Seabird assemblage at the mouth of the Amazon River and its relationship with environmental characteristics

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ABSTRACT

There is a paucity of data on seabird assemblages at sea in tropical waters, particularly in the western Atlantic Ocean, such as distribution and species occurrence. Here, we describe the seabird assemblage recorded near the Amazon River mouth, the greatest freshwater input in the marine environment globally, in North Brazil. Through two ship surveys conducted between March and May 2015, 219 seabird counts were carried out—118 during navigation and 101 point-counts; 443 individuals of 21 species were recorded. The species composition was almost all migrant taxa from both the Northern and Southern Hemispheres. We accessed the associations between bird assemblages (grouped by seabird families) and environmental variables, through univariate, two-part multiple regression models and canonical correspondence analysis. Seabirds aggregate in two main areas, each related to different mesoscale oceanographic features: the tidal mixing and saline front at the mouth of the Amazon River and the ring-formation zone on the border with French Guiana. For petrels (Procellariidae) and storm-petrels (Hydrobatidae), associations with sea surface temperature and distance from the coast were important. These groups were mainly observed in the ring-formation zone, and storm-petrels also occurred at the 20-m isobaths, where the advection process can cause local zooplankton enhancement. On the other hand, for terns (Sternidae), gulls (Laridae) and skuas and jaegers (Stercorariidae), chlorophyll-*a* and bathymetry were the most important factors. Their distributions were associated with the mouth of the Amazon River, where primary productivity is high. The oceanographic characteristics of these aggregation zones make them ecologically important areas for meso- and megafaunal marine taxa, particularly seabirds.

1. Introduction

The basic attributes used to characterize ecological assemblages are species composition, richness and abundance. Assemblages, defined as 'taxonomically related groups that occur together in space and time' (Stroud et al., 2015), are structured based on habitat heterogeneity, species diversity and their interactions (Begon et al., 2006). In the patchy marine environment, organisms are likely to be associated with some features shaped through oceanographic and physical processes. High primary production generated by available nutrients and physical forces accumulate biomass (Olson and Backus, 1985), creating ecologically important zones for several marine taxa (Hunt, 1990; Sournia, 1994; Bost et al., 2009). These structures are linked mainly to seabed topography, physical water properties, and oceanographic processes, such as fronts, eddies and local upwelling (Genin, 2004; Scales et al.,

2014b). These features influence prey availability and therefore, one can expect that top predators, such as seabirds, aggregate in these zones (Weimerskirch, 2007; Scales et al., 2014a; Grecian et al., 2016).

Different oceanographic conditions, such as water masses and nutrients, directly influence prey types and their availability. This has led to various seabird assemblages occurring in different oceanographic domains, even crossing large marine regions in offshore waters (Woehler et al., 2010; Commins et al., 2014; Jungblut et al., 2017). Globally, several environmental characteristics have been described as important drivers of seabird distributions, including bathymetry (Ainley et al., 1993; Yen et al., 2004; Hunt et al., 2014), sea ice cover (Ainley et al., 1993; Yen et al., 2004; Cushing et al., 2018), sea surface temperature, levels of chlorophyll-*a* (Bugoni et al., 2009; Blanco et al., 2017; Clay et al., 2017), and plumes of freshwater discharges (Urbanski et al., 2017; Phillips et al., 2018).

The major oceanic features, such as frontal zones, upwellings, and gyres are well known globally, as they are persistent in space and time (e.g., Acha et al., 2004; Belkin et al., 2009), but the monitoring of many of them in the Atlantic Ocean is lacking (Miloslavich et al., 2011). Many large marine regions worldwide have no data on seabirds, and this paucity of data is particularly notable in tropical regions and along the South American Atlantic coast (Mott and Clarke, 2018). In Brazil, which has over 7000 km of coastline, from 5°N to 34°S, a single published study was found in a recent global review on the study effort regarding at-sea seabird distributions (Mott and Clarke, 2018). This work was related to a single species and short time, from satellite-tracked Spectacled Petrels *Procellaria conspicillata* (Bugoni et al., 2009). Although a few other studies on seabird assemblages are also available for the region (Coelho et al., 1990; Neves et al., 2006; Krüger and Petry, 2010; Fey et al., 2017), they are all from the Southeast and South region, including assemblages attending fishing vessels (Olmos, 1997; Bugoni et al., 2008). With its extensive coastline, Brazilian marine environments play a key role in the entire ecosystem of the South Atlantic Ocean, which is widely variable in oceanographic characteristics, from tropical to sub-tropical environments, and is thus expected to host different seabird assemblages. The composition of the bird fauna along the Brazilian tropical area, including regions under influence of freshwater discharges, has not been described, although it is expected to be distinct from that studied from 23°S southward (Neves et al., 2006; Bugoni et al., 2008; Krüger and Petry, 2010).

At a global level, the largest freshwater discharge into the marine environment occurs by the Amazon River in northern Brazil, which influences the entire oceanographic pattern of the equatorial Atlantic Ocean (Hu et al., 2004; Coles et al., 2013). In terms of its biota and ecology, this is a poorly known area, despite its worldwide oceanographic importance (Miloslavich et al., 2011). Recently, a large mesophotic reef system discovered in the region calls attention to its ecological significance, given its unique formation and size (Moura et al., 2016; Francini-Filho et al., 2018). The northern area of the reef formation, as well as adjacent northern areas in Suriname, are regions undergoing current prospecting by the oil and gas industry (Willems et al., 2017; Francini-Filho et al., 2018), which causes concerns due to potential environmental issues. Due to the lack of information on seabird distributions in northern Brazil, in this study, we aim to describe the seabird assemblage associated with the Amazon River mouth and its adjacent areas, serving as a baseline for future studies in the region.

