

UNIVERSIDADE FEDERAL DO PARANÁ

ANDRÉ MENEGOTTO DOMINGOS

**MULTIPLE STATES OF TROPHIC CONNECTIVITY BETWEEN MANGROVES
AND SALT MARSHES ARE REVEALED THROUGH A SPATIAL AND
TEMPORAL APPROACH**

PONTAL DO PARANÁ

2014

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TEMPORAL APPROACH**

Dissertação apresentada como requisito parcial para obtenção do grau de Mestre em Sistemas Costeiros e Oceânicos. Curso de Pós-Graduação em Sistemas Costeiros e Oceânicos, Centro de Estudos do Mar, Setor de Ciências da Terra, Universidade Federal do Paraná.

Orientador: Prof. Dr. Paulo da Cunha Lana

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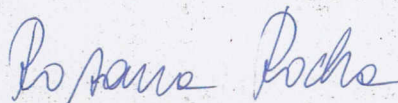
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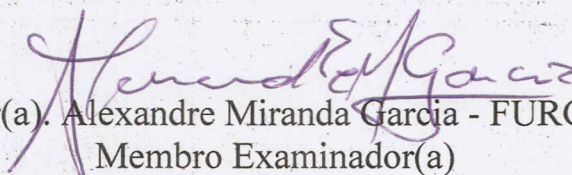
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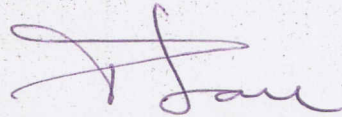
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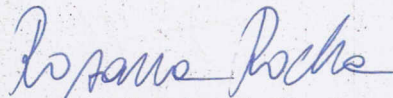
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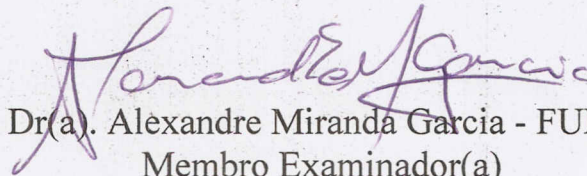
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"You see, but you do not observe.
The distinction is clear."

Sherlock Holmes
(*A Scandal in Bohemia*)

RESUMO

O gradiente de produtividade entre habitats adjacentes como manguezais e marismas pode flutuar sazonalmente, sugerindo que ambos possam ser alternadamente subsidiados ao longo do ano. Embora este processo seja bem conhecido para o subsídio de presas entre rios e matas ciliares, poucos estudos são disponíveis para outros sistemas ou tipos de subsídio. Avaliamos neste trabalho se a entrada de detrito e a assimilação de carbono alóctone por invertebrados bênticos residentes se alternam entre manguezais e marismas adjacentes da Baía de Paranaguá (sul do Brasil), durante os picos de produção de detrito (verão e inverno, respectivamente), usando armadilhas de detrito e isótopos estáveis de carbono. A amostragem foi conduzida nos setores estuarinos de menor (interno) e maior (externo) energia ambiental para avaliar a influência do vetor físico de transporte (correntes de maré) sobre a intensidade do fluxo de subsídios. A doação de detritos de marismas para os manguezais não variou significativamente entre estações, mas foi significativamente maior no setor externo. Do mesmo modo, invertebrados bênticos dos manguezais do setor externo foram mais enriquecidos em $\delta^{13}\text{C}$ que aqueles do setor interno, sem nenhuma variação sazonal significativa. O transporte de detritos do manguezal para as marismas ocorreu principalmente no verão em ambos os setores. Contudo, muito deste detrito permaneceu preso na borda da marisma. Assim, a contribuição sazonal dos manguezais para as marismas foi detectada apenas no setor interno da baía, onde a biomassa de detrito autóctone é baixa. A variação sazonal nos valores isotópicos de carbono também foi significativa apenas nas marismas do setor interno, nas quais os invertebrados são enriquecidos em ^{13}C devido à redução na disponibilidade de folhas do manguezal. Nossos resultados reforçam o modelo de que a conectividade trófica depende muito mais da proporção relativa entre o recurso alóctone (subsídio) e o autóctone do que apenas da produtividade assimétrica entre habitats. Diferenças nesta proporção relativa são resultantes da interação entre produtividade e transporte que levam a muitos estados de conectividade trófica, com um mesmo habitat atuando como doador ou recipiente em diferentes escalas hidrodinâmicas e sazonais.

Palavras chaves: Baía de Paranaguá; Bentos; Detrito; Estuário; Input alóctone; Isótopos estáveis; Subsídio recíproco.

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DISCLAIMER

A presente dissertação foi estruturada conforme o modelo exigido pelo programa de Pós-Graduação em Sistemas Costeiros e Oceânicos da Universidade Federal do Paraná, no qual as dissertações de mestrado ou teses de doutorado devem ser preparadas na forma de um ou mais artigos científicos formatados de acordo com as normas de uma revista alvo previamente determinada, para facilitar e acelerar o processo de publicação. Nesta dissertação apresento um manuscrito já em inglês que pretendemos, inicialmente, submeter à revista *Ecology*, Fator de Impacto (JCR 2012) = 5.175, Qualis CAPES = Estrato A1.

Multiple states of trophic connectivity between mangroves and salt marshes are revealed through a spatial and temporal approach

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Abstract. The productivity gradient between adjacent habitats can fluctuate over time due to seasonal cycles and lead to both habitats being alternately subsidized. Although this process is well known for prey subsidies in stream-riparian forest ecotones, few studies are available for other systems or subsidy types. We assessed if subsidy input and allochthonous carbon assimilation by resident benthic invertebrates alternated between adjacent mangroves and salt marshes during peaks of detritus productivity (summer and winter, respectively) by using detritus trapping techniques and stable carbon isotopes. Sampling was performed in the inner and outer estuarine sectors of the subtropical Paranaguá Bay (southern Brazil) to assess the influence of the physical transport vector (tidal currents) on the intensity of subsidy flow. Marsh litter supply to mangroves did not vary significantly between seasons but was significantly higher in the outer than in the inner sector. Likewise, benthic invertebrates from the outer sector mangroves were more enriched in ^{13}C than those from the inner mangroves, with no significant seasonal variations. Transport of mangrove litter into the salt marsh occurs mainly in the summer in both sectors; however, most of the litter remains trapped in the marsh boundary. Thus, the relative seasonal contribution of mangroves to salt marshes was detected only in the inner sector, where autochthonous litter biomass is lower. The seasonal difference in carbon isotopic ratios was also significant only in the inner marshes, where invertebrate isotopic values are enriched in $\delta^{13}\text{C}$ due to a decrease in available mangrove leaves. Our findings reinforce the model that trophic connectivity relies on the relative proportion of allochthonous (subsidy) and autochthonous resources rather than only on asymmetric productivity between habitats. Differences in this relative proportion result from productivity and transport interactions that lead to many connectivity states in which the same habitat can act as a donor or recipient at different hydrodynamic and seasonal scales.

Keywords: Allochthonous input; Benthos; Detritus; Estuary; Paranaguá Bay; Reciprocal subsidy; Stable isotopes.

Introduction

An innovative concept about ecosystem functioning suggests that food webs can be spatially subsidized, especially where there is a gradient of productivity between adjacent systems. According to this concept, the most productive habitat, the donor, can provide resources (material, energy, or organisms) to a less productive one, the recipient (Polis et al. 1997). Many recent studies have tested this idea and have revealed that subsidy flow can explain the high secondary productivity even in habitats with low primary production (Catenazzi and Donnelly 2007), regulate consumers' densities (Kato et al. 2003), and reduce predation pressure on autochthonous prey (Sabo and Power 2002). A growing number of empirical studies has led to a conceptual framework about the factors controlling subsidy flow and its effects on the recipient habitat (Polis et al. 1997, Talley et al. 2006, Marczak et al. 2007). However, most available studies have focused on land-water interfaces, such as streams and riparian forests (Nakano and Murakami 2001, Sabo and Power 2002, Kato et al. 2003) or land-sea ecosystems (Polis and Hurd 1995, Catenazzi and Donnelly 2007, Paetzold et al. 2008). More studies are needed in other habitats (e.g., Earl and Semlitsch 2012, Giery et al. 2013) to balance the current bias on the knowledge about spatial subsidies (Marczak et al. 2007).

