Ecosystems (2006) 9: 1076–1093
DOI: 10.1007/s10021-005-0188-1

ECOSYSTEMS

# Nutrient Addition to Experimental Rocky Shore Communities Revisited: Delayed Responses, Rapid Recovery

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## ABSTRACT

Coastal eutrophication may alter the dominance patterns of marine macroalgae, with potential consequences for the associated fauna and the entire ecosystem. Benthic macroalgae and animals in control and nutrient-enriched mesocosms were monitored to investigate eutrophication-induced changes in rocky shore communities. During a 3-year project, nutrient addition had only minor effects on the community structure, such as increased cover and biomass of green *Ulva* spp. and increased abundance of certain animal species at high nutrient levels. This study is a 4-year extension of a previously reported project, with 2 extra years of effect studies (altogether 5 years) and a subsequent 2 years for recovery. During the 4th year of nutrient enrichment, the cover of *Fucus vesiculosus* and *Fucus serratus* started to decline. In the 5th year, these canopy species crashed and there was an evident take-over by green algae at high nutrient addition levels. The previously observed abundance stimulation for fauna disappeared later in the time series, probably due to the loss of the macroalgal canopy. After less than 2 years on regular seawater, the algal and animal communities had returned to within the range of normal variability. The results indicate that established rocky shore communities of perennial algae with associated fauna are able to persist for several years, even at very high nutrient levels, but that community shifts may suddenly occur if eutrophication continues. They also indicate that rocky shore communities have the ability to return rapidly to natural undisturbed conditions after the termination of nutrient enhancement.

**Key words:** mesocosm; coastal eutrophication; intertidal communities; canopy algae; green tides; marine biodiversity; nutrient enrichment; long-term experiment.

## INTRODUCTION

During the 20th century, urban and industrial effluents, together with the intensified use of fertilizers, dramatically increased the transport of essential plant nutrients to the Sea (Gray 1992; Nixon 1995; Vitousek and others 1997; Cloern 2001), leading to widespread anthropogenic eutrophication of the coastal zone. Typical problems related to marine eutrophication include blooms of nuisance algae, anoxia events, loss of habitats and ecosystem functions, and impaired use of marine resources (Rosenberg 1985; Gray and others 2002; Karlson and others 2002). Although our understanding of responses to increased nutrient levels is generally adequate for the pelagic zone and seagrass systems (Duarte 1995; Valiela and others 1997; Vidal and others 1999), current knowledge of responses in rocky shore ecosystems is limited. Rocky intertidal habitats have characteristic traits that may render them partly resistant to nutrient enrichment. Dense populations of perennial macroalgae (Rhodophyceae/Phaeophyceae/Cholorophyceae) typically dominate intertidal

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Received 15 December 2005; accepted 16 December 2005;

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rocky shore communities, arising in an intense competition among individuals for space and light (Dayton 1971; Mann 1982; Worm and others 2001). The rocky intertidal is a highly energetic environment due to wave and tidal action, which may moderate the accumulation of excessive algal biomass through intense export (Lewis 1964; Kautsky 1991; Kiirikki 1996; Thompson and others 2002). Finally, large 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; Lotze and others 2001). All of these factors may modify primary eutrophication responses by reducing the development and dominance of opportunistic algae.

Conceptual eutrophication models (Cloern 2001) predict a stimulation of opportunistic algae by nutrient enrichment (Duarte 1995; Valiela and others 1997), and high loads of ephemeral algae are often observed at eutrophic sites (Rönnberg and others 1992; Middelboe and Sand-Jensen 2000; Diaz and others 2002). On rocky shores, eutrophication increases the growth of annual filamentous algae, thereby retarding perennial species, which are known to be important habitats for macrofauna (Weaver and others 1997; Schramm 1999; Benedetti-Cecchi and others 2001), but see also Kraufvelin and Salovius (2004) and Edgar and others (2004). Although increased nutrient supply also will affect the species composition of such systems (Valiela 1995; Worm and Sommer 2000), remarkably few experimental studies on the effects of nutrient enrichment have been conducted on intertidal rocky shores. In rocky littoral communities, high nutrient levels are generally considered to be responsible for stimulating the growth rates of photosynthetic organisms and for increasing the primary production of the ecosystem. Increased production will, however, not only manifest as an increased growth rate of the existing algae, but also as the replacement of slow-growing species by faster-growing opportunistic ones (Pedersen and Borum 1996; Valiela and others 1997). This change in the species composition of benthic algae (primary effect) may result in changes in the abundance and quality of food (species type and nutrient content), as well as habitat changes (Edgar 1990; Karez and others 2004; Salovius and Kraufvelin 2004), thereby causing changes in the animal community (secondary effects). However, the time scales required to exceed any buffering capacity of rocky shore ecosystems and cause either increased production or effects that are more undesirable remain unknown.

Recently, a high degree of resistance to disturbance caused by excessive nutrients has been documented in long-term mesocosm (Bokn and others 2002, 2003; Kraufvelin and others 2002; Barrón and others 2003) and field/whole-ecosystem experiments (Kraufvelin and others 2002). This phenomenon has several explanations. For negative changes, such as the loss of canopy algae, to occur in established communities, Kraufvelin and others (2002) and Bokn and others (2003) proposed that inadequately short time scale—that is, less than three years—was an important factor, together with a lack of sufficient light and free space for the settlement of opportunistic algae. Other explanations include an intense export from the macroalgal beds (Barrón and others 2003; Bokn and others 2003; Christie and Kraufvelin 2004) and intense grazing by macrofauna (Bokn and others 2003; Karez and others 2004; Kraufvelin and others 2006). Wave action, relevant in the present mesocosms due to the presence of continuously operating wave machines, may also modulate the impact of nutrient loading on intertidal community structure by increasing the rate of algal detachment and export. An inefficient experimental design with low statistical power (Kraufvelin 1998) as well as insufficiently low nutrient addition levels at the lower part of the gradient may be other explanations for the restricted response. Finally, the generally restricted realism of mesocosms may have interfered with the results (Kraufvelin 1999; Bokn and others 2003).

After the termination of the initial mesocosm experiment in August 2000, an opportunity to study temporal effects arose due to 2 additional years of nutrient dosing in 2001–02. At the end of nutrient enhancement in September 2002, a 2-year (2003–04) recovery survey of undisturbed mesocosms was conducted. This paper has therefore emerged as a long-term data synthesis covering macroalgal and macrofaunal community development in littoral rocky shore mesocosms over a period of 7 years. However, here the emphasis is placed on the last 2 years of effect studies (the 4th and 5th year) and the subsequent 2 recovery years, for which the data are previously unpublished. For the first years spanning 1997–2000, we refer mainly to Bokn and others (2002, 2003) and Kraufvelin and others (2002, 2006), although data from the year 2000 are included in this paper to illustrate the rapid changes in 2001–02. The main objective of this paper was to outline the importance of temporal effects for the occurrence and disappearance of eutrophication responses in rocky littoral macroalgal and macrofaunal assemblages.

# MATERIALS AND METHODS

## Solbergstrand Rocky Littoral Mesocosms

All measurements were made in eight rocky littoral mesocosms at the Marine Research Station Solbergstrand by the Oslofjord (59°37′N, 10°39′E) in southeast Norway. In 1997, all mesocosms received background fjord water and served as preexperimental controls. During the period from April 1998 to September 2001, nutrients were added to six mesocosms along a geometrical gradient corresponding to 1, 2, 4, 8, 16, and 32 μM of inorganic nitrogen (N) as well as 0.06, 0.12, 0.25, 0.5, 1.0, and 2.0 μM of inorganic phosphorus (P) above background levels. Two basins continued to serve as controls without extra nutrient addition. The highest nutrient addition level is similar to concentrations recorded in eutrophic areas locally (Kristiansen and Paasche 1982) and globally (Cloern 2001). During the period from March to September 2002, the four highest nutrient addition levels from the previous period (that is, 4–32 μM N and 0.25–2 μM P above background) were treated with 32 μM N and 2 μM P, respectively. In addition, the two previously lowest nutrient addition levels (that is, 1–2 μM N and 0.06–0.12 μM P above background) together with the two former controls became the new zero additions/controls. We changed the nutrient addition scheme to get real replicates under the same nutrient regime for analyses of variance (ANOVA) and to increase the relative differences in nutrient addition between treatments and controls, because these differences were often small at the lower end of the gradient due to large fluctuations in background ''fjord'' nutrient levels, thereby increasing the statistical power (Kraufvelin 1998). Nutrients were added as a mixture, which for the highest nutrient addition level consisted of 14.3 mol N as $NH_4NO_3$ and 0.9 mol P as $H_3PO_4$ with an N:P mol ratio of 16:1. Nutrient addition was stopped in September 2002 after 5 years of treatment; for the next 2 years (2003–04), all basins were fed with untreated seawater from the fjord to study recovery.

The Solbergstrand mesocosms (Figure 1) had a water volume of 6–12 $m^3$, depending on tidal level, and received water from a depth of 1 m in the Oslofjord at a rate of 5 $m^3\ h^{-1}$ (mean water 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, whereas a wave machine generated constant wave action (17 strokes/min). Apart from two incidents in 2003 with broken tide -regulators, which temporarily destroyed some of the upper intertidal algae in two control systems, the mesocosms worked well during the entire sampling period.