2. Methods

Two cruises were carried out from 27 March to 14 April, and from 23 April to 01 May 2015 onboard the F.P.V. *Jean Charcot*. Bird counts occurred between 5°26.753'N–0°02.391'S and 47°51.054'–59°57.179'W alongside the mouth of the Amazon River (Fig. 1). Transects encompassed shallow waters from ~10 m depth to offshore waters at ~3100 m depth. Two count methods were used: navigation counts while the vessel was underway and point counts while the vessel was stationary (see Section 2.2).

2.1. Study area and oceanographic characteristics

The Amazon River is the largest river in the world, with a discharge of approximately 6×10^{12} m^3/year of freshwater into the tropical Atlantic Ocean (Gibbs, 1967). This system helps to maintain the stability of salinity in the equatorial ocean, together with regional precipitation (Coles et al., 2013). Adjacent to the mouth of the Amazon River, the region is governed by the North Brazil Current (NBC), which flows northward towards the Caribbean Sea (Bourlès et al., 1999a) through the coastal Guiana Current (GC). Near 5–10°N, the NBC retroflexes and mixes into the North Equatorial Countercurrent (NECC), which flows eastward (Bourlès et al., 1999b; Silva et al., 2009). Shedding from the retroflection, eddies build and drift north-northwest to

the Caribbean Sea (Fratantoni et al., 1995; Bourlès et al., 1999b; Ffield, 2005). At least 2–3 rings are formed annually by this process, each of them transporting ~1 Sv (i.e., 10^6 m^3/s) of water, playing an important role in mass transport of Amazonian water across the equatorial-tropical gyre boundary (Fratantoni et al., 1995; Ffield, 2005; Silva et al., 2009).

2.2. Seabird counts

Seabird counts were undertaken for 27 days and represented *c.* 148 h of sampling effort, resulting in 219 counts: 118 during navigation and 101 point counts. The counts were carried out in scientific cruises, therefore sampling techniques varied by ship activity, i.e., during vessel navigation and at oceanographic stations. First, during navigation to reach the northern area near French Guiana, bird censuses were carried out following Tasker et al. (1984), adapted by Neves et al. (2006). This included snapshot and continuous counts of all birds at a given distance (300-m) from the vessel, after recording apart the ship-attending birds. This latter method involves counting birds that have typical ship-following behaviours, such as crossing the bow or flying in circles. Some birds even follow at a distance of 500–700 m from the ship; they commonly stay in the ship trail. This minimizes recounts of flying birds by identifying and counting them. Birds assigned as ship-followers were not counted nor included in the subsequent continuous and snapshot methods. Then, birds were recorded as stated by Tasker et al. (1984) by a continuous count of 10 min, followed by 10 snapshot counts 1 min apart, in a 300-m strip/band. All birds on the water and in flight were recorded. Continuous counts covered an area of 74.5 km^2, whereas snapshot counts covered 166.7 km^2.

Second, in the northern area, the vessel was operating at several oceanographic stations, collecting physico-chemical data. Therefore, without continuous velocity and no fixed heading, the methods described by Tasker et al. (1984) could not be used. Thus, birds were recorded at 1 h intervals, continuously, limited by a 300-m radius around the vessel; birds on the water and in flight were counted, avoiding recounting them within a sampling interval, as much as possible. More than an hour of activities occurred at some stations, so each 1-h of counting represented a new sampling period. Hereafter, we refer to this count method as point counts.

These methods were used in different areas; the first was during vessel navigation (including ship-followers, continuous and snapshot counts), while point counts were used in the northern region, when the vessel was stationary. The two methods are not directly comparable, although available bird species and their environmental associations should be equivalent. To support bird identification, two guides were consulted (Harrison, 1985; Onley and Scofield, 2007). Photographic records of the seabirds were made with a Nikon 7300 camera, Nikkor 70–400 mm lenses, and verified in the lab; photographs were also sent to experts when necessary.

Position and weather data were recorded at the beginning of each count, i.e., date, geographic coordinates, hour, cloud cover, sea state (on the Beaufort scale), and wind speed and direction. Censuses with a Beaufort value > 5 were not used in the subsequent analyses. The 300-m strips/band were calculated using the equations described by Heinemann (1981).

