Effect of nutrient enrichment on turf algae productivity

Eila Chin[1], Eliza Heery[1,2]

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[1] Friday Harbor Laboratories, University of Washington, Friday Harbor, WA 98250
[2] MarineGEO Program and Smithsonian Environmental Research Center, Edgewater, MD 21037

Contact Information
Eila Chin
Biology Department
Whitman College
Walla Walla, WA 99362
eilajchin@gmail.com

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ABSTRACT

Filamentous turf algae have become a dominant group in coastal marine ecosystems as coastal urbanization increases nutrient levels. These algae are multispecies assemblages composed of small macrophytes that are invariably coupled with a suite of epifaunal and microbial consumers. While photosynthetic productivity is generally assumed to be greater than turf assemblage respiration, turf assemblages may shift from being carbon sinks to carbon sources in urbanized, nutrient rich conditions. In San Juan Island, Washington, we examined the effect of nutrient enrichment and epifauna exclusion on turf assemblage productivity with a fully factorial design of nutrient enrichment and epifaunal exclusion treatments. Results suggested that fertilizer treatments increased the nitrogen content of turf assemblages. In turn, high nitrogen conditions coincided with lower overall productivity, but only when meiofauna were present. This suggested that meiofauna were partly responsible for decreasing productivity in nutrient rich turfs. Epifauna exclusions lowered respiration rates slightly and did not have a significant effect on productivity. The exclusions were performed with Carbaryl, an insecticide that targets arthropods, but Carbaryl treatments did not appear to influence densities of macrofauna. Thus, reduced respiration rates from Carbaryl were likely due to meiofaunal or microbial response. While our results from this experiment suggest that carbon absorption may be negatively affected in urban areas due to the expansion of turf algae, future studies repeating this approach are needed and should be performed at low flow-sites.

INTRODUCTION

Coastal marine habitats are some of the most productive and valued ecosystems worldwide (Costanza et al. 1997). However, coastal urban development has caused drastic changes to these systems. Agriculture and urbanization, for example, have altered marine biogeochemical cycles by significantly increasing nutrient loads and sediment deposition rates (Carpenter et al. 1998; Airoldi 2003; Firth et al. 2016). Additionally, artificial structures such as seawalls have altered abiotic conditions by increasing the amount of hard substrate in coastal habitats and altering water flow patterns (Bugnot et al. 2021; Chapman & Bulleri 2003). Altogether, these changes are causing shifts in the structure and functioning of coastal marine ecosystems (Airoldi et al. 1995; Gorgula & Connell 2004).

One of the main marine functional groups increasing in dominance as coastal urbanization expands is filamentous turf algae (Airoldi et al. 1995; Eriksson et al. 2002; Gorgula & Connell 2004). Filamentous turf algae is a multispecies assemblage composed of algal primary producers, such as Chlorophyta, Rhodophyta, and Phaeophyta, as well as a diverse community of epifauna and bacteria (Connell et al. 2014). The morphology and physiology of turf algae make it extremely effective at capturing nutrient-rich sediment, and this has allowed it to thrive along urbanized coasts (Airoldi 2003; Kendrick 1991; Vermeij et al. 2010).

The shift towards a turf-dominated system has significant implications for the biogeochemical cycles of coastal marine ecosystems and their ability to capture and store carbon (Costanza et al. 1997). Studies have shown that turf algae are replacing kelp and coral, both of which are highly productive ecosystems important in mediating marine carbon cycles (Costa et al. 2000; Dexter & Wernberg 2018). Kelp, for instance, has been shown to export up to 43% of its biomass to the deep ocean, where carbon is a limited resource (Krause-Jensen & Duarte 2016). Both kelp and coral are important mediators in the carbon cycle, and this brings into question how productivity and carbon sequestration of coastal marine ecosystems will change as they become more turf dominated.

