



# Macrophyte community response to nitrogen loading and thermal stressors in rapidly flushed mesocosm systems



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## ABSTRACT

A mesocosm system was developed to simulate estuarine conditions characteristic of short water-residence time ecosystems of the Pacific Coast of North America, and used to evaluate the response of multiple macrophyte metrics to gradients of NO<sub>3</sub> loading and temperature. Replicated experiments found that few responses could be directly attributed to NO<sub>3</sub> loading up to 6 x ambient. Some response metrics exhibited weak relationships with nutrient loading but could not be resolved with available statistical power. While direct nutrient responses were found for some species-specific metrics (e.g. green macroalgal growth and biomass, tissue N%, etc.), many patterns were confounded with temperature. Temperature generally had a larger effect on response metrics than did nutrient load. Experimental macrophyte communities exhibited community shifts consistent with the predicted effects of nutrient loading at 20 °C, but there was no evidence of other eutrophication symptoms (phytoplankton blooms or hypoxia) due to the short system-residence time. The *Z. marina* Nutrient Pollution Index (NPI) tracked the NO<sub>3</sub> gradient at 10 °C, but exhibited no response at 20 °C, which may limit the utility of this metric in areas with marked thermal seasonality. Results suggest that teasing apart the influence of temperature and nutrients on the expression of eutrophication symptoms will require complex multi-stressor experiments and the use of indicators that are sensitive across a broad range of conditions.

## 1. Introduction

Estuaries integrate the biology and geochemistry of terrestrial, riverine and oceanic drivers and respond to many forcing functions at both the land and ocean interface. Human activities have dramatically increased the input of nutrients, especially nitrogen inputs, into many ecosystems (Sobota et al., 2013). Increased nitrogen loading has been directly linked to the proliferation of planktonic and macroalgal blooms at a global scale (Glibert et al., 2005; Paerl and Scott, 2010), with negative impacts on estuarine ecology, human health and economics (Hoagland et al., 2002; Bricker et al., 2008; Compton et al., 2011).

Healthy seagrass communities are often considered an indicator of low anthropogenic impacts because seagrasses have relatively high light requirements and they thrive under low nutrient conditions. When estuarine macrophyte communities receive anthropogenic nutrient loading, algal species tend to dominate and there is increased competition among primary producers for light. This “nutrient loading hypothesis” (Short et al., 1991; Bricker et al., 2008; Brauer et al., 2012) suggests that under excessive anthropogenic nutrient loads, seagrass systems can be replaced by either macroalgae or phytoplankton

dominated systems.

Although this process is conceptually simple, determination of nutrient thresholds that negatively impact seagrass communities has been elusive due to the many factors involved (Valiela et al., 1997; Valiela et al., 2000; Nixon et al., 2001; Nielsen et al., 2004). This is further complicated because residence time influences the nutrient loading rate as well as the export of organic matter (Barrón et al., 2003) and biogeochemical processing rates. Valiela et al. (1997) hypothesized that under longer residence times, eutrophication impacts associated with a given nitrogen load would be more severe than at shorter residence times. Few studies have examined or quantified empirical load-response data within short residence time systems. Additionally, thermal characteristics of the water body likely influence susceptibility to eutrophication. Another potential complication includes colonization by non-native species that may be favored by increased nutrients or altered thermal regimes. Consequently, Cloern (2001) stated that the conceptual model of coastal eutrophication in response to nutrient loading will require addressing how system-specific attributes influence ecosystem response.

