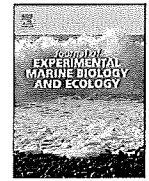




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Recreational clam harvesting affects sediment nutrient remineralization and the growth of the green macroalga *Ulva lactuca*

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ABSTRACT

Recreational clam harvesters at Northwest Penn Cove leave pools in the sediments that fill with porewater before being inundated by the incoming tide. We hypothesized that this nutrient-rich porewater may affect ulvoid algal growth. To test this, we measured nutrient concentrations in seawater, tidepools, shellfishers' pools, and in porewater from the top 9 cm of the sediment. On average, sediment porewater was 4495% higher in ammonium, 772% higher in nitrite, and 3238% higher in phosphate than nearby seawater; nitrate concentrations in porewater were 35% of the seawater concentrations. Water in shellfishers' pools was 291% higher in ammonium and 122% higher in nitrite than seawater. Nitrate and phosphate concentrations in shellfishers' pools and seawater did not differ significantly. We then transplanted *Ulva lactuca* around shellfishers' pools, tidepools, and onto the mudflat. Transplanted algae did not differ significantly in tissue carbon, nitrogen, and phosphorus concentrations after 2 days. However, the algae transplanted around shellfishers' pools grew 20% more over two weeks than the algae transplanted around tidepools and onto mud flats. Our results suggest that the nutrient-rich water in shellfishers' pools enhances algal growth near the pools and may contribute to the formation and persistence of the *Ulva* bloom at this site.

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1. Introduction

Large blooms of macroalgae occur throughout the world and are often associated with eutrophication (Fletcher, 1996; Morand and Briand, 1996; Schramm and Nienhuis, 1996; Valiela et al., 1997; Raffaelli et al., 1998; Raven and Taylor, 2003). Among the more common types of macroalgal blooms are those formed by ulvoid green algae (Phylum Chlorophyta, Order Ulvales), which are often referred to as "green tides". In temperate areas, these blooms can have a variety of detrimental effects that include fragmenting eelgrass meadows (Nelson and Lee, 2001), altering faunal community structure (Valiela et al., 1997; Hauxwell et al., 2001), and producing noxious odors (Frankenstein, 2000). The algae that produce the blooms can also produce toxins that negatively affect co-occurring algae and invertebrates (Magre, 1974; Johnson and Welsh, 1985; Jin and Dong, 2003; T. Nelson et al., 2003; Van Alstyne et al., 2006).

Although green tide blooms are generally thought to form in response to increases in seawater nutrient concentrations, they may also contribute to the maintenance of high nutrient concentrations. Ulvoid algal blooms are usually seasonal, with peak biomasses occurring from late spring to late summer, depending on the location and species composition of the bloom (T.A. Nelson et al., 2003; Zertuche-González et al., 2009). When algal mats decompose, they can add organic matter

containing both nitrogen and phosphorus to the underlying sediments (García-Robledo et al., 2008; Corzo et al., 2009). Once in the sediments, the organic matter is degraded by infaunal animals and microbes, ultimately resulting in the mineralization of nutrients. Mineralized nutrients may then be modified by a variety of processes including oxidation, ammonification, nitrification, and denitrification (Herbert, 1999). Ultimately, sediment nutrients may remineralize back into the overlying water column. Nutrients released from sediments can contribute to algal growth, especially when water column nutrient supplies are low (Lavery and McComb, 1991; Kamer et al., 2004). This suggests that the accumulation of nutrients in the sediments that results from the decomposition of macroalgal blooms and the later release of these nutrients from the sediments may contribute to the growth of blooms in subsequent years.

The movement of nutrients from the sediments to the water column can occur via diffusion, but may also be accelerated by mechanical disturbances such as bioturbation by infaunal animals (Blackburn and Henriksen, 1983; Hansen and Kristensen, 1997; Tuominen et al., 1999; Karlson et al., 2007). Disturbances caused by human activity can also increase nutrient remineralization. Larger-scale activities such as dredging (Falcao et al., 2003) and shellfish collection with hydraulic escalator harvesters (Coen, 1995) are known to decrease sediment nutrient concentrations and may affect primary productivity (Coen, 1995). However, it is possible that smaller-scale anthropogenic disturbances, such as recreational harvesting of shellfish in mud flats by individuals, also increase nutrient flux rates from the sediments. Although the effects of a single individual are not likely to have

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significant impacts at an ecosystem level, the cumulative effects of regular harvesting by large numbers of individuals may be locally important.

