

Climate-driven increases in nutrient runoff promote filamentous macroalgal mat development despite benthic grazer presence

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Research Article

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Abstract

Climate change is expected to alter precipitation patterns, terrestrial runoff, and nutrient delivery to shallow coastal ecosystems, potentially increasing the frequency and intensity of macroalgal blooms. Opportunistic filamentous green macroalgae are well adapted to exploit episodic nutrient enrichment, yet it remains unclear whether benthic grazers can effectively constrain macroalgal development under future nutrient-enriched conditions. To address this question, a six-week flow-through mesocosm experiment was conducted using intact sediments, with and without nutrient enrichment and natural populations of the polychaete *Hediste diversicolor*.

Nutrient enrichment significantly increased macroalgal biomass, whereas grazer abundance and biomass remained similar among treatments. The strongest algal development occurred in nutrient-enriched sediments despite the continued presence of *H. diversicolor*, suggesting that increased nutrient availability promoted algal growth beyond the capacity of grazers to effectively constrain mat development. In contrast, macroalgal growth was limited under ambient nutrient conditions, indicating that grazing may contribute to suppressing algal establishment when nutrient availability is low.

These findings suggest that even moderate increases in nutrient availability may favour the development of filamentous macroalgal mats despite the presence of abundant benthic grazers. As climate-driven increases in runoff are expected to increase the frequency of nutrient pulses in coastal ecosystems, opportunistic macroalgae may increasingly benefit from conditions that reduce the effectiveness of biological control.

Introduction

Climate change is expected to alter the functioning of coastal ecosystems through changes in precipitation patterns, more frequent extreme weather events, and altered terrestrial runoff. (IPPC, 2023). These hydrological changes are predicted to increase the transport of nutrients from land to coastal waters, potentially reinforcing eutrophication pressures even in regions where direct anthropogenic nutrient inputs have been reduced. As a result, nutrient enrichment is expected to remain a major driver of ecological change in shallow coastal ecosystems during the coming decades.

Among the primary producers that respond most rapidly to increased nutrient availability are filamentous green macroalgae (Wallentinus, 1984). Species such as *Ulva* and *Cladophora* are opportunistic algae characterized by high nutrient uptake rates, efficient nutrient storage, and rapid biomass accumulation following nutrient pulses (Pedersen and Borum, 1997; Wallentinus, 1984). Their ability to exploit short periods of elevated nutrient availability allows them to rapidly form extensive algal mats in shallow coastal environments. Consequently, climate-driven increases in nutrient runoff may create environmental conditions that favour the initiation, expansion, and persistence of filamentous macroalgal blooms.

Filamentous macroalgal mats are a widespread feature of shallow coastal ecosystems and have increased in frequency and extent in many regions worldwide (Louis et al., 2023; McGlathery et al., 2007; Valiela et al., 1997). Under favourable environmental conditions, these opportunistic algae can accumulate rapidly and form dense mats that alter ecosystem functioning. Such blooms may reduce light availability, suppress perennial vegetation, modify habitat structure, alter oxygen dynamics, and contribute to hypoxia during decomposition (McGlathery et al., 2001; Norkko and Bonsdorff, 1996; Olyarnik and Stachowicz, 2012; Sundbäck et al., 1990). The ecological consequences can extend throughout the food web and fundamentally alter benthic ecosystem processes.

Although nutrient availability is a major driver of filamentous macroalgal mat development, biological interactions may influence the extent to which opportunistic algae are able to establish and persist. In shallow soft-bottom habitats, benthic grazers can reduce algal recruitment and biomass accumulation through direct consumption of propagules and newly established filaments (Lotze and Worm, 2000; Worm et al., 1999). The polychaete *H. diversicolor* is among the most abundant benthic invertebrates in northern European coastal ecosystems and has previously been shown to suppress the development of filamentous green macroalgae through grazing (Engelsen and Pihl, 2008; Nordström et al., 2006). Such biological control may increase ecosystem resistance to macroalgal mat formation, although its effectiveness is likely to depend on prevailing environmental conditions. However, the effectiveness of grazer control may depend strongly on environmental conditions. Increased nutrient availability may stimulate algal production to levels that exceed grazing capacity, potentially reducing the relative importance of top-down regulation. In addition, climate-related stressors such as hypoxia, warming, and habitat degradation may negatively affect benthic grazer populations and further weaken biological control (Diaz and Rosenberg, 2008; Engelsen et al., 2010; Madeira et al., 2021). Together, these processes may increase the likelihood that future coastal ecosystems become increasingly dominated by opportunistic macroalgal mats.

Sediments may further amplify these responses. In addition to external nutrient inputs, coastal sediments represent important reservoirs of regenerated nutrients that can support macroalgal growth through benthic-pelagic coupling (Sundbäck et al., 2003; Trimmer et al., 2000). Enhanced organic matter accumulation associated with eutrophication may stimulate nutrient recycling and sediment nutrient release, creating positive feedbacks that reinforce macroalgal dominance. Consequently, future increases in nutrient runoff may interact with sediment nutrient dynamics and grazer activity to determine the trajectory of coastal ecosystem development.

Understanding how future increases in runoff-driven nutrient delivery influence the development of filamentous macroalgal mats is therefore of increasing importance. Although benthic grazers may contribute to ecosystem resistance, it remains unclear whether biological control can constrain macroalgal development under nutrient-enriched conditions representative of future climate scenarios.

The present study experimentally examined how moderate nutrient enrichment, representing future runoff-driven nutrient pulses, influences filamentous macroalgal mat development in shallow coastal

ecosystems. Using a replicated mesocosm experiment with natural populations of *H. diversicolor*, we assessed whether biological control remains effective under increased nutrient availability.

Materials & Method

The aim of the experimental setup was to test whether *H. diversicolor* can effectively graze down a developing or fully grown macroalgal mat under nutrient-enriched conditions. Surface sediments without *H. diversicolor* served as controls representing algal mat development in the absence of grazing pressure, such as may occur following anoxic events. These processes are central to understanding eutrophication dynamics and are increasingly important in the context of climate change, where both nutrient inputs and grazer populations can be expected to shift.

Experimental design

The experiment was conducted from June 19 to July 20, 2006, at the Kristineberg Marine Research Station (58° 15' N, 11° 30' E) on the west coast of Sweden, as part of a broader study on ephemeral green algal mat initiation and growth. The study site is microtidal with an average tidal amplitude of ~ 20 cm, and salinity in shallow coastal waters (~ 0.5 m depth) typically ranges from 20 to 25 PSU during summer (Pihl and Rosenberg, 1982).

