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Spatiotemporal patterns of carrion biomass of marine tetrapods at the ocean–land interface on the southern Brazilian coastline

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ABSTRACT: Quantifying how much carrion is produced temporally and spatially in ecosystems is considered one of the most important aspects of carrion ecology. Marine-derived inputs transferred from the ocean to terrestrial ecosystems are the principal source of energy and biomass for many coastal ecosystems. Here, we provide a comprehensive quantification of the carrion biomass of marine tetrapods across space and time at the ocean–land interface on the Brazilian coastline. Based on 3 large datasets, we estimated carrion biomass of 57 274 marine tetrapods beached along 1980 km of coastline over a 3 yr period (2016–2019). A total of 1 744 986 kg of carrion biomass was estimated from 76 species, ranging from a total of 30 g to 14 082 kg for each species. The 10 most abundant species accounted for 91.78% of total records but only 21.28% of total estimated biomass. We highlight the importance of both migratory and resident marine tetrapods as a predictable resource for the Brazilian coastline, especially in the winter and spring. Although baleen whales contributed higher values of carrion biomass, their true availability as a food source is affected by management procedures adopted after stranding events. A significant amount of carrion biomass is removed every year from the Brazilian coastal system. It is therefore imperative to assess the impacts of management procedures on the ecology of scavengers and the entire coastal system.

KEY WORDS: Carrion ecology · Carrion biomass · Ocean–land interface · Marine tetrapods · Brazilian coastline

1. INTRODUCTION

The interface between land and ocean is a unique geological, ecological, and biological region of vital importance to ecological connectivity in coastal areas (Fang et al. 2018). The ocean–land ecotone occupies around 8% of the earth's surface and provides an important site for the exchange of organic matter between aquatic and terrestrial habitats (Ray 1988, Polis & Hurd 1996). The dead organic matter found in this ecotone is derived from 2 main sources: vegetal (low quality) or animal (high quality) (Olea et al. 2019). Dead animal tissue (i.e. carrion) is a nutrient-rich matter that decomposes faster than plant litter and produces very different effects on ecosystems and their biota (Barton 2015). Carrion plays a crucial

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role in the health of ecosystems since it provides resources for a great number of scavengers (DeVault et al. 2003, Beasley et al. 2012, Barton et al. 2013, Moleón et al. 2014). Since the first publications about carrion in the 1960s (Payne 1965, Payne et al. 1968), the number of publications concerned with carrion and scavenging has grown (Moleón & Sánchez-Zapata 2015). However, the scientific attention given to carrion supply remains limited (Barton et al. 2019, Olea et al. 2019) compared with the scale of carrion consumption in ecosystems (Ackerman et al. 2004, Prugh 2005, Osterback et al. 2013).

Quantifying how much carrion is produced temporally and spatially in ecosystems is considered one of the most important aspects of carrion ecology (Barton et al. 2019, Bump et al. 2020, Moleón et al. 2020). It is possible to derive the carrion biomass of individual carcasses by scaling up from population- and community-level concepts such that comparisons among ecosystems can be made (Barton et al. 2019). However, the successful quantification of carrion biomass requires consideration of the spatiotemporal context and partitioning into carrion production and carrion availability, taking into account 4 hierarchical processes: production, distribution, partitioning, and availability (Moleón et al. 2020). Barton et al. (2019) and Moleón et al. (2020) agreed that the fundamental question is how much carrion is produced in different ecosystems. Resource production must therefore be quantified as an essential first step in investigations of availability (Bump et al. 2020). A few studies have provided estimates of carrion biomass production per unit of time and space in natural conditions, and most of them have focused on ungulates in terrestrial ecosystems (Moleón et al. 2019). Marine-derived inputs transferred from the ocean to the terrestrial ecosystem are the principal source of energy and biomass for many coastal terrestrial communities (Polis & Hurd 1996).

Brazil has one of the longest coastlines in the world, bordered by the Atlantic Ocean and extending for approximately 9000 km between 4° N and 34° S (Short & Klein 2016). The South Brazil Shelf (SBS) Large Marine Ecosystem, an important and productive area, is located between 23° and 34° S. The SBS is under the influence of 2 coastal upwelling systems (Cabo Frio, ~23° S and Cabo de Santa Marta Grande, ~28° S) as well as the Subtropical Convergence (~28°–34° S) and is one of the most energetic marine regions in the world, offering plentiful food resources for a variety of marine vertebrate species (Seeliger et al. 1997, Kämpf & Chapman 2016). Moreover, the SBS contributes about half of Brazil's commercial fisheries yield (Kämpf & Chapman 2016). Negative interactions between marine vertebrates and fisheries (e.g. bycatch) on the SBS have been well documented, especially among cetaceans, seabirds, and sea turtles (e.g. Secchi et al. 2003, Bugoni et al. 2008, Fiedler et al. 2012). In addition to incidental catches, marine tetrapods have also been affected by other causes of natural or anthropogenic mortality (e.g. disease, migratory starvation, pollution, boat collisions), resulting in thousands of carcasses stranding annually along the coastline (Mäder et al. 2010, Faria et al. 2014, Monteiro et al. 2016, Prado et al. 2016). Despite the great number of strandings along the Brazilian coastline, there are no studies evaluating carrion exchange between aquatic and terrestrial environments.

In this study, we quantified the carrion biomass of marine tetrapods in the ocean–land ecotone along nearly 2000 km of the southern Brazilian coastline over a 3 yr period. We gathered a large dataset of marine tetrapod strandings to provide a comprehensive quantification of carrion biomass and address one main question: How are beached marine tetrapod diversity and carrion biomass structured across space and time? We aimed to provide a baseline description of the spatial and temporal patterns of carrion biomass production, distribution, and availability. Moreover, this study advances the understanding of carrion ecology in this important and still understudied ecosystem: the ocean–land interface. We discuss the effects of the management of stranded marine tetrapods on carrion availability and highlight knowledge gaps to be addressed in further studies.

2. MATERIALS AND METHODS

2.1. Study area

The SBS Large Marine Ecosystem can be divided into 2 latitudinal areas according to their hydrographic features: the Southern Brazilian Bight (SBB), located between Cabo Frio and Cabo de Santa Marta Grande (~23°–28° S), and the Southern Subtropical Shelf (SSS), from Cabo de Santa Marta Grande towards the border with Uruguay (~28°–34° S). The 'arc' formed by the coastline between Cabo Frio near the limit of the tropical region and Cabo de Santa Marta Grande near the limit of the warm temperate region forms a transition zone (Mahiques et al. 2010). The SBB coastline, extending for 1700 km, is typified by rocky sections separating embayed beaches, inlets, and estuaries. On the other hand, the SSS coastline is 750 km long and consists of a near-continuous high-energy dissipative beach and backing barrier dominated by south-trending transgressive dunes, which in turn are backed by large freshwater lakes and lagoons (Short & Klein 2016).

The study area was divided into 46 transects, each 45 km long, following the coastline between Palmares do Sul (Transect 1) and Saquarema (Transect 46). This partially covered the SSS coastline and almost totally covered the SBB coastline (Fig. 1). Dataset 1 covers the area from Transect 1 to Transect 3. Dataset 2 covers the area from Transect 6 to Transect 32. Transects 4 and 5 received no sampling effort and were not considered in the analyses. Dataset 3 covers the area from Transect 33 to Transect 46. In total, we estimated the biomass of marine tetrapod carrion over an area of 1980 km of the Brazilian coastline.

