

Effects of eutrophication, grazing, and algal blooms on rocky shores

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Abstract

Eutrophication can profoundly change rocky shore communities. These changes often cause the replacement of perennial, canopy-forming algae such as *Fucus* spp. with annual, bloom-forming algae such as *Enteromorpha* spp. Grazing, however, can counteract eutrophication by eliminating the annual algae's susceptible recruits. We examine these generalizations across large scales. We use replicated "bioassay" experiments to compare the effects of eutrophication and grazing across four paired control versus eutrophied sites in the Northwest Atlantic and four eutrophied sites in the Baltic Sea in spring and summer. At each site, annual algal recruitment and grazing pressure were estimated using tiles seeded with *Enteromorpha intestinalis* propagules. Tiles were exposed for 3 weeks with grazers excluded or allowed access. Productivity of *E. intestinalis* recruits was strongly related to eutrophication (10-fold increase) and grazing (80% decrease) and was weakly related to season. While the absolute grazing rate increased in a linear fashion with algal productivity, the relative grazing rate remained surprisingly constant (~80%). Comparative field surveys showed that perennial algae decreased by 30–60%, while annual algae, filter feeders, and grazers increased across a gradient of eutrophication. As eutrophication increased from control to eutrophied to point source sites, rocky shore communities became increasingly dominated by single species of annual algae or filter feeders, and community diversity declined consistently by 24–46%. We conclude that grazers are important controllers of algal blooms but that, ultimately, they cannot override the effects of increasing eutrophication on rocky shore community structure and biodiversity.

Rocky shores are among the most dynamic and productive ecosystems on the planet. Biomass and primary productivity are typically dominated by canopy-forming perennial macroalgae such as fucoids and laminarians. Together with seagrasses on soft-bottom habitats, these algae generate up to 40% of the primary productivity of the coastal zone (Charpy-Roubaud and Sournia 1990) and a significant fraction of global marine plant biomass (Smith 1981). They also fulfill important ecosystem functions, including carbon storage, nutrient cycling, and the provision of food and habitat for a diverse invertebrate and fish fauna (Borg et al. 1997; Worm et al. 2000). Recently, perennial macroalgae and their associated communities have severely declined in abundance in regions such as the Baltic or the Adriatic Sea, where they have been replaced by few species of bloom-forming annual algae (Vogt and Schramm 1991; Munda 1993). These bloom-forming algae do not provide the same biogeochemical and habitat functions as perennial algae, and their mass occurrence often has strong negative effects on coastal ecosystems and their inhabitants, including humans (Valiela et al. 1997). Detailed observations and experiments have linked the increased occurrence of annual algal blooms to elevated nutrient loads from coastal eutrophication (Fong et al. 1993; Hauxwell et al. 1998; Lotze et al. 2000). In addition, it has been shown that grazers such as littorinid snails, isopods, and amphipods can reduce or even prevent algal blooms through selective feeding on their early life-history stages,

such as propagules and recruits (Lotze and Worm 2000; Lotze et al. 2000). The interplay of eutrophication and grazing may thus determine the occurrence of algal blooms and, on a larger scale, both structure and function of coastal ecosystems (Geertz-Hansen et al. 1993; Hauxwell et al. 1998; Worm et al. 2000).

In this paper, we attempt to quantify and compare the effects of eutrophication and grazing across four paired control versus eutrophied sites in the Northwest Atlantic and four eutrophied sites in the Baltic Sea. Sites were selected on the basis of documented differences in nutrient status and eutrophication, and they represent a broad range of background conditions. Specifically, we were interested in discovering how annual algal recruitment, grazing pressure, and community structure change with eutrophication. For example, it is an open question if grazing pressure is constant, increases, or decreases with increasing eutrophication. To answer this question, we developed a simple grazer-nutrient "bioassay" using tiles that were seeded with propagules of the bloom-forming green algae *Enteromorpha intestinalis* and enclosed in open and closed cages. Detailed experimental evidence shows that a high abundance of *E. intestinalis* is indicative of high nutrient supply, low grazing pressure, or both. Especially early life stages of *Enteromorpha* spp. (propagules and microscopic stages, hereafter called recruits) are extremely responsive to changes in nutrients and grazing (Lotze and Worm 2000, 2002; Lotze et al. 2001). This suggests that *E. intestinalis* can be used as an indicator organism to assay changes in both eutrophication and grazing pressure. In this study, we took advantage of this, using an experimental design that allowed us to separate the relative effects and potential interactions between eutrophication and grazing. As a further advantage, *E. intestinalis* thrives under a wide range of salinity, temperature, and light conditions (Woodhead and Moss 1975; Reed and Russell 1979), which

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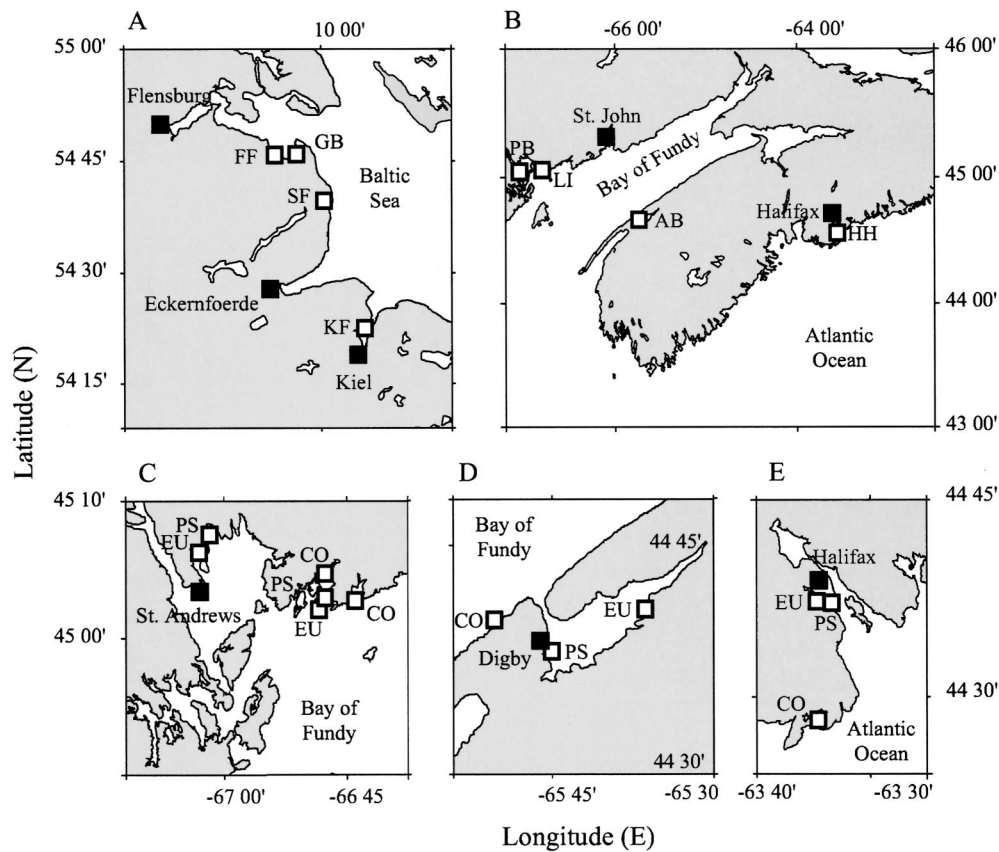


