

Dynamics of estuarine drift macroalgae

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2 3	Dynamics of estuarine drift macroalgae: growth cycles and contributions to sediments in shallow areas
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ABSTRACT: Blooms of opportunistic macroalgae play a major role in nutrient cycling in 35 shallow coastal areas. However, their short life cycles and rapid biomass remineralization can 36 promote feedbacks on sediment nutrient recycling, leading to self-regenerated blooms and the 37 consequent disruption of local biogeochemical cycles. We investigated the potential for algal 38 biomass-sediment nutrient feedbacks in shallow estuarine areas under natural scenarios of 39 40 biomass accumulation. To do so, the environmental factors driving the dynamics of drift macroalgal blooms and their biomass contributions to sedimentary organic matter were 41 assessed in a 2 yr field survey in shallow bays of the Patos Lagoon estuary, southern Brazil. 42 Interactive effects of hydrological and water physico-chemical parameters modulated the 43 abundance and persistence of algal biomass. The magnitude of the bloom biomass among 44 bays was positively correlated to wind exposure, reflecting the importance of drifting mat 45 advection by onshore wind-driven waves and currents on biomass accumulation. Large 46 biomass accumulations represented a substantial nutrient stock within the system. However, 47 no significant increases in the sediment total organic carbon or total nitrogen were observed. 48 Isotopic analysis revealed overall low contributions of macroalgal biomass to the sedimentary 49 organic matter during senescence, highlighting possible dual effects of wind exposure on 50 biomass accumulation and deposition. Our findings suggest that, in highly hydrodynamic 51 systems, feedbacks between biomass accumulation and sediment nutrient regeneration are 52 unlikely to occur. Given the unknown fate of algal-bound nutrients, more studies are 53 necessary to determine the effects of drift macroalgae-dominated phases on the long-term 54 balance of nutrients within the estuarine system. 55

KEY WORDS: Macroalgal blooms • Hydrology • Wind exposure • Sedimentary organic
 matter • Fate of nutrients • Patos Lagoon

INTRODUCTION

59 In shallow coastal areas worldwide, an increasing trend in the frequency of blooms of fast-

60 growing ephemeral macroalgae, also known as green tides, has been observed. Blooms of

opportunistic macroalgae, such as some species of *Ulva* and *Cladophora*, can outcompete

62 other autotrophs such as seagrasses and microphytobenthos for nutrients and light, causing

63 shifts towards the dominance of ephemeral primary producers (Lyons et al. 2014). While 64 nutrient enrichment is recognized as a primary cause of the excessive growth of ephemeral

nutrient enrichment is recognized as a primary cause of the excessive growth of ephemeral
 macroalgal species, the onset and magnitude of the bloom may be triggered by the interactive

effects of water physico-chemical and hydrodynamic conditions (Martins et al. 1999, 2007).

67 In shallow estuarine waters, the growth of macroalgae is controlled by the availability of light

at the bottom, water temperature and salinity, but the conditions for bloom formation depend

on the water residence time, which can enable or prevent the retention and accumulation of

the biomass produced (McGlathery et al. 2007).

71 Most green tides are composed of macroalgal mats that are detached from the substrata due to

72 waves and current action (hereafter termed 'drift macroalgae'). Due to their low erosion

thresholds, drift macroalgae can be easily transported as bedloads (i.e. mats drifting over the

sediment surface) or as floating mats in the water column (Flindt et al. 2004) by tidal and

vind-driven currents and waves (Biber 2007, Keesing et al. 2011). Consequently, local tidal

cycles and wind regimes can determine the occurrence and magnitude of the accumulations of
 the macroalgal biomass produced in shallow bays and estuarine shoals (Kennison & Fong

78 2013).

58

79 Once established, macroalgal blooms play a major role in nutrient cycling, acting initially as a

80 nutrient sink. Opportunistic macroalgae such as *Ulva* exhibit high uptake efficiency of

dissolved organic and inorganic nutrients from the water column and sediments (Tyler et al.

82 2003, Fong et al. 2004). However, due to their 'boom and bust' life cycles and high biomass

