Limnol. Oceanogr., 47(6), 2002, 1734–1741

Complex interactions of climatic and ecological controls on macroalgal recruitment

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Abstract

Little is known about the cumulative effects of multiple (>2) environmental controls on species performance and interactions in aquatic ecosystems. We asked how changes in climatic (temperature, ultraviolet radiation) and ecological controls (nutrients, grazing) affect recruitment of the green macroalga *Enteromorpha intestinalis*, which forms destructive algal blooms in coastal ecosystems worldwide. We designed factorial laboratory experiments to analyze the recruitment response to (1) single and combined effects of nutrient enrichment, grazing pressure, and grazer species composition and (2) the cumulative effects of ultraviolet (UV) radiation, temperature, nutrients, and grazing. Recruitment of *E. intestinalis* increased exponentially with nutrient enrichment. Grazers could control algal recruitment until a nutrient threshold was reached depending on grazer species composition. Snails (*Littorina littorea*) had strong negative effects on recruit density, whereas amphipods (*Gammarus oceanicus*) had weak grazing effects and favored algal recruitment through excretion when nutrient supply was low. Temperature and nutrients both enhanced algal recruitment but also the effects of grazers, which led to a significant three-way interaction among these factors. Similarly, effects of UV radiation depended on grazer presence and temperature. When grazers were absent, UV radiation reduced recruitment at 11 and 17°C but enhanced recruitment at 5°C. No effects were seen in the presence of grazers. Our results indicate that multiple human influences, such as climate change, eutrophication, and food web alterations, have interdependent effects and the potential for synergistically enhancing the development of macroalgal blooms in coastal ecosystems.

Natural fluctuations in the environment have shaped and altered ecosystems throughout evolutionary times. In the current era of global change, however, humans alter multiple abiotic and biotic environmental controls at rates, scales, and combinations fundamentally different from those at any other time in history (Vitousek et al. 1997). Human influences change the climate, resource supply, food web structure, water quality, and habitat availability, among other effects, and most of these changes co-occur in human-dominated areas such as coastal seas (Lotze and Milewski 2002). These changes affect species in manifold ways, altering their productivity, reproductive success, survival, interactions with other species, geographic distribution, or behavior. Understanding and predicting the cumulative effects of multiple human influences on species, communities, and ecosystems represents a key challenge for research and management (Breitburg et al. 1999; Harrington et al. 1999).

Multiple environmental controls can affect species performance and interactions in ways not predictable from single-factor studies because of nonadditive (synergistic or antagonistic) effects (Breitburg et al. 1999; Folt et al. 1999; Harrington et al. 1999; Lenihan et al. 1999). In order to identify cumulative effects, one needs to employ an experimental approach that can clearly distinguish between single and combined effects of multiple factors and their interactions. Such experiments are scarce (*but see* Folt et al. 1999; Lenihan et al. 1999). In this study, we explored the combined effects of four important climatic (temperature, ultraviolet radiation) and ecological (nutrient enrichment, grazing) controls, which are all subject to human-induced change, on the performance of the common, bloom-forming green macroalga *Enteromorpha intestinalis* Link.

Several species of annual macroalgae perform destructive mass blooms in eutrophied coastal waters worldwide, with negative and sometimes dramatic consequences on the perennial, habitat-building vegetation and its associated communities (Valiela et al. 1997; Raffaelli et al. 1998; Worm et al. 1999). This phenomenon has been linked to an unbalance between increasing nutrient supply and decreasing herbivore control caused by human activities (Valiela et al. 1997; Worm et al. 1999, 2000; Lotze et al. 2000). Recent field and laboratory studies showed that nutrient enrichment and grazing are especially effective controls during algal recruitment (i.e., the germination and growth from settled propagules) (Lotze et al. 2000, 2001; Lotze and Worm 2000). It remained unclear, however, how grazer density and different grazer species interact with increasing nutrient supply on recruit performance.

Recruitment and growth of annual macroalgae also depend on temperature and light and on their seasonal timing relative to other control mechanisms (Lotze et al. 1999, 2000). Relative nutrient and grazer effects were shown to change with season, but the effect of changing temperature or light climate on the nutrient–grazer–algae interaction could not be deduced from field experiments (Lotze et al. 2001). Increasing temperature can enhance algal recruitment and growth (Beardall et al. 1998), but it can also enhance grazer activity by increasing metabolic rate (Paul et al. 1989). Through warming, the vegetation period can start earlier, which can affect the timing of algal–grazer interactions in the field (Harrington et al. 1999). Ultraviolet (UV) radiation can harm photosynthetic performance and damage DNA (Franklin and Forster 1997). UV radiation can also

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Acknowledgments

We thank Ransom Myers, John Cullen, and Richard Davis for discussions and technical advice. Nutrient analyses were performed by Carol Anstey and Peter Strain. The comments of two anonymous reviewers strongly improved the manuscript. We are grateful for financial support from the German Research Council (DFG Lo 819/1-1, Wo 818/1-1).

alter nutrient uptake and pigment composition of plants, which can affect grazing patterns (Cronin and Hay 1996; Franklin and Forster 1997). Thus, climate change could accelerate or suppress algal blooms through either direct effects on algal performance or indirect effects on biological interactions.

