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Biomass, diversity and production of rocky shore macroalgae at two nutrient enrichment and wave action levels

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Abstract The littoral zone of temperate rocky shores is normally dominated by perennial macroalgae (e.g. *Fucus, Ascophyllum, Laminaria*), but nutrient enrichment and/or permanently decreased wave action may lead to structural community changes from dominance of perennials to increased amounts of annual opportunistic species (mainly green algae). Macroalgal biomass, diversity and production as well as relationships between the two latter were studied using Solbergstrand's rocky shore mesocosms in SE Norway in connection with a long-term experimental manipulation of nutrient addition and wave action (high and low levels of both factors applied in a crossed way to eight outdoor basins). After more than 2 years of experimental treatment, the total standing stock of macroalgae was larger in low nutrient than in high nutrient treatments as well as in high wave compared to low wave treatments (in autumn only). For macroalgal functional groups, bushy and filamentous brown and filamentous red algae were generally favoured by low nutrient concentrations, while annual filamentous and sheet-like green algae were stimulated by the nutrient enrichment. There was only one significant interaction between nutrient enrichment and wave action (for brown filamentous algae in autumn) and also only one significant main effect of the wave treatment (for bushy brown algae in autumn). Surprisingly, the high nutrient treatments supported a higher diversity of macroalgae, whereas the low nutrient treatments generally showed higher production rates. Moreover, significantly negative correlations were found between macroalgal diversity and primary productivity in both summer and autumn. This study shows that it is the biological components of the communities subjected to external forcing (nutrient addition or decreased wave action) that regulate production and this contradicts the common misperception that resource production in natural systems simply can be fast-forwarded by fertilization. The negative relationships between diversity and productivity, although a consequence of unexpected results for diversity and production, are also novel and hint towards species identities having more important functional consequences than general species dominance patterns and the amount of species per se. These results also emphasise the context dependency of findings within the field of biodiversity and ecosystem functioning.

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Introduction

Increased nutrient enrichment due to human activities is today commonly perceived as a major contributor to the deterioration of coastal ecosystems worldwide including vast structural and functional ecosystem changes (Nixon 1995; Schramm 1999; Cloern 2001; Eriksson et al. 2002). On temperate rocky shores, nutrient enrichment increases

the growth and dominance of annual filamentous and sheet-like algae (Valiela et al. 1997; Worm and Lotze 2006), which is linked to ecophysiological traits (growth rate, nutrient requirements and uptake rates), where thin algae are favoured above thick algae at higher nutrient levels (Wallentinus 1984; Pedersen and Borum 1996). This stimulation of annual ephemerals may accentuate the competition for light and space and retard perennial species or harm their recruitment or growth (Johansson et al. 1998; Råberg et al. 2005; Kraufvelin et al. 2007) and decrease their cover (Schramm 1999; Cloern 2001; Rabalais 2005). Loss of perennial algal species may in turn have consequences for the whole ecosystem, since the macroalgal canopy on rocky shores is known to form a mosaic of habitats for macrofauna and to constitute essential foraging and reproduction areas for fish (Weaver et al. 1997; Schramm 1999; Worm et al. 2000; Benedetti-Cecchi et al. 2001), but see also Kraufvelin and Salovius (2004), Edgar et al. (2004) and Engström-Öst et al. (2007) for a more diversified view of the possible consequences.

Generally, marine littoral communities are structured by a combination of physical factors and biotic interactions (Little and Kitching 1996; Wernberg and Connell 2008), and they possess a high structural and functional resistance against excessive nutrient availability as long as the communities are not seriously affected by other chemical, physical or biological processes (Connell 1985; Thompson et al. 2002; Worm and Lotze 2006). It is for example credible that the strong dominance of late successional and long-lived species, such as fucoids and kelps, by itself may prevent colonisation and development of ephemeral algae through strong competition for light and space. This may render rocky shore communities relatively resistant to nutrient enrichment (Sousa 1979; Bokn et al. 2003; Eriksson et al. 2006a; Kraufvelin et al. 2006b). Large macroalgae may also induce whiplash effects by which epiphytic or understory algae are prevented to settle or removed from their substrate (Kiirikki 1996; Irwing and Connell 2006). Wave action may further cause detachment or active removal and export of opportunistic algae and thereby moderate the accumulation of excessive algal biomass (Pihl et al. 1999; Thompson et al. 2002; Barrón et al. 2003; Kraufvelin 2007). Acting in combination, nutrient enrichment and decreased wave action may lower the diversity, which can be crucial for the ecosystem, if it is coupled to loss of functional groups and altered ecosystem function such as productivity (Naeem et al. 1994; Valiela et al. 1997; Johansson et al. 1998).

Due to concern about the outcome of current and future biodiversity decreases, relationships between biodiversity and ecosystem functioning (BEF) have become central ecological and environmental research topics during the past decade (Loreau et al. 2001). The ongoing debate about whether and how diversity at different organisational levels affects the stability of communities under fluctuating or monotonically changing environmental conditions has now produced hundreds of publications (reviewed by Balvanera et al. 2006; Fridley et al. 2007; Stachowicz et al. 2007). It is agreed that human impact on the earth's biological resources is significant and constantly increasing (Vitousek et al. 1997). This leads to dramatic changes in species composition and structure of natural communities, either through the loss of species or through the introduction of new species at new places. It is therefore crucial to determine, which consequences biodiversity changes may have on ecosystem functioning and on the goods and services that healthy ecosystems may provide (Hooper et al. 2005; Bracken et al. 2008). There is no single index for all traits characterising an ecosystem (Giller et al. 2004), but the most common variables that have been registered in BEF-studies have included direct or indirect measures of productivity as well as tolerance against or recovery capacity after disturbance or biological invasions (Benedetti-Cecchi 2006). As primary producers, plants constitute fundamental components of most ecosystems and have therefore been the central focus in the majority of the studies. The relationship between biodiversity and ecosystem function does not seem to be an absolute one, since different factors in nature, the applied spatial and temporal scale, the diversity level investigated, the diversity measure used and the response variable studied may give raise to different BEF-responses varying from strongly negative to strongly positive. Still, a number of studies (e.g. Naeem et al. 1994; Tilman 1996) have demonstrated that primary productivity often is positively related to biodiversity.

In this study, we measured macroalgal biomass, diversity and primary productivity in mesocosms that had been exposed in a crossed way to two levels of nutrient enrichment and two levels of wave exposure for 2 years. We used macroalgal functional groups and registered biomass calculated from cover data and primary productivity (g C produced over time) by measuring changes in pH levels in closed mesocosm water bodies over time during the spring (April), summer (June) and autumn (September) of 2006. We tried to discover structural (biomass/biodiversity) and functional (productivity) differences between treatments, i.e. nutrient and wave levels, but simultaneously we also wanted to check for possible significant BEF-relationships (as a by-product of the biomass/productivity responses to the studied treatments). We hypothesised that algal biomass, especially that of filamentous and sheet-like green algae, would be higher at high nutrient levels and low levels of wave action (due to decreased export and increased accumulation of algal matter). For canopy brown algae and most red algae, we expected a reverse relationship (more brown and red algae

at low nutrient and high wave action levels) due to the nutrient requirements of these groups or a better ability to withstand physical detachment. Regarding biodiversity and production, we hypothesised that algal diversity would be higher in low nutrient and high wave mesocosms, productivity lower in low nutrient and low wave mesocosms and that there would be a positive relationship between diversity and productivity. Following these ideas and with our treatment constellations, the most evident eutrophication effects should thus be found in mesocosms with high nutrient addition and low wave energy, followed by high nutrient addition and high wave action as well as low nutrient addition and low wave action, whereas the smallest effects would occur in mesocosms subjected to low nutrient levels and high wave action. Unique features of this experiment were not only the treatment combinations comprising strict long-term control of two nutrient enrichment levels and two wave energy levels, but also the high degree of internal similarity of parallel treatments with respect to physical background variables, the restricted accessibility to the mesocosms by humans, mammals and birds (and thereby known low levels of uncontrolled error) and known abundance of grazers and predators.

Materials and methods

Solbergstrand rocky littoral mesocosms

We made all measurements in eight rocky littoral mesocosms at the Marine Research Station Solbergstrand by the Oslofjord (59°37′N, 10°39′E) in SE Norway. Each mesocosm had a length of 4.75 m, a breadth of 3.65 m and a depth of 1.35 m (Fig. 1). The water volume was 6–12 m^3, depending on tide level, and the flow-through mesocosms received water from 1 m depth in the Oslofjord at a rate of 5 m^3 h^{-1} and with a short mean water residence time of 2 h, which meant a low influence from phytoplankton in the mesocosms (Bokn et al. 2003). A tidal regulator was coupled to the outlet pipes providing a tidal regime, which simulated natural changes in water level and reflected the local tidal amplitude of 36 cm. A wave machine generated constant wave action (18 strokes per minute, with an average wave amplitude of 11 cm in the high wave treatment and 5.5 cm in the low wave treatment). The effective wave action corresponded roughly to a wind force of up to 5 m/s in the high wave treatment and 2.5 m/s in the low wave treatment.

Since nutrient uptake among algae can saturate at relatively low flow speeds, depending on algal species, a description of the water circulation patterns and velocities is needed for the mesocosms. We carried out these measurements using a small stream cross at about 10 cm depth as well as near the bottom of the mesocosms. The stream cross was formed as a ball with 8 cm diameter, which together with the regular rhythm of the wave bar, enabled good estimates of water flow speed. These water flow speeds should be similar to natural sites in the Oslofjord subjected to comparable wave action.