Fig. 1. Locations of experimental and survey sites in the (A) Western Baltic Sea and (B) Northwest Atlantic. See Table 1 for site code definitions. Open squares represent individual sites, and black squares represent major cities. Location of eutrophied (EU), control (CO), and point source (PS) sites within PB: Passamaquoddy Bay and LI: Letang Inlet (C), AB: Annapolis Basin (D), and HH: Halifax Harbor (E) are shown. Experiments and surveys were conducted at all EU and CO sites in spring and summer; PS sites were surveyed in spring only.

facilitates comparisons across different sites. In addition to field experiments, we performed comparative field surveys across all sites to test how rocky shore community structure changes with eutrophication and how the abundances of perennial and annual algae, benthic filter feeders, grazers, and predators covary.

Methods

Study sites—To study the effects of anthropogenic eutrophication, we selected a total of 16 sites in the Northwest Atlantic and the Western Baltic Sea (Fig. 1). In the Northwest Atlantic, four large embayments in Nova Scotia (Halifax Harbor [HH] and Annapolis Basin [AB]) and New Brunswick (Letang Inlet [LI] and Passamaquoddy Bay [PB]) were chosen as study regions (Fig. 1B). Each of these regions has been settled by Europeans for >200 yr and has received large amounts of anthropogenic nutrient and organic inputs. Since its settlement in 1749, HH (Fig. 1E) has received untreated municipal sewage from up to 250,000 people (Dalziel et al. 1991). AB receives large amounts of agricultural runoff from the Annapolis River (Keizer et al.

1996b), which drains the largest agricultural area in the province and was the first of these sites to be settled by Europeans in 1605. LI and PB have been affected since about 1800 by logging, pulp mills, sewage, and fish processing, and since 1980, they have harbored some of the highest concentrations of salmon aquaculture farms in North America (Lotze and Milewski 2004). Recently, these four embayments were monitored by government agencies to document the extent of ongoing nutrient pollution and eutrophication from sewage, agricultural runoff, and aquaculture. Within each region, one control and one eutrophied site were established on the basis of published long-term monitoring data of dissolved nutrient and suspended chlorophyll *a* (Chl *a*) concentrations (Fig. 1C–E; Table 1) (data compiled from Dalziel et al. 1991; Keizer et al. 1996a,b; Strain and Clement 1996; and the database of the phytoplankton monitoring group, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada). While all eutrophied sites in the Northwest Atlantic showed elevated nutrient and chlorophyll concentrations compared with their respective control sites, background nutrient concentrations varied widely and overlapped among eutrophied and control sites of different regions (Ta-

Table 1. Experimental sites in the Northwest Atlantic (HH-PB) and Baltic Sea (FF-GB). Dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), and chlorophyll *a* averages (May–Aug) were derived from published monitoring sources; water temperature (T_{spring} : May–Jun, T_{summer} : Jul–Aug) and salinity (May–Aug) were measured directly. ND, no data.

| Region | Code | Eutrophication | DIN ($\mu\text{mol L}^{-1}$) | DIP ($\mu\text{mol L}^{-1}$) | Chl <i>a</i> ($\mu\text{g L}^{-1}$) | T_{spring} ($^{\circ}\text{C}$) | T_{summer} ($^{\circ}\text{C}$) | Salinity |
|-------------------|------|----------------|-----------------------------------|-----------------------------------|--|---|---|----------|
| Halifax Harbor | HH | Control | 0.44 | 0.34 | 0.55 | 10.7 | 16.8 | 30.1 |
| Halifax Harbor | HH | Eutrophied | 0.78 | 0.81 | 1.15 | 8.4 | 18.4 | 30.1 |
| Annapolis Basin | AB | Control | 4.84 | 0.45 | 2.28 | 9.7 | 13.5 | 31.8 |
| Annapolis Basin | AB | Eutrophied | 6.00 | 0.75 | 3.50 | 12.4 | 17.7 | 30.0 |
| Letang Inlet | LI | Control | 7.28 | 0.90 | 1.69 | 10.0 | 16.0 | 30.7 |
| Letang Inlet | LI | Eutrophied | 13.29 | 1.14 | 2.10 | 8.7 | 16.1 | 31.0 |
| Passamaquoddy Bay | PB | Control | 4.84 | 0.45 | ND | 9.4 | 15.1 | 30.8 |
| Passamaquoddy Bay | PB | Eutrophied | 5.97 | 0.62 | ND | 11.3 | 16.5 | 30.2 |
| Flensburg Fjord | FF | Eutrophied | 1.14 | 0.93 | 2.10 | 13.1 | 15.4 | 15.8 |
| Schlei Fjord | SF | Eutrophied | 1.35 | 0.23 | 6.71 | 16.1 | 18.8 | 14.5 |
| Kiel Fjord | KF | Eutrophied | 3.04 | 4.52 | 9.84 | 14.0 | 16.2 | 15.1 |
| Gelting Bay | GB | Eutrophied | ND | ND | ND | 16.0 | 19.0 | 15.9 |

ble 1). This was because the Bay of Fundy (AB, LI, and PB sites) (Fig. 1C,D) features strong tidal mixing and regional upwelling, whereas HH sites (Fig. 1E) receive nutrient-poor offshore waters (Keizer et al 1996a,b). We took into account these differences when designing the study, since it was our goal to analyze the effects of anthropogenic eutrophication across a broad range of background conditions. We further sampled four point source sites in spring that were located near (0.5–2 km) sewage outfalls (HH and AB) (Fig. 1D,E), a fish processing plant (LI) (Fig. 1C), and salmon aquaculture operations (PB) (Fig. 1C). This was done to see whether community changes observed at eutrophied versus control sites increase in magnitude near a nutrient point source.