Building on the knowledge gained from our previous field studies, we designed factorial laboratory experiments to analyze the single and combined effects of temperature, UV radiation, nutrient enrichment, grazer density, and grazer species composition on the recruitment response of *E. intestinalis.* Our motivation was threefold: (1) to expand the knowledge on multiple stressor effects, (2) to analyze effects of climatic factors on biological interactions (plant–herbivore) and ecological processes (bottom-up vs. top-down control), and (3) to explore whether a changing climate can alter the success of bloom-forming algae in eutrophied waters. In these experiments, it was not our aim to simulate specific scenarios for climate warming or increasing UV radiation due to ozone depletion but, more generally, to explore the potential for interactive effects between climatic and ecological controls.

Methods

In September–October 2001, a combination of two- and four-factorial laboratory experiments were performed. At this time, the annual green macroalga *E. intestinalis* (*Enteromorpha* hereafter) was fully reproductive in the rocky intertidal of our field site in Duncan's Cove (44°29.9′N, 63°31.7′W), Nova Scotia, Canada. This species is rare on the nutrient-poor open coast but is found abundantly near sewage outlets and other nutrient-enriched areas (Worm 2000). The most common grazer species in the field were *Littorina littorea* L. (*Littorina* hereafter) and *Gammarus oceanicus* Segerstrale (*Gammarus* hereafter).

Experimental design—Altogether, we established 144 experimental units, which were run for 4 weeks. Different combinations of experimental units addressed the following designs.

1. Nutrient gradient × grazing (4 × 2 design). Four nutrient (nitrate and phosphate) enrichment treatments were established: ambient (NO_3/PO_4 at 0/0 μmol L^{-1}) and three increasing levels of enrichment (NO_3/PO_4 at 4/0.4, 20/2, and 100/10 μmol L^{-1}, *see below*). These were combined with two grazer treatments: no grazers or one *Gammarus* plus one *Littorina.* There were four replicates and 32 experimental units.
2. Grazer density × nutrient enrichment (3 × 2 design). Three grazer treatments were established, which contained no, one, or two individuals of either *Gammarus* or *Littorina,* respectively. These were combined with two nutrient concentrations: ambient (0/0) or medium enriched (20/2). There were four replicates and 48 experimental units.
3. Grazer species composition × nutrient enrichment (4 × 2 design). Four grazer treatments were established that contained no grazer, two *Gammarus,* two *Littorina,* or one *Gammarus* plus one *Littorina* and combined with two nutrient concentrations: ambient (0/0) or medium enriched (20/2). There were four replicates and 32 experimental units.
4. UV radiation × temperature × grazing × nutrient enrichment (2 × 3 × 2 × 2 design). UV radiation was either present (PAR + UV, *see below*) or filtered out (PAR). Three temperature levels were established at 5, 11, and 17°C, respectively. Grazers were either absent or present with one *Gammarus* plus one *Littorina.* Nutrient concentrations were either ambient (0/0) or enriched (20/2). All treatments were fully crossed. There were four replicates and 96 experimental units.

The dependent variable in all experiments was recruit density of *Enteromorpha* after 4 weeks recruiting from settled propagules on preseeded 5 × 5 cm^2 unglazed ceramic tiles. Seeding was performed using fertile *Enteromorpha* thalli collected in the field and stored moist in a refrigerator over night. The next morning, all experimental tiles were arranged in a tub, algal thalli were placed on top and freshly collected seawater was spilled over the thalli up to 15 cm depth. The tub was exposed to natural sunlight over the day at around 20°C air temperature. The seeding procedure was repeated the next day with a second batch of *Enteromorpha.* We placed seeded tiles in 500-ml polycarbonate containers (10 × 10 cm^2) filled with 400 ml treatment medium (*see below*). Containers were installed at a distance of 36 cm to the light sources (*see below*). Light filters were mounted over the containers, leaving a 5-mm gap to allow for air circulation. Finally, we added *Littorina* and *Gammarus* individuals to the grazer treatments (*see below*). After 4 weeks, algal recruits were counted in 10 random subsamples of 4 × 4 mm^2 on each tile with a stereomicroscope (×25 magnification). Subsamples were pooled for analysis.

Light—We used a combination of three fluorescent tubes (Power Glo A-1630, 40 W, Hagen) as sources for photosynthetically active radiation (PAR) and 1 UVB light source (Light Sources FS40T12 UVB, Kelsun Distributors). Treatments with PAR + UV light were covered with a cellulose acetate sheet (General Electric), which eliminated UVC radiation <280 nm wavelength and slightly reduced UVB (280–320 nm) and UVA (320–400 nm) radiation emitted by the lamps. To prevent the aging effect, cellulose acetate sheets were exchanged weekly. Treatments without UV radiation were covered with an acrylic sheet, Acrylite-OP3 (CYRO Industries), which eliminated UVA and UVB radiation of <400 nm wavelength completely. The light treatments were run in a 14 : 10 light : dark cycle. Spectral irradiance emitted by the light sources was quantified using an OL 754 High Accuracy UV-Visible Spectroradiometer (Optronic Laboratories), from which irradiances and daily fluences were calculated (Fig. 1; Table 1). There was no difference in the spectral output of lamps or light intensity among the three temperatures at which the experiment was run. Readings from the local UVB monitoring station (Brewer MKIV 84, data from World Ozone and UV radiation Data Centre, North York, Ontario, Canada) served as a comparison with UVB field conditions; own field measurements with

