



## Dissolved inorganic nitrogen uptake kinetics and $\delta^{15}\text{N}$ of *Zostera marina* L. (eelgrass) in a coastal lagoon with oyster aquaculture and upwelling influence



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### ABSTRACT

Differences in dissolved inorganic nitrogen (DIN) availability can lead to intraspecific physiological differences in the DIN incorporation capacities of seagrasses. The objective of this study was to evaluate these physiological differences in *Zostera marina* (eelgrass) exposed to anthropogenic (oyster aquaculture) and natural (upwelling events) inputs of DIN in San Quintín Bay (Baja California, México). To this end, shoots from meadows in different sites within the bay (from the bay mouth to the inner parts of the bay), and differently exposed to nitrogen effluents from oyster aquaculture and upwelling events, were incubated with  $^{15}\text{N}$ -labeled tracers ( $^{15}\text{NH}_4^+$  and  $^{15}\text{NO}_3^-$ ) under laboratory controlled conditions. DIN uptake kinetics and  $\delta^{15}\text{N}$  isotopic signals were assessed in months without upwelling influence (February) and with recurrent upwelling events (June). Results showed that eelgrass is highly efficient in acquiring DIN (mostly  $\text{NH}_4^+$  by leaves and roots) from the water column and sediment pore-water to support their vegetative productivity. However, noticeable intraspecific differences in uptake kinetics strategies were observed. In both months, eelgrass shoots exposed to oyster aquaculture showed higher capacities (maximum uptake rate,  $V_{\text{max}}$  and/or affinity coefficient,  $\alpha$ ) to acquire  $\text{NH}_4^+$  compared to shoots from other meadows. This suggests that these plants are efficient in exploiting a valuable source of  $\text{NH}_4^+$  from oyster excretion or biodeposit remineralization. Shoots growing in the bay mouth which are the most exposed to upwelled waters, exhibited relatively low leaf  $V_{\text{max}}$  and  $K_m$  for  $\text{NO}_3^-$  in June. These properties allow these plants to restrict the uptake of  $\text{NO}_3^-$  from upwelling events, probably to avoid the potential toxicity resulting from its uptake in excess. Intraspecific differences in  $\delta^{15}\text{N}$  were also evident, probably related to the isotopic signal of the DIN source and the relative incorporation of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  by leaves and roots. Generally, higher values of  $\delta^{15}\text{N}$  were found in leaves and rhizomes of plants exposed to oyster aquaculture than those growing in the bay mouth. This indicated the incorporation of more  $^{15}\text{N}$ -enriched DIN (mainly  $\text{NH}_4^+$ ) by the shoots from the meadow near oysters, possibly resulting from biogeochemical processes enhanced by oyster biodeposition. The lower  $\delta^{15}\text{N}$  in plants growing in the bay mouth likely resulted from the higher uptake of more isotopically-depleted  $\text{NO}_3^-$  from oceanic waters relative to the total DIN incorporation.

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### 1. Introduction

Nitrogen (N) uptake in marine macrophytes, including seagrasses, is regulated by uptake kinetics. These basically involve key physiological and vegetative features (e.g. membrane transporters, capacities of N-assimilation, biomass allocation among plant modules, clonal integrity) which determine the specific uptake strategies exhibited by the plant

(Touchette and Burkholder, 2000). However, these mechanisms are also regulated by the complex interaction of external processes in the water column and sediments occurring at distinct spatio-temporal scales (e.g. input of new N, N-recycling and N-export; Risgaard-Petersen et al., 1998; Romero et al., 2006). These processes are responsible for the availability of N pools in the water column, and hence the capacity of N-acquisition by these plants (McGlathery et al., 2004; McGlathery, 2008).

Seagrasses can acquire dissolved inorganic N (DIN) species (i.e.  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) and organic-N (e.g. urea, free amino-acids) through above- and belowground tissues (Vonk et al., 2008; Alexandre et al., 2011, 2015; La Nafie et al., 2014). DIN-uptake by seagrasses can be described by the Michaelis–Menten kinetics although linear responses may occur (Paling and McComb, 1994; Alexandre et al., 2011). Generally, seagrasses exhibit higher uptake affinities- $\alpha$  and greater maximum

**Abbreviations:** DIN, dissolved inorganic nitrogen;  $V_{\text{max}}$ , maximum uptake rates;  $K_m$ , half-saturation constant;  $\alpha$ , uptake efficiency; %N, tissue nitrogen content;  $V_{\text{amb}}$ , uptake rates at ambient DIN concentrations;  $\delta^{15}\text{N}$ , nitrogen isotopic signal.