In the Baltic Sea, four fjordlike embayments were chosen as study regions, and one eutrophied study site was established in each (Fig. 1A; Table 1). These sites had high nutrient loading typical of inshore regions in the Baltic Sea. Control sites could not be established, as the whole Western Baltic suffers from the strong influence of anthropogenic eutrophication (Vogt and Schramm 1991). Nutrient and chlorophyll data (Table 1) were compiled from Schramm et al. (1996), Hillebrand (1999), Worm et al. (2000), and the coastal resource data base of the State Department for the Environment (Landesamt für Natur und Umwelt, Kiel, Germany). To compare hydrographic conditions among sites, water temperature and salinity at 1-m depth were recorded every time the sites were visited (Table 1).

Field experiments—Grazer-exclusion experiments were conducted at four eutrophied sites in the Baltic (Fig. 1A) and at four paired eutrophied and control sites in the Northwest Atlantic (Fig. 1B–E) in spring and summer 1998 and 1999, respectively. Point source sites were not included in these experiments. At each site, annual algal recruitment with and without grazers was quantified by exposing tiles seeded with *E. intestinalis* propagules in replicated cage experiments. First, heat-sterilized, unglazed ceramic tiles (5 × 5 cm) were seeded with 1 kg of fertile *E. intestinalis* thalli collected at the experimental sites. The algae were dripped dry and stored overnight in the dark at 8°C. Thalli were then

immersed in freshly collected seawater (8°C) with tiles underneath and exposed to natural daylight and temperatures around 15°C. This initiated the release and fertilization of propagules, which were allowed to settle on tiles for 30 h. Seeded tiles were stored for 1–2 d in filtered seawater in the dark at 10°C until they were used in the experiment. During each experimental run, five tiles were cultivated in the laboratory to quantify the initial settlement density of *E. intestinalis* propagules on the tiles. Each tile was placed in 500 ml of filtered and nutrient-enriched seawater (Provasoli 1965) and cultured for 23 d at 10°C and 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in a 14:10 light:dark cycle.

For the field experiment, tiles were enclosed in circular cages (closed cages: “No Grazer”; open cages: “Grazer” treatments) or exposed on uncaged control plots (“Grazer Control” treatments). We ran five replicates per treatment at each of 12 sites during spring and summer, giving a total of 24 individual experiments (Fig. 1). Cages were mesh bags (15 × 15 cm) made from a clear polyethylene mesh with 1-mm openings. Bags were closed at one end. The open end was fixed across an 8-cm-diameter polypropylene base made from sanitary tubing ends. A strong rubber ring (4-mm thickness) sealed the cage against the base. “Grazer” treatments had two 4.5- × 4.5-cm openings to provide access to grazers. In the Northwest Atlantic, cages were placed in the *Fucus vesiculosus* zone, which spans the lower to mid-intertidal. The chosen shore level corresponded to approximately 8–9 h of immersion per tidal cycle. Cages and uncaged tiles were fastened on sloping intertidal shorelines with 4-cm wedge anchors inserted into holes that were drilled with a gasoline-powered hammer drill. In the Baltic Sea, cages were also placed in the *F. vesiculosus* zone located between 0.6- and 0.9-m water depth and were secured with two tent picks.

Tiles were exposed for 23 d at the experimental sites (Baltic, 3–26 May and 6–29 July 1998; Northwest Atlantic, 16 May–8 June and 2–25 August 1999) and were then collected and analyzed in the laboratory. The later timing in the Northwest Atlantic corresponded to the later onset of spring and the slower warming of the water column in this region. In the laboratory, we estimated *E. intestinalis* recruit density at

×25 magnification under a dissecting microscope. *E. intestinalis* recruits were counted in 10 random 4- × 4-mm subsamples per tile. Other macroalgal recruits were rare and were not quantified. *E. intestinalis* recruit density was averaged from subsamples to a 1-cm² area for all experimental tiles. *E. intestinalis* productivity was calculated as the percentage of recruits that developed from settled propagules to germlings in the absence of grazing (settlement density was determined in the laboratory, *see above*). Grazing rate was calculated as the percentage of recruits that were lost in “Grazer” relative to “No Grazer” treatments.

Field surveys—Detailed field surveys were conducted at all 16 control, eutrophied, and point source sites during the spring experiments. At each site, 10 replicate frames (50 × 50 cm) were placed randomly along 100–150-m transects at the experimental shore level (corresponding to the *F. vesiculosus* zone, *see* “Field experiments”). Percentage covers of attached algae and sessile invertebrates were determined by species using a Plexiglas frame with 50 random points. We sampled epiphyte cover, secondary space cover, and primary space (understory) cover. The latter was determined after removing the fucoid canopy from the sample plots. Grazers and predators were removed by shaking the algae within a framed sampling net and were counted by species (except for gammarids, which could not be identified reliably). Species richness was calculated from these data. In the Northwest Atlantic, the four control and four eutrophied sites were resampled for species richness in summer to check whether patterns in spring were representative.

Data analysis—For analysis, we pooled all replicates within each site, as “site” was considered the appropriate experimental unit in this comparative study. We analyzed *E. intestinalis* recruit density on the experimental tiles as a function of eutrophication (“Control Northwest Atlantic” vs. “Eutrophied Northwest Atlantic” vs. “Eutrophied Baltic”), grazer presence (“Grazer” vs. “No Grazer” vs. “Grazer Control”), and season (spring vs. summer) using factorial fixed-factor analysis of variance (ANOVA). Data were log transformed to achieve homogeneity of variances tested by the Cochran test. The Tukey post hoc test was applied to compare different treatment levels. The variance explained by each factor was calculated as $SS_{\text{factor}}/SS_{\text{total}}$.

For the field surveys, we used analysis of covariance (ANCOVA) to analyze cover of perennial algae, annual algae, filter feeders, grazers, and predators as a function of eutrophication (“Control Northwest Atlantic” vs. “Eutrophied Northwest Atlantic” vs. “Point Source Northwest Atlantic” vs. “Eutrophied Baltic”). We included the abundance of consumers (grazers for algae and predators for filter feeders and grazers) and resources (annual algae for grazers and filter feeders for predators) as covariates, in order to account for site-specific differences in the variables. Percent cover data were angular (arcsine-square root) transformed, and grazer and predator data were log transformed to achieve homogeneity of variances.

