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Primary Research Paper

Positive and negative effects of riverine input on the estuarine green alga *Ulva intestinalis* (syn. *Enteromorpha intestinalis*) (Linneaus)

K.M. McAvoy & J.L. Klug*
Biology Department, Fairfield University, 1073 N. Benson Rd., Fairfield, Connecticut 06824,
*(*Author for correspondence: e-mail: jklug@mail.fairfield.edu)*

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Abstract

Freshwater inputs from rivers alter salinity of estuaries, and are also important conduits for the delivery of nutrients such as nitrogen and phosphorus. We studied the impact of freshwater inputs on primary producers in the lower Housatonic River estuary in Long Island Sound, U.S.A. We conducted a laboratory experiment with *Ulva intestinalis* (syn. *Enteromorpha intestinalis*) (Linnaeus), a common green macroalgae that can have a high biomass in eutrophic systems. *U. intestinalis* was collected from three sites around the estuary that varied in salinity and nutrient concentration. Algae from three sites were grown in four treatments containing different proportions of Housatonic River water to mimic the gradient in riverine influence in the estuary. As the percentage of Housatonic River water increased, nitrogen and phosphorus concentration increased and salinity decreased. Growth of *U. intestinalis* collected from lower salinity sites was higher in treatments containing Housatonic River water than in those containing only Long Island Sound water. Conversely, *U. intestinalis* collected from Long Island Sound grew best in the treatment with no river water. Previous studies showed that *U. intestinalis* growth is stimulated by high nutrient concentration and depressed by low salinity; however, the reduction in growth at low salinity may be mitigated by increased nutrients. Our results support these studies and suggest that for populations of *U. intestinalis* that have experienced reduced salinity in their environment, the negative impacts of reduced salinity may be outweighed by the positive impacts of the high nutrient concentration in Housatonic River water.

Introduction

Estuaries are highly impacted by the quality and quantity of their freshwater input (Hopkinson & Vallino, 1995). Freshwater inputs from rivers reduce salinity and are often significant sources of nitrogen, phosphorus, and sediment (Martins et al., 2001). Freshwater input may be variable across season and year and may affect the abundance and distribution of estuarine species. For example, Martins et al. (2001) showed that biomass of macroalgae in the Mondego Estuary in Portugal is regulated by the amount of freshwater and nutrients released from upstream rice fields. Dunton et al. (2001) found significant changes in saltmarsh vegetation following an extremely wet spring. Because changes in freshwater input affect multiple environmental factors (e.g, salinity and nutrients) it may be difficult to predict how a particular estuarine species will respond.

The distribution and abundance of *Ulva intestinalis* (syn. *Enteromorpha intestinalis*), a common estuarine green macroalga (Poole & Raven, 1997), may be affected by the variability in salinity and nutrient concentration caused by changes in freshwater input. Laboratory and field studies list

the optimal salinity for growth of *Enteromorpha* spp. at 18–22‰ (Martins et al., 1999; *E.* spp.), 24‰ (Kim & Lee, 1996; *E. intestinalis*), and 27.2‰ (Taylor et al., 2001; *E. linza*), but other field studies have shown that *Enteromorpha* is present at sites with salinities lower than optimal (Innes, 1987; this study). Experimentally, Kamer & Fong (2001) showed that although *Enteromorpha intestinalis* can tolerate very low salinities (0‰) for 24 h, it does not grow under those conditions. In general, *U. intestinalis* responds to increased nutrient levels with increased growth rates. (Fujita, 1985; Fong et al., 1993; Fong et al., 1996; Kamer & Fong, 2001), and increased nutrient levels also decrease the negative effects of reduced salinity (Kamer & Fong, 2001). Thus, *U. intestinalis* may be able to survive and grow in the lower salinity of high freshwater input areas if the freshwater input has a high nutrient concentration.

We studied the impact of increased freshwater input on the growth of *Ulva intestinalis* in the lower Housatonic River estuary, U.S.A. Specifically, we were interested in whether the positive effects of increased nutrient concentration outweighed the negative effects of reduced salinity. Because salinity and nutrient concentration are variable throughout the estuary, and prior environmental conditions can influence response to these factors (Reed & Russell, 1979; Fujita, 1985), we chose three sites along a gradient of freshwater influence. Our objective was to identify whether *U. intestinalis* collected from areas of different freshwater influence responded differently to changes in river input. We expected that *U. intestinalis* from all sites would benefit from the increased nutrients in the high river input treatments but that *U. intestinalis* from high salinity areas would be more negatively affected by the reduced salinity in high river input treatments than *U. intestinalis* from lower salinity areas.

