


## High incidence of sea turtle stranding in the southwestern Atlantic Ocean

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Sea turtles are globally threatened due to short- and long-term exposure to anthropogenic activities. Many life-history traits make it difficult to study these species in the wild. Stranding events provide invaluable data to infer key aspects of sea turtle ecology, such as regional occurrence, health status, mortality rates, and potential threats. In this study, we investigate spatial and temporal patterns of sea turtle occurrence and mortality in the southwestern Atlantic Ocean based on a systematic, large-scale survey programme covering 1040 km of coastline during 732 d of two consecutive years. From the 12 571 animals recovered, juvenile green turtles were the most common (90.4%), but four other species were also recorded. A significant non-linear effect of time and space in the number of stranding events was observed. The most parsimonious mixed linear model further indicated that stranding events were influenced by individual (sex, size), health (body condition, pathologies, decomposition), and oceanographic factors (chlorophyll-a, sea surface temperature, salinity, wave height). More than simply

describing the spatiotemporal occurrence and aspects of sea turtles' life history in an otherwise understudied area, this intensive field study provides evidence for relatively high mortality rates—an essential baseline information for guiding conservation efforts.

**Keywords:** anthropogenic threats, green turtle, hawksbill turtle, leatherback turtle, loggerhead turtle, mortality, olive ridley turtle, occurrence, stranding

## Introduction

The intensive anthropogenic activities in coastal areas have been challenging the marine biota. The list of threats to marine animals is long—overfishing, vessel traffic, noise pollution, chemical contamination from domestic, agricultural and industrial run-off, marine debris, and the multiple impacts caused by ports, dredging, and oil and gas exploration. Such environmental degradation is particularly problematic for long-lived, slow-growing animals with late sexual maturation, such as sea turtles. These traits typically accelerate population decline or protract population recovery, even when threats are reduced (Musick, 1999; Mazaris et al., 2017). The vulnerability of sea turtle populations is further aggravated by other life-history traits, such as extensive migrations between different areas combined to female nesting site fidelity and male-mediated gene flow (Plotkin, 2003). Globally, six of the seven sea turtle species are currently vulnerable to extinction, endangered, or critically endangered (IUCN, 2019).

Identifying critical areas for sea turtle conservation and management requires baseline information on turtle demography (e.g. population sizes and trends), population structure (e.g. sex ratio, age structure) and habitat use, and connectivity (e.g. migration routes between nesting, nurseries, and foraging sites) (Hamann et al., 2010; Bolten et al., 2011; Rees et al., 2016; Wildermann et al., 2018). However, assessing these parameters over large scales is logistically challenging (Rees et al., 2016; Wildermann et al., 2018). Given that anthropogenic impacts vary across space, relating human activities and sea turtle population status over regional scales is not only more feasible but also more biologically meaningful, as highlighted by the definition of regional sea turtle management units (RMUs, Wallace et al., 2010).

The RMUs in the southwestern Atlantic Ocean provide nesting and foraging habitats for five sea turtle species: hawksbill (*Eretmochelys imbricata*), green (*Chelonia mydas*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), and leatherback turtles (*Dermochelys coriacea*) (Marcovaldi and Marcovaldi, 1999; Wallace et al., 2010; Colman et al., 2019; IUCN, 2019). These RMUs comprise the coasts of southern Brazil, Uruguay, and northern Argentina, where the regional and local conservation status of sea turtles range from “critically endangered” for hawksbill and leatherback, to “vulnerable” for olive ridley, to “least concern” for green and loggerhead turtles (Santos et al., 2011; IUCN, 2019). This region is a crucial foraging ground for sea turtles of all life stages, but particularly for juveniles coming from different locations and genetic stocks (Wallace et al., 2010; Santos et al., 2011; Naro-Maciel et al., 2012; Coelho et al., 2018). Sea turtles travel and forage across latitudes in the southwestern Atlantic and so are exposed to a diverse set of potentially threatening anthropogenic activities (e.g. Gallo et al., 2006; Sales et al., 2008; González-Carman et al., 2011; Fiedler et al., 2012; González-Carman et al., 2012b; López-Barrera et al., 2012; Barceló et al., 2013; Monteiro et al., 2016; Silva et al., 2017; Vélez-Rubio et al., 2018; Tagliolatto et al., 2020; Fuentes et al., 2020).

Studying population structure and dynamics of such migratory species typically require laborious and expensive in-water surveys, long-term tagging, or automated tracking methods (e.g. Godley et al., 2008; Grossman et al., 2019; Kendall et al., 2019). Alternative, land-based methods such as stranding networks provide valuable quantitative baseline data, especially when the cause of death, health condition, and the stranding probability are determined (Epperly et al., 1996; Hart et al., 2006; Peltier and Ridoux, 2015; Monteiro et al., 2016; ten Doeschate et al., 2018). By monitoring stranding events over time and space, one can infer occurrence, distribution, mortality rates, and other demographic parameters necessary to guide conservation efforts (e.g. Hart et al., 2006; Vélez-Rubio et al., 2013; Monteiro et al., 2016; ten Doeschate et al., 2018; Tagliolatto et al., 2020). Understanding baseline spatiotemporal variation in occurrence and mortality is essential when using stranding data as ecological indicators (Santos et al., 2018a, b), and particularly relevant in developing countries where human impacts increase fast and resources for conservation are typically scarce.

