# FIDELITY BIAS IN MOLLUSK ASSEMBLAGES FROM COASTAL LAGOONS OF SOUTHERN BRAZIL

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ABSTRACT – The South America southern coast exhibits many outcrops with abundant shell beds, from the Pleistocene through the Recent. How much biological information is preserved within these shell beds? Or, what is the actual probability a living community has to leave a fossil record corresponding to these shell deposits? Although ecological and biogeographical aspects might had been pointed, considering these temporal scales, up to the moment there is no taphonomically-oriented studies available. Quantitative comparisons between living (LAs), death (DAs) and fossil assemblages (FAs) are important not only in strictly taphonomic studies, but have grown a leading tool for conservation paleobiology analysis. Comparing LAs, DAs and FAs from estuaries and lagoons in the Rio Grande do Sul Coastal Plain makes possible to quantitatively understand the nature and quantity of biological information preserved in fossil associations in Holocene lagoon facies. As already noted by several authors, spatial scale parts the analysis, but we detected that the FAs reflects live ones, rather than dead ones, as previously not realized. The results herein obtained illustrates that species present in DA are not as good preserved in recent (Holocene) fossil record as originally thought. Strictly lagoon species are most prone to leave fossil record. The authors consider that the fidelity pattern here observed for estuarine mollusks to be driven by (i) high temporal and spatial variability in the LAs, (ii) spatial mixing in the DA and (iii) differential preservation of shells, due to long residence times in the taphonomically active zone.

Key words: death assemblages, spatial mixing, time-averaging, estuaries, lagoons.

RESUMO – A costa sul da América do Sul apresenta diversos afloramentos com concentrações conchíferas, desde pleistocênicas até recentes. Quanta informação biológica está preservada nestas concentrações? Ou, qual a probabilidade de uma associação viva deixar um registro fóssil análogo a estas? Embora diferenças ecológicas e biogeográficas já tenham sido apontadas entre estas escalas temporais, até o presente momento nenhum trabalho analisou diferenças sob o ponto de vista tafonômico. A possibilidade de se comparar quantitativamente associações vivas, mortas e fósseis é importante não somente em estudos tafonômicos, como também tem se tornado uma ferramenta poderosa na paleobiologia da conservação. Este trabalho compara quantitativamente associações vivas, mortas e fósseis de lagunas e estuários da Planície Costeira do Rio Grande do Sul. Os resultados reforçam trabalhos anteriores, demonstrando que a escala espacial interfere na análise. Este trabalho também constatou que a associação fóssil reflete a associação viva. Além disso, as espécies estritamente lagunares têm maior probabilidade de deixar registro fóssil. Os resultados obtidos neste trabalho ilustram que as espécies presentes nas associações mortas não são tão bem incorporadas no registro fóssil recente. As espécies estritamente lagunares têm maior probabilidade de deixar registro fóssil. Foi aqui considerado que o padrão observado na fidelidade de moluscos estuarinos é ocasionado pela (i) alta variabilidade temporal e espacial na associações vivas, (ii) mistura espacial na associação morta e (iii) preservação diferencial, devido à destruição por um longo tempo na zona tafonomicamente ativa.

Palavras-chave: associações mortas, mistura espacial, condensação temporal, estuários, lagunas.

## **INTRODUCTION**

The resemblance between DAs and FAs to the original living community is a valuable appraisal of taphonomic bias (Behrensmeyer *et al.*, 2000; Lockwood & Chastant, 2006), and also provides data on broad temporal scales, which is important in conservation biology (see review by Kidwell, 2013). The comparison between assemblages (*i.e.* live-dead studies), called compositional fidelity or quantitative fidelity,

estimates how much of the original community (measured by its richness, abundance, structure and evenness) is preserved in a local fossil record (Kidwell & Bosence, 1991; Behrensmeyer *et al.*, 2000).