The nutrient loading hypothesis as applied to estuarine macrophyte

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communities was pioneered by researchers in New England (Short et al., 1991; Short et al., 1995; Valiela et al., 1997; Nixon et al., 2001), and supported by both field observations and manipulative mesocosm experiments (Hauxwell and Valiela, 2004; Howarth and Marino, 2006). However, manipulative experiments have only explored systems with long-residence times (e.g. coastal ponds, secondary and tertiary embayments, etc.). For example, pioneering mesocosm studies (Burkholder et al., 1992; Short et al., 1995; Taylor et al., 1995; Taylor et al., 1999) used long residence times (daily exchange of about ~10–20%) and warm water temperatures (> 20 °C), which favor development of eutrophic conditions (e.g. organic matter build up, high respiration rates, etc.). These conditions may exacerbate experimental effects and are not necessarily representative of field conditions in open coast estuaries along the Pacific Coast of North America (Hickey and Banas, 2003; Lee and Brown, 2009), or other upwelling regions such as the Iberian Peninsula, Chilean coast or Benguela Current system (Varela et al., 2005; Pitcher et al., 2010; Barton et al., 2015).

Many estuaries in upwelling-dominated areas may not conform to traditional estuarine paradigms (see Pitcher et al., 2010 for examples). Estuarine systems in the Pacific Northwest (PNW) region of the United States, such as Yaquina Bay, OR, receive large nutrient loads ( $2227 \text{ kg N km}^{-2} \text{ y}^{-1}$ ; Brown and Ozretich, 2009) primarily from natural sources and have not exhibited seagrass losses (Kaldy, 2014). In contrast to many systems with high nutrient concentrations, the primary nitrogen source (both riverine and oceanic) is  $\text{NO}_3$  coming from either nitrogen fixation by red alder trees in the watershed or coastal upwelling (Lee and Brown, 2009; Brown and Ozretich, 2009). Further, many estuaries along the Oregon coast are characterized by short residence times on the order of 2–12 days, with a large tidal prism relative to estuary volume, and are considered well mixed systems (Hickey and Banas, 2003; Lee and Brown, 2009; Lemagie and Lerczak, 2015). Likewise, the occurrence of hypoxic water and off-shore phytoplankton blooms are often linked to advection of recently upwelled water masses rather than estuarine eutrophication processes (Brown and Power, 2011). Consequently, we wondered if there was a nutrient loading rate that would trigger severe eutrophication expression in systems characterized by short system residence time, since this could be a factor contributing to the moderately low expression of eutrophication observed in many PNW estuaries (Bricker et al., 2007, 2008).

Another factor that has not generally been evaluated in estuarine ecosystems is the response of non-native species to eutrophication and the possible influence on community structure (Cloern, 2001). The non-native seagrass *Zostera japonica* has colonized many estuarine systems in the PNW and continues to spread (Shafer et al., 2014). The colonization process transforms mudflat to structured seagrass habitat, although the ecological consequences are unclear. *Z. japonica* colonization has led to control and eradication efforts (Shafer et al., 2014). Recent work concluded that this species is favored in high intertidal habitats with low bathymetric slope and by warm water temperatures (Shafer et al., 2014; Kaldy et al., 2015); however, little is known about the response to nitrogen loading which could influence colonization potential.

Many PNW estuaries have a moderately low expression of eutrophication symptoms (Bricker et al., 2007, 2008) despite high nutrient loads, which appear to contradict predictions of the nutrient loading hypothesis. Consequently, we wanted to determine if there was a nutrient loading threshold that would cause these systems to express more extreme eutrophication impairment. Estuarine plant communities, seagrass, macroalgae and microalgae, were subjected to a factorial experiment with a gradient of  $\text{NO}_3$  loading across two temperatures to assess a suite of morphological, physiological and biogeochemical response metrics. We chose nutrient loading rates that represent a realistic gradient of potential anthropogenic nutrient inputs. Likewise, we chose two thermal regimes that mimic conditions near the mouth (ocean dominated) and upstream near the limit of *Z. marina*

distribution (riverine dominated). We predicted that PNW estuarine macrophyte communities would exhibit most severe eutrophication symptoms (species shifts, algal blooms, increased production and respiration) under medium or high nitrate loading and warm thermal regimes. To test this hypothesis, we developed a mesocosm system that simulated estuarine conditions of PNW open coast estuaries, which are characterized by large tidal exchange and short residence time.

