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# Responses to nutrient enrichment, wave action and disturbance in rocky shore communities

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#### Abstract

A high degree of resistance against nutrient enrichment has previously been demonstrated for macroalgal-dominated rocky shore communities in the presence of moderate to large amounts of macroinvertebrate grazers. To experimentally examine, under controlled conditions, the possible roles for this resistance of two other factors, i.e. disturbance (presence/absence of the macroalgal canopy itself) and wave action, the canopy algae and associated algal and animal assemblages were removed by scraping from approximately one third of the area of eight littoral mesocosms, subjected to two different wave action regimes. After this, excessive nutrients were added to four mesocosms with the factor nutrients fully crossed with the factor wave action with two replicate mesocosm basins of each nutrient/wave treatment combination. Disturbance was added to the design as a within-basin factor thus making up a split-plot experiment. The abundance of grazers was allowed to vary freely and under the influence of the treatments. After 11 summer weeks, there were significant differences in community structure between nutrient enrichment levels for both algal and animal assemblages when examined by multivariate statistical techniques. Univariate analyses confirmed a significantly stimulated colonisation by green algae, mainly Ulva lactuca, in both disturbed (scraped) and undisturbed areas of nutrient-enriched mesocosms. In unenriched mesocosms, the green algae were absent from undisturbed areas and rare in disturbed areas, where mainly brown Ectocarpus spp. and red algae had settled. Among the macrofauna, the total abundance of grazers was stimulated in nutrient-enriched mesocosms with individuals of the amphipod genus Gammarus and the isopod genus Jaera being especially numerous. With regard to wave action, no significant differences occurred in community structure, although there were indications of significant nutrient  $\times$  wave effects for both the amount of exported red algae and the amount of accumulated brown algae. The study shows that eutrophication-related community shifts on rocky shores may occur very rapidly, regardless of the level of wave-energetic stress and the abundance of grazers, if the nutrient concentrations are high and the colonisation and growth of opportunistic algae are facilitated by disturbance such as (naturally or anthropogenically driven) canopy gap forming processes. © 2007 Elsevier B.V. All rights reserved.

Keywords: Mesocosm; Nutrient enrichment; Canopy gap formation; Rocky intertidal; Algal colonisation; Marine biodiversity

# 1. Introduction

Nutrient enrichment generally stimulates ephemeral macroalgae (Duarte, 1995; Valiela et al., 1997; Cloern, 2001; Worm and Lotze, 2006), which often, but not always, can be observed as high loads of excessive algal growth and accumulation in the littoral zone of eutrophic areas (Rönnberg et al., 1992; Bäck et al., 2000; Middelboe and Sand-Jensen, 2000; Diaz et al., 2002). On temperate rocky shores, eutrophication mainly increases the growth and dominance of annual filamentous and sheet-like algae, which is linked to ecophysiological traits (growth rate, nutrient requirements and uptake rates), where

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thin algae are favoured above thick algae at higher nutrient levels (Pedersen and Borum, 1996, 1997). This stimulation of annual ephemerals may accentuate the competition for light and space and retard perennial species or harm their recruitment (Berger et al., 2003; Råberg et al., 2005; Kraufvelin et al., 2007). A possible suppress on or disappearance 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 very important 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) and Edgar et al. (2004).

During a recent 3-year experiment in Norway, a high degree of resilience to community change following excessive nutrient

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addition was documented for moderately wave-exposed, moderately grazer-controlled, macroalgal-dominated rocky shores in mesocosm (Bokn et al., 2002, 2003; Barrón et al., 2003; Karez et al., 2004; Kraufvelin et al., 2006a) and field/ whole-ecosystem experiments (Kraufvelin et al., 2002). However, by prolonging the abovementioned mesocosm study with 2 more years, Kraufvelin et al. (2006b) observed a breakdown of canopy stands of Fucus vesiculosus L. and Fucus serratus L. between the fourth and fifth year of nutrient enrichment. This breakdown was probably due to limited fucoid recruitment and it occurred despite stimulated grazer abundances, which otherwise could be thought to buffer the negative effects on fucoid settlement by ephemeral algae in eutrophicated systems (Kraufvelin et al., 2006a, 2007). Apparently the increase in grazer populations was insufficient in these mesocosm studies for a prolonged buffering of eutrophication effects, as has been reported from field studies (Lotze and Worm, 2000; Lotze et al., 2000; Worm et al., 2002; Worm and Lotze, 2006). The demonstration of delayed eutrophication effects points out the importance of time for the occurrence and detection of responses, but also the relevance of controlled long-term and large-scale causative experimentation in order to be able to draw the right conclusions, particularly when dealing with longer-lived and larger-sized organisms, subtle (non-toxic) community stressors, and gradual change (Bokn et al., 2003; Kraufvelin et al., 2006a,b).

Marine littoral communities are generally structured by a combination of physical factors and biotic interactions (Little and Kitching, 1996). Due to several reasons, intertidal rocky communities may possess a high resistance against disturbance caused by an excessive nutrient availability as long as the communities are not seriously stressed or perturbed by other chemical, physical or biological processes (Connell, 1985; Thompson et al., 2002; Worm and Lotze, 2006). It is credible that the strong dominance of late successional and long-lived species, such as fucoids and kelps, in rocky shore ecosystems by itself may prevent colonisation and development of ephemeral algae through strong competition for light and space. This may therefore render rocky shore communities relatively resistant to nutrient enrichment (Sousa, 1979; Bokn et al., 2003; Eriksson et al., 2006; 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 (Dayton, 1971; Santelices and Ojeda, 1984; Kiirikki, 1996). Regarding eutrophication problems on rocky shores, a number of possible modifiers of primary eutrophication responses, such as the recruitment, development and persistence of opportunistic algae, have been listed (Lotze et al., 2000; Worm et al., 2002; Bokn et al., 2003; Worm and Lotze, 2006). Three of these seem to be especially important: the successional stage of the established macroalgal community, wave action and grazing. Dense populations of perennial macroalgae typically dominate intertidal rocky shore communities, arising in an intense competition among individuals for space and light with restricted opportunities for algal settlement, colonisation and growth in already established communities of later successional stages (Mann, 1982; Connell, 1985; Bokn et al., 2003). Some kind of disturbance of the rocky shore community, like opening up gaps in the canopy, can on the other hand lead to rapid community responses to nutrient enrichment (Worm et al., 2002; Eriksson et al., 2006; Jara et al., 2006; Valdivia and Thiel, 2006). Furthermore, the rocky intertidal is a highly energetic environment due to wave and tidal action, which may cause detachment or active removal and export of opportunistic algae and thereby moderate the accumulation of excessive algal biomass (Kiirikki, 1996; Pihl et al., 1999; Thompson et al., 2002; Barrón et al., 2003). Finally, efficient herbivores, capable of inducing strict top-down control, are often abundant in the intertidal zone of rocky coasts (Hawkins and Hartnoll, 1983; Duffy, 1990; Jenkins et al., 2005) and thereby, a considerable amount of the excessive algal production may simply be removed by grazing (Lotze and Worm, 2000; Kraufvelin et al., 2006a; Worm and Lotze, 2006). With regard to wave action and grazing, algal productivity seems to be more tightly linked to nutrient supply at sheltered sites (Mann, 1973; Nielsen, 2001) with grazers as the chief source of algal mortality, whereas physical disturbance probably is more important at waveexposed shores (Menge and Sutherland, 1987).