The taxonomy of the species we used has recently been revised. Linneaus originally placed *Enteromorpha* and *Ulva* in the same genus but they were split in the early 1800's. There is new molecular evidence that they are indeed the same genus and we will use the new nomenclature (Hayden et al., 2003). Therefore, when we refer to *Ulva intestinalis* we mean the species that has been recently known as *Enteromorpha intestinalis*. We have not changed the name when referring to previous studies.

Materials and methods

Study sites

The Housatonic River starts in western Massachusetts and drains through western Connecticut into Long Island Sound. The Housatonic River is the second largest source of freshwater and a major source of nutrients to Long Island Sound (NYSDEC and CTDEP, 2000). The last 20 km of the river downstream of the dam at Derby, CT is tidal. The lower river flows through a relatively urban area and water quality is influenced by industrial and sewage treatment plant discharges, navigational dredging, and sand and gravel mining. Nutrient concentrations throughout the estuary are high and late-summer phytoplankton blooms are common in the freshwater tidal reaches (J.L. Klug, personal observation).

We sampled *U. intestinalis* from three sites in or near the Housatonic River estuary (Fig. 1). The Long Island Sound site (LIS) is a sandy beach approximately 2 km east of the mouth of the river. Algae were collected from a shallow sub-tidal pool on the eastern side of a sand bar that isolates the area from direct flow from the Housatonic River. The second site (hereafter referred to as the Mouth site) was located on the western bank near the mouth of the Housatonic River. Algae were collected from large sub-tidal rocks. This site was more protected from wave action than the LIS site; however, the algae at this site are subject to strong current. The third site (hereafter referred to as the Upriver site) was located on the eastern bank approximately 4 km upstream from the Mouth site. There is strong riverine influence at this site, which causes the greatest variation in salinity between high and low tide. Algae were collected from a sub-tidal area with gravel substrate. Table 1 shows differences in salinity between the three sites. We identified the alga as *U. intestinalis* rather than another similar species common in Long Island Sound, *Enteromorpha linza* (Innes, 1987), because the tube was not united at any portion of the frond (Poole & Raven, 1997).

Experimental design

To explore the influence of riverine inputs on *U. intestinalis* growth, we collected algae from

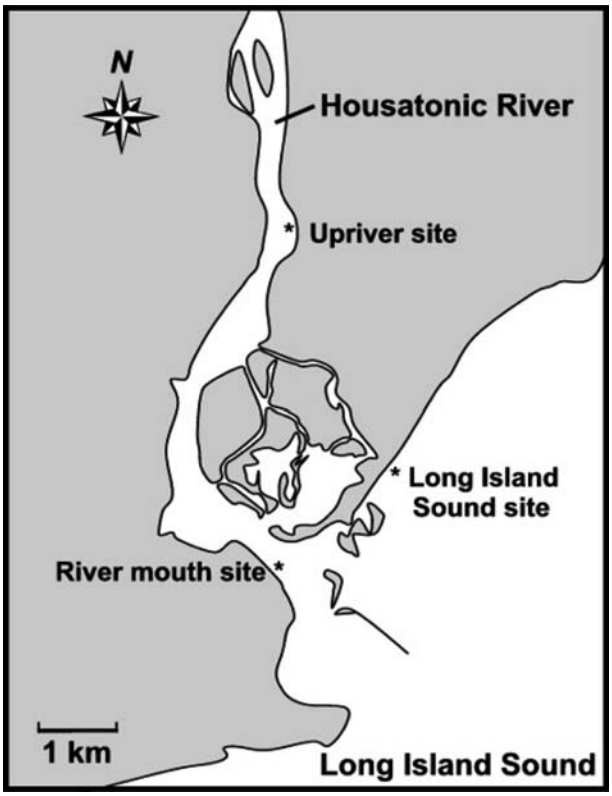

Figure 1. Map of the lower Housatonic River estuary and surrounding area.

three sites and grew it in water simulating different levels of riverine input. We conducted a factorial experiment under laboratory conditions that closely resembled early summer conditions experienced by *U. intestinalis* in the Housatonic River estuary. We grew algae from the 3 sites described above in four ratios of Housatonic River water to LIS water: 0% Housatonic: 100% LIS (denoted no river input), 15% Housatonic: 85% LIS (denoted low river input), 30% Housatonic: 70% LIS (denoted medium river input), and 45% Housatonic: 55% LIS (denoted high river input). We used water collected from the Upriver site at low tide for the Housatonic River water. Long Island Sound water was collected from the LIS site. Each site and water combination had 5 replicates for a total of 60 experimental units.