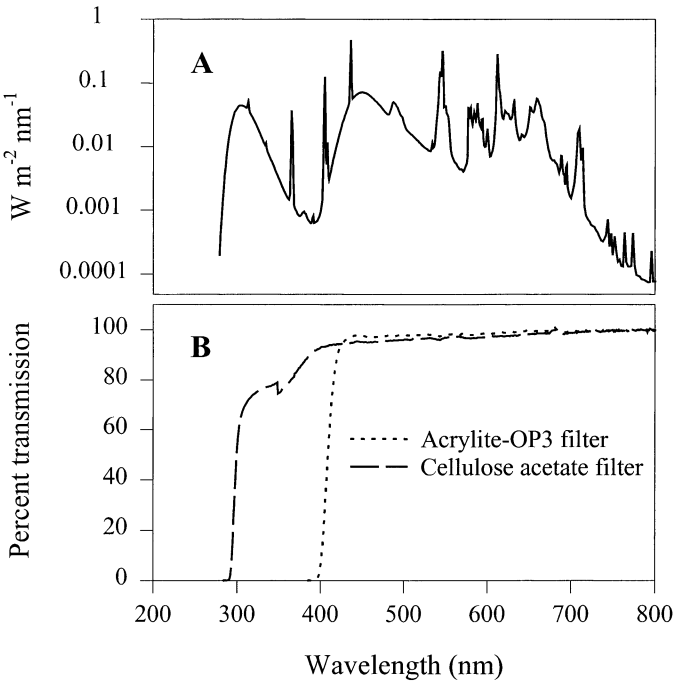

Fig. 1. (A) Spectral irradiance in the experiments of three fluorescent tubes and one UVB light source and (B) light transmission through cut-off filters.

a broadband dosimeter (RM-21, Gröbel UV-Elektronik) served as comparisons of PAR and UVA (Table 1) radiation. In our experimental setup, we reached realistic summer UVB irradiance and daily fluence when compared to UVB measurements at the Halifax monitoring station in June (Table 1). We did not enhance UVA radiation, and PAR was set at 20 W m^{-2}, which was sufficient for germination and growth of *Enteromorpha* (Lotze et al. 1999). Biologically weighed UVB irradiances for DNA damage (Green and Miller action spectrum, *see* Grobe and Murphy 1994) and General Plant damage (Caldwell action spectrum, *see* Grobe and Murphy 1994) were within the range of observed field values (Table 1) and those used in several other laboratory and field studies (*see discussion*).

Temperature—The three levels of temperature used in the experiment—5, 11, and 17°C—were chosen to represent spring (March–April), early summer (May–June), and late summer (August–September) seawater conditions in Nova Scotia, Canada (Lotze et al. 2001). Because of the large number of treatment units, the experiment had to be run in three adjacent constant-temperature rooms running at 5, 11, and 17°C. The three temperature rooms all showed similar temperature variations of ±1°C.

Grazer—Individual grazers were collected 1 d prior to the experiment at the study site. We collected *L. littorea* at a medium size of 5 mm and *G. oceanicus* at a medium size of 10 mm. Experimental treatment densities were one or two grazers per 5 × 5 cm^2 tile, representing a grazer density of 400 or 800 m^{-2}, respectively. This is comparable to medium to high densities in the field, where crustacean and gastropod grazers reach 200–1,000 m^{-2} (Lotze and Worm 2000; Lotze et al. 2001). Previous field experiments showed that both *Littorina* and *Gammarus* feed on juvenile *Enteromorpha* (Lotze et al. 2001), but feeding modes might differ between species (Lotze and Worm 2000). As a shelter and alternative food source, each treatment received a 5-cm thallus piece of *Fucus vesiculosus* L., which is the most common perennial intertidal macroalga in the field. Grazers commonly hid under the *Fucus* thalli, but none of the treatments showed any signs of consumption of *Fucus*; thus, no interference with the grazer treatment occurred. Because recruitment of *Enteromorpha* in low-nutrient treatments was extremely low, each treatment received a 5-cm piece of adult, nonfertile *Enteromorpha* thallus to provide grazers with additional food after 2 weeks. Because both grazer species immediately consumed these pieces, this procedure was repeated in the

Table 1. Irradiance and daily fluence (14 h light) applied in the experiment and reductions through cut-off filters. Measurements were made 36 cm from light sources, where experimental treatments were positioned. DNA weighed (Green and Miller action spectrum, see Grobe and Murphy 1994) and general plant weighed (Caldwell action spectrum, see Grobe and Murphy 1994) UVB irradiances were calculated for comparisons. Average UVB radiation in the field (1–30 June 2001) was calculated from readings at the local UVB monitoring stations in Halifax, Canada; average PAR and UVA radiation in the field were measured around noon during June–October 2001 (*see Methods for details*).