To explicitly focus on the roles of these abovementioned factors, i.e. disturbance (successional stage of the algal community/availability of free space/canopy gap formation), wave exposure and grazing by animals, for the timing and extent of eutrophication responses on rocky shores, a new longterm mesocosm experiment was initiated from June 2004 on (FAME 2004-2007, FActors Modifying Eutrophication responses in rocky shore communities). The present paper reports the role of disturbance) for early changes (weeks to months) in algal and animal community structure on disturbed (removal of canopy, understory algae and animals by scraping) and undisturbed mesocosm areas with consideration of the role of wave action (this factor being automatically built into the experimental design) and grazing by invertebrates. The unique features of this specific experiment are the treatment combination itself comprising strict control of two nutrient enrichment levels, two wave energy levels and presence and absence of disturbance, but also the high degree of similarity within physical background variables, the restricted accessibility to the mesocosms by humans, mammals, and birds (and thereby known low levels of extra stress), the known abundances of grazers and predators, as well as the ability to directly quantify algal export and accumulation from specific benthic areas.

# 2. Materials and methods

# 2.1. Solbergstrand rocky littoral mesocosms

All measurements were made in eight rocky littoral mesocosms at the Marine Research Station Solbergstrand by the Oslofjord ( $59^{\circ}37'N$ ,  $10^{\circ}39'E$ ) in SE Norway. The Solbergstrand mesocosms (Fig. 1) had a water volume of 6–12 m<sup>3</sup>, depending on tide level, and received water from 1 m depth in the Oslofjord at a rate of 5 m<sup>3</sup> h<sup>-1</sup> (mean water



Fig. 1. Solbergstrand mesocosm diagram showing four steps with intertidal (step number 1–2) and subtidal (step number 3–4) macroalgal communities, the wave generator and the tidal regulator.

residence time: 2 h). A tidal regime simulated natural changes in water level reflecting the local tidal amplitude of 36 cm, and comprising two high tides and two low tides diurnally. A wave machine further generated constant wave action (17 strokes per minute, wave amplitude on average 11 cm in the high wave treatment and 5.5 cm in the low wave treatment). The effective wave action was roughly corresponding 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 and the waves were facing the littoral communities in the same direction as natural waves in the inner Oslofjord (i.e. from the west).

Rocky shore communities were introduced in 1996 by transplanting small boulders from the Oslofjord, with macroalgae and associated animals attached, onto concrete steps in each mesocosm. These steps represented different water depths on a shoreline and consisted of two intertidal and two subtidal steps per mesocosm (Fig. 1). After the initiation phase, natural community development was allowed to contribute to the assemblages giving raise to mesocosm communities that corresponded very 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 after this for another 2 years of nutrient effect studies in 2001 and 2002, followed by a 2-year recovery survey in 2003–2004 (Kraufvelin et al., 2006b), prior to this study.

Over the years, over 40 species of macroalgae and 85 species of macrofauna have been identified in the mesocosms. Brown algae *Fucus serratus*, *Fucus vesiculosus*, *Fucus spiralis* L. and *Ascophyllum nodosum* (L.) Le Jol., the green algae *Ulva lactuca* L. and *Ulva intestinalis* L., and some seasonal red algae (mainly *Ceramium* spp., *Chondrus crispus* Stackh., *Polysiphonia* spp. and *Rhodomela confervoides* (Huds.) P.C. Silva) dominated the macroalgal assemblages. The green alga *U. intestinalis* consisted of several species formerly known as *Enteromorpha* (see Hayden et al., 2003), among which *Enteromorpha intestinalis* was most common. Amphipods, isopods, gastropods and blue mussels were the most important animal groups.

## 2.2. Experimental treatments

At the start of this investigation (in June 2004), it was first checked that both the algal and animal communities had fully recovered from previous experimentation during 1998-2004, i.e. that there were no significant differences in algal cover or animal abundance between any of the previous treatment and control mesocosms (Kraufvelin et al., 2006b). All loose-lying algae on the steps and on the mesocosm floor and all attached algae and animals on the mesocosm walls were removed by hand. Then, all macroalgae (including visible germlings) and macrofauna were removed from the middle part of all steps in all mesocosms (of 1.26 m breadth, i.e. 1/3 of the total area on each step, Fig. 1) by scraping (using a sharp iron scratch), cutting and active picking by hand. Only one area was disturbed/scraped (in the middle) due to practical difficulties with the scraping of many small areas. The resulting disturbed area of  $2 \text{ m}^2$  was smaller than the surrounding undisturbed areas of a total of  $2 + 2 = 4 \text{ m}^2$  in order to not disturb the original community too much and to allow for a "natural" recolonisation of macroalgae and animals over the years. The gap size could possibly reflect a dimension occurring in adjacent natural rocky shores. After the scraping, all boulders in the scraped area were turned around but left at their original places. This area is hereafter referred to as "disturbed". The remaining parts of the steps (2/3 of the total step area) on both sides of the disturbed area were left untouched with their established communities intact. This area is hereafter referred to as "undisturbed".

Nutrients, 32 µM inorganic nitrogen (N) and 2 µM inorganic phosphorus (P) above background fjord levels, were added continuously from June 18th 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 high nutrient addition levels have been utilised during previous enrichment experiments in these mesocosms (Bokn et al., 2003; Kraufvelin et al., 2006b). The nutrients were added as a mixture, which consisted of 14.3 mol N as NH<sub>4</sub>NO<sub>3</sub> and 0.9 mol P as H<sub>3</sub>PO<sub>4</sub> and had a N/P mol ratio of 16/ 1. In four mesocosms, the wave energy (and wave height) was reduced by 50% (maximum amplitude reduced from 11 to 5.5 cm) while retaining the same wave frequency. The two factors, nutrients and wave action, were applied 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).

The experiment for studying effects on macroalgae was set up as a split-plot design, where the treatment factor disturbance was entered as a fixed within-plot (i.e. within-basin) factor with two levels (two replicate transects in the disturbed area and two transects in the undisturbed area). The factor disturbance was orthogonal to nutrients and wave action (both of these were also fixed factors with two levels each). This means that there were eight orthogonal combinations of treatments (low and high nutrient levels, low and high wave action and disturbed and undisturbed areas). Eight "plots", i.e. basins, were available for the experiment and two basins were nested within each nutrient and wave action combination (Winer et al., 1991; Underwood, 1997). The effects on the animals and algal export and accumulation were studied with a two-way factorial model.