- turnover rates ranging from days to a few weeks, drift macroalgal blooms do not represent a
- long-term nutrient reservoir (McGlathery et al. 2007). During biomass active growth,
- senescence and collapse, the assimilated nutrients can be rapidly recycled in the water column
- as dissolved organic nitrogen and particulate organic nitrogen, where they are partly
- 87 processed by the microbial loop, mineralized or transferred to higher trophic levels through
- grazing (Tyler et al. 2001, Fong et al. 2004).
- 89 While a large bulk of the algal tissue is recycled in the water column, part of the material
- 90 contributes to temporary increases in the sediment organic matter content during bloom
- collapses (Pihl et al. 1999, Corzo et al. 2009, Hardison et al. 2010, Gao et al. 2013). The
- highly labile dead biomass is rapidly decomposed (Banta et al. 2004), increasing pore water
- 93 nutrients through bacterial activity and promoting subsequent effluxes of nutrients across the
- 94 sediment-water interface (García-Robledo et al. 2008, 2013, Hardison et al. 2010, Gao et al.
- ⁹⁵ 2013). Therefore, the rapid regeneration of nutrients may help initiate the further growth of
- macroalgae that, along with the mats continually drifting in from surrounding areas, help
- sustain the large accumulations of ephemeral macroalgae. This self-regeneration mechanism
 may cause the reoccurrence of macroalgal blooms and lead to the disruption of local
- ⁹⁸ hidy cause the reoccurrence of macroargar biobins and read to the disruption of it biogeochemical evalues in shallow estuaring areas (Sundhäck et al. 2002)
- biogeochemical cycles in shallow estuarine areas (Sundbäck et al. 2003).
- 100 To investigate the potential of self-regeneration by drift macroalgal blooms, most studies have
- 101 focussed on macroalgal nutrient removal and regeneration in the water column (e.g. Tyler et
- al. 2001, Fong et al. 2004). More recently, attention has turned to the sedimentary processes
- that link nutrient uptake in the water column to remineralization and release in the sediment
- during biomass deposition and senescence (e.g. Corzo et al. 2009, Hardison et al. 2010,
- 105 García-Robledo et al. 2013). However, most of these studies have been conducted in micro-
- and mesocosm experiments, over short spatial and temporal scales. Consequently, factors that
 affect both the spatio-temporal patterns of drift macroalgal blooms and their subsequent
- 108 contributions to sedimentary organic matter have not been considered at a field scale. This
- 109 knowledge gap, concerning the potential feedbacks of green tides on estuarine
- biogeochemical cycles, limits our current understanding of the processes contributing to the
- 111 occurrence and fate of drift macroalgae.
- 112 In the last decade, the Patos Lagoon estuary (PLE) in southern Brazil has undergone
- ecological changes, including reductions in the distribution and abundance of submerged
- 114 aquatic vegetation (i.e. Ruppia maritima meadows) and increases in the abundance of drift
- macroalgae (Odebrecht et al. 2010). Shifts towards the macroalgae-dominated state have
- 116 mainly been related to changes in the hydrological conditions (Lanari & Copertino in press),
- 117 but may also be associated with the increasing trend in the inorganic nitrogen concentrations
- in the water column and in the sediment pore water (e.g. Baumgarten & Niencheski 2010).
- 119 Local biogeochemical studies have shown that the estuarine sediments recycle a significant
- 120 portion of the primary production, subsequently providing inorganic nutrients to the water
- 121 column (Niencheski & Jahnke 2002). However, the role of drift macroalgae in estuarine
- 122 nutrient cycling is still poorly understood.
- 123 To assess the role of drift macroalgal blooms on estuarine nutrient cycling, we investigated
- the drivers of temporal and spatial variability in the occurrence and magnitude of drift
- macroalgal blooms in shallow estuarine areas based on 2 main hypotheses. First, we
- 126 hypothesized that while drift macroalgal blooms result from the coupling of factors affecting
- both drifting biomass production and retention in the system, the spatial variability in the
- timing and magnitude of biomass accumulations relies on wind exposure. Second, using the
- natural patterns of drift macroalgal bloom occurrence and persistence in the study area, we
- tested the hypothesis that drift macroalgae are an important source of sedimentary organic
- 131 matter. We suggest that the contribution of macroalgae to the sediments may be proportional

to the magnitude of the biomass accumulations, possibly creating conditions for feedbacks on
 sedimentary nutrient regeneration that trigger self-regenerated blooms.

134

135

MATERIALS AND METHODS

Study site

The warm temperate Patos Lagoon is one of the largest choked coastal lagoons in the world 136 (10360 km²; 30° 12' to 32° 12' S, 50° 40' to 52° 15' W; Fig. 1a). The estuarine area (PLE; 137 $\sim 1000 \text{ km}^2$) is influenced by a microtidal regime ($\sim 0.47 \text{ cm}$), further attenuated by a single 138 and narrow entrance channel (0.5 to 3 km wide); therefore, the hydrology of the PLE is 139 primarily controlled by fluvial discharge and wind patterns (Möller et al. 2001). The 140 prevailing northeast (NE) winds in spring and summer and southwest (SW) winds in autumn 141 and winter force the outflow and inflow, respectively, of water between the estuary and the 142 coastal region. During flood periods (mainly in winter/spring), the PLE becomes a river-143 dominated system, remaining fresh for several months (Möller et al. 2001). Conversely, 144 during low freshwater discharges (summer/autumn), southerly winds promote saltwater 145 intrusions, blocking freshwater outflow and increasing water retention within the estuary 146 (Odebrecht et al. 2015). Therefore, marine and euhaline conditions usually occur in 147 summer/autumn, while oligohaline conditions prevail in winter/spring. Overall, high levels of 148 nutrients in the water column (up to 40 μ M NO₂⁻+NO₃⁻, 40 μ M NH₄⁺ and 8.7 μ M PO₄³⁻) and 149 sediment (up to 710.7 μ M NH₄⁺ and 14.6 μ M PO₄³⁻) are maintained through inputs from the 150 watershed, macrophytes and anthropogenic sources (Baumgarten & Niencheski 2010, 151

152 Odebrecht et al. 2010).

153 From August 2012 to August 2014, macroalgal blooms and their contributions to sedimentary

organic matter were investigated in shallow shoals with different levels of exposure to the

prevailing SW and NE winds. Within each wind direction, 2 sites were selected according to

an *a priori* contrast between low (hereafter shelter-NE and shelter-SW) and moderate to high

exposure (exp-NE and exp-SW; Fig. 1b). The wind exposure of sites was determined

according to their average wave fetch values and their wave exposure (Burrows et al. 2008;

Fig. 1b). Wave exposure was determined based on a 200 m grid-based map of the PLE obtained from the high-resolution shoreline (GSHHS) digital coastline dataset

161 (www.ngdc.noaa.gov/mgg/shorelines/gshhs.html). For all coastal cells in the grid, the number

162 of 200 m grid cells representing water surface (i.e. sea cells) was calculated in 16 angular

163 sectors (22.5° each) and summed up. Therefore, for each coastal cell, wave exposure gradient

164 is given as the number of surrounding cells that do not represent land masses (i.e. land cells),

thus being available for wind drag on the water surface.

166

Hydrological and meteorological factors

167 Information regarding local freshwater discharge was provided by the Brazilian National

168 Water Agency (www.hidroweb.ana.gov.br). The sum of the flow of the 3 main rivers was

assumed to be a proxy for the total Patos Lagoon freshwater discharge (Möller et al. 2001).

