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Taphonomy of death assemblages of the freshwater bivalve *Corbicula fluminea* (Müller, 1774) (Veneroidea) after three and four decades in the upper Río de la Plata, Uruguay

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TAPHONOMY OF DEATH ASSEMBLAGES OF THE FRESHWATER BIVALVE *CORBICULA FLUMINEA* (MÜLLER, 1774) (VENEROIDEA) AFTER THREE AND FOUR DECADES IN THE UPPER RÍO DE LA PLATA, URUGUAY

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Abstract. The invasive bivalve *Corbicula fluminea* has been known in the Río de la Plata for approximately 40 years. This decadal time-lapse fill a gap in taphonomic studies. Our study is the second to investigate taphonomic modifications on valves of this species in Uruguay, expanding the temporal resolution of the first. We divided the valve into four sectors and recorded fragmentation, periostracum loss, and corrasion, categorizing these attributes into three severity levels. We also observed no attempts at bioerosion and bioencrustation. The central sector is the most frequent among all samples, and the posterior one is the least frequent. The differences in damage were tested using the X^2 test, the Bonferroni correction, and an average taphonomic score. We evaluated the extent of taphonomic damage over time by comparing the average taphonomic score using Kendall's *tau*. The tests revealed several statistically significant differences. The umbonal and posterior sectors are differently represented, with the 2008 sample being different in both cases. The central and anterior sectors do not exhibit differences. Fragmentation exhibits differences in all sectors except the anterior over the years; category 0 is the most represented in all years and sectors. Periostracum damage shows no statistically significant differences in sectors or years; category 2 is the most represented. Corrasion differs among the three samples, varying over the years in different sectors; category 2 is the most represented. In conclusion, there are statistically significant differences in the sectors represented and in fragmentation. However, no linear trend was observed over the years.

Key words. Actualistic Taphonomy. Death assemblage. *Corbicula fluminea*. Río de la Plata. Uruguay.

Resumen. TAFONOMÍA DE LOS ENSAMBLES DE VALVAS DEL BIVALVO INVASOR *CORBICULA FLUMINEA* (MÜLLER, 1774) (VENEROIDEA) LUEGO DE TRES Y CUATRO DÉCADAS DE SU REGISTRO EN EL ALTO RÍO DE LA PLATA, URUGUAY. *Corbicula fluminea* es un bivalvo invasor en el Río de la Plata desde hace aproximadamente 40 años, un lapso que no ha sido prácticamente estudiado desde la Tafonomía. Este estudio es el segundo sobre la especie, expandiendo la resolución temporal del primero. Dividimos las valvas en cuatro sectores, registrando la fragmentación, el daño del periostraco y la corrasión, clasificando la intensidad de estos atributos en tres categorías. El sector central fue el más representado siempre, y el posterior el menos frecuente. Para evaluar las diferencias en el daño tafonómico usamos el test de X^2, el de Bonferroni y un índice de daño promedio. Para correlacionar este índice con el paso del tiempo utilizamos la *tau* de Kendall. Los sectores umbonal y posterior están diferentemente representados, siendo la muestra de 2008 la diferente en ambos casos. El sector central y el anterior no exhiben diferencias. La fragmentación es diferente en todos los sectores excepto en el anterior, y la categoría 0 la más representada siempre. El daño del periostraco es similar en todas las muestras y sectores, siendo la categoría 2 la más frecuente. La corrasión es diferente entre las muestras, variando el sector afectado; la categoría 2 es la más representada. No encontramos signos de bioerosión o bioincrustación. En conclusión, se encuentran solamente diferencias significativas en la frecuencia de los sectores representados y en la fragmentación. De todos modos, no existe una tendencia a lo largo de los años ni para estos casos ni para el daño global.

Palabras clave. Tafonomía Actualística. Asociación de muerte. *Corbicula fluminea*. Río de la Plata. Uruguay.