Results

Field experiments—Cultivation of experimental tiles in the laboratory showed that the seeding procedure was successful. *E. intestinalis* propagules settled densely on the tiles ($2,210 \pm 308 \text{ cm}^{-2}$, mean $\pm 1 \text{ SE}$, $n = 20$), and densities were not significantly different among the four runs of the experiment (ANOVA, $F_{3,16} = 2.5$, $p = 0.098$). These densities are representative of daily settlement of *E. intestinalis* propagules on ceramic tiles in the Baltic (1,000–6,000 $\text{cm}^{-2} \text{ d}^{-1}$ from May to August) (Lotze et al. 2000).

In the field, only a fraction of settled propagules developed into recruits. Averaged across all experiments, recruit density after 23 d in the field was $174 \pm 25 \text{ cm}^{-2}$ (range = 0–2,665, $n = 259$), or 8% of settled propagules. *E. intestinalis* recruit density was strongly controlled by eutrophication, with a 10-fold increase between control and eutrophied sites (Fig. 2). Eutrophied sites in the Atlantic were significantly different from control sites (Tukey test, $p < 0.05$) but were not significantly different from eutrophied Baltic sites.

Grazers also had strong and consistent effects on *E. intestinalis*, causing an 80% decrease between “No Grazer” and “Grazer” treatments (Fig. 2). “No Grazer” treatments were significantly different from both “Grazer” as well as “Grazer Control” treatments. There were no detectable cage artifacts (Tukey’s test “Grazer” vs. “Grazer Control,” $p > 0.2$). Although both effects were statistically significant, eutrophication explained about twice as much of the variance as grazing (Table 2). No significant interaction between eutrophication and grazing was detected, suggesting that their effects were largely independent.

The effect of season was marginally nonsignificant ($p = 0.052$) and explained less than half of the variance compared with grazing and less than one fourth compared with eutrophication (Table 2). In spring, relative grazing effects were consistently strong in the Baltic and the Northwest Atlantic (Fig. 2A). In summer, grazing effects became more variable overall (Fig. 2B), and grazing control of annual algal recruitment vanished entirely at two sites in the Baltic (SF and GB) (Fig. 2B). Across all sites, recruit density without grazers was higher in spring ($346 \pm 131 \text{ cm}^{-2}$) than in summer ($201 \pm 139 \text{ cm}^{-2}$), and recruit density with grazers was lower in spring ($75 \pm 49 \text{ cm}^{-2}$) than in summer ($92 \pm 58 \text{ cm}^{-2}$). This may indicate higher nutrient supply and grazing pressure in spring and lower nutrient supply and grazing pressure in summer.

Overall, there was a highly significant log-linear relationship between recruit densities in “Grazer” and “No Grazer” treatments (Fig. 3A), indicating surprisingly consistent effects of grazing across several orders of magnitude in *E. intestinalis* density (this excludes two Baltic sites where grazing broke down in the summer). The regression line was significantly different from the 1:1 line ($t = -3.8425$, $p = 0.0011$), and the mean treatment effect was an 80% reduction in *E. intestinalis* density due to grazing. There was no linear trend of relative grazing rate with increasing *E. intestinalis* productivity, though grazer effects became more variable as *E. intestinalis* productivity increased (Fig. 3B).

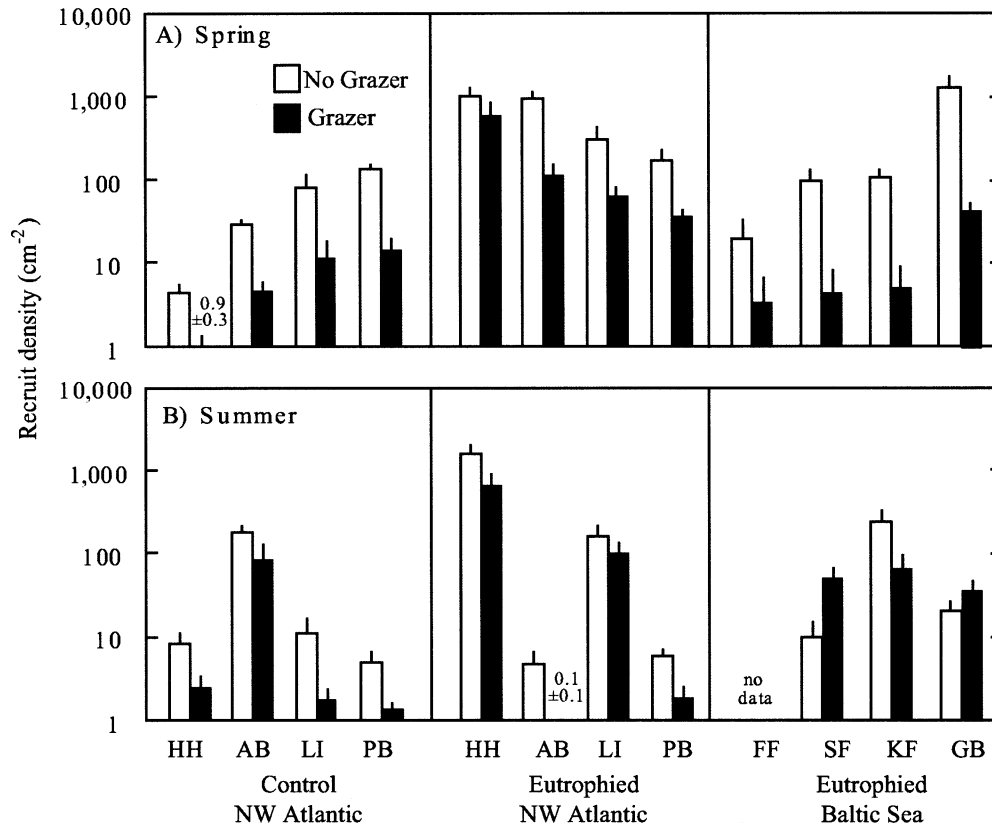


Fig. 2. Field experiments. Effects of eutrophication and grazing on recruit densities of the green alga *Enteromorpha intestinalis* at 12 sites in the Northwest Atlantic and Baltic Sea. (A) Spring experiment. (B) Summer experiment. Data are mean \pm 1 SE ($n = 5$). Grazer control treatments were not significantly different from caged grazer treatments and are not shown. For analysis, refer to Table 2.