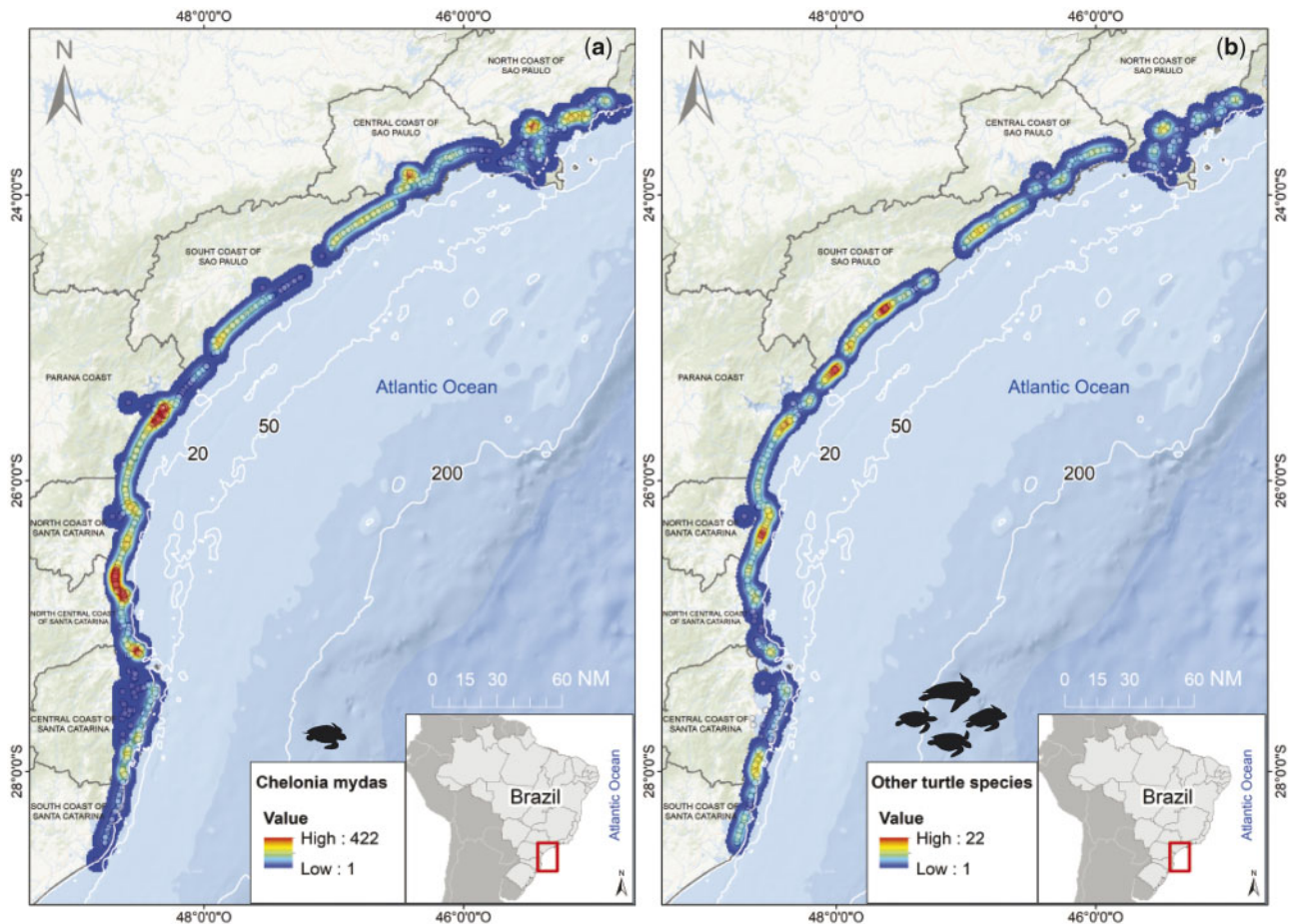
Here, we investigate the spatial and temporal patterns of sea turtle occurrence and mortality in the southwestern Atlantic Ocean based on a systematic, large-scale stranding survey programme, covering >1000 km of coastline nearly every day during 2 years by 11 research teams working simultaneously. This unmatched field effort in the area yielded the largest, most detailed dataset available on sea turtle stranding events in the southwestern Atlantic Ocean. Such unprecedented data provide insights into the occurrence and reveal high mortality, of five sea turtle species in this region.

## Methods

### Experimental design and sampling effort

Stranding events of marine animals were systematically monitored from 24 August 2015 to 24 August 2017, along 1040 km of coastline in the southern and southeastern Brazilian coast (23°22'31"S 42°44'00"W to 28°29'42"S 48°45'36"W), encompassing the states of São Paulo, Paraná, and Santa Catarina (Figure 1). This monitoring programme was part of the Santos Basin Beach Monitoring Project, a requirement set by the Brazilian Institute of the Environment (IBAMA) for the environmental licensing of the oil and natural gas production and transport by Petrobras at the pre-salt province (25°05'S 42°35'W to 25°55'S 43°34'W).

The coastal zone of the study area was monitored by car, motorcycles, four-wheel ATVs, bikes, foot, and boats, depending on the beach and coast characteristics. The tidal zone was surveyed during the low tide by trained observers searching for stranded animals, from the water line to the upper beach limit. Beaches were monitored either daily (65% of the area) or weekly (14% of the area), and in some beaches of difficult access (21% of the area), animals were collected by the field teams only when called by the general public. Given the logistical challenges of monitoring the 328 sites in 53 cities, the study area was split into



**Figure 1.** Spatial distribution of sea turtle stranding along the study area in southern Brazil, from August 2015 to August 2017. Colour code indicates kernel density for (a) green turtles (*Chelonia mydas*) and (b) the other four species combined: loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), olive ridley (*Lepidochelys olivacea*), and leatherback turtles (*Dermochelys coriacea*). Land delimitations indicate the eight sampling mesoregions; white lines indicate the three isobaths at which the oceanographic variables were measured. Inset indicates the location of the study area (red rectangle) in the southern Atlantic Ocean (for the spatial distribution of each species per austral season, see [Supplementary Figures S9–S15](#)). NM, nautical miles.

eight similar-sized mesoregions (mean = 102.1 km  $\pm$  31.9 SD, [Figure 1](#)), which were monitored by survey teams from 11 institutions, following the same, standardized field and laboratory protocols for data sampling. The mesoregions were defined combining Brazilian geographic and physiographical variables, including the “Coastal Sensibility Index” ([MMA, 2007](#)) to represent more than mere geopolitical divisions, but a set of habitats with similar physiographic characteristics, such as the coastline curvature, angle of beach exposure to the open sea, and geomorphological characteristics.

