

Mortality of seabirds migrating across the tropical Atlantic in relation to oceanographic processes

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Abstract

Large-scale climatic processes such as the El Niño-Southern Oscillation (ENSO) can have severe effects on the survival of seabirds in their breeding regions. However, there is a fundamental lack of understanding about how environmental factors are related to the mortality of these organisms in non-breeding areas of the tropics. We investigate here the direct and indirect effects of ENSO and oceanographic variables on the mortality of three migratory seabird species targeted by conservation programmes focused on human impacts: the Atlantic yellow-nosed albatross *Thalassarche chlororhynchos*, the Magellanic penguin *Spheniscus magellanicus* and the Manx shearwater *Puffinus puffinus* in a non-breeding area in Brazil, tropical Atlantic. We find that the intensification of ENSO increases the mortality of Manx shearwaters by enhancing the local storm activity. The mortality of Atlantic yellow-nosed albatrosses and Magellanic penguins is also related to a local increase in storm activity but regardless of the ENSO signature. Increased mortality of Magellanic penguins is observed when biological productivity falls below the annual average (1.7 mg m^{-3}). Adverse climatic conditions are highly deleterious for migratory seabirds and single storm episodes can cause massive deaths, thus exacerbating population declines. We argue that conservation and management strategies for migratory seabirds studied here should not only focus on direct human impacts but should also consider mitigating the effects of climate variability.

Introduction

The mitigation of the impacts of climate variability on marine life requires an understanding of the conditions under which organisms can thrive (Sydesman *et al.*, 2015). Variations in climate, such as those caused by the El Niño-Southern Oscillation (ENSO) influence the frequency and intensity of storms and wind boosts in the tropics and cause shifts in sea surface temperature (SST) and in biological productivity (Knutson *et al.*, 2010; Moon, Kim & Wang, 2015). Predators such as sea turtles, cetaceans and seabirds inhabit mainly the surface of the oceans and are thus likely to be affected by these adverse conditions (Flint *et al.*, 2017; Nicoll *et al.*, 2017; Jones *et al.*, 2018). The effects of ENSO, however, are highly variable and difficult to predict in some areas of the world, for example in the Pacific, where different organisms and species respond differently to El Niño phases (Lindgren *et al.*, 2018). In the tropical Atlantic, impacts can be heavily localized and variable (Fan *et al.*, 2017). Thus, investigations that integrate climatic and oceanographic observations in order to understand the

processes impacting the abundances of marine vertebrates are highly valuable, especially if we are to meet conservation requirements for these organisms.

Migratory seabirds are a particularly important component of marine ecosystems because they perform relevant ecological functions, such as nutrient transport and shape biological communities at large spatial scales (Doughty *et al.*, 2016). Global seabird populations have declined by almost 70% over the last 50 years (Paleczny *et al.*, 2015), mainly due to direct anthropogenic disruptions, including bycatch, habitat degradation, predation by exotic species and oil pollution (Croxall *et al.*, 2012; Lewison *et al.*, 2014). However, at least 65 out of the 346 seabird living species migrate through stormy regions of the tropical Atlantic and are exposed to climate-related mortality events every year (Carlos, 2009). Hundreds of Atlantic petrels *Pterodroma incerta*, for example, were found stranded in Southern Brazil after the hurricane Catarina hit the coastal regions of the South Atlantic in 2004 (Bugoni, Sander & Costa, 2007). Most of the research investigating the impacts of climatic variability on seabirds, however, focuses on colonies located in polar

and subtropical regions, where birds aggregate and it is easier to observe them there than in non-breeding areas (Jenouvrier, Barbraud & Weimerskirch, 2003; Tavecchia *et al.*, 2016). For the tropical Atlantic, information on the effects of climate variability and oceanographic conditions on seabird mortality is only available for the Cory's shearwater *Calonectris diomedea* and is based on data collected in breeding colonies (Genovart *et al.*, 2013).

Monitoring corpses of seabirds washed ashore is a non-invasive method for studying the ecology of species of conservation concern far from their breeding sites (Peltier & Ridoux, 2015). For many animal species, and especially for seabirds, stranded carcasses constitute a unique source of information for investigating diet (Petry *et al.*, 2008) and causes of death, which could be attributed to bycatch (Żydelis *et al.*, 2009) and pollution (Rodríguez *et al.*, 2012). The presence of carcasses on beaches also serves as a valuable indicator for at-sea mortality related to adverse weather (Newton *et al.*, 2009) and low food availability under decreased primary productivity (Parrish *et al.*, 2007; Jones *et al.*, 2018). Beach surveys for stranded birds can be conducted at relatively low-costs, a particularly convenient sampling method in tropical countries, where funding for environmental research projects is scarce (Fernandes *et al.*, 2017).

We investigate here the direct and indirect effects that large-scale climatic variations (ENSO) and local oceanographic conditions have on the mortality of far-ranging seabird species in non-breeding areas of the tropical Atlantic. For this, we use a modelling approach with a robust dataset of consecutive daily observations of seabird stranding, from November 2010 to September 2013 on the coast of Brazil, combined with at-sea seabird density data. Our investigations focus on: (1) the Atlantic yellow-nosed albatross *Thalasarche chlororhynchos* (Gmelin, 1789), (2) the Magellanic penguin *Spheniscus magellanicus* (Forster, 1781), and (3) the Manx shearwater *Puffinus puffinus* (Brünnich, 1764). These species are of conservation concern and, having contrasting characteristics, they represent the ecological variability of migratory seabirds in the Atlantic (Schreiber & Burger, 2002). Human direct impacts, such as fishery bycatch, oil pollution and habitat disturbance are considered as the main threats to these species. However, increased die-offs have been sparsely reported for the tropical Atlantic, but the causes of mortality remain unknown (Faria *et al.*, 2014; Godoy *et al.*, 2014; Tavares, Moura & Siciliano, 2016b; Cardoso *et al.*, 2018). Our study thus improves our understanding of the effects that climatic and oceanographic processes have on the mortality of iconic seabirds along their non-breeding areas in the South Atlantic.

