AK 5505), the flow rate was adjusted to 1 l d^{-1}. Twice a week the supply bottle was refilled, the flow-rate was controlled, and readjusted if it deviated by > 10% from 1 l d^{-1}. In the colonization experiments, all bottles contained the same nutrient concentrations (Table 2.1). By sampling one stone per week, the colonization process could be followed. Each stone sampled and taken out was replaced by a new one and at the end of the experiment all treatments were harvested again. In this way two series of samples were obtained. In the first series, the different incubation times had equal starting points and unequal harvesting points. In the second series (replacement stones) the starting points were unequal, but the harvesting points equal. Substrates for monthly and daily aspects were not replaced.

2.2.2 Sample preparation and analysis

Immediately after collecting, the substrates were transported to the laboratory, and the algae were scraped off quantitatively until no pigment colour could be detected on the stones. The biomass was suspended in organism-free filtered seawater (0.2 µm cellulose-acetate-filters). Subsamples were fixed with Lugol's iodine (10 g KI + 5 g I per 100 ml) and counted within five weeks. Algal cells were counted with an inverted microscope (Leitz DMIRB) at 400x magnification with standard Utermöhl-counting chambers (Hydrobios) (Utermöhl 1958). 1000 cells were counted at minimum per sample. To compare the different species, which spanned several orders of magnitude in size, biovolume was calculated by fitting nearest geometric models (Hillebrand et al. 1999). For this, linear dimensions were measured from 20 specimens of each species (except for rare species, which were present with fewer individuals). Measurements were done with an ocular scale, calibrated to an object micrometer.

Further subsamples were used for species determination. The species were determined alive during the first days following the sampling. Additionally, diatoms were analyzed on permanent slides. For these, a subsample was washed with bidest. H_2O, and subsequently oxidized in 30% H_2O_2 for 3-5 days. An aliquot was dropped on a slide and the liquid was vaporized by heating. Afterwards the sample was mounted in Naphrax (Biological Supplies Ltd.). Taxonomy of diatoms follows the nomenclature of Round et al. (1990) and Snoeijs (with co-editors 1993-98), beyond these Kuylenstierna (1989-90), Krammer & Lange-Bertalot (1986-91) and Pankow (1990) were used for determination. Taxonomy of other algae followed the nomenclature of Pankow (1990).

In order to know the planktonic species composition, pelagic samples were taken throughout the study period at the surface by a simple scoop. They were fixed by Lugol's iodine, counted and the species composition was determined as described above. Dissolved inorganic nutrients were analyzed from these samples with a Continuous Flow Analyzer using the methods of Grasshoff et al. (1983) for silicate, nitrate, ammonium and phosphate. All nutrient concentrations and ratios in this text are molar. Surface water temperature and mid-day irradiance level were read from continuous measurement devices of the institute.

2.2.3 Analysis of diversity and statistical analysis

Diversity comprises the number of taxa present and the equitability of the distribution of abundances among the different taxa. Diversity indices are proposed as univariate measures composed of both characteristics. The statistical behaviour of several diversity indices has widely been discussed and this discussion is far from being settled (Hurlbert 1971, Peet 1974, Pielou 1977, Robinson & Sandgren 1984, Krebs 1985, 1989; Valiela 1995). Therefore I employed two unrelated indices to show the robustness of my results. Since any two diversity indices are differently weighted regarding their sensitivity to species richness or equitability, they often show discrepancies in their response to changes in community composition (Hurlbert 1971). I adopted two statistics in common use, the Shannon-Weaver index H' and Simpson's index D', together with the species richness S and the evenness index J'. It was noted that H' is more sensitive to changes in rare species compared to D', which responds most strongly to changes in the most abundant species

(Krebs 1989). The insensitivity to the addition of rare species has been a major criticism against diversity indices (Sager & Hasler 1969, Brown 1973). However, rare species indeed make a minor contribution to communities and thus should have minor influences on community parameters like diversity (Hurlbert 1971). The insensitivity to minor changes enhances the reliability and objectivity of the indices, since the sampling effort is less influential.

Both diversity indices, H' and D', depend on contributions p_i of the ith species to the community or sample (Equ. 2.1 and 2.2). This can be expressed either in terms of contribution to total number of organisms or to total biomass. The calculation of H' based on biomass proportions was repeatedly recommended (Wilhm 1968, Hallegraeff & Ringelberg 1978, Cousins 1991). Some studies have used biovolume as biomass equivalent for benthic microalgae (Hill & Knight 1988, Carrick et al. 1988), since biovolume is an accessible way to measure the biomass of microbial species (Hillebrand et al. 1999) and includes size as a dominant denominator of biological processes in microbial communities (Steinman et al. 1992, Reynolds 1997, Sommer 1998). Since benthic microalgal species comprise several orders of magnitude in size, I decided to calculate the diversity indices on the basis of biovolume proportions throughout this study.

- Shannon-Weaver information theory index H'

$$H' = -\Sigma_{i=1}^{i=s} \ln p_i \cdot p_i \qquad \text{(Equ. 2.1)}$$

with pi : contribution of the ith species to the total biovolume of the community.

- complement of Simpson's index D

$$D' = 1 - D = 1 - \Sigma_{i=1}^{i=s} p_i^2 \qquad \text{(Equ. 2.2)}$$

Simpson's original index D measured the probability that two randomly depicted individuals represent one species. By using the complement D', the diversity of these organisms is analyzed (Krebs 1989).

- evenness J' (Pielou 1977)

$$J' = \frac{H'}{H\max} = \frac{H'}{\ln S} \qquad \text{(Equ. 2.3)}$$

This evenness index has recently been criticized for being dependent on species number (Smith & Wilson 1996). However, J' decreased with decreasing species number only if species numbers were <15. This threshold of species richness is exceeded in all microbial communities analyzed here.

- species richness S

The exact species number of a community cannot be estimated from samples. However, S can easily be compared if it is based on a standardized sample size, which was the case since I counted 3000 cells in the enrichment experiments and 1000 cells in the colonization experiments.

The development of diversity during colonization was analyzed with linear and non-linear model-I regression. In order to compare the species composition of the pelagic and benthic community, a multivariate graphic approach was used. Relative abundances according to Table A2 were used in order to avoid the separation of benthic and pelagic samples just by the different biomass magnitudes. For all experiments with benthic samples (n=30) and monthly pelagic samples (n=24), Euclidean distances were calculated and used to create a multidimensional scaling (MDS) plot.

2.3 Results

2.3.1 Taxonomic inventory

More than 230 species and varieties were determined in benthic and pelagic samples from the Kiel Fjord during the entire study (including the experiments described in Chapter 4). A complete species list is given in Appendix A2. However, more than 80% of total biovolume of microphytobenthos was contributed by less than 20 species throughout the study period 1996-1998. Tube-dwelling diatoms (*Berkeleya rutilans*, *Haslea crucigera* and *Navicula grevillei*) were highly dominant in spring, accompanied by the centric diatom *Melosira nummuloides* and the filamentous chlorophyte *Ulothrix flacca*. These were succeeded in summer by filamentous phaeophytes (*Ectocarpus siliculosus* and *Pilayella littoralis*), rhodophytes (mostly *Ceramium strictum* sensu Harvey) and the large centric diatom *Melosira moniliformis*. In autumn and winter, *Melosira moniliformis* was still

prevailing, partly together with *Odontella aurita*. Other important species were the epiphytic diatoms *Tabularia fasciculata* (mainly in spring), *Achnanthes longipes*, *Licmophora paradoxa* and *L. abbreviata* (summer), the mobile diatoms *Proschkinia complanata* (spring) and *Pleurosigma elongatum* (summer), and a second rhodophyte, *Aglaothamnion byssoides* (summer).

2.3.2 Seasonal aspects of colonization

There was a distinct seasonal development of abiotic parameters and of microalgal biomass (Fig. 2.3-2.6). Light and water temperature were positively correlated, with distinct maxima in summer (Fig. 2.3a). Nitrate, phosphate and silicate concentrations were highest in winter, whereas ammonium was highest in summer and autumn (Fig. 2.3b). Phosphate concentrations were less variable throughout the year, leading to shifts in the nutrient stoichiometry of the water column, with high N:P ratios in spring and low N:P ratios in summer (Fig. 2.3c). No data on salinity were obtained, but a distinct inflow of freshwater through the river Schwentine could be assumed from the proportion of oligohalobe species in plankton and benthic samples: Inferred from the salinity preferences shown in Table A2, the proportion of freshwater inhabiting species was highest in spring in both communities (Fig. 2.4).

The pelagic biomass also followed a seasonal trend, giving rise to a distinct diatom spring bloom, followed by additional biomass maxima of diatoms or dinoflagellates in summer and autumn (Fig. 2.5). The spring bloom of the diatoms occurred in March and April, dominated mainly by several *Chaetoceros* species (especially *Ch. cf. decipiens)* and *Rhizosolenia styliformis*. Highest biovolumes were found in late summer, consisting mainly of the chain-building diatom *Cerataulina pelagica* and *Skeletonema costatum*, as well as of several species of dinophytes (e.g. *Ceratium tripos, Heterocapsa triquetra, Katodinium rotundatum, Prorocentrum minimum)*.

The MDS-plot based on Euclidean distances (Fig. 2.6) visualizes that benthic and pelagic samples are clearly separated along the axis 1, with the exception of the August sample of the experiment season 1997, which was dominated by pelagic species after the interruption of the colonization process (see below). On the other hand, few distinct aggregations are visible, indicating high variability between years and between seasons.

a) light/temperature

b) nutrients

c) nutrient ratios
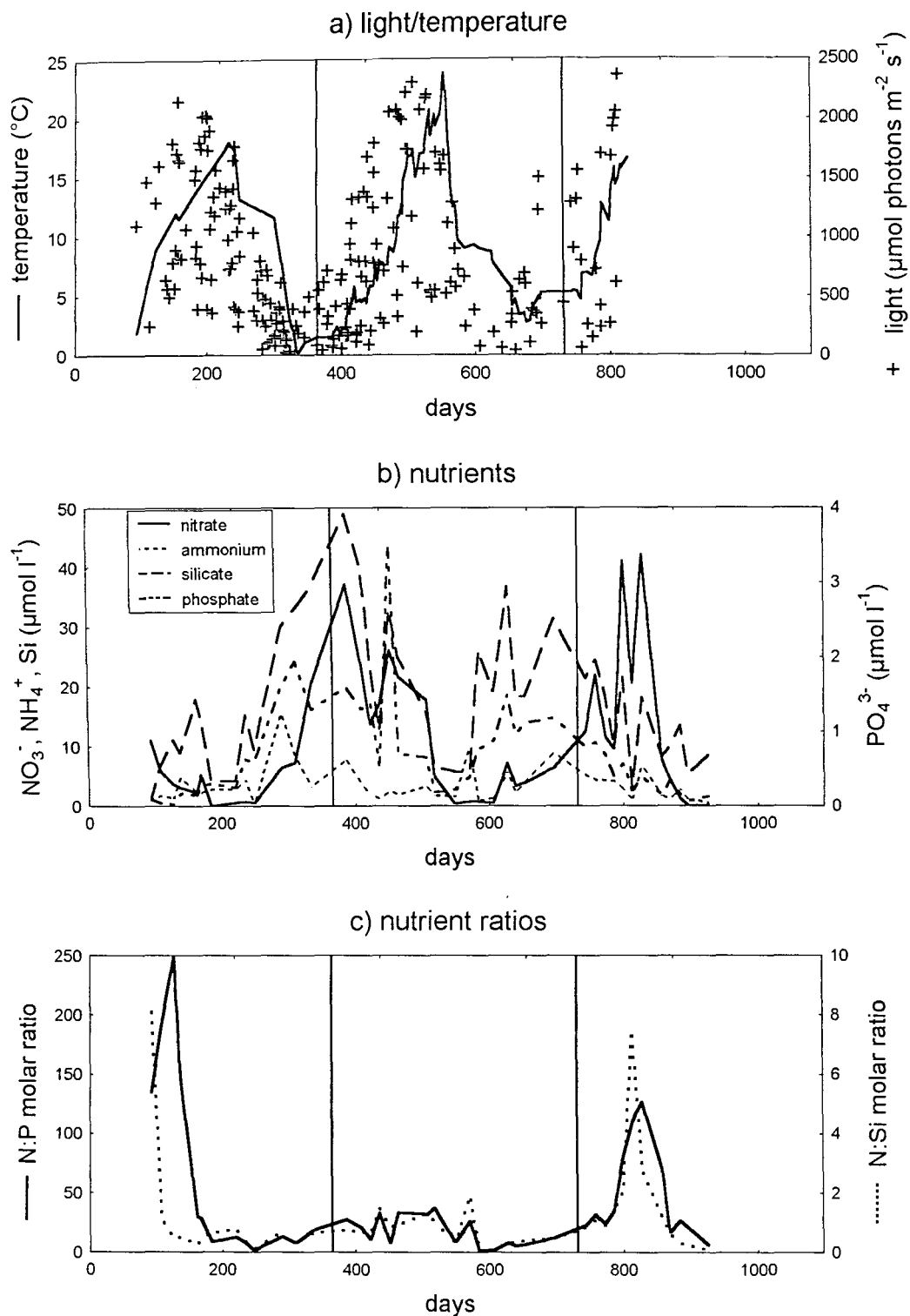
Fig. 2.3: Abiotic conditions during the study period April 1996 to July 1998. Days are given starting with Jan 1st 1996, the vertical lines indicate beginning of 1997 and 1998, respectively. a) Light and temperature data from continuous measurement devices of the institute. b) Concentrations of nutrients at the experimental site in the Inner Kiel Fjord. c) Molar nutrient ratios at the experimental site.
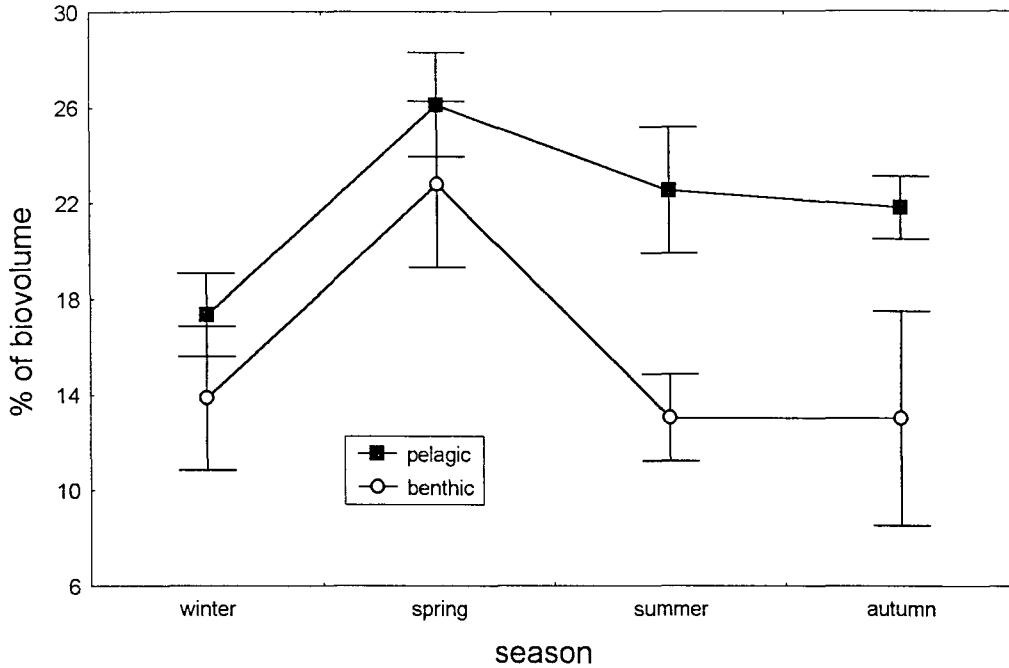
Fig. 2.4: Proportion of species (mean ± standard error) which are oligo- or oligomesohalob in benthic and pelagic samples. Proportions are inferred from relative abundances and literature data on salinity preferences (Table A2).
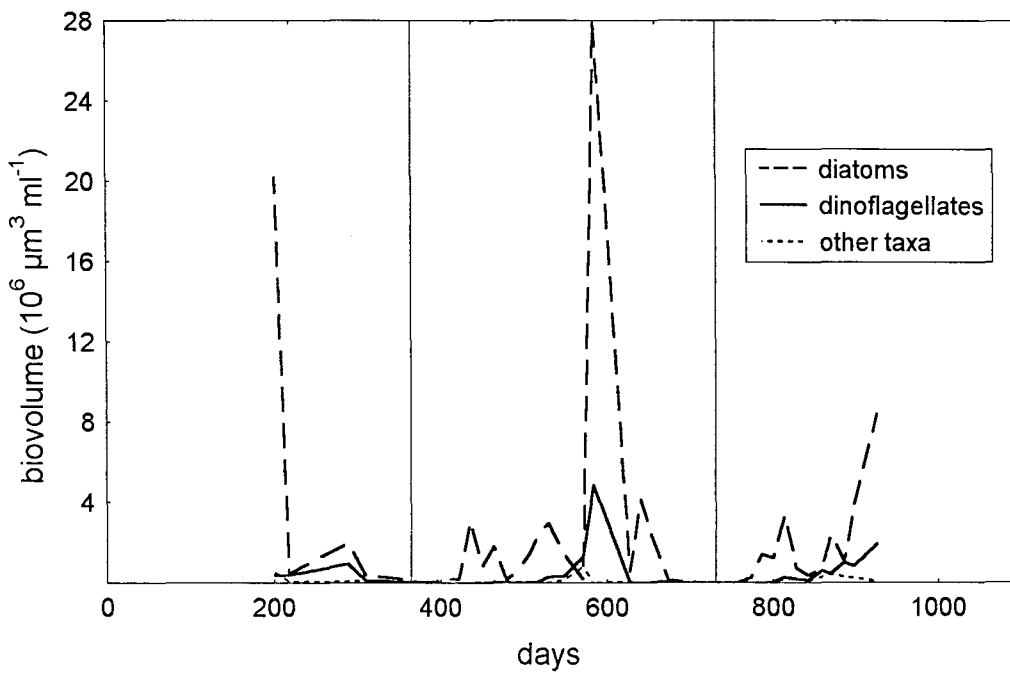
Fig. 2.5: Pelagic algal biovolume during the study period, differentiated for diatoms and dinoflagellates. For more details see Fig. 2.2.

○ spring □ summer △ autumn ◇ winter
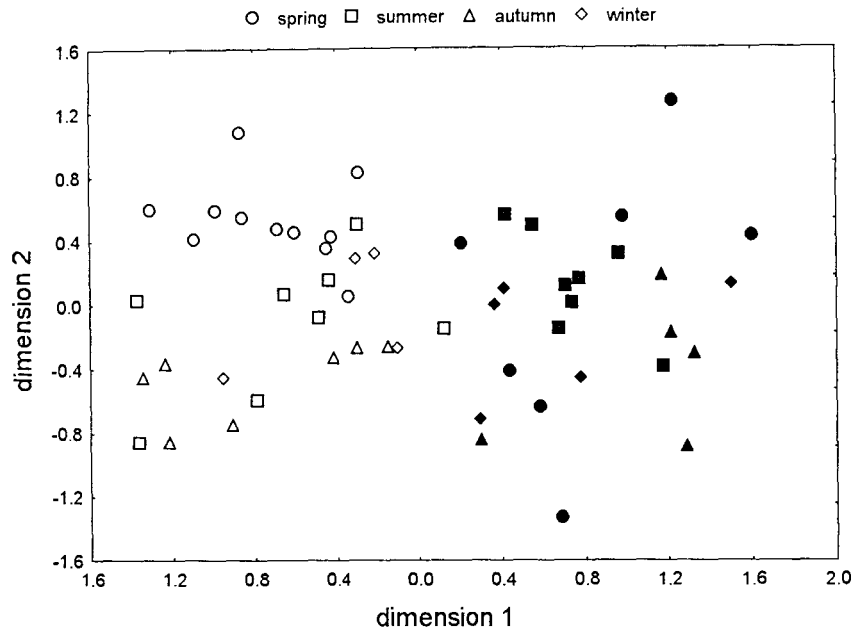
Fig. 2.6: MDS-plot of species composition of all pelagic and benthic samples, merged with Gutman-Lingoes procedure (Statistica 5.1). Different symbols denote different seasons, open symbols represent benthic samples and closed symbols pelagic samples. Plot represents final configuration of Euclidean distance matrix, final stress: 0.169, final alienation: 0.179.
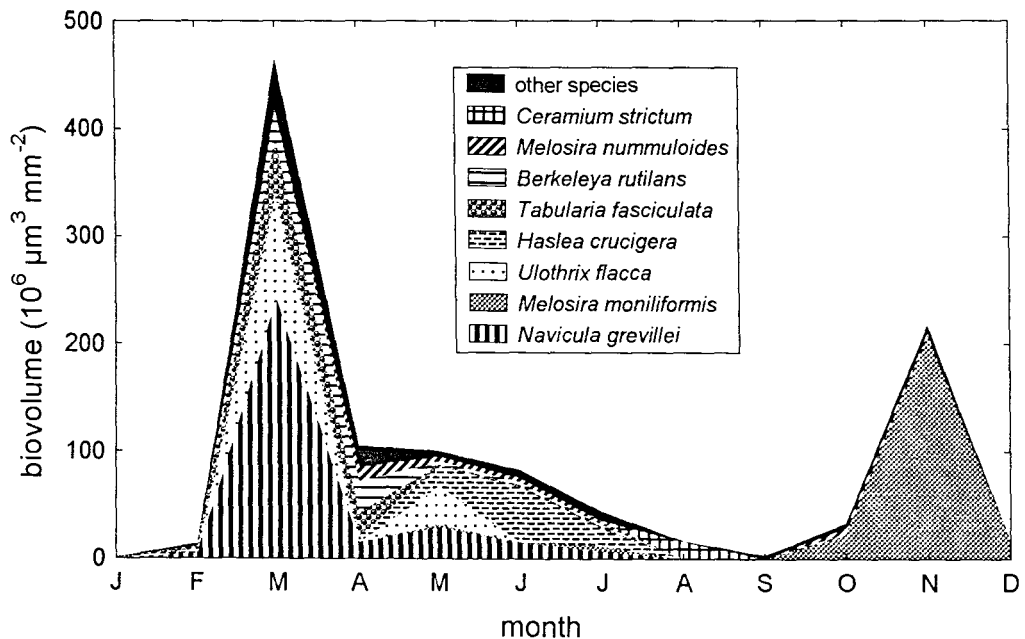
Fig. 2.7: Microphytobenthic biovolume and contribution of dominant species on artificial substrates, collected in monthly intervals in 1997.

In the experiment season 1997, the biomass of benthic microalgae reached a maximum peak in March, dominated by the tube-dwelling diatoms *Navicula grevillei* and *Haslea crucigera*. The biomass decreased during the summer months with a minimum in September, afterwards a second biomass peak occurred in late autumn (Fig. 2.7). This was dominated by the centric diatom *Melosira moniliformis*. Fig. 2.8 shows the contribution of different growth forms to the total biovolume. Single-celled species dominating in late winter were replaced rapidly by tube dwelling species, which dominated until August. After a sharp break, a new dominant group emerged, consisting of large chain-building species. This drastic change coincided with bivalve recruitment. This started in June and led to the visible dominance of small individuals of *Mytilus* on the substrates during July and August. The *Mytilus* colonization changed the character of the substrates, initializing a second colonization period, beginning with the loose attachment of pelagic species. Thus, the seasonal development of the community on these hard substrates was divided into two parts. The second part of the succession led to turfs of filamentous algae and large, chain-building diatoms inhabiting the space between the clusters of *Mytilus* individuals.

2.3.3 Short-term colonization of artificial substrates

The development of the microphytobenthic communities is shown in Fig. 2.9 and 2.10 for the 2 series of the 3 colonization experiments (Table 2.1). After an exponential growth phase lasting 4-6 weeks, a plateau of total biovolume was reached in these experiments (Fig. 2.9). Lower temperature in the autumn 1996 experiment increased the time until a plateau was reached (see autumn series 2 in Fig. 2.9).

At the beginning of each colonization series, the microphytobenthic community was a random sample of the benthic species suspended in ambient seawater, but at the end the dominant species were the same in the two series of one experiment (Fig. 2.10). In autumn, an overwhelming dominance of *Melosira moniliformis* was visible, in spring most biovolume was contributed by the tube-dwelling diatom species *Haslea crucigera*, *Berkeleya rutilans* and *Navicula grevillei*, together with the centric diatom *Odontella aurita*. Only in summer 1997, the second series of the experiment was dominated by *Enteromorpha* sp., which was not abundant in the first series.
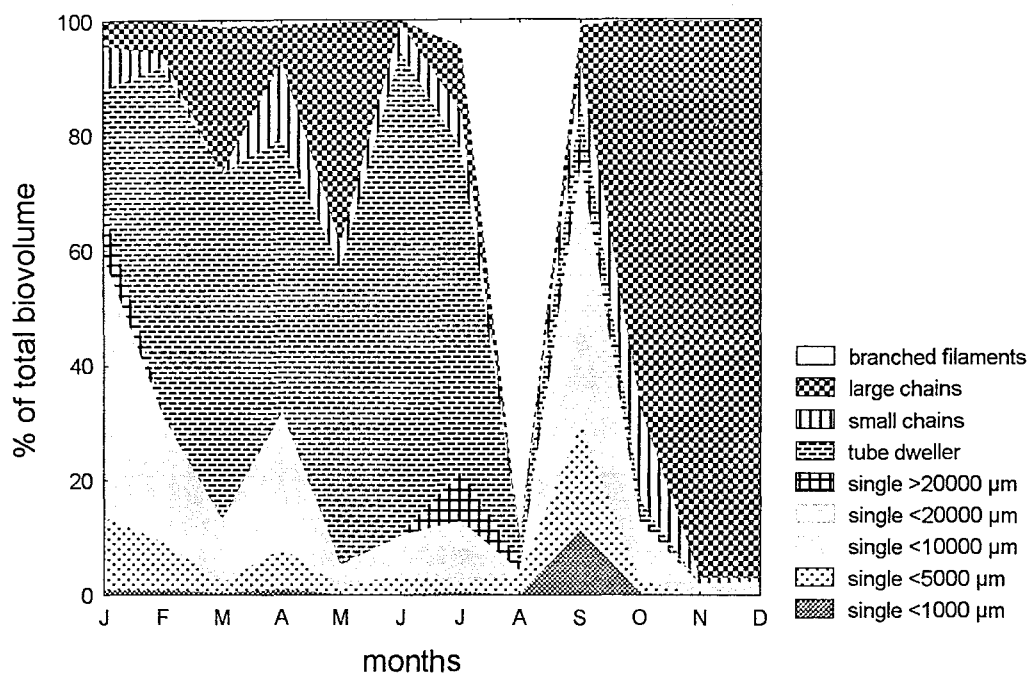
Fig. 2.8: Seasonal succession of growth forms in microphytobenthos on artificial substrates, based on data in Fig. 2.7. Single cells (including species occurring in small packages up to 5 cells) are divided on the basis of cell volume, chains are divided on the basis of chain diameter (threshold: 25 µm).
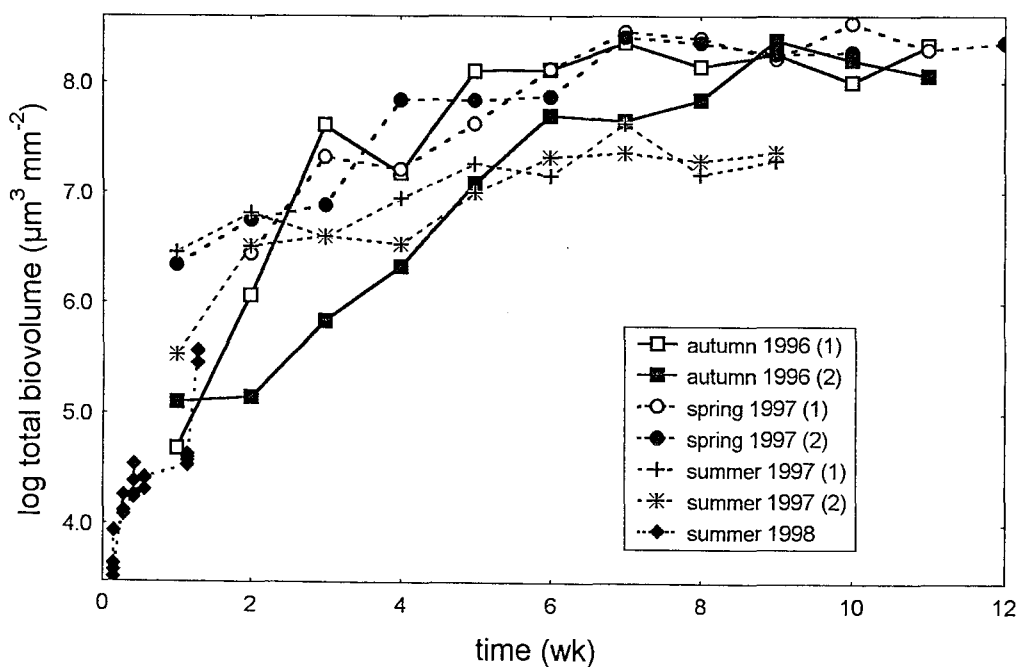
Fig. 2.9: Total biovolume of benthic microalgae in colonization experiments dependent on time. For each experiments two series are plotted since harvested substrates were replaced (see text and Table 2.1 for more details on experiments).

Only few species were distinctly early- or late successional. Among these were pelagic species like *Skeletonema costatum* in early colonization (Fig. 2.11), or *Melosira moniliformis* and some filamentous algae in later stages of colonization (Fig. 2.10). For many species, there was a distinct seasonal impact on the temporal performance during succession. *Navicula grevillei* and *Haslea crucigera* were dominant at later stages in spring, but in early stages in summer. *Berkeleya rutilans* dominated the late-successional communities only in spring, in summer it was a mid-successional subdominant. Other species changed from early to mid-successional maxima during seasons, e.g. *Odontella aurita*.

At the level of life-forms, a clear dominance of erect species was visible (Fig. 2.12), which established already during the first weeks. This corresponded to the dominance of erect species in the season 1997 experiment and in subsequent enrichment experiments (Chapter 4 and 5).

The species number found on artificial substrates after different times of incubation is shown in Fig. 2.13a. There was a steep increase in species number, reaching a plateau of ca. 25 species per 1000 cells. The dependence of species richness on incubation time could be described equally well with linear and nonlinear regression models (Table 2.2). On the other hand, there was also a significant decreasing trend of J', D' and H' during the successional development (Fig. 2.13b). This resulted in significant negative regressions of H' (slope b = -0.06, r= -0.46), J' (b= -0.03, r= -0.542) and D' (b= -0.02, r= -0.408) on incubation time (p<0.001, n=84). An initial increase could not be detected for any of these indices.

Table 2.2: Results of different regression models describing the dependence of species richness of benthic microalgae on incubation time. The table gives the model with equation, the parameter estimates and the coefficient of determination. All parameter estimates are given with their standard error and are significant at p<0.01.

model	equation	a (SE)	b (SE)	c (SE)	r^2
linear	$y = a + b{\cdot}x$	19.61 (1.06)	0.76 (0.18)	-	0.173
curvilinear	$y = a{\cdot}x\,/(b+x)$	25.44 (0.91)	0.14 (0.05)	-	0.214
polynominal	$y = a+ b{\cdot}x + c{\cdot}x^2$	17.16 (1.31)	2.55 (0.64)	-0.17 (0.06)	0.252
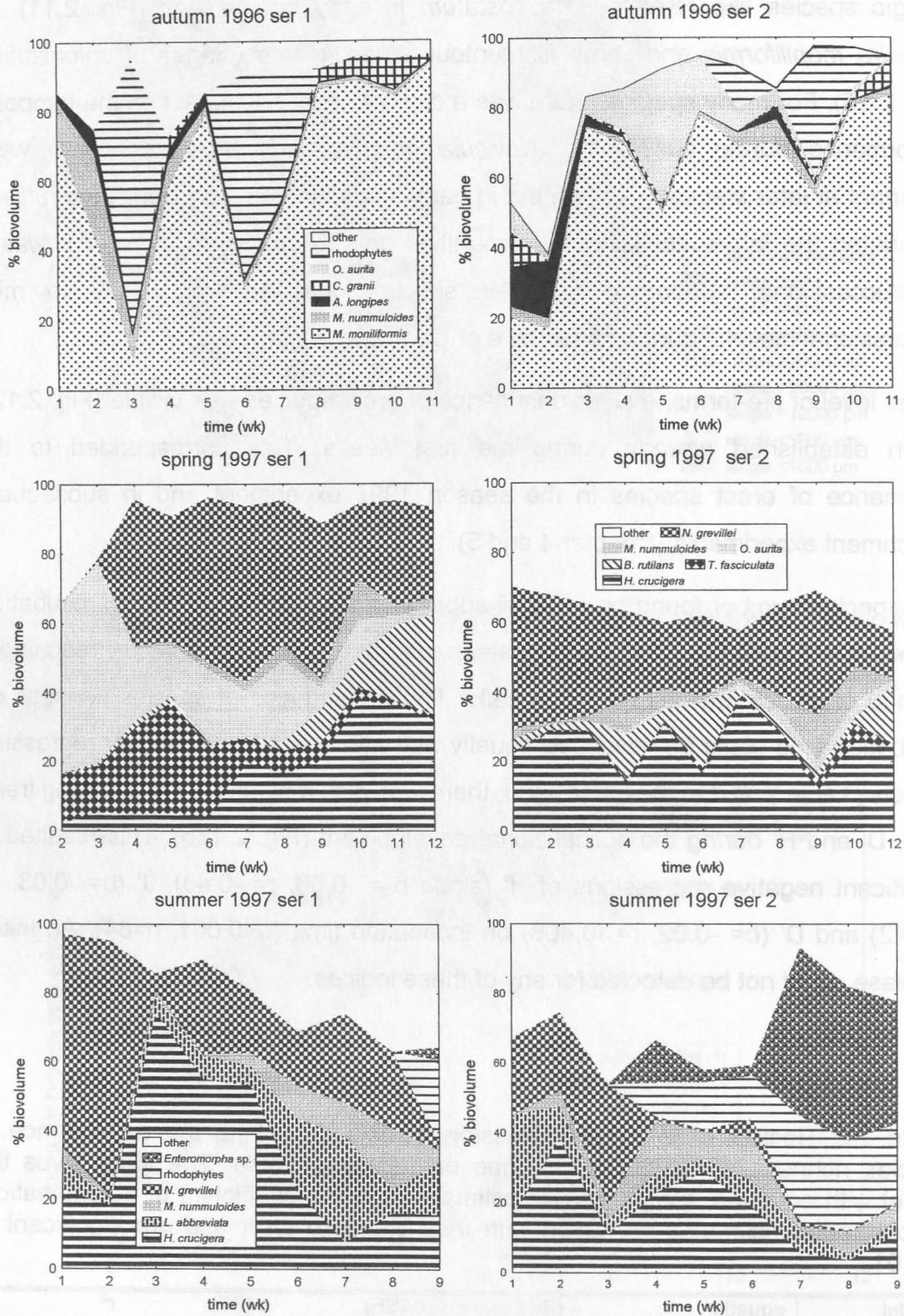
Fig. 2.10: Proportion of dominant species during colonization of artificial substrates, measured in weekly intervals. Corresponding total biovolume can be seen in Fig. 2.9.
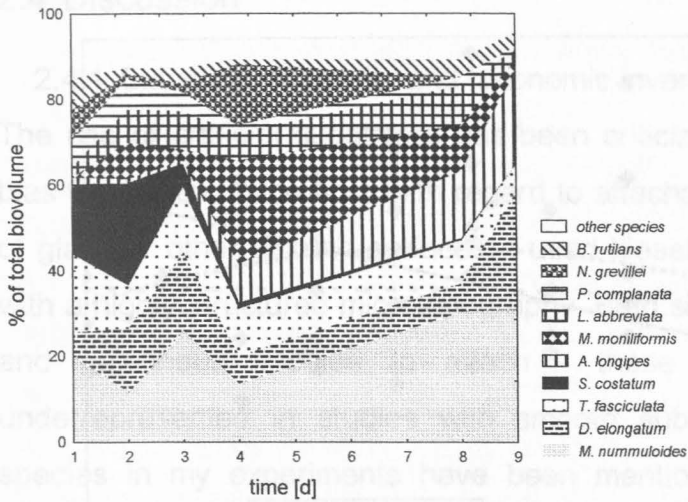
Fig. 2.11: Proportion of dominant species during colonization of artificial substrates, measured in daily intervals. Corresponding total biovolume can be seen in Fig. 2.9.

Legend (Fig. 2.11):
- other species
- B. rutilans
- N. grevillei
- P. complanata
- L. abbreviata
- M. moniliformis
- A. longipes
- S. costatum
- T. fasciculata
- D. elongatum
- M. nummuloides

autumn 1996 ser 1

autumn 1996 ser 2

spring 1997 ser 1

spring 1997 ser 2

summer 1997 ser 1

summer 1997 ser 2

Legend:
- pelagic
- epipelic
- epiphytic
- benthopelagic
- erect
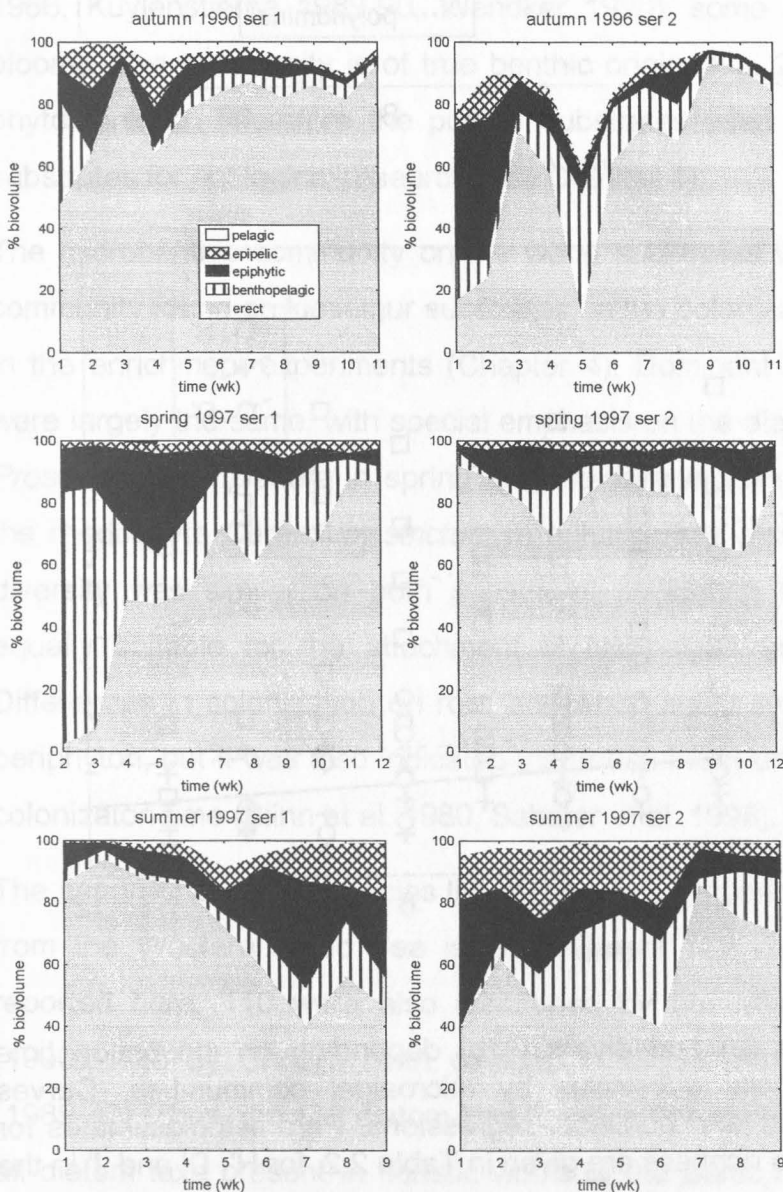
Fig. 2.12: Proportion of different life forms during colonization of artificial substrates. Corresponding total biovolume can be seen in Fig. 2.9. Life forms were attributed according to literature data and personal observations.
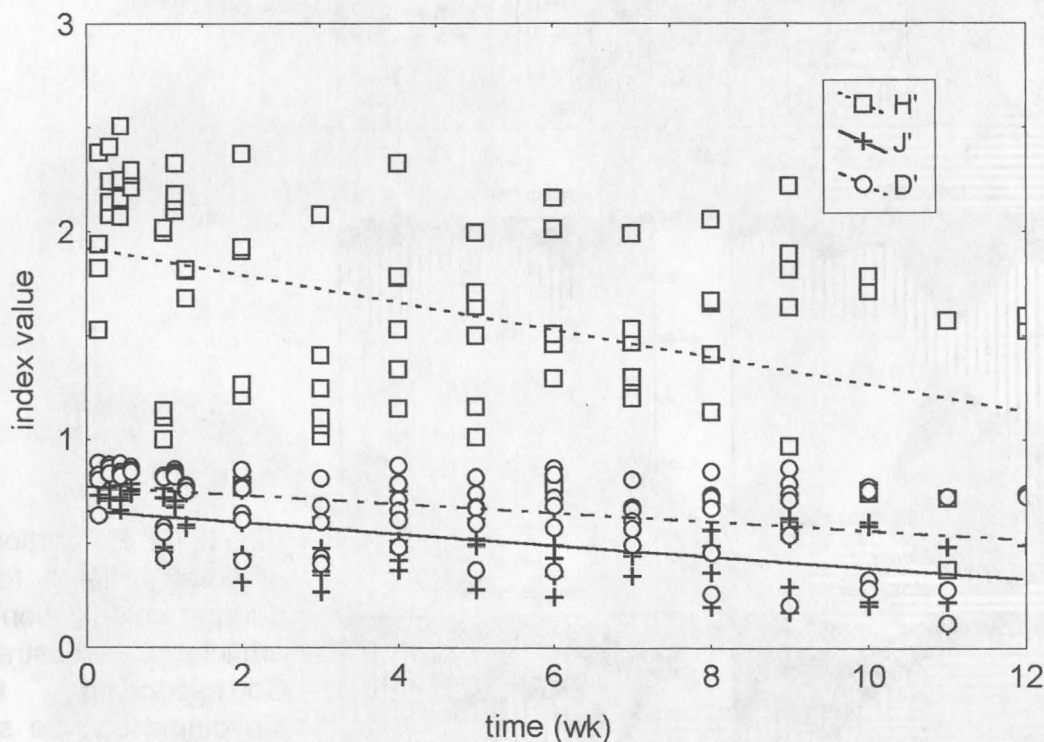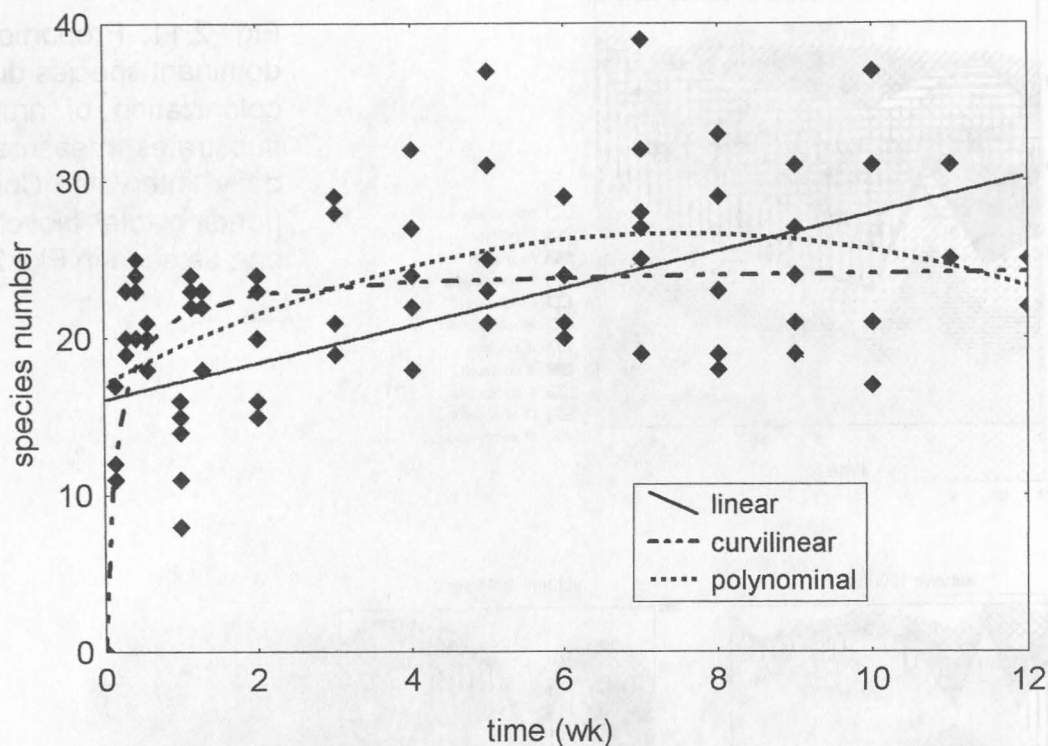
Fig. 2.13: Species richness (a) and diversity (b) depending on incubation time during colonization of artificial substrates by microalgal communities. Curves represent the results of linear and nonlinear regressions. Parameter estimates for regression results for species richness are given in Table 2.2, for H', D' and J' in the text.

2.4 Discussion

2.4.1 Substrate suitability and taxonomic inventory

The use of artificial substrates has been criticized, because they are assumed to bias the benthic microflora with regard to attachment ability (Snoeijs 1991). Instead of glass or other smooth surfaces, I used kieselgur stones and wood blocks, both with a highly structured microtopography. Both substrates allowed even filamentous and gelatinous species to attach - these groups were often missing or underrepresented in studies with smooth substrates (Snoeijs 1991). Dominant species in my experiments have been mentioned as common to Kiel Bight or Western Baltic in several floristic works (Karsten 1899, Simonsen 1962, Edsbagge 1966, Kuylenstierna 1989-90, Wendker 1990), some of them occurring in mass blooms. The community is of true benthic origin (Fig. 2.6) rather than sedimented phytoplankton. Therefore the porous substrates used are considered as reliable substrates for ecological research (see Chapter 4).

The microbenthic community on the wood substrates was generally similar to the community found on kieselgur substrates, in the colonization experiments as well as in the enrichment experiments (Chapter 4). Dominant species on both substrates were largely the same, with special emphasis on the diatoms *Berkeleya rutilans* and *Proschkinia complanata* in spring and *Melosira moniliformis* in autumn, as well as the rhodophyte *Ceramium strictum* in autumn (see also Chapter 4). The range of diversity was similar on both substrates, indicating that wood substrates were equally suitable for the attachment of microalgae as the kieselgur substrates. Differences in colonization on rock and wood substrates were reported for stream periphyton, but it was also indicated that these initial differences may vanish during colonizaton time (Blinn et al. 1980, Sabater et al. 1998).

The congruence of the species list of this work (Appendix A2) with previous reports from the Western Baltic Sea is high. Out of 172 diatom species and varieties reported here, 110 were also mentioned by Simonsen (1962), 156 by Pankow (1990), 128 by Snoeijs (with co-editors, 1993-1998), and 94 by Kuylenstierna (1989-90). Thus, the 172 diatom taxa found in this study comprise more than 20% of all diatom taxa present in floristic works of the Baltic Sea, although only a limited number of samples was analyzed at one site. Other studies reported even higher

diatom species richness (> 300) at one site (Kingston et al. 1983, Lange-Bertalot & Metzeltin 1996). This high local species richness is also common for other groups such as bacteria (Pedros-Alio 1993) and protozoa (Fenchel et al. 1997). The global species pool of ciliates is comparably low (Finlay et al. 1998). This can be explained by the high dispersal rate and high population sizes of microorganisms, leading to low rates of local extinction, low rates of allopatric speciation and thus to a high percentage of species that are cosmopolitic (Fenchel 1993, Fenchel et al. 1997). The contrast between high local and low global species richness results in very flat species-area curves found for ciliates (Fenchel et al 1997). For microorganisms, a saturation of local species richness from regional species pool can thus be assumed, whereas unsaturated local species pools and ineffective dispersion are generally reported for higher plants (Caley & Schluter 1997, Tilman 1997, Hubbell et al. 1999, see also Appendix 4). However, the actual rate of endemism (Snoeijs & Potapova 1998) and the dispersal abilities of diatoms remain largely unknown. High dispersal abilities may be assumed from the number of algae trapped in atmospheric aerosols (Brown et al. 1964) or by the overlap of species composition between distant sites stated for marine (Castenholtz 1967, McIntire & Moore 1977) and freshwater studies (cf. Hein 1990 and Krammer & Lange-Bertalot 1986-1991). However, these reports of high species overlap were criticized with respect to a finer taxonomic concept, which separates entities which so far had been lumped together. It is argued that this possibly reduces the proportions of cosmopolites (Mann & Droop 1996), but an increase in global species number due to finer separation of taxa may also lead to higher local species numbers.

Some species frequently present in these experiments have only been found rarely elsewhere in the Baltic Sea. *Cymbella helvetica* is mainly known from freshwater sites and was previously not described as a frequent contributor to brackish microphytobenthos (Krammer & Lange-Bertalot 1986-91). The presence of *Proschkinia complanata* was reported for the Kiel Fjord (Karsten 1899), but its taxonomic status is rather confusing. Judging by the dimensions and description, the species found in Kiel Fjord belongs to *Proschkinia complanata* sensu Karsten (1899) and Krammer & Lange-Bertalot (1986-91), whereas in other studies similar individuals were described as *Proschkinia poretzkajae* (Snoeijs, with co-editors,

1993-98). A taxonomic uncertainty exists for *Navicula grevillei*. Cox (1988) revived the genus *Parlibellus* and stated that the species name *Navicula grevillei* was used by Hustedt and subsequent taxonomists for specimen not matching the original description. *Navicula grevillei* sensu Hustedt was considered as a synonym to *Parlibellus delognei* by Cox (1988), but without further knowledge on type material etc., I preferred to stay with the name given in Pankow (1990). It should also be noted that *Navicula* cf. *perminuta*, *Navicula cincta* and *Nitzschia microcephala* were identified from permanent slides, but it cannot be excluded that different species of these genera may have been present in the counting samples which could not distinguished without frustule preparation.