Experiments took place in an outdoor greenhouse laboratory receiving approximately 80% of ambient natural daylight due to attenuation by greenhouse material. The study was conducted to coincide with the typical onset of green macroalgal mat development in the region. Figure 1 provides a schematic overview of experimental design and treatments. A total of 20 experimental units were established (five replicates per treatment), together with five baseline sediment cores used for initial measurements. Ten intact sediment cores (100 mm height, 165 mm internal diameter) and ten surface sediment samples (top 5 mm sliced from full cores) were used. These were divided into four treatments:

- **SedNu**: intact sediment with natural infauna and nutrient additions
- **Sed**: intact sediment with natural infauna, no nutrient additions
- **SurfNu**: surface sediment (macrofauna excluded) with nutrient additions
- **Surf**: surface sediment without nutrient additions

The intact cores (Sed and SedNu) were left undisturbed upon collection, characterized as silty with ~ 14% organic matter content (Engelsen et al., 2008). The commonly used approach of adding macrofauna to initially defaunated sediment was avoided because defaunation (e.g. by asphyxiation or freezing the sediment column with liquid N₂) can significantly alter pore-water distributions and sediment biogeochemical properties. Instead, an additional treatment was used, of cores with only the top 5 mm of natural sediment, i.e. a treatment without macrofauna but with pore-water concentrations more or less the same as those of the overlying water. This treatment was intended to simulate conditions where benthic grazers are absent, for example following hypoxic events that eliminate infauna from surface

sediments. All sediment samples contained a natural distribution of propagules originating from both sediment and inflowing seawater, thus reflecting natural coastal conditions.

Cores were transported to the laboratory and randomly assigned to basins supplied with flow-through seawater sourced from 2 m depth in a nearby bay, with a flow rate of approximately 10 L h⁻¹. Surface sediments (Surf and SurfNu) were spread on plates positioned at the same height as the sediment surface in intact cores, ensuring uniform light exposure across treatments. Each core received individual seawater flow, maintaining a 50 mm overlying water column to simulate *in situ* conditions. Water flow created turbulence that mixed the water column, and overflow was allowed to maintain core temperature close to ambient surface water (21–23°C).

Initially, macroalgal mats remained within core boundaries but occasionally extended beyond as they grew; these overgrown mats were included in final biomass estimates due to their cohesive association with respective cores.

Nutrient enrichment (SedNu and SurfNu) was applied every third day using uncoated fertilizer pellets (Hydro Agri OptiCrop NPK 21–3–10) contained in mesh bags at each core's water inlet. The enrichment approach followed the general principle of previous sediment nutrient addition experiments (Worm et al., 2000), while being adapted to the present experimental design. Approximately 5 g of fertilizer pellets were added per core at each fertilization event. Based on fertilizer composition (20.6% N and 2.4% P), this corresponded to approximately 1.03 g nitrogen (N) and 0.12 g phosphorus (P) per core per fertilization event. The enrichment treatment was designed to create sustained elevated nutrient conditions relevant to potential future scenarios of increased terrestrial runoff and enhanced nutrient loading associated with environmental change and climate-driven hydrological shifts. After fertilization, cores were closed for approximately 1 h to allow pellet dissolution. Background nutrient concentrations in inflowing water averaged approximately 3 µM dissolved inorganic nitrogen (DIN) and 0.45 µM phosphorus (P), indicating relatively low ambient nutrient conditions during the experiment. Temporal variation in environmental conditions (Table 1) may partly be explained by natural variability, including possible effects of wind-driven mixing (Schramm, 1999).

Table 1
Environmental conditions (temperature, salinity, and nutrient concentrations) measured during the experiment.

Date	Treatment	Salinity	Temperature	NH ₄ ⁺	NO ₃ ⁻	DIN	PO ₄ ³⁻	Si(OH) ₄
			° C	μmol L ⁻¹				
23 June	Sed	21	22	1.10	0.93	2.02	0.37	0.34
	SedNu	21	22	1.48	1.44	2.91	0.94	0.18
	Surf	21	22	0.85	0.78	1.63	0.31	0.20
	SurfNu	21	22	2.01	1.27	3.28	1.64	0.41
27 June	Sed	30	21	2.00	1.58	3.57	0.40	1.57
	SedNu	30	21	3.28	2.01	5.29	0.81	1.59
	Surf	30	21	1.85	1.58	3.44	0.41	1.62
	SurfNu	30	21	2.69	1.91	4.60	1.14	1.72
4 July	Sed	22	23	1.12	1.25	2.37	0.45	0.20
	SedNu	22	23	1.07	0.95	2.02	1.28	0.17
	Surf	22	23	0.59	0.79	1.38	0.34	0.32
	SurfNu	22	23	0.88	0.71	1.59	3.48	0.40
7 July	Sed	22	22	1.02	1.54	2.56	0.54	1.50
	SedNu	22	22	0.68	2.14	2.82	0.85	0.95
	Surf	22	22	0.70	1.05	1.75	0.44	1.49
	SurfNu	22	22	1.09	1.53	2.62	2.28	1.43
11 July	Sed	21	21	3.11	1.07	4.18	0.33	1.01
	SedNu	21	21	2.30	3.36	5.66	1.63	1.32
	Surf	21	21	0.70	1.28	1.98	0.36	1.09
	SurfNu	21	21	0.97	1.45	2.42	0.83	1.02
14 July	Sed	30	22	1.57	2.48	4.05	0.57	3.11
	SedNu	30	22	1.71	2.51	4.22	0.80	1.01
	Surf	30	22	0.80	2.23	3.03	0.49	4.51
	SurfNu	30	22	0.79	2.36	3.15	1.01	3.03

Initial sampling occurred 24 hours after setup (June 20), and final sampling on July 19. Water samples were collected every third day at inflow points to monitor nutrient concentrations. Weekly photographs documented macroalgal growth. Destructive sampling at the start and end quantified macroalgal biomass, microphytobenthic community composition and biomass, and benthic fauna abundance and biomass. Oxygen and nutrient fluxes were also measured to assess sediment characteristic changes during nutrient addition. At each sampling occasion, three of the five replicate cores per treatment were randomly selected. For an overview of the sampling days etc see Fig. 1.

Biological sampling

Macroalgal cover was visually assessed weekly and documented photographically to monitor mat development. At final sampling (July 19), macroalgae were removed, and wet weight (WW) and dry weight (DW) determined for biomass estimation.

During destructive sampling (June 20 and July 19), sediment was wet sieved through a 1 mm mesh to retrieve benthic macrofauna. Fauna was identified to the lowest possible taxonomic level, counted, and biomass estimated after correcting wet weight for shell weight (25%) (Rumohr et al., 1987). Abundance and biomass of *H. diversicolor* were converted from core-based measurements to area-standardized values (m^{-2}) using the inner core area (diameter: 16.5 cm).