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 (Figure 1). After the initiation phase, natural community development was allowed to contribute to the flora and fauna assemblages. Over the experimental period, over 40 species of macroalgae and 80 species of macrofauna were identified in the mesocosms. Green algal species—that is, *Ulva lactuca* L. and *Ulva intestinalis* L., as well as brown algae, *Fucus serratus* L., *Fucus vesiculosus* L., and *Ascophyllum nodosum* (L.) Le Jol, and some seasonal red algae dominated the macroalgal assemblages. The green alga *U. intestinalis* consisted of several species formerly known as *Enteromorpha* (see Hayden and others 2003), among which *Enteromorpha intestinalis* was most common. Bigger amphipods such as *Gammarus* spp. and *Hyale nilssoni* (Rathke), smaller amphipod taxa like Corophiidae, Stenothoidae, Ischyroceridae and Aoridae, isopods such as *Jaera* spp. and *Idotea* spp., gastropods such as *Littorina littorea* L. and *Rissoa* spp., and blue mussels were the most important animal groups.

## Sampling and Measurements

Macroalgal cover and animal abundance were measured one to five times each year, but for comparative purposes (to decrease the effects of seasonality), only measurements from late summer/autumn each year were used. The abundance of macroalgae was measured as percentage cover in 16 quadrats (42 × 42 cm, adjusted to the size of the steps) in each basin. Each quadrat was divided into 25 subquadrats to enable reliable estimaties of the algal cover, Murray and others 2006). The sum of species abundance in each quadrat may exceed 100% due to a multilayered community structure of primary cover, understory species, canopy, and epiphytes (algal cover was estimated in understory and canopy layers when present). Algal cover may be converted into biomass values using parallel biomass estimations (Bokn and others 2003), but in this study, nondestructive percentage cover was used, which is a straightforward and reliable estimate for macroalgal occurrence (Murray and others 2006). At each

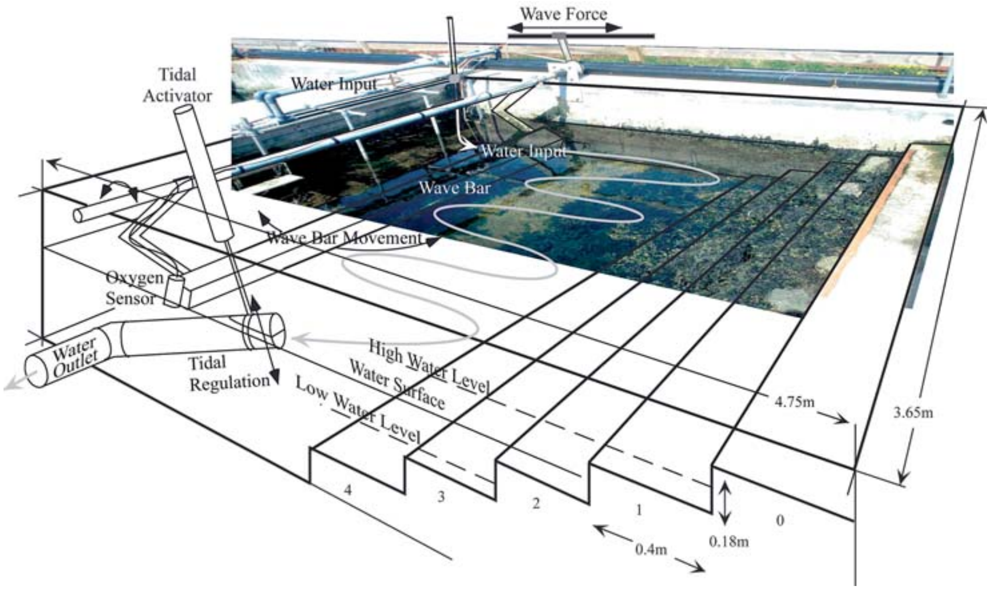

**Figure 1.** Solbergstrand mesocosm. The diagram shows four steps, with inter- and subtidal macroalgal communities, the wave generator, and the tidal regulator. All sampling was done on the steps.

sampling, the average macroalgal cover was calculated for each basin. Large motile and sessile animals were counted inside a grid covering the steps of the basins and additionally on the walls and bottom of each basin. The abundance of smaller motile animals was estimated by their colonization of artificial substrates. These substrates consisted of three 80-cm–long ropes, one stone, and one petri dish tied together. The substrates were able to collect an intermediate fraction of the animals normally present in the most dominant green, red, and brown algae (Kraufvelin and others 2002). These subtrates were used to provide for nondestructive sampling and to get samples of similar conditions from all mesocosms—that is, to counteract differences in faunal colonization due to differences in algal nutrient content and possible differences in algal morphology between controls and nutrient treatments (Kraufvelin and others 2006). Two substrates were placed into each mesocosm, one on an intertidal and one on a subtidal step, and exposed for 2 days in each basin, after which the animals were preserved in ethanol for later analysis. Because the main interest of this study lay in making comparisons between mesocosms, the two substrates were pooled and treated as one mesocosm measurement.

## Statistical Analysis

Algal cover and animal abundance versus nutrient addition level were analyzed by Pearson's correlation analysis for 2000–01 (Sokal and Rohlf 1995). From 2002 on, the data were analyzed by two-way ANOVAs with the factors N = Nutrient (two levels, fixed and orthogonal) and Y = Year (three levels, fixed and orthogonal) and the basic intention of looking for significant interactions, with 2002 representing extended/intensified dosing and 2003–04 representing possibilities for recovery from dosing. The model describing the data is: $X_{ijk} = \mu + N_i + Y_j + NY_{ij} + e_{k(ij)}$. Before running the parametric tests, it was checked for normality with Kolmogorov-Smirnov's test and homogeneity of variances with Cochran's C-test. To homogenize heterogeneous variances, arcsine transformations were used for algal data (percentages) and square-root-transformations, $\sqrt{(x + 1)}$, for animal data (counts). When appropriate, Student-Neuman-Keuls (SNK) tests were applied for a posteriori comparisons of the means. Hochberg's sequential Bonferroni (Hochberg 1988) was finally used to adjust the overall significance levels to the number of tests performed. For all significance tests, alpha was set at 0.05.

It may seem spurious that the four formerly highest-nutrient treatments were treated as real replicates in an ANOVA from 2002 onward—that is, that 4, 8, and 16 µM N all became 32 µM N during the last year of dosing, given that the obtained ''replicated'' mesocosms for this analysis were far from homogeneous in the past (Kraufvelin and others 2002; Bokn and others 2003). However, this solution was judged to be appropriate for effect detection and for testing a new research hypothesis, because it actually made it more difficult to reveal significant differences—that is, it implied a decreased risk of type I errors and increased the risk of type II errors (Kraufvelin 1998).

Multivariate nonmetric multidimensional scaling (NMDS) based on Bray-Curtis similarities was used to obtain a graphical overview of the temporal development in algal and animal communities in each mesocosm. In addition, one-way analysis of similarity (ANOSIM) was used to test for differences in algal and faunal community development between treatment and control mesocosms within and among years, as well as the similarity percentage breakdown procedure (SIMPER) for sorting species that contributed most to observed dissimilarities between mesocosms (Clarke 1993). The macroalgal data were analyzed untransformed due to rather small differences between the more common and the more rare algal groups, but the data were standardized prior to the multivariate analyses to deal with a total cover sometimes exceeding 100%. The macrofaunal data were transformed by the square root to balance the relative influences of dominant and rare species.

Finally, a correlation analysis between the abundance of the dominating macrofauna taxa (amphipods, *Jaera* spp., and *Littorina littorea*) and green, red, and brown macroalgal cover was carried out across all mesocosms over the years 2000–04.

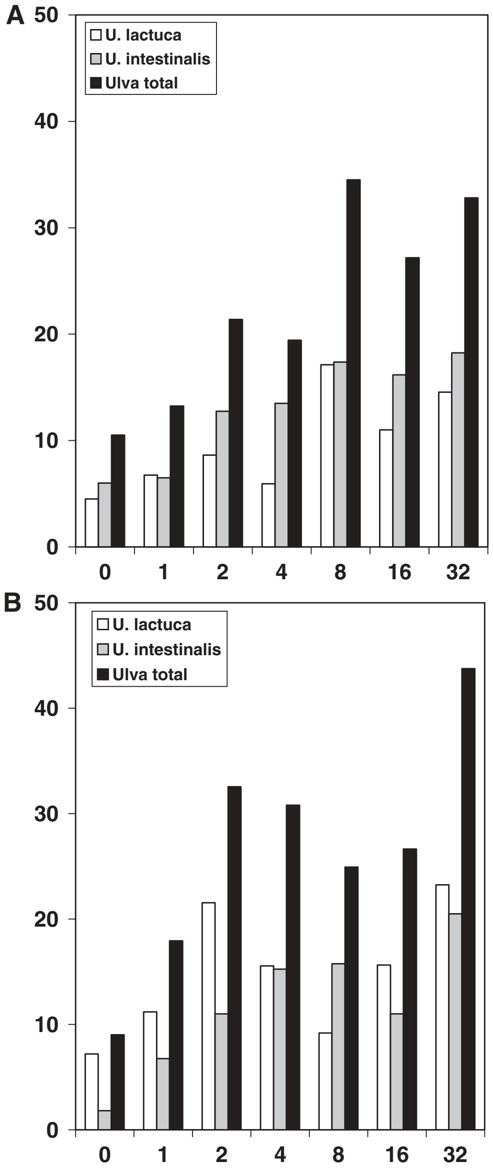

**Figure 2.** Percentage cover of *Ulva lactuca* and *Ulva intestinalis* and total *Ulva* along the nutrient-enrichment gradient (concentration in μM N; the two controls were pooled) in **A** 2000 and **B** 2001.