Materials and methods

Study site

This study was conducted along the Brazilian coast, in the tropical Southwestern Atlantic Ocean, between 21°S and 23°S (Fig. 1). This is an ecologically important region that harbours a diverse wildlife, including megafauna species of conservation concern (Branco *et al.*, 2014). The climate is

seasonal and marked by dynamic oceanographic processes. From December to March, when the Brazil Current prevails, waters are typically warm (more than 24°C) and depleted of inorganic nutrients (Moura *et al.*, 2016). From June to September, the Malvinas Current and stormy weather conditions prevail. From September (late Austral winter) to April (Austral autumn), the upwelling of the deep South Atlantic Central Water affects the area and waters are typically cold (<18°C) and rich with inorganic nutrient.

Studied species

The Atlantic yellow-nosed albatross reproduces in the Tristan da Cunha archipelago (37°06'S, 12°17'W), South Atlantic, during the Austral summer (del Hoyo *et al.*, 2018). This species migrates for about 3000 km to the coasts of South America and Africa mainly during the Austral winter (Fig. 1a). The species is classified as 'Endangered' at a global level, and the population of 33 650 breeding pairs shows a decreasing trend (del Hoyo *et al.*, 2018). The literature reports only of one mass stranding event of adults in the Southern coast of Brazil (Faria *et al.*, 2014). The Magellanic penguin breeds through southern South America (50°S, 60°W) during the Austral summer and migrates over 3000 km to the Brazilian coasts during the Austral winter. More than 90% of the penguins recovered along the Brazilian coast are juveniles, and the species is classified as 'Near Threatened' globally due to population declines in large colonies (Pozzi *et al.*, 2015; Marques *et al.*, 2018). Such declines are attributed to fisheries bycatch and oil pollution (Stokes *et al.*, 2014). The Manx shearwater breeds mainly along the Atlantic coasts of North America and Europe (63°N–33°N) during the Austral winter (del Hoyo *et al.*, 2018). Adults migrate for about 8000 km over stormy tropical areas to the Southern Atlantic Ocean mainly during the late Austral spring and summer (September–March) (del Hoyo *et al.*, 2018). The main known threats to this species include predation by rats at breeding sites, harvesting of eggs by humans, fisheries bycatch and oil pollution. Although the species is classified as 'Least Concern' globally, population declines were recorded in breeding colonies of North America (del Hoyo *et al.*, 2018). Precise information on dispersal ranges of the three species (e.g. distance in km travelled per day and duration of stopovers) is not available for the study site. Regarding the at-sea distribution, most of sightings of the three seabird species are from within 100 km from the coast (Supporting Information Figure S1).

Data collection

Seabird stranding data

We followed the sampling protocol recommended by previous studies focused in assessing the efficiency of stranded bird data for monitoring the causes of mortality at sea (Seys *et al.*, 2002; Parrish *et al.*, 2007; Newton *et al.*, 2009; Peltier & Ridoux, 2015; Tavares *et al.*, 2016b). Between November 2010 and September 2013, a staff of technicians recorded

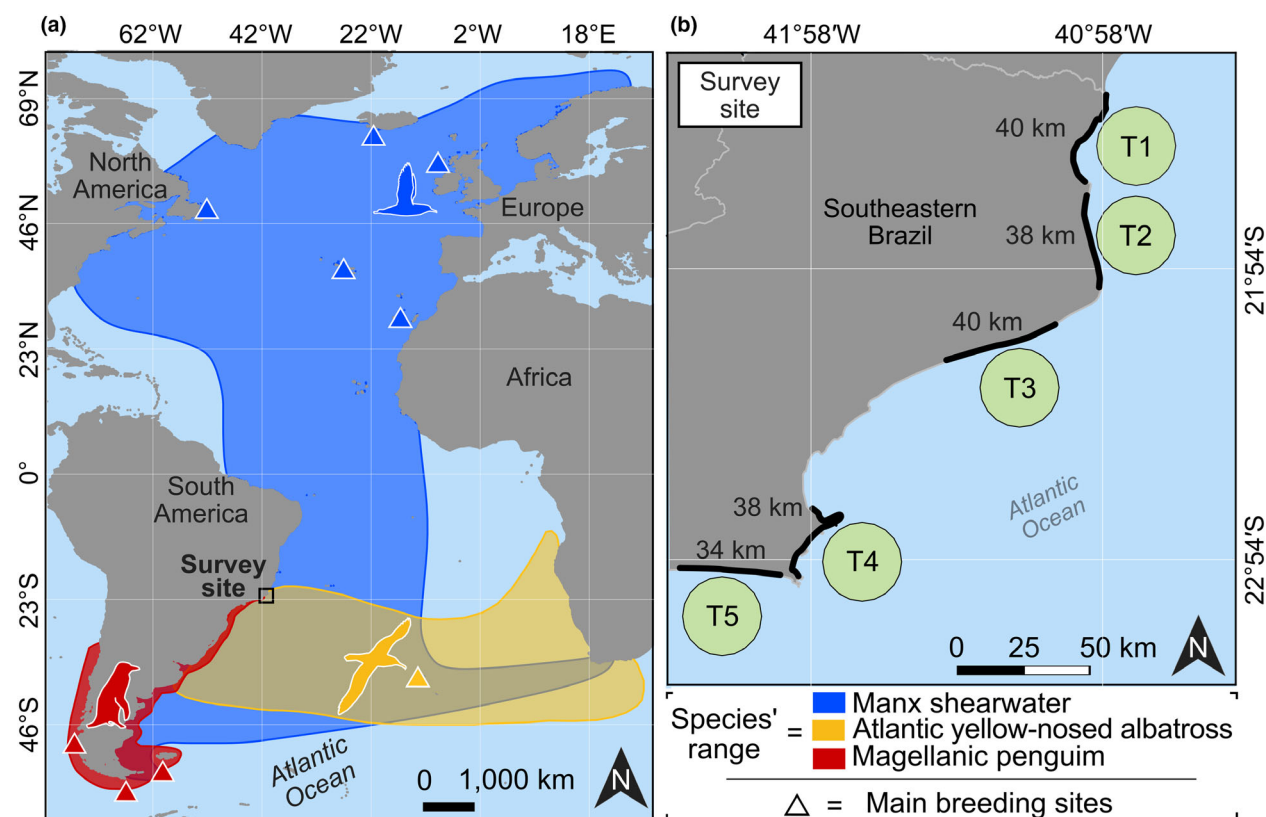


Figure 1 Distribution ranges of the seabird species analysed in this study and survey sites. The distributional ranges (a) were based on information available in the Handbook of Birds of the World Alive (del Hoyo *et al.*, 2018). Beach transects (black lines) and adjacent areas (circles marked T1–T5) from where we extracted satellite-derived oceanographic data (b). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