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uptake rates  $-V_{max}$  for  $\text{NH}_4^+$  in leaves than in roots. This has been related to the distinct characteristics of the N-transport at membrane level (i.e. number of uptake sites and their affinity for the substrate), as well as the differential availability of this substrate in the water column as compared to pore-water in sediments (1–10  $\mu\text{M}$  vs. >200  $\mu\text{M}$ ) (Lee and Dunton, 1999a, 1999b; Rubio et al., 2007). By contrast, seagrasses exhibit lower capacities to incorporate  $\text{NO}_3^-$  compared to  $\text{NH}_4^+$ , likely due to the metabolic costs of its assimilation (Raven, 1984; Touchette and Burkholder, 2000).

Dissolved inorganic nitrogen uptake capacity can be highly variable among seagrass species and within species, due, for instance, to seasonal-dependent patterns or adaptation to different environmental conditions (Lee and Dunton, 1999a; Lepoint et al., 2002). Differences may be even present among plant tissues (e.g. new leaves vs. old leaves) (Pedersen et al., 1997). In addition, some other sources of variability have been related to nutrient diffusion limits, to coverage with epiphytes or type of substrate (Stapel et al., 1996; Terrados and Williams, 1997; Cornelisen and Thomas, 2004; Apostolaki et al., 2012). However, the specific adaptation/acclimation to changes in the availability of DIN resources in the water column and sediments can be considered as a primary factor which can drive noticeable inter- and intraspecific differences in uptake kinetics of seagrasses. Indeed, availability of DIN pools can determine, at least in part, the differential integration of the uptake kinetics among plant tissues (i.e. leaf vs. roots), the plant biomass allocation, as well as the internal N-recycling and translocation capacities, which finally condition the DIN-acquisition strategies and the whole-plant N budget in seagrasses (Zimmerman et al., 1987; Hemminga et al., 1999; Lee and Dunton, 1999a; Marbá et al., 2002).

Dissolved inorganic nitrogen enrichment in seagrass-dominated habitats can result from natural factors such as sediment resuspension or ocean-derived nutrient delivery by upwelling events, and from man-induced activities (e.g. aquaculture, sewage inputs) (Burkholder et al., 2007; Hessing-Lewis and Hacker, 2013). Reported changes in the N metabolism of seagrasses in response to nutrient enrichment are the alterations of enzymatic-mediated assimilation, tissue N-content and nitrogen isotopic signal  $\delta^{15}\text{N}$  (Udy and Dennison, 1997; Burkholder et al., 2007; Touchette and Burkholder, 2007), while changes in seagrass uptake kinetics strategies remain comparably less studied. Marine aquaculture (e.g. fish farming and mariculture) represents a growing industry in many coastal areas worldwide (FAO, 2014), and their effluents can potentially alter water quality and sediment characteristics (Holmer and Kristensen, 1992; Burkholder et al., 2007). This can lead to changes in N fluxes, as well as in the N-isotopic signature and concentration of N-species available for submerged vegetation uptake (Ruiz et al., 2010; Kellogg et al., 2014). While there is information on the effects of fish farming on seagrass physiology (i.e. leaf  $\delta^{15}\text{N}$ ; Vizzini and Mazzola, 2004; Ruiz et al., 2010), studies on bivalve (e.g. oysters) aquaculture effects are very scarce and mostly based on vegetative responses (Everett et al., 1995; Wisheart et al., 2007; Vinther et al., 2008).

The eelgrass *Zostera marina* L. is the dominant submerged vegetation in coastal lagoons along the Pacific coast of the Baja California Peninsula like San Quintín Bay (Poumian-Tapia and Ibarra-Obando, 1999; Cabello-Pasini et al., 2003; Ward et al., 2003). In contrast to coastal lagoons at the southern end of the peninsula, eelgrass meadows at San Quintín Bay are exposed to human-induced and natural DIN inputs. Extensive oyster (*Crassostrea gigas* L.) aquaculture in this bay represents a long-term, relatively constant, DIN source, while the ocean represents a natural source with high variability in time, including pulsed tidal injection of DIN supplied by coastal upwelling events (Ibarra-Obando et al., 2001; Camacho-Ibar et al., 2003; García-Esquivel et al., 2004). Previous studies have documented that oyster farming effluents (e.g. biodeposits) can cause nutrient enrichment and change N fluxes in adjacent areas (Newell et al., 2005; Higgins et al., 2013; Kellogg et al., 2014). In San Quintín Bay, the release of  $\text{NH}_4^+$  from oyster excretion and nutrient upwelling pulses (mainly  $\text{NO}_3^-$ ) play a critical role in the