The history of the rocky littoral communities of the Solbergstrand mesocosms dates back more than 12 years. Rocky shore assemblages were introduced in 1996 by transplanting small boulders with attached macroalgae and associated animals, onto concrete steps in each mesocosm. These steps represented different water depths on a shoreline (Fig. 1). After transplantation, natural community

Fig. 1 Solbergstrand mesocosm diagram showing four steps with inter- and subtidal macroalgal communities, the wave generator and the tidal regulator. The sampling for this article took place all over the basins, i.e. on the steps, the bottom, the walls and the wave bar
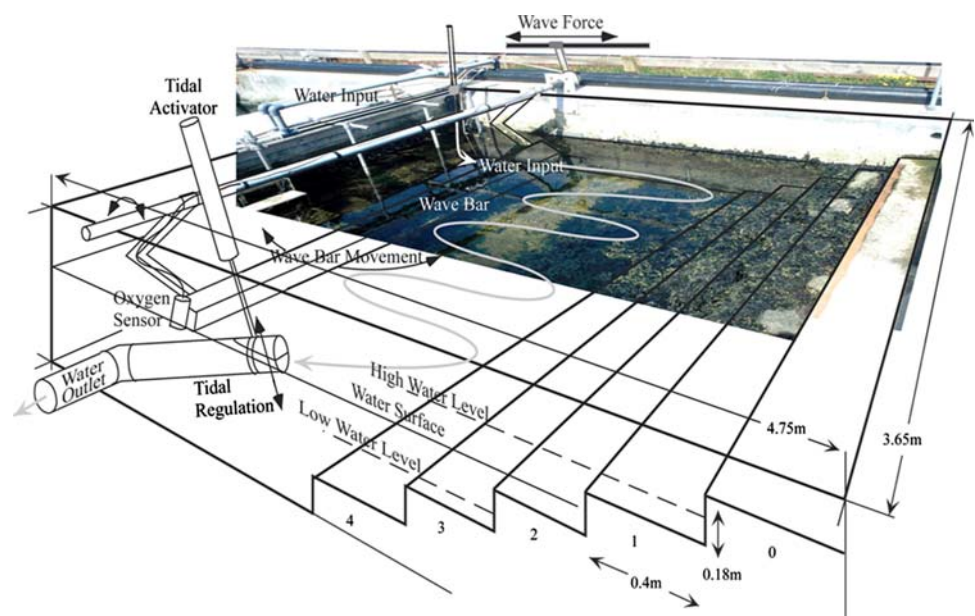
development was allowed to contribute to the assemblages giving raise to mesocosm communities that corresponded well with natural rocky shores of the inner Oslofjord (Bokn and Lein 1978). These mesocosms were first used for a 3-year eutrophication study 1998–2000 (e.g. Bokn et al. 2003) and immediately afterwards for another study on nutrient effects in 2001–2002, followed by a 2-year recovery survey in 2003–2004 (Kraufvelin et al. 2006b), prior to this study. This study started in June 2004, and some initial findings have already been reported by Kraufvelin (2007).

Over the years, more than 45 species of macroalgae and 90 species of macrofauna have been identified in the mesocosms. Brown algae *Fucus serratus* L., *Fucus vesiculosus*, *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jol. and *Laminaria digitata* (Huds.) J.V. Lamour., the red alga *Chondrus crispus* Stackh. and some seasonal red algae (mainly *Ceramium* spp., *Polysiphonia* spp. and *Rhodomela confervoides* (Huds.) P.C. Silva), as well as the green algae *Ulva lactuca* L., *Ulva intestinalis* L. and *Cladophora rupestris* (L.) Kütz. dominated the macroalgal assemblages. Amphipods, isopods, gastropods and blue mussels were the most important grazing animals, whereas sea stars, crabs and a few individuals of small fish (Gobiidae and Labridae) served as predators (Kraufvelin et al. 2002).

Experimental treatments

Before applying nutrient and wave treatments, it had been checked that both the algal and the animal communities had fully recovered from previous experimentation during 1998–2004 (Kraufvelin et al. 2006b; Kraufvelin 2007). We added nutrients, 32 μM inorganic nitrogen (N) and 2 μM inorganic phosphorus (P) above background fjord levels, continuously from 18th June 2004 on to four mesocosms. These nutrient addition levels are similar to concentrations recorded in eutrophic areas locally (Kristiansen and Paasche 1982) and globally (Cloern 2001), and corresponding nutrient addition levels have been utilised as "highs" during previous experiments in these mesocosms (Bokn et al. 2002, 2003; Kraufvelin et al. 2002, 2006a, b). We added nutrients during "summer months" (April–September) as a mixture, which consisted of 14.3 mol N as NH_4NO_3 and 0.9 mol P as H_3PO_4 and had an N/P mol ratio of 16/1. During the winter months (October–March), we did not add extra nutrients, because we considered the background nutrient levels in the fjord during this time of the year as sufficiently high for the enriched mesocosms to stay enriched (Bokn et al. 2002, 2003). In four mesocosms, we reduced the wave action (wave height) by 50% while retaining the same wave frequency. We applied the two factors, nutrients and wave action, to the eight mesocosms in a replicated two-way factorial design ($2 \times 2 \times 2 = 8$). This implied two mesocosms with high nutrient levels and high wave action (HN-HW), two mesocosms with high nutrient levels and low wave action (HN-LW), two mesocosms with low nutrient levels and high wave action (LN-HW) and two mesocosms with low nutrient levels and low wave action (LN-LW).

Sampling methods and grouping of macroalgae

We gathered data for this investigation in spring (April), in summer (June) and in autumn (September) 2006 after 2–2.5 years of nutrient and wave manipulation. Salinity and water temperature data were available for the entire period. During all three sampling periods, we registered the cover of all macroalgal species at the most feasible taxonomic resolution, i.e. without disturbing the communities too much and ripping off attached algae, which would have prevented subsequent mechanically unbiased sampling. We estimated cover layer by layer (including epiphytes) on the steps, on the basin walls, on the bottom and on the wave machine using a 40 cm× 40 cm grid. We transferred the cover values to biomass from known wet weights of known surface areas of all dominating algal species in the mesocosms (Kraufvelin and Lindholm unpublished). When we had all the species biomass data, we applied a functional group approach to the data merging together the species into nine different functional groups (Table 1). The functional group concept was based on algal class (brown, red or green), longevity (perennial or annual) and morphology (bushy, massive, filamentous, sheet-like or encrusting), but did not deviate crucially from the functional group concepts reviewed in Murray et al. (2006).

Estimating mesocosm primary production

Since algae take up and utilise carbon dioxide (CO_2) through photosynthesis, while CO_2 is released through the process of respiration, the pH level in a water body will vary during different times of the day depending on the light conditions and the amount of photosynthetic organisms (pH will raise during light day hours and decrease during dark night hours). Changes in pH over time are therefore useful for calculation of the total amount of carbon that is taken up from or released to a closed water body, if only the total alkalinity, the temperature and the salinity of the water are known (Hansson 1973; Almgren et al. 1975). Previously, Oviatt et al. (1986) have used pH changes in mesocosms to estimate production and respiration and they reported a good synchronicity with oxygen measurements, which are more commonly used for these purposes.

The pH-CO_2 method for measuring macroalgal productivity was based on registration of changes in pH values in entire mesocosms both during day time and during night

Table 1 List of the mapped macroalgal species in the study and arguments used for construction of functional groups

Species	Class	Longevity	Morphology	Functional group: abbreviation, description (number)
Ascophyllum nodosum (L.) LeJol.	Brown	Perennial	Bushy	BPB: brown perennial bushy (I)
Fucus vesiculosus L.	Brown	Perennial	Bushy	BPB: brown perennial bushy (I)
Fucus spiralis L.	Brown	Perennial	Bushy	BPB: brown perennial bushy (I)
Fucus serratus L.	Brown	Perennial	Bushy	BPB: brown perennial bushy (I)
Sargassum muticum (Yendo) Fensholt	Brown	Perennial	Bushy	BPB: brown perennial bushy (I)
Laminaria digitata (Huds.) J.V. Lamour	Brown	Perennial	Massive	BPM: brown perennial bushy (II)
Chordaria flagelliformis (O.F. Müller) C. Agardh	Brown	Annual	Filamentous	BAF: Brown annual filamentous (III)
Ectocarpus siliculosus (Dillwyn) Lyngb.	Brown	Annual	Filamentous	BAF: brown annual filamentous (III)
Pilayella littoralis (L.) Kjellm.	Brown	Annual	Filamentous	BAF: brown annual filamentous (III)
Chondrus crispus Stackh.	Red	Perennial	Bushy	RPB: red perennial bushy (IV)
Delesseria sanguinea (Huds.) J.V. Lamour	Red	Perennial	Bushy	RPB: red perennial bushy (IV)
Furcellaria lumbricalis (Huds.) J.V. Lamour	Red	Perennial	Bushy	RPB: red perennial bushy (IV)
Porphyra umbilicalis (L.) J. Agardh.	Red	Annual	Sheet-like	RAS: red annual sheet-like (V)
Hildenbrandia rubra (Sommerf.) Menegh.	Red	Perennial	Encrusting	No biomass estimated in the study
Phymatolithon lenormandii (Aresch.) W.H. Adey	Red	Perennial	Encrusting	No biomass estimated in the study
Callithamnion corymbosum (J.E. Smith) Lyngb.	Red	Perennial	Filamentous	RPF: red perennial filamentous (VI)
Ceramium spp.	Red	Perennial	Filamentous	RPF: red perennial filamentous (VI)
Polysiphonia spp.	Red	Perennial	Filamentous	RPF: red perennial filamentous (VI)
Rhodomela confervoides (Huds.) P.C. Silva	Red	Perennial	Filamentous	RPF: red perennial filamentous (VI)
Cladophora rupestris (L.) Kütz.	Green	Perennial	Filamentous	GPF: green perennial filamentous (VII)
Cladophora glomerata (L.) Kütz.	Green	Annual	Filamentous	GAF: green annual filamentous (VIII)
Chaetomorpha linum (O.F. Müller) Kütz.	Green	Annual	Filamentous	GAF: green annual filamentous (VIII)
Ulva intestinalis L.	Green	Annual	Filamentous	GAF: green annual filamentous (VIII)
Ulva lactuca L.	Green	Annual	Sheet-like	GAS: green annual sheet-like (IX)

time in spring, summer and autumn. Prior to each pH session, which consisted of pH monitoring during 2 h of maximum light (day time) or 2 h of darkness (night hours), we put all basins on high water, and after they all were totally filled with water (12 m^3) we shut down the water inlet. We closed the inlet, because the alkalinity of a closed water body does not change and because we did not want the incoming fjord water to affect the results. At each sampling occasion, we registered the pH value (to three decimals) and the temperature (to one decimal) once an hour in all mesocosms by the aid of a pH sensor of the model WRW pH 340i. We started and ended each pH session by a calibration measurement in a submerged bottle, which contained a standardised seawater buffer of 25 psu.