## RESULTS

### Changes in Algal Populations Examined by Univariate Techniques

Changes in the percentage cover of *Ulva* spp. along the nutrient gradient (2000–01) for each N addition level (controls pooled) and year are presented in Figure 2ab; the results of Pearson's correlation analysis are shown in Table 1. Mean cover values (± SE) of *Ulva lactuca* and *Ulva intestinalis* in replicated controls and treatments in 2002 and during the recovery period 2003–04 are presented in (Figure 3) and analyzed by two-way ANOVA in (Table 2). Although green algae, as *Ulva* spp. and as *U. lactuca*, have been reported to be significantly stimulated by the nutrient addition since the initial years of dosing (Bokn and others 2003), the significant relationships 2000–01 disappeared when we corrected for the number of comparisons by the sequential Bonferroni (Figure 2 and Table 1). In the two-way ANOVA 2002–04, *U. lactuca* responded with a significant interaction of Nutrient × Year Table 2. A posteriori SNK tests revealed that the percentage cover of *U. lactuca* was significantly stimulated by nutrients both during 2002 and during the first recovery year, 2003; whereas the cover in the nutrient treatments had decreased to the same level as in the controls by 2004, indicating recovery (Figure 3a and Table 2). For *U. intestinalis*, higher percentage cover in the treatments 2002–04 disappeared after Bonferroni- correction (Figure 3b and Table 2).

Red algae, comprised mainly of *Ceramium* spp., *Polysiphonia* spp., *Rhodomela confervoides* (Huds.) P.C. Silva, and *Chondrus crispus* Stackh, were significantly stimulated by nutrient addition in 2000

**Table 1.** Pearson's Correlation Analysis of Algal Cover 2000–01 along the Mesocosm Nutrient Gradient (0–32 μM N, 0–2 μM P)

| | 2000 | | 2001 | |
|---|---|---|---|---|
| Taxa | *r* | *P* value | *r* | *P* value |
| Total *Ulva* | 0.746 | **0.034** | 0.745 | **0.034** |
| *Ulva intestinalis* | 0.732 | **0.039** | 0.739 | **0.036** |
| *Ulva lactuca* | 0.679 | 0.064 | 0.633 | 0.092 |
| Red algae | 0.721 | **0.043** | 0.255 | 0.542 |
| *Fucus* spp. | 0.287 | 0.491 | –0.663 | 0.073 |
| *Fucus vesiculosus* | –0.078 | 0.854 | –0.480 | 0.229 |
| *Fucus serratus* | 0.544 | 0.163 | –0.434 | 0.282 |
| *Ascophyllum nodosum* | 0.022 | 0.959 | –0.026 | 0.951 |
| *Laminaria digitata* | 0.606 | 0.111 | 0.742 | **0.035** |
| Shannon | 0.663 | 0.073 | 0.501 | 0.206 |

*n = 8, r = correlation coefficients.*
*P values significant at the 0.05 level before a tablewise correction for the number of tests by Hochberg's sequential Bonferroni, but not after, are shown in bold face.*

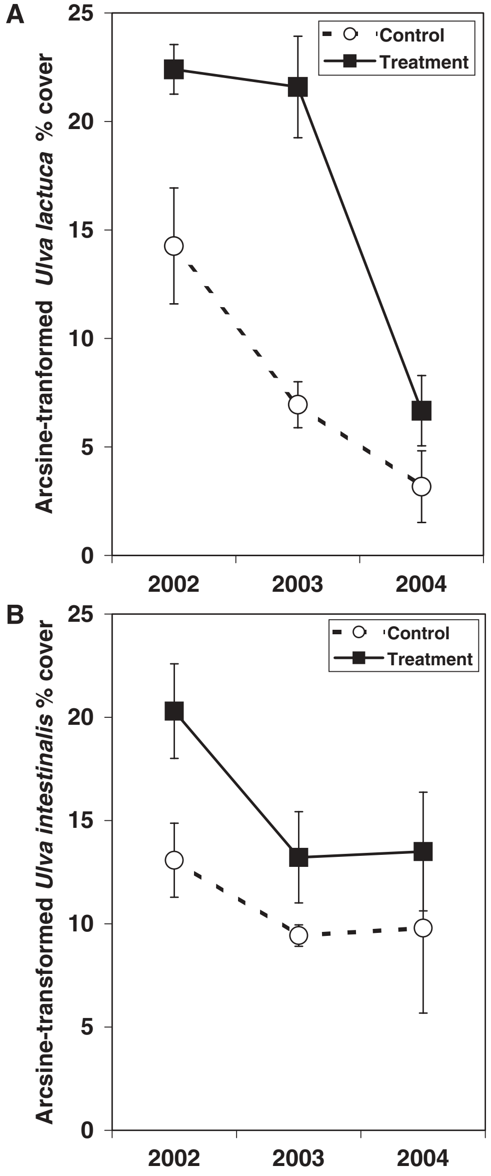

**Figure 3.** Percentage cover of *Ulva* spp. in controls and mesocosm treatments (addition of 32 μM N in 2002) and in the same systems during the recovery phase in 2003–04 (means ± SE). **A** *Ulva lactuca*. **B** *Ulva intestinalis*.

(Table 1), but this significant effect also disappeared after the Bonferroni -correction. Although red algae consisted of species that were functionally different from green algae—that is, mainly filamentous and coarsely branched species that may react differently to nutrient enrichment—no significant red algal responses to the nutrient enrichment were found. This was true both when the algae were regrouped into possible pollution-tolerant and pollution-sensitive species and when the species were tested separately (data not shown). The average abundance of upright red algal species was less than 5% cover and approximately 20% cover on average as a group. The average abundance of encrusting species was about 24% cover. The abundance of coarsely branched red algae (mainly *C. crispus*) increased slightly in all mesocosms during the recovery period, but the total abundance of red algae remained low.

The cover of brown algae—that is, *Fucus* spp.—was not affected by nutrient addition during the first 4 years of treatment (Bokn and others 2003) (Figure 4 and Table 1). In contrast, a highly significant negative response to the replicated nutrient addition was recorded for *Fucus serratus* in 2002 (Figure 5 and Table 2), with significant main effects for both Nutrient and Year in the two-way ANOVA. SNK tests showed that the cover of *F. serratus* was significantly lower in nutrient treatments than in the controls during 2002 and that these differences persisted throughout 2003 and 2004 (that is, there was still no recovery by June 2004, 21 months after the termination of dosing). With regard to changes over time, both the controls and treatments showed a strong increase in *F. serratus* cover in the recovery period (Figure 5a). The cover of *Fucus vesiculosus* did not respond significantly in the two-way ANOVA, but SNK-corrected pairwise tests demonstrated a decrease in the nutrient treatments in 2002 ($P < 0.05$), which had disappeared in 2003 (Figure 5b). The total cover of fucoids was reduced to 36%, as compared with approximately 85% cover in the controls (in 2002). This loss was preceded by a decrease in the cover of *Fucus* spp. germlings, which in 2001 showed

**Table 2.** Two-way Analysis of Variance (ANOVA) on Arcsine-Transformed Algal Cover Values and Untransformed Shannon-Wiener Diversity Values with Factors N = Nutrient Addition (Two Levels: Control versus Addition of 32 μM N and 2 μM P) and Y = year (Three Levels: 2002–04)

*Ulva intestinalis* Cover

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 144.51 | 5.59 | **0.029** |
| Year | 2,18 | 72.44 | 2.80 | 0.087 |
| N × Y | 2,18 | 8.03 | 0.31 | 0.737 |
| Residual | | 25.83 | | |

*Ulva lactuca* Cover

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 460.22 | 33.91 | **< 0.001** |
| Year | 2,18 | 378.46 | 27.88 | **< 0.001** |
| N × Y | 2,18 | 62.60 | 4.61 | **0.024** |
| Residual | | 13.57 | | |

*Fucus serratus* Cover

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 640.68 | 20.34 | **< 0.001** |
| Year | 2,18 | 352.00 | 11.18 | **< 0.001** |
| N × Y | 2,18 | 10.19 | 0.32 | 0.728 |
| Residual | | 31.49 | | |

*Fucus vesiculosus* Cover[a]

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,15 | 286.54 | 3.64 | 0.076 |
| Year | 2,15 | 145.70 | 1.85 | 0.191 |
| N × Y | 2,15 | 154.36 | 1.96 | 0.175 |
| Residual | | 78.71 | | |

Shannon-Wiener Diversity

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| **Nutrient** | **1,18** | **0.60** | **40.74** | **< 0.001** |
| **Year** | **2,18** | **0.22** | **15.18** | **< 0.001** |
| **N × Y** | **2,18** | **0.00** | **0.27** | **0.764** |
| **Residual** | | **0.01** | | |

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*P values significant at the 0.05 level after correction for the number of tests by Hochberg's sequential Bonferroni are underlined (the Bonferroni corrections were made separately for each algal variable).*

[a] *In 2003 and 2004, the control sample number was lower for intertidal Fucus vesiculosus due to broken tide regulators.*

significantly lower mean percentage cover (1.31 ± 0.41%) in treatment mesocosms than in the controls (3.46 ± 0.41%) (one-way ANOVA: $F$-ratio =13.82, $P$ = 0.010, $df$ =1, 6).