In this study, we investigated the trophic connectivity between adjacent mangroves and salt marshes from a subtropical bay, considering detritus as a resource for benthic invertebrates. In estuaries, the allochthonous input from highly productive coastal vegetation can benefit adjacent communities (Connolly et al. 2005) because many estuarine benthic animals do not move actively among habitats. However, the importance of allochthonous organic matter input in estuarine sediments is still controversial. Although reciprocal matter exchange (Hemminga et al. 1994, Slim et al. 1996) and allochthonous carbon assimilation by invertebrates (Connolly et al. 2005) have been documented, some studies suggest that only

autochthonous production is used because resource exchanges seem to never occur beyond the distance of 5 m at the interface of estuarine habitats (Guest and Connolly 2004).

However, the rates of primary production and thus detritus production are known to be highly variable over time. There is evidence that the mangrove litter contribution to an adjacent tidal flat occurs only in the summer, during the litterfall peak in the donor and low autochthonous production in the recipient habitat (Mfilinge et al. 2005). Detritus production by *Spartina* salt marshes occurs mainly in the winter when their leaves die (Dame 1982, Lana et al. 1991). Thus, the magnitude and/or frequency of subsidy flow can fluctuate seasonally according to the productivity in each system. The seasonal asynchrony in productivity of mangroves and salt marshes, which co-occur in subtropical estuaries, might result in both habitats being alternatively subsidized (Lana 2003), with resource exportation in high-productivity seasons and resource importation in low-productivity ones (see Nakano and Murakami 2001). Thus, we hypothesize that low autochthonous resources and a high subsidy input are expected in salt marshes in the summer and mangroves in the winter (H1).

In addition, the strength and frequency of tidal inundation can affect detritus exportation in intertidal vegetated systems (Lee 1995). In mangroves and salt marshes, limited inundation may reduce the exportation rate (Taylor and Allanson 1995) and enhance the accumulation of autochthonous organic matter (Bouillon et al. 2003). In highly dynamic regions, isotopic values of the sediment organic matter will not necessarily originate from the dominant local vegetation (Middelburg et al. 1997, Bouillon et al. 2003). Thus, the level of subsidy exchange might be higher in more energetic regions than in low-energy ones. Consequently, we also hypothesize that seasonal variations in subsidy exchange will be greater in the high-energy estuarine sector, where the physical transport vector effect is correspondingly higher (H2). Although the biological and physical transport vectors are commonly reported in the literature as extremely important for subsidy delivery (Witman et

al. 2004), there are few empirical tests available about effects of different transport vector intensities on subsidy flow (e.g., upwelling, Pulgar et al. 2011).

To test these two hypotheses of trophic subsidy exchange between mangroves and adjacent salt marshes, we first used trap-nets displayed within both habitats to quantify the amount of detritus transported in different estuarine sectors (high and low energy) and in different seasons (summer and winter). Secondly, we assessed the relative importance of autochthonous versus allochthonous resources in the diet of resident benthic invertebrates through carbon and nitrogen stable isotope analysis. Carbon isotopic ratios vary substantially among primary producers and can be used to determine original sources of dietary carbon in each habitat, either the C₄ *Spartina* or the C₃ mangrove trees. Nitrogen isotopic ratios, which increase with trophic transfers (Layman et al. 2012), can be additionally used to estimate the relative contribution of each food source to an animal diet.

Materials and Methods

Study area

The study was conducted in the Paranaguá Bay Estuarine Complex (Fig. 1), a subtropical estuarine system surrounded by 295.5 km² of mangroves and salt marshes (Noernberg et al. 2006). These mangroves display distinct structural heterogeneity along the bay and are composed of mono- and plurispecific stands of *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia schaueriana* (Martin 1992). The highest monthly averages of litterfall (values up to 50 g.m⁻²) occur from December–February (austral summer) and peak at 86 g.m⁻² in January (Sessegolo 1997). *Spartina alterniflora* marshes occur as monospecific, discontinuous belts in front of mangrove forests. Conversely, average marsh litter production up to 50 g.m⁻² occurs from May–July (late autumn/winter) and peaks at 82 g.m⁻² in May (Lana et al. 1991).

Autumn and winter are dry seasons, while a typical rainy season lasts from spring to summer with mean precipitation about three times higher than that of the dry season, from 280 up to 800 mm, respectively (Vanhoni and Mendonça 2008). A spatial salinity-energy gradient from freshwater to marine conditions divides the bay into: a) an oligo-mesohaline low-energy inner sector, which is subjected to greater influence of continental drainage and composed of silt-clay sediments; b) a middle polyhaline sector; and c) a euhaline high-energy outer sector, where sediments are dominated by fine sand (Netto and Lana 1997, Lana et al. 2001). Local tides are semi-diurnal mixed and display a mean range of 1.7 m in the outer sector to 2.7 m in the inner sector, with maximum current velocities of $0.8\text{--}0.85\text{ m}\cdot\text{s}^{-1}$ at ebb and $1\text{--}1.4\text{ m}\cdot\text{s}^{-1}$ at flood (Lana et al. 2001). Although current velocities increase toward the sheltered inner sector, only the high-energy outer sector is exposed to wave action (Lana et al. 2001).

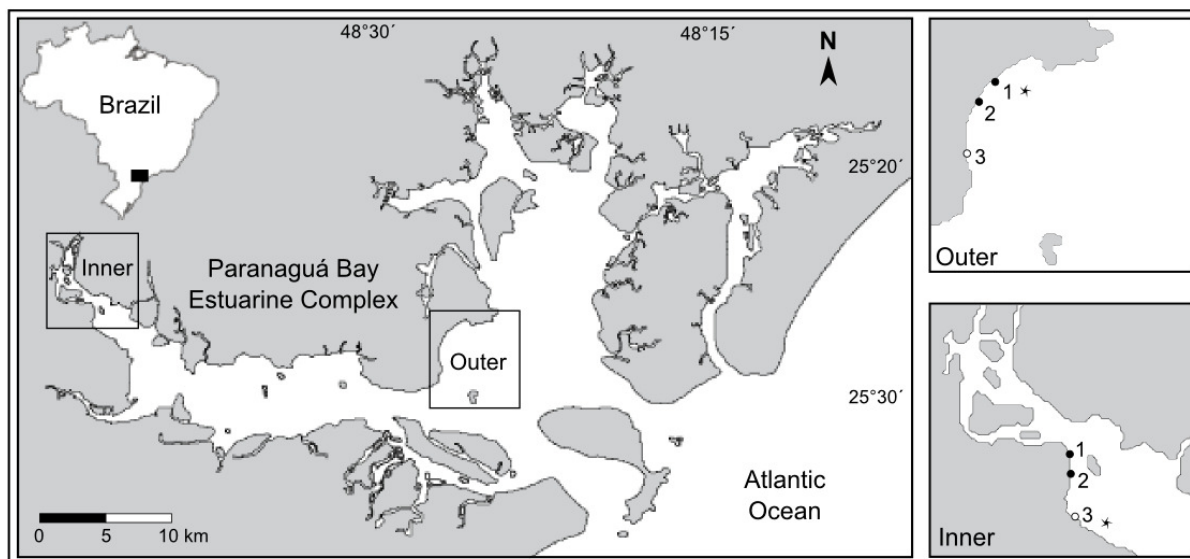


Fig. 1 Map of the Paranaguá Bay showing details of the inner and outer sectors; circles indicate sampling stations for the macro-detritus, and black stars indicate the position of the S4 current meter. Solid circles represent sampling sites for the stable isotope analysis.