## 2.3. Sampling of macroalgae and macrofauna

The algal communities were sampled in early September 2004 after 11 summer weeks of nutrient enrichment. During September 3rd to 8th, the macroalgal cover was registered along four transects in each mesocosm. Two randomly chosen transects were studied in the scraped/disturbed area and two in the undisturbed area, taking possible edge effects into consideration. With regard to the two transects in the undisturbed area, one was placed randomly in the northern area and one in the southern area. The transect placed in the southern area had the prerequisite of being at least 60 cm from the southern basin wall in order to prevent artificial shading effects from affecting the community structure. Each transect was therefore 42 cm wide and 168 cm long, going from the first

basin step down to the fourth step (Fig. 1). At the analysis of algal cover, only the surface layer of the algal assemblage was examined within the sampling area (not invisible algae in understory layers) in such a way that the total cover always was 100% (including bare uncovered substrate). This was done in order to minimise the disturbance of delicate species and can also be motivated by a better compatibility with non-destructive photographic documentation of the squares during periods in between samplings and during subsequent visits after the initial study period reported here. In the algal mapping, not all specimens of red and brown algae were determined to species level in order to save time and effort and to not disturb the communities too much. Therefore, some bigger collective groups as "red algae", Lithothamnia and "brown filamentous algae" have been used to lump together several species. This will have some impact on the characterisation of algal diversity and the detection of community effects, even though none of these undetermined species were dominant in the mesocosms.

The abundance of motile animals was estimated by their colonisation of artificial substrates. These substrates consisted of three 80 cm long ropes of hemp (thickness 8 mm), one stone, and one petri dish kept together with rubber bands. With regard to community composition (as seen in the ordination by nonmetric multidimensional scaling, NMDS), the substrates collected an intermediate fraction of the animals normally present in the most dominant types of green, red and brown algae (Kraufvelin et al., 2002). The basic ideas behind the use of subtrates were to provide an ability of non-destructive sampling and to get samples of similar conditions from all mesocosms, i.e. to counter-act differences in faunal colonisation due to differences in algal nutrient content and possible differences in algal morphology between controls and nutrient treatments (Depauw et al., 1986; Czerniawska-Kusza, 2004). Four substrates were placed into each mesocosm (two substrates in the undisturbed area and two in the disturbed area) at two different depths/steps (one intertidal and one subtidal step just below the tidal zone) and exposed for 2 days in each mesocosm (in the periods September 3rd-5th and 4th-6th), after which the animals were preserved in ethanol for later analysis. Since the main interests of this part of the study lay in making comparisons between factorially treated mesocosms of two nutrient and two wave action regimes, separately for disturbed and undisturbed areas, the two substrates from the same area (but from different depths) were pooled together.

The amount of exported algae was evaluated through the use of fine nets on the outlet pipes in September 2004. Algal samples were collected during 24 h and sorted and weighed (g ww). Loose-lying algae that had accumulated on the mesocosm floor during the period June–September was removed by hand and quantified (g ww).

# 2.4. Statistical analysis

Non-parametric multivariate techniques (Clarke, 1993) were applied to the algal and animal community data from the steps. In these analyses, the effects of wave action were ignored, just concentrating on responses to nutrient enrichment. This resulted in the necessary four replicates of both enrichment levels to be able to get *p*-values <0.05 in the permutation-based hypothesis testing. The macroalgal community data were analysed untransformed due to rather small differences between the more common and the more rare algal groups, whereas the macrofaunal data were transformed by the square root in order to even out the relative influence from dominant and rare species. Differences in community structure between the two nutrient treatment levels were tested for by one-way analysis of similarities (ANOSIM), separately for disturbed and undisturbed areas. NMDS based on Bray-Curtis similarities was further used to map samples and the similarity percentage breakdown procedure (SIMPER) for listing the species contributing most to the observed dissimilarities between the two nutrient regimes.

Differences in macroalgal cover and diversity, abundance and diversity of macrofauna, as well as algal export and accumulation were analysed by univariate means (Sokal and Rohlf, 1995; Underwood, 1997). The cover of brown and green algae, as well the Shannon-Wiener diversity along two disturbed and two undisturbed transects in each mesocosm were analysed by a split-plot ANOVA using the model  $X_{ijklm} = \mu + N_i + W_j + B_k(NW_{ij}) + D_l + NW_{ij} + ND_{il} + WD_{jl} + WD_{il} + WD_{i$  $DB_{kl}(NW_{ij}) + NWD_{ijl} + e_{m(ijkl)}$ , where  $X_{ijklm}$  represents the cover of algae (or Shannon-Wiener diversity) at disturbance l in basin k of nutrient level *i* and wave action level *j* (Winer et al., 1991; Underwood, 1997).  $N_i$ ,  $W_j$ ,  $B_k(NW_{ij})$  and  $D_l$  represent, if they exist, the effects of treatments N (nutrients), W (waves), D(disturbance) and basin B in treatments NW, respectively. NW<sub>ij</sub>, ND<sub>il</sub>, WD<sub>il</sub>, DB<sub>kl</sub>(NW<sub>ij</sub>) and NWD<sub>ijl</sub> represent interactions among these factors and  $e_{m(ijkl)}$  represents the error due to smaller-scale differences between samples because of spatial variability within basins.

Analyses of differences in abundance of macrofauna were performed separately for disturbed and undisturbed areas by a two-way ANOVA using the model  $X_{ijk} = \mu + N_i + W_j + NW_{i-j} + e_{k(ij)}$ , since no "replicated" artificial substrates had been taken within the disturbed and undisturbed mesocosm areas. Analyses of algal export and accumulation were similarly performed for whole mesocosms using the same model as for animal analyses.

The multivariate statistical analyses were run in PRIMER 6.0, whereas the univariate analyses were run in GMAV5 or SPSS 13.0. Before running the parametric univariate tests, the normality was checked 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-roottransformation,  $\sqrt{(x+1)}$ , or a logarithmic transformation, ln(x + 1). Percentage cover values of macroalgae were arcsinetransformed throughout. For all significance tests, alpha was set at 0.05. Hochberg's sequential Bonferroni (Hochberg, 1988) was used to adjust the overall significance levels to the number of tests performed. p-Values that initially were lower than 0.05, but then became non-significant with the Bonferroni correction, will still be brought up as potentially significant in the discussion, which is in accordance with the recommendations by Moran (2003).

#### 3. Results

#### 3.1. Changes in the algal community

If the four mesocosms, which received the same nutrient treatment, are used as replicates in the multivariate statistical analysis, significant differences in algal community structure between nutrient-enriched and un-enriched mesocosms can be seen in both disturbed and undisturbed areas (one-way ANOSIM, global R = 1.00, p = 0.029 in disturbed areas and global R = 0.84, p = 0.029 in undisturbed areas, which in both cases is the most extreme *p*-value at this level of replication). These differences between nutrient enrichment levels are also evident from the NMDS-ordination (Fig. 2a), where all samples receiving the same treatment (i.e. nutrients and disturbance). except one disturbed control area, cluster out within 60% Bray-Curtis similarity (the circles in the figure). In disturbed areas, SIMPER analyses show that the high degrees of cover of Ulva lactuca and Ulva intestinalis in nutrient-enriched mesocosms are responsible for almost 64% of the dissimilarities (average dissimilarity = 81%) between nutrient-enriched and unenriched mesocosms (Table 1a). In undisturbed areas, the average dissimilarity in the macroalgal community between nutrient-enriched and un-enriched mesocosms was less pronounced (44%) than in disturbed areas and the two nutrient enrichment groups were also closer to each other in the NMDSordination. Here Fucus serratus (more abundant in un-enriched mesocosms) and U. lactuca (more abundant in nutrient-



Fig. 2. (a) NMDS of macroalgal cover in disturbed and undisturbed areas of the eight mesocosms with nutrient addition level labelled as high or low (stress 0.07), circles indicate 60% Bray-Curtis similarity and (b) NMDS of macrofauna abundance in disturbed and undisturbed areas of the eight mesocosms with nutrient addition level labelled as high or low (stress 0.11), Circles indicate 70% Bray-Curtis similarity.