Despite most live-dead studies focuses on marine organisms that leave refractory remains (see generalization for the term "shell", by Kidwell, 2013), recent works have been done with different taxonomic groups and environments: estuarine diatoms (Hassan *et al.*, 2008), ostracodes (Allin &

Cohen, 2004; Michelson & Park, 2013), freshwater mollusks (Martello *et al.*, 2006; Erthal *et al.*, 2011; Tietze & De Francesco, 2012), terrestrial gastropods (Yanes *et al.*, 2008, 2011; Yanes, 2012), fruits and seeds (Vassio & Martinetto, 2012), small-mammals (Terry, 2010a,b) and stranding cetaceans (Pyenson, 2010, 2011).

The richness of DAs, for example, can differ from the corresponding LAs due to processes such as differential preservation, postmortem transport, differential turnover, natural temporal variability in the LAs and environmental change within the window of time-averaging (Olszewski & Kidwell, 2007; Olsewski, 2012; Kidwell, 2013). As has long been recognized, DAs are the complex product of the LAs (Johnson, 1965; Walker & Bambach, 1971).

In marine environments, death assemblages are richer than the local living community, due time-averaging, reaching up to 25% more species than the later (Kidwell, 2001, 2002a). In lagoon and estuarine environments, some authors have pointed out that the DAs virtually mirror the LAs. For example, a comparison between empty shells (DA) and living mollusk species from intertidal settings (Magu Lagoon), have indicated that shell mixing between habitats is not typical in these environments (Warme, 1969). Another study, conducted in Tomales Bay, California, shows that the DA is mostly composed of shells from mollusks living nearby, and within habitat transport is negligible (Johnson, 1965). However, more studies are needed to fully develop scenery of processes that affect the fossil preservation in lagoon environments, which need to be refined under the viewpoint of quantitative fidelity between live and death assemblages.

The aim of this paper is to determine fidelity of molluscan assemblages fossilization in coastal lagoons, illustrating how much information can actually be preserved in death and fossil assemblages originated during the Holocene in an estuarinelagoon (E-L) system (Rio Grande do Sul Coastal Plain, CPRS), at two different spatial scales, local and regional.

## Quaternary shell beds in South America

The southern South America coasts present high potential for taphonomic studies with mollusks, owing to the expressive presence of Quaternary shell concentrations (marine and E-L) from southern Brazil as far as Patagonia (Argentine) (Martínez *et al.*, 2013 and references therein). In Brazil, works conducted in the late 1960s and early 1970s dealt specifically with some of those shell assemblages in Rio Grande do Sul State (RS), regardless their taphonomy. Bianchi (1969), for example, described Pleistocene oyster beds in Pelotas municipality and surroundings, which are now lost due to mining activities. Closs & Forti (1971) listed mollusk species found in Holocene sediments. Studies in outcrops from the Chui region are still in early phases, addressing mainly taxonomic features (Lopes & Simone, 2012).

In addition, several sandy biodetritic deposits are present in the southern Brazilian continental shelf, informally named "bioclastic provinces" (Erthal, 2012). They are morphologically linear, distributed parallel to the present coastline (associated to ancient coastlines), and are mostly composed of molluscan shells, derived from inner shelf environments. These features have been mapped on shelf at water depths such as 20-25 m, 32-45 m, 60-70 m, 80-90 m and 120-130 m, but can be found even in present-day beaches (Corrêa *et al.*, 1996; Calliari *et al.*, 1999).

Shells from these "provinces" are commonly reworked, and along with biologic/bioclastic material, transported to the present shores during meteorological tides, mainly in the southern part of the CPRS (Calliari *et al.*, 1999). These reworking events, which happen since at least the late Pleistocene, mix temporally the molluscan shells, making it very difficult to attribute a reliable age.

Albeit the whole region shows potential for taphonomic studies, questions such as "what percentage of species living today in a province have also a Pleistocene record somewhere within it?" are still little addressed (see Kidwell, 2013). For example, from complementary data made available by Martínez *et al.* (2013) it is possible to state that nearly 90% of Holocene species are also recorded in the Pleistocene for the Uruguayan coast.