At this point, there is little known about the effects of recreational shellfish harvesting on nutrient fluxes from intertidal sediments or about the effects of changes in these fluxes on nearby primary production. Here, we hypothesize that small-scale anthropogenic disturbances to nutrient-rich sediments caused by the recreational shellfish harvesting result in the release of nutrients into the water column, which in turn, has localized effects on the growth and chemical composition of ulvoid algae. To test this hypothesis, we examined whether recreational clam harvesting at a mudflat in western Washington 1) affected localized fluxes of ammonium, nitrate, nitrite and phosphate, 2) caused changes in tissue carbon, nitrogen, and phosphorus concentrations in the bloom-forming ulvoid green alga *Ulva lactuca*, and 3) resulted in increases in growth rates of *Ulva* in areas adjacent to pools created by recreational clam harvesters (hereafter referred to as shellfishers' pools).

2. Materials and methods

2.1. Study site

The study site (48° 14' N, 122° 44' W), which is hereafter referred to as Northwest Penn Cove, is located 3.3 km NNE of the town of Coupeville in the northwest corner of Penn Cove, Washington on Whidbey Island. Although there is substantial temporal variation in the abundance of bloom-forming green algae in the Northwest Straits region of Washington, (Nelson et al., 2009), we have documented regular occurrences of ulvoid algal blooms at this site from 2006–2009 (Van Alstyne and Nelson, unpubl. data). The site is a shallowly sloping wave-protected, sand–mud beach that is ~1.3 km long. The algal cover is dominated by *U. lactuca*, but *Ulva prolifera* and *Ulva linza* are also common. By mid-summer, ulvoid algal mats often consist of several layers, with covers of 100% being common.

During summertime low tides, the site is frequented by recreational shellfishers collecting clams by digging holes in the sediments with shovels. The species harvested include *Saxidomus gigantea* (butter clams), *Protothaca staminea* (littleneck clams), *Venerupis philippinarum* (Manila clams), *Clinocardium nuttalli* (cockles), *Tresus nuttalli* (horse-clams) and *Tresus capax* (horseclams). The shellfishers' pools are usually 0.5 to 1 m in diameter and about 0.5 m depth. Typically, the sediment removed is not returned to the pools and water seeps into them from the surrounding sediments when the tide is out. Although we did not make any quantitative assessments of the clamming activity at this beach, it was not unusual to see five to ten different groups harvesting clams during a low tide, with each group leaving a number of pools. There were also numerous shallow tidepools located throughout the site, which were probably the remnants of old shellfishers' pools.

2.2. Seawater nutrient measurements

On 26 Jul 2007, water samples were taken from three locations (N = 8 per location): 1) the surface of the seawater where the depth was approximately 0.5 m, 2) "natural" tidepools, which were pools of standing water on the mud flat that showed no signs of being caused by recent clam harvesting, and 3) shellfishers' pools, pools of standing water on the mud flat that were created by clam harvesters within the previous hour. The samples were immediately filtered through 0.45 µm nylon filters and transported on ice to the Shannon Point Marine Center (SPMC) in Anacortes, Washington where they were stored at –4 °C for later analysis of ammonium, nitrate, nitrite, and phosphate concentrations. Nutrient measurements were made with a Lachat QuikChem 8500 autoanalyzer. Lachat method 30-107-06-1-A was used for ammonium, Lachat method 31-107-04-1-D was used for nitrate and nitrite, and Lachat method 31-115-01-1-H was used for orthophosphate.

The data were analyzed with a multivariate analysis of variance (MANOVA; SPSS 16.0) after being square-root transformed. After transformation, the ammonium and nitrite data still did not meet the assumption of homogeneity of variances; for this reason, we used a Pillai–Barlett V analysis, which is robust to moderate heteroscedasticity when the design is balanced or nearly so (Johnson and Field, 1993). An α value of 0.05 was used for all statistical analyses.