Table 1. Tissue nitrogen (%) for *Ulva intestinalis* collected from the three sites on July 2, 2002 and salinity at the three sites during summer 2002

Site	Initial tissue N (%)	Salinity at high tide (‰)	Salinity at low tide (‰)
Upriver	3.75 (0.23)	18.9 (2.95)	4.5 (1.16)
		range = 9.0–26.5	range = 0.6–10.3
Mouth	2.97 (0.08)	25.9 (0.57)	11.7 (1.50)
		range = 23.0–27.4	range = 5.1–17.9
LIS	0.78 (0.12)	27.2 (0.07)	26.6 (0.35)
		range = 27.0–27.5	range = 24.1–27.7

Data shown are means and standard errors for initial tissue N ($n = 4$) and means, standard error, and range for salinity ($n = 8$ for high tide, $n = 10$ for low tide).

Experimental methods and analysis

The experiment ran from July 2, 2002 to July 30, 2002. On July 2, 2002, we collected *U. intestinalis* consecutively from all three sites at low tide. At the same time, water was collected from the Upriver and LIS sites in 20 L polyethylene containers. Water for each riverine input treatment was mixed in the appropriate Housatonic River to LIS ratio in 20 L batches. Sixty clear 500 ml polyethylene containers were filled with 450 ml of one of the riverine input treatments. In the lab, algae were rinsed with LIS water to remove epifauna and excess water was removed by spinning in a hand centrifuge for ninety seconds (Fong et al., 1998). The algae from each site were divided into 2 g samples (± 0.08 g) and placed in the labeled filled containers. The containers were then placed in a randomly assigned location in a refrigerated recirculating water bath. The containers were maintained at 20.2 °C (± 2.05 °C) underneath fluorescent grow lights with an average photosynthetically active irradiance (PAR) of 152 μmol photons m^{-2} s^{-1} at the water surface. The water level in the cups was maintained at the initial marker point by adding distilled water every other day to replace that lost through evaporation.

The water in each container was replaced each week with water collected within the previous 24 h from the Upriver and LIS sites and mixed on the day of the water change. Algae were weighed each week at the time of water change and at the culmination of the experiment by pouring the contents of the cup into an individual nylon mesh bag. Before weighing, the algae in the bag were spun down for ninety seconds in a hand centrifuge to remove excess water. We removed algae from the mesh bag directly to a weigh boat, recorded mass, and then placed the algae immediately into its newly filled container and replaced it in the assigned location in the water bath. The algae were handled as little as possible and kept out of the container for as little time as possible to minimize stress and maintain uniformity. A subset of the *U. intestinalis* collected on July 2, 2002 was rinsed and dried at 50 °C for 18 h. Samples were ground and analyzed for nitrogen concentration using a Perkin–Elmer 2400 series II CHNS/O analyzer.

Whole and filtered (Whatman GF/F) water samples from the Upriver and LIS sites were frozen in 125 ml polyethylene bottles at the start of the experiment and at each water change. These samples were analyzed at the University of Connecticut's Environmental Research Institute for total nitrogen, total phosphorus, nitrate, phosphate, and ammonia. Salinity was measured using a YSI model 85 handheld salinity meter. Table 2 gives average nutrient concentrations and salinity for each water treatment.

Statistical Analysis

We used repeated measures ANOVA to assess the main effects of site, river input, and time as well as interactions between these factors. When a significant main effect or interaction was detected at $\alpha = 0.05$, we used pairwise contrasts (CONSTRAST statement within the GLM procedure in SAS) to evaluate differences within and among treatments.