2.4.2 Seasonality

The seasonal development of the epilithic microalgal biovolume with two distinct peaks, a first and high one in spring and a second one in late summer/autumn, has been described several times from different locations and on different surfaces (Underwood 1984, Wasmund 1986, Kawamura & Hirano 1992, Underwood & Paterson 1993, Asmus & Bauerfeind 1994, Snoeijs 1994). Several reasons were proposed to explain the sharp decline in microphytobenthic biomass after the spring bloom: desiccation stress (Underwood 1984), shading by the developing phytoplankton spring bloom (Hansson 1988), grazer impact and low nutrient availability (Underwood & Paterson 1993). Although the phenomenon seems to be quite common, no experimental tests of these factors have been performed so far. For grazing and nutrients, the possible impacts will be discussed throughout the following chapters of this thesis (Chapter 4 and 5). The phytoplankton spring bloom was not very dense in 1997 (Fig. 2.5), so this should not have been the cause for the decline of benthic microflora. Desiccation stress was inferred by microalgal biomass maxima at greater depth (Underwood 1984), but desiccation can be assumed to be low in a nontidal area. Contrary trends of higher biomass at higher elevations have been observed as well (Asmus & Bauerfeind 1994). Thus, desiccation might be a locally important phenomenon, but cannot explain the widespread pattern of summer biomass minima.

The dominance of tube-dwelling species during spring occurred both in the colonization and in the enrichment experiments (see Chapter 4). Increased grazer

resistance and higher tolerance of salinity variability was discussed as a reason for this life form which is exhibited by species living also unicellularly (Cox 1977, Houpt 1994, Sommer 1997). Densities of potential grazers were generally low in spring (Table A3 in the Appendix), but salinity should be greatly influenced by freshwater inflow from the river Schwentine (Fig. 2.4). Therefore, the tube dwelling life form may be an adaptation to salinity variability. Furthermore the erect growth form allows better access to nutrients and light (Riber & Wetzel 1987, see Chapter 5 and 6).

In addition to the decline following the spring bloom, there was a further discontinuity in the seasonal development of the periphyton, imposed by the settlement of bivalve larvae. *Mytilus* is a strong space competitor in eutrophic areas like the Western Baltic, reaching high recruitment rates in summer and dominating benthic assemblages if the bivalve abundance is not reduced by predators (Paine 1966, Reusch 1994). Especially in July, small mussels visibly dominated the artificial substrates. After the colonizaton of the mussels, the microphytobenthic succession started new, giving rise to a second biomass peak in late autumn.

2.4.3 Establishment of the epilithic community

The short-term colonization process could be divided into an exponential growth and a subsequent stationary phase with a reduced biomass variability (Fig. 2.9). This batch-culture like growth curve indicated the onset of resource limitation after 4-6 weeks, reflected by ongoing changes in species composition in the stationary phase (Fig. 2.10). The time span needed to establish a "mature" community was used as a minimum duration for subsequent enrichment experiments (Chapter 4). A similar sequence of an exponential and a stationary phase was described previously for stream periphyton, eventually leading to a degeneration of mats older than 10 weeks (Johnson et al. 1997). During my colonization experiments, no degeneration of the epilithic mat was detected, but my experiments did not exceed 12 weeks and might have been harvested before the onset of degeneration. Although the biovolume was stagnant in the stationary phase of my experiments, it can be assumed that this "mature" periphyton community is a transient phase of succession, since the marine littoral is dominated by large ephemeral or perennial macrophytes. At least the latter do not develop within the time these experiments

were conducted, so there might have been a bias against species with a short annual reproduction period, since new substrates were suspended for every experiment.

Since the sampling strategy was destructive, no direct analysis· of vertical structure of the epilithic microphytobenthos was possible. The architecture inferred from the life forms, however, was unambiguous and matched previous observations on the new establishment of periphyton mats. A modification of the surface by organic coating and bacterial colonization has been observed several times (Hoagland et al. 1982, Blinn et al. 1980) and can be assumed also for this study, although bacteria were not quantified. Generally, species with a pelagic or benthopelagic life-style were most abundant in the beginning of the colonization (Fig. 2.12), as had previously been shown for freshwater periphyton (Tuchmann & Blinn 1979). Afterwards, the colonization sequences were marked by an increasing dominance of erect species with time (Fig. 2.12). Shifts in dominance from adnate to erect species during colonization of free substrates are a very consistent pattern in periphyton development (Hudon & Bourget 1981, Hoagland et al. 1982, Johnson et al. 1997). These canopy species determined the response of benthic microflora to nutrient enrichment treatments (Paul & Duthie 1989, see Chapter 4 and 5). In Kiel Fjord, erect species were also dominant throughout the seasonal development process (Fig. 2.8). A third stage of higher structural complexity can be established through colonization of erect species by epiphytes, but this was not well expressed in my experiments (Fig. 2.12).

In my colonization experiments, diversity and evenness decreased linearly with colonization time, whereas species number increased initially and subsequently reached a plateau. Also a decrease of species richness at later stages of the succession could be detected, but was not marked (Fig. 2.13, Table 2.2). This decrease in diversity during succession has also been shown for freshwater periphyton, relating the decrease to lowered evenness (Stevenson 1984, Stevenson et al. 1991) or to both, lowered evenness and lowered species richness (Yount 1956). Theoretically, an increase of diversity was proposed for early successional stages, while competition should decrease diversity in late successional stages, resulting in an unimodal curve (Valiela 1995). In microbial communities, however,

the increasing part of the hypothesized unimodal time course of diversity may be very short and steep. This is indicated by the fact that high species richness can be reached after few days of colonization, as was described for freshwater periphyton (Stevenson et al. 1991) and for riverine protists (Franco et al. 1998). The rate of new colonization may thus be important only for a short period following the exposition of the substrate. Afterwards the growth on the substrates may be more influential. Peterson (1996a,b) found that periphytic algae were more abundant on colonized substrates as could be assumed from colonization alone, indicating the rapid growth of early colonizers. Especially unicellular organisms are able to proliferate immediately, whereas multicellular organisms have to develop vegetative structures to reproduce or fragmentate. Few species become dominant, leading to a reduced evenness, which offsets the increasing species number through new colonists and thus reduces also the diversity indices (Fig. 2.13).

2.4.4 Autogenic succession

The colonization of the artificial substrates can be considered a primary succession, i.e. the succession on newly established substrates as opposed to secondary succession which takes place following a disturbance (Begon et al. 1990). Hoagland et al. (1982) described the analogy of periphytic development to succession of terrestrial plants. In my experiments, species assemblages of periphyton with initially different composition showed convergent sequences during the colonization process (Fig. 2.10). This development was presumably based on processes which are also relevant for terrestrial vegetation. In their seminal contribution, Connell & Slatyer (1977) related succession to three different processes: facilitation, tolerance and inhibition. Late successional species may dominate, because early colonizers made a hostile environment more favourable for other species (facilitation), because late successionals are able to reduce resource concentrations to very low levels (tolerance), or because they are able to monopolize the substrate (inhibition) (Connell & Slatyer 1977). Early successional species survive because of their colonization advantage after a disturbance and because of high growth rates during short times of high resource concentrations (Pacala & Rees 1998).

All three driving forces of succession were described for microalgal succession. The organic and/or bacterial coating of the substrate may represent a first facilitation

step necessary for several species arriving later on the substrate (Hudon & Bourget 1981, Hoagland et al. 1982). Another facilitation process is represented by the beneficial effect of diatoms on colonization by the rhodophyte *Ceramium strictum* (see Chapter 4). Tolerance is an important trait, since the establishment of a thick periphyton mat changes the nutrient concentrations within the community via diffusional barriers (Johnson et al. 1997). Adnate species have only limited access to light (Hoagland et al. 1982) and water column nutrients (Burkholder et al. 1990, see also Chapter 5 and 6). Thus, during succession an erect life form becomes increasingly important (Fig. 2.12). Inhibition is e.g. attributed to allelopathy, which has not been observed among diatoms so far (Admiraal 1984), but was shown between diatoms and germlings of filamentous algae (Huang & Boney 1985).

These succession-driving processes are assumed to be independent of external forces (trends in the physicochemical environment), therefore succession is called autogenic. Succession is essentially a zero force process, i.e. a process taking place only without additional forcing affecting the development (Pickett & McDonnell 1989). That means, a successional sequence towards a more stable community may be interrupted or deflected by external influences. The seasonal variation in abiotic conditions can be assumed to be such an external force. Although the variability between years was high in my experiments (Fig. 2.6), the colonization process was convergent within one season regardless of starting conditions (Fig. 2.10) and the seasonal dominance of species was stable between different years (compare Fig. 2.7 and 2.10 as well as Chapter 4). This indicates an autogenic succession as it was observed for phyto- and zooplankton under stable conditions (stratification). For pelagic microalgae, a succession model has been established, linking convergent community development to biotic (zero force) interactions, which are disrupted by physical factors in autumn and winter, restarting the succession in the next spring (Sommer et al. 1986, Sommer 1991c). However, I followed the succession process only for weeks and months, and my experiments were thus not suitable to infer a restart of the seasonal succession by adverse winter conditions. Despite some analogous observations such as a benthic spring bloom, a summer biomass minimum resembling the pelagic "clear water phase" and a second biomass peak consisting of different species, there remains uncertainty about the

analogy of benthic and pelagic microalgal seasonality (see also Chapter 6). A thorough investigation of seasonal development in microphytobenthos should include explicit tests of internal forces (autogenic development sensu Connell & Slatyer 1977) *versus* external forces (e.g. changes due to temperatures, shading by phytoplankton) driving the observed community development.

The species sequence during colonization revealed two important patterns. Few species were consistently more abundant in early or late successional stages, which would have indicated colonization ability as a stable, species-specific trait. Instead, the early successional stages were markedly influenced by the species seasonally dominating the species pool. Tilman (1993) attributed the change of dominance during succession to a trade-off between colonization ability (immigration rate) and competitive ability. This is not evident in my colonization experiments. Stevenson et al. (1991) reported that diatoms dominating later successional stages showed relatively lower immigration rates, but a clear dichotomy between early and late successional dominants was lacking. However, colonization ability is not only influenced by the dispersal of propagules, but also by the maximum growth rates immediately after colonization and the abundance in the neighbourhood of the newly established substrates. For the "neighbourhood effect", there is no trade-off with competitive ability. The different position of species in the colonization sequence described above can therefore be regarded as a consequence of the abundance in the neighbourhood. A substrate opened in the bloom phase of spring species will be first colonized by those species, which are dominating the propagule pool. Thus, the initial periphytic assemblage is a random sample of the suspended algae, leading to a higher contribution of algae dominant at the time the substrates are provided. This initial assemblage is subsequently replaced and the late successional species are determined by competitive ability, i.e. the species composition is converging during colonization.

The relative importance of the neighbourhood effect compared to the trade-off between competition and colonization cannot be evaluated from my data. However, benthic microalgae have short generation times compared to seasonal time periods (Sommer 1991c) and high dispersal abilities (i.e. high local species richness). Thus, microalgae can generally be placed at the colonization end of the competition

versus colonization trade-off compared to filamentous or perennial macrophytes (Biggs et al. 1998). Only large, chain-forming diatoms like *Melosira moniliformis* (in this study) or *M. varians* (Biggs et al. 1998) are notable exceptions.

2.5 Conclusions

With regard to the questions raised in the introduction of this chapter, the following conclusions can be drawn:

(i) The artificial substrates used in this study allowed the attachment of a variety of benthic microalgae and filamentous macroalgae. No bias against different growth forms could be detected, since the species richness and form variety was high. However, the experimental duration did not allow the establishment of macroalgal vegetation. High local species richness indicated effective dispersal of benthic microalgae.

(ii) After 4-6 weeks the exponential growth phase ended and a more "mature" epilithic biofilm with stagnant total biovolume was established. The species composition changed with further development. This resulted in a decrease of evenness diversity with colonization time, whereas species number increased initially and subsequently reached a plateau. The diversity of periphyton was influenced more by the changes in species composition (i.e. evenness) than by the arrival of new colonists.

(iii) The "mature" epilithon was dominated by erect species, replacing early species with pelagic or adnate benthic life form. Changes in dominance could be observed on weekly and even daily time scales.

(iv) The colonization of artificial substrates was analogous to succession in terrestrial vegetation. Although some species were shown to be generally good colonizers, the initial species assemblage consisted mainly of seasonally dominating species.

3 Biomass stoichiometry of benthic microalgae

3.1 Introduction

The chemical composition of oceanic seston is known to be relatively constant at a C:N:P ratio of 106:16:1 (Redfield 1958, cf. Copin-Montegut & Copin-Montegut 1983). This biogeochemical ratio became widely known as "Redfield ratio" and was subsequently interpreted with respect to the physiology of phytoplankton. Droop (1974, 1975) investigated the nutrient content of phytoplankton subjected to different types and degrees of limitation and developed the cell quota growth model, relating growth rates to nutrient concentrations within the cells. Cell quotas can be based on carbon and thus are equivalent to internal nutrient ratios. Nitrogen and phosphorus supply supporting maximum growth rate was shown to lead to phytoplankton stoichiometry resembling the Redfield ratio (Goldman et al. 1979, Elrifi & Turpin 1985), and the internal nutrient ratios were proposed as an indicator of algal nutrient status (Healey & Hendzel 1980, Flynn 1990). Despite some criticism (Ryther & Dunstan 1971, Tett et al. 1985), biomass stoichiometry has been widely applied to assess nutrient supply to marine (Paasche & Erga 1988, Burkhardt & Riebesell 1997) and freshwater phytoplankton (Sommer 1991a, Hecky et al. 1993) and also to bacteria (Chrzanowski et al. 1996). It should be noted that C:N:P ratios close to the Redfield ratio do not indicate the absence of light limitation (Tett et al. 1985) or limitation by trace elements. They just indicate that neither N nor P are limiting factors of growth (Goldman 1986).

The use of nutrient ratios as an index of nitrogen or phosphorus limitation was also recommended for benthic microalgae (Borchardt 1996), because of the close phylogenetic relationship between benthic and pelagic microalgae. However, in benthic studies it has seldomly been applied to date (Engle & Melack 1993, Rosemond 1993, Rosemond et al. 1993). The infrequent use may be due to the fact that the relationship between cellular stoichiometry and growth rate has not yet been tested experimentally for marine microphytobenthos. Kahlert (1998) recently reviewed literature data on freshwater periphyton and found that C:N:P ratios are a

reliable tool for the assessment of the nutrient status of benthic algae, proposing an optimum ratio of 158:18:1.

In the present study, I wanted to answer the following questions: (i) Is there a consistent relationship between benthic microalgal growth rates and cellular stoichiometry, and (ii), Is this relation independent of abiotic conditions? If both criteria are met, the stoichiometry of benthic microalgae can be used to indicate N- and P-limitation.

3.2 Methods

To investigate the response of internal nutrient ratios to changes in nutrient regimes, I conducted laboratory experiments with natural inocula and a semicontinuous dilution of culture media combined with sampling in time intervals. I used natural inocula of algae to simplify comparison to natural assemblages. The algae for the inocula were scraped from an artificial substrate in the Kiel Fjord, Western Baltic Sea, ten days before the experiments were started. The algae were cultured in unenriched filtered seawater (0.2 µm cellulose-acetate filters) under the same abiotic conditions as the experimental treatments to allow acclimation (Table 3.1). At the beginning of the experiments, an aliquot of this precultured inoculum was added to each treatment. The experiments were conducted in flat bottom, transparent, polystyrene culture flasks with 30 ml total medium content. The algae grew as a biofilm on the bottom of the flasks, which were shaken once daily. This biofilm was a dense monolayer of cells lacking a canopy of large, erect species.

Table 3.1: Treatments in limitation experiments with natural algal inocula. The table lists the code of the experiment, the dilution rate, the duration of the experiment, the light intensity, the temperature and the media used.

code	dilution rate [d^{-1}]	time	light [µmol m^{-2} s^{-1}]	temp [°C]	applied media
H (high dilution)	0.5	22.9.-10.11.97	21	14	V, N$_{lim}$, P$_{lim}$, SI$_{lim}$
L (low dilution)	0.07	dito	21	14	V, N$_{lim}$, P$_{lim}$, SI$_{lim}$
C (cold temp.)	0.5	19.1.-9.3.98	35,8	5	V, N$_{lim}$, P$_{lim}$
M (medium temp.)	0.5	dito	34,7	14	V, N$_{lim}$, P$_{lim}$
W (warm temp.)	0.5	dito	32,2	19	V, N$_{lim}$, P$_{lim}$

Once per day, 15 ml of the culture was replaced by fresh medium, resulting in a dilution rate of 0.5 d^{-1}. Only treatment L (Table 3.1) was diluted thrice a week by only 5 ml, resulting in a dilution rate of 0.07 d^{-1}. It should be noted that the dilution rate did not affect the biomass of the attached benthic microalgae proportionately.

The media used in the experiments consisted of organism-free filtered seawater (0.2 µm cellulose-acetate filters) from the same location, enriched with nutrients and trace metals. The balanced medium (designated V) contained 80 µmol l^{-1} N (as $NaNO_3$), 80 µmol l^{-1} Si (as $Na_2O_3Si*5H_2O$) and 5 µmol l^{-1} P (as $Na_2HPO_4*2H_2O$), resulting in a medium N:P ratio of 16. For the N-limited medium (designated N_{lim}) the nitrogen concentration was reduced to 10 µmol l^{-1}. For the Si-limited medium (Si_{lim}), Si was reduced to 10 µmol l^{-1}, for the P-limited medium (P_{lim}), no phosphate was added, resulting in 1.0 µmol l^{-1} P. The experiments were conducted in autumn 1997 and spring 1998. In the autumn experiment, 4 different media were applied and the treatments consisted of an alteration of dilution rate (Table 3.1). In spring 1998, 3 different media were used and the temperature was altered (Table 3.1). The two experiments differed furthermore in the taxonomic composition of the inoculum and in the light intensity, which was measured with a LiCor LI 189 (Table 3.1). Each treatment was conducted in triplicate, resulting in 24 cultures in autumn (4 media x 2 dilution rates x 3 replicates) and 27 cultures in spring (3 media x 3 temperatures x 3 replicates).

Thrice a week the algae were counted alive in the flasks employing an inverted microscope (Leitz DMIRB) at 630x magnification. Up to 400 cells were counted per sampling date. To compare the different species, which span several size classes, biovolume was calculated by fitting appropriate geometric models (Hillebrand et al. 1999). In addition, thrice a week a sample was taken with a sterile pipette from the bottom of the flask. The sample volume corresponded to the dilution rate, i.e. 15 ml for treatments C, M, W, and H (for codes, see Table 3.1) and 5 ml for treatment L (see above). The samples were divided and filtered on precombusted Whatman GF/C filters for analyses of particulate CN and P, respectively. Particulate phosphate was determined as orthophosphate after a combined digestion with heat and acid (for details, see Chapter 4.2.2). Since this analysis needs a high amount of

material, the three replicates of one treatment had to be pooled. Particulate carbon and nitrogen were measured with a Fisons CN-Analyzer (NA 1500N).

The experiments were divided into two phases. After 28 days, the daily medium dilution was stopped in order to enforce a stronger limitation by decreasing the supply of new media. Sampling was carried out once a week. After sampling, the total volume of the cultures was filled up to 30 ml again. The L- treatment was stopped at day 28, the other experiments were conducted until day 49.

The daily growth rates µ were calculated from the total biovolume of each replicate according to Equ. 3.1.

$$\mu = \frac{\ln B_2 - \ln B_1}{t_2 - t_1}$$

(Equ. 3.1)

including   B: biovolume

            t: time

The ratios of C:N, N:P and C:P, respectively, were calculated on a molar basis. They were compared to the positive daily growth rates by a three-parameter exponential equation (Equ. 3.2) in a model-II nonlinear regression. The use of ratios in regression analysis is not without difficulties (Sokal & Rohlf 1995), but normal distribution of the ratio variables was affirmed (p>0.05, Kolmogorov-Smirnov-test).

$$R = a + e^{\left(b + c \cdot \mu\right)}$$

(Equ. 3.2)

with   R: molar ratio of C:N, N:P and C:P, respectively

        µ: daily growth rate

        a,b,c: parameters

With a negative estimate for c, the resulting curve decreases and approaches asymptotically to a horizontal line with y=a. Therefore, parameter a can be taken as an estimate of the optimal ratio. The validity of the regression model was estimated by an analysis of variance comparing the model-explained variance with the residual variance (Sokal & Rohlf 1995). The presence of a global convergence minimum in the regression procedure was affirmed by using different software and different estimation procedures (Statistica 5.1 and Statgraphics 6.1).
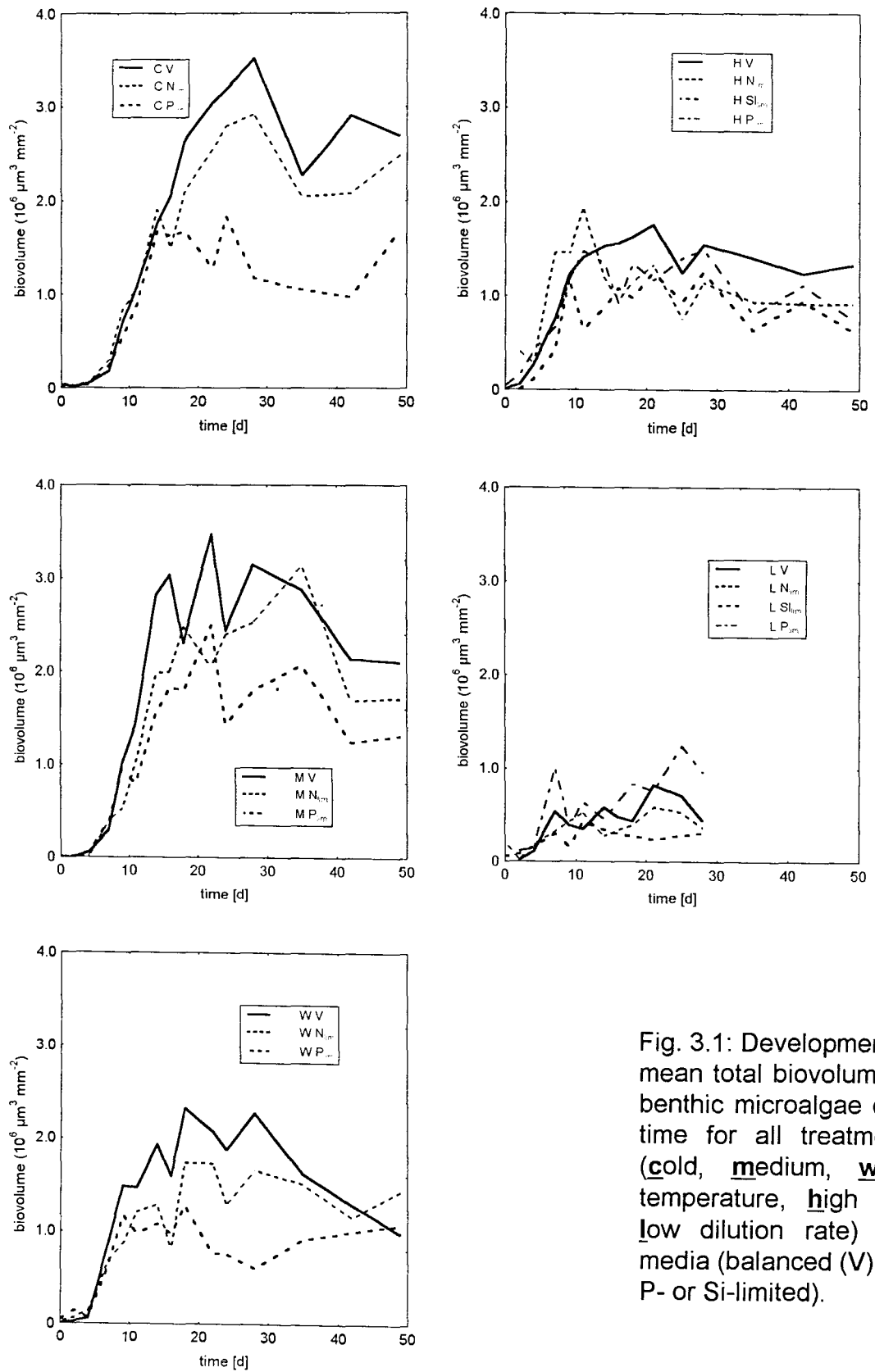
Fig. 3.1: Development of mean total biovolume of benthic microalgae over time for all treatments (cold, medium, warm temperature, high and low dilution rate) and media (balanced (V), N-, P- or Si-limited).

3.3 Results

Total biovolume of the treatments followed a sigmoidal curve in all cases, explaining 87.0 % ± 12.6 (mean ± standard deviation) of the variance. (Fig. 3.1). Final biovolumes were generally higher at lower temperature and lower in the N_{lim} treatments. Moreover, the spring experiments resulted in higher final biovolumes than the autumn experiments, the latter again was divided in lower biovolume in L-compared to H-treatments (Fig. 3.1). Daily growth rates increased in the beginning of the experiment and decreased afterwards. After attainment of the carrying capacity, the growth rate varied close to zero, mostly between +0.1 and -0.1 d^{-1} (Fig. 3.2). In the autumn experiments, 30 species were present, representing the Bacillariophyceae, Chlorophyceae and cyanobacteria. In spring, 30 species represented the Bacillariophyceae, cyanobacteria and Rhodophyceae. Almost all treatments were dominated by diatoms (unicellular, chain-forming and tube-dwelling), whereas non-heterocystous cyanobacteria became codominant at 19°C temperatures and high N-content.

C:N ratios increased with time (significant regression slopes over time, $p < 0.05$, except for LV, LN_{lim}, HSI_{lim}), up to 16 in SI_{lim}-, up to 20 in P_{lim}-, up to 23 in V- and up to 45 in N_{lim}-cultures, respectively. This increase reflected the increasing strength of nutrient limitation. The ratio of C:N decreased exponentially with increasing growth rate (Fig. 3.3, Table 3.2), independent of treatment and limiting nutrient. The regression model described the relationship between C:N ratios and growth rates significantly (F-ratio, $p < 0.01$, Table 3.2) for all media and treatments, except treatment L. The optimal ratio at high growth rates, estimated by parameter a of the regression, is plotted for the different treatments and media in Fig. 3.4 (except for the L treatment). The estimates of the optimal C:N ratios varied from 4.4 to 8.5, but showed widely overlapping confidence intervals (Fig. 3.4). A difference between the optimal C:N ratios at different abiotic treatments could therefore not be determined. However, the C:N ratios at low growth rates depended on the limiting nutrient (Fig. 3.5), indicating a steeper increase of C:N ratios under N-limitation compared to P- or Si-limitation.
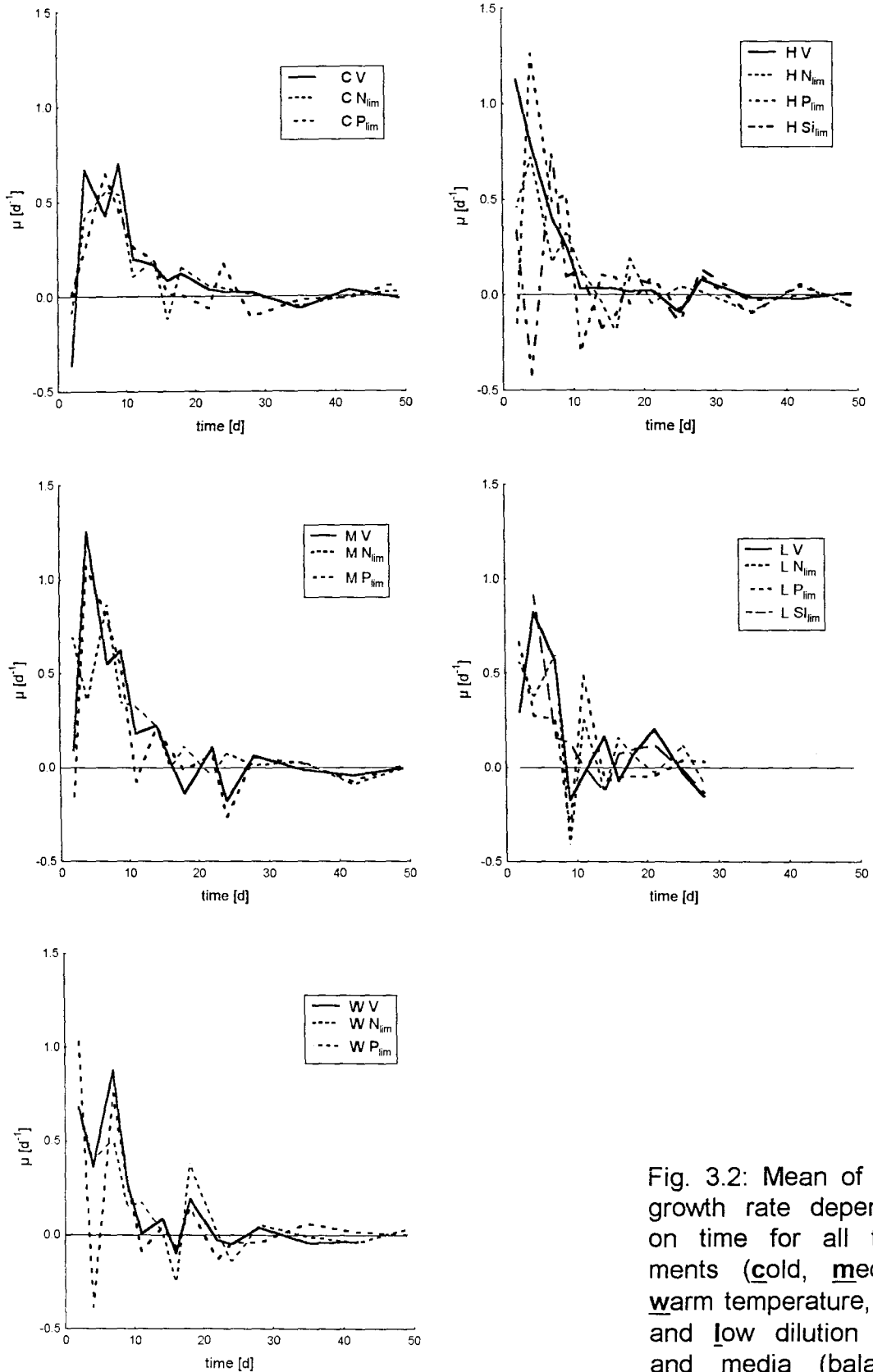
Fig. 3.2: Mean of daily growth rate depending on time for all treatments (cold, medium, warm temperature, high and low dilution rate) and media (balanced (V), N-, P- or Si-limited).
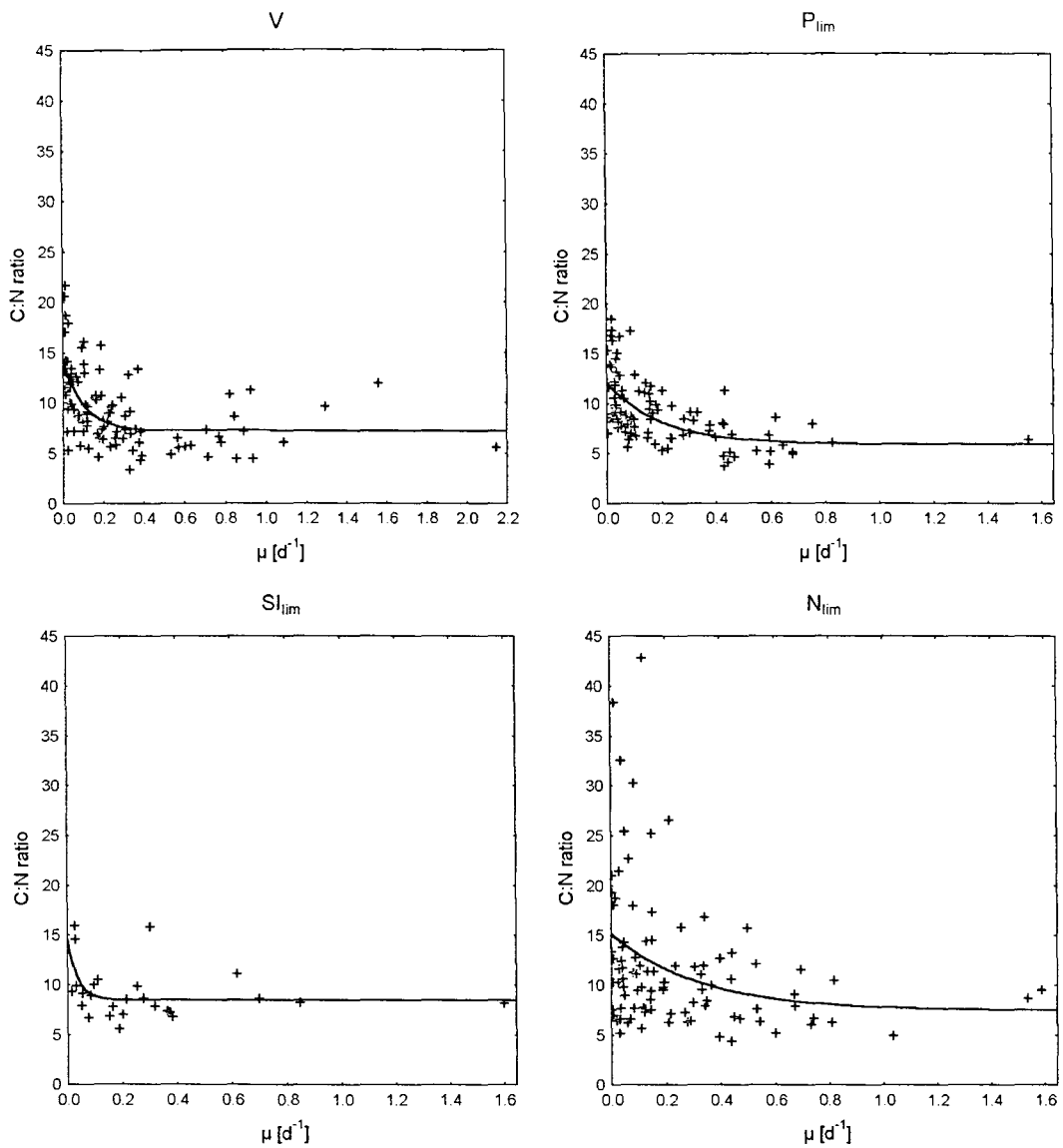
Fig. 3.3: C:N ratios of benthic microalgae dependent on growth rate, plotted for different media (balanced (V), N-, P- or Si-limited). Lines represent nonlinear fits of Equ. 3.2, parameter estimates are presented in Table 3.2.
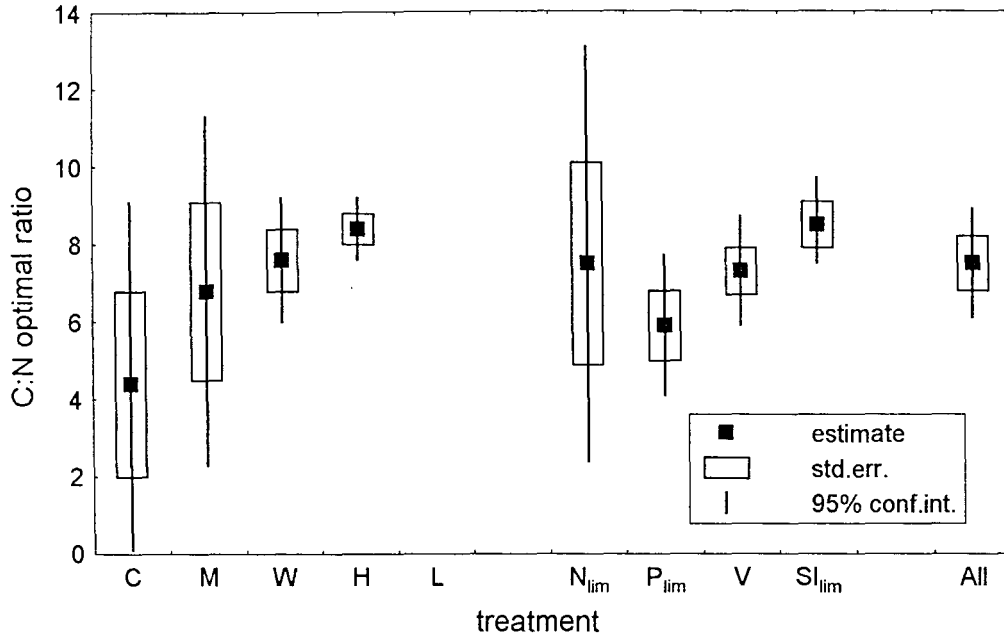
Fig. 3.4: Optimal C:N ratios of different treatments (cold, medium, warm temperature, high and low dilution rate) and media (balanced (V), N-, P- or Si-limited). Optimal C:N ratios are presented as estimate of parameter a (Equ. 3.2), its standard error and confidence interval. For treatment L, no optimal ratio could be fitted. "All" represents the optimal ratio fitted using all data.
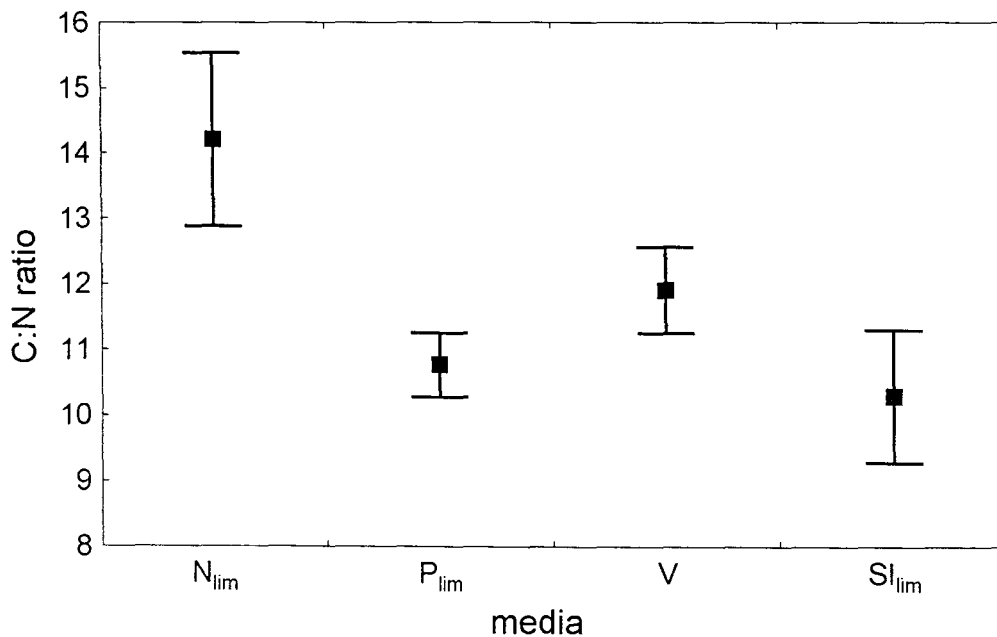
Fig. 3.5: C:N ratios of stagnant cultures under different nutrient limitation (balanced (V), N-, P- or Si-limited), depicted as mean ± standard error of all sampling dates with μ<0.1.

Table 3.2: Fit of an exponential function (Equ. 3.2) to C:N, C:P or N:P ratio dependent on µ. The table lists treatments (<u>c</u>old, <u>m</u>id and <u>w</u>arm temperatures, <u>h</u>igh and <u>l</u>ow dilution rates) and media, ratio for which the regression was calculated, number of observations, coefficient of determination r², and parameter estimates with standard error (which may be underestimated in a model-II regression). Furthermore the F-ratio for the explained and residual mean square is given (Sokal & Rohlf 1995). Significance level: *: p<0.05; **: p<0.01; ***: p<0.001; ns not significant. n.r.: no regression (estimation procedure did not converge).

treat	med	ratio	n	r²	a	b	c	$F_{(2;n-3)}$	
all	all	C:N	322	0.1669	7.5 ± 0.7	1.8 ± 0.1	-6.8 ± 2.6	32.04	***
all	V	C:N	102	0.3692	7.2 ± 0.6	1.9 ± 0.1	-9.9 ± 4.2	28.97	***
all	P_{lim}	C:N	98	0.362	5.9 ± 0.9	1.8 ± 0.2	-5.0 ± 2.3	26.96	***
all	N_{lim}	C:N	96	0.1118	7.5 ± 2.6	2.0 ± 0.2	-3.1 ± 2.5	5.78	**
all	Sl_{lim}	C:N	26	0.1952	8.5 ± 0.6	1.8 ± 0.6	-27.5 ± 18.3	10.18	**
C	all	C:N	77	0.3847	4.4 ± 2.4	2.2 ± 0.2	-3.3 ± 1.9	23.14	***
M	all	C:N	63	0.2253	6.8 ± 2.3	2.3 ± 0.3	-6.0 ± 4.3	7.99	**
W	all	C:N	63	0.2675	7.6 ± 0.8	2.6 ± 0.3	-26.2 ± 11.2	10.96	**
H	all	C:N	89	0.1796	8.4 ± 0.4	1.3 ± 0.2	-12.1 ± 7.3	9.42	***
L	all	C:N	30	n.r.	-	-	-	-	
all	all	C:P	122	0.0655	143.6 ± 48.5	5.1 ± 0.3	-8.2 ± 10.6	4.17	*
all	V	C:P	39	0.2380	119.0 ± 50.7	5.1 ± 0.4	-5.1 ± 4.2	3.28	*
all	P_{lim}	C:P	37	0.4306	139.2 ± 47.8	6.1 ± 0.2	-17.5 ± 8.0	12.85	**
all	N_{lim}	C:P	36	n.r.	-	-	-	-	
all	Sl_{lim}	C:P	10	0.4067	51.2 ± 53.8	4.9 ± 0.5	-8.6 ± 10.4	2.40	ns
C	all	C:P	23	0.2076	80.3 ± 61.9	5.0 ± 0.5	-5.8 ± 6.9	3.54	ns
M	all	C:P	20	0.2618	73.3 ± 120.4	5.7 ± 0.4	-5.4 ± 6.0	2.23	ns
W	all	C:P	21	0.1655	116.7 ± 27.4	4.6 ± 0.6	-20.7 ± 22.0	1.79	ns
H	all	C:P	26	n.r.	-	-	-	-	
L	all	C:P	18	0.1366	216.1 ±105.0	5.8 ± 0.7	-15.6 ± 15.0	1.17	ns
all	P_{lim}	N:P	37	0.2668	20.9 ± 2.6	3.1 ± 0.3	-24.7 ± 14.6	6.50	**

The three-parameter exponential regression on C:P data was significant at p<0.01 only for the P_{lim} media (Fig. 3.6), and at p<0.05 also for V and the pooled data (Table 3.2). The significant estimates for the optimal ratio varied between 119.0 and 143.6, whereas the C:P ratios increased dramatically after attainment of the carrying capacity (Fig. 3.7a). In a Si- or N-limited situation, there was no consistent relation between C:P ratios and growth rate, and the C:P ratios were not higher than the optimum in the stagnant phase of the culture (Fig. 3.7a).
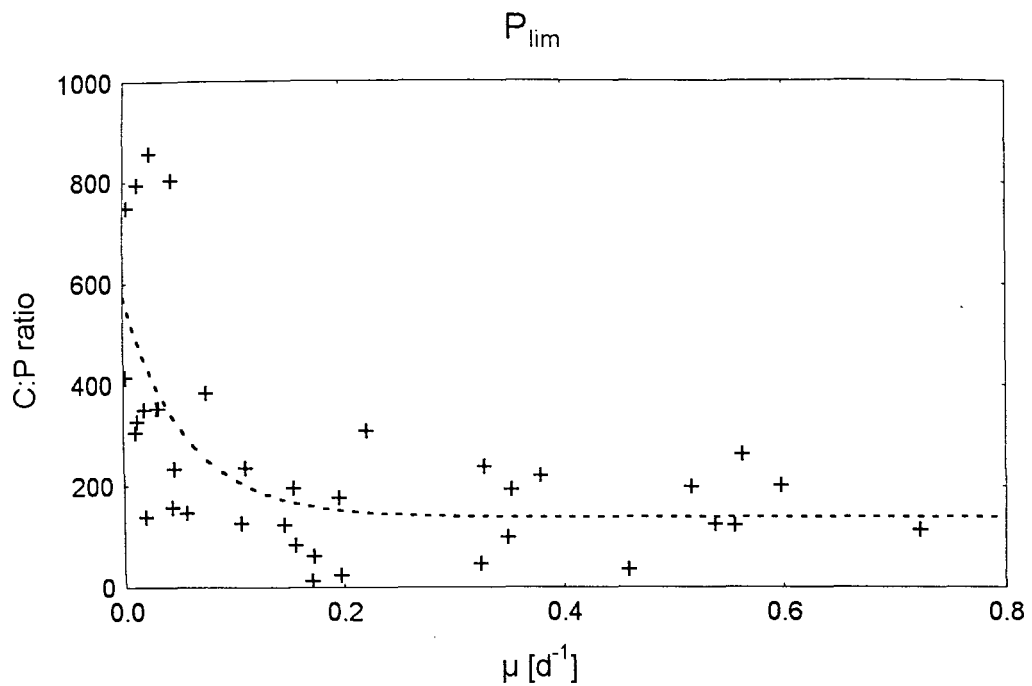
P_{lim}

Fig. 3.6: C:P ratios of benthic microalgae dependent on growth rates, plotted for P-limited cultures. Line represents nonlinear fit of Equ. 3.2, parameter estimates are given in Table 3.2.
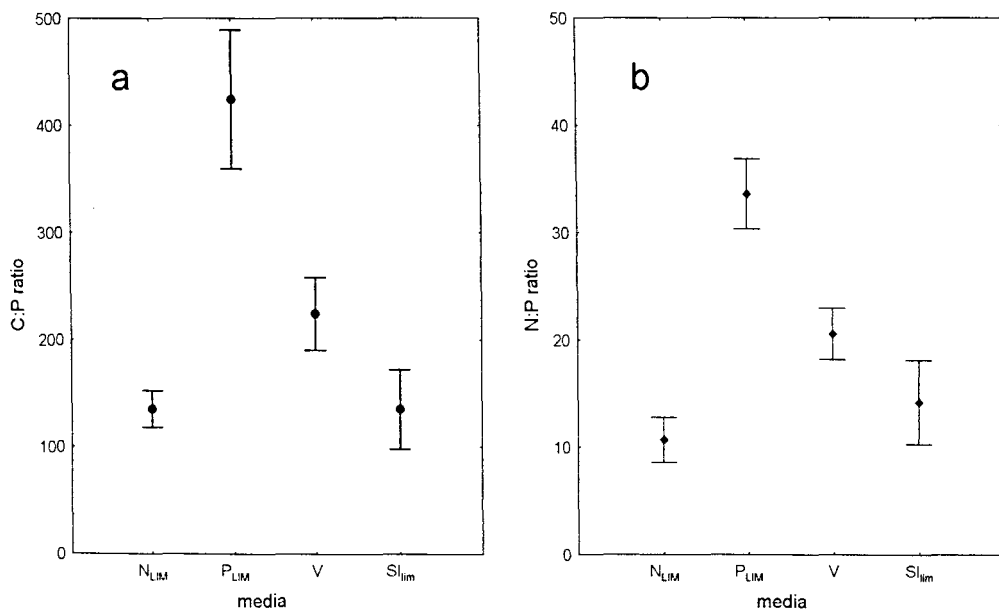
Fig. 3.7: C:P (a) and N:P (b) ratios of stagnant cultures under different nutrient limitation (balanced (V), N-, P- or Si-limited), depicted as mean ± standard error of all sampling dates with μ<0.1.

Only under P_{lim}-conditions, the N:P ratio increased exponentially with decreasing growth rate (Table 3.2). N:P ratios in the stationary phase ($\mu < 0.1$) were significantly different when comparing different media ($p < 0.05$; Kruskal-Wallis ANOVA on ranks; all pairwise multiple comparison by Dunn's method, Sigma Stat), but not between different abiotic conditions (Fig. 3.7b). The mean of the N:P ratio was significantly lower at N_{lim} (10.69) compared to P_{lim} (33.62), while the cellular N:P was intermediate at balanced medium N:P (for V 20.58, for SI_{lim} 14.22).

3.4 Discussion

My data support the view that biomass stoichiometry can be used as an indicator of nutrient status for benthic microalgae similar to phytoplankton, for which it was experimentally and conceptually developed (Droop 1974, 1975; Healey 1978, Healey & Hendzel 1980). Similar to my results, the C:P and N:P ratio of pelagic microalgae increased with decreasing growth rate specifically under P-limitation, while the C:N ratio increased with decreasing growth rate under P-, Si- and N-limitation. Moreover, the increase of C:N at low growth rates was higher under N-limitation than under Si- and P-limitation in my data (Fig. 3.5) and in phytoplankton studies (Perry 1976, Sakshaug & Holm-Hansen 1977, Goldman et al. 1979, Healey & Hendzel 1980). Under N-limitation, the C:P and N:P ratios of phytoplankton decreased below the optimum ratio with decreasing growth rates (Elrifi & Turpin 1985). In my N-limited experiments, the C:P ratio stayed near the optimum ratio (Fig. 3.7a), whereas the N:P ratio decreased (Fig. 3.7b). It can be concluded from these data that C:N ratios are applicable as general indicators of nutrient limitation, while C:P and N:P ratios allow indication of P- versus N-limitation (see below).

The deviation of the cellular C:N:P ratios from the optimal ratio under nutrient limitation is due to production of organic matter rich in carbon and low in nitrogen or phosphate (Conover 1975, Harrison et al. 1977) and to the depletion of internal pools of nutrients (Droop 1974, 1975; Dortch 1982, Dortch et al. 1984). The criticism concerning the indicator value of nutrient ratios pointed mainly at light limited conditions (Tett et al. 1985, Wynne & Rhee 1986), leading to the conclusion that

light limitation was not reflected by biomass stoichiometry. In agreement with Goldman (1986), the optimal ratios emerging from my autumn experiment with lower light intensities did not differ from the ratios from the spring experiment conducted at higher light levels (Fig. 3.4). This contradicts Wynne & Rhee (1986), who described changes in optimum N:P ratios in planktonic algae caused by changes in light intensity and wavelength. However, they calculated the optimum N:P ratio from minimal cell quotas, which refers to the stationary (i.e. limited) phase of cultures (μ = 0). This is a contradiction to the concept of optimal ratios (μ = μ_{max}), as becomes evident, if I approach my data in the same way. The minimal cell quotas (q_0) of N and P can be calculated from Equ. 3.2 by substituting μ=0 and inserting the estimates of a and b from Table 3.2. The mean ratio of q_0N:q_0P was 18.6 for all treatments, whereas the ratio for P_{lim} was 48.8. The latter ratio reflects the nutrient limited situation and not an optimal ratio. Besides, these calculations show that minimal cell quotas of benthic microalgae (ranges of q_0 are 0.060-0.083 mol N mol^{-1}C and 0.002-0.008 mol P mol^{-1}C, respectively) are within the same order of magnitude as those reported from freshwater phytoplankton (Sommer 1991a,b).