Research on seagrass ecosystems response to nutrients has focused primarily on simple, species specific metrics such as biomass or growth rates. Here, we use a variety of integrative metrics to assess responses including community structure, the nutrient pollution index, ecosystem metabolism, wasting disease index and shoot mortality. Community structure or dominance is a direct assessment of changes in macrophyte dominance and is directly related to the nutrient loading hypothesis. Consequently, we expected community structure to strongly reflect responses to mesocosm treatments. The Nutrient Pollution Index (NPI; Lee et al., 2004) is the ratio of leaf nitrogen to leaf mass and has been proposed as a metric to quantify nitrogen availability. Our experiments provide an opportunity to rigorously validate the efficacy of the metric, expecting that the metric would accurately track the  $\text{NO}_3$  loading gradient. We also use ecosystem metabolism measured as  $\text{O}_2$  dynamics to evaluate community response to  $\text{NO}_3$  and thermal stressors. We expected that as species composition shifted and organic matter accumulated there would be an increase in ecosystem respiration. Further, we evaluated the whole plant Wasting Disease Index (WDI; Burdick et al., 1993) because previous work has shown that *Z. marina* subjected to warming and  $\text{NO}_3$  loading may be more susceptible to wasting disease. Our expectation was that the WDI would increase with temperature and  $\text{NO}_3$  loading. Likewise, since shoot mortality is the ultimate manifestation of integrated response metrics, we examined mortality responses to  $\text{NO}_3$  and thermal stress, expecting greater mortality under high  $\text{NO}_3$  loads and warm temperatures. Our results indicate that there may be species specific responses to nitrate loading and that temperature and residence time may influence the expression of eutrophication symptoms.

## 2. Methods

### 2.1. Mesocosm conditions

The mesocosm facility (Kaldy, 2012, 2014; Shafer et al., 2011) consisted of 8 replicate cabinets (Fig. 1) that contained 2 banks of LED grow lights (180 W Advance Spectrum Max; AIBC International, LLC., Ithaca, NY, USA) suspended over a white polycarbonate tank (60 cm wide × 60 cm deep × 90 cm long). Each LED panel consisted of 119 LEDs in a 6:1:1:1 ratio of red (660 nm  $\lambda$ ), blue (465 nm  $\lambda$ ), orange (620 nm  $\lambda$ ) and white (6000 k). Photosynthetic photon flux density (PPFD) of photosynthetically active radiation (400–700 nm  $\lambda$ ) measured at the bottom of the tank with a spherical quantum sensor (LI-193SA) and LI-1400 data logger (LI-COR, Lincoln, Nebraska, USA) was > 200  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , which is above light saturation for *Z. marina* and *Z. japonica* (Shafer and Kaldy, 2014). Mesocosms were maintained on a 12:12 light:dark cycle. Each polycarbonate tank held 324 l and the ambient seawater delivery rate was  $500 \text{ ml min}^{-1}$  resulting in an exchange rate of about  $200\% \text{ d}^{-1}$ . Each cabinet had a separate seawater head tank that eliminated pressure changes and the water delivery rate was controlled using adjustable flowmeters (Model FR4L53BLBN-OM, FL2050; Omega, Stamford, CT, USA). Inflow was checked daily using a graduated cylinder and adjusted as needed. Estuarine tidal cycles were simulated twice daily in each mesocosm using dedicated small submersible pumps (Eco66, Sunlight Supply, Inc., Vancouver, WA., USA) and electronic timers (Apollo 7, Titan Controls, Sunlight Supply, Inc., Vancouver, WA., USA) that were synchronized between tanks. Water was removed by pumping over a 3-h period, such that at simulated low tide the mesocosm volume was reduced by 75%, and then the tank gradually refilled over the next 9 h before the cycle

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