Turf algae, particularly those located in non-urban, high flow environments, tend to be highly productive (Miller et al. 2009). Photosynthetic productivity per unit biomass is so high that despite epifaunal and bacterial respiration, turf assemblages are thought to be net autotrophs. However, turf algae assemblages may actually be net heterotrophic in urban environments. Firstly, increased nutrient concentrations in urban estuaries are likely to increase the abundance and respiration of bacteria (Smith & Kemp 2003). Turf algae are extremely effective at capturing sediments (Airoldi 1998), which means that in urban environments they are covered with nutrient rich organic matter. Thus, the increased nutrient inputs of urbanized coastlines may increase bacterial respiration enough to make turf algae assemblages net heterotrophic. Secondly, the low flow conditions and high rates of detrital deposition that are characteristics of urban marine environments may increase the abundances of small, epifaunal and meiofaunal arthropods (Gibbons 1988). Increases in faunal respiration may also therefore reduce net community production of turf algae assemblages in urban areas. Furthermore, other macrophyte systems have been shown to become net heterotrophs in nutrient enriched conditions (Egea et al. 2020; Gallagher 2022). Seaweed ecosystems were found to become net heterotrophic on a local scale when exposed to organic subsidies (Gallagher 2022). Additionally, a study in southern Spain found that the seagrass *Cymodocea nodosa* shifted from being net autotrophic to being net heterotrophic after nutrients were added (Egea et al. 2020). No study to date, however, has assessed whether turf algae shift to net heterotrophic systems under nutrient rich conditions.

This study examined how nutrient loading affects the trophic state of turf algae assemblages by comparing net community productivity of turf assemblages in nutrient enriched conditions vs ambient nutrient conditions. Both fertilizer treatments (nutrient addition vs nutrient control) as a categorical variable and nitrogen content as a continuous variable were used to assess how nutrient loading affects turf assemblage net community productivity. To provide greater insight into the factors affecting turf algae productivity, we also measured the effect of epifauna on net community productivity. As kelp and seagrass systems have been shown to become net heterotrophic in nutrient enriched conditions (Egea et al. 2020; Gallagher 2022), we predicted that turf algae in nutrient enriched conditions would have lower net community productivity.

METHODS

Study Site and Organisms

Our experiment was conducted on the floating docks at Friday Harbor Laboratories, located on San Juan Island, Washington, throughout the month of July 2022. Floating docks were convenient for our experiment because they provided easy surface access to subtidal algae, regardless of the tide. The docks also had an established community of filamentous rhodophytes, most of which belonged to the polysiphonous genera, Sy*mphiocladia* and *Polyostea*. The docks ran east to west, and all sites were south facing.

Experimental Design

This experiment used a two-way factorial design to test the effects of nutrient addition and epifauna exclusion on the productivity of turf algae communities. Each factor had two levels, resulting in four treatment combinations: 1) nutrient addition and epifauna exclusion, 2) nutrient addition and epifauna control, 3) nutrient control and epifauna exclusion and 4) nutrient control and epifauna control. All treatment combinations had 5 replicates, summing to a total of 20 plots. Nutrient treatments were deployed for four weeks and Carbaryl treatments were deployed for five days. The plots were placed every 2 m along the dock and treatments were assigned using a random number generator. The response variable was net community productivity of turf algae assemblages, which we measured using photorespirometry.

Treatment 1: Nutrient Addition

We used a pelleted plant fertilizer, Osmocote Smart Release (Sierra Chemicals; 15N-9P-5K; hereafter referred to Osmocote), to increase nutrient levels (Ramseyer et al. 2021).
While higher N:P ratios are generally favored for mimicking anthropogenic nutrient loading in marine environments, 15N:9P was selected for our experiment because it was available despite fertilizer shortages and because it was within the range of N:P ratios associated with urban wastewater (Mallin & McIver 2012). For nutrient addition plots, we added 2 falcon tubes each containing 40g of Osmocote for a total of 80g Osmocote per plot. Each tube had 35 holes (<2 mm diameter) spaced at 1 cm intervals to allow the fertilizer to diffuse into the plot. For nutrient control treatments, each plot received 2 empty falcon tubes. Each tube had 4 holes (<2 mm diameter) to ensure similar physical dynamics to nutrient addition tubes.

To secure the tubes to the dock, we ziptied falcon tubes to the middle section of a 4 ft strand of cotton rope (Figure 1a). We then ziptied each end of the rope to the dock ~50 cm apart so that the middle section of the rope was submerged (Figure 1b). We attached a weight between the 2 falcon tubes to ensure that the tubes remained fully submerged. Plots received nutrient enrichment for 4 weeks throughout the month of July.

Figure 1. **a)** Falcon tubes ziptied to cotton rope, with a weight in between the falcon tubes. **b)** The falcon tubes and weight hanging from the cotton rope, secured to the dock.

Treatment 2: Epifauna Exclusion

For the epifauna exclusion treatment we used Carbaryl, an aquatic insecticide. We chose Carbaryl because it has been shown to deter epifauna without affecting the growth or biomass coverage of macroalgae (Poore et al. 2009). For epifauna exclusion treatments, we incorporated Carbaryl into plaster blocks and attached the blocks to the docks so that the Carbaryl would be released as the plaster blocks dissolved. For epifauna control treatments, we used plaster blocks with no Carbaryl.