Table 2. Salinity and nutrient concentrations in Long Island Sound (LIS), Housatonic River (HR), and the low, medium and high river input treatments

	LIS (No input)	Low input	Medium input	High input	HR
Salinity (‰)	27.2 (0.06)	24.2 (0.20)	21.1 (0.38)	17.8 (0.51)	5.5 (0.91)
TN (μM)	28.4 (2.14)	36.2 (1.43)	43.0 (1.43)	49.7 (1.43)	74.25 (2.86)
TP (μM)	3.04 (0.097)	3.68 (0.129)	4.33 (0.226)	4.97 (0.355)	7.36 (0.807)
Nitrate (μM)	0.357 (0.143)	3.36 (0.214)	6.43 (0.286)	9.42 (0.357)	20.56 (0.714)
Ammonia (μM)	0.036 (0.036)	0.428 (0.143)	0.785 (0.286)	1.14 (0.500)	2.57 (1.07)
Phosphate (μM)	1.26 (0.032)	1.39 (0.065)	1.52 (0.161)	1.65 (0.258)	2.16 (0.581)
TN: TP (by atoms)	9.62 (0.37)	9.80 (0.36)	9.94 (0.42)	10.07 (0.50)	10.37 (0.71)

Data shown are means and standard errors of the 4 weeks of the experiment. TN denotes total nitrogen concentration and TP denotes total phosphorus concentration.

Results

The nutrient levels in Long Island Sound and the Housatonic River were fairly static, and consistently different from each other, for the duration of the experiment (Table 2). Water collected from the river had higher concentrations of nitrogen and phosphorus than water collected from Long Island Sound. Total nitrogen and total phosphorus concentrations in the Housatonic River were about 2.5 times greater than concentrations in LIS. However, the difference in inorganic nitrogen concentration was much larger (58 times greater in Housatonic River water than in LIS) than the difference in inorganic phosphorus concentration (1.7 times greater in Housatonic River water) leading to a much greater range of variability in inorganic nitrogen concentration than in inorganic phosphorus concentration across river input treatments (Table 2). The average salinity of the treatments was 27.2, 24.2, 21.2, and 17.8‰ for the no, low, medium, and high river input treatments (Table 2). TN:TP ratio did not greatly vary among treatments. Initial tissue nitrogen was highest in the Upriver site and lowest at the LIS site (Table 1).

There was a large difference in growth rates between *U. intestinalis* collected in the estuary sites relative to the Long Island Sound site. Average growth rate across treatments was 4.56, 4.65, and −0.08% d^{-1} in the algae collected at the Upriver, Mouth, and Long Island Sound sites respectively. Consequently, *U. intestinalis* biomass varied across sites and the effect of river input depended on site (Fig. 2, Table 3). Averaged across time, biomass was higher in algae collected at the Mouth and Upriver sites than in algae from LIS. In addition, algae collected at different sites responded differently to the river input treatments. At all sites, treatments that received some river input behaved

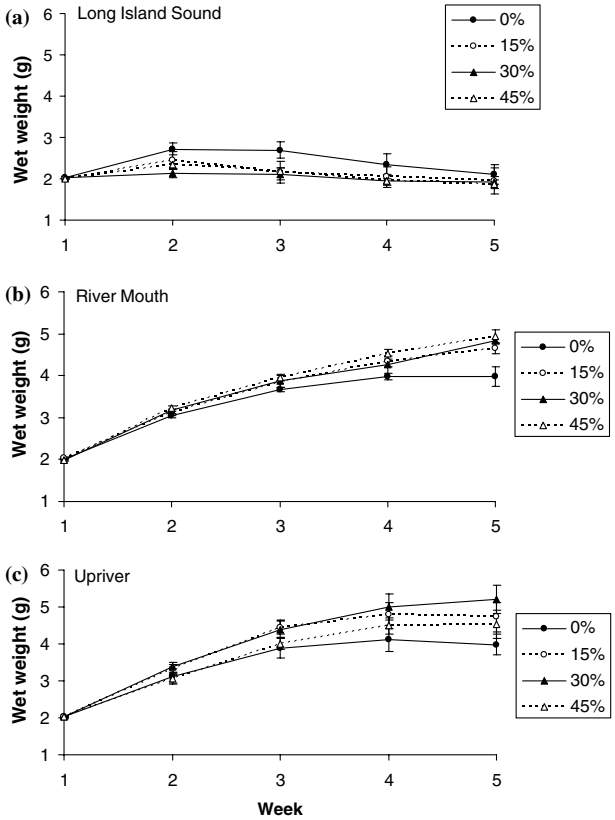

Figure 2. Biomass of *Ulva intestinalis* in treatments with different river water input for algae collected from the (a) Long Island Sound, (b) River Mouth, and (c) Upriver sites across the 4 weeks of the experiment. Symbols represent the mean of 5 replicates and the bars represent standard error of the mean.