To get total yearly production estimates per m^2 bottom area, we extrapolated the production values across seasons for each treatment type and divided the obtained values by the benthic area effectively available for production = 17.2 m^2 (i.e. the steps and the mesocosm bottom, not including vertical walls and the wave bar). Those values were compared to values from the literature and to direct production measurements from the mesocosms

between April and September 2006 using changes in standing stock, export and accumulation measurements as well as estimates of the grazed amount (Lindholm 2008).

Relating diversity to productivity

To explain our diversity/productivity findings and to test possible significant BEF-relationships, we related macroalgal diversity to productivity in spring, summer and autumn. We utilised Shannon–Wiener diversity (log base e) and Margalef's species richness as measures of diversity and net primary productivity (production estimates during light day hours minus respiration estimates during dark night hours, separately for different seasons due to differences in day length) as a measure of carbon production.

Statistical analysis

We analysed differences in macroalgal biomass, diversity and production by a two-way ANOVA using the model $X_{ijk} = \mu + N_i + W_j + NW_{ij} + e_{k(ij)}$, where X_{ijk} represents the dependent variable at nutrient level i and wave action level j, N_i and W_j represent the effects of treatments

N (nutrients) and W (waves), NW_{ij} represents interaction among these factors and $e_{k(ij)}$ represents the error due to smaller-scale differences between samples. We analysed the relationship between diversity and productivity by Pearson's correlation analysis. We run the statistical analyses in GMAV5 or in SPSS 16.0. Before running these parametric tests, we checked the normality by Kolmogorov–Smirnov's test and homogeneity of variances by Cochran's C-test. To homogenise variances, it was sometimes necessary to use a square-root transformation, $\sqrt{(x + 1)}$, or a logarithmic transformation, $\ln (x + 1)$. For all significance tests, alpha was set at 0.05.

Results

Mesocosm water flow, temperature and salinity

The water circulation patterns were similar in all mesocosms, while the flow speeds differed due to the level of wave action. At high tide, in all mesocosms, there was a regular surface circulation with water up-welling around the middle of the wave bar and streaming towards the middle of the mesocosm step zone, continuing along the step zone and turning back to the sides of the wave bar, where the water would sink or turn towards the middle of the bar again making another turn (see Fig. 1 for a picture of a mesocosm). The resulting water velocities were at high tide around 5–6 cm s^{-1} in high wave treatments and 2.5–3 cm s^{-1} in low wave treatments. At low tide, the main circulation was similar to the situation at high tide, but the speeds were now higher, about the triple, with velocities around 15–20 cm s^{-1} or 7.5–10 cm s^{-1} in high and low wave treatments, respectively. Just beneath and above the wave bar, regular water movements were even greater, 20–40 cm s^{-1}, directed in the same direction as the wave bar movement, but there were also vertical and irregular loops of similar speeds. This applies to the basin floor within 0.5–1 m from the wave machine. More than 1 m away from the wave bar, water movements along the basin floor were small, about 0–5 cm s^{-1} in the high wave treatments and half the velocity in the low wave treatments. Here it should also be pointed out that a halved flow speed in low wave treatments implies that the force acting on organisms is only one-fourth of the corresponding force in high wave treatments.

Both the water temperature and the salinity varied during the sampling period in 2006 (Fig. 2). The water temperature increased from 1.9°C in April to 22.7°C in July and dropped again to 17°C in September. The salinity ranged from 13.9 to 28.5 psu (Fig. 2) with highest salinities in May and September, but with an occasional low in early June due to heavy rainfall, which affected the salinity of the incoming water from the fjord.
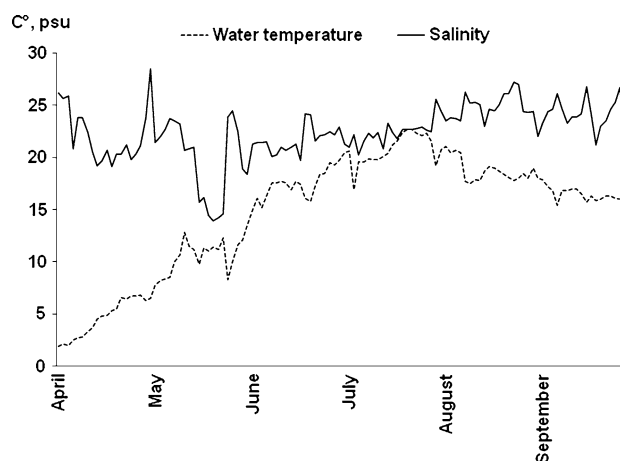

Fig. 2 Temperature (in °C) and salinity (in ‰) of the incoming water during 2006

Macroalgal biomass and biodiversity

Average standing stock of macroalgal biomass (across all mesocosms) increased from 35 kg wet weight (wwt) in spring to almost 50 kg in autumn, but less so in high nutrient than in low nutrient treatments (Fig. 3). There were no significant interactions between the applied nutrient and wave treatments on total macroalgal biomass, but nutrient enrichment caused a significantly lower total biomass of algae, a pattern that became more and more evident throughout summer (Table 2). There was only one significant effect of wave action on total biomass, i.e. in autumn, when we observed a higher biomass of macroalgae in high wave treatments (Figs 3; Table 2). At this stage, there was a clear decreasing sequence in total macroalgal biomass from LN-HW (highest values), via LN-LW and HN-HW, to HN-LW (lowest values) (Fig. 3).

When total macroalgal biomass was split into the nine functional groups (Table 1) contrasting responses among different macroalgal groups became evident. Perennial bushy brown macroalgae dominated all mesocosms at all sampling occasions, although the dominance was less obvious in the high nutrient mesocosms (Fig. 4a–h). During all three seasons, there were significantly more perennial bushy brown macroalgae in low nutrient mesocosms than in high nutrient mesocosms, and in the autumn there were also significantly higher biomass of perennial bushy brown macroalgae in high wave treatments than in low wave treatments (Fig. 4a; Table 3). Perennial massive brown macroalgae, i.e. *Laminaria digitata*, mainly occurred in the high nutrient treatments, but there were no significant differences due to high variability between replicates (Fig. 4b; Table 3). Annual filamentous brown macroalgae, on the other hand, had significantly higher biomass in low nutrient treatments in summer and a

Fig. 3 Total macroalgal biomass (g wet weight, mean ± SD) in the various treatments in spring, summer and autumn. Significant differences (two-way ANOVA) are marked as *$P \leq 0.05$ and **$0.001 < P \leq 0.01$; *LN* low nutrient, *HN* high nutrient, *HW* high wave, *LW* low wave
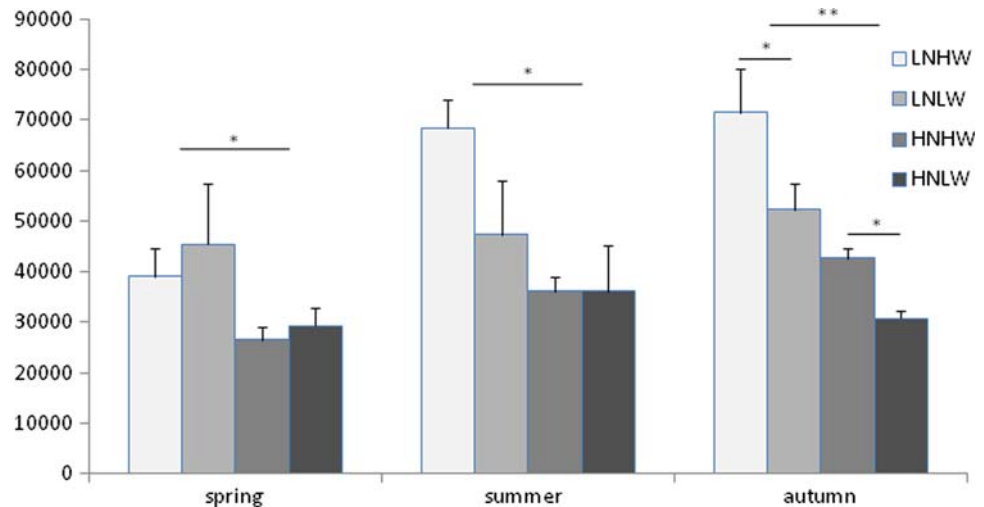

