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Alteration of microbial community composition and changes in decomposition associated with an invasive intertidal macrophyte

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Abstract

Data demonstrating the effects of biological invaders on microbial communities and microbial processes are scarce, especially in marine environments. Research was conducted at Padilla Bay, Washington, to examine the effect that an invasive intertidal eelgrass, *Zostera japonica* Aschers & Graebn, has on rates of decomposition, microbial community composition, and the possible implications for associated ecosystem processes in this estuarine environment. A series of observational and experimental studies were conducted in beds of *Z. japonica*, beds of its native congener, *Zostera marina*, and mixed eelgrass beds. These studies assessed decomposition of invasive and native eelgrass, enumerated bacterial abundance, and examined sole source carbon usage (SSCU) by microbial assemblages. *Z. japonica* decomposed more rapidly than its native congener throughout the study period although rates of decomposition were variable. Microbial abundance did not differ among different vegetation compositions although differences in SSCU by microbial assemblages were detected among beds of invasive, native, and mixed eelgrass. These results indicate that this abundant invasive species can accelerate rates of decomposition and alter the associative decomposer community, which may lead to higher carbon and nutrient turnover within Padilla Bay.

Abbreviation: SSCU – sole source carbon use

Introduction

Biological invasions often alter the community composition and dynamics of invaded areas (Posey 1988; Coles et al. 1999; MacIsaac et al. 1999) and can potentially alter ecosystem processes including productivity, decomposition, nutrient cycling, hydrology, and others (Elton 1958; Vitousek 1990; D'Antonio and Vitousek 1992; Vitousek et al. 1997). Quantitative data demonstrating such effects, however, are scarce, especially in marine environments (Ruiz et al. 1997, 1999). With anthropogenic activities introducing species outside of their natural range at an alarming rate (Lodge 1993; Cohen and Carlton 1995, 1998), understanding how invasive species may alter recipient communities and subsequent ecosystem properties is fundamental. One possible effect of invasive species is to modify the recipient community in such a way that subsequent changes in decomposition and/or nutrient cycling occur (Windham 2001). This may occur in one or both of the following ways: (1) providing organic material with a unique chemical composition and, (2) altering the decomposer community (primarily microbes) through either chemical or structural means. Because microbial processes are intricately linked to ecosystem level processes such as decomposition and nutrient cycling (Pedersen et al. 1999; Naeem et al. 2000), the consequences of an altered organic chemical regime or altered microbial community may be manifested as changes in the rate of decomposition or the ability

of the native microbial community to degrade organic materials.

Although invading species can potentially change the composition of microbial communities, to my knowledge, no previous research has specifically addressed this topic. This may be due to the inherent difficulty of studying microbial communities. Until recently, assessing differences among microbial communities has been costly and/or very labor intensive (Garland 1997). With the development of new methods that allow a rapid, community-level assessment of microbes, comparisons among different sites have become much more tractable (Garland and Mills 1991; Ellis et al. 1995; Garland 1997; Stephan et al. 2000).

The goal of this research was to examine the effects that *Zostera japonica* Aschers & Graebn, has on microbial processes, rates of decomposition, and their potential influence on associated community and ecosystem properties in Padilla Bay, Washington. *Z. japonica,* also known as Asian eelgrass or dwarf eelgrass, was unintentionally introduced to Washington State with shipments of oysters from Japan. The date of introduction is not known but falls somewhere between the date of first collection, 50 years ago, and the first importation of Japanese oysters to the area, 100 years ago (Harrison 1976; Harrison and Bigley 1982). *Z. japonica* has since spread along the coastline, replacing unvegetated mudflat habitat (Posey 1988) and possibly competing with the native eelgrass, *Zostera marina* L. (Harrison 1982; Nomme and Harrison 1991a, b). *Z. japonica* tends to grow higher in the intertidal than its native congener although in many areas the two species overlap forming beds of mixed vegetation (Harrison 1982; Nomme and Harrison 1991a, b; Bulthuis 1995). Thus, in any comparisons between *Z. marina* and *Z. japonica*, tidal height is a confounding factor and must be parsed out using manipulative experiments. *Z. japonica* has been shown to have significant effects on infaunal assemblages and sediment structure (Posey 1988), but no exploration of its effect on microbial communities has been conducted. Presented here are the results of a combination of observational and experimental studies that measured rates of decomposition of native and introduced eelgrass, and quantified the difference in bacterial abundance and microbial community assemblages in beds of native, introduced, and mixed eelgrass while separating out the confounding effect of tidal height.