Benthic oxygen and nutrient fluxes

Oxygen and inorganic nutrients (NH_4^+ , NO_3^- , PO_4^{3-} , Si(OH)_4) concentrations were measured in the water column of each core under light (12:00) and dark (24:00) conditions, ($n = 3$). During incubations, cores were sealed with acrylic lids and water flow was stopped. Oxygen concentration changes were kept below 20% to prevent oxygen-induced nutrient flux alterations (Dalsgaard et al., 2000). Incubation lasted ~ 1 hour (light) and ~ 2 hours (dark). The same cores were used for both oxygen and nutrient flux measurements.

Samples were collected using 20-ml glass syringes (oxygen) and disposable plastic syringes (nutrients). Time-zero samples were taken from open cylinders; post-incubation samples were taken through a 5 mm lid opening. Nutrient samples were filtered (0.45 μm Sartorius syringe filters) and frozen at -80°C until analysis by colorimetric auto-analyzer (TRAACS 800, Bran & L  bbe) following Strickland and Parsons (1972). Daily nutrient fluxes were calculated by scaling hourly fluxes to daylight and dark periods (Dalsgaard et al., 2000). Oxygen concentrations were measured immediately by Winkler titration (Strickland and Parsons, 1972). Net primary production (NPP) was calculated from oxygen flux measurements and scaled to daily rates using local irradiance data obtained from the Swedish Meteorological and Hydrological Institute.

Statistical analysis

Differences in the abundance and biomass of *H. diversicolor* between treatments were analysed using one-way analysis of variance (ANOVA), as only one factor (nutrient addition) was relevant for these variables.

The effects of nutrient addition and sediment depth on algal biomass, net primary production (NPP), community respiration (CR), and nutrient fluxes (NH_4^+ , NO_3^- , PO_4^{3-} , Si(OH)_4) were tested using two-factor ANOVA, with sediment depth (5 mm vs 100 mm) and nutrient addition (with vs without enrichment) as fixed factors, including their interaction. Surface sediment treatments (5 mm) effectively excluded macrofauna and were used to represent no-grazer conditions.

Initial sediment measurements were used as baseline values for comparison with final measurements. When relevant, differences between initial and final conditions within treatments were assessed using appropriate comparisons.

Assumptions of homogeneity of variances were tested using Cochran's test, and data were transformed when necessary to meet ANOVA assumptions. Statistical significance was accepted at $p \leq 0.05$. Significant effects were further explored using Tukey's honestly significant difference (HSD) post hoc test. Statistical analyses were performed using IBM SPSS Statistics (version 30). Statistical analyses were performed following standard ecological statistical procedures (Underwood, 1997). Data are presented as mean $\pm$ SE.

Results

Algal growth

Green algal mats consisting mainly of *Ulva compressa* started to grow in three out of four treatments: sediment with nutrient addition (SedNu), surface sediment (Surf) and surface sediment with nutrient addition (SurfNu). Grazers (*H. diversicolor*) were present only in 100 mm sediment treatments (Sed and SedNu). However, there was no macroalgal growth in the sediment treatment without nutrient addition (Sed) (Fig. 2). Treatment structure and experimental setup are shown in Fig. 1.

The macroalgal growth started day 4 in all cores. At the same time a cyanobacterial mat started to grow, particularly in SurfNu cores, but also in some SedNu cores. After further three days SedNu showed a green algal mat with a 50–100% degree of coverage in the cores, Surf showed a patchy coverage of approximately 15–20%, SurfNu had floating cyanobacterial mats and a growing macroalgal mat, while Sed still showed no sign of macroalgal growth. The following days the macroalgal mat increased in all cores, except in Sed cores, and became the dominating algal species. The mean macroalgal biomasses were 0 g m^{-2} (Sed), 134 g m^{-2} (SedNu), 42 g m^{-2} (Surf) and 92 g m^{-2} (SurfNu) at the end of the experiment (Fig. 2). There were significant ($p = 0.01$) differences in algal biomass between the treatments, where SedNu had the highest biomass, followed by SurfNu and Surf (Table 2). SedNu showed a biomass 3 times higher than Surf and 1.5 times higher than SurfNu (Fig. 2). Nutrient addition

significantly increased algal biomass, whereas sediment depth and the interaction between sediment depth and nutrient addition had no significant effect (Table 2).

Table 2

Summary of analyses of variance (ANOVA) where the one - factor ANOVA used sediment depth (100 mm and 5 mm) as fixed factor and the two - factor ANOVA used nutrient addition and sediment depth as fixed factors. Differences were accepted as significant at $p < 0.05$. Significance is highlighted in bold text in the table.

Treatment	df	MS	F	p
Hediste diversicolor (abundance)				
<i>Nutrient addition</i>	1	375	1.2	0.30
Hediste diversicolor (biomass)				
<i>Nutrient addition</i>	1	3	0.09	0.76
Algal biomass				
<i>Sediment depth</i>	1	6193	0.74	0.40
<i>Nutrient addition</i>	1	80538	9.66	0.01
<i>Sediment depth * Nutrient addition</i>	1	247	0.03	0.86
Net primary production (NPP)				
<i>Sediment depth</i>	1	399	0.62	0.45
<i>Nutrient addition</i>	1	295	0.46	0.51
<i>Sediment depth * Nutrient addition</i>	1	1329	2.08	0.19
Community respiration (CR)				
<i>Sediment depth</i>	1	821	2.43	0.16
<i>Nutrient addition</i>	1	286	0.85	0.38
<i>Sediment depth * Nutrient addition</i>	1	69	0.21	0.66
Ammonium (NH_4^+)				
<i>Sediment depth</i>	1	2754	0.10	0.75
<i>Nutrient addition</i>	1	4767	0.92	0.36
<i>Sediment depth * Nutrient addition</i>	1	50062	1.86	0.21
Nitrate (NO_3^-)				
<i>Sediment depth</i>	1	2437	4.97	0.05
<i>Nutrient addition</i>	1	1669	3.40	0.10
<i>Sediment depth * Nutrient addition</i>	1	5673	11.57	0.01

Treatment	df	MS	F	p
Phosphate (PO_4^{3-})				
<i>Sediment depth</i>	1	8169	1.48	0.26
<i>Nutrient addition</i>	1	35334	6.44	0.03
<i>Sediment depth * Nutrient addition</i>	1	15840	2.88	0.13
Silicate (Si(OH)_4)				
<i>Sediment depth</i>	1	34793	17.35	0.003
<i>Nutrient addition</i>	1	205	0.10	0.76
<i>Sediment depth*Nutrient addition</i>	1	197	0.10	0.76

Hediste diversicolor

Since the polychaete *H. diversicolor* was the main interest in this investigation, no attention is paid to other species found in the sediment, although species such as for example *Macoma baltica*., *Mya arenaria*, *Cerastoderma edule*, *Hinia reticulata*, *Pygospio elegans*, *Corophium volutator* and *Hediste virens* were found and are commonly found in this type of sediment (Engelsen et al., 2008). However, the abundance of *H. diversicolor* dominated the macrofauna. During the experiment, the polychaetes were seen grazing propagules on the sediment as well as on the edges of the cores where also macroalgal filaments had attached. Neither the abundance nor the biomass of *H. diversicolor* differed significantly between Sed and SedNu (Table 2, Fig. 3).