2.3. Oceanographic and physiographic variables

The environmental data used were sea surface temperature (°C; SST), sea surface salinity (SSS), wind direction (in degrees) and intensity (m/s), chlorophyll-*a* (mg of carbon/m^3; CHL), bathymetry (m; BAT), and distance from the coast (km; DIST). Data were obtained from open-access global source data, such as the HYbrid Coordinate Ocean Model (HYCOM – https://hycom.org/) for SST and SSS; for wind parameters, we used the European Centre for Medium-Range Weather Forecasts Re-Analysis (ERA-INTERIM-ECMWF – https://www.ecmwf.
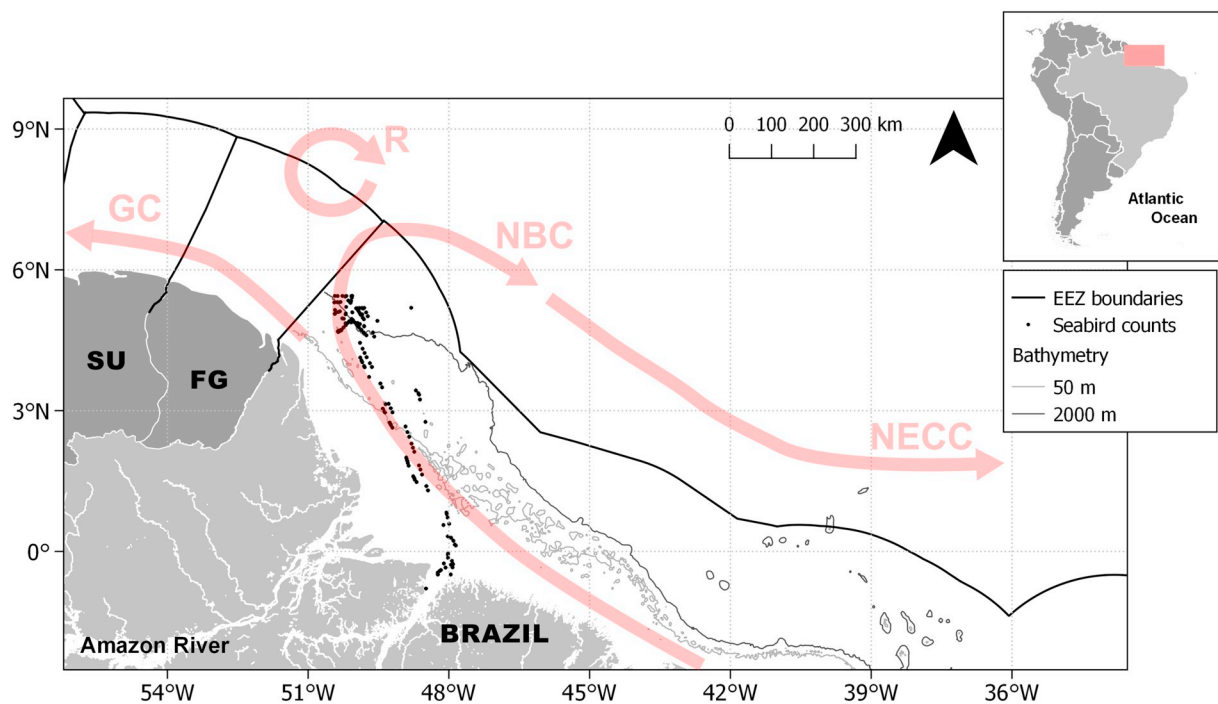
Fig. 1. Study area in northern Brazil (light grey) along the mouth of the Amazon River, with dots representing seabird counts (N = 219). A schematic diagram of the main surface currents and the zone of ring formations (R) are given (adapted from Bourlès et al., 1999b): GC = Guiana Current; NBC = North Brazil Current; NECC = North Equatorial Counter Current. In darker grey, South America, with SU = Suriname and FG = French Guiana. EEZ = Exclusive Economic Zone.

int/); chlorophyll-*a* data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua – https://oceancolor.gsfc. nasa.gov/data/aqua/); bathymetry data were obtained from the General Bathymetric Chart of the Oceans (GEBCO – https://www. gebco.net). The distance from the coast was calculated for each sample unit based on the minimum distance from the continental shoreline. Data were downloaded according to the proximate hour of the day associated with each sample and then interpolated in a 1000×1000 grid between 8.01°N–4.78°S and 43.26°W–52.71°W, ensuring a spatial resolution of 0.001° in longitude and 0.013° in latitude. Next, the most proximal value available for the sample unit was extracted with a nearest neighbour filter. These routines were carried out in MATLAB R2016b software.

2.4. Data analysis

Descriptive statistics were calculated according to the minimum and maximum numbers, mean, mean density (birds/km^2), and frequencies of occurrence for each species. Counts of ship followers and point counts did not have a fixed sampling area; therefore, we used mean values only. For subsequent analysis, sample units were considered the continuous counts during navigation, with the abundance data. The taxonomic arrangement follows Piacentini et al. (2015).

Birds were grouped based on phylogenetic proximity, which also encompasses similar ecological traits, as follows: shearwaters, Procellariidae (*Puffinus* + *Calonectris*); storm-petrels, Hydrobatidae (*Oceanodroma* + *Oceanites*); skuas and jaegers, Stercorariidae (*Stercorarius*); gulls, Laridae (*Leucophaeus*); terns, Sternidae (*Sterna*). Cabot's Terns *Thalasseus acuflavidus* and Large-billed Terns *Phaetusa simplex* were not included in the Sternidae group due to their ecological differences (Gochfeld and Burger, 1996) and limited sampling.

To address seabird-environment associations and to cope with many zeros in the dataset, we performed two-part multiple linear regressions, which are analogous to hurdle models (Zeileis et al., 2008). As a first step, we modelled the zero-part (i.e., the occurrence of seabird groups) based on binomial generalized linear models (GLMs) and a dataset of presence/absence matrix; then, we modelled the count-part (i.e., the abundance of seabird groups) based on a Poisson distribution with a zero-truncated dataset (Zeileis et al., 2008). Models fit was visually assessed with Quantile-Quantile plots and rootograms; the latter compares observed and expected values graphically, with observed values as bars (like those of histograms) and expected values as a curve (Kleiber and Zeileis, 2016). We also assessed the relationships between birds and their environment based on a multivariate approach through canonical correspondence analysis (CCA), which provides an ordination and ranks the influence of environmental parameters in the biological matrix (Legendre and Legendre, 1998; Quinn and Keough, 2002). This analysis helps to visualize the interactions between the seabird assemblages and environmental characteristics. The significance of the axes and explanatory variables in the CCA was assessed using ANOVA, with 99 permutations.

The environmental data were used as explanatory variables and bird counts as the response variable (absolute count) for grouped taxa in both analyses. The explanatory variables were selected after checking that they met assumptions of collinearity (Zuur et al., 2010). Therefore, we excluded SSS due to its high correlation with DIST and CHL ($r > 0.5$). All data from wind direction were from the northeast quadrant, so the explanatory power of this variable would be minimal; accordingly, we excluded wind direction and intensity, as these variables are likely to interact and have effects on bird abundance/distribution. The variance inflation factor (VIF) was low between the environmental variables, but, as a precaution, for the univariate linear models, we excluded DIST (VIF = 12.3) to ensure that the VIF values were < 3.

All statistical analyses were carried out in R v. 3.4.2 (R Core Team, 2017) with the packages 'vegan' 2.5-2 (Oksanen et al., 2018) and 'countreg' 0.2-0 (Zeileis and Kleiber, 2018). Spatial plots were created in QGIS 2.18.7 (QGIS Development Team, 2018). The R code used here are available in the Supplementary material S1.