stranded birds in 190 km of beaches per day in five specific areas (Fig. 1b), with the aid of vehicles and along the high tide line. Birds were recovered with daily frequency to avoid missing corpses that could be removed from the beach by scavengers and beach cleaning activities. The tidal variation in the study site, usually ranging from 0.5 m (low tide) to 0.8 m (high tide), does not affect carcass persistence and detectability at beach. To avoid recounting, bird corpses were systematically removed from the beach. The carcass level of decomposition is a proxy of post-mortem drift duration, and in the tropics, dead animals fully decompose in one single day due to warm waters and the quick action of decomposers (Peltier & Ridoux, 2015). Thus, to reduce the possibility that carcasses recorded in a given transect did not die in other adjacent studied sectors due to long drifting periods (Fig. 1b), we only considered alive and fresh specimens, that is, those with no missing body parts or exposed skeleton (Tavares *et al.*, 2016b). Considering only fresh specimens is reasonable because only 1–10% of drifting corpses make it to shore (Matsuura, 1975), and thus the presence of a few carcasses is a good proxy for high number of deaths at sea. Specimens showing signs of bycatch (i.e. lines and hooks) were also excluded from our analysis to avoid bias caused by non-climatic factors. In addition, the

body condition was estimated qualitatively based on a pectoral muscle index, which gives indications on the amount of protein reserves (Votier *et al.*, 2007). This index scores from 1 to 5, with 1 indicating poor body condition and 5 indicating excellent body condition.

At-sea seabird data

We estimated monthly fluctuations in the abundance of seabirds at-sea using data from 23 cruises, which were conducted from 1984 to 2013 in the studied region (Supporting Information Figure S1). Specific information on survey effort, bird abundances and data sources is listed in Supporting Information Table S1. These cruises covered linear transects and seabirds encountered along a research vessel were counted and identified to the lowest possible taxon (Tasker *et al.*, 1984; Camphuysen *et al.*, 2004). Transect length ranged from 14 to 236 km (mean = 118 km). Thus, to make the seabird abundance estimations comparable between different areas and months, we calculated the seabird density at sea as the number of birds recorded per km. All seabirds encountered in a radius of 200 m from a research vessel were counted and identified to the lowest possible taxon. For each species, we calculated the average density at-sea per month.

Predictors with local-scale influence

To examine the most important factors influencing seabird mortality events in the period from November 2010 to September 2013, we compiled daily oceanographic data that, according to previous literature, could be potentially related to seabird mortality and stranding (Newton *et al.*, 2009; Nicoll *et al.*, 2017; Jones *et al.*, 2018). Specifically, we collected: (1) wave height and wave period from the Global Wave Model (WaveWatch III); (2) atmospheric pressure (ATM) at sea level from the U.S. Navy Fleet Numerical Meteorology and Oceanography Center; (3) SST anomaly (SSTa) from the Advanced Very High Resolution Radiometer on-board the Polar-orbiting Operational Environmental Satellite; (4) chlorophyll-a concentration (considered here as a proxy of primary productivity) from the Moderate Resolution Imaging Spectroradiometer; and (5) wind components, from the microwave advanced scatterometer on-board the satellite Metop-A. These environmental variables covered five circular buffers 30 km in diameter (Fig. 1b, circles T1–T5), because drift card release experiments showed that the number of recoveries is markedly reduced when floating objects are released more than 30 km away from shore (Matsuura, 1975). Thus, birds that die far away from the coast are not expected to make it to the beach. Buffers larger than 30 km would introduce to our analysis conditions unrelated to the death of birds found on the beach. The circular buffers were chosen so that (1) their centres were aligned with the middle of the beach survey transects and (2) they were 1 km away from the coastline. In each circular region, we calculated spatial (over the circle) and temporal averages (over a month) of environmental variables. Basic statistics concerning the features of the investigated regions are summarized in Supporting Information Table S2.

Storm activity

Migratory seabirds are likely to experience exhaustion and starvation when facing stormy weather conditions during long migratory routes (Jones *et al.*, 2018). Some species may also starve to death due to reduced foraging under rough seas or die by traumas caused by waves and strong winds (Hass, Hyman & Semmens, 2012). Thus, we used wave height and wave period as metrics for storm intensity (Newton *et al.*, 2009). In the study region, waves higher than 2 m are indicative of stormy conditions (Machado *et al.*, 2016). Our analysis does not include frequency and duration of storms, because in the region studied, several peaks of wave height are observed over the months, preventing a precise distinction between stormy wave episodes (Machado *et al.*, 2016). Note, however, that by averaging wave height per month, we are also indirectly including the effects of storm frequency because months with higher storm frequency are expected to show higher mean wave height. We also considered ATM since it is associated to variations in ENSO and in storm intensity (Knutson *et al.*, 2010).

Prey availability

Migratory seabirds are likely to starve under decreased prey availability consequent to reduced primary productivity

(Parrish *et al.*, 2007). Thus, we considered chlorophyll-a concentration and upwelling intensity because these two variables are good proxies of primary productivity and correlate with prey availability at a regional scale (Devney, Short & Congdon, 2009; Silk *et al.*, 2016). The upwelling index (UI) was our proxy for upwelling intensity. This index is based on Ekman's theory of mass transport of surface water caused by wind stress and Coriolis force (Bakun, 1990). Positive and negative values of the UI indicate upwelling and downwelling respectively. We also considered the SSTa because this variable may influence primary productivity and prey availability.

Winds and currents

To assess the influence of these factors on carcass deposition at beach, we considered the speed and direction of winds and currents (Munilla *et al.*, 2011). We also calculated the offshore wind frequency by summing the proportion of offshore winds for each month based on daily-averaged estimates. Offshore winds are defined as winds parallel to the coastline or toward the land (Wilhelm *et al.*, 2009).

