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An evaluation of factors controlling the abundance of epiphytes on *Zostera marina* along an estuarine gradient in Yaquina Bay, Oregon, USA

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ABSTRACT

Epiphytes on seagrass (*Zostera marina*) growing in the lower intertidal were examined along an estuarine gradient within Yaquina Bay, Oregon over a period of 4 years. The Yaquina Estuary receives high levels of nutrients from the watershed during the wet season and from the ocean during the dry season. Mean epiphyte biomass per unit seagrass leaf surface area (epiphyte load) peaked during the summer, and thus epiphyte load was higher during dry season than wet season in both marine and riverine dominated regions. Epiphyte load was greater in marine than in riverine dominated areas in both wet and dry seasons, although only dry season differences were significant. There was no evidence that grazers controlled epiphyte load differences. Annual DIN concentration was inversely related to epiphyte load, principally because of elevated wet season dissolved inorganic nitrogen from river inputs. While there was a positive annual relation of epiphyte load to PO_4 concentration, it is not clear that phosphorus becomes a limiting nutrient for epiphyte growth. Water column light attenuation tends to increase linearly with distance from the estuary mouth, while both epiphyte load and *Z. marina* biomass tend to decrease. Both seagrass and seagrass epiphytes may be increasingly light limited in the upper estuary, and thus, epiphyte loads may have proportionally more impact on seagrass occurrence in this estuarine region.

1. Introduction

Epiphytic growth on the surface of seagrass leaves is a natural part of the seagrass community that may have high biodiversity (e.g. Saunders et al., 2003; Piazzi et al., 2004; Uku et al. 2007) and may contribute significantly to the overall seagrass community productivity (Penhale, 1977; Moncreiff et al., 1992; Wear et al., 1999). Additionally, epiphytes provide support to higher trophic levels (Jernakoff and Nielsen, 1997, 1998; Spivak et al., 2009; Whalen et al., 2013; Reynolds et al., 2014). However, dense epiphytic cover leads to decreased seagrass growth and can reduce survival because of light limitation (reviewed by Nelson, 2017b). High levels of anthropogenic nutrients have been associated with increases in seagrass epiphytes and decreased health of seagrass beds (reviewed by Nelson 2017a, 2017b). In some systems, light reduction to seagrasses from epiphyte load may reach 60–80%, at least seasonally (Harden, 1994; Dixon and Kirkpatrick, 1999). Mesograzers are believed to be an important factor that may influence the degree to which epiphyte load impacts seagrasses (Reynolds et al., 2014). Epiphyte load appears to be a major variable determining the ability of seagrasses to grow and survive under elevated nutrient conditions. Effects of epiphyte load on light available to seagrasses is thus an important factor which must be quantified to be able to develop accurate seagrass stressor response models for evaluating overall impacts of nutrients to seagrass systems (Kemp et al., 2000, 2004).

In contrast to seagrass systems such as Chesapeake Bay, (Stankelis et al., 2001; Kemp et al., 2004), Florida (Frankovich and Fourqurean, 1997; Fourqurean et al., 2010), and the Mediterranean (Piazzi et al., 2004; Balata et al., 2007), where many studies of effects of seagrass epiphytes have been conducted, estuaries on the west coast of the U.S. have important differences in fundamental ecological drivers. The estuaries have high natural loadings of nutrients, which occur both from the watershed in winter and from the coastal ocean in summer (Brown et al., 2007; Brown and Ozretich, 2009). Water temperatures are also strongly influenced by the coastal ocean and are typically low all year (flood tide, 8–16 °C) in the portion of the estuaries supporting seagrass/epiphyte systems (Brown and Folger, 2009). Tidal amplitudes ($\sim$3 m) are macrotidal (Monbet, 1992), and the majority of seagrass habitat is intertidal rather than subtidal. For example, less than 10% of the population coverage of *Z. marina* in three Oregon estuaries is found in subtidal areas $\leq$0.6 m below mean lower low water (MLLW) (Young et al., 2009). Thus, application of seagrass nutrient, stressor-response models requires calibration of the epiphyte load element to correctly capture the role of epiphytes in influencing seagrass growth and survival.

Quantitative knowledge of the dynamics of epiphytes on seagrasses

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remains relatively limited for the Pacific Northwest region of the USA (Thom, 1990; Thom et al., 1991; Williams and Ruckelshaus, 1993; Nelson and Waaland, 1997), and particularly for systems located outside of Puget Sound and adjacent waters (Kentula, 1982; Ruesink, 2016). Previous studies have not quantified seagrass epiphytes along the estuarine transition from marine dominated to river dominated regions of the system, nor has there been a spatial and temporal assessment of the impacts of epiphyte loads on light availability to seagrasses. Therefore, a study was conducted to assess the following hypotheses: 1) epiphyte load on *Zostera marina* varies along the estuarine gradient in Yaquina Bay, 2) spatial and temporal patterns of epiphytes on *Z. marina* correlate with spatial and temporal patterns of nutrient distribution, 3) epiphyte loads result in levels of light reduction to *Z. marina* that may impact the seagrass, and 4) mesograzer presence may ameliorate impacts of epiphyte load to *Z. marina*.