	PAR (400–700 nm)	UVA (320–400 nm)	UVB (280–320 nm)	Weighed UVB	
				DNA	General plant
Irradiance (W m^{-2})					
No filter	20.46	1.068	1.140	0.051	0.337
Cellulose acetate	19.88	0.967	0.626	0.008	0.125
Acrylite OP3	20.06	0.001	<0.0001	<0.0001	<0.0001
Halifax mean	231.29	15.300	1.092	0.0006	0.066
Halifax maximum	560.51	24.823	2.542		
Daily fluence (kJ m^{-2} d^{-1})					
No filter	1,031.18	53.424	57.443	2.557	17.007
Cellulose acetate	1,001.95	48.384	31.558	0.047	6.282
Acrylite OP3	1,011.02	0.050	0.0041	0.0002	0.0012
Halifax field	11,657.52	771.120	55.018	0.028	3.341

Table 2. Nitrate (NO_3) and phosphate (PO_4) concentrations (μmol L^{-1}) in background water (no enrichment, 0/0) and three nutrient enrichment levels. Water samples were taken in the treatments initially and after 4 d of the experiment ($n = 3$). Values are means (SE).

Nutrient enrichment		Initial concentration		Concentration after 4 d	
NO_3	PO_4	NO_3	PO_4	NO_3	PO_4
0	0	4.26(0.07)	1.11(0.05)	0.64(0.01)	0.55(0.01)
4	0.4	9.45(0.15)	1.39(0.10)	0.64(0.01)	0.42(0.05)
20	2	24.34(0.16)	2.97(0.08)	0.64(0.01)	0.64(0.06)
100	10	111.58(4.37)	11.57(0.37)	3.03(0.01)	2.17(0.18)

third week. The addition of *Enteromorpha* thallus pieces was also made to treatments without grazers, and pieces were removed at the time grazers had consumed their pieces.

Nutrients—Seawater for the treatments was taken from the Northwest Arm, a sheltered site near Halifax, Nova Scotia. The seawater was filtered (0.35 μm) and cooled down to treatment temperatures before application. Nutrients were added from concentrated stock solutions of $NaNO_3$ and KH_2PO_4, respectively, at a N:P ratio of 10:1 μmol L^{-1}, which is comparable to field conditions (Lotze et al. 2001). Nutrient enrichment treatments were chosen to represent summer background concentrations (0/0 μmol L^{-1} NO_3/PO_4, Lotze et al. 2001), winter concentrations in open coastal waters of the Nova Scotia coast (4/0.4 μmol L^{-1} NO_3/PO_4, Keizer et al. 1996), concentrations found in eutrophied estuaries of Atlantic Canada (20/2 μmol L^{-1} NO_3/PO_4, Strain and Clement 1996), and highly eutrophied areas such as parts of the Baltic Sea (100/10 μmol L^{-1} NO_3/PO_4, Nixon and Pilson 1983). Treatment media were exchanged twice a week; thus, nutrients were enriched in pulses, which is more natural than constant nutrient conditions (Lotze and Schramm 2000). Initial nutrient concentrations (NO_3, PO_4) at day 1 of the experiment and nutrient concentrations in treatments after 4 d were analyzed using a Technicon autoanalyzer (Table 2).

Statistical analysis—Following the designs of different experimental subsets, two- and four-factorial, fixed-factor analyses of variance were performed on the recruitment response of *Enteromorpha*. Recruit density data were log-transformed to achieve homogeneity of variances (Cochran's test). As a measure of relative effect size, we calculated the percent variance explained (Howell 1992). Post hoc multiple means comparisons were performed using the Tukey–Kramer procedure at the $\alpha = 0.05$ significance level.

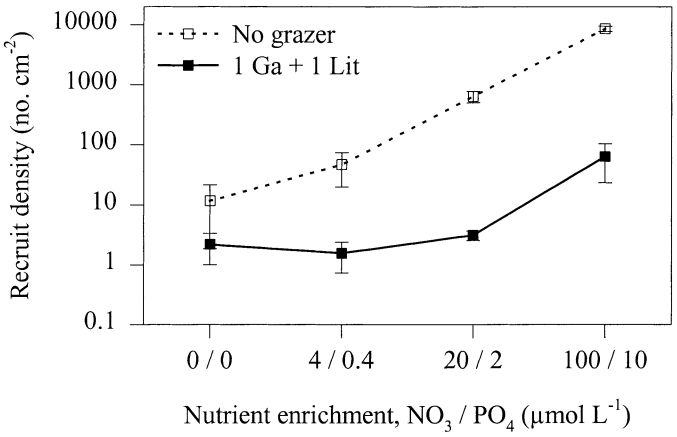

Fig. 2. Recruitment response of *Enteromorpha* (means ± 1 SE, $n = 4$) to the combined effects of nutrient enrichment (NO_3/PO_4) and grazing by one *Gammarus* (Ga) and one *Littorina* (Lit).