Macro-detritus sampling

A hierarchical sampling design was used to estimate the spatial variability in macro-detritus exchange between mangroves and salt marshes, comprising two sectors (inner = low energy and outer = high energy; scale of tens of kilometers), three stations in each sector (scale of hundreds of meters), and two transects separated by 10 m in each station (Fig. 1). At each transect, we collected macro-detritus at the salt marsh-mangrove interface and at 5, 10, and 15 m into both salt marsh and mangrove habitats (Fig. 2a) to assess if allochthonous macro-detritus enters the recipient habitat and does not remain at the interface.

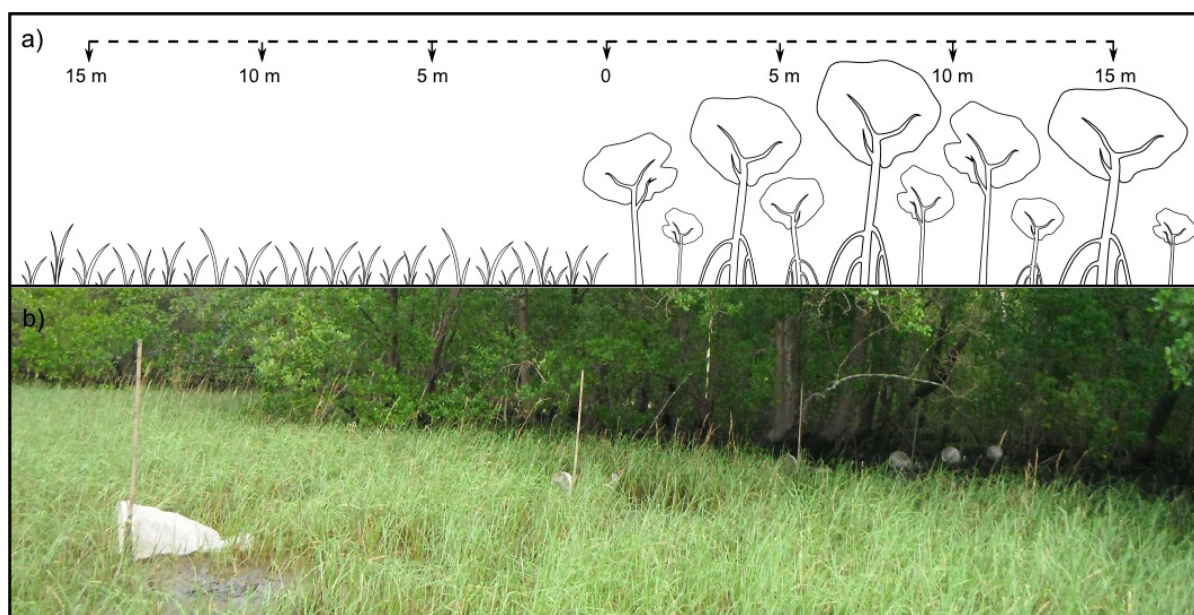


Fig. 2 Position of trap-nets in transects (a) and a view of their displacement in the field at low tide (b). Photo credit: Gisele C. Morais.

Macro-detritus was collected with nets (0.4 m in diameter and 1.5 m long; mesh size of 0.5 mm) set at the bottom during the low tide with their openings oriented toward the water flow (Fig. 2b). Before the slack water during the high tide, the nets were pulled up, carefully emptied, and turned around to sample the ebb tide.

This procedure was performed simultaneously in both sectors at three consecutive spring tides in the austral summer (25/01; 07/02; 25/02/2013) and winter (08/05; 22/05;

07/06/2013) when the mangrove litterfall and *Spartina* senescent leaves peak, respectively (Lana et al. 1991, Sessegolo 1997). Sampling occurred only at spring tides, when the tidal flow and detritus transport are higher (Whitfield 1988). Moreover, during most of the neap tides, the estuarine water does not reach into the mangrove forest. During each sampling, an S4 InterOcean current meter was positioned 0.5 m above the bottom at unvegetated flats in each sector and programmed to record the mean current velocity every 10 min.

In the laboratory, the macro-detritus was rinsed on a 0.5-mm sieve, sorted under a stereomicroscope, and dried to constant weight at 60 °C. Detritus dry weight was converted to a $\text{g}\cdot\text{m}^{-2}$ -estimate per tidal cycle. Only leaf biomass from the mangrove macro-detritus was used in the statistical analyses since it is the main litter component, can degrade faster than other components and, therefore, has a higher potential to represent the source of carbon for the fauna than other debris. *Spartina* detritus was not sorted and was considered total marsh litter.

Determination of stable isotopic ratios

A hierarchical design was used to evaluate the effects of variation in detritus productivity on carbon assimilated by resident benthic invertebrates. At each station (Fig. 1), three samples of benthic consumers and primary producers were collected in both mangrove and salt marsh habitats at a distance of 10–15 m from the interface to avoid possible edge effects (Guest and Connolly 2004). The sampling was performed throughout the first and last weeks of April and August of 2013, about three months after the peak in detritus production in mangroves and salt marshes, respectively (Lana et al. 1991, Sessegolo 1997). This interval was based on two important assumptions for temporal surveys involving stable isotopic ratios and benthic ecology: time for decomposition processes before detritus becomes fit for consumption (Wafar et al. 1997) and carbon turnover rates in invertebrates (Hentschel 1998).

Target species were chosen considering their relative restricted mobility and high density in each habitat. The deposit-feeder crab *Uca thayeri* (Ocypodidae) was chosen for analysis in mangroves from both sectors. Only adult males were collected, and each sample was composed of one individual. Unfortunately, we did not identify any species in high density and in a wide enough distribution range to choose as target species for this analysis in all salt marshes. Thus, different species were chosen in salt marshes from the inner and outer sectors, namely the predator polychaete *Nephtys fluviatilis* (Nephtyidae) and the deposit-feeder polychaete *Isolda pulchella* (Ampharetidae), respectively. About 10 individuals from each of these two species (lengths up to 20 and 10 mm, respectively) were collected and pooled as one sample. The choice of a secondary consumer was not a major issue because *N. fluviatilis* is a predator of deposit-feeder polychaetes (Schubert and Reise 1986); therefore, its primary organic matter source can be identified using the isotopic enrichment across these two trophic levels.

Leaf samples were collected from different individual plants of *S. alterniflora* and the three mangrove species and were washed with distilled water, whereas invertebrates were collected by hand or with a sieve. All samples were frozen after sampling except the polychaetes, which were maintained in filtered estuarine water for 24 h before freezing to allow the extrusion of gut contents. This procedure was not applied to crabs because the soft flesh from the chelae was selected for analysis. Samples were dried at 60 °C for 24–48 h (leaves) or freeze-dried (invertebrates) and ground to a fine powder using a mortar and pestle. These two drying techniques do not cause significant differences in isotopic values of macroinvertebrate samples (Carabel et al. 2006) or cause differences less than 1‰ (de Lecea et al. 2011). Therefore, considering the great isotopic distinction between mangroves and salt marsh plants, we do not consider these different techniques a source of bias. All samples were placed in tin capsules, and their carbon isotopic values were determined using a Carlo

Erba elemental analyzer coupled with a Delta Plus mass spectrometer at the Isotopic Ecology Laboratory, CENA-USP. In addition, nitrogen isotopic values from primary producers and invertebrates were analyzed for the calculation of the relative contribution of resources (see data analysis). The isotopic ratio was expressed in the δ notation relative to the international standards Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen, where $\delta^{13}C$ or $\delta^{15}N$ = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$ and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The analytical precision determined from the analysis of duplicate samples was $\pm 0.17\text{‰}$ for carbon and $\pm 0.23\text{‰}$ for nitrogen.