# STUDY AREA

The study area encompasses lagoon systems of the Coastal Plain of Rio Grande do Sul State (CPRS; Figure 1). The CPRS was formed during the Quaternary by the juxtaposition of sedimentary deposits from four barrier-lagoon systems designated as I (oldest) to IV (youngest) by Villwock *et al.* (1986). The first three are Pleistocene (Villwock *et al.*, 1986) while the younger barrier-lagoon system (Barrier-Lagoon IV) was formed during the Holocene (Villwock *et al.*, 1986; Tomazelli & Villwock, 2000).

The most recent lagoon-barrier depositional system of CPRS is represented by a suite of coastal lakes and lagoons, which were fully developed by the maximum Holocene transgression, such as the Tramandaí Lagoon (Tomazelli & Villwock, 2000; Dillenburg *et al.*, 2009). Then, most of the lowlands, presently constituting the Holocene lagoon plain, were flooded and formed large lagoon bodies that were connected to the ocean (Tomazelli & Villwock, 1991).

The Tramandaí Lagoon has an area of 12.86 km<sup>2</sup> and an average depth of 1.10 m (Schwarzbold & Schäfer, 1984); it receives, through the Tramandaí river, water inflow and fine sediments (silt and clay) originated in the rivers and lagoons situated northwards of the system. The Tramandaí estuary is linked to the Atlantic Ocean by a 1.5 km long channel with average depth of 3.0 m (Tabajara & Dillenburg, 1997).

## MATERIAL AND METHODS

Here, living assemblage -LA – refers to specimens collected alive; some original authors included empty shells with adhering flesh and even still-articulated empty shells in this category, but this is difficult to standardize post hoc. **DAs** refers to dead shells; herein are included fragments in their counts of dead individuals if unique (*e.g.* bivalve fragments that included the hinge, gastropods that included the apex).



**Figure 1.** Location of the study area. **A**, general overview of the study area, highlighting those sites where fossil mollusks have been found in E-L sedimentary facies, as well as living molluscan data for Patos Lagoon; **B**, DA data recovered in Tramandaí Lagoon by the authors (see Table 1), plus published work here used for FA.

**FAs** refers to specimens found in sedimentary deposits, at Holocene E-L facies, within the youngest barrier-lagoon system (Barrier-Lagoon IV).

## Living assemblages

Data for LA were compiled from only two lagoons from which data were available (or were of best quality): Tramandaí Lagoon (Pedroso & Girardi, 2003; Kapusta *et al.*, 2009) and Patos Lagoon (Bemvenuti & Neto, 1998). These three works surveyed benthic invertebrates in general. Growing human-induced alteration during the past few decades prevented the present LA data do be pristine (see Kidwell, 2007), mainly due to high estuaries alteration (Lötze *et al.*, 2006). Nevertheless, not every polluted areas show low live-dead agreement (Kidwell, 2008).

## **Death assemblages**

In this study were sampled 24 sites (= replicates) in the Tramandaí Lagoon. These sites were selected to represent a variety of environments (differing according to salinity regime) and to maximize the amount of sediments types and taphonomic bias (Figure 1B; Table 1). DA data for the Patos Lagoon are still not available in the bibliography. However, is assumed that whenever such kind of data becomes available, it will change the outcomes of our discussion only in side details, due to possible addition of rarer species to the DA. The effects of this sampling strategy will be justified in the Discussion section.

Samples were collected by the authors, with field logistic assistance provided by CECLIMAR/UFRGS and the site location was established using GPS (accurate to within 10 m). One sample was collected at each site (in autumn 2010) using Eckamm (recovering a volume of 4.6 L, with mesh sieve 1 mm). Whole specimens and identifiable fragments (DAs) were sorted under a dissecting microscope and identified to genus using a variety of general and specific shell guides (Abbott, 1974; Forti-Esteves, 1974; Rios, 2009; Mikkelsen & Bieler, 2008).