During 2000–02, the abundance of *Fucus* spp. and *Ulva* spp. were significantly negatively correlated with each other ($r = -0.513$, $P = 0.010$, $n = 24$), which is indicative of strong competition. After 2 years of recovery, total fucoid cover in the previously treated basins showed no significant difference from the controls (approximately 60% compared to 75%), mainly due to regrowth of *Fucus serratus*. The other common species of perennial brown algae in the mesocosms, *Ascophyllum nodosum* and *Laminaria digitata* (Huds.) J.V. Lamour, did not respond negatively to the nutrient additions. *L. digitata* was even significantly stimulated along the nutrient gradient, before the Bonferroni correction (Table 1).

Shannon-Wiener diversity indices calculated on algal data (log-base e) did not show any significant differences in the correlations 2000–01 (Figure 6a and Table 1), but in the two-way factorial ANOVA, there were significant main effects for both the factors Nutrient and Year (Figure 6b and Table 2). As shown in Figure 6b, these differences were due to higher diversity values in the nutrient treatments and lower values in 2004 compared to 2002 and 2003, but this could not be verified by SNK tests because these tests could not be computed for this variable.

## Changes in Algal Community Structure Examined by Multivariate Techniques

Temporal changes in the algal community structure (species/percentage cover) in both nutrient treatments and controls are illustrated by an NMDS ordination, in which lines have been drawn to group together samples of the same year (Figure 7). In this figure, the years (2000–04) cluster out as significantly different in a one-way ANOSIM (global $R = 0.267$, $P < 0.001$), which demonstrates that a natural ecological succession seems to be operating independently of the responses to and recovery from nutrient addition. Differences between ''controls'' (gray symbols) and high nutrient treatments (black symbols) increased steadily each year from 2000 through 2001, to 2002, which can be seen by the two groups diverging each year. In

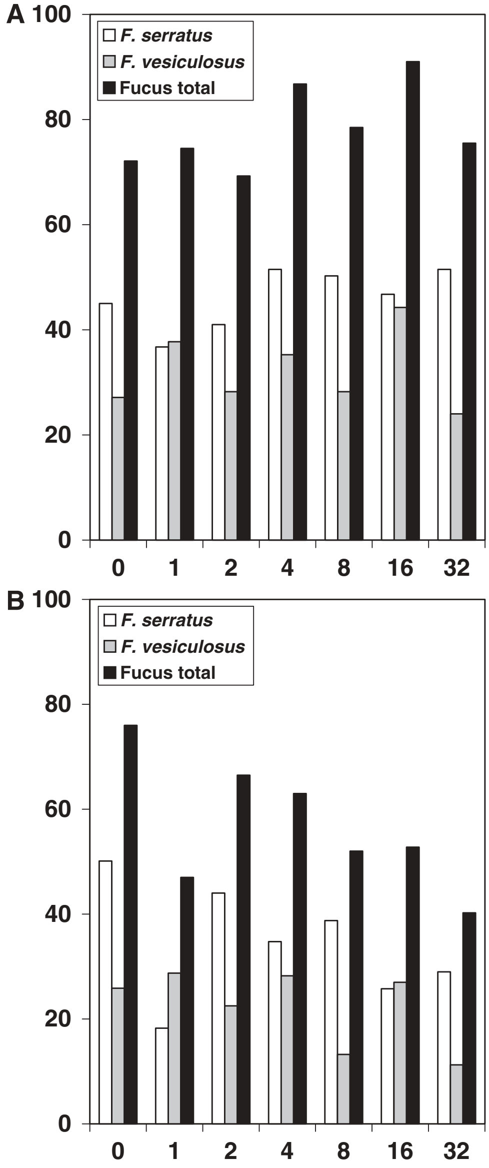

**Figure 4.** Percentage cover of *Fucus serratus*, and *Fucus vesiculosus* and total *Fucus* along the nutrient-enrichment gradient (concentration in µM N; the two controls were pooled) in **A** 2000 and **B** 2001.

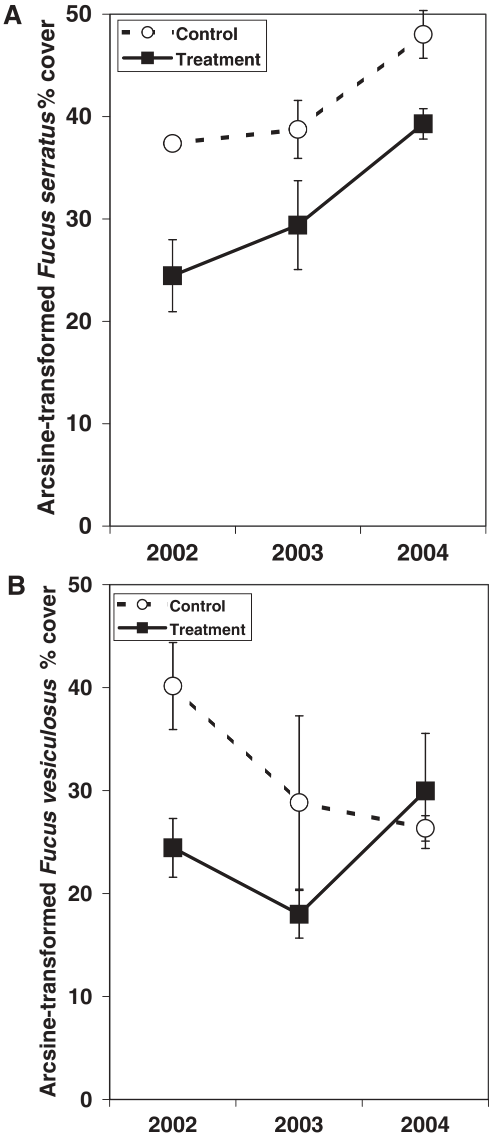

**Figure 5.** Percentage cover of *Fucus* spp. in controls and mesocosm treatments (addition of 32 µM N in 2002) and in the same systems during the recovery phase in 2003–04 (means ± SE). **A** *Fucus serratus*. **B** *Fucus vesiculosus*.

2002, the differences were also significant when analyzed by one-way ANOSIM ($R = 0.833$, $P = 0.029$). SIMPER analyses revealed that the two *Fucus* species, *Fucus vesiculosus* followed by *Fucus serratus*, both with lower percentage cover in the treatments, were responsible for 46% of the average dissimilarities of 35% between treatments and controls in 2002 (Table 3a). Judging from a significant one-way ANOSIM in 2003 ($R = 0.865$, $P = 0.029$), the algal community structure had not yet recovered, although the dissimilarity between treatments and controls had decreased to 31%. In this year, the two *Fucus* species contributed 47% of the average dissimilarities and *Ulva lactuca* contributed 17% (Table 3b). In 2004, the algal community structure had recovered ($R = 0.198$, $P = 0.200$), which also can be anticipated from the ordination by the fact that the highest nutrient treatments again have approached the controls (Figure 7). The two rightmost gray symbols represent the two ‘‘control’’ mesocosms, which suffered from destroyed *F. vesiculosus* and *Ascophyllum nodosum* stands due to excessive time at low water, after a local breakdown of the tidal system in 2003.

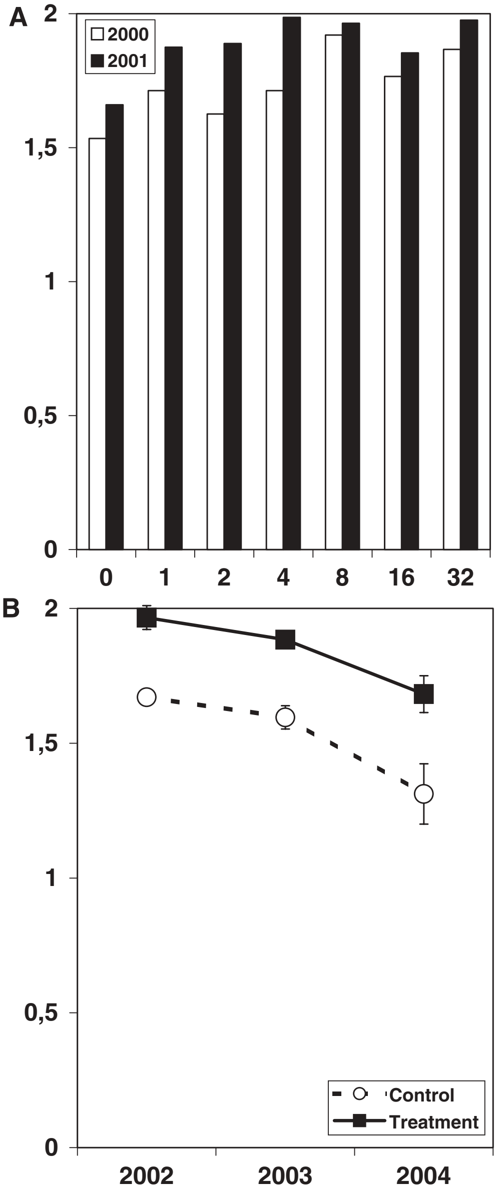

**Figure 6.** Shannon-Wiener diversity for algal data. **A** along the nutrient-enrichment gradient (concentration in µM N; the two controls were pooled), **B** in controls and mesocosm treatments (addition of 32 µM N in 2002), and in the same systems during the recovery phase in 2003–04 (means ± SE).

