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**MACROALGAS DE DERIVA NO ESTUÁRIO
DA LAGOA DOS PATOS (RS, BRASIL):
FATORES HIDROLÓGICOS, ESTOQUE DE
NUTRIENTES E EFEITOS NA COMUNIDADE
BENTÔNICA**

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ÍNDICE

LISTA DE SÍMBOLOS E ABREVIACÕES.....	vii
RESUMO.....	viii
ABSTRACT.....	ix
1. INTRODUÇÃO.....	1
1.1 Florações de macroalgas de deriva: forçantes ambientais.....	3
1.2 Contribuição ao estoque de nutrientes.....	5
1.3 Efeitos sobre a comunidade bentônica.....	8
2. OBJETIVOS.....	12
3. MATERIAIS E MÉTODOS.....	12
3.1 Área de estudo.....	12
3.2 Variabilidade temporal da abundância de macroalgas de deriva no período 2004-2007.....	15
3.3 Variabilidade espacial e temporal da abundância de macroalgas de deriva no período 2012-2014 e contribuições para a matéria orgânica sedimentar.....	20
3.4 Avaliação experimental dos efeitos da deposição transitória de macroalgas de deriva na comunidade bentônica.....	26
4. SÍNTESE DOS RESULTADOS.....	32
4.1 Artigo 1.....	33
4.2 Artigo 2.....	34
4.3 Artigo 3.....	36
5. DISCUSSÃO GERAL.....	38
6. CONCLUSÕES.....	54

REFERÊNCIAS BIBLIOGRÁFICAS.....	56
APÊNDICES.....	67

LISTA DE APÊNDICES

Apêndice 1: Drift macroalgae in the Patos Lagoon Estuary (Southern Brazil): effects of climate, hydrology and wind action on the onset and magnitude of blooms.

Apêndice 2: Dynamics of estuarine drift macroalgae: growth cycles and contribution to sediments of shallow areas.

Apêndice 3: Effects of short-term depositions of drift macroalgae on *Ruppia maritima* and associated benthic macrofauna.

LISTA DE SÍMBOLOS E ABREVIATÓES

AB: alta biomassa

ANOVA: análise de variância

BB: baixa biomassa

CC: controle cercados

CI: controle inicial

COT: carbono orgânico total

CR: controle referência

ELP: estuário da Lagoa dos Patos

ENSO: *El Niño Southern Oscillation*

MOD: matéria orgânica dissolvida

MOP: matéria orgânica particulada

MOPS: matéria orgânica particulada em suspensão

NE: nordeste

NNE: norte-nordeste

NT: nitrogênio total

NID: nitrogênio inorgânico dissolvido

PAR: *photosynthetic aquatic radiation*

PERMANOVA: análise de variância multivariada por permutação

SO: sudoeste

SSO: sul-sudoeste

VAS: vegetação aquática submersa

RESUMO

A dinâmica espacial e temporal de florações de macroalgas de deriva e seus efeitos sobre a matéria orgânica do sedimento e a comunidades bentônica foram investigados no estuário da Lagoa dos Patos (ELP). Amostragens semanais e mensais de macroalgas foram realizadas em enseadas rasas do estuário durante 2004-2007 e 2012-2014. Experimento de campo foi conduzido durante o Outono de 2014. Períodos dominados por macroalgas de deriva compostas predominantemente por *Ulva clathrata*, *U. intestinalis* e *Rhizoclonium riparium* foram observados, com altos valores de biomassa (até 2 kg PS m⁻²) indicando uma possível mudança de fase da vegetação aquática submersa. Teor de N próximo ou acima de 2% da biomassa de macroalgas evidenciou uma alta disponibilidade de nitrogênio para o crescimento. A formação de florações foi controlada principalmente pela descarga fluvial, a qual é influenciada por fatores climáticos (El Niño/La Niña) que afetam a precipitação na bacia de drenagem do estuário. A hidrodinâmica local determinou variações anuais e interanuais da ocorrência e persistência das florações e variações nos parâmetros físico-químicos da água determinaram a sua magnitude. Baixa descarga fluvial durante o verão e outono promoveu aumento na retenção d'água, proporcionando a permanência de macroalgas de deriva no estuário. Aumento na salinidade e irradiância e decréscimo na turbidez e nível d'água, associados a maiores valores de temperatura, favoreceram o crescimento algáceo. Ondas e correntes gerados por ventos também afetaram a magnitude e persistência das florações através da retenção/dispersão de biomassa. O sedimento apresentou baixos valores de carbono orgânico total e nitrogênio total em todos os períodos e enseadas investigadas. O modelo de mistura de isótopos estáveis indicou baixa contribuição da biomassa algácea para a matéria orgânica sedimentar (de 0,5% a 8,1%), independente da magnitude e persistência das florações. Acúmulos de macroalgas de deriva persistentes no tempo não foram traduzidos em maior incorporação de matéria orgânica no sedimento. Resultados experimentais evidenciaram uma alta instabilidade temporal e espacial de deposições de manchas de macroalgas de deriva sobre o fundo devido à advecção gerada pela alta hidrodinâmica local. Deposições transitórias (4-7 dias) de macroalgas ocasionaram decréscimos significativos na biomassa aérea e subterrânea, e parâmetros demográficos da fanerógama *Ruppia maritima*. Alterações na estrutura e abundância da macrofauna bentônica não foram significativas, embora efeitos negativos indiretos da deposição de macroalgas de deriva sobre o macrozoobentos são sugeridos, mediados pela remoção de *R. maritima*. A análise conjunta dos resultados sugere que, apesar dos recentes aumentos de nutrientes reportados na área de estudo, a dominância de macroalgas de deriva pode ocasionar a oligotrofização do ELP a longo prazo, com um possível decréscimo da produção secundária estuarina.

Palavras-chave: macroalgas de deriva, hidrologia, advecção, matéria orgânica sedimentar, *Ruppia maritima*, efeitos balísticos, macrozoobentos.

ABSTRACT

The spatio-temporal dynamics of drift macroalgae blooms and their effects on sedimentary organic matter and benthic communities were investigated in the Patos Lagoon estuary (PLE). Weekly and monthly surveys of macroalgal abundance were performed in shallow areas from 2004 to 2007 and 2012 to 2014. A field experiment was conducted in Autumn 2014. Macroalgal-dominated periods were detected, with biomass peaks up to 2 kg PS m⁻² of *Ulva clathrata*, *U. intestinalis* and *Rhizoclonium riparium*, which suggest a phase-shift of the submerged aquatic vegetation. Nitrogen content in algal tissue close or above 2% highlighted a high N availability for growth. The onset of macroalgal blooms was mainly driven by variations in freshwater discharges which, in turn, were influenced by climatic factors (El Niño/La Niña) that set precipitation regimes in the PLE watershed. Whereas variations in freshwater discharge determined annual and interannual patterns of blooms occurrence and persistence, associated changes in water physico-chemical parameters modulated their magnitude. Low freshwater discharges in early summer to late autumn enhanced water retention, enabling biomass maintenance in shallow areas. Increases in salinity and irradiance, and decreases in turbidity and level, associated to increased water temperatures, favored macroalgal growth. Wind-driven waves and currents also affected the magnitude and persistence of drift macroalgae blooms through biomass accumulation or dispersion. Sediment revealed low TOC and TN content for all periods and stations investigated. Stable isotopes mixing models indicated low contributions (from 0.5 to 8.1%) of drift macroalgae biomass to sedimentary organic matter, regardless blooms magnitude and persistence. Largest biomass accumulations were not translated into highest incorporations within sediments. Experimental results highlighted unstable depositions of drift mats resulting from their advection during high hydrodynamic conditions. Transitory depositions (4 to 7 days) of drift mats promoted significant decreases in *Ruppia maritima* above and belowground biomass, leaves and rhizome length and shoots and nodes density. No significant changes in the structure and abundance of associated benthic macrofauna were detected. However, indirect negative effects of transitory depositions of drift mats on macrozoobenthos through *Ruppia* meadows removal are suggested. The joint analysis of our results suggest that, although cultural eutrophication processes are reported in the study area, drift macroalgae-dominated periods may generate long term oligotrophication of the estuarine system, with a possible impoverishment of the secondary production.

Keywords: drift macroalgae, hydrology, advection, sedimentary organic matter, *Ruppia maritima*, ballistic effects, macrozoobenthos.

1. INTRODUÇÃO

Macroalgas são um importante componente dos produtores primários estuarinos juntamente com pradarias de fanerógamas submersas, fitoplâncton e microfitobentos (Valiela et al. 1997). Macroalgas são fonte alimentar para herbívoros e detritívoros, aumentam a complexidade estrutural do ambiente, fornecendo habitat e refúgio para a fauna bentônica e pelágica (Salovius & Bonsdorff 2004), além de participar da ciclagem dos nutrientes (Fong et al. 2004; Anderson et al. 2010). O deslocamento dos talos destas macroalgas pelas zonas rasas atua, ainda, como vetor de transporte da fauna local (Salovius et al. 2005) e favorece a remoção de epífitas sobre as folhas de fanerógamas marinhas (Irlandi et al. 2004). Consequentemente, macroalgas promovem o aumento da produção primária e secundária estuarina (Cebrián et al. 2014; Lyons et al. 2014).

Devido a menor disponibilidade ou ausência de substratos duros ou consolidados, macroalgas estuarinas crescem diretamente sobre a superfície dos sedimentos em enseadas rasas. Entretanto, devido à instabilidade do substrato e estruturas de fixação pouco desenvolvidas (discos ou filamentos basais pequenos e superficiais), estas algas são facilmente e frequentemente removidos do fundo e transportados pela ação de ondas e correntes (Flindt et al. 2004; Canal-Vergés et al. 2010). Formando massas flutuantes denominadas macroalgas de deriva, os talos mantêm o seu crescimento e reprodução na coluna d'água, desde que mantidos em condições favoráveis de luz, nutrientes e salinidade (Coutinho & Seeliger 1986).

Macroalgas de deriva estuarinas são compostas em geral por clorofíceas oportunistas, principalmente espécies de *Ulva*, *Cladophora* e *Chaetomorpha* (Morand & Merceron 2005). Outros grupos podem ocorrer como rodofíceas (algas vermelhas) dos

gêneros *Polysiphonia*, *Laurencia*, *Chondria* e *Gracilaria* (e.g. Irlandi et al. 2004; Biber 2007) e feofíceas (pardas) dos gêneros *Pylayella* (e.g. Luringson & Kotta 2006). Macroalgas de deriva verdes são caracterizadas por talos simples com morfotipo filamentoso, tubular ou laminar, baixo grau de especialização dos tecidos, alta relação superfície:volume e alto investimento em reprodução assexuada (por liberação de esporos) e vegetativo. Estas algas são eficientes na captação de luz e de nutrientes dissolvidos, tanto da coluna d'água como da interface com o sedimento (Tyler et al. 2001), resultando em alta taxa fotossintética e incremento da biomassa (Valiela et al. 1997).

Em densidades baixas a moderadas, macroalgas de deriva são benéficas e exercem importantes funções ecológicas no ambiente estuarino. Entretanto, a ocorrência de florações de macroalgas verdes densas e persistentes no tempo (conhecidas como “marés verdes”) podem alterar a estrutura e funcionamento de zonas rasas costeiras (Viaroli et al. 2008; Anderson et al. 2010), causando desequilíbrio ecológico, com prejuízos econômico e estético aos ambientes aquáticos costeiros (Morand & Merceron 2005). Nas últimas décadas, aumentos na frequência e magnitude das “marés verdes”, tem se tornado um fenômeno crescente em zonas costeiras de toda o globo, decorrentes principalmente de processos de eutrofização cultural (Teichberg et al. 2010; Smetacek & Zingone 2013; Lyons et al. 2014).

Os estudos sobre marés verdes e seus impactos ecológicos tem se restringindo a poucos ambientes estuarinos e costeiros, localizados principalmente em regiões temperadas (e.g. Europa, EUA e China), sendo escassos os estudos em regiões tropicais e subtropicais da América do Sul (e.g. Martinetto et al. 2010). No Brasil, não existem estudos sobre a ocorrência e nos fatores desencadeadores de marés verdes, e seus efeitos

nas comunidades bentônicas (Copertino et al. 2016). Tal fato é alarmante considerando a rápida ocupação e crescimento populacional em zonas costeiras brasileiras e resultantes aumentos das pressões antrópicas sobre ecossistemas marinhos nas últimas décadas (Dias et al. 2012). Portanto, a compreensão dos fatores que atuam na formação de marés verdes, bem como os seus efeitos no funcionamento dos ecossistemas costeiros e estuarino, é fundamental para o manejo e preservação desses sistemas.

1.1 Florações de macroalgas de deriva e formação de marés verdes: forçantes ambientais

O crescimento excessivo das macroalgas de deriva e a formação de marés verdes estão associados a processos de eutrofização e aumentos na disponibilidade de nutrientes inorgânicos, tais como nitrogênio e fósforo (Valiela et al 1997; Viaroli et al 2008; Fong & Kennison 2010; Teichberg et al. 2010). Embora o aumento no aporte e concentração de nutrientes na coluna d'água seja essencial para a proliferação de macroalgas oportunistas, uma complexa interação de variáveis hidrológicas e meteorológicas controla o crescimento e acúmulo de algas de deriva em áreas rasas estuarinas (Martins et al. 2001; Berglund et al. 2003; Kennison & Fong 2013). O desencadeamento de florações de macroalgas de deriva é também controlado pela hidrodinâmica local, a qual regula o tempo de residência da água e dos nutrientes, e a manutenção da biomassa de macroalgas no sistema (Martins et al. 2001; Viaroli et al. 2008; Fong & Kennison 2010). Enquanto a hidrodinâmica local determina o tempo de permanência da biomassa flutuante em áreas rasas, a interação de parâmetros físico-

químicos da água tais como salinidade, temperatura e irradiância modula a sua taxas de crescimento e consequente abundância (Martins et al. 1999, 2007; Malta et al. 2002).

Variações espaciais nos padrões de acúmulo da biomassa de macroalgas são também influenciadas pela ação dos ventos locais, os quais geram ondas e correntes que transportam as algas através das áreas estuarinas ou costeiras (e.g. Berglund et al. 2003; Liu et al. 2009). Dependendo da fisiografia da costa e da direção e velocidade dos ventos predominantes, o transporte de macroalgas de deriva promove a retenção ou acúmulo de biomassa produzida tanto localmente (autóctone) ou em áreas adjacentes (alóctone), resultando no empilhamento em grande extensão em determinadas áreas (e.g. Liu et al. 2009). Por outro lado, a ação de ventos também pode promover a dispersão da biomassa macrode macroalgas para zonas mais profundas e áreas adjacentes (Malta et al. 2002). Assim, os fatores responsáveis pelo desenvolvimento e acúmulo de macroalgas, assim como a sua persistência, variam nas diferentes regiões costeiras e entre locais de uma mesma costa ou estuário.

No estuário da Lagoa dos Patos (ELP), Rio Grande do Sul, Brasil, macroalgas de deriva são um componente importante da vegetação aquática submersa (VAS) e ocorrem associadas ou não a pradarias de fanerógamas enraizadas (e.g. *Ruppia maritima*, *Zannichellia palustri*; Copertino e Seeliger 2010). As macroalgas apresentam em geral um padrão sazonal, com maiores abundâncias no outono e primavera, enquanto pradarias de fanerógamas apresentam picos de verão. Entretanto, uma redução na distribuição e abundância da VAS tem sido observada nas últimas décadas, destacando-se o desaparecimento de pradarias de *R. maritima* de muitas das áreas rasas estuarinas. Entre as possíveis causas, destacam-se a precipitação pluviométria e a descarga fluvial anômala, durante eventos de El Niño forte (1997-98) e moderado

(2002-03), e o consequente aumento da remobilização de sedimentos e redução da irradiância sobre o fundo (Copertino & Seeliger 2010). Após o re-estabelecimento de condições hidrológicas favoráveis (i.e. redução do nível da água e aumento da penetração da luz), áreas rasas foram rapidamente dominadas por macroalgas deriva em detrimento às pradarias de *R. maritima* (Copertino & Seeliger 2010). Grandes e persistentes florações de macroalgas de deriva (mares verdes) foram observadas em zonas rasas do ELP (e.g. agosto-setembro de 2010; Gianasi et al. 2010) mas os fatores que desencadearam o fenômeno, assim como na sua magnitude e persistência, ainda são pouco entendidos.

1.2 Contribuições ao estoque de nutrientes

Macroalgas de deriva afetam os ciclos biogeoquímicos locais, contribuindo para uma ciclagem mais rápida dos nutrientes (McGlathery et al. 2007, Anderson et al. 2010). Massas flutuantes de macroalgas verdes oportunistas apresentam alta eficiência na captação dos nutrientes orgânicos e inorgânicos dissolvidos na coluna d'água e na interface sedimento-coluna d'água (Tyler et al. 2001). Devido à sua rápida taxa de crescimento e ciclo de vida muito curto (alguns dias a poucas semanas), os nutrientes assimilados são utilizados rapidamente, retornando à coluna d'água como matéria orgânica particulada (MOP) e dissolvida (MOD) durante o seu crescimento (exsudação, por fragmentação do talo e liberação de gametas e esporos), senescência, morte e decomposição. Tais compostos orgânicos são processados pela alça microbiana e repassados a níveis tróficos superiores (Tyler et al. 2001; Fong et al. 2004).

Por outro lado, florações de macroalgas de deriva podem provocar uma retroalimentação positiva e contínua no sistema, reforçando ou aumentando as consequências da eutrofização e das mudanças na estrutura da comunidade (Sündback et al. 2003). Uma menor parte da MOP e MOD liberada durante a deposição e posterior decomposição da biomassa de macroalgas é incorporada ao sedimento, contribuindo para o aumento dos teores de matéria orgânica, carbono e nitrogênio (Pihl et al. 1999; Corzo et al. 2009; Hardison et al. 2010; Gao et al. 2013). Todavia, aumentos de matéria orgânica do sedimento são transitórios devido à alta taxa de renovação (*turnover*) da biomassa das algas (Banta et al. 2004). A assimilação breve e rápida remineralização microbiana da matéria orgânica nas camadas óxicas do sedimento promove a subsequente liberação dos nutrientes reciclados na interface sedimento-coluna d'água (Hardison et al. 2010; García-Robledo et al. 2008, 2013). Por outro lado, o acúmulo de biomassas de macroalgas de deriva sobre o fundo intercepta os compostos inorgânicos liberados na interface sedimento-coluna d'água, suprimindo uma parcela significativa da demanda de nitrogênio e fósforo para manter a alta taxa de crescimento destas algas (Fong & Zedler 2000; Sündback et al. 2003, Tyler et al. 2001). Portanto, a remineralização da matéria orgânica nos sedimentos superficiais pode ser uma importante fonte de nutrientes que retroalimenta a taxa de crescimento e a persistência de florações de macroalgas em determinadas áreas rasas (Sündback et al. 2003).

O papel de florações de macroalgas nos ciclos biogeoquímicos locais e, particularmente, a contribuição da biomassa de macroalgas na concentração dos nutrientes estocados no sedimento, são poucos conhecidos. Estudos experimentais em baías costeiras e enseadas rasas estuarinas de áreas temperadas (e.g. América do Norte e Europa) demonstraram que parte da biomassa de macroalgas depositada sobre fundos

inconsolidados é retida nas camadas superficiais do sedimento (*e.g.* Garcia-Robledo et al. 2008, 2013; Corzo et al. 2009; Hardison et al. 2010). Entretanto, a maioria dos estudos tem sido realizada em laboratório ou estudos de campo em ambientes fechados ou controlados, não considerando fatores ambientais que possam influenciar os padrões espaço-temporais de acúmulos de biomassa e a sua subsequente incorporação no sedimento (Corzo et al. 2009; Hardison et al. 2010). Embora importantes para compreender os *feedbacks* da biomassa de macroalgas sobre a regeneração bêntica de nutrientes, os estudos experimentais fechados podem não reproduzir os padrões hidrológicos locais, limitando o conhecimento sobre os processos envolvidos no surgimento das florações e destino da matéria orgânica produzida por macroalgas de deriva.

No estuário da Lagoa dos Patos, o sedimento desempenha um papel importante na ciclagem de nutrientes, remineralizando uma parcela significativa da produção primária e, posteriormente, fornecendo nutrientes inorgânicos para a coluna de água (Niencheski & Jahnke 2002). Assim, áreas rasas onde florações de macroalgas de deriva têm sido observadas recentemente fornecem o cenário ideal para investigar a sua contribuição na matéria orgânica do sedimento, e os efeitos potenciais aos processos de auto-regeneração da biomassa.

Nesse contexto, a análise de isótopos estáveis é uma importante ferramenta na determinação das fontes de matéria orgânica no sedimento. Através do conhecimento das assinaturas isotópicas de distintas fontes, baseando-se na presença de diferenças entre elas e na manutenção das assinaturas durante o processo de decomposição da biomassa, e da mistura de interesse (no caso, o sedimento), é possível estimar o percentual de contribuição de cada fonte para a matéria orgânica sedimentar (Bouillon

et al. 2001). Usualmente, as razões isotópicas de carbono ($^{13}\text{C}/^{12}\text{C}$) e nitrogênio ($^{15}\text{N}/^{14}\text{N}$) são utilizados embora demais elementos como o enxofre (S) e biomarcadores como ácido graxos também possam ser utilizados. Com o avanço de modelos computacionais, estimativas de contribuição de distintas fontes para uma mistura de interesse utilizando dados isotópicos têm sido realizadas através de modelos de mistura bayesianos como o SIAR e, mais recentemente, o MixSIAR (Stock & Semmens 2013). Tais modelos levam em consideração informações obtidas *a priori*, erros associados tanto à variabilidade entre amostras como de origem desconhecida, e o fracionamento das assinaturas isotópicas das fontes durante a decomposição ou passagem entre níveis tróficos. A partir da geração de distribuições posteriores dos percentuais de contribuição de cada fonte, é possível estimar os seus valores médios e o intervalo de credibilidade de 95%.

1.3 Efeitos na comunidade bentônica

Extensas florações de macroalgas de deriva são um sintoma de mudanças de fase (i.e. *phase-shifts*) no estado de equilíbrio dos ecossistemas estuarinos, com subsequentes alterações na estrutura e abundância da VAS e da macrofauna associada (Viarolli et al. 2008). O acúmulo e deposição de massas de algas promove a competição por nutrientes com demais produtores primários e a redução da luz incidente sobre o fundo, sendo este último o principal fator associado ao desaparecimento de pradarias de fanerógamas marinhas durante eventos de marés verdes (Hauxwell et al. 2001; McGlathery et al. 2001). Adicionalmente, no interior de grandes massas de algas e na interface sedimento-água são formadas condições hipóxicas ou anóxicas resultantes da respiração e

senescência das algas, normalmente acompanhados por liberação de amônia e sulfetos durante a sua decomposição (Hauxwell et al. 2001; Pedersen et al. 2004). Sob tais condições adversas, ocorre a redução na taxa de crescimento, biomassa aérea e parâmetros demográficos de fanerógamas (i.e. comprimento de folha, densidade de hastes, entre outros; Hauxwell et al. 2001; Homer et al. 2011), assim como o decréscimo na abundância de organismos bentônicos epi e infaunais (Norkko & Bondorff 1996).

Os impactos deletérios de florações de macroalgas sobre comunidade bentônica ocorrem principalmente em áreas rasas com baixa hidrodinâmica, as quais são mais suscetíveis a acúmulos de biomassa estacionários e persistentes (Hauxwell & Valiela 2004; Cebrian et al. 2014). Entretanto, a deposição de massas de macroalgas de deriva sobre os fundos rasos estuarinos pode ser instável no tempo e espaço, visto que os acúmulos são controlados por fatores que atuam em distintas escalas temporais e espaciais (Kopecky & Dunton 2006). Dentre os fatores controladores, ressaltam-se ondas e correntes os quais podem transportar massas flutuantes de macroalgas mesmo sob baixas velocidades (i.e. $2-3 \text{ cm s}^{-1}$; Flindt et al. 2004). Esse processo ocasiona variações na deposição de macroalgas de deriva sobre pradarias de fanerógamas submersas em curtas escalas temporais (e.g. de um ciclo de maré a poucos dias; Biber 2007; Flindt et al. 2004) e espaciais ($\sim 1 \text{ m}^2$; Rasmussen et al. 2013), contrastando com os acúmulos de biomassa de longa duração usualmente fixados experimentalmente (Hauxwell et al. 2001; Cummins et al. 2004; Irlandi et al. 2004).

A movimentação frequente das massas de macroalgas de deriva pode atenuar os seus efeitos deletérios sobre as comunidades bentônicas devido à constante oxigenação da interface sedimento-coluna d'água (Hauxwell & Valiela 2004; Cebrián et al. 2014).

Contudo, impactos negativos do transporte de macroalgas de deriva sobre pradarias de fanerógamas foram sugeridos, resultantes da ressuspensão e erosão do sedimento (Valdemarsen et al. 2010; Canal-Vergés et al. 2014) e do aumento da força de arrasto sobre as plantas (Seeliger 2001). Uma vez que fundos vegetados tendem a suportar uma fauna mais diversa e abundante quando comparadas a fundos não-vegetados (Boström & Bonsdorff 1997; Rosa & Bemvenuti 2007), efeitos indiretos das macroalgas de deriva sobre a macrofauna bentônica são esperados. Entretanto, estudos considerando o comportamento dinâmico das macroalgas de deriva e seus efeitos sobre pradarias de fanerógamas são escassos (e.g. Irlandi et al. 2004), limitando a compreensão da direção e magnitude dos seus impactos sobre as comunidades bentônicas estuarinas.

O desenvolvimento de populações anuais de *R. maritima* no ELP é controlado pelo fotoperíodo, temperatura e salinidade da água (Copertino & Seeliger 2010). Durante a primavera, novas hastes brotam a partir da biomassa subterrânea (i.e. rizomas) remanescente e/ou novas plantas se originam a partir de sementes. Picos de biomassa e florescimento podem ser observados desde o final da primavera até o início do outono, seguido pela liberação dos frutos e senescência das plantas (Cafruni 1978). Reduções na abundância e distribuição de pradarias de *R. maritima* são reportadas nas últimas décadas associadas à aumentos da descarga fluvial durante eventos de El Niño (Copertino & Seeliger 2010). Embora populações de *R. maritima* sejam resilientes à distúrbios, devido a rápida recuperação baseada tanto na reprodução sexual e vegetativa (Anton et al. 2009; Cho et al. 2009), o re-estabelecimento de suas pradarias pode ser lento (até 10 anos), devido à remoção completa da rede de rizomas e do banco de sementes após distúrbios mais severos, como observado no ELP após fortes eventos El Niño (Copertino & Seeliger 2010). Efeitos aditivos ou sinérgicos de distúrbios distintos

podem afetar a resiliência de pradarias de fanerógamas submersas (Neto et al. 2010). Nesse sentido, sugere-se que a ocorrência de florações de macroalgas de deriva em áreas e períodos previamente dominados por pradarias de *R. maritima*, pode atrasar e/ou inibir o re-estabelecimento das plantas (Copertino & Seeliger 2010, Odebrech et al. 2010).

Em face às questões aqui apresentadas, o artigo 1 (i.e. Apêndice 1) dessa tese testou a hipótese de que, no ELP, enquanto o recrutamento e crescimento de macroalgas deriva estão relacionados a parâmetros físico-químicos da água, o acúmulo e distribuição da sua biomassa entre regiões meso e sublitoral de uma mesma enseada rasa depende da ação dos ventos locais. No segundo artigo (Apêndice 2), foi testada a hipótese de que florações de macroalgas de deriva resultam da interação de fatores atuando tanto na produção quanto na retenção da biomassa em áreas rasas, com a variabilidade espacial dos acúmulos de biomassa de macroalgas de deriva entre distintas enseadas estando relacionadas à diferentes graus de exposição aos ventos locais. Adicionalmente, através dos padrões naturais de ocorrência, magnitude e persistência de florações, o segundo artigo também testou a hipótese de que a biomassa macroalgácea é uma importante fonte de matéria orgânica para o sedimento, com contribuições sendo proporcionais à magnitude e persistência dos blooms. Finalmente, no terceiro artigo (Apêndice 3), foi testada a hipótese de que a deposição de massas de macroalgas de deriva sobre o fundo em curtos intervalos de tempo afeta negativamente plantas de *R. maritima*. A deposição de curta duração de macroalgas de deriva afeta ainda a macrofauna bentônica associada, através de efeitos indiretos mediados pela remoção das plantas de fanerógamas.

2. OBJETIVOS

Este estudo objetivou avaliar a variabilidade temporal e espacial de macroalgas de deriva do estuário da Lagoa dos Patos, investigando a influência dos fatores hidrológicos, a contribuição destas algas para a matéria orgânica no sedimento e suas interações com a flora e fauna bentônica. Os objetivos específicos foram:

- 1) Investigar a interação de fatores climáticos, hidrodinâmicos e hidrológicos que determinam o desenvolvimento, magnitude e persistência de florações de macroalgas de deriva em áreas rasas do ELP (Apêndices 1 e 2);
- 2) Analisar a variabilidade espacial da ocorrência e magnitude das florações de macroalgas de deriva em relação à direção e intensidade de ventos locais (Apêndice 2);
- 3) Investigar a contribuição da biomassa de macroalgas de deriva para a matéria orgânica estocada nos sedimentos e a sua variabilidade de acordo com a magnitude e persistência dos acúmulos e seus fatores atuantes (Apêndice 2);
- 4) Investigar os efeitos da ocorrência de macroalgas de deriva sobre as pradarias de *R. maritima* e a macrofauna bentônica associada, considerando padrões naturais de abundância, deposição e transporte (Apêndice 3).

3. MATERIAIS E MÉTODOS

3.1 Área de estudo

A Lagoa dos Patos é a maior lagoa costeira do tipo “estrangulada” no mundo com uma área de cerca de 10,000 km² (Kjerfve 1986; Figura 1). Com um regime de maré semi-diurno de baixa amplitude (~0,47 cm), a circulação da região estuarina, a qual abrange cerca de 10% da área total lagunar, é controlada pela interação entre a precipitação na bacia de drenagem da lagoa, a descarga fluvial e a ação de ventos locais e remotos (Möller et al. 2001). Picos de precipitação e descarga fluvial ocorrem durante o inverno/primavera enquanto cenários opostos ocorrem durante o verão/outono (Vaz et al. 2006). Variações interanuais e de longo prazo nos padrões de precipitação regional ocorrem associados à *El Niño Southern Oscillation* (ENSO), com anomalias positivas e negativas de precipitação ocorrendo durante suas fases quentes (El Niño) e frias (La Niña), respectivamente (Grimm et al. 1998).

Durante períodos de baixa descarga fluvial, os ventos predominantes de nordeste (NE) e sudoeste (SO) afetam, respectivamente, a saída e entrada de água entre o estuário e a costa adjacente. Tais processos são determinantes nos padrões de residência da água dentro do estuário (Odebrech et al. 2015). No entanto, em períodos de alta precipitação e descarga fluvial, o ELP se torna um sistema de água doce, com a área de mistura entre a água doce de origem continental e a água salgada, de origem marinha, ficando restrita à desembocadura do estuário. Durante esses períodos, somente fortes ventos de SO são capazes de reverter o fluxo de água do estuário para a zona costeira (Möller et al. 2001). Em contraste, durante períodos de descarga fluvial reduzida, a intrusão de água salina pode atingir os limites superiores do ELP (~45 km). Consequentemente, condições marinhas/eurihalinas são observadas durante o verão/outono enquanto condições de água doce/oligohalinas prevalecem durante o inverno/primavera. Em geral, o ELP é eutrófico, com altas concentrações de nutrientes inorgânicos na coluna d'água e nos

sedimentos decorrentes do aporte da bacia de drenagem, das macrófitas aquáticas e fontes antrópicas (Baumgarten & Niencheski 2010).

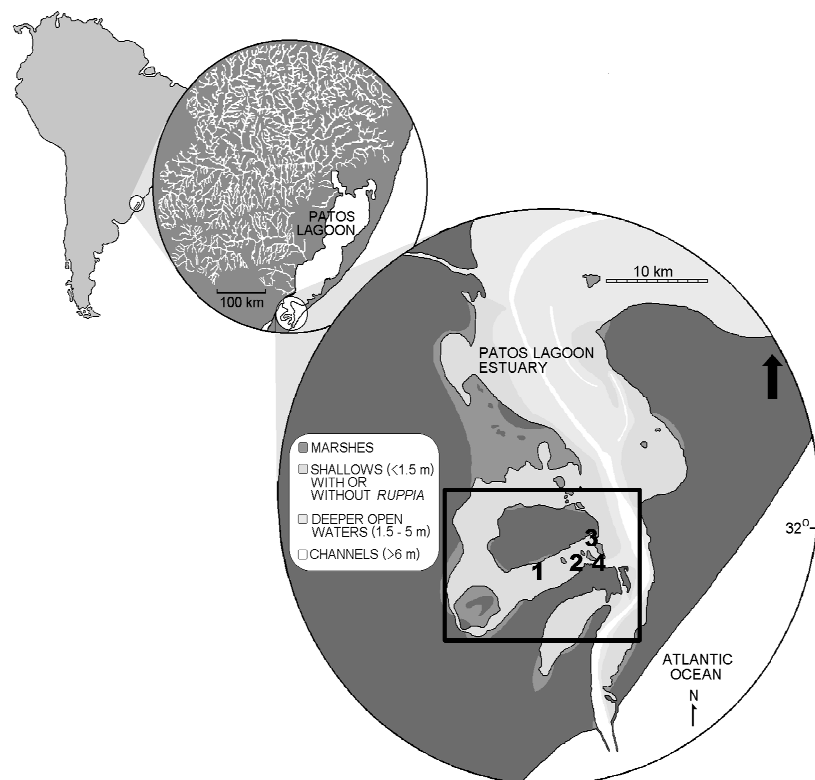


Figura 1. Localização do estuário da Lagoa dos Patos, no extremo sul do Brasil com a região mesomixohalina e enseadas investigadas em destaque (a) Enseadas são representadas como: (1) exp-SO, (2) exp-NE, (3) shelter-SO e (4) shelter-NE (ver item 3.2 para mais detalhes).

A vegetação aquática submersa ocupa extensas áreas rasas ($>120 \text{ km}^2$ com profundidade inferior a 2 metros) e é dominada por fanerógamas submersas eurihalinas e oligohalinas (*Ruppia maritima* e *Zannichellia palustris*, respectivamente) e macroalgas bentônicas dos gêneros *Ulva*, *Cladophora*, *Rhizoclonium* e *Polysiphonia* (Seeliger 2001). A abundância dos componentes da VAS varia sazonalmente com picos de produção de fanerógamas principalmente durante o verão e início do outono enquanto macroalgas predominam durante a primavera e o outono (Coutinho & Seeliger

1986; Silva & Asmus 2001). Entretanto, a análise da abundância da VAS no ELP durante os últimos 30 anos permitiu identificar anos com drásticas reduções da vegetação submersa (tanto fanerógamas como macroalgas) seguidos por períodos ou anos dominados por macroalgas de deriva (Copertino & Seeliger 2010; Gianasi et al. 2011).

O presente estudo foi realizado na região mesomixohalina da Lagoa dos Patos, no entorno do Saco do Arraial (Figura 1, em destaque), caracterizada pela presença de ilhas e enseadas rasas, com profundidade menor que 1,5 m margeadas por marismas e fundo composto por sedimentos finos (argila e silte) e arenosos (Calliari 1980). O Saco do Arraial, embora considerado protegido de eventos de alta energia, possui orientação no eixo nordeste-sudoeste estando sujeito à influência de ventos de nordeste (NE), mais frequentes, e do quadrante sudoeste (SO), de maior energia. Os locais de monitoramento, amostragem e experimentos foram definidos a partir de informações detalhadas sobre a ocorrência e abundância das pradarias de fanerógamas e macroalgas de deriva principalmente durante o verão e outono (Gianasi et al. 2011).

3.2 Variabilidade temporal da abundância de macroalgas de deriva no período 2004-2007

➤ Amostragens

Entre Janeiro de 2004 a Maio de 2007, a abundância de macroalgas de deriva foi investigada numa enseada rasa (<1 m de profundidade) da Ilha da Pólvora (shelter-NE, Figura 1 em detalhe), a qual é margeada por marismas compostos por *Spartina*

alterniflora, *S. densiflora* e *Scirpus maritimus*. A enseada investigada é exposta predominantemente aos ventos de NE, com a direção norte-nordeste (NNE) apresentando o maior *fetch* (Figura 1, Apêndice 1). A batimetria da enseada amostrada apresenta uma área central de depressão (60-90 cm de profundidade) cercada por bancos arenosos (5-50 cm de profundidade) com substrato inconsolidado composto por areia (50-90%), areia muito fina (20-30%) e silte e argila (até 10%).

Nessa enseada, a biomassa de macroalgas de deriva foi amostrada mensalmente utilizando-se quadrados amostrais (1 m^2) dispostos aleatoriamente nas regiões mesolitorais (da linha de marisma até 50 m) e sublitorais (até 90 cm de profundidade; $n = 3$ para cada região). De Janeiro 2006 a Maio 2007, a abundância de macroalgas foi monitorada mensalmente e semanalmente durante blooms. Nesses períodos, o percentual de cobertura e biomassa de macroalgas de deriva foi amostrada ao longo de três transectos (150 a 350 m de comprimento) perpendiculares à linha de costa e distanciados 300 m entre si. Para a estimativa do percentual de cobertura das macroalgas, o método de intersecção de linha foi utilizado (English et al., 1997). Esse método tem sido utilizado no estudo de recifes de corais e macroalgas devido à dificuldade de se estimar visualmente o percentual de cobertura desses organismos no ambiente subaquático. Para a sua utilização, transecções perpendiculares à linha de costa são instaladas na área de interesse a partir de pontos iniciais aleatórios. O comprimento total de cada transecção é determinado e a intercepção ao longo de cada transecção pelo organismo de interesse (no nosso caso, macroalgas de deriva) é registrada. O percentual de cobertura é determinado pela metragem total da transecção em que macroalgas de deriva estiveram presentes dividida pelo comprimento total da transecção.