170 Data on hourly wind speed and direction, obtained at the mouth of the PLE, were provided by

- the Rio Grande Maritime Pilotage (www.rgpilots.com.br/).
- 172

Water physico-chemical parameters

173 The estuarine water level (fixed ruler) in relation to the mean water level of the lagoon (40

- 174 cm) was obtained daily in an area approximately 3 km from the studied sites within the
- 175 Brazilian Long-Term Ecological Research Program (www.peld.furg.br/index.php/metadados).
- 176 Water salinity, temperature, turbidity (Multiparameter HI9829, Hanna Instruments) and

- 177 Secchi depth were monitored weekly at each site from August 2012 to August 2014. Water
- samples (N = 3) were collected monthly from each site for the analysis of dissolved inorganic
- nutrients (NH_4^+ , NO_2^- , NO_3^- and PO_4^{3-}). Underwater photosynthetically active radiation
- (PAR) at the bottom (I_z) was estimated according to the Lambert-Beer equation:
- $I_z = I_0 \times e^{-kz}$
- where I_0 is the PAR at the surface, k is the light extinction coefficient ($k = 1.7 \times \text{Secchi}^{-0.85}$;
- 183 Costa & Seeliger 1989), and *z* is depth. We assumed that PAR is 50% of the overall available
- 184 energy for photosynthesis and a 5% decrease in the incident light at the water surface (da
- 185 Silva & Asmus 2001). Data on the hourly surface radiation in the study area were provided by
- the Brazilian National Institute of Meteorology (www.inmet.gov.br/portal).
- 187

Macroalgal and sediment sampling

(1)

- 188 To assess the occurrence and magnitude of drift macroalgal blooms at each sampling site,
- 189 macroalgal cover was measured monthly along 3 transects (200 m each) laid out
- 190 perpendicular to the coast, 100 m apart from one another. Drift macroalgae coverage was
- estimated by visual census within 4 quadrats (0.25 m²) at 50 m intervals (N = 20 per transect). Each 50×50 cm quadrat was divided into 4 smaller ones (i.e. 12.5×12.5 cm, representing
- Each 50×50 cm quadrat was divided into 4 smaller ones (i.e. 12.5×12.5 cm, representing 25% coverage each) using lateral marks. Smaller quadrats were further mentally subdivided
- into 4 subquadrats. The total of subquadrats covered by drift mats was summed up, and
- 195 coverage was thus determined at 6.25% increments. When biomass coverage was far below
- 196 6.25%, it was assigned as 1%; otherwise, it was considered 6.25%. We used a PVC cylinder
- 197 (176.62 cm^2) to sample macroalgal biomass at 10 points where the coverage was 100%. To
- 198 evaluate the role of algal biomass as a source of sedimentary organic matter through
- leemental and isotopic analysis, samples of the surface sediment (N = 3) were collected with a
- 200 cylinder core (8 cm diameter, 3 cm depth) from below macroalgal mats within the transect
- area and placed in amber glass vials. The macroalgal and sediment samples were transported
- 202 on ice to the laboratory and prepared within the next 1 to 2 d.
- In the laboratory, the macroalgae were cleaned by removing associated fauna and detritus and
- rinsed with tap and distilled water; the dry weight (48 h at 60°C) was then determined.
- Subsamples (N = 3) of ~100 g fresh biomass were separated for elemental and isotopic
- analysis (see below for further details) and for taxonomic identification. For the latter,
- subsamples were fixed in a 4% formalin solution, and identification was based on
- morphological features. The average biomass (g dry weight $[DW] m^{-2}$) for each site was
- estimated by multiplying the biomass values by the mean percentage cover of the survey area estimated by visual consult (N = 60 guadrate)
- estimated by visual census (N = 60 quadrats).
- 211

Elemental and isotopic analysis

- 212 The sediment and macroalgal biomass subsamples were dried to a constant weight (48 h at
- 60° C) and ground to a fine powder using a mortar and pestle. Subsamples were weighed (25–
- 30 mg for sediments and 2.5–3.0 mg for macroalgae) and pressed into tin capsules for the
- analysis of total organic carbon (TOC), total nitrogen (TN) and their isotopic composition
- 216 (δ^{13} C and δ^{15} N). The sediment samples were analysed for TOC, TN, δ^{13} C and δ^{15} N for the
- sheltered sites (shelter-NE and shelter-SW) from August 2012 to August 2013 and up to
- August 2014 for the exposed sites (exp-NE and exp-SW). The δ^{13} C and δ^{15} N of the
- 219 macroalgal biomass were analysed only for 2014. The elemental and isotopic analyses were
- 220 performed using an automatic elemental analyser (2400 Series II CHNS/O System, Perkin-
- Elmer) and a mass spectrometer (Stable Isotope Laboratory, University of Georgia, USA),
- 222 respectively. Previous studies in the PLE have shown that sediments contain insignificant

- amounts of sedimentary calcium carbonate. Claudino et al. (2013) tested the need for a
- decarbonation treatment of PLE sediments and found no difference in the δ^{13} C value between
- acidified and non-acidified samples. Therefore, our sediment samples were not acidified prior
- to the analysis. Quality control for the elemental analysis of the macroalgal tissue was
 conducted using the certificate reference material acetanilide and the sediment MESS-3
- conducted using the certificate reference material acetanilide and the sediment MESS-3
 (National Research Council Canada). The percent TOC and TN content in the macroalgal
- tissue and sediment were converted to molar TOC:TN ratios, and the isotope ratios were
- expressed as parts per thousand (%). Pee Dee Belemnite was used as the standard for carbon,
- and atmospheric nitrogen was used for nitrogen. Based on the standard deviation of the
- internal standard replicates, the analytical precision for the carbon and nitrogen content and
- their isotopes was ± 0.16 , ± 0.05 , ± 0.08 and ± 0.12 , respectively.

Data analysis

235 Variation in water salinity has been used as a proxy for the water retention time in the study

- area (e.g. Odebrecht et al. 2015). Similarly, we used the average salinity and its variability
- 237 (i.e. coefficient of variation, CV) across season as a proxy for water retention within the
- estuary. In general, periods of higher water retention were identified by increases in salinity
- associated with a low CV, which reflected transitions from periods of outflow to inflow and the persistence of meso/euhaline waters in the estuary (Odebrecht et al. 2015).
- 241 Intercorrelations among freshwater discharge, level, salinity (mean and CV), turbidity,
- irradiance, temperature, NH_4^+ , NO_2^- and NO_3^- (expressed as dissolved inorganic nitrogen,
- 243 DIN) and PO_4^{3-} were analysed through principal component analysis (PCA). Since no
- significant spatial differences were found in the water physico-chemical parameters (level,
- salinity, turbidity, temperature and nutrients; see Fig. S1 in the Supplement at
- 246 **www.XXXXXX**), the abiotic data were averaged across all sites. All variables except
- 247 irradiance were log-transformed to achieve a normal distribution. The abiotic parameters were
- 248 grouped along the PCA axis according to their eigenvector coefficients. This procedure 249 provided ecological meaning for the PCA components and allowed data reduction. The
- relationships between the averaged macroalgal biomass across sites and the hydrological and
- 251 water physico-chemical parameters were thus investigated through multiple regression
- analysis using the eigenvalues of PC1, PC2 and PC3 as independent variables which
- explained, respectively, 47.10, 17.40 and 15.21% of the data variability. The residuals were
- 254 checked for data homoscedasticity and normality. Spatial patterns of the distribution and 255 abundance of drift macroalgal biomass among sites were analysed in relation to the local wind
- abundance of drift macroalgal biomassdirection, frequency and speed.