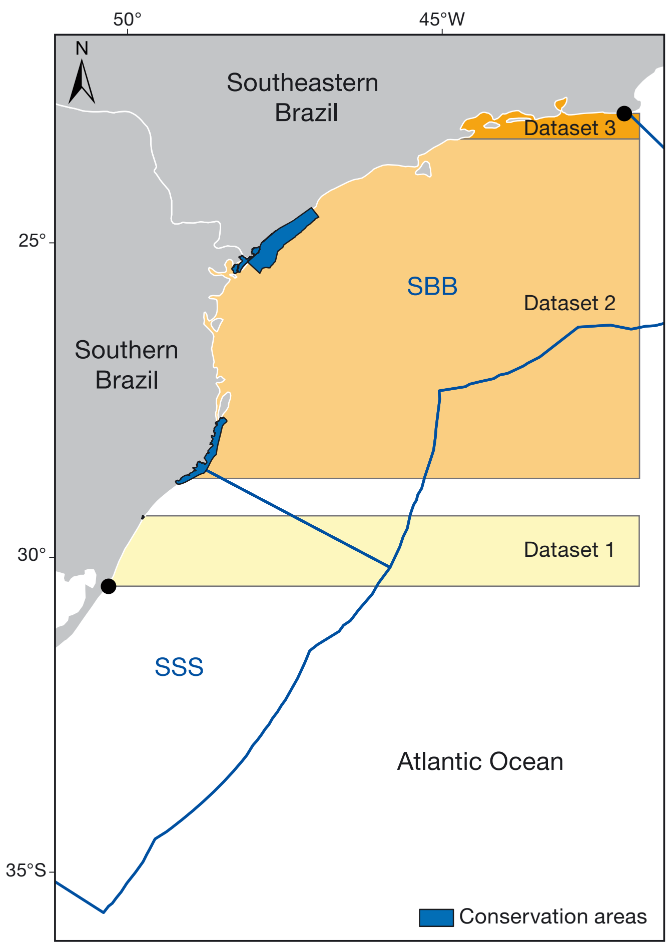

Fig. 1. Study area. Dataset 1: area surveyed by authors. Dataset 2: area surveyed by Santos Basin Beaches Monitoring Project (PMP-BS) Phase 1. Dataset 3: area surveyed by PMP-BS Phase 2. The conservation areas represented on the map are places where the carcasses were not buried by researchers after data collection or by local municipalities. SBB: Southern Brazilian Bight; SSS: Southern Subtropical Shelf

2.2. Marine tetrapod database

To investigate a broad pattern of marine tetrapod strandings and estimate carrion biomass along the Brazilian coastline, we compiled a database from 3 complementary datasets, one of them collected directly by us and 2 others accessed from a public online resource repository (https://simba.petrobras.com.br/simba/web/sistema/). Between 2012 and 2019, we conducted weekly beach surveys to document occurrence patterns of stranded marine tetrapod carrion in the State of Rio Grande do Sul (dataset 1). In alternating weeks we covered 2 complementary areas: (1) 80 km from Itapeva in Torres (29° 21′ S, 49° 44′ W) to Imbé (29° 58′ S, 50° 7′ W), and (2) 50 km from Tramandaí (29° 58′ S, 50° 7′ W) to Dunas Altas in Palmares do Sul (30° 24′ S, 50° 17′ W). In total, we covered ~130 km of the SSS coastline every 15 d. The beach surveys were carried out using a 4-wheel drive pickup truck at a speed up to 40 km h^{-1}, with 2–4 observers scanning the entire beach from the wash zone up to the base of the dunes. The data collection protocol for beached marine tetrapods was standardized including taxon (as specific as possible), date, geographical location, and decomposition state (adapted from Geraci & Lounsbury 2005) as follows: 1 = alive; 2 = freshly dead; 3 = moderate decomposition; 4 = advanced decomposition; 5 = mummified or skeletal remains. Each item of marine tetrapod carrion was collected and/or marked with spray paint to avoid multiple counting. Live animals were transported to the wildlife rehabilitation center (CERAM) of the Centro de Estudos Costeiros, Limnológicos e Marinhos (CECLIMAR) from the Universidade Federal do Rio Grande do Sul (UFRGS) for veterinary care. We only collected selected specimens from rare or target species (for research projects). Vouchers were kept in the scientific collections of the Museu de Ciências Naturais (MUCIN) from the UFRGS.

Datasets 2 and 3 were obtained from the 'Sistema de Informação de Monitoramento da Biota Aquática — 1.0.0 (SIMBA)'. These data encompass information obtained by 'Projeto de Monitoramento de Praias da Bacia de Santos' (Santos Basin Beaches Monitoring Project [PMP-BS]). This project was established by the Brazilian Institute of Environment and Natural Resources as a pre-requisite for the environmental licensing of drilling, exploration, production, and transportation of oil and natural gas in the Santos Basin Pre-Salt, Brazil. It is considered the largest beach survey program on the planet. The records of these 2 datasets covered the entire area of the SBB (~23°–28° S). Dataset 2 (PMP-BS, Phase 1) covered an area from Laguna, State of Santa Catarina (28° 29′ S, 48° 45′ W) to Praia de Camburi in Ubatuba, State of São Paulo (23° 22′ S, 44° 47′ W), incorporating data since August 2015. Dataset 3 (PMP-BS, Phase 2) included data since September 2016, covering the Brazilian coastline from Paraty, State of Rio de Janeiro (23° 13′ S, 44° 42′ W) to Saquarema, State of Rio de Janeiro (22° 56′ S, 42° 28′ W). The beach survey methodology adopted in datasets 2 and 3 was more variable and complex than the methodology we used in dataset 1 (Table 1). In datasets 2 and 3, the surveys were carried out in 3 different frequencies (daily, weekly, every 15 d), according to the type of beach. The beach surveys were carried out on foot (on small beaches), using a bicycle, a motorcycle, or using a 4-wheel drive vehicle (quadricycle or pickup truck). The number of observers varied from 1–2. The carcasses were removed or buried by researchers to avoid recaptures. In addition to the beach surveys, in datasets 2 and 3 there were aquatic surveys once a week to cover otherwise inaccessible beaches, as rocky sections, and some islands.

The difference of 168.44 km between the total survey effort presented in Table 1 (2148.44 km) and the total effort considered in our analyses (1980 km) is due to differences in the methodology and scale of measurement of the coastline. Any coastline is a fractal structure (Lloyd 2014), so whether measurements are taken at broad or fine scales will affect the results. For this reason, coastlines should be described at an appropriate scale for the analyses used. We measured the length of the transects on a regional spatial scale, to have a more uniform geographic distribution of samples. We excluded the coastline of islands and the local complexity of highly convoluted areas from our surveys. The aquatic survey of the 'Ilha Grande' located in dataset 2 was therefore mainly responsible for the difference in effort between dataset 1 and datasets 2 and 3. We believe that for our regional analysis, a broader, less detailed scale provides a better sampling design to describe the geographic pattern of diversity and carrion biomass distribution.

Despite the differences in the frequencies of effort, we matched all datasets and estimated carrion biomass for each species collected from September 2016 to August 2019, totaling 36 mo (3 yr) of effort and 3 periods: period 1 = September 2016–August 2017; period 2 = September 2017–August 2018; and period 3 = September 2018–August 2019.

Table 1. Effort frequency of surveys by dataset and methodology on the Brazilian coastline between September 2016 and August 2019. The aquatic survey covered rocky sections, islands, and inaccessible beaches. Dataset 1: original data from authors; dataset 2: Santos Basin Beaches Monitoring Project (PMP-BS) Phase 1; dataset 3: PMP-BS Phase 2. Efforts for datasets 2 and 3 are based on PMP reports

Dataset	Effort (km) of surveys by methodology					
	Land			Aquatic	Citizen	Total
	Daily	Weekly	Each 15 d	Weekly	science	
1			135.00			135.00
2	674.13	42.30		106.42	209.83	1032.68
3	108.78	3.07		739.32	129.59	980.76
Total (km)	782.91	45.37	135.00	845.74	339.42	2148.44
Total (%)	36.44	2.11	6.28	39.37	15.80	100

2.3. Biomass estimation

We estimated the mean biomass of birds, reptiles, and small marine mammals from beached, living specimens received by CERAM for dataset 1 and from necropsied freshly dead specimens from datasets 2 and 3. We found that this estimate more faithfully represented the biomass of stranded specimens in the area. According to the literature, adult Magellanic penguins have a mean body mass of up to 4.98 kg at the beginning of each breeding season (Boersma et al. 1990), whereas our estimate of the biomass of Magellanic penguins stranded on the Brazilian coastline was just 2.27 kg. This difference of about 45% would have resulted in a considerable and undesirable bias effect in our analyses. Given the potential bias, we opted to use the more realistic data derived directly from beached specimens in our study area. For whales, large pinnipeds, and leatherback turtles *Dermochelys coriacea*, we estimated carrion biomass of each species from the mean body length of all specimens recorded in the datasets, based on formulations given by Lockyer (1976), Trites & Pauly (1998), and Georges & Fossette (2006). Carrion biomass estimated for each species is given in Table S1 in the Supplement at www.int-res.com/articles/suppl/m672p057_supp.pdf.