#### Fossil assemblages

Data for fossil assemblages were compiled from publications concerning Holocene geological evolution of CPRS. We considered only species found at muddy facies, classified by the authors as E-L sedimentary deposits (Dillenburg, 1996; Buchmann *et al.*, 1998; Dillenburg *et al.*, 2004; Travessas *et al.*, 2005; Caron, 2007; Lima *et al.*, 2013) (Figures 1A, B). The authors also included data from previous taphonomic studies conducted in the area (Ritter *et al.*, 2013; Tramandaí

Site	Sediment	Depth (m)	Composition		
1	sand	0.90	absent		
2	fine sand	1.30	rare fragments of Tagelus plebeius		
3	fine sand	1.30	absent		
4	sand	1.30	rare fragments of T. plebeius		
5	sand	1.15	rare fragments of T. plebeius		
6	sand	0.75	absent		
7	sand	0.85	absent		
8	fine sand	1.05	absent		
9	sand	1.05	absent		
10	sand	0.95	absent		
11	sand	1.20	absent		
12	fine sand	1.40	absent		
13	fine sand	1.20	few shells of Erodona mactroides		
14	fine sand	1.10	rare fragments of T. plebeius		
15	sand	0.70	few shells of Heleobia sp. and E. mactroides		
16	sand	0.95	few shells of Heleobia sp. and E. mactroides		
17	sand	0.65	absent		
18	sand	1.60	absent		
19	silt	4.50	several shells		
20	silt	5.50	several shells		
21	silt	5.80	several shells		
22	silt	3.80	several shells		
23	silt	2.00	absent		
24	silt	2.50	absent		

Table 1. Details of the sites sampled (DAs) in the Tramandaí Lagoon.

Lagoon). Some classic publications (*e.g.* Closs & Forti, 1971; Forti-Esteves, 1974) were not included because they do not specify whether mollusks were found in E-L facies.

### **Fidelity analysis**

The fidelity analyses focused on the two indices proposed by Kidwell & Bosence (1991), including the so-called F1, the percentage of shelly species found alive that were also found dead  $[(NS \times 100)/(NS + NL)]$  (a measure of the preservation potential of species in their natural habitat); and F2, the percentage of species found dead that were also found alive  $[(NS \times 100)/(NS + ND)]$  (a measure of the spatial fidelity of skeletal remains to their original community); where NS =number of species shared by the two assemblages; ND =number of species found only in DA; and NL = number of species found only in LA. These indices were adapted to compare the fidelity of the FA in relation to the LA and DA (see also Erthal et al., 2011), as follows: F1, the percentage of species found alive that were also found in the FA, and the percentage of species found dead that were also found in the FA; F2, the percentage of species found in the FA that were also found live, and the percentage of species found in the FA that were also found in the DA.

The fidelity measures were conducted at the genus level, in order to avoid biases arising from possible misidentification of fossil species (Valentine, 1989), especially among species from geological studies. Two spatial levels were considered for the fidelity analysis: (i) local scale, considering only LA, DA and FA data from Tramandaí Lagoon; and (ii) regional scale, where LA data from Patos Lagoon were included as well as all FA data of all known fossil deposits from Holocene E-L facies in the CPRS. It is herein recognized that DA information is the same in both assessments, and any limitations are discussed. Species listed on only a single paper was excluded from de LA in the regional approach because they are punctual register and could be equivocates.

The Mann-Whitney-U test was used to test if live-deadfossil differed in median values. Statistical significance is considered at  $\alpha = 0,05$ . We performed a Non Metric Multidimensional Scaling (NMDS), using the Jaccard similarity index, which is appropriate for the available presence-absence data (Legendre & Legendre, 1998). In order to test whether groups of assemblages differed, was used the Multivariate Analysis of Variance with Permutation (PERMANOVA; Anderson, 2001). Statistical analyses were performed using PAST v2.17 software (Hammer *et al.*, 2001).

# RESULTS

Bottom samples from Tramandaí Lagoon (Figure 1B) yielded a few shell remains (Table 1). A total of 15 bivalves and 11 gastropods species were recorded across all modern (LA and DA) and fossil assemblages (Table 2). Of these, one bivalve genus (*Anomalocardia*) and one gastropod genus

(*Crepidula*) occurred only as fossils; one bivalve genus (*Macoma*) and one gastropod genus (*Melampus*) occurred only in modern assemblages (Tramandaí Lagoon; Table 2).