2.3. Sediment porewater nutrient measurements

On the same day, we also collected sediment cores by pushing five cm diameter plastic tubes approximately 9 cm into the mud. The cores were immediately split into a top and bottom half, sealed in plastic bags with as much of the air removed as possible, and transported on ice to SPMC where they were kept frozen at –70 °C for later analysis of porewater ammonium, nitrate, nitrite, and phosphate concentrations. To obtain porewater, the sediments were thawed and placed into 60 ml syringes. The porewater was collected as it drained from the bottoms of the syringes and was then filtered through 0.45 µm nylon filters. Ammonium, nitrate, nitrite, and phosphate concentrations were measured with a Lachat QuikChem 8500 autoanalyzer as described above. Because insufficient porewater was obtained to conduct all four analyses on all samples, we conducted nitrate analyses on all samples and phosphate, nitrite and ammonium analyses where possible on the rest.

Because we could not obtain all measurements from all samples, the data were analyzed with one-way analyses of variance (ANOVA) or Kruskal–Wallis tests comparing individual nutrient concentrations among seawater samples, porewater samples from the tops of the cores, and porewater samples from the bottoms of the cores (SPSS 16.0). Nitrate data were square root transformed to meet the assumption of normality and analyzed with a one-way ANOVA followed by a post hoc Tukey's test. Ammonium, nitrite, and phosphate data could not be transformed to meet the assumption of normality so they were analyzed with Kruskal–Wallis tests followed by post hoc Dunn's tests for multiple comparisons.

2.4. *U. lactuca* nutrient uptake experiment

To determine if *U. lactuca* growing near shellfishers' pools were affected by the high nutrient levels in the pools, we conducted a transplant experiment in Aug 2008. *Ulva* were collected from a single area on the mud flat and were transplanted around 1) shellfishers' pools, 2) tidepools, and 3) in a circle on the mud flat. The transplanting was done by placing nylon washers (2.5 cm in diameter) on either side of the alga and running a 30 cm long, 6 mm diameter stake through the washers, which was then embedded in the mud flat. In each of the six areas on the mud flat, we transplanted five *Ulva* around a recently dug shellfisher's pool, five around a similar-sized tidepool, and five in a circle of a similar diameter to the pools on the mud flat. Two days later, we collected the algae and returned them to SPMC for analyses of tissue carbon, nitrogen, and phosphorus levels.

Carbon and nitrogen measurements were made using the method described by Nelson et al. (2008). *Ulva* samples were dried in an oven at 60 °C for at least 24 h and stored in a desiccator until they were processed. Carbon and nitrogen concentrations were determined with a CE Elantech 1112 Elemental Analyzer, with atropine as a standard. Tissue phosphorus was measured using methods similar to those described by Wheeler and Björnsäter (1992). Briefly, approximately 5 mg of algae that had been dried in a 60 °C oven for at least 24 h was ground with a CPEX mixer/mill and was weighed on a microbalance. The algae were placed in a potassium persulfate/sodium hydroxide solution and were digested for 2 h in a 100 °C water bath. The solution was then acidified with 0.3 M hydrochloric acid, buffered with an alkaline borate buffer, and brought up to a volume of 50 ml with nanopure water. Phosphate was measured using Lachat method 31-115-01-1-H on a Lachat QuikChem 8500 autoanalyzer. Standards consisted of known concentrations of potassium dihydrogen phosphate that were run

through the same digestion process and analyzed on the autoanalyzer. After determining that there were no significant differences among the variances, the data were analyzed with MANOVA (SPSS 16.0) with area on the beach and transplant habitat type (tidepool, shellfishers' pool, or mud flat) as factors.

2.5. *U. lactuca* growth experiment

To determine if *Ulva* grew better near shellfishers' pools, we conducted a transplant experiment on 20 Aug 2009. Pieces of *Ulva* were collected from the beach at Northwest Penn Cove and were cut into squares with surface areas of 62 cm². The algae were transplanted around eight tidepools, eight shellfishers' pools, and in eight circles on the mud flat as described above (N=5–6 algal pieces around each). Two weeks later we recovered 64 of the algal pieces and transported them to SPMC where they were immediately photographed with a digital camera for later surface area measurements with Image Pro™ software. A one way ANOVA was used to compare the sizes of the pieces (SPSS 16.0) after the data were log transformed to meet the assumptions of normality and homoscedasticity.