Data analysis

Two procedures were used to test the potential macro-detritus exchange between mangroves and salt marshes. First, we ran an analysis of variance (ANOVA) testing the variability of allochthonous macro-detritus biomass inside the recipient habitat to discriminate factors affecting the subsidy transport. The analyzed factors were sector (fixed, two levels), site (random, three levels, nested in sector), season (fixed, two levels), day (random, three levels, nested in season), distance (fixed, four levels), and tide (fixed, two levels); transects were considered replicates. Second, we ran an ANOVA testing for differences in biomass between two macro-detritus types, inside each habitat, to assess the dominant resource and the factors affecting its dominance. A similar linear model was adopted including the nature of the macro-detritus as a factor (fixed, two levels), interpreting only terms with macro-detritus interaction. We used nested levels to avoid pseudoreplication and emphasized processes that occur at the scales of sectors and seasons. Homoscedasticity was evaluated by the Cochran's C test, and the fourth-root transformation was used to decrease the variance heterogeneity. After transformation, homoscedasticity was not met only for marsh litter data inside the mangroves. However, despite the fact that heterogeneous variance increases the Type I error, a balanced ANOVA design is considered robust

regarding these violations (Underwood 1997). When necessary, appropriate denominator mean squares and degrees of freedom were constructed for approximate F -ratios by the Satterthwaite method.

To test whether resource exchanges effectively altered carbon and nitrogen isotopic values of the resident invertebrates, an ANOVA was performed for these response variables considering the sector (fixed, two levels), site (random, two levels, nested in sector), season (fixed, two levels), and day (random, two levels, nested in season). Homoscedasticity was evaluated, and no transformation was necessary. The Student-Newman-Keuls (SNK) post hoc procedures were used to determine the rank order among treatment levels when significant ($p < 0.05$) macro-detritus exchange and stable isotope value differences were found. All statistical analyses were done using a beta version of GAD 1.1.1 (Sandrini-Neto and Camargo 2012), a package in R 3.0.3 software (R Development Core Team 2014).

We employed a Bayesian mixing model using SIAR 4.2 (Stable Isotope Analysis in R, Parnell and Jackson 2013) to estimate the relative contribution of subsidies as food sources to target species. This model takes into account the variability in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from resources and consumers and also allows for incorporation of the fractionation factor (Parnell et al. 2010). For the mixing analysis, we used the mean values from the *S. alterniflora* and mangrove trees isotopic data from this study but also included isotopic data of benthic diatoms from the literature to prevent neglecting the microphytobenthic contribution (see Appendix A). In accordance with methods described in Phillips et al. (2005), we combined *R. mangle* and *A. schaueriana*, since their isotopic values are similar. It was not possible to create a related group of carbon source including all three mangrove species because *L. racemosa* is ^{15}N -enriched (see results). Because methods for microphytobenthic extraction may be liable to contamination (Oakes et al. 2005), we used the isotopic data from benthic diatoms ($\delta^{13}\text{C} = -14.80\text{‰} \pm 2.70$; $\delta^{15}\text{N} = 7.70\text{‰} \pm 2.08$) reported by Ito (2002); these data

were obtained from benthic diatoms cultured in dialysis membrane tubes set in an estuarine environment. The $\delta^{13}\text{C}$ fractionation values were considered $0.4\text{‰} \pm 1.3$ for all species (Post 2002), while $0.53\text{‰} \pm 1.26$ and $1.59\text{‰} \pm 1.04$ were the $\delta^{15}\text{N}$ fractionation values adopted for ammonotelic detritivorous and carnivorous species, respectively (Vanderklift and Ponsard 2003). Because we were interested in assessing the organic matter source, we summed fractionation values of carnivorous and detritivorous species to remove the two trophic level enrichments of the predator *N. fluviatilis*.

Results

Macro-detritus exchange

Current velocity in the outer sector was higher during the flood than the ebb tide but with little difference between them (mean of $0.13 \text{ m}\cdot\text{s}^{-1}$ at ebb, $0.15 \text{ m}\cdot\text{s}^{-1}$ at flood). Conversely, in the inner sector, the flood was always lower than the ebb tide, varying from $0.17\text{--}0.27 \text{ m}\cdot\text{s}^{-1}$ (the highest recorded current velocity).

The presence of mangrove leaves inside the salt marshes differed significantly between seasons ($F_{1,08, 5.78} = 28.524$, $p = 0.002$). As expected, the highest biomass was recorded in the summer ($3.15 \pm 0.41 \text{ g}\cdot\text{m}^{-2}\cdot\text{tide}^{-1}$), and a significant reduction was recorded in the winter ($0.9 \pm 0.14 \text{ g}\cdot\text{m}^{-2}\cdot\text{tide}^{-1}$). This seasonal difference was significant at 0, 10, and 15 m but not at 5 m inside the salt marsh. No differences were detected between sectors, and spatial differences were significant only among distances ($F_{3,12, 23.61} = 68.998$, $p < 0.001$). The highest leaf biomass was recorded at the interface, and a significant and progressive decrease in mangrove leaves was observed from the interface to across the neighboring habitat (SNK-test, $0 > 5 \text{ m} > 10 \text{ m} = 15 \text{ m} / 4.89 \pm 0.77 > 1.32 \pm 0.24 > 0.88 \pm 0.17 = 1 \pm 0.2 \text{ g}\cdot\text{m}^{-2}\cdot\text{tide}^{-1}$). The results also indicated significant differences between tides within sectors ($F_{1,09, 7.94} = 7.457$, $p = 0.024$). In general, more mangrove leaves were transported during the ebb tide

than during the flood tide; however, this difference was only significant in the inner sector, where the ebb values ($3.99 \pm 0.55 \text{ g.m}^{-2}$) were remarkably higher than flood values ($0.42 \pm 0.08 \text{ g.m}^{-2}$). A complete table with the all ANOVA results is provided in Appendix B.

Despite the seasonal variation, the availability of mangrove leaves was never significantly higher than the availability of marsh litter inside the salt marshes, even in the summer (Fig. 3). The only interaction between the macro-detritus type and season was detected at the interface ($F_{19,11, 23.75} = 4.415, p = 0.007$), where there was no significant difference between the marsh and mangrove litter in the summer; however, higher marsh litter biomass was recorded in the winter. Nevertheless, the predominance of detrital resource differed significantly between sectors ($F_{1,02, 5.36} = 22.293, p = 0.004$). Although mangrove leaves did not differ spatially, the marsh litter biomass was higher than that of the mangrove and was the predominant resource in the outer-sector salt marshes (Fig. 3a). In the low-energy inner sector, less marsh litter was trapped, and no significant differences between autochthonous and allochthonous macro-detritus were detected inside the salt marshes.