2.4. Data analysis

We merged and cleaned the datasets before the analyses, selecting only marine or marine-related species as follows: seabirds and shorebirds (Procellariiformes, Sphenisciformes, Suliformes, and marine-related Charadriiformes), sea turtles (Cheloniidae and Dermochelyidae), and marine mammals (Cetacea and Pinnipedia). Other non-target taxa recorded in the datasets were excluded (e.g. terrestrial mammals and reptiles, Passeriformes, Pelecaniformes). Only specimens identified at the species level were considered for the abundance and richness analyses. Consequently, 2104 specimens were excluded from these analyses but were included in the quantification of biomass (Table S2).

We performed a network analysis with species abundance and occurrence (in each transect) to build a bipartite network looking for spatial patterns of beta diversity and abundance across the study area, following the biogeographical networks approach proposed by Vilhena & Antonelli (2015) and adapted by Leroy et al. (2019). A network represents the structure and properties of connections (network edges) between any collection of units (network nodes) interacting as a system (Proulx et al. 2005, Newman 2006). Biogeographical networks are bipartite networks composed of 2 categories of nodes representing space (sites) and biodiversity (species). In our study, the space is represented by coastal transects and species by records of marine tetrapod strandings. Undirected edges connect species to all the respective transects where strandings were recorded. Transect–transect and species–species connections are not allowed in biogeographical networks (Leroy et al. 2019). The bipartite network allows simultaneous visualization of transect richness, species occurrence, and the structure of connections. Network structure (modularity) can be assessed by the strength and distribution of the connections. Uneven distribution of connections segregates groups of nodes that are more densely interconnected than others, which indicates network communities (Newman 2006). In biogeographical networks, these communities indicate a spatial structure in the distribution of the species and are used for bioregionalization. In our study, we used modularity to identify groups of transects with more similar patterns of marine tetrapod strandings. To assess network structure, we generated a Pajek file using the 'biogeonetworks' library (Leroy 2019) in R version 3.6.0 (R Core Team 2019). We used the 'modularity' statistic from Gephi software version 0.9.2 to define the number of modules (network communities) with 'randomize', using edge weight, and with the resolution set to equal 1, where the size of nodes represents their degree (number of iterations) (Bastian et al. 2009). Different metrics of centrality can provide information on species/transect interactions (de Nooy et al. 2005). We chose the simplest metric — the centrality degree — to represent the number of iterations of a node in relation to the total number of iterations. To best view the network structure, we selected the Force Atlas 2 algorithm to disperse groups and give space around larger nodes.

To assess differences in carrion patterns across time, we adopted a circular statistical approach (Zar 2009). Our short time frame (3 yr) is more suited to circular statistics than to time-series analyses (Morellato et al. 2010). We searched for temporal patterns of stranding events for 6 groups: Mysticeti (baleen whales), Odontoceti (toothed whales, dolphins, porpoises), Pinnipedia (pinnipeds), Procellariiformes (albatrosses, petrels, etc.), Sphenisciformes (penguins), and sea turtles (Cheloniidae and Dermochelyidae). The dates of the stranding events were converted to degrees and tested for uniformity of the stranding data with Rao's spacing test. Circular analyses were performed with the 'circular' package (Agostinelli & Lund 2017) in R version 3.6.0 (R Core Team 2019).

We quantified carrion data by transect and by month to estimate carrion biomass km^{-1} mo^{-1} and km^{-1} yr^{-1}. In the same way, we calculated abundance in the study area. Due to the presence of many replicas with few or no records, in some graphics of abundance and carrion biomass, data were $\log_{10}(x)$ or $\log_{10}(x + 1)$ transformed to make the data clearer and easier to interpret.

To evaluate the origin of marine carrion, we classified the species into 3 categories: migratory, resident, and vagrant. The categories were defined as follows: a species was considered resident when it occurred year-round in the study area; vagrant when it occurred irregularly in the study area; and migratory when it moved from a breeding or feeding area to the study area annually (e.g. seabirds, baleen whales), except for sea turtles because of their complex life cycle. Sea turtles are well-known migratory animals; however, their occurrence in the study area shows different patterns when compared with a traditional definition of migration. The southern Brazilian coast is an important feeding area for sea turtles, where individuals spend many years during development (Lenz et al. 2017). Therefore, in our analyses, sea turtles were considered resident species because they occur year-round in the study area. Despite the complex definition of migration (see Dingle & Drake 2007), here we considered the post-reproductive dispersal movement of young individuals of some species of birds and mammals (e.g. Magellanic penguins and South American fur seals) as migration.

To evaluate the availability of carrion biomass in the study area, we divided the management of carcasses into 3 categories: (1) decomposition *in situ*, (2) beach burial, and (3) removal from the beach for necropsies or other analysis (e.g. oiled animals).

2.5. Management practices on marine carrion in the Brazilian coastline

The management practices adopted along the whole study area varied according to datasets. In dataset 1, the carcasses were not removed or buried by researchers, except for rare or target species collected for the scientific collections of MUCIN. The carcasses remained on the beach and followed the natural process of decomposition after data collection. On the other hand, in some cases local municipalities made beach burials an ongoing management practice due to frequent complaints from the local human population about the bad smell caused by the carcasses. These practices are much more common in the summer (beach season) because of the large numbers of people on the beaches on the Brazilian coastline. In datasets 2 and 3 (PMP-BS), there was a requirement to carry out necropsies on all specimens in decomposition codes 2 and 3, except for carcasses longer than 3 m or heavier than 100 kg (https://comunicabaciadesantos.petrobras.com.br/sites/default/files/Projeto_Executivo_Monitoramento_Praias_Integrado.pdf). In these cases, the necropsies were carried out on the beach and the carcasses buried by researches or by local municipalities.

There were only 5 conservation areas in which carcasses were not buried (Parque Estadual de Itapeva, Área de Proteção Ambiental da Baleia Franca, Parque Nacional do Superagui, Parque Estadual da Ilha do Cardoso, and Área de Proteção Ambiental Marinha do Litoral Sul), which together represented around 202 km of coastline (Fig. 1). All conservation areas are included in dataset 2, except Parque Estadual de Itapeva, a small conservation area included in dataset 1 (Fig. 1).

3. RESULTS

3.1. Carrion biomass in space and time

A total of 1 744 986 kg of carrion biomass was estimated from 57 274 marine tetrapods found stranded along the study area between September 2016 and August 2019 (Fig. 2). The estimated biomass of individuals from the 76 species recorded (for details see Table S1) ranged from 30 g (semipalmated plover *Charadrius semipalmatus*) to 14 082 kg (humpback whale *Megaptera novaeangliae*). An analysis by transect and by month for the 3 periods (n = 1584) showed that in 84.60% of transects less than 1000 kg of carrion biomass occurred per month (7.56% with