## Changes in Animal Populations Examined by Univariate Techniques

For the dominant animal species, there was generally a positive correlation between abundance and nutrient addition level during the early years (Kraufvelin and others 2002). Nevertheless, in this study, Pearson's correlation analysis (2000–01) yielded only two significant *P* values—for *Littorina littorea* (L.) in 2000 and for *Jaera* spp. in 2001—that still were less than 0.05 after the Bonferroni correction (Figure 8 and Table 4). In the two-way ANOVA, there were no significant results for the animals—that is, *L. littorea*, *Jaera* spp., *Gammarus* spp., and *Hyale nilssoni*—after the Bonferroni correction (Figure 9a–d and Table 5). Before the correction, however, there was a significant interaction for *H. nilssoni* due to higher abundances in nutrient treatments in 2002 and a rapid recovery in 2003 (Figure 9c). Due to the generally higher abundance of all the abovementioned species in nutrient treatments—that is, the stronger dominance of a few species—the Shannon-Wiener diversity for animals (log-base e) decreased along the nutrient gradient in 2001 (Figure 10a and Table 4), although this "significant" value also disappeared after the Bonferroni correction. In the two-way ANOVA, the Shannon-Wiener diversity was significantly lower in 2004 than in 2002 (Figure 10b and Table 5). All animal populations had recovered by the summer of 2003 and remained so during 2004 (Figure 9 and Table 5).

## Changes in Animal Community Structure Examined by Multivariate Techniques

The temporal development of the animal community structure (species abundance data, with years emphasized by drawn lines) in the NMDS ordination is even clearer than for the algal data (Figure 11) and is also highly significant in a one-way ANOSIM ($R = 0.751$, $P < 0.001$). On the other hand, no significant differences in animal community structure between nutrient addition levels were detectable by one-way ANOSIM within the relevant years. In 2001, *Jaera* spp., *Hyale nilssoni*, and *Gammarus* spp. made up 58% of the dissimilarities between treatments and controls in a SIMPER analysis. The two former taxa were on average four times as common in nutrient treatments, whereas *Gammarus* was twice as common. In 2002, *Jaera*, and the amphipods *H. nilssoni* and Stenothoidae made up 55% of the dissimilarities between treatments and controls. In the same year, *H. nilssoni* was on average 10 times as common, whereas *Jaera* and Stenothoidae were twice as common in nutrient treatments than in controls. By 2003 and 2004, the four former high-nutrient treatments approached the same part of the NMDS ordination scheme as the controls, indicating a "recovery" of the animal community structure (Figure 11).

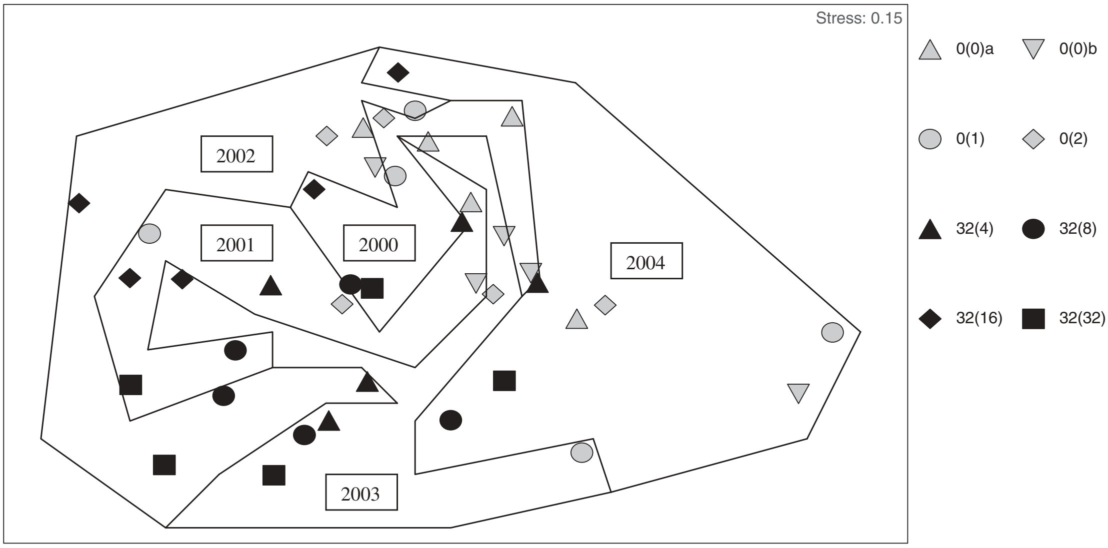

**Figure 7.** Nonmetric multidimensional scaling (NMDS) ordination describing changes in macroalgal community structure in the mesocosms over 2000–04 (stress 0.15). The lines help to group samples from the same year together. Dark labels indicate high-nutrient treatments, 32 μM N in 2002 (levels in parenthesis = dosing for 2000–01); gray labels indicate controls in 2002 (levels in parenthesis = dosing for 2000–01). In 2003–04 no dosing took place so we could study possible recovery.

**Table 3.** Each Plant Species' Contribution ($\delta_i$) to the Average Dissimilarities between Nutrient Treatments and Controls in **a** 2002 (total δ % = 34.91) and **b** 2003 (total δ % = 31.42)

| a Taxonomic Group | Average Algal Cover Controls | Average Algal Cover Treatments | Average Term $\delta_i$ | Ratio Dissim./SD | Percent Contrib. | Cumulative Percent |
|---|---|---|---|---|---|---|
| *Fucus vesiculosus* | 49.33 | 17.63 | 10.25 | 3.11 | 29.37 | 29.37 |
| *Fucus serratus* | 36.87 | 17.89 | 5.88 | 1.73 | 16.84 | 46.21 |
| *Ascophyllum nodosum* | 10.93 | 19.86 | 4.56 | 1.39 | 13.06 | 59.27 |
| *Ulva lactuca* | 6.64 | 14.60 | 3.86 | 1.97 | 11.06 | 70.34 |
| *Laminaria digitata* | 9.14 | 14.05 | 3.35 | 1.28 | 9.59 | 79.93 |
| *Ulva intestinalis* | 5.39 | 12.39 | 3.32 | 1.51 | 9.52 | 89.45 |
| *Cladophora rupestris* | 2.01 | 6.34 | 1.88 | 1.32 | 5.38 | 94.83 |
| Red algae | 17.89 | 14.91 | 1.81 | 1.57 | 5.17 | 100.00 |

| b Taxonomic Group | Average Algal Cover Controls | Average Algal Cover Treatments | Average Term $\delta_i$ | Ratio Dissim./SD | Percent Contrib. | Cumulative Percent |
|---|---|---|---|---|---|---|
| *Fucus serratus* | 39.37 | 24.97 | 8.38 | 2.90 | 26.67 | 26.67 |
| *Fucus vesiculosus* | 20.91 | 9.93 | 6.51 | 1.58 | 20.73 | 47.39 |
| *Ulva lactuca* | 1.56 | 13.90 | 5.46 | 10.36 | 17.39 | 64.78 |
| Red algae | 17.53 | 26.29 | 3.45 | 1.83 | 10.99 | 75.77 |
| *Ascophyllum nodosum* | 12.91 | 16.97 | 3.10 | 1.35 | 9.86 | 85.63 |
| *Laminaria digitata* | 7.16 | 10.34 | 1.82 | 1.49 | 5.78 | 91.41 |
| *Cladophora rupestris* | 2.05 | 5.61 | 1.46 | 1.49 | 4.65 | 96.06 |
| *Ulva intestinalis* | 2.71 | 5.64 | 1.24 | 1.37 | 3.94 | 100.00 |

*The first two columns give the actual cover values; the third column gives the contribution of each species to the total δ %; the fourth column is a measure of the variability (consistency within data); the fifth and sixth columns give the percentage contribution.*

## Faunal Assemblages in Relation to the Algal Community

In the whole data set spanning 2000–04 ($n = 40$), the total animal abundance, as well as the abundance of *Gammarus* spp. and *Hyale nilssoni*, indicated significantly positive correlations with *Ulva intestinalis* cover, whereas total animal abundance also indicated a similar relationship with *Ulva lactuca* (Table 6). Conversely, *Jaera* spp. seemed to correlate

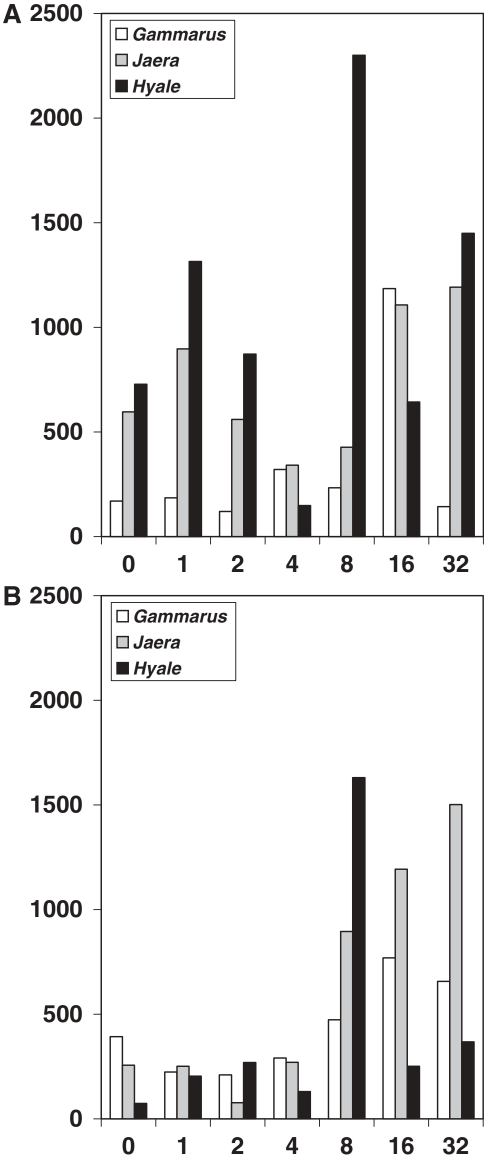

**Figure 8.** Abundance of *Gammarus* spp., *Jaera* spp., and *Hyale nilssoni* along the nutrient-enrichment gradient (concentration in μM N; the two controls were pooled) in **A** 2000 and **B** 2001.

negatively with *Fucus serratus* cover. After tablewise Bonferroni corrections, the only significant relationships that remained were *U. intestinalis* versus total abundance and abundance of *H. nilssoni*.