Ao longo dos transectos, a biomassa algácea foi amostrada a cada 50 m de intervalo através de método destrutivo (quadrados de 0,25 m²; n = 3). Em laboratório, a biomassa algácea foi lavada com água doce para remoção de detritos, sedimentos e fauna associada e teve seu peso seco determinado (estufa por 48h a 60°C). O conteúdo de carbono orgânico total (COT) e nitrogênio total (NT) nas algas foi obtido a partir de subalíquotas de biomassa (2–3 mg) lavadas com água destilada, secas e maceradas, utilizando-se um analisador elementar (2400 Series II CHNS/O System, Perkin-Elmer, USA). O material de referência certificado acetanilida foi utilizado para controle de qualidade das análises. Subalíquotas de biomassa de algas também foram fixadas em formol 4% na água do mar para posterior identificação taxonômica.

Durante o período estudado, os parâmetros hidrológicos nível d'água, salinidade e temperatura foram monitorados diariamente numa enseada próxima àquela investigada (~2 km) no âmbito do Programa de Pesquisa Ecológica de Longa Duração no Estuário da Lagoa dos Patos e Costa Adjacente (PELD, Sítio 8; <http://www.peld.furg.br/index.php/metadados>). Mensalmente, amostras de água em área próxima à amostrada (~0,5 km) foram obtidas para determinação das concentrações dos nutrientes inorgânicos dissolvidos na coluna d'água amônio (NH₄⁺), nitrito (NO₂⁻) + nitrato (NO₃⁻), fosfato (PO₄³⁻) e total de sólidos em suspensão (TSS) de acordo com metodologia previamente descrita em Haraguchi e colaboradores (2015).

Mensalmente, o índice *Oceanic Niño* (ONI) foi obtido a partir do *National Oceanic and Atmospheric Administration* (<http://www.noaa.gov>) para caracterizar a ocorrência de eventos de ENSO (*El Niño Southern Oscillation*). Condições de El Niño e La Niña foram caracterizadas, respectivamente, pela ocorrência de anomalias positivas (+0,5) e negativas (-0,5) da temperatura da superfície da água no oceano Pacífico

equatorial presentes por no mínimo cinco meses consecutivos. Dados diários de precipitação na bacia de drenagem da Lagoa dos Patos e descarga fluvial foram obtidos a partir da Agência Nacional de Águas (<http://www.ana2.gov.br>). Para este último, foram considerados os três principais rios tributários da Lagoa dos Patos (Jacuí, Taquari e Camaquã) cujos soma dos seus fluxos corresponde a cerca de 70% do deságue total na lagoa (Vaz et al. 2006). Dados horários de direção e velocidade do vento foram fornecidos pela Praticagem do Porto de Rio Grande (<http://www.rgpilots.com.br>).

➤ **Análises estatísticas**

A relação entre a precipitação pluviométrica na bacia de drenagem e a descarga fluvial no ELP foi analisada através de Regressão Linear simples. Posteriormente, os efeitos da descarga fluvial sobre os parâmetros hidrológicos nível d'água, salinidade, temperatura, TSS, PO_4^{3-} e nitrogênio inorgânico dissolvido na coluna d'água (NID, $\text{NH}_4+\text{NO}_2-\text{NO}_3$), assim como suas inter-relações, foram avaliados através da Análise de Componentes Principais (ACP). Para isso, médias sazonais foram utilizadas uma vez que estas tiveram um maior percentual de explicação da variabilidade dos dados comparadas às médias mensais. Estações do ano foram: inverno (Julho à Setembro), Primavera (Outubro à Dezembro), verão (Janeiro à Março) e outono (Abril à Junho). Variáveis foram checadas em relação à normalidade dos seus dados (teste de Shapiro-Wilk) e, quando necessário, foram logaritmizadas para se adequar aos pré-requisitos da análise. Variáveis hidrológicas foram agrupadas de acordo com as suas cargas (i.e. *loadings*) ao longo dos três primeiros eixos da ACP os quais explicaram, respectivamente, 50,8%, 23,3% e 13,1% da variabilidade total dos dados.

A relação entre a abundância total de macroalgas de deriva (i.e. zona mesolitoral e sublitoral) e as variáveis hidrológicas foi investigada através de uma Análise de Regressão Múltipla na qual os auto-valores dos três primeiros eixos da ACP foram utilizados como variáveis independentes. Para todas as análises de regressão, a análise dos resíduos foi conduzida para verificação dos pré-requisitos normalidade e homocedasticidade dos dados. Análises estatísticas foram conduzidas utilizando-se o programa R versão 3.2.2 (The R Foundation for Statistical Computing, 2015) e PAST versão 2.08.

Para avaliar os efeitos da ação de ventos sobre a distribuição espacial da abundância de macroalgas de deriva entre as zonas meso e sublitorais, as componentes zonais (τ_x) e meridionais (τ_y) da força de fricção do vento sobre a superfície d'água (i.e. *Wind stress*, τ) foram determinadas utilizando uma rotação horária de 22,5° no intuito de alinhar as componentes de acordo com a direção de maior *fetch* da área de estudo (NNE). Foram utilizadas as seguintes equações:

$$\tau_x = \rho \times c_d \times U_{10}^2 \times \sin\Theta$$

$$\tau_y = \rho \times c_d \times U_{10}^2 \times \cos\Theta$$

onde ρ representa a densidade do ar ($1,2 \text{ kg m}^{-3}$), c_d é o coeficiente de fricção ($2,5 \times 10^{-3}$; Elliot 1982), U_{10} é a velocidade do vento e Θ é o ângulo rotacionado da direção do vento em relação ao norte verdadeiro. Padrões temporais da ação dos ventos sobre a distribuição espacial das macroalgas de deriva foram analisados utilizando-se apenas a componente meridional, com valores negativos (positivos) indicando a ocorrência e magnitude de ventos de NNE (SSO).

3.3 Variabilidade espacial e temporal da abundância de macroalgas deriva no período 2012-2014 e contribuições para a matéria orgânica sedimentar

➤ Amostragem de campo

Entre Agosto de 2012 a Agosto de 2014, a ocorrência e abundância de macroalgas de deriva foram avaliadas em quatro áreas rasas selecionadas de acordo com um contraste *a priori* entre enseadas mais expostas e moderadamente expostas aos ventos predominantes na área de estudo, o qual reflete a susceptibilidade de cada enseada à ação de ondas e correntes geradas pela ação de ventos. Foram elas: uma enseada da Ilha das Pombas, representando um local exposto aos ventos de NE (exp-E); uma enseada da Ilha da Pólvora, local exposto aos ventos de NE, porém com um menor grau de exposição (shelter-NE); Coroa do Narciso, local altamente exposto a ventos de sudoeste (shelter-SO); e Coroa do Roque, exposto a ventos de sudoeste em menor intensidade (exp-SO; Figura 1, em detalhe). Para cada enseada, o seu grau de exposição aos ventos de NE e SO foi expresso através do seu valor médio de *Wave fetch* (i.e. pista de vento disponível para geração de ondas e correntes; Tabela 1), o qual foi determinado a partir da média dos comprimentos de linhas de *wave fetch* plotadas a cada 22.5° (total de 8 seções angulares; i.e., Figura 1, Apêndice 1). Em cada enseada, as linhas de *fetch* originaram-se a partir do ponto médio da costa, o qual foi representado pelo ponto inicial da transect central (veja seção *Amostragens* para mais detalhes).

Tabela 1. Principal direção de exposição aos ventos predominantes e o *Wave fetch* médio para cada enseada investigada. Valores representam a média dos valores individuais de *fetch* determinados a cada 22.5°.

Local	Exposição preferencial	Wave Fetch médio (km)
Exp-NE	NE	2.37
Exp-SO	SO	2.39
Shelter-NE	NE	1.38
Shelter-SO	SO	1.51

Em cada enseada investigada, a abundância das macroalgas foi avaliada mensalmente da região mesolitoral ao sublitoral raso, até aproximadamente 1,0-1,5 m de profundidade, ao longo de três transectos georeferenciados (200 m cada), perpendiculares à margem e distanciados 100 m entre si. Ao longo de cada transecto, o percentual de cobertura foi avaliado visualmente a cada 50 m, em quatro quadrados não-destrutivos (50 cm x 50 cm), posicionados adjacentes ao transecto (totalizando 20 quadrados amostrais por transecção). A biomassa de macroalgas foi amostrada nas proximidades das transecções, em quadrados onde o percentual de cobertura era 100%, através de tubo extrator de PVC de 15 cm diâmetro (área=176,62 cm²; n = 10). Amostras da camada superficial do sedimento (5 cm de profundidade amostradas com tubo extrator de 8 cm de diâmetro, n = 3) dentro da área dos transectos também foram obtidas para análise dos teores de COT, NT e suas razões isotópicas (¹²C/¹³C e ¹⁴N/¹⁵N). Em laboratório, a biomassa de macroalgas foi triada para a remoção de sedimento, detritos, fauna e flora associados. Subalíquotas de biomassa de macroalgas foram fixadas (formol 4%) para identificação taxonômica através da análise da morfologia do talo e anatomia do tecido com o auxílio de estereomicroscopia e microscopia ótica

segundo descrições de Baptista (1974), Coutinho (1982), Coto & Pupo (2009) e atualizações do banco de dados *AlgaeBase*. O peso seco da biomassa (estufa por 48h a 60°C) foi determinado e a abundância média das macroalgas de deriva em cada local foi expressa pelos valores de biomassa seca, corrigidos pelos valores médios de percentuais de cobertura.

Subamostras de biomassa de macroalgas de todo o período investigado foram lavadas com água destilada, secas, maceradas e encapsuladas (2-3 mg) em cápsulas de estanho para a avaliação dos teores de CO e NT no tecido (Analisador Elementar CHNS/O 2400 Series II, Perkin-Elmer, USA) no Laboratório de Hidroquímica (IO, FURG). Para as análises elementares, o controle de qualidade foi realizado a partir do material de referência certificado acetanilida. Os valores mínimos e máximos do percentual de recuperação da acetanilida foram 98,1 e 100,28%, 97,87 e 102,79% e 84,79 e 103,27% para o carbono, nitrogênio e hidrogênio, respectivamente (n = 9). Para as amostras de biomassa de macroalgas coletadas em 2014, suas razões isotópicas $^{12}\text{C}/^{13}\text{C}$ e $^{14}\text{N}/^{15}\text{N}$ também foram determinadas através de espectrômetro de massa junto ao Stable Isotope Laboratory da University of Georgia (USA). Procedimentos similares de secagem, maceração e encapsulamento (25-30 mg) foram adotados para as amostras de sedimento. Para a análise de COT no sedimento, é necessária a descarbonatação das amostras para a remoção do carbono inorgânico. Entretanto, visto que estudos pretéritos no ELP mostram que sedimentos de áreas rasas contêm baixos teores de carbono inorgânico (M. Wallner-Kersanach, comunic. pess.), as amostras de sedimento analisadas no presente estudo não foram acidificadas. De fato, Claudino e colaboradores (2013) testaram a necessidade de descarbonatação para amostras de sedimento de áreas rasas e não encontraram diferenças significativas nas assinaturas de ^{13}C entre amostras

acidificadas e não acidificadas. Análises isotópicas do tecido de macroalgas, e elementares e isotópicas do sedimento, foram realizadas em todo o período investigados para os locais exp-NE e exp-SO (2012-2014) e apenas no primeiro ano de amostragem (2012-2013) nos locais shelter-NE e shelter-SO, no Stable Isotope Laboratory (University of Georgia, USA). O material padrão para o carbono foi utilizado a Belemita de padrão Dee Pee e, para o nitrogênio, o nitrogênio atmosférico. Padrões internos dessa análise apresentaram desvios-padrão para TOC e ^{13}C de $\pm 0,16$ e $\pm 0,08$ e para TN e ^{15}N de $\pm 0,05$ e $\pm 0,12$, respectivamente.

Mensalmente, os parâmetros da água temperatura, salinidade turbidez (Multiparâmetro HI9829, Hanna Instruments, USA), secchi (disco de secchi) e nível (régua) foram obtidos em pontos adjacentes às transecções avaliadas. Amostras de água ($n = 3$) foram coletadas e filtradas para determinação da concentração de nutrientes inorgânicos dissolvidos (NH_4 , NO_2 , NO_3 e PO_4) (Strickland & Parsons 1972) e seston. Dados locais e horários da direção e intensidade do vento foram fornecidos pela Estação Meteorológica da Praticagem do Porto de Rio Grande (<http://www.rgpilots.com.br>). Dados diários de precipitação pluviométrica na bacia de drenagem do ELP foram fornecidos pela Agência Nacional das Águas (<http://www.ana2.gov.br>). Dados horários de radiação na superfície foram fornecidos pelo Instituto Nacional de Meteorologia (<http://www.inmet.gov.br/portal>). A radiação fotossinteticamente ativa subaquática (Underwater Photosynthetic Active Radiation, PAR) sobre o fundo foi estimada de acordo com a equação de Lambert Beer:

$$I_z = I_0 * e^{-kz}$$

em que I_0 é a radiação na superfície, k é o coeficiente de extinção ($k = 1,7 \cdot \text{secchi}^{-0,85}$; Costa & Seeliger 1989) e z é a profundidade. Foi assumido que cerca de 50% da PAR é fotossinteticamente ativa e uma perda de 5% da radiação incidente relativo à reflexão na superfície d'água (Silva & Asmus 2001).

➤ Análises estatísticas

A abundância total de macroalgas de deriva na área de estudo durante o período investigado foi expressa através da média dos valores de peso seco entre todos os locais. O coeficiente de variação (CV) sazonal da salinidade d'água foi utilizada como proxy para a retenção de água no ELP, o qual é indicativo do tempo de residência da água no sistema (Odebrecht et al. 2015). Períodos de maior retenção de água foram identificados por aumentos nos valores mensais médios de salinidade acompanhados por baixos coeficientes de variação, os quais refletiram a entrada e permanência de água de origem marinha no estuário.

Inter-relações entre todos os parâmetros hidrológicos investigados e seus efeitos sobre a abundância total de macroalgas de deriva, foram analisadas através de Análise de Componentes Principais e Regressão Linear Múltipla utilizando os mesmos procedimentos descritos na seção 3.2.2. Contudo, para a análise foram utilizadas médias mensais. Para os parâmetros hidrológicos amostrados em cada enseada (i.e. nível, salinidade, temperatura, seston, irradiância, fosfato e nitrogênio inorgânico dissolvido), a média entre todos os locais foram utilizadas devido à ausência de diferenças espaciais significativas (dados não mostrados). Como variáveis independentes na análise de Regressão Múltipla, foram utilizadas as três primeiras componentes principais, as quais explicaram, respectivamente, 47,1%, 17,4% e 15,2% da variabilidade dos dados.

Diferenças espaciais na ocorrência e magnitude dos blooms entre locais foram analisadas em relação à direção, intensidade e frequência dos ventos locais. Análises estatísticas foram conduzidas utilizando-se o programa R versão 3.2.2 (The R Foundation for Statistical Computing, 2015) e PAST versão 2.08.

A contribuição da biomassa de macroalgas de deriva para a matéria orgânica na camada superficial do sedimento foi avaliada através do modelo bayesiano de mistura MixSiar (Stock & Semmens 2013) nos programas R (versão 3.2.2) e JAGS. O pacote MixSiar fornece estimativas dos percentuais de contribuição de distintas fontes mesmo para sistemas indeterminados, levando em consideração a variabilidade associada às amostras e fontes de erro desconhecidas (Parnell et al. 2013). O modelo de mistura foi utilizado com as médias sazonais das assinaturas isotópicas de ^{13}C , ^{15}N e da razão elementar C:N das distintas fontes e os locais amostrados foram considerados um fator fixo. Além das macroalgas de deriva, demais fontes de matéria orgânica para o sedimento como a matéria orgânica particulada (MOP), a fanerógama *Ruppia maritima* e as halófitas *Spartina densiflora*, *Scirpus maritimus* e *S. olney* foram consideradas a partir de dados pretéritos obtidos na área de estudo (Claudino et al. 2013). A MOP representou o fitoplâncton e demais partículas em suspensão na coluna d'água e, apesar das amostras não terem sido acidificadas, assumiu-se que elas representaram o carbono orgânico particulado (COP) uma vez que testes de acidificação e não-acidificação realizados por Claudino e colaboradores (2013) evidenciaram um baixo teor de carbono inorgânico na matéria orgânica particulada no sedimento. *Ruppia maritima* e *Spartina densiflora* foram agrupadas como uma fonte única devido a similaridade em suas assinaturas isotópicas. O mesmo ocorreu para *Scirpus maritimus* e *S. olney*, as quais apresentam vias fotossintéticas semelhantes (plantas C3). Os percentuais de COT e NT

de cada fonte foram informados na análise. Valores de fracionamento para as fontes não foram incluídos uma vez que estudos preliminares no ELP indicaram a ausência de alterações nas concentrações elementares e isotópicas durante a diagênese da matéria orgânica (Claudino et al., em preparação). As distribuições posteriores das contribuições das distintas fontes de foram calculadas utilizando cadeias de Markov e Monte Carlo longas (*Markov Chains Monte Carlo*, comprimento de cadeia = 1.000.000, *burn-in* = 700.000, *thin* = 300) e sua convergência foi checada através testes de diagnósticos (*Trace plots*, *Gelman-Rubin test* e *Geweke test*; Stock & Semmens 2013).

3.4 Avaliação experimental dos efeitos de deposições transitórias de macroalgas de deriva sobre a comunidade bentônica

➤ Experimentos

No intuito de avaliar os efeitos do transporte e deposição de curta duração de macroalgas de deriva sobre pradarias de *R. maritima* e a macrofauna bentônica associadas, um experimento de campo foi conduzido em uma enseada rasa do ELP do final de Março ao início de Maio de 2014 (Outono). Para isso, biomassa fresca de macroalgas de deriva, compostas predominantemente por *Ulva clathrata* e *Rhizoclonium riparium*, foram adicionadas a cercados experimentais (0,5 X 0,5 m, 1 m de altura, abertos no topo) instalados sobre pradarias de *R. maritima*. Telas plásticas com malha de abertura de 1 cm² foram utilizadas para cercar os plots experimentais, enterradas no fundo com o auxílio de taquaras. A malha da tela era pequena o suficiente para a manutenção da biomassa de macroalgas dentro dos plots durante períodos de baixa hidrodinâmica sem, ao mesmo tempo, afetar a circulação da água no seu interior.

Por outro lado, durante eventos de alta energia (i.e., alta descarga fluvial e/ou ação de ventos), a malha não evitava a advecção da biomassa para fora dos cercados. Tal fato permitiu o controle das taxas de perda da biomassa de macroalgas ao longo do experimento (i.e. decréscimos de biomassa e cobertura de macroalgas) de acordo com o hidrodinamismo local. Os cercados experimentais foram instalados aleatoriamente (5 m de distância entre eles) em uma área de aproximadamente 200 m² ocupada por pradarias de *R. maritima* bem estabelecidas com manchas variando entre 0.5 a 1 m² de área. As pradarias eram homogêneas, com percentual de cobertura próximo a 100% e altura do dossel de 10 a 15 cm. Similarmente, a área experimental era homogênea quanto à granulometria do fundo (98% área, 1,2% silte e 0,8% argila) e profundidade d'água (0,3 a 1 m), variando de acordo com o nível médio d'água no estuário. Devido à topografia côncava do fundo, macroalgas de deriva não ocorriam naturalmente na área experimental, se acumulando nas depressões localizadas ao seu redor (obs. pess.).

Quatro tratamentos experimentais foram aplicados com quatro réplicas cada: (1) controle referência (CR; denominado RC no Apêndice 3) composto por áreas não manipuladas experimentalmente localizadas entre os cercados experimentais; (2) controle cercado (CC; FC no Apêndice 3), sendo plots cercados sem a adição de biomassa de macroalgas para controle dos efeitos da instalação do artefato experimental; (3) baixa biomassa (BB; LB no Apêndice 3) com plots cercados e a adição de 2 kg de biomassa fresca por m² (~200 g PS m⁻²) simulando a ocorrência natural de massas de macroalgas de deriva; e (4) alta biomassa (AB; HB no Apêndice 3), tratamento caracterizado pela adição de 10 kg de biomassa úmida por m² (~1000 g PS m⁻²) em cercados de acordo com cenário de florações observados no ELP. As réplicas de cada tratamento foram posicionadas aleatoriamente na área de experimento.

A biomassa de macroalgas utilizada no estudo foi coletada em áreas adjacentes à região experimental e defaunada manualmente com auxílio de pinça e lupa previamente à sua adição aos cercados.

Uma vez que macroalgas de deriva em zonas rasas do ELP têm um alto potencial para advecção mas, ao mesmo tempo, acúmulos se mostram persistentes em uma mesma área rasa, durando até 6 meses (ver resultados seção 4.1, Apêndice 1 e 4.2, Apêndice 2), simulou-se a ocorrência de deposições sequenciais de macroalgas de deriva sobre pradarias de *R. maritima*. Para isso, os cercados experimentais foram visitados durante seis intervalos de tempo para a avaliação da abundância de macroalgas de deriva perdida por advecção e readição de biomassa algácea aos cercados de acordo com patamares iniciais do experimento (i.e. reposição da biomassa). Os intervalos de tempo das visitas variaram de 4 a 7 dias, sendo eles: *t1*, que compreendeu entre 31 de Março a 4 de Abril; *t2*, composto de 4 a 7 de Abril; *t3*, de 7 a 14 de Abril; *t4*, de 16 a 23 de Abril; *t5*, de 23 a 29 de Abril; e *t6*, composto de 29 de Abril a 2 de Maio. Em cada intervalo de visita, a biomassa nos cercados era quantificada, possibilitando a determinação da sua taxa de perda dos cercados por advecção. Para isso, a biomassa de macroalgas remanescente nos cercados era cuidadosamente retirada manualmente para não afetar as plantas de *Ruppia* e a macrofauna associada. O volume da biomassa era estabelecido através da utilização de proveta plástica de 2 litros graduada, perfuradas do topo ao fundo em três fileiras, e acopladas com pistão de diâmetro semelhante ao do interior do cilindro. O pistão era utilizado para a compressão da biomassa algácea e consequente remoção do excesso de água (veja Robbins & Boese 2002 para mais detalhes). A partir do volume de biomassa fresca determinado (*x*), o seu peso seco (*y*) era estimado através da reta de regressão linear $y = -5,5 + 0,8399x$ ($p < 0,05$; $R^2 = 0,94$;

n = 40) obtida em testes preliminares na área de estudo. Devido à sua morfologia de talo simplificada, macroalgas de deriva de gêneros oportunistas como *Ulva* e *Rhizoclonium* apresentam rápida taxa de decomposição e, conseqüentemente, altas perdas de biomassa por decomposição (Banta et al. 2004). No intuito de controlar o percentual de redução de biomassa dentro dos cercados oriundo de processos de decomposição e não da sua advecção, sacolas de decomposição de dimensão similar aos cercados (0,5 x 0,5 m) e valores de biomassa de macroalgas similares aos tratamentos BB e AB (respectivamente LB e HB no Apêndice 3) foram instaladas aleatoriamente sobre o fundo da área experimental (n = 3 por tratamento de biomassa) durante os três últimos intervalos de tempo do experimento (i.e. t_4 , t_5 e t_6). As mesmas tiveram seus valores de perda de biomassa determinados a cada intervalo de tempo de acordo com a metodologia adotada nos cercados.

Após a determinação dos valores de perda de biomassa nos cercados, a sua reposição até valores iniciais era conduzida. A biomassa remanescente retirada dos cercados era recolocada neles e nova biomassa algácea fresca, previamente defaunada era também adicionada. Para as sacolas de decomposição, somente nova biomassa fresca foi adicionada. Os valores de biomassa repostos em cada intervalo de tempo foram similares às condições iniciais de biomassa no experimento (i.e. 200 g PS m⁻² para BB e 1000 g PS m⁻² para AB), as quais estiveram de acordo com padrões naturais de recorrência de macroalgas de deriva nas proximidades da área experimental. Esses foram investigados durante o experimento em uma área próxima à experimental (0,5 km², ~200 m distante) através do estabelecimento de sete plots fixos (0,25 m²) aleatoriamente posicionados. Nessa área, ao início e final do experimento, o percentual

de cobertura de macroalgas foi visualmente estimado em cada plot e coleta destrutiva de biomassa realizada para determinação do seu peso seco.

O experimento durou 33 dias (de 31 de Março a 2 de Maio de 2014), tempo suficiente para a ocorrência de expressivos declínios no percentual de cobertura de plantas de *R. maritima* dentro dos cercados (i.e. valores próximos a 10%). Ao final do experimento, amostragens destrutivas foram realizadas dentro dos cercados experimentais e no controle referência ($n = 4$ por tratamento) com o auxílio de tubo de PVC de 10 cm de diâmetro, enterrado a 15 cm de profundidade na coluna sedimentar. Dentro dos cercados, a amostragem foi realizada no seu centro para evitar efeitos de borda. Amostras foram peneiradas em malha de 500 μm de abertura e acondicionadas em sacos plásticos. Em laboratório, elas foram lavadas para a remoção de sedimentos, detrito e epífitas. A biomassa de *R. maritima* foi separada em biomassa aérea e subterrânea, cujo peso seco foi determinado (estufa a 60°C por 48h). Os parâmetros demográficos comprimento total do rizoma, número de hastes e densidade de nós foram determinados. O comprimento de 10 folhas selecionadas aleatoriamente também foi determinado. Subalíquotas (2-3 mg) de biomassa de *Ruppia* foram lavadas com água destilada, secas, maceradas e encapsuladas em cápsulas de estanho para análise do seu teor de COT e NT (2400 Series II CHNS/O System, Perkin-Elmer, USA). O material de referência certificado acetanilida foi utilizado para controle de qualidade das análises. A macrofauna bentônica associada a plantas de *R. maritima* foi fixada em formolina 4% na água do mar e identificada até o mínimo nível taxonômico possível com o auxílio de lupa com lente de aumento 40x.

Durante o período experimental, dados horários de direção e velocidade de vento na área de estudo foram obtidos através da Estação Meteorológica da Praticagem do

Porto de Rio Grande (<http://www.rgpilots.com.br>). Dados diários de descarga fluvial para a bacia de drenagem da Lagoa dos Patos, de acordo com os critérios citados no item 3.2.1, foram obtidos da Agência Nacional de Águas (<http://www.ana2.gov.br>).

➤ Análises estatísticas

O índice *Wave Exposure* (Burrows et al. 2008) foi utilizado como proxy da ação de ventos na área experimental, a qual, por sua vez, reflete a ação de ondas oriundas da fricção do vento local sobre a superfície da água. Para o cálculo desse índice, os comprimentos das linhas de *fetch* (pista de vento) sobre a água originados a partir de um ponto central da área experimental até à porção de terra mais próxima foram determinados em oito seções angulares (i.e. a cada 22.5° de direção do vento). Valores de *Wave Exposure* foram determinados a partir da frequência de ocorrência de ventos em cada direção, multiplicada pelo quadrado do valor médio de velocidade do vento (em nós) naquela mesma direção. Para avaliar a relação entre a hidrodinâmica local e a advecção de macroalgas de deriva sobre pradarias de *Ruppia*, efeitos individuais e interações da descarga fluvial e *Wave Exposure* sobre os valores de biomassa de macroalgas nos cercados experimentais ao longo do experimento foram investigados através de Regressão Linear Múltipla. Os pré-requisitos da análise paramétrica normalidade e homocedasticidade dos dados foram checados através da análise dos resíduos.

Para investigar a relação entre os distintos tratamentos experimentais (i.e. CR, CC, BB e AB) e a biomassa aérea e subterrânea de *Ruppia* e os seus parâmetros demográficos comprimento de folhas e rizomas, e densidades de nós e hastes, foi conduzida uma Análise de Componentes Principais (ACP). A ACP foi realizada através

de uma matriz de correlação dos dados brutos, a qual padronizou em uma mesma escala as variáveis mensuradas em distintas escalas de medida. Previamente à realização da ACP, variáveis foram checadas quanto à sua distribuição normal.

Os efeitos das deposições de macroalgas de deriva sobre a macrofauna bentônica associada a pradarias de *R. maritima* foram investigados através do ordenamento espacial das amostras utilizando a análise nMDS (*Non-metrical Multidimensional Scaling*). Devido à natureza dos dados (valores de abundância por organismo com a presença de zeros), a análise utilizou uma matriz de similaridade construída com o índice de dissimilaridade de Bray-Curtis e os dados foram previamente transformados para a sua raiz a quarta devido à dominância de algumas espécies na comunidade. Para testar diferenças significativas entre tratamentos, Análises de Variância Multivariadas Permutacional (PERMANOVA; Anderson 2001) foram conduzidas utilizando o índice de Bray-Curtis e 4999 permutações, seguidas por comparações par a par. Para a espécie numericamente dominante na comunidade, no caso, o crustáceo tanaidáceo *Monokalliapseudes schubarti* (ver Síntese dos Resultados, seção 4.3 e Apêndice 3), análise de PERMANOVA utilizando o índice de Bray-Curtis e 4999 permutação foi realizada para testar a presença de diferenças significativas na sua abundância entre tratamentos.

Todas as análises estatísticas foram conduzidas no programa R versão 3.2.2 (The R Foundation for Statistical Computing, 2015), PAST versão 2.08. Devido à baixa e desigual replicação das amostras, valores do conteúdo de COT e NT na biomassa aérea e subterrânea de *R. maritima* não foram analisados estatisticamente.

4 SÍNTESE DOS RESULTADOS

A seguir, os resultados estão apresentados de forma resumida. Resultados detalhados estão descritos nos três artigos apresentados no Apêndice desta tese.

4.1 Artigo 1: Dinâmica espacial e temporal de macroalgas de deriva no ELP entre 2004-2007 (Apêndice 1, artigo aceito para publicação no periódico *Marine Biology Research*).

A avaliação dos padrões temporais de abundância de macroalgas de deriva entre Janeiro de 2004 a Maio de 2007 evidenciou três ciclos de crescimento de macroalgas, os quais iniciaram-se no final da primavera (Novembro-Dezembro)/início do verão (Dezembro-Janeiro) e persistiram até o final do outono (Maio-Junho; Figura 6). A biomassa de macroalgas, composta predominantemente por *Ulva clathrata* e acompanhada por *U. intestinalis*, *U. flexuosa*, *Cladophora vagabunda*, *C. crispata* e *Rhizoclonium riparium*, apresentou valores médios entre 3 a 432,7 g PS m⁻², com picos na primavera e verão. Ciclos de crescimento diferiram em relação ao seu período de desencadeamento, magnitude e persistência entre os distintos anos investigados. A análise interanual das florações de macroalgas de deriva evidenciou que estas são fortemente afetadas por eventos de El Niño (*El Niño Southern Oscillation*), os quais determinam os padrões regionais de precipitação pluviométrica e consequentes variações na descarga fluvial no sistema (Figura 2a). As maiores florações de macroalgas de deriva foram observadas após eventos de El Niño fraco a moderado (Figuras 2a e 6). Anualmente, picos de biomassa ocorreram após diminuições da precipitação na bacia de drenagem do ELP e consequente redução na descarga fluvial

(Figura 2a,b). Conforme evidenciado pela Análise de Componentes Principais, a redução na descarga fluvial esteve relacionada a aumento de salinidade e tempo de retenção da água e decréscimo do nível e turbidez (Tabela I, Figuras 3 e 4). Tais condições favoreceram o crescimento de macroalgas, contudo, a relação entre esses parâmetros físico-químicos e a abundância de macroalgas não foi direta ($R^2 = 0.26$, $p = 0.96$). Similarmente, não foi encontrada uma relação direta entre a concentração de nutrientes inorgânicos dissolvidos na coluna d'água e a abundância de macroalgas de deriva (Figuras 5 e 6). Entretanto, resultados da concentração elementar de carbono orgânico e nitrogênio total no tecido algáceo e suas razões molares (C:N; Tabela II), indicaram a ausência de limitação de compostos nitrogenados para a formação das florações. Maiores florações na primavera de 2006 estiveram associadas ao aumento da concentração de fósforo na coluna d'água e consequentes decréscimo da razão N:P (Figuras 5 e 6). Uma vez estabelecidas as florações, variações temporais na distribuição espacial de acúmulos de biomassa foram observadas (Figuras 6 e 7). Ventos do quadrante N-NE, predominantes durante a primavera e o verão, carregaram a biomassa de macroalgas da região sublitoral para a mesolitoral, impedindo a permanência dessas algas na coluna d'água sob condições hidrológicas favoráveis ao desencadeamento de grandes florações (Figuras 7, 8 e 9).

4.2 Artigo 2: Dinâmica espacial e temporal de macroalgas de deriva no ELP entre 2012-2014 e contribuições para a matéria orgânica sedimentar
(Apêndice 2, artigo submetido ao periódico *Marine Ecology Progress Series*).

A análise dos padrões temporais (agosto de 2012 a agosto de 2014) da ocorrência e magnitude de florações de macroalgas de deriva em enseadas com distintos graus de exposição a ventos predominantes na área de estudo mostrou variações anuais e interanuais na sua abundância. A biomassa de *Ulva clathrata*, *U. intestinalis* e *Rhizoclonium riparium*, apresentou valores médios entre 0,38 (Agosto 2012) a 566 g de peso seco m² (Junho 2014), com picos durante o verão/outono de 2013 e outono/inverno 2014 (Figura 4). Maiores valores médios de biomassa foram observados em 2014 (223 g PS m⁻²) comparados a 2013 (43 g PS m⁻²). A abundância de macroalgas esteve positivamente relacionada ($R^2 = 0.67$, $F_{7,12} = 3.55$, $p = 0.02$) a redução da descarga fluvial e consequente aumento na retenção de água no estuário (i.e. aumento de salinidade associado à baixo CV, Tabela 1), salinidade, temperatura e irradiância sobre o fundo, e a decréscimos do nível d'água e turbidez (Figura 2a,b,c), variáveis agrupadas ao longo da PC1 (Tabela 2). Efeitos significativos da concentração de nutrientes inorgânicos na coluna d'água sobre a abundância de macroalgas de deriva não foram observados (Figuras 3 e 4). Entretanto, resultados do teor de COT e NT no tecido de macroalgas indicaram a ausência de limitação de nutrientes para o estabelecimento de florações de macroalgas de deriva (Figura 5). Variações espaciais na ocorrência, magnitude e persistência de marés verdes entre as enseadas estudadas foram detectadas. Enseadas mais expostas à ação de ventos foram mais suscetíveis a maiores acúmulos de biomassa de macroalgas de deriva, os quais coincidiram com o padrão temporal de ocorrência e intensidade dos ventos locais (Figuras 4 e 7). Nesses locais, blooms de macroalgas formados por manchas densas e extensas persistentes no tempo (2 a 5 meses; Figura 6) representaram estoques de até 0,18 toneladas de N por hectare. Valores do teor de COT e NT no sedimento foram, em geral, baixos e não variaram

espacialmente ou temporalmente de acordo com a distribuição espacial e temporal da biomassa de macroalgas observada (Figura S1). Modelos de mistura mostraram que, sazonalmente, as macroalgas de deriva tiveram uma baixa contribuição média para a matéria orgânica sedimentar (de 0,5% a 8,1%) comparadas com demais fontes como a halófito *S. densiflora* e a fanerógama *R. maritima* (9,6% a 61,9%), plantas C3 (0,2% a 28,5%) e MOP (15,5% a 88,5%; Figura 8 e S2). Similarmente ao observado para os resultados elementares do sedimento, padrões espaciais e temporais de contribuição da biomassa de macroalgas para a matéria orgânica incorporada no sedimento não refletiram diferenças sazonais na magnitude e persistência das florações entre locais. De maneira geral, a ocorrência de grandes florações persistentes no tempo não contribuiu para uma maior incorporação da biomassa de macroalgas no sedimento em enseadas rasas do ELP.

4.3 Artigo 3: Impactos de deposições transitórias de macroalgas de deriva sobre a comunidade bentônica. (Apêndice 3, artigo em preparação para submissão ao periódico *Journal of Experimental Marine Biology and Ecology*).

Experimento de campo realizado em outono de 2014 evidenciou que, apesar da persistência de florações de macroalgas deriva em área adjacente à experimental (Tabela 1; Apêndice 3), a distribuição de massas de macroalgas apresentou padrões temporais e espaciais dinâmicos de deposição. Ao longo dos intervalos de tempo estudados, a taxa média de perda da biomassa de macroalgas nos cercados experimentais variou de 12% ($\pm 2,34$) a 100% (± 0) para ambos os tratamentos de biomassa (i.e. BB e AB; denominados LB e HB no Apêndice 3, respectivamente),

refletindo os curtos períodos de deposição de macroalgas de deriva sobre o fundo (Figura 2). Perdas de biomassa de macroalgas nos cercados diferiram das taxas de perda mensuradas nas sacolas de decomposição ($8 \pm 4\%$ a $12,33 \pm 3,95\%$; Figura 2 em detalhe) e estiveram positivamente relacionadas aos efeitos interativos de aumentos da descarga fluvial e do índice *Wave Exposure* ($R^2 = 0.96$, $p = 0.02$; Figura 3). A Análise de Componentes Principais evidenciou maiores valores de biomassa aérea e subterrânea e dos parâmetros demográficos comprimento de folhas e do rizoma e densidade de hastes e nós em tratamentos sem a adição de biomassa macroalgácea (i.e. RC e FC; Figura 4). Reduções da biomassa de plantas de *Ruppia* e seus parâmetros demográficos foram observadas nos tratamentos BB e AB, sendo proporcionais à quantidade de biomassa manipulada nos cercados (Figura 5). Embora não testado estatisticamente, não houve diferença nos teores de COT e NT na biomassa aérea e subterrânea de plantas de *R. maritima* entre tratamentos (Figura 6). O ordenamento espacial dos dados de macrofauna não evidenciou a formação de grupos evidentes de amostras (Figura 7), não havendo diferenças significativas entre tratamentos (PERMANOVA, $p = 0,05$; Tabela 2a; Figura 8). A macrofauna associada às pradarias foi dominada pelo crustáceo tanaidáceo da infauna *M. schubarti*, seguido pelos poliquetas da infauna *Heteromastus similis*, *Nephtys fluviatilis* e *Laeonereis acuta*; organismos da epifauna como anfípodes, *Uromunna peterseni*, *Kupellonura* sp. e *Heleobia australis* apresentam baixa abundância (Figura 8). A riqueza de táxons e abundância total de indivíduos não variou entre tratamentos (Figura 8a,b). Entretanto, um decréscimo da abundância total superior àquele ocasionado pela manipulação experimental foi detectado em tratamentos com adição de biomassa de macroalgas (Figura 8b), resultante de variações na abundância da espécie dominante *M. schubarti* (Figura 8c). No entanto, variações na abundância de *M.*

schubarti entre tratamentos não foram significativas (PERMANOVA, $p = 0,09$; Tabela 2b).