3. Results

Nutrient concentrations in water samples collected from tidepools, shellfishers' pools, and the nearby seawater differed significantly (Fig. 1; Pillai's trace=0.994, F=3.458, hypothesis df=8, error df=28, P=0.007). Ammonium concentrations were approximately five times higher in shellfishers' pools than in seawater and tidepools (Fig. 1a; between-subjects effect of water source: F=8.688, df=2, p=0.003). Nitrite concentrations were also significantly higher in shellfishers' pools than tidepools (Fig. 1c; between-subjects effect of water source for nitrite: F=5.742, df=2, p=0.013). Nitrate (Fig. 1b; between-subjects effect of water source: F=3.421, df=2, P=0.058) and phosphate (Fig. 1d; between-subjects effect of water source for phosphate: F=3.357, df=2, p=0.061) concentrations did not differ significantly among the three habitat types.

Seawater and porewater from the tops and bottoms of the sediment cores had significantly different ammonium (Kruskal–Wallis test, H=9.89, df=2, P=0.007), nitrate (one-way ANOVA, F=13.173, df=2, P<0.001), nitrite (Kruskal–Wallis test, H=6.66, df=2, P=0.036), and phosphate (Kruskal–Wallis test, H=9.84, df=2, P=0.007) concentrations. Mean concentrations of ammonium in the tops and bottoms of the sediment cores were about 61 and 29 times higher than concentrations in seawater, respectively (Fig. 2a; Dunn's test: P<0.05), but they did not differ significantly from one another (Dunn's test: P≥0.05). Phosphate concentrations in porewater from the tops of the cores were 61 and 15 times as high as concentrations in seawater and porewater from the bottoms of the cores, respectively (Fig. 2d; Dunn's test: P<0.05); however, concentrations in seawater and porewater from the bottoms of the cores were not significantly different (Dunn's test: P≥0.05). Nitrate concentrations in porewater from the tops and bottoms of the cores were approximately one-quarter to half of the average concentration in seawater (Fig. 2b; Tukey's test: P<0.05), but they did not differ significantly from each other (Fig. 2b; Tukey's test: P≥0.05). Nitrite concentrations did not differ significantly in porewater from the tops and bottoms of the cores (Dunn's test: P≥0.05), but both were about 10 times higher than seawater concentrations (Fig. 2c; Dunn's test, P<0.05).

The algae that were transplanted to the shellfishers' pools, tidepools, and mud flats did not have significantly different tissue carbon, nitrogen, or phosphorus concentrations 2 days following transplantation (Fig. 3, Table 1; Pillai's trace=0.042, F=0.476, hypothesis df=6, error df=132, P=0.825). However, tissue carbon and nitrogen differed significantly among the 6 areas along the beach where the algae were transplanted (Table 1, Pillai's trace=0.500, F=2.680, hypothesis df=15, error df=201, P=0.001), suggesting that nutrient levels were affected by microtopographical features that differed at different