Based on the work of Healey & Hendzel (1980), Hecky et al. (1993) suggested limits of indicating values for phytoplankton nutrient ratios. Moderate N-limitation was indicated by C:N >8.3 and severe limitation >14.6, whereas moderate P-limitation was indicated by C:P >129 and severe limitation by C:P>258 and N:P>22. From my data, an optimal ratio of fast growing periphyton can be determined in analogy to the optimal phytoplankton ratios, based on the estimates of a (Equ. 3.2) for the balanced experiments (medium V). This results in a C:N:P ratio of 119:17:1. However, it seems to be more conservative to give ranges of internal ratios in non-limited conditions. These ranges were calculated from the estimates for the different media (V, P_{lim}, N_{lim} and Si_{lim}, Table 3.2), adding the standard error to the maximum estimate and subtracting it from the minimum. The optimum ranges are 5-10 for C:N and 90-185 for C:P. N:P ratios between 13 and 22 indicate balance between nitrogen and phosphate. These ranges allow the establishment of C:N:P ratios as indicators of nutrient limitation for periphyton, shown schematically in Fig. 3.8. Since C:N ratios were generally affected by nutrient limitation, a combination of ratios should be used to indicate nutrient limitation. With an N:P ratio below 13 **and**

a C:N ratio above 10, the peripyhton can be assigned N-limited. With a N:P ratio above 22 **and** a C:P ratio above 180, the microbenthic assemblage is P-limited. With any other combination of ratios, no statement on limiting nutrients can be made.

C:N ratio   C:P ratio

```
  50 ┐                                          ┌ 500

  40 ┤    N-limi-              P-limi-          ┤ 400
          tation               tation
  30 ┤                                          ┤ 300

  20 ┤                                          ┤ 200

  10 ┤                                          ┤ 100
              no lim.       no or other
                           limitation
       └───┬──────┬──────┬──────┬───┘
          10     20     30     40
```

N:P ratio
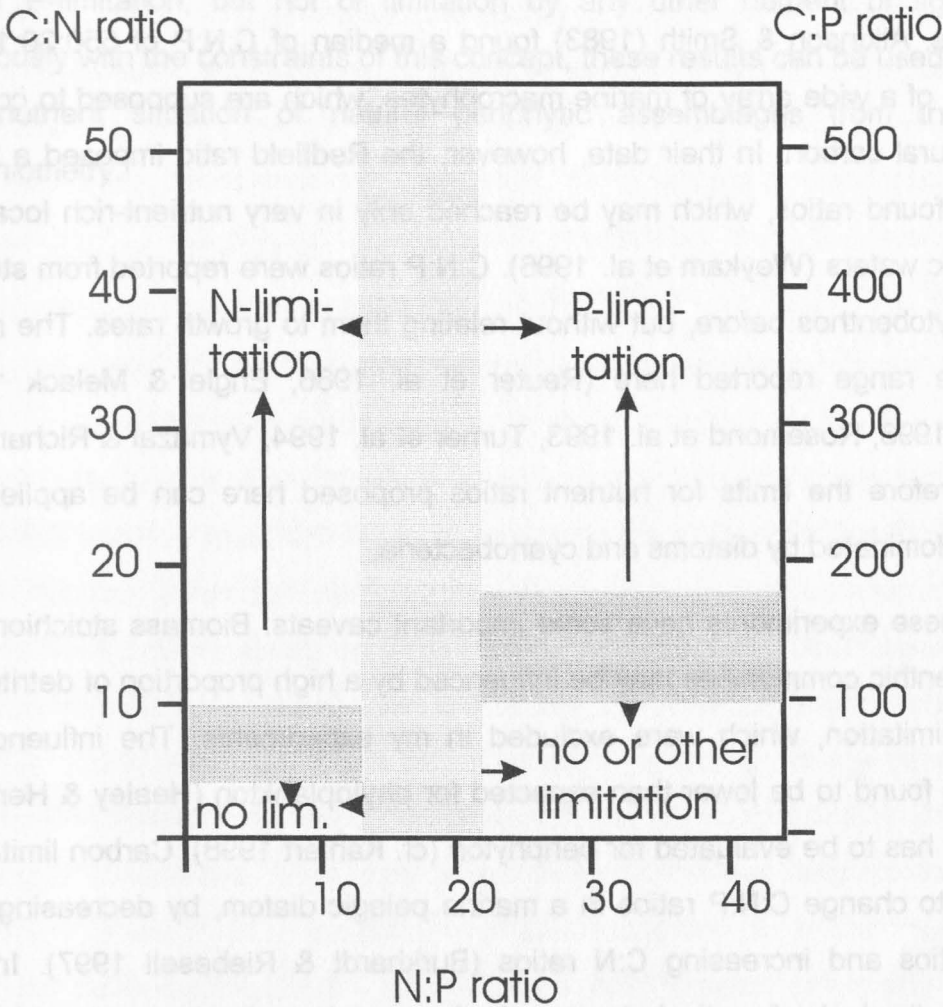
Fig. 3.8: Schematic diagram on the use of nutrient ratios as indicator of nitrogen or phosphorus limitation. Shaded bars represent the range of optimal ratios. Further explanations in the text.

These ratios are more similar to the Redfield ratio and the limits given by Hecky et al. (1993) for phytoplankton than to the optimal ratio proposed for freshwater periphyton by Kahlert (1998). Based on a literature survey, Kahlert (1998) found an optimum ratio for freshwater periphyton slightly higher than the Redfield ratio (C:N:P = 158:18:1) and proposed much higher indicators of limitation than Hecky et al. (1993): C:P>369 and N:P>32 for P-limitation and C:N>11 and N:P<12 for N-limitation. The reason for the discrepancy is probably that macrophytes (e.g. *Cladophora*) were included in the data survey, which are known to differ in their C:N:P ratios. Atkinson & Smith (1983) found a median of C:N:P of 550:30:1 in a comparison of a wide array of marine macrophytes, which are supposed to contain more structural carbon. In their data, however, the Redfield ratio imposed a lower limit of the found ratios, which may be reached only in very nutrient-rich localities like Antarctic waters (Weykam et al. 1996). C:N:P ratios were reported from studies on microphytobenthos before, but without relating them to growth rates. The ratios were in the range reported here (Reuter et al. 1986, Engle & Melack 1993, Rosemond 1993, Rosemond et al. 1993, Turner et al. 1994, Vymazal & Richardson 1995). Therefore the limits for nutrient ratios proposed here can be applied for periphyton dominated by diatoms and cyanobacteria.

However, these experiments have some important caveats: Biomass stoichiometry of natural benthic communities may be influenced by a high proportion of detritus or by carbon limitation, which were excluded in my experiments. The influence of detritus was found to be lower than expected for phytoplankton (Healey & Hendzel 1980), but it has to be evaluated for periphyton (cf. Kahlert 1998). Carbon limitation was shown to change C:N:P ratios in a marine pelagic diatom, by decreasing C:P and N:P ratios and increasing C:N ratios (Burkhardt & Riebesell 1997). In my experiments, the lack of vertical structure in the monolayerd cultures should have prevented CO_2-limitation, but it has not been tested if this limitation is also absent for periphyton mats *in situ*. Furthermore, attention should be paid to the fact that in dense biofilms the algae could have different access to nutrients from the water column or from the substrate, e.g. sediment pore water. Thus, sampling a periphytic mat results in pooling of organisms which experienced different degrees of limitation. Emerging nutrient stoichiometry may be the mean of this gradient.

3.5 Conclusions

My experiments showed that cellular nutrient ratios are a useful approach for the detection of nitrogen or phosphorus limitation in benthic microalgae as well as in phytoplankton. The cellular C:P ratio was a specific indicator of P-limitation, whereas the cellular C:N ratio indicated nutrient limitation in general. The N:P ratio distinguished between N- or P-limitation. Limitation should be determined with a combination of ratios following the diagram in Fig. 3.8. This allows the detection of N- or P-limitation, but not of limitation by any other nutrient or light. Dealing cautiously with the constraints of this concept, these results can be used to evaluate the nutrient situation of natural periphytic assemblages from their cellular stoichiometry.

4 Response of epilithic microphytobenthos to experimental nutrient enrichment *in situ*

4.1 Introduction

In his seminal series of reports on wadden sea microphytobenthos, Admiraal concentrated on abiotic influences on the community (Admiraal 1977 a,b,c, 1984; Admiraal & Peletier 1979, 1980), regarding nutrient competition as less important because of the high nutrient concentrations supplied from the pore water of the sediment they studied. This view, however, was revised by experiments with artificial eutrophication, resulting in increased microphytobenthic biomass on sediments due to nutrient enrichment (Sundbäck & Snoeijs 1991, Flothmann & Werner 1992, Nilsson 1995, Pinckney et al. 1995).

For epilithic algae, no sediment related nutrient pool is available, and the nutrient situation may be more deficient. It can be derived from studies on freshwater periphyton that the limitation may be severe in dense microalgal mats. In these mats, the supply of nutrients from the water column to the basal parts of the mat is low because of reduced flow and diffusive barriers (Riber & Wetzel 1987, Burkholder et al. 1990). Only canopy species growing above the nutrient-depleted boundary layer of the mat have access to the nutrient pool of the water column, whereas adnate growing species depend on nutrients recycled within the mat (Wetzel 1996). For marine epilithon, however, the degree of nutrient limitation has not been tested experimentally, whereas there are several analyses of freshwater periphyton subjected to different nutrient regimes, using nutrient-diffusing agar-plates (Pringle & Bowers 1984, Pringle 1987, 1990) or agar-filled clay-pots (Fairchild et al. 1985). These studies revealed distinct responses of periphyton biomass and species composition, but the nutrient supply via diffusion out of these substrates decreases exponentially with time, which is regarded not optimal for competition experiments (cf. Tilman 1982). In plankton research, continuous or semicontinuous culture techniques have been successfully used for competition experiments (Tilman 1977, Sommer 1983, 1994). For sediment inhabiting microflora, an experimental setup supplying the microphytobenthos continuously with additional

nutrients was proposed (Flothmann & Werner 1992), but when I started my studies no corresponding experimental setup for hard substrates was available.

I conducted *in situ* experiments on nutrient limitation and competition which were designed to warrant a continuous and adjustable supply of nutrients throughout the experiment. In two series of experiments, the main nutrients for benthic microalgae (N, P, Si) were manipulated in order to test the following hypotheses: (i) Nutrient availability limits the biomass of benthic microalgae, even if the water column is not nutrient depleted, and (ii) changes in nutrient supply shift the competitive balance within the epilithon and lead to reproducible taxonomical and structural shifts.

4.2 Methods

4.2.1 Experimental setup

The experimental setup described in Chapter 2.2.1 was used to supply artificial substrates continuously with nutrient-enriched liquid medium. For each experiment, 13 units as described in Fig. 2.2 were used. In contrast to the colonization experiments, incubation times were equal between the different treatments of one experiment and each substrate was sampled once (final harvest). But different experiments varied in their duration in order to account for slower colonization and smaller growth rates at lower temperatures (see Chapter 2). Two distinct series of experiments were conducted. The first series comprised 6 experiments, for which kieselgur substrates (aquaria air stone; 50 x 25 x 25 mm^3; material: kieselgur) and media enriched in N, P and N+P (Table 4.1) were used. The concentrations in the media were high compared to background concentrations, but due to low flow rates, the maximum supply of nutrients was rather low (Table 4.1). This first series was again divided in two groups differentiated by their nutrient supply ratios and concentrations. The kieselgur substrates used in these experiments contained and leaked out silicate. In order to control the Si supply as well, I used wood as a substrate for the second series of experiments (aquaria air woodblock; 25 x 15 x 15 mm^3; material: lime wood). These are used for aeration of aquaria and contain a plastic connection for tubes on the top side. The nutrient supply rates were arranged in two increasing gradients of Si (as Na_2O_3Si x 5 H_2O) concentrations, one with and one without supply of N and P in a 15:1 ratio (Table 4.1).

Table 4.1: Supply concentrations of nutrients during competition experiments. For each block of three experiments, the treatments are listed and the supply at maximum media concentrations ($\mu mol\ cm^{-2}\ day^{-1}$) are calculated. The name of each of the three experiments for each block is given with duration.

exper. group	treatment ($\mu mol\ l^{-1}$)	maximum supply	experiment	date
1st series/ 1st group substrate: kieselgur	C: control + N : 15, 45, 150, 450 + P : 1, 3, 10, 30 + NP: combined as above, ratio 15:1	N: 8.0 P: 0.53	spring 1996 late summer 1996 autumn 1996	30 Apr - 19 Jun 96 13 Aug - 23 Sep 96 30 Sep - 15 Nov 96
1st series/ 2nd group substrate: kieselgur	C: control + N: 15, 150, 450 + P: 10 + NP: P constantly 10 + N 0, 15, 10, 25, 50, 100, 150, 300, 450, 700	N: 12.4 P: 0.18	early spring 1997 late spring 1997 summer 1997	10 Feb - 7 Apr 97 7 Apr - 26 May 97 1 Jul - 7 Aug 97
2nd series substrate: wood	C: control + Si: 0, 10, 50, 100, 250, 500 + NP +Si: Si as above, additionally 450 N + 30 P	N: 26.0 P: 1.7 Si: 29.0	autumn 1997 winter 1997 spring 1998	2 Sep - 14 Oct 97 14 Oct - 9 Dec 97 17 Mar - 28 Apr 98

Following the results of increased abundance of a rhodophyte with high Si-supply (see Chapter 4.3), an additional experiment was conducted in order to reveal the effect of substrate conditioning and silicate concentrations on the abundance of *Ceramium strictum*. 12 wood substrates were suspended from June to July 1998 for 6 weeks. Half of these had previously been preconditioned in a mixed diatom culture for 2 weeks. In a factorial design, 3 of the preconditioned and 3 of the unconditioned substrates were supplied with high Si concentrations (500 $\mu mol\ l^{-1}$), and all treatments received N+P (450:30 $\mu mol\ l^{-1}$).

Sampling was done as described in Chapter 2.2.2. Subsamples were taken for counting (fixed with Lugol's iodine, 10 g KI + 5 g I 100 ml^{-1}), determination of particulate carbon, nitrogen and phosphate (filtered on Whatman GF/C filters - filters for CN-analysis had been heated at 545°C before use), and for taxonomic identification.

4.2.2 Biological and chemical analysis

Counting, taxonomic investigations and biovolume calculations were conducted as described in Chapter 2.2.2. Samples for microscopical analysis were diluted and counted in triplicate to minimize errors due to uneven distributed subsamples. Particulate carbon and nitrogen were measured with a Fisons CN-analyzer (NA 1500N). Particulate phosphate was determined after heating the filters to 545°C for 12 h, then the filters were transferred into Pyrex test-tubes, filled with 5 ml H_2O (Suprapure) and 0.1 ml H_2SO_4 (4M) and heated to 96°C in a heating block for 1 h (method communicated by T. Hansen). The liquid was thoroughly mixed and the particles were allowed to settle. The supernatant was used to measure particulate P as orthophosphate according to Grasshoff et al. (1983). Particulate silicate was analyzed for cultured individuals of the rhodophyte *Ceramium*, which were kindly supplied by Dr. A.F. Peters. The algae were digested by adding a base (8 ml 0.2 N NaOH) and heating (120°C for 12 min.). The liquid was neutralized thereafter (2 ml 1.0 N H_2SO_4) and dissolved Si was analyzed following Grasshoff et al. (1983).

4.2.3 Statistical analysis

In both series, the treatments were arranged in a gradient of nutrient supply rates rather than replicating single treatments, in order to be able to draw qualitative as well as quantitative conclusions (see below). Separate analyses have been conducted for the two experimental series. The qualitative analysis was done with a two-factor ANOVA on log_{10}-transformed total biovolume, with factors treatment and season of experiment. For this purpose, the different nutrient concentrations within one treatment were combined, resulting in three treatments for the first experiment series (+N, +P, +N+P, and control) and two (+Si, +N+P+Si, and control) for the second series. For the latter series, C:N ratios were used as a dependent variable as well. Homogeneity of variances was tested with Bartlett's χ^2-test. Posthoc tests were conducted with Tukey's HSD test (Statistica 5.1).

Quantitatively, the response of total biovolume to nutrient enrichment was evaluated with a Model I - linear regression model, with the log-transformed nutrient additions as independent and log-transformed biovolume as dependent variable. The log_{10}-transformation was adaequate because of the exponential increase in nutrient concentrations. In contrast to total biovolume, no linear relationship between

nutrient concentrations and species biovolume could be assumed. Therefore a non-parametric correlation was applied (Spearman rank correlation), pooling all experiments from one series (Table 4.1) and normalizing species biovolume by dividing it by the biovolume of that species in the control (all controls = 1). This was necessary to be able to compare the experiments with different total biovolume, allowing to analyze the deviation of species biovolume in comparison to the respective control. In the second series of experiments, the effects of N+P enrichment were analyzed with a Mann-Whitney U-Test between two samples.

Diversity was analyzed according to Chapter 2.2.3 as species richness and with indices of diversity (H' and D') and evenness (J'). Response of diversity to nutrient enrichment was analyzed with a linear model-I regression, whereas the relationship between different measures of diversity was done with Pearson correlation.

4.3 Results

4.3.1 Experimental setup

The flow-rate could be held constant in most cases, although readjustment was necessary after some weeks, when the stones were heavily colonized and flow-resistance became higher. Treatments with irregular flow (>10% deviation for more than 1 week) or microalgal growth in the tubes were excluded from analysis. Repeated nutrient analysis of media in the bottles showed that nutrient concentrations were nearly constant (max. difference to expected concentrations: 6.7 %), therefore bacterial consumption of nutrients in the darkened flasks was of no importance.

The substrates were suspended freely in the water column to minimize access of herbivores. Macrozoobenthic grazers of low mobility like gastropods were not found on the substrates, but ciliates, nematodes, copepods and sometimes amphipods were present (Appendix A3). However, the abundances were very low and estimated biovolumes of all herbivores at least one order of magnitude lower than those of autrotrophs. Nevertheless, the attached algae were of true benthic origin and different from plankton communities examined at the same time (Chapter 2).
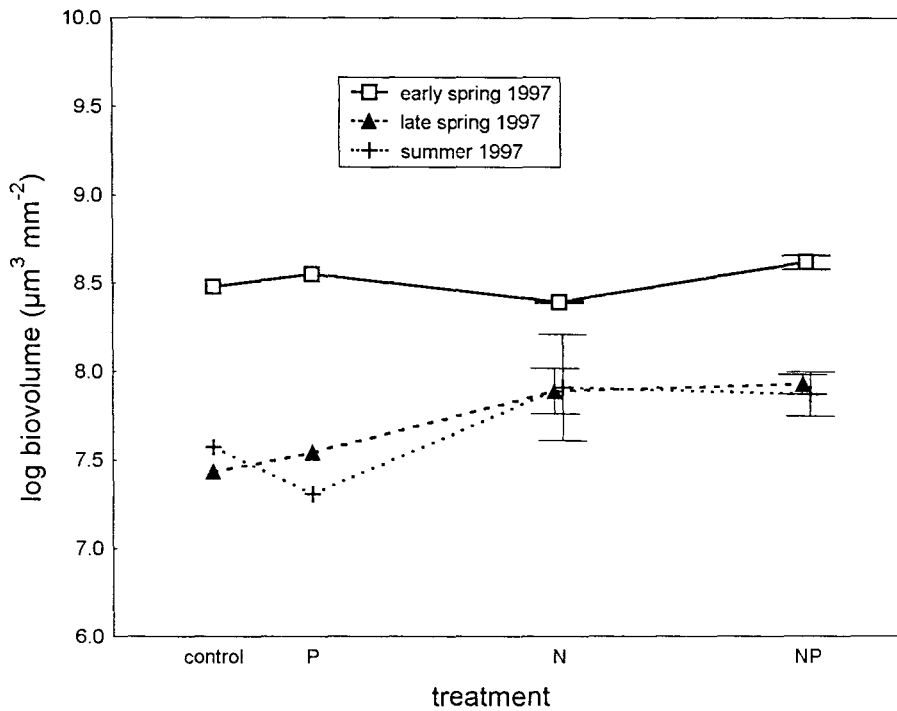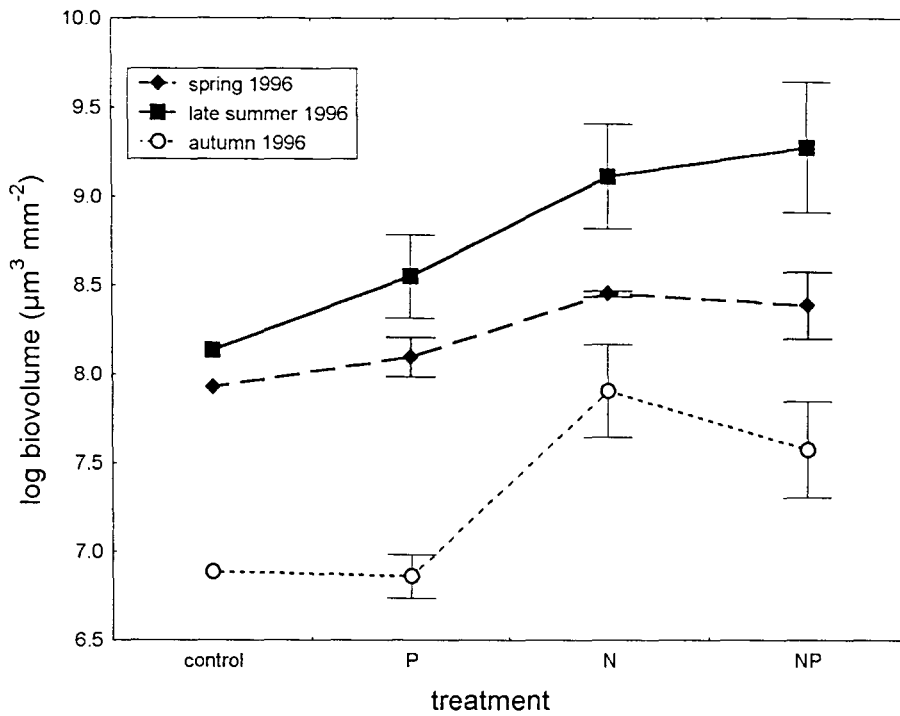
Fig. 4.1: Total biovolume (mean ± standard error) of benthic microalgae in 6 experiments. Nutrients were supplied as P, N and N+P. Note: controls consist only of one replicate, also P-treatments in lower graph. Upper graph: experiments from 1996. Lower graph: experiments from 1997.

4.3.2 Enrichment of N and P

Total biovolume varied significantly between the experiments and between the treatments (Table 4.2, Fig. 4.1). Biovolume increased with N and N+P addition, which were both significantly different from controls and enrichments of phosphate alone (Tukey's HSD, p<0.01). P-alone treatments did not differ significantly from controls (Tukey's HSD, p=0.966). Although the ANOVA detected no significant interaction, the quantitative increase of total biovolume depended on season: increases in total biovolume were higher in summer and autumn compared to spring experiments, resulting in higher regression slopes (Table 4.3).

Table 4.2: Effect of nutrient enrichment on log_{10}-transformed total biovolume, analyzed with a two-factor ANOVA (season of the experiment and nutrient enrichment). Log-transformation resulted in normal distribution (χ^2 = 11.38, p=0.251) and homogeneity of variances (Bartlett's χ^2 = 1.07, p=0.784)

source of variation	df	mean square	F-ratio	p-level
nutrients	3	0.91	7.72	<0.001
seasons	5	2.42	20.54	<0.001
nutrient x seasons	15	0.10	0.81	0.664
error	46	0.12		

Table 4.3: Linear regression of log_{10}-transformed biovolume dependent on log_{10}-transformed nutrient concentrations. The table lists the experiments, the enriched nutrients and the results of the linear regression: intercept, slope with standard error (SE), regression coefficient r^2 and significance level.

experiment	enrichment	intercept	slope (SE)	r^2	significance	
spring 1996	N	8.06	0.19 (0.11)	0.6099	0.219	ns
	P	7.91	0.24 (0.11)	0.6349	0.107	ns
	N+P (15:1)	7.79	0.33 (0.11)	0.7674	0.051	ns
late summer 1996	N	7.99	0.61 (0.15)	0.8553	0.024	*
	P	8.24	0.42 (0.26)	0.5648	0.249	ns
	N+P (15:1)	8.04	0.69 (0.07)	0.9773	0.011	*
autumn 1996	N	6.84	0.56 (0.16)	0.7993	0.041	*
	P	6.89	-0.05 (0.22)	0.0230	0.848	ns
	N+P (15:1)	6.79	0.45 (0.09)	0.9272	0.037	*
early spring 1997	N	8.51	-0.03 (0.04)	0.2317	0.519	ns
	N (+ 10 μM P)	8.58	0.02 (0.04)	0.0339	0.635	ns
late spring 1997	N	7.42	0.22 (0.02)	0.9950	0.045	*
	N (+ 10 μM P)	7.56	0.19 (0.02)	0.9106	<0.001	***
summer 1997	N	7.48	0.22 (0.15)	0.6745	0.387	ns
	N (+ 10 μM P)	7.23	0.37 (0.09)	0.7236	0.004	**
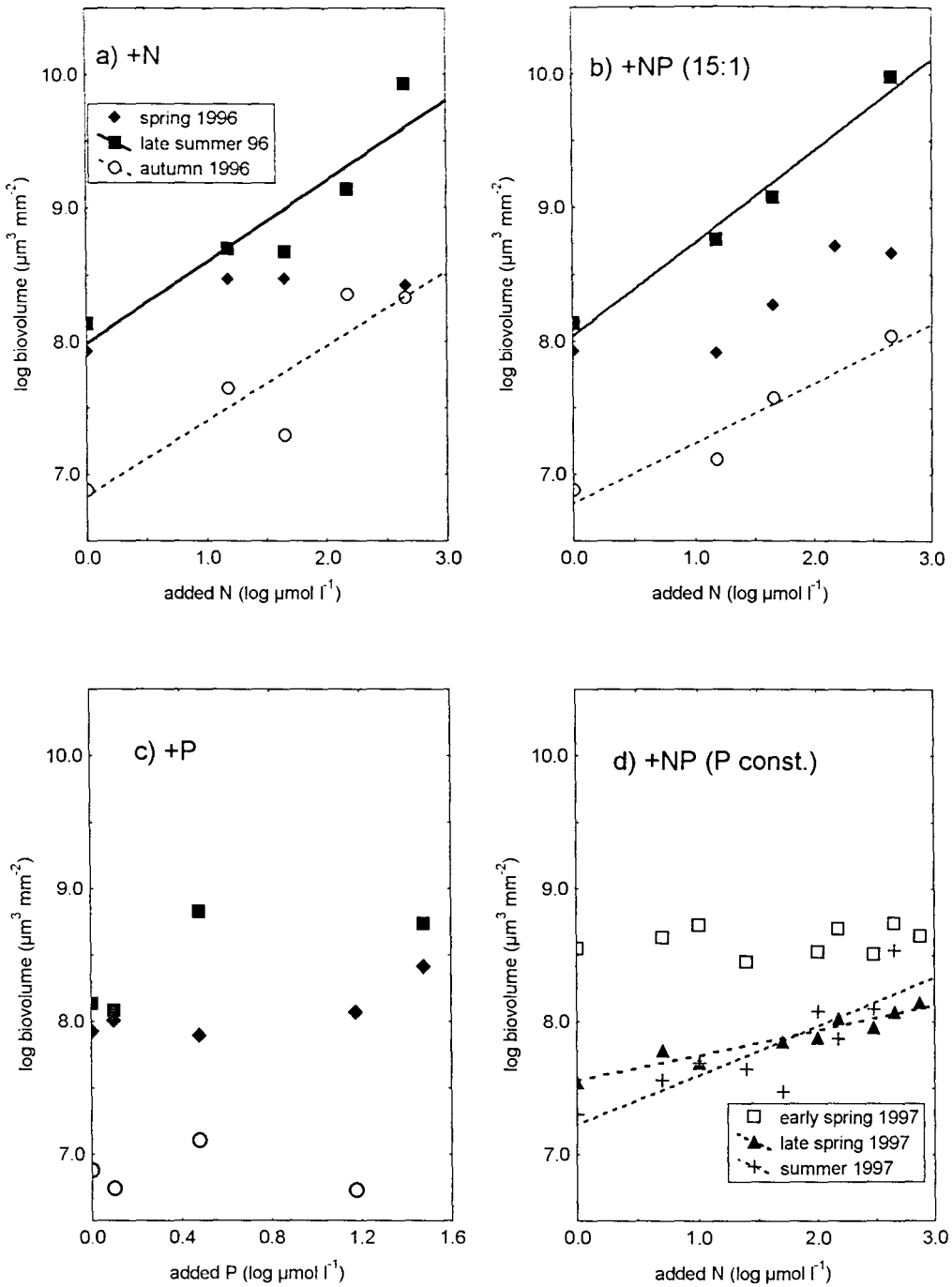
Fig. 4.2: Linear regression on total biovolume of benthic microalgae. Only significant regression lines are shown (see Table 4.3). a-c) experiments from 1996 with treatments supplying N (a), N+P (b) and P (c). d) experiments from 1997.

From late spring to autumn, only N-enriched treatments showed significant responses (Fig. 4.2, Table 4.3). During these experiments ambient nutrient ratios indicated a surplus of P relative to N (N:P < 16) (Fig. 2.3). In spring 1996, ambient N:P initially was as high as 50, but decreased to 12 (Fig. 2.3), and consecutively also a response of treatments receiving P-enrichment only was visible (Fig. 4.2 and 4.3). However, this was slightly insignificant for P-enrichment (p=0.107) and N+P enrichment (p=0.051) in the linear regression (Table 4.3). In early spring 1997, nutrient enrichment had no conspicuous effect on total biovolume (Table 4.3).

Table 4.4: Spearman-rank-correlation coefficients of species biovolume and nutrient enrichment. The table lists species name, correlation coefficients with significance level and number of valid observations (brackets). Annotation: seasonal occurrence of the respective species. m: missing or not dominant in the respective year.

species	1996			1997	annotation
	N	P	N+P	N+P	
Achnanthes longipes	1.00 *** (5)	0.61 ns (8)	0.40 ns (4)	0.60 ns (9)	summer
Berkeleya rutilans	0.71 ** (14)	0.41 ns (13)	0.75 ** (13)	0.59 ** (18)	all seasons
Ceramium strictum	1.00 *** (5)	0.80 ns (5)	1.00 *** (5)	0.95 *** (9)	summer
Haslea crucigera	0.06 ns (14)	0.17 ns (13)	0.07 ns (13)	0.47 ns (9)	spring
Licmophora paradoxa	-0.04 ns (13)	0.04 ns (12)	0.50 ns (12)	0.20 ns (18)	spring
Melosira moniliformis	0.74 * (10)	0.40 ns (8)	0.88 ** (8)	m.	sum. & aut.
Melosira nummuloides	0.50 ns (14)	-0.17 ns (13)	0.32 ns (13)	0.30 ns (18)	all seasons
Navicula grevillei	m.	m.	m.	0.77 * (9)	spring
Pleurosigma elongatum	0.80 ** (10)	0.12 ns (8)	0.39 ns (8)	0.70 * (9)	sum.& aut.
Proschkinia complanata	-0.10 ns (9)	0.72 ** (9)	0.89 ** (9)	0.63 ns (9)	spr. & sum.
Tabularia fasciculata	0.80 *** (14)	0.08 ns (13)	0.57 * (13)	0. 98 **	all seasons

The dominant taxa showed distinct reactions to nutrient treatments (Fig. 4.3, Table 4.4). Most of the species abundant in summer were stimulated only by increased nitrogen concentrations (Table 4.4), like *Ceramium strictum* and *Melosira moniliformis*. Others belonging to this group were *Tabularia fasciculata* and *Navicula grevillei*. *M. nummuloides* increased at low nitrogen-enrichment, but was replaced by other species at higher concentrations (150 or 450 μmol l^{-1}).
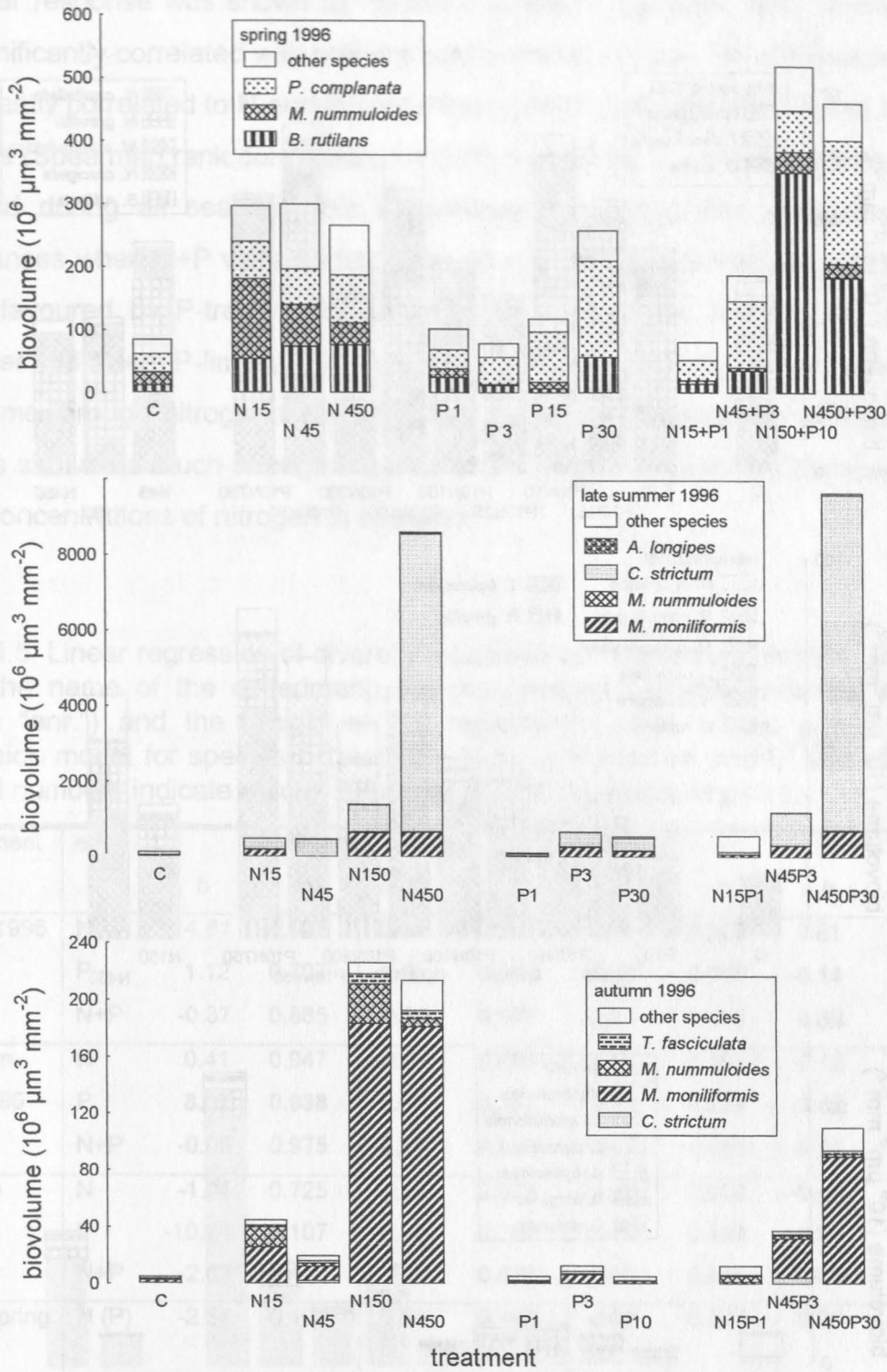
Fig. 4.3: Species composition of benthic microalgae in the 6 experiments of series 1. Treatments denote control (C), N-enrichments (N, concentrations are in µmol l^{-1}), P-enrichments (P) and N+P-enrichments in a ratio of 15:1 (N...P) or with constant supply of P (P...N). This page: experiments from 1996. Note different scales of Y-axes. Next page: experiments from 1997.
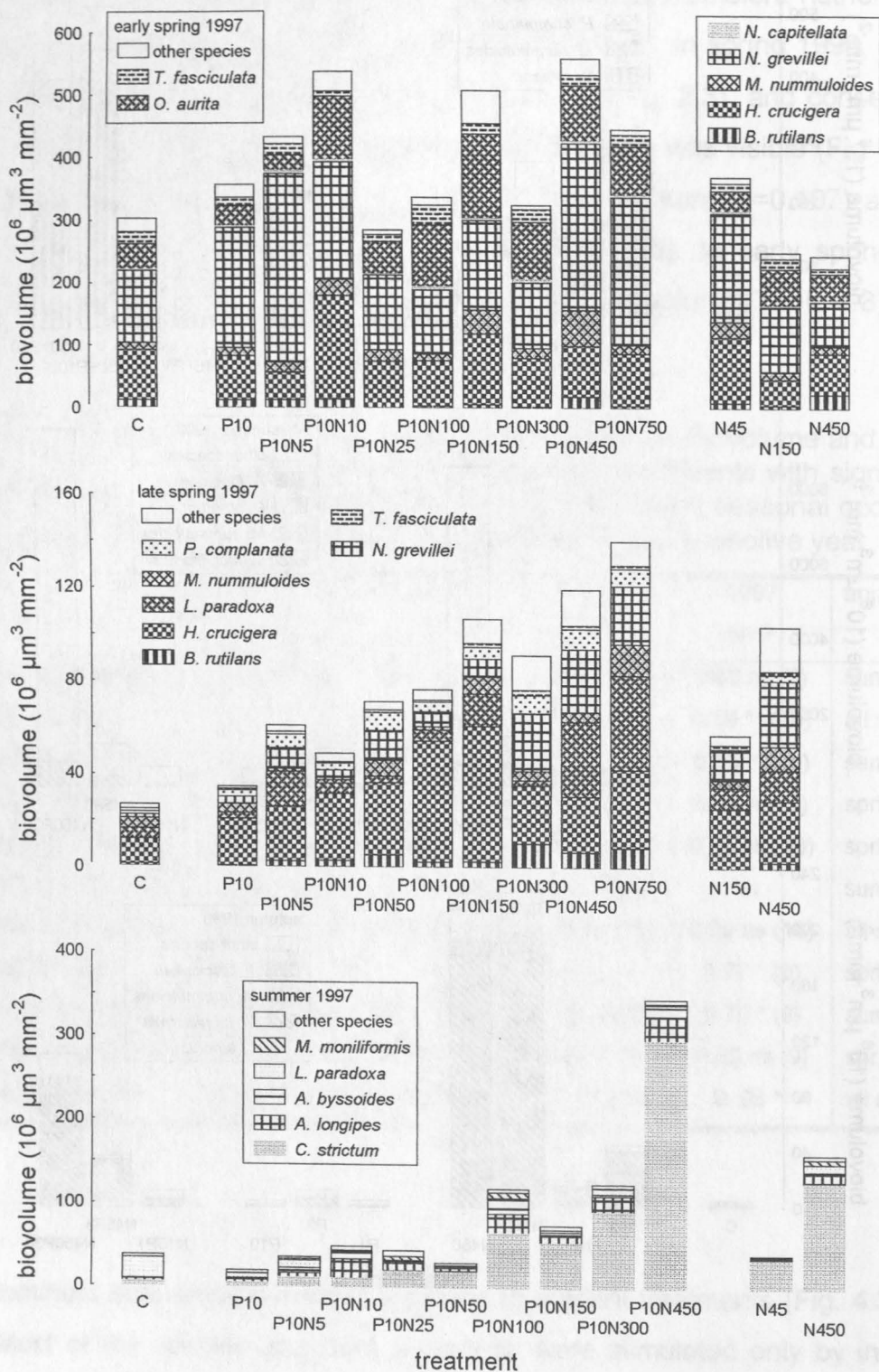
Fig. 4.3: *continued*

A similar response was shown by *Haslea crucigera*. Therefore, both species were not significantly correlated with nutrient supply (Table 4.4), but *M. nummuloides* was significantly correlated to N-enrichment if the highest treatment was omitted from the analysis (Spearman rank correlation, r = 0.70, p = 0.016, n = 11). *Berkeleya rutilans* occurred during all seasons, but it dominated in spring and showed greatest abundances when N+P were added. *Proschkinia complanata* was the only species highly favoured by P-treatments - regardless whether the N:P ratio of ambient seawater indicated P-limitation or not. Dominant spring species increased their biovolume through nitrogen treatments five- to tenfold at maximum, while summer species showed a much stronger augmentation (Fig. 4.3), probably because of the lower concentrations of nitrogen in seawater.

Table 4.5: Linear regression of diversity measures on nutrient enrichment. The table gives the name of the experiment, the independent variable (enriched nutrient, column "enr.") and the results of the regression: slope b and p-level of the regression model for species richness S, diversity indices H' and D' and evenness J'. Bold numbers indicate results significant at p<0.05, italics at p<0.1.

experiment	enr.	S		H'		D'		J'	
		b	p	b	p	b	p	b	p
spring 1996	N	*4.61*	*0.074*	0.07	0.568	0.03	0.326	0.01	0.873
	P	1.12	0.707	**-0.51**	**0.018**	*-0.16*	*0.089*	**-0.14**	**0.028**
	N+P	-0.37	0.885	*-0.30*	*0.097*	-0.07	0.310	-0.08	0.101
late sum-	N	0.41	0.947	*-0.43*	*0.059*	-0.18	0.169	*-0.12*	*0.081*
mer 1996	P	**8.87**	**0.038**	-0.39	0.367	-0.13	0.234	-0.12	0.312
	N+P	-0.06	0.975	**-0.54**	**0.049**	*-0.22*	*0.051*	**-0.14**	**0.044**
autumn	N	-1.04	0.725	-0.24	0.325	-0.10	0.302	-0.06	0.339
1996	P	-10.94	0.107	0.29	0.767	0.15	0.594	0.11	0.649
	N+P	-2.63	0.175	-0.26	0.576	-0.09	0.544	-0.06	0.596
early spring 1997	N (P)	-2.54	0.160	0.06	0.440	0.04	0.237	0.03	0.134
late spring 1997	N (P)	**1.31**	**0.038**	0.18	0.102	0.06	0.219	0.05	0.168
summer 1997	N (P)	1.54	0.444	**-0.52**	**<0.001**	**-0.22**	**<0.001**	**-0.16**	**<0.001**
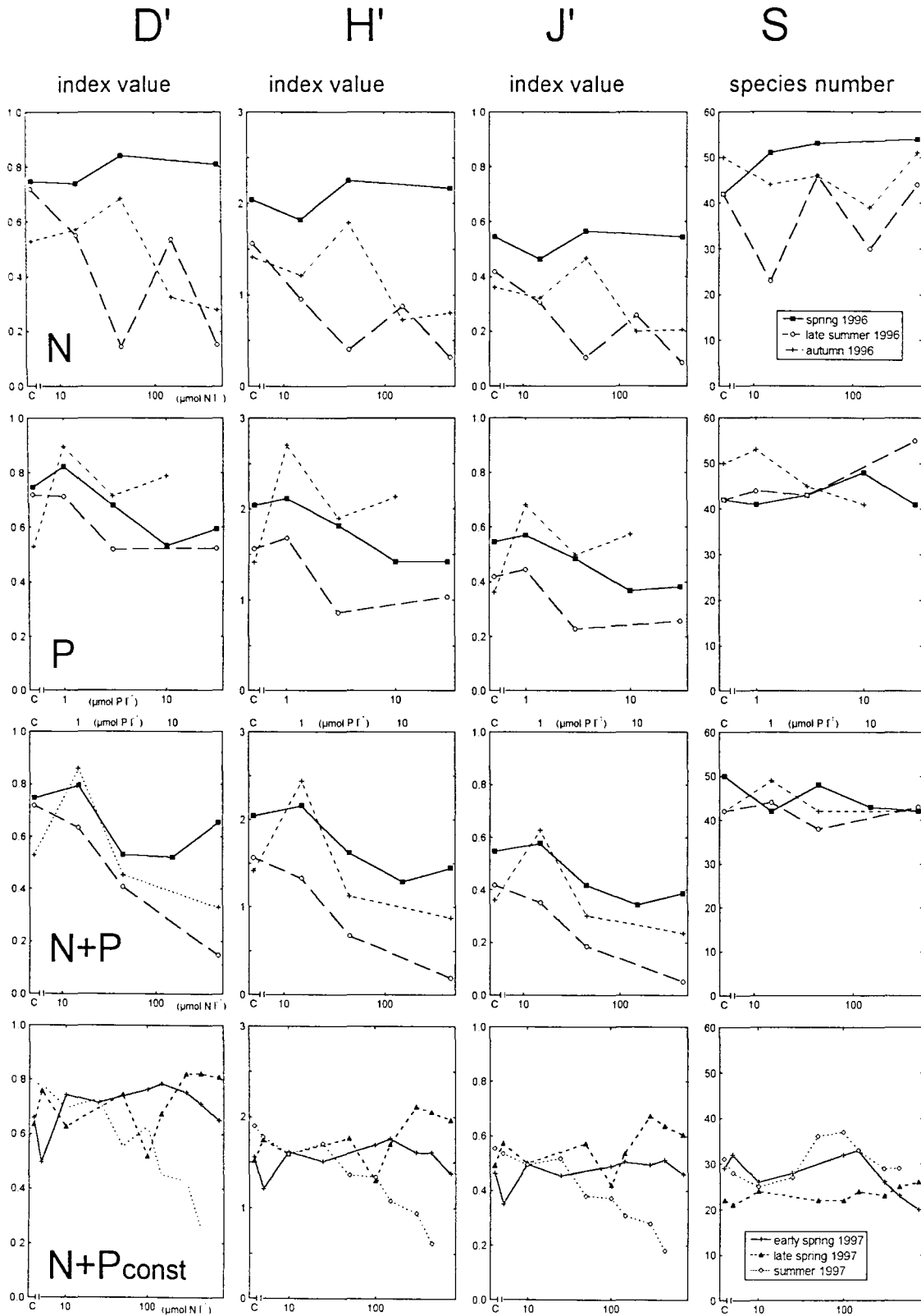
Fig. 4.4: Diversity of microalgal assemblages in the 6 experiments of the first series. Rows describe treatments as in Fig. 4.3. Diversity measures are D' and H', evenness J' and species number S. See text for further details.

Increasing nutrient supply led to a decrease in diversity of microphytobenthic communities (Fig. 4.4, Table 4.5). This decrease was due to enhanced dominance of few species and not to decreased species richness. While species number remained constant or increased insignificantly with enrichment, the evenness of the community decreased substantially, resulting in negative trends of H', D' and J'. In spring 1996, the negative trend of diversity with nutrient enrichment was associated with P-enrichment, whereas N-enrichment was effective in summer 1996 and 1997 (Table 4.5). The decrease of diversity with increasing nutrient supply resulted in a significant negative correlation of H' and J' with total biovolume (Fig. 4.5).