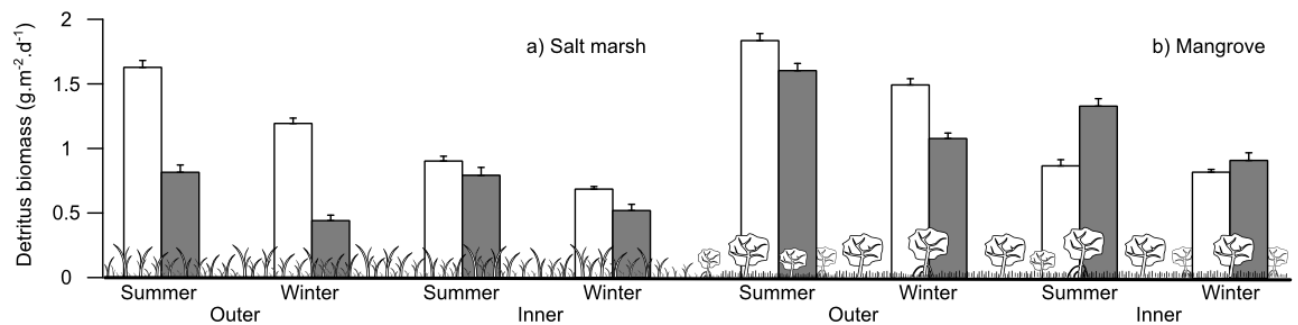


Fig. 3 Mean (\pm SE) marsh litter \square and mangrove leaf \blacksquare dry weight biomass inside salt marshes (a) and mangroves (b) from the outer and inner sectors of the bay during summer and winter. Fourth-root transformed data.

The marsh litter biomass inside the mangroves did not change significantly between seasons ($F_{1,33, 5.79} = 1.054, p > 0.05$). However, it differed significantly between sectors ($F_{1,02, 4.42} = 20.888, p = 0.008$), with higher values in the outer ($17.13 \pm 2.3 \text{ g.m}^{-2}.\text{tide}^{-1}$) compared

to the inner sector ($2.09 \pm 0.45 \text{ g.m}^{-2}.\text{tide}^{-1}$). Marsh litter biomass was significantly dependent upon the distance versus tide interaction in the outer sector ($F_{3,98, 20.07} = 4.209, p < 0.012$). The amount of trapped biomass increased from the interface into the mangrove habitat in the flood tide (SNK-test, $0 = 5 \text{ m} < 10 \text{ m} < 15 \text{ m} / 14.18 \pm 2.98 = 13.16 \pm 3.14 < 23.37 \pm 4.87 < 53.12 \pm 15.48 \text{ g.m}^{-2}$) but did not differ significantly among distances in the ebb tide or in the inner sector.

The predominant type of macro-detritus inside the mangroves was a reflection of spatial variability in marsh litter between sectors ($F_{1,04, 5.53} = 10.142, p = 0.021$). Marsh litter biomass was the main macro-detritus in mangroves from the high-energy sector, whereas mangrove leaves (the autochthonous resource) were dominant in mangroves from the inner sector of the bay (Fig. 3b). The significant interaction between macro-detritus and tide, detected inside the mangroves and salt marshes (see Appendix C), resulted from higher mangrove leaf biomass at the ebb tide than at the flood tide.

Stable isotopes composition

The $\delta^{13}\text{C}$ values for the dominant autotrophs could be clearly separated into enriched salt marsh grass (*S. alterniflora* = $-14.1\text{‰} \pm 0.1$) and depleted mangrove trees (*R. mangle* = $-29.98\text{‰} \pm 0.24$; *L. racemosa* = $-30.03\text{‰} \pm 0.24$; *A. schaueriana* = $-30.28\text{‰} \pm 0.24$). Nitrogen isotope values were independent of plant groups, as *A. schaueriana* ($1\text{‰} \pm 0.63$) and *R. mangle* ($0.8\text{‰} \pm 0.61$) were depleted relative to *Spartina* ($4.03\text{‰} \pm 0.22$) and *L. racemosa* ($5.58\text{‰} \pm 0.23$) especially in the inner sector, where the former two species had ^{15}N depletions of 2‰ and 1.6‰ , respectively (see Appendix A).

The $\delta^{13}\text{C}$ values for *Isolda pulchella* inside the salt marsh did not vary significantly in the outer sector between seasons ($-18.68\text{‰} \pm 0.05$). However, *Nephtys fluviatilis* varied from -19.43‰ to -18.63‰ in summer and enriched significantly to a range of -18.25‰ to -15.30‰

in the winter at salt marsh sites of the inner sector ($F_{2,4} = 13.182$, $p = 0.017$). *N. fluviatilis* $\delta^{15}\text{N}$ values were 4.4‰ higher than *I. pulchella* ($F_{1,2.08} = 1000.398$, $p < 0.001$), which were enriched 0.93‰ at station 1 in the winter ($F_{2,4} = 10.893$, $p = 0.024$). The results of the SIAR mixing model showed that autochthonous *Spartina* was the main carbon source in the diet of *I. pulchella* in the outer-sector salt marshes, with 39–66% of contribution (95% credibility interval). In the inner sector, the main carbon source to *N. fluviatilis* was the autochthonous microphytobenthos (35–68%), and *L. racemosa* was the second source in the summer (21–39%). The relative contribution of the mangrove tree was lower in the winter (8–27%) when *Spartina* (4–37%) became the second carbon source (Fig. 4).

The $\delta^{13}\text{C}$ values of mangrove crabs were more enriched in the outer compared to the inner sector (outer, -19.81‰ to -16.95‰; inner, -24.46‰ to -17.47‰), although the significance of this difference was influenced by sampling date ($F_{2,4} = 14.673$, $p < 0.014$). *Uca thayeri* was significantly more enriched in ^{15}N in the inner ($6.9\text{‰} \pm 0.16$) compared to the outer-sector mangroves ($4.45\text{‰} \pm 0.11$) ($F_{1.01,4} = 239.968$, $p < 0.001$). The allochthonous *Spartina* carbon contributed with 40–70% to the diet of crabs in the outer sector and <35% in the inner sector, where the diet was mainly composed of autochthonous mangrove (18–40%) and microphytobenthic (33–63%) components (Fig. 4).

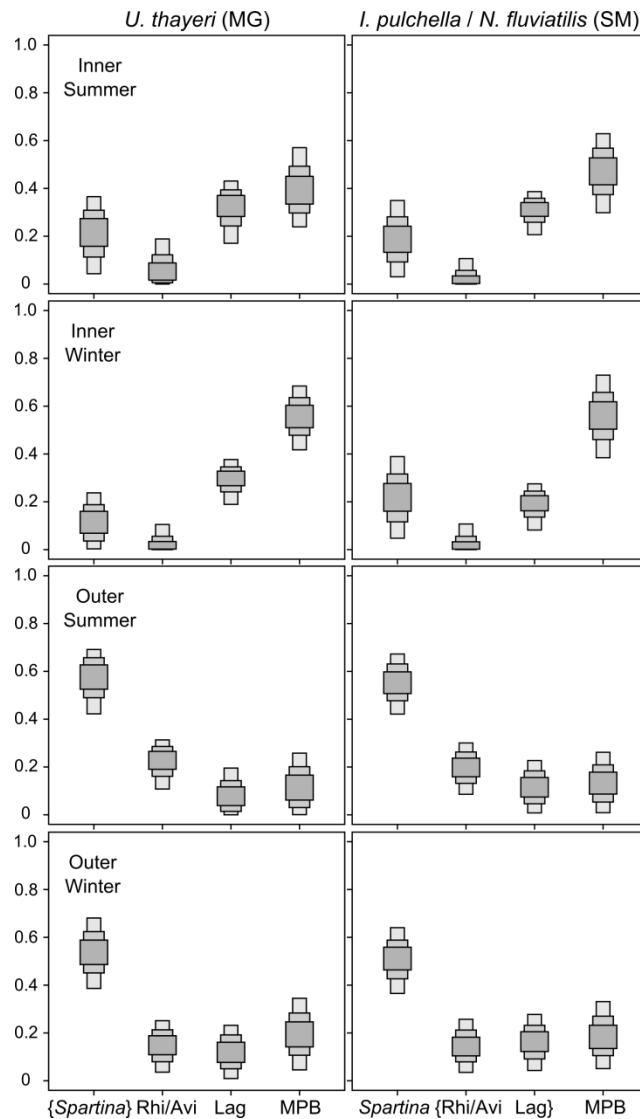


Fig. 4 Results of SIAR mixing models (with 95%, 75%, 50% credibility intervals) showing proportions of autochthonous and allochthonous (between curly brackets) food sources in the diet of resident benthic invertebrates of adjacent mangroves (MG) and salt marshes (SM) from the outer and inner sectors of the bay during summer and winter. *Spartina* = *S. alterniflora*, Rhi/Avi = *R. mangle*/*A. schaueriana*, Lag = *L. racemosa*, and MPB = microphytobenthos.