## DISCUSSION

This study demonstrates the need for long-term experiments to determine the ecological effects of perturbations. Extending the 3-year nutrient enrichment project described by Bokn and others (2003) resulted in very different conclusions about the effects of eutrophication on a rocky shore community. Although *Ulva* spp. responded within a couple of months after the initiation of nutrient addition with slight but significantly increased cover and biomass at higher nutrient addition levels, no dramatic changes in the algal community structure could be detected over the first 3 years of nutrient addition (Bokn and others 2003). After 3 years of nutrient enrichment, in 2000, the abundance of *Fucus* spp. (sum degree of cover) was actually higher in the four high-dosed environments than in the low-dosed enviroments and controls ($F = 6.80$, $P = 0.040$ in a one-way ANOVA with $df = 1, 6$) (Figure 4a). In contrast, the dominating perennial brown algae (*Fucus vesiculosus* and *Fucus serratus*) required more than 4 years and intensified nutrient dosing to show the expected loss of cover at higher nutrient addition levels (see Schramm 1999; Cloern 2001). In the 5th year of nutrient addition (2002), the rocky intertidal communities crashed, with a clear decrease in cover of the structuring canopy fucoids and substitution especially by the green algae *Ulva lactuca*. These results were consistent across all mesocosm treatments. It is important here to recognize that the percentage cover does not reflect true biomass. One individual of *Fucus* may cover the same area of a given surface as several overlapping individuals, which implies that the response time reported here does not necessarily reflect true changes in fucoid biomass. Nevertheless, it is difficult to measure biomass without conducting destructive harvesting. Within 2 years after the termination of nutrient addition, the algal communities had basically returned to the range of normal variability—that is, no significant differences remained between controls and previous nutrient treatments. An exception was *F. serratus*, but when examined as *Fucus*

**Table 4.** Pearson's Correlation Analysis of Macrofauna Abundance Values 2000–2001 along the Mesocosm Nutrient Gradient (0–32 μM N, 0–2 μM P)

| | 2000 | | 2001 | |
|---|---|---|---|---|
| Taxa | *r* | *P* value | *r* | *P* value |
| *Littorina littorea* | 0.863 | **0.006** | 0.694 | 0.056 |
| *Jaera* spp. | 0.704 | 0.051 | 0.931 | **0.001** |
| *Gammarus* spp. | 0.257 | 0.539 | 0.753 | **0.031** |
| *Hyale nilssoni* | 0.275 | 0.510 | 0.160 | 0.704 |
| Total abundance | 0.671 | 0.069 | 0.712 | **0.047** |
| Shannon diversity | –0.084 | 0.844 | –0.788 | **0.020** |

*n = 8, r = correlation coefficients.*
*Significant P values after a tablewise correction for the number of comparisons by Hochberg's sequential Bonferroni are underlined.*

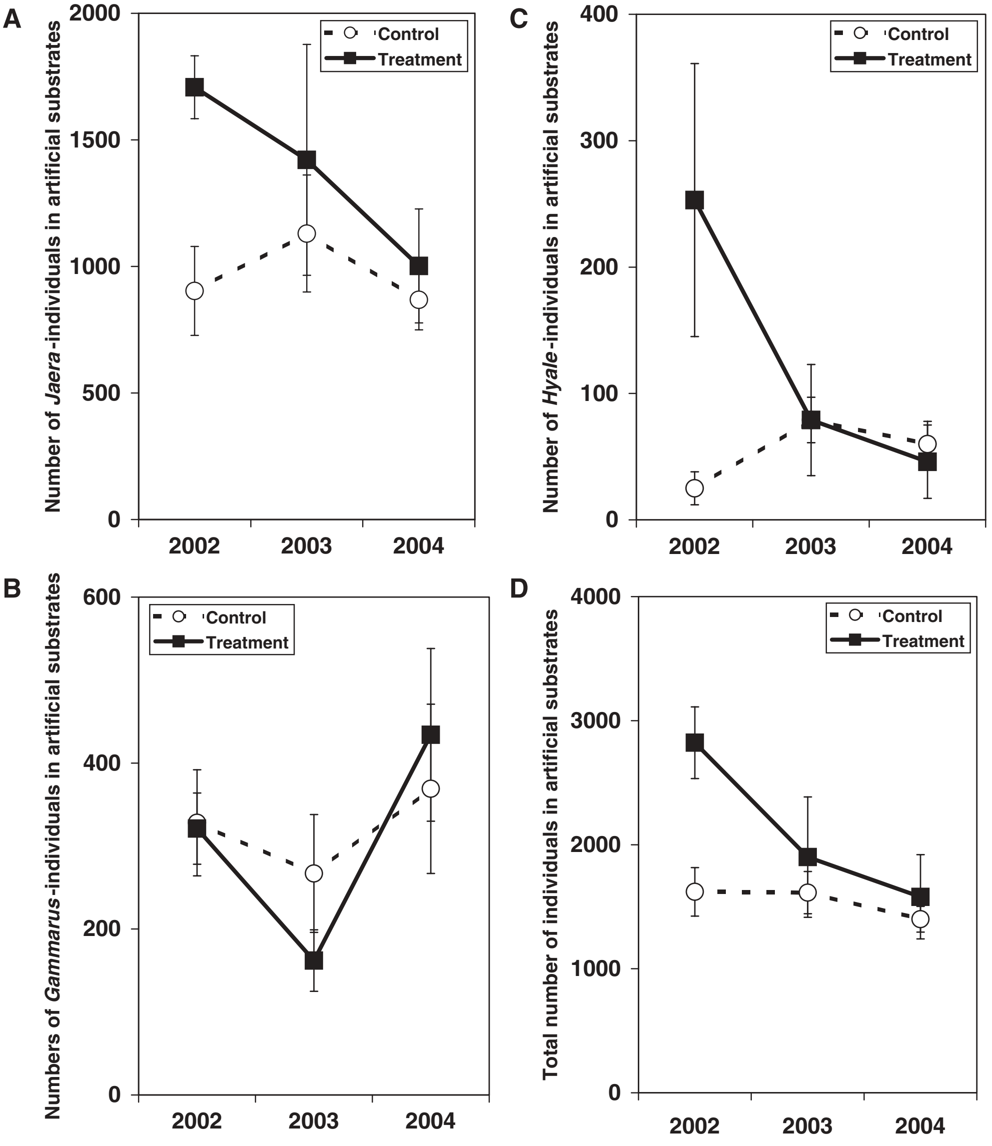

**Figure 9.** Macrofauna abundance in artificial substrates in controls and mesocosm treatments (addition of 32 μM N in 2002) and in the same systems during the recovery phase in 2003–04 (means ± SE). **A** *Jaera* spp. **B** *Gammarus* spp. **C** *Hyale nilssoni*. **D** total abundance (mean ± SE).

spp. (*F. serratus* and *F. vesiculosus* pooled) and when examined as algal community structure (multivariate ANOSIM), the algal canopy was found to have recovered in 2004.

The causative agent for the canopy crash was most probably an age-related mortality of *Fucus* specimens, which were not replaced by juveniles to the same extent in the nutrient treatments as in the controls. This may be due to increased competition for space, light, and nutrients by ephemeral algae, or to adverse effects on the reproduction and settlement of *Fucus* germlings at high nutrient levels (for example, Worm and others 2001; Berger and others 2003; Steen 2004; Råberg and others 2005). The significantly fewer numbers of *Fucus* germlings registered in the nutrient treatments in 2001 lend support to this theory, although in this project, the limited recruitment of *Fucus* was probably mainly caused by an increase in green, not brown or red ephemerals. In both 2001 and 2002, the cover of *Ulva* spp. had increased to approximately 30% in the nutrient treatments, or three times the background abundance. The abundance of *U. lactuca*, which grows primarily on rocks and other hard substrate, seems to be controlled by light limitation and increased more than twofold in response to the breakdown of the fucoid vegetation. *Ulva intestinalis* grows luxuriantly both on hard substrate and as epiphytes, especially on old fucoids, and its response measured as percentage cover is therefore affected by the availability of both types of substrates.