5 DISCUSSÃO GERAL

No estuário da Lagoa dos Patos, no extremo-sul do Brasil, macroalgas de deriva são um importante componente da produção primária estuarina em conjunto com pradarias de fanerógamas submersas, fitoplâncton e microfitobentos (Copertino & Seeliger 2010). Após a redução e desaparecimento da VAS durante eventos de El Niño fortes (1997/98) e moderados (2002/03), uma lenta recuperação de pradarias de *Ruppia maritima* foi reportada (Copertino & Seeliger 2010, Odebrecht et al. 2010). Nesse cenário, os resultados da análise interdecadal (2004-2007 e 2012-2014) da ocorrência e abundância de macroalgas de deriva aqui apresentados suportam estudos pretéritos que sugerem uma tendência de aumento na frequência de ocorrência e magnitude de marés verdes em enseadas rasas estuarinas (e.g. Copertino & Seeliger 2010, Odebrecht et al. 2010). Valores de biomassa dessas macroalgas aqui encontrados são similares, ou até superiores, àqueles reportados em áreas temperadas eutróficas (e.g. Hernández et al. 1997; Kamer et al. 2001; Martins et al. 2001; Hauxwell & Valiela 2004, entre outros). A análise das observações pretéritas e os resultados do presente estudo sugerem mudanças de fase (*phase-shift*) fanerógamas-macroalgas na estrutura da comunidade vegetal submersa. Entretanto, estudos de longo prazo e modelos são necessários para investigar essa hipótese, incluindo outros componentes da flora e fauna bentônica, assim como as consequências de tais mudanças no funcionamento do ecossistema.

Variações temporais na abundância de macroalgas de deriva

De maneira geral, florações de macroalgas de deriva ocorreram durante as primaveras de 2004 e 2007, verões de 2005, 2006, 2007 (Figura 6, Apêndice 1) e 2013, outonos de 2013 e 2014 e ao início do inverno de 2014 (Figura 4, Apêndice 2). Estas florações ocorreram durante períodos de anomalias negativas de precipitação pluviométrica na bacia de drenagem do estuário, que ocasionaram descargas fluviais baixas a moderadas. Tais condições favorecem a intrusão de água marinha no estuário, ocasionando aumentos no tempo de retenção da água no sistema (Odebrecht et al. 2015). Nessas condições, velocidades de corrente em zonas rasas do estuário são reduzidas de 1 m s^{-1} para em torno de $1 \text{ a } 25 \text{ cm s}^{-1}$ (Fernandes 2001). Esses valores encontram-se abaixo ou próximos aos limiares de velocidade de corrente necessários para o transporte de macroalgas de deriva suspensas na coluna d'água (i.e. $\sim 10 \text{ cm s}^{-1}$, Flindt et al. 2004), permitindo, assim, o acúmulo de biomassas nas áreas rasas. Desse modo, variações anuais e interanuais nos padrões de descarga fluvial no estuário determinam os padrões temporais de ocorrência e persistência de acúmulos de macroalgas e deriva no ELP.

Variações na descarga fluvial também determinam alterações na salinidade d'água, nível, irradiância e TSS (Figuras 2, 3 e 4, Apêndice 1; Figura 2, Apêndice 2), fatores que controlam as taxas de crescimento de macroalgas em zonas estuarinas rasas (Martins et al. 2001, 2007). Consequentemente, enquanto as variações de descarga fluvial e da penetração da água do mar (influenciando o tempo de retenção da água) determinam a permanência das macroalgas no ambiente, os parâmetros físico-químicos da água modulam a magnitude das florações. Macroalgas de deriva podem ser

beneficiadas com aumentos da salinidade (e.g. Martins et al. 1999; Taylor et al. 2001). As florações de macroalgas observadas no ELP ocorreram simultaneamente com aumentos da salinidade, acima dos valores críticos para a germinação de esporos (i.e. 5, Sousa et al. 2007) e próximos (ou dentro) de intervalos favoráveis ao crescimento de espécies oportunistas como *Ulva intestinalis* (10-22; Martins et al. 1999) e *U. clathrata* (10-30; Fitzgerald 1978). Aumentos de salinidade ocorreram junto com reduções no nível da água e das concentrações de TSS, as quais promoveram aumentos da disponibilidade de luz sobre o fundo. O aumento da incidência luminosa sobre o fundo, combinados a valores ótimos de temperatura d'água para o crescimento de clorofíceas oportunistas (15-20 °C; Taylor et al. 2001), estimulam o desenvolvimento e crescimento de macroalgas a partir de esporos e fragmentos remanescentes de florações anteriores (Malta et al. 2002). Dessa forma, efeitos interativos dos parâmetros físico-químicos provavelmente determinaram a formação de grandes florações de macroalgas de deriva em enseadas rasas.

Por outro lado, períodos caracterizados por aumentos de salinidade, irradiância (decréscimos no nível e turbidez da água) e temperatura nem sempre apresentaram grandes florações, com menores abundâncias normalmente observadas durante o verão (Figura 6, Apêndice 1; Figura 4, Apêndice 2). De fato, menores valores de abundância de macroalgas de deriva nesse período são historicamente reportados no ELP (e.g. Coutinho & Seeliger 1986; Copertino & Seeliger 2010) e indicam que a relação desses parâmetros físico-químicos da água com o crescimento de macroalgas não é direta. Por exemplo, valores de salinidade próximos a 35 têm se mostrado prejudiciais ao crescimento de espécies como *U. intestinalis*, as quais apresentam valores ótimos de crescimento entre 17-22 (Martins et al. 1999). Embora as espécies dominantes *U.*

clathrata e *R. riparium* sejam tolerantes a alta salinidade e temperatura de verão, valores de temperatura acima de 25-30° C podem inibir o crescimento destas espécies (Chao et al. 2005). Alta temperatura pode estimular a esporulação, com a alocação de biomassa para a formação e liberação de esporos, promovendo seu declínio (Niesenbaum 1988). A interação de altos valores de temperatura com baixos níveis da água no verão pode ainda provocar a exposição ao ar e consequente dessecação da biomassa (Martins et al. 2007). Assim, a combinação de baixos níveis d'água e altos valores de temperatura pode limitar a produção de macroalgas durante o verão, explicando as menores florações ocorrentes nessa estação.

A hidrodinâmica local também influencia o aporte de nutrientes em ecossistemas estuarinos através do tempo retenção da água. Um maior tempo de retenção da água favorece o acúmulo de macroalgas e a exposição aos nutrientes dissolvidos na coluna d'água (Martins et al. 2001; McGlathery et al. 2007). Nossos resultados mostram que alguns picos de nutrientes dissolvidas na coluna d'água ocorreram durante as altas descargas fluviais observadas no outono, inverno e primavera 2005 e inverno 2006 (Figura 5, Apêndice 1) e na primavera 2012, inverno e primavera 2013 e inverno 2014 (Figura 3, Apêndice 2). Nestes períodos, o menor tempo de residência da água no estuário, associado a menor disponibilidade de luz no fundo (alto TSS, alto nível da água), pode ter contribuído para a ausência de relação positiva entre biomassa das algas e nutrientes dissolvidos. Além disso, as amostragens pontuais de nutrientes, realizadas mensalmente, podem não representar a disponibilidade de nutrientes no sistema, já que as concentrações na coluna d'água variam em menor escala temporal (Kopecky & Dunton 2006). Adicionalmente, espécies oportunistas de *Ulva* proliferam rapidamente em ambientes eutróficos devido à sua alta taxa de captação de nutrientes associada a um

desacoplamento entre períodos de captação e assimilação (i.e., incremento de biomassa, Fong et al. 2004).

O conteúdo nutricional do tecido é considerado um melhor indicador da disponibilidade de nutrientes para o crescimento de macroalgas (Fujita 1985; Malta et al. 2002). Os valores de NT no tecido de macroalgas entre 2004-2007 (Tabela II, Apêndice 1) e 2012-2014 (Figura 5, Apêndice 2) foram sempre próximos ou superiores a níveis críticos para o crescimento de macroalgas (i.e. 2%, Fujita 1985). Limitações ao crescimento por nitrogênio, evidenciadas por decréscimos do % NT e consequentes aumentos das razões C:N, ocorreram somente após o estabelecimento das florações. Logo, nossos resultados demonstram a alta disponibilidade de compostos nitrogenados para a formação de grandes florações na área de estudo.

Sob altas concentrações de compostos nitrogenados na coluna d'água, o fosfato passa a ser o principal nutriente limitante ao crescimento de macroalgas (Teichberg et al. 2010). Similarmente, nossos resultados indicaram que, em períodos de baixa descarga fluvial, variações interanuais na magnitude de floração de macroalgas estiveram associadas às concentrações de fosfato, com maiores florações (i.e., primavera 2006 e outono e inverno de 2014) coincidentes a picos desse último. De fato, estudos pretéritos no ELP indicam que a intrusão de água marinha no estuário além de contribuir para uma maior retenção de biomassa de macroalgas em áreas rasas, também promove aumentos da salinidade d'água, os quais, por sua vez, favorecem processos de desorção do fósforo adsorvido aos hidróxidos de ferro e outros compostos presentes na coluna d'água e sedimento (Zarzur 2001). Logo sugere-se que, de acordo com o já observado para o fitoplâncton na área de estudo (e.g. Odebrecht et al. 2005), o crescimento de macroalgas é principalmente limitado por fósforo.

Variações espaciais na abundância de macroalgas de deriva

Uma vez desencadeadas as florações de macroalgas de deriva, ventos locais promoveram variações sazonais nos seus padrões de acúmulo de biomassa e persistência ao longo de distintas escalas espaciais (Figuras 6 e 7, Apêndice 1; Figuras 4 e 7, Apêndice 2). Nossos resultados demonstram que, devido ao baixo limiar de erosão de macroalgas de deriva (Flindt et al. 2004; Canal-Vergés et al. 2010), ondas e correntes geradas por ventos locais, além da própria circulação estuarina (i.e., processos de enchente e vazante, Möller et al. 2001), transportam as massas algais sobre o fundo. Tal processo ocorre mesmo sob baixa velocidade de correntes observada durante períodos de pouca descarga fluvial. A advecção desempenha um papel importante na formação de marés verdes uma vez que, dependendo da fisiografia local, este transporte pode tanto promover o acúmulo (e.g. Zieman et al. 1989; Berglund et al. 2003; Liu et al. 2009) ou a dispersão da biomassa de macroalgas (e.g. Bell & Hall 1997; Pihl et al. 1999; Loringston & Kotta 2006). Embora não avaliados aqui, a topografia e a heterogeneidade do fundo podem ainda influenciar o transporte de biomassa (Biber 2007) e seus consequentes padrões de distribuição espacial (Aníbal et al. 2007; Kotta et al. 2006).

A análise dos padrões de abundância de macroalgas entre enseadas com distintos graus de exposição aos ventos predominantes mostrou os efeitos positivos do estresse do vento sobre as macroalgas (Figuras 4 e 7, Apêndice 2). A maior incidência de ventos de NE e SO sobre a costa promoveu maiores acúmulos de biomassa nas enseadas expostas à tais direções, cenário resultante da maior retenção da biomassa local

(autóctone), mas também da importação de massas flutuantes de áreas adjacentes (alóctone) (Berglund et al. 2003; Liu et al. 2009). Portanto, considerando a alta disponibilidade de nutrientes no ELP para o crescimento de macroalgas, áreas com maiores acúmulos de biomassa podem representar um grande estoque de nutrientes no sistema, devido à concentração de biomassa enriquecida por nutrientes captados e/ou assimilados em distintas áreas do estuário (Rossi 2007). No entanto, acúmulos de macroalgas oportunistas representam um reservatório efêmero de nutrientes (McGlathery et al. 2007). Possuindo ciclos de vida de alguns dias a poucas semanas (e.g. ~12 dias para *U. clathrata* em tanques experimentais, Copertino et al. 2009) e liberando compostos orgânicos durante o crescimento, senescência e decomposição (Fong et al. 2004), os nutrientes assimilados pelas algas retornam rapidamente ao sistema.

A análise dos padrões de acúmulo de biomassa em escala local (i.e., mesolitoral *versus* sublitoral) evidenciou que a interação entre a magnitude das florações e o seu transporte advectivo pode afetar a persistência dos acúmulos e o destino dos nutrientes. A dispersão de valores biomassas baixos a moderados para zonas intermareais (Figuras 6 e 8, Apêndice 1) reduz o seu tempo de permanência no sublitoral, onde condições hidrológicas favoráveis poderiam sustentar um contínuo crescimento. Uma vez arribadas nas margens ou marismas, os nutrientes associados à biomassa de macroalgas podem prover um aporte nutricional para as plantas (Boyer & Fong 2005). Por outro lado, sob maior acúmulo de biomassa, como o observado na primavera 2006 (Figura 6, Apêndice 1) e em locais mais expostos no outono/inverno 2014 (Figura 4, Apêndice 2), o empilhamento das algas em direção à margem, não inibe totalmente a sua permanência no sublitoral. Com a manutenção de condições hidrológicas favoráveis ao

crescimento, florações persistem em manchas densas e estacionárias no tempo que podem cobrir extensas áreas rasas (Figura 8, Apêndice 1; Figura 6, Apêndice 2) e representar uma fonte de matéria orgânica para o sedimento durante a sua decomposição (Rossi 2007).

Contribuições da biomassa de macroalgas de deriva para a matéria orgânica no sedimento

Baixos valores de COT e NT no sedimento foram observados entre 2012-2014, com a ausência de um claro padrão de variação temporal e/ou espacial (Figura S2, Apêndice 2). De maneira geral, variações sazonais e espaciais na magnitude das marés verdes observadas no ELP nesse período não foram refletidas pelos valores de matéria orgânica incorporados no sedimento (Figura 4 e S2, Apêndice 2). Tal resultado indica que macroalgas de deriva contribuíram pouco ao TOC e TN sedimentar, independentemente do local e estação do ano, contrastando com aumentos do teor de C e N reportados durante acúmulos de macroalgas em zonas rasas (e.g. Pihl et al. 1999; Corzo et al. 2009 mas veja Sundbäck et al. 1999; García-Robledo & Corzo 2011).

Diversos fatores podem gerar aumentos transitórios no teor de CO e NT no sedimento, entre poucos dias (e.g. García-Robledo et al. 2008) a poucas semanas (e.g. Rossi 2007), impossíveis de serem detectados na escala mensal de monitoramento adotada no presente estudo. Devido à baixa complexidade estrutural e composição bioquímica dos talos algais filamentosos ou tubulares, o detrito das macroalgas incorporado no sedimento apresenta meia-vida de uma a duas semanas (Banta et al. 2004; Rossi 2007). A matéria orgânica é rapidamente reciclada através da assimilação

microbiana, liberando amônio (NH_4^+), nitrito (NO_2^-) e nitrato (NO_3^-) na interface sedimento-coluna d'água (García-Robledo et al. 2008). Esse processo é afetado pela concentração de oxigênio na interface sedimento-água (Middelburg & Lewin 2009) e a alta influência da ação de ventos em enseadas rasas do ELP pode maximizar a remineralização da matéria orgânica e subsequentes transferências de nutrientes para a coluna d'água (Rigaud et al., 2013). Nutrientes inorgânicos liberados do sedimento podem ser captados e assimilados pelo microfitobentos (Hardison et al. 2010) e posteriormente repassados à produção secundária estuarina através do consumo de microalgas bentônicas pela macrofauna bentônica, em especial comedores de depósito superficiais. Todos esses processos podem eliminar excessos de matéria orgânica no sedimento oriundos da deposição e decomposição de macroalgas (Rossi 2007).

Entretanto, aumentos transitórios da matéria orgânica sedimentar variando de 1.7% a 14% para C e 13.5% até 16% para N basearam-se na manipulação experimental de pequenas quantidades de biomassa (e.g. $\sim 40 \text{ g PS m}^{-2}$, Rossi 2007; 220 g PS m^{-2} , García-Robledo et al. 2008), similares a valores observados no presente trabalho nas enseadas mais protegidas e/ou períodos de florações moderadas. Sob maior magnitude e persistência de florações de macroalgas de deriva, como as observadas em enseadas expostas no outono e inverno de 2014 ($\sim 1900 \text{ g PS m}^{-2}$ e 572 g PS m^{-2} para os locais exp-SO e exp-NE, respectivamente), que cobriram até 75% da área (Figuras 4 e 6, Apêndice 2), ocorre auto-sombreamento da biomassa de macroalgas nas camadas inferiores. A subsequente senescência e decomposição da biomassa algácea pode promover a liberação de matéria orgânica na interface sedimento-água em quantidade superior às taxas de remineralização microbiana e assimilação pela fauna bentônica. Nesse caso, acúmulos de TOC e TN de macroalgas no sedimento seriam esperados

(Rossi 2007). Entretanto, acúmulos de COT e NT não foram detectados nas camadas superficiais dos sedimentos (Figura S1, Apêndice 2). Mais do que isso, a análise da composição isotópica e dos modelos de mistura indicaram uma baixa contribuição da biomassa de macroalgas à matéria orgânica sedimentar comparada às contribuições de demais fontes como a MOP, *R. maritima* e plantas de marisma (Figuras 8 e S2, Apêndice 2). Baixos valores de contribuição de macroalgas ocorreram independentemente da magnitude e persistência das florações.

A incorporação da biomassa de macroalgas nas camadas superficiais do sedimento depende das condições hidrodinâmicas locais as quais influenciam os seus padrões de deposição e soterramento (Hardison et al. 2010). Nossos resultados sugerem que, embora o transporte advectivo gerado por ventos locais promova grandes acúmulos de macroalgas de deriva em áreas mais expostas, este mesmo transporte impede a sua permanência prolongada e deposição, inibindo, portanto, a possível incorporação da biomassa de macroalgas no sedimento analisado. Estudos demonstram que os baixos limiares de erosão da biomassa de macroalgas (Flindt et al. 2004) podem ocasionar o seu constante deslocamento sobre o fundo e ressuspensão na coluna d'água, gerando deposições instáveis que variam em pequenas escalas espaciais (i.e., 1 m²) e temporais (i.e., poucas horas a poucos dias, Biber 2007; Rasmussen et al. 2013). Os resultados deste estudo sugerem que a constante ressuspensão e deslocamento das algas, principalmente nas enseadas expostas, inibe os efeitos de auto-sombreamento e consequente colapso da biomassa de macroalgas sobre o fundo. Estudos prévios demonstram que florações de macroalgas são uma fonte de matéria orgânica para o sedimento quando senescem e morrem no local (e.g. Pihl et al. 1999; Corzo et al. 2009). Entretanto, a manutenção da biomassa “saudável” sobre o fundo não promove aportes

significativos de detritos ao sedimento (Sundbäck et al. 1990; García-Robledo & Corzo 2011). Adicionalmente, uma alta hidrodinâmica inibe processos de anoxia na interface sedimento-água, mesmo durante a senescência da biomassa, possibilitando a reciclagem de grandes quantidades de matéria orgânica de macroalgas, através do consumo direto por herbívoros e detritívoros ou na coluna d'água pela alça microbiana estuarina (Fong et al. 2004; Cébrian et al. 2014).

Efeitos da deposição de macroalgas de deriva sobre pradarias de *R. maritima* e macrofauna associada

Os resultados do experimento de adição de macroalgas evidenciaram que, apesar da persistência mensal de uma floração na área rasa analisada (Tabela 1, Apêndice 3), variações ocorreram em escalas espaciais menores (cerca de 0,25 m²) e temporais (4 a 7 dias). Tais variações estiveram significativamente relacionadas aos efeitos interativos da descarga fluvial e ventos locais (i.e. *Wave Exposure*), os quais promoveram o transporte advectivo da biomassa de macroalgas (Figs. 2 e 3, Apêndice 3).

Efeitos negativos de florações de macroalgas de deriva sobre comunidades bentônicas têm sido observados sob acúmulos prolongados da biomassa de macroalgas (e.g. de 5 semanas, Holmer et al. 2011 a até 5 meses, Hauxwell 2001), os quais provocam atenuação da luz sobre o fundo e condições químicas adversas (i.e., anoxia e liberação de sulfetos) relacionadas à decomposição (Irlandi et al. 2004; Rasmussen et al. 2013). Os resultados experimentais do presente estudo mostraram que a pradaria de *R. maritima* foi afetada negativamente, mesmo com deposições algais transitórias (~ uma semana). As plantas mostraram decréscimos significativos na biomassa aérea e

subterrânea, comprimento de folhas, densidade de hastes e nós e comprimento de rizoma (Figs. 4 e 5, Apêndice 3), além de uma ausência de alterações significativas no conteúdo nutricional da biomassa (Fig. 6). Um dos principais efeitos deletérios das florações de macroalgas sobre pradarias é a atenuação da luz no fundo, devido ao auto-sombreamento (Hauxwell et al. 2001) e/ou ressuspensão dos sedimentos pelo movimento das algas (Canal-Vergés et al. 2010). Entretanto, as reduções de biomassa e dos parâmetros demográficos de *R. maritima* observadas demonstram que, embora reduções na luz disponível sobre o fundo possam ter ocorrido, essas por si só não foram suficientes para desencadear estratégias adaptativas a reduções crônicas de luminosidade. Essas incluem alongamento de folhas, aumento da razão biomassa aérea:subterrânea e reduções do conteúdo de C nos tecidos devido à sua mobilização para suprir requerimentos fisiológicos da planta (Cabaço & Santos 2007). Dessa forma, nossos resultados sugerem ocorrência de outros estresses pontuais sobre as plantas de *Ruppia*.

Em face ao caráter transitório das deposições de biomassa de macroalgas, é possível que as reduções da pradaria de *R. maritima*, observadas no presente estudo, foram causadas pelo estresse mecânico (i.e., efeitos balísticos *sensu* Canal-Vergés et al. 2010), devido ao deslocamento da biomassa de macroalgas, tanto sobre o fundo como através da coluna d'água (Flindt et al. 2004). As macroalgas de deriva do ELP são formadas por espécies oportunistas (*U. clathrata*, *Cladophora* spp, *R. riparium*) com talos filamentosos muito finos e densamente emaranhados, as quais se entrelaçam entre folhas e hastes das fanerógamas (Kopecky & Dunton 2006; Höffle et al. 2011). Desta maneira, o transporte advectivo das algas provoca a quebra das folhas e hastes das plantas (van Lent & Verschuure 1994). Hastes e rizomas de *R. maritima* são comumente

observadas entre massas de macroalgas de deriva no ELP (Fig. 9, Apêndice 3; Silva & Asmus 2001).

As observadas reduções na biomassa aérea e subterrânea, no comprimento dos rizomas e na densidade de nós também são respostas típicas de fanerógamas de pequeno porte, como *R. maritima*, à processos erosivos do sedimento (Cabaço & Santos 2007; Han et al. 2012). Populações anuais de *R. maritima* apresentam biomassa subterrânea reduzida, formada por redes delicadas de rizomas ancoradas nas camadas superficiais do sedimento (i.e., até 90% nos primeiros 5 cm de profundidade do sedimento, Kantrud 1991). Consequentemente, de acordo com o reportado para demais fanerógamas de pequeno porte (i.e. *Zostera noltii* Cabaço et al. 2008), plantas de *R. maritima* são bastante vulneráveis à hidrodinâmica alta e a remobilização do sedimento (Copertino & Seeliger 2010), as quais promovem a exposição dos rizomas na superfície e o seu consequente transporte advectivo por ondas e correntes. Contudo, nossos resultados sugerem que efeitos aditivos do alto hidrodinamismo local associado à ocorrência de florações de macroalgas de deriva podem maximizar esse processo, visto que o transporte advectivo de massas algais sobre o fundo promove uma maior erosão e ressuspensão dos sedimentos superficiais (Canal-Vergés et al. 2010). Estudos futuros investigando os efeitos do transporte advectivo de macroalgas de deriva sobre a dinâmica sedimentar são necessários para confirmar essa hipótese.

Impactos negativos de macroalgas de deriva sobre plantas de *R. maritima* ocorreram mesmo sob condições de biomassas baixas ($\sim 200 \text{ g PS m}^{-2}$, i.e. tratamento LB; Fig. 5, Apêndice 3), correspondentes a valores que ocorrem naturalmente em estuários eutróficos (e.g. Martins et al. 2001). Nesses cenários, espécies como *R. maritima*, de pequeno porte e caráter efêmero, podem rapidamente se recuperar da

fragmentação de pradarias através de uma rápida expansão horizontal por crescimento vegetativo (Cho et al. 2009; Han et al. 2012). Entretanto, essa recuperação depende da cessão do impacto (Han et al. 2012). Considerando os efeitos dos tratamentos de maior biomassa de macroalgas sobre plantas de *Ruppia* ($\sim 1000 \text{ g PS m}^{-2}$, i.e. Tratamento HB; Fig. 5, Apêndice 3) e os observados aumentos na magnitude e persistência de florações de macroalgas no ELP (Apêndices 1 e 2), os impactos negativos das macroalgas de deriva sobre as pradarias de fanerógamas submersas podem ser recorrentes, provocando depleções de biomassa acima da capacidade de recuperação das pradarias.

No ELP, grandes florações de macroalgas de deriva têm ocorrido simultaneamente a ciclos de crescimento de *R. maritima*, o que pode impactar períodos críticos para o estabelecimento das pradarias (primavera) e para a formação de bancos de sementes ao final do ciclo reprodutivo (outono). Plantas juvenis apresentam raízes e rizomas pouco desenvolvidos (Ailstock et al. 2010), sendo mais suscetíveis aos efeitos balísticos de macroalgas de deriva (Valdemarsen et al. 2010). Com a redução do crescimento vegetativo e da produção de sementes (Copertino & Seeliger 2010), o reestabelecimento de pradarias nos anos subsequentes é comprometido. Todos esses fatores podem talvez explicar a recuperação lenta de pradarias de *R. maritima* em áreas rasas do estuário após eventos de El Niño (i.e., 1997/98 e 2002/03, Copertino & Seeliger 2010), uma vez que períodos pós-El Niño foram dominados por macroalgas de deriva (Apêndice 1). Cenários similares são observados em outras regiões costeiras, onde a recuperação de pradarias de *Z. marina* é atrasada por efeitos balísticos de *Fucus* sp. em indivíduos juvenis (e.g. Odense Fjord, Valdemarsen et al. 2010).

Modificações na estrutura física do ambiente podem também afetar a produção secundária estuarina (Cébrían et al. 2014). A substituição de pradarias de *R. maritima*

por manchas algais instáveis no tempo e no espaço pode não compensar a perda das fanerógamas enraizadas, as quais aumentam a complexidade estrutural do ambiente e trapeiam a matéria orgânica em suspensão através da redução de correntes (Dolbeth et al. 2003). Entretanto, efeitos negativos de deposições transitórias de macroalgas de deriva sobre a riqueza e abundância da macrofauna bentônica não foram observados (Fig. 8a,b, Apêndice 3). Tal fato pode ser, em parte, explicado pela presença de poliquetas infaunais detritívoros como *L. acuta* e *H. similis* e predadores da meio e macrofauna como *N. fluviatilis*, os quais são pouco afetados pelas condições na superfície do sedimento (Bemvenuti 1987, 1997) e não demonstram dependência a fundos vegetados (Lee et al. 2001).

Por outro lado, maiores reduções na abundância do detritívoro superficial *M. schubarti* ocorreram no tratamento com biomassas altas (HB; Fig. 8c, Apêndice 3). Tais organismos habitam tubos em forma de U que podem atingir até 15 cm no interior do substrato (Bemvenuti, 1987) e, devido ao seu hábito de alimentação suspensívoro, dependem da camada superficial para alimentação. A inserção de elevada biomassa de macroalgas pode ter prejudicado sua atividade alimentar no material suspenso e ocasionado uma menor disponibilidade de alimentos devido à remoção de plantas de *Ruppia*. Sob tais condições, invertebrados infaunais e epifaunais podem colonizar manchas de macroalgas de deriva (Norkko & Bonsdorff 1996; Rosa & Bemvenuti 2007). Entretanto, enquanto o transporte advectivo de macroalgas de deriva favorece a dispersão dos organismos faunais (Salovius et al. 2005), a exportação das manchas algais para regiões adjacentes e/ou áreas mais profundas fornece habitats instáveis. Consequentemente, poderá ocorrer um empobrecimento a longo-prazo da macrofauna bentônica e pelágica associada, que utilizam as pradarias para alimento, proteção e

reprodução (Dolbeth et al. 2003). Nesse contexto, embora efeitos negativos de deposições instáveis de macroalgas de deriva sobre a macrofauna bêntica não tenham sido detectados, chama-se a atenção para a necessidade de estudos em escalas temporais maiores para detectar possíveis efeitos da substituição de *Ruppia* por macroalgas de deriva na produção secundária estuarina.

Através da análise integrada dos resultados deste estudo, conclui-se que os padrões de ocorrência de florações de macroalgas de deriva no ELP, e seus impactos sobre a matéria orgânica sedimentar e as comunidades bentônicas, podem ter implicações ecológicas relevantes para o funcionamento do ecossistema estuarino. Na ausência de demais produtores primários bentônicos que promovem a retenção de nutrientes a longo prazo, como o microfitobentos e pradarias de *R. maritima*, florações de macroalgas de deriva poderão atuar como o principal filtro de nutrientes em áreas rasas, contribuindo para a retenção da matéria orgânica no ELP. A baixa contribuição da biomassa de macroalgas ao C e N do sedimento indica que grande parte dos nutrientes são reciclados rapidamente na coluna d'água e na interface com o sedimento, consumidos e/ou exportados. Visto que macroalgas de deriva contribuem moderadamente à cadeia trófica estuarina do ELP (Claudino et al. 2013), mudanças de fase com o domínio de macroalgas de deriva podem aumentar a exportação da matéria orgânica (incluindo os organismos faunais) para fora das áreas rasas durante períodos de maiores descargas fluviais (Dolbeth et al. 2003; Martins et al. 2007). Consequentemente, mesmo em face aos recentes aumentos nas concentrações de nutrientes reportados no ELP (e.g. Niencheski & Baumgarten 2007; Haraguchi et al. 2015), uma oligotrofização do sistema pode ocorrer a longo prazo, com reflexos na produção secundária, (McGlathery et al. 2007; García-Robledo & Corzo 2011). Estudos

mais abrangentes sobre o balanço de nutrientes no sistema incorporando simultaneamente diferentes compartimentos bióticos (i.e., demais produtores primários e níveis tróficos superiores) e abióticos (i.e., coluna d'água e camada sedimentar) são necessários para investigar essa hipótese. Nesse sentido, cabe ressaltar a necessidade da inclusão de grupos comumente negligenciados no estudo da produção primária estuarina, como o microfitobentos (Sundbäck et al. 2003).

6 CONCLUSÕES

1. Períodos dominados por macroalgas de deriva evidenciam uma possível mudança de fase da VAS no ELP. Em face à uma alta disponibilidade nutrientes (em especial compostos nitrogenados) para o desencadeamento de florações de macroalgas de deriva, a sua ocorrência, magnitude e persistência são determinadas pela interação de fatores climáticos, hidrológicos e meteorológicos. Regimes de precipitação na bacia de drenagem do ELP, afetados por eventos de El Niño/La Niña, controlam os padrões temporais de descarga fluvial no estuário, os quais irão determinar variações anuais e interanuais na ocorrência de acúmulos de biomassa de macroalgas em enseadas rasas. Uma vez estabelecidas, a magnitude e persistência de florações são controladas por parâmetros físico-químicos da água e pelo transporte advectivo por ondas e correntes geradas pela ação de ventos.
2. Florações de macroalgas de deriva não fornecem contribuições significativas para a matéria orgânica acumulada no sedimento, independente da sua magnitude e persistência. O presente estudo indica que o transporte advectivo da

biomassa de macroalgas possivelmente tem efeitos opostos no seu acúmulo e na sua incorporação aos sedimentos. Tal processo inibe a persistência de florações sustentadas pela auto-regeneração bêntica da matéria orgânica de macroalgas, conforme sugerido na literatura. Nossos resultados evidenciam a importância de se considerar fatores ambientais diversos na investigação dos efeitos de florações de macroalgas de deriva sobre os ciclos biogeoquímicos locais.

3. Deposições de macroalgas de deriva sobre o fundo de enseadas rasas do ELP são instáveis no tempo e no espaço devido ao seu alto potencial de transporte advectivo. Apesar da presença de condições ambientais favoráveis na interface sedimento-água, evidenciadas pela ausência de alterações significativas na estrutura e abundância da infauna sedentária, impactos negativos de deposições de curto prazo de macroalgas sobre pradarias de *R. maritima* foram detectados. Nossos resultados indicam que, em contraste ao sugerido pela literatura, deposições instáveis de macroalgas de deriva afetam negativamente pradarias de fanerógamas submersas através do estresse mecânico gerado pelo transporte advectivo da biomassa de macroalgas.
4. A análise conjunta dos resultados evidencia que a dominância de grandes florações de macroalgas de deriva de caráter dinâmico pode ocasionar um empobrecimento do ecossistema estuarino investigado. A exportação da biomassa de macroalgas e dos nutrientes, juntamente com a fauna associada, para áreas adjacentes podem acarretar a oligotrofização do sistema e reduções na produção secundária estuarina a longo prazo.

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APÊNDICES

Apêndice 1

Esse apêndice refere-se ao artigo intitulado “Drift macroalgae in Patos Lagoon Estuary (Southern Brazil): effects of climate, hydrology and wind action on the onset and magnitude of blooms” aceito para publicação no periódico *Marine Biology Research*.

Drift macroalgae in the Patos Lagoon Estuary (Southern Brazil): effects of climate, hydrology and wind action on the onset and magnitude of blooms.

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Running head: Drift algae and hydrology

Abstract

Ephemeral macroalgae blooms have been increasing in frequency and abundance worldwide. We investigated the variability of drift macroalgae abundance in a shallow bay of the Patos Lagoon Estuary (PLE) in Southern Brazil to determine the influence of climate and hydrology on the onset and magnitude of blooms. During the study period (January 2004 to May 2007), three growth cycles were observed and differed in timing, magnitude and persistence. Macroalgal biomass (mostly *Ulva* species) varied annually and interannually (3 g DW m⁻² to 432.7 g DW m⁻²), peaking during the spring and summer. On an annual scale, macroalgal blooms occurred after reductions in freshwater discharge and associated decreases in water level and increases in salinity and retention. These hydrological parameters were influenced by precipitation which, in turn, is affected by the El Niño Southern Oscillation. On an interannual scale, the largest bloom was observed during a weak-moderate El Niño year. No direct relationship was found between biomass peaks and water nutrient concentrations, but tissue nitrogen content indicated no nitrogen limitation. However, a trend of increasing phosphorus concentration (resulting in decreased DIN:DIP ratios) may be associated with the largest bloom observed. Under favourable hydrological conditions for growth, wind action affected the algal transport in shallow areas, thereby controlling the magnitude and persistence of the blooms. The macroalgal abundance found in the PLE was comparable to that found in temperate eutrophic lagoons, highlighting an algal-dominated period triggered by the combined effects of climate and hydrological factors in a post-El Niño period.

Keywords: drift macroalgae blooms, El Niño Southern Oscillation, hydrodynamics, advective transport, phase-shift.

Introduction

Drift macroalgae are important primary producers in shallow estuarine waters, together with seagrasses, microphytobenthos and phytoplankton (Valiela et al. 1997). In eutrophic estuaries, macroalgae play a major role in nutrient cycling, acting both as sinks and sources of nutrients in the water column and sediment (Fong et al. 2004). Drift macroalgae are mainly composed of opportunistic species such as *Ulva* spp., *Cladophora* spp. and *Chaetomorpha* spp. Compared with rooted seagrasses and larger perennial macroalgae, these species present higher nutrient uptake and growth rates, therefore thriving in eutrophic conditions (Smetacek & Zingone 2013). Although recruiting first at the bottom, drift algae can be transported by wind-driven waves and currents (Flindt et al. 2004). Under favourable hydrological conditions, drift algae can grow and accumulate in shallow areas, forming green tides (Liu et al. 2009).

An increasing trend in the frequency and abundance of “green tide” events has been observed worldwide during recent decades, mostly attributed to coastal eutrophication (Smetacek & Zingone 2013). Excessive algal growth affects the water quality and benthic ecosystems by reducing light, causing anoxia and releasing toxic compounds during decay (Cummins et al. 2004). On soft bottoms, the thick algal mats intercept the flux of nutrients between the sediment and the water column, disrupting estuarine biogeochemical cycles (Fong & Kennison 2010). Thus, overgrowth of drift macroalgae can impair the structure and the function of estuarine and coastal ecosystems.

Increased nitrogen levels can stimulate the growth of opportunist macroalgae; however, the onset and persistence of green tides depend on multiple factors and differ among coastal regions and events within a region. Coastal eutrophication (e.g.

Teichberg et al. 2010), mariculture (e.g. Liu et al. 2009), overfishing and local hydrodynamics (e.g. Martins et al. 2001) are related to the growth and accumulation of opportunist algae. Furthermore, wind action determines the transport and accumulation of planktonic or drifting organisms throughout coastal areas (Liu et al. 2009). Therefore, identifying the causal factors of green tide events in different coastal areas may help to establish suitable management and mitigation measures for this increasing environmental problem (Smetacek & Zingone 2013).

In the Patos Lagoon Estuary (PLE), Southern Brazil, drift macroalgae are an important component of the submerged aquatic vegetation (SAV) along with seagrasses, freshwater grasses and microphytobenthos (Copertino & Seeliger 2010). The distribution, abundance and composition of drift algae in the PLE vary in space and time on different scales (Coutinho & Seeliger 1986). Over recent decades, large blooms and green tides have been observed in this estuary following periods of extreme precipitation (Copertino & Seeliger 2010). However, the driving factors behind the formation of the blooms as well as their frequency and persistence in the PLE are still poorly understood.