Table 1

The contribution from each plant species ( $\delta_i$ ) to the average Bray-Curtis dissimilarities between the two nutrient treatment levels in (a) disturbed (average  $\delta = 81\%$ ) and (b) undisturbed (average  $\delta = 44\%$ ) areas

Taxonomic group	Average cover	Average cover	Ratio $\delta_i$ /S.D.	Percent	
	un-enriched $\pm$ S.E.	nutrient-enriched $\pm$ S.E.			
(a) Disturbed areas					
Ulva lactuca	$0.0 \pm 0.0$	$48.5 \pm 5.4$	4.51	47.78	
Ulva intestinalis	$1.9 \pm 1.1$	$18.1 \pm 4.8$	1.79	15.91	
Red algae	$11.8 \pm 4.2$	$2.8 \pm 1.5$	1.76	9.06	
Brown filamentous	$8.9\pm2.2$	$0.0\pm0.0$	2.19	8.72	
Fucus serratus	$8.4 \pm 3.4$	$4.2 \pm 3.4$	1.47	6.59	
Fucus vesiculosus	$4.2 \pm 1.2$	$6.8 \pm 3.3$	1.20	3.88	
Fucus spiralis	$0.8\pm0.4$	$2.6\pm0.8$	1.24	1.92	
Ascophyllum nodosum	$1.1 \pm 0.2$	$2.0 \pm 1.4$	0.92	1.81	
(b) Undisturbed areas					
Fucus serratus	$31.6 \pm 5.7$	$16.7 \pm 2.1$	1.74	26.44	
Ulva lactuca	$0.0 \pm 0.0$	$11.5 \pm 2.0$	2.89	19.20	
Cladophora rupestris	$1.6 \pm 0.6$	$6.9\pm3.2$	0.99	9.31	
Fucus vesiculosus $8.7 \pm 0.4$		$12.4 \pm 4.4$	0.74	8.24	
$Ulva intestinalis$ $0.3 \pm 0.2$		$4.7 \pm 1.8$	1.33	7.37	
Ascophyllum nodosum	$7.5\pm2.2$	$9.0 \pm 2.5$ 1.07		7.33	
Chondrus crispus	$2.5 \pm 1.2$	$4.1 \pm 1.3$ 1.53		4.88	
Brown filamentous	$2.6 \pm 2.3$	$0.0\pm0.0$	0.64	4.49	
Laminaria digitata	$1.0 \pm 0.4$	$2.8 \pm 1.8$	0.94	4.23	
"Lithothamnia"	$3.4 \pm 0.7$	$2.1 \pm 0.7$	1.50	3.06	
Red algae	$2.3\pm0.6$	$2.7 \pm 1.0$	1.52	2.97	

The first two data columns give the actual cover values  $\pm$ S.E., the third column is  $\delta_i$  divided by S.D. of cover (consistency within data), whereas the fourth column gives the percentage contribution for each species (only the most common taxa are listed, cut-off cumulative percent = 95%).

enriched mesocosms) were the most important discriminators, together responsible for >45% of the differences (Table 1b).

Already within a couple of weeks, the disturbed areas of nutrient-enriched mesocosms (HN-HW and HN-LW) had been colonised by green algae, mainly *Ulva intestinalis* in the intertidal and *Ulva lactuca* in the subtidal, whereas the disturbed areas of un-enriched mesocosms still looked "clean" (as observed by the technical staff of Solbergstrand and documented with digital photos). At the sampling 2 months later, this pattern remained the same with very little green algae in the un-enriched mesocosms (LN-HW and LN-LW) and 40% average cover in HN-HW and 30% in HN-LW (Fig. 3). Green



Fig. 3. Stacked mean degrees of cover of brown, green and red algae in disturbed and undisturbed areas of the four nutrient and wave treatment combinations.

Ulva spp. were absent from LN-LW mesocosms, but covered 4% of disturbed areas in LN-HW mesocosms. The split-plot analysis of differences in degree of cover of green algae demonstrated a significant N × D interaction (Table 2). Pairwise SNK-corrected a posteriori analyses, performed to more specifically study the interactions, showed significantly more green algae in HN-mesocosms in both disturbed and undisturbed areas, as well as significantly more green algae in disturbed areas of HN-mesocosms compared to undisturbed areas of HN-mesocosms, but no differences between disturbed and undisturbed areas for LN-mesocosms. For brown algal cover there was significantly more brown algae in the undisturbed areas, but also a significant  $B(N \times W)$  interaction, i.e. parallel mesocosms deviated significantly from each other in some cases. For Shannon-Wiener diversity none of the interactions or the main factors were significantly different after the Bonferroni correction, although there were indications of significant  $D \times B(N \times W)$  and  $N \times D$  interactions (Fig. 4; Table 2).

#### 3.2. Changes in the animal community

Despite the short time period, changes took also place within the animal communities. The multivariate analyses (the different wave action levels were also pooled for animal data) suggested significant differences in macrofaunal community structure between nutrient-enriched and un-enriched mesocosms for both disturbed (one-way ANOSIM: global R = 0.792, p = 0.029) and undisturbed areas (one-way ANOSIM: global R = 0.865, p = 0.029). This can also be anticipated from the NMDS-ordination with 70% Bray-Curtis similarities superTable 2

Explained percent of the Total SS (%TSS) and *p*-values from a split-plot ANOVA using the model  $X_{ijkl} = \mu + N_i + W_j + B(NW)_{k(ij)} + D_1 + NW_{ij} + ND_{il} + WD_{il} + DB(NW)_{k(ij)} + NWD_{il} + e_{m(ijkl)}$  on differences in brown, green algae and algal Shannon-Wiener diversity

Source	d.f.	Brown algae	Brown algae		Green algae		Shannon diversity	
		%TSS	р	%TSS	р	%TSS	р	
N	1, 4	9.75	0.269	73.86	< 0.001	0.54	0.590	
W	1, 4	0.00	0.989	2.99	0.078	8.34	0.084	
$B(N \times W)$	4, 16	23.77	< 0.001	2.15	0.011	6.35	0.042	
D	1, 4	54.41	< 0.001	8.88	0.001	8.62	0.131	
$N \times W$	1, 4	2.39	0.560	0.03	0.824	3.25	0.226	
$N \times D$	1, 4	0.94	0.363	8.71	0.001	44.95	0.012	
$W \times D$	1, 4	0.02	0.897	1.01	0.045	0.02	0.925	
$D \times B(N \times W)$	4, 16	3.58	0.062	0.49	0.415	9.58	0.010	
$N \times W \times D$	1, 4	0.01	0.916	0.02	0.739	10.36	0.106	
Residual		5.12		1.87		7.99		