234

- 257 The contributions of drift macroalgal biomass to the organic matter in the sediments were
- estimated using the Bayesian mixing model MixSIAR (Stock & Semmens 2013). The
- 259 MixSIAR model provides estimates of the relative contributions of distinct sources to a
- 260 mixture even in undetermined systems, taking into account the uncertainty associated with
- both sample variability and unknown sources of error (Parnell et al. 2013). The mixing model was run for each season using the sampling sites as fixed factors. The sedimentary organic
- matter sources were suspended particulate organic matter (SPOM), drift macroalgae, the
- seagrass *Ruppia maritima* and the saltmarsh plants *Spartina densiflora*, *Scirpus maritimus* and
- 265 S. olney (**Table 1**). Seasonal elemental and isotopic values for *R. maritima*, *S. densiflora*, *S.*
- *maritimus, S. olney* and SPOM in the study area were obtained from Claudino et al. (2013). *R.*
- 267 *maritima* and *S. densiflora* presented similar isotopic signatures and were pooled as a single
- source. Due to their similar photosynthetic pathways, *S. maritimus* and *S. olney* were also
- 269 pooled together and denoted as C3 plants. TOC and TN were informed for each source.
- 270 Discrimination effects were not included due to the lack of significant changes in the

elemental and isotopic values of the sources during diagenesis in the study area (data not

shown). The posterior distributions of organic matter sources were calculated using long

273 Markov chain Monte Carlo chains (chain length = 1000000, burn-in = 700000, thin = 300),

and convergence was checked through diagnostic tests (see Stock & Semmens 2013 for more details).

276

RESULTS

277 Temporal variation in hydrological and water physico-chemical parameters

Water discharge, retention, level, salinity, turbidity and irradiance showed a strong seasonal 278 trend throughout the studied period (Fig. 2a,b, Table 2) and were highly correlated along the 279 first principal component (PC1; **Table 3**). PC1 reflected the associated changes in water 280 physico-chemical parameters related to water retention, therefore representing the balance 281 between outflow (i.e. freshwater discharge) and inflow (i.e. saltwater intrusion) in the PLE. 282 Periods of high freshwater discharge, predominantly in winter and spring, were followed by 283 increases in water level and turbidity and decreases in salinity, underwater irradiance and 284 water retention (i.e. indicated by high salinity CV values). Water temperature varied 285 seasonally, with the lowest values recorded during winter, and was positively correlated with 286 PC2 (Fig. 2c, Table 3). 287

Nutrient concentrations in the water column showed no consistent seasonal trend (**Fig. 3** and

Fig. S1). Peaks of NH_4^+ were found mainly during October and November 2012 (spring; Fig. 3a). Higher concentrations of $NO_2^- + NO_3^-$ were observed during October and November

2012 (austral spring), from April to July 2013 (autumn to winter) and in July 2014 (mid-

winter; Fig. 3a). The variability in the PO_4^{3-} concentrations was less pronounced, although an

increasing trend towards autumn and winter of 2014 was observed (Fig. 3c). All nutrient
 concentrations increased along PC3 (Table 3).

295

Temporal and spatial dynamics of drift macroalgal blooms

Annual and interannual variability in the abundance and composition of drift macroalgae were 296 found. Mixed mats of tubular Ulva species (formerly Enteromorpha) occurred during 297 summer/autumn 2013 and autumn/winter 2014, while mats dominated by Rhizoclonium sp. 298 occurred only in autumn/winter 2014. Polysiphonia sp. occurred at negligible abundances in 299 summer 2013 and was not considered in the total algal weight. Peaks of biomass occurred 300 during early summer and autumn 2013 and in autumn and early winter 2014 (Fig. 4a). The 301 average biomass values across all sites ranged from 0.38 g DW m⁻² (winter, August 2012) to 302 566 g DW m⁻² (winter, June 2014) and, overall, higher mean biomass values were found 303 during 2014 (223 g DW m⁻²) compared to 2012–2013 (43 g DW m⁻²). The results of the 304 regression analysis showed that PC1, representing freshwater discharges and associated 305 306 changes in water retention and physico-chemical parameters, was the best predictor of the average values of drift macroalgal biomass ($R^2 = 0.67$, $F_{7,12} = 3.55$, p = 0.02). On the other 307 hand, no significant effects of water temperature (here represented by PC2) or nutrient 308 concentrations (PC3) on drift macroalgal abundance were detected. Macroalgal tissue TOC 309 and TN presented slight spatial differences (see Fig. S2 in the Supplement) and were averaged 310 across all sites for analysis. The mean values for C content varied from 31.5% (March 2014) 311 312 to 39% (July 2014), and N content ranged from 1.5% (December 2013) to 3.6% (November 2013; Fig. 5a). Temporal changes in the algal tissue C:N ratios reflected variation in the drift 313 macroalgal abundance, with peaks during bloom periods (Fig. 5b). 314