Field surveys—Surveys at the 12 experimental sites and four point source sites (see Fig. 1) showed trends of decreasing cover of perennial algae and increasing annual algae, filter feeders, grazers, and predators with eutrophication (Fig. 4). There was, however, considerable variability among sites, and not all trends were statistically significant (Table 3). Baltic sites showed on average higher annual algal cover and higher grazer densities than Northwest Atlantic sites but lower perennial algal cover. Perennial algae were mostly fucoids

Table 2. ANOVA. Effects of eutrophication, grazing, and season on *Enteromorpha intestinalis* recruit density in the field experiments. Data were (log + 1) transformed. MS, mean square.

| Source | df | MS | F | p | % variance |
|-------------------------|----|-----|-----|--------|------------|
| Eutrophication (E) | 2 | 4.1 | 8.3 | 0.0007 | 19.0 |
| Grazing (G) | 2 | 2.1 | 4.3 | 0.0192 | 9.7 |
| Season (S) | 1 | 1.9 | 4.0 | 0.0522 | 4.5 |
| E \times G | 4 | 0.0 | 0.1 | 0.9903 | 0.3 |
| E \times S | 2 | 1.0 | 2.0 | 0.1435 | 4.6 |
| G \times S | 2 | 0.4 | 0.9 | 0.4061 | 2.1 |
| E \times G \times S | 4 | 0.2 | 0.4 | 0.8052 | 1.8 |
| Residuals | 51 | 0.5 | | | |

(*F. vesiculosus*, *Ascophyllum nodosum*), and annual algae were mostly ulvoids (e.g., *E. intestinalis*, *Ulva lactuca*) or ectocarpoids (e.g., *Pilayella littoralis*, *Ectocarpus* spp.). Filter feeders were mostly mussels (*Mytilus edulis*, *Mytilus trossulus*) and barnacles (*Balanus crenatus*, *Balanus improvisus*). Grazers were mostly gastropods (e.g., *Littorina littorea*, *Littorina saxatilis*), isopods (e.g., *Idotea baltica*, *Idotea chelipes*), or amphipods (*Gammarus oceanicus*, *Gammarus locusta*). Predators were mostly starfish (*Asterias vulgaris*), whelks (*Nucella lapillus*), and crabs (*Carcinus maenas*). Negative trends with eutrophication were significant for perennial algae, and positive trends were significant for grazers and marginally nonsignificant for annual algae (Table 3). In addition to eutrophication, grazer density (as a covariable) explained much of the variance in annual algal cover. This means that algal blooms typically occurred at those eutrophied sites that had low grazer densities, namely eutrophied sites HH, LI, FF, KF, GB, and point source site PB (Fig. 4). Predator density was a significant covariate for both filter feeder and grazer abundance, which may indicate significant effects of secondary consumers. Grazer abundance was also significantly related to annual algal cover, which may indicate simultaneous resource control of grazer populations (Table 3). Eutrophication and consumer-resource covariates ex-

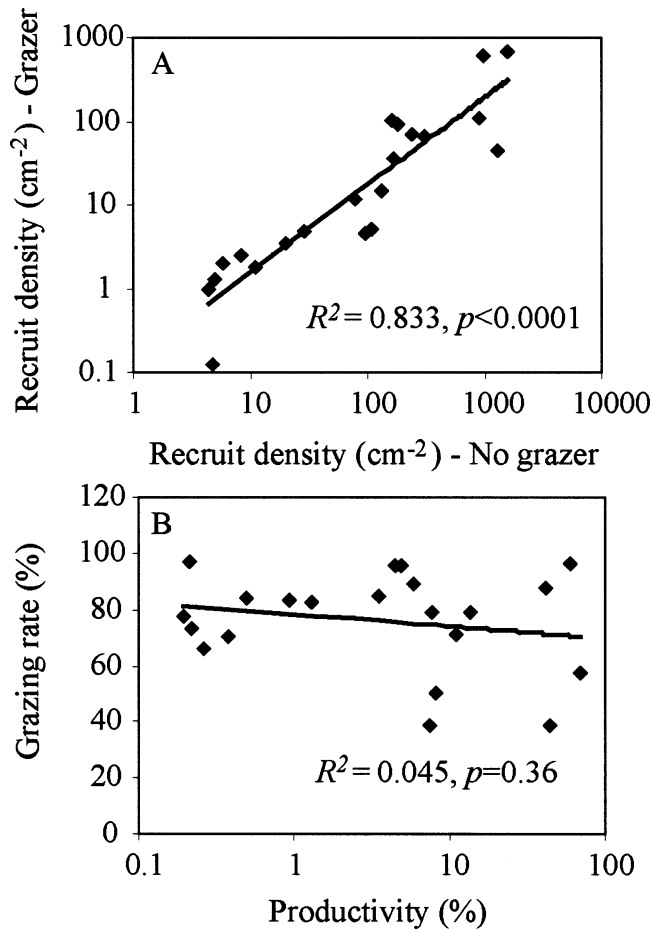


Fig. 3. Grazing and *Enteromorpha intestinalis* productivity. (A) Densities of *E. intestinalis* recruits in experimental “Grazer” versus “No Grazer” treatments followed a strong linear relationship. (B) Grazing rate (percentage of recruits removed) showed no trend with *E. intestinalis* productivity (percentage of settled propagules that recruited in the absence of grazing) across all field experiments. Points represent means of five replicates per site.

plained 48–93% of the variance in abundance of these functional groups (Table 3). In addition, there was a positive trend for annual algae ($R^2 = 0.26, p = 0.088$) and a negative trend for perennial algae ($R^2 = 0.27, p = 0.083$) with *E. intestinalis* productivity as measured in the experiments. Filter feeder abundance was strongly positively correlated with Chl *a* concentrations ($R^2 = 0.71, p = 0.0044$), as derived from published long-term monitoring sources (Table 1).

Changes in community structure with eutrophication led to declining species richness (Fig. 5; Table 3). Richness declined by 24% with eutrophication in the Northwest Atlantic and by 46% at sites that were close to a nutrient point source. Species loss with eutrophication was most pronounced in perennial algae, followed by annual algae, grazers, predators, and filter feeders. Declines in species richness between Northwest Atlantic control and eutrophied sites were consistent in spring and summer (Fig. 5) (ANOVA, eutrophication [E] $F_{1,11} = 4.5, p = 0.056$, season [S] $F_{1,11} = 0.2, p = 0.698$, E \times S $F_{1,11} = 0.1, p = 0.807$).