lagoon's N budget, and have been shown to impact the productivity of *Z. marina* and other macrophytes (e.g. *Ulva* sp.) (Hernández-Ayón et al., 2004; Camacho-Ibar et al., 2007; Zertuche-González et al., 2009). However, the differential impact of oyster farming waste products and upwelling derived nutrients on the DIN-uptake strategies of *Z. marina* populations within this lagoon is still unknown.

The objective of this study was to evaluate if the exposure of *Z. marina* to different DIN sources within San Quintín Bay, leads to different plant uptake kinetics strategies. Uptake kinetics for DIN of leaves and roots were examined among plants from four meadows differently exposed to oyster aquaculture and upwelled waters. This was studied by means of individual shoot incubations in laboratory, by using  $^{15}\text{N}$ -labeled ammonium and nitrate as tracers. Total nitrogen content and the nitrogen isotopic signal of plant tissues were also analyzed. These measurements were made in two months with contrasting nutrient regimes and environmental conditions: February (end of winter season without upwelling) and June (early summer with upwelling influence). To our best knowledge, this work represents the first contribution to compare the variation of the strategies of eelgrass' DIN-uptake kinetics due to natural and anthropic inputs of DIN sources.

## 2. Material and methods

### 2.1. Study area: San Quintín Bay

Plant collection and field work were carried out in San Quintín Bay (SQB), which has extensive intertidal and shallow subtidal flats mainly occupied by monospecific seagrass beds of *Z. marina* (~46% of the substratum) (Ward et al., 2003; Ibarra-Obando et al., 2007) (Fig. 1). SQB is a coastal lagoon located in the northwestern Pacific coast of the Peninsula of Baja California, Mexico (30° 30' N, 116°W). SQB is Y-shaped (43 km<sup>2</sup>, average 2 m depth) with a single mouth, 800 m wide, connecting with the ocean, and with two arms; an eastern and a western arm known as Bahía San Quintín and Bahía Falsa, respectively (Fig. 1). Oyster (*C. gigas*) aquaculture is an important economic activity that is restricted to Bahía Falsa, covering approximately 33% of the surface area of this arm (Ward et al., 2003; García-Esquivel et al., 2004). Since land inputs of water (i.e. domestic wastes, surface and groundwater flows) are limited, water exchange and circulation are mainly dominated by semidiurnal tidal flows (average tidal amplitude of 1.6 m) between the lagoon and the coastal ocean. Water circulation largely occurs through narrow and deep (5–7 m) tidal channels which extend along the length of both arms. Geomorphology and distance from the bay mouth lead to increasing of water residence times toward the inner lagoon (from ~2 days near the bay mouth to ~5 days in Bahía Falsa), as estimated by Camacho-Ibar et al. (2003) based on water and salt budgets under neap tidal conditions. Water residence time together with evaporation processes result in some gradients of increasing salinity and temperature from the bay mouth to the two heads of both arms (Table 1). Oceanic supply of new nutrients, particularly during the upwelling season, creates a pattern of decreasing nitrate from the mouth to the heads of the lagoon. See further detail of biogeochemical characteristics of the bay in Camacho-Ibar et al. (2003), Hernández-Ayón et al. (2004) and Ribas-Ribas et al. (2011).

### 2.2. Plant collection

Shoots with intact rhizomes and roots of *Z. marina* were collected in February (winter) and in June (spring) 2014 by scuba diving at four dense subtidal meadows (max. depth of 2.5 m during high tides). Meadows were selected by their differential exposure to oyster aquaculture and upwelling influence (Fig. 1). Two of the meadows are located within the area designated for oyster aquaculture at the inner and the outer Bahía Falsa (i-BF and o-BF, respectively) which show slightly different environmental conditions (Table 1). Shoots were also collected from a meadow located at the bay mouth (BM), being the most exposed

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