315 We found marked spatial variability in the timing and magnitude of drift macroalgal blooms.

316 The exposed sites showed the highest values of biomass throughout the studied period, with

- algal accumulations forming persistent, extensive patches covering up to 90% of the surveyed
- area (Fig. 4a,b). Conversely, sheltered sites showed lower values of accumulated biomass
- deposited onto the substrata as scattered thin patches. Temporal shifts in biomass
- accumulation between the exposed sites were in accordance with the local wind patterns (data
- presented in Fig. S3 in the Supplement). The largest algal blooms at the exp-SW site occurred
- during autumn (March to May) 2013 and 2014 under an increasing frequency and intensity (from 2.1 up to $> 11 \text{ m s}^{-1}$) of winds from the SW was during C_{2} and C_{3} and C_{4} and C_{4}
- (from 2.1 up to >11 m s⁻¹) of winds from the SW quadrant. Conversely, the exp-NE site showed large algal blooms, mainly in summer 2013 (December to February) and early winter
- 2014 (June), under the predominance of moderate (5.7 to 8.8 m s⁻¹) to strong (8.9 to 11.1 m s⁻¹)
- 326 ¹) N to E winds.
- 327

Contribution of drift macroalgal biomass to sediment organic matter

Sediment elemental and isotopic values showed no clear seasonal or spatial trends (**Fig. 6**a–

d), indicating that algal biomass did not promote significant increases in sedimentary organic

matter. Accordingly, the mixing model results showed that drift macroalgae, with isotopic

signatures varying from -13.5 to -17.5% for δ^{13} C and 7.4 to 8.2‰ for δ^{15} N (Table 1), had a

- much lower contribution $(3.56 \pm 2.96\%; \text{mean} \pm \text{SD} \text{ across all sites and seasons})$ to the
- sedimentary organic matter compared to other sources such as SPOM ($54.14 \pm 29.40\%$), *S*.
- 334 *densiflora* and *R. maritima* $(30.24 \pm 19.34\%)$ and C3 plants $(11.68 \pm 11.10\%;$ **Fig. 7**).
- In spite of the large credible intervals, the highest average values of contributions of
- macroalgae to the sedimentary organic matter across all sites occurred during summer (4.5 \pm
- 337 0.36%) and winter $(8 \pm 2\%)$ 2013 and autumn $(6.4 \pm 2.4\%)$ and winter $(4 \pm 2.26\%)$ 2014,
- periods of the highest macroalgal biomass accumulation (Figs. 4a,b & 7). The only exception

to this pattern was winter 2013, a post-bloom period. However, there was a spatio-temporal

decoupling between algal contributions to the sediments and the observed patterns of drift

macroalgal abundance. Algal contributions were not proportional to the annual and
 interannual variations in algal bloom magnitude and persistence. Furthermore, the largest

- biomass blooms at exposed sites were not translated into the higher values of organic matter
- incorporated into the sediments. Indeed, the values of algal contribution to the sedimentary
- organic matter were not significantly different among the exposed and sheltered sites.
- 346

DISCUSSION

347 Our results showed that interactive effects of hydrological and meteorological factors create

favourable conditions for the onset of large drift macroalgal accumulations in shallow areas.

- Nonetheless, regardless of their magnitude and persistence, macroalgal blooms made a minor
- contribution to the sediment organic matter pool compared to other primary producers, such
- as seagrasses and salt marsh plants. These findings contrast with those from previous
- experimental studies showing that drift algae may make significant, although transitory, contributions to the sedimentary organic matter (e.g. Corzo et al. 2009). Most of these
- previous studies, however, did not take into account the natural patterns in their abundance
- and their driving factors (but see Pihl et al. 1999). Therefore, our study highlights the
- importance of considering the environmental context in the assessment of macroalgal bloom
- 357 feedbacks on benthic nutrient regeneration.

358

Temporal and spatial patterns of drift macroalgal blooms

359 Drift macroalgal blooms have been a common feature in the PLE in the last decade,

- 360 suggesting a shift towards a macroalgal-dominated state (Lanari & Copertino 2017). Although
- 361 opportunistic macroalgal blooms are often regarded as a symptom of eutrophication
- 362 (Teichberg et al. 2010), we did not observe significant effects of water column nutrients on

- the development of macroalgal biomass on a monthly basis (i.e. PC2; Figs. 3 & 4a). However,
- the tissue TN values found here were close to or above the critical values required for
- maximum growth (i.e. 2.2%; Pedersen & Borum 1996) and those found under nutrient-
- enriched conditions (i.e. 3.5%; Martinetto et al. 2011), highlighting that nitrogen availability
- 367 was sufficient to trigger drift macroalgal blooms. The largest blooms in 2014 coincided with a
- period of increased PO_4^{3-} concentrations in the water column (Figs. 3c & 4a,b), indicating
- that in nitrogen-enriched systems such as the PLE, phosphorus supply may limit the growth of
- bloom-forming macroalgae (Teichberg et al. 2010).
- The effects of nutrient availability on bloom onset are also mediated by local hydrology,
- 372 which in turn controls the variability in water physico-chemical parameters in the PLE.
- During very high freshwater discharge (spring 2012 and late winter/spring 2013; Figs. 2a &
- 374 3), water level and turbidity increase, which reduces the light levels in the water column and
- 375 limit the growth of algae (Lanari & Copertino 2017). Conversely, low/moderate freshwater
- discharges and increased saltwater intrusions and water retention (i.e. summer/autumn 2013
- and autumn/early winter 2014; Fig. 2) improve underwater light conditions through decreased
 water turbidity and levels. Together with the reduced currents, the latter conditions enable
- biomass growth and accumulation in shallow areas. Blooms of *Ulva* species benefit from
- increased salinity and temperature in summer/early autumn (Coutinho & Seeliger 1986,
- Martins et al. 1999), whereas *Rhizoclonium* sp. thrives at lower salinities, temperatures and
- irradiances in mid-autumn to winter (Hall & Walmsley 1991, Matsuyama-Serisawa et al.
- 2004). Thus, seasonal differences in the timing, persistence and composition of blooms reflect
- the annual and interannual variability in the local hydrology and covarying water physico-
- 385 chemical parameters.
- Bloom-forming species may be an important food resource for some consumers in the
- mudflats of the PLE during warmer seasons (Claudino et al. 2013). Juvenile and adult crabs,
- such as *Neohelice granulata* and *Callinectes sapidus*, are found grazing on drifting mats in
- 389 shallow areas (M. Copertino pers. obs.). Nonetheless, bloom-forming macroalgae do not
- contribute significantly to the diets of herbivorous fish in the PLE (Mont'Alverne et al. 2016,
- 391 Garcia et al. 2017). As in many temperate estuaries, the PLE harbours few species of
- herbivorous fish and crustaceans (Mont'Alverne et al. 2016), and herbivory therefore cannot
- 393 control macroalgal blooms. Furthermore, top-down controls on algal blooms can be limited
- under nutrient-enriched conditions, such as in the PLE (e.g. Martinetto et al. 2011).
- Exposure had a positive effect on the magnitude of algal blooms, with the site of the largest
- biomass accumulations varying seasonally according to the prevailing NE and SW winds.
- 397 Large drift mat accumulations occur at exposed shallow bays due to their import from nearby
- areas in addition to the retention of *in situ* growth (Berglund et al. 2003). Accordingly, the
- average wind speeds observed here (6 m s^{-1}) were within or above values reported to trigger
- 400 onshore algal transport/accumulation in coastal areas worldwide through wind-induced waves
- 401 and superficial currents (i.e. 5 to 10 m s⁻¹ in China, Keesing et al. 2011; 3–5 m s⁻¹ in 402 Denmark, Rasmussen et al. 2013). Thus, our findings indicate that interactive effects of
- 402 Definition, Rashussen et al. 2013). Thus, our midnings indicate that interactive effects of 403 exposure and local wind patterns can cause predictable patterns of biomass accumulation in
- 404 shallow estuarine areas.
- 405 However, the low spatial replication here limited our conclusions. Drift mat advection and
- 406 accumulation may also co-vary with other factors such as substratum complexity (e.g.
- 407 presence of seagrass meadows; Biber 2007) and bottom topography (Kotta et al. 2008).
- 408 Consequently, contrasting effects of exposure on drift macroalgae accumulations have been
- reported (e.g. Pihl et al. 1999, Berglund et al. 2003, Rasmussen et al. 2015), and studies
- 410 conducted over large spatial scales are needed to test the generality of our results.