Plaster blocks were made by mixing 70 mL of liquid Carbaryl (43%) with 3.929 L of chilled water, and then adding that to 2.0 kg of plaster of Paris (Poore et al. 2009). This yielded a 7.6% Carbaryl plaster block by dry weight. We poured the plaster mixture into 4 oz paper cups and allowed them to air dry for ~5 min. After allowing the plaster to air dry, we removed the plaster blocks from the paper cups and dried them in a 60°C oven for 3 days. We used the same methods to prepare the epifauna control plaster blocks, but added no Carbaryl. We attached the plaster blocks to each site by putting each block into a mesh bag and hanging the bag from the cotton rope (Figure 2).

Figure 2. Carbaryl plaster block in a mesh bag, next to the weight so that it remains submerged.

Data Collection

After four weeks of the nutrient treatment and five days of the Carbaryl treatment, we collected one turf sample (~3 cm diameter) from each plot. We then processed each turf sample to evaluate: (1) net community productivity, (2) turf taxa, (3) epifauna abundance, and (4) nutrient levels. When collecting turf samples, we preferentially chose polysiphonous red algae.

We measured net community productivity because it accounts for epifaunal respiration and would allow us to measure the effect of nutrient enrichment and epifauna exclusion on turf assemblages as a whole system. To measure net community productivity, we used alternating dark/light incubations to calculate rates of respiration and photosynthesis (*sensu* Tait and Schiel 2010). First, we placed each turf sample in 480 mL glass bottle and filled the rest of the bottle with filtered seawater so that no air bubbles were present. Since seawater still contains phytoplankton that photosynthesizes, we added two control bottles that had filtered seawater only. All the bottles were submerged in 16°C water for the incubation treatments. To measure respiration rates, we let the turf acclimate to dark incubation for 15 minutes, recorded initial dissolved oxygen (DO) concentrations, let the bottles respire in complete darkness for 30 minutes, and then recorded final DO concentrations at the end of the dark incubation period. We measured photosynthesis rates using the same methodology, except that we used a light incubation (100 µmol) rather than a dark incubation. Finally, we used the DO measurements and a photosynthetic quotient of 1.1 to compute net community productivity (Kirk 1994). Since different turf taxa may have different photosynthetic capacities, we also identified the primary algal taxa from each turf sample. Additionally, we used the dry weight of each sample to standardize net community productivity values.

We also measured epifauna abundances to assess whether the carbaryl was effective at deterring epifauna. We processed epifauna by sieving the turf through 0.05 mm mesh and submerging turf samples in fresh water for ~12 hrs. We then identified epifauna to the phyla level and calculated relative abundances. Counts were standardized by turf dry weights, which were measured after drying the algal material from each sieved sample for 24 hr at 60°C.

To confirm that Osmocote additions raised nutrient levels on a local level we also evaluated the relative N and P composition. After we dried the turf samples and measured dry weight, we ground the samples into a powder using a mortar and pestle and sent the resulting powder to UW's Analytical Services Center for elemental analysis (relative N and P composition).

Statistical Analysis

Rates of production and respiration, as well as the relative abundances of epifauna and algal N and P concentrations, were compared between treatments using a simple two-way

ANOVA. These analyses were performed in R using the base function lm() and model assumptions and performance were evaluated via diagnostic plots, F statistics, and adjusted R^2 values.

RESULTS

We used a two-way ANOVA to test for significant differences in net productivity from fertilizer, carbaryl, and/or the interaction between fertilizer and carbaryl. ANOVA assumes the response variable is normally distributed, and we confirmed this assumption by looking at residual plots (Figure 3) and with a Shapiro test ($P > 0.05$). ANOVA also assumes that variances are equal across our different treatment groups. We performed Levene's test for equal variances and found that variances were equal (test statistic = 1.06, $P = 0.395$).

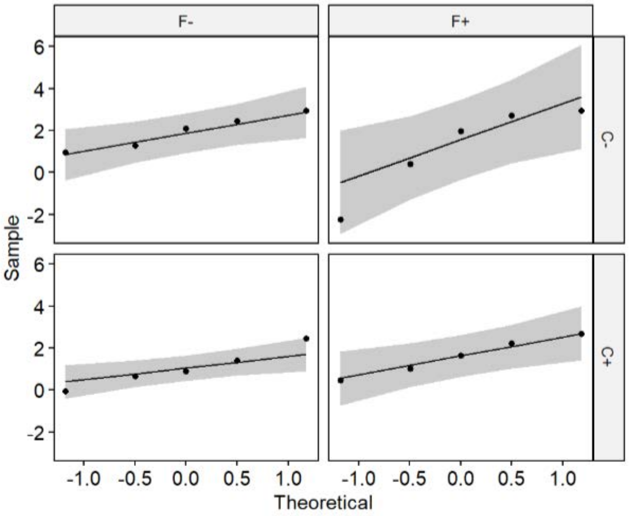

Figure 3. QR plots of model residuals for all treatment groups: fertilizer control / Carbaryl control, fertilizer addition / Carbaryl control, fertilizer control / Carbaryl addition, fertilizer addition / Carbaryl addition.