### Ethical note

The licences and research permits for monitoring programme and the biological sampling were issued by the Brazilian government (IBAMA-ABIO 640/2015); all animal handling procedures and protocols followed the required ethics and welfare practices.

### Data sampling

Upon finding a stranded sea turtle, the survey teams identified the species, assigned an individual identification code, and recorded date and geographical coordinates. Animals found alive

( $n = 1186$ ; 9.4%) were transferred to local rehabilitation centres for potential posterior reintroduction; those found dead ( $n = 11\,385$ ; 90.6%), whenever possible, were taken to laboratories to be necropsied by veterinary pathologists. In the field, the team also recorded variables regarding (i) environmental sampling conditions, (ii) individual attributes, (iii) carcass condition, and (iv) suggestive signs of interaction with anthropic activities.

The (i) environmental variables describing the sampling conditions were: substrate type (sandy, rocky, water, or mangrove); cloud cover (good = sunny, partially cloudy, cloudy; bad = rainy, foggy); and wind intensity ( $\text{km h}^{-1}$ ). The (ii) individual variables were: sex, body size, and development stage. Sex (male/female) was inferred in the field only for adults through visual inspection of the tail ([Wyneken, 2001](#)) and then confirmed by gonadal analysis during necropsy or through histological evaluation ([Wibbels, 2003](#); [Supplementary Table S1](#)). For all juveniles, sex was determined by gonadal analysis during necropsy and applying histological examination. The curved carapace length (CCL, measured at  $\pm 0.1$  cm precision), which is highly correlated with other body length measurements ([Balazs, 1999](#)), was used as a proxy for body size ([Supplementary Table S2](#), [Supplementary](#)

Figures S1 and S2). A development stage (hatchling, juvenile, or adult) was assigned based primarily on gonadal analysis (Supplementary Table S3); when not available, the stage was inferred through body size considering juveniles as those with CCL smaller than the minimum size at the nearest nesting sites for each species (green: 90 cm; loggerhead: 83 cm; leatherback: 139 cm; hawksbill: 86 cm; olive ridley: 63 cm; following Monteiro *et al.*, 2016).

The (iii) carcass variables were: individual condition (dead/alive) and decomposition state. Decomposition was classified in five states [adapted from Geraci and Lounsbury (2005), Reis *et al.* (2017)] as code 5 (mummified or skeleton only); code 4 (severely decomposed); code 3 (moderately decomposed); code 2 (freshly dead, likely within the last 24 h); and code 1 (alive). The (iv) health and anthropic interactions variables were overall body condition (good/bad based on body mass) and incidence of amputation of limbs, pathologies (macroscopic analysis), epibionts, and suggestive signs of interaction with anthropic activities. Anthropic interactions were further classified into entanglement or any clear interaction with fishing gear; external signs of ingestion of any type of marine debris; external signs of human aggression (e.g. knife cuts); and signs of collision with vessels or dredge. Each of these categories was ranked based on the level of evidence for each interaction from 1 (low) to 3 (high). All these variables were first assessed by visual inspection by the field teams and later updated during necropsy performed by veterinarians.

Finally, four oceanographic variables were retrieved from the Physical Oceanography Distributed Active Archive Center (NASA's Jet Propulsion Laboratory, <https://podaac.jpl.nasa.gov>): sea surface temperature (SST), chlorophyll-*a* concentration, salinity, and significant wave height. The SST (°C) and the chlorophyll-*a* concentration data ( $\text{mg m}^{-3}$ ) were retrieved from satellite imagery collected by a moderate-resolution spectroradiometer, every 8 d. The SST data are available in cell grids of 1/24 geographic degree of resolution (ca. 9.3 km at the study area), while the chlorophyll-*a* data are in cell grids of  $0.04 \times 0.04$  degree of resolution (4 km). The salinity data (measured in practical salinity units) were collected from the soil moisture active passive satellite, roughly every 3 d, in cell grids of  $0.25^\circ \times 0.25^\circ$  with approximate resolution of 70 km. The significant wave height data (m) have resolution of one (1) geographic degree, measured daily (AVISO Near Real Time). For each sea turtle stranding event, the oceanographic variables (Table 1) were extracted from the satellite images at three isobaths ranges (0–20, 20–50, 50–200 m), averaging the values at these depth intervals in front of the corresponding mesoregion, using ArcGIS® 10.2.2 for Desktop (ESRI, 2014).

### Stranding distribution

Sea turtle stranding events were plotted and analysed using kernel density models, using a bandwidth of 10 km in ArcGIS® 10.2.2. The kernel maps aimed to describe the spatiotemporal distribution of stranding events of each sea turtle species during each austral season. They were also used to visually identify stranding hotspots along the study area, using a 10-km influence radius to minimize overlap. The maps were produced using the “Percentual Clip” tool (e.g. uniform kernel density), a linear stratification between the minimum and maximum values of all pixels in the image used for the calculations (*sensu* Silverman, 1986).

### Modelling stranding incidence

The sea turtle stranding incidence was evaluated by counting stranding events per units of space (20 km) over time (week). The study area was divided into 31 latitudinal bands of 20 km and recorded the number of stranded animals during each of the 107 weeks from August 2015 to August 2017. The dataset yielded 3317 sampling units of 20 km band/week. This spatiotemporal scale was chosen because it is compatible with the average field survey (total survey length/total number of surveys = 15.5 km) and for providing a good compromise between the total number of sampling units, variation in stranding incidence, and number of zeroed band/week sampling units ( $n = 944$ ). Nevertheless, a sensitivity analysis was performed to test whether the final model performed well when considering coarser ( $40 \text{ km month}^{-1}$ ) and finer ( $5 \text{ km week}^{-1}$ ) sampling units (see Supplementary Figures S3 and S4).