411

Contribution of drift macroalgae to sediment C and N

Ephemeral macroalgal blooms are short-lived (McGlathery et al. 2007). Accordingly, 412

senescent understory biomass was observed within bloom periods, corroborating the short life 413

cycles (~12 d for U. clathrata; Copertino et al. 2009) and high decomposition rates (~4 wk in 414

litter bags; data not shown) of the opportunistic species observed in the PLE and reported 415

elsewhere (e.g. Castaldelli et al. 2003, Conover et al. 2016). Although increases in sediment C 416

and N content can result from macroalgal biomass depositions and senescence (Pihl et al. 417

418 1999, Corzo et al. 2009, Hardison et al. 2010), our results did not support these findings. No

significant increases in sediment TOC and TN were observed, regardless of the temporal and 419

spatial differences in the magnitude of biomass accumulations. 420

Many factors may have resulted in transitory increases in sedimentary organic matter of a few 421

days or weeks that could not be detected at the monthly time scale adopted in our study (Rossi 422

423 2007, García-Robledo et al. 2008). Due to the fast turnover of opportunistic macroalgal

detritus, biomass deposited on the sediment is quickly recycled through bacterial assimilation, 424 resulting in effluxes of ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) across the 425

sediment-water interface (García-Robledo et al. 2008, 2013). In shallow estuarine areas

426 similar to the PLE, wind action maintains high oxic conditions at the water-sediment 427

- interface, thus enhancing the microbial mineralization of organic matter and its transfer to the 428
- 429 water column (Rigaud et al. 2013). Nutrients released from sediment can be assimilated by
- microphytobenthos (Hardison et al. 2010), which is subsequently consumed by surface 430

431 deposit feeders, transferring nutrients from the sediment to secondary consumers (Rossi et al.

2007). Indeed, transitory increases (i.e. 2 wk) in sedimentary TOC (1.7 to 14%) and TN (13.5 432

to 16%) have been observed during experimental additions of low algal biomass (e.g. ~ 40 g 433

DW m⁻², Rossi et al. 2007; 220 g DW m⁻², García-Robledo et al. 2008). Nonetheless, at 434

higher levels of biomass accumulation such as those found here, up to 1900 g DW m⁻², 435

biomass inputs would override sediment mineralization rates, thereby causing C and N 436

accumulations and increasing the potential for algal biomass feedbacks on nutrient cycling 437

(Rossi 2007). 438

No evidence of macroalgal C and N accumulation was observed. The stable isotope analysis 439

showed that, overall, the low sedimentary TOC and TN contents were explained by a low 440 incorporation of algal biomass, regardless of the magnitude and persistence of the

441 accumulations. The incorporation of algal biomass within sediments relies on the existence of 442

hydrodynamic conditions promoting the deposition and burial of macroalgal tissue (Hardison 443

444 et al. 2010). We suggest that, although advective transport may promote large accumulations

of drift biomass in shallow shoals, the driving force behind its accumulation, i.e. wind action, 445

also hampers its deposition and burial within sediments during senescence. The low erosion 446

thresholds of drift mats cause their frequent translocation by waves and currents (Flindt et al. 447

2004), leading to unstable deposition on the sediment surface at small spatial (i.e. 1 m^2) and 448

temporal scales (i.e. a few hours to a few days; Biber 2007, Rasmussen et al. 2013). 449

Accordingly, wind-driven weekly variation in the spatial distribution of drift macroalgae has 450

been reported in shallow shoals of the PLE (Lanari & Copertino 2017), indicating transitory 451

mat depositions on the sediment surface. In addition, although decaying biomass was detected 452

during the sampling periods, the relocation of drift mats may have alleviated extensive 453

biomass die-offs through shelf-shading, diminishing mass transfers to superficial sediments 454

(García-Robledo & Corzo 2011). Therefore, our study indicates that in high hydrodynamic 455 systems where unstable depositions of algal mats occur, feedback mechanisms between algal

456

blooms and nutrient regeneration within sediments are unlikely to occur. 457

As algal blooms had a minor contribution to the sediment organic matter pool, the fate of 458 nutrients bound to algal biomass in the PLE is still unclear. Dense biomass accumulations 459