Predictors with large-scale influence

ENSO is one of the most important coupled ocean-atmosphere phenomenon of climate variability at large scale and can be examined by means of several indices (Fan *et al.*, 2017). Both the Multivariate ENSO Index (MEI) and the Southern Oscillation Index (SOI) are routinely used to quantify the effects of large-scale climate processes on populations of apex predators. However, both indices are strongly correlated (Pearson correlation coefficient = 0.99). Therefore, we investigated the effects of ENSO using MEI (which was obtained from the NOAA's Earth System Research Laboratory) because it combines more climate parameters than SOI (Towner *et al.*, 2013). The values of this index typically range from −2 to 3, with negative scores indicating a cold ENSO phase (La Niña), and positive scores indicating a warm ENSO phase (El Niño). The events were determined as weak, moderate or strong based on the historic ranks of MEI values.

Data organization

In contrast to mortality events related to low productivity, which prolong over weeks, deaths related to adverse weather conditions are subtle (Parrish *et al.*, 2007; Haney, Geiger & Short, 2014; Jones *et al.*, 2018). Also, floating corpses may drift, on average, for 8 days before they reach the shores of the study site (Matsuura, 1975). To include the effects of predictors on both subtle and prolonged mortality events and to account for drifting times, we averaged both stranding and oceanographic data within 30-day intervals. This time span is also reasonable because, in general, birds were recovered throughout each month rather than in specific days (i.e. early month). After 35 months of daily sampling in the five areas (Fig. 1b), we covered about 200 000 km of beach and

obtained a total of 175 samples. Our data include months in which the species considered do not aggregate in breeding colonies and normally occur in the study site in order to (1) avoid false zeros, i.e. situations in which wrecks are not observed because birds are absent (or in low abundance) and (2) avoid exceptionally high values of the relative mortality index, which would not reflect high mortality, but casual deaths of vagrant individuals. Our analyses, thus, included April–September for the Atlantic yellow-nosed albatross, June–November for the Magellanic penguin and September–March for the Manx shearwater (del Hoyo *et al.*, 2018).

Data analysis

To investigate seabird mortality in relation to habitat variables, we considered the relative mortality index proposed by Newton *et al.* (2009), which is calculated as the number of carcasses and wrecked birds recorded on the beach divided by the sum of density recorded at sea and number of carcasses and wrecked birds recorded on the beach. The number of carcasses and wrecked birds is also included as a divisor in the index to avoid problems with undefined numbers when at-sea abundance is zero. The values of this index range from 0 to 1, with the extreme values indicating low and high mortality respectively (Newton *et al.*, 2009). The predictors included: wave height, wave period, ATM, chlorophyll-*a* concentration, SSTa, UI, wind speed and direction, frequency of offshore winds, vertical and horizontal current components and the MEI. The core statistical analyses were preceded by a data exploration phase aiming at detecting outliers and zero inflation (Zuur *et al.*, 2009). Collinearity was assessed using the Variance Inflation Factor and cross correlations among predictor variables (see Supporting Information Table S2).

Using Random Forests (RFs), we identified the most important variables related with the stranding events of the three bird species. This method simulates multiple conditional classification trees to estimate the importance of each variable for predicting the response variable (Strobl *et al.*, 2007). The classification trees framework allows data to be analysed without the assumptions required for classical parametric tests, such as balanced designs and independence between samples (Hothorn, Hornik & Zeileis, 2006). For each species, we fitted a full model, with the relative mortality index fitted as functions of the predictors. The variable importance scores (IS) were estimated based on permutations of the area under the curve, which is a more robust method to analyse unbalanced response variables (Genuer, Poggi & Tuleau-Malot, 2010; Janitzka, Strobl & Boulesteix, 2013). We set the number of permutations (trees) to 1 000 000, because smaller numbers were leading to imprecise IS estimations, due to the relatively high number of predictors. The variables are considered significant if their values are greater than the absolute value of the variable with the lowest negative value (Ming Lee *et al.*, 2015).

To examine direct and indirect effects of predictors on seabird mortality, inferred with the relative mortality index, we performed structural equation models (SEM). This

method is suitable for investigating chain processes in ecological systems because it allows to define and explore relationships/paths between predictors (Grace *et al.*, 2010). For each species, we initially fitted SEMs with the mortality index as response variable as functions of environmental variables with significant RF IS (described in the paragraph above). In order to detect indirect effects of variables on the mortality index and increase model performance, we then increased SEM complexity by adding predictors with non-negative RF IS. SEM goodness-of-fit was evaluated with chi-square tests and other relevant metrics (Grace *et al.*, 2016). Models were fitted via diagonally weighted least squares (Bandalos, 2014).

To account for spatial correlations in the data associated to the hierarchical nature of our sampling design (Fig. 1 and Supporting Information Figure S2) and potential nonlinear relationships between mortality patterns and predictor variables, we also analysed the relative mortality of each seabird species using Generalized Additive Mixed Models, GAMMs (Wood, 2006). In practice, GAMMs are linear models with smoothing functions linked to the predictor variables, which allow for both linear and nonlinear regressions (Zuur *et al.*, 2009). Different from other linear methods, these models generate a number of slopes rather than a singled fixed one, thus allowing for the detection of non-uniform responses of the relative mortality index to predictors. For each of the investigated seabird species, we fitted a GAMM including significant predictors with direct effects on the relative mortality index, according to the results obtained with SEMs. The surveyed transects were set as random effects, thus accounting for spatial correlations in the data (Supporting Information Figure S2). We fitted models with Gaussian family because it provided the best fits according to the visual inspection of regression residuals (Zuur, Ieno & Elphick, 2010). Parameters were estimated using restricted maximum likelihood (Wood, 2006). For each species, we plotted smooth splines of the relative mortality index as function of predictors. Average values for model slopes were obtaining by calculating the mean of the list of slopes obtained with the GAMM. During the data exploration phase, we also analysed data using linear models and Generalized Linear Mixed Models, but the results showed poor model residual fits in comparison to those obtained with GAMMs.

All the statistical analyses were conducted with R (version 3.0.2), using the packages ‘party’ for calculating variable IS based on RFs, ‘lavaan’ for the SEMs and ‘gamm4’ for generalized additive mixed models.