Brown and green algal cover values were arcsine-transformed. Underlined values indicate significance at the 0.05-level after correction for the number of comparisons with Hochberg's sequential Bonferroni. N = Nutrients (fixed, orthogonal factor), W = Wave (fixed, orthogonal factor), B = Basin (random factor nested in combinations of N  $\times$  W, D = Disturbance (fixed within-plot factor, orthogonal).

imposed by circles (Fig. 2b). Although the group distinctions for the animal community are less clear than for algal data, it is noteworthy that all samples from the nutrient-enriched mesocosms cluster out together, well separated from samples from un-enriched mesocosms. SIMPER analyses show that *Gammarus* spp. (49%) followed by *Jaera* spp. (28%), both more common in nutrient-enriched mesocosms, were the most important discriminators between disturbed areas of nutrientenriched and un-enriched mesocosms (average dissimilarity = 66%), whereas *Jaera* spp. (66%) followed by *Gammarus* spp. (15%) were the most important discriminators in undisturbed areas (average dissimilarity = 64%; Table 3). Other



Fig. 4. Shannon-Wiener diversity of algae (+S.E.) in disturbed and undisturbed areas of the various nutrient and wave treatment combinations.

important contributors were *Rissoa* spp., *Hyale nilssoni* and the amphipod group Stenothoidae (generally more common in nutrient-enriched mesocosms) as well as the amphipod group Aoridae (more common in un-enriched mesocosms).

Total invertebrate abundance was significantly stimulated by the nutrient enrichment in both disturbed and undisturbed areas (Fig. 5a, Table 4) and this increase was largely due to bigger populations of *Gammarus* spp. and *Jaera* spp. (Fig. 5b), although the individual *p*-values for the abundance of these species did not pass the sequential Bonferroni correction. The same applies for the Shannon-Wiener diversity for animals, although there are signs of lower diversity values both in disturbed and undisturbed areas of nutrient-enriched mesocosms compared to un-enriched mesocosms (Fig. 5c, Table 4). Neither *Idotea* spp. nor *Littorina littorea* L., two dominant grazers, showed any significant responses to the treatments at this early stage of experimentation (data not shown).

#### 3.3. Algal export and accumulation

With regard to algal export, there was a significantly higher export rate of green algae from HN-mesocosms (Table 5a, Fig. 6a), and there was also a significant N  $\times$  W interaction for red algae, although the latter did not pass the Bonferroni correction. The red algal interaction was expressed as higher export rates at high wave action and low nutrient levels and lower export rates at high wave action and high nutrient levels. Regarding accumulation of algae, i.e. the amount of loose-lying algae that were removed from the mesocosm bottoms, there were no significant differences for this variable after the correction for the number of comparisons with a sequential Bonferroni (Table 5b, Fig. 6b), although a stimulated accumulation of green algae was indicated at high nutrient levels as well as a significant N × W interaction for brown algae. The latter observation seemed mainly to be due to higher brown algal accumulation at low wave action and low nutrient levels and higher accumulation at high wave action level and high nutrient levels.

Table 3

The contribution from each animal taxa ( $\delta_i$ ) to the average Bray-Curtis dissimilarities between the two nutrient treatment levels in (a) disturbed (average  $\delta = 66\%$ ) and (b) undisturbed (average  $\delta = 64\%$ ) areas

Taxonomic group	Average cover un-enriched $\pm$ S.E.	Average cover nutrient-enriched $\pm$ S.E.	Ratio $\delta_i$ /S.D.	Percent
(a) Disturbed areas				
Gammarus spp.	$41.8 \pm 15.8$	$459.5 \pm 74.2$	2.50	49.48
Jaera spp.	$65.8 \pm 16.1$	$308.8 \pm 84.8$	1.60	27.60
Aoridae	$93.2 \pm 31.6$	$38.2 \pm 8.6$	1.24	6.88
Stenothoidae	$35.5 \pm 15.2$	$82.2\pm36.0$	1.01	6.58
Hyale nilssoni $28.5 \pm 14.1$		$15.5 \pm 5.2$	0.92	2.31
Rissoa spp. $31.0 \pm 8.6$		$36.8 \pm 7.0$ 1.25		1.93
Mytilus edulis	$14.0\pm 6.2$	$9.8\pm4.6$	1.27	1.30
(b) Undisturbed areas				
Jaera spp.	$125.8 \pm 36.5$	$952.0 \pm 144.2$	4.64	66.50
Gammarus spp.	$111.0 \pm 20.3$	$300.5 \pm 20.4$	4.49	15.48
Hyale nilssoni	$23.0\pm8.4$	$72.8\pm20.6$	1.67	4.90
Stenothoidae	$12.0 \pm 4.7$	$70.0 \pm 34.2$	1.18	4.66
Rissoa spp.	$15.2 \pm 4.9$	$43.0 \pm 12.8$	1.17	2.47
Aoridae	$55.2\pm14.2$	$34.2\pm5.6$	1.26	2.22

Abundance values  $\pm$  S.E. refer to average number of individuals in two artificial substrates per area and mesocosm (only the most common taxa are listed, cut-off cumulative percent = 95%).

# 4. Discussion

Within 11 summer weeks, green opportunistic algae, i.e. Ulva lactuca and Ulva intestinalis, had conquered large parts of the disturbed areas in the nutrient-enriched mesocosms. Since no corresponding increase in green algae did occur in the undisturbed area, the absence of competition for light and space with adjacent perennial canopy species or the absence of active removal of opportunists by sweeping large macroalgae must be important prerequisites for the occurrence of these early responses. The suspected buffering of eutrophication effects by adjacent established macroalgae (see Bokn et al., 2003; Kraufvelin et al., 2006b) was effectively controlled thanks to the disturbance of relatively large areas. With insufficient nutrient concentrations for a clear stimulation of green algae in un-enriched mesocosms, the disturbed areas here remained mainly uncovered, although they were to a certain extent colonised by brown filamentous species (mainly Ectocarpus spp.) and red algae, groups that apparently were out-competed by the green algae in the nutrient-enriched mesocosms. An extreme green algal colonisation to free space of nutrientenriched systems could also be anticipated from the findings of Bokn et al. (2003) and Karez et al. (2004) based on colonisation studies of clean granite chips and various sampling equipment placed out in mesocosms. On these substrates, green algae were also to a similar extent dominating at high nutrient levels and brown and red algae at lower nutrient levels.