- comprise a substantial stock of labile organic matter with high nutritional value (Banta et al.
 2004, Britton-Simmons et al. 2012). For instance, biomass peaks of up to 982 g DW m⁻² with
 a nitrogen content of 2.1% (i.e. exp-SW in autumn 2014) can store up to 0.18 t N ha⁻¹.
 Simultaneously, biomass accumulated through mat advection may promote influxes of
 macroinvertebrates from adjacent areas and enhance the biotic structural complexity in
- shallow areas, increasing macrofaunal diversity and abundance (Salovius et al. 2005). Under
- the maintenance of oxic conditions, herbivory and detritivory may partly account for the
 recycling of organic matter, thus creating hotspots of secondary productivity in areas of algal
- 468 accumulations (Cebrian et al. 2014). Released organic and inorganic nutrients in the water
- 469 column during biomass senescence and decomposition can also be taken up by other primary
- 470 producers, such as salt marsh plants (Newton & Thornber 2013) and phytoplankton (Wang et
- al. 2012), or may sustain further macroalgal growth (Hanisak 1993).
- 472 Macroalgal-bound nutrients were ultimately flushed out from shallow areas by increased
- 473 freshwater discharges (i.e. winter 2013 and 2014). In the absence or loss of perennial primary
- 474 producers that promote long-term nutrient retention, such as seagrasses, the mass export of
- 475 plant-bound nutrients may be enhanced (Flindt et al. 2004, McGlathery et al. 2007). The
- advection of drift biomass from shallow areas may fuel deep secondary production through
- substantial fluxes of energy and nutrients to recipient communities, creating spatially
- subsidized food webs (Britton-Simmons et al. 2012, Hyndes et al. 2014). However, low
 contributions of drift macroalgae to herbivores and detritivores occurring in deeper areas have
- 479 controllous of drift macroargae to heroryores and deutifyores occurring in deeper areas have
 480 been reported in the PLE (Mont'Alverne et al. 2016). Thus, according to the hydrological
- 481 (Britton-Simmons et al. 2009) and basin-shape conditions (Britton-Simmons et al. 2012,
- 482 Filbee-Dexter & Scheibling 2016), much of the biomass advected to deep channels can be
- exported to adjacent coastal areas, hence representing nutrient loss from the system (Martins
- et al. 2007). If so, eutrophication in shallow areas may ultimately cause a long-term
- oligotrophication of the system (McGlathery et al. 2007, García-Robledo & Corzo 2011).

In conclusion, our study highlights the role of drift macroalgal blooms as either a sink or 486 source of nutrients within a subtropical, highly dynamic estuarine system. The combined 487 effects of local hydrology, water physico-chemical parameters and wind action promote large 488 algal biomass accumulations representing short-lived nutrient stocks in shallow areas. 489 Although nutrient regeneration within sediments can sustain the onset of macroalgal blooms 490 (Sundbäck et al. 2003), our findings indicate that feedbacks of biomass accumulations on 491 sedimentary organic matter are unlikely to occur due to the dual effects of wind action on mat 492 accumulations. Therefore, meteorological and hydrodynamic conditions must be considered 493 when assessing the fate of algal-bound nutrients in shallow coastal areas. To evaluate the 494 generality of our results, more studies assessing the incorporation of algal biomass within 495 sediments under distinct spatio-temporal scales of mat deposition are needed, preferably using 496 additional tracers. Moreover, as the fate of macroalgal-bound nutrients is still unclear, 497 investigations on the effects of algal-dominated phases on nutrient cycling and transfers 498 across different biotic compartments and at distinct spatial scales (i.e. shallow and deep areas) 499

500 may provide insights on nutrient balance within the ecosystem.

501

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- 693

Fig. 1. (a) Patos Lagoon estuary along the southern Brazilian coastline and (b) the

- mesomixohaline area of the estuary, with coastal wave exposure highlighted by colours; wave
- 696 fetch values of each sampling site are indicated. Sampling sites are indicated by squares
- 697 (circles) for sites with preferential exposure to SW (NE) winds. Filled and empty symbols
- represent exposed and sheltered sites, respectively. Wave exposure gradients for each coastal
- cell are given in grid cell units which represent the number of 200 m grid cells covered by sea
- and available for calculating wind drag on the water surface in 16 angular sectors of 22.5°
- Fig. 2. Variation of the hydrological and physico-chemical parameters. (a) Freshwater
- discharge, water level and salinity, (b) water column turbidity (FNU: formazin nephelometric
- units) and irradiance, and (c) temperature from August 2012 to August 2014. Values are
- means (\pm SE) among all sites. W: winter, Sp: spring, Su: summer and Au: autumn
- Fig. 3. Monthly variation in (a) NH_4^+ , (b) $NO_2^- + NO_3^-$ and (c) PO_4^{3-} concentrations in the
- water column between August 2012 and August 2014. Values are means (\pm SE, N = 12)
- among all sites. W: winter, Sp: spring, Su: summer and Au: autumn
- Fig. 4. Temporal variation in drift macroalgal (a) biomass and (b) coverage among sites from
- August 2012 to August 2014. Values are means \pm SE (N = 10 and 60 per station for biomass
- and coverage, respectively). Note the broken *y*-axis in panel a. DW: dry weight, W: winter,
- 711 Sp: spring, Su: summer and Au: autumn. Sites were labelled according to low ('shelter') and
- moderate to high exposure ('exp') and wind direction (northeast: NE, or southwest: SW)
- Fig. 5. Monthly variation in (a) total organic carbon (TOC) and total nitrogen (TN) and (b)
- C:N molar ratios in algal tissue between August 2012 and August 2014. Values are means (±
- SE, N = 12) among all sites. W: winter, Sp: spring, Su: summer and Au: autumn. Note the
- 716 broken *x*-axis depicting only drift macroalgal blooming periods
- Fig. 6. Monthly variation in (a) % total nitrogen (TN), (b) % total organic carbon (TOC), (c)
- δ^{15} N and (d) δ^{13} C in sediment sampling sites from September 2012 to August 2014 (at sites
- exp-SW and exp-NE; site abbreviations as in Fig. 4) and from September 2012 to August
- 720 2013 (shelter-SW and shelter-NE). Values are means \pm SE
- Fig. 7. Estimated contributions of (a) drift macroalgae, (b) *Ruppia maritima* and *Spartina*
- 722 *densiflora*, (c) C3 plants and (d) suspended particulate organic matter (SPOM) to sedimentary
- organic matter among sites from spring 2012 to winter 2014. Bars represent the posterior
- probability means \pm 95% credible intervals. Site abbreviations as in Fig. 4. W: winter, Sp:
- spring, Su: summer and Au: autumn. Note the different *y*-axis scales