Regardless molluscan class, the presence of living species found also in death assemblages, at local scale, is slightly lower than at regional scale, while the spatial fidelity is low for both spatial scales here considered, reaching less than 20% (Figure 2A). Dead species are represented far well in fossil assemblages at regional scale than at local scale, with more than 80% of spatial fidelity (F2), at both spatial scales (Figure 2B). Living species are fully represented in fossil layers at regional scale (100%), but reach less than 60% at local scale. Their spatial fidelity is very low at regional scale, becoming higher at local scale (up to 80%; Figure 2C).

Accordingly to the Mann-Whitney U test, the LAs differ significantly from DA at both spatial scales (local: Z=-3.937, p<0.001; regional: Z=-3.574, p<0.001) and FAs at regional scale (Z=-3.64, p<0.01), but not at local scale (Z=-0.6425,

p>0.05). DA showed significant difference from FA at local scale (Z=-4.472, p<0.001), but not at regional scale (Z=-1, p>0.05).

NMDS shows that the FAs are scattered regarding the mollusk composition (Figure 3). The two LAs here considered are within the space encompassed by the group formed by FAs, while the DA is considerably different from the first two assemblages. The PERMANOVA showed no significant difference between living, death and fossil assemblages (F=1.401, p=0.1009).

In the DA, richness is considerably higher than in LA and FA at both scales (Table 2). Considering the data only from Tramandaí Lagoon (local scale), living gastropods are better preserved in the DA than bivalves, which present more resemblance (living x dead) at regional scale (Figure 4A). The preservation of spatial fidelity (F2) is very low for bivalves and gastropods at both scales (Figure 4B). The preservation of species found dead into FA, for both gastropods and bivalves is remarkably low at local scale, and overall high at regional,

Table 2. Presence/absence data compiled from coastal lagoons of Rio Grande do Sul State. Fossil<sup>1</sup>, data only from Tramandaí Lagoon; Fossil<sup>2</sup>, species found across all Holocene lagoon deposits. Abbreviations: E, estuarine; M, marine.

Classification	Genus	Live	Dead	Fossil <sup>1</sup>	Fossil <sup>2</sup>	Environmental preference
Gastropoda						
Calyptraeidae	Calyptraea		х		х	М
	Crepidula				х	М
Cochliopidae	Heleobia	х	х	х	х	E
Columbellidae	Costoanachis		х			М
Olivellidae	Olivella		х		х	М
Pyramidellidae	Turbonilla		х			М
	Parodizia	х			х	Е
Bullidae	Bulla		х		х	М
Cylichnidae	Cylichnella		х			М
	Acteocina		х		х	М
Ellobiidae	Melampus	х				Е
Gastropoda total		3	8	1	7	
Bivalvia						
Nuculidae	Nucula		х	х	Х	М
Mytilidae	Mytilus		х			М
Ostreidae	Ostrea		х		Х	М
Lucinidae	Ctena		х			М
Carditidae	Carditamera		х		х	М
Cardiidae	Laevicardium		х			М
Tellinidae	Tellina	х		х	Х	E
	Macoma					E
Veneridae	Anomalocardia		х		х	М
	Pitar		х		Х	М
	Transennella		х			М
Mactridae	Mactra		х		х	М
Corbulidae	Corbula		х		Х	М
	Erodona	х	х	х	х	Е
Solecurtidae	Tagelus	х	х	х	х	Е
Bivalvia total		3	13	4	10	
TOTAL		6	21	5	17	



Figure 2. Fidelity indices (F1 and F2) comparing living, death, and fossil assemblages at local and regional scales pooled data for gastropods and bivalves.

larger scale, where data from Patos Lagoon were included (Figure 4C). However, the spatial fidelity for preservation of dead species in FA is quite high, being slightly lower for bivalves at local scale (Figure 4D).

Although the preservation of living species in FA is higher at regional scale (with 100% of preservation for both gastropods and bivalves) than at local scale (Figure 4E), the spatial fidelity is much lower in regional scale than in local scale (where gastropods present 100% of preservation), when LA and FAs are compared (Figure 4F).