The few significant changes in macroalgal cover in the undisturbed zone, despite the nutrient enrichment, i.e. only green algae showed stimulation, are in accordance with the previous finding that established communities of perennial algae and associated fauna on rocky shores may resist or withstand a take-over by bloom-forming opportunistic algae over prolonged periods of time (Bokn et al., 2002, 2003; Karez et al., 2004; Kraufvelin et al., 2006b). The undisturbed areas of the un-enriched mesocosms in this study also clearly resembled the previous control mesocosms and low dose treatments of the previous 3-year eutrophication project (Bokn et al., 2003; Kraufvelin et al., 2006b). These undisturbed un-enriched areas retained a very high dominance of brown fucoids and thereby a

Table 4

Results from two-way ANOVAs on differences in macrofaunal abundance due to nutrient addition and wave action in (a) disturbed and (b) undisturbed areas (d.f. = 1, 4 for all F-ratios)

Source	Jaera %TSS	р	Gammarus %TSS	р	Total %TSS	р	Shannon %TSS	р
(a) Disturbed	areas							
Ν	56.90	0.078	83.46	0.010	83.95	0.002	86.60	0.005
W	0.02	0.971	0.65	0.707	2.30	0.310	1.80	0.468
$\mathbf{N}  imes \mathbf{W}$	2.08	0.676	0.02	0.953	1.54	0.395	0.41	0.721
Res	41.00		15.88		6.81		11.20	
(b) Undisturb	ed areas							
Ν	83.72	0.010	87.87	0.005	88.08	0.004	81.03	0.012
W	0.57	0.722	0.59	0.675	1.77	0.449	0.40	0.773
$\mathbf{N}  imes \mathbf{W}$	0.03	0.934	0.03	0.924	0.12	0.835	1.64	0.566
Res	15.67		11.52		10.04		16.92	

Underlined values indicate significance at the 0.05-level after correction for the number of comparisons with Hochberg's sequential Bonferroni.



Fig. 5. (a) Total abundance of macrofauna (+S.E.), (b) Mean abundance for *Gammarus* spp. and *Jaera* spp. (+S.E.) and (c) Shannon-Wiener diversity (+S.E.). The animals have been sampled from artificial substrates collected from disturbed and undisturbed areas of the various nutrient and wave treatment combinations.

lower Shannon-Wiener diversity (although not significantly so after Bonferroni correction) than the undisturbed areas of nutrient-enriched mesocosms. This is no spectacular finding, however, but only in accordance with the intermediate disturbance hypothesis (Connell, 1978), which predicts a depressed diversity in the absence of disturbance due to the competitive exclusion of inferior competitors by one or a few dominant species and an increased diversity at low to moderate stress 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; Patricio et al., 2006; Valdivia et al., 2005) and also previously in these mesocosms (Kraufvelin et al., 2006b).

The macrofaunal responses are also in accordance with previous findings (Kraufvelin et al., 2002, 2006a,b; Bokn et al., 2003), e.g. a stimulation of total abundance (mainly by bigger populations of *Jaera* spp. and *Gammarus* spp.) and tendencies of a decreased Shannon-Wiener diversity in nutrient-enriched mesocosms due to the intense dominance of only a few taxa. On the other hand, *Littorina littorea* did not respond with significant abundance stimulation during the course of this experiment as for example in the study by Kraufvelin et al. (2002), which probably mainly was due to the short time scales.

Results non two way fire vision differences in (a) agai export and (b) agai accumulation due to nutrient addition and wave action (d.i. = 1, + 10) and i matching							
Source	Green %TSS <sup>a</sup>	р	Red %TSS	р	Brown %TSS <sup>a</sup>	р	
(a) Algal export							
Ν	87.08	< 0.001	59.02	0.011	38.43	0.179	
W	7.28	0.052	3.55	0.330	2.92	0.677	
$\mathbf{N}  imes \mathbf{W}$	1.76	0.248	25.85	0.040	0.64	0.844	
Res	3.88		11.59		58.01		
(b) Algal accumu	ulation						
N	57.27	0.013	14.80	0.382	20.80	0.100	
W	14.95	0.095	8.88	0.490	0.53	0.751	
$\mathbf{N}  imes \mathbf{W}$	15.16	0.093	14.72	0.384	60.43	0.022	
Res	12.61		61.60		18 24		

Results from two-way ANOVAs on differences in (a) algal export and (b) algal accumulation due to nutrient addition and wave action (d.f. = 1, 4 for all F-ratios)

The underlined value indicates significance at the 0.05-level after correction for the number of comparisons with Hochberg's sequential Bonferroni. <sup>a</sup> Data were transformed by ln(x + 1).

The stimulation of total animal abundance in nutrient-enriched mesocosms was, however, more pronounced and rapid than expected from previous experience. This is probably related to the much stronger and more rapid stimulation of green algae in this experiment, since green algae together with periphytic microalgae are among the preferred food sources for the dominating animal taxa (Kraufvelin et al., 2006a). The contrasting results for *Gammarus* and *Jaera* with one taxon responding with a stronger abundance increase in the disturbed

Table 5



Fig. 6. Stacked (a) g ww of exported macroalgae per 24 h, (b) kg ww of accumulated macroalgae during June–September 2004 (11 weeks).

zone (Gammarus) and the other (Jaera) with a stronger abundance increase in the undisturbed zone is interesting. This pattern may have several explanations: (1) a stronger dependence on Ulva lactuca and Ulva intestinalis as a food source for Gammarus (Kraufvelin et al., 2006a); (2) a higher degree of mobility of Gammarus spp. possibly leading to more frequent visits outside the denser algal assemblages (Christie and Kraufvelin, 2004); (3) an active avoidance of the physically more open disturbed zone by Jaera to escape predators during light hours, since the animal samples were collected during day-time (Christie and Kraufvelin, 2004); or (4) a direct avoidance of large Gammarus-assemblages by Jaera, since the former taxa may predate on the latter (Dick et al., 2005). Even though these obvious stimulations of grazing macrofauna took place, it must be noted that the grazer populations were clearly not large enough to be able to control the algal responses to nutrient enrichment, see e.g. Kraufvelin et al. (2006a) in contrast to Worm and Lotze (2006).

At this early stage of experimentation (11 weeks), wave action had only minor impacts on the existing community structure on the steps, which also may be due to the rather small differences between the two wave action levels, although tidal and wave action (Lewis, 1964), in combination with export of organic matter, may moderate the accumulation of ephemeral algae and, thus also, render some rocky shore communities relatively resistant to nutrient enrichment. Intermediate to high wave exposure may continuously detach ephemeral algae from their substrate (Sousa, 1979), because they are more delicate than the perennial species otherwise dominating the communities (Littler and Littler, 1980). Fast water exchange may subsequently prevent accumulation of the detached algae through export from the littoral zone (Barrón et al., 2003; Bokn et al., 2003). The findings by Pihl et al. (1999) support this hypothesis by demonstrating the importance of wave exposure for excluding any occurrence of beds of filamentous algae in eutrophic areas of the Swedish west coast. Coastal macroalgal communities are also by themselves considered as export systems, providing food/nutrient supplies to deeper adjacent systems (Hawkins et al., 1992; Barrón et al., 2003; Bokn et al., 2003; Christie and Kraufvelin, 2004). Despite the lack of responses to wave action in the algal and animal communities,

wave action seemed indeed to be a significant factor for the detachment, export and accumulation of macroalgae. The higher export rate through the outlets of HN-HW mesocosms for green algae (Fig. 6a), as well as the tendencies of a higher accumulation rate in HN-LW mesocosms (Fig. 6b) can most likely be explained by the differences in wave action and its impact on algal detachment and transport. A justification for the  $N \times W$  interaction effects on red algal export can be sought in variable species composition with more wave tolerant species in the HN-HW mesocosm, since there were no significant differences in the total amount of red algae in the mesocosm step assemblages. For brown algae, the reasons behind the extremely low accumulation of loose algae in HN-LW coupled with the relatively high accumulation in LH-LW are harder to explain, but continued experimentation will probably show if these results are merely coincidental or if they turn out to be more consistent in time and space.

