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Are seagrass beds indicators of anthropogenic nutrient stress in the rocky intertidal?

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ABSTRACT

It is well established that anthropogenic nutrient inputs harm estuarine seagrasses, but the influence of nutrients in rocky intertidal ecosystems is less clear. In this study, we investigated the effect of anthropogenic nutrient loading on *Phyllospadix* spp., a rocky intertidal seagrass, at local and regional scales. At sites along California, Washington, and Oregon, we demonstrated a significant, negative correlation of urban development and *Phyllospadix* bed thickness. These results were echoed locally along an urban gradient on the central California coast, where *Phyllospadix* shoot $\delta^{15}\text{N}$ was negatively associated with *Phyllospadix* bed thickness, and experimentally, where nutrient additions in mesocosms reduced *Phyllospadix* shoot formation and increased epiphytic cover on *Phyllospadix* shoots. These findings provide evidence that coastal development can threaten rocky intertidal seagrasses through increased epiphytism. Considering that seagrasses provide vital ecosystem services, mitigating eutrophication and other factors associated with development in the rocky intertidal coastal zone should be a management priority.

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1. Introduction

Foundation species provide essential ecosystem services including storm protection and carbon sequestration, and they are often nurseries for commercially important marine species (Barbier et al., 2008; Bruno et al., 2003; Smale et al., 2013; Waycott et al., 2009). However, many coastal foundation species are in global decline via direct threats including land transformation, overexploitation, and pollution, and indirect threats like trophic downgrading and climate change (Estes et al., 2011; Jackson et al., 2001; Waycott et al., 2009). For example, seagrass beds along the western coast of the United States are potentially threatened by nearly 50 million people who disproportionately occupy coastal areas (Halpern et al., 2009; Merrifield et al., 2011), highlighting the need to understand the role of anthropogenic nutrient inputs as an underlying mechanism for seagrass decline (Burkholder et al., 2007; Hughes et al., 2013).

Over a century of studies have demonstrated negative effects of anthropogenic nutrient input on seagrass beds in estuaries (e.g. Burkholder et al., 1992; Duarte, 1995; Harlin and Thorne-Miller, 1981; Hughes et al., 2013; Kaldy, 2014; Letts and Adeney, 1908; Orth and van Montfrans, 1984; Orth et al., 2006; Schubert et al., 2013; Short et al., 1995; Short and Burdick, 1996; Tomas et al., 2011; Waycott et al., 2009). These studies show that excessive nutrient loading can impose

physiological and biological consequences to estuarine seagrasses via nitrogen toxicity, increased turbidity, and epiphytic overgrowth (Burkholder et al., 2007; Valiela et al., 1997). However, relatively little is known about the consequences of anthropogenic nutrient inputs to foundation species in the rocky intertidal.

Here we use the only seagrass genus to grow on rocky habitat, *Phyllospadix*, to investigate the associations of seagrass beds and epiphyte growth with anthropogenic nutrient loading. *Phyllospadix* forms expansive and dense beds in rocky intertidal and subtidal habitats along the north Pacific coast (den Hartog and Kuo, 2010). Along much of the eastern Pacific, two species, *Phyllospadix torreyi* and *P. scouleri*, grow together and occupy both the lower intertidal and upper subtidal zones (Ramirez-Garcia et al., 1998). Both species have broad and almost completely overlapping distributions that span from Baja, California to Alaska (den Hartog, 1970; Phillips, 1979). While *P. torreyi* is often found in higher abundances at lower tidal heights due to its sensitivity to air exposure during low tides (Ramirez-Garcia et al., 1998), *P. scouleri* has been found to coexist with *P. torreyi* (Ramirez-Garcia et al., 1998; Ramirez-Garcia et al., 2002) and in our study these species were almost always found together at sites and within plots. A third species, *P. serrulatus* is known to exist in Oregon and Washington (den Hartog, 1970; Phillips, 1979), but was not detected. *Phyllospadix* beds play a key functional role in the intertidal by moderating temperatures and community composition (Shelton, 2010). Like other seagrasses, leaves of *Phyllospadix* create substrate for fast-growing algal epiphytes, such as diatoms, *Ulva* sp., *Ectocarpus* sp., *Melobesia* sp. and *Smithora* sp. (Willcocks, 1982). *P. scouleri* are characterized by flat, 2–4 mm wide leaves whereas *P. torreyi* leaves are tubular, <2 mm wide and firm