To model the spatiotemporal patterns of stranding events in the area, we focused on the green turtles because they were overwhelmingly more frequent (90.4%) than all the other species combined (Supplementary Table S3). A stranding event was modelled by considering it as a compound probability of three events—occurrence, death, and drift. That is, for a stranded animal to be recorded, it should have occurred in the study area, be dead or impaired, and be washed close to shore to be found by the survey teams. To describe the probability of occurrence in the study area, three biological (sex, development stage, and body size) and three environmental variables (chlorophyll-*a* concentration, SST, and salinity at the 20, 50, and 200 m isobaths) were used. To describe the probability of death, two health variables (body condition and presence of pathologies) and one anthropic variable (evidence of anthropic interaction) were used. Interaction with fisheries interaction is a critical threat for sea turtles in the area (Gallo *et al.*, 2006; Fiedler *et al.*, 2012; González-Carman *et al.*, 2012b; López-Barrera *et al.*, 2012; Guebert *et al.*, 2013; Kotas *et al.*, 2004); while fishing effort would be relevant variable, it was not included in the models because the data available are fragmented in space and time and likely underestimated. To describe the probability of drift ashore, two health variables (carcass condition and presence of epibionts) and one oceanographic variable (significant wave height at the 20, 50, and 200 m isobaths) were used (since oceanic waves might be generated mostly by wind acting on the water surface for long periods, they can contribute to drift and here served as proxies of surface mass transportation, which is intensified when closer to the coast). Other factors that could affect drift or carcass buoyancy (see Hart *et al.*, 2006) were either unavailable (proximity of the carcass to strong currents, spatial proximity of mortality sources) or accounted for in our other models (e.g. body size, water temperature).

To evaluate the probability of sea turtles occurring in the study area, modelling was used to determine how the set of individual and oceanographic variables was related to stranding rates. The tested hypothesis is that sea turtle abundance increases with SST and chlorophyll-*a*, reflecting a correlation between occurrence and temperature/sea productivity (Table 1). To evaluate the probability of individual death, the set of health and anthropogenic interaction variables was modelled relative to the stranding rates. The overall hypothesis is that poor health conditions and signs of interaction with anthropic activities increase death probability (Table 1). To evaluate the probability of an individual to

**Table 1.** Summary of the candidate independent variables used in the five hypothesis-specific GLMMs to describe the dependent variable number of stranded green turtles (*Chelonia mydas*) per sampling unit (20 km band week<sup>-1</sup>).

Hypothesis-specific model	Hypothesized influence on stranding rates	Independent variables	Variable type (unit)	Variable description	Variable summary (mean ± SD)
Time	Seasonal variation	Season	Categorical	Four austral seasons	Spring, $n = 3\ 140$ Summer, $n = 1\ 894$ Fall, $n = 2\ 845$ Winter, $n = 3\ 414$ $-25.815 \pm 1.485$
Space	Heterogeneous distribution	Latitude	Continuous (degree)	Mean latitude within 20 km band	$-25.815 \pm 1.485$
Occurrence	Individual variation	Sex	Proportion	Females/male	$0.416 \pm 0.464$
		Body size	Continuous (cm)	Mean curved carapace length	$40.296 \pm 5.753$
		Development stage	Proportion	Juvenile/adult	$0.922 \pm 0.206$
	Positive influence of oceanographic conditions	Chlorophyll-a at 0–20 m isobath	Continuous (mg m <sup>-3</sup> )	Average/month/mesoregion	$3.663 \pm 2.411$
		Chlorophyll-a at 20–50 m isobath	Continuous (mg m <sup>-3</sup> )	Average/month/mesoregion	$1.465 \pm 1.467$
		Chlorophyll-a at 50–200 m isobath	Continuous (mg m <sup>-3</sup> )	Average/month/mesoregion	$0.643 \pm 0.910$
		Sea surface temperature at 0–20 m isobath	Continuous (°C)	Average/month/mesoregion	$22.211 \pm 2.906$
		Sea surface temperature at 20–50 m isobath	Continuous (°C)	Average/month/mesoregion	$22.054 \pm 2.877$
		Sea surface temperature at 50–200 m isobath	Continuous (°C)	Average/month/mesoregion	$22.478 \pm 2.522$
		Salinity at 0–20 m isobath	Continuous (PSU)	Average/month/mesoregion	$34.313 \pm 1.529$
Salinity at 20–50 m isobath	Continuous (PSU)	Average/month/mesoregion	$34.400 \pm 1.473$		
Salinity at 50–200 m isobath	Continuous (PSU)	Average per month per mesoregion	$35.378 \pm 1.028$		
Death	Negative influence of health conditions	Pathology	Proportion	Presence/absence	$0.085 \pm 0.193$
		Anthropic interaction	Proportion	Presence/absence	$0.010 \pm 0.214$
		Body condition	Proportion	Bad/good	$0.461 \pm 0.380$
Drift	Positive influence of carcass state	Decomposition	Ordinal (state)	Mean state of decomposition (1–5)	$3.499 \pm 0.838$
		Epibiont	Proportion	Presence/absence	$0.327 \pm 0.350$
	Positive influence of oceanographic conditions	Significant wave height at 0–20 m isobaths	Continuous (m)	Average/month/mesoregion	$1.978 \pm 0.522$
		Significant wave height at 20–50 m isobath	Continuous (m)	Average/month/mesoregion	$1.997 \pm 0.517$
		Significant wave height at 50–200 m isobath	Continuous (m)	Average/month/mesoregion	$2.010 \pm 0.506$

SD, standard deviation;  $n$  = sample size; PSU, practical salinity unit.

drift ashore, the relationship of stranding rates and the set of carcass condition and oceanographic variables were modelled. Wave height may reflect the intersection between wind and current directions and velocities, and the hypothesis tested is that higher waves could wash more and larger carcasses ashore (Table 1). The stranding incidence could also be influenced by the SST as it could accelerate carcass decomposition process, and severely decomposed animals may be more buoyant and drift longer distances (Santos *et al.*, 2018a, b). Live animals in poor health conditions may also have more epibionts due to lower levels of activity (slower swimming speeds). Finally, time dependence was considered by modelling the influence of seasons and considered space dependence by modelling the influence of latitude on weekly stranding rates (Table 1).