When interpreting the results from mesocosm studies, and experimental studies in general, one cannot totally neglect the issue of study realism. For the present paper this may have been especially relevant with regard to the applied treatment levels. The nutrient levels were within the ranges found at natural field sites locally and globally, although the nutrient-enriched mesocosms received nutrients in the upper end of this range (i.e. they were highly eutrophic). Both wave action levels were clearly in the smaller end of the wave action range, definitely 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. With regard to scraping/disturbance, i.e. the removal of whole algal and animal assemblages (not only the canopy), which was done due to practical reasons, this measure can be perceived as rather extreme, but as a matter of fact, such situations can also often be found at natural field sites of cold temperate coasts, e.g. in connection with extended periods of low water coupled with extreme temperatures and even ice scouring (Kiirikki and Ruuskanen, 1996).

According to this study, eutrophication-related community shifts on rocky shores may occur rapidly (within weeks for algae/within months for animals), regardless of the level of wave-energetic stress, if the enrichment levels are sufficiently high and the colonisation and development of opportunistic algae are facilitated by (natural or anthropogenic) gap forming processes. The availability of free substrate for algal colonisation thus seems to be an important prerequisite for a rapidly developing green tide and subsequent changes in the macrofaunal community. If similar disturbance measures had been taken within the previous eutrophication project, the reported community responses, i.e. resistance (Bokn et al., 2003) and delay (Kraufvelin et al., 2006b), may well have become different. Since present work also is a part of a longer term study (at least continuing until the autumn of 2007), it will be of interest to follow the community development in the various treatment combinations over the seasons and years, not to forget the long-term importance of wave energy (Pihl et al., 1999) and grazing (Geertz-Hansen et al., 1993; Hillebrand et al., 2000; Kraufvelin et al., 2006a; Worm and Lotze, 2006), since the effects of these factors may be expected to be expressed more evidently later on in the time series.

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## References

- Bäck, S., Lehvo, A., Blomster, J., 2000. Mass occurrence of unattached *Enteromorpha intestinalis* on the Finninsh Baltic Sea coast. Ann. Bot. Fenn. 37, 155–161.
- Barrón, C., Marbà, N., Duarte, C.M., Pedersen, M.F., Lindblad, C., Kersting, K., Moy, F., Bokn, T., 2003. High organic carbon export precludes eutrophication responses in experimental rocky shore communities. Ecosystems 6, 144–153.
- Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance: large-scale loss of canopy algae on rocky shores. Mar. Ecol. Prog. Ser. 214, 137–150.
- Berger, R., Henriksson, E., Kautsky, L., Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. Aquat. Ecol. 37, 1–11.
- Bokn, T., Lein, T.E., 1978. Long-term changes in fucoid associations of inner Oslofjord, Norway. Norweg. J. Bot. 25, 9–14.
- Bokn, T.L., Moy, F.E., Christie, H., Engelbert, S., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Marbà, N., Pedersen, M.F., Sørensen, K., 2002. Are rocky shore ecosystems affected by nutrient enriched seawater? Some preliminary results from a mesocosm experiment. Hydrobiologia 484, 167–175.
- Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marbà, N., Moy, F.E., Barrón, C., Bjerkeng, B., Borum, J., Christie, H., Engelbert, S., Fotel, F.L., Hoell, E.E., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Olsen, M., Sommer, U., Sørensen, K., 2003. The response of experimental rocky shore communities to nutrient additions. Ecosystems 6, 577–594.
- Christie, H., Kraufvelin, P., 2004. Mechanisms regulating amphipod population density within macroalgal communities with restricted predator impact. Sci. Mar. 68 (Suppl. 1), 189–198.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. 210, 223–253.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
- Connell, J.H., 1985. Variation and persistence of rocky shore populations. In: Moore, P.G., Seed, R. (Eds.), The Ecology of Rocky Coasts. Hodder and Stoughton Educational Press, Kent, England, pp. 57–69.
- Czerniawska-Kusza, I., 2004. Use of artificial substrates for sampling benthic macroinvertebrates in the assessment of water quality in large lowland rivers. Pol. J. Environ. Stud. 13, 579–584.
- Dayton, P.K., 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41, 351–389.