Table 2 Differences in total biomass as analysed by two-way factorial ANOVAs

Season	Source	df	MS	F	P
Spring	Nutrient	1	411.27	8.34	0.044*
	Wave	1	42.23	0.86	0.406
	Nutrient × wave	1	6.20	0.13	0.740
	Error	4	49.04		
Summer	Nutrient	1	935.71	15.58	**0.017***
	Wave	1	227.48	3.79	0.124
	Nutrient × wave	1	224.79	3.74	0.125
	Error	4	60.04		
Autumn	Nutrient	1	1,263.78	46.96	**0.002****
	Wave	1	483.45	17.96	**0.013***
	Nutrient × wave	1	27.71	1.03	0.368
	Error	4	26.91		

Significant *P*-values are in bold style, * $P \leq 0.05$, ** $P \leq 0.01$

significant interaction between nutrient and wave treatments in autumn (Fig. 4c; Table 3). SNK-corrected a posteriori analyses revealed that this interaction was due to a significantly higher biomass in low nutrient treatments at low wave action. For red algae, there were no significant differences for perennial bushy algae and for annual sheet-like algae, but there was a significantly higher biomass of perennial filamentous red algae in low nutrient treatments in summer (Fig. 4d, e; Table 3). Perennial filamentous green algae were not significantly different between the treatments (Fig. 4f; Table 3), but both annual filamentous and annual sheet-like green algae had throughout significantly higher biomass in high nutrient treatments with the exception of annual filamentous green algae in spring (Fig. 4g, h). There were also some clear sequences along mesocosm treatments with regard to biomass of perennial

bushy brown algae in summer and autumn, i.e. from LN-HW (highest values), via LN-LW and HN-HW, to HN-LW (lowest values) and a complete reverse sequence for annual sheet-like green algae in spring, summer and autumn and for annual filamentous green algae in autumn.

Both Margalef's species richness and Shannon–Wiener diversity (as well as Pielou's evenness, data not shown) were higher in high nutrient than in low nutrient treatments, although not significantly so for Margalef's species richness until the autumn (Fig. 5a, b; Table 4), whereas for the wave treatment, there were no significant differences and neither were there any significant interactions The Shannon–Wiener diversity sequence from LN-HW (lowest values), via LN-LW and HN-HW, to HN-LW (highest values) in autumn (Fig. 5b; Table 4) is very clear and also very interesting, since it was again the same sequence that was found for green annual sheet-like and filamentous algae above and exactly the opposite sequence to the one that was found for total biomass and perennial bushy brown algal biomass in summer and autumn (Figs. 3, 4a, g, h; Tables 2, 3, 4). Moreover, it was totally opposite to what had been hypothesised at the start of the experiment. The higher diversity indices in high nutrient treatments are not only due to a more even distribution of macroalgae over species, but also due to a higher biomass of green algae (*Cladophora rupestris*, *Ulva intestinalis* and *Ulva lactuca*) and the brown alga *Laminaria digitata*.

Macroalgal production

The total mesocosm production and respiration values measured by the pH-CO_2 method were lower in spring (production below 4 g C h^{-1}, respiration around 1 g C h^{-1}) than in summer or autumn (production almost 6 g C h^{-1}, respiration around 3 g C h^{-1}) (Fig. 6a–c). There was no significant effect of wave action on
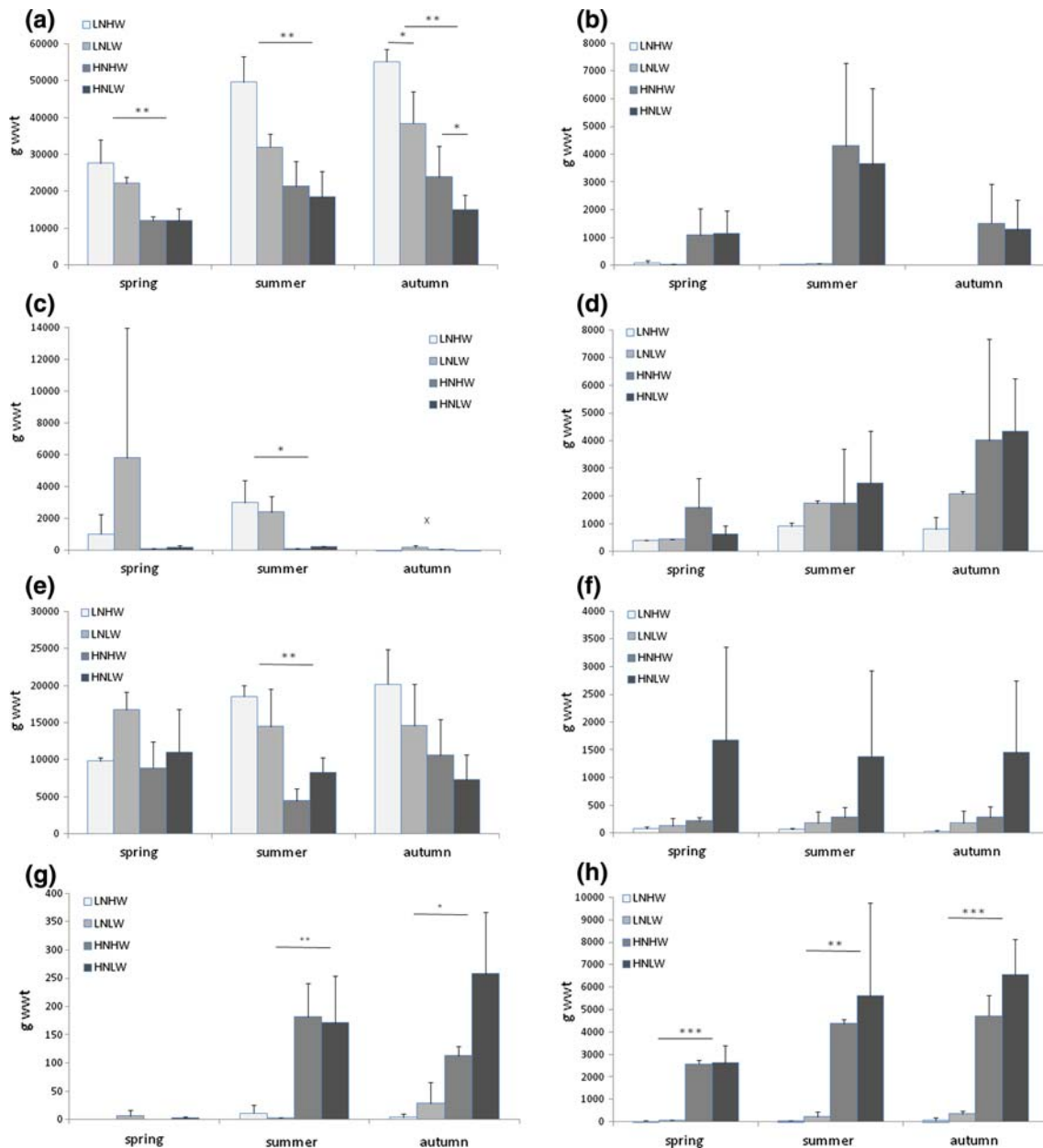
Fig. 4 Total biomass of different functional groups of macroalgae (g wet weight, mean ± SD) in the various treatments in spring, summer and autumn: **a** brown perennial bushy, **b** brown perennial massive, **c** brown annual filamentous (X = significant interaction), **d** red perennial bushy, **e** red perennial filamentous, **f** green perennial filamentous, **g** green annual filamentous, **h** green annual sheet-like macroalgae. Significant differences (two-way ANOVA) are marked as *$P \leq 0.05$, **$0.001 < P \leq 0.01$ and ***$P \leq 0.001$; *LN* low nutrient, *HN* high nutrient, *HW* high wave, *LV* low wave

production and neither were there any significant interactions. In spring, there were no significant effects of nutrient treatment on production during the day or on respiration during the night (Fig. 6a; Table 5). In summer, there was a significantly higher production during the day in low nutrient systems and a significantly higher respiration during the night in high nutrient systems (Fig. 6b; Table 5). In autumn, there was a significantly higher respiration during night in high nutrient systems (Fig. 6c; Table 5).

Table 5). An averaging of the mesocosm production numbers over the seasons and across treatments would give a yearly total estimate of 9,360 g C per mesocosm in the low nutrient treatments and 15–25% less in the high nutrient treatments. The actual estimated yearly numbers (excluding the mesocosm walls and the wave bar) from pH-CO_2 measurements are LN-HW = 542 g C m^{-2}, LN-LW = 539 g C m^{-2}, HN-HW = 465 g C m^{-2} and HN-LW = 398 g C m^{-2}.