### Model construction

First, generalized additive models (GAMs; Zuur *et al.*, 2009; Wood, 2017) were fitted to the number of green turtles stranded,

under the hypothesis that stranding events vary between days and across latitudes. In the temporal GAM, the response variable was the number of turtle strandings per day and modelled as a smooth function (thin plate regression spline) of day; in the spatial GAM, the number of stranded turtles in a week was modelled as a smooth function of the mean latitude of the stranding events along 20 km intervals. This type of count data is usually slightly overdispersed, and to be conservative they were modelled using negative binomial distribution with log link functions (see the poor support for other distributions in Supplementary Table S4). Diagnostic plots were used to check for model validation (Supplementary Figures S5 and S6). For all the other species, a smoothing function was used to only visualize trends, if any, of stranding events over time and space. GAMs were compared to corresponding null models with only the intercept (Supplementary Table S5) using the Akaike information criterion (AIC; Burnham and Anderson, 2002).

In addition, generalized linear mixed models (GLMMs) were built to evaluate which descriptors of the three probability events

**Table 2.** Nested unifying spatiotemporal GLMMs describing the number of stranded green turtles (*Chelonia mydas*) per sampling unit (20 km band week<sup>-1</sup>) ranked by the lowest AICc.

Stranding component	Independent variable <sup>a</sup>	Unifying GLMM 1 <sup>b</sup>	Unifying GLMM 4	Unifying GLMM 3	Unifying GLMM 2	Null model
	Intercept	8.690	6.544	6.644	6.359	1.409
Time	Season	Positive	Positive	Positive	Positive	–
space	Latitude	0.247	0.238	0.246	0.242	–
Occurrence	Sex proportion	0.446	0.449	0.453	0.452	–
	Body size	–0.007	–0.006	–0.008	–0.008	–
	Chlorophyll-a (20–50 m)	–0.087	–0.047	–	–	–
	SST (20–50 m)	–0.024	–	–	0.008	–
	Salinity (20–50 m)	–0.035	–	–	–	–
Death	Body condition	0.135	0.141	0.127	0.128	–
	Pathology	–0.196	–0.210	–0.183	–0.186	–
Drift	Decomposition state	0.209	0.210	0.216	0.215	–
	Wave height (20–50 m)	0.135	0.169	0.214	0.215	–
DF		17	15	14	15	4
Log-likelihood		–5 562.390	–5 566.590	–5 575.720	–5 575.430	–5 749.970
AICc		11 159.000	11 163.400	11 179.600	11 181.100	11 508.000
ΔAICc		0.000	4.340	20.580	22.020	348.920
AICc weight		0.898	0.102	0.000	0.000	0.000

The number of stranding events within weeks and within mesoregions was set as random effects.

<sup>a</sup>The units of the variables are explained in Table 1.

<sup>b</sup>GLMMs were initially built with the selected variables from the hypothesis-specific GLMMs (Table 1) than reduced by dropping the least significant variables.

Each column gives the variables retained in the GLMM. Model formulae are found in Supplementary Table S9.

DF, degrees of freedom; ΔAICc, difference between the best-fitting model and a given model; AICc weight, conditional probability for each model.

better explained the incidence of stranded green turtles in time and space (Harrison *et al.*, 2018). Due to the broad set of predictors (22), the modelling approach was incremental, that is, by starting with models with only additive effects and then building more complex models. This way, the stranding events were modelled considering each component of the stranding probability separately to test specific hypotheses related to the influence of occurrence in the area, death, and drift descriptors on the stranding probability (Table 1). The significant variables in these models were then used to build unifying spatiotemporal models (Table 2).

In all GLMMs, the dependent variable was the number of green turtle stranding events per sampling unit of 20 km band week<sup>-1</sup>, again using negative binomial distribution (with log link function) to be conservative and account for the slightly overdispersion of the count data (Supplementary Table S6). As for the independent variables (fixed effects), all binary variables (presence/absence of pathologies, anthropic interactions, epibionts) and categorical independent variables (classes of sex, development stage, and body condition) were transformed in proportions of incidence of the most common class per sampling unit. For all continuous variables, the average value per sampling unit was considered, while for the oceanographic variables, the average monthly values per mesoregion was used (Table 1). Prior to building the models, potential collinearity among independent variables was examined using Pearson correlations (e.g. Begger and Possingham, 2008) and considered  $r < 0.60$  a cut-off for keeping the variable with greater ecological importance in the analysis.

Despite a study design prioritizing a uniform sampling across the entire study area, there could be variations in sampling effort. To account for the possibility that the temporal and spatial variation in stranding incidence along the study period and area could result from any variation in sampling effort, all models were built

using the week of the year and the mesoregion as temporal and spatial random effects, respectively (Bolker *et al.*, 2009). To evaluate whether there was any spatiotemporal bias in the data, they were controlled for the number of stranding events within weeks (the temporal sampling unit) and within mesoregion. This approach accounted for the possible variations in sampling due to different survey teams working in different areas and weather conditions, as well as for the stranding events coming from the areas of difficult access (21% of the sampling area, yielding 23% of the stranded sea turtles).