The C:N ratios of biomass were regularly higher than the optimum ratio of 7.2 (see Chapter 3), whereas cellular N:P ratios were generally lower than 17 (Fig. 4.6), except for some treatments of 1997 experiments. The combination of high C:N and low N:P ratios indicated nitrogen limitation (see Chapter 3). The effect of the nutrient supply was shown by a positive correlation between N:P ratios in the supplied media and in the biomass ($r=0.299$, $p=0.013$, $n=68$). Since this correlation was dominated by some exceptionally high N:P ratios in the medium, the correlation was conducted again leaving out treatments with a medium N:P >100. This did not affect the conclusion ($r=0.307$, $p=0.019$, $n=58$, Fig. 4.7). Also the C:P ratios in the biomass were positively correlated with N:P ratios of the supply medium, with all treatments ($r=0.360$, $p=0.003$, $n=68$) and with treatments supplying N:P in a ratio < 100 ($r=0.289$, $p=0.028$, $n=58$). C:N ratios in the biomass were not correlated with the supply ratio of N:P ($r=0.03$, $p=0.824$).
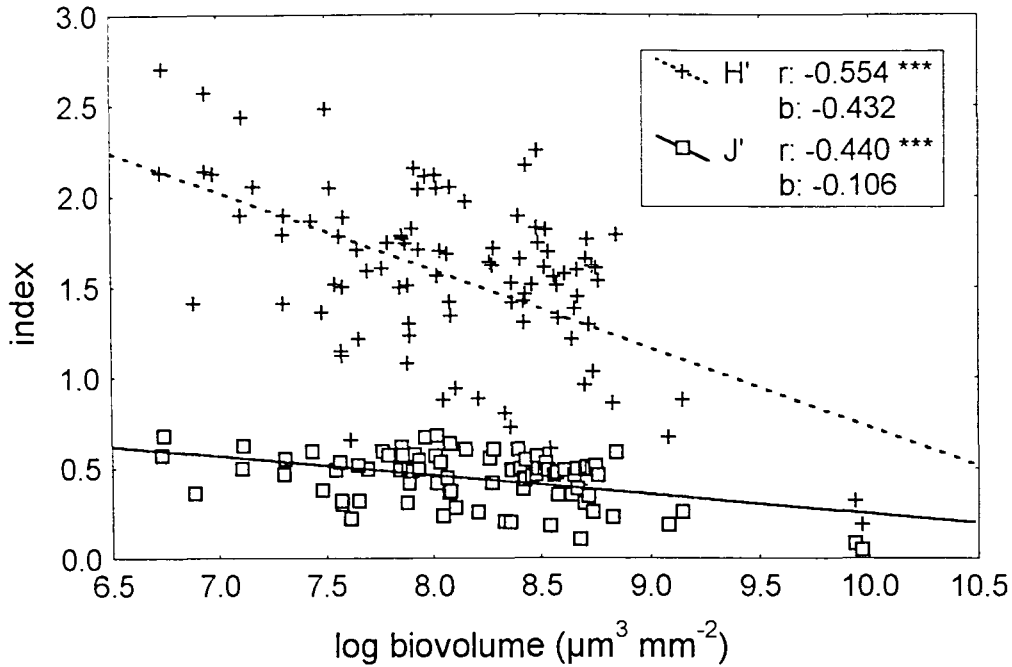
Fig. 4.5: Shannon-Weaver diversity H' and evenness J' of microalgal assemblages dependent on total biovolume. Correlation coefficient r and slope b of linear model-II regression are given with significance level (***: p< 0.001).
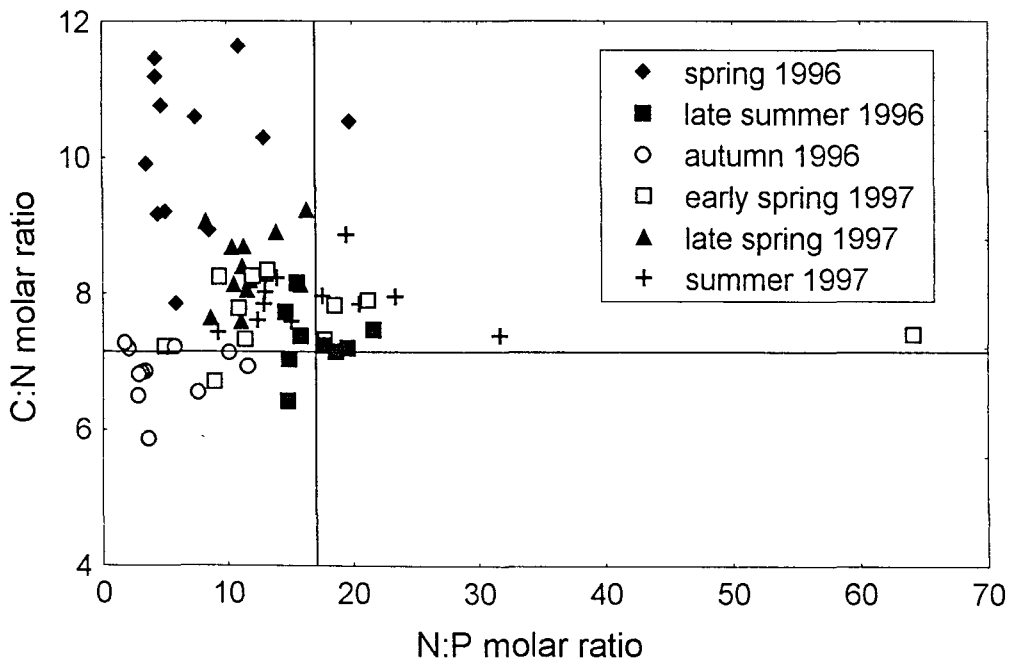
Fig. 4.6: Relationship between N:P and C:N molar ratios of benthic microalgae. Solid lines indicate optimal ratios derived from experiments in Chapter 3.
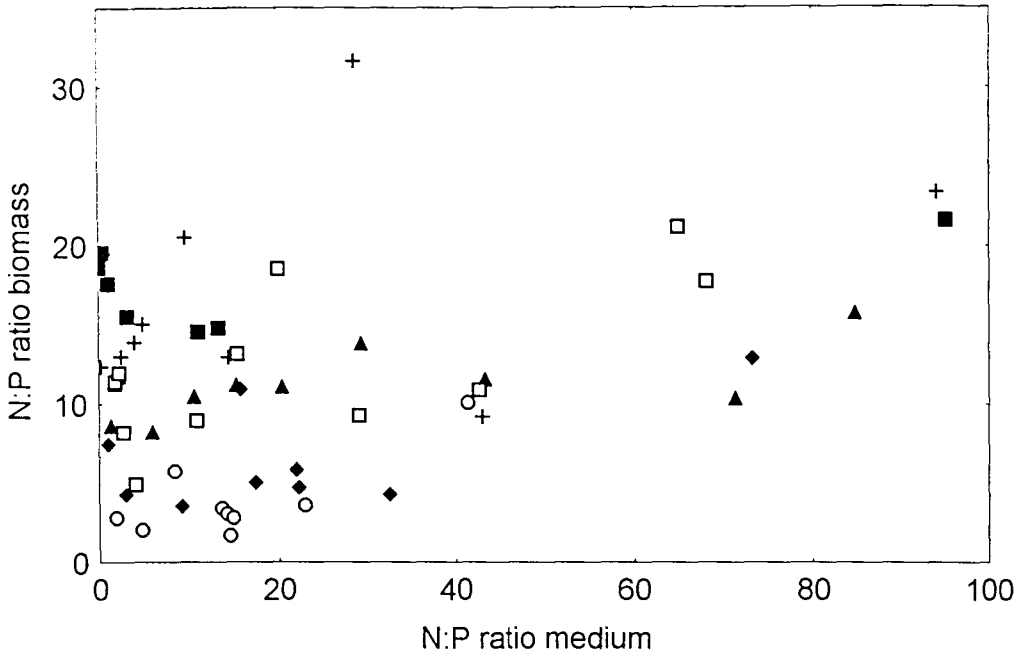
Fig. 4.7: Correlation between biomass N:P ratio and N:P ratio of the supplied medium. Symbols as in Fig. 4.6.
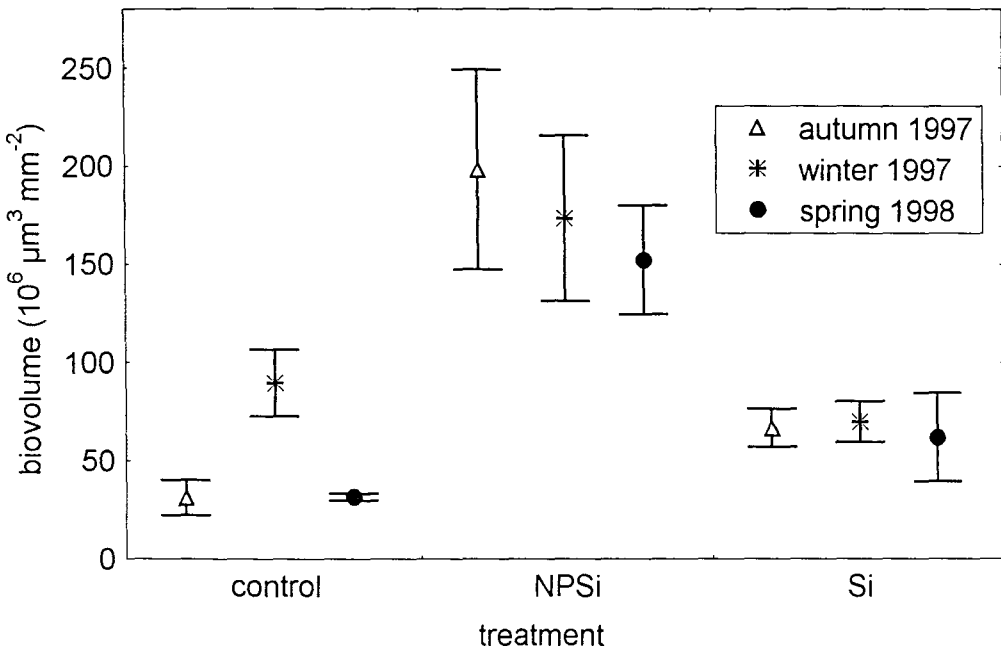
Fig. 4.8: Total biovolume (mean and standard error) of benthic microalgae in the 3 experiments of the second series, with control and addition of N+P+Si and Si.

4.3.3 Enrichment of Si

In the second series of experiments, total biovolume was affected by nutrient treatment, but not by the season of the experiment (Fig. 4.8, Table 4.6). The biomass increased due to N+P-enrichment, which was significantly different from controls and Si-enrichments (Tukey's HSD, p<0.01). No significant difference was detected in the ANOVA for total biovolume between controls and Si-enrichments (Tukey's HSD, p=0.422). However, the increase in medium Si-concentration resulted in a linear increase in total biovolume in autumn 1997 and in spring 1998, but in the latter experiment only in combination with N+P enrichment. In winter 1997, the Si-concentrations had no significant effects (Fig. 4.9, Table 4.7).

Table 4.6: Results of a two-factor ANOVA on log-transformed total biovolume with treatment (C, NPSi or Si) and season of experiment (autumn, winter, spring) as factors. Log-transformation resulted in normal distribution (χ^2 = 1.95, p=0.930) and homogeneity of variances (Bartlett's χ^2 = 6.09, p=0.637).

Effect	df	MS effect	F-ratio	p-level
treatment	2	0.907	18.218	<0.001
season	2	0.109	2.192	0.131
treatment x season	4	0.051	1.015	0.417
error	27	0.050		

Table 4.7: Linear regression of $\log_{10}$-transformed biovolume dependent on $\log_{10}$-transformed Si-concentrations. The table lists the experiments, the enriched nutrient and the results of the linear regression: intercept, slope with standard error (SE), regression coefficient r^2 and significance level (ns: not significant, *: p<0.05; **: p<0.01, ***: p<0.001).

experiment	enrichment	intercept	slope (SE)	r^2	significance	
autumn 1997	Si	7.46	0.18 (0.05)	0.7601	0.011	*
	Si+N+P	7.75	0.29 (0.06)	0.8669	0.007	**
winter 1997	Si	7.88	-0.01 (0.05)	0.0069	0.859	ns
	Si+N+P	7.93	0.16 (0.10)	0.5792	0.239	ns
spring 1998	Si	7.51	0.10 (0.09)	0.2220	0.345	ns
	Si+N+P	7.84	0.18 (0.04)	0.8545	0.008	**
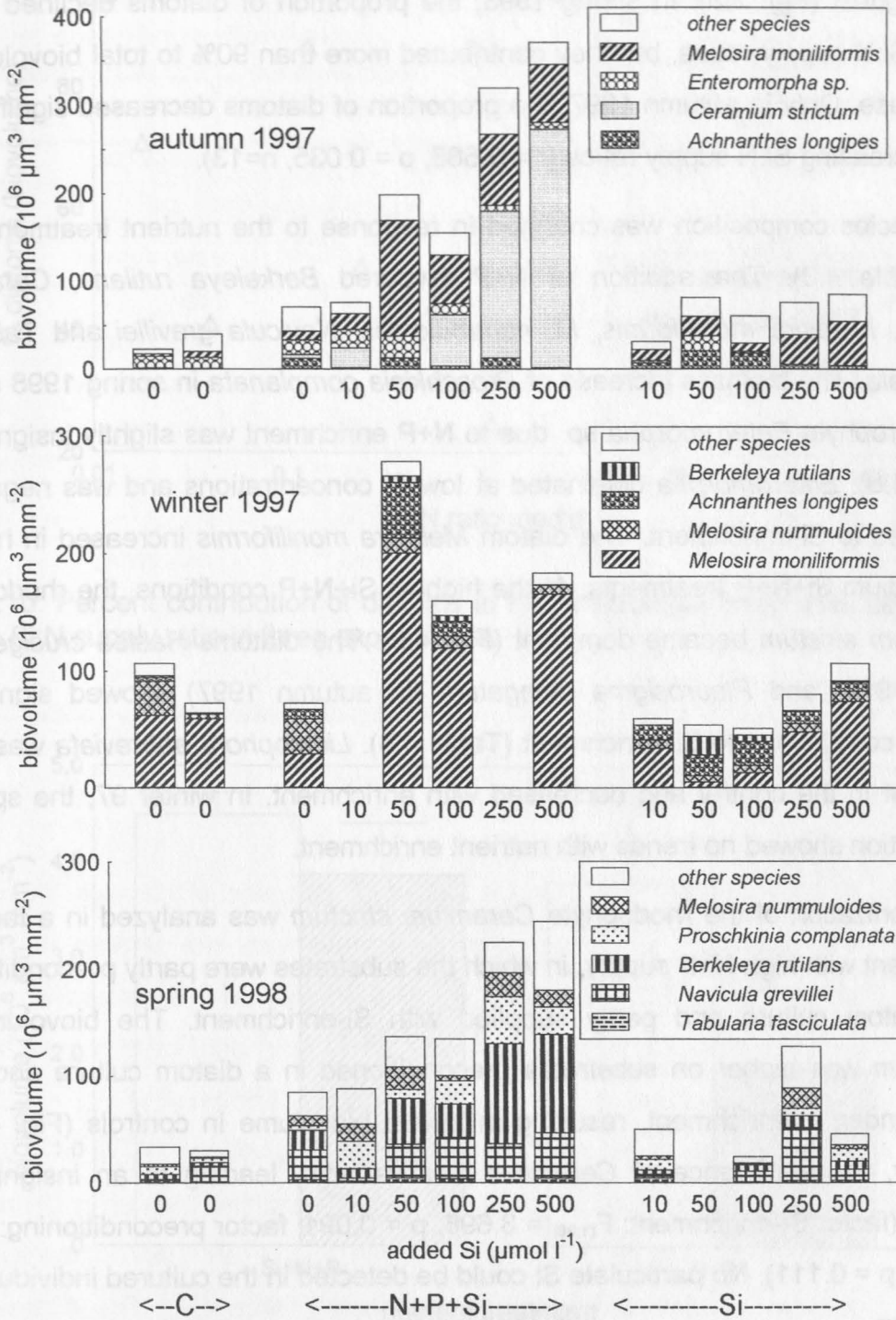
Fig. 4.9: Species composition of benthic microalgae in three experiments with control (C) and addition of N+P+Si and Si.

In general, diatoms were the most dominant group (Fig. 4.10). They stayed dominant throughout all treatments in winter 1997, when ambient Si-concentrations were highest (Fig. 2.3). In spring 1998, the proportion of diatoms declined at the lowest Si:N supply ratios, but they contributed more than 90% to total biovolume in every case. Only in autumn 1997, the proportion of diatoms decreased significantly with decreasing Si:N supply ratios (r = 0.588, p = 0.035, n=13).

The species composition was changed in response to the nutrient treatment (Fig. 4.9, Table 4.8). The addition of N+P favoured *Berkeleya rutilans*, *Ceramium strictum*, *Melosira moniliformis*, *M. nummuloides*, *Navicula grevillei* and *Tabularia fasciculata*. The biomass increase of *Proschkinia complanata* in spring 1998 and of the chlorophyte *Enteromorpha* sp. due to N+P enrichment was slightly insignificant (Table 4.8). *Enteromorpha* dominated at low Si concentrations and was negatively correlated to Si-enrichment. The diatom *Melosira moniliformis* increased in high Si and medium Si+N+P treatments. At the highest Si+N+P conditions, the rhodophyte *Ceramium strictum* became dominant (Fig. 4.9). The diatoms *Haslea crucigera* (in spring 1998) and *Pleurosigma elongatum* (in autumn 1997) showed significant positive correlations to Si-enrichment (Table 4.8). *Licmophora abbreviata* was most abundant in the control and decreased with enrichment. In winter 97, the species composition showed no trends with nutrient enrichment.

The colonization of the rhodophyte *Ceramium strictum* was analyzed in a factorial experiment with high N+P supply, in which the substrates were partly preconditioned in a diatom culture and partly supplied with Si-enrichment. The biovolume of *Ceramium* was higher on substrates preconditioned in a diatom culture and also higher under Si-enrichment, resulting in lowest biovolume in controls (Fig. 4.11). However, the abundance of *Ceramium* was variable, leading to an insignificant ANOVA (factor Si-enrichment: $F_{(1;28)}$ = 3.698, p = 0.091; factor preconditioning: $F_{(1;28)}$ = 3.209, p = 0.111). No particulate Si could be detected in the cultured individuals of *Ceramium*.
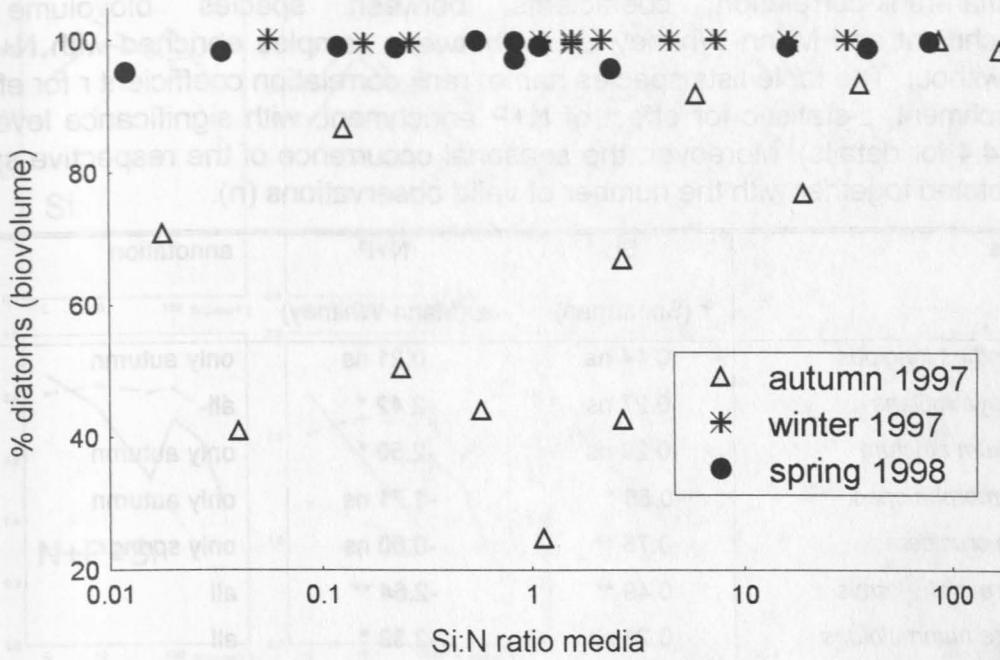
Fig. 4.10: Percent contribution of diatoms to total microalgal biovolume, depending on the Si:N supply ratio in three experiments.
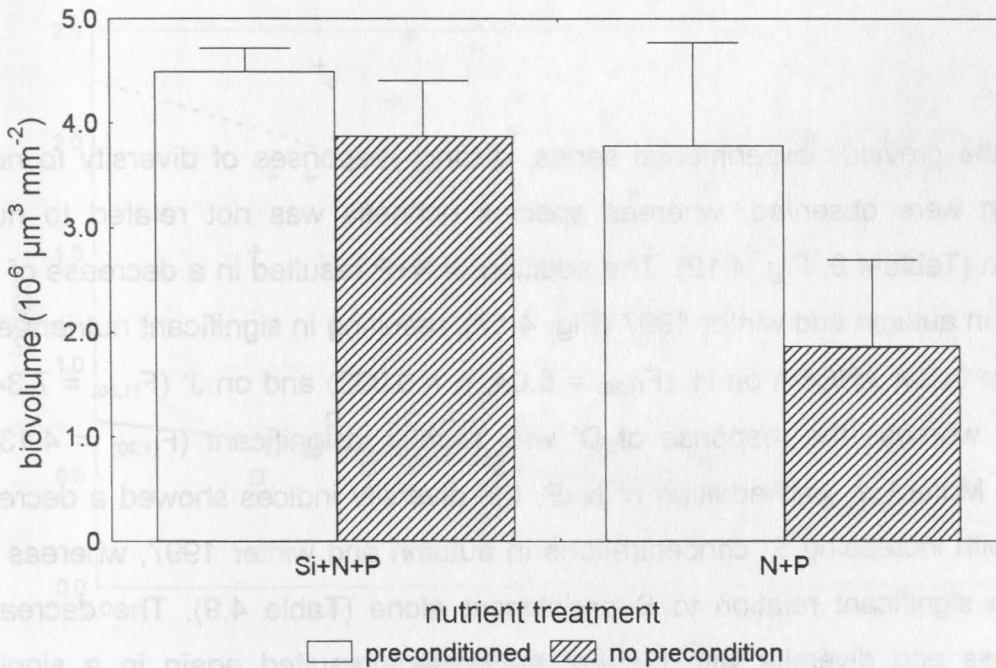
Fig. 4.11: Biovolume (mean ± standard error) of *Ceramium strictum* on substrates preconditioned in a diatom culture compared to unconditioned substrates (hatched bars) for two nutrient treatments (+Si+N+P or +N+P).

Table 4.8: Response of dominant species to nutrient enrichment: Spearman-rank-correlation coefficients between species biovolume and Si-enrichment and Mann-Whitney U-test between samples enriched with N+P and those without. The table lists species name, rank correlation coefficient r for effect of Si enrichment, z-statistic for effect of N+P enrichment, with significance level (see Table 4.4 for details). Moreover, the seasonal occurrence of the respective species is annotated together with the number of valid observations (n).

species	Si	N+P	annotation	n
	r (Spearman)	z (Mann-Whitney)		
Achnanthes longipes	0.14 ns	0.21 ns	only autumn	13
Berkeleya rutilans	0.27 ns	-2.42 *	all	36
Ceramium strictum	0.29 ns	-2.50 *	only autumn	13
Enteromorpha spec.	-0.56 *	-1.71 ns	only autumn	13
Haslea crucigera	0.75 **	-0.80 ns	only spring	12
Melosira moniliformis	0.49 **	-2.64 **	all	36
Melosira nummuloides	0.21 ns	-2.39 *	all	36
Navicula grevillei	0.24 ns	-2.88 **	only spring	12
Pleurosigma elongatum	0.71 **	-0.71 ns	only autumn	13
Proschkinia complanata	0.50 ns	-1.92 ns	only spring	12
Tabularia fasciculata	0.41 *	-2.39 *	all	36

As in the previous experimental series, distinct responses of diversity to nutrient addition were observed, whereas species richness was not related to nutrient addition (Table 4.9, Fig. 4.12). The addition of N+P resulted in a decrease of H', J', and D' in autumn and winter 1997 (Fig. 4.12), resulting in significant nutrient effects in a two factor ANOVA on H' ($F_{(1;30)}$ = 5.04, p = 0.032) and on J' ($F_{(1;30)}$ = 7.34, p = 0.011), whereas the response of D' was slightly insignificant ($F_{(1;30)}$ = 4.13, p = 0.051). Moreover, with addition of N+P, the diversity indices showed a decreasing trend with increasing Si concentrations in autumn and winter 1997, whereas there was no significant relation to Si-enrichment alone (Table 4.9). The decrease of evenness and diversity with nutrient enrichment resulted again in a significant negative trend of diversity with increasing biovolume (Fig. 4.13). Regression slopes were slightly higher in the second series of experiments.
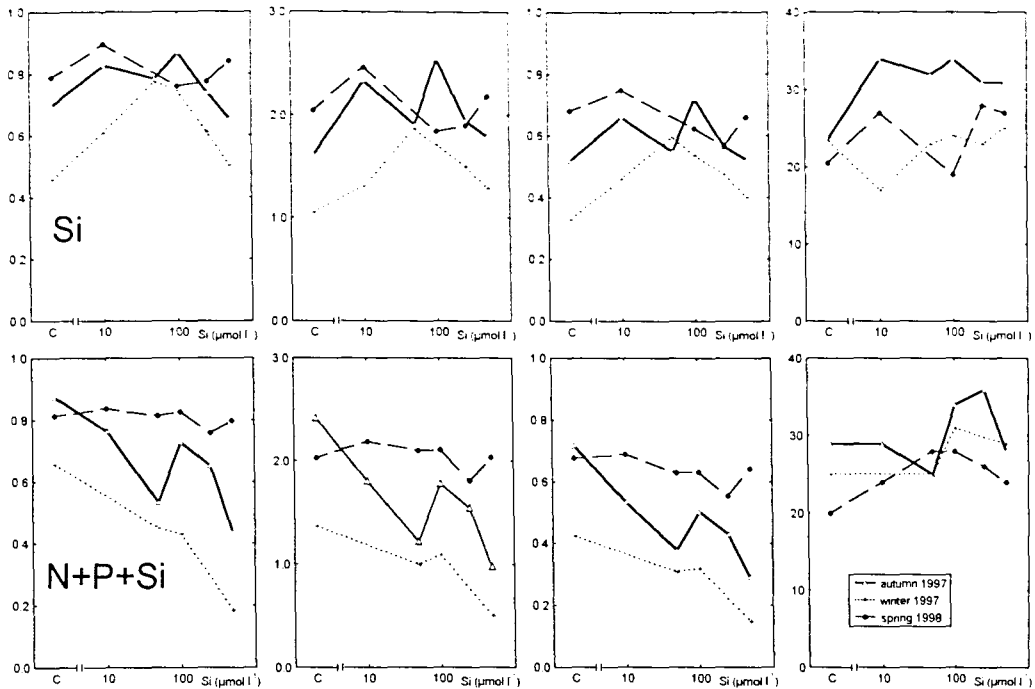
Fig. 4.12: Diversity of microalgal assemblages in the 3 experiments of the second series. Rows describe treatments (+Si and +Si+N+P). Diversity measures are D' and H', evenness J' and species number S.
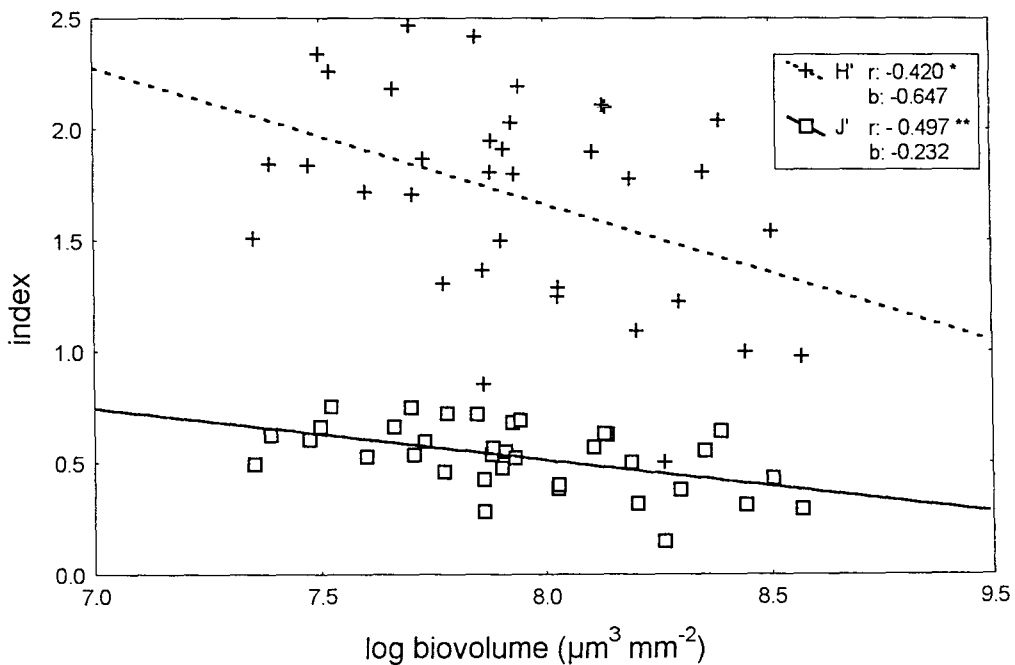
Fig. 4.13: Shannon-Weaver diversity (H') and evenness (J') of microalgal assemblages depending on total biovolume in three experiments of the second series. Correlation coefficient r and slope b of linear modell-II regression are given with significance level (*: p<0.05, **: p<0.01).

Table 4.9 Linear regression of diversity measures on nutrient enrichment. The table gives the name of the experiment, the independent variable (enriched nutrient, column "enr.") and the results of the regression: slope b and p-level of the regression model for species richness S, diversity indices H' and D' and evenness J'. Bold numbers indicate results significant at p<0.05, italics at p<0.1.

experiment	enr.	S		H'		D'		J'	
		b	p	b	p	b	p	b	p
autumn	Si	*3.04*	*0.079*	0.13	0.380	0.01	0.772	0.21	0.550
1997	Si (NP)	1.51	0.885	**-0.50**	**0.045**	*-0.15*	*0.053*	**-0.15**	**0.022**
winter 1997	Si	0.58	0.645	0.18	0.163	0.06	0.330	0.05	0.190
	Si (NP)	2.20	0.329	*-0.36*	*0.086*	**-0.20**	**0.028**	*-0.12*	*0.058*
spring 1998	Si	1.88	0.258	-0.04	0.755	-0.002	0.942	-0.03	0.394
	Si (NP)	2.08	0.107	-0.07	0.387	-0.02	0.240	-0.04	0.119

Combining the data of both experimental series, the different response of species richness and evenness to nutrient enrichment led to a lack of correlation between S and H' ($r = -0.097$, $p = 0.336$, $n = 100$) and a negative correlation between S and J' ($r = -0.340$, $p < 0.001$, $n = 100$), respectively D' ($r = -0.206$, $p = 0.040$, $n = 100$). Between the indices H', D' and J', the correlation was always highly positive ($r > 0.90$, $p<0.001$, $n = 100$).

In all experiments, the biomass stoichiometry changed with the nutrient treatment. C:N ratios decreased in the NP-enriched treatments (Fig. 4.14, Table 4.10), whereas controls and Si showed similar C:N ratios. The cellular C:N ratio was also influenced by the season of the experiments, since nutrient conditions changed during the year (Table 4.10, cf. Fig. 2.3). N:P ratios were generally lower than 17 in autumn and winter 1997 and varied broadly in spring 1998 (Fig. 4.15). In autumn 1997, the C:N:P ratios indicated a N-limited situation, whereas in spring 1998 the data were less clearcut (cf. Chapter 3).
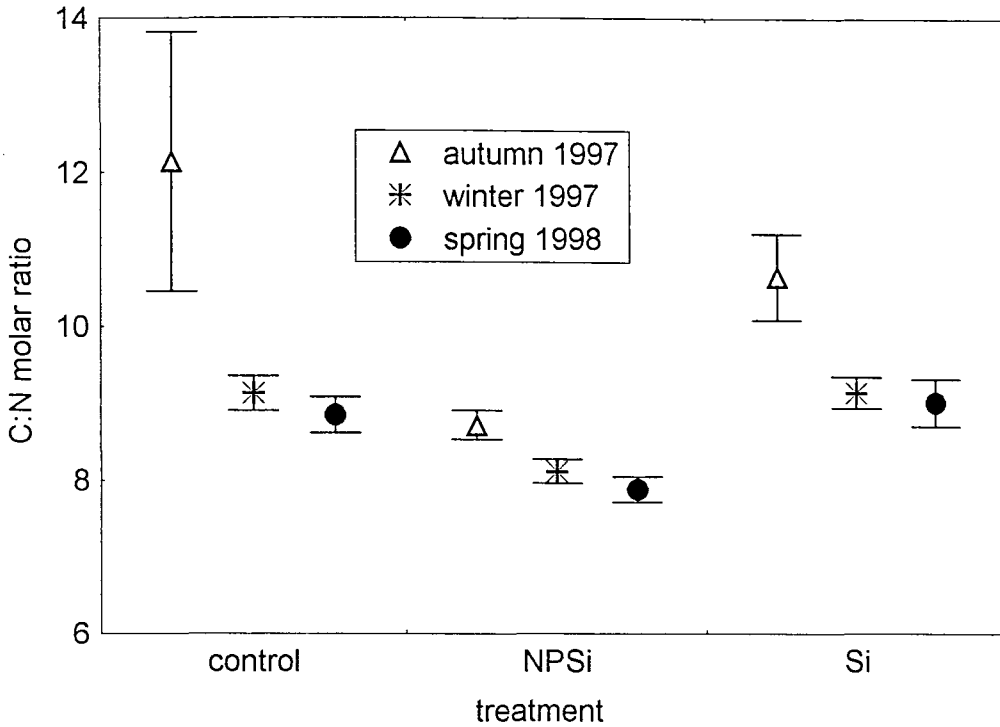
Fig. 4.14: C:N ratios (mean and standard error) of benthic microalgae in three experiments of the second series with addition of Si and Si+N+P.
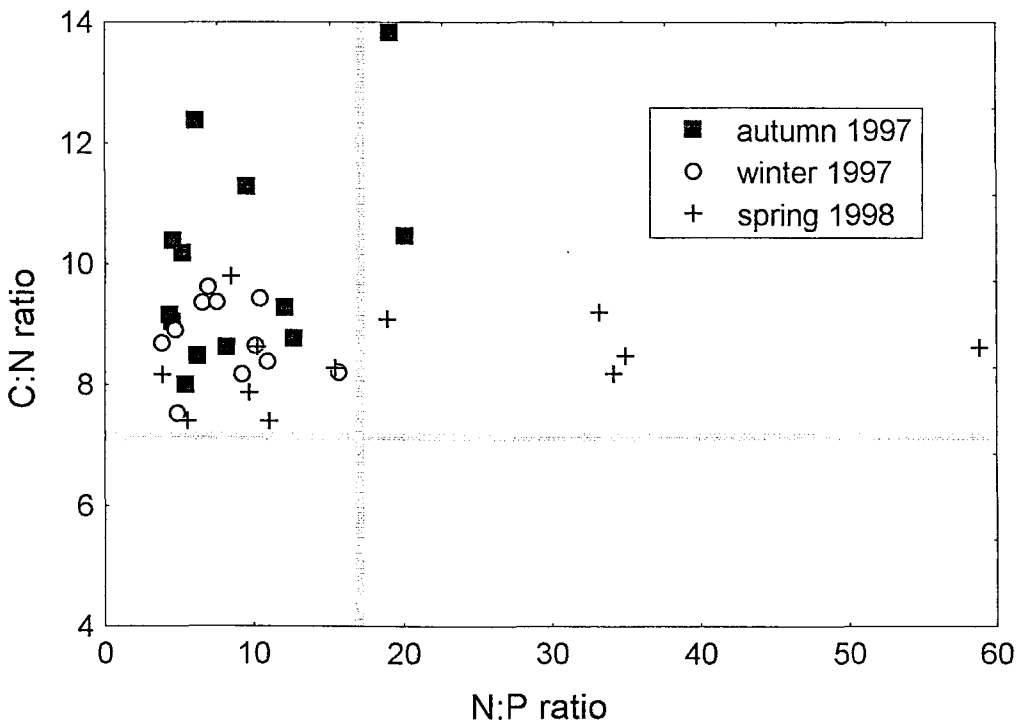
Fig. 4.15: Relationship between C:N, N:P and C:P ratios of benthic microalgae in 3 experiments of the second series. Solid lines indicate optimal ratios derived from experiments in Chapter 3.

Table 4.10: Results of a two-factor ANOVA with treatment (C, NPSi or Si) and season of experiment (autumn, winter, spring) as factors on C:N ratio as dependent variable. Homogeneity of variances was achieved by squareroot transformation of the dependent variable (Bartlett's χ^2 = 12.58, p=0.127), whereas normal distribution was not achieved (χ^2 = 13.80, p=0.008).

Effect	df	MS effect	F-ratio	p-level
treatment	2	0.060	20.667	<0.001
season	2	0.057	19.637	<0.001
treatment x season	4	0.006	2.146	0.101
error	28	0.003		

4.4 Discussion

4.4.1 Method

The advantages of the experimental setup presented here are the continuous and constant supply of nutrient concentrations and ratios to the benthic community, besides the simplicity and the low costs of the setup. It was furthermore possible to use very low supply rates, which presumably were near to natural nutrient sources (Table 4.1). The constant supply rates make this experimental design superior to diffusing substrates with exponentially declining rates, where nutrient regime changes permanently during experimental time. Both artificial substrates allowed the settlement of a wide variety of species, as was shown in Chapter 2. The duration of the experiments was chosen according to the results of the colonization experiments (Chapter 2). Pinckney et al. (1995) mentioned that experiments may often be too short to detect reactions on nutrient treatments, and suggested to conduct experiments for more than 15 days. The shortest of my experiments was run for 38 days (Table 4.1). The colonization experiments (Chapter 2) showed that biovolume had reached a plateau at the time when enrichment experiments were harvested.

In principle, there are two alternatives of experimental treatments at a constant level of effort: either many different nutrient levels distributed along a gradient of concentrations or only one enrichment level with higher number of replicates. By using different nutrient levels, more information was gained on the quantitative

response of benthic microalgae to nutrient enrichment, than would have been possible from replicated treatments with only one concentration per treatment (Table 4.3 and 4.7). Combining the different concentrations for an analysis of variance (Table 4.2) is a conservative approach, since the inherent variation due to the different nutrient concentrations should increase the error term. For linear regression, however, it should be remembered that insignificant relationships may be due to the small data basis or to nonlinearities in the response.

Further shortcomings of these experiments were: Every treatment could only be harvested once, so the results reflect a benthic community, for which the developmental history is not known (McIntire & Overton 1971). However, this development can be inferred from the colonization studies conducted simultaneously (Chapter 2). Besides, my experiments were enrichment experiments, i.e. only the additional supply of nutrients to the benthic community was controlled, while the algae were exposed to ambient nutrient concentrations as well. Therefore, the final nutrient regime was dependent on both and on hydrographic conditions around the stones. From previous experiments and from the results presented below it can be concluded that periphytic algae may have limited access to water column nutrients (Riber & Wetzel 1987, Chapter 4.4.2). Therefore, I used exponentially increasing nutrient concentrations in order to cover a wide range of influences within the limited number of experimental units.

The free suspension of the substrates prevented effectively the invasion by grazers like gastropods or large isopods (Appendix A3). Few meso- and micrograzers like amphipods, nematodes and ciliates were recorded. Although several studies have shown an influence of these taxa on benthic algal biovolume, they are less effective than larger herbivores in regulating microalgal biovolume (Hargrave 1970, McCormick 1991, Balczon & Pratt 1996). The abundance of herbivores was not systematically correlated to algal biovolume or nutrient treatment, but most groups were more abundant in summer and almost absent in early spring (Appendix A3). Therefore they are not considered as possible cause for changed community composition between the treatments.

4.4.2 Nutrient limitation

Two criteria were employed to assess nutrient limitation *in situ*: the response of biomass to nutrient enrichment and the cellular stoichiometry of benthic microalgae. The increase of total biovolume due to enrichment indicated nutrient limitation in the unenriched treatments. During late spring, summer and autumn, nitrogen was limiting for the benthic microalgae in Kiel Fjord (Table 4.3). For spring 1996, a colimitation of nitrogen and phosphate could be deduced from the fact that microalgal biovolume increased as well with nitrogen as with phosphate enrichment (see also below). Nitrogen limitation seemed to be strongest in the summer and autumn experiments with the highest biomass stimulation (i.e. highest slopes in Table 4.3) compared to the control. In winter and early spring the nutrient treatments failed to produce higher biovolume yields than the control (Table 4.3 and 4.7). It can be assumed that low light conditions (irradiance and daylength) and low temperature in combination with high ambient seawater nutrients (Fig. 2.3) precluded nutrient limitation during winter and early spring. Addition of silicate increased the total biovolume as well, but this increase was significant only in autumn 1997, and in spring 1998 in combination with N+P enrichment. The pattern in spring 1998 indicated a shift towards a Si-limited situation after the addition of N and P. Although the water column concentrations were >15 µmol l^{-1} Si in autumn 1997 (Fig. 2.3), this was obviously not sufficient to meet the demands of the developing biofilm (see below).

The dependency of cellular stoichiometry on nutrient limitation has been established for benthic marine microalgae during this study. On the basis of the optimal ratios and of the limitation indices developed in my laboratory experiments (Chapter 3), the cellular biomass composition in my *in situ* experiments supported the conclusion that the microflora was nitrogen limited for most parts of the year. C:N was seldom lower than 7.0 and raised up to 13, whereas the N:P ratio <17 and the C:P ratio <119 indicated a P-surplus. The internal N:P ratios of the biomass ranged from 1 to 64 and increased conspicuously, if media with an increased N:P ratio were supplied (Fig. 4.7). Similar results were obtained by Myklestad (1977) in experiments with two diatom species. From these data, it can be deduced that internal nitrogen pools were not saturated in unenriched treatments (cf. Droop 1983), supporting the

observed biomass increase in the enriched treatments. The significant correlation indicated also that the addition of nutrients was effective, i.e. the nutrients have been assimilated by the microalgae. This was supported by the decrease of C:N ratios under N-enriched conditions in the second experiment series (Fig. 4.14)

Thus, both criteria of nutrient limitation indicated a N-limitation for Kiel Fjord microphytobenthos, at least from late spring to autumn. The response to P-addition in spring 1996 and the N:P variability in spring 1998 indicated a P-limitation at the beginning of the year. This is corroborated by the peaks in N:P ratios in the ambient seawater in spring 1996 and 1998 (Fig. 2.3). The data are not unambiguous, however, because the epilithon had low internal N:P ratios in spring 1996 (Fig. 4.6). A shift from P- to N-limitation in spring may be caused by high inflow of freshwater, which is more likely to be P-deficient (Hecky et al. 1993). For this I cannot present direct evidence, but the increase in freshwater species in spring may indicate higher inflow from the river Schwentine (Fig. 2.4), which is less than 1 km across the Fjord opposite to my experimental site (Fig. 2.1). A shift from P-limitation in spring to N-limitation in summer was reported from several other freshwater influenced ecosystems (D'Elia et al. 1986, Malone et al. 1996). Taking into account also the Si-limitation indicated for diatoms, my experiments showed a mosaic of nutrient effects, which may differ seasonally and for different taxonomic groups. It is therefore a oversimplification to apply Liebig's law of the minimum (limitation by a single nutrient) to natural communities (D'Elia et al. 1986). The changing importance of nutrient conditions during seasonal succession is well understood for freshwater phytoplankton (Sommer et al. 1986). Also for periphyton, nutrients may be important for seasonal development (Chapter 2 and 6), but further research is needed to reveal the combined influence of nutrients, grazing, and abiotic conditions on seasonality of the microphytobenthos.

This study moreover showed that nutrient limitation may still be in effect, even if nutrients are detectable in the water column. The maximum winter concentrations of nitrate in Kiel Fjord clearly exceeded 30 μmol l^{-1} and ambient nutrient pools were never depleted (Fig. 2.3). Nevertheless, the periphytic algae responded significantly to the increased nutrient concentrations. This indicated the existence of diffusion barrieres which limit the access of benthic microalgae to water column nutrients

(Riber & Wetzel 1987, Burkholder et al. 1990). Bothwell (1985, 1989) showed the higher nutrient demands of intact periphyton mats compared to species-specific demands in single-celled cultures. In a review on freshwater periphyton, Wetzel (1996) emphasized the importance of nutrient recycling within the epilithic microflora, since periphyton was shown to be impervious to water currents and thus did not respond to slightly changed water column concentrations of essential resources. He also pointed at an increasing importance of regeneration with increasing biomass of epilithic mats. It can be assumed that regeneration is more effective in natural communities than in my experiments due to the low herbivore abundances on the suspended substrates. By supplying nutrients from the bottom, I presumably overcame this nutrient barrier and additionally reversed the vertical nutrient supply: In natural periphytic mats, the outermost species have access to nutrients first, while in my experiments the nutrients were supplied first to species growing adnate to the substrate. Nevertheless, most of the species responding to nutrient enrichment growed erectly: directly on the substrate (*Tabularia*), in chains (*Melosira*), on stalks (*Achnanthes*) or in tubes (*Berkeleya*) (Table 4.4 and 4.8). The vertical position of the mobile unicellular species (*Pleurosigma*, *Proschkinia*) could not be determined. A more direct response of erect growing species to nutrient enrichment of the water column was also proposed for freshwater periphyton (Paul & Duthie 1989, Rosemond et al. 1993). Even in situations where nutrients are supplied from below the mat, the adnate species may be less effective than erect species at using additional nutrients, since they are limited as well by light. In conclusion, nutrient limitation of epilithic microalgae may be possible in a wide variety of aquatic habitats, not only under oligotrophic conditions. This has implications for the nutrient competition within the epilithon (see below), the trade-off between nutrient availability and herbivore resistance (see Chapter 5) and for the competition between benthic and pelagic microalgae (see Chapter 6).

Epilithic microalgae depend only on nutrients from the water column and recirculation within the biofilm, but sediment-inhabiting microalgae may also use the pore-water nutrients. This may lead to differences in the response of epilithic and epipelic algae to nutrient enrichment (for freshwater, see Blumenshine et al. 1997). Therefore, a direct application of these results to microphytobenthos on sediments

is not possible. However, studies from marine to freshwater habitats revealed biomass stimulation through nutrient enrichment on a variety of substrates, including sediments (Fairchild et al. 1985, Sundbäck & Snoeijs 1991, Flothmann & Werner 1992, Rosemond et al. 1993, Coleman & Burkholder 1994, Nilsson 1995). Thus, the conclusion has to be drawn that nutrient limitation is often present in microphytobenthic communities of different substrate quality. This contradicts the assumption by Admiraal (1984) and co-workers that sediment-inhabiting microalgae may not be nutrient limited.

4.4.3 Nutrient competition

Competition can be expected to play an important role for the structure of epilithic communities as a consequence of the nutrient-limited situation during most of the year in the Kiel Fjord. This is also suggested when comparing the large species pool and wide ecological tolerance of benthic microalgae in contrast to the dominance of few species regularly observed (Chapter 2, for freshwater see McCormick 1996). Predicting species performance during in situ experiments according to competition theory (Tilman 1982) would require the knowledge of zero net growth resource concentrations (R^*) for the species and additionally an exact calculation of the supply ratios. Only for few microbenthic species, resource based growth kinetics have been calculated, and this was done only under a limited array of laboratory conditions (Deegen 1997, Hillebrand unpubl. data). Mortality rates during the experiment could not be measured, and presumably were not constant throughout the experiment, therefore one important factor for net growth is unknown. Moreover, the supplied media mixed with the surrounding water column, and thus another source of variation was added to the supply ratios experienced by the microalgae. In situ experiments do not adequately match the assumptions of equilibrium competition theory (Tilman 1982). However, in my experiments, a constant nutrient inflow in exponential concentration intervals changed the growth of epilithic microalgae and led to reproducible shifts in taxonomic composition. Therefore it is possible to evaluate the effect of nutrient competition on the natural, non-equilibrium assemblage of benthic microalgae in my experiments. The importance of resource competition will be discussed by means of the dominance distribution and the contribution of higher taxa and species to the community.

Dominance distribution: Diversity decreased significantly with nutrient enrichment (Fig. 4.4 and 4.12). Although not all regressions of diversity on nutrient concentrations were significant (Table 4.5 and 4.9), the results were consistent: The decrease of diversity was based on the enrichment of the respective limiting nutrient, i.e. P in spring, N in summer and Si at N+P enriched conditions. This decrease of diversity was due to an increase in dominance of few species (i.e. lowered evenness), whereas species numbers were stable within the experiments. The opposing effect of experimental eutrophication on species number and evenness can be attributed to the absence of species exclusion in these experiments. Suspending an artificial substrate in a natural aquatic habitat permitted the permanent colonization by species from the surrounding environment (McIntire & Overton 1971), including a recolonization of species that could not withstand the competitive pressure on the artificial substrates. Thus, changes in competitive dominance were reflected only by evenness (J') and not by species numbers (S). These different effects of added nutrients on S and J' resulted in a negative correlation between both measures (Chapter 4.3.3). The lack of correlation between H' and S can be explained by the fact that H' is unaffected by species number if S > 15 (Sager & Hasler 1969). D' was negatively correlated to S, since it is even more resistant against changes in the presence of rare species and more influenced by evenness than H' (Krebs 1989). Previous studies on microalgae reported a similar lack of correlation between S and H' (Robinson & Sandgren 1984), but also a positive correlation (McIntire & Overton 1971).

The decrease of evenness with increasing nutrient supply stressed the importance of enhanced dominance of single or few species outgrowing their competitors. Only few species responded significantly to the nutrient enrichment, leading to steeper dominance distributions. This pattern was previously reported for periphyton in freshwater enrichment experiments (Sullivan 1976, Fairchild et al. 1985, Carrick et al. 1988) and also for phytoplankton (Revelante & Gilmartin 1980, Agusti et al. 1991). These results clearly point at an impact of competitive displacement (but not exclusion) on the structure of the marine epilithic microphytobenthos. The shifts in dominance distribution indicate shifts in competitive ability with changed resource supply.

However, other studies found a positive correlation between diversity and nutrient enrichment, especially in nutrient-poor environments (Marcus 1980, Pringle 1990). These controversial findings can be explained by an unimodal relationship between nutrient richness and diversity, which was proposed as a universal pattern for regional diversity and productivity (Rosenzweig & Abramsky 1993, Tilman & Pacala 1993, but see Abrams 1995). This pattern emerges from the interaction of negative and positive effects of nutrient enrichment on the diversity of a species assemblage. Nutrient enrichment thus enhances diversity in oligotrophic environments because more species are able to exhibit positive net growth rates (Tilman 1982), because more individuals are present, presumably comprising more species (Srivastava & Lawton 1998), because rare species are less subjected to random extinctions because of increased population size (Rosenzweig & Abramsky 1993, Abrams 1995), and because more specialization is possible on single nutrients (Abrams 1995) or on different segments of the allocation trade-off between resource utilization and defense (Tilman & Pacala 1993, Chapter 5). On the other hand, nutrient enrichment decreases diversity in nutrient rich habitats because nutrient enrichment can shift resource supply in regions, in which supply variability is not sufficient to sustain stable coexistence (Tilman 1982), because succession may be faster resulting in shorter time frames for temporal fugitives (Tilman 1993), and because of higher instability of population dynamics (Rosenzweig 1971). The anthropogenic eutrophication of coastal areas is further characterized by the fact that anthropogenic nutrient enrichment is imbalanced with respect to some essential resources (Si, Fe, light), thus decreasing the possibility of stable coexistence.

Despite the criticism on diversity indices (Hurlbert 1971, Brown 1973), these results showed that diversity indices are appropriate measures of changes in microalgal assemblages and allow to evaluate the response to an experimental manipulation. This can be extended to geological time scales, as was shown for paleoecological investigations of diatoms in Chesapeake Bay (Cooper 1995). In this study, a decrease of H' was correlated to land use patterns and agricultural fertilization. However, diversity measures may be valid for microbial assemblages only on local spatial scales reflecting ecological gradients which influence the abundance of microalgae. Benthic microalgae show horizontal aggregations in scales of 1 dm^2

(Blanchard 1990, Saburova et al. 1995) and even smaller scales of vertical distributions (Berninger & Huettel 1997, Johnson et al. 1997). Diversity of periphyton should be cautiously interpreted if it is calculated for areas very much larger than these scales (Biggs et al. 1998). This is supported by the high local variability of diversity found in a literature survey on benthic microalgae, resulting in blurred gradients of diversity on large spatial scales (Appendix 4).