Results

Seabird mortality and ENSO events

The MEI indicates a moderate-strong La Niña event between November 2010 and January 2012, followed by a moderate-strong El Niño between April and September 2012 (Supporting Information Figure S3). From October 2012 to September 2013 the MEI oscillated around zero. Unusual mortalities of Atlantic yellow-nosed albatrosses and Magellanic

penguins occurred when MEI was relatively weak and during a peak of El Niño (Supporting Information Figure S2). Also, unusual mortalities of Manx shearwaters were recorded during both moderate-strong El Niño and La Niña conditions (Supporting Information Figure S3). The monthly variations of seabird recovered on the beach, at-sea abundance, relative mortality index and main predictor variables directly associated to mortality are shown in Supporting Information Figure S3.

Most of the birds recovered during our monitoring campaign showed poor body conditions (Atlantic yellow-nosed albatross: 79%, $n = 61$; Magellanic penguins: 92%, $n = 1650$; Manx shearwaters: 85%, $n = 46$). The Atlantic yellow-nosed albatrosses and Manx shearwaters included mostly adults, comprising 77% and 93% of the wrecks recorded for each species respectively. Magellanic penguins included mostly juveniles, comprising 92% of the specimens of this species. Moreover, a relevant proportion of recovered birds were still alive (Atlantic yellow-nosed albatrosses = 10%, Magellanic penguins = 35% and Manx shearwaters = 22%).

The most important predictors of seabird mortality

Figure 2 summarizes the IS of each environmental variable for predicting the mortality of Atlantic yellow-nosed albatrosses, Magellanic penguins and Manx shearwaters. The frequency of offshore winds, wave height, wind speed and ATM are the most important predictors ($IS > 4.0 \times 10^{-4}$) of the mortality of Atlantic yellow-nosed albatrosses (Fig. 2a). Wave height, ATM, chlorophyll-a concentration and the MEI are significant predictors ($IS > 4.9 \times 10^{-4}$) of the mortality of Magellanic penguins (Fig. 2b). The most important variables associated with the relative mortality of Manx shearwaters include ATM, wave height, the MEI and wind speed ($IS > 6.9 \times 10^{-5}$, Fig. 2c).

Direct and indirect effects of ENSO and oceanographic conditions on seabird mortality

The multiple metrics of goodness-of-fit and regression parameters obtained from the best-fitting SEMs are summarized respectively, in the Supporting Information Tables S3 and S4. The best-fitting SEM revealed that the mortality of the Atlantic yellow-nosed albatross (Fig. 3a) is positively correlated to increased ATM and wave height (a proxy for storm intensity), but not to large-scale climatic processes, and negatively correlated to the frequency of offshore winds. The mortality of Magellanic penguins (Fig. 3b) is positively correlated to increased wave height and reduced chlorophyll-a concentration (a proxy for prey availability). The mortality of Manx shearwaters is positively correlated to ENSO, which is associated to an increase in wave height. More specifically, a positive MEI index (El Niño conditions) is associated to an increase in ATM at sea level in areas close to the Brazilian shores, which in turn increases wave height and thus the mortality of Manx shearwaters (Fig. 3c).

The Generalized Additive Mixed Models confirm the direct effects of wave height on the mortality of Atlantic yellow-nosed albatrosses, Manx shearwaters and Magellanic penguins (Fig. 4; Table 1). The frequency of offshore winds plays also a significant direct effect on the mortality of Atlantic yellow-nosed albatrosses, and the concentration of chlorophyll-a has a significant direct effect on Magellanic penguins (Fig. 4; Table 1). Increasing the wave height increases the mortality for all three species, but for the Magellanic penguins, the number of stranded birds does not change substantially when monthly wave height exceeds 2.1 m (Fig. 4; Table 1). In addition, the mortality of Magellanic penguins is reduced when the concentration of chlorophyll-a is higher than the annual average (Fig. 4d). Figure 4 also shows the combined effect of wave height and chlorophyll-a concentration on the mortality of Magellanic penguins.

Discussion

Our results show that the mortality of Manx shearwaters is related to indirect effects of a large-scale climate condition (ENSO), which promote localized changes in oceanographic conditions. The intensification of ENSO increased ATM and storm activity in Brazilian coastal waters. These environmental variables are positively correlated with the mortality of Manx shearwaters. In contrast, the mortalities of Atlantic yellow-nosed albatrosses and Magellanic penguins are associated to local changes in habitat. These differences are explained by variations in the arrival time of the three species in the Brazilian coast. The mortality of Manx shearwaters is higher during the late Austral summer of 2012 and early Austral spring of both 2012 and 2013, months with moderate-intense El Niño events and anomalously storm activities, conditions that in the Brazilian coast occur typically during the winter months (Pianca, Mazzini & Siegle, 2010). Atlantic yellow-nosed albatrosses arrive mainly in autumn and their mortality is related to local increased storm activity during early winter (June and July). The Magellanic penguins arrive in the Brazilian coast mainly during late-winter (July), under increased stormy activity, and remain until late spring (November), when biological productivity (a proxy for prey availability) is below the annual average. A range of physical processes causes mortality of seabirds migrating along the tropical Atlantic and call for a variety of mitigation measures.

Adverse oceanographic conditions in non-breeding areas are an additional, often overlooked, threat for endangered seabird species and may explain why conservation strategies aiming at reducing direct human impacts, including bycatch, oil pollution and predation by exotic species have not been fully successful in programmes of population recovery (Stokes *et al.*, 2014; Phillips *et al.*, 2016; BirdLife International, 2017). As a consequence of climate change, stormy weather is becoming more frequent and intense in tropical regions (Knutson *et al.*, 2010). Storm conditions, e.g. increased wave height, can impair the capacity of seabirds to catch food, a particularly adverse situation for animals with