One of the primary issues about taphonomic processes is the time needed to produce recognizable signatures. In other words, how much time is required to reach a given taphonomic condition? Recently, the answers have come mainly from evaluating death assemblages and experimental taphonomy (Kidwell, 2002; Kowalewski & Labarbera, 2004; Martínez *et al.*, 2020a).

Time averaging in death assemblages comprises, at best, hundreds of years (Kidwell & Bosence, 1991; Flessa, 1993; Flessa *et al.*, 1993; Meldahl *et al.*, 1997; Kosnik *et al.*, 2009; Martínez & Rojas, 2023; Ritter *et al.*, 2023), meanwhile experimental taphonomy (*i.e.*, artificial conditions) in

real-time implies a resolution of months or a few years (*e.g.*, Flessa & Brown, 1983; Briggs, 1995; Chattopadhyay *et al.*, 2013). The Shelf and Slope Experimental Taphonomy Initiative —SSETI— field experiment (Powell *et al.*, 2002, 2008, 2010, 2011a, 2011b; Parsons-Hubbard *et al.*, 2011) began around two decades ago, trying to recreate realistic conditions. Still, it implies direct human intervention by introducing samples into the environment.

Molluscan shells are one of the most frequent protagonists in the study of taphonomic processes because of their abundance in present and past assemblages along with their high preservation potential (*e.g.*, Parsons & Brett, 1991; Powell *et al.*, 1992; Best & Kidwell, 2000a, 2000b; Erthal & Ritter, 2017).

The use of a mollusk bioinvader with a well-documented arrival time in a given area enables us to observe natural taphonomic processes in action on a timescale that is typically not achievable. Martínez *et al.* (2020b), Antuña *et al.* (2021), and Gómez *et al.* (2023) are a series of published papers that evaluate the shells from a taphonomic point of view of the invasive gastropod *Rapana venosa* (Valenciennes, 1846) in Uruguay, concluding that taphonomic damage is reached very quickly. Through a process that lasts approximately 20 years, taphonomic conditions equivalent to those observed in millennial shells can be achieved.

Regarding freshwater environments, Kusnerik *et al.* (2020) compared the taphonomic damage in the invasive gastropod *Melanoides tuberculata* (Müller, 1774) with that of the native *Polygyra septemvolva* Say, 1818 in Florida (USA), finding rapid shell alteration. Meanwhile, Gómez *et al.* (2021) investigated the taphonomy of the invasive bivalve *Corbicula fluminea* (Müller, 1774) in Uruguay. The present paper continues that work, reevaluating the samples used therein and adding a new one collected several years earlier. *Corbicula fluminea* has been present in Uruguay for approximately forty years (see Ituarte, 1982; Veitenheimer-Mendes & Olazarri, 1983; Clavijo, 2021), providing a decadal resolution for the taphonomic processes involved. The goal of this paper is to determine whether the conclusions reached previously using the invasive estuarine gastropod *Rapana venosa* are valid when applied to an invasive freshwater bivalve.

MATERIALS AND METHODS

Sampling was carried out on a Río de la Plata beach known as Barrancas de San Pedro (34° 21′ 1″ S; 57° 54′ 60″ W) (Fig. 1). This area is part of the upper and intermediate Río de la Plata, being its coast part of the "Southwest littoral" landscape (Evia & Gudynas, 2000; López Laborde, 2003). This zone is characterized by coarse sand and gravel beaches limited by sedimentary cliffs. Waves and currents are usually of low energy. Nevertheless, wind-dominated tides are important, sometimes reaching the base of the cliffs.

We collected by hand all bioclasts of *C. fluminea* larger than 10 mm found in a rectangle limited by the low tide line up to about 5 m towards the cliffs, along about 30 m parallel to the water line, on three occasions (March 2008, April 2016, and May 2018), obtaining 223, 318, and 303 bioclasts, respectively. The specimens are housed in the Departamento de Paleontología, Facultad de Ciencias, Universidad de la República.