Discussion

Some studies on trophic connectivity between habitats (Nakano and Murakami 2001, Kato et al. 2003) suggest a cyclic pattern of subsidy flow, which can be seasonally reversed due to a shift in productivity gradients. Although our results support the idea that both mangroves and salt marshes are subsidized, we partially rejected the working hypotheses that mangroves and salt marshes might be alternatively subsidized due to seasonal asynchrony in

productivity (H1), with greater subsidy exchange in the high-energy estuarine sector (H2). Only mangrove leaves are supplied to adjacent salt marshes during litter production peaks, while only marsh litter is subsidized to mangroves in the outer estuarine sector.

Many environmental drivers may affect the responses of marsh and mangrove litter to differing seasonal and hydrodynamic conditions. At first glance, the high marsh litter biomass trapped in nets in the high-energy sector may reflect variations in salt marsh productivity along the bay (Netto and Lana 1999); the taller and denser *S. alterniflora* stands in the inner sector of the bay compared to stands in the outer sector could also limit litter transport. Local salt marshes are, in fact, more productive in the inner sector (Netto and Lana 1999), but differences in marsh cover do not necessarily affect flow and particle transport (Leonard et al. 2002). This paradox may result from differences in physical conditions between the two sectors of the bay. The outer sector is more exposed to strong winds and storms; in addition, turbulence generated by wind-waves coupled with low tidal ranges are more effective in mechanically detaching dead and alive *Spartina* leaves, which are always present inside the mangroves and in the traps, regardless of season. Conversely, mangrove leaves will be available for tidal transport only after falling upon ground; thus, the amount of transported mangrove litter may reflect seasonal senescence more precisely. The differing responses of detritus types to seasonality and transport dynamics open different possibilities of direction and periodicity in subsidy flow. This complex and unexpected pattern may lead to a better understanding of trophic connectivity between mangroves and salt marshes.

Marsh litter is supplied to mangroves in the outer sector in both seasons, regardless of the amount of autochthonous mangrove production. On the other hand, autochthonous mangrove leaves were always the main detritus source inside the mangroves in the inner, low-energy sector. The isotopic data are clearly consistent with this spatial variation in marsh supply to local mangrove forests. Carbon isotopic ratios of crabs displayed a similar spatial

pattern with carbon enrichment in the outer sector. Since mangrove trees are depleted in $\delta^{13}\text{C}$, this carbon enrichment indicates the contribution from a richer source, such as the C_4 salt marshes. Marsh consumption already has been recorded in other *Uca* species (Weis et al. 2002). Allochthonous marsh litter greatly contributed to the crabs' diet in the outer sector, whereas a dietary shift was recorded in the inner-sector mangroves, with a small subsidy input (see Bouillon et al. 2004). In general, the diet of mangrove crabs in the inner sector was mainly composed of microphytobenthic- and mangrove-derived carbon.

The supply of mangrove leaves to salt marshes was tremendously limited by the low permeability of the marsh vegetation, even during peaks of mangrove litterfall. This pattern was spatially consistent along the bay, but since marsh litter was always the predominant resource inside marshes, there was no diet shifts or depletion of values in the benthic isotopic data in the outer sector. On the other hand, there were no differences in the amount of autochthonous and allochthonous detritus inside the salt marshes from the inner sector, where marsh litter availability was always low. The differences in the relative contribution of resource sources increased only in the winter, when the amount of mangrove leaves decreased. Variation patterns in detritus availability are consistent with variations in the benthic isotopic ratios, as shown by the clear ^{13}C -enrichment of *N. fluviatilis* in the winter. Although mangrove-derived detritus is not the main carbon source to the predator *N. fluviatilis*, its contribution to the worm diet is reduced nearly by half in the winter. Enriched $\delta^{13}\text{C}$ values of -14.65‰ were recorded for *N. fluviatilis* in *Spartina* marshes without associated mangroves in southern Brazil (Hoeinghaus et al. 2011). Despite the low nutritional quality of mangrove leaves (Alongi et al. 1989), their higher availability in the inner marshes in the summer clearly influenced the isotopic ratios of *N. fluviatilis*. This suggests that the quality over quantity paradigm (Marcarelli et al. 2011) does not always apply, at least when

generalist species such as capitellid polychaetes, the preferred prey of nephtyids (Schubert and Reise 1986), are involved. However, this hypothesis still requires empirical tests.

The interpretation of our data could be affected by other potential carbon sources on the diet of target species, such as seagrasses. However, extensive seagrass meadows are absent from the bay and only occur as small patches of *Halodule wrightii* (Sordo et al. 2011). Mangrove and marsh litter accounted for 95% of all plant components trapped in the studied habitats. Microphytobenthos was the only potential carbon source not analyzed directly in this study. Though we have used isotopic values from the literature, the large contribution of microphytobenthic carbon in the inner sector matched the field's visual record of a dense biofilm over the sediment. Temporal variation in carbon isotopic ratios of benthic microalgae is common and may induce seasonal changes (Claudino et al. 2013). However, such variation may not be associated with ^{13}C enrichment in *N. fluviatilis* because microphytobenthic carbon is known to become depleted in winter (Oakes et al. 2005). The use of different target animals, such as crabs and polychaetes, could also imply a bias in stable isotope results due to metabolic differences, but the extent of such variation is still poorly understood. However, since the stable isotope and mixing model results closely agree with detritus dynamics, our results may well represent the trophic connectivity between mangroves and salt marshes.

Most available reports on trophic subsidy studies focused on unidirectional flow between habitats (Sabo and Power 2002, Kato et al. 2003, Paetzold et al. 2008). The few studies that addressed bidirectional flows dealt mainly on stream ecosystems with prey as the unit of flux (Marczak et al. 2007). Ours is the first study to test subsidy reciprocity in an estuarine environment at different spatial and temporal scales. Previous studies about carbon exchanges between mangroves and salt marshes suggested that assimilation of the allochthonous carbon by resident fauna is strongly restricted to the interface between these habitats (< 5 m, Guest and Connolly 2004). We have shown that this is not always the case.

Multiple states of trophic connectivity may be present depending on the spatial (hydrodynamic) and temporal (seasonal detritus) scales involved. Intertidal habitats from a subtropical estuary can vary; they can be donors, recipients, seasonally connected, or seasonally disconnected (Fig. 5). Trophic disconnection may be an expected pattern in sheltered environments (Guest and Connolly 2004), at least during periods of low detritus availability.

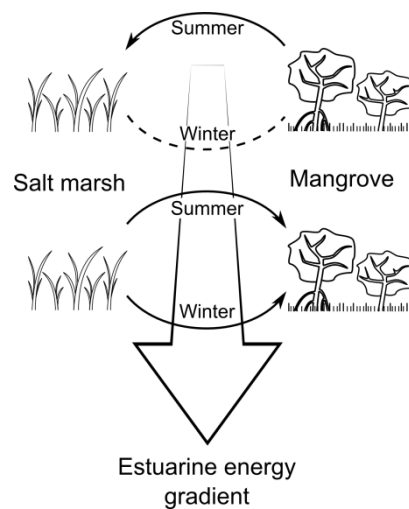


Fig. 5 Conceptual drawing of the trophic connectivity between mangroves and salt marshes based on the flux of detritus subsidies to deposit-feeder invertebrates. Arrows indicate the flow direction, and the dashed line indicates trophic disconnection.

