PRIMARY RESEARCH PAPER

Estuary hydrogeomorphology affects carbon sources supporting aquatic consumers within and among ecological guilds

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Abstract The relative importance of carbon sources supporting aquatic food webs within and among estuaries may be influenced by factors that affect relative availability of autotrophic carbon sources, as well as movement of individuals among marine, estuarine and freshwater zones. We used stable isotopes of carbon and nitrogen to examine (1) the relative importance of carbon sources supporting estuarine consumers among estuaries with different hydrogeomorphic characteristics, (2) stable isotope signatures of consumer ecological guilds defined by dependence on estuarine habitats and residence time, and (3) if patterns in stable isotope signatures of ecological guilds repeat across estuaries with distinct hydrogeomorphological features. At the assemblage level, consumer carbon isotope signatures reflected the consumption of locally abundant primary production sources and differed across estuary types (choked lagoon, coastal river). Consumer ecological guilds differed in $\delta^{13}C$ within sites, and the same trend repeated across sites but with differing magnitudes. This variation is attributed to movement and residence patterns in addition to differences in the relative abundances of autotrophic sources across sites. Although within-estuary variation in consumer resource use is to be expected, estuarine food webs may be broadly classified according to landscape-scale hydrogeomorphic factors that allow an initial prediction of the relative importance of carbon sources to secondary production. Predictions may be refined at the species level using knowledge of habitat use and residence time. Such predictions are useful as a starting point for poorly studied regions such as ours in southern Brazil, as well as for global-scale analyses of patterns in estuarine food webs.

Keywords Brazil · Food web · Migration · Salt marsh · South America · Subsidies

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Introduction

Estuaries are spatially complex, formed by forces of freshwater inflow meeting marine water across narrow to broad areas, and may vary greatly in physicochemical conditions due to tidal flux and

season. Patterns of dominance of primary producers often change along estuarine gradients (Day et al., 1989; Kennish, 1990; Isacch et al., 2006), such as in a gradient of marsh grasses or mangroves occupying relatively higher elevations or the inter-tidal zone and seagrass and algae occurring in lower elevations. Corresponding with such changes in dominance of primary producers, prior food web studies have shown that the relative importance of autotrophic carbon sources supporting secondary production of aquatic consumers often changes along gradients within estuaries (Peterson et al., 1985; Deegan & Garritt, 1997; Garcia et al., 2007; Kanaya et al., 2007).

Estuarine food web studies have identified similarities as well as differences in the relative importance of autotrophic production to consumers (e.g., Hsieh et al., 2002; Kang et al., 2003; Winemiller et al., 2007; Rodriguez-Grana et al., 2008). Similar hydrogeomorphic factors that drive patterns of spatial variation within estuaries should also result in variation among estuaries with different characteristics. For example, tidal creeks, lagoons and bays vary greatly in their relative proportion of littoral to open water area, and may also vary in the relative size of the estuarine zone in general. Based on findings from inland freshwater ecosystems where landscape-scale hydrogeomorphic features have a strong influence on food web structure and carbon flow (Hoeinghaus et al., 2007, 2008), we expect differences in the relative importance of carbon sources among estuaries to correspond to hydrogeomorphic characteristics that affect patterns of dominance of primary producers.

Patterns of carbon flow in estuarine food webs may also be affected by the movement of individuals among marine, estuarine, and freshwater zones. Local estuarine food webs may receive subsidies of marine and freshwater production via marine and freshwater visitant species that serve as transport vectors (e.g., Deegan, 1993; Garman and Macko, 1998; MacAvoy et al., 2000) or by direct flux in the environment (e.g., Connolly et al., 2005). Isotopic differences in source signatures among freshwater, estuarine, and marine systems may be retained to certain degrees in non-resident individuals (dependent on length of time since arriving, body size, feeding rate, e.g., Rubenstein & Hobson, 2004; Bardonnet & Riera, 2005; Herzka, 2005) or assimilated by resident estuarine species through trophic interactions. For example, in