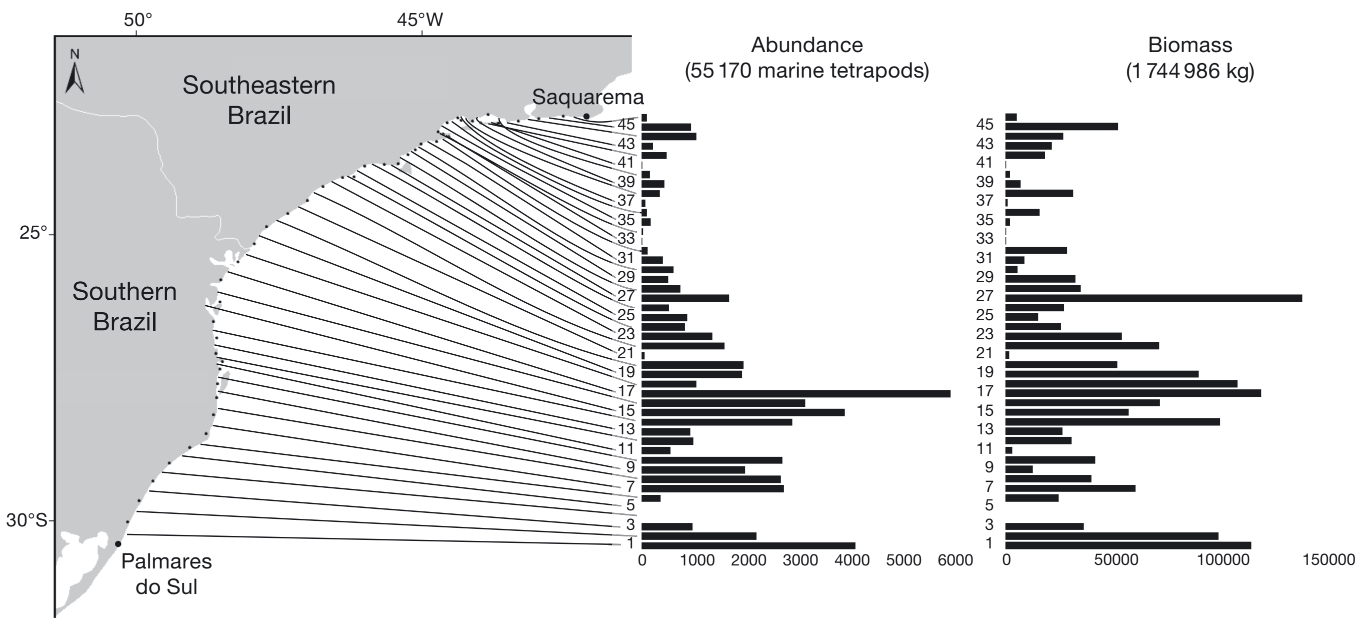

Fig. 2. Total abundance and total estimated carrion biomass by transect, from September 2016 to August 2019, between Palmares do Sul, State of Rio Grande do Sul and Saquarema, State of Rio de Janeiro, on the coastline of South Brazil Shelf, for the 76 marine tetrapod species analyzed

no records of carrion biomass), 11.99% between 1001 and 10 000 kg, 2.90% between 10 001 and 20 000 kg, 0.32% between 20 001 and 30 000 kg, 0.13% between 30 001 and 40 000 kg, and 0.06% more than 40 000 kg (Fig. S1). The mean input of carrion biomass in period 1 was 287.73 kg km^{-1} yr^{-1} or 23.98 kg km^{-1} mo^{-1}; in period 2: 351.73 kg km^{-1} yr^{-1} or 29.31 kg km^{-1} mo^{-1}; and in period 3: 241.87 kg km^{-1} yr^{-1} or 20.16 kg km^{-1} mo^{-1}.

Together, the Mysticeti, Odontoceti, Pinnipedia, Procellariiformes, Sphenisciformes, and sea turtles accounted for 99.74% of total carrion biomass. The least abundant group (Mysticeti) also contributed the most carrion biomass, accounting for 70.88% of the total (Fig. 3A). The second largest group in terms of carrion biomass was the sea turtles (17.16%), followed by Odontoceti (7.91%), Sphenisciformes (2.37%), Pinnipedia (1.03%), and Procellariiformes (0.39%) (Fig. 3B–F). Mysticeti showed an irregular pattern, with sporadic records along the whole study area and no records in 10 transects. Sea turtles and Odontoceti showed a similar pattern, with carrion biomass well distributed in the study area. Sphenisciformes, Pinnipedia, and Procellariiformes showed a similar pattern, with a trend of increasing biomass to the south denoting the temperate habitat preferences of their most representative species: Magellanic penguins, South American fur seals *Arctocephalus australis*, and yellow-nosed albatrosses. Alone, humpback whales accounted for 45.19% of the total carrion biomass in the study area. Four species were among the 10 most important in both abundance and biomass: green turtles, loggerhead turtles, Magellanic penguins, and Guiana dolphins. Together, these species accounted for 74.39% of the total abundance (Fig. S2) and 19.79% of total carrion biomass (Fig. S3).

Although carrion is considered an unpredictable resource, carrion biomass showed a consistent seasonal pattern of input deposition in the study area for all 6 taxonomic groups (Fig. 4). According to Rao's test, uniformity was rejected for all 6 groups (p < 0.01), suggesting the presence of non-random tempo-

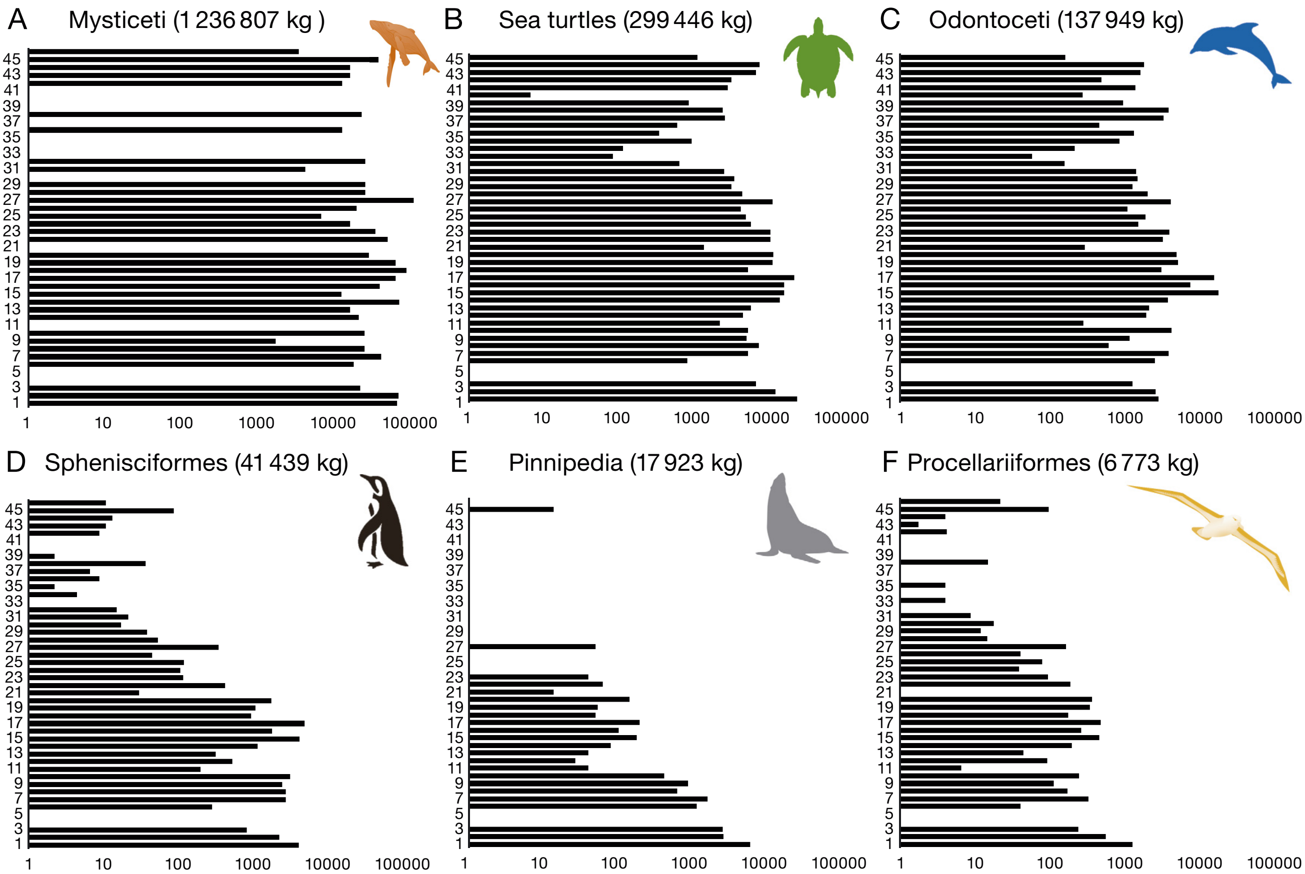

Fig. 3. Spatial distribution of total carrion biomass (kg) by group: (A) Mysticeti, (B) sea turtles, (C) Odontoceti, (D) Sphenisciformes, (E) Pinnipedia, and (F) Procellariiformes, between September 2016 and August 2019 on the coastline of South Brazil Shelf. Carrion biomass data were log10(x) transformed to make the figures easier to interpret. Two groups of birds were excluded from this analysis: Charadriiformes and Suliformes