In summary, the subsidy flow from donor to recipient habitats is not simply related to asymmetry in habitat productivity (Polis et al. 1997). Conversely, our results exemplify a little explored pattern, in which trophic connectivity relies on the relative proportion of subsidy and autochthonous resources (Marczak et al. 2007). This proportion is affected by subsidy availability, which does not necessarily result only from the productivities of adjacent habitats. For instance, although the amount of marsh detritus is higher in inner estuarine regions (Netto and Lana 1999), it is more available to resident benthic fauna from mangrove stands in the high-energy sector. Likewise, only a small fraction of subsidy from the high litter-producing mangroves can cross the low permeable boundary of the salt

marshes. Thus, subsidy availability clearly seems to result from an interaction between productivity of adjacent habitats, interface permeability, and transport vector (Witman et al. 2004). In most available studies, the analyzed vector (Paetzold et al. 2008, Giery et al. 2013) or subsidy are mobile invertebrates, such as insects (Nakano and Murakami 2001, Sabo and Power 2002, Kato et al. 2003), which can be highly efficient in transferring donor productivity with seasonal precision (Nakano and Murakami 2001). However, limitations on subsidy transport due to weak vectors or low permeability at the habitat interface may reduce resource availability regardless of the productivity (see Kato et al. 2003). These complex interacting factors may affect the relative proportion of autochthonous and subsidy resources, thus generating multiple states of trophic connectivity.

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Supplemental Material

Appendix A

Appendix A. Carbon and nitrogen isotopic ratios (overall mean \pm SE) of primary producers and target benthic invertebrates of adjacent mangroves and salt marshes from the outer and inner sectors of Paranaguá Bay during summer and winter.

	n	Inner/Summer	Inner/Winter	Outer/Summer	Outer/Winter
$\delta^{13}\text{C}$					
Primary producers					
<i>Spartina alterniflora</i>	6	-14.50 \pm 0.23	-13.65 \pm 0.12	-13.91 \pm 0.09	-14.20 \pm 0.17
<i>Avicennia schaueriana</i>	6	-30.48 \pm 0.45	-30.28 \pm 0.77	-29.85 \pm 0.22	-30.51 \pm 0.36
<i>Laguncularia racemosa</i>	6	-29.51 \pm 0.51	-29.60 \pm 0.54	-30.66 \pm 0.33	-30.35 \pm 0.48
<i>Rhizophora mangle</i>	6	-29.44 \pm 0.58	-30.14 \pm 0.43	-29.80 \pm 0.49	-30.55 \pm 0.35
MPB*	6	-14.80 \pm 2.70			
Target species					
<i>Uca thayeri</i>	12	-20.26 \pm 0.56	-19.29 \pm 0.35	-18.65 \pm 0.23	-18.02 \pm 0.18
<i>Nephtys fluviatilis</i>	6	-19.02 \pm 0.07	-17.09 \pm 0.26	-	-
<i>Isolda pulchella</i>	6	-	-	-18.73 \pm 0.07	-18.63 \pm 0.06
$\delta^{15}\text{N}$					
Primary producers					
<i>Spartina alterniflora</i>	6	3.65 \pm 0.51	3.72 \pm 0.65	4.31 \pm 0.14	4.46 \pm 0.31
<i>Avicennia schaueriana</i>	6	-1.83 \pm 1.24	-1.37 \pm 0.39	3.98 \pm 0.27	3.20 \pm 0.23
<i>Laguncularia racemosa</i>	6	6.25 \pm 0.38	6.09 \pm 0.63	5.17 \pm 0.21	4.80 \pm 0.22
<i>Rhizophora mangle</i>	6	-1.24 \pm 1.71	0.05 \pm 0.79	2.93 \pm 0.30	1.46 \pm 1.08
MPB*	6	7.70 \pm 0.80			
Target species					
<i>Uca thayeri</i>	12	6.37 \pm 0.21	7.43 \pm 0.10	4.09 \pm 0.14	4.81 \pm 0.07
<i>Nephtys fluviatilis</i>	6	9.00 \pm 0.08	9.09 \pm 0.14	-	-
<i>Isolda pulchella</i>	6	-	-	4.30 \pm 0.10	4.90 \pm 0.06

* Data extracted from Ito (2002).

Appendix B

Appendix B. Summary of the analysis of variance (ANOVA) results for the effects of the seasons (summer vs. winter), sectors (inner vs. outer), distances (0, 5, 10, and 15 m), tides (flood vs. ebb), days (nested in season), and sites (nested in sector) on mangrove leaves (mgL) inside salt marshes (SM) and marsh litter (smL) inside mangroves (MG). Significant differences in bold.

	df	mgL inside SM		smL inside MG	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>p</i>
Season = Sea	1	28.524	0.002	1.054	0.372
Sector = Sec	1	0.718	0.717	20.888	0.008
Distance = Dis	3	68.998	<0.001	0.864	0.520
Tide = Ti	1	38.127	0.001	0.064	1.000
Day (Sea)	4	0.784	0.552	5.805	0.004
Site (Sec)	4	1.316	0.306	5.312	0.006
Sea x Sec	1	3.123	0.078	2.849	0.144
Sea x Dis	3	3.144	0.029	0.830	0.592
Sea x Ti	1	2.287	0.183	0.496	0.684
Sec x Dis	3	1.296	0.294	2.387	0.090
Sec x Ti	1	7.457	0.024	5.140	0.056
Dis x Ti	3	0.373	0.995	4.335	0.012
Day (Sea) x Sec	4	0.344	0.844	0.277	0.888
Day (Sea) x Dis	12	0.439	0.939	1.723	0.091
Day (Sea) x Ti	4	0.655	0.632	4.654	0.011
Site (Sec) x Sea	4	0.184	0.943	1.373	0.287
Site (Sec) x Dis	12	0.338	0.978	3.451	0.001
Site (Sec) x Tide	4	1.742	0.190	11.241	<0.001
Day (Sea) x Site (Sec)	16	2.555	0.001	7.302	<0.001
Sea x Sec x Dis	3	0.628	0.899	0.869	0.569
Sea x Sec x Tide	1	1.408	0.291	1.598	0.277
Sea x Dis x Ti	3	0.584	0.906	1.192	0.344
Sec x Dis x Tide	3	1.104	0.393	4.209	0.012
Day (Sea) x Sec x Dis	12	1.042	0.428	1.405	0.196
Day (Sea) x Sec x Tide	4	1.465	0.259	5.559	0.005
Day (Sea) x Dis x Tide	12	1.377	0.210	0.427	0.945
Site (Sec) x Sea x Dis	12	0.977	0.483	1.161	0.337
Site (Sec) x Sea x Tide	4	2.394	0.094	0.437	0.780
Site (Sec) x Dis x Tide	12	2.135	0.032	1.291	0.255
Day (Sea) x Site (Sec) x Dis	48	1.091	0.327	0.766	0.868
Day (Sea) x Site (Sec) x Tide	16	1.569	0.076	2.074	0.010
Sea x Sec x Dis x Tide	3	1.345	0.272	2.312	0.066
Day (Sea) x Sec x Dis x Tide	12	0.945	0.512	0.499	0.905
Site (Sec) x Sea x Dis x Tide	12	1.057	0.416	0.856	0.595
Day (Sea) x Site (Sec) x Dis x Tide	48	1.061	0.374	0.778	0.853
Residuals	288				