Study site and methods

This research was conducted at the Padilla Bay National Estuarine Research Reserve located in northern Puget Sound (latitude 48°28′ N, longitude 122°31′ W). Tidal fluctuations are quite large with a maximum range of nearly 4 m. With its predominance of intertidal flats, Padilla Bay supports one of the largest contiguous beds of *Z. marina* (native eelgrass) on the west coast of North America (Bulthuis 1995, for a more thorough site description and map see Bulthuis 1996). In addition to beds of the native eelgrass the bay also has extensive beds of the invasive *Z. japonica* as well as mixed eelgrass beds. Bulthuis (1991) mapped the eelgrass beds in 1989 finding ca. 2900 ha of *Z. marina*, 236 ha of *Z. japonica*, and 88 ha of mixed eelgrass. The coverage of both *Z. japonica* and mixed beds has increased substantially over the past decade (Hahn, pers. obs.). The zone of overlap between the native and invasive eelgrass is widest in the middle part of the bay and narrowest in the northern part of the bay (Hahn, unpub. data).

Eelgrass transplants

Within naturally occurring beds of eelgrass, the effects of bed composition and tidal height are confounded (Harrison 1982; Nomme and Harrison 1991a,b; Bulthuis 1991,1995). To separate the effects of these two factors, a series of transplants was conducted. These transplants moved the various bed compositions (*Z. japonica*, *Z. marina*, and mixed) to each tidal zone (upper or *Z. japonica* zone, lower or *Z. marina* zone, and the intermediate or mixed zone) with control beds transplanted back into the zone from which they originated. A total of nine transplants were established for this research and these transplants were conducted in the central portion of the bay where the mixed zone tends to be largest.

In the process of relocating each bed of eelgrass, turfs of eelgrass and sediment to a depth of ca. 10–15 cm were transplanted. This depth included the rhizomes and the majority of roots for both eelgrass species. Transplants measured 1 m^2 in size and were cut into 16 equal pieces to facilitate transport. Transplants were moved between sites using a plastic snow sled and each piece of sod was placed on a piece of plastic tarp to keep the sod together during handling. Once each transplant was in place, a 20 cm border was cleared around the plot to minimize the effect of surrounding vegetation

on the transplant. Transplants were conducted in May of 2000 and beds were allowed to establish and grow for at least 4 weeks before any samples were taken.

Estimating decomposition rates

To determine decomposition rates, decomposition bags were placed in the field. In order to get accurate measures of the mass lost during experiments, eelgrass was collected fresh and oven dried at 40 °C. Each 8 cm × 10 cm bag was constructed of fine mesh (nylon sheer, 0.83 mm × 0.38 mm pore size) and contained 5 g (dry weight) of either *Z. japonica* or *Z. marina*. Bags were anchored to the sediment surface by attaching them to a loop in the end of a 30 cm piece of heavy gauge zinc wire. Within naturally occurring beds of eelgrass, 3 replicate bags of each vegetation type (18 bags total) were haphazardly deployed in early June 2000 and left in the field for 39 days. Within the transplanted beds, 3 replicate bags of each vegetation type were haphazardly placed in each plot (54 bags total) in mid June 2000 and left in the field for 27 days. Upon collection, all bags were rinsed thoroughly with tap water to remove sediments, dried at 40 °C, and reweighed.

Extraction of microbes for direct counts and SSCU

Microbial samples were obtained from the sediments by collecting soil cores in mid-July using a soil-coring device fitted with a 5 cm (internal diameter) by 15 cm aluminum sleeve. Within naturally occurring beds of eelgrass, cores were taken haphazardly with a total of five cores from *Z. japonica* beds (upper intertidal), eight cores from *Z. marina* beds (lower intertidal), and three cores from mixed eelgrass beds (intermediate tidal height). Within the transplanted eelgrass beds, three cores were haphazardly taken from each of the plots. Once a core was extracted, the sleeve was removed, capped at both ends, and kept refrigerated until processing the next day. In order to obtain workable levels of bacteria a dilution of the sediments was conducted. The top 5 cm of the core were homogenized and 5 g (wet weight) was sub-sampled from the homogenate. The 5 g of sediment was placed in a sterile 60 ml polyethylene centrifuge tube with 45 ml of filter-sterilized seawater, capped, and shaken vigorously for 30 min. One millilitre of the resulting suspension was removed from the centrifuge tube and transferred to a sterile 25 ml test tube to which an additional 9 ml of sterile seawater was added. At this point (1 : 100 dilution), 9 ml of the dilution was transferred to a scintillation vial and preserved with formalin for later use in assessing relative bacterial abundance. The remaining 1 ml was again diluted with 9 ml of sterile seawater for a final dilution of 1 : 1000 and was used in SSCU.