Higher taxa: Diatoms were generally the dominant higher taxon in all experiments, except for summer, when filamentous algae were more abundant (mostly rhodophytes, but also chlorophytes and phaeophytes). Cyanobacteria were present in several experiments, especially in summer and autumn, but never contributed more than 2% to total biovolume. The minor contribution of cyanobacteria may be due to the low water temperatures (Fig. 2.3a), which were shown to be suboptimal for cyanobacteria (Duncan & Blinn 1989, Watermann et al. submitted, Chapter 3).

In the first series of experiments (spring 1996 to summer 1997) only N and P were supplied, resulting in a decrease of Si:N and Si:P supply rates at increasing N and P supply. From previous experiments (Nilsson 1995, Sommer 1996a), a decreasing dominance of diatoms was expected at high N:P enrichment. However, shifts in higher taxonomic groups were found only in summer and autumn experiments. This may in part be due to the used substrates and to the colonization bias against long-lived species. The kieselgur stones used in the first experiment series contained and leaked silicate. This was shown by placing one kieselgur stone in 500 ml silicate-rich seawater: After one week, the Si-concentrations reached 34.0-42.3 μmol l^{-1}, compared to 28.4-30.0 in the control without stone. Thus, the stones as an additional Si-source may have mitigated the effect of N+P-enrichment. This argument was also proposed by Sundbäck & Snoeijs (1991), who found no dominance-shift during N+P addition and attributed this to their use of sediment, which acted as a silicate-pool. Therefore, the substrate and the nutrient supply was changed in the second series of experiments (autumn 1997 to spring 1998). The effect of Si on higher taxonomic composition in these experiments must be regarded as minor, since again only in autumn 1997 a distinct dominance shift could be observed (Fig. 4.10).

It was surprising that a rhodophyte profited from the nutrient treatment more than chlorophytes and phaeophytes which often form mass blooms in eutrophicated habitats (Lotze 1998). This may be due to the temporal coincidence of rhodophyte reproduction and low Si concentrations. In the Schlei estuary, the propagule concentrations and the percent cover of dominant filamentous and perennial algae were measured from 1997 to 1998 (Worm, unpublished data). It became obvious that the reproductive period of the rhodophyte *Ceramium strictum* was extended later into the year than the reproductive periods of *Pilayella littoralis* and *Enteromorpha* spec. Thus the reproduction of *Ceramium* may fall into phases of low Si-concentrations (Fig. 2.3), allowing this species to compete successfully with diatoms for N and P. However, this assumption has to be analyzed experimentally, since the critical Si:N ratio reducing the dominance of diatoms is still under debate. During my experiments, ambient Si:N ratios varied around 1, but were lowered in late summer and peaked in spring (Fig. 2.3c). The reduced importance of diatoms in phytoplankton observed in coastal areas was correlated to an *in situ* decrease of winter Si:N ratios from 1 to 0.25 (Radach et al. 1990). In contrast, Sommer (1994) reported a reduced dominance of diatoms in phytoplankton below an Si:N ratio of 25 and in periphyton below an Si:N ratio of 1.5 (Sommer 1996a). The high critical Si:N ratios observed in the phytoplankton experiments (Sommer 1994) were later on explained by the high Si-demand of the species selected for the experiments (Sommer 1996b)

In contrast to my investigation, other studies reported more substantial changes in dominance of higher taxa following the manipulation of nutrient ratios: In laboratory experiments benthic algae grown with different nutrient ratios showed responses similar to higher taxa of phytoplankton, with diatoms dominating at high Si:N and Si:P ratios and - at low silicate concentrations - chlorophytes dominating at high N:P ratios and cyanobacteria at low N:P ratios (Sommer 1996a). These patterns are corroborated by an experimental study on sediment inhabiting microalgae: Cyanobacteria became more important when only phosphate (lowering of supplied N:P) was added because of their ability to fix N_2 (Pinckney et al. 1995). In experiments by Nilsson (1995), diatoms were only replaced at high N+P addition without extra silicate and stayed dominant when Si+N+P were added. Only few

studies on nutrient competition in freshwater periphyton have compared the effects of Si- and N+P- enrichment on benthic microalgae. In fact few studies have considered Si at all, which is surprising since diatoms often dominate the periphyton (Borchardt 1996). In experiments with combined control of Si and N+P, the community composition was altered by enrichment of N+P (Carrick et al. 1988), but the enrichment of Si alone did not increase the biomass (Carrick & Lowe 1988).

Species composition: While the dominance of higher taxa was changed only in summer, distinct shifts in dominance at the level of species were visible in most of my experiments. The proportion of species responding to nutrient enrichment was small in my experiments (see also Chapter 5) and in freshwater enrichment studies (Fairchild et al. 1985, Carrick et al. 1988). However, the most abundant species differed clearly in their response to the supplied nutrients, leading to altered community composition (Fig. 4.3 and 4.9, Table 4.4 and 4.8). In spring 1996, this is illustrated by the alternate dominance of *Berkeleya rutilans* on N-enriched treatments and *Proschkinia complanata* on P-enriched treatments and the co-dominance of both species in N+P enriched treatments. These dominance patterns were stable, since *P. complanata* was favoured by N+P enrichment in late spring 1997 and spring 1998, but not by enrichment of N alone in late spring 1997 and Si alone in spring 1998. The species shifts were also consistent between the two series of experiments conducted in Kiel Fjord. In the second experimental series on wood blocks, several trends could be confirmed, which had already become visible in the experiments with kieselgur stones, e.g. the high N-demand of *Berkeleya rutilans*, *Ceramium strictum*, *Melosira moniliformis* or *Tabularia fasciculata* (Table 4.4. and 4.8).

Also a comparison to other studies on nutrient competition reveals a high degree of congruence regarding the effects of nutrient treatments on dominant species. Whereas some studies reported only slight changes on the species level (Sundbäck & Snoeijs 1991, Pinckney et al. 1995), distinct dominance changes within higher taxa were described for laboratory experiments by Sommer (1996a). When Sommer used species also abundant in my *in situ* experiments, the responses to nutrient treatments were similar in both investigations. *Melosira nummuloides* was favoured in his culture experiments by high silicate and a N:P ratio around 15, *in situ* it was

favoured at low nitrogen enrichments resulting in a similar N:P supply. *Berkeleya rutilans* (= *Amphipleura rutilans* in Sommer 1996a) increased in importance at high N:P-ratios in the laboratory (N:P 145-22:1) as well as *in situ*. The higher demand of nitrogen of this species may be due to the unique formation of tube walls, which contain proteins unlike all other investigated tube dwellers (Daniel et al. 1987).

Quite unexpectedly, with N+P enrichment and increasing Si addition, a non-silicified algae, the red algae *Ceramium strictum*, became increasingly dominant in the autumn 1997 experiment. In fact, *Ceramium strictum* was also dominant in late summer 1996 and summer 1997 at high N concentrations on Si-leaking substrates (Fig. 4.3). The reliance on high N-concentrations can be explained by high N-demands of *Ceramium* species (Pedersen & Borum 1997) and leads to the lack of response to Si-Enrichment without additional N+P (Fig. 4.9). For the positive response to silicate at high N+P, two possible explanations can be discussed: A direct explanation assumes a Si-utilization by this rhodophyte, which to my knowledge has not been reported up to now. It was shown that Si is utilized by some filamentous algae, but these reports do not include rhodophytes (Parker 1969). The analysis of the Si content of *Ceramium* individuals which were free from epiphytes did not reveal measurable concentrations of particulate Si. An indirect explanation is based on the succession often found during the colonization of free substrates by periphyton (Hudon & Bourget 1981, Hoagland et al. 1982, Chapter 2). This would imply that microorganisms (in this case diatoms profiting from the additional Si) alter the surface of the substrate and thus facilitate the adherence of *Ceramium*, thereby increasing the abundance of attached individuals as well as prolonging the growth phase of the attached individuals until the experiment was harvested. This is consistent with the results on the effect of Si-supply and substrate preconditioned in summer 1998, although the effects were not significant (Fig. 4.11). Therefore I assume that *Ceramium* is favoured by high N-concentrations (Pedersen & Borum 1997) and the modification of the surface provided by diatoms under increased Si-concentrations.

The role of competition: Whereas competition has been successfully analyzed experimentally in the laboratory, the structuring influence of competition on natural communities in a non-equilibrium state has been a matter of wide debate (Connell

1980, Sommer 1990, see also Krebs 1985, Begon et al. 1990). As was stated above, my experiments did not allow the application of equilibrium competition models (Tilman 1982) and the exclusion of species was not observed due to possible recolonization by species competitively excluded from the substrates. Moreover, the poor knowledge on species-specific nutrient requirements of benthic microalgae did not allow to make predictions on competitive outcome. Nevertheless, the structuring role of competition can indirectly be inferred from the observed presence of nutrient limitation as a result of nutrient consumption and the shifts in dominance following the experimental manipulation of nutrient supply (Sommer 1990, McCormick 1996). There was a striking consistency of the taxonomic responses to nutrient treatments. The species gaining dominance at a certain nutrient treatment were similar for different years, different substrates and in comparison to other studies. Besides the species responding positively to nutrient enrichment, competitive displacement was strongly indicated by the decline of *Enteromorpha* with Si enrichment, the decrease of *Licmophora* in N+P enriched treatments and the decline of *Melosira nummuloides* at highest N supply rates (Table 4.4 and 4.8). These results point to the importance of competition, which is determined by physiological traits of the species. It is important to notice, however, that almost none of the species that became dominant at enriched conditions was rare or even absent in the unenriched community. The nutrient shift does not allow a cryptic species (e.g. a dormant winter species) to re-establish its dominance. Abiotic constraints inhibit the reversion of the nutrient poor summer assemblage into an assemblage resembling the community dominant at high ambient nutrient levels in early spring. Therefore competition is one of the major factors influencing species composition and community structure, but its influence is bound by external factors.

4.5 Conclusions and outlook

My hypotheses for the *in situ* experiments included (i) the possibility of nutrient limitation and (ii) the importance of resource competition. A complex pattern of nutrient limitation was revealed for the epilithic microflora in Kiel Fjord. Nutrient limitation was of seasonally varying importance, and concentration shifts in the ambient seawater led to shifts in limiting nutrients. Phosphate was limiting in spring,

but from late spring to autumn nitrogen was the main limiting nutrient for most species. Silicate might be deficient for diatoms in summer on natural substrates. This pattern was indicated by the response of the benthic microalgae to nutrient enrichment and by the stoichiometry of microalgal biomass.

Nutrient enriched treatments led to altered or enhanced dominance of a single or a few species, whereas higher taxa were less affected. Mainly species of an erect growth habit were favoured by the nutrient enrichment. The changes in species composition due to the addition of N, P or Si were consistent between years and substrates, indicating the existence of species-specific traits of nutrient affinity. Thus, competition may act as an important factor determining microphytobenthic species composition. The nutrient enrichment favoured only a small number of species, leading to a less diverse community. This was due to the decrease of evenness with increasing concentrations of the limiting nutrient, whereas species richness was not related to enrichment. Diversity indices were shown to be a reliable tool to measure the response of benthic microalgae to experimental treatments.

The experimental setup as used here was shown to be a reliable tool to manipulate the nutrient supply to epilithic microflora. This setup allowed the continuous and controlled supply of nutrients to benthic microalgae. Conceivably, these experiments should be combined with an approach including other biotic interactions (e.g. herbivory) and other groups of benthic organisms (bacteria, protists). It is e.g. largely unknown how benthic bacteria respond to this kind of nutrient enrichment.

5 Interaction of nutrient and herbivore control on epilithic microphytobenthos

5.1 Introduction

Marine littoral communities have a long and intensive history of research on trophic interactions, revealing the structuring role of herbivores (Lubchenco 1978) and predators (Paine 1966, Lubchenco & Menge 1978). Coastal areas are, on the other hand, widely affected by anthropogenic nutrient enrichment (Ryther & Dunstan 1971, Valiela et al. 1997), leading to changes in the composition and biomass of benthic macrophytes, and to mass blooms of filamentous algae (Lavery et al. 1991, Duarte 1995, Raffaeli et al. 1998). Therefore, littoral autotrophs are exposed to a combination of top-down and bottom-up influences. The antagonistic effects of grazing and nutrient supply was shown for the interaction of epiphytes and their substrate plants, macroalgae or seagrass (Cattaneo 1983, Borum 1987, Neckles et al. 1993, Jernakoff et al. 1996). The interaction of nutrient and herbivore effects on ephemeral and perennial macrobenthic vegetation has become a research focus recently (Lotze 1998, Worm et al. in prep.).

However, so far this focus has not been extended to benthic microalgae. Herbivory on epilithic microalgae has been studied sporadically in the marine environment (Castenholtz 1961, Nicotri 1977, Hunter & Russell-Hunter 1983, Sommer 1997). These experiments showed the possibility of top-down control and the differential influence of herbivore types on species composition and vertical structure of the algae. Besides, there have been a few attempts to analyze herbivore control on sediment-inhabiting microphytobenthos (Admiraal et al. 1983, Smith et al. 1996). To my knowledge, combined experimental manipulations of nutrients and grazing have not been conducted in marine microbenthos.

This lack of studies on grazing effects in the marine epilithon is contrasted by the thorough investigation of grazing effects on freshwater periphyton, especially in streams (reviewed by Steinman 1996). These studies showed that natural densities of herbivores can strongly reduce algal biomass (Hill & Knight 1987, Steinman et al. 1987), change the physiognomy of the community by removing their upper layers

(Lowe & Hunter 1988, Steinman et al. 1991), and influence successional patterns of the community (Tuchman & Stevenson 1991). Very few studies from freshwater habitats considered the interaction of nutrients and grazing, revealing a combined influence of bottom-up and top-down regulation and strongest effects if herbivores and nutrients were manipulated simultaneously (Marks & Lowe 1989, Rosemond 1993, Rosemond et al. 1993). However, it remains unresolved if conclusions drawn from studies in streams with an unique matrix of habitat constraints (Biggs et al. 1998) can be transferred to marine microbenthos.

Within the context of a broader study of grazer-macrophyte-nutrient interactions (Lotze 1998, Worm et al. in prep.), I investigated the effect of grazers and nutrient enrichment on benthic microalgae in field experiments. I tested the following hypotheses: (i) Herbivores and nutrients antagonistically control the biomass of epilithic microalgae, (ii) Herbivores and nutrients exert selective control by preferentially removing or favouring certain species or growth types, (iii) The impact of herbivores on microphytobenthos is mitigated by fish predation on herbivores (trophic cascades).

5.2 Methods

The effects of nutrient enrichment and herbivory on benthic microalgae were surveyed from May to July 1998 (Table 5.1). The main experiment (G1) was conducted at Maasholmer Breite, a sheltered broadening of the Schlei estuary, Western Baltic Sea (Fig. 2.1). Grazer abundance (via exclusion) and nutrient concentration were manipulated simultaneously (Table 5.1). Exclusion was provided by cages (25 x 25 x 25 cm³), which were closed by a 1-mm polyethylene mesh ("without grazer" treatment). In half of these cages, one side was cut out to allow grazer access to the cages ("with grazer" treatment). Uncaged control plots were used to test for cage artifacts. Light intensities within the cages were reduced by only 8% (Li-Cor LI-192SA). The cages were brushed weekly in order to remove fouling algae growing on the mesh. Background grazer densities were determined in May and July on the control plots (n=16, Table 5.1). All experiments were conducted in the *Fucus* zone of the littoral, at a water depth of 60-80 cm.

Nutrient enrichment was performed with commercial slow-release NPK fertilizers (Plantacote Urania Agrochem, Hamburg), consisting of pellets with a semipermeable polyutherane layer (Worm et al. in prep.). These pellets were enclosed in polyethylene mesh rolls with 4 cm diameter and variable length. The respective length of the diffusor rolls and the amount of pellets corresponded to 6 different nutrient enrichment levels (length of mesh roll: 2.5, 5, 10, 20, 40 and 80 cm, respectively; amount of pellets: 5, 10, 20, 40, 80, 160 g, respectively). Each treatment combination was replicated twice, the nutrient control treatment without enrichment was replicated fourfold. The experiment was run in a 2x7 factorial randomized block design with 2 blocks. The nutrient concentrations on experimental plots were analyzed with an continuous flow analyzer (CFA) using the methods of Grasshoff et al. (1983). Background nutrient levels were 9.85 μmol l^{-1} Si, 0.16 μmol l^{-1} NO_3^-, 0.33 μmol l^{-1} NH_4^+ and 0.49 μmol l^{-1} PO_4^{3-}.

In all experiments, ceramic tiles (5 x 5 cm) were used as standard substrates for benthic microalgae, in order to minimize the effect of different microtopography of the natural sites (Nicotri 1977). The tiles were placed onto the surface of experimental plots and harvested after exposure for 23 or 25 days (Table 5.1). The biomass was scraped off with a razor blade, suspended in 25 ml of filtered seawater (0.2 μm cellulose-acetate filters) and fixed with Lugol's iodine. A subsample of the suspension was filled into Utermöhl counting chambers and at least 1000 cells per sample were counted with an inverted microscope (Leitz DMIRB). Biovolume was calculated for each of the species following Hillebrand et al. (1999).

In the second experiment (G2), grazer exclusion experiments were conducted at three different sites in order to reveal variability of herbivory across sites (Table 5.1). The chosen sites were sheltered embayments in the Western Baltic Sea: Maasholmer Breite, Wackerballig and Geltinger Noor (Fig. 2.1). Grazer presence was manipulated as described above (closed and open cages, control plots without cages, each with four replicates), but here small circular cages (8 cm in diameter) were used, covered with 1mm polyethylene mesh. In order to minimize the variability due to different recruitment of filamentous algae, the substrates were seeded in the laboratory with spores of the chlorophyte *Enteromorpha* sp. (see Worm et al. in prep. for details).

Table 5.1: Experimental setup of grazing experiments, listing the name, duration and location of the experiment, as well as background grazer abundances. Grazer densities were evaluated on control plots (G1 and G3, n=16) and are given as individuals m^{-2}. In G2 the grazer fauna was evaluated by using 25x25 cm frames (n=10), abundances were calculated for an area of 1 m^2. *Idotea* sp. is *I. baltica* and *I chelipes*, *Gammarus* sp. is *G. locusta*, *G. salinus* and *G. zaddachi*.

exp.	duration	location	background grazer densities N m^{-2} mean (standard error)	
G1	9.5.-1.6. 1998	Maasholmer Breite	*Littorina saxatilis*	4031 (408)
			Littorina littorea	0 (0)
			Hydrobia ulvae	200 (45)
			Idotea sp.	25 (11)
			Gammarus sp.	0 (0)
			other	10 (5)
G2	6.5.- 29.5. 1998	Maasholmer Breite	*Littorina saxatilis*	1104 (370)
			Littorina littorea	41 (17)
			Idotea sp.	444 (96)
			Gammarus sp.	24 (25)
		Wackerballig	*Littorina saxatilis*	0 (0)
			Littorina littorea	235 (43)
			Idotea sp.	115 (56)
			Gammarus sp.	56 (31)
		Geltinger Noor	*Littorina saxatilis*	325 (119)
			Littorina littorea	10 (4)
			Idotea sp.	35 (10)
			Gammarus sp.	13 (7)
G3	3.7.-26.7. 1998	Maasholmer Breite	*Littorina saxatilis*	63 (24)
			Hydrobia ulvae	312 (57)
			Idotea sp.	13 (9)
		Geltinger Noor	no data	

In the last experiment (G3), I attempted to evaluate (i) whether herbivore effects vary between spring and summer, and (ii) whether fish can potentially affect microalgal colonization through enhanced feeding on herbivores (trophic cascades). This experiment was conducted at two of the three sites of G2, Maasholm and Geltinger Noor. Fish densities were evaluated at Geltinger Noor and Maasholm on June 28th and July 25th 1998 by counting 5 replicate transects (30m x 1m) parallel to the shore at 0.5-1 m depth (data courtesy of B. Worm). Fish densities were low at these sites (<0.1 m^{-2}) and thus fish density was enhanced rather than to exclude fish. I used the same experimental setup as described for G2 (open, closed cages, uncaged controls). As an additional treatment, uncaged tiles were exposed at a distance of 10-20 cm from fish-burrows inhabited by individuals of *Gobius niger*, a common demersal fish that feeds on crustacean herbivores.

Statistical analysis for G1 was done with a 2-way fixed factor ANOVA, including grazers (presence vs. absence) as the categorical variable and nutrients (control and 6 enrichment levels) as a continuous variable. Block was added as a third, non-interactive variable. The cage effect was analyzed with the same ANOVA setup, with cage (presence vs. absence) replacing the grazer factor. The analysis was performed with total biovolume and nutrient concentrations as dependent variables. Experiments G2 and G3 were analyzed with 2-way fixed factor ANOVAs, including site and grazer presence as independent factors. The response variables were total biovolume and diversity. The data were log-transformed for G2 in order to assure normal distribution. Homogeneity of variances was tested with Bartlett's χ^2-test. Posthoc tests were conducted with Tukey's honest significant differences (HSD). Linear regression analyses (model I) were performed to evaluate the quantitative response of microalgae to nutrients in experiment G1. The significance of differences between slopes was tested with an F-test (Sokal & Rohlf 1995). As measures of microbenthic diversity, species richness (S) as well as Shannon-Weaver Index (H') and evenness (J') were calculated (see Chapter 2.2.3). To evaluate the significance of the unimodal model of the relationship between diversity and nutrient supply, a second-order polynominal was fitted in a nonlinear model-I regression procedure. A significant unimodal relationship is characterized by a positive estimate for the linear term and a negative estimate for the quadratic term and a maximum of the response curve within the experimental range of the dependent variable.

5.3 Results

5.3.1 Experiment G1

The stoichiometry of background nutrient levels indicated nitrogen deficiency during experiment G1 (N:P<16). Nitrogen availability was significantly raised in the cages by NPK-fertilizer addition (ANOVA, for NH_4^+: $F_{(1,23)}$ = 7.45, p=0.012, for NO_3^-: $F_{(1,23)}$ = 4.93, p=0.037), whereas phosphate and silicate were not significantly affected (p>0.4). Presence of grazers had no significant effect on nutrient concentrations (ANOVA, p>0.1). The DIN concentrations increased linearly with pellet tube length

(slope b = 0.016 ± 0.007, p = 0.032). Nitrogen concentrations at highest NPK-enrichment were 1.45 µmol l^{-1} NH$_4^+$ and 0.47 µmol l^{-1} NO$_3^-$.

Both grazer removal and nutrient enrichment significantly increased the total biomass of benthic microalgae (Table 5.2, Fig. 5.1). Highest total biovolume was found in grazer-exclusion treatments with high nutrient addition (Fig. 5.1). This is underlined by the significant grazing x nutrient interaction of the ANOVA (Table 5.2) and the small difference between grazed and ungrazed communities in unenriched treatments (Fig. 5.1). The slope of the linear regression was used to indicate the strength of the algal response to nutrients (Table 5.3). Regression on total biovolume showed that nutrient enrichment had more direct effects (i.e. higher slopes) on total biovolume in grazer-exclusion treatments than in grazer-access cages ($F_{(1,28)}$ = 6.45, p<0.05) and control plots ($F_{(1,28)}$ = 4.23, p<0.05). Regression slopes for total biovolume in grazer access cages and on control plots were not significantly different ($F_{(1,28)}$ = 0.002). A curvilinear regression on total biovolume in ungrazed cages gave partially insignificant results (model: y = a•x/(b+x); a = 869943, p<0.001; b = 3.42, p = 0.090; r^2 = 0.6039).

There was a significantly higher total biovolume in the control plots compared to the cages with grazer access, indicating a cage artifact (ANOVA, $F_{(1;26)}$ = 42.0, p<0.001). However, there was no significant nutrient effect between open cages and control plots (ANOVA, $F_{(1;26)}$ = 42.0, p=0.082). The cage artifact was caused by the reduced abundance of one species, Licmophora abbreviata, in the open cages (see below). Abundance of the snail Littorina saxatilis was significantly lowered in open cages compared to control plots (cage: 1084 ± 238 individuals m^{-2}, control: 4031 ± 408). This was presumably due to the weekly brushing procedure. Gammarid amphipods (cage: 68 ± 19, control 0) and the isopod Idotea spp. (cage 125 ± 33, control 25 ± 11) were more abundant in the cages than in the control plots.
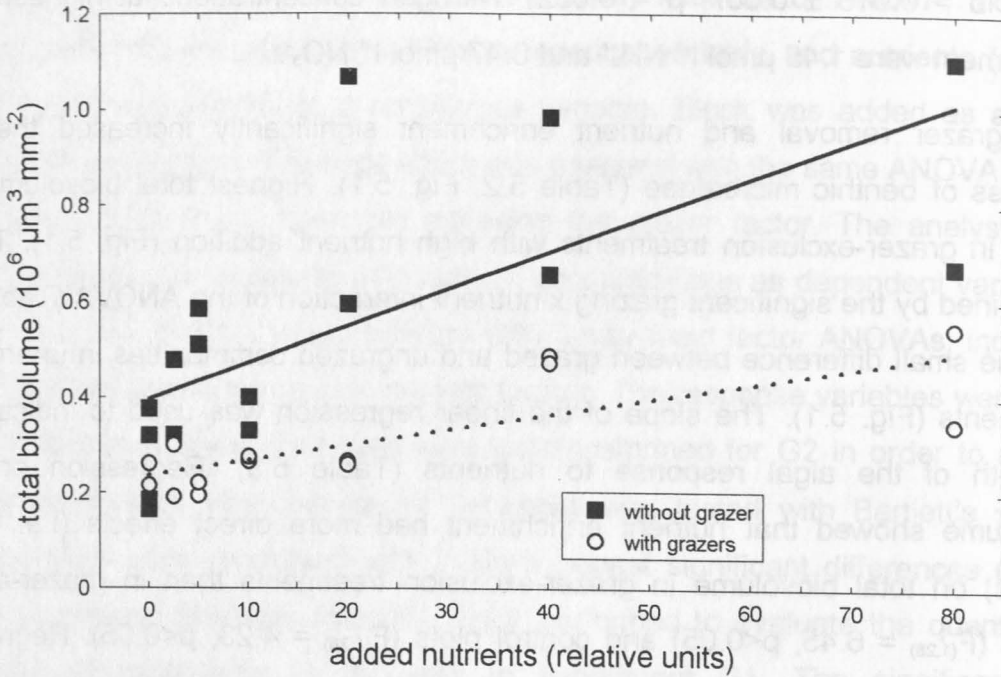
Fig. 5.1: Total biovolume of benthic microalgae in experiment G1 in relation to nutrient addition for ungrazed ("without grazer") and grazed ("with grazers") treatments. Lines represent linear regression models (see Table 5.3). Nutrient addition is given as pellet tube length, which resulted in a linear increase of DIN (slope = 0.016).
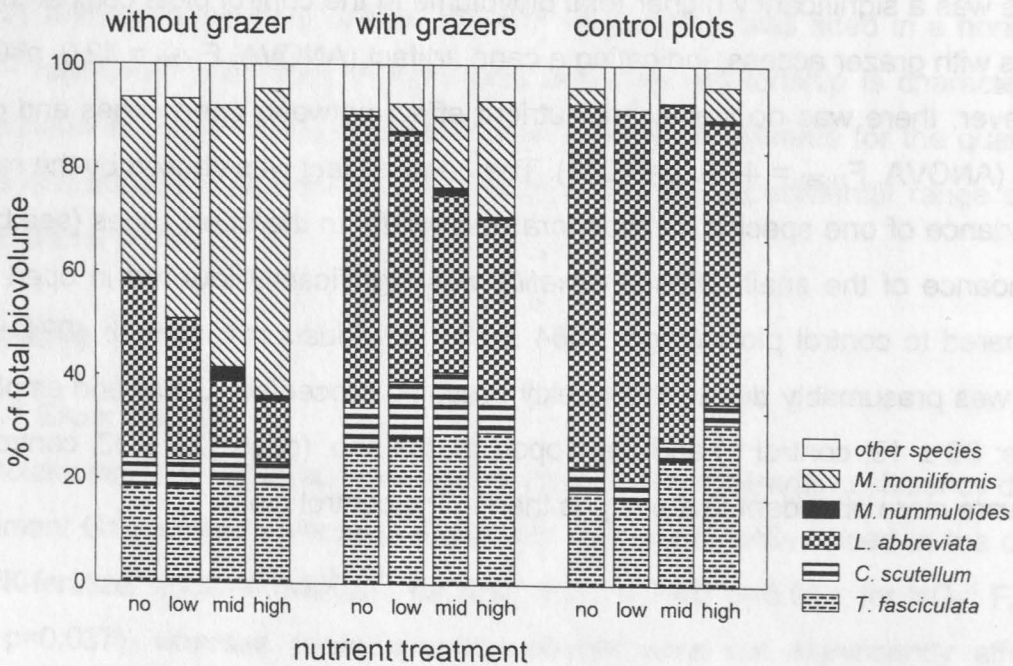
Fig. 5.2: Species composition of benthic microalgae in experiment G1, presented as mean % contribution to total biovolume. To calculate means, nutrient treatments were combined to no enrichment, low (pellet tube length: 2.5 and 5 cm), mid (10 and 20 cm) and high (40 and 80 cm) enrichment.

Table 5.2: Results of 2-way fixed factor ANOVA with grazing and nutrient enrichment as independent factors, block as non-interactive variable and total biovolume as dependent variable. Untransformed data gave normal distribution (χ^2 = 7.45, p=0.114) and homogeneity of variances (Bartlett's χ^2 = 30.5, p = 0.062). A significant cage artifact was revealed by the control experiment (p<0.001).

source of variation	df	mean square	F-ratio	p-level
grazing	1	$1.325 \cdot 10^{11}$	5.490	0.027
nutrient enrichment	1	$6.333 \cdot 10^{11}$	26.230	<0.001
grazing x nutrients	1	$1.059 \cdot 10^{11}$	4.388	0.046
block	1	$5.77 \cdot 10^{10}$		
error	27	$2.41 \cdot 10^{10}$		

The epilithic community consisted of 68 algal species and was dominated by benthic diatoms, only small proportions (<5% of total biovolume) of cyanobacteria were present (Fig. 5.2). Shifts in species composition due to the treatments were characterized by the fact that the species being most susceptible to grazing, the centric diatom *Melosira moniliformis*, was also highly influenced by nutrient enrichment (Fig. 5.2, Table 5.3). The grazer removal had positive effects on *Melosira nummuloides*, whereas *Cocconeis scutellum* and *Licmophora abbreviata* contributed more biovolume in the presence of grazers. *Tabularia fasciculata* was not significantly affected by herbivore presence (Fig. 5.2). *L. abbreviata* was the only dominant species which was more abundant in the control plots compared to open cages, in terms of absolute and relative biovolume.

The response of the epilithic microphytes to the nutrient enrichment was analyzed with a linear regression model. A significant increase of biovolume with added nutrient amounts was observed for *M. moniliformis*, and significantly higher slopes were found in the absence of grazers ($F_{(1,28)}$ = 43.98, p<0.001), indicating a more direct response to the enrichment (Table 5.3). *T. fasciculata* and *M. nummuloides* were also favoured by N+P addition, the latter, however, significantly only in uncaged plots. The response of *T. fasciculata* was not significantly altered by the presence of grazers ($F_{(1,28)}$ = 0.501, p>0.05). *L. abbreviata* and *C. scutellum* were not positively influenced by additional nutrients. The relative biovolume of *L. abbreviata* decreased with increasing nutrient enrichment (Fig. 5.2).
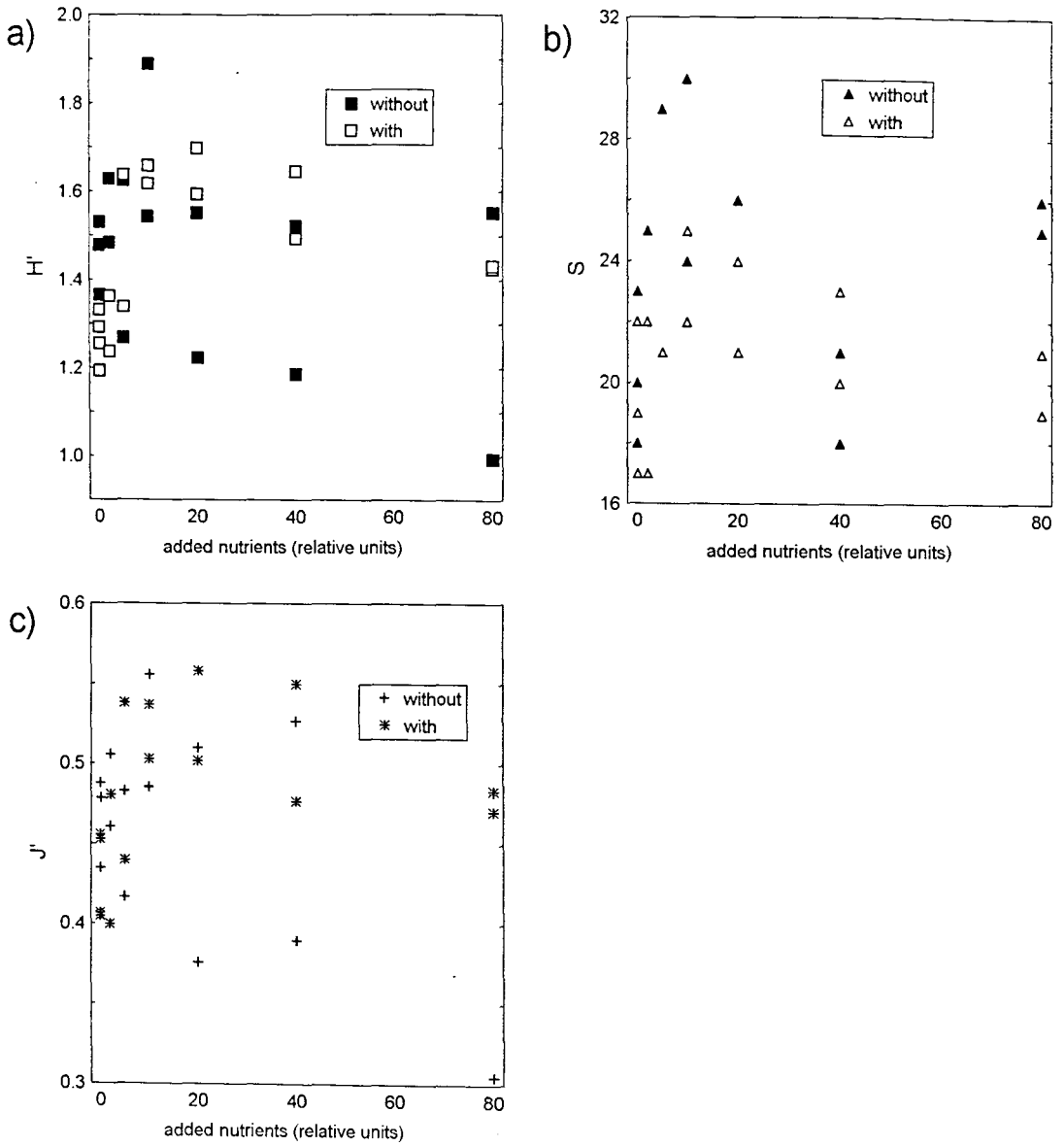
Fig. 5.3: Effects of nutrient enrichment and grazing on (a) diversity (H'), (b) evenness (J') and (c) species richness (S) of benthic microalgae. Grazer presence was manipulated with open cages ("with") and closed cages ("without"). Nutrient enrichments are given as pellet tube length, which is linearly related to DIN concentrations (slope = 0.016). Results of nonlinear regression models are given in Table 5.4.

Table 5.3: Linear regression analysis of nutrient concentrations on total and specie biovolume of all dominant species. The table gives regression slopes b wit standard error, significance of the slope (ns: not significant, *: p<0.05, **: p< 0.01 ***: p<0.001) and coefficient of determination (r^2).

dependent	without grazer		with grazers		control plots	
	b ± SE	r^2	b ± SE	r^2	b ± SE	r^2
total biovolume	7688.2 ± 2056.9 **	0.499	3192.0 ± 660.3***	0.625	3126.6 ± 1471.2 ns	0.244
M. moniliformis	5917.4 ± 1792.4 **	0.438	1095.6 ± 465.2 *	0.284	466.6 ± 194.6 *	0.291
L. abbreviata	-100.7 ± 427.6 ns	0.004	591.9 ± 358.9 ns	0.163	812.0 ± 1203.11 ns	0.032
T. fasciculata	1293.8 ± 376.5 **	0.458	1199.5 ± 150.6***	0.819	1851.3 ± 401.6 ***	0.603
M.nummuloides	101.2 ± 92.1 ns	0.079	4.3 ± 34.3 ns	0.001	110.5 ± 24.7 ***	0.588
C. scutellum	183.6 ± 132.7 ns	0.120	118.5 ± 76.0 ns	0.147	8.72 ± 103.4 ns	0.001

The combined effects of grazing and nutrient enrichment on species compositior was reflected by species richness and diversity (Fig. 5.3). In the presence o grazers, an unimodal relationship between nutrient enrichment and diversity coulc be determined. At low nutrient levels, diversity increased rapidly with increasing enrichment, but decreased slowly at higher enrichment levels. The fit of the second-order polynominal was significant for H' and J' (Table 5.4), whereas foi species number the parameter estimates had marginally insignificant p-levels o 0.069 (linear term b) and 0.067 (quadratic term c). The effect of grazers on diversit) was insignificant, except for species richness which decreased significantly ir grazed compared to ungrazed communities (ANOVA, $F_{(1,27)}$ = 7.13, p=0.013) Without grazer, however, the differences between replicates were greater for al three dependent variables (Fig. 5.3), resulting in insignificant nonlinear regressior models (Table 5.4).

5.3.2 Experiment G2

Microalgal biomass differed significantly across sites. Grazers reduced microalga biovolume at all three sites (Fig. 5.4, Table 5.5). The highest total biovolume an the strongest grazer effect were found in Maasholm (significant difference betwee grazer-access and grazer-exclusion treatments, as well as significant difference t both other sites, Tukey's HSD, p<0.05). In Geltinger Noor, overall biovolume wa

lower and the grazer removal resulted in a distinct increase in total biovolume (Tukey's HSD, p=0.224 for unplanned comparison). In Wackerballig, the biovolume also decreased in grazed treatments, but this was less distinct. In this experiment no cage artifact was detected, microalgal biovolume in control plots was not significantly different from open cages ($F_{(1;20)}$ = 0.052, p=0.822).

Table 5.4: Results of nonlinear regression analysis of the effect of nutrient enrichment on diversity (H'), evenness (J') and species richness (S). Analysis was performed with a second-order polynominal ($y=a+b \cdot x+c \cdot x^2$) for data from grazed ("with grazers") and ungrazed ("without grazer") cages. Parameter estimates or a, b and c are given with standard error and p-level as well as the coefficient of determination (r^2).

dependent	a (SE)	p	b (SE)	p	c (SE)	p	r^2
with grazers							
H'	1.332 (0.046)	<0.001	0.017 (0.004)	0.002	$-0.2 \cdot 10^{-3}$ ($0.06 \cdot 10^{-3}$)	0.003	0.5385
J'	0.446 (0.015)	<0.001	0.045 (0.002)	0.008	$-0.05 \cdot 10^{-3}$ ($0.02 \cdot 10^{-3}$)	0.013	0.4298
S	19.91 (0.78)	<0.001	0.148 (0.075)	0.069	$-1.87 \cdot 10^{-3}$ ($0.94 \cdot 10^{-3}$)	0.067	0.5385
without grazer							
H'	1.491 (0.080)	<0.001	-0.001 (0.008)	0.863	$-0.02 \cdot 10^{-3}$ ($0.10 \cdot 10^{-3}$)	0.844	0.1264
J'	0.472 (0.023)	<0.001	0.0002 (0.002)	0.934	$0.01 \cdot 10^{-3}$ ($0.03 \cdot 10^{-3}$)	0.603	0.1751
S	23.63 (1.36)	<0.001	-0.074 (0.130)	0.581	$1.12 \cdot 10^{-3}$ ($1.63 \cdot 10^{-3}$)	0.506	0.0429

Table 5.5: Results of a two-way ANOVA with site and grazing as independent factors and log-transformed total biovolume as dependent variable. Log_{10}-transformation resulted in normal distribution (χ^2 = 5.33, p=0.255) and homogeneity of variances (Bartlett's χ^2 = 7.87, p = 0.248). No cage artifact was detected in the control experiment (p<0.822).

source of variation	df	mean square	F-ratio	p-level
site	2	1.154	8.468	0.002
grazing	1	3.073	22.557	<0.001
site x grazing	2	0.092	0.675	0.519
error	22	0.136		

Fig. 5.4: Total biovolume (mean ± standard error) of benthic microalgae in experiment G2 for uncaged control plots, open cages ("with grazer") and closed cages ("without grazer").

Fig. 5.5: Species composition of benthic microalgae in experiment G2, presented as mean % contribution to total biovolume, for uncaged control plots, grazer access cages (with) and grazer exclusion (without) treatments.

The species composition was similar to experiment G1, with 51 species recorded and diatoms contributing >90% to the total biovolume. Dominant species were similar among the different sites (Fig. 5.5), the epilithon consisted mostly of *T. fasciculata*, *L. abbreviata* and *C. scutellum*. However, *C. scutellum* was less abundant in Wackerballig, while *L. abbreviata* showed highest relative biovolume there. In the grazer exclusions, there was a significant increase of *Berkeleya rutilans* in Maasholm and Wackerballig and of *M. moniliformis* in Maasholm and Geltinger Noor. *L. abbreviata* had lower relative biovolume in the ungrazed communities, the proportions of *T. fasciculata* and *C. scutellum* were not changed by exclusion of herbivores. Species number was significantly reduced by grazing at all three sites (ANOVA, $F_{(1;22)}$ = 29.54, p<0.001), whereas H' and J' were unaffected (ANOVA, p>0.3).

5.3.3 Experiment G3

In the summer experiment, no significant grazer or site effect on microalgal biovolume could be detected (Table 5.6). Biovolume tended to be higher in Maasholm compared to Geltinger Noor (Fig. 5.6), but this was significant only for open plots. Fish density had no significant effect on the total biovolume (Tukey's HSD, p=0.999) or on the presence of any species. Neither fish density nor grazing had significant effects on species richness or diversity (ANOVAs, p>0.1).

50 species were recorded in this experiment. The species composition was slightly altered compared to the previous experiment G2 (Fig. 5.6). The proportion of cyanobacteria increased in Maasholm, and the diatom community was shifted to higher contribution of small, mobile diatoms, e.g. *Cylindrotheca closterium* and *Navicula* cf. *perminuta*. However, *L. abbreviata*, *T. fasciculata* and *C. scutellum* were still the dominant species.

Table 5.6: Results of a two-factor ANOVA for experiment G3: Effects of site and grazing in caged plots (with grazers vs. without grazer) and effects of predation on open plots (control vs. fish). Untransformed data were normally distributed (χ^2 = 2.65, p=0.266), whereas homogeneity of variances could not be established (Bartlett's χ^2 = 30.31, p<0.001). No significant cage artifact was detected in the control experiment (p=0.422).

source of variation	df	mean square	F-ratio	p-level
grazing				
site	1	$1.089\ 10^{10}$	2.692	0.120
grazing	1	$6.90\ 10^{9}$	1.707	0.210
site x grazing	1	$7.0\ 10^{8}$	0.173	0.684
error	1	$4.04\ 10^{9}$		
fish predation				
site	1	$1.448\ 10^{10}$	10.629	0.006
predation	1	$0.6\ 10^{8}$	0.047	0.832
site x predation	1	$3.49\ 10^{9}$	2.563	0.133
error	16	$1.36\ 10^{9}$		

Fig. 5.6: Biovolume and species composition of benthic microalgae in experiment G3, for uncaged control plots, grazer access cages ("with") and grazer exclusion cages ("without"), and uncaged fish treatments. Whiskers represent 1 standard error of total biovolume.

Table 5.3: Linear regression analysis of nutrient concentrations on total and species biovolume of all dominant species. The table gives regression slopes b with standard error, significance of the slope (ns: not significant, *: p<0.05, **: p< 0.01, ***: p<0.001) and coefficient of determination (r^2).

dependent	without grazer		with grazers		control plots	
	b ± SE	r^2	b ± SE	r^2	b ± SE	r^2
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The combined effects of grazing and nutrient enrichment on species composition was reflected by species richness and diversity (Fig. 5.3). In the presence of grazers, an unimodal relationship between nutrient enrichment and diversity could be determined. At low nutrient levels, diversity increased rapidly with increasing enrichment, but decreased slowly at higher enrichment levels. The fit of the second-order polynominal was significant for H' and J' (Table 5.4), whereas for species number the parameter estimates had marginally insignificant p-levels of 0.069 (linear term b) and 0.067 (quadratic term c). The effect of grazers on diversity was insignificant, except for species richness which decreased significantly in grazed compared to ungrazed communities (ANOVA, $F_{(1,27)}$ = 7.13, p=0.013). Without grazer, however, the differences between replicates were greater for all three dependent variables (Fig. 5.3), resulting in insignificant nonlinear regression models (Table 5.4).

5.3.2 Experiment G2

Microalgal biomass differed significantly across sites. Grazers reduced microalgal biovolume at all three sites (Fig. 5.4, Table 5.5). The highest total biovolume and the strongest grazer effect were found in Maasholm (significant difference between grazer-access and grazer-exclusion treatments, as well as significant difference to both other sites, Tukey's HSD, p<0.05). In Geltinger Noor, overall biovolume was

lower and the grazer removal resulted in a distinct increase in total biovolume (Tukey's HSD, p=0.224 for unplanned comparison). In Wackerballig, the biovolume also decreased in grazed treatments, but this was less distinct. In this experiment no cage artifact was detected, microalgal biovolume in control plots was not significantly different from open cages ($F_{(1;20)}$ = 0.052, p=0.822).

Table 5.4: Results of nonlinear regression analysis of the effect of nutrient enrichment on diversity (H'), evenness (J') and species richness (S). Analysis was performed with a second-order polynominal ($y=a+b{\cdot}x+c{\cdot}x^2$) for data from grazed ("with grazers") and ungrazed ("without grazer") cages. Parameter estimates or a, b and c are given with standard error and p-level as well as the coefficient of determination (r^2).

dependent	a (SE)	p	b (SE)	p	c (SE)	p	r^2
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J'	0.446 (0.015)	<0.001	0.045 (0.002)	0.008	$-0.05\ 10^{-3}$ ($0.02\ 10^{-3}$)	0.013	0.4298
S	19.91 (0.78)	<0.001	0.148 (0.075)	0.069	$-1.87\ 10^{-3}$ ($0.94\ 10^{-3}$)	0.067	0.5385
without grazer							
H'	1.491 (0.080)	<0.001	-0.001 (0.008)	0.863	$-0.02\ 10^{-3}$ ($0.10\ 10^{-3}$)	0.844	0.1264
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site x grazing	2	0.092	0.675	0.519
error	22	0.136		

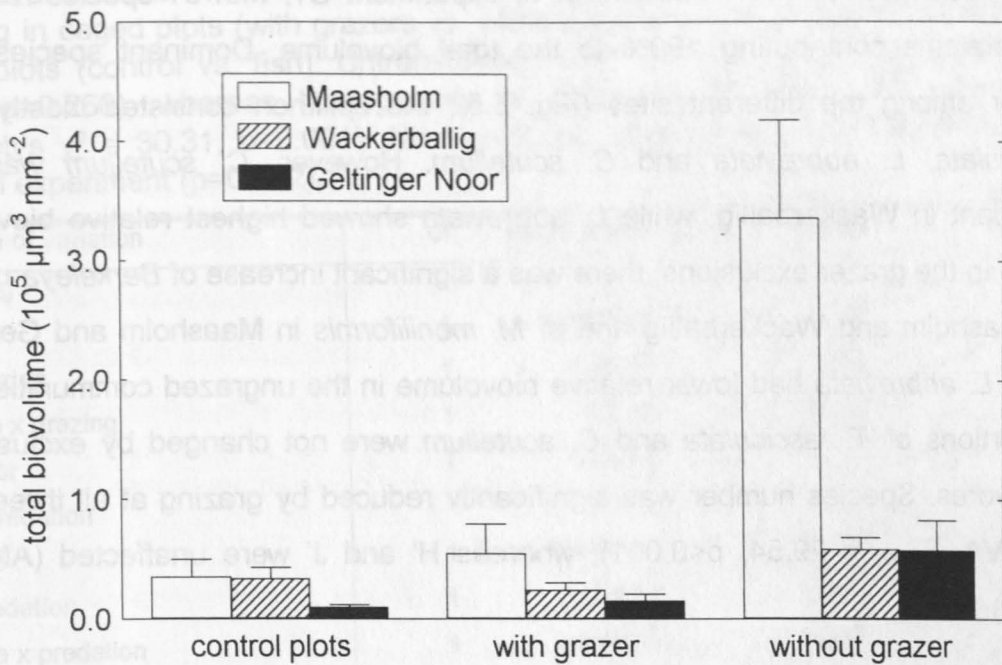Fig. 5.4: Total biovolume (mean ± standard error) of benthic microalgae in experiment G2 for uncaged control plots, open cages ("with grazer") and closed cages ("without grazer").
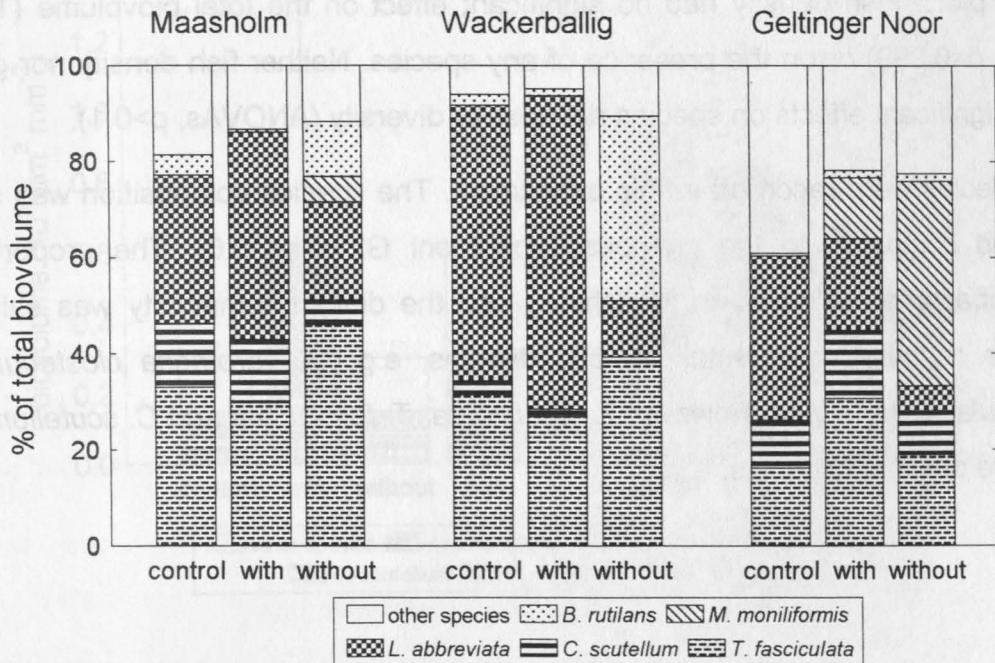

Fig. 5.5: Species composition of benthic microalgae in experiment G2, presented as mean % contribution to total biovolume, for uncaged control plots, grazer access cages (with) and grazer exclusion (without) treatments.