### Model selection

The modelling was started building the full GLMMs for each hypothesis (Table 1) and used a backward stepwise procedure, dropping one independent variable at a time and computing changes in the AIC (Zuur *et al.*, 2007). The variance inflation factor (VIF) was calculated to ensure that predictors in the full models were not correlated to each other (low multicollinearity indicated by  $VIF < 3$ ; Zuur *et al.*, 2010). The significant variables from each hypothesis-specific GLMM were then used to build a final unifying spatiotemporal model. To evaluate whether less complex, nested models could provide better fit to the observed data, the full unifying spatiotemporal GLMM was then subjected to the same variable selection described previously. To select the most parsimonious models, both among the hypothesis-specific and unifying models, the nested models were ranked by the lowest AIC and evaluated their relative likelihoods using AIC weights (Burnham and Anderson, 2002, Johnson and Omland, 2004). As a benchmark, a null model was considered with only the intercept. When the level of support for the models (ΔAIC) was  $< 2$ , the model with the highest AIC weight was considered the most probable model to explain data variation (Burnham and Anderson, 2002).

## Model validation

To validate the selected model, the plots of residuals against fitted data (which represents the stochastic component of the model) and deviance residuals against predicted data were visually inspected. When the residuals were neither consistently over nor under the  $x$ -axis, the model was considered appropriate for the data. The Normal Q–Q plots were inspected, which evaluates the stochastic component of the model, given that deviance residuals are approximately normally distributed (Supplementary Figure S7). When the bulk of the observations fell along the Q–Q line, the chosen distribution was considered appropriate for the data. Simulations of the residuals were also performed to test for overdispersion and for spatial and temporal autocorrelation of the data (Hartig, 2018) using Moran's I test and Durbin–Watson test, respectively (Supplementary Figure S8). To measure the proportion of variation accounted by the predictors (fixed effects) of the chosen unifying spatiotemporal model, that is how close the model was to achieving the closest fit, a marginal  $R^2$  was calculated (Nakagawa and Schielzeth, 2013). Finally, the marginal  $R^2$  was compared to the conditional  $R^2$  to evaluate the influence of the random effects (week and mesoregion) in explaining the stranding events, attempting to isolate such potential spatial and temporal bias from the effects of the independent variables (Nakagawa and Schielzeth, 2013). All analyses were performed on the R environment, version 3.2.4 (R Core Team, 2018).

## Data availability

All stranding data are part of the open SIMBA database (Sistema de Informação de Monitoramento da Biota Aquática), which can be accessed at <https://segurogis.petrobras.com.br/simba/web/>. The formatted dataset used here and all R codes to replicate models are available upon request.

## Results

During 732 sampling days between 24 August 2015 and 24 August 2017, the survey teams carried out a total of 94 681 surveys (85 993 in land; 8688 by boat) along the eight mesoregions, covering a total of 1 468 200 km. Despite variation in weather conditions, the sampling effort was similar between years (August 2015–August 2016 = 49 730; September 2016–August 2017 = 44 951 surveys) and among months (ratio km/survey: mean = 6.79, median = 6.72, range = 4.67–10.30). The field teams recovered a total of 12 571 stranded sea turtles (stranding per unit of effort = 0.007 stranding  $\text{km}^{-1}$ ), with 94.6% of them being found on regularly monitored beaches (daily and weekly). Most animals were found in sandy beaches (91.4%,  $n = 11 488$ ) during good weather conditions (80.3%) with weak winds (mean wind intensity =  $1.43 \text{ km h}^{-1} \pm 1.19 \text{ SD}$ ).

Stranded sea turtles were mostly found dead (90.6%) and in intermediate to advanced decomposition state (code 2 = 6.4%; code 3 = 19.1%; code 4 = 50.9%; code 5 = 14.2%). The advanced decomposition prevented the species identification of 2.7% of the carcasses ( $n = 341$ ). Green turtles accounted for 90.4% of the stranding events in which the species were identified (green  $n = 11 362$ , loggerhead  $n = 659$ ; olive ridley  $n = 92$ ; hawksbill  $n = 66$ ; leatherback  $n = 51$ ).

Considering all species, sex could be determined in 29% of the cases ( $n = 3620$ ), out of which 77% were females and 23% were males. The development stages were determined in 92% of the cases, mostly represented by green turtles (Supplementary Figures

S1 and S2; Supplementary Table S3): juveniles were much more common (96.3%) than adults (3.4%) and hatchlings (0.3%). Regarding health descriptors, the overall body condition could be determined in 74% of the cases ( $n = 9254$ ), the majority in poor conditions (65.7%). Amputated limbs were recorded for 6.9% of 10 947 evaluated individuals; pathologies were identified in 11.3% among 8759 examined individuals during necropsy (macroscopic analysis); and evident signs of anthropic interactions were found in 14.1% of 9020 individuals. Among these, signs of collision with vessels or dredging operations were found in 378 (3.0%) individuals (evidence code ranging from 1 to 3, mean =  $2.29 \pm 0.85 \text{ SD}$ ); entanglement in fishing gear was recorded for 1488 (11.8%) individuals (mean =  $2.54 \pm 0.70 \text{ SD}$ ); external signs of ingestion of plastic debris were recorded for 798 (6.3%) individuals (mean =  $2.80 \pm 0.52 \text{ SD}$ ); and 40% of the individuals had epibionts on the body surface.

