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Reduced macrofauna diversity and abundance in response to red macroalgal detritus

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ABSTRACT

Macrophyte detritus from exogenous sources can play an important role in structuring benthic communities. Macrofaunal responses to seagrass wrack, mangrove leaf litter, and detritus from brown and green macroalgae have previously been examined through enrichment experiments. Yet effects from red macroalgal detritus, which is a major component of algal drift in many regions, are not well understood. In this study, enrichment experiments were performed on a shallow subtidal sandflat in Puget Sound, Washington, USA with detritus from three species of red macroalgae to assess: (1) whether macrofaunal assemblages were affected by two different "dosages" of red macroalgal enrichment (100 ml vs 500 ml per 0.079 m^3 of sediment); (2) whether macrofaunal response differed between one-time and repeated (weekly) additions of red macroalgae; and (3) whether responses to red macroalgal enrichment changed over time. There appeared to be little or no effect on macrofauna from one-time enrichment regardless of the amount/dosage of algae added. However, weekly additions of red macroalgae led to negative responses across macrofaunal taxa. These responses occurred rapidly, within the first 3 weeks, and were largely unchanged after 7 weeks, intensifying for only 2 of the 10 most common taxa. No opportunistic responses to weekly additions were observed. Frequent influx of some types of red macroalgae may degrade the quality of sedimentary habitats by leaching chemically defensive compounds or through other mechanisms, which should be investigated in future studies. Although weekly enrichment treatments were informed by previous estimates of detrital delivery rates near hard-bottom habitats in the same locality, further research is needed to assess detrital influx frequency and community response in other regions where red macroalgal detritus is common, and to understand the broader implications of exogenous detritus from red macroalgae on benthic ecosystems.

1. Introduction

Macrophyte detritus from exogenous sources is an important factor structuring benthic marine communities (Duggins et al. 1989; Gooday and Turley 1990; Mann 1988; Moore et al. 2004) and may be an increasingly prominent driver of ecosystem dynamics with greater storminess due to climate change (Baring et al. 2014; Bishop and Kelaher 2007; Brodie et al. 2014). Benthic responses to macrophyte detritus depend on a variety of factors, including the composition, magnitude, frequency, and duration of detrital influx (Bishop et al. 2010; Bishop and Kelaher 2008, Bishop and Kelaher, 2007; Godbold et al. 2009; Hanley et al. 2017; Lee 1999; O'Brien et al. 2017; Olabarria et al. 2007; Rossi et al. 2013). Although impacts of detrital material from seagrasses, mangroves, brown macroalgae, and green macroalgae have been explored experimentally in past studies (Bishop et al. 2010; Gladstone-Gallagher et al. 2014; Kelaher and Levinton 2003; O'Brien et al. 2010; Olabarria et al. 2010; Taylor et al. 2010), effects of red macroalgal detritus on benthic communities are not well understood.

Red macroalgae are a common component of macroalgal drift in many coastal areas, particularly in the northern hemisphere and Antarctica (Amsler et al. 1999; Biber 2007; Eklund et al. 2005; Norkko et al. 2004). Many species are perennial or pseudo-perennial, with thalli or parts of thalli detaching from substrate during seasonal storms or other disturbances (Cecere et al. 2011). Red macroalgal drift is transported to adjacent habitats by water currents and, in some cases, by organisms such as urchins (Amsler et al. 1999; Biber 2007). In soft-bottom environments specifically, exogenous sources of red macroalgal detritus can become readily incorporated into surface sediments (Heery and Sebens unpublished data) and sedimentary food webs (Norkko et al. 2004).

As a detrital resource, red macroalgae may differ from other types of macrophytes in several ways. Red macroalgae are highly efficient at taking up and storing nutrients (Jones et al. 1995; Vergara et al. 1993) and they decay rapidly (Rice and Tenore 1981; Tenore et al. 1984).

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High content of essential fatty acids and proteins could make them an important nutritional source for recipient communities (Fleurence et al. 1999; Galloway et al. 2012; Leduc and Probert 2009; Pereira et al. 2012). Yet many red macroalgal species are also rich in chemically defensive compounds that deter consumers, including acetylene-containing lipids and halogenated secondary metabolites (Amsler et al. 1998; Boettcher and Targett 1993; Fenical 1975; Pedersen et al. 1974). Whether exogenous sources of red macroalgal detritus primarily serve as a resource subsidy, lethal toxin, or usable, yet minor energetic resource for recipient assemblages is presently unclear (Eklund et al. 2005; Ince et al. 2007; Norkko et al. 2004).

Past studies assessing the role of red macroalgal detritus in shaping benthic assemblages have found mixed results. In some cases, it causes rapid shifts in community structure and decreases in diversity (Norkko and Bonsdorff 1996). In other cases, it enhances the abundance of selected organisms and increases species richness (Ince et al. 2007), even as other types of macroalgal detritus negatively impact diversity (Cardoso et al. 2004). Benthic response may be particularly influenced by the amount, delivery rate, and duration of detrital influx (Bishop and Kelaher 2007; Hanley et al. 2017; Sundbäck et al. 1990). Studies that evaluate the relative importance of these factors are essential for understanding the likely effects of red macroalgal detritus on benthic communities given a variety of environmental conditions and future trajectories for disturbance.

This study examined the effect of red macroalgal detritus on soft-sediment assemblages through a series of field experiments in Puget Sound, Washington, USA. Enrichment experiments were performed in a shallow subtidal sandflat to assess: (1) whether macrofaunal assemblages were affected by two different amounts, or "dosages," of red macroalgal detritus; (2) whether macrofaunal response differed between one-time and repeated (weekly) additions of red macroalgal detritus; and (3) whether responses changed over time. Additions of red macroalgae were hypothesized to have a subsidizing effect on deposit feeders and their predators at low doses, but act as a stressor at higher dosage levels and with repeated additions over time.