Table 1

Summary of seabird assemblage data from northern Brazil, along the mouth of the Amazon River, in March–May 2015.

Count-method	Navigating (N = 118)																		Stations (N = 101)				Total
	Ship followers				Continuous counts					Snapshot counts					Point counts								
Taxon	Max	n	Mean	FO%	Max	n	Mean	Density	FO%	Max	n	Mean	Density	FO%	Max	n	Mean	FO%					n
Procellariiformes																							
Procellariidae (shearwaters)																							
Calonectris borealis	1	2	0.0169	1.69	2	2	0.0169	0.0268	0.85	1	1	0.0008	0.0060	0.85	1	1	0.0099	0.99					6
Puffinus puffinus	5	11	0.0932	5.93	7	9	0.0763	0.1208	1.69	23	24	0.0203	0.1439	1.69	2	8	0.0792	6.93					52
Puffinus sp.	0	0	0	0	1	1	0.0085	0.0134	0.85	0	0	0	0	0	1	1	0.0099	0.99					2
Hydrobatidae (storm-petrels)																							
Hydrobatidae	0	0	0	0	0	0	0	0	0	1	1	0.0008	0.0060	0.85	1	1	0.0099	0.99					2
Oceanites oceanicus	2	8	0.0678	5.93	1	5	0.0424	0.0671	4.24	3	5	0.0042	0.0300	2.54	1	2	0.0198	1.98					20
Oceanodroma leucorhoa	1	2	0.0169	1.69	1	2	0.0169	0.0268	1.69	1	3	0.0025	0.0180	2.54	2	9	0.0891	7.92					16
Suliformes																							
Fregatidae (frigatebirds)																							
Fregata magnificens	1	3	0.0254	2.54	0	0	0	0	0	1	2	0.0017	0.0120	1.69	2	11	0.1089	8.91					16
Sulidae (boobies)																							
Sula dactylatra	1	6	0.0508	5.08	0	0	0	0	0	0	0	0	0	0	0	0	0	0					6
Sula sula	1	1	0.0085	0.85	0	0	0	0	0	0	0	0	0	0	0	0	0	0					1
Charadriiformes																							
Scolopacidae (curlew)																							
Numenius hudsonicus	1	1	0.0085	0.85	0	0	0	0	0	0	0	0	0	0	1	2	0.0198	1.98					3
Stercorariidae (skuas and jaegers)																							
Stercorarius skua	1	1	0.0085	0.85	0	0	0	0	0	0	0	0	0	0	1	10	0.0990	9.90					11
Stercorarius pomarinus	1	1	0.0085	0.85	0	0	0	0	0	0	0	0	0	0	3	7	0.0693	3.96					8
Stercorarius parasiticus	0	0	0	0	1	1	0.0085	0.0134	0.85	0	0	0	0	0	1	2	0.0198	1.98					3
Stercorarius longicaudus	4	6	0.0508	2.54	0	0	0	0	0	1	2	0.0017	0.0120	1.69	1	1	0.0099	0.99					9
Stercorarius sp.	1	1	0.0085	0.85	2	5	0.0424	0.0671	3.39	0	0	0	0	0	3	5	0.0495	2.97					11
Laridae (gulls)																							
Leucophaeus atricilla	4	17	0.1441	6.78	16	23	0.1949	0.3087	5.93	3	8	0.0068	0.0480	3.39	1	4	0.0396	3.96					52
Sternidae (terns)																							
Anous stolidus	1	2	0.0169	1.69	0	0	0	0	0	0	0	0	0	0	1	5	0.0495	4.95					7
Onychoprion fuscatus	15	17	0.1441	1.69	0	0	0	0	0	4	6	0.0050	0.3598	1.69	20	31	0.3069	2.97					54
Phaetusa simplex	0	0	0	0	9	9	0.0763	0.1208	0.85	0	0	0	0	0	6	22	0.2178	10.89					31
Sterna hirundo	11	30	0.2542	5.08	3	5	0.0424	0.0671	1.69	1	3	0.0025	0.0180	2.54	40	42	0.4158	2.97					80
Sterna dougallii	1	1	0.0085	0.85	0	0	0	0	0	0	0	0	0	0	7	7	0.0693	0.99					8
Sterna paradisaea	3	3	0.0254	0.85	0	0	0	0	0	0	0	0	0	0	1	2	0.0198	1.98					5
Sterna sp.	1	3	0.0254	2.54	2	5	0.0424	0.0671	2.54	15	15	0.0127	0.0900	0.85	2	2	0.0198	0.99					25
Thalasseus acuflavidus	1	1	0.0085	0.85	1	2	0.0169	0.0268	1.69	0	0	0	0	0	0	0	0	0					3
Thalasseus maximus	7	12	0.1017	2.54	0	0	0	0	0	0	0	0	0	0	0	0	0	0					12
Total		129				69					70					175							443
Species richness		20				9					9					17							21

Data are presented for the four different count methods. For each species, the maximum, total and mean number per count method is given. Density (birds/km^2) is computed for continuous and snapshot counts, which have an associated defined area. The minimum count for all species across all count methods was zero. Therefore, these values are not shown. FO = frequency of occurrence (%); N = sample size, n = number of birds counted.

3. Results

3.1. Seabird assemblage

A total of 443 birds from 8 families and 21 species (Table 1) were recorded. During the ship-follower and point count methods, the numbers of records and species richness were similar (129 and 175 records; 20 and 17 species, respectively). Likewise, the continuous and snapshot count records and richness were also similar (69 and 70 records; nine species each, respectively) (Table 1). Spatially, a high abundance of seabirds occurred in Brazil's northern limit of the Economic Exclusive Zone, between the isobaths of 200 and 2000 m depth, followed by the coastal area adjacent to the Amazon River mouth < 20 m depth (Fig. 2).