The abundance was 299 ind m^{-2} for Sed and 234 ind. m^{-2} for SedNu, and the biomass was 84 g m^{-2} for Sed and 62 g m^{-2} for SedNu (Fig. 3).

Biogeochemical fluxes

Patterns in nutrient fluxes differed between treatments and over time (Fig. 4). Inorganic nutrient fluxes were measured at the beginning and in the end of the experiment.

The initial flux represents the condition before an algal mat starts to grow, and the terminal flux measurement shows the conditions after four weeks in the different treatments. Ammonium was the only nutrient species released in the initial measurement, while nitrate, phosphate and silica were consumed by the sediment (Fig. 4). At the end of the experiment, ammonium was consumed in all treatments but Sed (Fig. 4), which instead showed a release. Nitrate showed an uptake for all treatments while phosphate was released where nutrients had been added (SedNu and SurfNu) and uptakes where no nutrients were added (Sed and Surf) (Fig. 4). SedNu showed a high mean release of phosphate at the

end of the experiment, although this was not statistically significant due to high variation among replicates. Silica appeared to mirror sediment thickness, with 100 mm sediments showing uptake and 5 mm sediments showing release (Fig. 4). Silicate fluxes differed significantly between sediment depths ($p = 0.003$), whereas neither nutrient addition ($p = 0.76$) nor the interaction between sediment depth and nutrient addition ($p = 0.76$) had significant effects (Table 2). Intact sediment treatments (Sed and SedNu) showed net uptake of silicate (-9.85 and $-25 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively), whereas surface sediment treatments (Surf and SurfNu) showed net release (90 and $89.8 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively) (Fig. 4).

Significant differences between sediment depths were also found for nitrate ($p = 0.05$) whereas phosphate showed a significant difference between treatments (Table 2). A significant interaction between sediment depth and nutrient addition was also detected for nitrate fluxes ($p = 0.01$), suggesting that nutrient effects varied between sediment treatments.

Primary production

Net primary production (NPP) was similar between treatments and over time (Table 2, Fig. 5), although there was a tendency of oxygen uptake at the beginning (Initial) of the experiment. All NPP treatments however, showed an oxygen release at the end of the experiment (Fig. 5).

Highest daily mean NPP m^{-2} was shown for Surf treatment ($50 \text{ mmol m}^{-2} \text{ d}^{-1}$), although the variation between replicates within the treatment was high. The range between the treatments was from 20 to 50 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 5).

Community respiration was similar between treatments and over time (Table 2) and showed an oxygen uptake during the experiment for all treatments. The range between the treatments was from -44 for Sed to $-18 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for SurfNu (Fig. 5).

Species composition of benthic micro algae

Not only filamentous macroalgae responded to the additional nutrient supply. Microscopic examination of benthic microalgae revealed a community composed of both diatoms and cyanobacteria. Cyanobacteria, including *Anabaena* spp., were present alongside diatoms such as *Pleurosigma* spp., *Nitzschia* spp., and *Navicula* spp. In the nutrient-enriched surface sediment treatment (SurfNu), cyanobacterial growth was particularly pronounced, leading to the formation of buoyant mats that detached from the sediment and floated to the water surface. This phenomenon was exclusively observed in the SurfNu mesocosms with a 5 mm sediment layer.

Discussion

The present study suggests that nutrient availability may play an important role in determining whether benthic grazers are able to constrain the early development of filamentous macroalgal mats. Nutrient-enriched treatments developed substantially greater macroalgal biomass than unenriched treatments

despite the continued presence of the polychaete *H. diversicolor*. Although grazer abundance and biomass remained similar between treatments, nutrient enrichment was associated with a marked increase in macroalgal growth, indicating that relatively modest increases in nutrient supply may reduce the effectiveness of biological control under conditions of increased nutrient availability.

Filamentous green macroalgae are widely recognized as opportunistic primary producers capable of rapidly exploiting transient increases in nutrient availability (Pedersen and Borum, 1997; Wallentinus, 1984). High nutrient uptake rates, efficient nutrient storage, and rapid growth allow these species to respond quickly to nutrient pulses, often resulting in substantial biomass accumulation over short periods. The results obtained here are consistent with this general pattern. While grazing appeared sufficient to constrain macroalgal development under ambient nutrient conditions, nutrient enrichment was associated with substantial algal growth despite the continued presence of grazers.

The findings may be particularly relevant in the context of ongoing climate change. In northern Europe, future climate scenarios predict increasing precipitation, more frequent extreme rainfall events, and enhanced terrestrial runoff (IPPC, 2023). Such changes are expected to increase the transport of nutrients from catchments to coastal waters, potentially generating more frequent nutrient pulses in shallow coastal ecosystems. Under these conditions, opportunistic filamentous algae may be favoured because of their capacity to rapidly assimilate and store nutrients following episodic enrichment events (Schramm, 1999; Wallentinus, 1984). Although the nutrient additions used in the present experiment were moderate, they were sufficient to promote substantial macroalgal growth despite grazer presence, suggesting that even relatively small increases in nutrient availability may favour macroalgal mat development despite the continued presence of benthic grazers. This sequence of processes is summarized conceptually in Fig. 6.

At the same time, long-term trends in macroalgal blooms are not necessarily straightforward. In several coastal regions, nutrient management programmes have reduced external nutrient loading during recent decades, yet filamentous macroalgal blooms remain common and continue to occur in many shallow coastal ecosystems (Louis et al., 2023; McGlathery et al., 2007). This suggests that factors other than direct anthropogenic nutrient inputs may increasingly influence bloom dynamics. Internal nutrient cycling, sediment nutrient release, altered hydrological regimes, and biological interactions may all contribute to sustaining macroalgal growth under contemporary environmental conditions. These interacting pathways are incorporated into the conceptual framework presented in Fig. 6.

An alternative future scenario may occur in systems where external nutrient inputs decrease or where runoff becomes less important during extended dry periods. Under such circumstances, nutrient regeneration from sediments may become proportionally more important as a source of nutrients supporting benthic primary production. Previous studies have shown that shallow coastal sediments can constitute substantial nutrient reservoirs and may supply regenerated nutrients to overlying waters through benthic-pelagic coupling (Engelsen et al., 2008; Sundbäck et al., 2003). Sediment nutrient release has been identified as an important contributor to primary production in shallow coastal systems

and may support both microalgal and macroalgal growth even when external nutrient loading is relatively low. Consequently, future macroalgal dynamics are likely to depend on interactions between external nutrient delivery and internal nutrient recycling. Both external nutrient inputs and internal sediment nutrient recycling are included as complementary pathways in the conceptual model (Fig. 6).