Although the green algae responded to nutrient enrichment as expected and the brown algae responded with a delay, the cover of red algae declined

**Table 5.** Two-way Analysis of Variance (ANOVA) on Macrofauna Abundance Values with Factors N = Nutrient Addition (Two Levels: Control versus Addition of 32 μM N and 2 μM P) and Y = Years (Three Levels: 2002–04)

*Littorina littorea* Abundance, square root (x+1)

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 1.45 | 0.11 | 0.744 |
| Year | 2,18 | 13.41 | 1.02 | 0.380 |
| N × Y | 2,18 | 3.87 | 0.29 | 0.748 |
| Residual | | 13.13 | | |

*Jaera* spp. Abundance, square root (x+1)

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 181.94 | 3.33 | 0.085 |
| Year | 2,18 | 67.41 | 1.23 | 0.315 |
| N × Y | 2,18 | 56.61 | 1.04 | 0.375 |
| Residual | | 54.69 | | |

*Gammarus* spp. Abundance

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 1488 | 0.07 | 0.800 |
| Year | 2,18 | 70675 | 3.15 | 0.067 |
| N × Y | 2,18 | 14558 | 0.65 | 0.535 |
| Residual | | 22465 | | |

*Hyale nilssoni* Abundance, square root (x+1)

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 39.70 | 2.12 | 0.162 |
| Year | 2,18 | 14.95 | 0.80 | 0.465 |
| N × Y | 2,18 | 83.41 | 4.46 | **0.027** |
| Residual | | 18.69 | | |

Total Abundance

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | $1.9 \times 10^6$ | 5.44 | **0.032** |
| Year | 2,18 | $1.1 \times 10^6$ | 3.21 | 0.064 |
| N × Y | 2,18 | $0.6 \times 10^6$ | 1.85 | 0.186 |
| Residual | | $0.3 \times 10^6$ | | |

Shannon-Wiener Diversity

| Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Nutrient | 1,18 | 0.00 | 0.05 | 0.830 |
| Year | 2,18 | 0.40 | 5.25 | **0.016** |
| N × Y | 2,18 | 0.00 | 0.02 | 0.976 |
| Residual | | 0.08 | | |

*P values significant at the 0.05 level after correction for the number of tests by Hochberg's sequential Bonferroni are underlined (the Bonferroni corrections were made separately for each animal variable).*
*Transformed variables are indicated in the table heads.*

in all mesocosms (Bokn and others 2003). With the exception of a stimulated abundance of red algal species by nutrient addition in 2000, no other significant responses were observed, either to increased nutrient addition or to recovery conditions. One possible cause is their different life strategies. *Ceramium* spp. (filamentous group) grew mainly as epiphytes and were thus dependent on both *Fucus* abundance and conditions. *Chondrus crispus* (coarsely branched group) prefers shading and is in this respect dependent on *Fucus* abundance, which may explain an increased abundance of *C. crispus* during the recovery phase, when the cover of fucoids increased. Overall, changes in the abundance of red algae were probably too small compared to natural variability for responses to be detected.

Because enhanced nutrient levels are expected to improve the food quality for animals in several ways, including increased N and P content of algae, lowered levels of grazer deterrents, stimulation of generally preferred periphyton and green algae, and increased amounts of detritus and other food items (Mattson 1980; Hemmi and Jormalainen 2002), a stimulated animal abundance along a nutrient enrichment gradient is not very surprising. By 2001, three dominating groups of macrofauna—*Littorina littorea* (an intertidal surface grazer), *Jaera* spp. (intertidal interstitial grazers), and *Gammarus* spp. (ubiquitous grazers/omnivores)—had shown significant stimulation of the number of individuals with nutrient enrichment (Table 4). After 2001, the abundance of these animals dropped despite an intensified dosing, which could be related in part to the loss of the macroalgal canopy or the changed algal community composition (Benedetti-Cecchi and others 2001; Duffy and others 2001), although other explanations are also possible. The presence of other agents is supported by the fact that there were no significant positive correlations between the abundance of these animals and the amount of canopy brown algae when examined over the period 2000–04 (Table 6). Instead, *Jaera* spp. indicated a negative response to the percentage cover of *Fucus serratus*, whereas both *Gammarus* spp. and *Hyale nilssoni* were indicative of positive responses to green algal cover, which continued to increase during 2002. The animal responses to *Fucus* spp. are therefore probably masked by responses to green algae, because these two algal groups correlated significantly and negatively to each other during the treatment period.

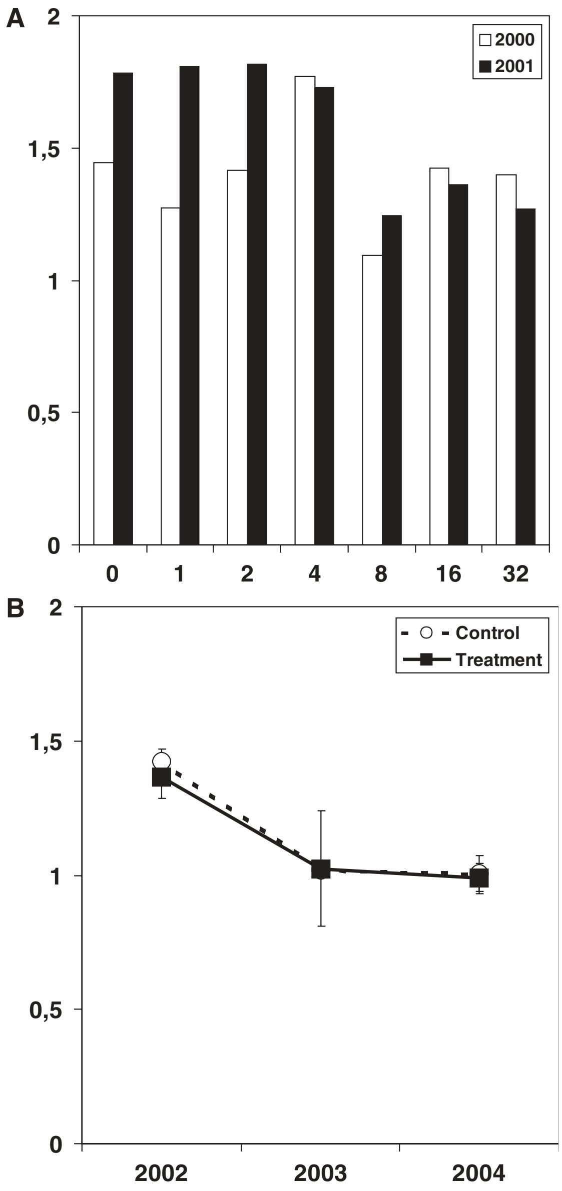

**Figure 10.** Shannon-Wiener diversity for macrofaunal data. **A** along the nutrient-enrichment gradient (concentration in μM N; the two controls were pooled), **B** in controls and mesocosm treatments (addition of 32 μM N in 2002) and in the same systems during the recovery phase in 2003–04 (means ± SE).

The different development of the Shannon-Wiener diversity index for algae and animals over time deserves some attention. For algae, the very high dominance of brown fucoids in the controls throughout the experimental period implied a clearly lower Shannon-Wiener diversity index than was seen in the nutrient-enriched mesocosms. This is 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 (for example, Lubchenco 1978; Paine and Levin 1981; Valdivia and others 2005; Patricio and others 2006). Moreover, the stimulated algal diversity in this study is also supported by the findings by Bracken and Nielsen (2004), who suggested that below a critical nutrient level, local-scale nutrient additions may increase algal diversity, but above the critical level, algal diversity declines with enrichment. For animals, the pattern was the reverse, with a slight decrease in the Shannon-Wiener diversity index along the increasing nutrient gradient in 2001. This decrease was basically due to the strong dominance of a few animal species that were favored by nutrient enrichment.

When analyzed by multivariate statistical techniques, the algal community (not surprisingly) responded more readily to nutrient enrichment than the animal community, which did not show a significant difference in community structure between controls and nutrient treatments when whole communities were examined simultaneously. This may have a natural explanation, because primary community responses to eutrophication probably have to be maintained for a longer period of time before secondary community responses can be expected to express themselves (Kraufvelin and others 2002). In addition, algal–animal interactions on eutrophic rocky shore systems have a very complex nature. It seems that eutrophication provides more and better-suited algal food but less suitable habitats for animals, making the whole pattern of responses extremely difficult to assess (for example, Thompson and others 2002; Bokn and others 2003; Kraufvelin and others 2006). With higher nutrient concentrations, a more homogeneous environment for the fauna could be generally expected, with either higher biomasses of the animal species favored by the new environment, fewer species because there are now fewer different niches, or both reduced biomass and diversity due to increased emigration (see Christie and Kraufvelin 2004) as a result of spatial competition.