Discussion

This study suggests that eutrophication and grazing are key variables that explain much of the patterns and processes on rocky shores subject to anthropogenic influences. Throughout our experiments, eutrophication increased the productivity of bloom-forming green algae, which are normally kept in check by grazing. We found surprisingly constant effects of grazing across several orders of magnitude in algal productivity. While the absolute number of recruits removed increased in a linear fashion with *E. intestinalis* productivity (Fig. 3A), the relative grazing pressure remained constant at about 80% on average (Fig. 3B). Thus, grazers are important controllers of algal blooms, but ultimately, they cannot override the effects of increasing eutrophication. The apparent constancy of grazing effects may be explained by the functional response of the main grazer species, the gastropods *L. littorea* and *L. saxatilis*. Sommer (1999) found that *L. littorea* ingestion rates for benthic microalgal films increased with algal biomass in a saturating function. At subsaturating food levels, *L. littorea* increased the area grazed per time but not the grazing intensity in that area. The grazing rates we found may thus correspond to the average area that is grazed, not the grazing intensity per area.

Using *E. intestinalis* propagules as a grazer-nutrient “bio-assay” proved successful in our experiments. *E. intestinalis* responds quickly to changes in nutrient supply and grazing pressure and thrives under a wide range of environmental conditions (Woodhead and Moss 1975; Reed and Russell 1979; Lotze and Worm 2002). Thus, this simple methodology could be a useful tool to compare and monitor biological processes across many sites and to assess eutrophication status across a wide range of environments. Similar “grazer assays” were used on coral reefs (Hay et al. 1983) and rocky shores to quantify spatiotemporal gradients in grazing pressure (Worm and Chapman 1998). These previous experiments showed that grazing pressure varied predictably with water depth and time of day (coral reef) and shore height and season (rocky shore), respectively. In our experiments, grazing pressure was surprisingly constant across sites and seasons but became more variable in summer (Fig. 2B) and at high levels of *E. intestinalis* productivity (Fig. 3B). In the Baltic Sea, grazer effects were strong in spring but weakened considerably in summer (Fig. 2). This pattern was also seen in previous field experiments and linked to increasing predator abundance and consumer control of grazer populations in the summer months (Worm et al. 2000). *E. intestinalis* recruitment in the absence of grazing was lower in summer than in spring in both oceans. This probably indicates increasing nutrient limitation of bloom-forming green algae in summer (Pedersen and Borum 1996). Although we cannot exclude high temperature or other limiting factors that may vary seasonally, patterns of increasing nutrient limitation, decreasing algal biomass, and decreasing grazing pressure from spring to summer have also generally been found in phytoplankton communities (Sommer et al. 1986).

In accordance with the experimental results, our field surveys showed that massive blooms of annual algae typically occurred at eutrophied sites with reduced grazer densities.

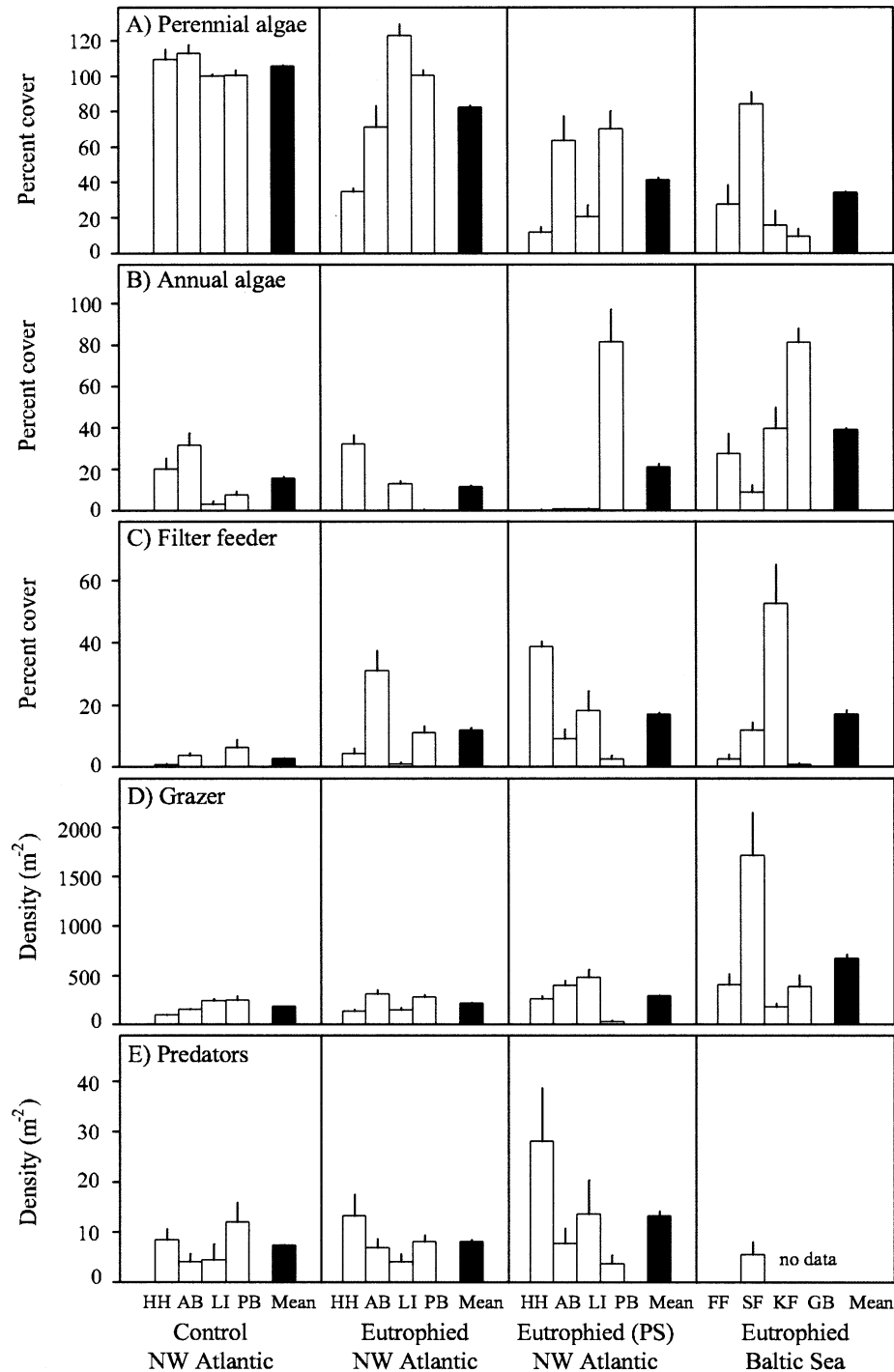


Fig. 4. Field surveys. Four control sites are contrasted with four eutrophied sites and four point source (PS) sites in the Northwest Atlantic, as well as four eutrophied sites in the Baltic Sea. White bars represent means of 10 replicates per site (± 1 SE), and black bars represent means across four sites (± 1 SE). For analysis, refer to Table 3.