Table 1. Mean values (\pm 1 SD) of δ^{13} C, δ^{15} N, %C and %N for the sources *Ulva* sp. and *Rhizoclonium* sp. (drift macroalgae), *Ruppia maritima*, *Spartina*

densiflora, *Scirpus maritimus* and *Scirpus olney* and suspended particulate organic matter (SPOM) collected in mudflats of the Patos Lagoon estuary, Brazil, across seasons (spring, summer, autumn and winter). Lowercase letters indicate sources grouped for mixing models analysis. ND:

	Summer					Autumn				Win	ter	Source	
	$\delta^{13}C$	$\delta^{15}N$	%C	%N	$\delta^{13}C$	$\delta^{15}N$	%C	%N	$\delta^{13}C$	$\delta^{15}N$	%C	%N	
Drift macroalgae	-15.7 ± 1.5	8.2 ± 1.4	33 ± 0	1.9 ± 0	$\begin{array}{c}-17.5\pm\\1.6\end{array}$	$\begin{array}{c} 7.5 \pm \\ 0.9 \end{array}$	34.1 ± 3	3.4 ± 1.4	-13.5 ± 3.3	7.4 ± 1.3	36.5 ± 2	3 ± 1	Claudino et al. (2013), this study
Spartina densiflora ^a	-12.1 ± 0.2	6.2 ± 0.5	41 ± 1.4	0.7 ± 0.2	$\begin{array}{c}-12.3\pm\\0.3\end{array}$	6.2 ± 0.7	$\begin{array}{c} 40.7 \pm \\ 0.7 \end{array}$	0.8 ± 0.2	$\begin{array}{c}-12.2\pm\\0.6\end{array}$	4.5 ± 0.6	40.6 ± 1.2	0.9 ± 0.1	Claudino et al. (2013)
Ruppia maritimaª	-10.5 ± 1.4	7.3 ± 0.4	40.3 ± 1.6	3.2 ± 0.4	$\begin{array}{c}-13.9\pm\\0.9\end{array}$	$\begin{array}{c} 7.2 \pm \\ 0.8 \end{array}$	28.6 ± 4	2 ± 0.1	$\begin{array}{c}-10.7\pm\\1.2\end{array}$	6 ± 0.8	41 ± 2.1	3.8 ± 0.7	Claudino et al. (2013), this study
Scirpus maritimus ^b	$\begin{array}{c}-25.2\pm\\0.9\end{array}$	7 ± 0.5	41.7 ± 1	1.3 ± 0.2	$\begin{array}{c}-28.1 \pm \\0.6\end{array}$	5.7 ± 0.8	39.9 ± 1.9	2.2 ± 0.1	-27 ± 1.1	4 ± 2.1	41.3 ± 1	1.6 ± 0.3	Claudino et al. (2013)
Scirpus olney ^b	$\begin{array}{c}-26.7\pm\\1\end{array}$	6 ± 0.5	$\begin{array}{c} 39.8 \pm \\ 1.5 \end{array}$	1.5 ± 1.1	ND	ND	ND	ND	-28 ± 1.1	6 ± 1.2	$\begin{array}{c} 40.3 \pm \\ 0.2 \end{array}$	1.5 ± 0.2	Claudino et al. (2013)
SPOM	$\begin{array}{c}-18.4\pm\\0.4\end{array}$	6.6 ± 0.3	$\begin{array}{c} 1.8 \pm \\ 0.1 \end{array}$	0.2 ± 0	-19.5 ± 1.3	1.8 ± 1.6	$\begin{array}{c} 0.9 \pm \\ 0.5 \end{array}$	0.2 ± 0.1	$\begin{array}{c}-18.5^{\mathrm{c}}\pm\\0.8\end{array}$	4.2 ^c ± 0.9	1.4 ^c ± 0.3	0.2* ±	Claudino et al. (2013)

^aDenoted as a single source due to the similarities in their isotopic signature

⁷³⁰ ^bDenoted as a single source (C3 plants) due to their same photosynthetic pathway

⁷³¹ ^cValues are averages between summer and autumn

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Table 2. Mean, standard deviation (SD) and coefficient of variation (CV) of water salinity from Spring 2012 to Winter 2014

Spring			Summer			Autumn			Winter			
Year	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
2012-	10.57	1.43	0.13	18.66	4.76	0.25	14.45	3.22	0.22	6.45	1.48	0.22

2013												
2013– 2014	2.25	1.56	0.69	6.41	4.13	0.64	5.46	0.31	0.05	2.03	0.44	0.21

Table 3. Eigenvector coefficients of hydrological and water physico-chemical parameters in

relation to the 3 first axes of the PCA. PC1, PC2 and PC3 explained 47.1, 17.4 and 15.21% of

data variability, respectively. Highest coefficient values for each factor are highlighted in
bold; DIN: dissolved inorganic nitrogen, CV: coefficient of variation

Parameter	PC1	PC2	PC3
Freshwater discharge	0.68	-0.24	-0.16
DIN	-0.23	0.03	0.84
PO ₄	0.14	-0.56	0.64
Level	0.92	-0.16	-0.16
Temperature	-0.30	0.81	0.18
Salinity	-0.88	-0.29	0.04
Turbidity	0.74	0.47	0.33
Irradiance	-0.83	0.27	-0.20
Salinity CV ^a	0.83	0.33	0.06

⁷³⁸ ^aProxy for water retention in the study area