Table 3 *P*-values for differences in biomass for different algal functional groups and seasons as analysed by two-way factorial ANOVAs

Source	I	II	III	IV	V	VI	VII	VIII	IX
Spring									
N	**0.008****	0.073	0.315	0.112	NA	0.265	0.118	0.718	**<0.001***[a]**
W	0.359	0.992	0.790	0.312	NA	0.148	0.208	0.306	0.620
N × W	0.365	0.902	0.884	0.229	NA	0.401	0.280	0.551	0.683
Summer									
N	**0.009****	0.051	**0.013***	0.132	NA	**0.008****	0.176	**0.009****	**0.002***[b]**
W	0.080	0.838	0.715	0.788	NA	0.965	0.301	0.812	0.366
N × W	0.167	0.826	0.593	0.319	NA	0.129	0.509	0.974	0.446
Autumn									
N	**0.004****	0.089	0.144	0.135	0.136	0.066	0.081	**0.015***	**<0.001****
W	**0.050***	0.864	0.482	0.614	0.966	0.256	0.176	0.107	0.180
N × W	0.443	0.864	**0.041*[a]**	0.760	0.812	0.744	0.426	0.215	0.292

N Nutrient addition, *W* wave action, *I–IX* algal functional groups in the following way: *I* brown perennial bushy, *II* brown perennial massive, *III* brown annual filamentous, *IV* red perennial bushy, *V* red annual sheet-like, *VI* red perennial filamentous, *VII* green perennial filamentous, *VIII* green annual filamentous, *IX* green annual sheet-like, *NA* not analysed, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

[a] Transformed with $\sqrt{(x + 1)}$

[b] Transformed with $\ln (x + 1)$

Fig. 5 a Margalef's species richness index and **b** Shannon–Wiener diversity index for the various treatments (mean ± SD) in spring, summer and autumn (*labels as previously mentioned*)
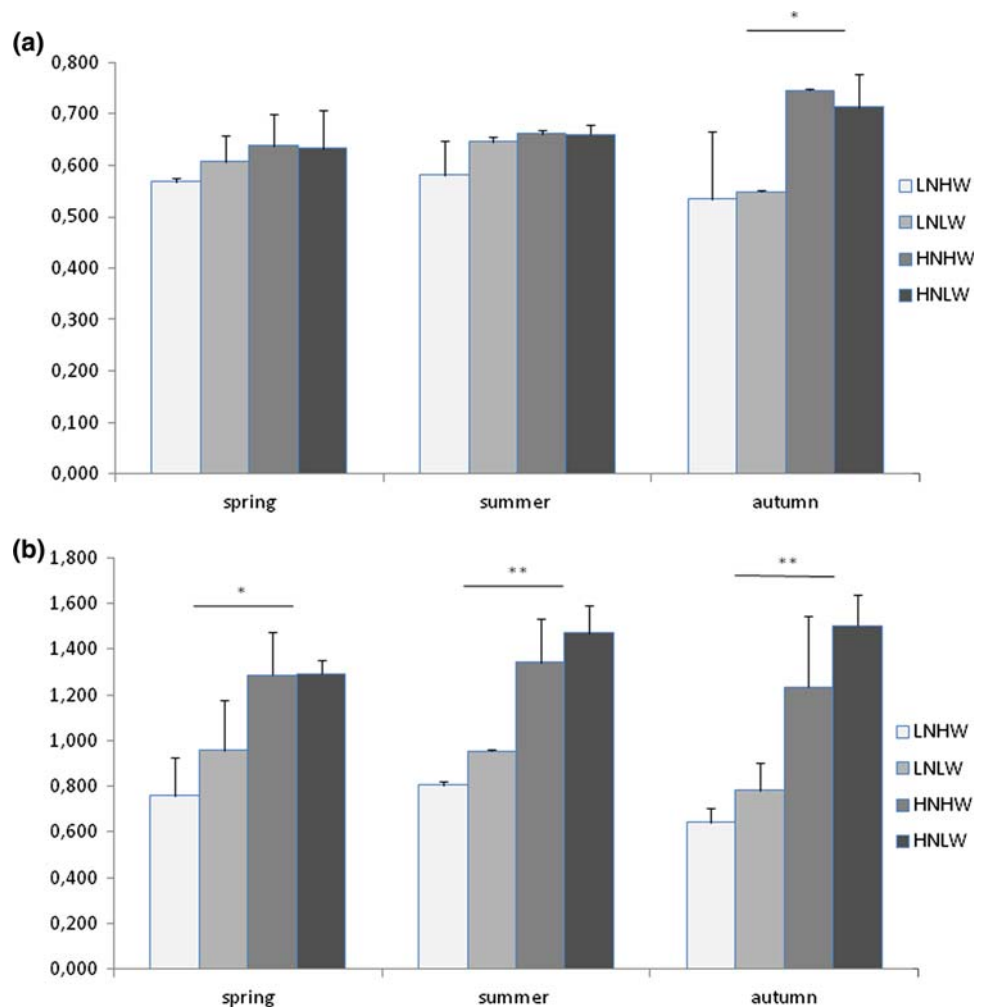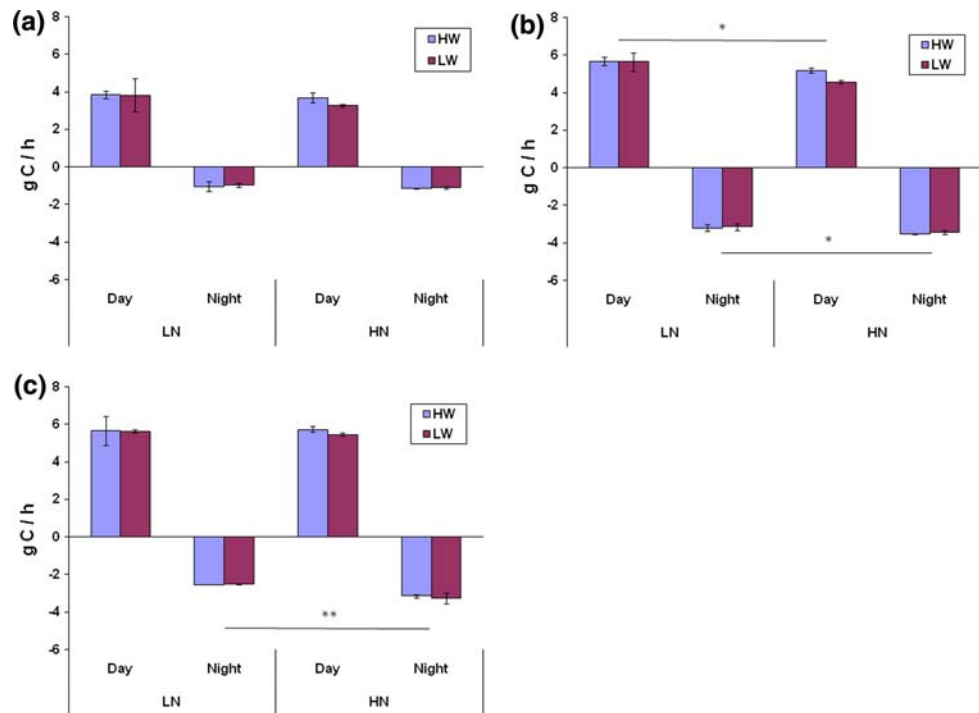
Table 4 Differences in Margalef's species richness and Shannon–Wiener diversity as analysed by two-way factorial ANOVAs

Season	Index	Source	df	MS	F	P
Spring	Shannon	Nutrient	1	0.376	12.85	**0.023***
		Wave	1	0.021	0.71	0.447
		Nutrient × wave	1	0.190	0.65	0.465
		Error	4	0.029		
	Margalef	Nutrient	1	0.004	1.49	0.289
		Wave	1	0.001	0.18	0.695
		Nutrient × wave	1	0.001	0.31	0.605
		Error	4	0.003		
Summer	Shannon	Nutrient	1	0.556	43.94	**0.003****
		Wave	1	0.038	3.00	0.158
		Nutrient × wave	1	0.000	0.01	0.912
		Error	4	0.013		
	Margalef	Nutrient	1	0.005	3.65	0.129
		Wave	1	0.002	1.60	0.274
		Nutrient × wave	1	0.002	1.71	0.261
		Error	4	0.001		
Autumn	Shannon	Nutrient	1	0.861	25.99	**0.007****
		Wave	1	0.085	2.55	0.185
		Nutrient × wave	1	0.008	0.24	0.651
		Error	4	0.033		
	Margalef	Nutrient	1	0.071	13.31	**0.022***
		Wave	1	0.000	0.03	0.872
		Nutrient × wave	1	0.001	0.20	0.675
		Error	4	0.005		

$* P \leq 0.05$, $** P \leq 0.01$

Examination of BEF-relationships

Nutrient enrichment caused a higher biodiversity and a lower productivity suggesting a negative relationship between the two. This was verified by a significant negative Pearson's correlation between Shannon–Wiener diversity (and Pielou's evenness, data not shown) and net primary productivity estimated by the pH method in summer (Fig. 7a–c). We also found a significant negative correlation between Margalef's species richness and net primary productivity in autumn (Fig. 7d). For the significant relationship between Shannon diversity and productivity in summer (Fig. 7b), it is noteworthy that the two lowest diversity values represented LN-HW mesocosms, the following two represented LN-LW mesocosms, the next two represented HN-HW mesocosms, while the two highest diversity values represented HN-LW mesocosms. With regard to production estimates, the reverse sequence could be seen for nutrient enriched mesocosms in both summer and autumn, i.e. the lowest net primary productivity was always found in the two HN-LW mesocosms, followed by the HN-HW mesocosms.