The data in Fig. 4 suggest that blooms are likely to occur at <500 grazers m^{-2} in the Baltic and at <100 grazers m^{-2} at eutrophied Northwest Atlantic sites; the cause for this difference is speculative. This corroborates the results of previous experiments showing that increased nutrient loading and reduced grazer densities are both conditions that favor

intense macroalgal blooms (Geertz-Hansen et al. 1993; Hauxwell et al. 1998; Lotze et al. 2000). Field surveys also showed that perennial algae declined between 30% and 60% in abundance with eutrophication. This is likely linked to interference with annual algae, which block perennial recruitment, as demonstrated by previous field experiments in

Table 3. ANCOVA. Effects of eutrophication (main effect) and consumer and resource abundance (covariates) on rocky shore communities. Cover data were angular transformed, and abundance data were log transformed. MS, mean square.

| Dependent | Source | df | MS | F | p | % variance |
|------------------|----------------|----|------|------|--------|------------|
| Perennial algae | Eutrophication | 3 | 0.35 | 4.7 | 0.0240 | 56.0 |
| | Grazer | 1 | 0.00 | 0.1 | 0.8194 | 0.2 |
| | Residuals | 11 | 0.07 | | | |
| Annual algae | Eutrophication | 3 | 0.13 | 3.0 | 0.0761 | 19.8 |
| | Grazer | 1 | 1.09 | 25.6 | 0.0004 | 56.1 |
| | Residuals | 11 | 0.04 | | | |
| Filter feeder | Eutrophication | 3 | 0.05 | 2.1 | 0.1768 | 32.1 |
| | Predators | 1 | 0.13 | 5.4 | 0.0485 | 27.4 |
| | Residuals | 8 | 0.02 | | | |
| Grazer | Eutrophication | 3 | 0.28 | 15.2 | 0.0019 | 43.7 |
| | Annual algae | 1 | 0.73 | 39.1 | 0.0004 | 37.5 |
| | Predators | 1 | 0.23 | 12.5 | 0.0095 | 12.0 |
| | Residuals | 7 | 0.02 | | | |
| Predators | Eutrophication | 3 | 0.18 | 0.6 | 0.6196 | 12.2 |
| | Filter feeder | 1 | 1.54 | 5.4 | 0.0485 | 35.4 |
| | Residuals | 8 | 0.29 | | | |
| Species richness | Eutrophication | 3 | 83.4 | 5.7 | 0.0115 | 58.8 |
| | Residuals | 12 | 14.6 | | | |

the Baltic Sea (Worm et al. 1999, 2000). Annual algae and grazers on average increased with eutrophication, as did filter feeders and predators on some sites (Fig. 4). However, increased abundance of some generalist species with increasing eutrophication was accompanied by declining species richness across all groups, most notably in the algae (Fig. 5). Thus, eutrophication may shift the competitive balance, such that few species can monopolize abundant resources, leading to a marked decline in diversity. Similar declines in diversity were caused by experimental eutrophication (and

removal of grazers) on rocky shores and other aquatic ecosystems (Worm et al. 2002).

On the basis of the results obtained in this study as well as in previous experiments, we propose the following conceptual model of rocky shore community responses to eutrophication, as set forth in the three paragraphs that follow (Fig. 6A).

Nutrients and algae: Increases in nutrient supply by eutrophication favor phytoplankton and annual bloom-forming algae, which can displace canopy-forming perennial algae. This leads to the disruption of habitat and the loss of biodiversity on rocky shores. Such changes in diversity were also shown to diminish some ecosystem functions, namely carbon storage and nitrogen retention (Worm et al. 2000, 2002).

Grazers: Invertebrate grazers strongly reduce recruitment and subsequent colonization of annual algae. This appears to be a general process on rocky and some sedimentary shores (Lubchenco and Menge 1978; Hawkins and Hartnoll 1983; Duffy and Harvilicz 2001), leading to the suppression of algal blooms and the maintenance of perennial algae and seagrasses under normal conditions (indirect positive effect in Fig. 6A). However, despite the increased abundance of some grazer species at high nutrient loads (Worm et al. 2000), consumer control often breaks down under eutrophication, leading to the proliferation of annual algae (Worm et al. 1999, 2000; Lotze and Worm 2002). The present study indicates the probable reason for this pattern: constant or slightly decreasing grazing rates with increasing nutrient supply and annual algal productivity.

Filter feeder and predators: Control of filter feeders such as mussels and indirect maintenance of macroalgae by “key-

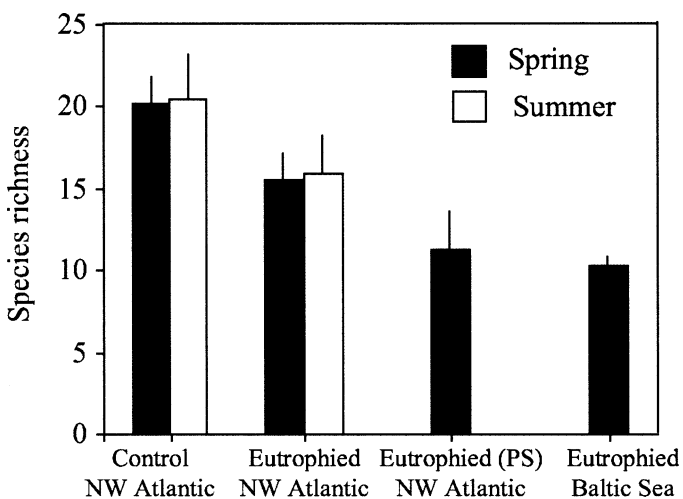


Fig. 5. Diversity and eutrophication at rocky shores. Total species richness of benthic macrophytes and invertebrates was sampled in the Northwest Atlantic at four control sites, four eutrophied sites, four point source (PS) sites, and four eutrophied sites in the Baltic. Data are mean \pm 1 SE ($n = 4$). For analysis, refer to Table 3.