For the record of taphonomic features, valves were delimited in four sectors: umbonal, anterior, central, and posterior (Fig. 2.1). Fragmentation, the integrity of periostracum, and corrasion were registered and recorded on a three-state scale in each of the sectors: Fragmentation, 0: more than 80% of the section of the valve is present, 1: between 80% and 20% of the valve is present, and 2: less than 20% of the section of the valve is present. Periostracum, 0: periostracum is present in at least 80% of the surface, 1: periostracum is present in 80 to 20% of the surface, and 2: periostracum is present in less than 20% of the surface. Corrasion, 0: less than 20% of the external surface has signs of corrasion, 1: 80% to 20% has corrasion, 2: more than 80% of the external surface has signs of corrasion. To facilitate comparisons, this scale is identical to that used in our earlier works on invasive species (*e.g.*, Gómez *et al.*, 2023). Bioerosion and bioencrustation were not recorded in any bioclast.

Additionally, we calculated an average taphonomic score for total taphonomic damage and for each sector, using an adaptation of the formula developed by Meldahl *et al.* (1997): $g1+2(g2)+3(g3)+4(g4)/n$. We used 0, 1, and 2 for our categories rather than the 1, 2, 3, and 4 chosen by Meldahl *et al.* (1997), but because of operational problems, we avoided

Figure 1. Geographic location of the sampled locality. Image from Landsat/Copernicus 2023; Google Earth, accessed November 2023. Scale bar= 50 km.

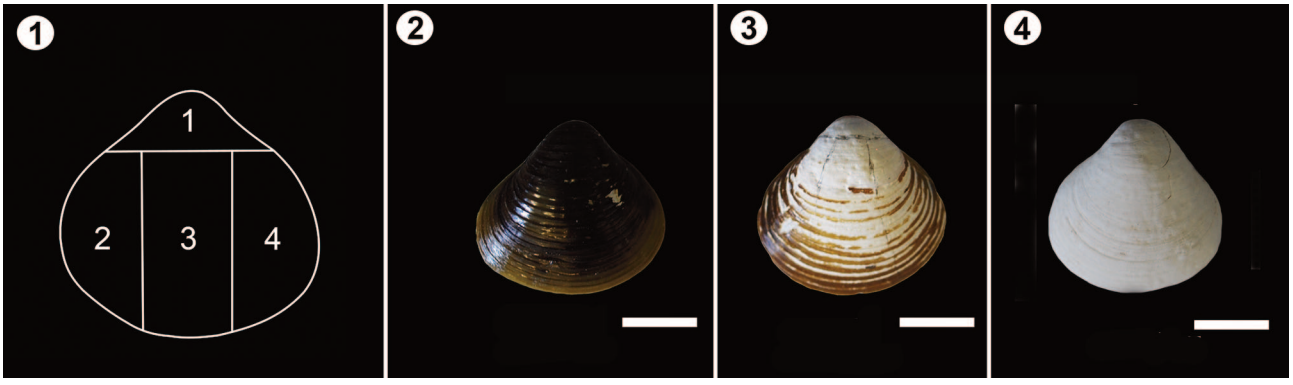

Figure 2. ***Corbicula fluminea***. **1,** Sectors of the valves: 1, umbonal; 2, anterior; 3, central; 4, posterior. **2,** Shell illustrating fragmentation, periostracum, and corrasion category 0. **3,** Shell illustrating periostracum and corrasion category 1. **4,** Shell illustrating periostracum and corrasion category 2. Scale bar= 1 cm.

the 0 for the equation. Hence, the categories became 1, 2, and 3, and a new term (-1) was introduced to the equation, resulting ($c1+2(c2)+3(c3)/n)-1$. Here, $c1$ represents the shells included in our category 0, $c2$ those in category 1, and $c3$ those in category 2; n is the total number of shells, and the (-1), as said above, is introduced to compensate for the use of different numbers for the categories.

Data (Tab. 1) were summarized in histograms and compared using the *chi*-squared (X^2) test, with a $p < 0.05$ significance level. For pairwise comparisons, the post hoc Bonferroni correction was applied. To evaluate temporal tendencies, we used Kendall's *tau* correlation. The software used was PAST, version 5.2.2 (Hammer *et al.*, 2001).