Elemental analysis of turf samples showed that fertilizer treatments had a weakly significant effect on nitrogen content (F=4.00, d.f.=1, P=0.0608), with greater nitrogen content in nutrient addition plots and lower nitrogen content in nutrient control plots (Figure 4). However, there was considerable variation in this relationship. When fertilizer treatment was included as a categorical variable in two-way ANOVA, it did not significantly affect net community productivity of turf assemblages (F=0.05, d.f.=1, P=0.8344) (Figure 5). Mean turf assemblage productivity from nutrient addition plots was 1.39 mg O 2 g -1 hr -1 ± 0.50 SE and 1.51 mg O 2 g -1 hr -1 ± 0.30 SE from nutrient control plots.

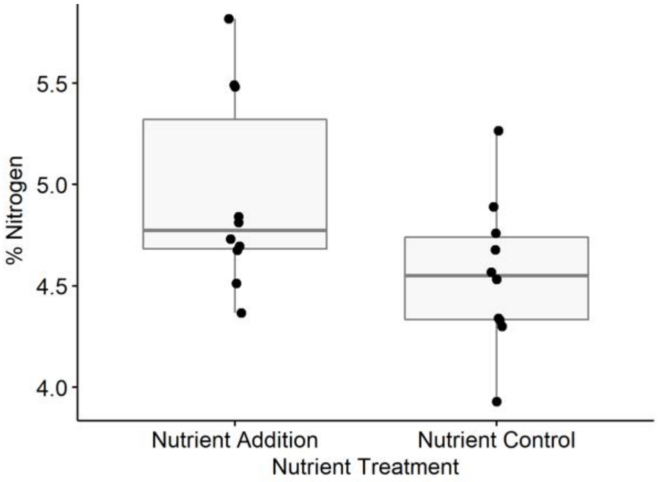

Figure 4. Turf samples that received nutrient addition for 4 weeks had slightly greater nitrogen content than turf samples that received no additional nitrogen.

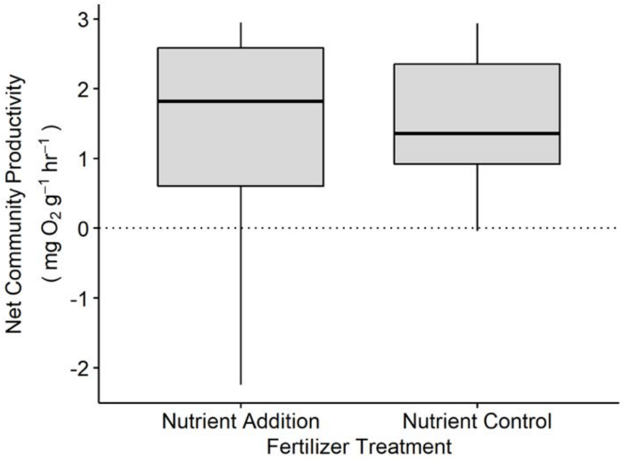

Figure 5. Fertilizer treatment as a categorical variable did not have a statistically significant effect on net community productivity of turf algae assemblages at our study site on San Juan Island, Washington.

When we used nitrogen content rather than the categorical variable for fertilizer treatment, we found a statistically significant effect on net community productivity (F=4.96, *d.f.*=1, P=0.04). Net community productivity of turf assemblages decreased as nitrogen content increased (Figure 6). Furthermore, there was a significant interaction between nitrogen content and Carbaryl; effects of nitrogen loading were primarily limited Carbaryl control plots (F=14.87, *d.f.*=1, P=0.0014). In Carbaryl addition plots, net community productivity was comparable regardless of nitrogen. Nitrogen content also had a weakly significant effect on respiration (F=4.0322, *d.f.*=1, P=0.0618), with respiration increasing as nitrogen increased (Figure 7).