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(Phillips and Menez, 1988). Algal epiphytes are commonly concentrated on the tips (the older leaf portions) of both species and along the edges of *P. scouleri* blades (Harlin, 1980; Willcocks, 1982). *P. scouleri* may carry a higher algal epiphyte load due to its greater blade surface area and tendency to be found in areas that are protected from sand-scour and have higher irradiance relative to *P. torreyi* (Harlin, 1980; Kozloff, 1983; Trautman and Borowitzka, 1999). Anthropogenic nutrient inputs to *Phyllospadix* beds may lead to epiphytic overgrowth and associated physiological and biological consequences such as reduced productivity (Hughes et al., 2013; Spivak et al., 2009; Whalen et al., 2013; Willcocks, 1982; Zimmerman, 2010). The objective of this study was to investigate the role of coastal nutrient enrichment on intertidal *Phyllospadix* beds. While there may be species differences as discussed above, we were specifically interested in comparing seagrass beds among sites rather than within sites and between species. We therefore lumped *P. scouleri* and *P. torreyi* together and focused analyses at the genus level because these two species were found intermixed at our field sites, and we therefore could not assess species-specific differences quantitatively.

We examined the relationship between coastal urban development, a proxy for nutrient loading (Short and Burdick, 1996), and adjacent *Phyllospadix* beds along the west coast of the United States. We then used nitrogen stable isotope analysis to quantify the influence of nutrient loading on *Phyllospadix* beds at a local scale along an urban gradient of development. Finally, we performed a mesocosm experiment to understand the mechanisms that drive regional and local patterns. We focused the mesocosm solely on *P. scouleri* so that we would remove only single rhizomes with shoots for replicates in our experiments. We performed this work with the prediction that nutrient enrichment decreases metrics of *Phyllospadix* productivity and increases algal epiphyte loading. Because the rocky intertidal is exposed to wave action and high mixing, the number of studies examining anthropogenic nutrient loading to this ecosystem is minimal but we believe is critical to understand as a potential threat in highly populated areas.

2. Materials and methods

2.1. Coastal development and *Phyllospadix* beds

To determine the relationship between coastal development and *Phyllospadix* (*P. scouleri* and *P. torreyi*) bed metrics, we examined long-term seagrass data in relation to estimates of development in adjacent watersheds (e.g. Short and Burdick, 1996). We used a long-term monitoring dataset of monthly *Phyllospadix* surveys conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) from 2001 to 2012 at 28 rocky intertidal sites between Pt. Conception, California to Port Angeles, Washington (Fig. 1). At each site, surveyors measured *Phyllospadix* bed thickness (cm) along 10 m replicate transects ($n = 3$ per site). To quantify epiphyte cover at each site, surveyors assigned qualitative ranks of 'none' = 0%, 'low' = 1–20%, 'medium' = 21–50%, and 'high' $\geq 50\%$ cover of algal epiphytes on *Phyllospadix* shoots. We converted these categories into numerical data values of 0, 11, 36, and 76 respectively to reflect mean cover, rounded to the nearest integer. We then averaged thickness and epiphyte scores by year for each site.

To estimate the extent of coastal urban development at each site surveyed by PISCO, we used The Nature Conservancy's (TNC) Conservation Assessment of West Coast (USA) Estuaries Geodata Viewer (Gleason et al., 2011; Merrifield et al., 2011), which measured the development per catchment in coastal watersheds. Developed land considered areas that contain some to significant amounts of constructed materials used and maintained by humans and includes areas of heavy urban use, family housing, land-use planning such as irrigation, and areas for recreation (Gleason et al., 2011; Merrifield et al., 2011). This database was intended to describe watershed impacts on estuaries, but the proximity of watersheds to the rocky intertidal zone allowed us to quantify watershed development (urban land use) across PISCO sites using

watersheds as our proxy. We used Google Earth (Google earth V 7.1.2.2041, 2014) to quantify the linear distance (km) between each PISCO rocky intertidal site and neighboring watersheds. We then chose the nearest watershed and assigned the TNC development per catchment (in acres) value to that rocky intertidal site. In some cases, watershed development data from one watershed was used for two or three PISCO sites. Distances between rocky intertidal sites and their associated watersheds were between 0.36 and 30.83 km with an average of $7.78 \text{ km} \pm 7.52 \text{ SD}$.