TABLE 1 – Number of bioclasts by sample, sector of the valve, taphonomic attribute, and its category.

	San Pedro 2008				San Pedro 2016				San Pedro 2018			
	0	1	2	abs	0	1	2	abs	0	1	2	abs
umbo												
fragmentation	178	14	13	18	245	47	14	12	194	53	19	37
periostracum	0	3	202	18	1	3	302	12	1	9	256	37
corrasion	0	5	200	18	0	6	300	12	3	20	243	37
anterior												
fragmentation	152	47	12	12	246	44	17	11	204	62	14	23
periostracum	2	18	191	12	8	23	276	11	12	23	245	23
corrasion	10	18	183	12	2	14	291	11	8	22	250	23
center												
fragmentation	148	58	11	6	265	36	14	3	192	94	13	4
periostracum	2	24	191	6	9	22	284	3	12	25	262	4
corrasion	5	29	183	6	3	13	299	3	8	22	269	4
posterior												
fragmentation	134	40	23	26	249	30	23	16	187	47	25	44
periostracum	5	15	177	26	11	20	271	16	15	20	224	44
corrasion	8	20	169	26	4	13	285	16	8	21	230	44

abs= absent

RESULTS

The frequencies of the taphonomic attributes are presented in Figure 3; the results of the X^2, Bonferroni, and Kendall tests are summarized in Tables 2–5.

The 2018 specimens had the lowest percentages of lost sectors (Tab. 2). Regarding the percentages, the central sector was the most represented, with a peak in 2008. The less frequent was the posterior one. The Kendall test (Fig. 4; Tab. 3) indicated that there is no correlation between lost sectors and damage by sector with time. The X^2 and Bonferroni tests (Tab. 2) showed that the umbonal and posterior sectors are differently represented, with 2008 being the distinct sample in both cases. Meanwhile, the central and anterior sectors did not exhibit differences.

Table 4 shows the frequency of taphonomic attributes. Fragmentation exhibited statistically significant differences in all sectors except the anterior over the years. In the umbonal sector, statistically significant differences were observed in 2008 and 2018. Significant differences were also noted in the central sector for 2016 and 2018, and in the posterior sector for 2016.

Periostracum damage had no statistically significant differences in sectors or years. Category 2 was most represented in more than 85% of the bioclasts, followed by categories 1 and 0.

Corrasion was statistically different among the three samples. The distinct sample in the umbo was 2018, in the anterior 2016, in the center 2008 and 2016, and in the posterior 2016. Category 2 was represented in more than 80% of the bioclasts, followed by 1 and 0.

Category 0 was by far the most represented in all years and sectors, accounting for 88% or more of the bioclasts, followed by categories 1 and 2 in descending order. The X^2 and Bonferroni tests (Tab. 5) show that 0 was statistically

TABLE 2 – Valve sectors. X^2 squared and Bonferroni post hoc tests, and Kendall's tau.

	umbo	anterior	center	posterior
X^2	15.122	51.426	27.895	21.761
p (no assoc.)	0.00052	0.07643	0.24789	1.88E-01

Bonferroni p (no assoc.)

	umbo		anterior		center		posterior	
	pres	abs	pres	abs	pres	abs	pres	abs
2008	1	1	1	1	0.62352	0.6235	0.29792	0.29792
2016	0.00301*	0.00301*	0.28534	0.28534	1	1	0.02795*	0.02795*
2018	0.00354*	0.00354*	0.24213	0.24213	1	1	1.87E-01*	1.87E-01*