2. Methods

2.1. Study Area

Yaquina Bay is a small (19 km^2) estuary located on the central coast of Oregon, USA (Fig. 1). The watershed (660 km^2) is 85% forested, 6.5% grasslands, and is < 1% developed land, with the remaining area as wetlands and estuary. Population density is relatively low (12 km^{-2}). Within Yaquina Bay and in the Pacific Northwest coastal region in general, there are two distinct hydrological seasons. In the winter wet season, river flows are high and can be five times greater than during the summer dry season, and the dominant (74%) source of dissolved inorganic nitrogen (DIN) into the estuary is the watershed. During the summer period of low river flow, coastal upwelling is a major (82%) source of nitrogen and phosphorus into Yaquina Bay (Brown et al., 2007). Relative to river flow and upwelling, atmospheric deposition, wastewater input, and benthic recycling are minor (1–2 orders of magnitude lower) sources of nitrogen to both the estuary and the watershed (Brown and Ozretich, 2009). Through analysis of new cruise data, historical water quality data, hydrodynamic modeling and stable isotope analyses of nitrogen sources, Yaquina Bay has been divided into Marine and Riverine zones which tend to be dominated by differing sources of nutrients (Brown et al., 2007). The division is approximately associated with a median salinity of 26 (Fig. 1).

2.2. Epiphyte abundance

Epiphytes growing on *Z. marina* leaves were collected at six stations, located within the lower intertidal zone between 3.5 and 17 km upriver from the estuary mouth, over the period from August 2000 through November 2004 (Fig. 1). Stations WN1-WN4 were all within the elevation range + 0.2 to − 0.2 m MLLW, while due to bathymetric variation up-estuary, WN5 was at + 0.7 and WN6 was at − 1.6 m MLLW. Over the course of the study, sampling intensity was reduced and sampling was discontinued at Stations WN2 and WN5 in February 2002, and at Station WN6 in March of 2003. As resources varied, sampling occurred at approximately monthly intervals from 2000 to 2001 and again in 2003, and at approximately bimonthly intervals in 2002 and 2004. Sampling dates and locations are provided in Supplementary Table 1.

At each station, 6 eelgrass shoots were collected into plastic bags. Because epiphyte load varies with blade age within a shoot, to obtain an average estimate for load within a shoot, one exterior leaf (older) and one internal leaf (younger) were selected from each shoot in the laboratory. Variation among shoots within a station was not a prime focus of the current study, and the replicate observations for the 6 shoots were pooled to calculate mean values of all parameters per site and date, which were used for subsequent analyses. Epiphytes were scraped from both sides of each leaf collected, and both epiphytes and seagrass leaves were separately placed in a drying oven for 24–36 h at 60–70 °C and dry weights of the material removed were determined for each leaf. While the term epiphyte biomass is used to refer to dry weight (g) of the material collected, the measurements included inorganic material since this material also reduces light available to the

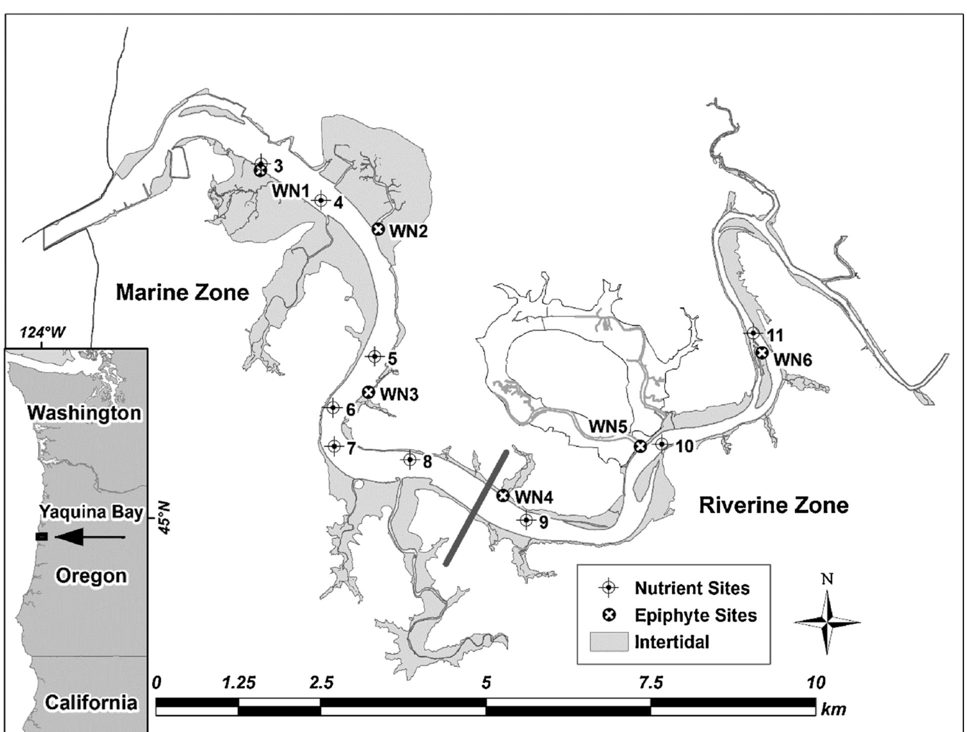

Fig. 1. Sample locations for seagrass epiphytes and nutrients along the length of the Yaquina estuary. Three epiphyte stations were located within both the Marine and Riverine zones. Gray bar indicates the approximate boundary of the two estuarine zones.