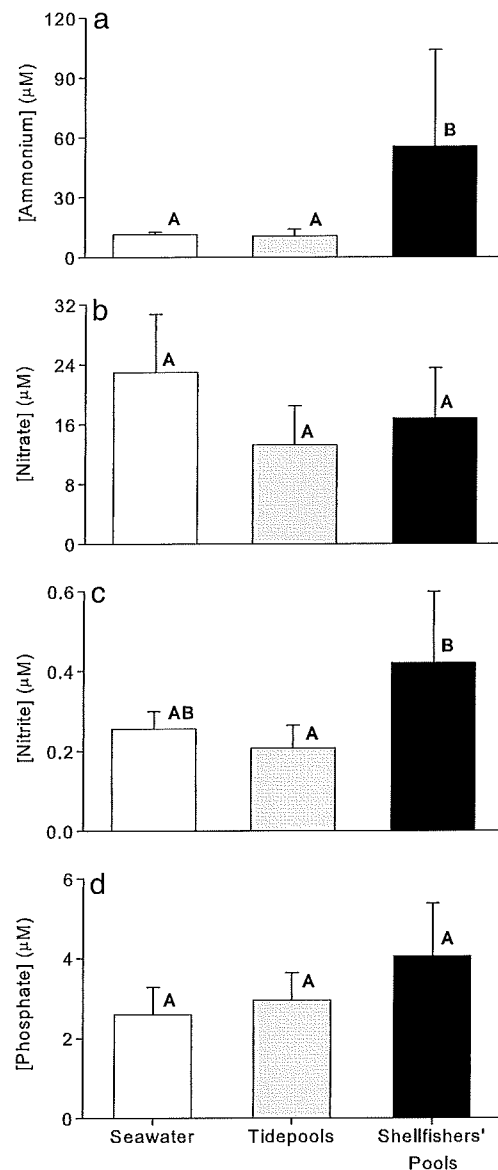


Fig. 1. Concentrations of a) ammonium, b) nitrate, c) nitrite, and d) phosphate in seawater (open bars), tidepools (grey bars) and shellfishers' pools (black bars). Data are means ± 1 SD (N=8). Different capital letters above the bars indicate significant differences (Tukey's test: P<0.05).

sites along the beach. Average tissue N:P ranged from 12.04 ± 2.55 in algae from the mud flat to 12.24 ± 3.91 in algae from the tidepools. Tissue N:P was not significantly different among algae from shellfishers' pools, tidepools and mud flats (one-way ANOVA: F=0.038, P=0.963).

On average, the growth rates of *Ulva* transplanted around shellfishers' pools were about 20% higher than the growth rates of *Ulva* transplanted around tidepools or onto the mudflat (Fig. 4; one-way ANOVA: df=2, F=3.436, P=0.039, Tukey's test, P<0.05). The growth rates of algae transplanted around tidepools and onto the mudflat were not significantly different from each other (Tukey's test: P≥0.05).

4. Discussion

Our study found that recreational clamming at the Northwest Penn Cove study site was responsible for remineralizing significant amounts

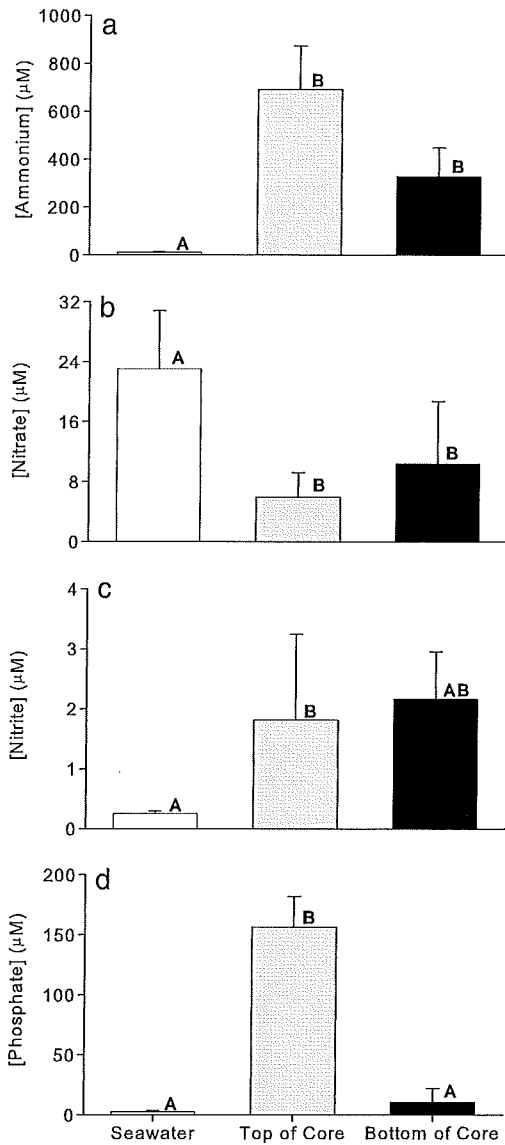


Fig. 2. Concentrations of a) ammonium (N=3–7), b) nitrate (N=7–10), c) nitrite (N=4–7), and d) phosphate (N=4–7) in seawater and in porewater from the top and bottom halves of sediment cores. Data are means \pm 1 SD. Different capital letters above the bars indicate significant differences (ammonium, nitrite, phosphate: Dunn's test, $P < 0.05$, nitrate: Tukey's test: $P < 0.05$).

of ammonium and nitrite from nutrient-rich sediments into the water that filled pools left behind by clam harvesters. *Ulva* growing adjacent to shellfishers' pools grew about 20% faster than *Ulva* adjacent to tidepools or on mud flats, but it did not contain higher concentrations of nitrogen, phosphorus, or carbon in its tissues.