#### DISCUSSION

The lack of surveys of living communities through broader time spans, enough to capture all its natural variability, is one of the leading problems in live-dead comparisons (Kidwell, 2001, 2008; Olszewski & Kidwell, 2007). Moreover, DAs present some degree of time-averaging (that may reach up to tens of thousands of years; see Flessa & Kowalewski, 1994; Kidwell, 2002a, 2013) and within-habitat spatial condensation, which naturally produces some departing in live-dead similarities (Kidwell & Bosence, 1991; Tomašových & Kidwell, 2009a, 2011).

Here is assumed that the living community data came from patchy samples and may not represent a wide sample (see Lockwood & Chastant, 2006 for a temporal series over 20 years of LA sampling). This sampling bias would matter in studies evaluating relative species abundance, since the numerical dominance influence live-dead comparisons (Tomašových & Kidwell, 2009a).

In addition, E-L environment is known to be poorer in species than marine environments, due to limiting factors such as salinity variation, low depths, restricted water circulation, etc. However, the fidelity data herein presented are not of poorer quality, since the live-dead-fossil comparison here performed was done considering a wide spatial scale. Though some species might be absent from DA, and either LA or FA, due to limited sampling effort, some studies suggest the contrary (Tomašových & Kidwell, 2009a, 2010b). The magnitude of the diversity excess in DAs, relative to LAs, will decrease with decreasing spatial resolution from alpha to beta scales, because each local assemblage is increasingly likely to (i) be colonized by species from the shared species pool and (ii) experience habitat conditions that occur in adjacent communities, thus reducing spatial variation in species composition and abundance (Tomašových & Kidwell, 2009a, 2010b).

## Fidelity

Three main processes are probably responsible for fidelity pattern observed here: (i) high temporal and spatial variability of the living communities. Given many generations, and in consequence to time-averaging in the DA, the LA becomes very different (and rarefied in species) than the DA; (ii) spatial mixture in the DA, with the addition of (dead) shells from other environments, mainly strictly marine species (low spatial fidelity at regional scale in the live x dead comparison) (Figure 2A; Table 2); and (iii) differential preservation, since shells may reside for a long time after destruction in the surficial E-L sediment (Ritter & Erthal, 2011), determining the dissimilarity with the LA and the FA at local scale. DAs may acquire higher richness than the corresponding LAs by multiple factors (shell input more than shell destruction and sedimentation rate).

The low richness recorded in LAs may be consequence of undersampling (see Lockwood & Chastant, 2006). Estuaries and coastal lagoons may be aggressive environments, allowing poorer mollusc faunas to develop (Lerberg *et al.*,



Figure 3. Scatter plot showing the NMDS analysis conducted with living (crosses), death (square) and fossil assemblages (diamonds) of coastal lagoons from southern Brazil. Stress = 0.1568. Abbreviations: LA-Tra, living assemblage from Tramandaí Lagoon; LA-Pat, living assemblage from Patos Lagoon; DA-Tra, death assemblage from Tramandaí Lagoon. Fossil assemblages: R-2013-1, fossil data from Ritter *et al.* (2013), outcrop 1; R-2013-2, data from Ritter *et al.* (2013), outcrop 2; L-2013, Lima *et al.* (2013); C-2007, Caron (2007); T-2005, Travessas *et al.* (2005); D-2005, Dillenburg *et al.* (2004); B-1998, Buchmann *et al.* (1998); D-1996, Dillenburg (1996).

2000), mainly due to the high osmotic pressure this setting is subject (Shumway, 1977; Rhodes-Ondi & Turner, 2010). This may be true for the Patos and Tramandaí lagoons, as Coutinho & Seeliger (1984) found salinity varying from 3 to 36‰. Also, the low depths, typical of CPRS coastal lagoons (including Patos Lagoon to some degree; Möller & Castaing, 1999), may complicate the thriving of more marine species (Allen, 1978, 2008). E-L molluscan LAs may be highly variable, with little persistence of less abundant species in the community through time (Kidwell, 2002a; Zuschin & Oliver, 2003; Kidwell & Rothfus, 2010; Olszewski, 2012). DAs may, on the other way, acquire higher richness than corresponding LAs by multiple factors. Time-averaging, as a leading agent, results in accumulating ecologically persistent species (sometimes rare) over long-term time spans (Kidwell & Bosence, 1991; Flessa & Kowalewski, 1994; Kidwell & Flessa, 1995; Kowalewski et al., 2000; Kidwell, 2002a;