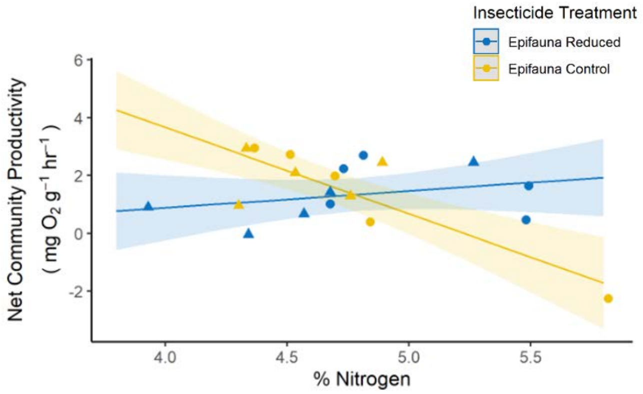

Figure 6. When epifauna were present, greater nitrogen content correlated with decreased net community productivity. Nitrogen content did not have a statistically significant effect on net community productivity when epifauna were reduced.

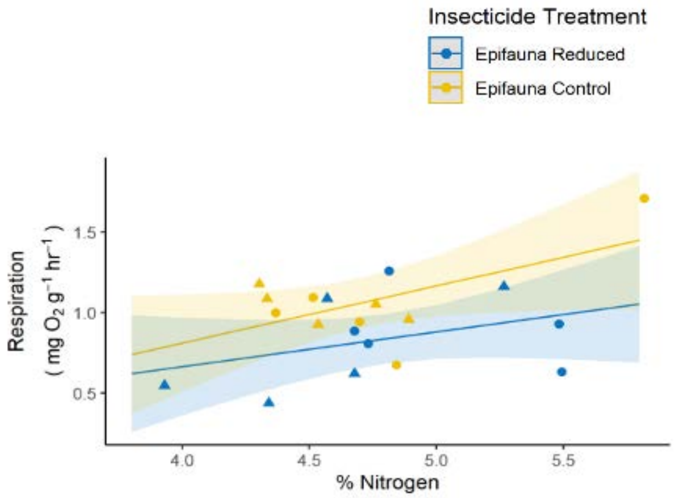

Figure 7. Respiration of turf algae decreased as nitrogen content increased, regardless of whether epifauna were present.

Carbaryl treatments had a weakly significant effect on respiration levels (F=3.45, *d.f.*=1, P=0.0797). Turf assemblages treated with Carbaryl had lower respiration levels than those with no Carbaryl (Figure 8a). Carbaryl did not have a statistically significant effect on net community productivity (F=0.12, *d.f.*=1, P=0.7305) (Figure 8b). While Carbaryl addition plots had a mean productivity of 1.35 mg O_2 g^{-1} hr^{-1} ± 0.30 SE and Carbaryl control plots had a mean productivity of 1.56 mg O_2 g^{-1} hr^{-1} ± 0.50 SE, this difference was not statistically significant.

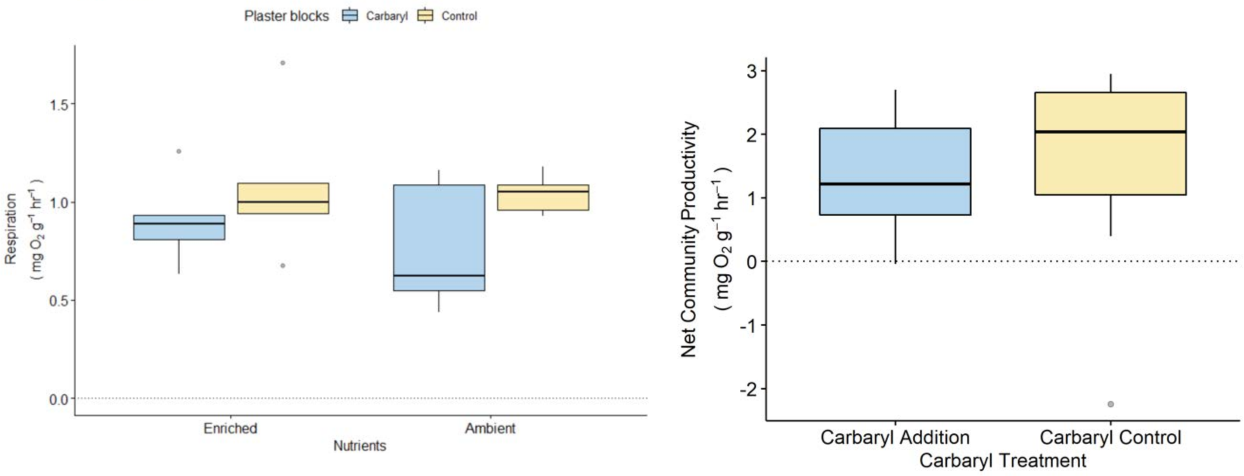

Figure 8. a) Turf algae assemblages from carbaryl addition treatments had slightly decreased respiration levels. **b)** Net community productivity of turf algae assemblages did not vary between Carbaryl addition vs. Carbaryl control treatments.