The observed nutrient flux patterns provide some support for this interpretation. Despite substantial differences in macroalgal biomass, net primary production did not differ significantly among treatments, suggesting that increased biomass was not accompanied by proportional increases in areal oxygen production over the duration of the experiment. Nutrient-enriched treatments showed altered sediment-water nutrient exchange compared with unenriched treatments, suggesting that nutrient enrichment may influence not only algal growth directly but also the sediment processes that regulate nutrient availability. Such feedback mechanisms have previously been proposed as important drivers of macroalgal bloom persistence (McGlathery et al., 2007; Sundbäck et al., 2003; Trimmer et al., 2000). The conceptual model (Fig. 6) integrates these sediment feedbacks with the direct effects of nutrient enrichment on macroalgal growth.

The absence of macroalgal development in the unenriched sediment treatment further suggests that grazing may contribute to suppressing algal establishment when nutrient availability is low. Similar effects of *H. diversicolor* have been reported previously, where grazing reduced the establishment and development of filamentous macroalgae (Engelsen and Pihl, 2008; Nordström et al., 2006). However, the results suggest that the occurrence of abundant grazers alone may not prevent macroalgal mat development when nutrient availability increases. Under such conditions, opportunistic algae may rapidly exploit nutrient pulses and accumulate biomass despite the continued presence of benthic consumers. This illustrates the reduced effectiveness of grazing under elevated nutrient availability depicted in Fig. 6.

Overall, the results suggest that future changes in nutrient delivery may influence the capacity of benthic grazers to regulate filamentous macroalgal mats. Increased runoff associated with climate change may favour opportunistic macroalgae by increasing the frequency and magnitude of nutrient pulses, whereas nutrient regeneration from sediments may continue to support algal growth under conditions of reduced external loading. Understanding how these external and internal nutrient sources interact with benthic consumer communities will be important for predicting the future occurrence of filamentous macroalgal blooms in shallow coastal ecosystems. Together, these findings support the conceptual model presented in Fig. 6, in which climate-driven increases in runoff enhance nutrient availability, stimulate rapid macroalgal growth, and reduce the relative effectiveness of benthic grazing while sediment nutrient recycling provides an additional reinforcing pathway.

Conclusion

The present study suggests that relatively modest increases in nutrient availability can promote the development of filamentous macroalgal mats in shallow coastal ecosystems. Nutrient enrichment

stimulated substantial algal growth despite the continued presence of abundant benthic grazers, highlighting the capacity of opportunistic macroalgae to rapidly exploit increased nutrient availability.

As climate change is expected to alter precipitation patterns and increase terrestrial runoff in many coastal regions, nutrient pulses may become increasingly important drivers of macroalgal mat development. The results indicate that even moderate increases in nutrient delivery may favour filamentous macroalgae and contribute to mat formation under future environmental conditions. Understanding how climate-driven changes in nutrient supply influence coastal primary producers will therefore be important for predicting and managing future eutrophication-related impacts in shallow coastal ecosystems.

Declarations

Ethics approval and consent to participate

Not applicable. The study did not involve human participants or vertebrate animals requiring ethical approval.

Consent for publication

Not applicable.

Competing interests

The author declares that there are no competing interests.

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Authors' contributions

Anna Engelsen conceived and designed the study, conducted field and laboratory work, analyzed the data, interpreted the results, and wrote the manuscript.

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Figures

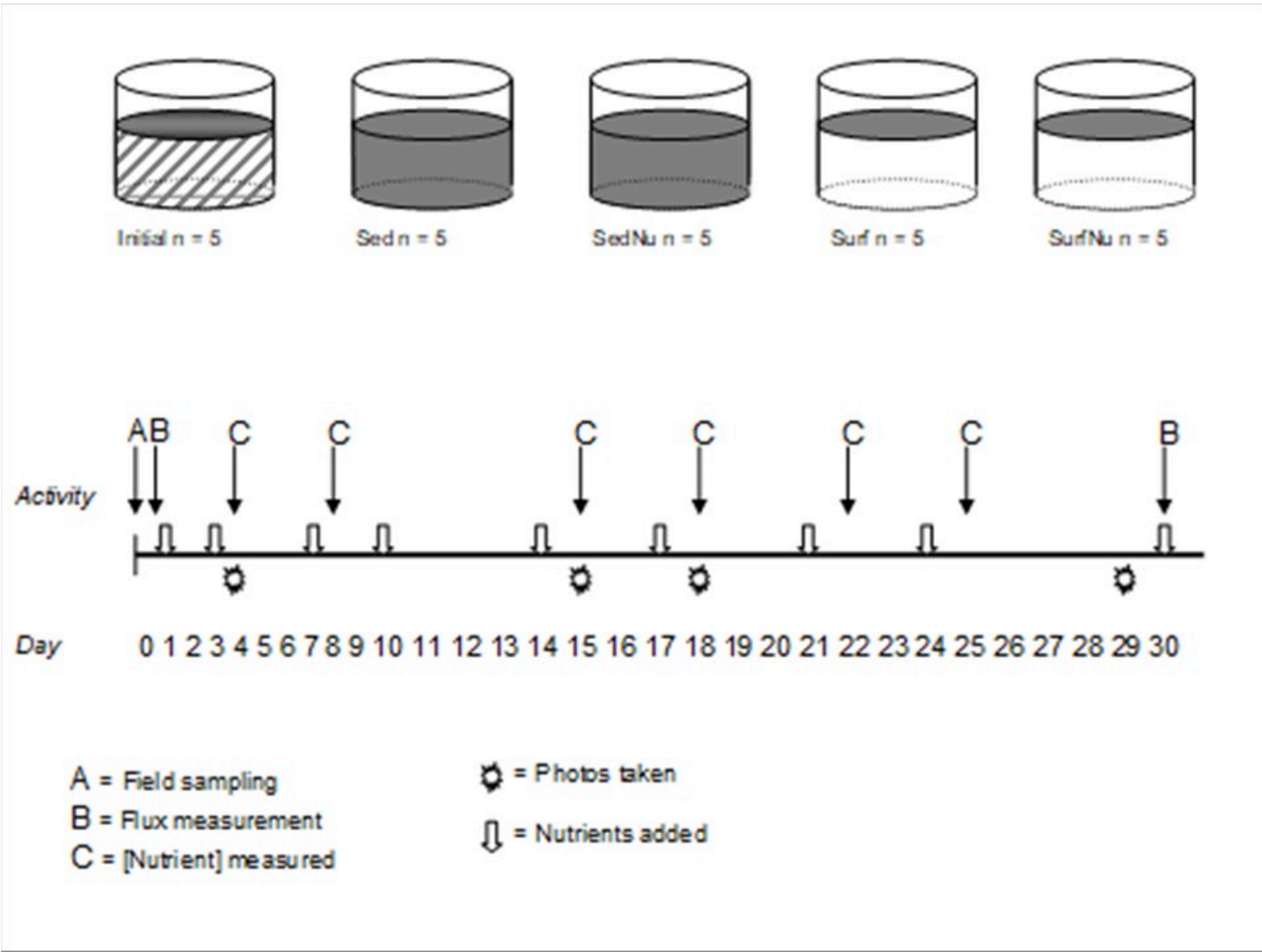


Figure 1

Treatments, timing of sampling and measurement activities (above time scale), nutrient additions and photos taken (below time scale) during the experiment. Sed (10-cm intact sediment); SedNu (10-cm intact sediment exposed to continuous nutrient addition); Surf (5-mm of surface sediment, no macrofauna) and SurfNu (5-mm of surface sediment, no macrofauna, with nutrient addition). *n* = 5 + SE.