- Depauw, N., Roels, D., Fontoura, A.P., 1986. Use of artificial substrates for standardised sampling of macroinvertebrates in the assessment of waterquality by the Belgian biotic index. Hydrobiologia 133, 237–258.
- Diaz, P., Gappa, J.J.L., Piriz, M.L., 2002. Symptoms of eutrophication in intertidal macroalgal assemblages of Nuevo Gulf (Patagonia Argentina). Bot. Mar. 45, 267–273.
- Dick, J.T.A., Johnson, M.P., McCambridge, S., Johnson, J., Carson, V.E.E., Kelly, D.W., MacNeil, C., 2005. Predatory nature of the littoral amphipod *Echinogammarus marinus*: gut content analysis and effects of alternative food and substrate heterogeneity. Mar. Ecol. Prog. Ser. 291, 151–158.
- Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41, 87–112.
- Duffy, J.E., 1990. Amphipods on seaweeds: partners or pests? Oecologia 83, 267–276.
- Edgar, G.J., Barrett, N.S., Morton, A.J., Samson, C.R., 2004. Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. J. Exp. Mar. Ecol. Biol. 312, 67–87.
- Eriksson, B.K., Rubach, A., Hillebrand, H., 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. Ecology 87, 246–254.
- Geertz-Hansen, O., Sand-Jensen, K., Hanen, D.F., Christiansen, A., 1993. Growth and grazing control of abundance of the marine macroalgae *Ulva lactuca* L. in a eutrophic Danish estuary. Aquat. Bot. 46, 101–109.
- Hawkins, S.J., Hartnoll, R.G., 1983. Grazing on intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. 21, 195–282.
- Hawkins, S.J., Hartnoll, R.G., Kain, J.M., Norton, T.A., 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), Plant-Animal Interactions in the Marine Benthos. Clarendon Press, Oxford, pp. 1–32.
- Hayden, H.S., Blomster, J., Maggs, C.A., Silva, P.C., Stanhope, M.J., Waaland, J.R., 2003. Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. Eur. J. Phycol. 38, 277–294.
- Hillebrand, H., Worm, B., Lotze, H., 2000. Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. Mar. Ecol. Prog. Ser. 204, 27–38.
- Hochberg, Y., 1988. A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75, 800–802.
- Jara, V., Miyamoto, J.H.S., Da Gama, B.A.P., Molis, M., Wahl, M., Pereira, R.C., 2006. Limited evidence of interactive disturbance and nutrient effects on the diversity of macrobenthic assemblages. Mar. Ecol. Prog. Ser. 308, 37–48.
- Jenkins, S.R., Coleman, R.A., Della Santina, P., Hawkins, S.J., Burrows, M.T., Hartnoll, R.G., 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. Mar. Ecol. Prog. Ser. 287, 77–86.
- Karez, R., Engelbert, S., Kraufvelin, P., Pedersen, M.F., Sommer, U., 2004. Biomass response and changes in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment. Aquat. Bot. 78, 103–117.
- Kiirikki, M., 1996. Experimental evidence that *Fucus vesiculosus* (Phaeophyta) controls filamentous algae by means of the whiplash effect. Eur. J. Phycol. 31, 61–66.
- Kiirikki, M., Ruuskanen, A., 1996. How does *Fucus vesiculosus* L. survive ice scraping? Bot. Mar. 39, 133–139.
- Kraufvelin, P., Christie, H., Olsen, M., 2002. Littoral macrofauna (secondary) responses to experimental nutrient addition to rocky shore mesocosms and a coastal lagoon. Hydrobiologia 484, 149–166.
- Kraufvelin, P., Salovius, S., 2004. Animal diversity in Baltic rocky shore macroalgae: can *Cladophora glomerata* compensate for lost *Fucus vesiculosus*? Est. Coast. Shelf Sci. 61, 369–378.
- Kraufvelin, P., Salovius, S., Christie, H., Moy, F.E., Karez, R., Pedersen, M.F., 2006a. Eutrophication-induced changes in benthic algae affect the behaviour and fitness of the marine amphipod *Gammarus locusta*. Aquat. Bot. 84, 199–209.
- Kraufvelin, P., Moy, F.E., Christie, H., Bokn, T.L., 2006b. Nutrient addition to experimental rocky shore communities revisited: delayed responses, rapid recovery. Ecosystems 9, 1076–1093.
- Kraufvelin, P., Ruuskanen, A.T., Nappu, N., Kiirikki, M., 2007. Winter colonisation and succession of filamentous algae and possible relationships to

*Fucus vesiculosus* settlement in early summer. Est. Coast. Shelf Sci. 72, 665–674.

- Kristiansen, S., Paasche, E., 1982. Nitrogen nutrition of the phytoplankton in the Oslofjord. Est. Coast Shelf. Sci. 14, 237–249.
- Lewis, J.R., 1964. The Ecology of Rocky Shores. English Universities Press, London.
- Little, C., Kitching, J.A., 1996. The Biology of Rocky Shores. Oxford University Press, Oxford.
- Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am. Nat. 116, 25–44.
- Lotze, H.K., Worm, B., 2000. Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. Mar. Ecol. Prog. Ser. 14, 1428–1447.
- Lotze, H.K., Worm, B., Sommer, U., 2000. Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. Oikos 85, 46–58.
- Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112, 23–39.
- Mackey, R.L., Currie, D.J., 2001. The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82, 3479–3492.
- Mann, K.H., 1973. Seaweeds: their productivity and strategy for growth. Science 182, 975–981.
- Mann, K.H., 1982. Ecology of Coastal Waters. A System Approach. Blackwell, Oxford.
- Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130, 730–757.
- Middelboe, A.L., Sand-Jensen, K., 2000. Long-term changes in macroalgal communities in a Danish estuary. Phycologia 39, 245–257.
- Moran, M.D., 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100, 403–405.
- Nielsen, K.I., 2001. Bottom-up and top-down forces in tide-pools: test of a food chain model in an intertidal community. Ecol. Monogr. 71, 187–217.
- Paine, R., Levin, S.A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51, 145–178.
- Patricio, J., Salas, F., Pardal, M.A., Jørgensen, S.E., Marques, J.C., 2006. Ecological indicators performance during a re-colonisation field experiment and its compliance with ecosystem theories. Ecol. Indicators 6, 43–57.
- Pedersen, M.F., Borum, J., 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. Mar. Ecol. Prog. Ser. 142, 261–272.
- Pedersen, M.F., Borum, J., 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. Mar. Ecol. Prog. Ser. 161, 155–163.
- Pihl, L., Svenson, A., Moksnes, P.O., Wennehage, H., 1999. Distribution of green algal mats throughout shallow soft bottoms of the Swedish Skagerrak archipelago in relation to nutrient sources and wave exposure. J. Sea Res. 41, 281–295.
- Råberg, S., Berger-Jönsson, R., Björn, A., Granéli, E., Kautsky, L., 2005. Effects of *Pilayella littoralis* on *Fucus vesiculosus* recruitment: implications for community composition. Mar. Ecol. Prog. Ser. 289, 131–139.
- Rönnberg, O., Ådjers, K., Ruokolahti, C., Bondestam, M., 1992. Effects of fish farming on growth, epiphytes and nutrient contents of *Fucus vesiculosus* L. in the Åland archipelago, northern Baltic Sea. Aquat. Bot. 42, 109–120.
- Santelices, B., Ojeda, F.P., 1984. Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. Mar. Ecol. Prog. Ser. 19, 73–82.
- Schramm, W., 1999. Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. J. Appl. Phycol. 11, 69–78.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry, third ed. Freeman and Company, New York.
- Sousa, W.P., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49, 227–254.
- Thompson, R.C., Crowe, T.P., Hawkins, S.J., 2002. Rocky intertidal communities, past environmental changes, present status and predictions for the next 25 years. Environ. Conserv. 29, 168–191.

- Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.
- Valdivia, N., Thiel, M., 2006. Effects of point-source nutrient addition and mussel removal on epibiotic assemblages in *Perumytilus purpuratus* beds. J. Sea Res. 56, 271–283.
- Valdivia, N., Heidemann, A., Thiel, M., Molis, M., Wahl, M., 2005. Effects of disturbance on the diversity of hard-bottom macrobenthic communities on the coast of Chile. Mar. Ecol. Prog. Ser. 299, 45–54.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42, 1105– 1118.
- Weaver, M.J., Magnuson, J.J., Clayton, M.K., 1997. Distribution of littoral fishes in structurally complex macrophytes. Can. J. Fish. Aquat. Sci. 54, 2277–2289.
- Winer, B.J., Brown, D.R., Michels, K.M., 1991. Statistical Principles in Experimental Design, third ed. McGraw-Hill, New York.
- Worm, B., Lotze, H.K., 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnol. Oceanogr. 51, 569–579.
- Worm, B., Lotze, H.K., Sommer, U., 2000. Coastal food web structure, carbon storage and nitrogen retention regulated by consumer pressure and nutrient loading. Limnol. Oceanogr. 45, 339–349.
- Worm, B., Lotze, H.K., Hillebrand, H., Sommer, U., 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417, 848–851.