The species composition was similar to experiment G1, with 51 species recorded and diatoms contributing >90% to the total biovolume. Dominant species were similar among the different sites (Fig. 5.5), the epilithon consisted mostly of *T. fasciculata*, *L. abbreviata* and *C. scutellum*. However, *C. scutellum* was less abundant in Wackerballig, while *L. abbreviata* showed highest relative biovolume there. In the grazer exclusions, there was a significant increase of *Berkeleya rutilans* in Maasholm and Wackerballig and of *M. moniliformis* in Maasholm and Geltinger Noor. *L. abbreviata* had lower relative biovolume in the ungrazed communities, the proportions of *T. fasciculata* and *C. scutellum* were not changed by exclusion of herbivores. Species number was significantly reduced by grazing at all three sites (ANOVA, $F_{(1;22)}$ = 29.54, p<0.001), whereas H' and J' were unaffected (ANOVA, p>0.3).

5.3.3 Experiment G3

In the summer experiment, no significant grazer or site effect on microalgal biovolume could be detected (Table 5.6). Biovolume tended to be higher in Maasholm compared to Geltinger Noor (Fig. 5.6), but this was significant only for open plots. Fish density had no significant effect on the total biovolume (Tukey's HSD, p=0.999) or on the presence of any species. Neither fish density nor grazing had significant effects on species richness or diversity (ANOVAs, p>0.1).

50 species were recorded in this experiment. The species composition was slightly altered compared to the previous experiment G2 (Fig. 5.6). The proportion of cyanobacteria increased in Maasholm, and the diatom community was shifted to higher contribution of small, mobile diatoms, e.g. *Cylindrotheca closterium* and *Navicula* cf. *perminuta*. However, *L. abbreviata*, *T. fasciculata* and *C. scutellum* were still the dominant species.

Table 5.6: Results of a two-factor ANOVA for experiment G3: Effects of site and grazing in caged plots (with grazers vs. without grazer) and effects of predation on open plots (control vs. fish). Untransformed data were normally distributed (χ^2 = 2.65, p=0.266), whereas homogeneity of variances could not be established (Bartlett's χ^2 = 30.31, p<0.001). No significant cage artifact was detected in the control experiment (p=0.422).

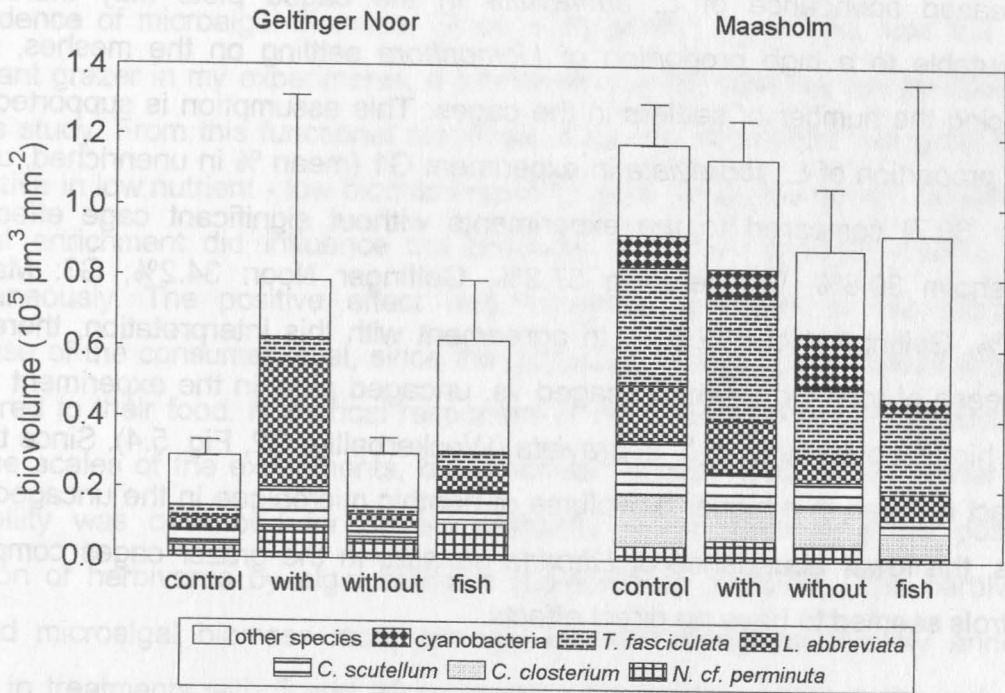| source of variation	df	mean square	F-ratio	p-level
grazing				
site	1	$1.089 \cdot 10^{10}$	2.692	0.120
grazing	1	$6.90 \cdot 10^{9}$	1.707	0.210
site x grazing	1	$7.0 \cdot 10^{8}$	0.173	0.684
error	1	$4.04 \cdot 10^{9}$		
fish predation				
site	1	$1.448 \cdot 10^{10}$	10.629	0.006
predation	1	$0.6 \cdot 10^{8}$	0.047	0.832
site x predation	1	$3.49 \cdot 10^{9}$	2.563	0.133
error	16	$1.36 \cdot 10^{9}$		

Fig. 5.6: Biovolume and species composition of benthic microalgae in experiment G3, for uncaged control plots, grazer access cages ("with") and grazer exclusion cages ("without"), and uncaged fish treatments. Whiskers represent 1 standard error of total biovolume.

5.4 Discussion

5.4.1 Experimental setup

The nutrient enrichment with increasing pellet tube length resulted in a linear increase in water column nitrogen concentrations. Nitrogen was deficient compared to phosphate in the water column, and the increase in NH_4^+ and NO_3^- showed conclusively the effectiveness of the NPK-fertilizer. The combination of the categoric grazer removal with a continuous increase of nutrients enabled me to combine the factorial experimental design with quantitative statements on nutrient effects.

A cage artifact was detected in experiment G1, but not in experiments G2 and G3. In experiment G1, the higher microalgal biovolume in control plots compared to grazer-access cages was due to the pennate diatom *L. abbreviata*, which was the only species developing more biovolume in the uncaged plots. *Licmophora* species often belong to the first and prominent colonizers in the Western Baltic Sea, and they are able to settle on thin, finely branched macroalgae (Ramm 1977). The decreased abundance of *L. abbreviata* in the caged plots may therefore be attributable to a high proportion of *Licmophora* settling on the meshes, thereby reducing the number of settlers in the cages. This assumption is supported by the high proportion of *L. abbreviata* in experiment G1 (mean % in unenriched, uncaged plots: 69.7) compared to the experiments without significant cage effects (G2: Maasholm 30.8%, Wackerballig 57.3%, Geltinger Noor: 34.2%; G3: Maasholm 12.7%, Geltinger Noor 12.8%). In agreement with this interpretation, there was a decrease of total biovolume in caged vs. uncaged plots in the experiment with the next highest proportion of *L. abbreviata* (Wackerballig, G2, Fig. 5.4). Since the cage artifact resulted in a higher biovolume of benthic microalgae in the uncaged control plots, the lower abundance of *Littorina saxatilis* in the grazer cages compared to controls seemed to have no direct effects.

5.4.2 Effects of grazing and nutrients on total biovolume

Grazers controlled the biomass and species composition of benthic microalgae in both spring experiments (G1 and G2). This is consistent with previous studies from marine (Castenholtz 1961, Nicotri 1977, Hunter & Russell-Hunter 1983) and freshwater habitats (Hill & Knight 1987, Steinman 1996). For sediment inhabiting

diatoms, top-down control was assumed to be ineffective (Admiraal et al. 1983). Grazing impact was strongly dependent on nutrient supply (Fig. 5.1), and varied between different sites (Fig. 5.4) and between different seasons (Table 5.2, 5.5 and 5.6).

The effects of grazing and nutrient enrichment on microalgal biomass was antagonistic. Grazing removed a significant part of microalgal biomass in all enriched treatments, but not in the unenriched control (Fig. 5.1). In enriched treatments, benthic microalgal biovolume increased, but at the same time consumption of algae increased, resulting in a twofold increase of microalgal biovolume in ungrazed compared to grazed communities (Table 5.3). Stronger grazing effects in nutrient enriched vs. unenriched plots have been described also for freshwater experiments (Marks & Lowe 1989, Rosemond et al. 1993). In a literature survey, Cattaneo & Mousseau (1995) found a positive correlation between herbivore removal rates and peripyhtic biomass. Sommer (1999a) found a curvilinear type-II functional response of the periwinkle *Littorina littorea* in dependence of microalgal biomass. Since a congener, *L. saxatilis*, was the most abundant grazer in my experiments, a similar functional response can be assumed for this study. From this functional response, it can be concluded that grazers are ineffective in low nutrient - low biomass environments. Thus, the bottom up effect of nutrient enrichment did influence the producer and the consumer trophic level simultaneously. The positive effect was, however, restricted to the functional response of the consumer level, since the generation times of gastropods are long compared to their food. Numerical responses of herbivores could not be tested on the time scales of the experiments, but a somatic growth response to higher food availability was described for stream caddisfly larvae, indicating the possible limitation of herbivores by algal biomass (Lamberti et al. 1987). The herbivores reduced microalgal biomass most strongly in experiments moderately enriched (>60% in treatments with 5 and 20 cm pellet tube length), whereas the reduction was lower in higher enrichments (<50% in treatments with 40 and 80 cm pellet tube length). This may indicate the starting saturation of the functional response of the herbivores and the ability of benthic microalgae to outgrow their losses at highest nutrient enrichment.

Moreover, grazing reduced the variability in biomass of the benthic microalgal community, whereas in ungrazed, highly enriched communities total biovolume was highly variable (Fig. 5.1). A similar pattern was found for filamentous algae (mainly *Enteromorpha intestinalis*), which showed decreased variation of canopy height and percent cover in grazed vs. ungrazed treatments (Lotze 1998, Worm unpubl. data). Because of their bulldozer-like feeding type, gastropods tend to increase spatial heterogeneity of periphytic mats by producing grazing tracks (Sommer 1999a). However, in my experiments the abundance of *L. saxatilis* was more than a magnitude higher than the abundance of *L. littorea* in the experiments by Sommer (1999b). Therefore the heterogeneity may decrease if the grazing tracks show substantial overlap, which may explain the decreased biomass variability observed in the grazed cages (Fig. 5.1).

Maasholm showed the strongest degree of grazing control, which can be explained by the higher abundance of herbivores at this site, especially evident for the gastropod *Littorina saxatilis* (Table 5.1). Increased abundance of *L. saxatilis* may also explain the stronger grazing effect in Geltinger Noor compared to Wackerballig (Table 5.1, Fig. 5.4). Lotze (1998) showed that *L. saxatilis* was a main consumer of germlings of filamentous algae *(Enteromorpha* sp., *Pilayella littoralis)*, whereas it did not feed on adults. The germlings are in the same order of size as the benthic microphytes dealt with in this study. The decreasing abundance of herbivores, especially of *L. saxatilis*, may also explain the decreasing seasonal shift of grazing impact observed between May and July in Maasholm and Geltinger Noor (Table 5.5 and 5.6).

The reason for the seasonal decline in grazing pressure remains speculative. Due to decreasing nutrient availability from spring to summer, microalgal biomass production may become nutrient limited (see Chapter 4), and microalgae may cease to serve as a good nutritional basis for herbivores. This is supported by the fact that biomass production of microalgae in Maasholm was substantially lower in summer (Fig. 5.6) compared to spring (Fig. 5.1 and 5.4). Increased predation on herbivores could also affect grazing pressure in summer, but no evidence for a trophic cascade could be found in experiment G3. Three- to four-level trophic cascades are known from freshwater pelagic communities (McQueen et al. 1989) and marine

This is also indicated by the overproportional decrease of the tube dwelling diatom *Berkeleya rutilans* in grazed cages of experiment G2. This species builds gelatinous tubes lowering its nutritional value and was grazed with low rates when offered to the isopod *Idotea baltica* (Sommer 1997) or the periwinkle *L. littorea* (Sommer 1999a). Therefore an avoidance was expected rather than a preference. But *Berkeleya rutilans* also exhibits an erect life form, and thus may have a higher probability to be removed physically. Dislodging is equivalent to loss from the community in my *in situ* experiments, whereas in the lab experiments conducted by Sommer (1999a) dislodged individuals stay within the aquarium. This may explain the different results for tube-dwelling species. Generally, physical dislodging of the algae due to the mechanical activity of the grazers (Castenholtz 1961, Sumner & McIntire 1982) may cause removal rates much higher than ingestion rates (Cattaneo & Mousseau 1995).

The adnate growth form explains also the low grazing impact on the adnate species *Cocconeis scutellum*, which often dominated in grazed treatments in freshwater experiments (Colletti et al. 1987, Pan & Lowe 1994). Adnate growth form can be conceived as a spatial refuge from herbivores like *Littorina* which have limited access to this basal layer of periphyton (Sommer in press). The grazing resistance of *Licmophora abbreviata*, however, was more surprising, since the congeneric species *L. ehrenbergii* was heavily grazed in experiments with *Idotea baltica* (Sommer 1997). Again, the vertical position of adherence may determine the grazing loss, since individuals growing epiphytically in the canopy layer may be ingested together with their substrate algae, while individuals colonizing directly on the substrate may be less susceptible (Sommer 1999a, in press). In my experiments, *Licmophora* attached directly to the substrate with a short stalk (Daniel et al. 1987) and was seldomly observed epiphytically or in multicellular aggregations. It was probably the flexibility of the stalk that made the attachment of *Licmophora* more resistant to mechanical forces provided by the radula of gastropods compared to the more picking grazing type of isopods (Sommer 1997). The increase of *Licmophora* in relative and absolute biovolume in the grazed cages indicated competitive release, as it was described previously for other groups, e.g. cyanobacteria in a freshwater study (McCormick & Stevenson 1991, Rosemond et

al. 1993). The overall low contribution of cyanobacteria in my experiments was most probably caused by temperature, since cyanobacteria tend to dominate only at high water temperatures (Tilman et al. 1986, Duncan & Blinn 1989, Watermann et al. submitted, Chapter 3). This view is supported by the higher proportion of cyanobacteria in July (Fig. 5.6).

Melosira moniliformis was not only least resistant against herbivory, but simultaneously it was the species with the highest response to the nutrient enrichment in experiment G1 (Table 5.3). This is in accordance with results from my nutrient enrichment experiments conducted in the nearby Kiel Fjord, where this species was highly favoured by nitrogen additions in summer and autumn (see Chapter 4). *Tabularia fasciculata* was also favoured by high nutrient levels, whereas *Licmophora abbreviata* was unaffected or - if relative biovolume is accounted for - reduced, in the present experiments and also in the Kiel Fjord (see Chapter 4).

Consequently, there is an allocation trade-off between grazing resistance and nutrient uptake, indicated by the significant interaction grazer x nutrients (Table 5.2) and the differences between regression slopes for the dominant species (Table 5.3). Growth versus resistance trade-offs are a general pattern in plant communities: Eutrophicated coastal areas are often dominated by blooms of ephemeral, filamentous algae, which are on the other hand sensitive to herbivore pressure (Valiela et al. 1997, Lotze 1998). In their functional form model for macroalgae, Littler & Littler (1980) demonstrated an inverse relationship between growth rate and grazing resistance by investment in supportive structure and thalli toughness. For higher plants, the trade-off is attributed to the allocation of resources in growth or in chemical defense compounds (Coley et al. 1985, Bazzaz et al. 1987). For benthic microalgae, however, this trade-off is presumably not related to the production of antiherbivore compounds or toughness, but to growth form constraints: erect species do not resist mechanical forcing (e.g. grazing), but can sequester nutrients from the water column overlying the nutrient-depleted periphyton (Riber & Wetzel 1987, Steinman et al. 1992, Rosemond et al. 1993). Microalgae living adnately to the surface are resistant to grazing and mechanical forcing (Poff & Ward 1995, Steinman 1996), but they pay for their resistance by increased isolation from the water column as a nutrient source (Burkholder et al. 1990). These conclusions are

supported by other experimental studies: The response to nutrient addition was attributed mainly to overstory species in a well-developed periphyton mat (Paul & Duthie 1989, Chapter 4), and a positive correlation between growth rate and grazing susceptibility was shown for epilithic microalgae (Sommer 1997).

5.4.4 Effects of grazing and nutrients on diversity

Nutrient enrichment and grazing resulted in an unimodal dependence of diversity, evenness and species number on nutrient concentration. This hump-backed relationship was proposed as a general ecolgical pattern for the response of diversity to productivity (Rosenzweig & Abramsky 1993, Tilman & Pacala 1993), although it is not without criticism (Abrams 1995). In my experiments, the unimodal pattern was observed only within grazer-access cages, but not within grazer-exclusion treatments. Similarily, a recent metaanalysis implies that grazing tends to reduce plant species richness at oligotrophic sites, but enhanced richness at eutrophic sites (Proulx & Mazumder 1998). These contrasting effects are based on the increased dominance of few species following nutrient enrichment (Chapter 4) and the preferential removal of those opportunistic but grazer-susceptible species by herbivores described above. By removing the dominant species, herbivores prevent the monopolization of the community (Lubchenco 1978, Proulx et al. 1996, Proulx & Mazumder 1998). In oligotrophic habitats, grazing does not counteract enhanced dominance and may lead to the local extinction of species. The significant decrease of species richness in grazed and unenriched treatments observed in experiments G1 and G2 supports this view. Surveying freshwater grazing experiments, Steinman (1996) stated a diversity decrease due to grazing in half of the studies surveyed, and attributed this decrease mostly to reduced species richness. A decrease of periphytic diversity and species richness was shown to be linked to preferential grazing on subdominant species (Swamikannu & Hoagland 1989).

Without grazers, the variability of benthic microalgal diversity increased, leading to a loss of significance of linear or unimodal regression models. In laboratory experiments, low abundances of herbivores increased spatial variability and diversity in periphyton (Sommer 1999b). The contrary impact in my experiments may be explained by the higher abundance of grazers in my experiments, resulting in a

uniform prostrate microalgal assemblage with low biomass variability and decreased species richness (see above). This is supported by the decrease of diversity reported by Sommer (1999b) for higher abundance levels of *L. littorea* and *I. baltica*. Herbivores may thus compensate for the variability introduced by stochastic germination and colonization processes (Hart 1992) and differences in maximum growth rates under nutrient enriched conditions.

It becomes obvious that eutrophication effects are consumer-dependent (Proulx & Mazumder 1998, Worm et al. in prep.). It cannot be concluded from my experiments, however, if the proposed unimodal relationship between diversity and nutrient enrichment (Rosenzweig & Abramsky 1993) is generally dependent on the presence of grazers. However, it is plausible to assume a shift of the optimum diversity to higher nutrient richness in grazed communities. Maximum diversity is assumed to be established at low resource concentrations (Tilman 1982, Huston & De Angelis 1994). Following this assumption, diversity increases with increasing resource supply only over a narrow range which allows more species to grow (Marcus 1980). At more benign conditions, increased nutrient supply results in a decrease of diversity (Tilman 1982, see Chapter 4). In grazed communities, the plants face higher losses and more nutrients may be necessary to compensate these losses. In this case, highest diversity may be established at higher resource levels. However, more experimental studies are necessary to unravel the dependency of diversity on nutrient supply and consumer density.

5.5 Conclusions

Benthic microalgae were simultaneously and antagonistically influenced by nutrient supply and herbivory, in terms of biomass, diversity and species composition (and by this the architecture of the community). Herbivores significantly reduced algal biomass, but this effect was partly compensated when nitrogen supply was doubled. Relative herbivore effects on microalgal biomass increased with increasing nutrient availability, indicating a functional response of herbivores to prey availability. The response of microalgae on the species level suggested a trade-off between nutrient use and grazing resistance, which appeared to be linked to algal growth form. Large

erect species were most responsive to both, nutrient enrichment and herbivory, compared with other growth forms. Microalgal diversity showed an unimodal response to nutrient enrichment when herbivores were present but there was no significant response when grazers were excluded. The presence of herbivores reduced the variability of microalgal biomass and species composition. Herbivore effects varied considerably among different sites and were stronger in spring than in summer. Manipulations of fish density during summer did not have any effects on microalgal community structure.

6 General Discussion

6.1 General conclusions regarding the effects of biotic interactions on the structure of microphytobenthos

The results of my experiments on the impact of biotic interactions on periphyton were presented and discussed in the previous chapters. The following general conclusions can be drawn from this study:

- The colonization of substrates by benthic microphytes involved a sequence of species and life-forms, beginning from a random collection of unicells and resulting in a late successional microalgal mat dominated by large and erect species. Species richness on the artificial substrates was saturated within few days of incubation time, whereas the ongoing succession led to a decrease of diversity due to lower evenness. The successional trade-off between fast colonizers and good competitors was strongly influenced by seasonal fluctuations in the species pool.

- The response of biomass stoichiometry to artificial nutrient enrichment was a reliable tool to determine limiting nutrients. Biomass stoichiometry and the response of total algal biovolume to nutrient supply indicated nutrient limitation of the benthic microalgae in Kiel Fjord. During most of the growth season, nitrogen was limiting, but phosphate could be limiting in spring and silicate for diatoms, indicating a complex pattern of shifts in nutrient limitation.

- The microlgal community was consistently altered through nutrient supply, with more changes on the species level than on higher taxonomic levels. When supplemented with additional nitrogen, filamentous algae displaced the usually dominating diatoms only during summer. At the species level, a persistent dependence of certain species on either nitrogen or phosphate supply was exhibited. Erect species profited most strongly from the nutrient enrichment. The diversity of benthic microalgae was negatively correlated to the supply of the limiting nutrient, based on an increased dominance of few species (i.e. reduced evenness). Nutrient competition was an important factor structuring the microalgal assemblage, especially from late spring to autumn, while in winter

and early spring adverse physical conditions and high nutrient availability prevented nutrient competition.

- The effects of nutrient enrichment were partly compensated by herbivores, which were able to reduce algal biomass significantly and increased their removal rates with algal production. Algal species faced a growth form trade-off between mechanical (i.e. grazing) resistance and sequestration of resources (nutrient and light). Generally, algal species richness was lower in grazed compared to ungrazed communities. In the presence of herbivores, algal diversity was unimodally related to nutrient enrichment, indicating that herbivores are able to counteract negative influences of eutrophication.

- Diversity was a suitable response variable to measure environmental effects on a community (e.g. nutrient enrichment, successional sequence), but for microalgae an extrapolation beyond the observed or experimentally manipulated site might be difficult.

Although my experiments were conducted in a limited array of habitats, it became evident that biotic interactions impose complex control mechanisms on the microbenthic flora. Besides the contribution to an understanding of the distribution and abundance of benthic microalgae (see Chapter 6.2), some general patterns emerged, which are valid beyond the periphyton community, affecting a broad variety of autotrophs in aquatic and terrestrial habitats:

The increased dominance of few taxa in nutrient enriched environments can be re-garded as a general feature of autotrophic communities. The increasing dominance of one or few taxa with increasing eutrophication was shown for benthic microalgae in marine (this study) and freshwater habitats (Stevenson et al. 1991), for marine and freshwater phytoplankton (Revelante & Gilmartin 1980, Agusti et al. 1991), aquatic (Lotze 1998) and terrestrial vegetation (Tilman 1982, Wedin & Tilman 1996). The theory underlying this feature stems from resource-based competition models (Tilman 1982, Rosenzweig & Abramsky 1993, Tilman & Pacala 1993). The loss of diversity can be explained by a reduced heterogeneity of nutrient supply, the imbalance of nutrient supply ratios due to anthropogenic enrichment of single nutrients, and the ability of species with highest μ_{max} to outgrow their competitors.

A second general feature across ecosystems is the herbivore influence on the response of the autotrophic guild to nutrient enrichment. Mitigation of eutrophication effects through herbivores has been repeatedly described for aquatic plants in microbenthic (this study) and macrobenthic communities (Lotze 1998, Worm et al. in prep.), for phytoplankton (Mazumder & Lean 1994) and for terrestrial vegetation (see examples in Proulx & Mazumder 1998). Herbivores are able to enhance diversity at eutrophic sites, whereas they reduce diversity at oligotrophic sites (Proulx & Mazumder 1998). This reflects the preferential grazing of dominant species at high nutrient concentrations (Lubchenco 1978, this study) and the species loss due to grazing at low nutrient concentrations. Related to this topic is the existence of an autotrophic trade-off between growth and defense. This has been found for terrestrial plants (Coley et al. 1985), aquatic macrophytes (Littler & Littler 1980), phytoplankton (Van Donk & Hessen 1993) and benthic microalgae (this study). However, the mechanisms of grazing deterrence are different, comprising morphology, noxious chemicals, growth form and adhesion to the substrate.

My results further highlighted the similarities between periphyton and phytoplankton, regarding nutrient requirements, biomass stoichiometry and grazing susceptibility. Also the kind of seasonal succession may be similar between both communities (Sommer et al. 1986, this study), although the succession of periphyton has not been studied intensively enough to allow a direct comparison. However, limitations of the transfer of concepts have become visible as well: Benthic microalgae do not simply live within their nutrient media, but establish an environment which differs widely from their surrounding aquatic habitat, exhibiting strong vertical structuring and steep gradients of resources and abiotic conditions. Since macrozoobenthic grazers are reported to be more influential on periphyton composition (Steinman 1996), the main grazers of periphyton are large and long-lived compared to main grazers of phytoplankton. These aspects possibly pose a limit to the transfer of biological models from phytoplankton to periphyton.

6.2 A conceptual model of interactions affecting benthic microalgae

The following conceptual model of interactions in the microbenthos integrates the findings of this thesis and several marine and freshwater studies. This model is proposed to visualize the effect of biotic and abiotic forces on the benthic microalgae (Fig. 6.1). It serves to discuss the interactions between periphyton and other important components of littoral ecosystems, those living within the architecture provided by microalgae (termed "periphyton community") and those living outside. Moreover, the model will allow to predict qualitatively the changes in the microbenthic community following the eutrophication of their habitat. These predictions will be based on my experiments, which were a small-scaled and artificial counterpart of eutrophication processes, and on literature data. The rationale for this discussion is the increasing human impact on the global nitrogen cycle and the increasing nutrient load into aquatic habitats (Vitousek et al. 1997, Carpenter et al. 1998). Coastal ecosystems are especially affected by eutrophication and a variety of negative consequences have been described, including the loss of perennial vegetation (i.e. spatial structure important for recruitment of benthic invertebrates and vertebrates), mass blooms of ephemeral filamentous algae and toxic phytoplankton species, loss of biotic diversity, sediment anoxia and the change of biogeochemical cycles (Larsson et al. 1985, Cederwall & Elmgren 1990, Hallegraeff 1993, Duarte 1995, Valiela et al. 1997, Lotze 1998, Raffaeli et al. 1998).

It should be kept in mind, however, that some of the connections presented in this model are still speculative and originate only from a limited array of studies. Moreover, this model is proposed explicitly for coastal marine and lentic freshwater habitats, whereas stream periphyton may be influenced more directly by the hydrologic regime (Biggs et al. 1998).

Fig. 6.1: Schematic diagram visualizing the interactions structuring the periphyton community. Bold arrows indicate interactions influenced by nutrient supply. For further details, see text.
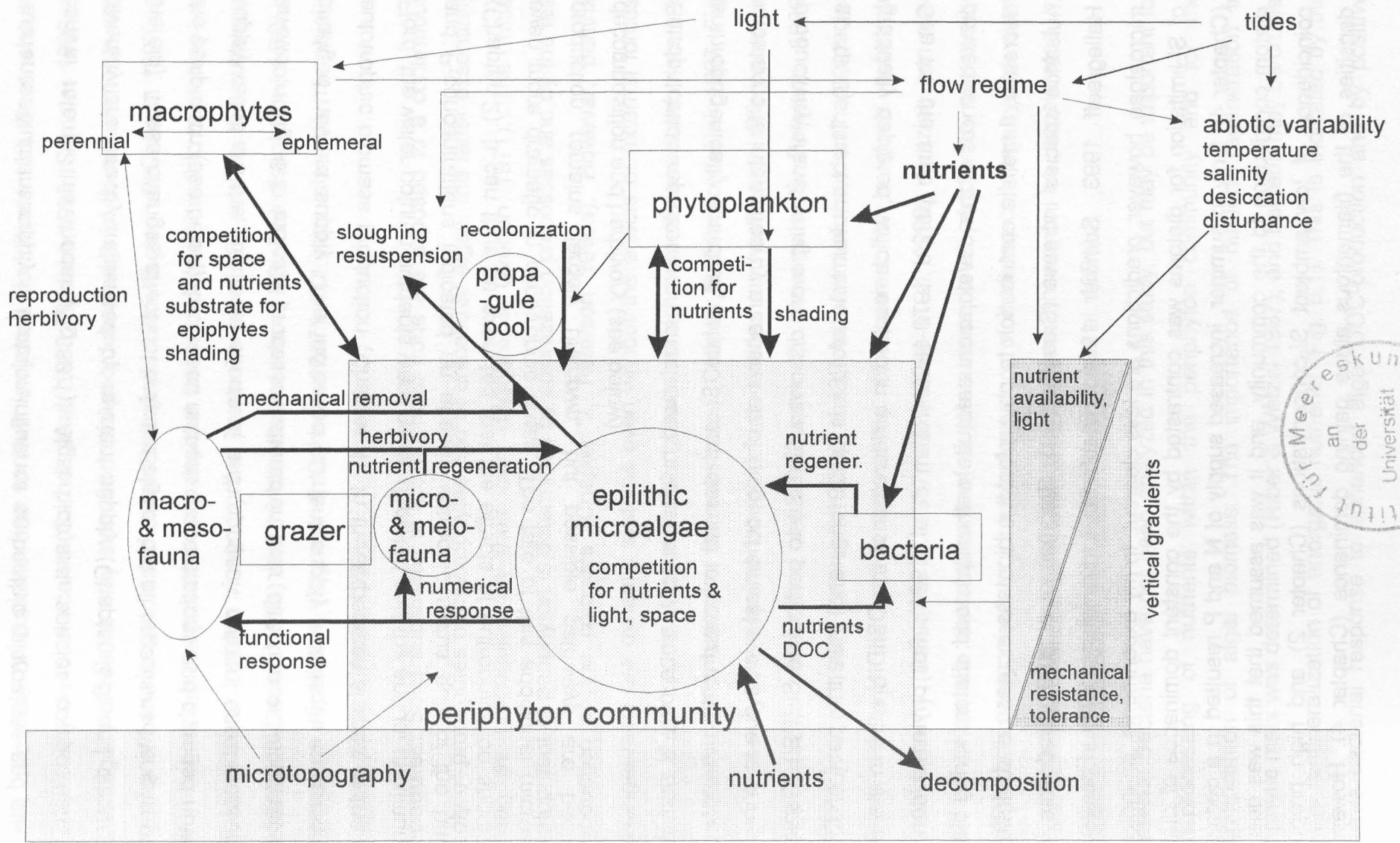
correlations between benthic bacteria and autotrophic production (Hepinstall & Fuller 1994, Lopez et al. 1995). Besides this correlation, however, information on the response of benthic bacteria to changes in nutrient supply and subsequently changed autotrophic biomass are scarce. Nilsson et al. (1991) found no effects of eutrophication on marine benthic bacteria, whereas Tufail (1987) reported increased bacterial abundances in enriched sediments. Weisse (1991) reviewed data for pelagic bacteria and proposed a reduced relative importance of microbial food webs in eutrophic habitats. Sanders et al. (1992) reported a higher degree of top-down control in microbial food webs of eutrophic habitats, leading to a decreased impact of nanoplankton on bacteria. The integration of bacteria into a functional model of periphyton ecology remains a challenging goal for future research.

Herbivores: Grazing invertebrates are able to reduce the biomass of benthic microalgae substantially and furthermore alter the species composition and structure of the periphyton (Chapter 5). This in turn imposes a strong trade-off on the algae between grazer resistance and nutrient sequestering (Chapter 5, see vertical gradients in Fig. 6.1). Besides the ingestion of algae, herbivores remove upperstory algae mechanically (Castenholtz 1961, Sumner & McIntire 1982, Cattaneo & Mousseau 1995) and thus increase the resuspension of benthic microalgae, affecting the propagule pool (Fig. 6.1). As discussed for bacteria, another important impact of herbivores is presumably the regeneration of nutrients, but quantitative data are missing for microbenthic communities.

The herbivores can be divided into species much larger and long-lived compared to the periphyton mat (e.g. gastropods, isopods, or insect larvae in freshwater) and those living within the mat (e.g. protozoa, nematodes, copepods). Both groups of consumers can be assumed to have different effects on the periphyton. Large herbivores (macrozoobenthos) profited from enhanced biomass due to nutrient enrichment, since the additional production is provided by loosely attached overstory species (Chapter 5). These macrograzer exhibit only passive preference and ingest a broad variety of prey species (Nicotri 1977, Sommer 1997, 1999a). The response of macrozoobenthic grazers to prey density is proximately functional, i.e. these organism increase their ingestion or removal rates but are not able to increase their fecundity immediately (Fig. 6.1). However, large herbivores are able

to migrate into patches of high algal densities. In contrast, small herbivores (protists and meiobenthos) are capable of developing higher reproductive rates due to higher food supply because of their shorter generation times (Fig. 6.1, numerical response). Micrograzers are more specialized consumers because of their size and their food uptake mechanisms (Hargrave 1970, Romeyn & Bouwman 1983, McCormick 1991, Balczon & Pratt 1996, Bott 1996, Sundbäck et al. 1996b). There is no information available, whether benthic microalgae can escape meiobenthic grazers by increasing cell size, as was reported for phytoplankton species grazed by *Daphnia* (Van Donk & Hessen 1993). The grazer-prey interaction is influenced by the competition of both herbivore groups, the ingestion of small herbivores by large and essentially omnivorous grazer, and by predation. Trophic cascades by predatory fish can be assumed to affect large and poorly-armoured herbivores (crustacea) more than small (meiofauna) or heavily-armoured ones (gastropods) (Dahl 1998, Chapter 5).

Since eutrophication favours mainly large and erect species (Chapter 4 and 5, Cattaneo 1987), small herbivores may experience a different habitat structure and food abundances in nutrient-enriched habitats. Another consequence of eutrophication may be a lower efficiency of grazers in very nutrient-rich situations (Chapter 5). If a saturation of functional or numerical responses of herbivores is achieved in nutrient-rich habitats, an increased proportion of the autotrophic biomass is directed to the decomposition food web. This may thus add to benthic hypoxia due to oxygen-consumptive decomposition processes, which again is supposed to decrease herbivore abundance (Raffaelli et al. 1998), resulting in a reinforcing feedback.

Phytoplankton: During my experimental work, I concentrated on direct influences on benthic microalgae, but a full account of biotic interactions has to consider other photoautotrophs as well (Fig. 6.1). Benthic macrophytes (see below) and phytoplankton are the most important autotrophic competitors of periphyton. These three groups experience markedly different physico-chemical gradients and exhibit different growth requirements and growth rates (Sand-Jensen & Borum 1991). The balance of competition between benthic and pelagic microalgae can be influenced by the source of nutrient enrichment. Principally, additional nutrients can be

supplied to the water column (riverine inflow, atmospheric deposition) and to the sediment (groundwater inflow, release of previously deposited nutrients). Benthic microalgae are able to control nutrient release by the sediment, thereby reducing the availability of nutrients for phytoplankton (Hansson 1988, Sundbäck & Graneli 1988, Sundbäck et al. 1991). The limited access of periphytic algae to water column nutrients (see discussion in Chapter 4) imposes a competitive advantage to phytoplankton, if the water column is nutrient-enriched. Thus, eutrophication tends to favor pelagic over benthic algae, although species-specific growth requirements are similar (Bothwell 1985, 1989). The increased phytoplankton biomass shades the benthic vegetation, shifting the limiting factor from nutrients to light (Hansson 1988, 1992; Duarte 1995) and leading to a curvilinear correlation between periphyton biomass and lake trophic state (Cattaneo 1987, Hansson 1992). The limited access to water column nutrients is important for epilithic mats (Riber & Wetzel 1987) and presumably also for the sediment-inhabiting microflora due to the production of exopolymers by epipelic diatoms (Underwood & Paterson 1993, Smith & Underwood 1998).

The competitive dominance is changed if the nutrients are supplied via the sediment or via the porous substrate as in my *in situ* experiments (Chapter 4). Benthic microalgae may profit from the "benthic eutrophication" much more than from water column nutrients (Pringle 1987, Fairchild & Sherman 1992). Hagerthey & Kerfoot (1998) showed the increase of benthic algal biomass in groundwater-inflow regions of a temperate sepage lake, confirming the hypothesis of increased nutrient availability to benthic microalgae with enriched nutrient content in the substrate.

Macrophytes: For benthic microalgae, macrophytes represent competitors for space and resources (see above) as well as substrates for epiphytes (Fig. 6.1). In fact, the interaction between epiphytes and their substrate plants is a well documented example of biotic control in community ecology on its own (Sand-Jensen 1977, Cattaneo 1983, Borum 1987, Neckles et al 1993, Coleman & Burkholder 1994, Jernakoff et al. 1996). Eutrophication-based shifts from perennial to ephemeral and pelagic algae were described (Duarte 1995, Lotze 1998). Ephemeral filamentous and unicellular algae require more nutrients to balance their losses and to sustain their growth, whereas perennial vegetation is favoured in

oligotrophic conditions due to low mortality and higher storage capacities (Pedersen & Borum 1996, 1997). To my knowledge, no reports on competition between edaphic microflora and macrophytes have been published. Direct competition between macrophytes and benthic microalgae was observed only for epiphytes (Neckles et al. 1993, Coleman & Burkholder 1994), showing the competitive advantage of epiphytes under enriched conditions, based on the same mechanisms: shifting the limiting factor from nutrient to light by overgrowing their substrate plants (Sand-Jensen 1977).

Apart from this, mass blooms of ephemeral macrophytes occur as drifting or settling mats and may change the habitat for benthic microalgae considerably. In experiments with drifting green algal mats, microbenthic biomass was shown to be insensitive to a high degree of shading and possible hypoxia (Sundbäck et al. 1996a, see also Sundbäck et al. 1990). Hypothetical explanations of this phenomenon include shading from UV-radiation, shade adaptation, vertical migration of diatoms, and sediment supply of organic nutrients (heterotrophy) (Sundbäck et al. 1996a). Thus, benthic microalgae seem to be robust against drastic changes in their environment - a view supported by the results of the Dutch Ems-Dollart study on tolerance of benthic diatoms to abiotic harshness (Admiraal 1977a,b,c, 1984; Admiraal & Peletier 1979, 1980).

Physical conditions: The conceptual model discussed so far gives the impression of a complex web of biotic interactions structuring the periphyton community. However, the strength and the interrelations of these biotic forces were shown to be spatially and temporally variable, e.g. colonization processes between seasons (Chapter 2), limiting resources between seasons (Chapter 4), species composition on temporal and spatial scales (Chapter 2, 4 and 5) and grazing effects between similar habitats (Chapter 5). The scales of temporal and spatial variability receive increasing attention by marine ecologists (Underwood & Chapman 1998, Hughes et al. 1999). Therefore, the importance of physicochemical variability will be briefly outlined.

Differences between habitats in colonization, competition, herbivory and photosynthetic activity have often been observed for microbenthic assemblages and explained e.g. by flow velocity (Poff & Ward 1995, Berninger & Hüttel 1997), habitat

heterogeneity including substrate microtopography (Poff & Nelson-Baker 1997, Sabater et al. 1998, Watermann et al. submitted), temperature (Duncan & Blinn 1989), chemical composition (Admiraal 1984) and disturbance (Wootton et al. 1996). It becomes obvious that biotic interactions cannot be separated from the abiotic conditions of the habitat. Biggs et al. (1998) proposed a habitat matrix model for stream periphyton, involving resource supply and disturbance as primary axes and thus resembling Grime's concept of competitive, ruderal and stress-tolerant plant strategies (Grime 1977, Grace 1991). In this habitat matrix model, biomass and species composition of stream periphyton are considered as a function of habitat stability and resource supply, mediated by grazing intensity. Biggs et al. (1998) concluded that competition and grazing effects are minor in unstable, highly disturbed habitats. Although stream periphyton may be more directly influenced by the hydrological regime, it can be derived from this model that the importance of biotic interactions may be overridden by abiotic conditions in extremely harsh habitats, as was proposed for intertidal sediment-inhabiting microphytobenthos (Admiraal 1984, but see Flothmann & Werner 1992). However, experimental tests of the interplay of biotic and abiotic interactions in periphyton are rare (but see Poff & Ward 1995, Wootton et al. 1996).

Spatial variability can be found also within habitats. Benthic microalgae (and their consumers) are often distributed in horizontal patches of small size (around 100 cm²), which may be aggregated in patches of higher order again (Blanchard 1990, Saburova et al. 1995). These patches can influence nutrient availability and grazer-prey encounters, but may as well be the result of biotic interactions, as described for algal patches defended by larvae of a territorial caddisfly (Hart 1985). Another dimension of spatial complexity is added by vertical gradients of microalgal biomass on hard substrates (Johnson et al. 1997) and in sediments (Berninger & Hüttel 1997, Wiltshire in press). The vertical position of an algae determines nutrient and light availability and decreasing mechanical resistance of benthic microalgae and, thus, may shift the balance between top down and bottom up interactions within the periphyton community (Fig. 6.1).

Temporal variability is imposed with very different time periods, e.g. based on disturbance frequency (Peterson 1996a,b; Wootton et al. 1996), sloughing and

recolonization cycles (Hoagland et al. 1982, Johnson et al. 1997), or intraannual variation in abiotic conditions. In this seasonal perspective, biotic interactions may be most important from spring to autumn, whereas from late autumn to early spring adverse growth conditions and high nutrient supply may suppress algal competition. Simultaneously, grazing impact is low because of low herbivore abundances and activity (Chapter 2 and 5). The favourable temperature and light conditions, the low nutrient concentrations and the higher herbivore abundance (respectively activity) during the summer period as well as the increased growth of phytoplankton can be assumed to intensify biotic interactions.

Summary: The conceptual model described in Fig. 6.1 shows the multi-level web of connections between abiotic and biotic structuring forces. It became obvious that biotic interactions strongly influence the species composition and biomass in the periphyton community. Furthermore, it is evident that linear interactions as those shown in Fig. 6.1 are simplifications because of a multitude of mitigating and reinforcing interactions. In a modelling study, McCann et al. (1998) showed the stabilizing effect of weak and nonlinear interactions in complex trophic webs. In ecological research, the complexity of ecosystem is often viewed as "noise" masking simple relationships (Polis & Strong 1996, Polis 1998, Berlow 1999). The study by McCann et al. (1998) brought up the question if complexity itself may be an important factor regulating ecosystem function. This should especially be considered in management issues of ecosystems dominated by humans (e.g. coastal areas) for which complexity is often neglected (De Leo & Levin 1997).

6.3 Outline of future research on benthic microalgae

Despite increasing knowledge on the ecology of marine benthic microalgae and a substantial transfer of concepts derived from freshwater and terrestrial vegetation, it became obvious throughout this discussion that several important questions concerning the microbenthos cannot be answered adequately, if at all. Concluding this thesis, I want to present three fields of research which may be promising for the future in order to reveal further forces shaping microbenthic communities and to allow the application of results from this thesis for monitoring purposes.

- **Extending the stoichiometric view.** The importance of nutrient regeneration was shown for benthic microalgal mats, caused by the limited access to water column nutrients (Riber & Wetzel 1987, Burkholder et al. 1990). The regeneration can be provided by herbivores and bacteria, and different stoichiometric requirements of these organisms may lead to imbalanced nutrient supply. It was shown that different groups of herbivorous zooplankton resupplied nutrients in different ratios, e.g. higher N:P re-supply ratios by cladocerans compared to copepods (Sterner et al. 1992). The dominant group of zooplankton was capable of shifting freshwater habitats from N- to P-limitation or vice versa (Elser et al. 1988, Sterner et al. 1992). Furthermore, a feedback of nutrient regeneration on phytoplankton composition was established, diminishing the proportion of poor P-competitors in cladoceran dominated lakes (MacKay & Elser 1998). Also bacteria seem to have an optimal stoichiometry different from unicellular algae (Chrzanowski et al. 1996). However, the importance of these differences has not been assessed for microbenthic communities, although several indications exist. Internal biomass stoichiometry of benthic microalgae was shown to be sensitive to nutrient supply ratios and limitation scenarios (Chapters 3 and 4). Without specifying the resupply ratios, a decrease of C:N ratios by nutrient regeneration of herbivores was shown for periphyton (Hunter & Russell-Hunter 1983, Rosemond 1993). Compared to the pelagic environment, the coupling of uptake and regeneration processes may be even closer in microbenthic communities because of the spatial integration of microalgae, bacteria and herbivores. Therefore, it can be assumed that (i) specific supply ratios should alter the nutrient situation and the competitive performance of periphyton species, (ii) nutrients regenerated by bacteria, protozoa, meiofauna and macrofauna will differ in their nutrient ratios, and (iii) the differential influence of macro- and micrograzer will be reinforced by the destruction of the periphyton matrix by macrograzers, resulting in a changed pattern of nutrient regeneration. An analysis of stoichiometric properties of biotic interactions should involve a test of recycling ratios of different organism groups (bacteria, micro-, meio- and macrofauna), distinguishing between regeneration rates which are species specific and those which are dependent on the nutritional status of the food. The quantitative importance of nutrient regeneration compared to new

production has to be assessed. Finally, an experimental test of changes in microalgal species composition and biomass following changes in dominant heterotrophs should be conducted

- **Relating ecosystem function to diversity**: The role of diversity in stabilizing communities and securing ecosystem function has been widely debated in the last decade. In a series of experiments, the correlation between the stability of grassland communities and species richness was shown (Naeem et al. 1994, 1996, Tilman & Downing 1994, Tilman 1996, Tilman et al. 1996). But these experiments have been heavily criticized for reflecting hidden treatments rather than diversity effects (Huston 1997) or for reflecting statistical effects rather than ecological ones (Doak et al. 1998, Tilman et al. 1998). Subsequent experiments emphasized the presence of functional groups and the number of these groups rather than the presence and number of species as a determinant of stability (Hooper & Vitousek 1997, Tilman et al. 1997, Wardle et al. 1997b, Symstad et al. 1998, but see Martinez 1996). Microalgae would serve as simple test objects for this issue, since they exhibit short generation times and a high natural variability of genotypes. Explicit tests of the effect of aquatic unicellular diversity on ecosystem function are rare (but see Naeem & Li 1997). In soil food webs based on microbes, however, diversity was not related to ecosystem function (Wardle et al. 1997, Mikola & Setälä 1998) and experimental results were idiosyncratic, reflecting the importance of species characteristics rather than species diversity (Mikola & Setälä 1998). An experimental analysis should combine the assembly of communities with increasing diversity with a measure of ecosystem function (e.g. productivity) and ecosystem stability (e.g. the resilience to different, successive disturbances) (Karez & Hillebrand, unpublished data).

- **Use of microbenthic assemblages as bioindicators**. The response of benthic microalgae to nutrient enrichment was shown to be consistently species-specific and explicit on small spatial scales. Therefore an analysis of diatom communities could serve as a monitoring tool to allow conclusions on the trophic status of coastal waters. The use of diatoms as indicators of eutrophication (Lange-Bertalot 1978, 1979, McCormick & Stevenson 1998, Rott et al. 1998) or

abitotic conditions (e.g. pH-values, Pan et al. 1996) has been proposed for freshwaters (Lowe & Pan 1996). Principally, three different modes of indications can be used: the description of discriminant species, whose presence allows the conclusion on trophic status (Lange-Bertalot 1978, 1979) or the calculation of indices (Rott et al. 1998) or the assignment of indicator values to different taxa (Van Dam et al. 1994). Whereas my thesis gives important suggestions, which species could serve for either purpose, a thorough investigation of diatom assemblages at different sites and under different abiotic conditions in the laboratory would be required to establish a monitoring system.

7 Summary

Benthic microalgae play an important role in littoral communities, but so far only few studies have investigated the biotic interactions influencing the distribution and abundance of these organisms. During this study, the impact of facilitation, competition and herbivory on the structure of periphytic communities on hard substrates was analyzed with *in situ* and laboratory experiments.

The internal ratios of C:N:P of algal biomass have widely been applied to indicate nutrient limitation in phytoplankton, but not in marine benthic microalgae. The response of biomass stoichiometry of benthic microalgae to nutrient limitation was analyzed in laboratory experiments with natural species assemblages. C:N:P ratios of benthic microalgae were measured under an array of altered abiotic conditions (temperature, light, and dilution rate) and with different forms of nutrient limitation (N, P, Si and balanced). Microalgae with optimal growth rates showed a C:N:P ratio of 119:17:1, which is close to the Redfield ratio. C:N ratios increased with increasing nutrient limitation irrespective of the limiting nutrient, whereas C:P ratios increased only under P-limitation. The N:P ratio decreased under N-limitation and increased under P-limitation. Thus, biomass stoichiometry was shown to be a useful approach to indicate N- or P-limitation of benthic microalgae. A combination of low N:P ratios (N:P<13) and high C:N ratios (C:N>10) indicated N-limitation, whereas high N:P (N:P>22) combined with high C:P ratios (C:P>180) indicated P-limitation.