Turf algae samples were dominated by polysiphonous red algae from the genera *Symphiocladia*, *Polyostea*, and *Polysiphonia*. However, two of the 20 samples were instead dominated by genera in the family Rhodomelaceae: *Neorhodomela* and *Rhodomela*. Some samples also included secondary components of green filamentous *Chaetomorpha* and red foliose *Cryptopleura*. We found that algal compositions did not influence net community productivity measurements (by primary genus: $F_{(1,18)}$=0.189, P=0.6690) but did have a significant effect on epifauna densities ($X^2_{(1,18)}$ = 12.6, P = 0.0004). Epifauna were found in polysiphonous red algae only, with zero epifauna found in Rhodomelaceae algae (Figure 9).

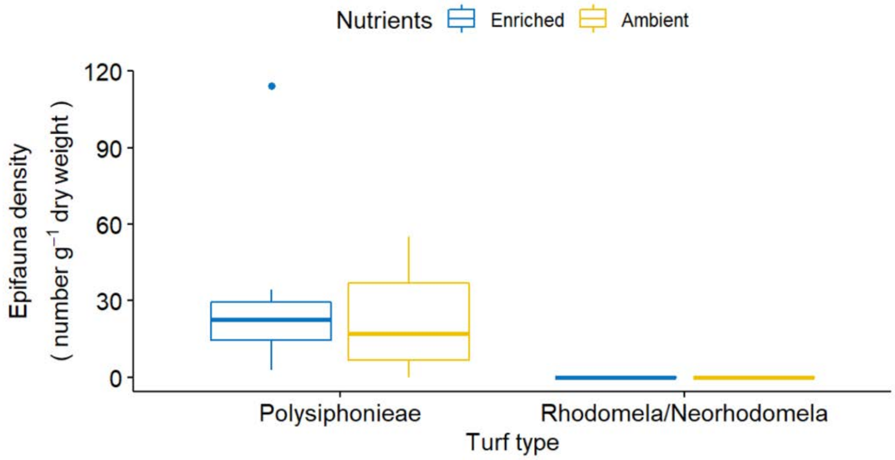

Figure 9. Epifauna abundances for turf algae samples dominated by Tribe Polysiphonieae vs turf algae samples dominated by Rhodomela or Neorhodomela (Family Rhodomelaceae). Note that there were only two samples dominated by Rhodomela or Neorhodomela.

We also evaluated epifauna counts across the nutrient and Carbaryl treatments and analyzed the effect of epifauna on net community productivity. We found that epifauna counts did not vary between nutrient addition vs nutrient control treatments ($X^2_{(1,18)}$= 0.273, P=0.6014). Additionally, Carbaryl did not have a significant effect on epifauna counts ($X^2_{(1,18)}$=0.259, P=0.6108). When analyzing the effect of epifauna on productivity, we found that there was a significant relationship between epifauna density and net community productivity ($F_{(1,18)}$ =19.54, P=0.00033). Greater epifauna density was correlated with lower net community productivity (Figure 10), with epifauna density explaining 52% of the variation in net community productivity.

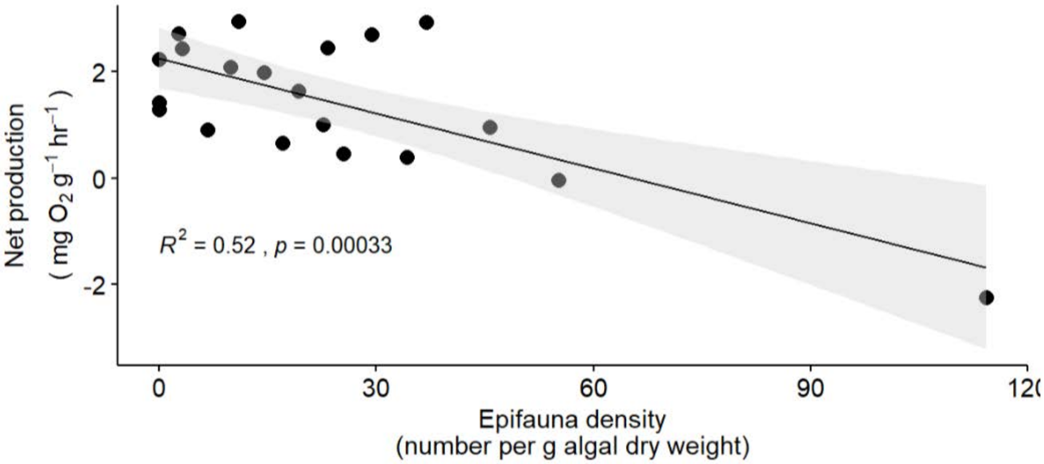

Figure 10. Net community production of turf algae assemblages was negatively correlated with epifauna density.