abs= absent; pres= present; *= statistically significant at 0.05%

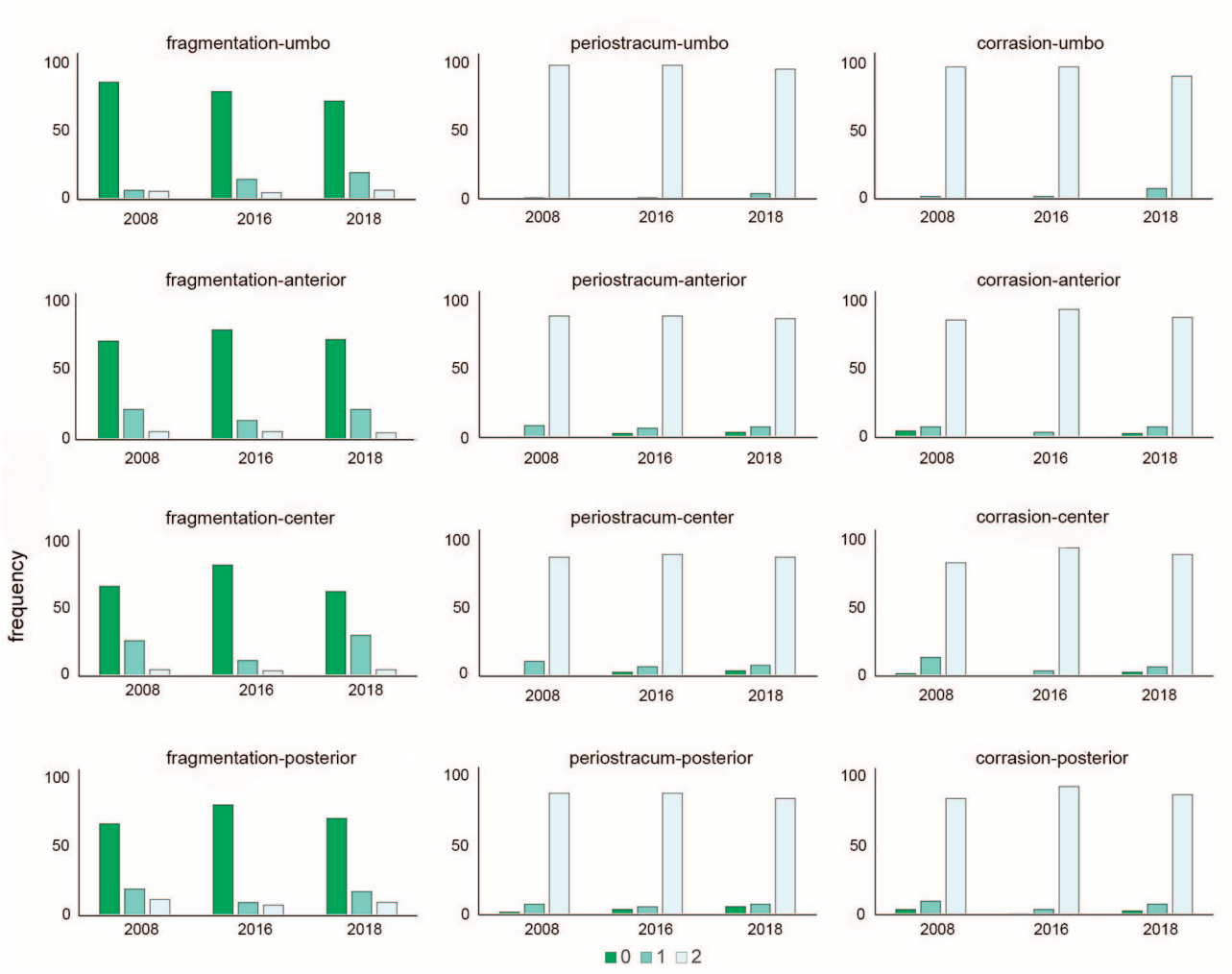

Figure 3. Frequency of taphonomic attributes over time by category, valve sector, and sample.

TABLE 3 – Kendall's tau for lost sectors, damage by sector, and taphonomic category.

	Lost sectors	Damage by sectors		Taphonomic category
	All cases	**Umbo, anterior, center**	**Posterior**	**All cases**
tau	0.33333	0.33333	-1	0.33333
p (uncorr.)	0.60151	0.60151	0.11719	0.60151

TABLE 4 – Frequency of taphonomic attributes by sector. X^2 squared and Bonferroni post hoc tests.