Notably, four species accounted for 54% of all records: Common Tern *Sterna hirundo* (n = 80), Sooty Tern *Onychoprion fuscatus* (n = 54), Manx Shearwater *Puffinus puffinus* (n = 52) and Laughing Gull *Leucophaeus atricilla* (n = 52). These species had at least one point of occurrence with more than 15 birds in a flock, reflecting their apparent dominance when compared to other species (Fig. 3). However, such a result does not reflect directly on the frequencies of occurrences, as Wilson's Storm-Petrel *Oceanites oceanicus* was one of the most frequent

species in three different types of counts (ship-followers, continuous and snapshot). Four other species were the most frequent in point counts (*Oceanodroma leucorhoa*, *Fregata magnificens*, *Stercorarius skua*, and *Phaetusa simplex*), while *Numenius hudsonicus*, *Stercorarius parasiticus*, *Thalasseus acuflavidus*, and *Sula sula* had fewer than three records (Table 1).

3.2. Seabird-environmental relationships

According to the univariate multiple regression approach, the zero-part of the models points to the importance of cooler SSTs (negative estimates) for three groups: Procellariidae, Laridae and Sternidae (Table 2). Although the model estimates are low, this result may indicate that these groups associate with different water edges, which influence the chlorophyll-*a* levels, also a significant parameter for Sternidae. Effects of SST and CHL were additionally identified in the count-models for Stercorariidae, Laridae and Sternidae, with negative estimates for SST and positive estimates for CHL, even though they reached statistical significance only for Laridae (Table 2). However, some models with good mathematical fit had unreliable estimates, such as for Procellariidae, or had large standard errors, e.g. for Stercorariidae, likely due to the low number of counts with > 0 birds, which
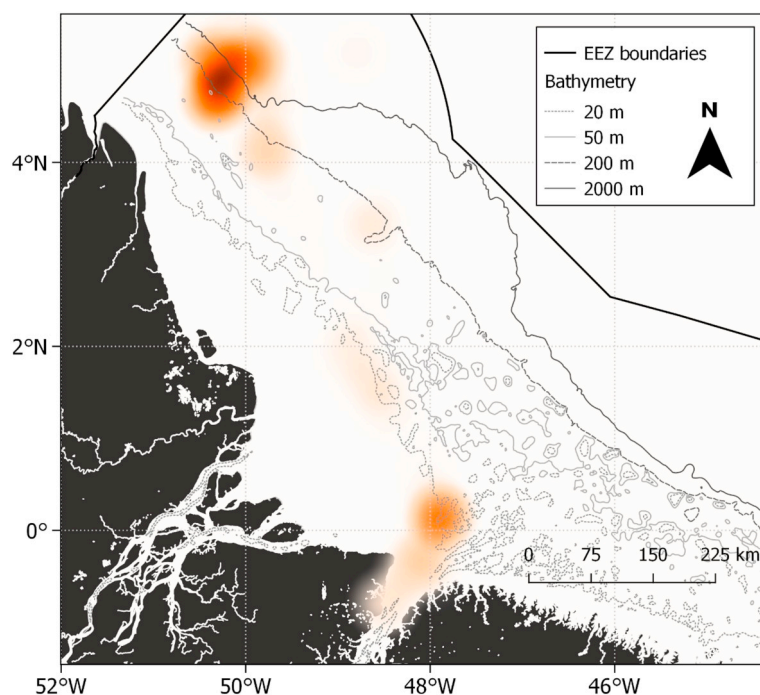
Fig. 2. Heatmap of all seabird records according to total count numbers, exhibiting two areas of aggregation, along the mouth of the Amazon River, Brazil, in March–May 2015.
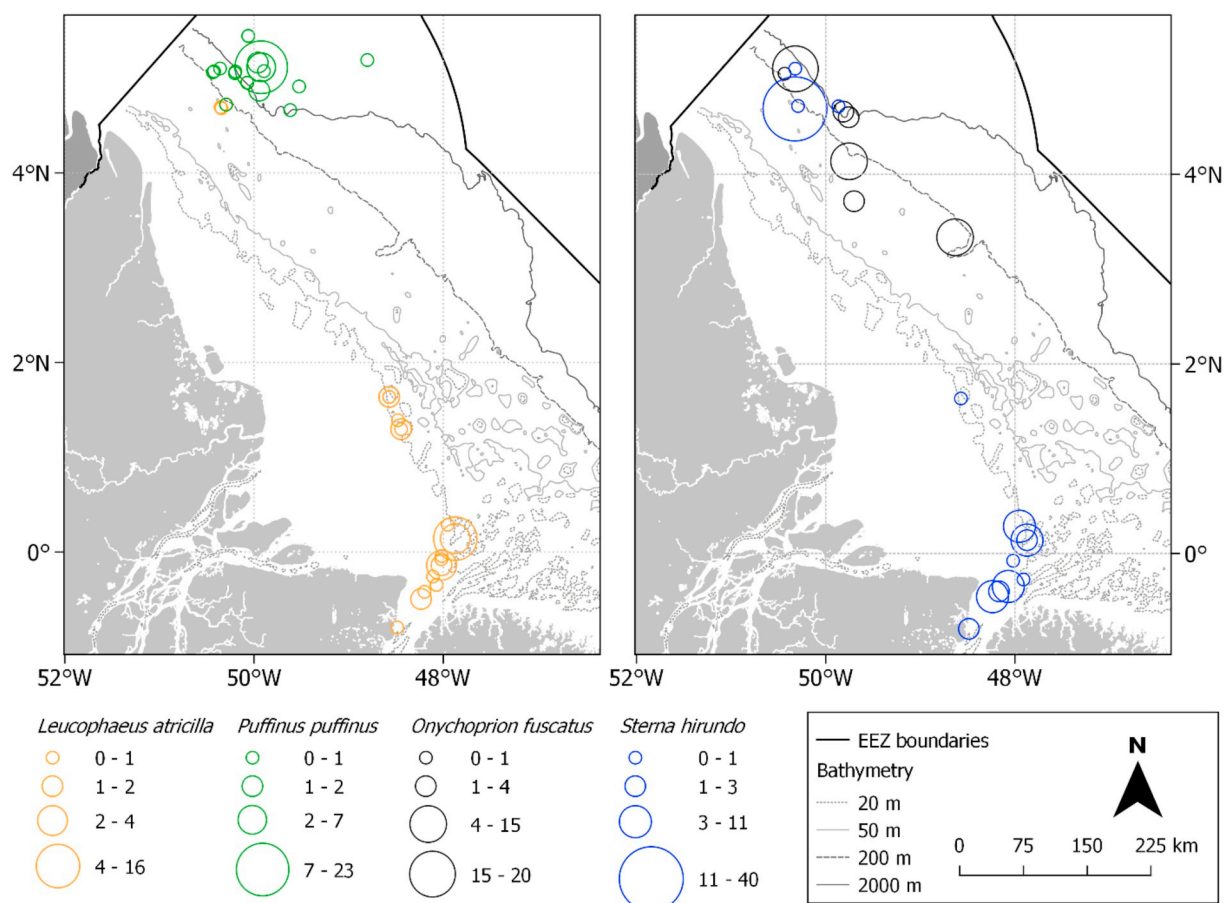