previous research in this region of South America, stable isotope signatures of carbon were useful to identify movement of individuals from freshwater into estuarine zones within a large coastal lagoon (Garcia et al., 2007). In this manner, the functional composition of the estuarine consumer assemblage, specifically the relative composition of estuarine resident and visitant species, may affect the relative importance of carbon sources identified at the assemblage level and also may be expected to vary among functional groups.
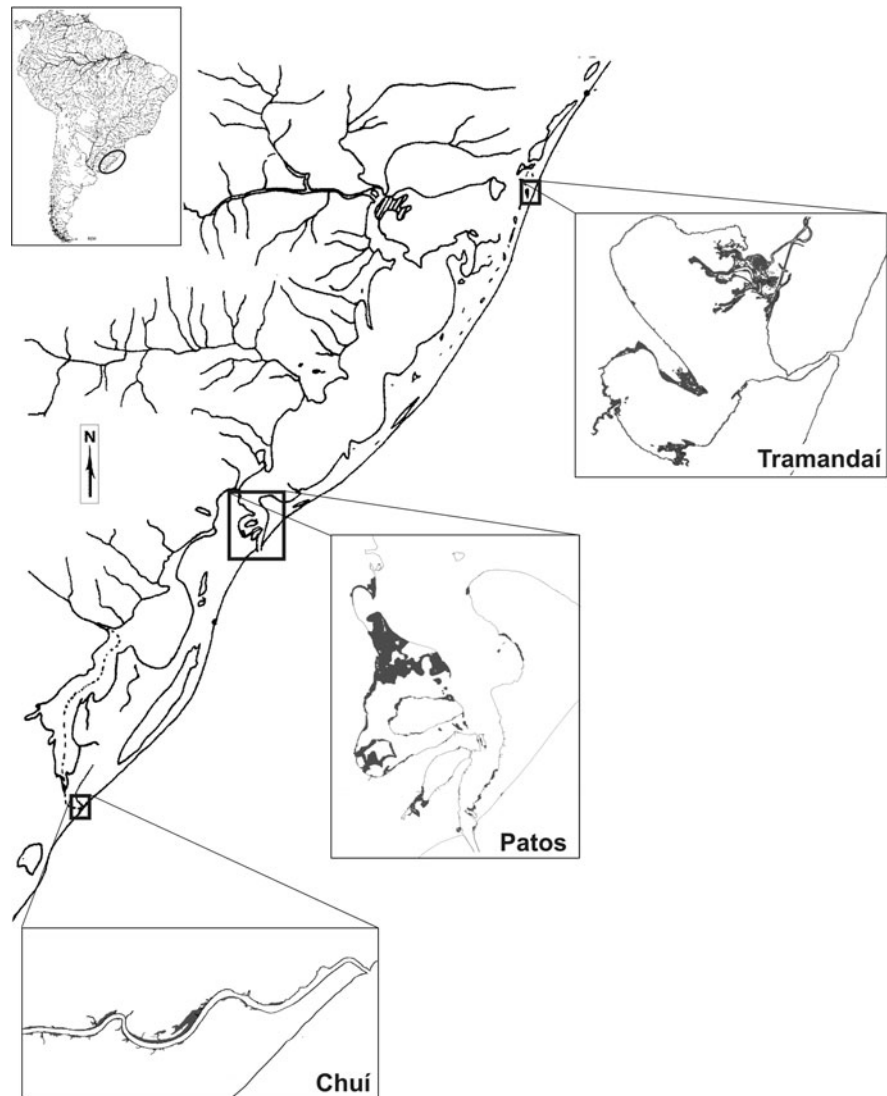
In this study, we used stable isotopes of carbon and nitrogen to examine food web structure of three estuaries of subtropical Brazil. This study provides new data on an understudied region, and further investigates underlying drivers of structure in estuarine food webs in general. We were interested in whether the relative importance of carbon sources supporting estuarine consumers differed among estuaries with different hydrogeomorphic characteristics, and to what extent functional roles had an effect on consumer resource use and isotopic signature. Specifically, we ask the following questions: (1) within estuaries, do consumer ecological guilds defined by dependence on estuarine habitats and their time of residence differ in their carbon isotope signatures?, and (2) do patterns in carbon isotope signatures of ecological guilds within an estuary repeat in a similar manner across estuaries situated in the same coastal plain but with distinct hydrogeomorphological features?

Materials and methods

Regional description and study sites

Estuarine food webs were investigated at three locations along the southern Brazilian coast (Fig. 1). Hydrogeomorphologic characteristics differ among the estuaries (Table 1), primarily being classified as "choked lagoons" (sensu Kjerfve, 1986; Tramandaí-Armazén lagoon complex and Patos Lagoon, although Patos Lagoon is far larger than the Tramandaí-Armazén lagoon complex) and a coastal river (Chuí). The studied estuaries are located in Rio Grande do Sul (RS), the southernmost state of Brazil, across a 500 km stretch of coastline from the northern-most site (Tramandaí, 30°S, 50°W) to the Brazil–Uruguay border (Chuí, 33°S, 53°W; Fig. 1).

Fig. 1 Map of South America, with detail of the Rio Grande do Sul, Brazil, coastline depicting the location and spatial structure of Tramandaí, Patos Lagoon and Chuí estuaries. *Shading in inset* maps for each site indicate saltmarsh area

This coastal zone is influenced by the convergence of oligotrophic and nutrient-rich subtropical waters of the Brazil and Malvinas currents, respectively, as well as large amounts of continental freshwater inflow into the coastal zone from the La Plata River and Patos-Mirim lagoon complex. These unique conditions make this area one of the most productive in the southwestern Atlantic (Seeliger et al., 1996).

The Tramandaí-Armazém lagoon complex (hereafter Tramandaí) has an area of 30 km². Its main tributaries are a river draining highland areas and several lakes, which together comprise a drainage basin of 2,697 km². The estuarine zone is restricted to Armazém lagoon and the area near the connection

with the sea, which is 1.5 km long, 0.3 km wide, with depths ranging from 1.5 m in the shallow waters and 5 m in the main channel (Fig. 1). Strong variations in its environmental conditions over short time periods and throughout the year usually occur due to sudden changes in wind patterns. Salinity is influenced by changes in tides and freshwater inflow (Schwarzbold & Schäfer, 1984).

Patos Lagoon is the better studied of the three estuarine systems (Seeliger et al., 1996; Seeliger, 2001). The lagoon is 250 km long and 60 km wide, which gradually narrows into a channel (700 m wide) connected with the sea (Fig. 1). The estuarine zone is restricted to its southern region and comprises

Table 1 Hydrogeomorphic and vegetation characteristics of Tramandaí, Patos Lagoon, and Chuí estuaries

Features	Estuary		
	Tramandaí	Patos Lagoon	Chuí
Drainage basin (km^2)	2,698	201,626	276
Surface area (km^2)	30	10,360	18
Area mixohaline zone (km^2)	19.4[a]	971	0.3
Area mixohaline zone/surface area (%)	64.6	9.37	1.67
Saltmarsh longitudinal distribution (km)[b]	7.7	42.5	4.5
Saltmarsh spatial coverage (ha)[c]	92.4	6,837.5	7.5
Mean depth (m)	1.5	5.0	2.0
Maximum depth (m)	5.0	18.0	3.0
Salinity (mean)	3.6	9.6	3.3
Water transparency (cm)	34.4	39.6	25.0

[a] Based on the spatial distribution of saltmarsh

[b] Distance from the mouth of the estuary to the upstream limit in distribution of saltmarsh vegetation