	Fragmentation			Periostracum			Corrasion		
Umbo									
X^2	18.207			54.039			19.234		
p (no assoc.)	0.00112			0.2483			0.00071		
Anterior									
X^2	76.917			52.414			13.215		
p (no assoc.)	0.10355			0.26341			0.01027		
Center									
X^2	39.039			69.996			18.494		
p (no assoc.)	<0.000001			0.13591			0.00099		
Posterior									
X^2	16.085			36.297			11.007		
p (no assoc.)	0.00291			0.45843			0.02649		
				Bonferroni p (no assoc.)					
	Fragmentation			Periostracum			Corrasion		
	0	1	2	0	1	2	0	1	2
Umbo									
2008	0.01975*	0.01975*	1	1	1	1	1	1	1
2016	1	1	1	1	1	1	1	0.17866	0.07189
2018	0.01151*	0.02546*	1	1	0.30326	0.27664	0.14543	0.00259*	0.00024*
Anterior									
2008	1	1	1	0.55181	1	1	0.13988	1	0.17644
2016	0.13416	0.05418	1	1	1	1	0.07234	0.44746	0.01585*
2018	1	1	1	0.47224	1	1	1	1	1
Center									
2008	0.53244	0.67096	1	0.48408	1	1	1	0.00246*	0.00403*
2016	6.67E-04*	1.15E-04*	1	1	1	1	0.99678	0.02277*	0.00464*
2018	0.00034*	5.85E-01*	1	0.90724	1	1	1	1	1
Posterior									
2008	0.06027	0.25101	1	1	1	1	1	0.49289	0.1298
2016	0.00151	0.00581*	1	1	1	1	0.59603	0.12651	0.01626*
2018	1	1	1	0.79481	1	1	1	1	1

*= statistically significant at 0.05%

TABLE 5 – Damage by taphonomic category. X^2 and Bonferroni post hoc tests.

X^2	60.908		
p (no assoc.)	<0.000001		
	Bonferroni p (no assoc.)		
	0	1	2
2008	1	0.083632	1
2016	0.044167*	2.4639E-13*	0.23789
2018	0.51034	6.6107E-07*	0.89604

*= statistically significant at 0.05%

significant in the 2016 sample, and 1 in the 2016 and 2018 samples. The Kendall test (Tab. 3) indicated that there is no correlation between taphonomic categories with time.

The average taphonomic score was nearly identical across the three samples, differing only in the third decimal (2008 = 1.3658; 2016 = 1.3612; 2018 = 1.3641) (Fig. 4).

DISCUSSION

Preservation

In general, the taphonomic attributes observed in *C. fluminea* showed scarce variability, as depicted by the three samples studied. The X^2 tests revealed statistically significant differences in the sectors represented and fragmentation, but there is no linear tendency over the years.

The central valve sector was the most frequent in the samples, while the posterior one was the least frequent. The causes seem to be morphological. The central sector is the most protected against fragmentation due to its topological position, and the valve is not too convex to form an abrasion pattern, such as in the whorls of a gastropod.

Regarding the posterior area and considering the entire molluscan death assemblages of the Touro Passo River in southern Brazil, Kotzian & Simões (2006) found that the most fragmented sector was the posterior one, as in our case. Unfortunately, it was not provided data discriminated by species. We suggest that, again, morphology is the root of this pattern. The posterior area of the *C. fluminea* shell is larger and slightly thinner than the anterior area, and as a result, it is more fragile against mechanical efforts. Newell *et al.* (2007) stated that in *Unio,* the umbo is the tallest and most exposed zone to particle impact, and consequently, the first to be abraded, and subsequently more prone to fragmentation. As seen above, this is not the case for *C. fluminea*. This can be attributed primarily to the different morphology of both species. Newell *et al.* (2007) noted that the umbonal cavity in their *Unio* specimens was very thin and prone to abrasion and perforation, which notably favored the occurrence of fractures. This is not the case for *C. fluminea*, which has a rather thick umbonal part of the shell. The microstructure of both types of shells is also different and may play a role in the distinct preservation styles observed. Unionid shells are aragonitic, with an outer prismatic layer and an inner nacreous layer, which comprise most of the shell thickness (Checa & Rodríguez-Navarro, 2001, and references). However, the shell of *Corbicula fluminea*, which is also aragonitic, comprises three layers,