The region of Southern Brazil is strongly affected by the El Niño Southern Oscillation (ENSO) mode and its effects on regional climatology. Precipitation anomalies leading to wet and dry periods are associated with ENSO's warm and cold phases (i.e. El Niño and La Niña respectively; Grimm et al. 1998). Autumn–winter anomalies in the year following El Niño events have been associated with extreme floods in the region. Because the Patos Lagoon receives the precipitation and fluvial discharge from an extensive watershed ($\sim 200,000 \text{ km}^2$), the influence of ENSO on the hydrology and ecology of the estuary is impressive (e.g. Odebrecht et al. 2010). During

El Niño years, the PLE is dominated by high river flow, water level, turbidity and low salinity. The very low light levels reaching the bottom, in combination with high wave energy and sediment resuspension, causes decreases in SAV distribution and abundance, as observed during El Niño events in 1997-1998 and 2002-2003 (Copertino & Seeliger 2010). After El Niño periods, shallow areas are quickly covered by drift macroalgae to the detriment of seagrass and other benthic primary producers in the PLE (Copertino & Seeliger 2010).

Therefore, the present study aimed to investigate the onset and variability of drift macroalgae abundance and distribution in the PLE during the SAV reductions following the strong-moderate El Niño in 2002-2003. We analysed the influence of climate and hydrology based on the hypothesis that while the recruitment and growth of drift macroalgae are related to favourable water physico-chemical parameters, their accumulation and distribution across a shallow area depend on wind action and patterns.

Materials and Methods

Study site

The Patos Lagoon is the largest (10,000 km²) choked coastal lagoon in the world (Kjerfve 1986). With a semi-diurnal microtidal regime (~0.47 cm), the driving forces behind the estuarine hydrology are regional precipitation, fluvial discharge and wind patterns (Möller et al. 2001). Peaks of discharge occur during winter-spring, while drought periods prevailed during summer-autumn (Vaz et al. 2006). Long-term, interannual variability is strongly affected by ENSO, with anomalous flows occurring during El Niño years. The prevailing northeasterly (NE) and southwesterly (SW) winds

affect the outflow and inflow of water, respectively, between the estuary and the adjacent coast. During flood periods, the PLE becomes a river-dominated system with the mixing zone restricted to the mouth of the estuary; only strong SW winds can reverse the outflow forces (Möller et al. 2001). During drought periods, seawater enters the inner estuary and shallow areas, with the mixing zone advancing to the upper limits of the PLE. Consequently, marine and euryhaline conditions usually occur in the summer/autumn, while freshwater and oligohaline conditions prevail in the winter/spring. Overall, high levels of nutrients in the water column and sediment are maintained through nutrient inputs from the watershed, macrophytes and anthropogenic sources (Baumgarten & Niencheski 2010).

Submerged aquatic vegetation (SAV) can occupy extensive areas ($>120 \text{ km}^2$) of the shallow bottoms ($< 2 \text{ m}$ depth), peaking during summer (Copertino & Seeliger 2010). SAV is dominated by the euryhaline species *Ruppia maritima* Linnaeus and the oligohaline species *Zannichellia palustris* Linnaeus. Several attached or free-floating macroalgae species of *Ulva*, *Cladophora*, *Rhizoclonium* (Ulvophyceae) and *Polysiphonia* (Florideophyceae) are present amongst the SAV, and species abundance varies seasonally (Coutinho & Seeliger 1986).

Between January 2004 and May 2007, we studied drift macroalgae in a shallow ($<1 \text{ m}$ depth) bay of the PLE adjacent to Pólvora Island (Figure 1), a marshland dominated by the halophytes *Spartina alterniflora* Loisel, *S. densiflora* Brongn and *Bolboschoenus maritimus* (Linnaeus) Palla. The bay is exposed to the prevailing NE winds, with the NNE direction presenting the highest wave fetch (Figure 1). Local bathymetry shows a depression (60-90 cm in depth) surrounded by shallower sand banks (5-50 cm) with the unconsolidated substrate composed of 50-90% sand, 20-30%

very fine sand, up to 10% clay and silt and 2-4% organic matter (Margareth Copertino 2005, personal observation).

Climate, hydrology and physical-chemical parameters

The Oceanic Niño Index (ONI; National Oceanic and Atmospheric Administration, NOAA) was used for measurement of ENSO events. These events were defined as 5 consecutive overlapping 3-month periods at or above the $+0.5^{\circ}$ anomaly for El Niño events and below the -0.5° anomaly for La Niña events. Total monthly rainfall and fluvial discharge data for the Patos Lagoon watershed were obtained from the Brazilian Water National Agency, and local wind speed and direction data were obtained from the Port of Rio Grande Meteorological Station. The flow of the three main tributary rivers (Jacuí, Taquari and Camaquã rivers), which accounts for 70% of the inflow into the Patos Lagoon (Vaz et al. 2006), was assumed to be a proxy for the total fluvial discharge.

Water parameters were monitored near the study site (Figure 1), within the meso-mixohaline region of the PLE, as part of the Brazilian Long-Term Ecological Research (BR-LTER). Water monitoring sites were close enough to the surveyed area (~ 0.8 to 3 km apart) and their abiotic parameters are well representative of those in the shoal surveyed, once no significant spatial variations has been detected among these sites (data not shown). Water level (fixed ruler), salinity (refractometer A366ATC, Atago, Japan) and temperature (thermometer) were monitored daily. Water was sampled monthly and immediately filtered with glass fibre filters for analysis of inorganic nutrients (NH_4^+ , NO_2^- , NO_3^- and PO_4^{3-}) and total suspended solids (TSS), following the methodology described previously for the study area (see Haraguchi et al.

2015 for details).

Drift Macroalgae

Between January 2004 and May 2007, drift macroalgae were sampled monthly and randomly for percentage of cover and biomass within 1 m² quadrats at intertidal flat zones (in which the salt marsh reaches the lowest water level, ~ 0-50 m) and subtidal zones (up to 90 cm in depth) (N = 3 for each zone). From January 2006 to May 2007, macroalgae was monitored monthly and weekly (during blooms) within the depression area (~ 0.5 km²), where they recruited, drifted and accumulated within the bay. The percentage of cover and biomass were assessed along three transects (150-350 m long, 300 m apart) perpendicular to the coast. The Line Intercept Transect (LIT) method was used to estimate macroalgal cover within the surveyed area. This method is designed to sample within-plot variation and quantify temporal changes in plant cover using transects located within the macroplot (English et al. 1997). Along each transect, macroalgae were considered present in a given line segment if data lines intersected the plane of the line segment, from the bottom to the surface. Cover was recorded as the number of metres intersected along the transect. Percentage of cover was then calculated by dividing the number of metres intersected by the total length of the transect. The biomass was destructively sampled at 50 m intervals within quadrats (0.25 m²; N = 3).

In the laboratory, the biomass was washed and cleaned by the removal of invertebrates, debris and sediment, after which the dry weight was obtained (48 h at 60°C). The carbon and nitrogen contents were obtained from a 2–3 mg dried, powdered tissue aliquot using an elemental analyser (2400 Series II CHNS/O System, Perkin-

Elmer, USA). Algal sample subsets were fixed (4% formalin solution) for taxonomic identification.

Data Analyses

The relationship between precipitation and freshwater discharge was assessed through linear regression analysis. Effects of freshwater discharge on water level, salinity, temperature, TSS, PO_4^{3-} concentration and dissolved inorganic nitrogen (DIN , $\text{NH}_4+\text{NO}_2-\text{NO}_3$) concentration were investigated through Principal Component Analysis (PCA). Average seasonal values were used once it explained a higher proportion of the variability than the monthly averages, and variables were log transformed when necessary. The seasons were austral winter (July to September), spring (October to December), summer (January to March), and autumn (April to June). Hydrological parameters were grouped along the PCA axes according to their loadings, which are analogous to Pearson correlation coefficients. This procedure allowed data reduction and provided ecological meanings for the principal components. As PCA axes are independent, variables that are highly correlated along the same axis are inter-correlated, and the opposite is true for variables correlated to different axes. The relationship between drift macroalgal biomass and hydrological parameters was investigated through multiple regression analyses using eigenvalues of PC1, PC2 and PC3, which explained 50.88%, 23.32% and 13.16% of total hydrological data variation, respectively, as independent variables. All statistical analyses were performed using R software (version 3.2.2).

To assess the effects of wind on the distribution of macroalgal abundance, hourly zonal (E-W) and meridional (N-S) components of wind stress (τ), which

represents the horizontal force of wind on the water surface, were calculated using a 22.5° clockwise rotation according to equations (1) and (2), respectively:

$$\tau_x = \rho \times c_d \times U_{10}^2 \times \sin\Theta \quad (\text{Eq. 1})$$

$$\tau_y = \rho \times c_d \times U_{10}^2 \times \cos\Theta \quad (\text{Eq. 2})$$

where ρ is the density of air (1.2 kg m^{-3}), c_d is the drag coefficient (2.5×10^{-3} ; Elliot 1982), U_{10} is the wind speed and Θ is the rotated angle of the wind vector from true north. This procedure made the meridional component (τ_y) coincident with the direction of the highest wave fetch in the bay surveyed (i.e., NNE winds). Positive and negative values of τ_y represented SSW and NNE winds, respectively. In turn, the values reflected conditions of low and high wind action. Temporal patterns of drift mat distribution along inter- and subtidal areas were analysed in relation to τ_y . The spatial variability of algal coverage throughout different time intervals (7 to 30 days) was also plotted and analysed in relation to wind action (i.e., direction and intensity). Wind plots were constructed using WRPLOT View software (The et al. 2011).

Results

Climatic and hydrological conditions

Between January 2004 and May 2007, the ONI index ranged from -0.7 to 1.0, oscillating among neutral conditions (2004, 2005-2006) and weak El Niño events (2004-2005, 2006-2007) (Figure 2a). Total precipitation varied seasonally, with higher precipitation during austral winter and spring compared with summer months (Figure

2a). Freshwater discharge was significantly correlated to seasonal precipitation (linear regression analysis; $r^2 = 0.38$; $p = 0.03$; $N = 12$; Figure 2b). In turn, increases in freshwater discharge promoted increases in water level and reductions in TSS and salinity (Figures 3a, b, c). All these parameters were highly correlated along PC1 (Table I; Figure 4).

The monthly values of dissolved inorganic nutrients were highly variable with no apparent seasonal trend (Figure 5a). Despite instances of increases during high water flows, the relationship between nutrients and fluvial discharge was not direct. An increasing trend was observed for phosphate concentrations over the study period, with peaks in the springs of 2005 and 2006 (Figure 5a). Reductions in DIN:DIP ratios during the spring of 2006 and early summer of 2007 were caused by the increases in phosphate levels (Figure 5a, b). PO_4^{3-} concentration in the water column loaded on the PC2 axis along with water temperature (Table I; Figures 4 and 5a, c). Water temperature varied seasonally, with peaks during the summer and early autumn (Figure 5c). Dissolved inorganic nitrogen (DIN) concentration was highly correlated with PC3 axis (Table I; Figures 4 and 5a).

Drift macroalgae

Multispecific mats of macroalgae were found in the area, composed mainly of *Ulva clathrata* (Roth) C. Agardh along with *U. intestinalis* Linnaeus, *U. flexuosa* Wulfen, *Cladophora vagabunda* Linnaeus (Hoek), *C. glomerata* var. *crassior* (C.Agardh) Hoek and *Rhizoclonium riparium* (Roth) Harvey. Algal biomass varied substantially from 3 g DW m^{-2} (June 2006) to 432.7 g DW m^{-2} (November 2006) and started to grow in late winter/early spring, mainly peaking during the spring (Figure 6). Three main growth cycles were observed and differed in timing, magnitude and

persistence. Cycle I lasted approximately 8 months (September 2004 to April 2005) and presented 2 peaks (spring and late summer/early autumn), with an average maximum biomass of 49 g DW m^{-2} and the larger biomass (256 g DW m^{-2}) measured in the spring. Cycle II was the shortest (January to June 2006), presenting low average (19 g DW m^{-2}) and maximum (58 g DW m^{-2}) biomasses peaking in the summer (January 2006). Cycle III (November 2006 to May 2007) presented the highest average values of biomass (124 g DW m^{-2}) with peaks (432 g DW m^{-2}) during the spring.

Tissue nutrient content varied among macroalgae growing cycles and periods, with N content ranging between 1.2% (spring 2006 and summer 2007) and 2.2% (autumn 2006) at the end of the growth season (Table II). Carbon:nitrogen (C:N) molar ratios in tissues ranged from 12.59 (summer 2007) to 23.73 (spring 2006), with higher values measured during biomass peaks.

The influence of environmental conditions on drift macroalgae

On a short-term (annual) scale, the macroalgal blooms occurred after high flow periods when there were reductions in water levels and increases in salinity (i.e., PC1 axis), temperature and PO_4^{3-} (i.e., PC2), i.e. spring/summer conditions (Figures 3, 5 and 6). However, there were no statistically significant relationships among macroalgal abundance and PCA axes (multiple regression analysis; $r^2 = 0.26$, $p = 0.96$, $N = 12$), highlighting that the effects of hydrological factors on macroalgal blooms were not direct. Interestingly, on a long-term (interannual) scale, the highest biomasses did not match with the years of lowest water levels and highest salinity. The highest algal bloom was observed during the late spring of a weak-moderate El Niño year (2006), which correlated with increased PO_4^{3-} concentrations and decreased DIN:DIP ratios

when compared to data from other years. Nevertheless, no statistically significant relationships were observed between macroalgal biomass and DIN (represented by PC3) and DIN:DIP ratios (Figures 5a, b and 6).

The persistence of the macroalgal biomass and its spatial distribution across the shallow area varied according to wind action. Large amounts of algal biomass (~ 30 to 100% of occurring dry weight) were found throughout the intertidal flat during spring 2004 and 2006, associated with higher frequency and intensity of NNE winds (high negative values of WS; Figures 6 and 7). In contrast, during periods of low wind stress (summer/autumn), macroalgae prevailed in the subtidal zone. The spatial distribution of algal cover supported this trend among the different time scales investigated. As winds from the N-E quadrant became more intense and frequent, subtidal mats were translocated across the sampled area, leading to deposition and high coverage in the intertidal flat (~ 0-100 m from the coast; Figures 8 and 9a). Conversely, during calmer conditions, drift biomass remained in the subtidal zone (Figure 9b). Patterns of macroalgal transport were predominantly shoreward. Because the surveyed area was protected from SSW winds, the wrecked biomass persisted on the intertidal flat until its decomposition and disappearance.

Discussion

Our results showed that the onset, magnitude and permanence of drift macroalgae in the PLE are controlled by the variability in freshwater discharge, mainly due to its effects on water retention, nutrient availability, light levels (measured as water level and turbidity) and salinity. The amount of freshwater entering the PLE is

significantly affected by regional precipitation, which in turn varies according to ENSO episodes (Möller et al. 2001). During the strong El Niño of 2002-2003, the anomalous fluvial discharge caused reductions in the distribution and abundance of SAV in PLE (Copertino & Seeliger 2010). Seagrasses were absent during our study period, contrasting with previous years when *Ruppia maritima* meadows prevailed from spring to late summer and drift macroalgae occurred under low to moderate abundances from autumn to early spring. Therefore, there were large areas of bare sediment available to be colonized by the fast growing macroalgal mats. The present study shows that these macroalgal mats can attain high coverage and biomass comparable to that of blooms reported in other eutrophic coastal areas (e.g. Hernández et al. 1997; Valiela et al. 1997; Martins et al. 2001). We suggest that transitions to opportunistic macroalgae-dominated periods can occur on a multi-annual scale in the PLE, driven by climate and local hydrology.

Seasonal and interannual variability

Blooms of drift macroalgae followed decreases in freshwater discharge. These decreases were accompanied by increasing water salinity resulting from the inflow of coastal saltwater, a process regarded to enhance water retention within the system (Odebrecht et al. 2015). Increased water retention reduces flushing forces out of the PLE, which can attenuate currents speeds from 1 m s^{-1} to $1\text{-}25 \text{ cm s}^{-1}$ in shallow areas (Fernandes 2001). Advective transport is an important mechanism controlling drift biomass retention (Flindt et al. 2004). Current speeds below erosion thresholds for suspension, as well as transport and export of free-floating mats in the water column (i.e. $\sim 10 \text{ cm s}^{-1}$; Flindt et al. 2004) enables the accumulation of greater amounts of algal

biomass in shallow areas. Thus, in the PLE, annual and inter-annual variations of freshwater discharges will determine the occurrence of favourable hydrodynamic conditions for the onset of algal blooms, with temporal variations in their timing and persistence.

Variations in freshwater discharge determined changes in water salinity, level and TSS, factors known to control algal biomass production in shallow estuarine waters (Martins et al. 2001, 2007). We suggest that while freshwater discharges control the occurrence of algal blooms, associated changes in water physico-chemical parameters modulate seasonal variations in magnitude. Our results support the notion that water salinity positively affects the growth of bloom-forming macroalgae (Martins et al. 1999; Taylor et al. 2001). Accordingly, build-up phases of macroalgal blooms were associated with increased values of salinity (~10-19) in the PLE. The salinity levels were above the critical range for spore germination (i.e. 5; Sousa et al. 2007) and within the range of optimal growth rates of *Ulva intestinalis* (10-22; Martins et al. 1999) and *U. clathrata* (10-30; Fitzgerald 1978). These conditions occurred simultaneously with reductions in water level and intermediate values of TSS, which possibly promoted sufficient light availability for algal growth at the bottom. Consequently, the conjunction of changes in level and salinity, associated with temperatures close to optimum values for opportunistic algal growth (15-20 °C; Taylor et al. 2001) may contribute to the onset of high-drift macroalgae blooms in PLE during the spring.

Reductions in algal abundance occurred towards summer/autumn, which can be partly explained by further increments in water salinity (30-35) above optimum reported ranges for bloom-forming species growth (i.e. 17-22, Martins et al. 1999; 23-27, Taylor et al. 2001). However, the dominant species at the PLE (*U. clathrata*) exhibits high

growth rates in increased saline conditions (Coutinho & Seeliger 1986), which indicates that other factors, such as light and temperature, may have contributed to the observed biomass reductions. Opportunistic macroalgae can withstand high water temperatures, with tolerance ranges varying according to the temperatures experienced in their natural habitat (Taylor 2001). High growth rates of *U. clathrata* have been observed in the PLE during midsummer (Coutinho & Seeliger 1986; Copertino et al. 2009), when water temperatures approach optimum reported values for growth (i.e. 25°C, Fitzgerald 1978). However, when temperatures reach seasonal highs, moving allocation of biomass to the formation and release of spores (swarmers) is greatest, thereby resulting in declining biomass (Niesenbaum 1988). In addition, the lowest water levels during the summer promoted air exposure and desiccation of algal biomass in shallow areas. Thus, the combined effects of the lowest water levels and highest temperatures during the study period may have caused the decline in biomass observed in summer/autumn.

In shallow coastal areas, the most noticeable effect of nutrient enrichment on primary producers is the shift from the dominance of perennial macroalgae and seagrasses towards ephemeral macroalgae (Valiela et al. 1997; Fong & Kennison 2010). Fast growing species of *Ulva*, *Cladophora*, *Rhizochlonium*, among others, are capable of quickly taking advantage of nutrient pulses or high nutrient concentrations (Fong et al. 2004). The PLE is a nutrient-replete system (Haraguchi et al. 2015); the excess of dissolved inorganic nutrients is related not only to increases in freshwater discharge but also to anthropogenic and sedimentary sources (Baumgarten & Niencheski 2010). However, we did not find a statistically significant, direct relationship between drift macroalgal blooms and nitrogen concentrations in the water column. This can be explained by the rapid nitrogen uptake and decoupling between uptake and growth of

opportunistic species (Fong et al. 2004). *Ulva clathrata*, as other *Ulva* species, is highly efficient in nitrogen uptake, stripping up to 80% of DIN from its environment within 3 days when cultivated in extremely high nitrogen concentrations (>50 mM; Copertino et al. 2009). Consequently, tissue nutrient content is a better proxy of nutrient availability for algal growth (Fujita 1985). During high biomass blooms, such as in the spring of 2006, tissue nitrogen contents were below to critical values for growth (i.e. ~2%, Fujita 1985). Despite sufficient nutrient availability to promote blooms, it is likely that nitrogen limitation may have occurred after the biomass build-up phases. Accordingly, high C:N ratios (23) in this period reflect the use of tissue N during growth. Tissue nitrogen did not reach values well below the critical values for growth in the summer-autumn. These data support our previous assertion that similar to other studies (e.g. Hernández et al. 1997; Martins et al. 2007), interactive effects of abiotic factors other than nutrient may control biomass abundance in this period.

In nitrogen-enriched systems, P supply controls the growth rates of bloom-forming macroalgae (Teichberg et al. 2010) and primary production has been shown to be P-limited in the PLE during drought periods (Haraguchi et al 2015). We suggest that the increasing trend in phosphorus concentration (resulting in low DIN:DIP ratios) is responsible for the largest blooms observed during the spring of 2006. Competition among different groups of primary producers mediated by increasing N and P concentrations has been reported in coastal lagoons worldwide, leading to phase shifts dominated by macroalgae mats (Fong et al. 1993). Nonetheless, although our results may suggest an on-going, similar process, more studies are necessary to investigate this hypothesis in our study area.

Drift macroalgae spatial distribution

Northeasterly winds promoted the deposition of drift macroalgae biomass to the intertidal and the lower salt marsh, corroborating the hypothesis that wind-driven currents and waves affect the transport and accumulation of drift biomass between subtidal and intertidal stock. In this context, we suggest that local wind action may play an additional role in controlling macroalgal blooms. Under favourable hydrodynamic conditions, such as those observed in the spring of 2006, the permanence of mats in subtidal areas promoted excessive algal growth and may trigger extensive green tides. As reported here, the large macroalgal biomass during these periods and high productivity in the PLE enable the mats to outcompete microalgae possibly through nutrient competition and the release of toxic allelopathic compounds (Copertino et al. 2009). Following high biomass peaks, drift algae suffer quick decomposition, leading to anoxic conditions, toxic concentrations of ammonia and sulphides and the consequent collapse of benthic communities (Cummins et al. 2004). Advective transport caused by strong northeasterly winds during highest biomass peaks dispersed significant amounts of drift biomass to intertidal flats, preventing the build-up of large stagnant blooms and limiting their potentially deleterious effects in subtidal areas. Nonetheless, consequent adverse effects may still occur in intertidal areas as a result of the wrecked biomass decomposition (Sutula et al. 2014).

In conclusion, the combined effects of climate (i.e., ENSO and rainfall) and hydrology (i.e. freshwater discharge and water physico-chemical parameters) drive the onset and magnitude of drift macroalgae blooms in the shallow areas of the PLE. During bloom periods, wind action further controls the persistence and possible occurrence of large green tides. Our results support studies showing that hydrodynamics

is the major factor controlling the occurrence of algal blooms in warm temperate eutrophic estuaries (e.g. Martins et al. 2001), highlighting that similar mechanisms may apply in subtropical areas. Further studies based on a larger spatial scale as well as the integration of experimental and modelling approaches could provide better information for locations most prone to green tide events, facilitating a more effective management of the estuarine ecosystem. Furthermore, long-term studies are necessary to determine if the algal-dominated periods observed reflect a phase-shift in the SAV and consequent effects on the estuarine structure and function.

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TABLES

Table I. PCA loadings (correlation coefficients of variables making up PCs) of the hydrological factors in relation to the axis PC1, PC2 and PC3 which explained, respectively 50.88, 23.32% and 13.16% of total data variation. Values in bold highlight the highest loadings for each factor.

	PC1	PC2	PC3
Freshwater discharge	-0.91	0.14	-0.18
DIN	-0.32	0.36	0.86
PO₄	-0.24	0.86	-0.09
Level	-0.81	0.31	-0.06
Temperature	0.36	0.58	-0.14
Salinity	0.86	-0.08	0.29
Total suspended solids	0.88	0.40	-0.15

Table II. Values of tissue nitrogen and carbon content and C:N molar ratio (mean $\pm$ SE) of the drift macroalgae *Ulva clathrata*, Patos Lagoon Estuary. Samples without replicates are indicated by NR.

	% N	% C	C:N
Summer 2005	1.93 (± 0.18)	23.21 (± 0.21)	14.50 (± 1.09)
Summer 2006	1.99 (± 0.30)	13.56 (± 1.90)	14.19 (± 5.92)
Autumn 2006	2.20 (nr)	25.25 (nr)	13.39 (nr)
Spring 2006	1.21 (nr)	24.68 (nr)	23.73 (nr)
Summer 2007	1.20 (± 0.48)	11.37 (± 1.30)	12.59 (± 3.75)
Autumn 2007	1.65 (± 0.14)	18.26 (± 2.24)	13.23 (± 0.12)

FIGURE LEGENDS

Figure 1. Patos Lagoon Estuary in South America and the location of the studied site, next to Pólvora Island. Closed circles represent the initial point of transects T1, T2 and T3 and arrows show the monitoring sites for water parameters. Lines and number show wave fetch values (in km) at each 22.5° for the shoal surveyed. Please note that highest wave fetch line (i.e. 14.3 km, NNE) is not totally depicted in order not to lose resolution of the studied shoal.

Figure 2. Data on a) total precipitation (full line) and ONI index (dotted line) and b) freshwater discharge. Grey areas are daily values and black lines the mean of 30 running days (January 2004 to May 2007).

Figure 3. Monthly variation of a) water level, b) salinity and c) total suspended solids (TSS) from January 2004 to May 2007. Grey areas are daily values and black lines the mean of 30 running days.

Figure 4. Results of PCA on the relationships among the hydrological parameters freshwater discharge (Disc), level (Lev), salinity (Sal), temperature (Temp), dissolved inorganic nitrogen (DIN), phosphate (PO_4^{3-}) and total suspended solids (TSS) and the principal components axis. PC1, PC2, PC3 explained, respectively, 50.88%, 23.32% and 13.16% of total data variation. Data are seasonal values.

Figure 5. Monthly variation of a) total ammonium nitrogen (NH_4^+ , bold line), nitrite+nitrate ($\text{NO}_2^- + \text{NO}_3^-$, dotted line) and phosphate (PO_4^{3-} , open circles), b) DIN:DIP ratios and c) water temperature from January 2004 to May 2007.

Figure 6. Variability of drift macroalgae dry biomass (mean $\pm$ SE; N=3) at intertidal (grey) and subtidal (black) areas at the NE face of Pólvora Island (August 2004 to May 2007). Areas represent the cumulative average values ($\pm$ SE) for each zone.

Figure 7. Daily variation (mean values of hourly measures) of a) wind direction and magnitude and b) meridional wind stress (WS) at the mouth of Patos Lagoon Estuary from August 2004 to May 2007.

Figure 8. Drift macroalgae percentage cover in the study area at Pólvora Island, Patos Lagoon Estuary, and the prevailing wind from mid-January to mid-March 2006. The wind rose shows the frequency of average wind speed and direction 7-27 days prior to sampling.

Figure 9. Drift macroalgae percentage cover in the study area at Pólvora Island, Patos Lagoon Estuary, and the prevailing wind from a) mid-November to early-December of 2006 and b) late-January to mid-February of 2007. The wind rose shows the frequency of average wind speed and direction 7-10 days prior to sampling.