Assessing bacterial abundance

Formalin-preserved samples were stained with DAPI (4′,6-diamidino-2-phenylindole) at a concentration of 0.4 μg/ml and microbes were collected by running 0.1–0.5 ml of the sample through a 0.2 μm membrane filter (modified from Porter and Feig 1980; Bird et al. 2000). Filters were mounted on microscope slides, covered with immersion oil and a coverslip, and counted at 1000× using an epifluorescence microscope. Ten fields were counted per sample and these counts were averaged to give a single estimate of relative bacterial abundance for each sample.

SSCU

The final 1 : 1000 dilution, obtained from the sediment cores, was plated onto Biolog EcoPlates (Biolog Inc., Hayward, California) at a volume of 150 μl per well. Biolog EcoPlates contain 31 unique carbon sources (one sole carbon source per well) and a redox colorant (tetrazolium violet). When bacteria are able to use a carbon source for growth, the reduction of the colorant causes the well to turn purple and indicates that the inoculant microbial community is able to utilize that carbon source. Plates were incubated at room temperature and were read after 4, 12, 24, 48, 72, 96, and 120 h using a Biolog Microlog Microstation Plate Reader. For consistency, data presented here are from the 72 h reading which showed a significant amount of color development.

Statistical analysis

Inferential statistics are applied to the data collected in this study to provide a basis for examining patterns among treatments (Oksanen 2001, but see Hurlbert 1984). Data from decomposition bags and from microbial enumeration were analyzed using ANOVA. Because many of the 31 measures of SSCU obtained from Biolog EcoPlates were highly correlated, these data were reduced to their principal components. Subsequently the first three principal components were

subjected to MANOVA to test for effects of vegetation type and tidal zone on microbial SSCU. All analyses were conducted using SYSTAT 9.0 (SPSS Inc., 1999).

Results

Decomposition

Decomposition of eelgrass in the field showed a considerable amount of variation (Figure 1) with overall losses ranging from 50% to 80% during 39 days of incubation in naturally occurring beds and 38–60% during the 27-day deployment in transplanted beds. Within naturally occurring beds of eelgrass, bed composition/tidal zone did not have a significant effect on the rate at which either eelgrass species decomposed (Figure 1A, Table 1A). Similarly, within the transplanted eelgrass beds, neither the tidal height nor the composition of the eelgrass bed had a significant effect on the rate of decomposition (Figure 1B, Table 1B). In all cases, however, *Z. japonica* decomposed significantly faster than the native eelgrass (Figure 1, Table 1).

Bacterial enumeration

Direct counts of microbes using DAPI epifluorescence microscopy revealed no significant differences in the number of bacteria among vegetation types or tidal zones (Figure 2). This was true for bacteria isolated from sediments in naturally occurring beds of eelgrass (Figure 2A) as well as transplanted vegetation which separated out the effects of the bed composition from those of the tidal zone (Figure 2B).

SSCU

Multivariate data (results from 31 unique carbon sources) were reduced to their principal components and the first 3 principal components explained a total