Fig. 3. Laughing Gull *Leucophaeus atricilla*, Manx Shearwater *Puffinus puffinus*, Sooty Tern *Onychoprion fuscatus*, and Common Tern *Sterna hirundo* distributions along the mouth of the Amazon River, Brazil, in March–May 2015. Records based on all count methods are included.

Table 2
Summary of the two-part regression models, grouped by seabird families.

	Zero-part		Count-part	
	Estimate ± SE	*p*-value	Estimate ± SE	*p*-value
Procellariidae				
SST	−0.117 ± 0.063	0.063	−6.490 ± NA	NA
CHL	−1.037 ± 2.393	0.665	342.366 ± 0.705	< 0.001
BAT	−0.0003 ± 0.0006	0.627	−0.056 ± NA	NA
Hydrobatidae				
SST	0.003 ± 0.048	0.935	n.f.	n.f.
CHL	−0.183 ± 0.117	0.118	n.f.	n.f.
BAT	0.028 ± 0.018	0.129	n.f.	n.f.
Stercorariidae				
SST	0.013 ± 0.057	0.809	−0.565 ± 232.273	0.998
CHL	−0.202 ± 0.133	0.129	2.037 ± 113.363	0.986
BAT	0.043 ± 0.026	0.096	0.658 ± 488.841	0.999
Laridae				
SST	−0.149 ± 0.087	0.089	−0.591 ± 0.186	0.001
CHL	0.231 ± 0.149	0.121	0.662 ± 0.221	0.002
BAT	0.016 ± 0.044	0.705	−0.418 ± 0.107	< 0.001
Sternidae				
SST	−0.433 ± 0.203	0.033	−0.765 ± 0.636	0.229
CHL	0.724 ± 0.386	0.060	0.984 ± 0.798	0.218
BAT	−0.001 ± 0.005	0.810	−0.390 ± 0.296	0.188

Full models are presented (y ~ SST + CHL + [BAT*(-1)]) to represent the importance of each explanatory variable for each family. SST = sea surface temperature; CHL = chlorophyll-*a*; BAT = bathymetry; SE = standard error; n.f. = no fit.

were fit using zero-truncated GLMs, and thus interpretation should be undertaken with caution. For Hydrobatidae, the count-model did not fit.

The two principal CCA axes were statistically significant (CCA1, $F = 10.05$, $p = 0.01$; CCA2, $F = 6.21$, $p = 0.01$), while the other two axes were not significant. All variables were significant in terms of building the axes (DIST, $F = 6.06$, $p = 0.01$; BAT, $F = 5.16$, $p = 0.01$; CHL, $F = 3.39$, $p = 0.03$; SST, $F = 3.03$, $p = 0.03$). The CCA indicates a similar pattern to the GLM models, with Procellariidae associated with SST and DIST; DIST was also important for Hydrobatidae, as they were frequently recorded near the 20-m isobaths. Laridae and

Fig. 4. Canonical correspondence analysis of seabird-environmental relationships from the data from two cruises in the mouth of the Amazon River, Brazil, in March–May 2015. Data represent scores of families of seabirds (triangles) and scores of environmental variables (arrows).

Sternidae, were associated most highly with CHL and BAT (Fig. 4). Maps with records of the continuous counts for both Procellariiformes and Charadriiformes demonstrated distinct patterns of occupancy, with the former concentrated in the northern areas, whereas the latter occurred mostly near the mouth of the Amazon River (Fig. 5). This reinforces, spatially, the results from the CCA.