[c] Based on analysis of satellite images (LANDSAT-7, CBERS-2, QuickBird-2) of the dominant vegetation at each site: *S. olneyi* and *J. kraussii* at Tramandaí; *S. alterniflora*, *S. densiflora* and *J. kraussii* at Patos Lagoon; *S. olneyi* and *J. acutus* at Chuí

approximately 10% of the entire lagoon (976 km^2). Apart from a deeper navigation channel, about 80% of the estuarine zone is less than 2 m deep. Tidal influence in the estuary is minimal (mean tidal amplitude is 0.47 m). Wind and seasonal pulses of freshwater inflow influence longitudinal and vertical patterns of water circulation and salinity (Seeliger et al., 1996), and have strong effects on the spatio-temporal dynamics of the fish assemblages (Garcia et al., 2004). The lagoon has a large drainage basin (201,626 km^2) formed by rivers characterized by a mid-latitude flow regime: high discharge in late winter and early spring and low to moderate discharge through summer and autumn (Moller et al., 2001). There is great habitat heterogeneity within the estuary, particularly associated with C_4 plants such as widgeon grass (*Ruppia maritima*), which forms extensive meadows during spring and summer (Costa et al., 1997), and saltmarsh plants such as *Spartina densiflora* and *Spartina alterniflora* that occur in higher and lower saltmarsh elevations, respectively (Costa et al., 1997). These vegetated habitats provide nursery grounds for several marine fishes and shrimp species (Garcia et al., 1996; Garcia & Vieira, 1997; Costa et al., 1997), which are abundant in the lagoon and sustain an artisanal fishery that provides livelihood for ~3,500 fishermen (Vieira & Castello, 1996; Reis & D'incao, 2000).

In contrast with the other two choked lagoon estuaries, Chuí is formed by a 60 km river that empties into the sea through a narrow channel just 60 m wide (Fig. 1). Depth ranges from 1.5 to 3 m, and the small estuarine zone (only 0.3 km^2) extends ~1 km up-river and with more prevalence of oligohaline conditions in comparison with the other two estuaries (Pereira et al., 1998). This site, therefore, has less diversity of typical estuarine vegetated habitats (seagrass meadows and saltmarshes) that are commonly found in the other estuaries, especially at Patos Lagoon. Rather, the dominant vegetated habitats along its margins are the C_3 plants *Scirpus olneyi* and *Juncus acutus* in the lower and higher elevations, respectively (C. S. Costa, unpublished data).

Vegetation surveys, and field collection and sample processing for isotopic analyses

Patterns of dominance were characterized for vegetation at each estuary from satellite images and field surveys (Table 2). High resolution digital aerial photographs (for Patos Lagoon) and QuickBird-2 satellite images (Tramandaí and Chuí) were classified by supervised pixel-based algorithm (maximum likelihood classification, MAXVER) and used to generate land cover thematic maps of the marginal salt marshes. In each estuary, image classifications, cover

Table 2 Patterns of dominance (spatial coverage) and carbon stable isotope values for the representative vegetation at each site

	Tramandaí	Patos Lagoon	Chuí	Mean δ^{13}C
Marsh vegetation				
Cyperus spp (C_3)	Sparse	Rare	Rare	−28.0
Juncus spp. (C_3)	Sparse	Abundant	Abundant	−27.0
Panicum elephantipes (C_4)	Sparse	–	–	
Paspalum vaginatum (C_4)	Sparse	Rare	Sparse	−12.5
Salicornia gaudichaudiana (C_3)	Rare	Rare	Sparse	−29.7
Scirpus californicus (C_3)	Sparse	Rare	Rare	−26.1
Scirpus maritimus (C_3)	Rare	Sparse	–	−27.0
Scirpus olneyi (C_3)	Abundant	Sparse	Abundant	−28.5
Spartina alterniflora (C_4)	–	Abundant	–	−11.4
Spartina densiflora (C_4)	Rare	Abundant	Sparse	−12.2
Submerged aquatic vegetation				
Ruppia maritima (C_4)	Abundant	Abundant	–	−11.8
Enteromorpha sp. (C_4)	Abundant	Sparse	–	−12.9

Marsh vegetation abundance based estimates of species cover in percents: rare $0.1 \leq x\% < 4.0$; sparse $4.0 \leq x\% < 16.0$; abundant $x\% \geq 16.0$. Submerged aquatic vegetation abundance is from Costa et al. (1997) and Rosa-Filho et al. (2004). Mean δ^{13}C values from this study, Garcia et al. (2007), and Abreu et al. (2006)

maps and salt marsh area were estimated using GIS SPRING software (Camara et al., 1996). During the extensive ground verification, ocular estimates of percent cover by species were recorded in 57, 585, and 65 quadrads (0.25 m^2) along transects perpendicular to the estuarine margins of Tramandaí, Patos Lagoon, and Chuí estuaries, respectively. The percentage cover occupied by each species was used to calculate mean cover value that was assigned to an abundance class, based on an octave scale (logarithmic to the base 2; Gauch, 1984), as follows: rare $0.1 \leq x\% < 4.0$; sparce $4.0 \leq x\% < 16.0$; abundant $x\% \geq 16.0$.

Fishes, macroinvertebrates and primary producers were sampled at several points in each estuary during a 1 week period of November 2004 (late austral spring). Late spring is an important season for these ecosystems because of high primary production and the presence of diverse guilds of consumers (see below). Fishes were collected using multiple gears (beach seines, cast nets and gillnets) to collect representative samples of the fish diversity at each site. Benthic macroinvertebrates and infauna were collected using cores, and some larger invertebrate species (e.g., *Callinectes sapidus*) were also collected using seines. Dominant floating and emergent macrophytes were collected by hand. Our δ^{13}C data for plants (including some previously published by

Garcia et al., 2007) was complemented with information reported by Abreu et al. (2006) for Patos Lagoon (Table 2).