Figure 1

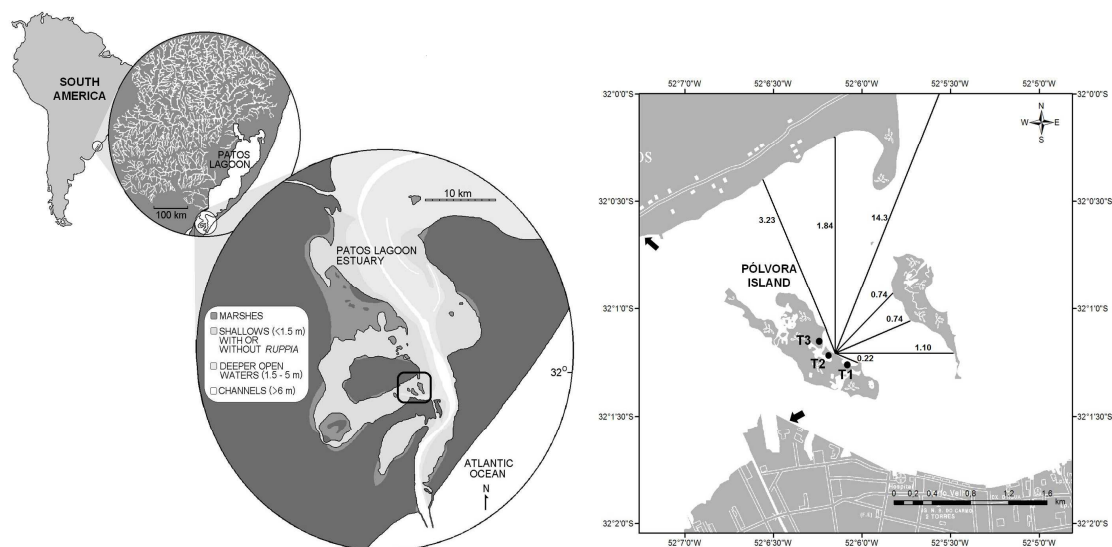


Figure 2

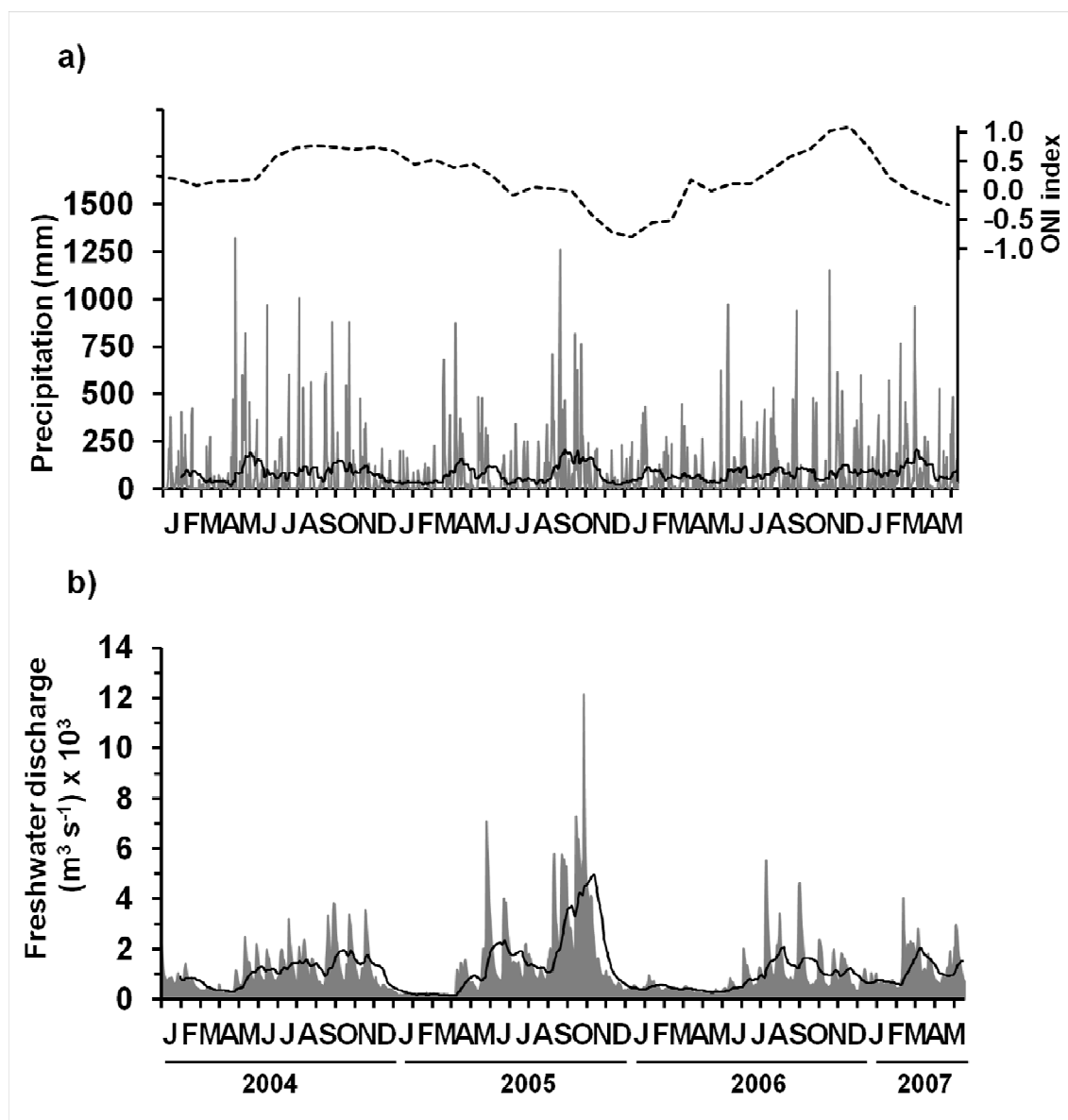


Figure 3

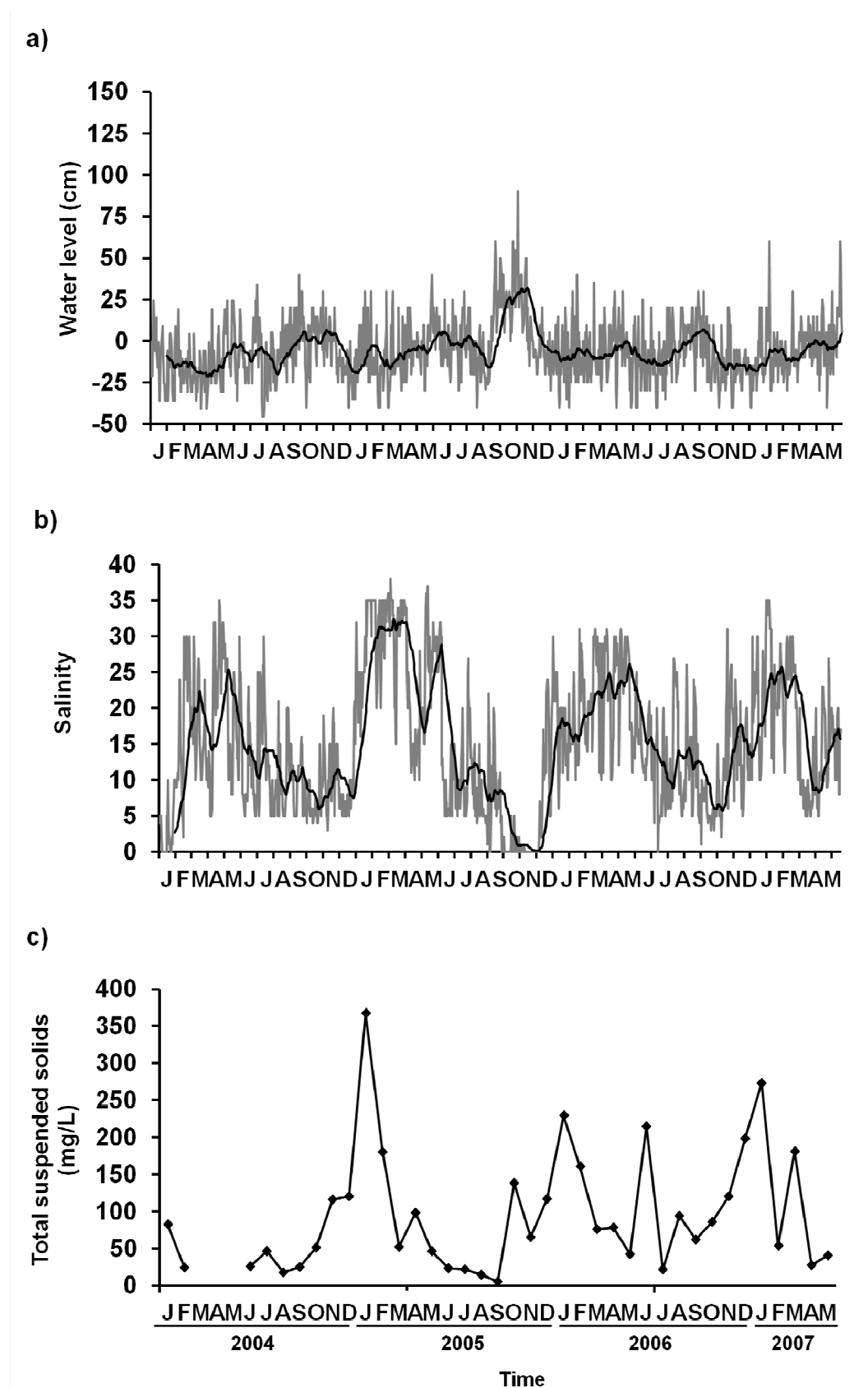


Figure 4

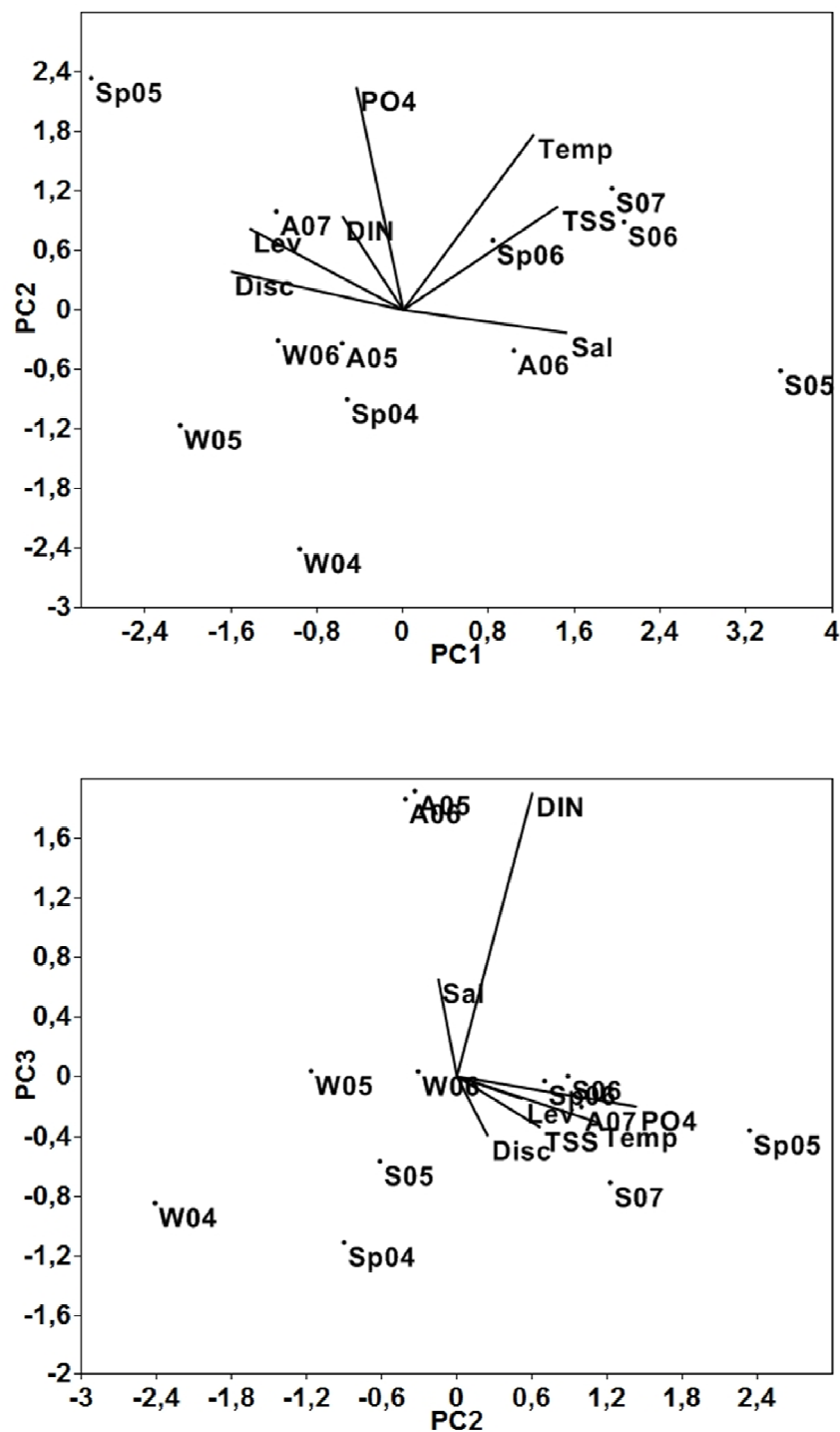


Figure 5

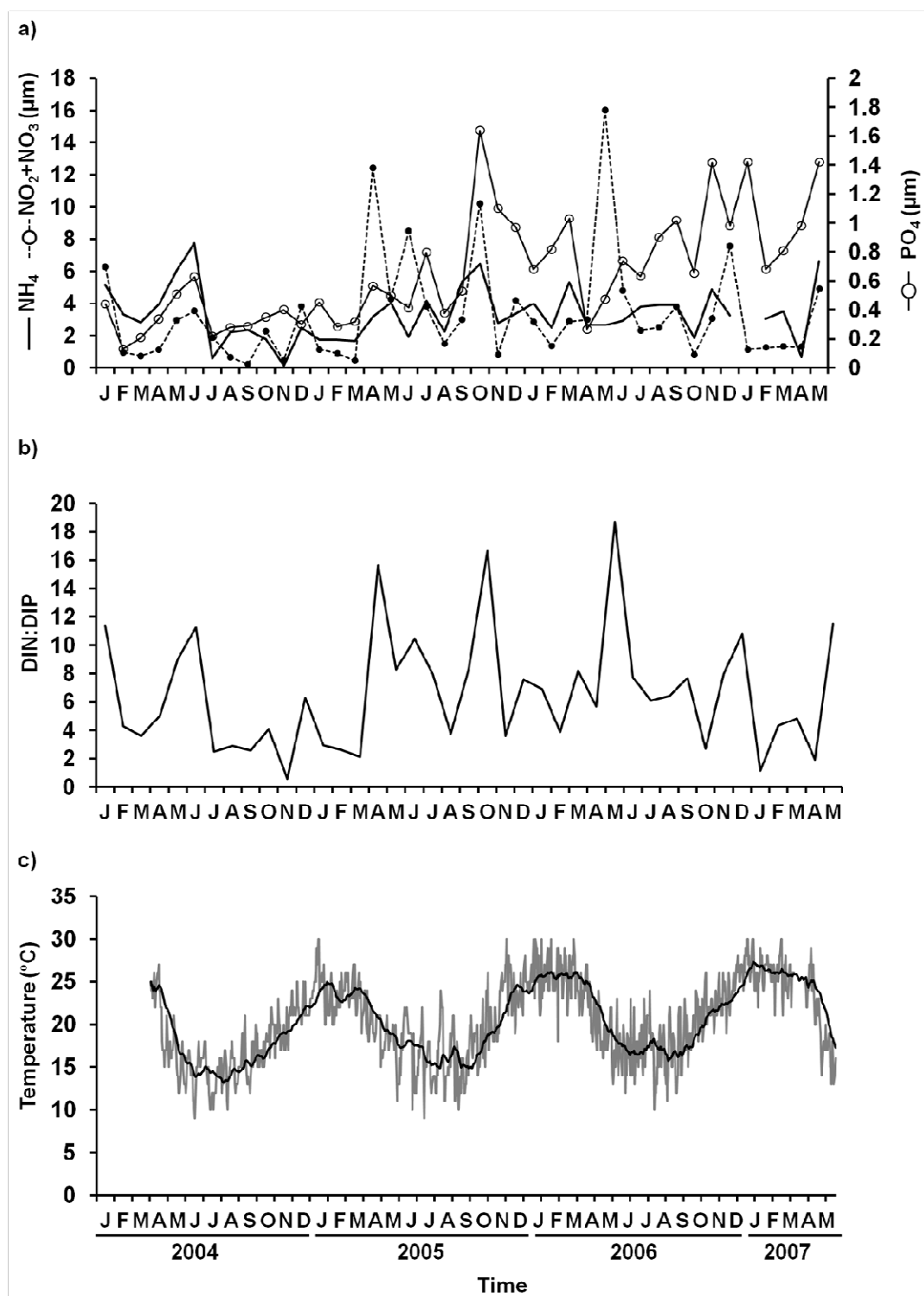


Figure 6

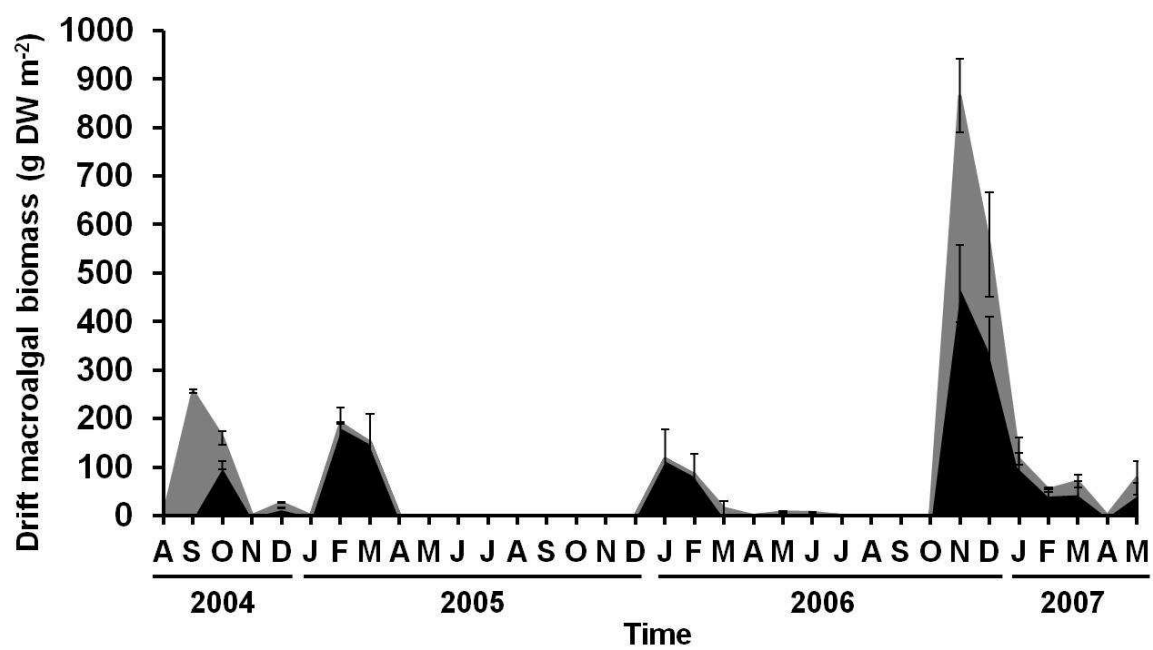


Figure 7

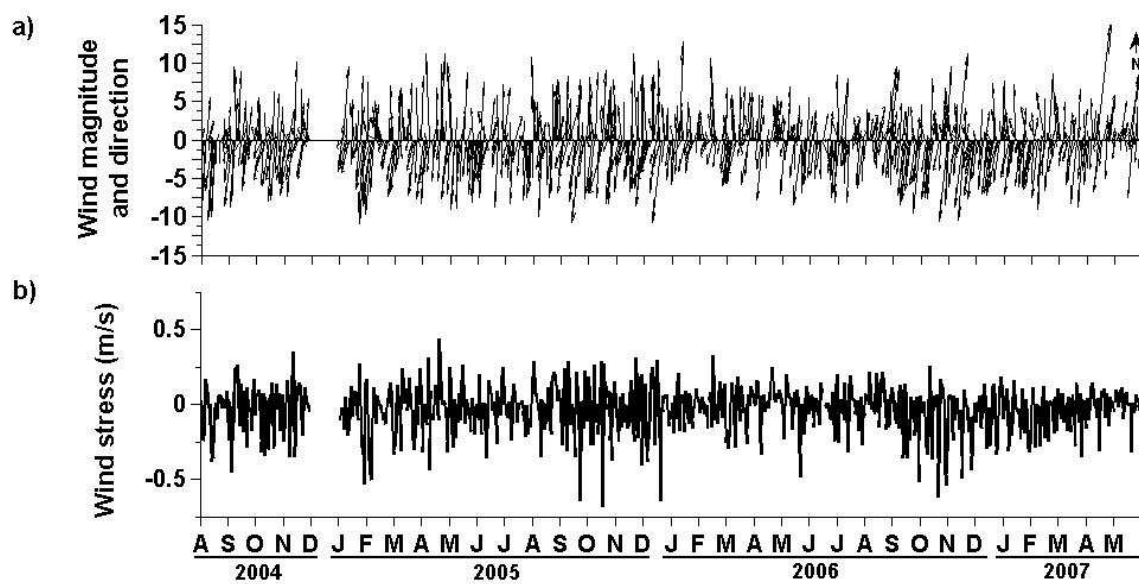


Figure 8

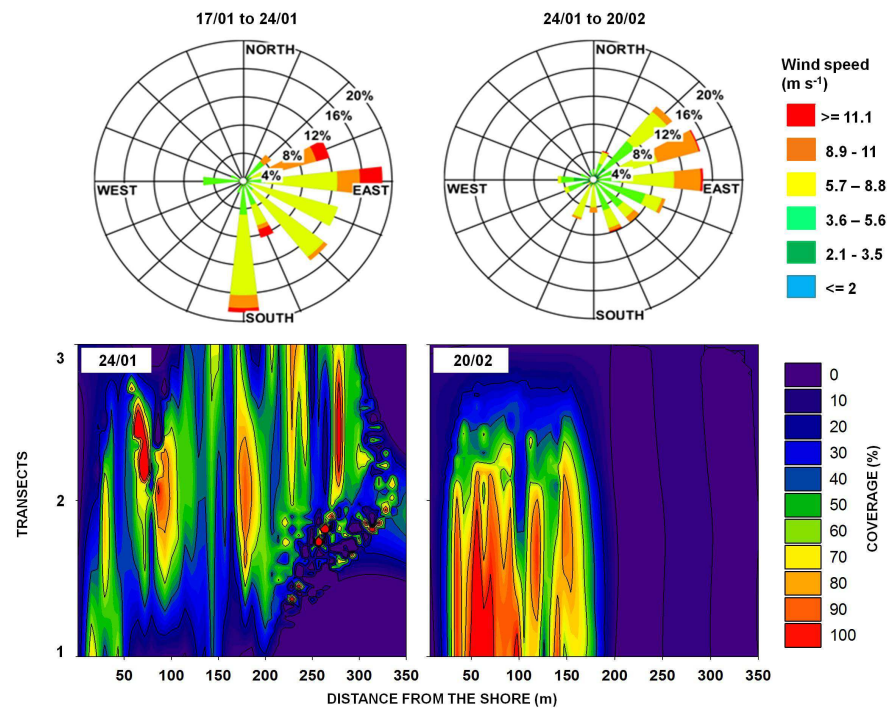
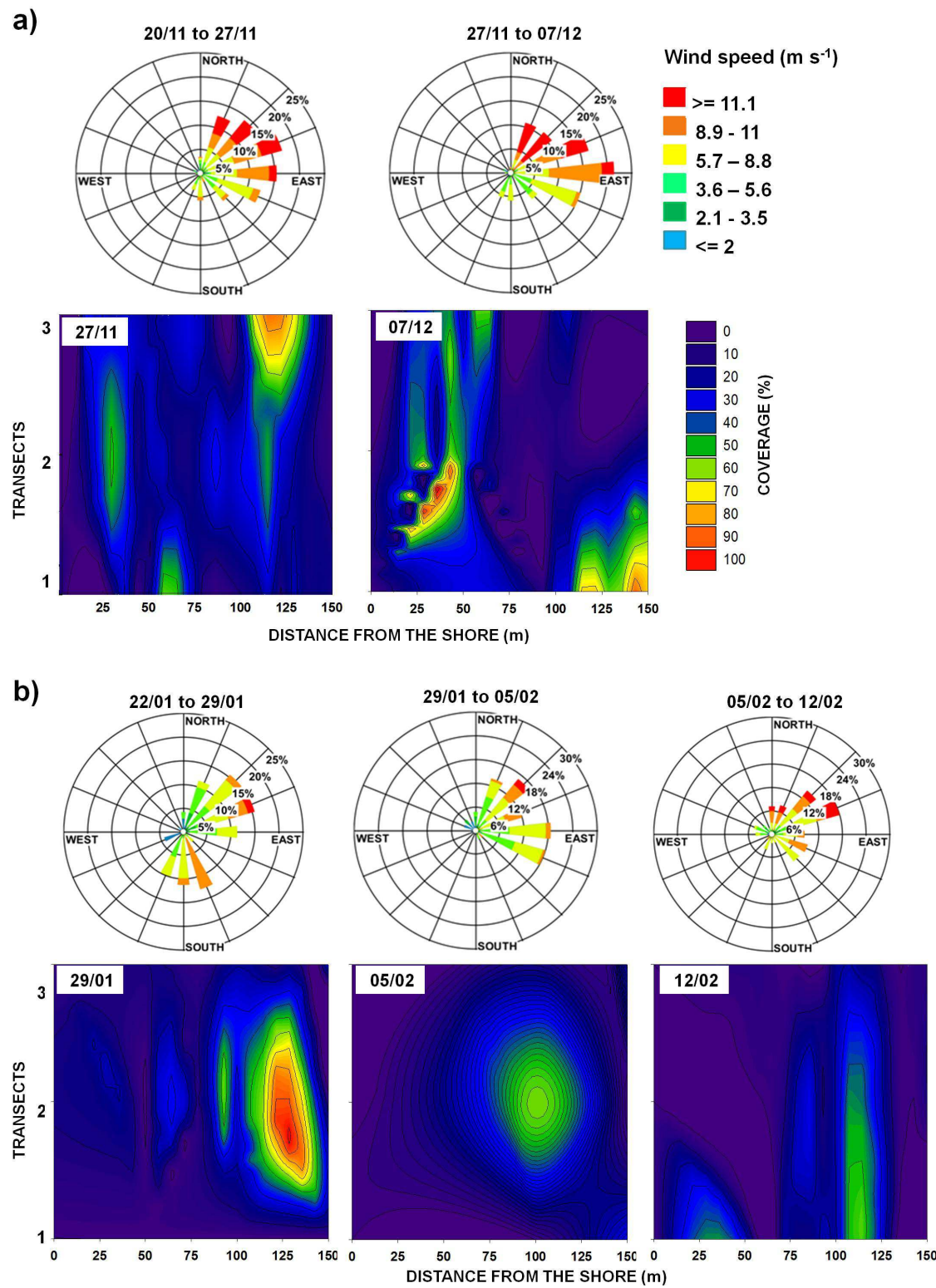


Figure 9



Apêndice 2

Esse apêndice refere-se ao artigo intitulado “Dynamics of estuarine drift macroalgae: growth cycles and contributions to sediments of shallow areas” submetido para análise no periódico *Marine Ecology Progress Series*.

Dynamics of estuarine drift macroalgae: growth cycles and contributions to sediments of shallow areas

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Running page head: Macroalgal contributions to sedimentary organic matter

ABSTRACT

Large accumulations of opportunistic green macroalgae represent either a sink and a source of nutrients in the water column and sediments, potentially leading to self-regenerating blooms in eutrophic areas. We investigated the contributions of drift macroalgae blooms to sedimentary organic matter considering their natural patterns of abundance and their driving factors. The hydrological and meteorological conditions determining the occurrence, magnitude and persistence of drift macroalgae blooms, along with macroalgal biomass contributions to total organic carbon and total nitrogen in the sediments, were monitored in a two-years field campaign in estuarine shallow bays of the Patos Lagoon estuary (southern Brazil) under different wind exposure. Our results showed that effects of a high nutrient availability for the onset of macroalgal blooms were modulated by variations in freshwater discharges and associated changes in water retention and physico-chemical parameters. Once established, blooms magnitude and persistence were positively affected by onshore wind-driven waves and currents, with largest accumulations in the most exposed stations representing substantial stocks of nutrients within the system. Regardless spatio-temporal differences in the magnitude and persistence of accumulations, no significant increases in sediment TOC and TN were observed. Isotopic analysis revealed overall low contributions of macroalgal biomass to the sedimentary organic matter, indicating that larger wind-driven biomass accumulations were not translated into higher incorporation within sediments. Therefore, the present study highlights the influence of hydrodynamics conditions on macroalgal blooms feedbacks on nutrient cycling with possible effects on long-term nutrients balance within estuarine systems.

Keywords: macroalgal blooms, hydrology, advective transport, plant bound nutrients, sedimentary organic matter.

INTRODUCTION

In shallow estuarine areas worldwide, an increasing trend in the frequency of blooms of fast growing ephemeral macroalgae has been observed (Lyons et al. 2014). Blooms of macroalgae such as the species of the genera *Ulva* can outcompete other autotrophs such as seagrass and microphytobenthos for nutrients and light, causing shifts in primary producer dominance (Valiela et al. 1997). While nutrient enrichment is recognized as a primary cause of ephemeral macroalgae excessive growth, the onset and magnitude of the bloom may be triggered by the right combination of water physico-chemical and hydrodynamic conditions. In shallow estuarine waters, the growth of macroalgae are controlled by the availability of light at the bottom, water temperature and salinity, but the conditions for bloom formation depends on water residence time, which enable (or not) the retention and accumulation of the biomass produced (Martins et al. 2001, McGlathery et al. 2007).

Most green tides are composed of macroalgal mats which are detached from the substrate due to waves and currents action (hereafter drifting macroalgae). Due to their easy transportation as part of the bedload or as floating mats, drifting macroalgae blooms can be quite unstable, presenting unpredictable patterns of spatial distribution (Berglund et al. 2003, Flindt et al. 2004, Kennison & Fong 2013). In this context, studies have called into attention the importance of physical processes such as wind-driven waves and currents determining the occurrence and magnitude of the accumulations of the macroalgal biomass produced in shallow bays and estuarine shoals

(Pihl et al. 1999, Berglund et al. 2003, Liu et al. 2013). In exposed areas, larger drift macroalgal blooms tend to occur resulting from the accumulation of locally produced biomass as well as from mats drifting in from the surrounding areas (e.g. Berglund et al 2003, Liu et al 2013).

Once established, macroalgae blooms play a major role in nutrient cycling acting initially as a sink of nutrient. Opportunistic macroalgae species such as *Ulva* exhibit high uptake efficiency of dissolved organic and inorganic nutrients from the water column and sediments (Tyler et al. 2003, Cohen and Fong 2004, Fong et al. 2004). However, due to their “boom and bust” life cycles and high tissue turnover rates ranging from days to a few weeks, drift macroalgae blooms do not represent a long-term nutrient reservoir (McGlathery et al. 2007). During biomass active growth, collapse and senescence, the assimilated nutrients are rapidly recycled to the water column as dissolved (DON) and particulate organic nitrogen (PON), where they are partly processed by the microbial loop, mineralized or transferred to higher trophic levels through grazing (Tyler et al. 2001, Fong et al. 2004).

Although a large bulk of the algal tissue is decomposed in the water column, some material can also become incorporated into the sediments during bloom collapse, increasing the organic matter content (Pihl et al. 1999, Corzo et al 2009, Hardison et al. 2010, Gao et al. 2013). The increase in sediment organic matter may be transitory as dead macroalgae are rapidly decomposed due to the lability of their tissues (Banta et al. 2004). During decomposition pore water nutrients are raised through bacterial activity, promoting subsequent effluxes of nutrient across the sediment-water interface (Hardison et al. 2010, García-Robledo et al. 2008, 2013, Gao et al. 2013). In this context, the rapid regeneration of nutrients may help initiate further growth of macroalgae, that along with

mats continually drifting in from the surrounding area help sustain the large accumulations of ephemeral macroalgae that occur in shallow areas. This self-regeneration mechanism would set the reoccurrence of macroalgal blooms and lead to the disruption of local biogeochemical cycles in estuarine shallow areas.

To address the issue of self-regenerating drift macroalgal blooms, most studies have focused on macroalgal nutrient removal and regeneration in the water column. Recently, attention has turned to the sedimentary processes that link nutrient uptake in the water column to remineralisation and release in the sediment during biomass deposition and senescence onto the substrate. Most of these studies have been conducted in micro- and mesocosm experiments, over short spatial and temporal scales (e.g. Corzo et al. 2009, Hardison et al. 2010). Consequently, studies measuring the environmental factors that affect both the spatio-temporal patterns of drift macroalgal blooms and their subsequent contributions to sedimentary organic matter on a field scale have not been considered. This knowledge gap, concerning the potential feedbacks of green tides on estuarine biogeochemical cycles, provides a limit to our current understanding of the processes contributing to drift macroalgae occurrence and fate.

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 aquatic vegetation (SAV) and increases in the abundance of drift macroalgae (Odebrecht et al. 2010). Shifts to macroalgae-dominated states have been mainly related to changes in hydrological conditions, but may be also associated with the increasing trend of inorganic nitrogen concentrations in the water column (e.g. Haraguchi et al. 2015) and in the sediment pore-water (e.g. Baumgarten & Niencheski 2010). Local biogeochemical studies have shown that sediments play an important role in nutrient

cycling of the PLE, recycling a significant portion of primary production and subsequently providing inorganic nutrients to the water column (Niencheski & Jahnke 2002). But the role of drift macroalgae on estuarine nutrient cycling is still poorly understood. The frequent occurrence of drift macroalgae algae in PLE and its variability in time and space is an ideal setting for investigating the conditions under which those ephemeral algae are incorporated into the sediment, potentially leading to the self-regeneration processes.

In the present study, we investigated the drivers of temporal and spatial variability of the occurrence and magnitude of drift macroalgae blooms in estuarine shallow areas based on two main hypotheses. First, we hypothesized that while drift macroalgae blooms will result from the coupling of factors affecting both drifting biomass production and retention in the system, the spatial variability in their magnitude will be associated to different scenarios of wind exposure. Second, using the natural occurrence of drift macroalgal blooms at the study area, we tested the hypothesis that drift macroalgae are an important source of sedimentary organic matter. We suggest that, while the hydrological factors may act more uniformly on generating macroalgal blooms, contribution of macroalgae to the sediments may be proportional to the magnitude of macroalgal blooms (i.e. biomass and coverage).

METHODS

Study site

The warm temperate Patos Lagoon situated in southern Brazil is the largest choked coastal lagoon in the world (10,000 km²) (Fig. 1a) (Kjerfve 1986). Water exchange between the estuary and the South Atlantic Ocean occurs through a narrow

and deep channel (0.5-1 km wide, 14-18 m depth), maintained for navigation. The region is influenced by a microtidal regime (~ 0.47 m) and tidal effects are attenuated within the lagoon. With a large catchment area ($200,000 \text{ km}^2$), the local hydrology is driven mainly by rainfall, freshwater discharge and wind circulation, which are also the main factors affecting water level and salinity. The prevailing NE winds (dominant in austral spring and summer) and SW winds (dominant in autumn and winter) force, respectively, the outflow and inflow of water between the estuary and the coastal region. During flood periods the PLE becomes a river-dominated system, remaining fresh for several months (Möller et al. 2001). Under strong southerly winds, associated to the passage of atmospheric fronts, larger saltwater intrusions occur, blocking freshwater outflow from the PLE, a process that increases water retention within the estuary (Odebrecht et al. 2015). Therefore, marine and euhaline conditions usually occur in summer/autumn, while freshwater and oligohaline conditions prevail in winter/spring. Nonetheless, short-term salinity oscillations are observed and the PLE may alternate between fresh-oligohaline, over mesohaline to marine in the time scale of hours to days (Abreu et al. 2010). The estuary is eutrophic, due to both large natural and anthropogenic sources, with nutrient concentrations in the water column ranging from ~ 0.1 to $40 \text{ } \mu\text{M NO}_2^- + \text{NO}_3^-$; ~ 0.1 to $40 \text{ } \mu\text{M NH}_4^+$; and ~ 0.1 to $8.7 \text{ } \mu\text{M PO}_4^{3-}$. Sediment pore water nutrients range from ~ 33.6 to $710.7 \text{ } \mu\text{M NH}_4^+$ and from ~ 0.1 to $14.6 \text{ } \mu\text{M PO}_4^{3-}$ (Baumgarten & Niencheski 2010, Odebrecht *et al.* 2010).

About 75% of the estuarine area is comprised of shallow shoals (<2 m depth) covered in unconsolidated sediments, surrounded by salt and brackish-marshes and suitable for the growth of submerged aquatic vegetation (SAV). SAV is dominated by the widgeon grass *Ruppia maritima*, the oligohaline *Zannichellia palustris*, and several

attached or free-floating macroalgae species of *Ulva*, *Cladophora*, *Rhizoclonium* and *Polysiphonia* (Copertino & Seeliger 2010). For the present study, different scenarios of exposure to local winds, here represented by the action of the prevailing southwest (SW) and northeast (NE) winds, were investigated. Within each wind direction, two stations were selected according to an a priori contrast between low (hereafter shelter-NE and shelter-SW) and moderate-high exposure (exp-NE and exp-SW; Fig. 1). Wind exposures of stations were determined according to their wave fetch index (Burrows et al. 2008; Fig. 1 highlighted).

Physico-chemical water parameters

Regional and local hydrological data were provided by the Brazilian National Water Agency (<http://www.hidroweb.ana.gov.br>) or locally obtained during the studied period. The sum of the flow of the three main rivers was assumed to be a *proxy* of the total Patos Lagoon freshwater discharge (Möller et al. 2001). Estuarine water level (fixed ruler) was obtained daily distant approximately 3 km from the studied stations within the Brazilian Long-Term Ecological Research Program (<http://www.peld.furg.br/index.php/metadados>). Data on hourly wind speed and direction, obtained at the mouth of the Patos Lagoon estuary, were provided by the Rio Grande Maritime Pilotage (<http://www.rgpilots.com.br/>).

The parameters water salinity, temperature, turbidity (Multiparameter HI9829, Hanna Instruments, USA) and Secchi depth were monitored weekly in each location from August 2012 until August 2014. Water samples ($N = 3$) were collected monthly from each station for analysis of dissolved inorganic nutrients (NH_4^+ , NO_2^- , NO_3^- and

PO_4^{3-}). Underwater Photosynthetic Active Radiation (PAR) at the bottom (I_z) was estimated according to Lambert-Beer's equation:

$$I_z = I_0 * e^{-kz} \quad (1)$$

where I_0 is the PAR at the surface, k is light extinction coefficient ($k = 1.7 * \text{secchi}^{-0.85}$; Costa & Seeliger 1989) and z is depth. We assumed that PAR is 50% of overall available energy for photosynthesis and a 5% decrease in incident light at the water surface (Silva & Asmus 2001). Data on hourly surface radiation in the study area was provided by the Brazilian National Institute of Meteorology (<http://www.inmet.gov.br/portal>).

Macroalgal and sediment sampling

Sampling was conducted monthly from August 2012 to August 2014. In each location, macroalgal cover was measured along three 200 m transects laid out perpendicular to the coast, distant 100 m apart from each other, covering approximately 40,000 m² of surveyed area. Drift macroalgae coverage was estimated by visual census, within four 0.25 m² quadrats, at each 50 m intervals ($N = 20$ per transect). Macroalgae biomass was sampled in ten points where coverage was 100% with a PVC cylinder (176.62 cm²). Samples of the surface sediment were collected with a cylinder core (diameter of 8 cm, 3 cm depth, $N = 3$) below macroalgal mats within the transects area and placed in amber glass vials. Macroalgal and sediment samples were transported in ice to the laboratory and prepared within the next 1-2 days.

In the laboratory, macroalgal biomass was cleaned from associated fauna and detritus, rinsed with tap and distilled water and the dry weight (48h at 60°C) was determined. Subsamples (~ 100 g of fresh weight) were fixed (4% formalin solution) for

taxonomical identification. The average biomass (g dry weight per m²) for each station were estimate by multiplying the punctual biomass values by the mean percentage cover of the survey area, estimated by visual census (N = 60 quadrats). Macroalgal biomass and sediment samples were dried (48h at 60°C) and grounded for analysis of total organic carbon (TOC), total nitrogen (TN) and their isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Elemental and isotopic analysis

The sediment samples were analyzed for TOC, TN, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in triplicate for sheltered stations (shelter NE and shelter-SW) from August 2012 up to August 2013 and for exposed ones (exp-NE and exp-SW) up to August 2014. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the macroalgae were analyzed only for 2014. Elemental and isotopic analyses were performed using an automatic elemental analyzer (2400 Series II CHNS/O System, Perkin-Elmer, USA) and a mass spectrometer (Stable Isotope Laboratory, University of Georgia, USA), respectively. Previous studies in Patos Lagoon have shown the sediments to contain insignificant sedimentary calcium carbonate. Claudino et al. (2013) tested the need for decarbonation treatment of Patos lagoon sediments and found no difference in $\delta^{13}\text{C}$ value between acidified and non-acidified samples. Therefore, sediment samples of the present study were not previously acidified. The quality control for the elemental analysis in macroalgal tissue was conducted using the certificate reference material acetanilide and the sediment MESS-3 (National Research Council Canada). Percent TOC and TN content in macroalgal tissue and sediment were converted to molar TOC:TN ratios and isotope ratios were expressed as parts per thousand (‰). The Pee Dee Belemnite was used as the standard for carbon, and

atmospheric nitrogen for nitrogen. Based on the standard deviation of the internal standard replicates, the analytical precision for carbon and nitrogen content and their isotopes were ± 0.16 , ± 0.05 , ± 0.08 and ± 0.12 , respectively.

Data Analysis

Differences in mean values of biotic and abiotic parameters were compared among the seasons, which were: austral spring (September to November), summer (December to February), autumn (March to May) and winter (June to August).

Variations in water salinity have been used as a *proxy* of water retention time in the study area (e.g. Odebrecht et al. 2015). Similarly, we used average salinity and variability (i.e. coefficient of variation, CV) per season as a *proxy* of water retention within the estuary. In general, periods of higher water retention were identified by increases in salinity associated with low CV, which reflected, respectively, transitions from periods of outflow to inflow and the persistence of meso/euhaline waters in the estuary (Odebrecht et al. 2015).

Intercorrelations among the hydrological parameters freshwater discharge, level, salinity (mean and CV), turbidity, irradiance, temperature, NH_4^+ , NO_2^- and NO_3^- (expressed as dissolved inorganic nitrogen, DIN) and PO_4^{3-} were analyzed through Principal Component Analysis (PCA). Since no significant differences were found among locations in water physical-chemical parameters (level, salinity, turbidity, temperature and nutrients), the abiotic data was averaged among all stations. All variables except irradiance were log-transformed to achieve a normal distribution. Hydrological parameters were grouped along PCA axis according to their eigenvector coefficients. This procedure provided ecological meanings for the PCA components and allowed data reduction (see section Results for more details). The relationship between

macroalgal biomass and hydrological parameters were thus investigated through a Multiple Regression Analysis using eigenvalues of PC1, PC2 and PC3 as independent variables which explained, respectively, 47.10%, 17.40% and 15.21% of hydrological data variability. Residuals were checked for data homoscedasticity and normality. Spatial patterns of drift macroalgae biomass distribution among stations were analyzed in relation to local wind direction, frequency and speed.

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 MixSIAR model provides estimates the relative contributions of distinct sources to a mixture even in undetermined systems taking into account the uncertainty associated to 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. Sedimentary organic matter sources were suspended particulate organic matter (SPOM), drift macroalgae, the euryhaline grass *R. maritima* and the saltmarsh plants *Spartina densiflora* (C4 plant) and *Scirpus maritimus* and *Scirpus olney* (C3 plants). Seasonal elemental and isotopic values for *R. maritima*, *S. densiflora*, *S. maritimus*, *S. olney* and SPOM in the study area were obtained from Claudino and collaborators (2013) (see Table S1). *R. maritima* and *S. densiflora* were pooled in as a single source due to similarities in their isotopic signatures. TOC and NT was informed for each source. 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). Organic matter sources posterior distributions were calculated using long Markov Chain Monte Carlo chains (chain length = 1.000.000,

burn-in = 700.000, thin = 300) and convergence was checked through diagnostics tests (see Stock & Semmens 2013 for more details).

RESULTS

Temporal and spatial variation in hydrological parameters and dissolved nutrients

The hydrological parameters water discharge, retention, level, salinity, turbidity and irradiance showed a strong seasonal trend throughout the studied period (Fig. 2a,b, Table 1) and were highly correlated along the first principal component (Table 2). PC1 reflected the associated changes in water physico-chemical parameters related to water retention, therefore representing the balance between outflow (i.e. freshwater discharge) and inflow (i.e. saltwater intrusion) in the PLE. Periods of high freshwater discharge, predominantly in winter and spring, were related to increases in water level and turbidity, and decreases in salinity, underwater irradiance and water retention (i.e. indicated by high values of salinity CV). Water temperature varied seasonally with the lowest values during winter and was positively correlated along PC2 (Fig. 2c, Table 2).

In general, nutrient concentration in water column showed no consistent seasonal and spatial trend (Figs 3a,b,c). Higher concentrations of $\text{NO}_2^- + \text{NO}_3^-$ were observed during the spring 2012 (mainly October and November) and autumn and winter of 2013 and 2014 (April to July, Fig. 3a). Variability in PO_4^{3-} concentrations were less pronounced though an increasing trend toward autumn and winter 2014 was observed (Fig. 3c). Peaks of NH_4^+ were found mainly during spring 2012 (Fig. 3b). Average nutrient concentrations among all stations increased along PC3 (Table 2).

Temporal and spatial dynamics of drift macroalgae blooms

Drift macroalgal biomass were composed by mixed mats of mainly *Ulva clathrata*, *U. intestinalis* and *Rhizoclonium riparium*, which showed annual and interannual variability. Peaks of biomass occurred during early summer and autumn 2013 and autumn and early winter 2014 (Fig. 4). Average biomass values across all stations ranged from 0.38 g DW m⁻² (winter, August 2012) to 566 g DW m⁻² (winter, June 2014) and, overall, higher mean biomass values were found during 2014 (223 g DW m⁻²) compared to 2012-2013 (43 g DW m⁻²). Results of Regression Analysis showed that PC1, representing freshwater discharges and associated changes in water retention and physico-chemical parameters, was the best predictor of the average values of drift macroalgal biomass values ($R^2 = 0.67$, $F_{7,12} = 3.55$, $p = 0.02$). On the other hand, no significant effects of water temperature (here represented by PC2) or nutrient concentrations (PC3) on drift macroalgal abundance were detected. Macroalgal tissue TOC and TN presented slight spatial differences with more dissimilar values in the station exp-SW (Fig. 5a,b). Mean values for C content varied from 25% (station exp-SE, April 2014) to 41.6% (exp-NE, May 2014) and N content ranged from 0.84% (exp-SW, April 2014) to 4.12% (exp-NE, May 2014). Temporal variations in C:N ratios among stations reflected variations in drift macroalgal abundance, with peaks during bloom (Fig. 5c).

The results showed a marked spatial variability in the occurrence and magnitude of drift macroalgal blooms. The most exposed stations to the prevailing winds (i.e. exp-NE and exp-SW) showed the highest values of biomass throughout the studied period with algal accumulations forming persistent, extensive patches covering up to 90% of the area surveyed (Fig. 4 and 6). Conversely, sheltered stations (shelter-NE and shelter-SW) showed lower values of biomass accumulation deposited onto the substrate as

scattered thin patches. Temporal patterns of biomass accumulation at exposed stations were in accordance with seasonal variations in local wind action (Fig. 7). The largest algal blooms at the exp-SW station occurred during autumn (March to May) 2013 and 2014, periods characterized by an increasing frequency and intensity of winds from the S-W quadrant. For the exp-NE station, large algal blooms occurred mainly in summer 2013 (December to February) and early winter 2014 (June) under the predominance of moderate to strong N to E winds.

Contribution of drift macroalgal biomass to sediment organic matter

Sediment isotopic values showed no clear seasonal trend and no consistent pattern in spatial variability (Fig. S1). The isotopic signature of the drift macroalgae varied from -13.5 to -17.5‰ for $\delta^{13}\text{C}$ and 7.4 to 8.2‰ for $\delta^{15}\text{N}$ (Table S1). Mixing model results showed that drift macroalgae had a much lower contribution ($3.56 \pm 2.96\%$; mean $\pm$ SD across all stations and seasons) as a source of organic matter to the sediment compared to other sources such as SPOM ($54.14 \pm 29.40\%$), *S. densiflora* and *R. maritima* ($30.24 \pm 19.34\%$) and C3 plants ($11.68 \pm 11.10\%$; Fig. 8 and S2). Furthermore, algal biomass contributions to the sediment promoted no significant increases in sediment TOC and/or TN content (Fig. S1).