4. Discussion

This is the first study describing the at-sea seabird assemblage adjacent to the mouth of the world's largest river. Results presented here demonstrate high species richness at the mouth of the Amazon River. The species compositions were similar to those described for Suriname, composed mainly of migratory species (de Boer et al., 2014; Willems et al., 2017). Procellariiformes, Stercorariidae and Scolopacidae (Charadriiformes) are all migrants from the Southern and Northern Hemispheres (Harrison, 1985). The recorded Suliformes can be both from islands off north-eastern Brazil or from the Caribbean Sea (Harrison, 1985); however, *Sula* are likely from the Caribbean, as they do not disperse widely, while *Fregata* can be from either location. On the other hand, Sternidae are both resident (e.g., Large-billed Terns, which breed on sand banks in Amazonian rivers or the coast) and migratory (e.g., the Common Tern); Laughing Gulls (Laridae) are also migrants from the Northern Hemisphere (Harrison, 1985).
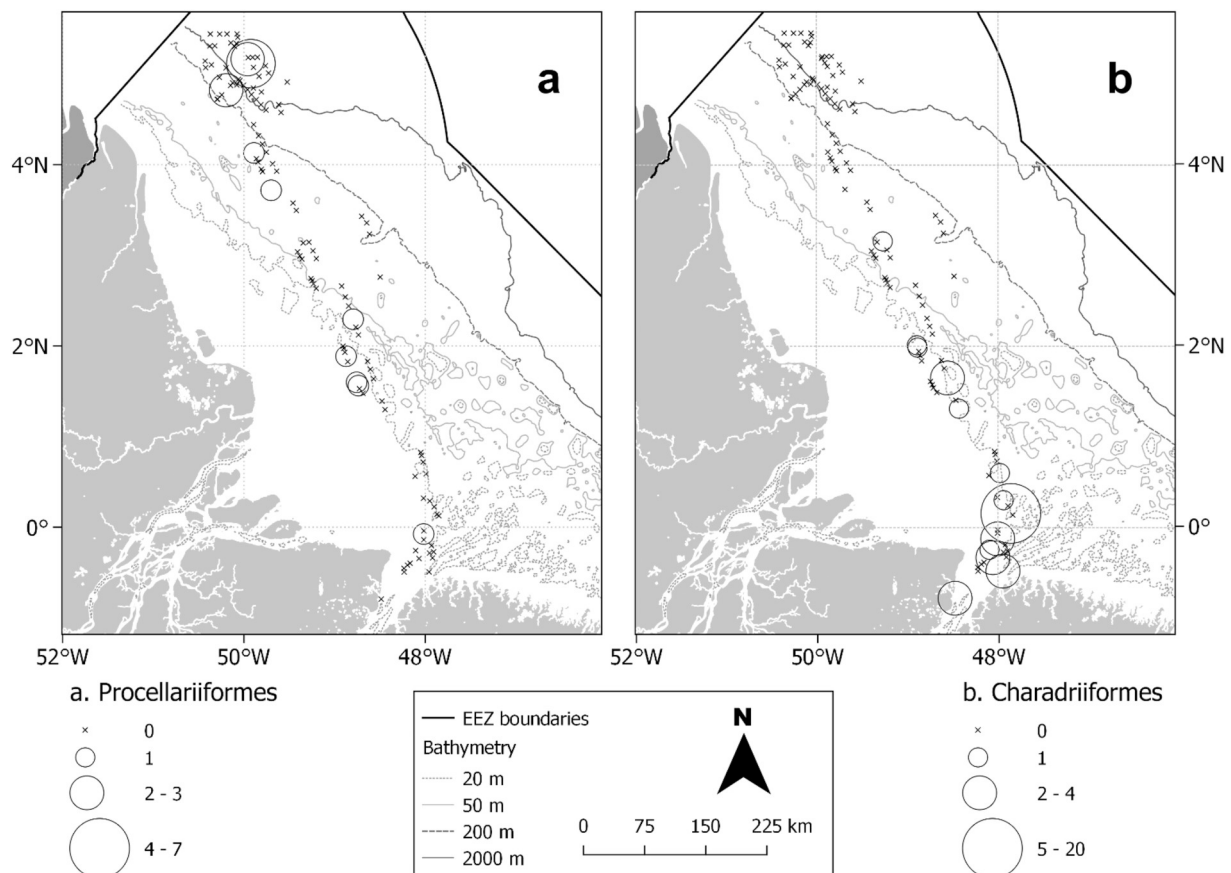
Seabirds recorded along the mouth of the Amazon River have low frequencies of occurrence and lower densities than in other areas. This might be due to their distinct species composition, with approximately 18 out of 21 species being migrants. Indeed, northern Brazil serves as a pathway for many transequatorial migrants, including pelagic (such as shearwaters and skuas) and coastal (terns and gulls) species (Guilford et al., 2009; Mostello et al., 2014; Neves et al., 2015; van Bemmelen et al., 2017; Pollet et al., 2019). Low density of seabirds is expected for tropical waters, similar to the Pacific and Indian Oceans (Ribic et al., 1997; Jaquemet et al., 2004), as the composition of tropical seabird assemblages is usually based on species breeding on nearby lands (Jaquemet et al., 2004; Ballance et al., 2006). The recorded coastal seabirds, mainly terns, commonly feed at sea and roost on the coast, being able to feed more than once a day (Bugoni et al., 2005).

Spatially, two seabird aggregation sites were noted. In patchy environments, this likely indicates potential feeding zones (e.g., Davoren, 2013). Oceanographically, these two areas have their own singularities, pointing to important ecological features in each one. The surveyed northern area is where the NBC retroflects into the NECC, generating the starting point of ring development (Bourlès et al., 1999b; Ffield, 2005). The edges of these rings have Amazon water, which is fresher, more nutrient rich and warmer than the NBC water, entrapped in the ring (Ffield, 2005). In the same way, but through different physical processes, the discharge at the mouth of the Amazon River produces a suitable foraging area for seabirds. In addition to transporting nutrients (Santos et al., 2008), freshwater river discharges influence the vertical turbulence at the boundaries of their plume and the edge of the saltwater mass (Largier, 1993); this frontal zone causes mixture that influence physical and biological processes (Largier, 1993; Karati et al., 2018). The position, extent and intensification of the Amazon River salinity front is driven by its discharge, amount of suspended sediment in the water column, and tidal processes (Geyer, 1995). The bottom saline front extends ahead of the mouth of the Amazon River, between the isobaths of 10 and 20 m, where it supports strong frontogenesis (Geyer, 1995). As a result, the bottom-up process in the trophic chain creates dynamic opportunities for seabird feeding (Cox et al., 2013; Scales et al., 2014b; Phillips et al., 2018).