Tomašových & Kidwell, 2009a, 2010a,b, 2011). It provides a window of opportunities for postmortem transportation to homogenize species composition, mixing skeletal remains from multiple generations of living populations and environmental randomness, and from ecological succession and environmental change occurrences in a spatial fashion (Tomašových & Kidwell, 2009a,b). Furthermore, these models are neutral in terms of preservation: they assume that all species have the same (stochastic) per-individual rate of shell destruction or removal from the DA (Tomašových & Kidwell, 2010a,b, 2011).

Although with a considerably time-averaging, and including long-lasting elements (with high durability), the E-L DA here recorded shows high preservation potential, mainly for bivalves at regional scale (Figures 4A,C). This may be a result of processes such as high input of marine shells from the inner shelf during meteorological tides, low biogenic destruction (De Francesco & Hassan, 2008; Ritter *et al.*, 2013) and high sedimentation rates (the sedimentation rate at the mouth of Tramandaí River is 4.2-4.4 mm/yr.; Dillenburg & Burnett, 1995). Those processes may explain why DA is located far the LA and FA cloud in the NMDS (Figure 3).

E-L environments, being transitional sedimentary settings, also display a transitional preservation pattern, at least for mollusks, for several reasons. The LA is preserved in the FA (Figures 3, 4C), even though the DA may be 'polluted' by non-indigenous shells, raising the DA richness with species that will not further preserve in FA (Figure 4B), at least at local scale. The differential preservation of lagoon shells may be the reason for their persisting in the recent fossil record, whilst, as already examined by Ritter et al. (2013), the main destructive process in the E-L sedimentary column is dissolution, a typical fluvial agent (see also Pip, 1988; Kotzian & Simões, 2006; Erthal et al., 2011), which could cause low preservation in lagoon environments. However, the high production of mollusk shells in E-L environments, observed for Erodona mactroides Bosc, 1802 both presently in the Patos Lagoon (Colling et al., 2010) and in lagoon outcrops in CPRS (Ritter et al., 2013) possibly mean constant input of shells through the taphonomically active zone (TAZ).

The live-dead agreement, for mollusks, is on average poorer on shelves than in estuaries and lagoons (Kidwell, 2001, 2002b), and taphonomic processes other than within-habitat time-averaging (probably environmental condensation) are more important there (Tomašových & Kidwell, 2011). Indeed, the present results indicate that both LA and FA in E-L environments are basically constituted by indigenous species, though FA may be somehow enriched with marine species which resisted differential destruction in E-L TAZ (Ritter *et al.*, 2013; Figures 4D,F). In addition, marine species found in FA (at estuarine facies) might have not been transported, but are instead relicts of earlier populations which lived at approximate locations during sea-level variations (see Flessa, 1998 for a close example).

Despite transport of non-indigenous species may be an important factor for the discordance, the leading process is time-averaging. Kidwell (2013) found that richness and composition of molluscan DAs overwhelmingly reflect the effects of time-averaging rather than postmortem bias, due time averaged nature of the DAs, which captures rare and patchy species not sampled alive during a one-time survey, and by lateral shifting in habitats within the window of timeaveraging.

#### Spatial scale issues

The question 'What percentage of species sampled alive is also encountered dead?' can be asked for any spatial scale: at a site, in a habitat, in a region and across scales (*e.g.* 'What percentage of species in a regional checklist can be found among the dead at a single site?'). Presenceabsence tests of live-dead agreement can be applied to a broad array of groups and settings and thus allow crossscale comparisons (Kidwell, 2013), although they may be significantly homogenized by time-averaging (whilst spatial mixture may mash relative abundance; Olszewski & West, 1997). These approaches provide a relatively simple means of quantifying per-taxon 'fossilization rates', although none are true rates (Kidwell, 2013).