In spite of the large credible intervals, highest average values of contributions of macroalgae to the sediment organic matter across all stations occurred during summer ($4.5 \pm 0.36\%$) and winter 2013 ($8 \pm 2\%$), and autumn ($6.4 \pm 2.4\%$) and winter 2014 ($4 \pm 2.26\%$), periods of highest macroalgal biomass accumulation (Fig. 4 and 8a). The only exception to this pattern was winter 2013, a post-bloom period. However, a spatio-temporal decoupling between algal contributions to the sediments and the observed

patterns of drift macroalgae abundance were observed. Algal contributions were not proportional to the seasonal and interannual variations in algal blooms magnitude and persistence observed. In addition, the largest biomass blooms, observed at exposed stations, were not translated into the highest values of organic matter incorporated into the sediments. Indeed, the values of algal contribution to sedimentary organic matter were not significantly different among exposed and sheltered stations.

DISCUSSION

Although the interaction between blooms and the underlying sediment have been studied in the field using small enclosures (e.g. Corzo et al. 2009), to our knowledge, no study has explicitly investigated the role of drift macroalgae blooms as a source of sedimentary organic matter taking into account natural patterns of their abundance and their driving factors (but see Pihl et al. 1999). Our results showed that interactive effects of hydrological and meteorological factors created favorable conditions for the onset of large drift macroalgal accumulations in shallow areas. Nonetheless, regardless their magnitude and persistence, macroalgal biomass had a minor contribution to the sediment organic matter pool, compared to other primary producers such as widgeon grass (*R. maritima*) and salt marsh plants. Therefore, our study highlights the importance in considering hydrodynamics forces, such as waves and currents, in the assessment of macroalgal blooms feedbacks on benthic nutrient regeneration.

Temporal and spatial patterns of drift macroalgae blooms

Blooms of drift macroalgae have been documented previously at both seasonal and interannual scale at the PLE (e.g. Lanari & Copertino in review) following floods-

driven severe reductions of meadows of the widgeon grass *R. maritima* (Odebrecht et al. 2010). Drift macroalgae biomass reported here, attaining peaks up to 2 kg DW m⁻² (i.e. station exp-SW Autumn 2014), are comparable to those seen in other coastal areas undergoing anthropogenic nutrient enrichments (e.g. Kamer et al. 2001, Martins et al. 2001). Our results support suggested ongoing transitions to opportunistic macroalgae-dominated periods in the last decade simultaneous to increases in total nitrogen in the study area (Haraguchi et al. 2015, Lanari & Copertino in press).

Although opportunistic macroalgae blooms is a worldwide commonly reported symptom of eutrophication (Teichberg et al. 2010, Lyons et al. 2014), we did not observe a direct relationship between monthly averages values of algal biomass and nutrient concentrations in the water column (i.e. PC2, Figs 3 and 4). This fact may indicate that monthly sampling is not representative of nutrient availability in the system once concentrations in the water column may vary at shorter time scales. Fast-growing species such as *Ulva* can also quickly take advantage of nutrient pulses and/or high nutrient concentrations through rapid nitrogen uptake and decoupling between uptake and growth (Fong et al. 2004). Consequently, tissue nutrient content is a better proxy of nutrient availability for macroalgal growth than nutrient concentrations in the water column (Fujita 1985). Temporal variations of nutrient content in macroalgal tissue among sites agreed with the spatio-temporal dynamics of drift macroalgae blooms (Fig. 4 and 5). At the beginning of the growing seasons (i.e. late spring 2012 and autumn 2014), values of TN content around 4% were above critical values for growth (i.e. 2%, Fujita 1985) and similar to those reported in locations experiencing nutrient enrichment worldwide (e.g. Teichberg et al. 2010). Reductions in tissue TN and increases in C:N ratios were observed only after blooms establishment and possibly

reflected nitrogen use during biomass build-up phases. Thus, our results suggest sufficient nitrogen availability to trigger large drift macroalgae blooms at the study area

In nitrogen-enriched systems, P supply may limit the growth rates of bloom-forming macroalgae (Teichberg et al. 2010). Accordingly, largest macroalgal blooms during autumn and winter 2014 were simultaneous to raised concentrations of PO_4^{3-} in this period (Fig. 3c and 4), which likely alleviated already suggested P-limitations for primary producers at the study during drought periods (Odebrecht et al. 2005, Lanari & Copertino in review). However, P content in macroalgal tissue were not analysed and more studies assessing both nitrogen and phosphorus content in macroalgal biomass are needed to elucidate this question.

Effects of increased water nutrient concentrations in shallow areas are further mediated by local hydrodynamics since water retention within a location regulates the time exposure of the macroalgae to water column nutrients (Martins et al. 2001, McGlathery et al 2007). In Patos Lagoon, annual mean values of chlorophyll a decreases significantly with mean values of rainfall in its drainage basis above 1500 mm per year; beyond this threshold, high freshwater discharges promote biomass washing out of the estuary, inhibiting phytoplankton blooms even under high nutrient concentrations in the water column (Abreu et al. 2010). Similarly, drift macroalgae did not accumulate during peaks of DIN and PO_4^{3-} associated to the high freshwater discharges observed in spring 2012, late winter and spring 2013 and mid-winter 2014 (Fig. 2a and 3). In these periods, increased freshwater discharges blocked saltwater intrusions (i.e. low salinity values, Fig. 3a) and reduced water retention within the lagoon (i.e. high values of salinity CV, Table 1), which may hamper macroalgal blooms

through the advective transport of biomass to adjacent and/or deeper areas (Martins et al. 2001).

In contrast, low to moderate freshwater discharges and subsequent increased saltwater intrusions and water retention during summer/autumn 2013 and autumn/early winter 2014 (Fig. 2) reduce currents speeds ($1\text{--}25\text{ cm s}^{-1}$, Fernandes 2001) below thresholds for macroalgal advective transport (i.e., $\sim 10\text{ cm s}^{-1}$; Flindt et al. 2004), maintaining drift macroalgal biomass in the system. Co-occurring increased water salinity, temperature and irradiance may enhance growth rates of opportunistic macroalgae such as *Ulva* and *Rhizoclonium* species, leading to the onset of large drift macroalgae blooms (Martins et al. 1999, Taylor et al. 2001). Therefore, while local hydrodynamics is the key factor setting annual and interannual patterns of occurrence and persistence of algal blooms, associated changes in water physico-chemical parameters will set their magnitude.

Effects of wind action set a marked spatial variability in the timing and magnitude of drift macroalgal blooms. Largest biomass accumulations were detected in the most exposed stations (i.e. exp-NE and SW, Fig. 4) and likely resulted from onshore wind-driven waves and currents promoting the collection of locally produced biomass and of mats imported through advective transport from surrounding areas (Berglund et al. 2003, Liu et al 2013). Thus macroalgae may accumulate away from the areas that represented their nutrient sources and recruitment (Pihl et al. 1999, Kennison & Fong 2013). Largest macroalgal blooms in exposed areas can represent accumulations of nutrient-replete biomass, representing substantial stocks of nutrients within the system (Rossi 2007). For instance, in autumn 2014 mean macroalgal N content was 2.09% of dry weight in the exp-SW station. Given that the mean macroalgal biomass across

stations was 982 g DW m^{-2} , this represents a N store of 0.18 tonnes of N per hectare. Thus, in a nutrient-replete system such as the PLE, drift biomass can play a major role as a sink of nutrients slowing their seaward transport and increasing their retention within the system.

Contribution of drift macroalgae to the sediment C and N

Although increases of sediment C and N content can result from macroalgal biomass depositions (Pihl et al. 1999, Corzo et al. 2009, Hardison *et al.* 2010), our results did not support these findings but is in accordance with the results of other experimental set-ups with opportunistic macroalga (e.g. Sundbäck et al. 1990, García-Robledo & Corzo 2011). During drift macroalgae blooms, no significant increases in sediment TOC and TN were observed, regardless the significant differences in the magnitude and spatial patterns of biomass accumulations among stations.

Many factors may have resulted in transitory increases in sedimentary organic matter of a few days to a few weeks that cannot be detected at the monthly time-scale adopted in our study (Rossi 2007, García-Robledo et al. 2008). Due to the fast turnover of opportunistic macroalgae detritus, the senescing biomass can be quickly recycled through bacterial assimilation, resulting in effluxes of ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) across the sediment-water interface (García-Robledo et al. 2008, 2013). In this process, O_2 concentration in the water column influences the biogeochemical characteristics of sediments (Middelburg & Lewin 2009). Under the influence of the high wind action observed in shallow areas of the PLE, the promotion of oxic conditions in the water-sediment interface may have enhanced microbial mineralization of organic matter, increasing the lability of elements in porewater and

transport mechanisms that induce their transfer to the water column (Rigaud et al., 2013). Nutrients released from sediment can be assimilated by microphytobenthos (Hardison et al. 2010), and subsequently consumed by surface deposit feeders transferring nutrient from the sediment to secondary consumers (Rossi et al. 2007). Although in our study the persistent large biomass accumulations in the exposed stations occurred as extensive dense mats which may outcompete microphytobenthos for light (Hardison et al. 2013).

Transitory small increases in sedimentary organic matter ranging from 1.7% to 14% for C and 13.5% up to 16% for N have been observed during experimental additions of low algal biomass to sediments (e.g. $\sim 40 \text{ g DW m}^{-2}$, Rossi et al. 2007; 220 g DW m^{-2} , García-Robledo et al. 2008), in which the values were similar to the ones found here in the sheltered stations. At higher levels of biomass accumulations, such as the ones found in our exposed stations with dense mats (i.e. up to 1900 g DW m^{-2} and 572 g DW m^{-2} in stations exp-SW and exp-NE, respectively) covering up to 75 % of the surveyed areas (i.e. autumn and winter 2014, Fig. 6), shelf-shading on lower layers of algal mats may occur (Hardison et al. 2013). Subsequent algal biomass die-offs may cause anoxic conditions and the release of plant-bound nutrients in the sediment-water interface may occur (Hardison et al. 2010). It would be expected that biomass inputs would override sediment mineralization rates, therefore causing C and N accumulations to occur (Rossi 2007) and increasing the potential for algal biomass feedbacks on nutrient cycling in these areas.

No evidence of macroalgal C and N accumulation was observed. In fact, stable isotope analysis showed that overall the low TOC and TN contents in the sediments are explained by a low incorporation of algal biomass, regardless of the magnitude and

persistence of accumulations. Algal biomass incorporation within sediments relies on the existence of hydrodynamic conditions promoting the deposition and burial of macroalgal tissue (Hardison et al. 2010). We suggest that, although advective transport may promote large accumulations of drift mats in shallow shoals, the driving force behind their accumulation, i.e. wind action, may help sustain the growth of the bloom and also hamper its long-term deposition and burial in the sediment (Hardison et al. 2010). Studies have shown that the low erosion thresholds of drift mats (Flindt et al. 2004, Canal-Vergés et al. 2010) cause resuspension resulting in unstable deposition on the sediment surface at small spatial (i.e., 1 m²) and temporal scales (i.e., few hours to a few days; Biber 2007, Rasmussen et al. 2013). Accordingly, wind-driven weekly variations in the spatial patterns of drift macroalgae depositions are reported in the PLE (Lanari & Copertino, *in press*). The constant relocation of the drift algal mats in the most exposed stations may have inhibited biomass die-offs through shelf-shading and the maintenance of healthy drift biomass disable mass transfers to superficial sediments (Sundbäck et al. 1990, García-Robledo & Corzo 2011. Even when the bloom collapses, large amounts of macroalgal derived organic matter may be recycled in the water column, through higher levels of herbivory and detritivory under normal oxic conditions (Cébrian et al. 2014).

In this context, low contributions of drift macroalgae to secondary production reported in the study area (Claudino et al. 2013) suggest that our results may have important ecological implications on estuarine nutrients retention. Macroalgal accumulations can have negative impacts on benthic primary producers that promote long-term nutrients retention, such as microphytobenthos and seagrasses (Hauxwell et al. 2001, Hardison et al. 2013). The absence or loss of perennial primary producers (i.e.

seagrasses), which act to retain nutrients within the estuary or lagoon, may enhance the mass export of macroalgal-bound nutrient to adjacent coastal areas during high freshwater discharges (McGlathery et al. 2007). Although this process may alleviate possible deleterious impacts resulting from self-regenerating blooms, it may also generate system oligotrophication in a long-term (McGlathery et al. 2007, García-Robledo & Corzo 2011).

In conclusion, the present study highlights the importance of considering the environmental context when assessing the initiation, persistence and subsequent transport of macroalgae as well as the potential feedbacks of drift macroalgae blooms on estuarine nutrient cycling. Although sediment nutrient effluxes may trigger drift macroalgal blooms (Sundbäck et al. 2003), our results showed that new inputs of algal-derived fresh organic matter to sustain this process rely on local hydrodynamic conditions. The hydrodynamic forces in the Patos Lagoon drive advection of macroalgae from their recruitment areas and their accumulation in the shallow of exposed areas of the lagoon. These same hydrodynamic forces likely help sustain the accumulated material in the water column resulting in little incorporation within sediments. To determine the generality of these results more studies evaluating the effects of dynamic spatio-temporal scales of mats deposition on biomass incorporation within sediments are needed, preferably through additional tracers of sedimentary organic matter sources. Long-term monitoring, over shorter time intervals than adopted here, of the effects on algal-dominated phases on nutrient cycling may also provide insights on nutrient balance within estuarine or lagoon systems.

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FIGURES AND LEGENDS

Figure 1. Location of the Patos Lagoon estuary at southern Brazilian coastline and the mesomixohaline area of the estuary with coastal Wave Exposure Indexes highlighted. Stations are indicated as: (1) exp-SW, (2) exp-NE, (3) shelter-SW and (4) shelter-NE. Fetch values are given as the number of grid cells units (200 m each) adjacent to a point.

Figure 2. Variation of the hydrological parameters freshwater discharge, water level and salinity (a), water column turbidity, irradiance and pH (b) and temperature (c) from August 2012 to August 2014. Values are monthly means ($\pm$ SE) among all stations. W = Winter, Sp = Spring, S = Summer and A = Autumn.

Figure 3. Monthly variation of $\text{NO}_2^- + \text{NO}_3^-$ (a), NH_4^+ (b) and PO_4^{3-} (c) in the water column of the sampling stations between August 2012 to August 2014. Values are means ($\pm$ SE, N = 3). W = Winter, Sp = Spring, S = Summer and A = Autumn.

Figure 4. Temporal variation of drift macroalgal biomass (mean $\pm$ SE) from August 2012 to August 2014 among stations. Areas represent the cumulative average values ($\pm$ SE) for each station. Grid lines separate different seasons. W = Winter, Sp = Spring, S = Summer and A = Autumn.

Figure 5. Monthly variation in total organic carbon, TOC (a), total nitrogen, TN (b) and C:N ratios in algal tissue of the sampling stations between August 2012 to August 2014. Values are means ($\pm$ SE, N = 3). W = Winter, Sp = Spring, S = Summer and A = Autumn.

Figure 6. Seasonal spatial patterns of drift biomass coverage for each station along transects during blooms periods. Coverage data were obtained at each 50 m (N = 4) along 200 m transects deployed 100 m apart. Bold and dotted lines represent 10% and 5% coverage intervals, respectively.

Figure 7. Wind roses showing the prevalent wind directions during Summer and Autumn 2013 and Autumn and Winter 2014. The length of the diamonds shows the percentage of hours that wind blew from a given direction. Different shades of gray within diamonds represent speed intervals.

Fig 8. Estimated contributions of drift macroalgae biomass (a), suspended particulate organic matter, POM (b), *Scirpus maritimus* and *S. olney*, C3 plants (c) and *Ruppia maritima* and *Spartina densiflora* (d) to sedimentary organic matter in different seasons

and sampling stations. Data are MixSIAR posterior probability means and $\pm$ 95% credible intervals. W = Winter, Sp = Spring, S = Summer and A = Autumn. Please note different y-scales.

Figure 1.

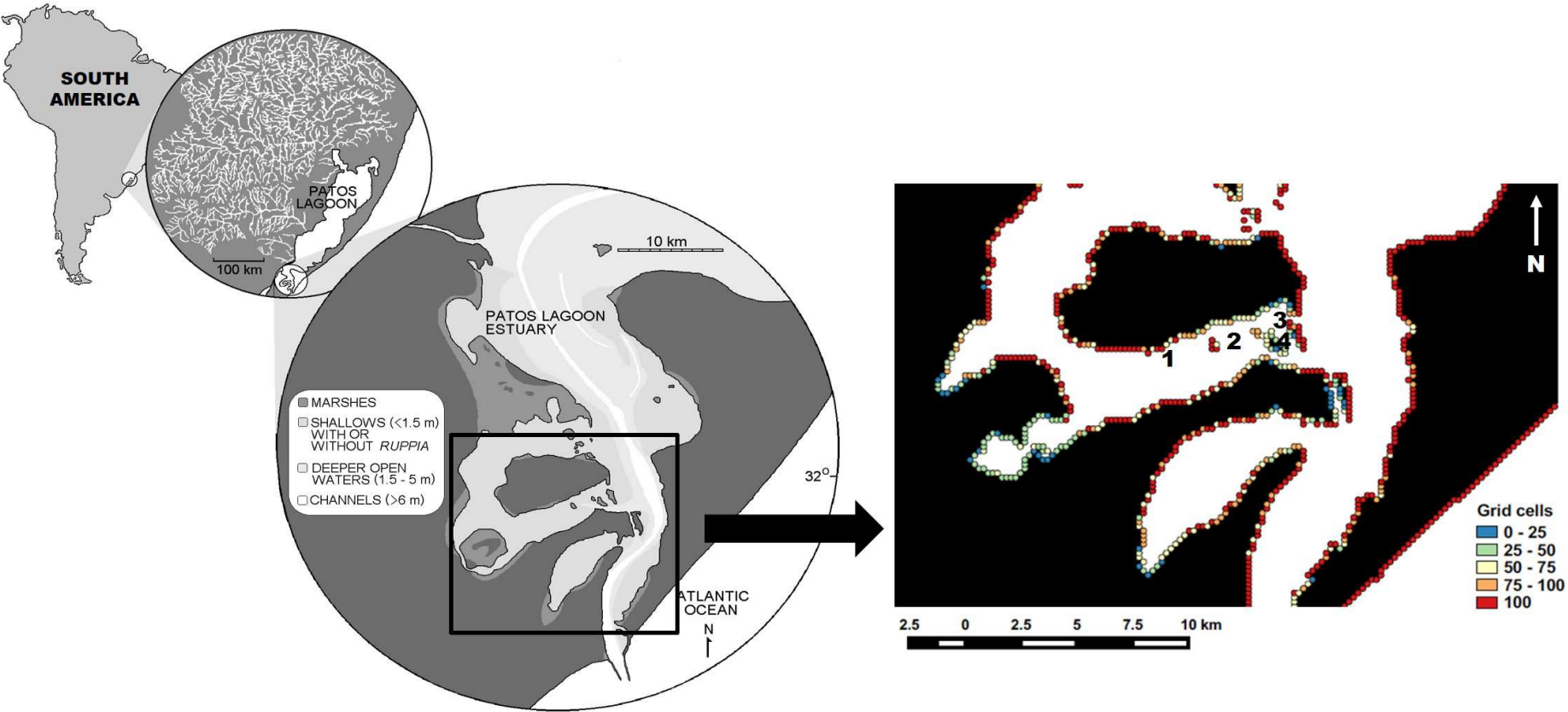


Figure 2.

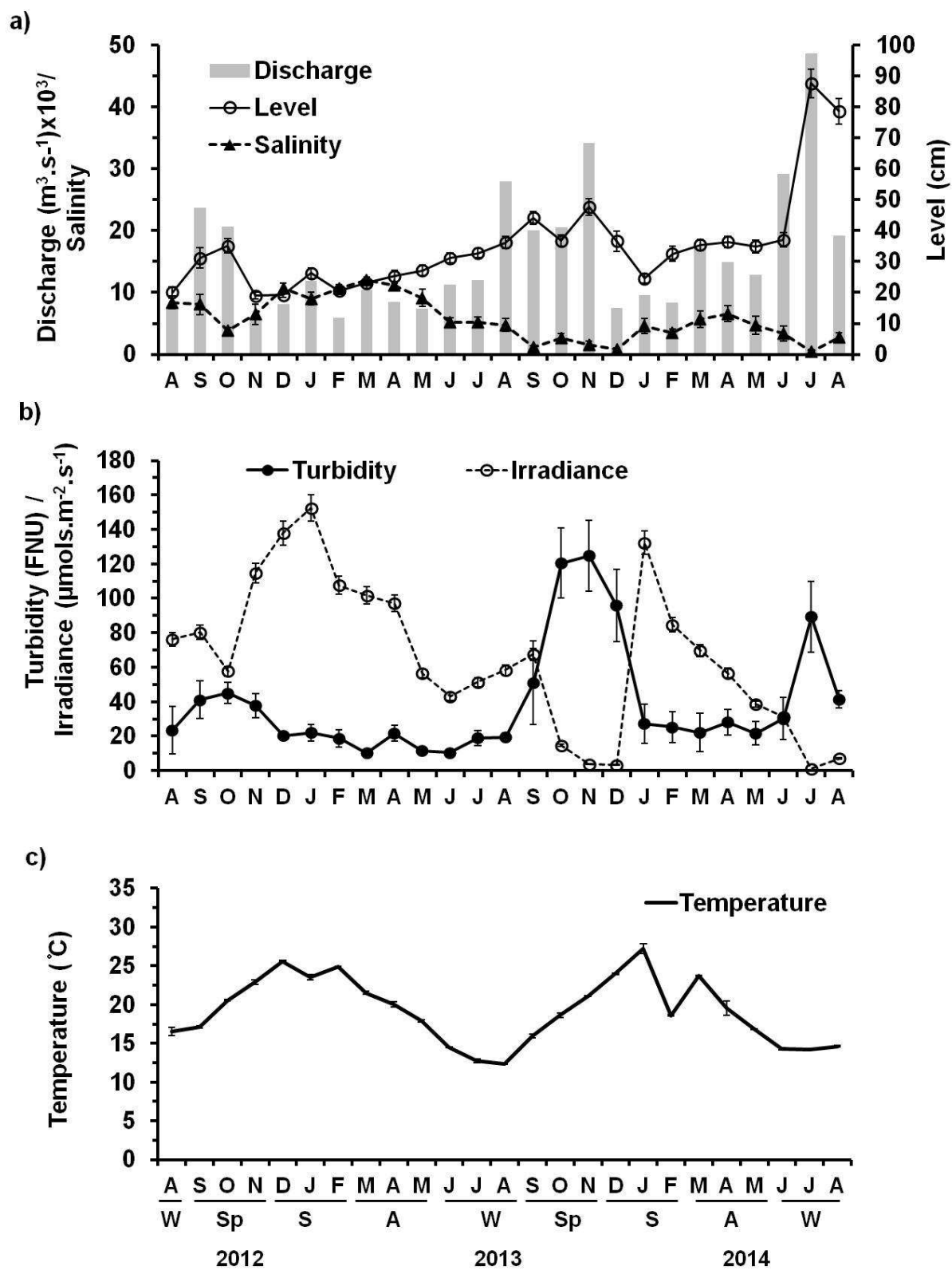


Figure 3.

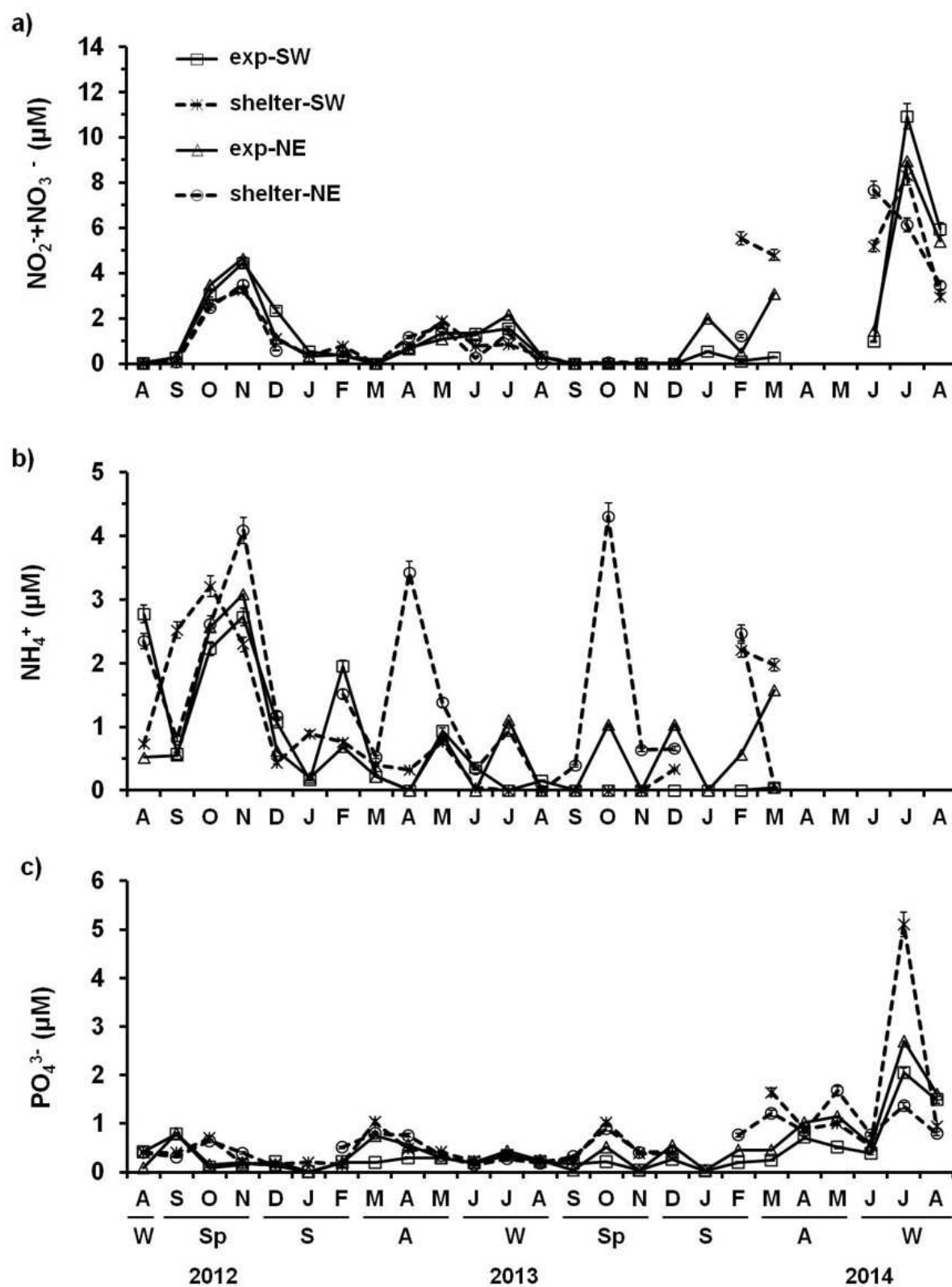


Figure 4.

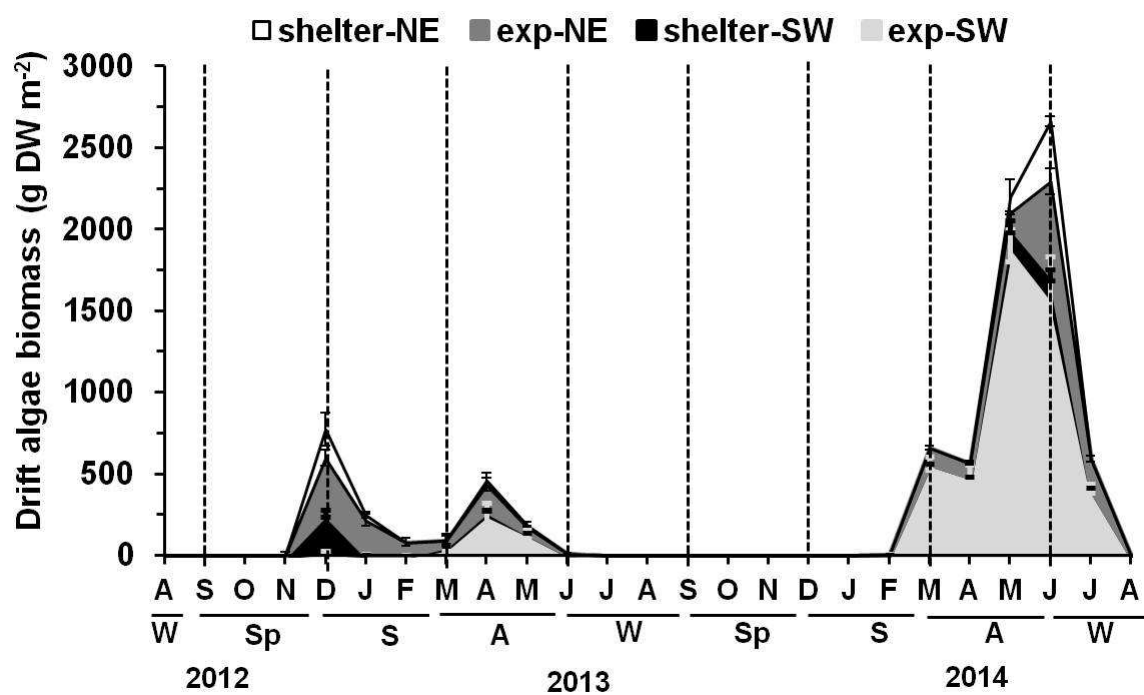


Figure 5.

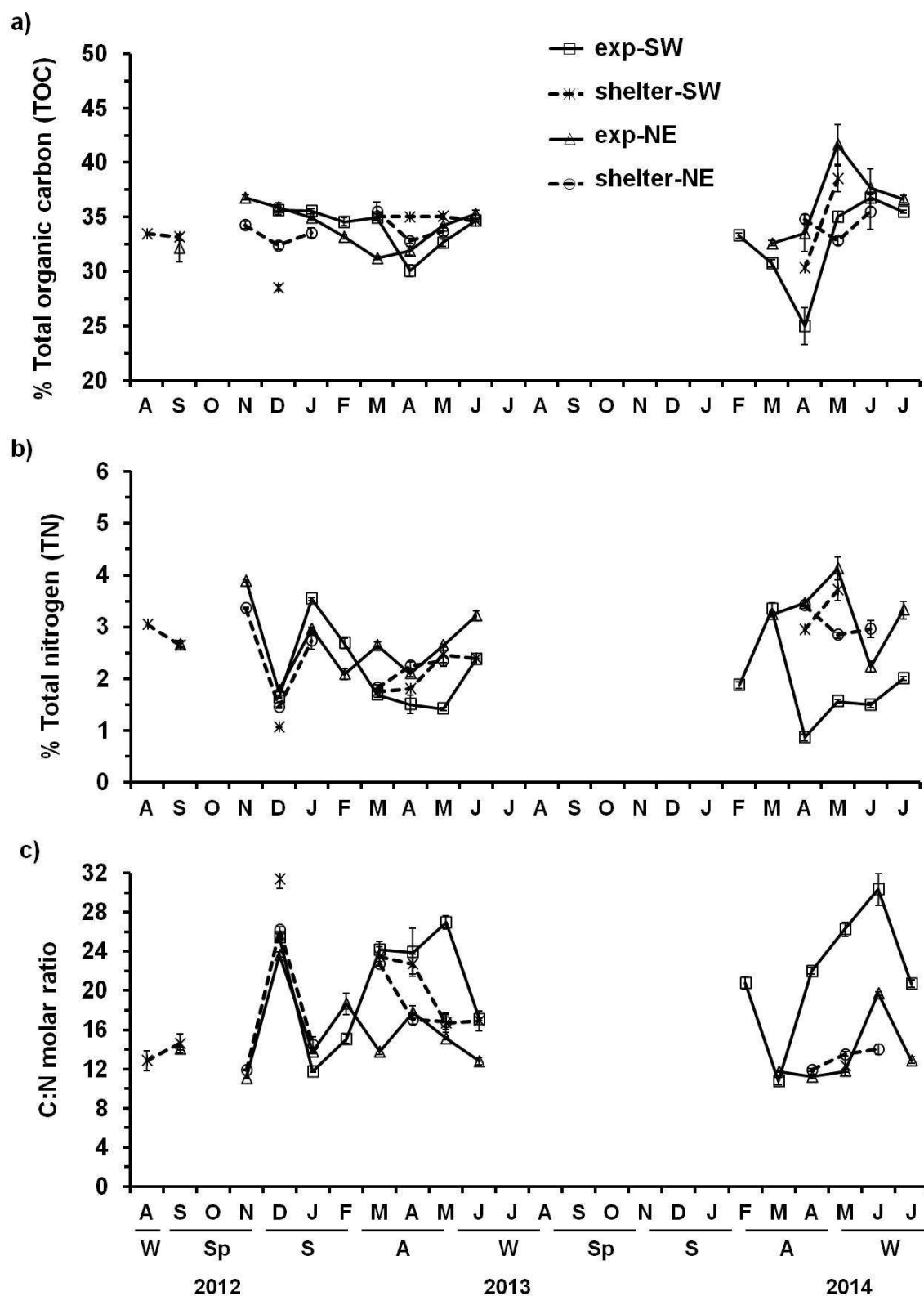


Figure 6.

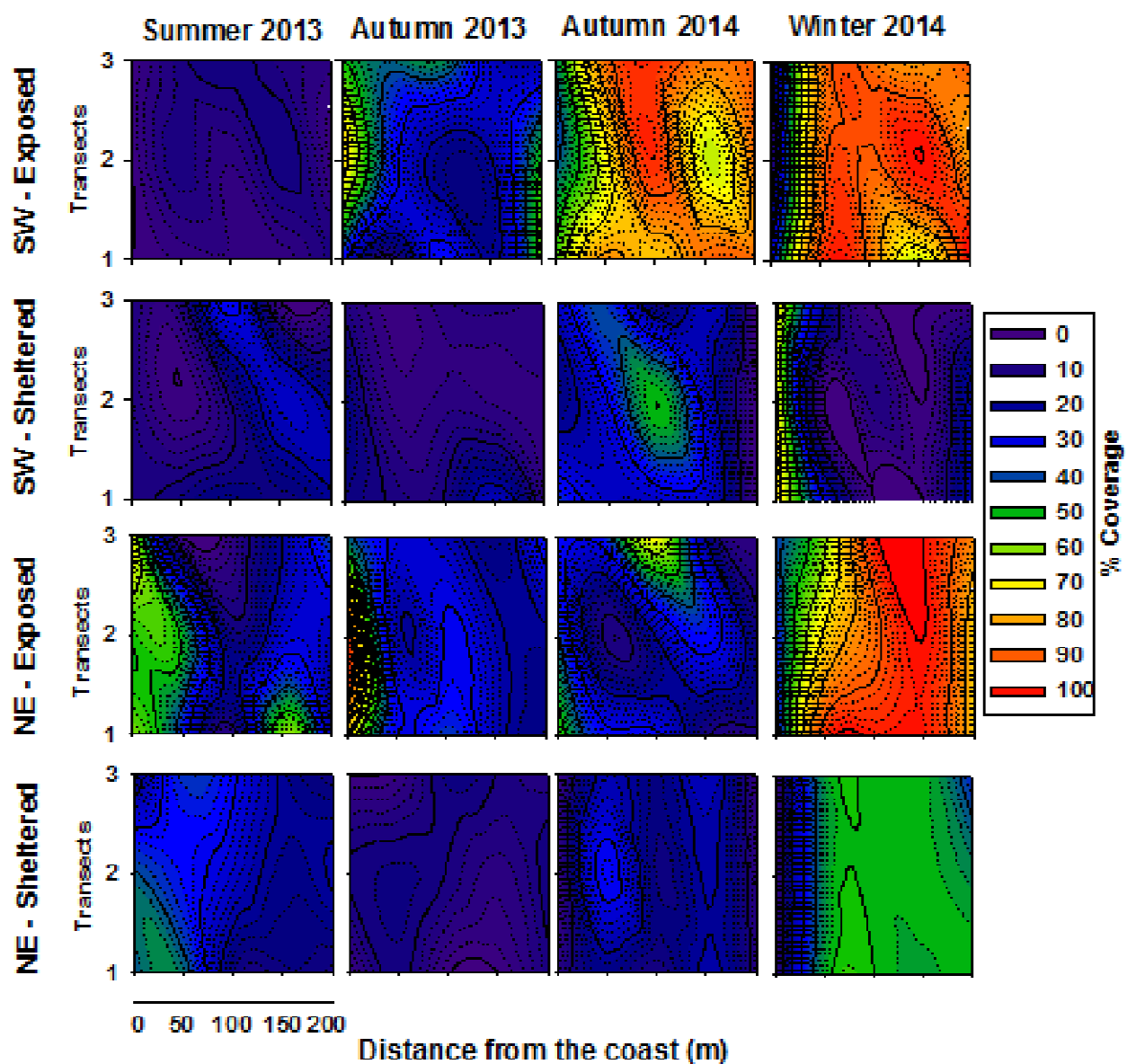


Figure 7.