Table 3. Results from repeated measures ANOVA on *Ulva intestinalis* biomass. Treatments that are underlined are not significantly different from one another

Source	DF	F	*p*	Contrasts
River input	3	0.81	0.50	
Site	2	138.44	< 0.0001	LIS < Mouth Upriver
River input × Site	6	2.29	0.05	no > low med high at LIS
				no < low med high at Mouth Upriver
Time	4	437.25	< 0.0001	
Time × River input	12	3.18	0.012	no low med high
Time × Site	8	119.83	< 0.0001	LIS Mouth Upriver
Time × River input × Site	24	0.069	0.123	

similarly and were different from the treatment that received no river input. Algae collected at LIS had higher biomass in the no river input treatment than in treatments with river input. In contrast, algae collected at the Mouth and Upriver sites had higher biomass in the treatments with river input than in the no river input treatment (Table 3).

At all sites, growth was higher in the early part of the experiment than in the later weeks (Fig. 2). Biomass of algae collected from the three sites showed different trajectories through time as evidenced by the significant time × site interaction (Table 3). Averaged across all treatments, there was a strong increase in biomass in algae collected from the Mouth and Upriver sites and slight or no growth of the algae collected from LIS. Biomass of algae collected from Upriver leveled off at the end of the experiment whereas biomass of algae collected at the Mouth continued to increase (except in the no river input treatment).

Discussion

Our objective was to test how *U. intestinalis* collected from sites along a nutrient and salinity gradient would respond to changes in Housatonic River input. The Housatonic River has a large influence on the abiotic conditions in the study area and can influence growth of *U. intestinalis* by altering both nutrient concentration and salinity. Previous studies that have varied nutrients and salinity independently have conclusively shown that decreasing salinity from the optimum range decreases growth (Martins et al., 1999; Kamer & Fong, 2001) and that increasing nutrients from a minimum requirement increases growth (Fong et al., 1993; Fong et al., 1996; Kamer & Fong, 2001). In addition to the predictable effects of nutrients and salinity on *U. intestinalis*, different populations may respond to changes in nutrient concentration and salinity in unexpected ways because of genetic differences in sensitivity or because physiological acclimation to particular nutrient and salinity conditions determines the subsequent response to changes in those conditions.

U. intestinalis collected from each site had been growing under different environmental conditions at the time of collection. The LIS site had higher salinity and lower nutrient concentration than the Mouth and Upriver sites. In the experiment, algae from each site grew best in treatments that approximated the conditions of the habitat from which they were collected. *U. intestinalis* from the Mouth and Upriver sites grew better in the high nutrient, lower salinity water than in the low nutrient, high salinity water. It appears that for Mouth and Upriver algae, the reduced salinity in the river input treatments was not enough to prevent increased growth due to the higher nutrient concentration. Salinity in our highest river input treatment averaged 17.8‰, which is not much lower than the optimal range given for *Enteromorpha* spp. by Martins et al. (1999) and is well within the range of salinity measured at these sites (Table 1). In contrast, *U. intestinalis* collected from the LIS site rarely experience salinity below 26‰. Thus, differences in salinity between river input treatments are more likely to be important for algae collected from LIS than algae collected from the Mouth or Upriver. *U. intestinalis* from LIS had lower growth in the river input treatments than in the no river input treatment. These algae

may not have been able to use the elevated nutrients in the river input treatments because of the lower salinity. Despite optimal salinity, growth of LIS *U. intestinalis* in the no river input treatment was minimal, presumably due to the low concentrations of inorganic nitrogen.