Results

Nutrient gradient × grazing—Nutrient concentrations followed the chosen enrichment levels (Table 2). Although background nutrient concentrations were high (4 μmol NO_3 L^{-1}, 1 μmol PO_4 L^{-1}), rapid nutrient depletion in the treatments occurred, and after 4 d, nitrate and phosphate concentrations were depleted below 1 μmol L^{-1}, except for the highest enrichment level (Table 2). Exchange of the nutrient medium re-established the experimental nutrient levels every 3–4 d. In the absence of grazers, recruit density of *Enteromorpha* increased exponentially with nutrient enrichment (linear regression on log-transformed data: $y = 0.028x + 1.31$, $r^2 = 0.72$, $p < 0.0001$) and was enhanced by three orders of magnitude toward the highest nutrient level (Fig. 2). In the presence of grazers (one *Gammarus* and one *Littorina*), recruit density remained low at the three lower nutrient levels but increased by one order of magnitude toward the highest nutrient level (Fig. 2, linear regression on log-transformed data: $y = 0.012x + 0.36$, $r^2 = 0.74$, $p < 0.0001$). This indicates that grazers were able to suppress the effects of nutrient enrichment up to a threshold level of 100/10 μmol NO_3/PO_4 L^{-1}, at which *Enteromorpha* could outgrow grazing pressure. This difference in the effects of nutrients in the absence versus presence of grazers was statistically significant (Table 3A).

Grazer density × nutrient enrichment—The two grazer species had contrasting effects on *Enteromorpha* recruitment. In the absence of grazers, nutrient enrichment (20/2) enhanced recruit density by two orders of magnitude (Fig. 3). *G. oceanicus* did not appear to use *Enteromorpha* recruits as a food source (Fig. 3A), but it consumed adult *Enteromorpha* pieces (*see Methods*). When nutrients were enriched, addition of one or two *Gammarus* had no effects on *Enteromorpha* recruitment (Fig. 3A, solid line). Without nutrient enrichment, *Enteromorpha* recruitment increased in the presence of *Gammarus* (Fig. 3A, dotted line). The interaction between *Gammarus* density and nutrient enrichment was statistically significant (Table 3B). In contrast, *L. littorea*

Table 3. Results of fixed-factor ANOVA on the effects of (A) nutrient gradient and grazing, (B) grazer density (*Gammarus* and *Littorina* separately) and nutrients, and (C) grazer species composition and nutrients on recruit density of *Enteromorpha* (cm^{-2}). Data were log-transformed to achieve homogeneity of variances.

Source	df	MS	*F*	*P*	Effect size
A Grazing (G)	1	16.683	89.613	<0.0001	0.33
Nutrients (N)	3	7.779	41.785	<0.0001	0.45
G × N	3	1.959	10.522	0.0001	0.11
Residuals	24	0.186			
B *Gammarus* (Ga)	2	0.877	3.635	0.0472	0.66
N	1	10.797	44.761	<0.0001	0.53
Ga × N	2	1.482	6.144	0.0092	0.12
Residuals	18	0.241			
Littorina (Lit)	2	6.630	59.959	<0.0001	0.54
N	1	3.443	31.133	<0.0001	0.14
Lit × N	2	2.641	23.885	<0.0001	0.21
Residuals	18	0.111			
C Grazer composition	3	8.607	54.764	<0.0001	0.65
N	1	3.353	21.336	0.0001	0.08
G × N	3	1.872	11.909	<0.0001	0.13
Residuals	24	0.157			

strongly reduced *Enteromorpha* recruitment (Fig. 3B). Nutrient enrichment increased recruitment in the presence of one, but not in the presence of two, *Littorina.* This interaction between *Littorina* density and nutrient enrichment was statistically significant (Table 3B).

Grazer species composition × nutrient enrichment—When comparing the effects of different grazer species compositions (no grazer, two *Gammarus,* two *Littorina,* one *Gammarus* plus one *Littorina*), we found significant differences among grazers and their influence on the nutrient enrichment effect. In the presence of two *Gammarus,* algal recruitment increased in nonenriched treatments, whereas no effects occurred in nutrient-enriched treatments (Fig. 3A). In contrast, two *Littorina* overrode nutrient effects by reducing *Enteromorpha* in enriched and nonenriched treatments to low levels (Fig. 3B). A mix of one *Gammarus* and one *Littorina* resulted in intermediate recruit densities in both nutrient treatments (Fig. 2, compare 0/0 and 20/2 nutrient levels). The interaction between nutrient enrichment and grazer species composition was statistically significant (Table 3C).