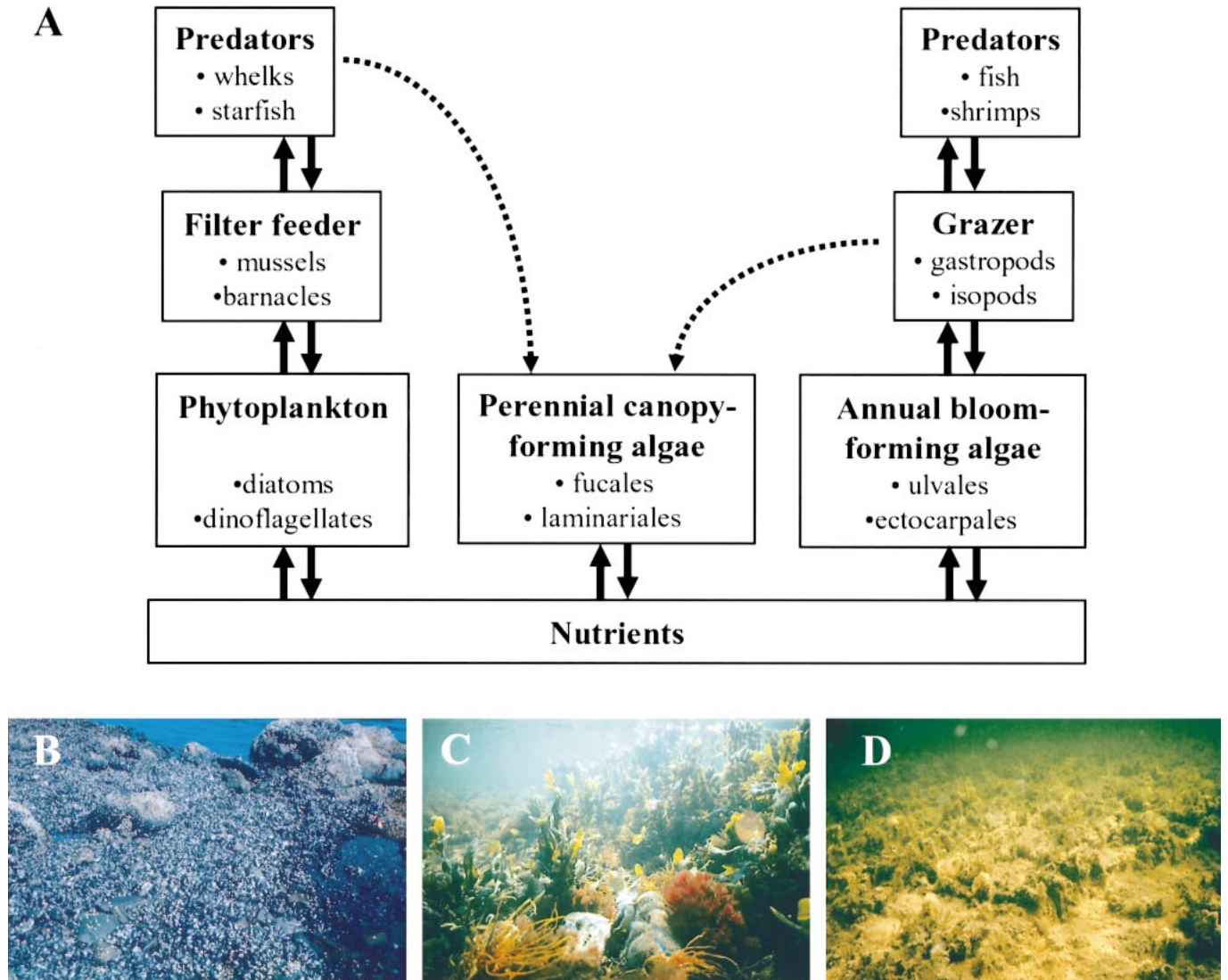


Fig. 6. (A) Food web interactions and (B–D) alternative community states on rocky shores. Upward arrows indicate resource (“bottom-up”) effects, and downward arrows indicate consumer (“top-down”) effects. Dotted arrows indicate indirect positive effects. Nutrient enrichment stimulates the growth of phytoplankton (and indirectly filter feeders) as well as annual bloom-forming algae over the growth of perennial algae. Predators and grazers limit the growth of filter feeders and annual algae and may indirectly maintain perennial algae. Excessive eutrophication can override top-down control and favor the development of (B) mussel beds or (D) annual algae, both of which displace (C) perennial algal canopies.

stone” predators are classic patterns in community ecology (Fig. 6A) (Paine 1966; Lubchenco and Menge 1978). However, there is increasing evidence that nutrient supply can overrun this powerful interaction. Nutrient-rich conditions favor phytoplankton growth and, indirectly, filter feeders, which can then escape predator control and begin to dominate the substratum (Menge et al. 1997, 1999). Our field surveys showed that filter feeders increased strongly at some eutrophied sites. All eutrophied sites had elevated Chl *a* concentrations compared with their respective control sites, and there was a strong positive correlation between Chl *a* and filter feeder abundance. Furthermore, the density of predators (mostly starfish, whelks, and crabs) was positively related to filter feeder abundance, which may indicate the transmission of bottom-up effects to higher trophic levels. These results are

consistent with observations and experiments in Oregon (Menge et al. 1997) and New Zealand (Menge et al. 1999), indicating higher filter feeder and predator density and higher predation rates at nutrient-enriched sites.

In conclusion, comparative experiments and observations in the Baltic and Northwest Atlantic indicate that community structure on rocky shores is controlled and maintained both by nutrient supply and consumer pressure (Fig. 6A). While grazers and predators control their prey under normal conditions, increased nutrient supply can change the interaction from predominant consumer control to predominant resource control. This can lead to the replacement of perennial algal canopies (Fig. 6C) either to mussel beds (Fig. 6B) or annual algal blooms (Fig. 6D) and to marked declines in community diversity. Whether these alternative community states on

rocky shores are stabilized by positive feedbacks and are therefore difficult to reverse is an important question that remains to be tested experimentally (Scheffer and Carpenter 2003). On the positive side, recent field surveys indicate the recovery of *F. vesiculosus* populations and associated fauna in the Baltic Sea following the reduction of nutrient loads (Nilsson et al. 2004; Worm pers. comm.). This may be interpreted as a hopeful sign that wise management actions can reverse the deleterious trends discussed in this paper, even over large spatial scales.

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