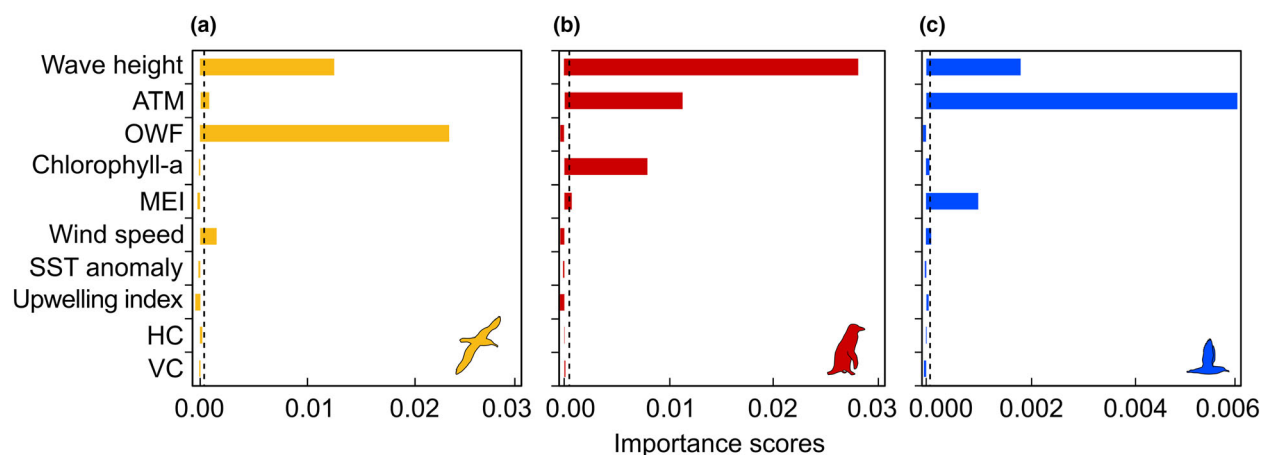


Figure 2 Ranking of environmental variables according to their relative importance, as estimated by random forests, to predict the mortality of the Atlantic yellowed-nosed albatross (a), the Magellanic penguin (b) and the Manx shearwaters (c) in non-breeding areas of the tropical Atlantic (21°–23°S). HC, horizontal currents; MEI, Multivariate El Niño–Southern Oscillation Index; OWF, offshore wind frequency; ATM, atmospheric pressure at sea level; VC, vertical currents. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

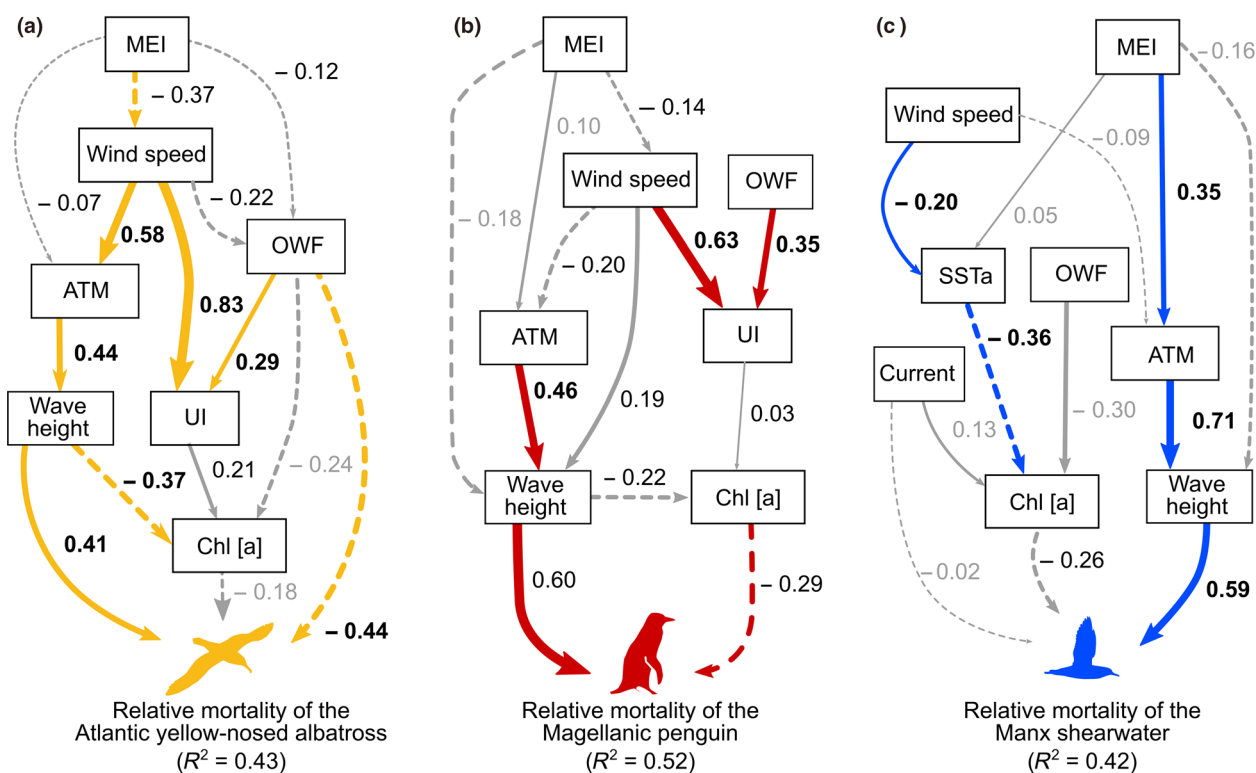


Figure 3 Best-fitting structural equation models for predicting the mortality of the Atlantic yellowed-nosed albatross (a), the Magellanic penguin (b), and the Manx shearwater (c). ATM, atmospheric pressure; Chl, chlorophyll-a; MEI, Multivariate El Niño–Southern Oscillation Index; OWF, offshore wind frequency; SSTa, sea surface temperature anomaly; UI, upwelling index. Continuous and dashed coloured lines indicate positive and negative significant effects respectively, while grey lines indicate non-significant paths ($P > 0.05$). Numbers adjacent to arrows indicate standardized path coefficient estimates. The higher the coefficient, the greater the magnitude of the relationship between variables. The width of the arrows is proportional to the value of the coefficients. The relative mortality of the birds is estimated by the relative mortality index (Newton *et al.*, 2009). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