Seabirds are known to be associated with eddies, shelf-fronts, and river plumes (Scales et al., 2014b; Cox et al., 2016; Phillips et al., 2018), and the two areas of aggregation shown here seem to attract seabirds through the coupling of physical and biological processes. Procellariiforms, which comprise the majority of birds in the northern region, are
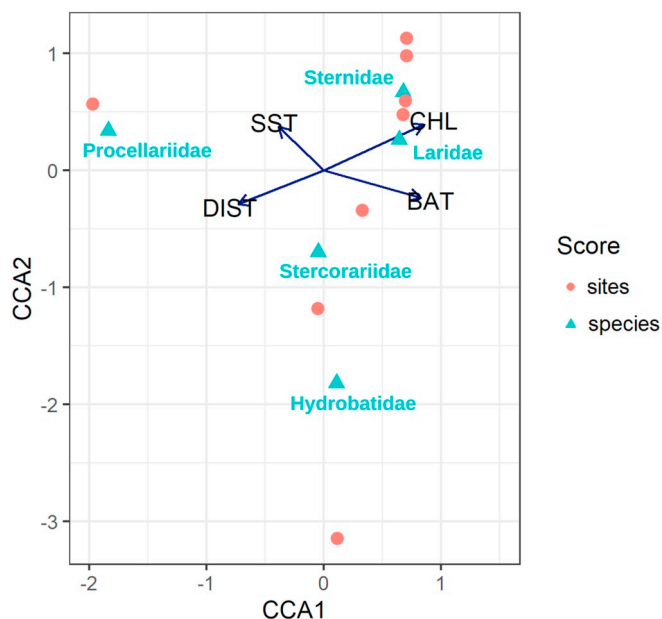
Fig. 5. Procellariiformes (a; Procellariidae + Hydrobatidae) and Charadriiformes (b; Stercorariidae + Laridae + Sternidae) distribution along the mouth of the Amazon River, Brazil, in March–May 2015. Only records from the continuous count method are included.

known to be associated with mesoscale features (Weimerskirch, 2007; Phillips et al., 2018). As they are predominantly oceanic, not surprisingly, they are concentrated in this area off the 200-m isobath, near the NBC retroflexion, which is supported by the CCA results that show association with sea surface temperature (SST) and distance from the coast (DIST) for Procellariidae. However, some Hydrobatidae were recorded on the border of the 20-m isobath. In that region, tidal processes appear to sustain conditions for the accumulation of zooplankton (see Geyer, 1995; Santos et al., 2008), possibly through the advection of bottom water, likely benefiting storm-petrels, which are mainly zooplanktivores.

The tidal process and the salinity front are key elements at the mouth of such a source of freshwater discharge. Coupling these oceanographic processes that influence lower trophic-level accumulation, with the coastal habit of the majority of the charadriiforms recorded, explains seabird aggregations next to the mouth of the Amazon discharge. The CCA results indicate a positive association with chlorophyll-*a* (CHL) for Sternidae and Laridae, in addition to bathymetry (BAT), as their main densities occurred in shallow waters. They can benefit from prey availability, as estuaries are nursery grounds for fishes, and by facilitative interactions provided by subsurface predators (Goyert et al., 2018). At the confluence of the Amazon River and the Atlantic Ocean, the water is very productive, with high CHL concentrations (Santos et al., 2008). The salinity front and tidal processes likely also influenced seabird foraging sites (Cox et al., 2013; Phillips et al., 2018), although we removed salinity from our models due to collinearity with DIST and CHL. Proximity to shore was additionally documented in other seabirds (Ainley et al., 1993), likely allowing them to expend less energy during their commute between feeding sites and coastal breeding and/or roosting sites.

The seabird survey presented here show a species-rich assemblage,

even with limited at-sea sampling and data from a single season (boreal spring). With a typical migratory seabird assemblage, there is room for increased species richness with increasing sampling effort. In Suriname, six seabird species were documented as new for the country in a two-and-a-half month at-sea survey (in boreal spring to summer), totalling 18 species (de Boer et al., 2014). Likewise, Willems et al. (2017) recorded 25 seabird species (in boreal spring, winter, and early fall), with Bulwer's Petrel *Bulweria bulwerii* new to Suriname. We did not recorded some of the species documented by these studies, though it is plausible that they all pass through Brazilian waters (e.g., Bulwer's Petrel, Red-billed Tropicbird *Phaethon aethereus*, and Audubon's Shearwater *Puffinus lherminieri*). In addition, this study did not coincided with large migrating flocks, as those reported in austral autumn in areas eastward, as the Brazilian corner (Metcalf, 1966) and is not in the corridor between south and north Atlantic Ocean (e.g. González-Solís et al., 2009; Hedd et al., 2012). In fact, northern Brazil and Caribbean South America have a paucity of marine biological studies (Miloslavich et al., 2011). For seabirds, new records are frequently reported in this region (de Boer et al., 2014; França et al., 2016; Flood et al., 2017; Willems et al., 2017).

The absence of studies in the region allows new discoveries, such as the remarkable mesophotic reef formation (Moura et al., 2016; Francini-Filho et al., 2018). The improvement of biological surveys and ecological understanding is urgently needed, as the lack of those information do not allow predict/understand the possible environmental impacts of current (e.g. fisheries) or future (e.g. oil and gas exploration) activities. Given the comprehension of the macro- and meso-oceanographic processes at the mouth of the Amazon River and in adjacent areas, biological studies should focus on the two aggregation sites reported here, at the mouth of the Amazon River per se and the zone of ring formation near the French Guiana border. The process of tidal

mixing along the 20-m isobath may provide insights into the bottom-up process influencing meso- and megafauna distributions associated with the Amazon River discharge. Notwithstanding, these two areas seem to be profitable hotspots, serving as ecologically important areas for seabirds.

Declaration of competing interest

None.

Authors' contribution

N.W.D. and L.B. design the study analysis; S.P.M and L.B. delineated sampling and identified birds; S.P.M. collected data onboard the vessel; E.P.K. gather the oceanographic data; N.W.D. analyze the data; N.W.D. wrote the manuscript, and all authors contribute to the final version.

Role of funding sources

Sponsors had no role in study design, sampling, analysis and interpretation of data, writing and in the decision to submit the article for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2019.101826.

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