Although they were often much higher than the concentrations in the nearby seawater, the porewater ammonium, nitrite, and phosphate concentrations that we measured (Fig. 2) were comparable to previously reported values at comparable depths (Hansen and Kristensen, 1997; Murray et al., 2006). Marine sediments, particularly those underlying large growths of macroalgae, often contain higher concentrations of nutrients than the seawater that overlies them. The high ammonium and nitrite concentrations in the sediment porewater (Fig. 2) explain why nutrient concentrations were also higher in the shellfishers' pools relative to the nearby seawater (Fig. 1). Thus, our

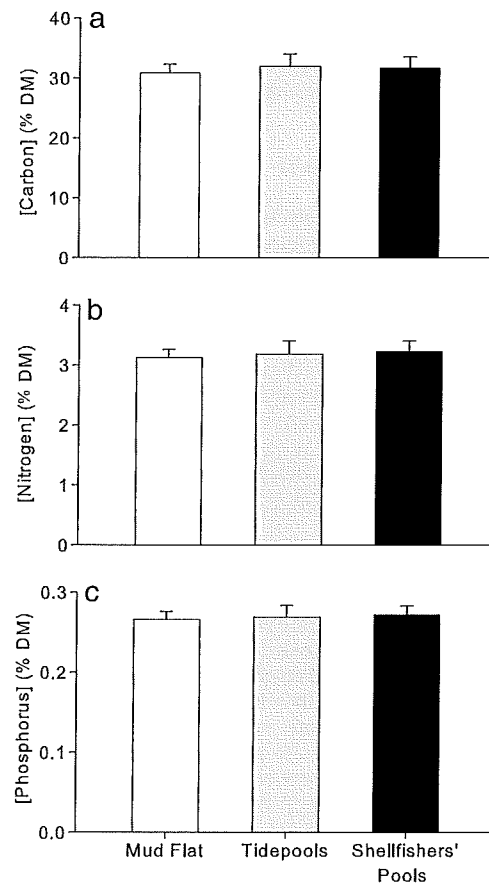


Fig. 3. Concentrations of tissue a) carbon b) nitrogen and c) phosphorus in transplanted *Ulva* after 2 days on mud flats and around tidepools and shellfishers' pools. Data are means \pm 1 SE (N=6). DM: dry mass.

results show that disturbance to the sediments caused by recreational shellfishing at Northwest Penn Cove resulted in the remineralization of sediment nutrients on a highly localized scale.

The sources of the high concentrations of nutrients in sediment porewater at Penn Cove have not been documented; however, it is possible that the ulvoid algal mats may be contributing to their

Table 1

Between-subject effects from a multivariate analysis of variance of tissue carbon, nitrogen, and phosphorus concentrations in *Ulva lactuca* that were transplanted to three different habitats (tidepools, shellfishers' pools, and mud flats) at six locations on the beach at Northwest Penn Cove.

Source	Dependent variable	Sum of squares	df	Mean square	F	P
Habitat	Carbon	15.716	2	7.858	0.872	0.423
	Nitrogen	0.265	2	0.133	0.511	0.602
	Phosphorus	0.223	2	0.112	0.095	0.910
Location on beach	Carbon	318.758	5	63.752	7.078	<0.001
	Nitrogen	5.086	5	1.017	3.917	0.004
	Phosphorus	4.751	5	0.950	0.807	0.549
Habitat x location	Carbon	1016.311	10	101.631	11.284	<0.001
	Nitrogen	8.718	10	0.872	3.358	0.001
	Phosphorus	19.074	10	1.907	1.619	0.120
Error	Carbon	603.456	67	9.007		
	Nitrogen	17.396	67	0.260		
	Phosphorus	78.913	67	1.178		
Total	Carbon	85958.908	85			
	Nitrogen	892.925	85			
	Phosphorus	2559.985	85			