Appendix C

Appendix C. Summary of the analysis of variance (ANOVA) results of both mangrove and salt marsh macro-detritus (MDt) in different seasons (summer vs. winter), sectors (inner vs. outer), distances (0, 5, 10, and 15 m), tides (flood vs. ebb), days (nested in season), and sites (nested in sector) inside each habitat. Only macro-detritus interaction terms (in bold) are of interest. Significant differences in bold.

	df	Inside Salt marsh		Inside Mangrove	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>p</i>
Macro-detritus = MDt	1	21.090	0.002	0.106	0.999
Season = Sea	1	6.760	0.056	8.614	0.019
Sector = Sec	1	6.950	0.039	16.698	0.008
Distance = Dis	3	35.766	<0.001	2.057	0.124
Tide = Ti	1	12.030	0.010	1.005	0.372
Day (Sea)	4	3.964	0.020	3.322	0.037
Site (Sec)	4	2.673	0.070	5.876	0.004
MDt x Sea	1	0.161	0.998	1.416	0.302
MDt x Sec	1	22.293	0.004	10.142	0.021
MDt x Dis	3	18.811	<0.001	1.732	0.172
MDt x Ti	1	27.211	0.001	8.302	0.040
Sea x Sec	1	3.643	0.096	1.569	0.266
Sea x Dis	3	0.923	0.531	0.465	0.920
Sea x Ti	1	1.620	0.257	0.402	0.806
Sec x Dis	3	1.983	0.128	3.293	0.030
Sec x Ti	1	5.676	0.046	5.313	0.060
Dis x Ti	3	0.404	0.988	2.164	0.119
Day (Sea) x MDt	4	4.961	0.009	8.075	0.001
Day (Sea) x Sec	4	0.607	0.664	1.062	0.407
Day (Sea) x Dis	12	0.976	0.484	2.894	0.004
Day (Sea) x Ti	4	1.078	0.400	2.617	0.074
Site (Sec) x MDt	4	3.258	0.039	4.472	0.013
Site (Sec) x Sea	4	0.104	0.979	2.260	0.108
Site (Sec) x Dis	12	0.658	0.781	1.596	0.125
Site (Sec) x Tide	4	2.282	0.106	9.434	0.000
Day (Sea) x Site (Sec)	16	7.410	<0.001	3.398	0.000
MDt x Sea x Sec	1	0.914	0.528	1.494	0.290
MDt x Sea x Dis	3	4.415	0.007	1.787	0.135
MDt x Sea x Ti	1	1.763	0.264	0.205	0.997
MDt x Sec x Dis	3	1.393	0.224	0.699	0.766
MDt x Sec x Ti	1	1.285	0.338	0.808	0.539
MDt x Dis x Ti	3	0.474	0.949	1.255	0.316
Sea x Sec x Dis	3	0.662	0.755	0.880	0.566
Sea x Sec x Tide	1	1.036	0.399	1.731	0.232
Sea x Dis x Ti	3	0.678	0.817	1.278	0.285
Sec x Dis x Tide	3	1.490	0.240	0.615	0.759

Day (Sea) x MDt x Sec	4	0.573	0.686	0.891	0.492
Day (Sea) x MDt x Dis	12	0.534	0.882	0.820	0.629
Day (Sea) x MDt x Ti	4	0.850	0.514	2.995	0.051
Day (Sea) x Sec x Dis	12	1.793	0.077	1.320	0.239
Day (Sea) x Sec x Tide	4	1.135	0.375	2.616	0.074
Day (Sea) x Dis x Tide	12	0.818	0.631	0.705	0.739
Site (Sec) x MDt x Sea	4	1.267	0.324	0.658	0.630
Site (Sec) x MDt x Dis	12	0.719	0.725	1.801	0.075
Site (Sec) x MDt x Ti	4	0.725	0.588	0.120	0.973
Site (Sec) x Sea x Dis	12	1.334	0.231	1.097	0.384
Site (Sec) x Sea x Tide	4	2.293	0.104	2.148	0.122
Site (Sec) x Dis x Tide	12	2.454	0.014	3.207	0.002
Day (Sea) x Site (Sec) x MDt	16	2.288	0.003	2.414	0.002
Day (Sea) x Site (Sec) x Dis	48	1.113	0.285	0.978	0.518
Day (Sea) x Site (Sec) x Tide	16	3.748	<0.001	2.633	0.001
MDt x Sea x Sec x Dis	3	1.041	0.476	0.874	0.661
MDt x Sea x Sec x Ti	1	1.140	0.425	0.193	0.998
MDt x Sea x Dis x Ti	3	0.484	0.977	0.911	0.576
MDt x Sec x Dis x Ti	3	0.768	0.692	1.495	0.226
Sea x Sec x Dis x Tide	3	0.680	0.807	3.036	0.028
Day (Sea) x MDt x Sec x Dis	12	0.348	0.975	0.584	0.844
Day (Sea) x MDt x Sec x Ti	4	1.798	0.179	2.927	0.054
Day (Sea) x MDt x Dis x Ti	12	1.822	0.071	0.781	0.666
Day (Sea) x Sec x Dis x Tide	12	0.894	0.559	0.778	0.669
Site (Sec) x MDt x Sea x Dis	12	0.719	0.725	0.733	0.713
Site (Sec) x MDt x Sea x Ti	4	0.161	0.955	2.356	0.098
Site (Sec) x MDt x Dis x Ti	12	1.486	0.163	1.445	0.179
Site (Sec) x Sea x Dis x Tide	12	1.373	0.212	0.578	0.849
Day (Sea) x Site (Sec) x MDt x Dis	48	1.038	0.407	0.810	0.817
Day (Sea) x Site (Sec) x MDt x Ti	16	1.537	0.082	1.253	0.223
Day (Sea) x Site (Sec) x Dis x Tide	48	1.150	0.232	1.044	0.396
MDt x Sea x Sec x Dis x Ti	3	2.549	0.050	0.740	0.759
Day (Sea) x MDt x Sec x Dis x Ti	12	0.825	0.625	1.063	0.411
Site (Sec) x MDt x Sea x Dis x Ti	12	0.592	0.838	0.953	0.505
Day (Sea) x Site (Sec) x MDt x Dis x Ti	48	0.937	0.596	0.707	0.932
Residuals	576				

Appendix D

Appendix D. Summary of the analysis of variance (ANOVA) results for the effects of the seasons (summer vs. winter), sectors (inner vs. outer), days (nested in season), and sites (nested in sector) on carbon and nitrogen stable isotope ratios in benthic invertebrates from mangroves and salt marshes. Significant differences in bold.

	df	Salt marsh		Mangrove	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
(a) Carbon					
Season = Sea	1	8.669	0.089	1.339	0.346
Sector = Sec	1	2.171	0.248	4.521	0.149
Day (Sea)	2	0.600	0.592	14.386	0.015
Site (Sec)	2	17.471	0.011	1.307	0.366
Sea x Sec	1	5.857	0.096	0.117	0.948
Sea x Site (Sec)	2	13.182	0.017	2.770	0.176
Sec x Day (Sea)	2	3.287	0.143	14.673	0.014
Site (Sec) x Day (Sea)	4	1.137	0.357	0.246	0.910
Residual	32				
(a) Nitrogen					
Season = Sea	1	2.518	0.243	11.435	0.070
Sector = Sec	1	1000.398	<0.001	239.968	<0.001
Day (Sea)	2	0.692	0.552	2.924	0.165
Site (Sec)	2	4.664	0.090	0.539	0.620
Sea x Sec	1	1.524	0.351	3.565	0.173
Sea x Site (Sec)	2	10.893	0.024	0.107	0.901
Sec x Day (Sea)	2	0.093	0.913	0.534	0.623
Site (Sec) x Day (Sea)	4	0.495	0.739	1.332	0.279
Residual	32				