All samples were placed on ice for transport to the laboratory where they were stored frozen, and later processed following standard procedures for isotopic analyses (Garcia et al., 2007, Hoeinghaus & Davis, 2007). Briefly, samples consisted of several leaves for plant species, ~5 g of pure muscle tissue from individual fish and large invertebrates. In the case of smallest size-classes (<50 mm total length for fishes, <100 mm carapace width for crabs) and taxa (shrimp, bivalves, and polychaetes), a composite sample of individuals of approximately the same size was taken by combining pure muscle tissue from 5–15 individuals from the same site. Because isotopic signatures of crustacean exoskeletons reflect assimilated calcium carbonate derived from the environment, only pure muscle samples were used for stable isotope analysis. Pure muscle tissue was dissected from crabs and shrimp using a sterile scalpel. For bivalves, the adductor was removed and processed in the same manner. Polychaetes were processed whole. Thawed samples were carefully inspected to remove non-muscle matter (e.g., bone or scales in fish tissue), rinsed with distilled water, placed in sterile Petri dishes, and dried in an oven at 60°C to constant weight (minimum of 48 h). Dried samples were

ground to a fine powder with a mortar and pestle and stored in clean glass vials.

Sub-samples were weighed to the nearest 0.01 mg, and pressed into Ultra-Pure tin capsules (Costech Analytical, Valencia, California), and sent to the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia, for analysis of carbon and nitrogen isotope ratios. Results are expressed in delta notation (parts per thousand deviation from a standard material): $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] * 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material for carbon is Pee Dee Belemnite (PDB) limestone, and the nitrogen standard is atmospheric nitrogen. Standard deviations of $\delta^{13}C$ and $\delta^{15}N$ replicate analyses ($n = 18$, each) were 0.14 and 0.13‰, respectively.

Data analysis

Subsequent analyses are based on carbon and nitrogen isotopic ratios of 140 consumer samples (Tramandaí: $n = 36$; Patos: $n = 71$; Chuí: $n = 33$). Individuals of some large-bodied fish species were separated into size classes to reduce potential bias due to ontogenetic diet shifts. Bi-plots of $\delta^{15}N$ and $\delta^{13}C$ values of fishes and macroinvertebrates were used to visualize patterns of isotopic variation across sites. The relative importance of various sources of organic carbon assimilated by consumers is indexed by relative positions of consumers on the x-axis ($\delta^{13}C$ values), whereas trophic position is indicated by relative position on the y-axis ($\delta^{15}N$) (Peterson & Fry, 1987). Analysis of variance (ANOVA) was used to compare $\delta^{13}C$ and $\delta^{15}N$ of fish and invertebrate consumer assemblages among sites. Within each site, ANOVA was used to compare consumer $\delta^{13}C$ among four ecological guilds identified by Garcia et al. (2003): (1) estuarine residents—species typically occurring and breeding within the estuary; (2) estuarine dependents—marine or freshwater spawning species found in large numbers within the estuary during certain periods of their life cycle; (3) marine vagrants—species typically inhabiting marine habitats and rarely occurring within the estuary; and (4) freshwater vagrants—species typically inhabiting freshwater habitats and rarely occurring within the estuary. When a significant main effect was observed, pairwise comparisons of site or guild means were performed using Tukey's post-hoc procedure. For post-hoc analyses of guild means at

Chuí and Tramandaí, the marine vagrant guild was excluded because it was represented by only a single species at both sites.

Results

Between 46 and 76% of the mean plant cover of the salt marshes was accounted for by five or fewer species, and dominant plants were not the same among estuaries (Table 2). The South American cordgrass S. densiflora was the most abundant species in the mesohaline Patos Lagoon estuary, whereas S. olneyi occurred in dense stands in low marshes of the oligohaline estuaries of Chuí and Tramandaí. Salt marsh areas of Tramandaí and Patos Lagoon were 10 and 100 times larger than Chuí, respectively. The choked lagoons also showed extensive beds of widgeon grass Ruppia maritima and macroalgae Enteromorpha spp. (especially Tramandaí), more diversified salt marsh flora and site specific C_4 plants such as S. alterniflora (low marshes of Patos Lagoon) and Panicum elephantipes (marsh-land border of Tramandaí) (Table 2).

A total of 31 fish species and 8 invertebrate species was collected across the three sites (Table 3). A similar number of fish and invertebrate species were collected at Patos Lagoon (19 fish species and 5 invertebrate species) and Chuí (20 fish species and 3 invertebrate species), whereas fewer species were collected at Tramandaí (7 fish species, 5 invertebrate species; Table 3). Species representing all four ecological guilds were collected at Patos and Chuí (Table 3), although freshwater vagrant species dominated Chuí (17 species) and estuarine resident and estuarine-dependent species dominated Patos Lagoon (12 and 9 species, respectively). Aside from the marine vagrant Pomatomus saltatrix (bluefish), only estuarine resident and estuarine dependent species were found at Tramandaí (Table 3). Across all sites, the marine vagrant guild was represented by either a single species (Tramandaí, Chuí) or two species (Patos Lagoon). The estuarine resident Odonthestes argentinensis (silverside) and estuarine-dependent species C. sapidus (blue crab), Micropogonias furnieri (whitemouth croaker), and Mugil liza (mullet) were collected at all three sites (Table 3).

