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The impact of short-term depositions of macroalgal blooms on widgeon-grass meadows in a river-dominated estuary

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ABSTRACT

Macroalgal blooms can trigger adverse biogeochemical conditions at the sediment-water interface of shallow coastal areas, hence threatening critical habitats such as seagrasses meadows. The direction and magnitude of macroalgal blooms impacts on the aquatic ecosystem can be context-dependent, varying according to the local hydrodynamic conditions. Thus, studies investigating the impacts of stagnant algal depositions on the benthos may fail to address realistic situations and interactions which are common in well-flushed systems. This is especially true for the South America coast, where no study has investigated the effects of macroalgal blooms on seagrasses meadows. To fully understand the impacts of macroalgal blooms on sediment biogeochemistry and seagrass habitats across distinct environmental conditions and biogeographical regions, two independent, complementary field experiments replicated the natural temporal patterns of drift macroalgal mats depositions on unvegetated and vegetated (*Ruppia maritima* meadows) shoals of the Patos Lagoon estuary (PLE), a subtropical, high hydrodynamic system in southern Brazil. Transitory depositions of algal mats alleviated deleterious biogeochemical conditions in the sediment-water interface of unvegetated bottoms. Nevertheless, these unstable algal depositions promoted significant reductions in *R. maritima* biomass, by reducing their shoot height and density, and rhizome length. That plant biomass reductions were followed by a decrease in the abundance of the dominant infaunal tanaidacean *Monokalliapseudes schubarti*, indicating that algal impacts on seagrasses were transferred to higher trophic levels. Our results suggest that, although unstable deposition of drift algal mats can attenuate potential adverse impacts at the sediment-water interface, the physical stress during mats advection can still trigger small seagrass losses. This process may diminish the resilience of *R. maritima* meadows in the PLE, with impacts on estuarine nutrient cycling and secondary production. We conclude that, although harmful drift macroalgal blooms area global phenomenon, the mechanisms through which macroalgae impair seagrass habitats may vary according to the environmental context. Therefore, further studies are necessary to identify the underlying mechanisms of drift macroalgae-seagrass-macrofauna interactions in high hydrodynamic systems and their generality across distinct biogeographical areas.

1. Introduction

Seagrass meadows support a high primary productivity in coastal systems, increasing habitat complexity and food availability for consumers, enhancing coastline protection through wave action attenuation, stabilizing sediments and filtering terrestrial run-off (Waycott et al., 2009; Duarte et al., 2013). Together with other vegetated coastal ecosystems, seagrasses sequester significant amounts of carbon into their sediments, therefore playing a fundamental role in climate change mitigation and adaptation (Duarte et al., 2013). Despite their recognized ecological importance and the numerous ecosystem services that seagrasses provide, seagrass meadows are among the most threatened ecosystems on Earth. Thirty percent of the areal extent was lost in the last century and the rates of decline have been faster in the last few decades (Waycott et al., 2009).

Eutrophication has been pointed out as the main driver of seagrass decline worldwide. Increasing nutrient inputs promote blooms of opportunistic macroalgae that outcompete seagrasses for nutrient and light (Lyons et al., 2014; Thornber et al., 2017). In temperate regions, several estuarine and coastal areas are experiencing phase shifts of persistent macrophytes to ephemeral macroalgae (McGlathery et al., 2007; Moreno-Marín et al., 2016). Stagnant depositions of algal blooms trigger hypoxic/anoxic conditions and high ammonia and sulphide concentrations at the water-sediment interface during biomass

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respiration and decomposition (Hauxwell et al., 2001; McGlathery et al., 2007; Wang et al., 2012), leading to declines in seagrasses meadows (Holmer et al., 2011; Thomsen et al., 2012a) and their associated benthic macrofaunal assemblage (Cummins et al., 2004).

The direction and magnitude of macroalgal blooms and their further impact on seagrasses are highly variable and context-dependent, depending on the local oceanographic and hydrodynamics conditions (Hessing-Lewis et al., 2011; Cebrian et al., 2014), as well as the macroalgae and seagrasses features (i.e., size, abundance, morphology; Thomsen et al., 2012a, b). Most deleterious impacts of macroalgal blooms on seagrasses are documented for experiments simulating shallow, low-energy conditions where stationary algal mats accumulate and decompose (Cebrian et al., 2014). Nonetheless, drift macroalgae mat accumulations can be highly unstable once their aggregations are driven by factors operating at distinct spatial and temporal scales (Kopecky and Dunton, 2006). Tidal and wind-driven waves and currents can translocate drift mats, first as bedloads and then suspended in a water column, at increasing current speeds (Canal-Vergés et al., 2010). In highly hydrodynamic systems, the frequent relocation of drifting mats hence leads to temporary accumulations of macroalgal biomass (e.g., ~ 6 h, Biber, 2007; 2–3 days, Rasmussen et al., 2013) that may alleviate oxygen depletion and high porewater ammonium concentrations on seagrass communities (Cebrian et al., 2014; Gustafsson and Boström, 2014; Hessing-Lewis et al., 2015). Thus, experiments simulating stagnant algal depositions may fail to address realistic stress scenarios and the mechanistic basis of macroalgal bloom impacts on seagrass communities in well-flushed areas.

Although showing lower diversity and abundance compared to that of other global seagrass bioregions, seagrass meadows are widely distributed along the entire Brazilian Coast, forming nursery grounds for important fishing resources (Creed, 2003; Copertino et al., 2016). The conservation status of seagrass ecosystems in that region is critical, and significant reductions have been reported by long-term studies (*SeagrassNet* and LTER sites) caused mainly by coastal degradation and extreme climatic events (Short et al., 2006, Barros et al., 2013, Copertino et al., 2016). Nevertheless, the specific effects or contributions of the drift macroalgal blooms to seagrass structure and functioning (Copertino et al., 2016) have not been investigated. The lack of studies on macroalgae-seagrass interactions in South America represents a knowledge gap, which may limit the comprehension of ecosystem functioning, seagrass conservation ecology and coastal management plans.