2. Methods

2.1. Study area

Puget Sound is a large, fjordal system with estuarine circulation and extensive sedimentary habitat. Red macroalgae are a dominant component of algal drift in shallow sedimentary environments in the region (Heery and Sebens unpublished data). The degree of deposition and integration of red macroalgal detritus in sediments varies spatially and temporally, though is elevated after major storms (typically in late autumn) and near hard-substrate habitats. During summer months, concentrations of red macroalgal detritus can reach as much as 2700 ml/m^3 and average 655 ± 190 ml/m^3 in sediments within a meter of hard substrates (compared with 157 ± 57 ml/m^3 in sediments 15 m away) and turnover rapidly, degrading or being expelled from sediments within 4 days (Heery and Sebens unpublished data).

Experiments in this study were conducted on a subtidal sandflat at approximately 4–6 m depth near Alki Point, Washington (47° 34′ 13″ N, 122° 24′ 54″ W; Fig. S1). The site was selected because it had limited drift accumulation, was relatively far (> 50 m) from hard substrate habitats, and had a gradually sloping bottom profile, which facilitated establishment rectangular grids of experimental plots over a small depth range. Prior surveys indicated that *Chondracanthus exasperatus*, *Polyneura latissima*, and *Sarchodiotheca gaudichaudii* dominated algal drift in the area (Heery and Sebens unpublished data). C:N ratios for *C. exasperatus* and *P. latissima* were estimated at 9.9 and 7.1, respectively, but were not available for *S. gaudichaudii* (Table S1). From the literature, phenolic content for *C. exasperatus* and *S. gaudichaudii* was estimated at 0.1% and 4.3% of dry weight, respectively (Pennings et al. 2000; Tibbetts et al. 2016), but was unknown for *P. latissima.*

2.2. Experimental design

Two enrichment experiments were conducted – one ("Experiment 1") in the summer of 2013 and the other ("Experiment 2") in the summer of 2015. Experiment 1 tested the effect of two different quantities of red macroalgal detritus on macrofaunal assemblages. Experiment 2 tested the effect of one-time versus repeated, weekly additions of red macroalgal detritus on macrofauna. Algal material used for enrichment treatments in both experiments comprised 50% *C. exasperatus*, 30% *P. latissima*, and 20% *S. gaudichaudii*, to reflect composition of red macroalgae in drift in the region (Heery and Sebens unpublished data). Methods for incorporating algal material into sediments were based on those described by Bishop et al. (2010) and adapted for subtidal deployment on SCUBA, as described below.

2.2.1. Experiment 1

To test macrofaunal response to different amounts of red macroalgal detritus, 28 circular experimental plots (0.5 m diameter, center points separated by 1.5 m) were established at the study site in a rectangular grid on 3 June 2013. The grid spanned a depth range of < 1 m, with the shallowest plot situated at 4.8 m and the deepest plot at 5.4 m. Each plot was marked at the center with a small construction flag. Plots were randomly assigned to one of four treatments: (n = 7 replicate plots per treatment level; Table 1): low-dose (100 ml) algal addition (A1), high-dose (500 ml) algal addition (A2), hand-churned control (C1), and undisturbed control (C2). The volumes of algae used in treatments A1 and A2 were selected based on detritus loads in the area as quantified in prior surveys (Heery and Sebens unpublished data) and coincided with sediment detrital concentrations of 256 and 1282 ml per m^3 of sediment, respectively. Based on volume:weight ratios estimated in lab (0.10085 g dry weight per ml of shredded macroalgae), 100 ml and 500 ml treatments were estimated to roughly correspond to 10 and 50 g of dry weight, or 26 and 130 g/m^3 of sediment. To prepare algal treatments, red macroalgae (*C. exasperatus*, *P. latissima*, and *S. gaudichaudii*) were collected from the field the day before and shredded into 0.5–1 cm pieces using a large cheese grater, with care taken to minimize exposure time to air. Measured quantities of shredded macroalgae were then delivered to the study site at slack tide in closed zip-lock bags, which were stored in a dark cooler with cold seawater. Algae were deposited onto experimental plots by scooping sediment from plots into zip-lock bags and emptying a mixture of algae and sediment back onto plots. The mixture was then hand-churned into the top 5 cm of sediment until evenly distributed. C1 plots were additionally hand-churned without algal material, while C2 plots were left undisturbed.

Sediment core samples were collected from experimental plots after 8 weeks and 16 weeks, on 29 July and 23 September 2013. Two replicate cores (10 cm diameter, 8 cm depth) were removed from experimental plots on each sampling date. Cores were stored in zip-lock bags and transported to the laboratory in a dark cooler over ice. The

Table 1
Summary of treatments in Experiments 1 and 2. Sediment samples were collected from experimental plots after 8 and 16 weeks in Experiment 1, and after 3 and 7 weeks in Experiment 2.

Treatment	Type	Dosage	Frequency
Experiment 1			
A1	Algal Addition	100 ml	One-time
A2	Algal Addition	500 ml	One-time
C1	Hand-churned control	*na*	One-time
C2	Undisturbed control	*na*	One-time
Experiment 2			
A1	Algal Addition	120 ml	One-time
A3	Algal Addition	120 ml	Weekly
C1	Hand-churned control	*na*	One-time
C3	Hand-churned control	*na*	Weekly