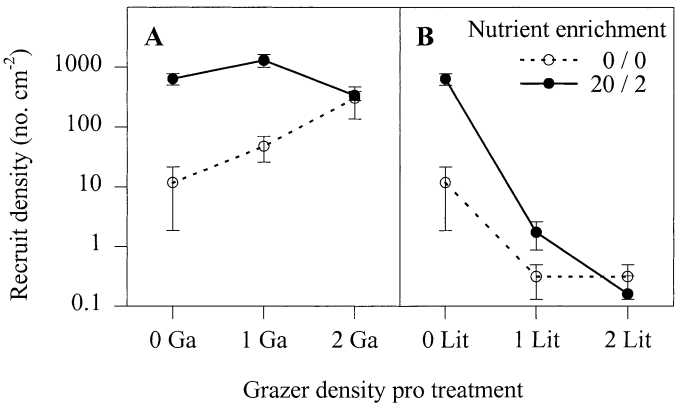

Fig. 3. Effects of (A) *Gammarus oceanicus* (Ga) and (B) *Littorina littorea* (Lit) density and nutrient enrichment (NO_3/PO_4) on recruitment of *Enteromorpha* (means ± 1 SE, $n = 4$).

UV radiation × temperature × grazing × nutrient enrichment—The four-factorial experiment revealed strong and interacting effects of temperature, grazers, and nutrients and weaker interacting effects of UV radiation. In the control treatments (no grazer, no nutrients, no UV radiation), temperature increase alone enhanced recruit density by one order of magnitude with each 6°C increase (Fig. 4). At 5°C, recruitment rate was extremely low (0.2–4.8 recruits cm^{-2}). Overall, nutrients increased and grazers reduced recruit density (Fig. 4). The strength of these interacting effects, however, varied with temperature (Fig. 5A), resulting in a significant three-way interaction (T × G × N, Table 4). Nutrients strongly increased recruitment in the absence of grazers at 11 and 17°C, but only slightly at 5°C, where recruitment likely was limited by temperature. Relative grazer effects were weak at 5°C but increased with temperatures and were stronger when nutrients were enriched (Fig. 5A). Taken together, the main and interacting effects of temperature, nutrients, and grazers explained 87% of the variance (effect size, Table 4).

UV radiation had less pronounced and more variable effects, which depended on temperature and the presence of grazers. When grazers were absent, UV radiation reduced *Enteromorpha* recruitment by 37–65% at 11 and 17°C but enhanced recruit density at 5°C (Fig. 4). In the presence of grazers no significant UV effects occurred. These patterns resulted in a significant temperature × grazer × UV interaction, which explained 1% of the variance (Fig. 5B; Table 4).

Discussion

Our experiments revealed strong and interacting effects of temperature, nutrient enrichment and grazing on recruitment

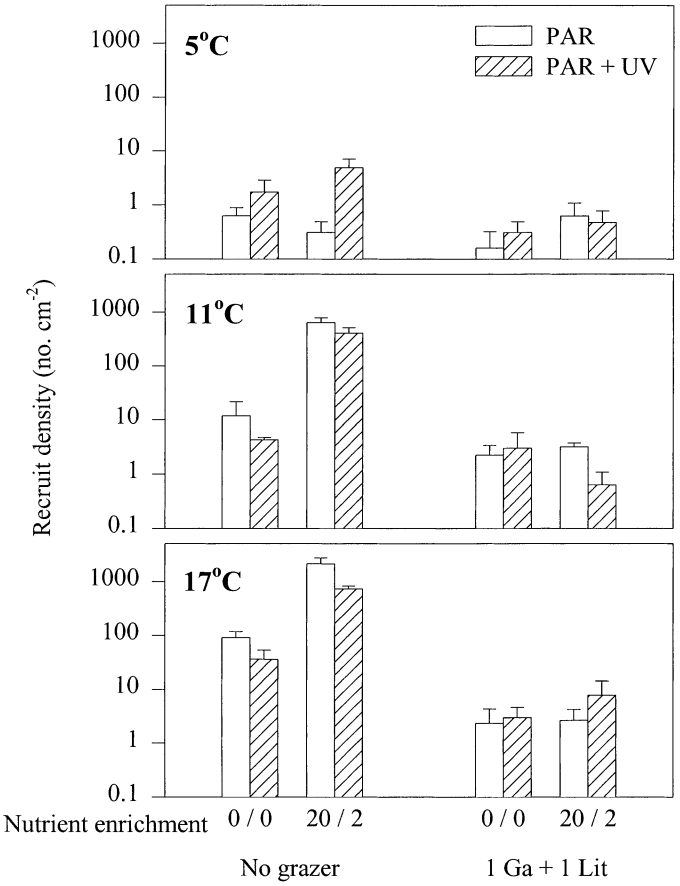

Fig. 4. Cumulative effects of UV radiation (PAR vs. PAR + UV), temperature (5, 11, 17°C), grazing by one *Gammarus* (Ga) and one *Littorina* (Lit), and nutrient enrichment (NO_3/PO_4) on recruit density of *Enteromorpha* (means ± 1 SE, $n = 4$).