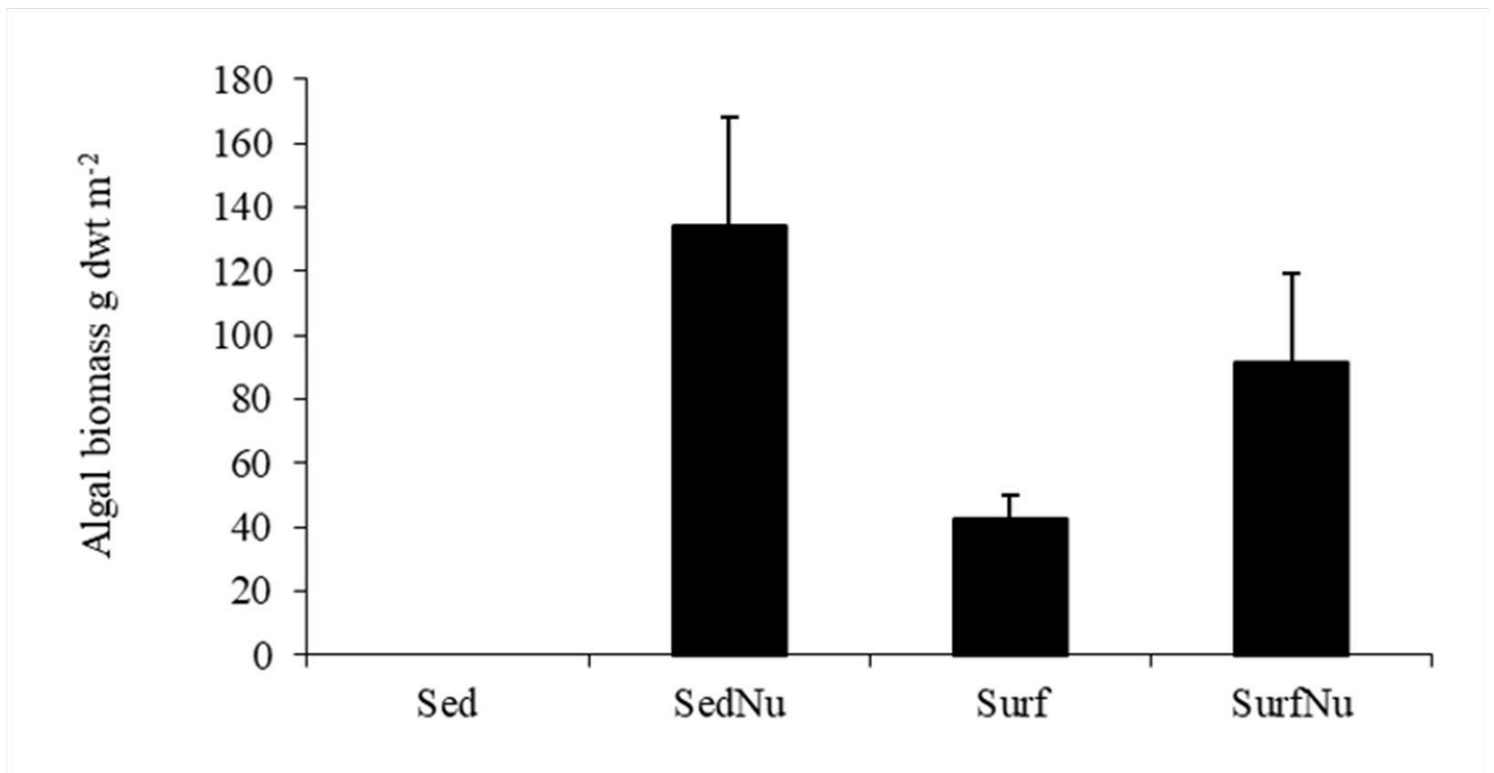


Figure 2

Biomass of green algae on Day 30 in the four treatments. Sed (10-cm intact sediment); SedNu (10-cm intact sediment exposed to continuous nutrient addition); Surf (5-mm of surface sediment, no macrofauna) and SurfNu (5-mm of surface sediment, no macrofauna, with nutrient addition). $n = 5 + \text{SE}$.

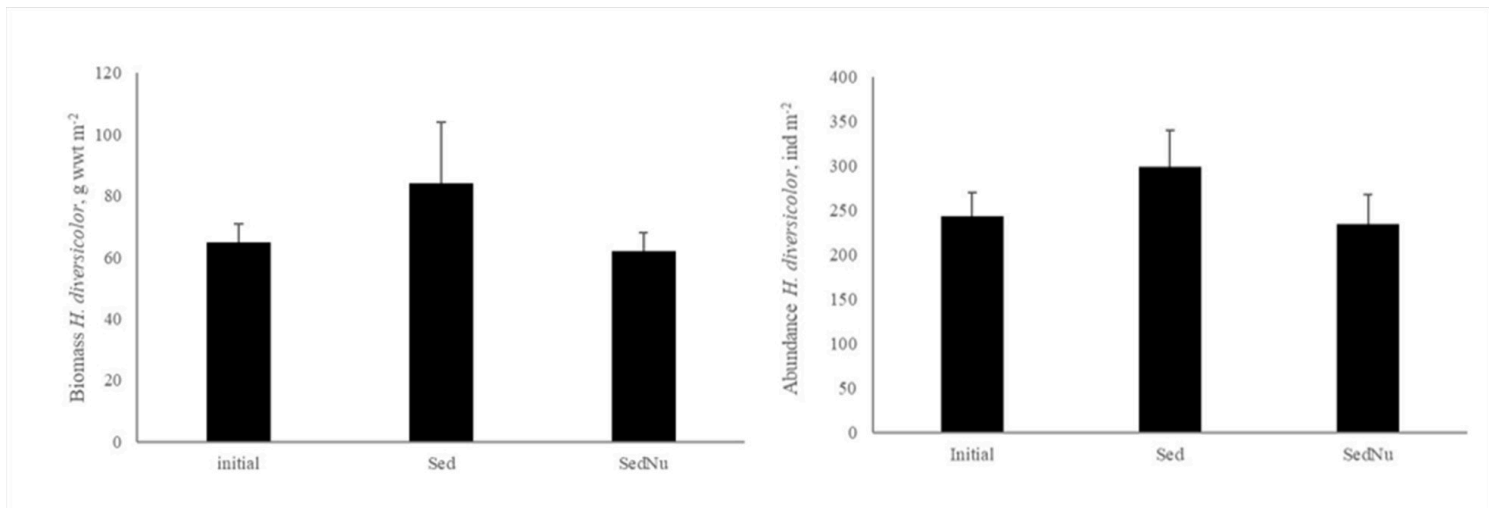


Figure 3

Abundance and biomass of live *Hediste diversicolor* initial and at the end of the experiment. Sed (10-cm intact sediment); SedNu (10-cm intact sediment exposed to continuous nutrient additions during the experiment). $n = 5 + \text{SE}$.