We also found a spatial gradient of net community productivity and epifauna density. Productivity decreased from east to west ($F_{(1,18)}$ = 8.29, P = 0.0100), with plot location explaining 32% of the variation in productivity (R^2 = 0.32) (Figure 11a). While we did collect samples from west to east, collection time was not found to have a statistically significant effect on productivity ($F_{(1,18)}$ = 0.36, P = 0.557). For epifauna density, we found an opposite spatial pattern in which epifauna density increased from east to west ($X^2_{(1,18)}$ = 3.94, p = 0.0471) (Figure 11b).

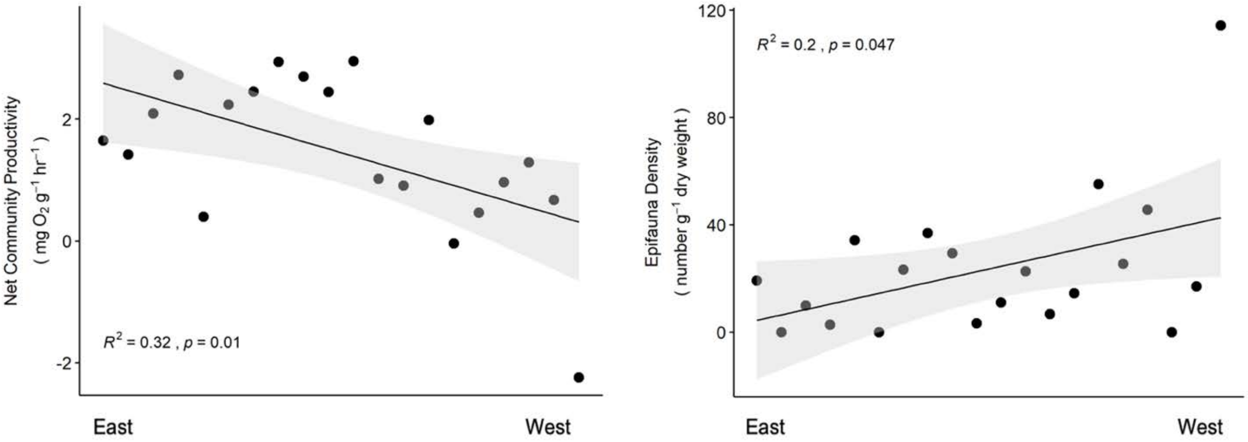

Figure 11. a) Net community productivity of turf algae assemblages decreased from east to west. **b)** Epifauna density increased from east to west.

DISCUSSION

The effects of nutrient enrichment on net community productivity of turf algae assemblages were minimal at our study location on San Juan Island, Washington. Nutrient additions increased nitrogen content of turfs, and this in turn coincided with slightly lower productivity levels. However, this effect was not detectable using categorical designations (nutrient addition vs nutrient control), either because of insufficient statistical power, spillover of nutrients between experimental plots, or both of these. While relevant literature has shown that other macrophytes can shift from net autotrophic to net heterotrophic in nutrient rich environments (Egea et al. 2020; Gallagher 2022), we found that this response was not dramatic for turf assemblages in high flow area within the Salish Sea.

Elemental analyses showed that fertilizer treatments were marginally effective. While fertilizer treatments did increase nitrogen content, nitrogen levels were only slightly greater in nutrient addition plots than nutrient control plots. Flow rates, which were estimated to be as high as 1 m s $^{-1}$, may have caused nutrients to bleed between plots and may have reduced the effectiveness of using nutrient addition and nutrient control plots as separate categories. While these results indicate that turf algae productivity may be only minimally affected by changes in nutrient levels, this experiment should be repeated in a low flow environment that creates a more distinct difference in nutrient level.

Productivity decreased slightly as nitrogen levels increased. This indicates that turf assemblages can shift to become net heterotrophic under nutrient rich conditions, which aligns with previous studies that have found both seagrass and seaweed systems to become heterotrophic in nutrient rich environments (Egea et al. 2020; Gallagher 2022). This suggests that the takeover of turf algae in coastal marine ecosystems may have the potential of altering these systems' carbon absorption capacity.