At the assemblage level, nitrogen isotopic signatures of consumers ranged from ∼6–16‰ (Fig. 2),

Table 3 Fishes and invertebrates collected at each site, with ecological guild, size range, and mean (±1 SD) carbon and nitrogen isotope values

Species	Guild	n	Size class (mm)	$\delta^{15}N$	±1 SD	$\delta^{13}C$	±1 SD
Tramandaí							
Lycengraulis grossidens	ED	3	90–96	12.5		−19.0	
Micropogonias furnieri	ED	2	87–98	13.2	0.11	−15.3	0.43
Micropogonias furnieri	ED	3	127–128	13.5	0.12	−14.7	1.08
Mugil liza	ED	8	27–34	7.6		−20.0	
Mugil liza	ED	3	99–101	9.1	1.21	−13.5	2.26
Mugil liza	ED	3	214–240	9.3	0.53	−15.4	3.18
Genidens barbus	ED	3	319–357	14.9	0.24	−14.9	0.63
Atherinella brasiliensis	ER	6*	83–129	13.0	0.33	−16.7	0.87
Odonthestes argentinensis	ER	5	36–50	12.3		−16.3	
Odonthestes argentinensis	ER	3	153–155	13.8	0.46	−15.3	0.93
Odonthestes argentinensis	ER	3	229–255	12.8	0.09	−16.2	0.37
Pomatomus saltatrix	MV	3	146–176	14.8	1.80	−16.3	0.37
Callinectes sapidus	ED	5	53–84	13.1		−16.1	
Farfantepenaeus paulensis	ED			9.9	0.21	−11.4	0.53
Heteromastus similis	ER			8.6		−18.0	
Laeonereis acuta	ER			9.8		−14.3	
Nephtys fluviatilis	ER			10.8		−14.8	
Patos Lagoon							
Brevoortia pectinata	ED	25	35–40	9.5		−17.2	
Lycengraulis grossidens	ED	1	85	11.0		−17.8	
Micropogonias furnieri	ED	30*	48–100	12.1	0.76	−15.0	0.85
Micropogonias furnieri	ED	9	120–179	11.3	1.87	−14.7	1.25
Micropogonias furnieri	ED	3	211–223	13.6	3.46	−17.7	2.05
Mugil liza	ED	21*	23–50	8.4	0.36	−16.1	2.90
Mugil liza	ED	3	395–415	9.2	1.11	−15.2	1.20
Genidens barbus	ED	4	88–100	15.5		−15.3	
Genidens barbus	ED	10*	102–153	10.9	0.51	−18.3	0.75
Paralichthys orbignyanus	ED	2	98–106	11.6		−12.4	
Catathyridium garmani	ER	3	125–137	11.0	0.60	−14.8	1.36
Atherinella brasiliensis	ER	2	94–96	12.3		−14.6	
Genidens genidens	ER	5	87–101	12.0		−16.5	
Ctenogobius shufeldti	ER	9	50–70	9.6		−13.3	
Odonthestes argentinensis	ER	35*	36–100	10.1	0.45	−17.2	0.85
Jenynsia multidentata	ER*	8	33–54	8.1		−18.6	
Astyanax eigenmanniorum	FV	11	35–47	7.7		−23.9	
Astyanax sp.	FV	6	56–67	10.6		−18.7	
Hoplias aff. malabaricus	FV	3	270–281	10.8	0.35	−22.0	0.21
Platanichthys platana	FV	8	50–93	11.1		−19.2	
Geophagus brasiliensis	FV*	3	104–113	8.8	0.64	−17.8	3.84
Geophagus brasiliensis	FV*	3	140–162	11.1	1.13	−16.3	2.03
Citharichthys spilopterus	MV	1		10.6		−15.2	

Table 3 continued

Species	Guild	n	Size class (mm)	$\delta^{15}N$	±1 SD	$\delta^{13}C$	±1 SD
Symphurus jenynsi	MV	4*	51–104	12.7	0.85	−14.9	1.80
Callinectes sapidus	ED	16*	36–145	8.3	1.13	−15.9	0.64
Farfantepenaeus paulensis	ED	7	70–105	9.0		−12.5	
Erodona mactroides	ER	6	4–7	5.7		−16.9	
Laeonereis acuta	ER	2		7.8	1.16	−14.7	1.45
Nephtys fluviatilis	ER	1		10.1		−14.5	
Chuí							
Micropogonias furnieri	ED	4	82–93	14.4		−16.3	
Mugil liza	ED	21*	35–75	9.4	1.04	−16.6	0.27
Mugil liza	ED	4*	205–254	9.7	0.38	−17.8	2.87
Paralichthys orbignyanus	ED	1	146	12.0		−17.8	
Ctenogobius shufeldti	ER	2	98–108	9.4		−24.4	
Odonthestes argentinensis	ER	4	54–60	11.7		−25.5	
Odonthestes argentinensis	ER	1	125	11.9		−25.1	
Jenynsia multidentata	ER*	15	21–56	10.7		−22.3	
Astyanax jacuhiensis	FV	5	64–76	8.5		−24.7	
Astyanax fasciatus	FV	3	55–75	8.9		−29.2	
Astyanax fasciatus	FV	2	137–156	11.3		−28.3	
Charax stenopterus	FV	3	72–85	10.4		−27.7	
Crenicichla lepidota	FV	2	115–188	10.1	0.87	−28.0	1.41
Crenicichla punctata	FV	1	113	11.3		−26.7	
Cyphocharax voga	FV	1	74	8.2		−24.0	
Hoplias aff. malabaricus	FV	1	355	11.3		−25.7	
Oligosarcus robustus	FV	1	72	10.8		−23.9	
Oligosarcus robustus	FV	1	153	10.8		−25.4	
Pimelodella australis	FV	3	79–87	10.6		−27.5	
Platanichthys platana	FV	1	84	12.5		−20.7	
Pseudocorynopoma doriae	FV	4	69–81	10.8		−25.6	
Rineloricaria longicauda	FV	2	138–142	10.8		−26.5	
Geophagus brasiliensis	FV*	3	84–104	9.2		−25.8	
Geophagus brasiliensis	FV*	1	218	7.2		−29.2	
Paralonchurus brasiliensis	MV	2	99–124	13.6		−18.6	
Callinectes sapidus	ED	10*	40–100	11.5	0.33	−19.0	0.29
Cyrtograpsus angulatus	ER	3	22–24	12.0		−18.4	
Palaemonetes argentinus	FV*	4	52–59	10.4		−25.1	