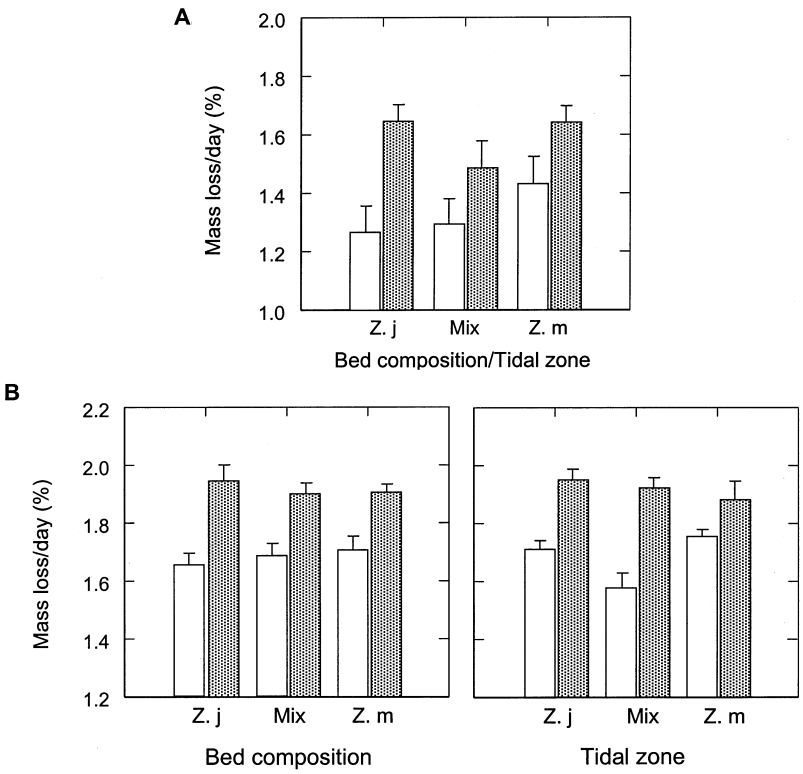

Figure 1. Decomposition of invasive eelgrass, *Z. japonica* (shaded bars) and native eelgrass, *Z. marina* (open bars) in eelgrass beds of different composition. A: Naturally occurring beds. B: Transplanted eelgrass beds. Values shown are mean ± SE. *Z.j* = *Zostera japonica*, Mix = mixed vegetation (*Z. japonica* and *Z. marina*), *Z.m* = *Z. marina*. See Table 1 for ANOVA results.

of 40% of the variance associated with the original 31 measures of SSCU. These first three principal components were used in the subsequent MANOVA to test for effects of bed composition, tidal zone, and any possible interaction between them (Table 2). Results of the MANOVA revealed that the bed composition had a significant effect on the microbial assemblage while tidal height did not have a significant effect. The interaction between vegetation and tidal zone was significant for the first principal component, but the multivariate test statistics was not significant.

Table 1. ANOVA results for decomposition of invasive and native eelgrass in eelgrass beds of different composition.

Source	SS	df	MS	*F*	*P*
A. Within naturally occurring beds					
Bed composition/ tidal zone	0.037	2	0.019	2.126	0.162
Vegetation type	0.240	1	0.240	27.475	<0.001
Interaction	0.026	2	0.013	1.494	0.263
Error	0.105	12	0.009		
B. Transplanted eelgrass beds					
Bed composition	0.022	2	0.011	0.039	0.961
Tidal zone	1.672	2	0.836	2.960	0.065
Vegetation type	19.051	1	19.051	67.466	<0.001
Bed comp. × T. zone	0.994	4	0.248	0.880	0.485
Bed comp. × Veg. type	0.510	2	0.255	0.903	0.415
T. zone × Veg. type	2.536	2	1.268	4.491	0.018
Bed comp. × T. Zone × Veg. type	0.256	4	0.064	0.227	0.921
Error	10.166	36	0.282		

Discussion

Over the course of this study, *Z. japonica* decomposed faster than *Z. marina* in all tidal zones and bed compositions. There are several reasons why *Z. japonica* might decompose more rapidly. The simplest explanation is that, morphologically, it is smaller than *Z. marina* and thus may have a higher surface area to volume ratio. This, in turn, could lead to the higher observed rates of decomposition. An alternative explanation is that its chemical or structural composition makes it easier to break down than its native congener. Because incubation in the field was relatively short, four to six weeks, the initial degradation is the more labile compounds in the eelgrass and hence *Z. japonica* may contain more of these labile compounds while *Z. marina* contains more structural compounds. The detrital food web is important for transferring energy and nutrients from seagrasses to associated organisms (Newell 1965; Harrison and Mann 1975; Harrison 1977; Phillips 1984) and the added material contributed by *Z. japonica* is readily broken down, making it quickly available to detritivores.

On the basis of SSCU, the sediment microbial assemblage associated with *Z. japonica* differed from that of the native eelgrass. Microbial assemblages isolated from transplanted beds of invasive, native, and mixed eelgrass showed different patterns of SSCU based on the composition of the eelgrass bed. However, patterns of SSCU did not differ when compared among different tidal heights. This suggests that the vegetation is