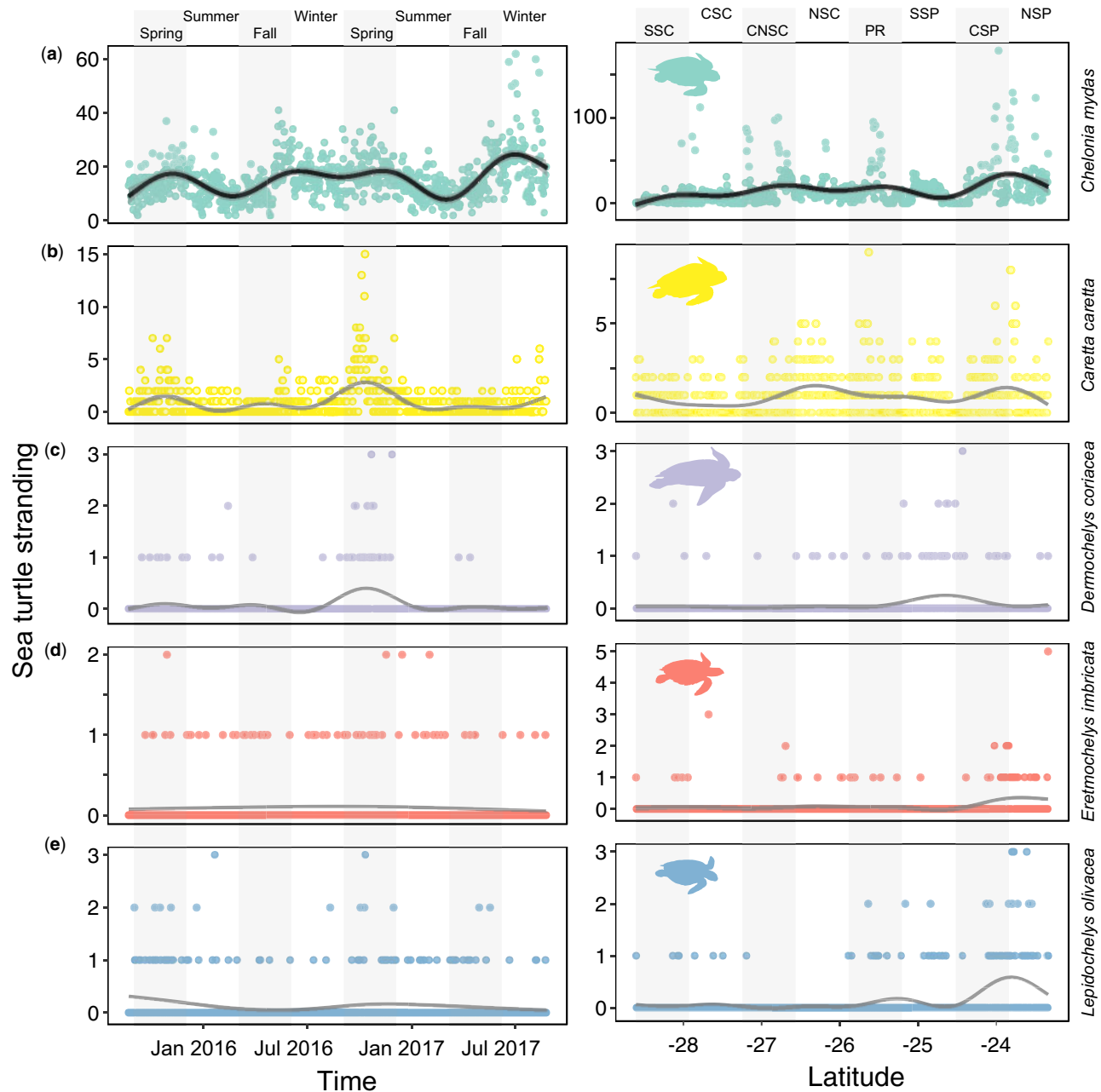
## Spatiotemporal stranding patterns

Stranding events of each sea turtle species were not evenly distributed throughout the study period and study area (Figures 1 and 2; see also additional maps as Supplementary Figures S9–S15). Green turtles stranding varied seasonally, with generally lower incidence in the austral summer than in the winter—there was a significant non-linear effect of time and space in their number of stranding events (Supplementary Figure S10). Smoothing curves (Figure 2a) showed the number of green turtle stranding incidence increased in the last winter (adjusted  $R^2 = 0.289$ , deviance explained = 31.8%,  $p < 0.001$ ), and that there was a high number of stranding events towards the north of the surveyed area (adjusted  $R^2 = 0.153$ , deviance explained = 19.3%,  $p < 0.001$ ). The number of loggerhead turtle stranding events oscillated over time and space, although less markedly (Figure 2b, Supplementary S11); there were some increase in stranding events between 2016 and 2017 and a slight variation across latitudes. For the other three species, there were no clear temporal or spatial trends (Figure 2c–e), likely due to the few stranding events (Supplementary Figures S12–S15).

In terms of body size, the distributions of green and loggerhead turtles were similar across seasons and along the latitude range (Figure 3a and b). The individuals recorded across seasons and latitudes showed similar ranges of body sizes. While only juvenile green turtles were recorded, adult and juvenile loggerheads were observed during all seasons and mesoregions. The spatiotemporal occurrence of leatherback turtles differed from the other species (Figure 3c). Stranding events of both juveniles and adults were rare but appeared seasonal, with increased incidence during winter and spring, and more frequent at latitude 25° S. Finally, hawksbill and olive ridley turtles (Figure 3d and e) also occurred in the entire area along all seasons, varying both the average and range of body size across seasons and latitudes. All stranded hawksbill turtles were juveniles; there was a slight tendency for smaller animals to strand in winter and a slight tendency for animals of a wider range of body sizes to strand in spring. Seasonal variation was also observed for the olive ridley turtle, with larger animals being more common during the fall. The occurrence of both species was more common in the northern areas and with a greater size range.