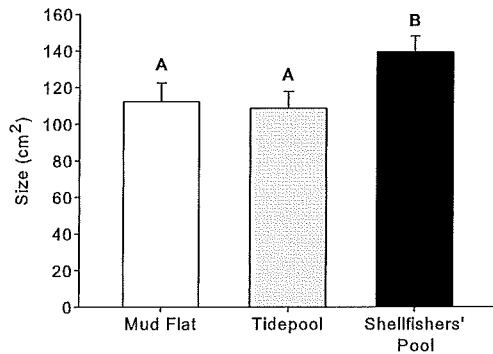


Fig. 4. Growth rates of algae in mud flats, tidepools, and shellfishers' pools at Penn Cove (N = 18–24). Mean growth rates are significantly different (one-way ANOVA: $df=2$, $F=3.436$, $P=0.039$). Growth rates around shellfishers' pools are higher than growth rates on mud flats and around tidepools (Tukey's test: $P<0.05$).

accumulation. Ulvoid algal blooms have been occurring regularly at the site since at least 2006 (Van Alstyne and Nelson, unpubl. data). In other locations, decomposing ulvoid algae have been documented to be a source of sediment nutrients and carbon (Herbert, 1999; Garcia-Robledo et al., 2008; Corzo et al., 2009). Filter-feeding animals, such as bivalves, which are abundant at the Penn Cove site, are also known to increase nutrient concentrations in sediments (Magni et al., 2000).

Remineralized sediment nutrients can cause increases in ulvoid algal growth (Herbert, 1999; Sundback et al., 2003; Kamer et al., 2004). At Northwest Penn Cove, the large inputs of ammonium to the shellfishers' pools from the sediments were the most likely cause of the higher growth rates of *Ulva* that occurred adjacent to the pools. Although the algae were not in the pools, they would have been subjected to a pulse of nutrient-rich water as the incoming tide caused the pools to flood. The tissue N:P that we measured in the algae was about 12, a ratio that is indicative of nitrogen limitation in *U. lactuca* (reported as *Ulva fenestrata*) in this region (Björnsäter and Wheeler, 1990). If these algae were nitrogen rather than phosphorus limited, as suggested by the N:P ratio, then any increase in seawater phosphate that resulted from the movement of phosphate from the porewater to the sediments should have had no effect on algal growth. Both nitrate and ammonium can be rapidly assimilated by ulvoid algae (Naldi and Wheeler, 2002), but the nitrate concentrations in the shellfishers' pools were comparable to those in seawater, whereas the ammonium concentrations were about five times higher (Fig. 1). Nitrite was also significantly higher in the shellfishers' pools but it made up less than 1% of the nitrogen measured so it was unlikely to have had an impact on algal growth rates.

The lack of a change in tissue nitrogen and phosphorus concentrations in the transplanted algae may have been a result of the algae immediately allocating nutrients to the formation of new tissue, rather than storing the compounds. In laboratory experiments, where nitrogen was maintained at consistently higher concentrations, *U. lactuca* both grew and increased their tissue nitrogen concentration over 10 days (Nelson et al., 2008). However, in our field experiments, the algae surrounding the shellfishers' pools should have received only a single pulse of nutrients as the pools were flooded by the incoming tides. If the extra nutrients taken up from this pulse were immediately used to increase growth, then no differences in tissue nutrient concentrations would be expected among the algae surrounding the shellfishers' pools, the tidepools, and on the mud flat.

This is one of the first studies to document the effects of recreational shellfish harvesting on the productivity of macroalgae via an effect on nutrient remineralization. Disturbances resulting from clam harvesting are known to impact the diversity of benthic plant and animal communities and the survival of individual species. For example, clam harvesting that involved both digging and tilling sediments reduced shoot densities and biomass in seagrass (*Zostera noltii*) meadows in

southern Portugal (Cabaço et al., 2005). Reserves where harvesting is prohibited in Washington State, USA had higher abundances of the clams *P. staminea* and *V. philippinarum* and a more diverse community of clams, other infauna, and epifauna than similar areas where clam harvesting is allowed (Griffiths et al., 2006). Commercial harvesting of worms and clams in Maine, USA affected the diversity of polychaete worms as well as the densities of some, but not all, polychaete species (Brown and Wilson, 1997). Thus, disturbances resulting from shellfish harvesting can affect marine benthic communities in multiple ways, including altering the availability of nutrients, changing the abundances of primary producers, and altering the abundances and diversity of infaunal and epifaunal invertebrates.

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