ED estuarine dependent, *ER* estuarine resident, *ER** freshwater species, but abundant in the estuary year-round, *MV* marine vagrant, *FV* freshwater vagrant, *FV** freshwater species that is salinity tolerant, being frequently found in the estuary (second order freshwater fish). Blank lines within sites separate fish from invertebrate species. Species or size-classes with multiple individuals sampled but no standard deviations are composite samples (see "Materials and methods" section); sample sizes with an *asterisk* include one or more composite samples
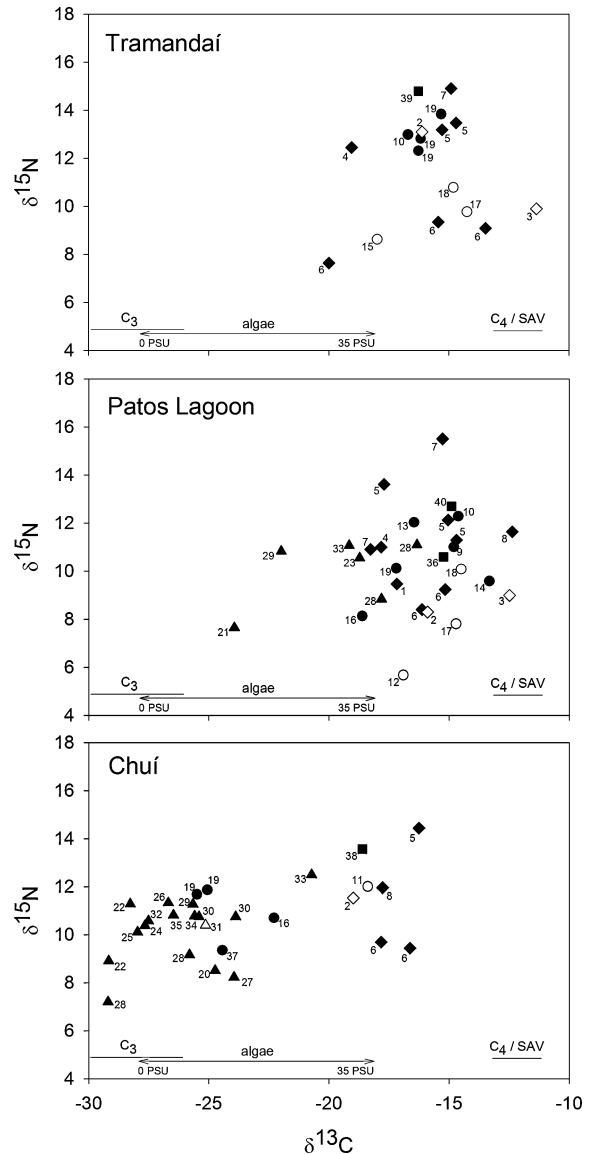
and did not differ among sites ($F_{2,71} = 2.68$, $P = 0.08$). This range of variation in consumer nitrogen isotope ratios corresponds to approximately three to four trophic levels considering a trophic fractionation of between +2.5‰ (Vanderklift & Ponsard, 2003) and +3.4‰ (Post, 2002). Consumer $\delta^{13}C$ values differed significantly among sites ($F_{2,71} = 52.38$, $P < 0.001$), and post-hoc analyses

Fig. 2 Carbon and nitrogen isotope bi-plots of fish and ▶ macroinvertebrate consumers in Tramandaí, Patos Lagoon and Chuí estuaries. *Bars* represent ranges of $\delta^{13}C$ for C_3 macrophytes, C_4 macrophytes and submerged aquatic vegetation (SAV). The *arrow* represents the range of $\delta^{13}C$ for algae along a freshwater to marine salinity gradient (Fry, 2002). *Filled symbols* are fishes and *open symbols* are invertebrates. Ecological guilds and species codes: estuarine dependents (*filled diamonds*): 1, *Brevoortia pectinata*; 2, *Callinectes sapidus*; 3, *Farfantepenaeus paulensis*; 4, *Lycengraulis grossidens*; 5, *Micropogonias furnieri*; 6, *Mugil liza*; 7, *Genidens barbus*; 8, *Paralichthys orbignyanus*; estuarine residents (*filled circle*): 9, *Catathyridium garmani*; 10, *Atherinella brasiliensis*; 11, *Cyrtograpsus angulatus*; 12, *Erodona mactroides*; 13, *Genidens genidens*; 14, *Ctenogobius shufeldti*; 15, *Heteromastus similis*; 16, *Jenynsia multidentata*; 17, *Laeonereis acuta*; 18, *Nephtys fluviatilis*; 19, *Odonthestes argentinensis*; freshwater vagrants (*filled triangles*): 20, *Astyanax bimaculatus*; 21, *Astyanax eigenmanniorum*; 22, *Astyanax fasciatus*; 23, *Astyanax* sp.; 24, *Charax stenopterus*; 25, *Crenicichla lepidota*; 26, *Crenicichla punctata*; 27, *Cyphocarax voga*; 28, *Geophagus brasiliensis*; 29, *Hoplias* aff. *malabaricus*; 30, *Oligosarcus robustus*; 31, *Palaemonetes argentinensis*; 32, *Pimelodella australis*; 33, *Platanychthys platana*; 34, *Pseudocorynopoma doriae*; 35, *Rineloricaria longicauda*; marine vagrants (*filled squares*): 36, *Citharichthys spilopterus*; 37, *Gobionellus oceanicus*; 38, *Paralonchurus brasiliensis*; 39, *Pomatomus saltatrix*; 40, *Symphurus jenynsi*

distinguished the comparatively ^{13}C depleted freshwater vagrant-dominated assemblage at Chuí from the more ^{13}C-enriched estuarine resident- and estuarine dependent-dominated assemblages at Patos Lagoon and Tramandaí (Fig. 2; Table 3). At both Patos Lagoon and Tramandaí, consumer $\delta^{13}C$ values were mostly between −12 and −20‰, whereas consumer $\delta^{13}C$ values at Chuí ranged from ∼ −16 to −30‰ (Fig. 2; Table 3).