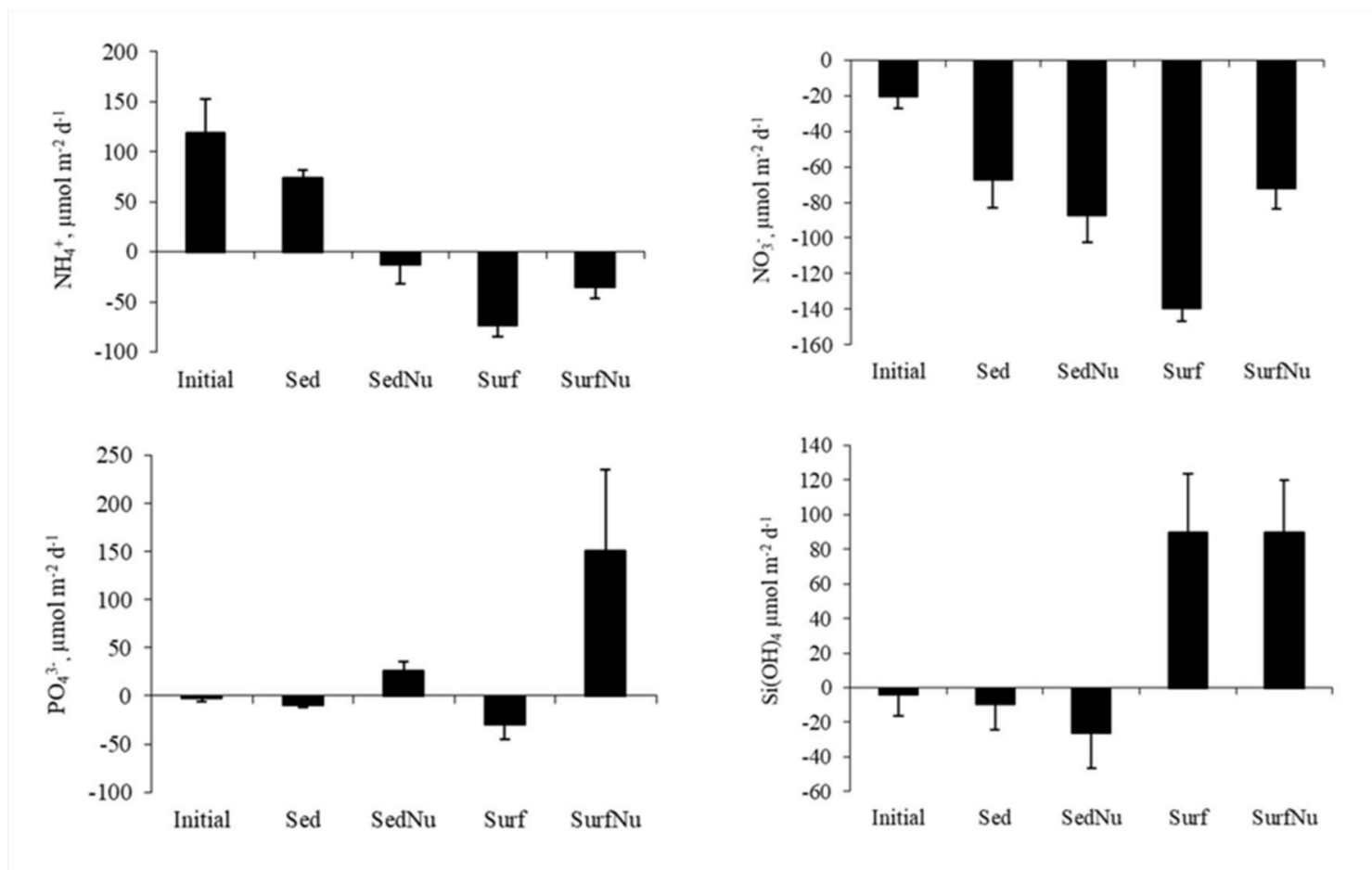


Figure 4

Daily (24-h) fluxes of ammonium (NH_4^+), Nitrate (NO_3^-), phosphorus (PO_4^{3-}) and silica Si(OH)_4 on Day 1 (Initial) and at the end of the experiment in the four treatments Sed (10-cm intact sediment); SedNu (10-cm intact sediment exposed to continuous nutrient addition); Surf (5-mm of surface sediment, no macrofauna) and SurfNu (5-mm of surface sediment, no macrofauna, with nutrient addition). $n = 5 + \text{SE}$.