While Carbaryl did not affect macrofauna associated with filamentous turf algae, its negative effect on respiration rates could have been driven by reduced meiofaunal abundances. Meiofauna were not captured by our methods, and studies on meiofaunal response to high nutrients are limited. However, previous studies have found epifauna to increase in abundance in nutrient rich conditions (Gibbons & Griffiths 1986; Gil, Armitage, & Fourqurean 2006; Tuya et al. 2013). Thus, meiofaunal abundance and respiration may have increased in nutrient rich environments, ultimately lowering net community productivity of turf assemblages. This study suggests that meiofauna are partly responsible for decreasing net community productivity of turf assemblages in high nutrient conditions, although future studies are needed to determine how meiofauna respond to changes in nutrient levels.

We found no difference in net community productivity of turf algae assemblages between Carbaryl addition vs Carbaryl control treatments. However, because epifauna counts did not vary between Carbaryl addition and Carbaryl control plots, this is likely due to ineffective Carbaryl treatments rather than a non-effect of epifauna on turf assemblage productivity. Supporting this, epifauna counts were shown to be negatively correlated with productivity, which indicates that methods for counting relative epifauna abundance were likely effective. One reason Carbaryl treatments may not have affected macrofauna is that they were only deployed for five days before we collected turf samples. While Carbaryl is relatively fast-acting, this may not have been enough time to exclude macrofauna, which have a longer life cycle than most meiofauna. In addition, macrofauna are more mobile than meiofauna, potentially adding variability to their distribution patterns relative to Carbaryl treatments. Furthermore, high water flow rates may have diluted the Carbaryl to a low enough concentration that it was non-lethal and insufficient as a deterrent for arthropods with slower metabolic rates, which presumably includes more macrofauna than meiofauna.

We did find that respiration was slightly lower in Carbaryl addition plots than in Carbaryl control plots. When we measured epifauna abundance we focused on macrofauna and did not measure meiofauna. While Carbaryl was not found to affect macrofauna counts, it could have been effective against meiofauna. If meiofauna were responsive to Carbaryl treatments, then lower meiofaunal abundances could explain the lower respiration levels measured in Carbaryl addition treatments. Ultimately, future studies are needed to determine the relative contribution of meiofauna vs macrofauna to turf assemblage respiration.

Turf algae composition was found to affect epifauna counts, as epifauna were found in samples dominated by polysiphonous algae but not in those dominated by Rhodomelaceae algae. This is consistent with previous findings that epifauna prefer more structurally complex habitats, since polysiphonous algae are more structurally complex than Rhodomelaceae algae at their respective organismal scale (Chemello & Milazzo 2002; Hauser et al. 2006). However, net community productivity was not found to vary between polysiphonous samples and Rhodomelaceae samples despite differences in epifaunal densities. This could indicate that the photosynthetic ability of polysiphonous algae is greater than Rhodomelaceae algae, potentially enough to make up for its greater epifaunal respiration. Alternatively, Rhodomelaceae algae could have more meiofauna than polysiphonous algae. Epifauna counts only measured macrofauna, which means that greater meiofauna abundance in Rhodomelaceae algae could have raised respiration rates enough to lower its net community productivity to be similar to that of polysiphonous algae.

The eastern-most plots within our study site had greater net community productivity and fewer epifauna than western plots. The productivity gradient can be explained by the epifaunal gradient because greater epifaunal densities would increase respiration rates and therefore decrease net community productivity. The epifauna gradient may be due to the spread of turf taxa along the dock. When we collected turf samples, we observed that Rhodomelaceae algae were more common on the eastern side of the dock while polysiphonous algae were more common on the western side of the dock. Rhodomelaceae algae are less structurally complex than polysiphonous algae, and previous studies have shown that greater structural complexity of algae supports greater epifaunal abundance (Chemello & Milazzo 2002; Hauser et al. 2006). Thus, epifauna would be more abundant on the western side of the dock, where the more structurally complex polysiphonous algae are more dominant. We also observed that the eastern side of the dock was more frequently submerged by waves from boat traffic, and this may explain why Rhodomelaceae algae are more common on the eastern side of the dock. As less structural complexity may decrease water retention, Rhodomelaceae algae may prefer an environment in which it is frequently submerged and not water limited. Wave patterns may impact the spread of turf taxa along the dock and affect epifauna abundance, although future studies will need to confirm this.

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