Several censuses and/or sampling many sites of LAs are necessary to obtain meaningful relationships among LAs and DAs. In marine settings, this procedure has yielded values around 62%-88% for F1, and 63%-94% for F2, (Kidwell & Bosence, 1991; Zuschin *et al.*, 2000; Kidwell, 2002a; Kowalewski *et al.*, 2003; Zuschin & Oliver, 2003; Lockwood & Chastant, 2006). In fluvial settings, Erthal *et al.* (2011) found lower values for F1 and F2, ranging from 30% to 58% at the species level and from 66% to 75% at the genus level. In the present study, the values range from 75-100% for F1 and from 12.5-100% for F2.

It is conceivable that spatial scale of sampling influences the fidelity outcomes. In small scales, sometimes, the proximity between sampling sites may alone explain the resemblance between LAs and DAs (spatial autocorrelation; Tomašových & Kidwell, 2009a). In the present study, the difference between scales (local x regional) is observed in the living x fossil comparison (Figure 2C). Despite lagoon species, in both scales, display high relative probability of preservation, F2 values at regional scale show that FA actually reflects the DA. In other words, lagoonal species are in fact preserved, but owing to time-averaging (*e.g.* Olszewski & Kidwell, 2007) and spatial mixing (*e.g.* Fürsich, 1978) processes the richness is increased and then incorporated to the recent fossil record.

The degree of transport is basically determined by the habitat spatial scale, *i.e.*, whether there is within- of multi- habitat spatial mixing (Kidwell & Bosence, 1991; Kidwell, 1998). The basic premise is that DAs suffer a natural increase in the richness due to time-averaging, but also as a consequence of transport between contiguous areas (spatial mixing), transferring diversity from  $\beta$  (beta levels, between sites) to  $\alpha$  (local, at facies level) (Kidwell & Bosence, 1991; Olszewski & Kidwell, 2007; Tomašových & Kidwell, 2009a,b). For example, local DAs on average capture 80% of regional richness whereas LAs capture only 60% (Tomašových & Kidwell, 2009a).

It is still not all clear how taphonomic, and even ecological factors, may influence the resemblance of living, death and fossil assemblages in estuaries and lagoons. Dissolution is the main taphonomic process altering biological information in those environments (Ritter *et al.*, 2013), but differential preservation may be, perhaps, the responsible for introducing bias from living to fossil assemblages. It may considerably dilute the increase in DA richness, accounted by the time-averaging and within- and multi-habitat and spatial mixing.

# CONCLUDING REMARKS

The results above indicate that DAs and FAs in E-L environments present significant spatial multi-habitat mixing, by the addition of inner shelf species and considerable timeaveraging, since most of DA richness is captured by local



Figure 4. Fidelity indices (F1 and F2) comparing living, death, and fossil assemblages at regional scales, separately for bivalves and gastropods.

FA. Fossil mollusk assemblages found in strictly lagoon sedimentary environments in the CPRS present multi-habitat spatial condensation, probably with significant time-averaging, and are not a strong reflection of lagoon DA species. Therefore, these assemblages represent more than a single depositional environment, with several mollusk generations. As a consequence, the age of a supposedly life-positioned shell do not temporally reflect the facies as a whole, but a single episode instead, probably from a late depositional event.

Several taphonomic factors (both intrinsic ant extrinsic to the mollusks) may operate in the formation of the assemblages here studied, such as preferential preservation of infaunal elements. Nevertheless, more knowledge about LAs and DAs (*e.g.* abundance) are still needed, since long-term fidelity studies with mollusks are absent in the CPRS.

Additionally, the inclusion of live-dead-fossil information from adjacent areas (such as the coast of the State of Santa Catarina, in Brazil, and the coasts of Uruguay and Argentina) would improve our understanding of fidelity in a wider spatial scale, as well as temporal, with data from the Pleistocene. Yet, intersecting information from quantitative fidelity and paleobiogeography can, in concert, lead to new insights into the faunistic change in South America coastal area all along the Quaternary.

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