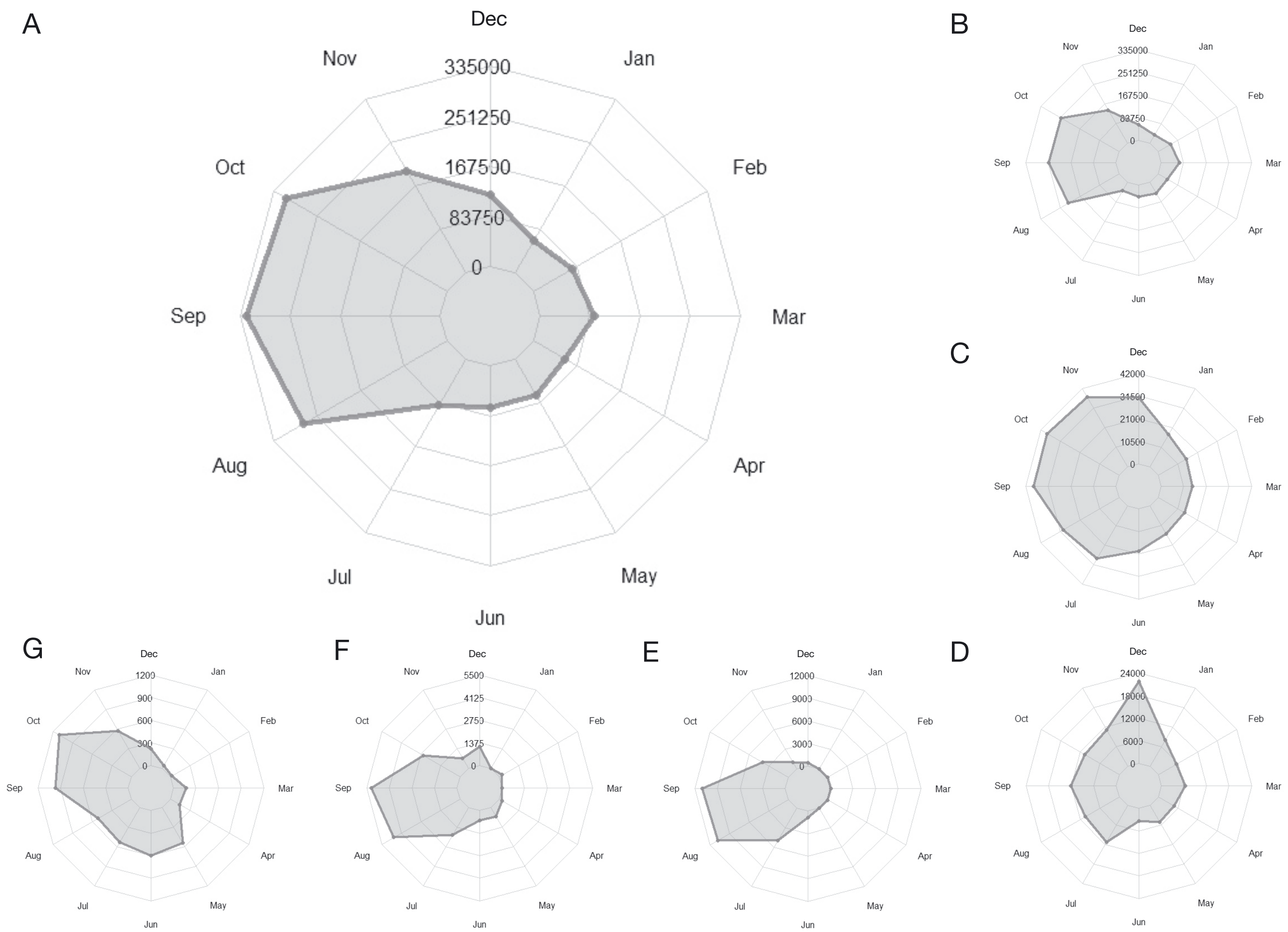

Fig. 4. Temporal patterns of carrion biomass (kg) production (shaded areas), by groups (B–G), on the coastline of South Brazil Shelf, between September 2016 and August 2019. (A) Total carrion biomass, (B) Mysticeti, (C) sea turtles, (D) Odontoceti, (E) Sphenisciformes, (F) Pinnipedia, and (G) Procellariiformes

ral patterns in the stranding events (Fig. S4). The overall pattern between September 2016 and August 2019 showed that August, September, and October were the months with a higher deposition of carrion biomass at the ocean–land interface in the study area (Fig. 4A). The Mysticeti defined the overall pattern since they accounted for more than 70% of total carrion biomass (Fig. 4B). Sea turtles showed a regular deposition year-round, with more carrion biomass input between July and December and a clear peak between September and November (Fig. 4C). The Odontoceti showed a pattern similar to sea turtles, although a high peak was detected in December (Fig. 4D). This peak, however, can be explained by a single event of a stranded sperm whale *Physeter macrocephalus* recorded in December 2017. The sperm whale alone had the second heaviest estimated biomass in this study at 13 985 kg. When we excluded the sperm whale from the analysis, the Odontoceti showed a regular input of carrion biomass between July and December. The Sphenisciformes (Magellanic penguins) showed a pattern typical of temperate species, with the input of carrion biomass concentrated in the austral winter season (August and September; Fig. 4E). The Pinnipedia followed practically the same pattern as penguins (Fig. 4F). The Procellariiformes showed a pattern similar to penguins and pinnipeds, with their peak of carrion biomass input between September and October (Fig. 4G).

3.2. Richness and abundance of marine carrion in the Brazilian coastline

We compiled 55 170 records (52.53% Aves, 40.97% Reptilia, and 6.50% Mammalia) from 76 species (61.84% Aves, 31.58% Mammalia, and 6.58% Reptilia) and 25 families (60% Aves, 32% Mammalia, and

8% Reptilia) of marine tetrapods stranded along the study area between September 2016 and August 2019 (Table S1). The green turtle *Chelonia mydas* was the most abundant species and alone accounted for 34.37% of total records. The only species of Sphenisciformes recorded, the Magellanic penguin *Spheniscus magellanicus*, was the most abundant seabird with 18 255 individuals. Together, these 2 species accounted for 67.46% of total records. The next 8 most abundant species, in decreasing order of abundance, were Manx shearwater *Puffinus puffinus*, loggerhead turtle *Caretta caretta*, Franciscana dolphin *Pontoporia blainvillei*, brown booby *Sula leucogaster*, yellow-nosed albatross *Thalassarche chlororhynchos*, kelp gull *Larus dominicanus*, neotropic cormorant *Nannopterum brasilianus*, and Guiana dolphin *Sotalia guianensis*. The 10 species cited above accounted for 91.78% of total records. Together, all baleen whales accounted for only 0.16% (n = 88) of total abundance. The most abundant baleen whale was the humpback whale *M. novaeangliae*, with 56 records.

The deposition of marine carrion along the Brazilian coastline was irregular and varied monthly in each of the 45 km transects, ranging from 0–1754 marine tetrapods (Fig. S5), with a mean of 35 ind. transect^{-1} mo^{-1} or 9 ind. km^{-1} yr^{-1}. Most of the time (65.15%), few animals (0–24) stranded by transect mo^{-1}. However, there were 2 events with 1116 and 1754 strandings, where Magellanic penguins accounted for 1022 and 1549 individuals, respectively.