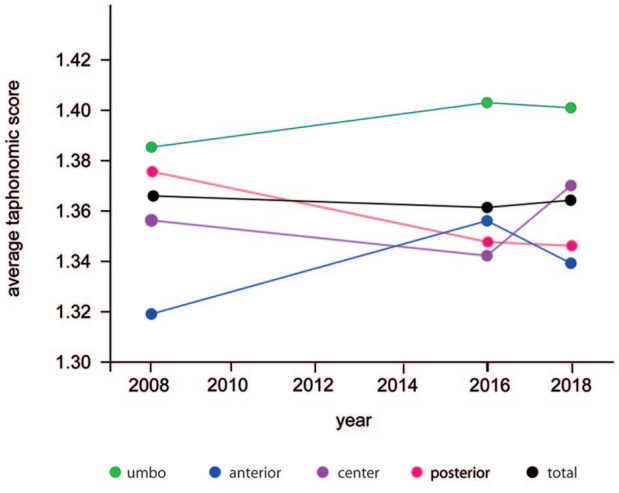

Figure 4. Average taphonomic scores over time.

from the outer to the inner: crossed-lamellar, prismatic (pallial myostracum), and complex crossed-lamellar (Fritz *et al.*, 2022, and references).

In addition, the usual low energy of the river in the study area and the absence of bioerosion may also explain the scarce fragmentation in general. The absence of bioerosion and bioencrustation reflects the low-salinity conditions in which *C. fluminea* lives. It is very improbable to find these structures in freshwater conditions (Kotzian & Simões, 2006; Tietze & De Francesco, 2014).

Worldwide, *Corbicula* species have various predators that break the shells, such as fish, birds, and crabs (Robinson & Wellborn, 1988; Cadée, 2003; Cadée & Soes, 2004; Pla Ventura *et al.*, 2018; Sanders & Mills, 2022; Kroboth *et al.*, 2024), but predation on *Corbicula fluminea* has not been yet studied in the study area.

Corrasion exhibits differences among the years: the statistically significant ones are 2018 in the umbonal sector, 2016 and 2018 in the central sector, and 2016 in the anterior and posterior sectors. In all cases, category 2 was the predominant one. The high chemical dissolution present in freshwater and estuarine conditions may not infrequently erase the eventual accumulation of taphonomic signals (Tietze & de Francesco, 2014). This is not the case, but it is interesting to note the presence of dissolution pits in some specimens (although their frequency was not quantified).

Specifically, the periostracum is the first barrier against abrasion and corrosion (Taylor & Kennedy, 1969; Harper, 1997, among others), and a correlation between periostracum loss and corrasion (specifically corrosion) has been noted (*e.g.*, Pereira *et al.*, 2021, and references). In our case, although category 2 predominates in both attributes, their distribution over the years and sectors is not linearly correlated.

Contrary to our findings, Kotzian & Simões (2006) reported small levels of corrasion for the mollusks of the Touro Passo Stream. Still, since they did not discriminate among species, their results and ours are hardly comparable. However, a different time of exposure to the taphonomic agents and/or the differing sedimentary environments of both studies (river vs. fluvial beach) may also contribute to the observed taphonomic patterns.

On the contrary, Kusnerik *et al.* (2020) found intense taphonomic damage in *Melanoides tuberculata*, an invasive gastropod that has been present in their study area (spring-fed river systems in Florida, USA) for approximately 50 years.