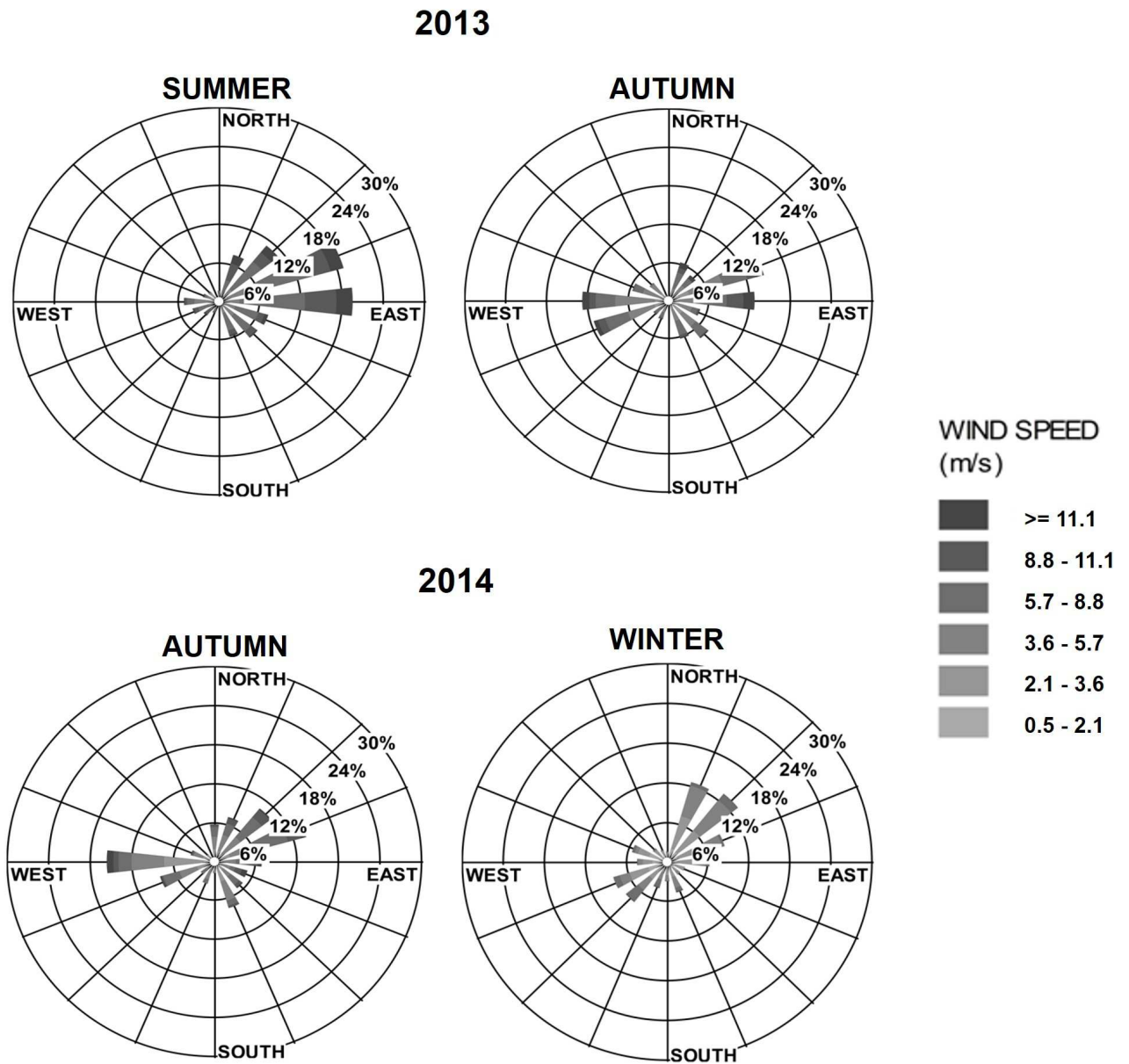
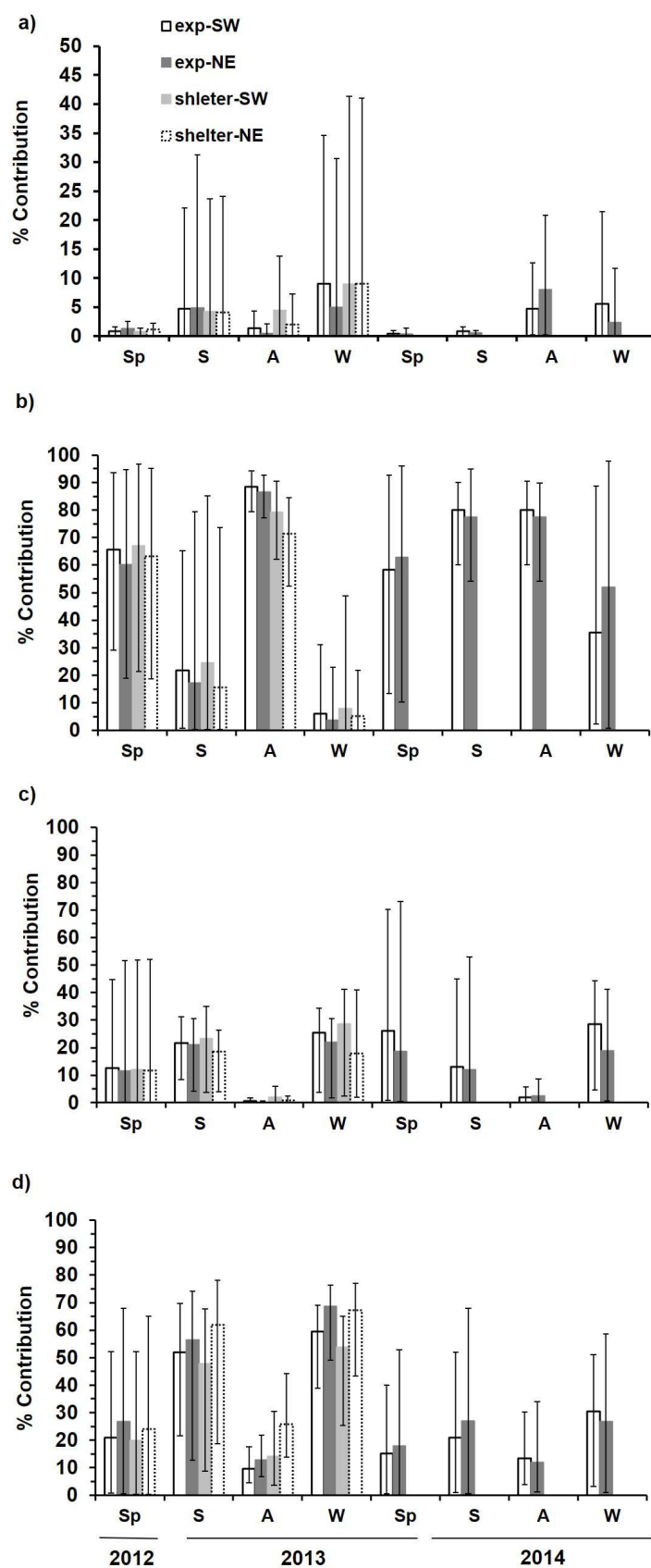


Figure 8.



SUPPLEMENTARY MATERIAL

Figure S1. Monthly variation in %TN (a), %TOC (b), $\delta^{15}\text{N}$ (c) and $\delta^{13}\text{C}$ (d) in sediment sampling stations from September 2012 to August 2014 (stations exp-SW and sw-NE) and from September 2012 to August 2013 (stations shelter-SW and shelter-NE). Values are means ($\pm$ SE).

Figure S2. MixSIAR estimated posterior distributions of the contributions of drift macroalgae, suspended particulate organic matter (POM), *Scirpus maritimus* and *S. olney* (C3 plants) and *Ruppia maritima* and *Spartina densiflora* (denoted as C4 for simplicity) to sedimentary organic matter among stations from Spring 2012 to Winter 2014.

Figure S1.

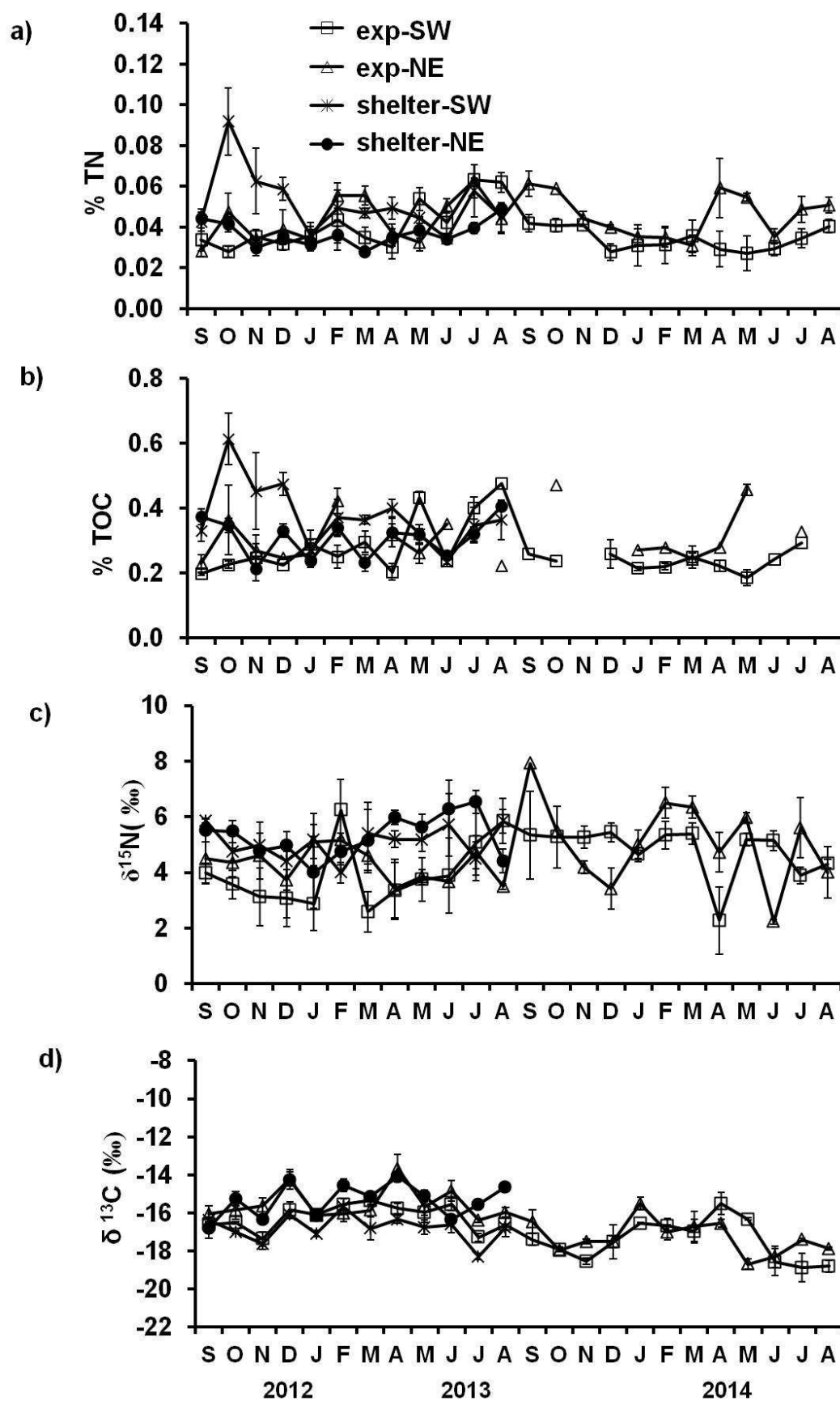
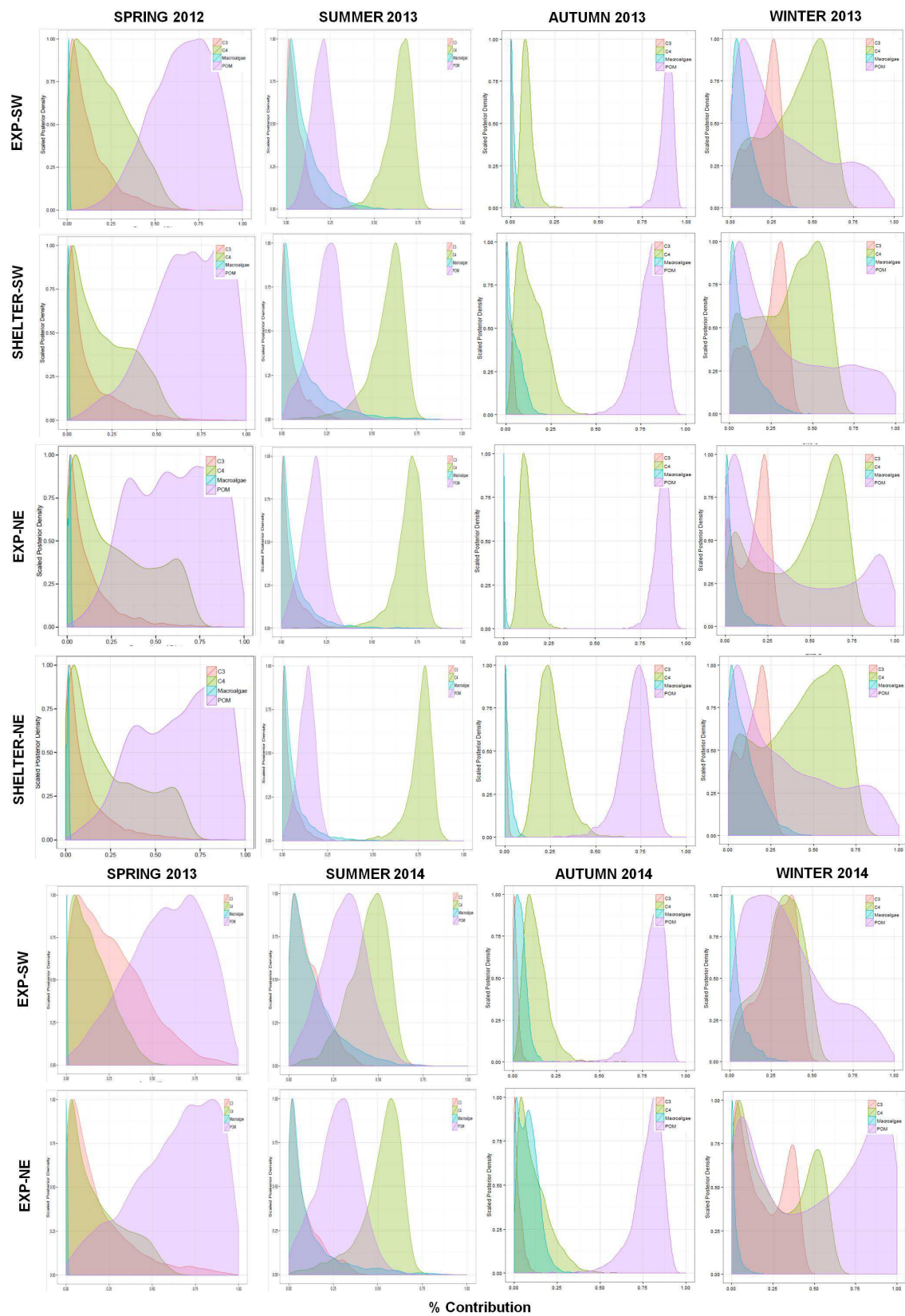


Figure S2.



TABLES

Table 1. Seasonal mean, standard deviation (SD) and coefficient of variation (CV) of water salinity from Spring 2012 to Winter 2014.

	Year	Spring			Summer			Autumn			Winter		
		Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Salinity	2012-13	10.57	1.43	0.13	18.66	4.76	0.25	14.45	3.22	0.22	6.45	1.48	0.22
	2013-14	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 2. Eigenvectors coefficients of hydrological factors in relation to the three first axis of the PCA. PC1, PC2 and PC3 explained 47.1%, 17.4% and 15.21% of hydrological data variability, respectively. Values highlighted are the highest coefficients values for each factor.

Hydrological factor	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 [#]	0.83	0.33	0.06

A proxy for water retention within the study area.

SUPPLEMENTARY MATERIAL

Table S1. Mean values (± 1 SD) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C and %N for the sources *Ulva* sp. and *Rhizoclonium riparium* (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 across seasons (spring, summer, autumn and winter). Lower case letters indicate sources grouped for mixing models analysis.

	Summer				Autumn				Winter				Data obtained from
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	
Drift macroalgae	-15.7 ± 1.5	8.2 ± 1.4	33 ± 0	1.9 ± 0	-17.5 ± 1.6	7.5 ± 0.9	34.1 ± 3	3.4 ± 1.4	-13.5 ± 3.3	7.4 ± 1.3	36.5 ± 2	3 ± 1	Claudino et al. 2013 and present study
<i>Spartina densiflora</i> ^a	-12.1 ± 0.2	6.2 ± 0.5	41 ± 1.4	0.7 ± 0.2	-12.3 ± 0.3	6.2 ± 0.7	40.7 ± 0.7	0.8 ± 0.2	-12.2 ± 0.6	4.5 ± 0.6	40.6 ± 1.2	0.9 ± 0.1	Claudino et al. 2013
<i>Ruppia maritima</i> ^a	-10.5 ± 1.4	7.3 ± 0.4	40.3 ± 1.6	3.2 ± 0.4	-13.9 ± 0.9	7.2 ± 0.8	28.6 ± 4	2 ± 0.1	-10.7 ± 1.2	6 ± 0.8	41 ± 2.1	3.8 ± 0.7	Claudino et al. 2013 and present study
<i>Scirpus maritimus</i> ^b	-25.2 ± 0.9	7 ± 0.5	41.7 ± 1	1.3 ± 0.2	-28.1 ± 0.6	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
<i>Scirpus olney</i> ^b	-26.7 ± 1	6 ± 0.5	39.8 ± 1.5	1.5 ± 1.1	ND	ND	ND	ND	-28 ± 1.1	6 ± 1.2	40.3 ± 0.2	1.5 ± 0.2	Claudino et al. 2013
SPOM	-18.4 ± 0.4	6.6 ± 0.3	1.8 ± 0.1	0.2 ± 0	-19.5 ± 1.3	1.8 ± 1.6	0.9 ± 0.5	0.2 ± 0.1	-18.5* ± 0.8	4.2* ± 0.9	1.4* ± 0.3	0.2* ± 0	Claudino et al. 2013

^a Denoted as a single source in the model due to the similarities in their isotopic signature.

^b Denoted as a single source (C3 plants) due to the same photosynthetic pathway.

*Values are averages between Summer and Autumn.

APÊNDICE 3

Esse apêndice refere-se ao artigo intitulado “Effects of short-term depositions of drift macroalgae on *Ruppia maritima* and associated benthic macrofauna” em preparação para submissão ao periódico *Journal of Experimental Marine Biology and Ecology*.

Effects of short-term depositions of drift macroalgae on *Ruppia maritima* and associated benthic macrofauna

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ABSTRACT

Large drift macroalgal blooms generate adverse environmental conditions in the sediment-water interface during stationary depositions and subsequent biomass collapse and decomposition. Consequently, declines in seagrass populations and associated benthic macrofauna are observed. However, many blooms are composed of unstable depositions of drifting mats which are suggested to alleviate deleterious conditions on benthic communities. To investigate the effects of short-term depositions of drifting macroalgal mats on the widgeon grass *Ruppia maritima* plants and associated macrozoobenthos, macroalgal abundance was experimentally manipulated in a shoal of the Patos Lagoon estuary, southern Brazil. Mixed mats of *Ulva clathrata* and *Rhizoclonium riparium* equivalent to natural levels of biomass abundance ($\sim 200 \text{ g DW m}^{-2}$) and to bloom conditions ($\sim 1000 \text{ g DW m}^{-2}$) were added to experimental plots (0.5 m^2) deployed on *Ruppia* meadows. The experiment ran for about a month and assessments of experimental plots (each 4-7 days) were performed to record biomass losses and to maintain initial conditions of biomass within plots according to natural patterns observed in surrounding areas. Depositions of drift macroalgae mats were highly unstable with average percentages of biomass loss along the experiment ranging from 12.25 % (± 2.34) to 100% (± 0), with similar patterns between biomass treatments. Rates of biomass losses within plots were positively related to high fluvial discharges

and wind action. Significant reduction in *R. maritima* above and belowground biomass and the demographic parameters leaves length, shoots and nodes density and rhizome length were detected, with reductions proportional to the amount of algal biomass added (except for nodes density). Slight reduction in macrofauna taxonomic richness and no significant changes in total macrofauna abundance were observed under short-term drift mats deposition. Nonetheless, decreases of the dominant infaunal tanaidacean *Monokalliapseudes schubarti* beyond those explained by experimental manipulation were detected in biomass plots. Our results indicate the potential of transitory depositions of drift macroalgal blooms to promote extensive plants dislodgements, which may be contributing to the slow recovery of *R. maritima* meadows reported for the study area. Moreover, indirect effects of drift macroalgal mats on benthic macrofauna structure and abundance may occur through *Ruppia* removal, leading to long-term impoverishment of benthic macrofauna. Therefore, the present study supports that transitory drift macroalgae mats can negatively impact benthic communities, a not yet widely recognized problem in estuarine shallow areas.

Keywords: macroalgal blooms, local hydrodynamics, advection, ballistic effects, estuarine shallow areas.

1. INTRODUCTION

An increasing trend in frequency and intensity of macroalgal blooms has been observed worldwide during last decades, mostly attributed to coastal eutrophication (Valiela et al., 1997). Mainly occurring as accumulations of floating mats that are

detached from the substrate due to waves and currents action (hereafter drifting macroalgae), macroalgal blooms are composed of opportunistic species of green algae such as *Ulva*, *Cladophora* and *Chaetomorpha*. Due to their very high nutrient uptake and growth rates, drift macroalgal mats can attain high abundances in nutrient-enriched coastal shallow areas (Valiela et al., 1997). Excessive macroalgal growth and die-off cause reductions in light penetration, release of toxic compounds, sediment anoxia, with profound changes in primary and secondary production, biogeochemical cycles and species composition (McGlathery et al. 2007; Cebrián et al., 2014).

Many of the negative effects of macroalgal blooms have been reported over seagrass meadows and macrozoobenthic communities (eg. Hauxwell et al. 2001; Cummins et al. 2004). Adverse impacts of macroalgal mats deposition primarily include nutrient competition and shading by algal biomass, this last being the main factor leading to decreases in seagrass growth and recruitment (Hauxwell et al., 2001; McGlathery et al., 2001). Harmful biogeochemical conditions within the drift mats and at water-sediment interface also occur due to hypoxic/anoxic conditions related to algal biomass respiration and senescence, accompanied by high ammonia and sulphide concentrations during decomposition (Hauxwell et al., 2001; Pedersen et al., 2004). Under these conditions, overall decreases in aboveground biomass, demographic parameters and growth rates are reported for seagrasses (Hauxwell et al., 2001; Homer et al., 2011), and the survival of infaunal and epifaunal invertebrate communities is impaired (Norkko & Bondorff, 1996).

Most of the deleterious impacts of excessive growth of drift algae on benthic communities rely on shallow, low energy conditions where stationary algal mats accumulate (Hauxwell & Valiela, 2004; Rasmussen et al., 2012; Cebrián et al., 2014).

Nonetheless, drift macroalgae mats accumulations can be highly unstable once aggregations are driven by factors operating at different spatial and temporal scales (Kopecky & Dunton, 2006). High water flow and wind-driven waves and currents can translocate drift mats firstly as bedloads and then suspended in water column at increasing current speeds (Flindt et al., 2004; Biber, 2007). This process leads to variations in drift macroalgae depositions on seagrass beds at small spatial (i.e., 1 m²) and temporal scales (i.e., one tidal cycle up to a few days; Biber, 2007; Flindt et al., 2004; Rasmussen et al., 2013), contrasting with the fixed nature of mats commonly simulated in field and mesocosm experiments (e.g., Hauxwell et al., 2001; Cummins et al., 2004; Irlandi et al., 2004).

The frequent relocation of drifting mats may shorten the exposure of benthic communities to their deleterious impacts once the algal movement promotes well-oxygenated conditions in the water-sediment interface for macrozoobenthos and seagrass to thrive (Cebrián et al., 2014). However, drift mats short-term depositions have still been suggested to hamper the reestablishment of seagrass beds at large spatial scales possibly through enhanced sedimentary dynamics (Valdemarsen et al., 2010; Canal-Vergés et al., 2014) and physical stress (Seeliger, 2001). Once seagrass meadows support more abundant and diverse faunal communities due to increased structural complexity compared to unvegetated areas (Bomstron & Bonsdorff, 1997; Rosa & Bemvenuti, 2007), indirect effects of drift mats on macrozoobenthos may occur through if the plants are removed. In this context, negative effects of short-term depositions of drift mats on seagrasses still remain untested (but see Irlandi et al., 2004). Furthermore, considering the dynamic behaviour of drift mats in shallow areas, further studies

replicating their natural patterns of deposition are necessary to fully understand the magnitude and direction of their impacts on benthic communities.

In the Patos Lagoon estuary (PLE), Southern Brazil, the shallow areas are covered by submerged aquatic vegetation (SAV) dominated by eurihaline and oligohaline grasses (mainly *Ruppia maritima* L. and *Zannichellia palustris* L.), together with benthic macroalgae (mainly drift mats of *Ulva* spp, *Cladophora* spp and *Rhizoclonium riparium* (Seeliger, 1996). The development of the annual *R. maritima* populations is controlled by photoperiod, water temperature and salinity (Copertino & Seeliger, 2010). Plants develop during spring from perennial rhizomes and seed banks, with biomass and fructification peaks occurring from late spring to early autumn, followed by senescence and seed releasing (Cafruni et al., 1978). Reductions of *R. maritima* abundance and distribution have been reported during last decades, resulting from high water flow and extreme floods during *El Niño* events (i.e., 1997/98 and 2002/03). Although *R. maritima* populations can be highly resilient to disturbances, recovering quickly from seed banks and left over rhizomes after the reestablishment of favourable environmental conditions (Anton et al., 2009; Cho et al., 2009), a slow recovery of the meadows was observed in PLE due to reductions in rhizome nets and seed banks after severe storms and high sediment remobilization (Copertino & Seeliger, 2010).

The overlap of several disturbances may reduce the resilience of seagrass meadows (Neto et al., 2010). While climate anomalies (*El Niño* events) and associated higher fluvial discharge reduce seagrass abundance and distribution in Patos Lagoon (Southern Brazil), it is suggested that the slow recovery of the seagrass meadows in post-*El Niño* periods is further inhibited by the fast colonization of opportunistic drift

macroalgae (Copertino & Seeliger, 2010; Odebrecht et al., 2010). In a nutrient-replete system such as the PLE (Haraguchi et al., 2015), macroalgal blooms are mainly triggered by the combination of decreasing freshwater discharges and water level and consequent increasing water residence times and salinity (Lanari & Copertino, *in press*). Wind-driven waves and currents promote biomass dispersion to intertidal and /or adjacent areas, thereby preventing the development of large, stagnant blooms (Lanari & Copertino, *in press*; Lanari et al., *in press*). In this way, the PLE provides an ideal scenario to investigate the effects of drift macroalgae on seagrass meadows and associated macrozoobenthos, considering natural patterns of abundance and time frames of short-term algal deposition.

Throughout a combination of a field survey and experiment, we tested the hypothesis that short-term depositions of drifting macroalgal mats can affect the growth of *R. maritima* plants, therefore contributing for the slow recovery of the meadows, after natural disturbances. Furthermore, indirect effects of drift algal mats on macrozoobenthos may occur mediated by removal of the plants. To test these hypotheses, we simulate sequential depositions of drifting mats on *R. maritima* meadows in experimental plots, and quantified seagrass demographic parameters as well as the abundance and structure of associated benthic macrofauna.

2. MATERIAL AND METHODS

2.1. Study area

The warm temperate Patos Lagoon situated in southern Brazil is the largest choked coastal lagoon in the world (10,000 km²; Kjerfve, 1986; Fig.1). Water exchange between the estuary and the South Atlantic Ocean occurs through a narrow and deep channel (0.5-1 km wide, 14-18 m depth), maintained for navigation. The region is influenced by a microtidal regime (~ 0.47 m) and tidal effects are attenuated within the lagoon. With a large catchment area (200,000 km²), the local hydrology is driven mainly by rainfall, freshwater discharge and wind circulation, which are also the main factors affecting water level and salinity. The prevailing NE winds (dominant in austral spring and summer) and SW winds (dominant in autumn and winter) force, respectively, the outflow and inflow of water between the estuary and the coastal region. During flood periods the PLE becomes a river-dominated system, remaining fresh for several months. Under strong southerly winds, associated to the passage of atmospheric fronts, larger saltwater intrusions occur, blocking freshwater outflow from the PLE (Möller et al., 2001). Therefore, marine and euhaline conditions usually occur in summer/autumn, while freshwater and oligohaline conditions prevail in winter/spring. Nonetheless, short-term salinity oscillations are observed and the PLE may alternate between fresh-oligohaline, over mesohaline to marine in the time scale of hours to days (Abreu et al., 2010). The estuary is eutrophic, due to both large natural and anthropogenic sources, with nutrient concentrations in the water column ranging from ~ 0.1 to $40 \mu\text{M NO}_2^- + \text{NO}_3^-$; ~ 0.1 to $40 \mu\text{M NH}_4^+$; and ~ 0.1 to $8.7 \mu\text{M PO}_4^{3-}$. Sediment pore water nutrients range from ~ 33.6 to $710.7 \mu\text{M NH}_4^+$ and from ~ 0.1 to $14.6 \mu\text{M PO}_4^{3-}$ (Baumgarten & Niencheski, 2010; Odebrecht et al., 2010). Our study was conducted in a shallow shoal (>1.5 m depth) of the PLE moderately exposed to wind action.

2.2. Experimental design

To assess the effects of short-term depositions of drifting macroalgal mats on seagrasses and benthic macrofauna, we conduct a field experiment during austral autumn of 2014 where mixed drifting algal mats, composed mainly of *Ulva clathrata* (Roth) C. Agard and *Rhizoclonium riparium* (Roth) Harvey, were added to a *R. maritima* bed. Drift macroalgae abundance were manipulated by adding fresh biomass within fenced experimental plots (0.5 X 0.5 m, 1 m high). A plastic mesh was used to fence the plots, which were open at the top. The fence bottom was buried into the substrate by using bamboo poles. Mesh-size (1cm²) was small enough to retain macroalgae biomass during calm hydrodynamic conditions, here represented by low fluvial discharge and wind action, and at same time did not constrain water circulation and minimized flow reductions within plots. Under high hydrodynamic periods (i.e. high fluvial discharge and/or wind action), the mesh-size enabled the movement of the algal mats out of the plots or their filaments entanglement in the surrounding mesh. This allowed us to simulate naturally occurring time frames of algal depositions and to control the rates of drifting macroalgae losses (i.e. decreases in biomass, percentage cover and canopy height) according to different scenarios of local hydrodynamism. The experimental plots (16 in total) were deployed 5 m apart of each other in a random design over a ~200 m² area occupied by established *R. maritima* meadows. Meadows presented a patchy arrangement, varying in size from 0.5 to 1m². Experimental plots were set up in relatively homogeneous meadows, where coverage was 100% and canopy was ~ 10 cm. Experimental area was also homogeneous in terms of bottom granulometry (98% sand, 1.2% silt and 0.8% clay) and variations in water level which

ranged from 0.3 m (drought period) to 1 m (flood period), depending on the inflow/outflow regime. Due to the bottom topography (i.e. a concave bank), drift algal mats did not occur naturally at the experimental area once they accumulated in surrounding depressions (*pers. Obs.*).

Four treatments were applied, each having 4 plot unities ($N = 4$): (1) reference control (RC), composed by undisturbed plots without fences; (2) fenced control (FC), fenced plots with no addition of algal biomass; (3) low biomass (LB), which 2 kg wet weight m^{-2} (~ 200 g DW m^{-2} , 50% of coverage and a 5 cm thick mat) of drift macroalgae biomass were added to the plots, representing naturally occurring abundances; (4) high biomass (HB), whereby the addition of 10 kg wet weight m^{-2} (~ 1000 g DW m^{-2} , 100% of coverage and a 20 cm thick mat) simulated recurrent blooming events in the study area (Lanari & Copertino, *in press*). Plots were randomly deployed in the study area. Drifting biomass of *U. clathrata* and *R. riparium* used in the experiment was collected from adjacent areas and defaunated manually prior to addition in the plots.

Once drift algal mats present a high potential for advection whilst, at the same time, their biomass accumulations within an area can persist up to six months (Lanari & Copertino *in press*; but also see results in sections 4.1 and 4.2 of this thesis), we simulated sequential depositions of drifting mats over *R. maritima* meadows. To this, experimental plots were assessed during six time intervals to assess reductions in macroalgae abundance through biomass advection and to reallocate algal biomass within plots to maintain initial experimental conditions. Assessment time intervals comprised 4 up to 7 days (t_1 , from 31 March to 4 April; t_2 , from 4 to 7 April; t_3 , from 7 to 14 April; t_4 , from 16 to 23 April; t_5 from 23 to 29 April; t_6 , from 29 April to 2 May). At each time interval, remaining algal biomass within plots was recorded to estimate biomass

losses originated from advection. Remanescent biomass within plots was manually removed from the plots with care not to disturb *Ruppia* plants and the associated fauna. Algal biomass volume was determined using a plastic 2000 ml graduated cylinder with a plunger with a diameter approximately similar to the cylinder's inside diameter. The plunger was used to compress biomass within the cylinder and drain holes, drilled from the top to the bottom of the cylinder in three parallel rows, enabled water removal (see Robbins & Boese 2002 for more details). Using the determined algal biomass volume (x), its dry weight (y) was estimated through their linear relationship express as the equation $y = -5.5 + 0.8399x$ ($p < 0.05$; $R^2 = 0.94$; $N = 40$), which was previously obtained in pilot sampling in the study área. Due to the simple thallus morphology of opportunistic macroalgae such as *Ulva*, rapid biomass losses through decomposition occurs (Banta et al. 2004). To disentangle biomass losses associated from biomass decomposition from those related to their advective transport, litter bags with similar dimensions to the plots (i.e. 50 cm X 50 cm) and similar biomass to the experimental plots (i.e. LB and HB) were deployed ($N = 3$) during the last three time interval (i.e. t_4 , t_5 and t_6) to control for the amount of macroalgal biomass being lost due to decomposition. Biomass reductions within litter bags were determined according to the same procedures use for the experimental plots.

After determination of biomass losses within the plots, new fresh biomass was added to the plots to maintain initial biomass conditions. Remanescent biomass was returned to the plots and new fresh biomass, previously defaunated, was added to meet the initial biomass conditions for LB (i.e. $\sim 200 \text{ g DW m}^{-2}$) and HB treatments (i.e. $\sim 1000 \text{ g DW m}^{-2}$). For litter bags, only fresh biomass was added. These values of biomass were in accordance with natural drift mats reoccurrence observed in the

adjacent areas, which were assessed during the experiment using seven fixed plots (0.5 m²) randomly positioned in a 0.5 km² area located outside the experimental area (~ 200 m apart; i.e., non-experimental area) prone to drift macroalgae accumulations (pers. obs.) and with similar hydrodynamic conditions and substrate features. The abundance of drift macroalgae was weekly assessed and, at the beginning and at the end of the experiment, percentage cover was visually estimated and plots had its biomass cleared for dry weight determination in laboratory (60°C for 48 hrs).

The experiment lasted 33 days (from March 31st to May 2nd), until significant decreases in *R. maritima* coverage (~10%) was observed within experimental plots. At the end of the experiment, destructive sampling was conducted. We collected one core per treatment plot using a PVC corer (10 cm diameter, 15 cm depth) inserted in the centre to avoid edge effects. Samples were sieved through a 500 µm mesh and stored in plastic bags. In the laboratory, samples were washed to remove debris and *R. maritima* biomass was sorted out into above and below-ground biomass. The demographic parameters leaf length, total rhizome length, number of shoots and nodes were recorded and above and below-ground dry weight (60°C for 48hrs) were obtained. Sub-samples (N = 1 to 3) of above and belowground biomass were ground to fine powder, inserted into tin capsules and analyzed for total organic carbon (TOC) and total nitrogen (TN) content using an automatic elemental analyzer (2400 Series II CHNS/O System, Perkin-Elmer, USA). Macrofaunal organisms were sorted out, fixed with 4% buffered formalin/seawater, identified to the lowest taxonomic level (40x stereomicroscopes) and preserved in ethanol (70%).

During the experiment, hourly wind speed and direction data were obtained from the Rio Grande Maritime Pilotage (<http://www.rgpilots.com.br/>) located at the PLE

mouth. Daily fluvial discharge for the Patos Lagoon hydrographic basin was obtained from the Brazilian National Water Agency (<http://www.hidroweb.ana.gov.br>). The flow of the three main tributary rivers (Jacuí, Taquari and Camaquã rivers), which accounts for 70% of the inflow into the Patos Lagoon (Vaz et al. 2006), was assumed to be a proxy for the total fluvial discharge.

2.3.Data analysis

To test the effects of local hydrodynamics on variations of drift macroalgal biomass within experimental plots, the main and interactive effects of fluvial discharge and wind action on mean percentages of biomass loss were investigated through Multiple Linear Regression. Wind action for the experimental area was expressed as the index Wave Exposure (WE; Burrows et al. 2008) which combines the wave fetch of the area with local wind regime (direction, speed and frequency). Assumptions of normality and homogeneity were checked by visual inspection of residual plots.

To investigate the relationship between the experimental treatment and *Ruppia*'s above and belowground biomass and its demographic parameters leaves and rhizome length and nodes and shoots density, we performed a Principal Component Analysis (PCA). PCA was conducted using the correlation matrix among the replicates of each treatment, thus standardizing all variables to the same scale. Prior to analysis, data was checked for normal distribution.

Effects of drift algal biomass deposition on benthic macrofauna associated to *Ruppia* meadows were investigated through data ordination of all treatments replicates using Non-metrical Multidimensional Scaling (nMDS). Due to the characteristic of

macrofauna data (i.e. abundance data with the presence of zeros), nMDS analysis was performed using a resemblance matrix among samples based on Bray-Curtis dissimilarity index. To this, data was previously transformed to its fourth root due the dominance of few species. Subsequently to nMDS analysis, to test for significant differences among treatments, Permutation-based Multivariate Analysis (PERMANOVA, Anderson 2001) were conducted using Bray-Curtis dissimilarity index and 4999 permutations, followed by pairwise comparisons. For the dominant species in the community (in our case, *Monokalliapseudes schubarti*), individual PERMANOVA was conducted using Bray-Curtis dissimilarity index and 4999 permutations, followed by pairwise comparisons, to test for significant differences in their abundance among treatments.

All analyses were performed in the software R (version 3.2.2) and PAST (version 2.08). Due to the low and unequally replication of carbon and nitrogen content in *R. maritima* above and belowground biomass, these results were visually analyzed.