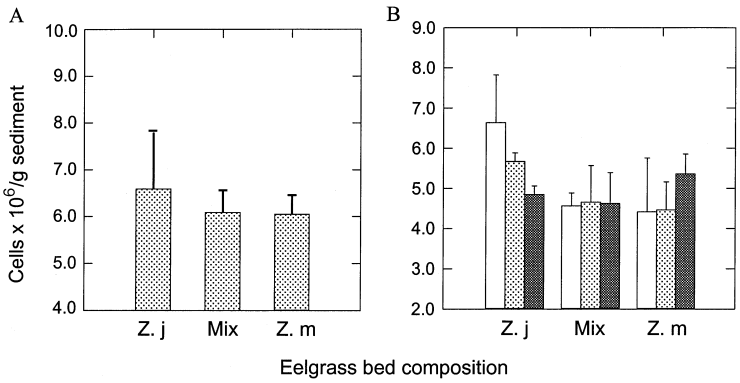

Figure 2. Abundance of bacteria from eelgrass beds of different composition as assessed by direct counts (DAPI epifluoresence microscopy). A. Naturally occurring eelgrass beds, ANOVA testing for the effect of bed composition/tidal zone: df = 2, $F = 0.21$, $P = 0.816$. B. Transplanted eelgrass beds, ANOVA testing for the effect of bed composition, tidal zone, and their interaction: bed composition – df = 2, $F = 2.92$, $P = 0.080$; tidal zone – df = 2, $F = 0.20$, $P = 0.819$; interaction – df = 4, $F = 1.25$, $P = 0.372$. Values are mean ± SE and abbreviations are as in Figure 1.

Table 2. MANOVA results (Univariate *F*-test) based on the first three principal components of SSCU obtained from the 31 unique carbon sources. The first three principal components explained 40% of the total variance associated with SSCU.

Effect	SS	df	MS	*F*	*P*
Test for the effect of bed composition					
Factor(1)	4.013	2	2.006	3.654	0.047
Error	9.883	18	0.549		
Factor(2)	9.994	2	4.997	5.907	0.011
Error	15.226	18	0.846		
Factor(3)	0.897	2	0.449	0.412	0.668
Error	19.589	18	1.088		
Multivariate test:					
Wilks' Lambda = 0.377		6, 32	–	3.357	0.011
Test for the effect of tidal zone					
Factor(1)	1.846	2	0.923	1.681	0.214
Error	9.883	18	0.549		
Factor(2)	0.505	2	0.253	0.299	0.745
Error	15.226	18	0.846		
Factor(3)	4.745	2	2.373	2.180	0.142
Error	19.589	18	1.088		
Multivariate test:					
Wilks' Lambda = 0.670		6, 32	–	1.180	0.342
Test for an interaction between bed composition and tidal zone					
Factor(1)	10.258	4	2.564	4.670	0.009
Error	9.883	18	0.549		
Factor(2)	0.274	4	0.069	0.081	0.987
Error	15.226	18	0.846		
Factor(3)	0.769	4	0.192	0.177	0.948
Error	19.589	18	1.088		
Multivariate test:					
Wilks' Lambda = 0.450		12, 41	–	1.251	0.282

having a strong influence on the microbial assemblage. Also of note was the interaction between bed composition and tidal height for the first principal component. The first principal component mainly comprises color development across all carbon sources and the interaction indicates that within a given bed composition, the total color development may vary among tidal zones. However, the multivariate test statistic is not significant for the interaction indicating that the overall measure of microbial community composition remains consistent within a particular bed composition across all tidal zones. Because there was no corresponding difference in microbial abundance, the differences in SSCU likely correspond to changes in microbial community composition rather than simply an alteration of microbial abundance. Changes in microbial composition could lead to different patterns or rates of nutrient mineralization, immobilization, retention, and subsequently the interaction between the microbes and the vegetation (Pedersen et al. 1999; Naeem et al. 2000).

The results of this study indicate that the abundant *Z. japonica* has the potential to alter ecosystem level processes such as decomposition and nutrient cycling in addition to the more obvious effects on habitat and infauna (e.g. Posey 1988). The rapid decomposition of the introduced eelgrass could lead to more rapid nutrient cycling which could in turn feed back into higher levels of both primary and secondary production within this system. Results also suggest that *Z. japonica* alters the associated decomposer assemblage and the functional diversity of microbes which may lead to further changes in decomposition, nutrient cycling, and nutrient retention.

Further research is needed to determine how these microbial communities differ between native and invasive eelgrass beds and to what extent the changes in the microbial assemblage affect decomposition and nutrient cycling. Additionally, the mechanism by which *Z. japonica* alters the microbial community was not elucidated in this study and warrants further investigation. In both marine and terrestrial systems, more research should focus on the effects of invaders on the microbial component of the recipient community as these microbial communities may strongly affect broader ecosystem processes.

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