Even though the consumer assemblages of Patos Lagoon and Tramandaí were enriched in ^{13}C compared to Chuí, $\delta^{13}C$ values of the freshwater vagrant guild were consistently more depleted than the other guilds within sites when present (Fig. 2; Table 3). At Patos, consumer $\delta^{13}C$ values differed significantly among guilds ($F_{3,25} = 6.35$, $P = 0.002$), and post-hoc analyses distinguished the relatively ^{13}C-depleted freshwater vagrant guild from all three other guilds. Significant differences in consumer $\delta^{13}C$ values were also observed among guilds at Chuí ($F_{3,24} = 22.50$, $P < 0.001$), with the freshwater vagrant, estuarine dependent and estuarine resident guilds all significantly different in post-hoc analyses. Freshwater vagrants were the most depleted in ^{13}C, estuarine residents had intermediate values, and estuarine-dependent species were relatively enriched in ^{13}C (Fig. 2). No difference in $\delta^{13}C$ values was observed among guilds at Tramandaí ($F_{2,14} = 0.08$, $P = 0.925$), where species in the freshwater vagrant guild were not present.

The four species collected at all three sites exhibited different patterns in their $\delta^{13}C$ values. Carbon isotopic signatures of the estuarine-dependent species *C. sapidus*, *M. furnieri*, and *M. liza* differed little among sites, although at Tramandaí the smallest size class of mullet *M. liza* was depleted more than 4‰ compared to the two larger size classes sampled, and *C. sapidus* at Chuí were slightly depleted in ^{13}C compared to the other sites (Table 3). The silverside *O. argentinensis*, an estuarine-resident species, had similar $\delta^{13}C$ values at Tramandaí and Patos (approximately −16 and −17‰,

respectively), but both size classes collected at Chuí were ∼8‰ more depleted (−25‰, Table 3).

Discussion

Estuary hydrogeomorphology and community-level variation in isotope signatures

The three subtropical estuaries examined in this study were broadly classified based on landscape-scale hydrogeomorphological characteristics as choked lagoons (Patos Lagoon, Tramandaí) and a coastal river (Chuí). The primary characteristics that distinguish these classifications are the total area of the mixohaline zone, size of the mixohaline zone relative to adjacent freshwater zones, cross-sectional elevation profile, and the relative proportion of open water habitat. These hydrogeomorphological differences affected the composition and relative abundances of primary producers (Isacch et al., 2006). For example, typical saltmarsh vegetation such as *Spartina* spp. occupied much greater areas in both choked lagoon estuaries compared with Chuí (Fig. 1; Table 2) because these lagoons have a greater proportion of lower elevation littoral and larger mixohaline zones. Widgeon grass (*R. maritima*) also can form extensive meadows in the open water zones of choked lagoons during spring and summer, and macroalgae (*Enteromorpha* spp.) are common or abundant. In contrast, littoral vegetation at Chuí was dominated by *S. olneyi* and *J. acutus*, and the total area covered was lower because of steeper littoral elevation profiles.

These differences in primary producer composition and relative abundance are well represented by stable isotope ratios of carbon, because *Spartina* spp., *R. maritima* and *Enteromorpha* spp. are C_4 plants ($\delta^{13}C$ between −13‰ and −10‰), whereas *Juncus* spp. and *S. olneyi* are C_3 plants ($\delta^{13}C$ between −29‰ and −26‰; Table 2). Phytoplankton also typically vary in $\delta^{13}C$ along salinity gradients because of differences in carbon isotope signatures of dissolved inorganic carbon (DIC), becoming more depleted as the relative contribution of DIC of freshwater origin increases (Peterson et al., 1994; Canuel et al., 1995; Bouillon et al., 2000; Fry, 2002; Kaldy et al., 2005). Therefore, the relative area of mixohaline versus surrounding freshwater zones may affect the carbon isotope signature of algae being utilized by consumers, following the same trend of more enriched values in the choked lagoons.

Carbon isotope signatures of consumers across all three estuaries appear to reflect the consumption of local sources of primary production. As described above, the dominant primary producers at Chuí are considerably ^{13}C-depleted compared with those from the two choked lagoon estuaries (i.e., C_3 sources and depleted algae at Chuí, and C_4 sources and enriched algae in the choked lagoons). This comparatively ^{13}C-depleted resource base was reflected in tissues of consumers at the assemblage level (i.e., regardless of ecological guild). Carbon isotope ratios of consumers at Chuí were significantly depleted ($\delta^{13}C$ range of −30 to −16‰) compared with the consumer assemblages of Patos Lagoon and Tramandaí ($\delta^{13}C$ range of −20 to −12‰). Winemiller et al. (in press) observed a shift from C_3-dependent food webs along the fluvial gradient to the C_4-based food web of the seagrass/mangrove zone for a coastal river in Belize. A similar trend was observed by Garcia et al. (2007) along a gradient within Patos Lagoon, where consumers in estuarine zones appear to assimilate greater amounts of carbon from C_4 production sources (e.g., *Spartina* spp., widgeon grass) and enriched benthic algae compared with upper freshwater reaches of the lagoon that are dominated by C_3 production sources (e.g., *Scirpus californicus*, floating aquatic macrophytes such as *Eichhornia* spp.) and algae with depleted $\delta^{13}C$. Comparable spatial variation in the relative importance of carbon sources to consumers within estuaries has been repeatedly observed among diverse temperate, subtropical and tropical estuaries (e.g., Peterson et al., 1985; Deegan & Garritt, 1997; Chanton & Lewis, 2002; Hsieh et al., 2002; Richoux & Froneman, 2007, but see also Rodriguez-Grana et al., 2008).