3. RESULTS

3.1. Patterns of drift macroalgae deposition

Drift macroalgal blooms were persistent at the PLE with recurrent depositions of dense mats during the studied period, in both experimental and non-experimental areas. In the areas adjacent to experimental plots (i.e. non-experimental), drift macroalgal mats occurred in high abundances from late March to early May (Table 1), with no significant differences between these two periods (T-test for Coverage, t-value = 1.36, *p*

= 0.19; and Biomass, t -value = 0.07, p = 0.94). Algal depositions and abundances varied among the fixed non-experimental plots between two successive samplings, reflecting the natural movement of drifting mats.

Within the experimental plots, the frequency and abundance of depositions of drift macroalgae mats were highly variable across weekly assessments, generally with short durations. Macroalgal biomass within the experimental plots significantly varied along assessment time intervals with biomass losses (mean $\pm$ SE) ranging from 12.25 % ($\pm$ 2.34) to 100% ($\pm$ 0), with similar patterns between Low Biomass (LB) and High biomass (HB) treatments (Fig. 2). The lowest biomass loss (12.25 $\pm$ 2.34%) occurred during t_2 whereas total biomass loss (100%) was observed in t_3 . Percentages of biomass losses kept high during the following time intervals (96.5 $\pm$ 1.72%, 91.14 $\pm$ 2.09% and 89.43 $\pm$ 4.44% during t_4 , t_5 and t_6 , respectively). Biomass losses within experimental plots differed from those observed in the litter bags. The latter showed lower biomass losses than the experimental plots, with mean values ranging from 8 $\pm$ 4% (t_5) to 12.33 $\pm$ 3.95% (t_6 ; Fig. 2, in detail).

The losses of macroalgal biomass within the experimental plots were significantly related to increases in fluvial discharge (Multiple Linear Regression; R^2 = 0.97, p = 0.01) and wind action (Multiple Linear Regression; R^2 = 0.96, p = 0.01), with a significant interaction between these two factors (Multiple Linear Regression; R^2 = 0.96, p = 0.02). Highest biomass reductions occurred under moderate fluvial discharge ($> 2000 \text{ m}^3 \text{ s}^{-1}$) and/or high WE (≥ 50), as observed during t_3 , t_4 , t_5 and t_6 time intervals (Figs. 2 and 3). Conversely, biomass losses were minimal during the short periods of low discharge ($\sim 1000 \text{ m}^3 \text{ s}^{-1}$) and WE (≤ 40) (i.e. t_2). Although not quantified, similar temporal patterns of mats translocation were observed in the adjacent

surveyed area (i.e. non-experimental area), where algal retention and dispersion occurred during low and high hydrodynamic conditions, respectively.

3.2. Effects of drift macroalgae deposition on seagrass and benthic macrofauna

Seagrass above and belowground biomass and leaves and rhizome length and shoots and nodes density were inversely correlated to LB and HB plots (PCA; Fig. 4). Accordingly, reductions in seagrass demographic parameters and biomass values were observed in these treatments, which were proportional to the amount of algal biomass added to the plots (Fig. 5). Although not tested statistically, changes in TOC and TN in *Ruppia*'s above and belowground biomass were not observed (Fig. 6).

In relation to the associated benthic macrofauna, no variability in the spatial ordination of replicates were detected among treatments (nMDS; Fig. 7). This result was corroborated by the PERMANOVA analysis which showed no significant differences in macrofauna abundance and structure among treatments (Table 2a).

The number of benthic macrofauna taxa was generally low and total macrofauna abundance did not varied among biomass treatments (Fig. 8a and b, respectively). Changes in total abundance were explained mainly by the reductions of the tanaidacean *M. schubarti* (Mañé-Garzón, 1949), the dominant species in the community (Fig. 8c), followed by the infaunal polychaete worms *Heteromastus similis* (Southern, 1921), *Nephtys fluviatilis* (Monro 1937) and *Laeonereis acuta* (Treadwell, 1923; Figs 8d, e, f). Lower abundances of *M. schubarti* in LB and HB treatments were observed, but also coincided with reductions in FC plots in a lesser extent, highlighting the effects of experimental manipulation (i.e. fenced structures; Fig. 8c). Furthermore, differences in

the abundance of *M. schubarti* among treatment were not significant (PERMANOVA, $p = 0.09$; Table 2b). For infaunal polychaete worms, no variations were observed among treatments (Fig. 8d,e,f). Epifaunal species such as amphipods, the isopods *Uromunna peterseni* (Vanin, 1985) and *Kupellonura* sp. and the snail *Heleobia australis* (Marcus & Marcus, 1963) occurred in very low abundances (Figs. 8 g,h,i,j).

4. DISCUSSION

The present study investigated the effects of drift macroalgae on a widgeon grass (*R. maritima*) meadow and their associated macrozoobenthos in a shallow estuarine area, under natural conditions of algal mat depositions. During the experimental period, the algal bloom persisted for a month over the meadow, although biomass retention within the plots did not last more than a week. Our results corroborate previous studies emphasizing the high temporal and spatial dynamics of drift macroalgal mats over a seagrass bed, driven by the algal advective transport (e.g. Biber, 2007; Rasmussen et al., 2013).

It is suggested that under conditions of short residence time of water and low to moderate algal retention within an area, the blooms may not cause deleterious impacts on seagrasses and macrozoobenthos communities, due to alleviation of light attenuation and adverse sedimentary conditions (Hauxwell & Valiela, 2004; Irlandi et al., 2004; Cebrián et al., 2014). However, our study found that drifting algal mats can negatively affect seagrass plants, even when the accumulations last shortly (i.e. few days) with low-moderate and high algal biomass. Significant reductions in all *R. maritima* demographic parameters and biomass were detected, regardless the amount of drift

macroalgal biomass deposited. Reductions in light availability to the bottom are the first and immediate impact of persistent algal blooms, due to both direct shading (Hauxwell et al., 2001) and sediment resuspension (Canal-Vergés et al., 2010). However, the decreases in the demographic parameters and biomass of *R. maritima* found here contrast with reported survival strategies to cope with chronic light deprivation. These include leaf elongation, increased above: belowground biomass ratios (Hauxwell et al. 2001), and carbon content reductions due to remobilization to meet plants requirements (Cabaço & Santos 2007). Therefore, although intermittent light deprivation may have occurred at some extent throughout unstable mats deposition, these were probably not sufficient to promote the reductions detected.

Given the transitory character of the drift mats, the mechanical stress triggered by algal advective transport may have contributed to the observed decline in all *R. maritima* parameters. Due to their densely packed morphology, clumps of filamentous algae are prone to get tightly entangled among seagrass leaves and shoots (Kopecky & Dunton, 2006; Höffle et al. 2011). The advective transport of drift mat by waves and currents promotes the break-off of leaves (Van Lent & Verschuure, 1994) and, similarly, *Ruppia* leaves are commonly observed among drift macroalgal mats (Fig. 9; Silva & Asmus, 2001).

Observed reductions in above and belowground biomass and rhizome length are also typical responses of small-sized seagrasses to sediment erosion (Cabaço & Santos, 2007; Han et al., 2012). Small seagrass species, such as *R. maritima*, have low belowground biomass formed by thin roots and rhizomes with shallow anchorage depth (i.e. 90% of belowground biomass in the first 5 cm sediments depth; Kantrud, 1991). Consequently, as reported for others small seagrasses (e.g. *Zostera noltii*, Cabaço et al.,

2008), *R. maritima* plants are highly vulnerable to sediment remobilization, which cause plant detachment and advection (Cho et al., 2009). Previous studies at the study area have reported dislodgment of *R. maritima* plants and meadows due to sediment remobilization during high hydrodynamic events (Copertino & Seeliger, 2010). Nonetheless, our results indicated that depositions of drift macroalgae mats may enhance plant dislodgment since the sweep of algal biomass over the bottom disrupt sediment surface, reducing the thresholds for sediment erosion and increasing resuspension (Canal-Vergés et al. 2010). This hypothesis, however, still needs to be confirmed by studies focusing on the effects of the algal mats advective transport on sediment erosion. Furthermore, we were not able to determine the rate of *R. maritima* reductions across distinct time intervals but a gradual decrease in plant density was notable, suggesting gradual effects of drift mats along the experiment.

The dislodgement of *R. maritima* plants by drift macroalgae have been observed in the PLE, mainly at the end of the growing season (Seeliger 2001; Silva & Asmus 2001). Our study quantified reductions in the widgeon grass even at low biomass values of macroalgal deposition (LB treatment), indicating that this may be a recurrent process in the area. Small, opportunistic species such as *R. maritima* can rapidly recover from rhizome exposure and bed fragmentation through fast horizontal expansion during vegetative growth (Cho et al. 2009; Han et al. 2012). However, recovery depends on ceasing physical stress (Han et al. 2012). In this context, the magnitude and persistence of the algal blooms observed here, and blooms reported for the study area (e.g. Lanari & Copertino, *in press*), indicates that the ballistic effects of macroalgae on *R. maritima* plants can be recurrent, potentially leading to the depletion of belowground reserves.

In PLE, transitory drift algal blooms have been occurring during *R. maritima* growing season (i.e. late spring to late autumn) (Lanari & Copertino, *in press*), which may impair critical periods for meadow establishment and seed bank formation. Seedlings lack rhizome net and have low developed roots, therefore are highly susceptible to uprooting by the ballistic effects of drift mats (Ailstock et al., 2010; Valdemarsen et al., 2010). Once seeds production can vary according to meadow abundance and permanence in the shallow areas (Copertino & Seeliger, 2010), the development of *R.maritima* population in the following year may be drastically reduced under the influence of transitory algal mats. We suggested that this process contributed to the slow recovery of *R. maritima* meadows in the PLE after *El Niño* events (i.e. 1997/98 and 2002/02; Copertino & Seeliger, 2010), since drift macroalgae dominated the estuarine shallow areas during post-*El Niño* periods (Lanari & Copertino, *in press*). Similar scenarios are reported in Odense Fjord where the recovery of *Zostera marina* meadows has been delayed by *Fucus* sp. ballistic effects on seedlings at large spatial scales, even after the restoration of water quality (Valdemarsen et al., 2010; Canal-Vergés et al., 2014).

In spite of *R. maritima* reductions, no significant changes in the macrozoobenthos community were observed. However, *M. schubarti*, the dominant species, presented reduced abundances in biomass plots, beyond those explained by experimental manipulation (Fig. 8c). Differently from polychaetes that inhabit deeper sediments *strata* and have been shown not to rely on benthic vegetation to thrive (e.g. Lee et al., 2001), *M. schubarti* is a shallow-burrowing suspension feeder that may benefit from the higher structural complexity and suspended organic matter trapping, promoted by *R. maritima* beds (Bemvenuti, 1987).

Due to their planktonic life, drift macroalgae are mobile corridors and can enhance faunal dispersion (Salovius et al. 2005). Furthermore, due to their low morphological complexity and associated high palability for herbivores and detritivores, increases in secondary production may occur under the dominance of drift microalgae in shallow areas (Cébrain et al 2014). However, due to their short-life cycle and high vulnerability to be washed out to deeper and/or external areas during high water flow (Martins et al. 2001), drift algal mats provide an unstable temporary habitat, compared to the rotted seagrass meadows. Hence, they cannot compensate for seagrass reductions, leading to a long-term impoverishment of the macrofaunal community (Dolbeth et al. 2003). We call into the attention that, despite negative effects of unstable drift mats on benthic macrofauna were not detected in the present study, long-term studies are necessary in order to establish the effects that the replacement of *Ruppia* meadows by drift macroalgal beds can have in estuarine secondary production over longer time scales.

In conclusion, our study showed that drift algal mats can impact seagrass meadows in Patos Lagoon estuary, even at small time scales and under low biomass accumulations. The short-term depositions may negatively affect *R. maritima* plants, through direct (e.g. mechanical) and indirect (e.g. shading, increasing resuspension) effects. Moreover, indirect effects of transitory drift macroalgal mats on macrozoobenthos may occur mediated by seagrass removal, leading to long-term changes in the abundance and structure of benthic macrofauna. Negative effects of drift macroalgal mats on seagrasses meadows has not been widely recognized in estuarine shallow areas (Valdemarssen et al. 2010) and more studies are necessary to test the generality of our results. The ballistic effects of drift mats may vary according to algal morphology, which influences their transport (Flindt et al., 2004; Canal-Vergés et al.,

2010) and the type of interactions with seagrasses (Höffle et al. 2011). Similarly, seagrass size determines their vulnerability to sediment erosion and macroalgal dragging force (Cabaço et al, 2008; Thomsen et al., 2012). Finally, studies combining small and large spatial scales investigations, coupled with modelling (e.g. Canal-Vergés et al. 2014), may be a powerful tool to forecast the magnitude and consequences of drift macroalgae at the ecosystem level.

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TABLES

Table 1. Temporal variation of drift macroalgae coverage and biomass within fixed 0.5 m² plots surveyed in an area adjacent to the experiment at the beginning and at the end of the experiment (~one month interval). Destructive biomass sampling within quadrats implied that quadrats were cleared after cover assessment. Biomass dry weight is expressed by m².

Plot	Initial		Final	
	Coverage (%)	Biomass (g DW m ⁻²)	Coverage (%)	Biomass (g DW m ⁻²)
1	100	476.16	20	323.8591
2	100	1377.42	50	462.0088
3	100	483.52	50	662.4391
4	100	1931.83	80	951.1947
5	10	120.59	50	723.0212
6	100	432.56	100	1114.257
7	50	354.99	50	806.81
Mean (± SE)	80 (± 13.62)	882.44 (± 335.28)	57.14 (± 9.68)	720.51 (± 102.72)

Table 2. Results of PERMANOVA and pairwise comparisons for benthic macrofauna (a) and for the dominant species *M. schubarti* (b). Codes are: Reference Control (RC), Fenced Control (FC), Low Biomass (LB) and High Biomass (HB).

Source	df	SS	Pseudo-F	P(permanova)
a)				
Treatments	3	1602.04	1.98	0.05
Residuals	12	3226.8		
<i>Pairwise comparisons</i>				
	RC	FC	LB	
RC				
FC	0.11			
LB	0.06	0.63		
HB	0.06	0.14	0.09	
b)				
Treatments	3	7025.4	2.18	0.09
Residuals	12	12882		
<i>Pairwise comparisons</i>				
	RC	FC	LB	
RC				
FC	0.28			
LB	0.20	0.34		
HB	0.05	0.11	0.36	

FIGURES AND LEGENDS

Figure 1. Location of the Patos Lagoon estuary at the Brazilian southern coastline with the experimental area highlighted.

Figure 2. Drift macroalgae biomass within experimental plots ($N = 4$) after biomass additions according to the treatments Low (L) *versus* High (H) biomass at different time intervals (t_1 , t_2 , t_3 , t_4 , t_5 and t_6 , see Methods for more details). Horizontal dashed lines represent initial biomass values for the treatments highlighted. *In detail:* final values of algal biomass in the litter bags ($N = 3$) at the time intervals t_4 , t_5 and t_6 . All values are means ($\pm$ SE).

Figure 3. Daily variation of the Wave Exposure index (black bold line) and fluvial discharge (gray dotted line) from 31 March to 2 May 2014. Assessments time intervals are indicated.

Figure 4. Principal Component Analysis (PCA) of above and belowground biomass, rhizome and leaves length, and nodes and shoots density of *R. maritima* over treatments. PC1 and PC2 explained, respectively, 85.02% and 8.63% data variability. Treatments are: RC = reference control; FC = fenced control; LB = low biomass; HB = high biomass. Leav. = leaves length, Nod. = nodes density, Shoot = shoots density, Abo = aboveground biomass, Bel = belowground biomass, Rhiz. = rhizome length.

Figure 5. Variation of (a) above and (b) below-ground biomass, (c) shoots density, (d) rhizome length and (e) nodes density and (f) leaves length across the experimental treatments. Values are means $\pm$ SE. Treatments are: RC = reference control; FC = fenced control; LB = low biomass; HB = high biomass.

Figure 6. Variation of (a) above and (b) belowground total organic carbon (TOC) and total nitrogen (TN) content across the experimental treatments. Values are means $\pm$ SE. Treatments are: RC = reference control; FC = fenced control; LB = low biomass; HB = high biomass.

Figure 7. Non-metrical multidimensional scaling (nMDS) ordination of benthic macrofauna based on transformed abundances (fourth root) and Bray-Curtis similarities (N = 4 samples). Treatments are: RC = reference control; FC = fenced control; LB = low biomass; HB = high biomass.

Figure 8. Mean ($\pm$ SE) number of species (a), total abundance (b) and abundance per species or taxonomic group of benthic macrofauna across the experimental treatments. Treatments are: RC = reference control; FC = fenced control; LB = low biomass; HB = high biomass.

Figure 9. Drifting mats as bedloads on unconsolidated bottoms (a) and *Ruppia maritima* biomass entangled in an algal mat floating at the surface (b) at the Patos Lagoon Estuary. Photo: Marianna Lanari.

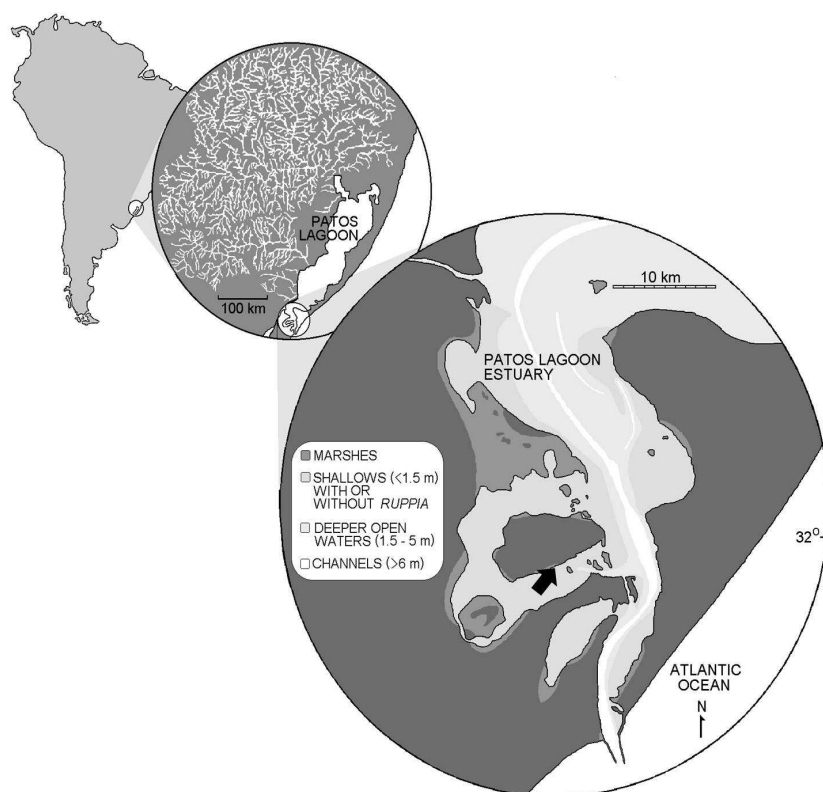
Figure 1.

Figure 2.

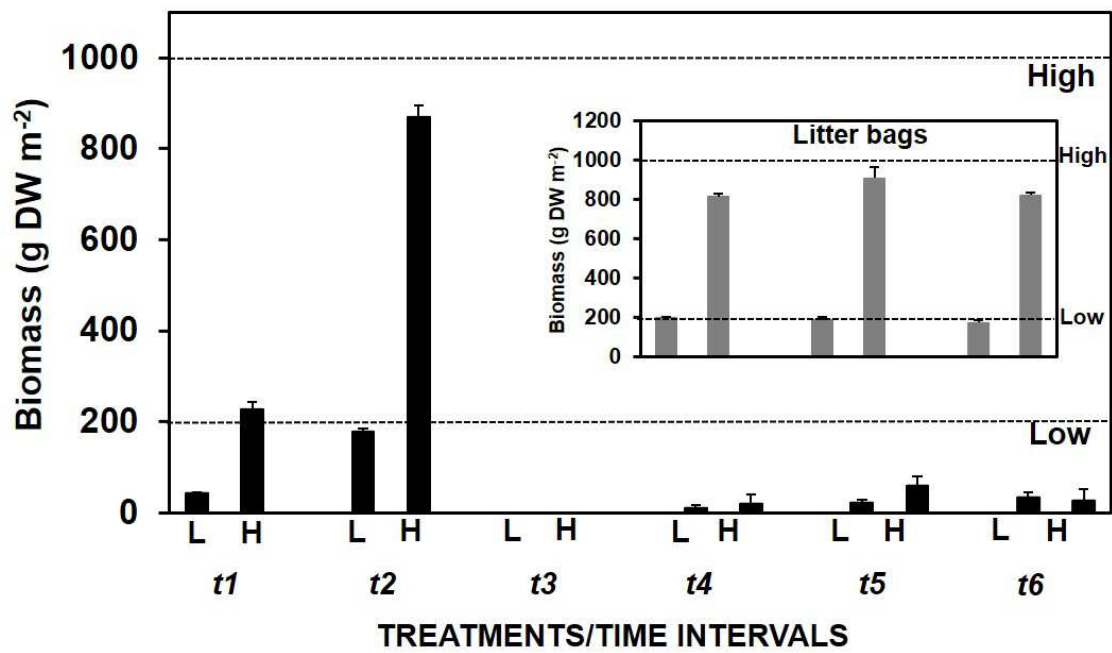


Figure 3.

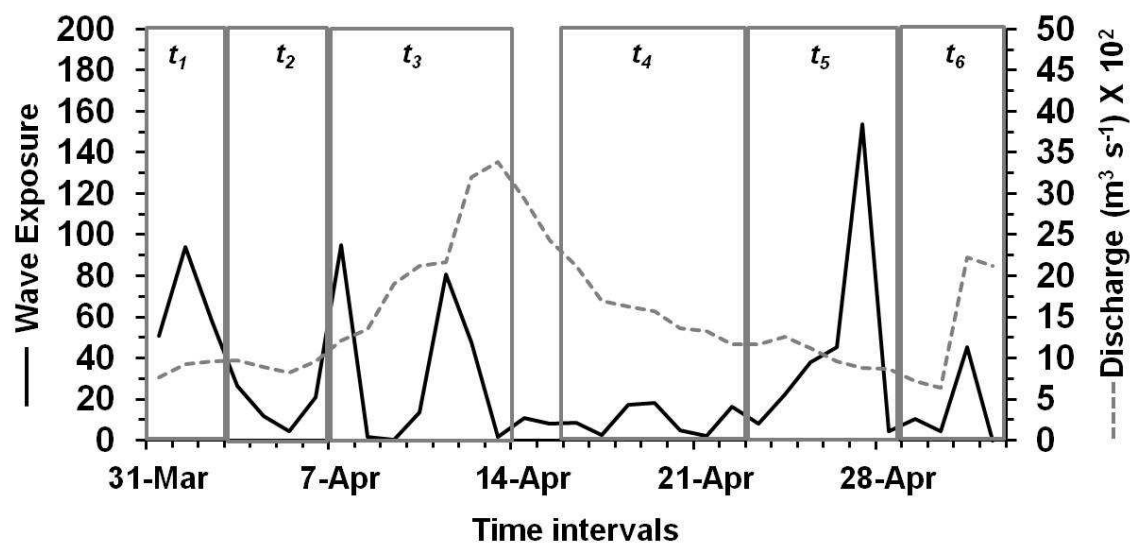


Figure 4.

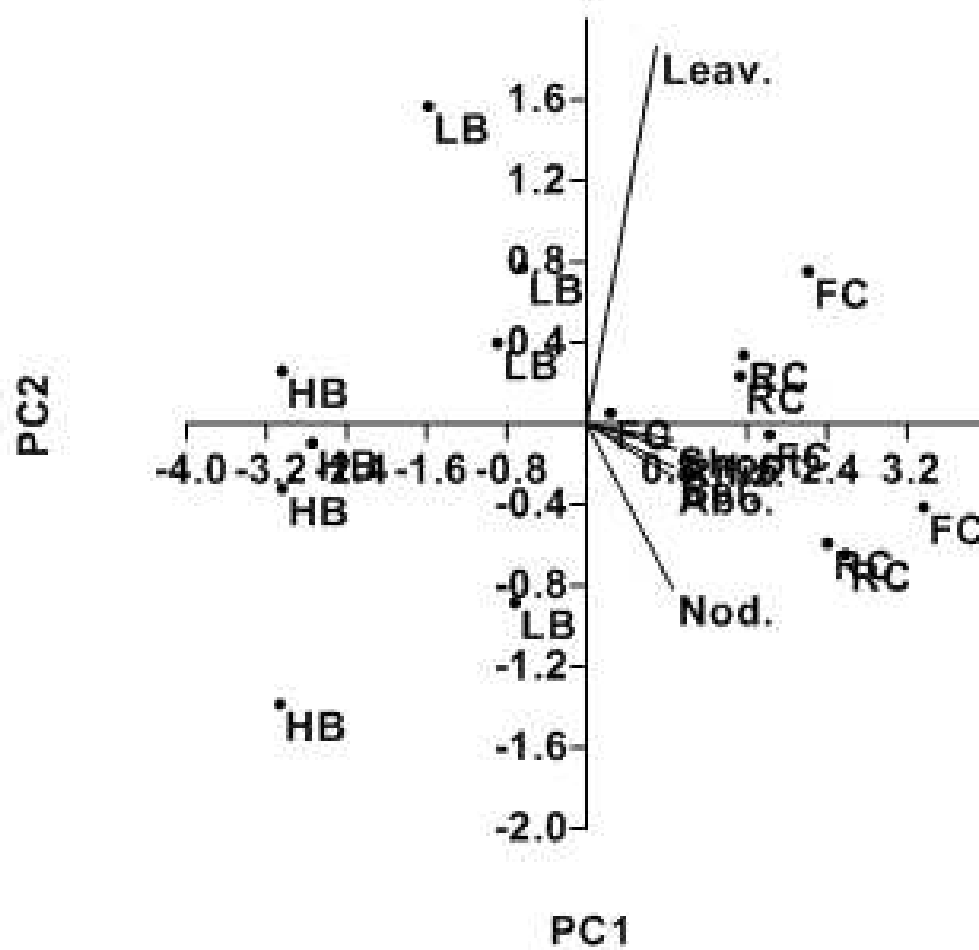


Figure 5.

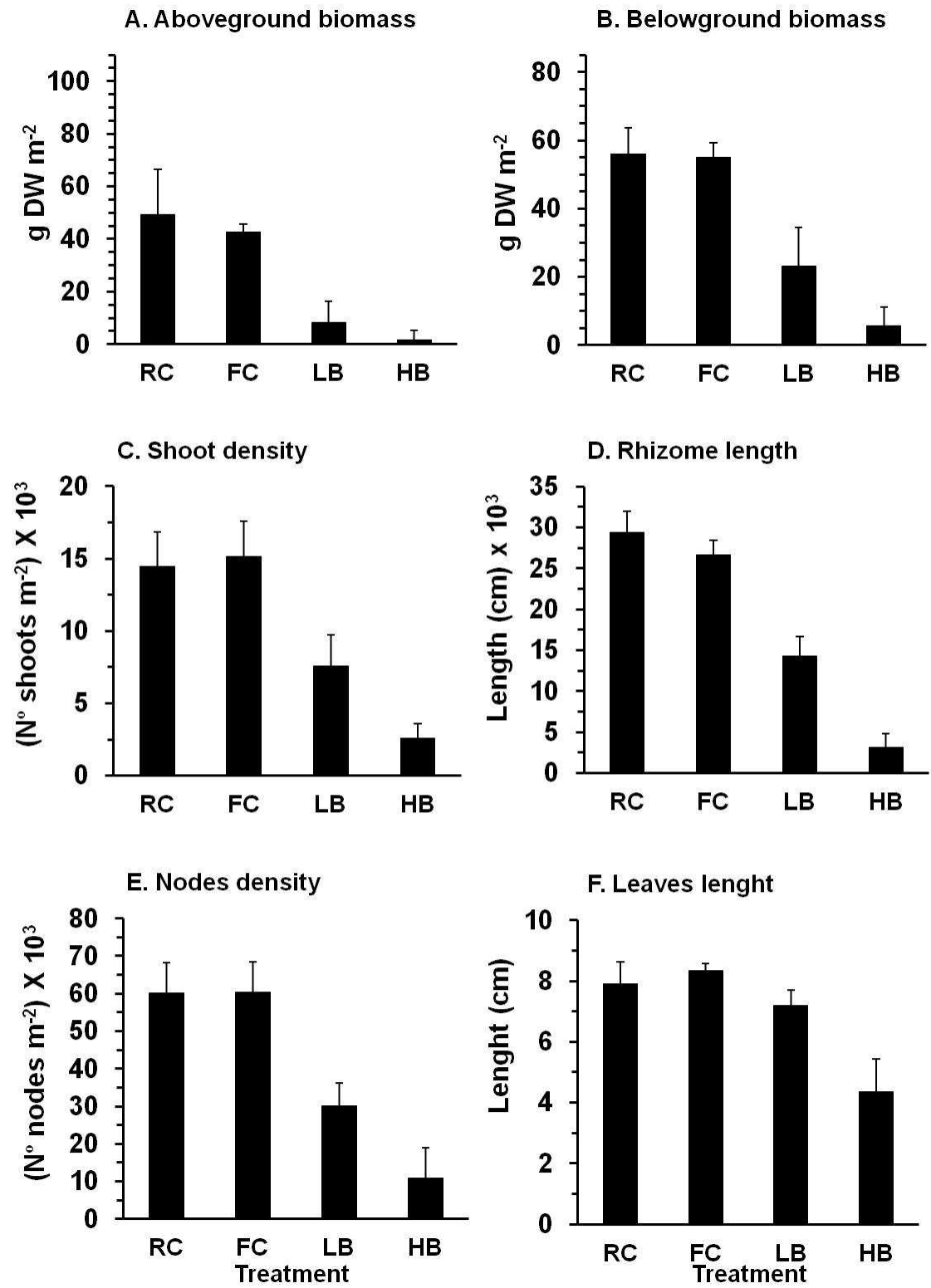


Figure 6.

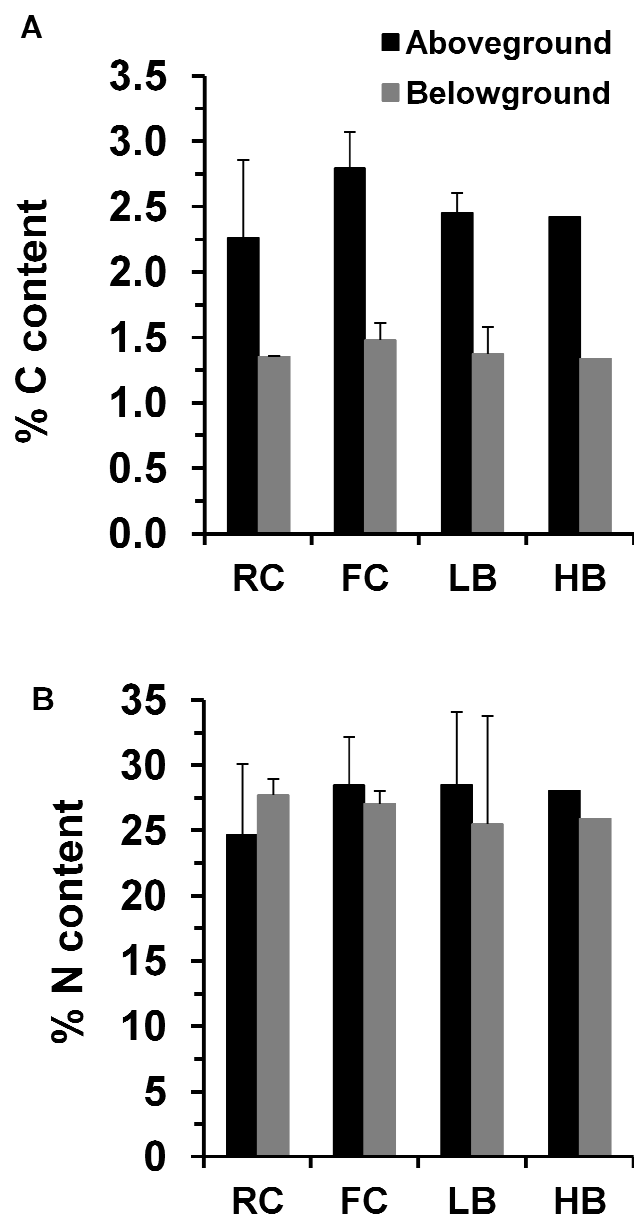


Figure 7.

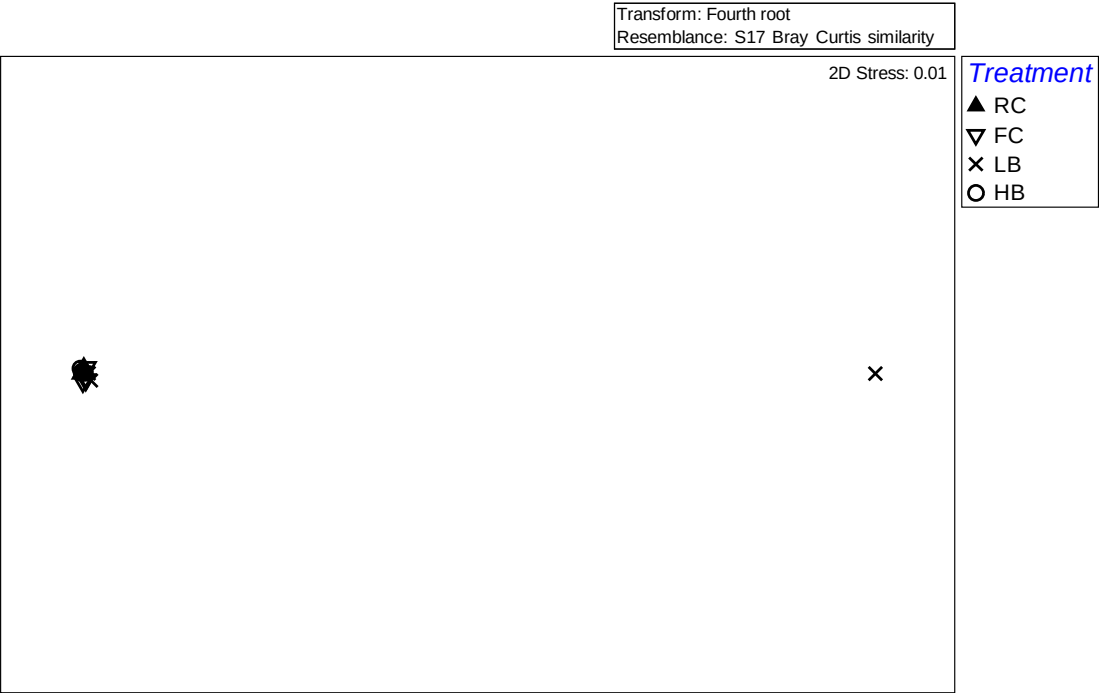


Figure 8.

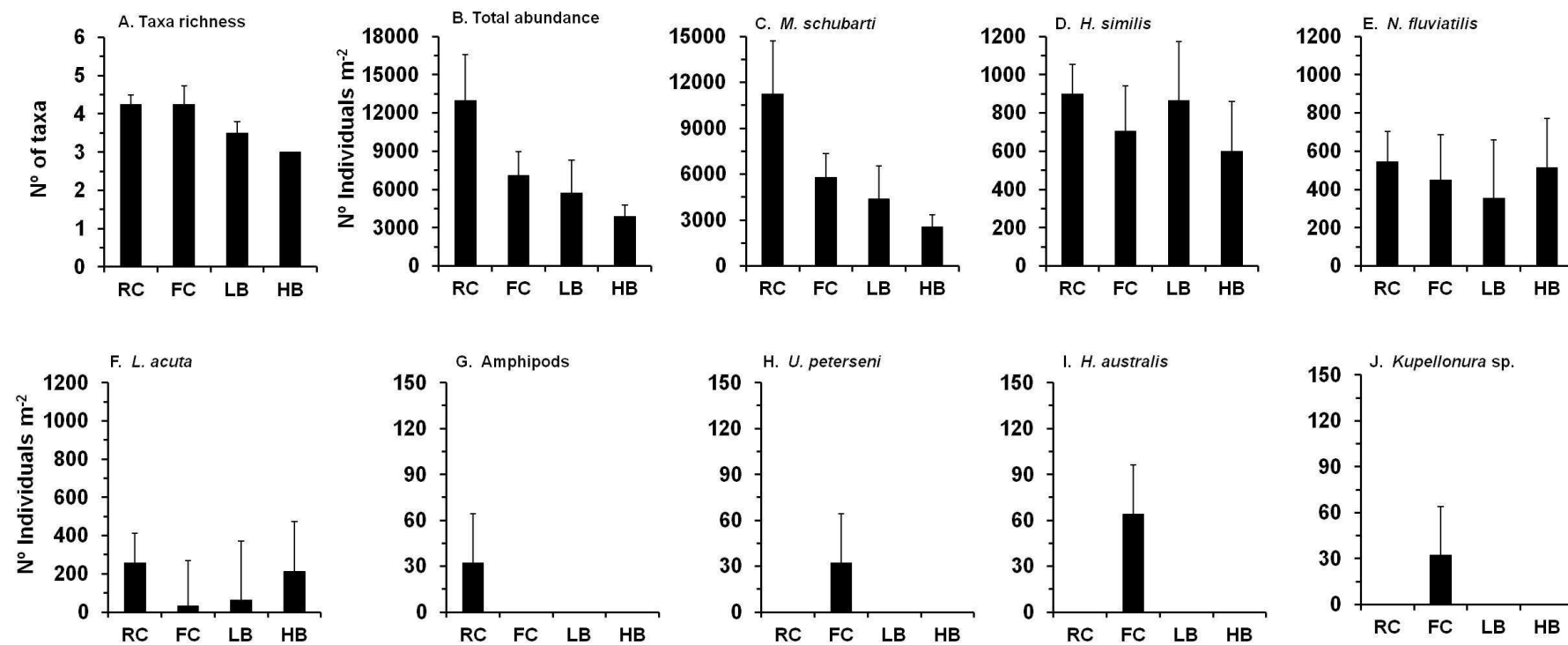


Figure 9.