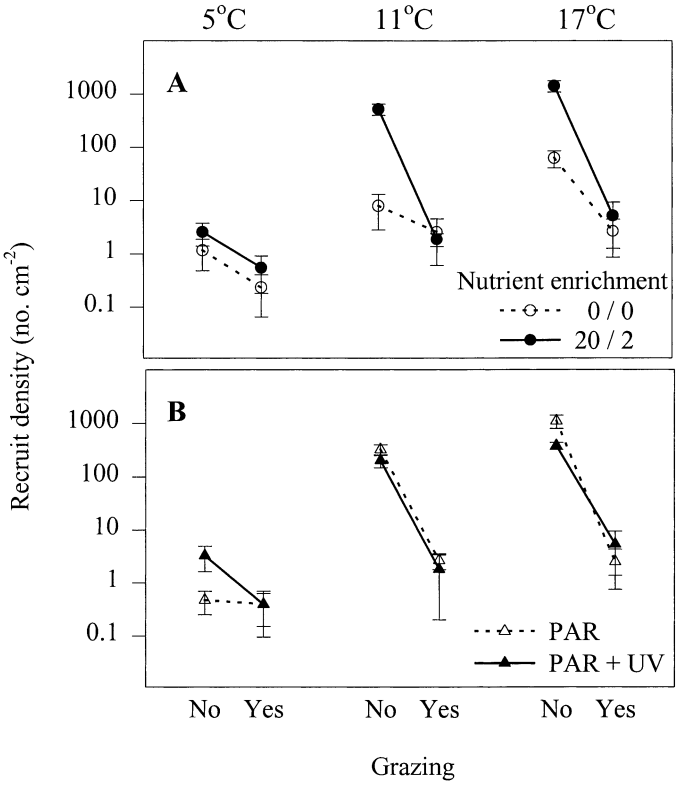

Fig. 5. Three-way interaction plots of (A) the temperature × nutrient enrichment (NO_3/PO_4) × grazing (one *Gammarus* and one *Littorina*) interaction (data were pooled over UV radiation treatments) and (B) the temperature × UV radiation (PAR vs. PAR + UV) × grazing interaction (data were pooled over nutrient enrichment treatments) on *Enteromorpha* recruit density (means ± 1 SE, $n = 8$). For statistical analysis refer to Table 4.

of the bloom-forming macroalga *E. intestinalis.* Effects of UV radiation were less pronounced but also interactive with grazing and temperature effects. These results demonstrate the potential for strong interactions among multiple environmental controls.

Interactions of nutrient enrichment, grazer density, and grazer species composition—Recruitment of *Enteromorpha* increased exponentially with nutrient enrichment. Grazers could control algal recruitment until a nutrient threshold was reached. Previous field experiments demonstrated this exponential increase of annual green algae (*Enteromorpha, Cladophora*) with nutrient enrichment, as well as strong counteracting grazer effects (Lotze and Worm 2000; Lotze et al. 2001). However, a threshold nutrient level was not detected, probably because of lower nutrient concentrations in the field experiments. In concordance with previous field studies, our results clearly indicate that a suppression of macroalgal blooms in eutrophied waters can result from strong grazing pressure that masks the effects of nutrient enrichment. In turn, macroalgal blooms can occur when nutrient concentration exceeds a threshold level or grazer abundance is reduced. This hypothesis is supported by large-scale field surveys in Atlantic Canada, which indicated the occurrence of macroalgal blooms only in those estuaries that were both eutrophied and had reduced grazing pressure (Worm 2000).

Not only reduction in grazing pressure, but also shifts in grazer species composition might favor the occurrence of macroalgal blooms. Shifts in grazer species composition can be caused by direct exploitation, pollution, changes in habitat structure, or altered food web composition (Laughlin et al. 1984; Lotze and Worm 2000; Worm 2000; Lotze and Milewski 2002). *L. littorea* had strong negative influences on *Enteromorpha* recruitment, whereas algal recruitment increased in the presence of *G. oceanicus* when nutrient supply was low. This was most likely a fertilization effect (Sterner 1986). However, both species consumed adult *Enteromorpha* thalli, which were provided as an additional food source. Although both littorinid snails and gammarid amphipods are known to feed on palatable annual green macroalgae such as *Enteromorpha* (Shacklock and Doyle 1983; Norton et al. 1990), species-specific, site-specific and life-stage–specific preferences occur. In the Baltic, *G. locusta* feeds heavily on *Enteromorpha* recruits but has only weak effects on adult stages, whereas *L. littorina* has only weak effects on both recruits and adults (Lotze and Worm 2000). This pattern is in contrast to our recent results and could be explained by local consumer–food adaptations. Together, our experimental results indicate that restrictions on nutrient loading in com-

Table 4. Results from fixed-factor ANOVA on the combined effects of temperature, UV radiation, grazing, and nutrient enrichment on *Enteromorpha* recruit density. Data were log-transformed to achieve homogeneity of variances. MS, mean square.