We found 2 distinct network communities that were geographically structured along the study area, hereafter named 'North' and 'South' groups. The 2 groups shared 50 species; North had 13 exclusive species represented by 24 individuals, and South had 13 exclusive species represented by 88 individuals (Fig. 5). Together, the exclusive species of both groups only accounted for 0.20% of total abundance. North and South groups recorded 30 261 and 24 909 individuals, respectively. The Magellanic penguin was the most abundant species in the South group (n = 12 613), while the green turtle was the most abundant in the North group (n = 15 212).

3.3. Origin of carrion biomass

Fourteen species of birds, all sea turtles, one species of baleen whale, and about 63% of cetacean species recorded were considered residents in Brazilian waters. Concerning migratory species, 11 were seasonal visitors coming from the Northern Hemisphere and 30 were seasonal visitors coming from the Southern Hemisphere. The 5 sea turtles were considered migratory species compared to the seasonal visitors coming from Northern or Southern Hemispheres (Table S1).

3.4. Carrion biomass availability

The analysis of the management of carcasses revealed that 46% of the total (n = 57 724) were removed from the beach for necropsies or other analyses, 36% remained until decomposition *in situ*, and 18% were buried on the beach (Fig. 6A). In terms of carrion biomass, 1 082 306 kg remained until decomposition *in situ*, 376 568 kg were removed from the beach for necropsies or other analyses, and 286 112 kg were buried on the beach (Fig. 6B). Most carcasses (64%) were found in decomposition code 4 and accounted for 1 123 754 kg, followed by code 3 (17%; 181 839 kg), code 5 (14%; 388 198), and code 2 (5%; 51 195) (Fig. 6).

4. DISCUSSION

We described the multi-species input of carrion biomass spatiotemporally at the ocean–land interface along the southern coastline of Brazil. Based on inputs from the ocean to the land of 76 marine tetrapod species, we provide baseline levels for the spatial and temporal pattern of the abundance of carrion specimens and the amount of carrion biomass in this important ecosystem. Our results show a complex pattern of abundance and richness of marine tetrapod species. According to Miloslavich et al. (2011), the Brazilian Shelf region is one of the most biodiverse marine regions of South America. This high biodiversity can be explained by the 3 energetic oceanographic regions that influence the study area: the 2 coastal upwelling systems (Cabo Frio and Cabo de Santa Marta Grande) and the Subtropical Convergence (Seeliger et al. 1997, Kämpf & Chapman 2016). These oceanographic regions offer rich food supplies for various species of megafauna, supporting large numbers of young marine mammals and seabirds every year (e.g. South American fur seals, Magellanic penguins) and sea turtles (e.g. green turtles, loggerhead turtles) which arrive for foraging and development. For other species, the study area represents a crucial site for resting and building up stores of energy (it is a wintering ground for migratory shorebirds and Procellariiformes) or as a breeding ground for baleen whales such as Southern right

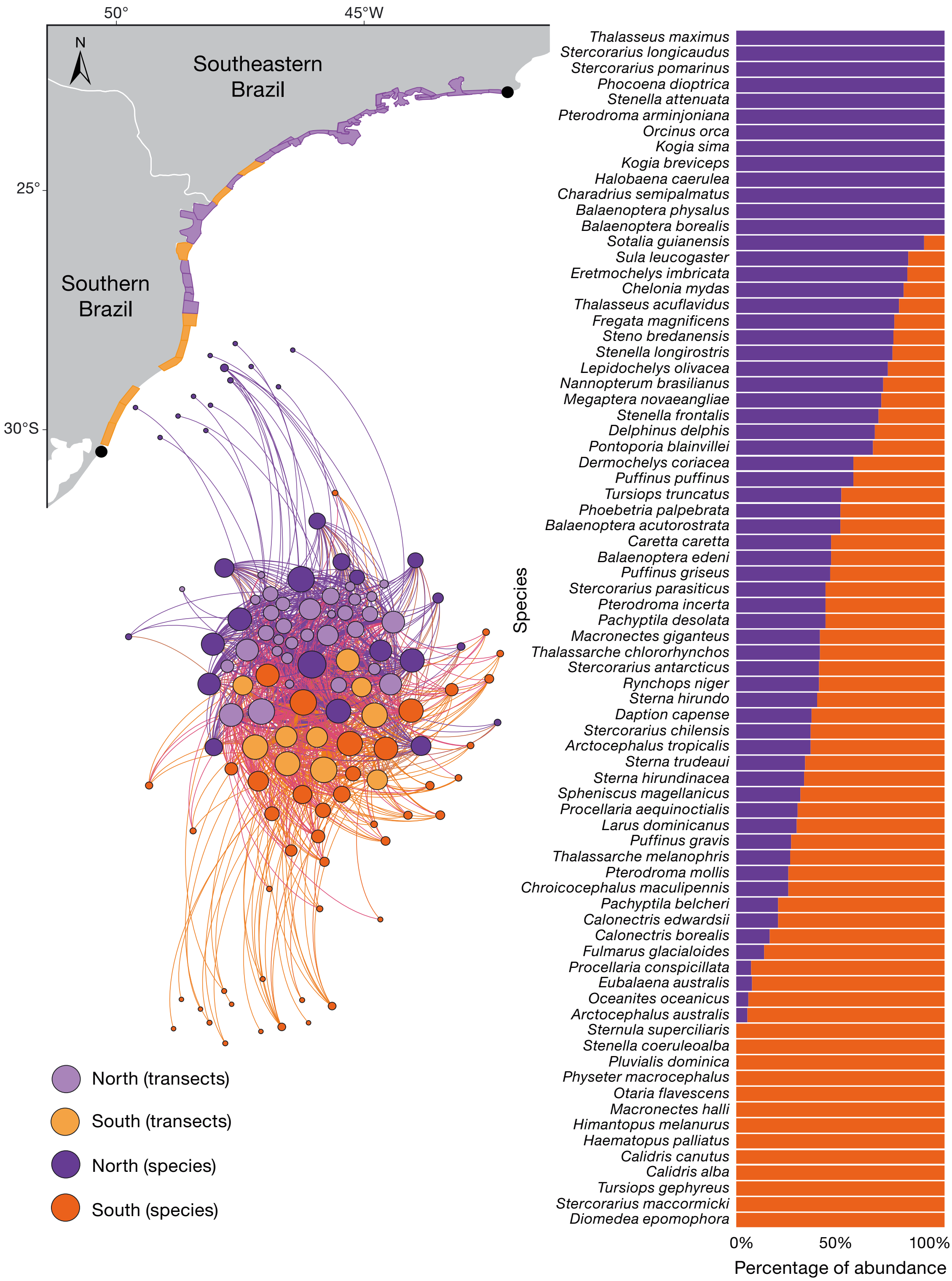

Fig. 5. Network for species and transects (nodes) showing the 2 groups (North and South communities) detected by the modularity maximization method. The size of the nodes (circles) is dependent on the number of connections (centrality degree). The geographic distribution of the groups is highlighted in the map by light purple and light orange colors attributed to transects. The 26 species exclusive to both groups (13 to North and 13 to South), as well as the 50 species shared between the 2 groups are represented by the percentage in the bars at the right side of the figure (dark purple: North species; dark orange: South species). In the spatialization of the network, we used the Force Atlas 2 to disperse groups and give space around larger nodes. The 13 species exclusive for each group were manually distanced to make the figure easier to interpret