As stated earlier, Martínez *et al.* (2020b), Antuña *et al.* (2021), and Gómez *et al.* (2023) have pioneered studies on the taphonomy of the invasive gastropod *Rapana venosa*. In this case, they also found a pattern of early damage comparable to those shown by the Holocene or even Pleistocene mollusks from the area in this study. Comparing the taphonomic features of the shells of this species and *C. fluminea*, the primary difference is that the *R. venosa* shells underwent a considerably more intense fragmentation. This can be attributed to the presence of bioerosion structures, which weaken the shell, and to the higher energy of the environment. Both species share a high corrasion pattern, which, in the case of *R. venosa*, was attributed to physical factors (high energy). In *C. fluminea*, the principal factor may be chemical, such as the low pH of the water.

Time averaging

Other actualistic studies on shell ages and taphonomic conditions have previously concluded that the latter cannot be regarded as a straightforward indicator of age (*e.g.*, Flessa *et al.*, 1993), but the decadal time-lapse was only investigated in the latest years (Kusnerik *et al.*, 2020; Martínez *et al.*, 2020b; Antuña *et al.*, 2021; Gómez *et al.*, 2021, 2023). Specifically, regarding *C. fluminea*, Gómez *et al.* (2021) demonstrated that specimens with substantial taphonomic modifications coexist with scarcely modified exemplars after nearly four decades.

In the present work, we evaluated shells sampled apart by a decade and by only two years, and we did not find a temporal trend. For example, taphonomic damage to the shells is not more severe over time. There is no statistically significant difference when comparing samples separated by ten years with those separated by only two years. In other words, the older samples are globally as damaged as the younger ones. Then, taphonomic damage emerged very early, especially in terms of periostracum loss and corrasion. Moreover, fragmentation did not increase over the years.

At least two hypotheses can explain this situation. One

is that the specimens are not replaced in the sampling area, and thus, the taphonomic characteristics are acquired early after death, and in the following years, there are no notable modifications of the shells. The second hypothesis is that there is a partial or total replacement of the shells in the study area, and we are dealing with assemblages partially or totally composed of new shells. In this case, the assemblage would be (partially or totally) rejuvenated or reset, *i.e.*, including shells that have been exposed to taphonomic agents for a very short time, and we are recovering dissimilarly aged shells over the years (mainly). The data seem to better support the idea that shells are rapidly altered after death and that no substantial rejuvenation occurs over time. Even if there were partial or total replacement of the assemblage, we would expect to see at least some shells with better-preserved features, such as the periostracum. However, its consistent absence across samples suggests that this component is quickly lost post-mortem, and therefore, the shells observed—even if newly deposited—are already in an advanced stage of taphonomic alteration. This supports the idea that taphonomic changes occur rapidly and that the assemblage remains relatively stable in its overall condition.

We sampled without replacement, and in consequence, these shells were removed from the system, modifying the future universe of available specimens. Nevertheless, we consider that the magnitude of the alteration in such a big area with a considerable number of available shells is negligible. In any case, the conclusion regarding very early after-death taphonomic damage, in terms of periostracum loss and intense corrasion, remains unchanged. The taphonomic characteristics of the older and younger samples are very similar.

CONCLUSIONS

Within a maximum period of 36 years, the most prominent taphonomic attributes in the shells of *C. fluminea* were periostracum loss and corrasion, which followed similar trends, as expected due to the loss of the protective function of the periostracum. Surface shell modifications in *C. fluminea* in the study area are interpreted as being more chemically induced than mechanically induced.

Fragmentation was not an important taphonomic attribute in this inner Río de la Plata fluvial beach, which is typically exposed to a low-energy regime.

Beyond the details of this research, taphonomic alterations in this freshwater environment are recognized in a short time-lapse, not exceeding 36 years, which has interesting consequences for the interpretation of fossil and death assemblages.

Comparing the taphonomic features of the shells of *C. fluminea* with previous studies on the estuarine invasive gastropod *Rapana venosa*, the most notable difference is that the shells of this species suffered considerably more intense fragmentation. This can be attributed to equally intense bioerosion and the higher energy of the environment.

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