In the Patos Lagoon estuary (PLE), southern Brazil, historic reductions in the abundance and distribution of the seagrass *Ruppia maritima* L. resulted from anomalous precipitations and high fluvial discharge associated with *El Niño* events (e.g., 1997/98 and 2002/03; Odebrecht et al., 2010). The seagrass *R. maritima* is small and ephemerous, with low resistance to physical disturbances, but it quickly recolonizes disturbed areas throughout seed banks and rhizome growth (Anton et al., 2009). Although being resilient to disturbance, the recovery of *R. maritima* meadows in PLE took up to ten years, after periods of extreme reductions in their distribution and abundance (Copertino et al., 2016). Extreme reductions in rhizome net and seed bank, low rates of seed viability and seedling survival may be the cause of the delay in seagrass recovery following high freshwater discharges and sediment remobilization. Furthermore, reductions in seagrass meadows were followed by blooms of drift macroalgae, which fast occupied the bare sediment after the return of favourable water conditions. Indeed, an increasing trend in the frequency and magnitude of those algae have been reported in PLE, triggered mainly by nutrient increases and changes in N:P ratios (Lanari and Copertino, 2017; Lanari et al., 2017). Although the genus *Ruppia* is widely distributed across the world coastal regions (Short et al., 2007) and is highly resilient to environmental disturbances, knowledge about the potential impacts of macroalgal blooms on this small seagrass is scarce (but see Harlin and Thorne-Miller, 1981).

The abundance of drift macroalgae in the PLE is triggered by interactive effects of hydrological (mainly freshwater discharge) and water physical-chemical parameters (i.e., dissolved inorganic nutrient concentrations, salinity, water level and turbidity), which modulate the occurrence, magnitude and persistence of the blooms (Lanari et al., 2017). River flow and wind-driven currents vary from 1–25 cm s^{-1} (i.e., calm periods) to up to 1 m s^{-1} (i.e., during high fluvial discharges; Fernandes, 2001), values that are very much above the reported erosion thresholds for algal mat advection (e.g., 2–3 cm s^{-1}, Canal-Vergés et al., 2010; 20–50 cm s^{-1}, Biber, 2007). In contrast to stationary algal blooms, simulated in most previous field and laboratory experiments (e.g., 6 months, Holmquist, 1997; 3–4 months, Hauxwell et al., 2001; 12 weeks, Cummins et al., 2004; 2–3 months, Irlandi et al., 2004; five weeks, Holmer et al., 2011), natural waves and currents thus promote unstable drift mat depositions that may last from a few hours of up to five days in the PLE (Lanari and Copertino, 2017). Therefore, similar to other coastal shallow areas worldwide (e.g., Rasmussen et al., 2013; Canal-Vergés et al., 2014), persistent drift macroalgal accumulations can be continuously rearranged and advected over the same spots on shorter timescales, thereby preventing the development of stagnant blooms.

The present study investigated the impacts of drift macroalgal blooms on *Ruppia maritima* meadows and associated benthic communities under the natural conditions of water flow and algal movement in a highly hydrodynamic estuary in southern Brazil, South America. For this study, we performed two independent, complementary field experiments to investigate 1) the influence of unstable depositions of drift macroalgae on physical-chemical parameters at the sediment-water interface and 2) the effects of transitory algal mat depositions on *R. maritima* plants and their associated benthic macrofauna. We first hypothesized that unstable depositions of drift macroalgae can alleviate adverse environmental conditions in the sediment-water interface. Second, we hypothesized that drift algal mats can negatively impact *R. maritima* plants even in the absence of deleterious biogeochemical conditions, with negative effects being transferred to the benthic macrofaunal assemblage dwelling on meadows.

2. Methods

2.1. Study area

The subtropical PLE is located within the Patos Lagoon, the largest choked coastal lagoon in the world (10,360 km^2; 30°12´-32°12´S; 50°40´-52°15´W; Fig. 1). The estuarine area (~1000 km^2) is influenced by a microtidal regime (~0.47 cm), which is attenuated by a single and narrow entrance channel (0.5–3 km wide). Thus, the hydrology of the PLE is primarily controlled by fluvial discharge and wind patterns. During high fluvial discharges (winter/spring), the PLE becomes a river-dominated system. During low discharges (summer/autumn), the prevailing NE winds in spring and summer and SW winds in autumn and winter force the outflow and inflow, respectively, of water between the estuary and the coastal region. Therefore, marine and euhaline conditions occur in summer/autumn, whereas oligohaline conditions prevail in winter/spring (Möller et al., 2001).

Two field experiments were performed in early Autumn (late March to early May) of 2013 and 2014 to investigate the effects of drift macroalgal depositions on sediment-water interface physical-chemical parameters (i.e., oxygen saturation, redox potential and organic matter content; hereafter, Experiment 1) and on *Ruppia maritima* meadows and their associated benthic macrofauna (hereafter, Experiment 2) in a well-flushed system. Experiments were performed in two adjacent shallows shoals (< 1 m depth) with similar exposure to S-W winds and bottom granulometry (98% sand, 1.2% silt and 0.8% clay). Both experiments simulated depositions of drift algal mats (dominated by *Rhizoclonium* sp. and minor contributions of *Ulva* sp.) by adding previously manually defaunated algal biomass to experimental plots. The biomass values