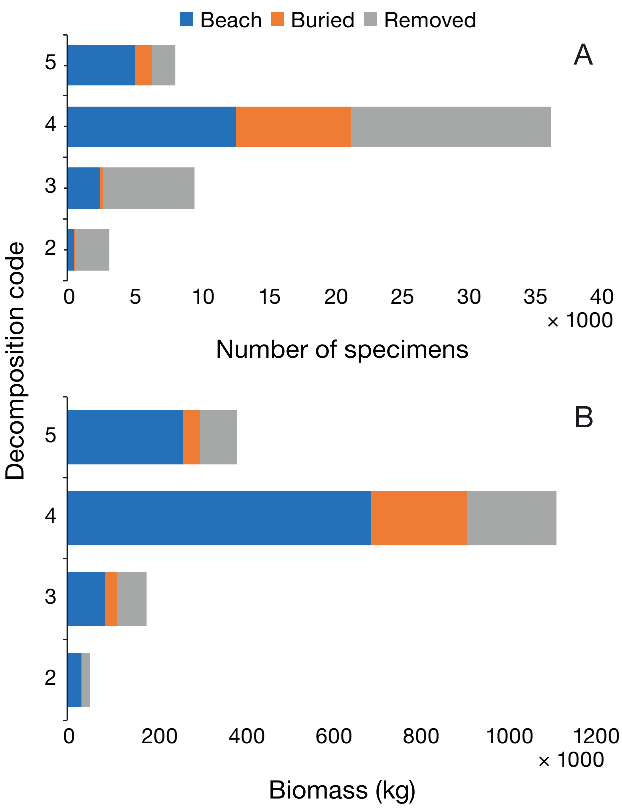

Fig. 6. Management categories of carcasses by decomposition code on the coastline of the South Brazil Shelf between September 2016 and August 2019. (A) Number of specimens of marine tetrapods managed by category and (B) total carrion biomass managed by category. Beach: decomposition *in situ*; buried: beach burial; removed: removal from the beach for necropsies or other analysis. Decomposition codes follow Geraci & Lounsbury (2005)

whales *Eubalaena australis* (Danilewicz et al. 2017). Most of the recorded species (66%) were present in both the North and South groups as detected by network analysis, while a few rare species occurred exclusively in the North group (17%) or the South group (17%). The weak group structure (only 2 network communities) was expected because of the great number of shared species between the 2 groups. Furthermore, the exclusive species were much less abundant than the other species. The exception was the South America sea lion *Otaria flavescens*, with 40 records exclusively in the South group. Given the observed pattern, the network analysis was successful in recognizing North–South differences in composition, but predominantly in the latitudinal differences in abundance seen for many species. Overall, a few species showed high abundance and accounted for most of the records, while most species showed low abundance. Most of the time only a few specimens stranded each km mo^{-1}, but sporadically there were mass strandings of Magellanic penguins. The estimates of individual carrion biomass were highly variable, ranging from the small semipalmated plover (lightest species) to the enormous humpback whale (heaviest species). Therefore, in terms of biomass, a few very large specimens accounted for most of the carrion detected.

In the present study, we estimated a carrion input up to 352 kg km^{-1} yr^{-1} along the southern Brazilian coastline. In terrestrial ecosystems, carrion biomass produced by natural causes (e.g. predation, disease) can be highly variable, ranging from 10s to 100s of kg km^{-2} (Moleón et al. 2019). Barton et al. (2019) estimated a carrion input of 75 and 600 kg km^{-2} yr^{-1} from rabbit *Oryctolagus cuniculus* and kangaroo *Macropus giganteus* populations in Southern Australia, respectively. In island ecosystems, carcass supply can be substantially higher than in mainland ecosystems. Carrion biomass produced in the grey seal *Halichoerus grypus* colony on the Isle of May (Scotland) was estimated at 6893 kg yr^{-1}, including placentae and carcasses (pups and adults) (Quaggiotto et al. 2018). Polis & Hurd (1996) estimated carrion biomass (110, 340, and 530 kg km^{-1} yr^{-1}) of marine animals (vertebrates and invertebrates) in 3 sites along the shoreline of the Gulf of California. However, comparisons across environments should be made with caution because the quantitative scales and the kind of carrion are very different. We recommend the approaches suggested by Barton et al. (2019) and Moleón et al. (2020) for measuring carrion biomass properly, including spatial and temporal boundaries with standardized units of mass per unit area and time. For example, kg km^{-1} yr^{-1} on shorelines and kg km^{-2} yr^{-1} in inland ecosystems.

4.1. The true availability of carrion biomass at the ocean–land interface

In ecology, there are 4 distinct relationships between body size and abundance, but all of them show that small species occur at higher densities than large species (White et al. 2007). In their review, Barton et al. (2019) also found that carcass densities were lowest for large animals and highest for small animals. In our study, the 10 most abundant species accounted for 91.78% of total records, but only 21.28% of total estimated biomass; therefore, we recorded many species with low abundance and few species with high abundance. Four of the 10 most abundant species are also among the 10 with the greatest total biomass: green turtles, loggerhead turtles, Magellanic penguins, and Guiana dolphins. Because they occur at high densities, these 4 species (19.79% of total carrion biomass) are more important in terms of food supply to vertebrate scavengers at the ocean–land interface than all baleen whales recorded (70.88% of total biomass).

Although whale supply accounted for the greatest contribution to the total carrion biomass in our study, its true availability is very low because of the most frequently used management procedures adopted after a whale strands in the study area. Although they represent an extraordinary concentration of mass and nutrients, the carcasses of baleen whales are sporadically distributed along the coastline and occur at low densities compared with other tetrapod species. Additionally, these nutrients, most of the time, are available for very short periods because baleen whales are typically buried on the beach soon after stranding events as a management procedure on the Brazilian coastline.

In this study, a great number of individuals (64%) and a significant amount of carrion biomass (662 680 kg) was buried or removed from the beach system (Fig. 6) across the study area. However, if we compare dataset 1 (State of Rio Grande do Sul) with datasets 2 and 3 (from State of Santa Catarina to State of Rio de Janeiro), there is an astonishing difference in the management of carcasses. In the area included in dataset 1, few carcasses were removed from the beach system by researchers (0.5%) or buried on the beach (2.5%) compared with the rest of the study area (datasets 2 and 3), where 54% of carcasses were removed for necropsies and 20% buried to avoid recaptures. Only in a small fraction (10.2%) of the study area, in 5 conservation units, were the carcasses not buried following the management protocols of conservation unit managers (Fig. 1). Four of these conservation units are located in dataset 2 and one of them in dataset 1. In the whole dataset 3, all carcasses codes 2 and 3 were removed from the beach for necropsies or buried at the beach when exceeding more than 3 m or heavier than 100 kg. Moreover, the numbers of baleen whales buried is likely to be higher than reported here, since the decision on the final disposal site of carcasses found on the beach is made by local authorities that avoid the do-nothing approach in areas frequented by beach users. Beach burial of large carcasses is an ongoing practice by local municipalities along the Brazilian coastline. The study area comprises several touristic beaches and large cities and represents almost the entire coast of the southeast and south political Brazilian regions with about 107 million inhabitants (Instituto Brasileiro de Geografia e Estatística; www.censo2010.ibge.gov.br, accessed 30 Apr 2021). According to Tucker et al. (2018), beach burial is one of the most cost-effective and logistically viable options to manage a stranded whale carcass. However, there are limited studies into the impacts of carcass burial on beaches. For example, Tucker et al. (2019) studied the effects of humpback whale carcass leachate plumes in beach groundwater and found they are a possible shark attractant to the surf.

When a whale carcass is buried, a plethora of organisms are prevented from accessing the huge amount of resources it could provide. In the study of marine systems, knowledge about the ecology of whale falls has increased since 1989, and their importance to the deep-sea floor is indisputable — they support a widespread, characteristic fauna, with extraordinary local species richness (Smith & Baco 2003, Smith et al. 2015). Whale carcass decomposition on beaches and the ecological relationships involved in this complex process remain an unexplored world in carrion ecology, and this area requires research. The effects of the removal of carcasses on ecological processes at the individual, population, and ecosystem levels at the ocean–land interface are completely unknown and deserve special attention. According to Beasley et al. (2012), much attention has been given to contrasting carrion cycling among terrestrial and marine ecosystems, but there are no studies focused on carrion consumption. The inadequate management of carcasses results in a significant loss of carrion to wildlife in an important, poorly studied, and little understood ecosystem. Therefore, there is an increasing need to understand how anthropogenic perturbations to the ocean–land interface influence the efficiency and resiliency of scavenging communities on the Brazilian coastline.