Source	df	MS	*F*	*P*	Effect size
Temperature (T)	2	11.736	95.293	<0.0001	0.23
UV radiation	1	0.084	0.684	0.4108	
Grazing (G)	1	30.210	245.305	<0.0001	0.30
Nutrients (N)	1	9.094	73.841	<0.0001	0.09
T × UV	2	0.321	2.604	0.0809	
T × G	2	5.818	47.241	<0.0001	0.11
T × N	2	1.746	14.174	<0.0001	0.03
UV × G	1	0.020	0.163	0.6877	
UV × N	1	0.005	0.042	0.8378	
G × N	1	7.187	58.359	<0.0001	0.07
T × UV × G	2	0.530	4.302	0.0172	0.01
T × UV × N	2	0.115	0.932	0.3987	
T × G × N	2	1.896	15.392	<0.0001	0.04
UV × G × N	1	0.056	0.456	0.5016	
T × UV × G × N	2	0.026	0.207	0.8132	
Residuals	72	0.123			

bination with an abundant and diverse herbivore guild might be the best insurance to prevent destructive macroalgal blooms in coastal ecosystems (Valiela et al. 1997; Raffaelli et al. 1998; Worm et al. 1999, 2000).

Interactive effects of UV radiation, temperature, grazing, and nutrient enrichment—We were interested in how climatic factors might interact with the bottom-up versus top-down control of annual macroalgae. Recruitment of *Enteromorpha* was strongly limited at 5°C. At this low temperature, nutrient enrichment, grazing, and UV radiation had no or weak effects (*see below*). The recruitment rate of *Enteromorpha* was enhanced by one order of magnitude with each 6°C temperature increase. Previous studies revealed that recruitment is initiated when water temperatures exceeded 5°C, germination rate strongly increases toward 10°C, and growth rate further increases up to 15°C (Lotze et al. 1999). These results suggest that rising temperatures in spring and early summer might accelerate macroalgal bloom development. Besides the temperature effect, nutrient enrichment further enhanced *Enteromorpha* recruitment by one to two orders of magnitude. The interaction of temperature and nutrients indicates the potential for synergistic effects of eutrophication and climate warming on macroalgal recruitment in the field.

Relative grazer effects in our experiment increased with rising temperature as well as with nutrient enrichment. Grazer activity increased, probably because of increasing metabolic activity related to temperature (Paul et al. 1989), and with higher food supply because of nutrient enrichment and rising temperature. Overall, increasing grazer effects masked the positive nutrient and temperature effects on *Enteromorpha* recruit density (Fig. 5A). This suggests the potential for antagonistic grazer effects on climate warming and eutrophication. As discussed above, however, increasing nutrient loads, changes in grazer species composition, or reduction of grazer abundance, all of which are related to human activities, could impair this natural control against macroalgal blooms.

Compared to the other treatments, UV radiation effects on *Enteromorpha* recruitment were less pronounced but also interactive with temperature and grazer effects. Strong grazing pressure masked UV radiation effects on recruit density at all temperatures (Figs. 4, 5B). When grazers were absent, however, a positive UV radiation effect was seen at 5°C and negative UV radiation effects at were seen at 11 and 17°C. As an intertidal species, *Enteromorpha* might be well adapted to natural UV radiation stress (Hanelt et al. 1997*b*; Bischof et al. 1998), and it was shown that *E. prolifera* dominated filamentous algal communities from tropical origin under UV radiation exposure for 2 weeks, whereas other species dominated under UV radiation exclusion (Santas et al. 1998). However, there is no real explanation for a positive UV radiation effect at 5°C only (Vincent and Roy 1993; Franklin and Forster 1997). Recruitment was very sparse and partially clumped at this low temperature, which might have resulted in incorrect density estimates creating a spurious UV radiation effect. On the other hand, UV radiation reduced *Enteromorpha* recruitment by 37–65% at higher temperatures, and these negative effects were stronger at 17 than at 11°C (Fig. 5B). In short-term experiments with similar UVB radiation exposure, adult *E. intestinalis* from England and *E. bulbosa* from Antarctica both showed 10–15% reduction in photosynthesis (Cordi et al. 1997; Bischof et al. 1998), and *Ulva expansa* showed 10–30% reduced growth rate under UVB radiation exposure in outdoor experiments in California (Grobe and Murphy 1994). The early life stages in our experiments might be more sensible to UV radiation than adult thalli, and acclimatization to UV radiation stress could occur during the maturation process (Hanelt et al. 1997*a*). Thus, in long-term exposure under natural conditions, UV radiation effects might weaken over time (Hanelt et al. 1997*a*,*b*; Bischof et al. 1998; Santas et al. 1998). As our results indicate, however, the magnitude and direction of UV radiation effects could depend on temperature, and there is the potential for interdependent effects between increasing UV radiation and warming that could limit recruitment of bloom-forming macroalgae in the summer months.

Rising temperatures and increasing nutrient loads can synergistically enhance the recruitment of annual macroalgae, triggering increased macroalgal blooms in coastal waters. High grazer densities can counteract these effects until a threshold nutrient concentration is reached, depending on grazer species composition. Reductions of grazer abundance or alterations of grazer species composition through direct harvesting, pollution, or habitat or food web alterations could impair natural grazer control of macroalgal blooms. Furthermore, increasing UV radiation might be more harmful in combination with rising temperatures and could limit recruitment of bloom-forming macroalgae in summer. We could demonstrate that multiple human influences have the potential of synergistic effects with strong negative effects on the environment.

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Received: 8 March 2002
Accepted: 16 July 2002
Amended: 11 August 2002