Consumer isotope signatures among ecological guilds

Even though differences in isotope signatures of locally dominant primary production sources may account for the broad differences observed in $\delta^{13}C$ of consumers at the assemblage level, we also observed significant differences in $\delta^{13}C$ among ecological guilds within Patos Lagoon and Chuí estuaries. These within-site differences among ecological guilds may be attributed to movement and residence patterns in

addition to relative abundances of different auto-trophic resources (e.g., Herzka, 2005). For example, freshwater vagrant species collected in Patos Lagoon estuary were significantly depleted in ^{13}C compared with the other ecological guilds present. However, these individuals were enriched in ^{13}C compared with freshwater vagrant species collected in freshwater zones of this same lagoon where they naturally occur (Garcia et al., 2007) as well as freshwater vagrant species collected at Chuí. This suggests that the freshwater vagrant species collected in Patos Lagoon estuary colonized the area from upper freshwater reaches of the lagoon, but were present in the estuary long enough to have assimilated local ^{13}C-enriched carbon sources, resulting in an intermediate carbon isotope signature.

In addition to freshwater vagrant species being more ^{13}C depleted than other ecological guilds at Chuí (having an almost completely "freshwater" signature), estuarine-dependent and estuarine-resi-dent species also differed in their carbon isotope signatures. Estuarine-dependent species had the most enriched signatures and were only very slightly ^{13}C depleted compared with the same ecological guild at Patos and Tramandaí lagoons. These species (*C. sapidus*, *M. furnieri*, *M. liza*, *Paralichthys orbignyanus*) appeared to have retained an isotopic signature characteristic of choked lagoons, perhaps due to recent colonization of Chuí following movement from other nearby estuaries, such as Patos Lagoon, for reproduction in the adjacent marine environment. It is unlikely that the enriched signatures observed for these species are due to selectively feeding on less abundant C_4 production sources because their diets can be characterized as omnivorous or detritivorous. Unlike the estuarine-dependent species that move offshore for spawning, estuarine resident species complete their entire life cycle in the estuary and had carbon isotope signatures only slightly less depleted than freshwater vagrant species collected at Chuí, but significantly depleted compared with estuarine dependent species. In choked lagoons, estuarine resident, and estuarine-dependent species did not differ in their isotopic signatures. At Chuí, estuarine resident species, therefore, appear to be assimilating local autotrophic sources, which happened to have depleted carbon isotope signatures. Evidence from tropical estuaries of eastern Australia indicates that the area (patch size) of saltmarsh vegetation affects the relative importance of that source to consumers within those patches (Guest & Connolly, 2006). Therefore, the limited patch size of C_4 saltmarsh vegetation at Chuí (due to a comparatively small mixohaline zone and steep littoral) could preclude the importance of this source even for species that occur most frequently in association with littoral vegetation zones where C_4 saltmarsh plants may be present. The slight difference in freshwater vagrant and estuarine resident species at Chuí may be due to frequent movement of freshwater vagrant species between purely freshwater reaches and the estuarine zone.

Hydrogeomorphology and the relative importance of carbon sources supporting secondary production

Estuaries are dynamic mixing zones where potential autotrophic sources supporting secondary production could derive from in situ, freshwater or marine origin. The relative importance of diverse production sources to estuarine consumers may be influenced by multiple factors, including hydrogeomorphologic features that affect the relative size of the estuarine zone, patterns of freshwater inflow, type of connection with the marine ecosystem, and slope/extent of the littoral zone relative to open water. As discussed above, studies conducted across fluvial/salinity gradients within estuaries have found patterns similar to our findings comparing across three estuaries that differed in hydrogeomorphology. But can hydrogeo-morphic factors identified at the landscape scale be useful for making generalizations or predictions regarding the relative importance of autotrophic carbon sources supporting secondary production of estuarine consumers?

Detecting patterns of resource utilization using stable isotopes requires isotopic differentiation of autotrophic sources (e.g., C_3 and C_4 vegetation, relationship between salinity and algal δ^{13}C). This appears highly feasible for most estuarine ecosystems, especially when including analyses of sulfur isotopes (e.g., Connolly et al., 2004). Although consumers in estuarine food webs typically rely on multiple resource pathways and functional groups may differ in their resource use (e.g., Alfaro et al., 2006), predictions may be made regarding dominant energy sources support-ing consumers at the level of the entire assemblage. For example, carbon derived from C_4 marsh grasses, such

as *Spartina* spp. may be expected to be a major contributor to secondary production in those estuaries having expansive littoral zones and high densities of saltmarsh vegetation relative to open water area (e.g., Richoux & Froneman, 2007; Winemiller et al., 2007). In contrast, secondary production in estuaries characterized by expansive open water zones relative to littoral area may depend on large contributions from various algal sources and submerged aquatic vegetation (e.g., Kang et al., 2003; Riera & Hubas, 2003; Garcia et al., 2007). Similar to our data from Chuí, secondary production in coastal river estuaries with high freshwater inflow may rely on C_3 productions sources, including ^{13}C-depleted algae (e.g., Chanton & Lewis, 2002).

Several studies have found that estuarine consumers often rely most heavily on locally abundant autotrophic sources produced in situ (e.g., Wainright et al., 2000, and the above cited references). Therefore, hydrogeomorphic factors that determine the relative abundance of such sources may also correlate with resource use by consumers. Although within-estuary variation is to be expected, estuaries may be broadly classified according to landscape-scale hydrogeomorphic factors (e.g., choked lagoon and coastal river as in this study) that allow an initial prediction of the relative importance of carbon sources to secondary production. Similar to our analyses of ecological guilds, predictions may be refined at the species level using ecological knowledge such as habitat use, ecomorphology and residence time. Such predictions are useful as a starting point for poorly studied regions such as ours, as well as for global-scale analyses of patterns in estuarine food webs. Future studies should directly measure aspects of hydrologic variation and geomorphology across a range of estuaries to test our generalizations and identify specific relationships and causal mechanisms. Continuing research should address interacting effects of latitude, seasonality/climatic factors, tidal amplitude, biogeography, functional composition of the consumer assemblage, and degree of movement of organisms among freshwater, estuarine, and marine environments.

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