4.2. Bias in carrion biomass estimation

We estimated the carrion biomass from the mean biomass of selected specimens beached alive (code 1) or freshly dead (code 2). This method of estimation more faithfully represents the biomass of stranded specimens in the area than using biomass estimates of live specimens from the literature. However, there is another potential bias with regards to code 4 and 5 carcasses. These kinds of carcasses can exhibit a significant loss of fluids or body parts of the specimen during the decomposition process. In these cases, overestimation of the carrion biomass of the carcasses is possible, especially for code 5 carcasses (Fig. 6). Experiments to calculate the mean loss of weight for each species during the decay of carcass would be beneficial; although decomposition has been extensively studied in animals and humans, many variables have been found to affect its progress (e.g. Brooks 2016), making this parameter very difficult to estimate. For large animals (e.g. whales), the formulations used to estimate carrion biomass based on the mean body length have been adjusted to allow for blood and fluid losses: 6% body weight in baleen whales and 10% body weight in the toothed sperm whale (Lockyer 1976).

Another potential bias could be related to the frequency of beach surveys when these are not conducted daily. In dataset 1, the beach surveys had a maximum interval of 15 d. In 2017, only 16.16% of carcasses of loggerhead turtles (n = 464) were recaptured in dataset 1 with the retention time ranging from 12–132 d, and 13.97% of green turtles (n = 186) were recaptured, ranging from 12–43 d of the retention time at the beach (M. Tavares et al. unpubl. data). In the same study, the authors concluded that carcass removal on the beach during the summer season by local managers or lifeguards influenced the detection and persistence of both studied sea turtle species.

The retention time of marine tetrapod carcasses on the beach can also be influenced by vertebrate scavengers, especially for small carcasses that can be completely removed by large scavengers (i.e. birds of prey). According to Huijbers et al. (2013), urbanization alters the processing of marine carrion on sandy beaches because it substantially influences the structure of the scavenger guild. In non-urbanized areas, large raptors were more abundant and removed 98% of carcasses (experimentally placed fishes) within 24 h (Huijbers et al. 2013). There are no studies on the Brazilian coastline about trophic relationships between vertebrate scavengers and carrion of marine tetrapod species. Observations in the area covered by dataset 1 recorded the presence of 3 main birds of prey (*Caracara plancus*, *Cathartes aura*, and *Coragps atratus*) feeding on marine tetrapod carcasses (M. Tavares pers. obs.), but how these species affect the retention time of carrion at the beach is still unknown.

4.3. Origin of carrion biomass

More than half of the species recorded in this study were migratory, accounting for 53.95% (n = 41) of the total and 70.74% (1 234 304 kg) of biomass. About 45% (n = 34) are resident species and only one species, *Phocoena dioptrica* (spectacled porpoise), is considered a vagrant in Brazilian waters, accounting for 29.25% (510 462 kg) and 0.01% (220 kg) of biomass, respectively. The spectacled porpoise has a circumpolar distribution in cool temperate, sub-Antarctic, and Antarctic waters (Goodall & Brownell 2018).

The diversity of migratory patterns in nature is broad and occurs at an astonishing range of spatial and temporal scales (Chapman et al. 2014). Since annual migrations are round-trips synchronized with the annual cycles of the migratory species, we can compare the stranding patterns we identified with the spatiotemporal patterns of carrion biomass. In this way, we can consider some migratory species as a predictable resource on the Brazilian coastline. Only in the State of Rio Grande do Sul, southern Brazil, thousands of Magellanic penguins and up to hundreds of South American fur seals are found dead and stranded on the beach every year (Mäder et al. 2010, Prado et al. 2016) between the winter and spring. We recorded the same pattern for these species and albatrosses of the genus *Thalassarche* in the South group (Fig. 4E–G).

According to Moleón et al. (2019), carrion is a relatively unpredictable resource in space and time in natural conditions. There are few exceptions, such as grey seal carrion on the Isle of May (Scotland) that is considered a predictable resource for coastal ecosystems (see Quaggiotto et al. 2018). However, patterns of carrion occurrence are rapidly changing at a global scale, shifting from a pulsed, random resource to a more predictable food source depending on human activities (Moreno-Opo & Margalida 2019). Fishing exploitation is a good example of a human activity that produces huge amounts of carrion (e.g. marine animal catches without commercial interest). The SBS is a recognized hotspot of megafauna bycatch in the southwestern Atlantic Ocean (Lewison et al. 2014). In this context, some important resident species can also be considered as predictable resources on the Brazilian coastline. The Guiana dolphin, Franciscana dolphin, green turtle, and loggerhead turtle are amongst the 10 most abundant species recorded and are spatially well distributed (Fig. 3B,C) over the whole study area year-round, with higher abundance in winter and spring (Fig. 4C,D). They accounted for 44.26 and 18.52% of the total abundance and carrion biomass, respectively. These 4 species are typically bycaught in gill nets or trawl fisheries in Brazilian waters (Secchi et al. 2003, Monteiro et al. 2016, Flores et al. 2018), resulting in high numbers of stranded individuals at the ocean–land interface of the study area.

Baleen whales are also migratory species with a seasonal stranding pattern on the Brazilian coastline. In a recent review of records of the genus *Balaenoptera* on the east coast of South America from 1865–2018, Milmann et al. (2020) showed that most of the species occurred in higher numbers during the winter and spring. Prado et al. (2016) reviewed a dataset spanning 1976–2013 and also found a seasonal stranding pattern for baleen whales in the State of Rio Grande do Sul, with most stranding events recorded during the winter and spring. In the present study, we found the same pattern for baleen whales. Despite low abundance (0.16% of the total), whale supply provided the greatest contribution to the total carrion biomass in our study (70.88%). Humpback whales alone accounted for 63.64% of the total Mysticeti records. Until the 1980s, humpback whale records were rare on the Brazilian coastline (see Pinedo 1985), but after 1992 stranding records increased with a peak in 2010 (Moura et al. 2013). In the mid-1950s, humpback whales in the southwestern Atlantic were on the brink of extinction; however, protection led to a strong recovery and the current population is estimated to be at 93% of its pre-exploitation size (Zerbini et al. 2019). According to Pyenson (2011), the cetacean stranding record faithfully reflects patterns of richness and relative abundance in living communities, especially for coastlines greater than 2000 km long and at latitudinal gradients of greater than 4°. Our study area extends to around 2000 km and comprises a latitudinal gradient of 8°, suggesting carrion biomass from marine tetrapods may be a predictable resource for coastal ecosystems in the study area.

4.4. Concluding remarks

Our study provided the first comprehensive quantification of carrion biomass over a large area of the ocean–land interface on the east coast of South America. We highlighted the importance of both migratory and resident marine tetrapods as a predictable resource for the Brazilian coastline, especially in the winter and spring. Although baleen whales provided greater quantities of carrion biomass, their true availability is affected by the management procedures adopted after stranding events. Only in 5 conservation areas are the carcasses of marine tetrapods not buried. We recommend further studies about carrion ecology in these areas, especially with regards to baleen whales, to measure the complex ecological relationships between this great amount of carrion biomass and scavengers. The increasing sightings of humpback whales on the Brazilian coast as well as the increasing numbers of stranding events in the last decade provides an opportunity to study this resource which provides energy to migratory species. On the other hand, the number of carcasses removed and buried in the study area may have serious implications for coastal food webs. For this reason, it is important to evaluate these practices and propose less harmful methods of carcass management which can reduce the impact on scavenging species but still take into account the health issues involved for humans in handling the carcasses. We would also like to highlight the importance of open-access public data. The public dataset (SIMBA) accessed in the present study was crucial for building a comprehensive quantification of carrion biomass along the southern Brazilian coastline. It provided us with access to high-quality information and large datasets (datasets 2 and 3) about stranded marine tetrapods (e.g. photos, decomposition code, geolocation, the destination of carcasses, necropsy information, etc.), which enabled a wide range of analyses. Finally, we encourage further studies about carrion ecology on the Brazilian coastline to generate useful data for comparisons between other ecosystems, especially long-term studies that maintain good temporal data series.

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