Nutrient history appears to have played a role in determining the tissue nitrogen concentration of our field collected samples. *U. intestinalis* from the low nutrient LIS site had lower tissue N concentrations than *U. intestinalis* from the higher nutrient Mouth and Upriver sites. These results are similar to previous studies (Fujita, 1985; Fong et al., 1994; Barr & Rees, 2003) that showed that tissue nitrogen concentration in *Enteromorpha* is a function of nutrient history and are interesting because tissue nitrogen concentration and nutrient history may affect uptake rates of nutrients. Fujita (1985) measured ammonium uptake rates of *Enteromorpha* spp. grown under different nitrogen concentrations. Uptake rates were highest in *Enteromorpha* which had been starved of nitrogen for 10 days and lowest in the algae which had been cultured under high nitrogen concentration. *Enteromorpha* cultured under low nitrogen concentration had intermediate uptake rates. Similarly, Barr & Rees (2003) found that N-specific and chlorophyll-specific rates of ammonium uptake were negatively correlated with tissue nitrogen concentration. Based on these studies, *U. intestinalis* collected from LIS should have had high uptake rates of the ammonium (and potentially other N sources) in the river input treatments. The lack of growth in these treatments suggests that the lower salinity may have affected their ability to use the increased nutrients for growth.

Past salinity history has also been shown to affect how *U. intestinalis* responds to changes in salinity. Reed & Russell (1979) found that *E. intestinalis* from estuarine habitats had a wider range of salinity tolerance than individuals from high salinity habitats. The offspring of these individuals had similar patterns of salinity tolerance which suggests that salinity tolerance has a genetic basis. Innes (1987) showed genetic differences in tolerance to low salinity in two clones of *Enteromorpha linza* collected from adjacent high (19–30‰) and low salinity (0–11‰) sites in Long Island Sound. Both clones had higher growth rates at salinity = 28‰ than at salinity = 4‰ but the clone associated with the high salinity sites had a much greater reduction in growth at low salinity than the clone associated with the low salinity sites. These results are consistent with our interpretation that *U. intestinalis* from the LIS site were negatively affected by the reduced salinity in the low, medium, and high river input treatments but algae from the Mouth and Upriver sites were not.

Despite differences in nutrient concentration and salinity among no, low, medium, and high river input treatments, we only saw significant differences in biomass between the presence and absence of Housatonic River water. This may be related to the relative magnitude of differences in nutrients vs. differences in salinity. Salinity decreased by ~3‰ at each level of river input. In contrast, nitrate and ammonium increased by ~10 fold from the no to low river input treatments and only by ~2 fold from the low to medium to high river input treatments. The significant differences in growth rate for the Mouth and Upriver sites correspond to the large difference in nutrient concentration between no and low river water input and not to the steady change in salinity, further suggesting that nutrient differences were more important than salinity for the Mouth and Upriver sites and that high nutrient concentrations in the river input treatments mediated the potential negative effects of reduced salinity (Kamer & Fong, 2001).

We showed that algae from different sites respond differently to changes in riverine input. The magnitude of response to changes in riverine input depends on the relative effects of changes in nutrient concentration and changes in salinity. The salinity and nutrient concentration of river water vary across years and there may be interannual variability in the effect of river water on *U. intestinalis* growth. For example, 2002 was a very dry year in the Housatonic River watershed and freshwater input to the estuary was low relative to 2003. During 2002, TP and TN concentrations in Housatonic River water were higher than in 2003 but nitrate and ammonium concentrations were lower (J. Klug, unpublished data). Salinity at different sites in the estuary is also affected by flow. For example, the average salinity at low tide at the Mouth site in 2002 (the dry year) was 11.7‰ (n = 10), range = 5.1–17.9‰, whereas average salinity at the same site in

2003 was 7‰ (n = 5), range = 0.5–12.7‰. Thus, the impact of riverine input on estuarine macroalgae will depend not only on differences in population response to nutrients and salinity but on difference in composition of river water among years.

Conclusion

Riverine inputs to estuaries have a significant impact on the organisms that live there. In many systems, including the Housatonic River estuary, human activities in the watershed play a large role in determining how river input affects salinity and nutrient concentration within the estuary. For example, mandated reductions in nitrogen loading (NYSDEC & CTDEP, 2000) to the Housatonic River will decrease the nitrogen concentration of the river input to the estuary over the next 10 years. Thus, the high nutrient, low salinity river water which currently has a positive impact on populations of *U. intestinalis* within the estuary may eventually have a neutral or negative impact as nitrogen concentration decreases. This may reduce the area of the estuary in which *U. intestinalis* can persist. A better understanding of the relative importance of acclimation to particular environmental conditions vs. genetic differences in tolerance between populations may help predict the impact of future changes in riverine input on the growth and distribution of estuarine macroalgae.

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