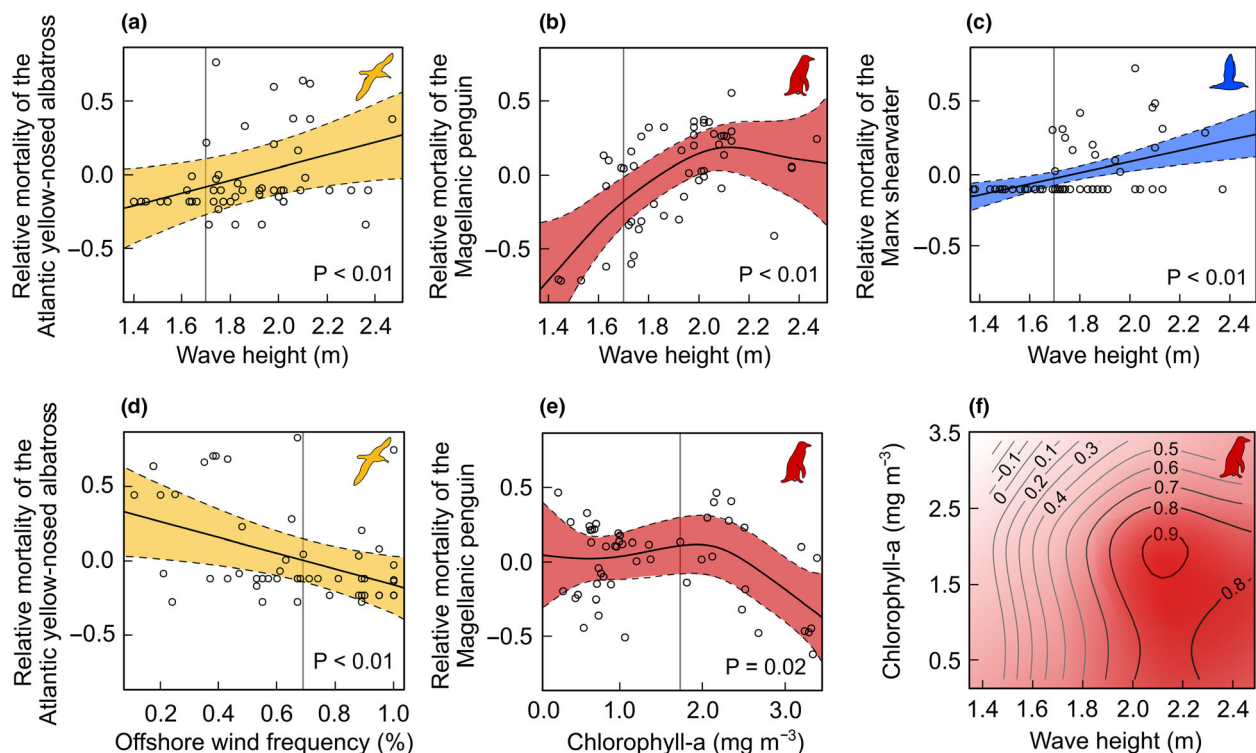


Figure 4 Smoothing splines for predicting the mortality of the seabird species in response to significant predictors, which are: wave height (a–c), offshore wind frequency (d), and chlorophyll-a (e). The contour plot (f) indicates spline values for the mortality of Magellanic penguins as functions of the interaction between wave height and chlorophyll-a concentration. The smoothing spline (continuous black line) and the 95% confidence bands (shaded areas) were obtained by fitting the relative mortality as function of environmental variables using Generalized Additive Mixed Models. Vertical grey lines indicate the annual averages of the predictor variables. The colours were added behind the contours to facilitate visual interpretation. Higher values and colour saturation indicate higher mortalities. Empty circles indicate partial residuals. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com)]

Table 1. Summary statistics for Generalized Additive Mixed Models (GAMM) fits

Seabird species	Predictors	β	P	R^2
Atlantic yellow-nosed albatross	Wave height	0.012	<0.01	0.29
	Offshore wind frequency	−0.014	<0.01	
Magellanic penguin	Wave height	0.073	<0.01	0.43
	Chlorophyll-a concentration	0.028	0.02	
Manx shearwater	Wave height	0.009	<0.01	0.18

The slope averages (β), P -values (P) and coefficient of determination (R^2) were obtained for models fitted for each seabird species, including predictors with significant direct effects on the mortality index, according to the structural equation models (see Materials and methods). Slope averages were calculated based on the different slopes of each GAMM.

high energetic demands during the long-distance migrations (Finney, Wanless & Harris, 1999; Parrish *et al.*, 2007). Stormy conditions through non-breeding areas result in sudden mortalities of sexually mature Atlantic yellow-nosed albatrosses and Manx shearwaters, a particularly worrisome

finding given that these adults contribute to the maintenance of the population stocks. Future increases in the intensity and frequency of stormy weather can exacerbate the mortality of the species we studied, with negative consequences for their populations. The conservation of these species should not only focus on the effects produced by direct human disturbances (i.e. bycatch prevention and protection of breeding sites), but also on predicting demographic parameters under future climate change, e.g. increased cyclone intensity and frequency in the tropics (Şekerciöğlu, Primack & Wormworth, 2012; Bacmeister *et al.*, 2018).

Mathematical models can help to predict how seabird mortality rates and global population abundances change over time in response to human disturbances (e.g. bycatch and oiling rates) and adverse climate (e.g. rates of deaths due to starvation). Our results show that wave height, a proxy for storm intensity, can be useful to predict mortality rates. This variable can also contribute to carcass deposition along shore (Kenow *et al.*, 2016). However, despite having relatively similar body shape and mass (Atlantic yellow-nosed albatross: 2.5 kg, Magellanic penguin: 3.4 kg, Manx shearwater: 0.43 kg), the three seabird species responded differently to wave height. If wave height had played an

important role in carcass deposition, predictive curves would have been the same for the three species. Even corpses featuring different shape and mass, such as bottles and sea turtles tend to show similar stranding patterns in response to drifting forces (Hart, Mooreside & Crowder, 2006). A total of 34% of the 1757 birds in our data were recovered alive, a further indication of the role of wave height as a proxy for storm intensity. Inter and intraspecific trait variability related to bird survival abilities, such as preferred diet, feeding strategy, body mass and age (Tavares *et al.*, 2019), can help us understand how these organisms respond to oceanographic conditions. Predictive models should consider that, on average, about 17% of dead birds are recovered on beaches (Munilla *et al.*, 2011), thus bird deaths estimated by beach monitoring programmes represent only a small component of bird mortality.