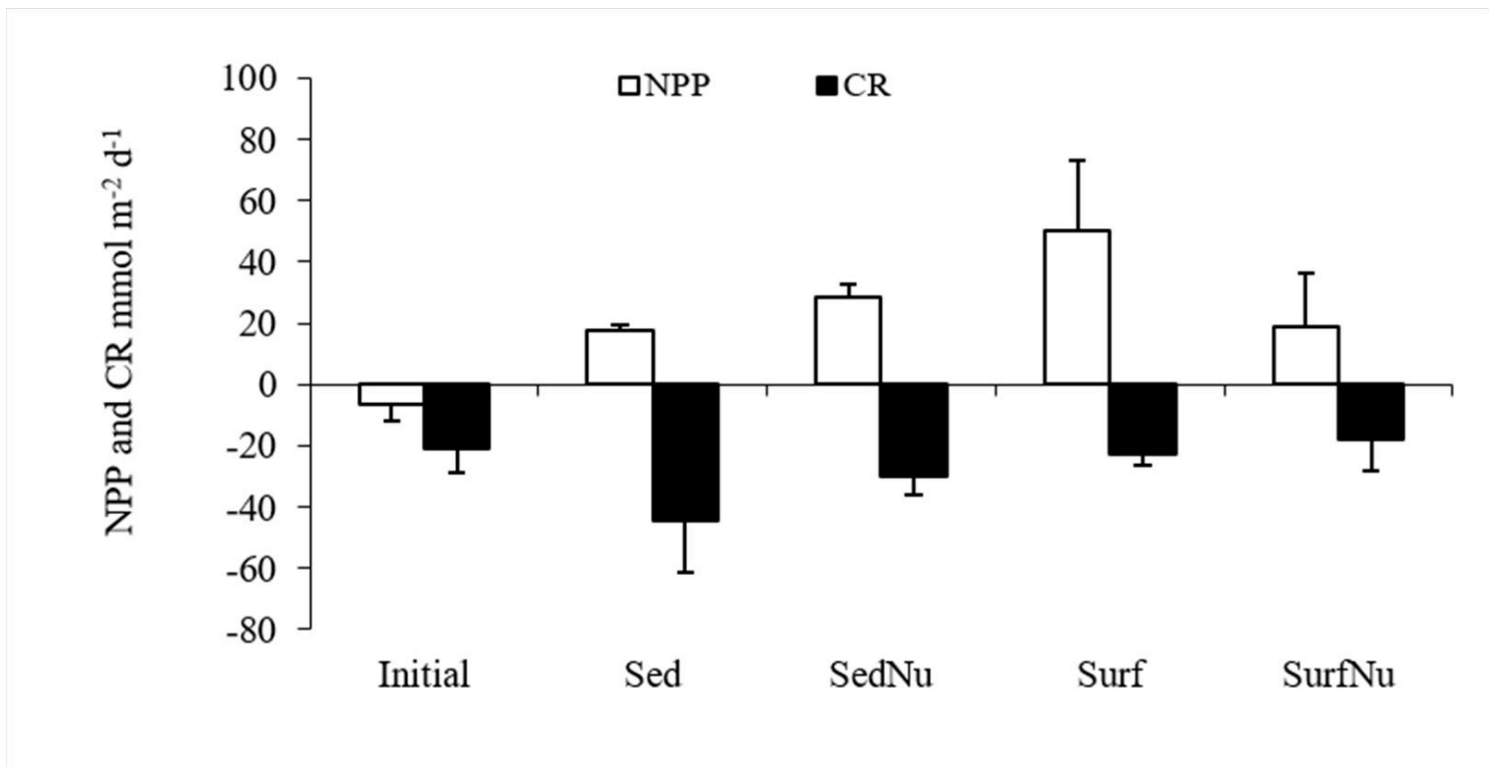


Figure 5

Daily net primary production (NPP) and community respiration (CR) on Day 1 (Initial) and in the four treatments; Sed (10-cm intact sediment); SedNu (10-cm intact sediment exposed to continuous nutrient addition); Surf (5-mm of surface sediment, no macrofauna) and SurfNu (5-mm of surface sediment, no macrofauna, with nutrient addition). $n = 5 + SE$.

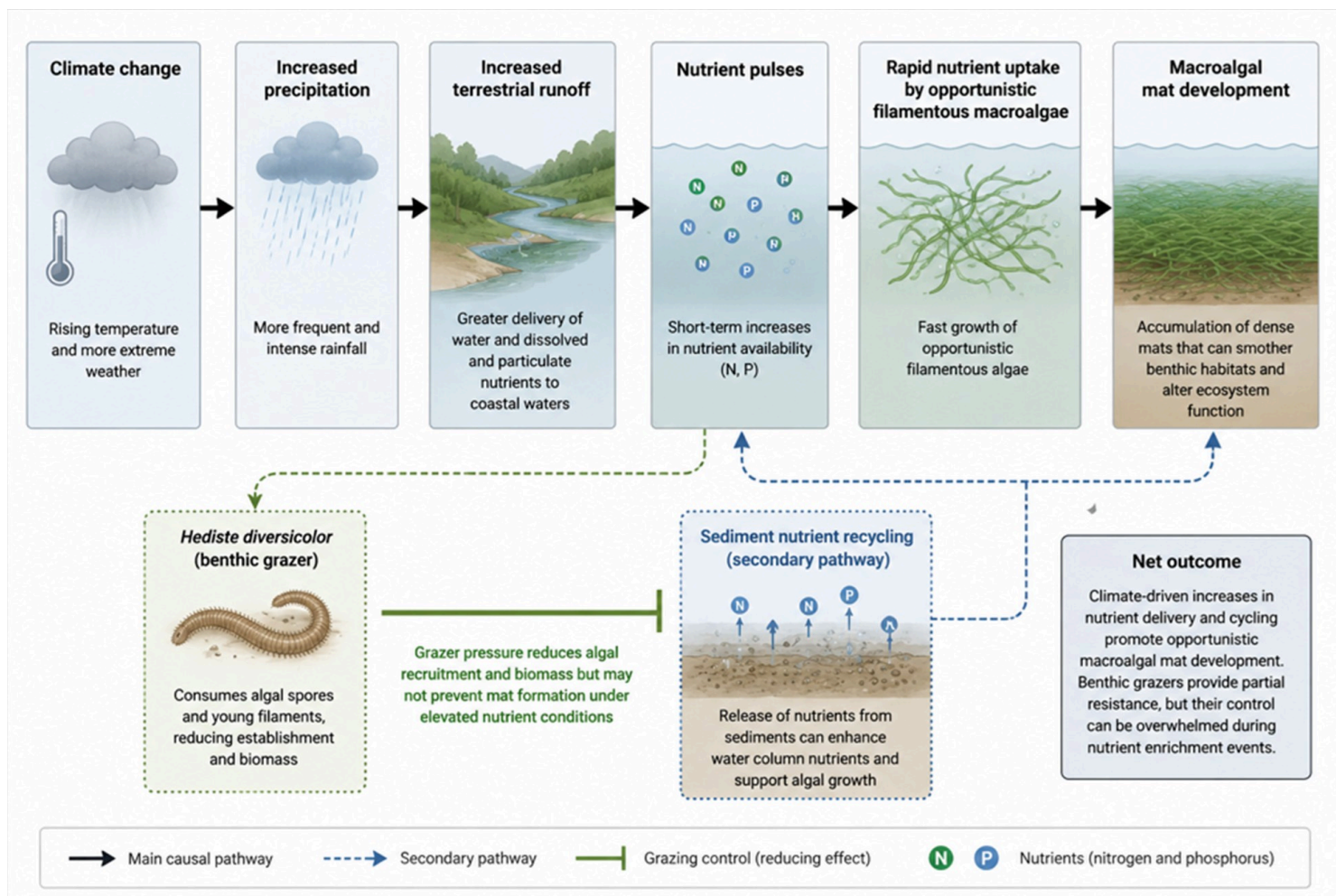


Figure 6

Conceptual model showing how climate-driven increases in runoff and nutrient delivery may promote filamentous macroalgal mat development. Opportunistic macroalgae rapidly exploit nutrient pulses, while benthic grazers may only partially constrain mat formation. Sediment nutrient recycling may further support algal growth.