For the field experiments, a novel experimental setup was developed, allowing the supply of liquid media with controlled nutrient content to artificial substrates. These substrates consisted of porous stones or porous wood blocks, which were connected with tubing to flasks containing the medium. The liquid trickled through the substrates with a constant flow rate, which was adjusted by a mechanic regulation device. This experimental setup allowed to supply nutrients at low concentrations and at different ratios. Employing this experimental design, colonization and competition experiments were performed at the pier of the institute in the inner Kiel Fjord.

The artificial substrates were rapidly colonized during an exponential growth phase, which lasted for 4-6 weeks. The total biovolume remained rather constant in the following "mature" stage of the periphyton, but still the dominance of species changed during time. This was reflected by a decreasing diversity and evenness during the development of the algal mat, whereas species richness was saturated within few days. Dominant species at later successional stages were always erect-growing, benthic species, whereas pelagic or benthopelagic species were most abundant in the beginning of the colonization. The assemblage of early colonizers consisted mostly of species dominating the surrounding vegetation, indicating an important role of the "neighbourhood" on the colonization process. However, some species were distinctly early or late successional. In general, the colonization of substrates by benthic microalgae was analogous to succession in terrestrial vegetation. Moreover, these experiments revealed the suitability of the artificial substrates used, indicated by the high species numbers (>230 in total) and the abundance of growth forms like tube-dwelling diatoms, which previously were reported to be underrepresented on artificial substrates.

The nutrient enrichment experiments revealed two important aspects: the presence of nutrient limitation and the competitive shifts in dominance of algal species due to changed nutrient supply. The nutrient limitation was indicated by the C:N:P ratios of benthic microalgae and by the increased biovolume of benthic microalgae following the nutrient enrichment in the field experiments. The pattern of limitation was characterized by a phase of P-limitation in spring and a major influence of N-limitation from late spring to autumn. For diatoms, an Si-limitation was also indicated. The limitation was strongest in summer and autumn, although the nutrient pool in the water column was never totally depleted. This indicated a limited access of periphytic algae to nutrients from the overlying water column.

The nutrient-limited situation resulted in shifts in the competitive dominance due to the nutrient supply. On higher taxonomic level, a consistent dominance of diatoms was evident, which was overcome only in summer, mainly by filamentous red algae. This shift in dominance might be based on the temporal coincidence between maximum reproductive output of the red algae and low water column Si-concentrations. Within the diatoms, a distinct separation was observed between

species profiting from N-addition (*Melosira moniliformis*, *Tabularia fasciculata*, *Berkeleya rutilans*), those profiting from P-addition (*Proschkinia complanata*) and those most abundant in unenriched (*Licmophora paradoxa*) and low N-enriched (*Melosira nummuloides*, *Haslea crucigera*) treatments. Mainly species of erect growth form profited from the nutrient enrichment. Moreover, the nutrient supply resulted in a decrease of diversity of the microbenthic community, based on the increased dominance of single species (i.e. reduced evenness), whereas species numbers were constant within experiments. The presence of nutrient limitation and the consistency of changes in species composition following nutrient enrichment strongly indicated the structuring role of nutrient competition. The different impact of enrichment on evenness and species number was due to the limited number of species responding to the enrichment on the one hand and the presence of a propagule pool allowing recolonization of competitively excluded species on the other hand. These experiments showed that diversity indices are suitable response variables to measure the local environmental impact on benthic microalgae.

The combined influence of herbivory and nutrient supply was investigated in 3 additional field experiments, conducted in shallow embayments of the Western Baltic Sea (Maasholmer Breite, Geltinger Noor and Wackerballig). In these experiments, the natural herbivore population was excluded by a cage with 1 mm mesh size, and nutrients were added in one grazing experiment by slow release fertilizers, enhancing the ambient N concentration significantly. Strong and antagonistic effects of both factors were observed: Nutrient enrichment led to increased microalgal biovolume and favoured mainly large, erect species, especially *Melosira moniliformis*. Herbivores (mainly gastropods) removed substantial parts of the algal biovolume and reduced especially these erect species. Thus, herbivores were more effective under enriched conditions, since they had more access to loosely attached species. Highest microalgal biovolume was found in ungrazed and enriched treatments. The microalgae faced a trade-off between access to water column nutrients (erect growing, but loosely attached species) and mechanical resistance (adnately growing species). Species richness was lowered by the herbivores, whereas the diversity of benthic microalgae was unimodally related to enrichment in the grazed communities. This confirmed the negative effect of

eutrophication on microalgal diversity, but indicated also a shift of the optimum diversity to higher nutrient concentrations due to the grazing losses. The comparison of the results for different sites and different parts of the year showed a high temporal and spatial variability of herbivore control on benthic microalgae. In order to test for trophic cascades, fish-densities were increased, but this had no effect on periphyton biomass.

Several of my experimental results can be generalized beyond the benthic microphytes. The monopolizing effect of nutrient enrichment on plant communities is an universal pattern, depending on the loss of spatial heterogeneity of nutrient supply, the imbalance of supply ratios and the ability of opportunistic species to outgrow their competitors. Herbivores are able to counteract these effects of eutrophication on plants by reducing the dominance of single species. Plants generally are subjected to a trade-off between growth and defense against herbivores, although different groups of autotrophs differ in their defense mechanisms.

In conclusion, these experimental results revealed a pattern of interacting biotic forces structuring the periphyton in terms of microalgal biomass, biomass stoichiometry, species composition and diversity. The degree of regulation imposed by top-down (grazing) and bottom-up (nutrient competition) factors on microalgae depended on the variability of abiotic conditions and on the interaction with other compartments of the littoral community (phytoplankton, macrophytes). It was shown that nutrient supply is of central importance for the structure of microbenthic communities and thus distinctive changes of this community have to be assumed following anthropogenic nutrient load into coastal ecosystems.

8 Zusammenfassung

Benthische Mikroalgen stellen eine wichtige Komponente des marinen Litorals dar. Dennoch ist wenig über die biotischen Faktoren bekannt, die die Artenzusammensetzung und die räumliche Struktur dieser Gemeinschaft beeinflussen. In dieser Arbeit wurde der Effekt von Facilitation, Konkurrenz und Herbivorie auf die Struktur periphytischer Gemeinschaften auf Hartsubstraten *in situ* und im Labor untersucht.

Das interne Verhältnis von C:N:P wird für Phytoplankton als Indikator von Nährstofflimitation verwendet, aber die Gültigkeit dieses Konzeptes für benthische Mikroalgen ist zuvor nicht untersucht worden. In Laborexperimenten wurde die Veränderung der C:N:P-Stöchiometrie einer natürlichen benthischen Mikroalgengemeinschaft unter verschiedenen Nährstoffbedingungen (N-, P-, oder Si-limitiert) und bei verschiedenen Kulturbedingungen (Temperatur, Licht, Verdünnungsrate) untersucht. Das Periphyton zeigte bei hohen Wachstumsraten eine Annäherung an ein C:N:P Verhältnis von 119:17:1, welches nahe dem sogenannten Redfield-Verhältnis liegt. Die C:N-Verhältnisse stiegen unspezifisch bei steigender Nährstofflimitation an, während das C:P-Verhältnis spezifisch nur auf eine P-Limitation mit einem Anstieg reagierte. Das N:P Verhältnis sank bei N-Limitation und stieg bei P-Limitation. Damit läßt sich die Biomasse-Stöchiometrie der benthischen Algen als Indikator einer P- oder N-Limitation verwenden ähnlich der Verwendung des Redfield-Verhältnisses für das Phytoplankton: N:P Verhältnisse <13 und C:N Verhältnisse >10 indizieren eine N-Limitation, während hohe N:P Verhältnisse (N:P>22) in Kombination mit hohen C:P Verhältnissen (C:P>180) eine P-Limitation anzeigen.

Für die Feldexperimente wurde ein Verfahren entwickelt, bei dem künstliche Substrate kontrolliert mit nährstoffangereicherten Flüssigmedien versorgt wurden. Diese Substrate bestanden aus porösem Material (Kieselgur oder Lindenholz) und waren über Silikonschläuche mit den Vorratsbehältern verbunden. Das darin befindliche Medium tropfte mit konstantem Durchfluß aus den Substraten aus, die Durchflußrate wurde mechanisch mit einem Präzisionstropfenregler eingestellt.

Somit war eine kontrollierte Zufuhr von geringen Nährstoffkonzentrationen und eine Veränderung der Nährstoffverhältnisse möglich. Experimente zur Kolonialisierung und Konkurrenz wurden in dieser Art an der Pier des Instituts für Meereskunde an der Kieler Förde durchgeführt.

Die Kolonialisierung der künstlichen Substrate begann zunächst mit einer exponentiellen Wachstumsphase, die etwa 4 bis 6 Wochen andauerte. In der anschließenden "reiferen" Phase der Periphytongemeinschaft variierte das gesamte Biovolumen wenig, aber die Artenzusammensetzung veränderte sich weiterhin. Dies resultierte in einer abnehmenden Diversität und Evenness während der Kolonialisierung, während die Artenzahl schon nach wenigen Tagen ein Plateau erreichte. Das Periphyton zeigte eine deutliche sukzessionale Entwicklung, die der in terrestrischen Pflanzengemeinschaften glich. Die dominanten Arten spätsukzessionaler Stadien waren aufrecht wachsende, benthische Arten, während die ersten Kolonialisten oft eine pelagische oder benthopelagische Lebensweise aufwiesen. Die Zusammensetzung der ersten Besiedler war stark von den dominanten Arten der Umgebung geprägt, es gab jedoch auch Arten, die stetig früh- oder spätsukzessional auftraten. Die Kolonialisierungsexperimente bestätigten außerdem die Eignung der künstlichen Substrate, die von einer Vielzahl von Arten besiedelt wurden (insgesamt >230), darunter auch röhrenbildende, gelatinöse Diatomeen, die in anderen Studien auf künstlichen Substraten unterrepräsentiert waren.

Die Nährstoffanreicherung in den Konkurrenzexperimenten offenbarte sowohl eine vorhandene Nährstofflimitation der Mikroalgen als auch eine Dominanzverschiebung in der Artenzusammensetzung als Folge der veränderten Nährstoffzufuhr. Die Nährstofflimitation begann mit einer P-Limitation im Frühjahr, die in eine N-Limitation für den Rest der Vegetationsperiode überging. Für Diatomeen ließ sich auch eine mögliche Si-Limitation zeigen. Diese Muster wurde sowohl durch den Anstieg der Algenbiomasse nach der Nährstoffanreicherung angezeigt als auch durch die stöchiometrische Zusammensetzung der Algenbiomasse. Die Nährstofflimitation war besonders deutlich im Sommer und im Herbst, obwohl die Nährstoffe der umgebenden Wassersäule niemals völlig

aufgezehrt waren. Somit scheint das Periphyton von den Nährstoffen des umgebenden Wasserkörpers weitgehend isoliert zu sein.

Die Zufuhr von Nährstoffen führte zu einer Veränderung in der kompetitiven Dominanz der nährstofflimitierten Algen. Auf höherem taxonomischen Niveau wurde die Artenzusammensetzung weitgehend durch Diatomeen bestimmt, deren Dominanz nur im Sommer durch filamentöse Algen (v.a. Rhodophyta) unterbrochen wurde. Die erhöhte Bedeutung von Rotalgen im Sommer beruhte vermutlich auf dem zeitlichen Zusammentreffen zwischen der Reproduktion der Rotalgen und geringen Si-Konzentrationen im Umgebungswasser. Innerhalb der Diatomeen konnten Arten unterschieden werden, die von der Zugabe des Stickstoffs profitierten (*Melosira moniliformis*, *Tabularia fasciculata*, *Berkeleya rutilans*) oder von der Zugabe des Phosphors (*Proschkinia complanata*). Andere Arten waren in den unangereicherten (*Licmophora paradoxa*) oder in gering N-angereicherten (*Melosira nummuloides*, *Haslea crucigera*) besonders häufig. Vor allem aufrecht wachsende Arten profitierten von der Nährstoffanreicherung. Außerdem führte die Nährstoffanreicherung zu einer Verringerung der Diversität der periphytischen Algengemeinschaft, die vor allem auf der erhöhten Dominanz einzelner Arten (d.h. verringerte Evenness) beruhte, denn die Artenzahl blieb innerhalb der Experimente relativ konstant. Die vorhandene Nährstofflimitation und die konstanten Veränderungen der Artengemeinschaft durch Anreicherung legen einen bedeutenden Einfluß der Konkurrenz auf die Struktur des Periphytons nahe. Der unterschiedliche Einfluß der Eutrophierung auf Artenzahl und Diversität läßt sich durch die geringe Anzahl opportunistischer Arten erklären, die auf die Anreicherung reagierten und damit die Evenness reduzierten, während gleichzeitig die Möglichkeit zur Rekolonialisierung der Substrate bestand, so daß einer kompetitive Exklusion entgegengewirkt wurde. Diese Experimente zeigten außerdem, daß Diversitätsindices eine geeignete Variable sind, um lokale Umwelteinflüsse auf benthische Mikroalgen zu verfolgen.

Der gleichzeitige Einfluß von Herbivorie und Nährstoffanreicherung wurde in weiteren Experimenten überprüft, die in flachen Buchten der westlichen Ostsee (Maasholm, Geltinger Noor, Wackerballig) durchgeführt wurden. In diesen Experimenten wurde die natürliche Herbivorenpopulation durch Käfige mit 1mm

Maschenweite ausgeschlossen. Zusätzlich wurden in einem Experiment Nährstoffe mit Langzeitdüngern zugeführt, die eine signifikante Erhöhung der N-Konzentration hervorriefen. Beide Faktoren hatten starke und entgegengesetzte Wirkungen: Das Biovolumen des Periphytons stieg mit der Nährstoffanreicherung an, wobei besonders aufrecht wachsende Arten wie *Melosira moniliformis* profitierten. Die Grazer (vor allem Gastropoden) reduzierten die Algenbiomasse sehr stark, und zwar bevorzugt die aufrecht wachsenden Arten. Daher waren die Herbivoren besonders effektiv unter nährstoffangereicherten Bedingungen, da ihnen mehr der aufrechten, schwach festgehefteten Algen zur Verfügung standen. Die größte Algenbiomasse wurde dementsprechend in grazer-freien, nährstoffreichen Ansätzen gefunden. Die benthischen Mikroalgen unterlagen somit einem *trade-off* zwischen der Aufnahme von Nährstoffen aus der Wassersäule (aufrechtes, aber wenig fesgeheftetes Wachstum) und der mechanischen Widerstandsfähigkeit gegenüber dem Fraß (substratnahes, stark festgeheftetes Wachstum). Die Artenzahl der Mikroalgen wurde durch die Herbivoren reduziert, gleichzeitig war die Diversität des Periphytons in den Grazeransätzen unimodal mit der Nährstoffanreicherung verbunden. Dies bestätigt zum einen den negativen Effekt der Eutrophierung auf die Diversität der Mikroalgen, zum anderen benötigen die Algen jedoch eine erhöhte Ressourcenkonzentration, um die Grazingverluste auszugleichen und die maximale Diversität zu erreichen. Ein Vergleich der Ergebnisse für die drei verschiedenen Standorte ergab eine hohe zeitliche und räumliche Variabilität der *top-down* Kontrolle des Mikrophytobenthos. In einem Experiment wurde die Fischdichte experimentell erhöht, um die Möglichkeit von trophische Kaskaden zu testen, es konnte jedoch kein signifikanter Effekt festgestellt werden.

Einige der experimentellen Ergebnisse haben eine über das Periphyton hinausgehende Bedeutung. Der dominanzfördernde Effekt von Eutrophierung scheint für autotrophe Gemeinschaften universell zu sein, hervorgerufen durch die verringerte räumliche Variabilität der Nährstoffzufuhr, die einseitge Zufuhr einzelner Nährstoffe und die Fähigkeit einiger opportunistischer Arten, ihren Konkurrenten zu entwachsen. Herbivore sind in der Lage, diesen Effekten entgegenzuwirken, in dem sie die Dominanz einzelner Arten reduzieren. Die Pflanzen sind generell einem *trade-off* zwischen Wachstum und Verteidigung ausgesetzt, obwohl es

weitegehende Unterschiede in den Verteidigungsmechanismen zwischen verschiedenen Pflanzengruppen gibt.

Zusammengefaßt ergeben diese Experimente ein Muster biotischer Interkationen, die einen steuernden Einfluß auf die Biomasse, die Biomasse-Stöchiometrie, die Artenzusammensetzung und die Diversität des Periphytons haben. Die Stärke des Einflusses der verschiedenen Faktoren ist variabel und hängt von der der Variabilität abiotischer Bedingungen ebenso ab wie von der Interaktion mit anderen Gemeinschaften des Littorals (Phytoplankton, Makrophyten). Der überragende Einfluß der Nährstoffsituation auf das Periphyton wurde in dieser Studie deutlich, so daß aufgrund der anthropogenen Nährstoffeinträge in die Küstengewässer eine deutliche Veränderung dieser Gemeinschaft erwartet werden kann.

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10 Acknowledgements

Diese Arbeit wäre nicht möglich gewesen ohne die konstruktive und unschätzbare Hilfe der folgenden Personen:

Prof. Dr. Ulrich Sommer danke ich für die thematische Einführung in die Ökologie und die Betreuung dieser Arbeit, für die er mir jeden Freiraum in der Ausgestaltung ließ. Seine uneingeschränkte Sichtweise ökologischer Zusammenhänge half mir, eigene Fragestellungen anzugehen und thematische Verbindungen innerhalb und außerhalb der marinen Ökologie zu suchen. Für diese hervorragende Betreuung bin ich sehr dankbar.

Dr. Ulrike-G. Berninger kam zur rechten Zeit in die Abteilung Meerebotanik, um meine Schriftwerke rot anlaufen zu lassen. Ihre Mithilfe verhinderte viele grobe sprachliche Schnitzer und diplomatische Ungeschicke. Vor alle jedoch danke ich für ihre Ermunterung, ihren Enthusiasmus und ihre Anteilnahme, die mich oft über Wasser gehalten haben.

Anja Göbel, Maria Kahlert und Dr. Rolf Karez haben dieses Werk korrekturgelesen und viele Verbesserungsvorschläge gemacht. Anja hat außerdem inhaltlich das Werden (und leider auch Vergehen) mehrerer potentieller Nobelpreise mit unterstützenden Kommentaren begleitet. Rolf war eine tragende Säule des Institutsalltags, der diverse Gespräche mit dem richtigen Wort zur richtigen Zeit würzte. Latürnich. Maria regte nicht nur die Versuche zur C:N:P- Stöchiometrie an, sondern eröffnete auch die Möglichkeit einer Zusammenarbeit.

Heike Lotze und Boris Worm ermöglichten mir die Auswertung von Mikrobenthosgemeinschaft aus ihren Grazingexperimenten, die sie in Maasholm und in der Geltinger Bucht durchgeführt haben. Außerdem gaben sie viele gedankliche Impulse, stellten von ihnen erhobene Begleitdaten zur Verfügung und korrigierten vorherige Fassungen des Kapitels 5 dieser Arbeit.

Den Mitarbeitern der Abteilung Meeresbotanik sei für die konstruktive und hilfreiche Atmosphäre der letzten 3 Jahre gedankt. Dieser Dank gilt besonders Thomas Hansen, ohne dessen Mithilfe kein Datenpunkt aus Autoanalyzer und C:N-Analyzer

entstanden wäre, Cordula Stielau für die alltäglichen Hilfestellungen, Wolfgang Hukriede für die Mithilfe bei Poster- und Vortragserstellung, und Dr. Akira F. Peters für den Zuspruch in Leiden. Petra Deegen hat als Diplomandin und Hiwine in diesem Projekt gearbeitet und wichtige Beiträge zu Daten und Betriebsklima geleistet. Dr. Herwig Stibor danke ich für einige interessante Aspekte meiner Diskussion und die dazu passenden Literaturzitate.

Außerhalb der Abteilung wurde diese Arbeit beeinflußt durch Diskussionen mit der AG Marine Ökologie von Dr. M. Wahl an der CAU Kiel, mit Maria Kahlert vom Erkenlabor (Universität Uppsala) und (kurz nur, aber sehr hilfreich) Dr. Alan Steinman (SFWD Florida). Frau Oelrichs danke ich für die Fotoarbeiten.

Das Projekt wurde finanziert von der Deutschen Forschungsgemeinschaft (DFG-SO-145/15-1&2).

Meine Eltern und meine Geschwister haben mich in all den Jahren meines Studiums und meiner Promotion selbstlos unterstützt, wofür ihnen nicht genug gedankt werden kann. Darüberhinaus haben sie mir handwerklich beratend zur Seite gestanden.

Desweiteren danke ich Elisabeth & Eckart Liebl, Birgit Scheuerbrandt, Olli Schliep, Andrea Janssen, Elsbeth & Claus Feiling, Birgit Kürzel-Seidel (und den anderen Mitarbeitern der "alten" AG BiGePro des ICBM) und Frank Watermann.

Mein ganz besonderer Dank gilt Monika Feiling für das Durchsehen der Literaturzitate, das Miterleben aller Hochs und Tiefs, und ihre Zuneigung.

Monika und meinen Eltern gewidmet

Appendices

Appendix 1: Abbreviations and definitions

allocation	division of resources to different processes
ANOVA	analysis of variance
Bartlett's χ^2	test for homogeneity of variances
competition	negative interaction between populations exploiting a common resource, resulting in a decreased growth rate of at least one competitor
df	degrees of freedom
DIN	dissolved inorganic nitrogen
diversity	combination of the taxonomic richness and the evenness of a multispecies assemblage
DOC	dissolved organic carbon
edaphic algae	algae inhabiting the substrate in contrast to epiphytic algae
evenness	measure of the distribution of individuals on species
homogeneity of variances	prerequisite of ANOVA, homoscedasticity
HSD	honest significant difference, post-hoc test
Kolmogorov-Smirnov-test	test for normal distribution
limitation	restriction of the growth rate or the biomass yield of a population (individual, assemblage)
Mann-Whitney U-test	non-parametric test between independent variables
microphytobenthos	see periphyton
Model-I-regression	regression analysis with a fixed independent variable (X-variable is without error)
Model-II-regression	regression analysis with a measured independent variable (X-values are subject to variation or measurement error)
MS	mean sqaure
n	total number of replicates
p	significance level

periphyton	Periphyton and microphytobenthos are used as synonyms in this text. Generally, periphyton is more often used in freshwater research to describe a mixture of multicellular and unicellular algae growing on hard or soft substrates or plants, whereas microphytobenthos is often used to describe diatom assemblages inhabiting sediments in coastal areas.
r	correlation coefficient (product-moment-correlation)
r^2	coefficient of determination
SE	standard error
Spearman-rank-correlation	non-parametric correlation using ranks instead of parametric values
structure	Since structure is a poorly defined term in ecology, it will be used here explicitly to denote the periphytic species assemblage and the architecture based on this species composition.
substrate	Substrate is defined here general as the material benthic organisms are attached to, without referring to the difference to growth media supplying nutrients.
trade-off	mutual exchange between different ecological strategies, e.g. allocation of resources to growth or reproduction
treatment	combination of experimental manipulations

Appendix 2: Species list

Table A2: Alphabetical list of species with common synonyms and taxonomic position. Additional information: Maximum relative biovolume reached in every season (r: <1%; v: 1<10%; c: 10<25 %; p: 25<40%; d 40+% of total biovolume), frequency of the taxon (number of occurences in benthic experiments (n=30) and pelagic samples (n=24)), and salinity preference (derived from Snoeijs et al. 1993-1998, with additional information from Pankow 1990, Kuylenstierna 1989-90).

Achnanthes brevipes CA Agardh
  Achnanthidium brevipes (CA Agardh) Cleve
  Achnanthes seriata CA Agardh
  Fragilaria salina Kützing
  Cymbosira agardhii Kützing
  Achnanthes salina (Kützing) Kützing
      Bacillariophyta - Bacillariophyceae -
      Achnanthales - Achnanthaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	19
pelagic	r	r	-	v	5

Achnanthes clevei Grunow
  Actioneis clevei Cleve
  Karayevia clevei (Grunow) Round & Bukhtiyarova
      Bacillariophyta - ... - Achnanthaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	5
pelagic	-	-	-	-	-

Achnanthes fimbriata (Grunow) R Ross
  Schizostaurum fimbriatum Grunow
  Achnanthes manifera Brun
  Achnanthes stroemii Hustedt
      Bacillariophyta - ... - Achnanthaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	r	r	2
pelagic	-	-	-	-	-

Achnanthes longipes CA Agardh
  Achnanthes carmichaeli Greville
  Conferva amilaris OF Müller
      Bacillariophyta - ... - Achnanthaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	v	c	c	r	19
pelagic	-	r	r	-	2

Achnanthes marginestriata Simonsen
      Bacillariophyta - Bacillariophyceae -
      Achnanthales - Achnanthaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Achnanthes spec. A
      Bacillariophyta - Bacillariophyceae -
      Achnanthales - Achnanthaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Achnanthidium cf. *delicatulum* Kützing
  Achnanthes delicatula (Kützing) Grunow
  Achnanthes hauckiana v *rostrata* Schulz
  Achnanthes hauckiana v *elliptica* Schulz
  Microneis delicatula Cleve
  Achnanthes delicatula v *robusta* Hustedt
  Planothidium delicatulum (Kützing) Round & Buk.
      Bacillariophyta - ... - Achnanthaceae

salinity preference: B(F)

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	-	-	-	-	-

Achnanthidium hauckianum (Grunow) Czarnecki
  Achnanthes hauckiana Grunow
  Achnanthes fonticola Hustedt
  Planothidium hauckianum (Grun.) Round & Buk.
  Achnanthes delicatula ssp *hauckiana* (Grunow)
        Lange-Bertalot & Ruppel
      Bacillariophyta - .. Achnanthaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	-	-	-	-	-

Achnanthidium lanceolatum de Breb. ex Kützing
  Achnanthes lanceolata (de Brebisson) Grunow
  Planothidium lanceolatum (De Breb.) Round & B.
  Achnanthes haynaldii v *oblongo-elliptica* Schaars.
  Stauroneis truncata Schumann
  Achnanthes pseudoantiqua, pagesi Peragallo
      Bacillariophyta - ... - Achnanthaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	5
pelagic	-	-	-	-	-

Achnanthidium rostratum Oestrup
  Achnanthes lanceolata v rostrata (Oestrup) Hust.
  Achnanthes lanceolata f crassa Cleve-Euler
  Achnanthes lanceolata ssp rostrata (Oe.) L.-Bert.
  Planothidium rostratum (Oestr.) Round & Bukht.
  Achnanthes rostrata Oestrup
     Bacillariophyta - ... - Achnanthaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	
pelagic	-	-	-	-	

siehe A. *lanceolatum*

Actinastrum cf. *hantzschii* Lagerheim
     Chlorophyta - Chlorophyceae -
     Chlorococcales - Coelastraceae

salinity preference: ?

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic	r	-	-	-	1

Actinoptychus senarius (Ehrenberg) Ehrenberg
  Actinocyclus senarius Ehrenberg
  Actinocyclus undulatus JW Bailey
  Actinoptychus undulatus (JW Bailey) Ralfs
     Bacillariophyta - Coscinodiscophyceae -
     Coscinodiscales - Heliopeltaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	8
pelagic	-	-	-	-	

Aglaothamnion byssoides (Arn.) L'Hardy-Hal.&Rue.
  Callithamnion byssoides Arnott
  Callithamnion arnotii Trevisan
  Callithamnion furcellariae JG Agardh
  Aglaothamnion furcellariae (JG Agardh)Feld.-Mar.
     Rhodophyta - Rhodophyceae -
     Ceramiales - Ceramiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	v	c	-	9
pelagic	-	-	-	-	

Amphidinium crassum Lohmann
     Dinophyta - Dinophyceae -
     Gymnodiniales - Gymnodiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	v	-	-	4

Amphidinium spec. A
     Dinophyta - Dinophyceae -
     Gymnodiniales - Gymnodiniaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	r	-	-	v	2

Amphora coffeaeformis (CA Agardh) Kützing
  Frustulia coffeaeformis CA Agardh
  Amphora salina W Smith
     Bacillariophyta - Bacillariophyceae -
     Thalassiophysales - Catenulaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	22
pelagic	-	-	-	-	-

Amphora copulata (Kützing) Schoeman & Archibald
  Amphora libyca Ehrenberg
  Amphora affinis Kützing
  Amphora ovalis v libyca (Ehrenberg) Cleve
  Amphora ovalis v affinis (Kützing) van Heurck
  Frustulia copulata Kützing
  Amphora ovalis v pediculus (Kützing) Cleve
     Bacillariophyta - ... - Catenulaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1
pelagic	-	-	-	-	

Amphora cf. *exigua* Gregory
     Bacillariophyta - Bacillariophyceae -
     Thalassiophysales - Catenulaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Amphora holsatica Hustedt
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	9

Amphora cf. *laevis v laevissima* (Gregory) Cleve
Amphora laevissima Gregory
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	2

Amphora ostrearia de Brebisson ex Kützing
Amphora membranacea W Smith
Amphora littoralis Donkin
Bacillariophyta - ... - Catenulaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	17
pelagic	-	-	r	-	-

Amphora cf. *ovalis* (Kützing) Kützing
Navicula amphora Ehrenberg
Frustulia ovalis Kützing
Amphora gracilis Ehrenberg ex Kützing
Bacillariophyta - ...- Catenulaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	8
pelagic	-	-	-	-	-

Amphora pediculus (Kützing) Grunow
Cymbella pediculus Kützing
Amphora minutissima W Smith
Amphora borealis, globosa Schumann
Amphora ovalis v *pediculus* (Kützing) van Heurck
Bacillariophyta - ... - Catenulaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	5
pelagic	r	-	r	-	3

Amphora pseudohyalina Simonsen
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	2

Amphora cf. *veneta* Kützing
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	2
pelagic	-	-	r	-	1

Amphora spec A
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Amphora spec B
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Amphora spec C
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	6

Amphora spec D
Bacillariophyta - Bacillariophyceae -
Thalassiophysales - Catenulaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	6

Anabaena cf. *spiroides* Klebahn
Cyanophyta - Cyanophyceae -
Nostocales - Nostocaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
pelagic	v	-	-	-	2

Anorthoneis excentrica (Donkin) Grunow
   Cocconeis excentrica Donkin
      Bacillariophyta - Bacillariophyceae -
      Achnanthales - Cocconeidaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1

Asterionella formosa Hassall
   Asterionella inflata Heiberg
      Bacillariophyta - Fragilariophyceae -
      Fragilariales -Fragilariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	7
pelagic	v	-	v	r	6

Aulacoseira islandica (O Müller) Simonsen
   Melosira islandica O Müller
   Melosira transsilvanica, temperi Pantocsek
   Melosira granulata v hungarica Pantocsek
   Melosira polymorpha ssp granulata v isl. Bethge
   Melosira venerensis A Cleve
      Bacillariophyta - Coscinodiscophyceae -
      Aulacoseirales - Aulacoseiraceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	19
pelagic	r	r	r	c	10

Bacillaria paxillifer (OF Müller) Hendey
   Vibrio paxillifer OF Müller
   Bacillaria paradoxa Gmelin in Linnaeus
   Nitzschia paxillifer (OF Müller) Heiberg
   Nitzschia paradoxa (Gmelin) Grunow
      Bacillariophyta - Bacillariophyceae -
      Bacillariales - Bacillariaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	21
pelagic	v	-	r	-	4

Berkeleya rutilans (Trentepohl ex Roth) Grunow
   Amphipleura rutilans (Trentepohl ex Roth) Cleve
   Conferva rutilans Trentepohl ex Roth
   Schizonema dillwynii CA Agardh
   Schizonema obtusum Grunow
   Berkeleya dillwynii (CA Agardh) Grunow
   Berkeleya obtusa (Greville) Grunow
   Schizonema rutilans (Trentepohl ex Roth) CA Ag.
   Berkeleya harveyana Grunow
   Berkeleya antarctica (Harvey) Grunow
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Berkeleyaceae

salinity preference: B(M)

sample	spr	sum	aut	win	freq
benthic	p	v	v	v	29
pelagic	v	r	v	v	14

Berkeleya scopulorum (De Brebisson) EJ Cox
   Navicula scopulorum de Brebisson ex Kützing
   Pinnularia johnsonii W Smith
   Navicula johnsonii (W Smith) O'Meara
   Navicula mesotyla Kützing
   Climaconeis frauenfeldii Grunow
   Stictodesmis australis Greville
   Climacosphenia linearis Janisch & Rabenhorst
   Okedenia scopulorum Mereschkowsky
   Navicula romanowii Pantocsek
      Bacillariophyta - ...- Berkeleyaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	3
pelagic	-	r	-	-	1

Brebissonia lanceolata (CA Ag.) Mahoney & Reimer
   Cocconema boeckii Ehrenberg
   Doryphora boeckii (Ehrenberg) W Smith
   Brebissonia boeckii (Ehrenberg) Grunow
   Gomphonema lanceolatum CA Agardh

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Navicula boeckii (Ehrenberg) Heiberg
Vanheurckia boeckii (Ehrenberg) Schütt
    Bacillariophyta - Bacillariophyceae -
    Cymbellales - Cymbellaceae

Caloneis silicula (Ehrenberg) Cleve
Navicula ventricosa Ehrenberg
Navicula leptogongyla Ehrenberg
Navicula silicula Ehrenberg
Caloneis ventricosa (Ehrenberg) Meister
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Pinnulariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic	-	-	-	-	-

Catenula cf. *adhaerens* (Mer.) Mereschkowsky
Navicula adhaerens Mereschkowsky
Amphora sabyii Salah
    Bacillariophyta - Bacillariophyceae -
    Thalassiophysales - Catenulaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	3
pelagic	-	-	-	-	-

Ceramium strictum sensu Harvey, non *C. strictum*
    Roth, nec (Kützing) Harvey
    Rhodophyta - Rhodophyceae -
    Ceramiales - Ceramiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	d	d	-	13

Cerataulina pelagica (Cleve) Hendey
Zygoceros pelagicum Cleve
Cerataulus bergonii H Peragallo
Cerataulina bergonii (H Per.) H Per.ex Schütt
    Bacillariophyta - Coscinodiscophyceae -
    Hemiaulales - Hemiaulaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	v	-	6
pelagic	c	d	d	c	13

Ceratium fusus (Ehrenberg) Dujardin
Peridinium fusus Ehrenberg
    Dinophyta- Dinophyceae -
    Gonyaulacales - Ceratiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	-	v	-	-	1

Ceratium tripos (OF Müller) Nitzsch
Cercaria tripos OF Müller
    Dinophyta- Dinophyceae -
    Gonyaulacales - Ceratiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	v	-	-	5
pelagic	-	v	c	v	8

Chaetoceros cf. *cinctus* Gran
    Bacillariophyta - Coscinodiscophyceae -
    Chaetocerotales - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	r	2
pelagic	-	v	v	-	4

Chaetoceros cf. *compressus* Lauder
Chaetoceros contortus Schütt
    Bacillariophyta - Coscinodiscophyceae -
    Chaetocerotales - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
pelagic	-	-	-	c	1

Chaetoceros cf. *danicus* Cleve
Chaetoceros wighamii Van Heurck
Chaetoceros boreale Schütt
    Bacillariophyta - ...Chaetocerotaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	-	-	r	4
pelagic	r	r	r	r	7

Chaetoceros debilis Cleve
  Chaetoceros vermiculatum Schütt
    Bacillariophyta - Coscinodiscophyceae -
    Chaetocerotales - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	-	-	c	3

Chaetoceros cf. *decipiens* Cleve
  Chaetoceros grunowii Schütt
  Chaetoceros decipiens v *concreta* Grunow
  Chaetoceros concretus (Grunow) Engler
    Bacillariophyta - ... - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	12
pelagic	p	c	p	c	16

Chaetoceros cf. *diadema* (Ehrenberg) Gran
  Syndendrium diadema Ehrenberg
  Chaetoceros curvisetus, groenlandium Cleve
  Chaetoceros paradoxum H & M Peragallo
  Chaetoceros subsecundum (Grun.) Hustedt
  Chaetoceros distans v *subsecundum* Grunow
    Bacillariophyta - ... - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	r	-	v	5

Chaetoceros cf. *didymus* Ehrenberg
  Goniothecium gastridium Ehrenberg
  Chaetoceros gastridium Ehrenberg
  Chaetoceros protuberans Schütt
  Chaetoceros mamillanum Cleve
  Chaetoceros furcellatus v *anglica* Grunow
    Bacillariophyta - ... - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	6
pelagic	v	-	v	c	9

Chaetoceros cf. *mitra* (JW Bailey) Cleve
  Dicladia mitra JW Bailey
  Dicladia groenlandica Cleve
    Bacillariophyta - ... - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	-	v	v	-	2

Chaetoceros cf. *simplex* Ostenfeld
  Chaetoceros subsalsus sensu Hust., non Lemm.
    Bacillariophyta - Coscinodiscophyceae -
    Chaetocerotales - Chaetocerotaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	10
pelagic	r	-	-	v	5

Chaetoceros subtilis Cleve
    Bacillariophyta - Coscinodiscophyceae -
    Chaetocerotales - Chaetocerotaceae

salinity preference: B

sample	spr	sum	aut	win	freq
pelagic	-	v	-	v	2

Chaetoceros spec. A
    Bacillariophyta - Coscinodiscophyceae -
    Chaetocerotales - Chaetocerotaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	c	-	-	-	1

Chlorella spec.
    Chlorophyta - Chlorophyceae -
    Chlorococcales - Chlorellaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	2

Chroococcus spec.
    Cyanophyta - Cyanophyceae -
    Chroococcales - Chrococcaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1
pelagic	-	-	r	-	1

Chrysochromulina spec.
    Chromophyta - Prymnesiophyceae -
    Prymnesiales - Prymnesiaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	v	r	r	-	3

Cladophora spec.
    Chlorophyta - Chlorophyceae -
    Cladophorales - Cladophoraceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2

Closterium spec.
    Chlorophyta - Conjugatophyceae -
    Desmidiales - Desmidiaceae

salinity preference: -

sample	spr	sum	aut	win	freq
pelagic	r	-	-	-	2

Cocconeis costata Gregory
    Rhaphoneis scutelloides Grunow
    Pleuroneis costata (Gregory) Cleve
    Surirella quarnerensis Grunow
    Bacillariophyta - Bacillariophyceae -
    Achnanthales - Cocconeidaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	19

Cocconeis pediculus Ehrenberg
    Cocconeis depressa Kützing
    Cocconeis salina (Kützing) Rabenhorst
    Cocconeis tenera, sigmoidea Schumann
    Bacillariophyta - ... - Cocconeidaceae

salinity preference: BF

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	10
pelagic	-	-	v	-	1

Cocconeis placentula Ehrenberg v *placentula*
    Cocconeis reicheltii, producta A Schmidt
    Cocconeis punctata Schumann
    Cocconeis grovei Oest., non C. *grovei* A Schmidt
    Cocconeis placentula v *genuina* A Mayer
    Bacillariophyta - ...- Cocconeidaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	20
pelagic	v	-	r	-	2

Cocconeis placentula v *euglypta* (Ehr.) Grunow
    Cocconeis euglypta Ehrenberg
    Cocconeis trilineata Heribaud & Peragallo
    Cocconeis placentula v *trilineata* (Her.& Per.) Cl.
    Bacillariophyta - ...- Cocconeidaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	8
pelagic	r	-	-	-	1

Cocconeis scutellum Ehrenberg v *scutellum*
    Rhaphoneis scutellum Ehrenberg
    Cocconeis adriatica , mediterranea Kützing
    Cocconeis morrisii W Smith
    Rhaphoneis marginata Grunow
    Cocconeis pethoei, haradaae Pantocsek
    Cocconeis baldjikiana, adjuncta A Schmidt
    Bacillariophyta - ...- Cocconeidaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	12
pelagic					

Cocconeis scutellum v *parva* (Grun.in V.H.) Cleve
    Cocconeis scutellum f *parva* Grun. in van Heurck
    Cocconeis scutellum v *minuta* Grunow
    Cocconeis aggregata, consociata Kützing
    Cocconeis transversalis Gregory
    Cocconeis scutellum v *minor* A Schmidt
    Bacillariophyta - ...- Cocconeidaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	3
pelagic					

Corymbellus aureus Green
    Chromophyta - Prymnesiophyceae -
    Prymnesiales - Prymnesiaceae

salinity preference: ?

sample	spr	sum	aut	win	freq
pelagic	v	-	-	-	1

Coscinodiscus granii Gough
    Bacillariophyta - Coscinodiscophyceae -
    Coscinodiscales - Coscinodiscaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	-	v	-	4
pelagic	-	-	v	-	1

Coscinodiscus jonesianus v *commutatus* (Gr.) Hust.
   Coscinodiscus commutatus Grunow
   Coscinodiscus concinnus v *jonesiana* Rattray
   Coscinodiscus radiatus v *jonesiana* Van Heurck
   Coscinodsicus biconicus Van Breemen
     Bacillariophyta - ...- Coscinodiscaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1
pelagic	-	-	-	-	-

Cosmioneis pusilla (W Smith) Mann & Stickle
   Navicula pusilla W Smith
   Navicula tumida W Smith sensu Grunow
   Navicula tumida v *subsalsa* Grunow
   Navicula anglica v *subsalsa* (Grunow) Cleve
   Navicula gastroides Gregory
   Navicula tumida v *genuina, jamalinensis* Grunow
     Bacillariophyta - Bacillariophyceae -
     Naviculales - Cosmioneidaceae

salinity preference: B(F)

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	3
pelagic	-	-	-	-	-

Craticula cuspidata (Kützing) Mann
   Frustulia cuspidata Kützing
   Navicula cuspidata (Kützing) Kützing v *cuspidata*
   Navicula accurata Hustedt
   Bacillaria fulva Nitzsch
   Cymbella latefasciata CA Agardh
   Navicula reinickeana Rabenhorst
   Vanheurckia cuspidata (Kützing) De Brebisson
     Bacillariophyta - Bacillariophyceae -
     Naviculales - Stauroneidaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	4
pelagic	-	-	-	-	-

Cyclostephanos dubius (Fricke) Round
   Cyclotella dubia Fricke in A Schmidt
   Stephanodiscus dubius (Fricke) Hustedt
   Stephanodiscus pulcherrimus A Cleve
     Bacillariophyta - Coscinodiscophyceae -
     Thalassiosirales - Stephanodiscaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	5
pelagic	r	-	-	r	3

Cyclotella cf. *meneghiniana* Kützing
   Cyclotella rectangula De Brebisson
   Surirella melosiroides Meneghini
   Cyclotella melosiroides Meneghini
   Cyclotella salina Marsson
   Cyclotella kuetzingiana Thwaites
   Cyclotella laevissima Van Goor
     Bacillariophyta - ...- Stephanodiscaceae

salinity preference: BF

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	15
pelagic	v	r	r	-	10

Cyclotella cf. *radiosa* (Grunow) Lemmermann
   Disclopea comta Ehr. 1845, 1854, non Ehr. 1844
   Cyclotella comta v *radiosa* Grunow
   Cyclotella comta Kützing 1849 pro parte
   Cyclotella comta v *melosiroides* Kirchner
   Cyclotella melosiroides (Krichner) Lemmermann
   Cyclotella comta (Ehrenberg) Kützing v *comta*
     Bacillariophyta - ... - Stephanodiscaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	3

Cyclotella cf. *striata* (Kützing) Grunow
  Coscinodiscus striatus Kützing
  Coscinodiscus dallasiana W Smith
  Cyclotella dallasiana W Smith
  Cyclotella sinensis (Ehrenberg) Ralfs
  Discoplea sinensis Ehrenberg
      Bacillariophyta - ... - Stephanodiscaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	12
pelagic	-	-	-	-	-

Cylindrotheca closterium (Ehr.) Reiman & Lewin
  Ceratoneis closterium Ehrenberg
  Nitzschia closterium (Ehrenberg) W Smith
  Nitzschiella tenuirostris Mereschkowsky
      Bacillariophyta - Bacillariophyceae -
      Bacillariales - Bacillariaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	v	r	r	r	26
pelagic	v	r	r	r	15

Cymatopleura elliptica (de Brebisson) W Smith
  Surirella elliptica de Brebisson ex Kützing
  Denticula undulata (Ehrenberg) Kützing
  Surirella ovum Naegeli ex Kützing
  Cymatopleura angulata Greville
  Cymatopleura turicensis Meister
      Bacillariophyta - Bacillariophyceae -
      Surirellales - Surirellaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	2
pelagic	-	-	-	-	-

Cymatopleura solea (de Breb. & Goday) W Smith
  Cymatopleura librile (Ehrenberg) Pantocsek
  Navicula librile Ehrenberg
  Frustulia quinquepunctata Kützing
  Cymbella solea de Brebisson & Godey
  Surirella solea (De Brebisson & Godey) de Breb.
  Cymatopleura apiculata W Smith
  Surirella albaregiensis Pantocsek
      Bacillariophyta - ...- Surirellaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic	-	-	-	-	-

Cymbella aspera (Ehrenberg) H Peragallo
  Cocconema asperum Ehrenberg
  Cymbella lanceolata v aspera (Ehrenberg) Brun
  Cymbella gastroides (Kützing) Kützing
      Bacillariophyta - Bacillariophyceae -
      Cymbellales - Cymbellaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1
pelagic	-	-	-	-	-

Cymbella cistula (Ehrenberg) Kirchner
  Bacillaria cistula Ehrenberg
  Cocconema cistula (Ehrenberg) Ehrenberg
      Bacillariophyta - ... - Cymbellaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	8
pelagic	-	-	-	r	1

Cymbella helvetica Kützing
  Cymbella gallica Heriband
  Cymbella compacta Östrup
  Cymbella helvetica v compacta (Östrup) Hustedt
      Bacillariophyta - ... - Cymbellaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	14
pelagic	-	-	-	-	-

Cymbella pusilla Grunow
      Bacillariophyta - Bacillariophyceae -
      Cymbellales - Cymbellaceae

salinity preference: B(F)

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	10
pelagic	-	-	-	r	1

Detonula confervacea (Cleve) Gran
   Lauderia confervacea Cleve
     Detonula cystifera Gran
       Bacillariophyta - Coscinodiscophyceae -
       Thalassiosirales - Skeletonemataceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	-	-	-	1

Diatoma constricta (Grunow) Williams
   Diatoma vulgare v *constricta* Grunow
      Bacillariophyta - Fragilariophyceae -
      Fragilariales -Fragilariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	4

Diatoma tenuis CA Agardh
   Diatoma elongatum v *tenuis* (CA Agardh) van H.
   Diatoma tenuis v *elongatum* Lyngbye
   Diatoma elongatum (Lyngbye) CA Agardh
   Diatoma mesoleptum Kützing
   Diatoma gracillimum Naegeli
      Bacillariophyta - ... -Fragilariaceae

salinity preference: BF

sample	spr	sum	aut	win	freq
benthic	c	c	r	r	16
pelagic	d	r	-	v	6

Diatoma vulgare Bory
   Bacillaris vulgare (Bory) Ehrenberg
   Diatoma fenestratum Kützing
   Diatoma flocculosum CA Agardh
   Denticula obtusa Kützing, non *D. obtusa* W Smith
      Bacillariophyta - ... -Fragilariaceae

salinity preference: BF

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1
pelagic	-	-	-	-	-

Dictyocha speculum Ehrenberg
   Distephanus speculum (Ehrenberg) Haeckel
      Chromophyta - Cryptophyceae -
      Dictyochales - Dictyochaceaeceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	9
pelagic	r	r	r	-	6

Dimeregramma minor (Gregory) Ralfs in Pritchard
   Denticula minor Gregory
      Bacillariophyta - Coscinodiscophyceae -
      Triceratiales - Plagiogrammaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	3

Dinobryon cf. *balticum* (Schütt) Lemmermann
   Dinodendron balticum Schütt
      Chromophyta - Prymnesiophyceae -
      Prymnesiales - Prymnesiaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
pelagic	v	r	-	-	5

Dinophysis norvegica Claparede & Lachmann
   Dinophysis norvegica v *debilior* Paulsen
      Dinophyta- Dinophyceae - Dinophysales -
      Dinophysiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	r	r	v	v	6

Diploneis bomboides (A Schmidt) Cleve
   Navicula bomboides A Schmidt
   Navicula williamsonii O'Meara
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Diploneidaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic					

Diploneis didyma (Ehrenberg) Cleve
   Navicula didyma Ehrenberg
   Pinnularia didyma Ehrenberg
      Bacillariophyta - ... - Diploneidaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	5

Diploneis interrupta (Kützing) Cleve
  Navicula interrupta Kützing
    Bacillariophyta - ... - Diploneidaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	-	-	r	2

Diploneis papula (A Schmidt) Cleve
  Navicula papula A Schmidt
    Bacillariophyta - ... - Diploneidaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	2

Diploneis smithii (de Brebisson) Cleve
  Navicula smithii De Brebisson
  Diploneis major Cleve
  Navicula elliptica W Smith
  Pinnularia scutellum O'Meara
  Navicula scutellum (O'Meara) O'Meara
  Navicula fusca v *permagna* Pantocsek
  Navicula gyrinidae Mann
  Diploneis gyrinidae (Mann) FW Mills
  Diploneis smithii v *permagna* (Pant.) A Cleve
    Bacillariophyta - ... - Diploneidaceae

salinity preference: M(B)

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	5
pelagic	-	-	-	-	-

Ditylum brightwellii (T West) Grunow
  Triceratium brightwellii T West
  Ditylum trigonum JW Bailey
    Bacillariophyta - Coscinodiscophyceae -
    Lithodesmiales - Lithodesmiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	6
pelagic	-	-	v	-	1

Ectocarpus siliculosus (Dillwyn) Lyngbye
  Conferva siliculosus Dillwyn
  Ectocarpus gedanensis Lokowitz
    Phyaeophyta - Phaeophyceae -
    Ectocarpales - Ectocarpaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	v	r	-	15
pelagic	-	-	-	-	-

Encyonema prostratum (Berkeley) Kützing
  Monema prostratum Berkeley
  Cymbella prostrata (Berkeley) Brun
    Bacillariophyta - Bacillariophyceae -
    Cymbellales - Cymbellaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	-	1	-	r

Encyonema silesiacum (Bleisch) DG Mann
  Cymbella silesiaca Bleisch
  Cymbella ventricosa v *silesiaca* (Blei.) Cl.-Euler
  Cymbella ventricosa Kützing pro parte
  Cymbella minuta v *silesiaca* (Bleisch) Reimer
    Bacillariophyta - ... - Cymbellaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
pelagic	r	-	r	-	4