The SEMs allowed us to uncover processes related to seabird mortality that are otherwise not detectable by RFs and other techniques such as regression models. The RFs IS of ATM for predicting the mortality of Atlantic yellow-nosed albatrosses are relatively low. However, SEMs showed that the ATM indirectly contributes to mortality patterns, via its effect on wave height. Moreover, the MEI is a significant predictor of the mortality of Manx shearwaters, but the mechanisms driving this correlation cannot be understood without looking at the processes, i.e. the paths, linking these variables. Using SEMs, we demonstrated that increased MEI has an indirect effect on the mortality of Manx shearwaters, through positive impacts on ATM and wave height. In contrast to most approaches to data modelling, SEMs offers a framework for defining path/network relations between predictor variables (Grace *et al.*, 2010) and it allowed us to investigate multiple oceanographic processes, defined as direct and indirect pathways, in relation to the mortality of seabirds.

A total of 83% of 1757 birds were recovered in the southern region of our study site, (T4 and T5, Fig. 1 and Supporting Information Figure S2). A relatively high mortality of resident birds, i.e. brown boobies *Sula leucogaster* and Kelp gulls *Larus dominicanus* was previously observed in this region, due to the high abundance of these species in colonies located nearby (Tavares *et al.*, 2016a, 2016b). By using the mortality index, we showed that the mortality of migratory seabirds is related to oceanographic processes rather than to an increased abundance of birds during migratory influxes in the region. Beach monitoring programmes and conservation strategies may be focused on areas close to T4 and T5, where we found a higher number of seabird wrecks.

Out of the three species studied here, only the Magellanic penguin is negatively affected by a local decrease in primary productivity. The mortality of this species occurred mainly during the Austral winter when upwelling is weak in our study site (Valentin, 2001) and primary productivity is typically below the annual average (1.7 mg m^{-3}). Under these conditions, the abundance of prey (e.g. fish and cephalopods) is low (Moura *et al.*, 2018). Also, 92% of the 1650 penguins we recovered were juveniles with poor body conditions and clear signs of starvation. Poor body conditions and the

relatively small body size of the juveniles makes it difficult for these birds to search and capture preys through the water column, especially in rough seas and under limited prey availability (Walker & Boersma, 2003; Cardoso *et al.*, 2011). These observations are consistent with the hypothesis that these birds are sensitive to decreased prey availability at the local scale as also suggested by an atypical die-off of penguins along the Brazilian coast in 2008 during anomalous cold waters and decreased prey availability (García-borboroglu *et al.*, 2010).

The population declines of Magellanic penguins have been largely attributed to the mortality caused by oil pollution and bycatch in fisheries during the migration along South America's Atlantic (García-Borboroglu *et al.*, 2006; Cardoso *et al.*, 2011). The conservation strategies for protecting the species are thus centred on marine zoning, which requires ambitious international efforts (Stokes *et al.*, 2014). In our study site, 0.78 penguins per km are recorded with signs of starvation annually. This mortality rate is 15 times higher than the one reported for penguins showing death related to oil, which is 0.05 of penguins per km, over 8000 km of South American Atlantic coast (García-Borboroglu *et al.*, 2006). For reducing these sources of mortality, mitigation strategies could include also the establishment of rehabilitation programs for reintroducing penguins recovered in poor body conditions and the optimization of rehabilitation protocols (Martins *et al.*, 2015). Only about 25 seabird rehabilitation centres are available along the whole South Atlantic Ocean (García-Borboroglu *et al.*, 2006). An appropriate number of rehabilitation centres is particularly important for Magellanic penguins because 35% ($n = 577$) of the individuals we recovered were still alive.

Large-scale climatic processes like ENSO are often related to changes in prey availability and abundance of top predators in the tropics (Sprogis *et al.*, 2017). For example, El Niño events negatively impacted shearwaters *Puffinus carneipes* in Australia (Bond & Lavers, 2014) and dolphins *Cephalorhynchus commersonii* in Argentina because they reduce prey availability (Dellabianca *et al.*, 2012). Recent research has shown that tropical cyclones related to ENSO intensifications can have contrasting effects on petrels of the Indian Ocean by simultaneously increasing mortality and improving foraging opportunities (Nicoll *et al.*, 2017). Manx shearwaters migrate to our study region during upwelling (late Spring), when high primary production fuels higher trophic levels and improves foraging opportunities for these birds (Guilford *et al.*, 2009; Freeman *et al.*, 2013). Thus, the mortality of Manx shearwaters is not affected by low prey availability, but by intensified ENSO, which leads to untimely increased storm intensity during spring months (Pianca *et al.*, 2010).

In conclusion, the mortality of migratory seabirds in non-breeding sites of the tropical Atlantic is related to changes in local oceanographic conditions and to indirect effects of ENSO. Bird species arriving during the late austral spring and summer, i.e. Manx Shearwaters, show increased mortality under anomalously storm activity driven by intensified El Niño conditions. Species migrating during the austral winter, i.e. the Magellanic penguin and the Atlantic yellow-nosed

albatrosses, show greater mortality under increased adverse oceanographic conditions at local scale. Human-induced climate change is expected to increase the frequency and intensity of storms and climate variability in the tropics (IPCC, 2014). Periodic climatic variations can thus exacerbate the decline in population abundances of seabird species, such as the Atlantic yellow-nosed albatrosses, Magellanic penguins and Manx shearwaters, which are already under threat by fishery bycatch, oil pollution and introduction of exotic species. Our study also highlights the importance of comprehensive data on year-round seabird stranding to assess at-sea mortality patterns.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. At-sea abundance of Atlantic yellow-nosed albatrosses *Thalassarche chlororhynchos* (Gmelin, 1789), Magellanic penguins *Spheniscus magellanicus* (Forster, 1781) and Manx shearwaters *Puffinus puffinus* (Brünnich, 1764) in the Southeastern Brazilian coast.

Figure S2. Number of corpses of migratory seabird species recorded at the beach transects.

Figure S3. Monthly variation of seabird carcasses recovered on the beach (a), density at-sea (b), relative mortality index (c), and the main predictor variables (d).

Table S1. Information on data sources, number of birds recorded and survey effort of seabird cruises carried out in Southeast Brazilian coast.

Table S2. Description of climatic and oceanographic predictor variables and their potential effects on the seabird species studied.

Table S3. The goodness-of-fit of structural equation models for predicting seabird mortality.

Table S4. Summary statistics for the structural equation models fitted.