When the sudden and dramatic community changes reported in this study are viewed in contrast to the less dramatic effects reported previously (Bokn and others 2002, 2003; Kraufvelin and others 2002, 2006; Karez and others 2004), it be-

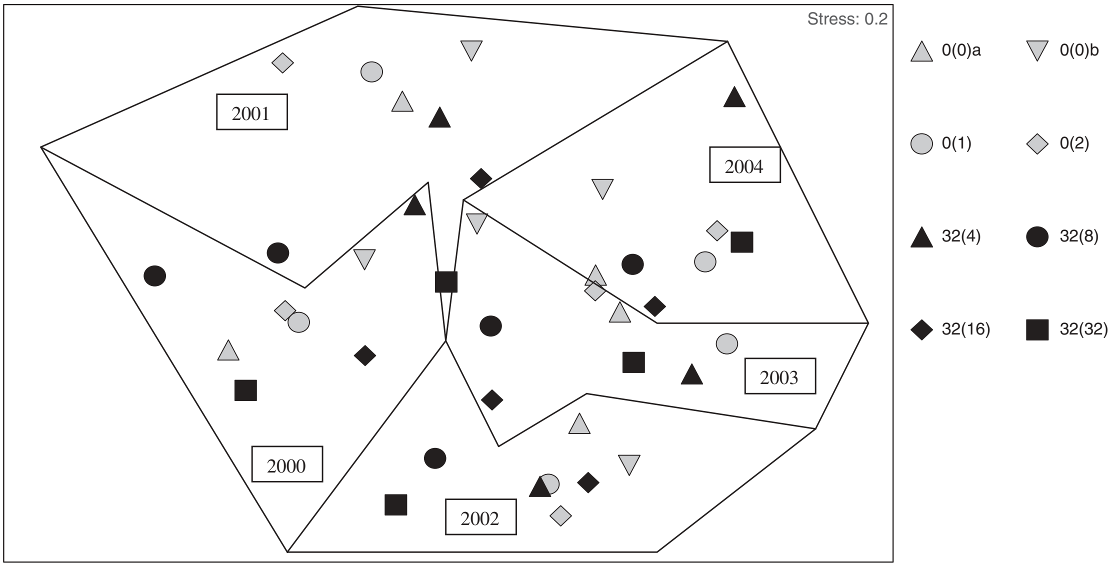

**Figure 11.** Nonmetric multidimensional scaling (NMDS) ordination describing changes in macrofaunal community structure in the mesocosms from 2000–04 (stress 0.20). The lines help to group samples from the same year together. Dark labels indicate high-nutrient treatments, 32 μM N in 2002 (levels in parenthesis = dosing for 2000–01); gray labels indicate controls in 2002 (levels in parenthesis = dosing for 2000–01). In 2003–04, no dosing took place so we could study possible recovery.

**Table 6.** Pearson's Correlation Analysis between Algal Degree of Cover and Macrofaunal Abundance Data within Treatment Mesocosms from 2000 to 2004 ($n = 40$)

| Taxa | Statistics | *Ulva intestinalis* | *Ulva lactuca* | Red algae | *Fucus vesiculosus* | *Fucus serratus* |
|---|---|---|---|---|---|---|
| *Jaera* spp. | *r* | 0.117 | 0.155 | 0.126 | –0.204 | –0.327 |
| | *P* value | 0.473 | 0.338 | 0.438 | 0.207 | **0.039** |
| *Gammarus* spp. | *r* | 0.362 | 0.001 | 0.020 | 0.157 | 0.125 |
| | *P* value | **0.022** | 0.997 | 0.901 | 0.334 | 0.442 |
| *Hyale nilssoni* | *r* | 0.527 | 0.285 | 0.166 | 0.082 | 0.172 |
| | *P* value | **< 0.001** | 0.074 | 0.307 | 0.615 | 0.288 |
| Total | *r* | 0.605 | 0.404 | 0.266 | –0.004 | –0.151 |
| | *P* value | **< 0.001** | **0.010** | 0.097 | 0.979 | 0.353 |

*Significant P values after a tablewise correction for the number of comparisons by Hochberg's sequential Bonferroni are underlined.*

comes clear that our understanding of eutrophication responses in rocky shore communities is far from complete. Rocky intertidal communities may have a high resistance to disturbance caused by excessive availability of nutrients as long as the communities are not seriously stressed or perturbed by other chemical, physical, or biological processes (Connell 1985; Thompson and others 2002). For every new factor added, numerous new uncertainties and questions arise, some of which are interrelated. The results from our mesocosm studies highlight three factors relevant in the context of community resistance: (a) grazing by animals, (b) wave exposure and the export of matter, and (c) the successional stage of the algal community and the longevity of the key algal species. These factors have already been discussed by Pihl and others (1999), Schramm (1999), Bokn and others (2003), and Kraufvelin and others (2006).

The results indicated that rocky shore communities are able to resist a loss of brown algal canopy and a shift to dominance of bloom-forming opportunistic algae for several years. Nevertheless, community shifts may ultimately occur if the high nutrient levels persist over longer periods. Dramatic shifts to contrasting states are not uncommon in ecosystems subjected to gradual change (Scheffer and others 2001; Scheffer and Carpenter 2003), especially in situations where interspecific competition exceeds intraspecific competition (van Nes and Scheffer 2004)—that is, in this case, green *Ulva* spp. versus brown canopy *Fucus* spp. This study further indicates that rocky shore communities have a high degree of resilience—that is, an ability to rapidly return to natural undisturbed conditions after termination of the disturbance, as long as the communities are situated within the range of natural spore and larval dispersion. In this sense, it must be pointed out that the mesocosms were always fed with untreated seawater from adjacent relatively undisturbed rocky shore areas, which may affect both the responses (delay) and the recovery (speedup). The responses and recovery patterns presented here have also only been demonstrated for moderately wave-exposed mesocosm communities with established macroalgal dominance. Because the realism of mesocosm studies and other experiments is open to debate (for example, Perez 1995), the types and timing of effects and recovery in natural ecosystems may differ from these findings depending on geographical location, site history, distance to unaffected areas, and specific additional chemical, physical, and biological stressors (natural or human-induced). However, the consistency within control and treatment mesocosms and the fact that the mesocosm communities have persisted like natural rocky shore communities throughout the 7-year study period further argue for the validity of our results.

Different species showed different recovery patterns; the recovery for green algae implied a decreased cover, whereas the opposite was true for fucoids. Green algae recovered faster than the brown algae; this difference can be attributed to differences in the lifespans of the two groups, but also to the fact that green algal growth was stimulated more directly by, and dependent on the actual nutrient-enrichment levels than the perennial brown algae, which are capable of nutrient storage. Without any nutrient addition and with a low availability of substrates (that is, fucoids), the abundance of *Ulva intestinalis* was already reduced to normal by the first summer of the recovery phase. Conversely, the abundance of *Ulva lactuca* did not decrease before the 2nd year of recovery, when the canopy of fucoids again had been established, because *U. lactuca* probably benefited from a lower density of fucoids. *Fucus vesiculosus* and *Fucus serratus* do compete for space in the lower littoral zone, and the conditions seemed to favor the growth of *F. serratus* during the recovery phase, which here was expressed as a strong increase in abundance both in controls and treated mesocosms during the 2nd year of recovery (Figure 5a). The faster recovery of the animal populations as compared to that the algae, may be due to less intense changes (only stimulation), but also to the stronger seasonality of the animal assemblages that had very low abundances in late autumn, winter, and spring, after which time community development begins again (Kraufvelin and others 2002; Christie and Kraufvelin 2004).

Nutrient enrichment on rocky shores cannot be expected to occur as a simple dose response (for example, Dye 1998; Lopez-Rodriguez and others 1999; Kraufvelin and others 2002; Karez and others 2004). The degree of wave exposure, water exchange rates, water currents, weather conditions, shore profiles, successional stage of the algal community, and amount of grazers and predators also affect eutrophication processes (Worm and Sommer, 2000; Duggins and others 2001; Bokn and others 2003; Kraufvelin and others 2006), making the resulting community difficult to predict. At the same times the impact of nutrient loading on top-down and bottom-up processes must not be forgotten (Worm and Sommer 2000; Lotze and others 2001; Bracken 2004; Nielsen and Navarrete 2004). This paper has demonstrated the significance of time for the occurrence and detection of eutrophication responses (at least 5 years for a canopy crash), and has shown that recovery after termination of nutrient enrichment can be relatively rapid (1 to 2 years) despite dramatic effects. It is noteworthy that both processes (effects and recovery) expressed themselves similarly in all the replicated mesocosm basins. The large time lag before the effects of eutrophication were reflected in these artificial rocky shore communities needs also to be mentioned in the context of investigations and monitoring. Such time lags underscore the need for more long-term experiments, particularly when dealing with larger and longer-lived organisms, subtle community stressors, and creeping change (Kraufvelin and others 2006).

## ACKNOWLEDGEMENTS

The European Commission (through MAST III program MAS3–CT97-0153), MARICULT, and Norsk Hydro financed the first part of this work. From May 2001 on, the project was supported by a financial contribution from Åbo Akademi University, Carl Cedercreutz stipendiefond at Svenska Kulturfonden, Ella och Georg Ehrnrooths Stiftelse, Svenska Litteratursällskapet i Finland (Ingrid, Margit och Henrik Höijers donationsfond II), Oskar Öflunds Stiftelse, Societas pro Fauna et Flora Fennica, Letterstedska Föreningen, and the Academy of Finland (P.K.). K. O'Brien kindly served as editor. This study could never have been completed without the aid of the Norwegian Institute for Water Research, which agreed to keep the mesocosms running over the 4 extra years despite a lack of external funding. The paper is contribution number 54 from Marine Research Station Solbergstrand. The Solbergstrand mesocosms and the Oslofjord can be viewed live at the following Web-cam link: http://151.157.160.150/view/index.shtml (user name and password = mfs).

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