Discussion

Macroalgal biomass and diversity

At this stage of experimentation (2–2.5 years), the changes in macroalgal community structure due to both nutrient

Fig. 6 Produced g carbon (C)/h during daytime and consumed amount during night time for the various treatments (mean ± SD) estimated by the pH-CO_2 method in **a** spring, **b** summer, **c** autumn (*labels as previously mentioned*)

Table 5 Differences in production and respiration (measured as g C h^{-1} during day and night, respectively) as analysed by two-way factorial ANOVAs

Month	Index	Source	df	MS	F	P
April	Production	Nutrient	1	0.242	1.10	0.353
		Wave	1	0.099	0.45	0.538
		Nutrient × wave	1	0.073	0.32	0.602
		Error	4	0.219		
	Respiration	Nutrient	1	0.031	1.48	0.290
		Wave	1	0.007	0.34	0.590
		Nutrient × wave	1	0.000	0.00	0.963
		Error	4	0.021		
June	Production	Nutrient	1	1.240	16.38	**0.016***
		Wave	1	0.202	2.66	0.178
		Nutrient × wave	1	0.171	2.26	0.207
		Error	4	0.076		
	Respiration	Nutrient	1	0.183	9.81	**0.035***
		Wave	1	0.015	0.82	0.416
		Nutrient × wave	1	0.000	0.03	0.865
		Error	4	0.019		
September	Production	Nutrient	1	0.007	0.05	0.840
		Wave	1	0.045	0.29	0.618
		Nutrient × wave	1	0.029	0.19	0.689
		Error	4	0.155		
	Respiration	Nutrient	1	0.062	53.43	**0.002****
		Wave	1	0.000	0.32	0.600
		Nutrient × wave	1	0.000	0.39	0.564
		Error	4	0.001		

* $P \leq 0.05$, ** $P \leq 0.01$

enrichment and decreased wave action (and largely expressed as decreased biomass of brown and red algae and increased biomass of green algae) partly contradicts previous findings in these mesocosms, especially with regard to timing and intensity (Bokn et al. 2002, 2003; Kraufvelin et al. 2006a), although some hint of these kinds of responses already could be given by Karez et al. (2004), Kraufvelin et al. (2006b) and Kraufvelin (2007). Generally, perennial bushy brown algae still dominated in all mesocosms, although their biomass decreased in high nutrient treatments, while green algae did relatively badly in low nutrient treatments and increased their biomass markedly in high nutrient treatments. These changes were mainly driven by changes in abundance of the brown alga *Fucus serratus* (a more abundant species at low nutrients) and the green algae *Ulva lactuca* and *Ulva intestinalis* (more abundant species at high nutrients). Although most red algae were represented by filamentous species, these do not seem to have been affected in the same way as green filamentous algae. On the contrary, there were occasionally significantly more red algae in low nutrient treatments than

in high nutrient treatments (i.e. in summer 2006). The reason behind this is unclear, since red algae have a good ability to absorb light and should therefore not be limited by overshadowing, but only benefit from enhanced nutrient levels. In a long-term investigation in the Skagerrak area, a general increase in both perennial bushy red algae and annual filamentous red algae was registered as a result of increased nutrient levels (Johansson et al. 1998).

A wave reduction over more than 2 years had clear negative effects on the macroalgal community structure compared with the minor early impact (2 months) reported by Kraufvelin (2007). It is generally accepted that tidal currents and wave action (Lewis 1964), in combination with an effective export of organic matter, may moderate the accumulation of ephemeral algae and, thus also, render some rocky shore communities relatively resistant to nutrient enrichment. In the Solbergstrand mesocosms, a fast water exchange may prevent accumulation of detached algal assemblages through export from the littoral (Barrón et al. 2003; Bokn et al. 2003; Christie and Kraufvelin 2004). Moreover, water movement has been shown to directly stimulate the growth of aquatic organisms. Leigh et al. (1987) gave examples on communities where macroalgal growth had increased with intermediate and high wave action. Along exposed coasts, waves increase the ability of algae to take up nutrients and sunlight and may also protect already attached perennial algae by repelling competing annual species. These explanations may also hold true for the mesocosms, since there were many signs of positive influence on the amount of macroalgae by wave action (e.g. Figs. 3, 4; Tables 2, 3). In addition to the effects caused by the physical force from the wave action (i.e. higher export rate and less accumulation), the differences in wave energy also affect the macroalgal community by causing differences in water movement. A halved water movement causing decreased nutrient uptake may also partly explain the smaller standing stocks of total macroalgae (brown annual bushy) and the improved competitive abilities for annual algae (green filamentous and sheet-like algae) in the low wave treatments. According to McGlathery et al. (2007), the water exchange rate may also be a possible key factor originally determining whether it will be phytoplankton or macroalgae that will contribute the most when a system becomes eutrophicated. If the water exchange rate is slow, the phytoplankton will not be flushed away, but will instead stay and eventually outcompete the benthic macroalgae through shadowing (Valiela et al. 1997; McGlathery et al. 2007). In the Solbergstrand mesocosms, however, the water exchange rate was rather rapid. This means that treatment specific plankton communities never really were allowed to form, accumulate in the water column and have influence on the results (Bokn et al. 2003).
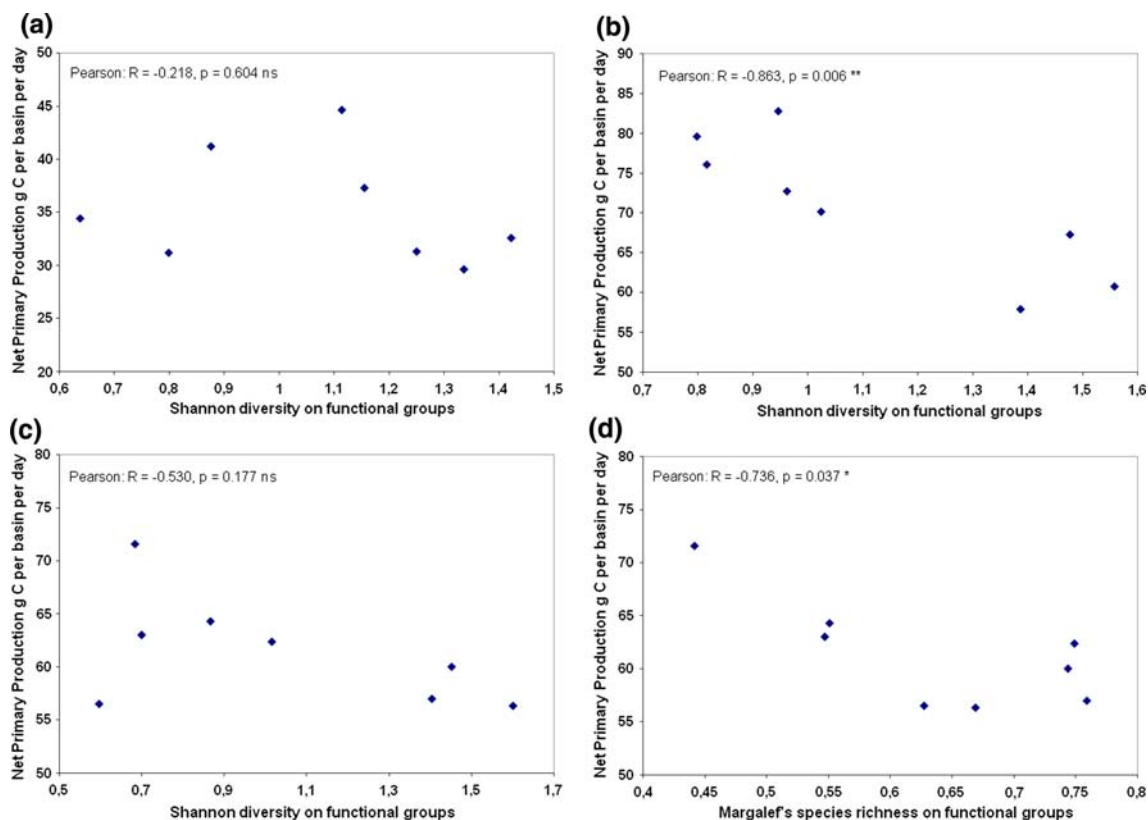
Fig. 7 Correlation between diversity and net primary production (NPP) as g C produced day^{-1} mesocosm^{-1} (estimated by the pH-CO$_2$ method): **a** Shannon–Wiener diversity versus NPP in spring, **b** Shannon–Wiener diversity versus NPP in summer and **c** Shannon–Wiener diversity versus NPP in autumn, **d** Margalef's species richness versus NPP in autumn; R = Pearson's correlation coefficient, P = significance level

Loss of biodiversity through the loss of perennial species is often coupled to eutrophication (e.g. Valiela et al. 1997; Johansson et al. 1998; Rabalais 2005; Worm et al. 2006), but this could not be supported by the present study. The degree of nutrient enrichment or the differences in wave action may not have been strong enough to entirely remove species from the mesocosms. Instead a more even species distribution was observed at high nutrient treatments, and later at low wave treatments, which in turn gave higher values for the diversity indices in these treatments. It must also be remembered here that nutrient addition does not necessarily equal eutrophication, which is basically due to the supposed unimodal relationship between the two, i.e. on the right side of the relationship we have eutrophication, but on the left side of the relationship we may have positive effects on diversity. In the view of this, the diversity results are not very spectacular, but only in accordance with the intermediate disturbance hypothesis (Connell 1978), which predicts depressed diversity at low disturbance due to the competitive exclusion of inferior competitors by one or a few dominant species and an increased diversity at increasing, but moderate stress/disturbance levels. Although this hypothesis is somewhat controversial

(Mackey and Currie 2001), it has often been supported by studies from marine hard bottom communities (e.g. Lubchenco 1978; Paine and Levin 1981; Valdivia et al. 2005) and also previously in these mesocosms (Kraufvelin et al. 2006b; Kraufvelin 2007).

Together with nutrient enrichment, grazing has been suggested as a key factor capable of explaining quite a few of the patterns and processes that can be seen on rocky shores affected by human activity (Kraufvelin et al. 2006a; Worm and Lotze 2006; Russell and Connell 2007; Masterson et al. 2008) and in nutrient-rich and nutrient-poor ecosystems in general (Proulx and Mazumder 1998). Primary consumers may also have a positive effect on algal diversity, since selective grazing on algal propagules may prevent mass occurrence of algae (Worm et al. 2000). Hillebrand (2003) found that grazing and nutrients had opposite effects on species diversity of epiphytic algae, i.e. nutrient enrichment increased and grazing decreased species richness. Worm et al. (2002) manipulated the nutrient availability and grazing pressure on two sheltered rocky shore communities of different productivity and showed strong reverse effects on diversity by these factors, but that they switched roles between high and low productive

systems following the pattern described by Proulx and Mazumder (1998). In high productive systems, nutrient enrichment decreased diversity, while grazing increased diversity. In low productive systems, the case was the reverse. Similarly, Masterson et al. (2008) found, during a nutrient limited period of the year, that positive effects of nutrient enrichment on macroalgal cover were generally lower than the negative effects of grazer control; although at the peak of algal cover, nutrient effects were apparent irrespective of grazer treatment. According to this, the grazers affect the diversity of primary producers regardless of nutrient levels, although they do not seem to be capable of buffering the effects of heavy nutrient loads (Kraufvelin et al. 2006a; Worm and Lotze 2006; Russell and Connell 2007; Masterson et al. 2008).