To test the association between coastal development, *Phyllospadix* bed thickness, and epiphyte cover on shoots, we used linear and generalized linear mixed-effects models. Mixed-effects models are useful when including both fixed and random effects (Bates et al., 2016). We tested for the relationship between response variables and Coastal Development (fixed effect) and included the random effects of Year, Watershed, and Year * Watershed into the model. Using AICc model selection, we compared models with every unique combination of random factors, and selected the lowest scoring (best-fit) models within two AICc units (Burnham and Anderson, 2002). To perform linear mixed-model (LMM) selection for drivers of *Phyllospadix* bed thickness ($n = 216$) we used the lmer function using the lme4 package (Bates et al., 2016) in R (v. 3.2.2; R Core Team, 2015). Since data for epiphyte cover ($n = 162$) was generated with rank scores we used a generalized linear mixed model (GLMM) using a Poisson error distribution to compare competing models.

2.2. Local nutrient enrichment and *Phyllospadix* beds

To determine the relationship between nutrient enrichment and *Phyllospadix* bed metrics at a local scale, we conducted surveys at accessible *Phyllospadix* beds along a developmental gradient on the central California coast (Fig. 1). Watersheds in this location transition from highly urbanized to relatively undeveloped from south to north (Fig. 1). Our southernmost site, Pleasure Point, had nearly 300 times more development per catchment (acres) compared to more northerly sites (<http://www.tnccmaps.org/estuaries/>). We surveyed each site ($n = 5$) within three consecutive days in May 2013 at low tide (at least -0.5 m). At each site we measured the average *Phyllospadix* bed thickness (cm) in replicate $0.25 \times 0.25 \text{ m}$ quadrats at the high, medium, and low tidal ranges of each bed. We did this to account for possible variation in *Phyllospadix* parameters as a function of tidal height and to account for any partial depth zonation between the two species, of which we found none. (e.g. Boese and Robbins, 2008). We collected replicate *Phyllospadix* shoots ($n = 5$) from each quadrat and transported samples on ice to Long Marine Laboratory at the University of California, Santa Cruz. We rinsed shoots and scraped off algal epiphytes from the shoots. We dried shoots and algal epiphytes at $60 \text{ }^\circ\text{C}$ for 24 h to determine dry biomass.

We used stable isotopes to estimate anthropogenic signals at each site we sampled. Stable nitrogen isotope ratios ($\delta^{15}\text{N}$) can be used to identify sources of coastal pollution in adjacent freshwater, estuarine, and marine producers because many anthropogenic sources of nitrogen, particularly sewage effluent, are enriched in $\delta^{15}\text{N}$ compared to baseline values due to trophic fractionation (e.g. Costanzo et al., 2005; Huntington and Boyer, 2008; Leavitt et al., 2006; McClelland et al., 1997). We analyzed *Phyllospadix* shoot tissue by site (we haphazardly chose 18 shoots per site: two shoots per quadrat with three quadrats per transect and three transects per site) for $\delta^{15}\text{N}$ using an isotope ratio mass spectrometer (ThermoFinnigan Delta-Plus XP) coupled to an elemental analyzer (Carlo Erba 1108) at the University of California Santa Cruz Stable Isotope Laboratory. Prior to quantifying $\delta^{15}\text{N}$ in *Phyllospadix* shoots, we homogenized shoots with a mortar and pestle. To test for the relationship between mean shoot $\delta^{15}\text{N}$ and *Phyllospadix* bed thickness, we performed a linear regression among sites. We repeated this analysis to quantify the relationship between shoot $\delta^{15}\text{N}$ and algal epiphyte loads. To confirm that we were sampling a true

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