Enteromorpha spec.
    Chlorophyta - Chlorophyceae -
    Ulvales -Ulvaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	v	r	-	11

Entomoneis paludosa (W Smith) Reimer
  Amphiprora paludosa W Smith
    Bacillariophyta - Bacillariophyceae -
    Surirellales - Entomoneidaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	16

Epithemia cf. *smithii* Carruthers
  Epithemia proboscidea W Smith, non Kützing
    Bacillariophyta - Bacillariophyceae -
    Rhopalodiales - Rhopalodiaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Epithemia cf. *sorex* Kützing
    Bacillariophyta - Bacillariophyceae -
    Rhopalodiales - Rhopalodiaceae

salinity preference: B(F)

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	2

Epithemia turgida (Ehrenberg) Kützing
   Navicula turgida Ehrenberg
   Eunotia turgida Ehrenberg
   Frustulia picta Kützing
   Epithemia pictum (Kützing) De Brebisson
    Bacillariophyta - ... - Rhopalodiaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Euglena spec.
    Chlorophyta - Euglenophyceae -
    Euglenales - Euglenaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	11
pelagic	r	r	-	r	4

Eutreptia cf. *viridis*
    Chlorophyta - Euglenophyceae -
    Euglenales - Eutreptiaceae

salinity preference:

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	2
pelagic	v	r	-	v	8

Fallacia cf. *cryptolyra* (Brockmann) Stickle & Mann
   Navicula cryptolyra Brockmann, *N. misella* Hust.
   Navicula praestoeensis Möller
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Sellaphoraceae

salinity preference: B(F)

sample	spr	sum	aut	win	freq
benthic	r	r			5

Fallacia forcipata (Greville) Stickle & Mann
   Navicula forcipata Greville v *forcipata*
   Navicula forcipata v *minor* A Schmidt
    Bacillariophyta - ... - Sellaphoraceae

salinity preference: M(B)

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	4
pelagic	-	-	-	-	-

Fragilaria construens (Ehr.) Grunow v *construens*
   Staurosira construens Ehrenberg
   Odontidium tabellaria W Smith
   Fragilaria rhombica Oestrup
   Dimeregramma tabellaria (W Smith) Ralfs
    Bacillariophyta - Fragilariophyceae -
    Fragilariales -Fragilariaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	4
pelagic	-	-	-	-	-

Fragilaria crotonensis Kitton
   Synedra crotonensis v *prolongata* van Heurck
   Fragilaria crotonensis v *prolongata* (Gr.) De Toni
   Nitzschia pecten Brun
   Fragilaria pecten (Brun) Castracane
    Bacillariophyta - ... -Fragilariaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	10

Fragilaria vaucheriae (Kützing) JB Petersen
   Fragilaria capucina v *vaucheriae* (Kütz.) L.-Bert.
   Exilaria vaucheriae Kützing
   Synedra vaucheriae (Kützing) Kützing
   Fragilaria intermedia Grunow
    Bacillariophyta - ... -Fragilariaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	-	r	r	10
pelagic	r	-	-	-	1

Gomphonema acuminatum Ehrenberg
   Gomphonema brebissonii Kützing
    Bacillariophyta - Bacillariophyceae -
    Cymbellales - Gomphonemataceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	2

Gomphonema olivaceum (Hornemann) de Breb.
  Gomphoneis olivaceum (Hornemann) P Dawson
  Ulva olivaceum Hornemann
  Echinella olivacea (Hornemann) Lyngbye
      Bacillariophyta - ... - Gomphonemataceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	6
pelagic	-	-	-	-	-

Gomphonema parvulum (Kützing) Kützing
  Sphenella parvula Kützing
  Gomphonema micropus v *minor, exilis* Grunow
      Bacillariophyta - ...- Gomphonemataceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	-	-	r	2
pelagic	-	-	-	-	-

Gomphonemopsis pseudexigua (Simonsen) Medlin
  Gomphonema pseudexiguum Simonsen
      Bacillariophyta - Bacillariophyceae -
      Cymbellales - Rhoicospheniaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	-	r	r	r	3

Grammatophora oceanica Ehrenberg
  Grammatophora marina v *communis* Van Heurck
      Bacillariophyta - Fragilariophyceae -
      Striatellales - Striatellaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	5

Guinardia delicatula (Cleve) Hasle
  Rhizosolenia delicatula Cleve
      Bacillariophyta - Coscinodiscophyceae -
      Rhizosoleniales - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	-	-	-	3

Guinardia flaccida (Castracane) H Peragallo
  Rhizosolenia flaccida Castracane
  Phyxilla baltica sensu Hensen, non Grunow
  Rhizosolenia castracanei Cleve
  Guinardia baltica Schütt ex De Toni
  Henseniella baltica Schütt ex De Toni
      Bacillariophyta -... - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	2
pelagic	v	-	c	r	4

Guinardia striata (Stolterforth) Hasle
  Eucampia striata Stolterforth
  Rhizosolenia stolterforthii H Peragallo
      Bacillariophyta - ... - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Gymnodinium simplex (Lohmann) Kofoid & Swezy
  Dinophyta - Dinophyceae -
  Gymnodiniales - Gymnodiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	10
pelagic	v	v	c	c	20

Gymnodinium spec. A
  Dinophyta - Dinophyceae -
  Gymnodiniales - Gymnodiniaceae

salinity preference: -

sample	spr	sum	aut	win	freq
pelagic	r	-	v	-	5

Gyrodinium aureolum Herbert
  Dinophyta - Dinophyceae -
  Gymnodiniales - Gymnodiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
pelagic	v	-	-	-	2

Gyrosigma acuminatum (Kützing) Rabenhorst
  Frustulia acuminata Kützing
  Pleurosigma acuminatum (Kützing) W Smith
  Pleurosigma lacustre W Smith
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Pleurosigmataceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	13

Gyrosigma balticum (Ehrenberg) Rabenhorst
  Navicula baltica Ehrenberg
  Pleurosigma balticum (Ehrenberg) W Smith
    Bacillariophyta - ...- Pleurosigmataceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	2

Hantzschia baltica Simonsen
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Hantzschia virgata v *gracilis* Hustedt
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	2

Haslea crucigera (W Smith) Simonsen
  Schizonema crucigera W Smith
  Navicula crucigera (W Smith) Cleve
  Stauroneis crucigera (W Smith) Heiberg
  Dickieia crucigera De Toni
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Naviculaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	d	v	r	c	27
pelagic	c	v	r	c	7

Heterocapsa triquetra (Ehrenberg) Balech
  Glenodinium triquetrum Ehrenberg
  Peridinium triquetrum (Ehrenberg) Lebour
  Protoperidinium heterocapsa (Stein) Meunier
    Dinophyta- ... - Peridiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r		5
pelagic	v	c	v	-	11

Hippodonta capitata (Ehr.) L.-Bert., Metz. & Witk.
  Navicula hungarica v *capitata* (Ehrenberg) Cleve
  Pinnularia garganica Rabenhorst
  Navicula humilis Donkin
  Navicula capitata Ehrenberg
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Naviculaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	r		5
pelagic					

Katodinium rotundatum (Lohmann) Loeblich III
  Amphidinium rotundatum Lohmann
  Marsartia rotundata (Lohmann) Schiller
    Dinophyta - Dinophyceae -
    Gymnodiniales - Gymnodiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	r	1
pelagic	c	c	-	-	4

Kirchneriella spec.
    Chlorophyta - Chlorophyceae -
    Chlorococcales - Ankistrodesmaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1

Licmophora abbreviata CA Agardh
  Podosphenia lyngbyei Kützing
  Licmophora lyngbyei (Kützing) Grunow
  Podosphenia abbreviata (CA Agardh) Ehrenberg
  Rhipidophora abbreviata (CA Agardh) Kützing
  Podosphenia abbreviata Rabenhorst
    Bacillariophyta - Fragilariophyceae -
    Licmophorales - Licmophoraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	c	c	r	r	18
pelagic	v	-	-	r	5

Licmophora hyalina (Kützing) Grunow
  Podosphenia hyalina Kützing
    Bacillariophyta - ... - Licmophoraceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	v	r	r	r	22

Licmophora paradoxa (Lyngbye) CA Agardh
   Echinella paradoxa Lyngbye
   Gomphonema paradoxum (Lyngbye) CA Agardh
   Rhipidophora paradoxa (Lyngbye) Kützing
   Stylaria paradoxa (Lyngbye) Bory
   Rhipidophora australis Kützing
   Podosphenia paradoxa (Lyngbye) Rabenhorst
   Podosphenia australis (Kützing) Rabenhorst
   Stylaria australis (Kützing) Trevisan
       Bacillariophyta - ... - Licmophoraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	c	p	c	v	23
pelagic	r	-	-	-	1

Lyngbya confervoides CA Agardh
       Cyanophyta - Cyanophyceae -
       Oscillatoriales - Oscillatoriaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	v	r	-	5
pelagic	r	r	-	-	3

Lyrella abrupta (Gregory) DG Mann
   Navicula abrupta (Gregory) Donkin v *abrupta*
   Navicula lyra v *abrupta* Gregory
   Navicula connectens Grunow
   Navicula abrupta v *linearis* Schulz
       Bacillariophyta - Bacillariophyceae -
       Lyrellales - Lyrellaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	12
pelagic	-	-	r	-	1

Lyrella lyra (Ehrenberg) Karayeva
   Navicula lyra Ehrenberg
   Pinnularia lyra Ehrenberg
   Navicula gregoryana Greville
       Bacillariophyta -... - Lyrellaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	r	3
pelagic	-	-	-	-	-

Martyana martyi (Heribaud) Round
   Opephora martyi v *robusta, capitata* Heribaud
   Opephora martyi f *anomala* Heribaud
   Fragilaria mutabilis f *subsolitaris* Grunow
   Opephora martyi Heribaud
   Fragilaria leptostauron v *martyi* (Her.) Lange-Bert.
   Opephora cantalense Heribaud
       Bacillariophyta - Fragilariophyceae -
       Fragilariales -Fragilariaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1
pelagic	-	-	-	-	-

Melosira moniliformis (OF Müller) CA Agardh
   Conferva moniliformis OF Müller
   Melosira borreri Greville
   Lysigonium moniliforme Link
   Gaillonella moniliformis Bory
   Gaillonella borreri Pelletan
   Melosira lentigera Harvey
       Bacillariophyta - Coscinodiscophyceae -
       Melosirales - Melosiraceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	v	d	d	v	24
pelagic	v	-	c	c	5

Melosira nummuloides CA Agardh
   Melosira salina Kützing
   Melosira borreri sensu Waytt, non Greville
   Conferva nummuloides Dillwyn
   Fragilaria nummuloides Lyngbye
   Gaillonella nummuloides Bory
   Sphaerophora globulifera Hassall
   Melosira discigera CA Agardh
       Bacillariophyta - ... - Melosiraceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	c	c	c	v	29
pelagic	v	v	-	r	12

Melosira varians CA Agardh
  Conferva fasciata Dillwyn
  Nematoplata quadrata Bory
  Gaillonella varians Ehrenberg
  Vesiculifera composita Hassall
  Lysigonium varians De Toni
  Melosira aequalis CA Agardh
  Melosira coarctata Ehrenberg
  Melosira varians v *aequalis* Kützing
      Bacillariophyta - ... - Melosiraceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	-	v	r	-	4
pelagic	-	-	-	v	1

Meridion circulare (Greville) CA Agardh
  Echinella circularis Greville
  Meridion zinckenii Kütz. *M. flabellum* Ehr.
  Meridion heribaudi Per., *M. vernale* Ag.
  Exilaria flabellum Ehrenberg
  Frustulia circularis Duby
      Bacillariophyta - Fragilariophyceae -
      Fragilariales -Fragilariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic	-	-	-	-	-

Merismopedia glauca (Ehrenberg) Nägeli
  Gonium glaucum Ehrenberg
  Merismopedia mediterranea Nägeli
      Cyanophyta - Cyanophyceae -
      Nostocales - Nostocaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
pelagic	-	-	r	-	1

Monoraphidium cf. *contortum* (Thuret) Kom.-Legn.
      Chlorophyta - Chlorophyceae -
      Chlorococcales - Ankistrodesmaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	-	-	r	3
pelagic	r	v	v	r	11

Myrionecta rubra

salinity preference: ?

sample	spr	sum	aut	win	freq
pelagic	v	-	c	v	5

Navicula arenaria Donkin
  Navicula lanceolata v *arenaria* (Donkin) V.Heurck
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Naviculaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	16

Navicula cincta (Ehrenberg) Ralfs
  Navicula cari v *cincta* (Ehrenberg) Lange-Bertalot
  Pinnularia cincta Ehrenberg
  N.heufleri Gr., *N.umida* Bock, *N. inutilis* Krasske
      Bacillariophyta - ...- Naviculaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	v	r	r	r	29
pelagic	v	r	r	v	6

Navicula directa (W Smith) Ralfs in Pritchard
  Pinnularia directa W Smith
      Bacillariophyta - ... - Naviculaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	4

Navicula duerrenbergiana Hustedt
  Navicula stundlii Hustedt
      Bacillariophyta - ... - Naviculaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	2

Navicula gregaria Donkin
   Navicula cryptocephala Kütz. pro p. (excl. Lect.)
   Navicula gregalis Cholnoky
   Navicula gotlandica Grunow sensu Hustedt
   Navicula phyllepta sensu Brockm. & sensu Hend.
     Bacillariophyta - ... - Naviculaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	14
pelagic	-	-	r	r	3

Navicula grevillei -> *Parlibellus delognei*

Navicula heterovalvata Simonsen
   Bacillariophyta - Bacillariophyceae -
   Naviculales - Naviculaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	2

Navicula lanceolata (CA Agardh) Ehrenberg
   Frustulia lanceolata CA Agardh, non *N. lanceolata*
     sensu Kützing nec Hustedt
   Cymbella lanceolata (Ag.) Ag., non (Ehr.) Kirchn.
     Bacillariophyta - ...- Naviculaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	14
pelagic	-	-	r	-	1

Navicula cf. *menisculus* Schumann
   Bacillariophyta - Bacillariophyceae -
   Naviculales - Naviculaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	v	r	r	r	8
pelagic	-	-	-	r	1

Navicula palpebralis De Brebisson
   Bacillariophyta - ... Naviculaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Navicula cf. *pavillardii* Hustedt
   Navicula pavillardii v *constricta* Cleve-Euler
     Bacillariophyta - ... Naviculaceae

salinity preference: M

sample	spr	sum	aut	win	freq
siehe *N. duerrenbergiana*					

Navicula perminuta Grunow
   Navicula diserta Hustedt
   Navicula hansenii Möller
   Navicula cryptocephala v *perminuta* (Gr.) Cleve
   Navicula dulcis Patrick non Krasske
     Bacillariophyta - .... Naviculaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	c	r	c	r	28
pelagic	v	r	v	r	18

Navicula phyllepta Kützing
   Navicula lanceolata v *phyllepta* (Kützing) Van H.
   Navicula minuscula v *istriana* Grunow
     Bacillariophyta - ... - Naviculaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	5

Navicula ramosissima (CA Agardh) Cleve
   Schizonema ramosissima CA Agardh
     Bacillariophyta - ... Naviculaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	7

Navicula reinhardtii Grunow
   Stauroneis reinhardtii Grunow
     Bacillariophyta - ... - Naviculaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Navicula rhynchocephala Kützing
   Bacillariophyta - ... - Naviculaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	3

Navicula tripunctata (OF Müller) Bory v tripunctata
  Vibrio tripunctatus OF Müller
  Navicula gracilis Ehrenberg
    Bacillariophyta - ... - Naviculaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	18
pelagic	v				2

Navicula spec. A
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Naviculaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Nitzschia cf. *amphibia* Grunow
  Nitzschia amphibia v *acutiuscula* Grunow
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Nitzschia cf. *capitellata* Hustedt
  Nitzschia subfrequens Simonsen
  Nitzschia subcapitellata, balcanica, diserta Hust.
  Nitzschia salinicola Aleem & Hustedt
    Bacillariophyta - ...- Bacillariaceae

salinity preference: BF

sample	spr	sum	aut	win	freq
benthic	v	v	v	v	29
pelagic	v	r	r	-	8

Nitzschia cf. *fasciculata* (Grunow) Grunow
  Nitzschia sigma v *fasciculata* Grunow
    Bacillariophyta - ...- Bacillariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic	r	-	-	-	1

Nitzschia cf. *gracilis* Hantzsch
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	11
pelagic	r	-	-	r	4

Nitzschia longissima (de Brebisson) Grunow
  Ceratoneis longissima de Brebisson
  Nitzschia birostrata JE Smith
    Bacillariophyta - ... - Bacillariaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	v	r	12
pelagic	v	-	v	-	4

Nitzschia microcephala Grunow
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	22
pelagic	v	r	r	r	9

Nitzschia cf. *pusilla* Grunow
  Nitzschia kuetzingiana Hilse, non sensu Hustedt
  Nitzschia kuetzingii Rab., *N. indistincta* Mich.
  Synedra pusilla Kützing, *parvula* Kütz. p.p.
  Nitzschia kuetzingiana v *exilis* Grunow
    Bacillariophyta - ... - Bacillariaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Nitzschia cf. *reversa* W Smith
  Nitzschia longissima v *reversa* Grunow
    Bacillariophyta - ... - Bacillariaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	-	-	-	r	1

Nitzschia sigma (Kützing) W Smith v *sigma*
  Synedra sigma Kützing
    Bacillariophyta - ...- Bacillariaceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	16

Nitzschia tubicola Grunow
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	-	-	r	11

Nitzschia spec. A/B
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	1/1

Odontella aurita (Lyngbye) CA Agardh
  Biddulphia aurita (Lyngbye) de Brebisson
  Diatoma auritum Lyngbye
    Bacillariophyta - Coscinodiscophyceae -
    Triceratiales - Triceratiaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	v	r	v	c	22
pelagic	v	-	-	r	3

Opephora olsenii M Möller
    Bacillariophyta - Fragilariophyceae -
    Fragilariales -Fragilariaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	3

Oscillatoria cf. *amphibia* CA Agardh
    Cyanophyta - Cyanophyceae -
    Oscillatoriales - Oscillatoriaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	-	r	r	r	6
pelagic	-	r	-	-	-

Oscillatoria cf. *margaritifera* (Kützing) Gomont
    Cyanophyta - ...- Oscillatoriaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
pelagic	r	-	-	-	1

Parlibellus delognei (Van Heurck) Cox
  Schizonema grevillei sensu W Smith, non CA Ag.
  Navicula grevillei sensu Hust., non (CA Ag.) Heib.
  Navicula grevilleana Hendey
  Navicula delognei Van Heurck
  Libellus adnatus Heiden & Kolbe
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Berkeleyaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	d	c	r	d	23
pelagic	c	-	-	-	2

Pediastrum boryanum (Turpin) Menegini
  Helierella boryanum Turpin
    Chlorophyta - Chlorophyceae -
    Chlorococcales - Hydrodictyaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	2
pelagic	r	-	-	-	1

Phacus spec.
    Chlorophyta - Euglenophyceae -
    Euglenales - Euglenophyceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1

Phaeodactylum tricornutum Bohlin
  Nitzschia closterium f *minutissima* Allen & Nelson
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Phaeodactylaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1

Pilayella littoralis (Linné) Kjellman
  Conferva littoralis Linné
    Phyaeophyta - Phaeophyceae -
    Ectocarpales - Ectocarpaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	v	r	-	r	4

Pinnularia quadratarea (A Schmidt) Cleve
  Navicula quadratarea A Schmidt
  Navicula pinnularia Cleve
  Pinnularia quadratarea v *baltica* Grunow
    Bacillariophyta - Bacillariophyceae -
    Naviculales - Pinnulariaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	3
pelagic	-	-	-	-	-

Placoneis clementis (Grunow) Cox
  Navicula inclementis Hendey
  Navicula clementis Grunow
  Navicula exigua (Greg.) Grun. sensu Grun. 1880
      Bacillariophyta - Bacillariophyceae -
      Cymbellales - Cymbellaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	2
pelagic	-	-	-	-	-

Plagiogramma staurophorum (Gregory) Heiberg
  Denticula staurophora Gregory
  Plagiogramma gregorianum Greville
  Plagiogramma minutissimum Heiden
      Bacillariophyta - Coscinodiscophyceae -
      Triceratiales - Plagiogrammaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	r	3
pelagic	-	-	-	-	-

Pleurosigma angulatum (Quekett) W Smith
  Navicula angulatum Quekett
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Pleurosigmataceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	6
pelagic	-	-	-	-	-

Pleurosigma elongatum W Smith
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Pleurosigmataceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	r	c	v	r	25
pelagic	c	-	-	-	1

Proboscia alata (Brightwell) Sundström
  Rhizosolenia alata Brightwell
      Bacillariophyta - Coscinodiscophyceae -
      Rhizosoleniales - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	-	-	-	1

Prorocentrum baltica (Lohmann) Loeblich
  Exuviella baltica Lohmann
      Dinophyta- Dinophyceae -
      Prorocentrales - Prorocentraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	7
pelagic	v	d	-	-	9

Prorocentrum micans Ehrenberg
      Dinophyta- Dinophyceae -
      Prorocentrales - Prorocentraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	7
pelagic	-	c	v	-	10

Prorocentrum minimum (Pavillard) Schiller
  Exuviella baltica Pavillard
  Exuviella marie-lebouriae Parke & Ballantine
  Prorocentrum marie-lebouriae (Par.& Ball.) Loebl.
  Prorocentrum triangulatum Martin
      Dinophyta- ... - Prorocentraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	v	v	-	10
pelagic	r	c	v	-	11

Proschkinia complanata (Grunow) DG Mann
  Navicula complanata (Grunow) Grunow
  Amphora complanata Grunow
  Libellus complanatus (Grunow) De Toni
  Amphora hyperborea Grunow
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Proschkiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	p	v	v	r	23
pelagic	r	p	-	p	8

Protoperidinium bipes (Paulsen) Balech
  Peridinium bipes Paulsen
      Dinophyta- Dinophyceae -
      Peridiniales - Protoperidiniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	2
pelagic	v	r	r	r	6

Protoperidinium spec. A
    Dinophyta- Dinophyceae -
    Peridiniales - Protoperidiniaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	v	r	-	5
pelagic	-	v	v	-	13

Prymnesium spec.
    Chromophyta - Prymnesiophyceae -
    Prymnesiales - Prymnesiaceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	5
pelagic	v	c	v	v	13

Pseudo-nitzschia pungens (Grunow) Hasle
  Nitzschia pungens Grunow f *pungens*
    Bacillariophyta - Bacillariophyceae -
    Bacillariales - Bacillariaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	-	r	r	8
pelagic	v	-	c	v	7

Pseudanabaena catenata Lauterborn
    Cyanophyta - Cyanophyceae -
    Nostocales - Nostocaceae

salinity preference: ?

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	4

Punctaria plantaginea (Roth) Greville
  Ulva plantaginea Roth
  Phycolapathium plantagineum (Roth) Kützing
  Laminaria plantaginea (Roth) CA Agardh
  Zonaria plantaginea (Roth) CA Agardh
    Phyaeophyta - Phaeophyceae -
    Dyctiosyphonales - Punctariaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	-	-	-	-	-

Rhabdonema minutum Kützing
  Fragilaria striatula Greville
  Tessella catena Ralfs
  Fragilaria carmichaeli Harvey
  Rhabdonema oestrupii A Cleve
    Bacillariophyta - Fragilariophyceae -
    Rhabdonematales - Rhabdonemataceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	r	-	r	-	3

Rhizosolenia pungens A Cleve
    Bacillariophyta - Coscinodiscophyceae -
    Rhizosoleniales - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	4
pelagic	c	-	v	c	6

Rhizosolenia setigera Brightwell
  Rhizosolenia japonica Castracane
  Rhizosolenia hensenii Schütt
    Bacillariophyta - ... - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
pelagic	-	-	v	-	1

Rhizosolenia styliformis Brightwell
  Rhizosolenia styliformis v *longispina* Hustedt
    Bacillariophyta - ... - Rhizosoleniaceae

salinity preference: M

sample	spr	sum	aut	win	freq
pelagic	d	v	-	-	4

Rhodomonas cf. *pelagica* Lohmann
    Chromophyta -Cryptophyceae -
    Cryptomonadales - Cryptomonadaceae

salinity preference: M(B)

sample	spr	sum	aut	win	freq
benthic	-	r	r	r	9
pelagic	v	v	v	c	21

Rhoicosphenia curvata (Kützing) Grunow
  Gomphonema abbreviatum CA Agardh
  Gomphonema curvatum Kützing
  Rhoicosphenia abbreviata (CA Ag.) Lange-Bert.
  Gomphonema minutissimum Kützing
    Bacillariophyta - ... - Rhoicospheniaceae

salinity preference: BF

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	16
pelagic	v	-	r	-	2

Rhopalodia cf. *brebissonii* Krammer
  Rhopalodia musculus v *succincta* sensu Perag.
  Rhopalodia gibberula v *succincta* sensu Fricke
      Bacillariophyta - Bacillariophyceae -
      Rhopalodiales - Rhopalodiaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	3
pelagic	-	-	-	-	-

Rhopalodia cf. *operculata* v *constricta* (W Sm.)Ross
  Epithemia constricta W Smith
  Rhopalodia musculus v *constricta* (W Smith) Per.
  Rhopalodia constricta (W Smith) Krammer
  Rhopalodia gibberula v *constricta* (W Sm.) Karst.
      Bacillariophyta - ...- Rhopalodiaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	r	r	-	3
pelagic					

Scenedesmus spec.
      Chlorophyta - Chlorophyceae -
      Chlorococcales - Scenedsmaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	7
pelagic	r	-	v	-	7

Skeletonema costatum (Greville) Cleve
  Melosira costata Greville
  Stephanopyxis costata (Greville) Hustedt
      Bacillariophyta - Coscinodiscophyceae -
      Thalassiosirales - Skeletonemataceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	d	v	r	r	26
pelagic	d	r	p	v	22

Spirulina subsalsa Oersted
      Cyanophyta - Cyanophyceae -
      Oscillatoriales - Oscillatoriaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	-	r	r	r	13
pelagic	-	-	r	-	1

Staurastrum spec.
      Chlorophyta - Conjugatophyceae -
      Desmidiales - Desmidiaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	-	-	r	-	1
pelagic	-	-	v	-	1

Stauroneis cf. *kriegerii* Patrick
  Stauroneis pygmaea Krieger
      Bacillariophyta - Bacillariophyceae -
      Naviculales - Stauroneidaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r			4

Stauroneis simulans (Donkin) R Ross
  Amphiprora constricta Ehrenberg
  Navicula simulans Donkin
  Stauroneis constricta (Ehr., W Smith?) Cleve
  Stauronella constricta (Ehr.) Mereschkowsky
  Libellus constrictus (Ehrenberg) Cleve
      Bacillariophyta - ... - Stauroneidaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	v	v	r	r	23
pelagic	-	-	v	-	5

Stephanodiscus binderanus (Kützing) Krieger
  Melosira binderana Kützing
  Melosira oestrupii A Cleve
  Melosira zachariasii Castracana
      Bacillariophyta - Coscinodiscophyceae -
      Thalassiosirales - Stephanodiscaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	5
pelagic	-	-	-	r	1

Stephanodiscus hantzschii Grunow f *hantzschii*
  Stephanodiscus hantzschianus Grunow
  Cyclotella operculata sensu Hantzsch
  Stephanodiscus balticus Schumann
  Stephanodiscus zachariasii Brun, *S. minor* Rev.
      Bacillariophyta - ... - Stephanodiscaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1
pelagic	-	-	-	-	

Surirella brebissonii Krammer & Lange-Bertalot
   Surirella ovata sensu Hustedt
   Surirella ovata v *marina* De Brebisson
      Bacillariophyta - Bacillariophyceae -
      Surirellales - Surirellaceae

salinity preference: FB

sample	spr	sum	aut	win	freq
benthic	r	r	r	r	17
pelagic	-	-	-	-	-

Synedra ulna (Nitzsch) Ehrenberg
   Bacillaria ulna Nitzsch
   Frustulia splendens Kützing
   Fragilaria ulna (Nitzsch) Lange-Bertalot
   Bacillaria paxillum Bory, *lyngbyei* Bory
   Synedra splendens (Kützing) Kützing
   Synedra mesolepta Kützing, *interrupta*
      Auerswald, *bicurvata* Biene
   Synedra subaequalis Pant.
      Bacillariophyta - Fragilariophyceae -
      Fragilariales - Fragilariaceae

salinity preference: F

sample	spr	sum	aut	win	freq
benthic	v	-	-	-	3
pelagic	r	r	-	-	2

Tabularia fasciculata (CA Agardh) Williams & Round
   Synedra fasciculata (CA Agardh) auct. non. Kütz.
   Diatoma fasciculatum CA Agardh
   Synedra affinis Kützing
   Fragilaria fasciculata (CA Agardh) Lange-Bertalot
   Synedra affinis v *fasciculata* (CA Agardh) Grunow
   Synedra tabulata v *fasciculata* (CA Agardh) Hust.
      Bacillariophyta - ... - Fragilariaceae

salinity preference: B(M)

sample	spr	sum	aut	win	freq
benthic	p	c	c	d	30
pelagic	v	v	v	v	20

Tabularia investiens (W Smith) Williams & Round
   Synedra investiens W Smith.
   Fragilaria investiens (W Smith) Cleve-Euler
      Bacillariophyta -...- Fragilariaceae

salinity preference: M(B)

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	-	-	-	-	-

Tetraselmis spec.
      Chlorophyta - Prasinophycae -
      Chlorodendrales - Chlorodendraceae

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1

Thalassionema nitzschoides (Grunow) Grunow
   Synedra nitzschoides Grunow
   Thalassiothrix nitzschoides (Grunow) Grunow
   Thalassiothrix curvata Castracane
   Thalassiothrix frauenfeldii Cleve, non Grunow
      Bacillariophyta - Fragilariophyceae -
      Thalassionematales -Thalassionemataceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	v	-	r	15
pelagic	v	c	v	v	13

Thalassiosira anguste-lineata (A Schm.) Fryx.& Has.
   Coscinodiscus anguste-lineatus A Schmidt
   Coscinodiscus polychorda Gran
   Thalassiosira polychorda (Gran) Jörgensen
   Thalassiosira ornata Proschkina-Lavrenko
   Coscinosira polychorda (Gran) Gran
      Bacillariophyta - Coscinodiscophyceae -
      Thalassiosirales - Thalassiosiraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic	v	r	-	v	8

Thalassiosira baltica (Grunow) Ostenfeld
   Coscinodiscus polyacanthus v *baltica* Grunow
   Coscinodiscus balticus (Grun.) Grunow ex Cleve
   Thalassiosira subsalina Proschkina-Lavrenko
      Bacillariophyta - ... - Thalassiosiraceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	v	r	r	r	12
pelagic	r	-	p	v	4

Thalassiosira cf. *decipiens* (Grunow) Jörgensen
   Coscinodiscus eccentricus v *decipiens* Grunow
   Coscinodiscus decipiens Grunow
   Thalassiosira gelatinosa Hensen
      Bacillariophyta - ... - Thalassiosiraceae

salinity preference: BM

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	7
pelagic	r	r		r	3

Thalassiosira eccentrica (Ehrenberg) Cleve
   Coscinodiscus excentricus Ehrenberg
   Coscinodiscus labyrinthus Roper
   Odontodiscus excentricus Ehrenberg
   Coscinodiscus minor A Schmidt, *labyrinthus*
      Roper, *heliozoides* Siddall
      Bacillariophyta - ... - Thalassiosiraceae

salinity preference: M

sample	spr	sum	aut	win	freq
benthic	r	-	-	-	1

Thalassiosira nordenskioeldii Cleve
      Bacillariophyta - ... - Thalassiosiraceae

salinity preference: M

sample	spr	sum	aut	win	freq
pelagic	v	-	r	v	6

Thalassiosira cf. *proschkinae* Makarova
      Bacillariophyta - Coscinodiscophyceae -
      Thalassiosirales - Thalassiosiraceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	-	-	5
pelagic	r	-	-	-	1

Triceratium favus Ehrenberg
   Triceratium muricatum Brightwell, *fimbricatum*
      Wallich, *ferox* Castracane, *sarcophagus*
      Castracane, *comptum* Ehr.
   Biddulphia favus (Ehrenberg) Grunow
      Bacillariophyta - Coscinodiscophyceae -
      Triceratiales - Triceratiaceae

salinity preference: ?

sample	spr	sum	aut	win	freq
benthic	-	r	-	-	1
pelagic					

Trichormus variabilis (Kütz.) Komarek & Anagnost.
   Anabaena variabilis Kützing
      Cyanophyta - Cyanophyceae -
      Nostocales - Nostocaceae

salinity preference: F(B)

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	7
pelagic	r	-	r	r	4

Tryblionella apiculata Gregory
   Synedra constricta Kützing
   Nitzschia constricta (Kütz.) Ralfs, non (Greg.) Gr.
   Nitzschia apiculata (Gregory) Grunow
      Bacillariophyta - Bacillariophyceae -
      Bacillariales - Bacillariaceae

salinity preference: B

sample	spr	sum	aut	win	freq
benthic	r	r	r	-	4
pelagic	-	-	-	-	-

Tryblionella punctata W Smith
   Pyxidicula compressa Bailey
   Nitzschia compressa (Bailey) Boyer
   Nitzschia punctata (W Smith) Grunow
      Bacillariophyta - ... - Bacillariaceae

salinity preference: MB

sample	spr	sum	aut	win	freq
benthic	r	-	r	-	5
pelagic	-	-	-	-	-

Ulothrix flacca (Dillwyn) Thuret
   Conferva flacca Dillwyn
   Ulothrix pseudoflacca Wille
      Chlorophyta - Chlorophyceae -
      Ulotrichales - Ulotrichaceae

salinity preference: ?

sample	spr	sum	aut	win	freq
benthic	p	r	r	v	20
pelagic	r	-	-	r	3

Ulothrix implexa (Kützing) Kützing
   Hermidium implexum Kützing
   Ulothrix subflaccida Wille
   Ulothrix achorhiza Kornmann
     Chlorophyta - ... - Ulotrichaceae

salinity preference: ?

sample	spr	sum	aut	win	freq
benthic	r	r	-	r	8

Unidentified flagellate species

salinity preference: -

sample	spr	sum	aut	win	freq
benthic	-	-	-	-	-
pelagic	v	r	c	v	20

Appendix 3: Abundance of zoobenthos

Table A2: Abundance of zoobenthos groups (cm^{-2}) in the experiments 1996/1997. Note for comparison with phytobenthos data that the latter are given per mm^{-2}. n.d.: not determined.

taxonomic group		spring 1996	late summer 1996	autumn 1996	early spring 1997	late spring 1997	summer 1997
Protozoa	Ciliata	50.6	n.d.	n.d.	28.6	244.71	3.2
Cnidaria	Hydrozoa	-	-	-	-	7.17	-
Plathelminthes	Turbellaria	0.1	-	-	-	-	-
Nemathelminthes	Nematoda	0.14	24.75	1.53	0.74	144.4	4.12
	Rotatoria	0.24	2.25	0.22	9.38	19.87	3.61
Annelida	Polychaeta	-	0.39	1.64	0.25	0.01	-
Arthropoda	Copepoda	0.03	35.05	6.00	5.93	13.59	5.46
	Amphipoda	0.01	2.95	-	-	-	0.34
	Cirripedia	-	0.22	-	-	-	-
	Isopoda	0.01	0.09	0.11	-	-	-
Mollusca	Bivalvia	-	18.55	-	-	-	29.23

Appendix 4: Spatial scales of unicellular diversity

It became obvious from the experiments presented in this thesis that diversity of benthic microalgal assemblages was a suitable response variable to measure the effect of environmental factors on the structure of benthic microflora. However, these experiments were conducted on small spatial scales. Most studies employing diversity measures of benthic microalgae investigated local assemblages in experimentally manipulated situations (Sullivan 1976, Marcus 1980, Sundbäck & Snoeijs 1991, this study), whereas comparably few studies of regional changes in microalgal diversity have been published (but see Blinn 1993). Regional diversity is defined to be influenced by biogeography and evolution (i.e. distribution, dispersal and speciation), whereas local diversity is influenced by ecological processes (Cornell & Lawton 1992, Gaston & Williams 1996). For macroscopic organisms, local species richness was shown to be an increasing function of regional species richness, and the relationship was often linear indicating that local species richness was not saturated (Ricklefs 1987, Caley & Schluter 1997). This view was supported by recent experiments showing conclusively that local species richness of higher plants was constrained by dispersal and recruitment limitation (Tilman 1997, Hubbell et al. 1999).

Fenchel (1993) proposed a different view for unicellular organisms. Based on a high local species richness compared to low global species numbers and a high proportion of cosmopolitic species, a minor influence of dispersal and distribution barriers on ciliate diversity was proposed. This pattern was reflected by a flat species-area curve for ciliate diversity (Finlay et al. 1998). It becomes obvious from these thoughts that regional species richness gradients should be rare for protists. Since benthic microalgae are of a similar size range, it can be hypothesized that benthic microalgae, too, exhibit stronger local than regional gradients of diversity.

To test these hypotheses, I conducted a literature survey, using the Aquatic Science and Fisheries Abstracts, in order to obtain values for H' and S from studies on benthic microalgae giving the geographic position of the study site (Table A4.1). Latitudinal gradients belong to the most prominent patterns in diversity. These have been found for several biota (Tilman & Pacala 1993, Gaston & Williams 1996),

including marine benthic communities (Rex et al. 1993, Roy et al. 1998). I chose H' as it was often calculated or can be calculated from given species-abundance lists. Since different log-bases were used in the original studies, I transferred all H' to values based on log_2, using the equations given by Krebs (1989). Species-abundance lists have been employed, if at least 15 taxa were listed.

The references for the literature survey on latitudinal gradients are given in Table A4.1. The range and mean values for H' are plotted in Fig. A4.1, showing a high variance for every given latitude. The published studies often revealed a local range of H' comprising almost the complete theoretical range of H' for the given species richness (0-log_2S) (see e.g. McIntire & Overton 1971, Sullivan 1975). Therefore no significant trend for mean or maximum H' values with latitude emerged, neither for the whole data set nor for the freshwater, marine or brackish subset of data ($p>0.1$), except for the means of the marine-coastal subset (slope -0.038; $p=0.036$, $r^2=0.192$). The latter trend, however, seems to be redundant taking into account the wide range of values around the mean. Species richness was also not correlated to latitude ($p=0.585$).

However, the survey relied on studies very different in their scope and their study effort. The survey comprised only the latitudinal range from 20°-70° N and ecological and floristic studies were confounded as well as different substrates (sediments, artificial substrates and epiphytes). It seems thus necessary to investigate if a correlation with latitude is masked by the poor data basis.

It can be cautiously concluded that regional gradients of microalgal diversity are less distinct than local gradients, if not absent. I am aware of only one study reporting significant trends of unicellular diversity with environmental variables on the regional scale (Blinn 1993). The small scales of microalgal distribution (Saburova et al. 1995) and of the related environmental gradients (Biggs et al. 1998) may prevent the emergence of robust patterns on scales extending along thousands of km (Caley & Schluter 1997).

Table A4.1: Literature survey on diversity of benthic microalgae from freshwater and marine sites. The table gives the site, the geographic position (position in italics: not given in original text, but estimated from standard maps). In the column "sal.", M denotes marine habitats, B brackish and F freshwater. The substrates are divided in sed. (sediment), hard (hard substrates, e.g. stone, wood), and plt. (plants). Column "T" indicates, if natural or artificial substrates were sampled (nat., art.) and if any further treatment was applied (exp.). Mean and range of H' are given as bits ind^{-1}, reflecting log$_2$-basis. Italics indicate calculation from species list, while boldface numbers indicate calculation from graphs in the respective study. Species number (S) are given, if given in the respective reference. [a]: H' based on biovolume.

site	lati-tude	sal.	substr.	T	H' mean	H' range	S	reference
La Jolla, Ca. USA	32.8 N	M	sed.	nat	3.28	3.17-3.38	93	Amspoker 1977
Yaquina estuary, Oregon USA	44.6 N	B	sed.	nat	4.07	1.74-5.11	-	Amspoker & McIntire 1978
Oak Creek, Arizona USA	34.9 N	F	hard	nat	2.41	2.26-2.49	44	Blinn et al. 1980
Elk Lake, Vancouver Island, Canada	48.5 N	F	hard	art	2.67	1.95-3.18	28	Brown 1973
Cuyahoga River, Ohio USA	*41.2 N*	F	hard/plt.	nat	*3.72*	*1.98-4.93*	140	Brown & Olive 1995
Lake Michigan, Little Traverse Bay, USA	*45.0 N*	F	hard	exp/ art	**3.00**[a]	**1.8-4.1**	-	Carrick et al. 1988
Grand Bayou Blue, Louisiana USA	29.4 N	B	sed.	nat	4.37	3.96-5.02	112	Cook & Whipple 1982
Montezuma Well, Arizona USA	34.7 N	F	sed.	nat	3.14	1.62-3.94	75	Czarnecki 1979
Montezuma Well, Arizona USA	34.7 N	F	hard	nat	3.30	1.99-3.71	59	Czarnecki 1979
Upper Florida Bay, USA	*25.2 N*	M	sed.	nat	4.69	-	161	De Felice & Lynts 1978
Upper Florida Bay, USA	*25.2 N*	M	plt.	nat	3.09	-	dito	De Felice & Lynts 1978
St. Lawrence River, Montreal, Canada	*45.5 N*	F	sed.	nat	2.24	0.35-3.34	-	De Seve & Goldstein 1981
Tourujoki river, Finland	62.3 N	F	hard	art	2.46	1.46-3.25	108	Eloranta & Kunnas 1979
Adak Island, Alaska	*51.9 N*	F	hard	nat	3.38	1.78-4.68	321	Hein 1990
Forked River, New Jersey, USA	*41.0 N*	F	hard	art	**4.5**	**1.0-5.8**	223	Hein & Koppen 1979
Barnwell & Fox Creek, Ca. USA	37.7 N	F	hard	exp/ art	*3.09*[a]	*2.88-3.20*	-	Hill & Knight 1988
Kiel Fjord, Western Baltic Sea	54.3 N	B	hard	exp/ art	2.26[a]	0.27-3.91	180	Hillebrand & Sommer 1997
Geltinger Noor, Western Baltic Sea	54.8 N	B	hard	exp/ art	2.74[a]	1.49-3.55	-	Hillebrand, Worm & Lotze (chapter 5)
Maasholm, Western Baltic Sea	54.7 N	B	hard	exp/ art	2.27[a]	1.21-3.64	-	dito
Wackerballig, Western Baltic Sea	54.8 N	B	hard	exp/ art	1.72[a]	0.77-2.45	-	dito
Pawnee Reservoir, Nebraska USA	*40.8 N*	F	hard	art	**3.3**	**3.0-3.5**	81	Hoagland 1983
Vineyard Sound, Ma. USA	*41.4 N*	M	hard	exp/ art	**2.3**	**0.3-3.6**	96	Hunter & Russell-Hunter 1983
Created Wetland, Perth, Australia	33.0 S	F	sed.	nat	2.03	0.93-3.99	62	John 1993

| site	latitude	sal.	substr.	T	H' mean	H' range	S	reference
Lake Michigan, Grand Traverse Bay, USA	45.0 N	F	sed.	nat	4.39	3.54-5.74	425	Kingston et al. 1983
Oak Metropark, Ohio	40.0 N	F	sed.	nat	2.30	-	138	Krejci & Lowe1987
River Main near Mühlheim, Germany	50.2 N	F	hard	nat	2.75	1.69-3.79	-	Lange-Bertalot 1979
Gulf of Finland, Baltic Sea	59.9 N	B	hard	art	3.6	2.4-4.3	99	Leskinen & Sarvala 1988
Hyalite Creek, Montana USA	45.0 N	F	hard	exp/art	2.08	1.69-2.63	61	Marcus 1980
Avon-Heathcote Estuary, New Zealand	43.6 S	M	sed.	nat	3.46	3.27-3.61	53	McClatchie et al. 1982
Yaquina Estuary Oregon USA	44.6 N	B	hard	art	3.22	0.22-5.21	256	McIntire & Overton 1971
Kuparuk River, Alaska	68.5 N	F	hard	exp/art	3.53	2.93-3.77	187	Miller et al. 1992
Tidal Flat, West Coast of Korea	35.8 N	M	sed.	nat	2.91	2.5-3.2	371	Oh & Koh 1995
Carp Creek, Michigan USA	45.6 N	F	hard	exp/art	2.7	1.0-3.6	-	Pringle 1990
Everglades, Florida,	26.0 N	F	sed.	nat	2.73	2.12-3.92	116	Raschke 1993
Baie de Morlaix, France	48.7 N	M	sed.	nat	3.1	0.5-4.1	-	Riaux 1983
Mack Creek, Oreg.USA	45.0 N	F	hard	art	1.0	0.1-2.5		Sabater et al. 1998
Swedish Coast, Baltic Sea	59.5 N	B	plt.	nat	1.6	0.9-3.2	86	Snoeijs 1994
Äskö, Baltic Sea	59.5 N	B	hard	art	1.5	0.4-3.3	85	Snoeijs & Kautsky 1989
Gulf of Finland, Baltic Sea	59.9 N	B	hard	nat	4.17	4.01-4.32	126	Snoeijs et al. 1990
Fleming Creek, Michigan, USA	46.0 N	F	hard	art	2.5	1.9-3.5	185	Stevenson 1984
Harts Run, Kentucky, USA	38.0 N	F	hard	exp/art	2.8	1.0-3.5	-	Stevenson et al. 1991
Maple River, Michigan, USA	45.2 N	F	all subst.	nat	5.0	4.6-5.4	233	Stevenson & Hashim 1989
Canory Creek Salt Marsh, Delaw. USA	38.8 N	M	sed.	nat	4.03	0.47-5.22	104	Sullivan 1975
Canary Creek Salt Marsh, Delaw. USA	38.8 N	M	sed.	nat	4.6	4.1-4.9	105	Sullivan 1976
Graveline Bay, Mississippi, USA	30.4 N	M	sed.	exp	3.8	2.8-4.5	119	Sullivan 1978
Falsterbo, Sweden	55.3 N	M	sed.	nat	3.86	3.3-4.2	74	Sundbäck 1984
Tjärnö, Swedish West Coast	58.9 N	M	sed.	exp	4.16	3.75-4.76	-	Sundbäck & Snoeijs 1991
Colne Estuary, U.K.	51.7 N	B	sed.	nat	3.25	2.27-3.57	-	Underwood et al. 1998
Haapsalu Bay, Estonia	58.3 N	B	sed.	nat	4.3	4.2-4.9	239	Vilbaste 1992
Schlei Estuary, Western Baltic Sea	54.6 N	B	hard	nat	3.29	2.73-3.95	-	Wendker 1990
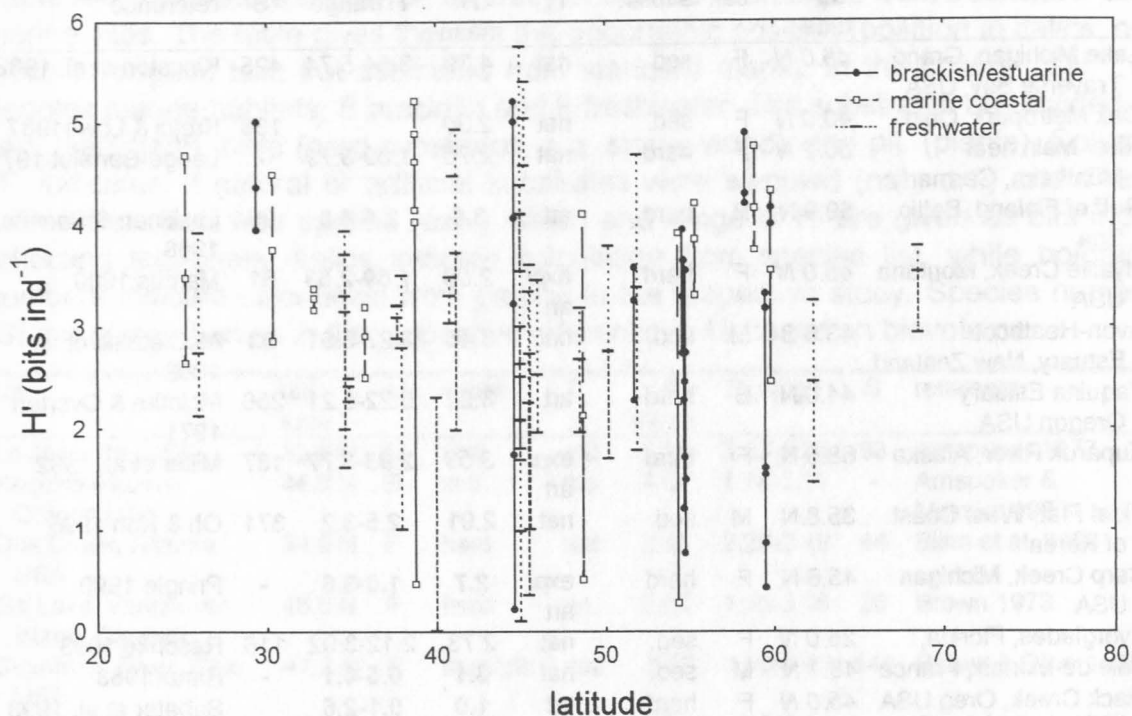
Fig. A4.1: Published values for Shannon-Weaver diversity index (H') related to latitude of the site from which the data were obtained. References and values are given in Table A4.1. From each study, mean and range (min-max) of H' were obtained.

It was noted before that regional and local species richness are determined predominantly by biogeographic and ecological processes, respectively. It can be derived from the lack of regional patterns that biogeographic processes are less influential on microalgal diversity than ecological processes. This is consistent with reports on ciliates (Fenchel et al. 1997, Finlay et al. 1997) and the high local species richness observed in several unicellular groups (ciliates: Fenchel et al. 1997; bacteria: Pedros-Alio 1993; diatoms: this study).

These findings have important implications for the conservation of biodiversity (Finlay et al. 1997) and for the emerging field of macroecology, which is in search of general ecological patterns beyond the variability of community ecology (Gaston & Blackburn 1999, Lawton 1999). Relationships between diversity and global gradients (latitude, productivity, body size) belong to the most prominent macroecological patterns, but these may be invalid on the microbial level.