Macroalgal production

Macrophytic communities are generally considered to be autotrophic, i.e. to produce more than what is being consumed (Gattuso et al. 1998). This excessive production should lead to increased biomass standing stock, increased accumulation and increased export of organic matter (Barrón et al. 2003). Since rocky shores are subjected to both waves and tidal action, macroalgal communities will have a higher degree of export than accumulation and degradation within the system (Duarte and Cebrian 1996). The amount of export depends on the floating capacity of the algal material and how much wave action the community is subjected to (Cebrian 2002). In the Solbergstrand mesocosms, we could also add the role of the outlet pipe and its operation, i.e. the additional constraints this put on the macroalgal export compared to the function of open natural shores. The outlet pipe in combination with much lower maximum wave sizes will mean that the relative roles of macroalgal accumulation and degradation probably were much bigger in the present study than the role of the export.

The total yearly carbon production estimated from the values measured in this study, i.e. a range of 398–542 g C m^{-2} (lower in high nutrient treatments and higher in low nutrient treatments) fits into the range of 300–1,300 g C m^{-2} year^{-1}, which previously has been reported for fucoid dominated communities (Lüning 1990; Barrón et al. 2003). For comparison, the direct estimations of produced carbon during April–September, which were made parallel to this study, rendered values in the size of 320–676 g C m^{-2} (Lindholm 2008), i.e. a little bit higher (since the winter season was not included) and a little bit more variable (because also export, grazing and degradation now influenced the results). When looking at the data, one must also remember that the mesocosm area used for the calculation does not include all available substrates,

since the mesocosm walls, the vertical parts of the steps and the wave bar were excluded. At the same time, parts of the mesocosm floor did not support maximum presence of macroalgae, which means that at least the values estimated from pH-CO$_2$ measurements may be slightly underestimated.

An increased primary productivity is a typical symptom related to nutrient enrichment, although this does not always have to be the case, as may be exemplified by the present study. Even though fast growing algae and plankton have a greater productivity per unit weight than slow growing algae, the latter may compensate their slow production speed by having a bigger biomass (Sand-Jensen and Borum 1991). Due to interspecific differences in nutrient demands, bigger long-lived macroalgae can maintain almost a maximum growth rate also at low nutrient levels, while fast growing algae are much more restricted by low nutrient concentrations (Pedersen and Borum 1996). In this study, the total biomass and the total productivity were highest in LN-HW. The second highest total biomass was found in LN-LW, which also had the second highest productivity values.

Coupling diversity to ecosystem functioning

Only few experiments have investigated BEF-relationships on rocky shores and hard substrata (Benedetti-Cecchi 2006), and only a handful of these studies has explicitly investigated the roles of macroalgal diversity (Allison 2004; Bracken and Nielsen 2004; Bruno et al. 2005, 2006; Stachowicz et al. 2008a, b; Arenas et al. 2009). Allison (2004) investigated responses to heath stress among intertidal communities of various diversity levels and found that original biomass tended to determine the sensitivity against disturbance more than species richness. Bracken and Nielsen (2004) investigated changes in intertidal macroalgal diversity with nitrogen loading by invertebrates and found that a fourfold increase in the ammonium loading rate was associated with a doubling in the number of macroalgal species and that macroalgal assemblages in more species-rich pools were characterised by higher rates of biomass-specific ammonium uptake. Bruno et al. (2005) conducted field and mesocosm experiments to measure the effects of macroalgal identity and number of species on primary productivity and biomass and noticed that the effect of the number of species on biomass increase was positive and statistically significant, but mostly weaker than the pure influence of species identity. In a field and mesocosm study on the influence of macroalgal identity and richness on the primary productivity of coral reefs, Bruno et al. (2006) found positive effects of species identity, while the effects of diversity were marginal. Stachowitz et al. (2008ab) demonstrated the importance of

long-term experiments and field contra mesocosm experiments in their studies showing that seaweed species richness increased biomass accumulation and they therefore supposed that the strength of diversity on ecosystem processes in natural marine ecosystems likely had been underestimated in the past. Finally, Arenas et al. (2009) reported positive relationships between macroalgal species richness and productivity for natural intertidal boulder assemblages.

Opposite to most other BEF-studies on macroalgae our long-term experiment demonstrated significantly negative relationships between diversity and productivity, which on the whole may be attributed to a greater significance of species identity (e.g. the role of brown Fucales) above the number of species per se. However, it must be pointed out here that this study did not specifically test the effects on production from diversity levels (number of species) that had been manipulated in a controlled way (this part of the study is merely derived as a by-product) and that there is a causality problem, since the treatments in themselves also have effects on production. Nevertheless, different macroalgal densities were obtained naturally by changing the environmental conditions, and the significant negative relationships may be attributed both to the diversity of the assemblages present and to the applied treatments. In addition to the somewhat surprising results for diversity and production and thereby the negative BEF-relationships, another take home message of the present study may thus be the very same as in Allison (2004) and Goodsell and Underwood (2008), i.e. that the influence of diversity on community dynamics is complex and will depend on the characteristics of the stress as well as the characteristics of the species present in the community. Our results also echo those of Jiang et al. (2008) in the sense that for a particular function (here productivity), the exact form of the BEF-relationship may depend on how the functional groups relate to their competitive abilities in the community. Finally, the recent results from the cross-system analyses of fertilization effects on producer richness and productivity by Hillebrand et al. (2007) and Gruner et al. (2008) are supportive of our negative correlation between primary production and diversity. These studies also highlight the context dependency of the findings.

Several recent experiments on grasslands (e.g. Fridley 2002) and in aquatic environments (Downing and Leibold 2002; Bruno et al. 2005, 2006; O'Connor and Crowe 2005; Arenas et al. 2006) have shown that species composition and number or identity of functional groups also can have a bigger influence than diversity on ecosystem functions. The effects of plant and algal diversity on primary productivity can often be marginal and sometimes impossible to discover, since highly productive species often fail to dominate in highly diverse plant communities by so called

negative selection (Hooper and Dukes 2004; Bruno et al. 2005). Even though the diversity in our study did not show very strong significant negative relationships with productivity and for all investigated variables at all times, there were clear shifts in species composition between the treatments and also clear differences in production estimates. With regard to single diversity variables, Shannon–Wiener diversity gave more significant results than Margalef's species richness, which shows that there is a difference if only the number of species is counted or both the number of species and the density are registered (see also Arenas et al. 2009). Due to the use of functional groups and the general dominance of only a few species in the mesocosms, we considered Shannon–Wiener diversity to be a more relevant and informative diversity index than Margalef's species richness. More quantitatively oriented variables (Shannon) are also considered better than qualitative (Margalef) when differences between macroalgal communities are investigated (Middelboe and Sand-Jensen 2000). It may also be noted here that Pielou's evenness, in this study, gave exactly the same significant differences between treatments and significant correlations as Shannon-Wiener diversity (Table 4; Figs. 5b, 7b).

Although much focus has been put on studying the relationships between diversity and productivity, the underlying general explanatory patterns are still unknown (Mittelbach et al. 2001). In many ecosystems, a unimodal pattern, where the diversity is highest at intermediate levels of productivity and a decrease in diversity can be seen both at decreased and increased productivity, has been found (Huston 1994; Eriksson et al. 2006b). A decrease in diversity at higher productivity levels has been explained with competitive species exclusion (Worm et al. 2002). In the 1960's and 1970's, many studies where the productivity was negatively correlated with species richness were documented (Huston 1994). This pattern appeared to be especially common in aquatic systems, where nutrient enrichment can increase production but decrease diversity (e.g. Patrick 1963, cited in Huston 1994). Although our investigation also gave negative relationships between diversity and productivity, it must be remembered that our nutrient enrichment results for diversity (increase) and productivity (decrease) were exactly the opposite to the ones presented by Patrick (1963).

Positive relationships between biodiversity and ecosystem functioning seem to be the trend at least in the published literature. In the meta-analysis by Balvanera et al. (2006) comprising 446 measurements of biodiversity effects, it was found that biodiversity overall had a positive effect on the studied ecosystem functions. In marine environments, Worm et al. (2006) noticed general positive effects on ecosystem functions with increased species diversity. At the same time, it was found that the effects of diversity were

weaker in less controlled study systems (field versus aquaria) due to greater abiotic and biotic variability under more natural conditions. With regard to levels of biological organisation, the positive effects of biodiversity were weaker at the ecosystem level than at the community level and at the population level they were negative (Balvanera et al. 2006). This seems to be due to individual populations shifting more with increased biodiversity, while the community stability should increase at higher levels of diversity (Tilman 1996). The reason for the rarity of negative BEF-relationships can be that negative relationships only occur under special circumstances, but it may also be due to a publication advantage of studies reporting positive BEF-relationships above neutral or negative ones. With regard to BEF-relationships, it has also been stressed that it is difficult to make simple generalisations between different ecosystem types, ecosystem characteristics or trophic levels (Allison 2004; Bracken and Nielsen 2004; Balvanera et al. 2006; Goodsell and Underwood 2008).

Evaluation of the applied methodology

When interpreting the results from mesocosm studies one cannot totally neglect the issue of study realism. The general advantage of using mesocosms lies in the possibility to replicate study systems and to control and manipulate factors and investigate response variables in a semi-natural to natural environment (Lawton 1995). Mesocosms have proved to serve as valuable experimental tools in pollution research and are often the best alternative, unless one accepts to discharge large amount of pollutants into the real environment for research purposes (Bokn et al. 2001). The major disadvantage with mesocosm studies is that their realism is always lower than the one of natural field studies, while the amount of control always is lower than what can be achieved under laboratory conditions (Kraufvelin 1998, 1999).

The mesocosms that were used in the present study have a relatively high ecological relevance. The species assemblages totally mimic the ones that can be found in the Oslofjord, the mesocosms were subjected to natural variations in light, temperature and salinity and a continuous flow-through system of water allowed organisms to be imported to and exported out of the system. In addition, these mesocosms have once again proven to function well over long time periods, which is important when dealing with long-lived organisms and assemblages (Kraufvelin et al. 2006b).

With regard to the specific treatments used in present paper, the applied nutrient and wave treatment levels were also realistic. For the nutrient treatment, it is worth noting that we added nutrients during the growth season, i.e. when nutrients are likely to be limiting, but not during the winter season (when background nutrients are high, but the system production is low). Thus, the enriched mesocosms experienced around 30 μM N year-round, whereas non-enriched mesocosms fluctuated from ∼1 μM N in summer to >30 μM N in winter. We therefore manipulated both the supply of nutrients and their variability, but are unable to distinguish between these two potential nutrient effects. The wave action levels were indeed clearly in the smaller end of the wave action range, mimicking only sheltered and very sheltered shores. On the other hand, the wave machines were operating continuously, which means that there were never any entirely calm days. However, since extreme wave action caused by incidental storms may be instrumental in causing gap formation and also in general structuring of rocky shore assemblages, this experiment could not assess the full role of the wave factor.

The applied macroalgal biomass and production measurements delivered data of varying reliability. The measurement of biomass in marine systems is not as easy as in terrestrial systems, since a huge amount of the marine biomass is lost due to disturbance, is transported away from the growth place by currents or waves or is simply grazed down by herbivores (Cebrian 1999). Again mesocosms are well suited for these kinds of studies, because all the earlier mentioned factors can be taken into account. To estimate macroalgal biomass through degree of cover worked reasonable well and already three measurements during one summer season gave a satisfactory precision of the standing stocks at various times (e.g. Murray et al. 2006). For the purpose of this study, concentrating on changes in macroalgal budgets, the transfer of cover values to biomass was in fact a prerequisite, although cover values alone may work fairly well as a non-destructive method for other main purposes (see Masterson et al. 2008).

The pH measurements for the productivity estimates had the advantage of being cheap and easy to carry out, while the major disadvantage may be that the method (and its performance) is not well known/used in the published literature. Even though the production values originating from pH and oxygen measurements are similar (Oviatt et al. 1986), species-specific differences in the relationship between pH and oxygen production may render comparisons of different communities questionable. Björk et al. (2004) have, for example, shown that *Ulva lactuca* and *Ulva intestinalis* preferentially use bicarbonate as a carbon source and that *U. intestinalis* in particular by this action increases the pH of rockpools, which makes the environment unsuitable for other seaweeds (e.g. *Chondrus* and *Fucus*). Axelsson (1988) showed that fucoid algae exhibited a CAM-like (Crassulacean Acid Metabolism) photosynthesis, resulting in a change in the ratio of oxygen production to pH at high photosynthetic rates. However, even though the method using the pH-CO_2 relationship and the

oxygen method clearly estimate production with some conceptual differences, the deviations should not be crucial with regard to the values presented in this paper. The central question is what the pH-CO_2 method used in our study actually estimates. In some studies, this method is compared to the oxygen method: Oviatt et al. (1986) on a pelagic to sublittoral community, Axelsson (1988) on mostly littoral algal species. The pH method of Oviatt et al. (1986) did not probably give sufficient precision (± 0.02 units) to compare day to day results, but combined over many days it gave reasonable relationships between changes in pH-CO_2 and O_2 (pH in their experiments varied in the total range of 7.1–9). The results of Axelsson (1988) using high precision methods followed a modified photosynthetic quotient of P'Q = 1.17 ± 0.02 where P'Q = Change of O_2/change of pH calculated as CO_2-carbon. This was obtained under controlled conditions with many species of brown, red and green algae, and each species came close to the common result (pH was in the range of about 8–8.5). With his accurate measurements, Axelsson (1988) was able to discuss variation between species and the influence of other substances than carbonate. A generalised C/N/P relation of marine macrophytes suggests that CO_2 differences calculated from pH will be about 5% too high if the aim is to estimate organic carbon production. This is due to the corresponding uptake and reduction in nitric and phosphoric acid. Conceivably, this additional proton uptake will vary with species according to their C/N/P-relation. Additional proton uptake could apply to uptake and reduction in sulphuric acid and hydrogenation of organic compounds as well. Thus, the pH-CO_2 method appears quite related to the O_2 method as it comprise protons removed to reduce the additional substances and also protons to reduce organic carbon to different levels, for example reduce carbohydrates to oil. Axelsson and Uusitalo (1988) studied the relationships between pH and changes in dissolved inorganic carbon (DIC) in controlled experiments with a number of algae. *U. lactuca* followed the theoretical relation until 40% of the initial DIC was left (pH about 10). They stated that the way of uptake, either as CO_2 or as HCO_3^-/OH^- exchange did not alter the relation. From about pH 10.1–10.2, DIC was reduced without further increase in pH. Tests with reduced magnesium content indicated that this was due to precipitation of magnesium hydroxide, thus reducing alkalinity. Fucaceans started to reduce alkalinity at a lower pH (about 9.5) probably due to proton excretion from CAM. One sublittoral species (*Desmarestia aculeata* (L.) J.V. Lamour) caused reduced alkalinity of the water at much lower pH (about 8.3) and excretion of malic or sulphuric acid were suggested explanations. As a whole, littoral algae showed no pronounced deviation from the theoretical pH-CO_2 model until pH was above 9 (Axelsson and Uusitalo 1988).

In our study, the highest pH values during production tests were seen in June 2006 and ranged from 8.7 to 8.8. These, then, should not be affected by substantial deviations from the main pH-CO_2 relationship, although different species composition in the mesocosms may have been responsible for some differences. Our data are adjusted to, and presented on, a seawater pH scale. We used Hansson's (1973) tris buffer for 25 psu salinity as standard. His standards for 35 psu are the same as more recent standard values for synthetic seawater tris buffers (cf. Millero et al. 1993). Differences are in the range of 0.000 to 0.003 units, which are near the measurement precision. This suggests that we can talk about *the* seawater pH scale, and not only one of them. The advantage of Hansson's buffers is that they define pH in waters of reduced salinity as well, which is the case in the Oslofjord. Our own precision of measurements based on readings of a standard (25 psu) kept in one mesocosm at the start and end of each measuring event was SD = 0.0067 pH units.

Conclusive remarks

This study has shown that after more than 2 years of experimental treatment, the total standing stock of macroalgae was larger at low nutrient levels than at high nutrient levels as well as in high wave systems compared to low wave systems (in autumn only). For macroalgal functional groups, bushy and filamentous brown algae and filamentous red algae were generally favoured by low nutrient concentrations, while annual filamentous and sheet-like green algae were stimulated by the nutrient enrichment. There was only one significant interaction between nutrient enrichment and wave action (for brown filamentous algae in autumn) and also only one significant main effect of the wave treatment (for bushy brown algae in autumn). Surprisingly, the high nutrient treatments supported a higher diversity of macroalgae, whereas the low nutrient treatments generally showed higher production rates and for many of the studied variables there were clear sequences rating the mesocosms from LN-HW (least negatively affected) via LN-LW and HN-HW, to HN-LW (most negatively affected). Most apparently, nutrients decreased production since less productive (valuable) algae were favoured in the long-term. Compared to previous investigations in these mesocosms both the more rapid and the more intense responses are striking. Summarised, it is the biological components of the communities subjected to external forcing (nutrient addition or decreased wave action) that regulate the production in these mesocosms, and this contradicts the common misperceived "farmer" view that resource production in natural systems simply can be fast-forwarded by fertilization. As a consequence of these findings, significantly negative correlations were also

found between macroalgal diversity and primary productivity in both summer and autumn.

Due to the escalating loss of species and populations in marine ecosystems under human influence (Worm et al. 2006), it has become evident that there is a huge need for general knowledge about the underlying mechanisms as well as the functional consequences of altered community structure. In this context, aquatic ecosystems have proven well suited for the study of BEF-questions with a great potential also for the contribution of general ecological theory (Gessner et al. 2004). A decreased diversity may decrease the recovery potential, the stability and the water quality of marine ecosystems, but a restored biodiversity may multiply the productivity and decrease the variability in the ecosystem (Worm et al. 2006). Today, the scientific community has reached agreement with regard to several aspects of BEF-relationships, including many factors that are important within ecosystem management. Continued progress demands knowledge about how abiotic and biotic factors control ecosystem characteristics, how ecological communities are organised, and which forces are driving species extinctions and invasions (Hooper et al. 2005). In this respect, it must be remembered that human activities more often affect the relative amount of species than they affect presence or absence of species. Changes in the relative dominance patterns of species thus demand more attention than the species richness itself, since the evenness of species will respond faster and may express more important ecosystem consequences far earlier than a species is threatened by extinction (Chapin et al. 2000).

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