## Stranded green turtles: occurrence, death, and drift

For green turtles, all the hypothesis-specific GLMMs were more parsimonious than the null model (Supplementary Tables S7 and S8), indicating the effects of time, space, and the descriptors of



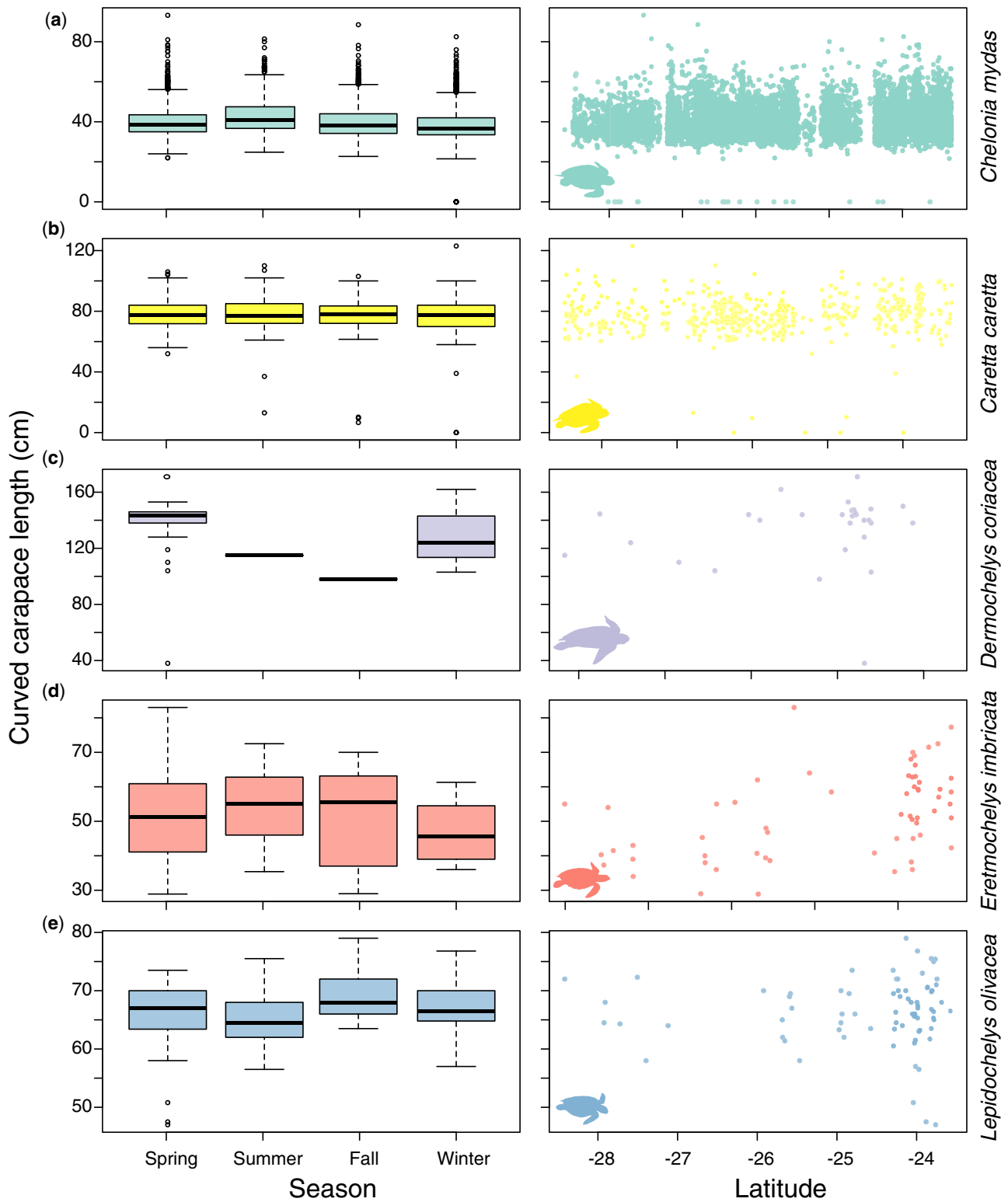
**Figure 2.** Stranding incidence of five species of sea turtles in the southern Brazilian coast over time and space: daily stranding events during the entire study period (August 2015–August 2017) and along the entire study area ( $-28.60^{\circ}\text{S}$  to  $-23.33^{\circ}\text{S}$ ) per  $0.01^{\circ}$  of latitude. (a) green turtles (*Chelonia mydas*), (b) loggerhead turtles (*Caretta caretta*), (c) leatherback turtles (*Dermochelys coriacea*), (d) hawksbill turtles (*Eretmochelys imbricata*), and (e) olive ridley turtles (*Lepidochelys olivacea*) (icons from phylopic.org). In (a), the black lines and accompanying grey shades (a) represent fit and confidence intervals of GAMs (Supplementary Table S5); in (b)–(e), the grey lines represent a smoothing function to visualize suggesting trends. Vertical stripes indicate austral seasons and sampling mesoregions. NSP, north coast of São Paulo; CSP, central coast of São Paulo; SSP, south of São Paulo; PR, Paraná coast; NSC, north of Santa Catarina; SSC, south of Santa Catarina.

occurrence, death, and drift in the stranding incidence of green turtles. From these GLMMs, unifying models were built (Table 2, Supplementary Figure S9).

The most parsimonious unifying model (GLMM1) suggested that the incidence of green turtle stranding was related to season, latitude, and descriptors of individual traits, death, and drift (Table 2). The combined explanatory power of all these fixed terms accounted for 33% (marginal  $R^2$ ) of the incidence of green

turtle stranding, reaching 41% when considering both fixed and random effects (conditional  $R^2$ , Table 3). This 8% increase indicated that the data variation did not have a major bias from spatial (mesoregion) or temporal (weekly) sampling effort. There was no overdispersion of the data (nonparametric dispersion test via  $SD$  of residuals fitted vs. simulated: ratio observed/simulated = 1.045,  $p = 0.552$ ), neither there was spatial (Moran's  $I$  test, observed = 0.0020, expected =  $-0.0004$ ,  $SD = 0.0011$ ,  $p = 0.0323$ )





**Figure 3.** Body size distribution of stranded sea turtles in the southern Brazilian coast over time (austral seasons) and space (latitude). (a) Green turtles (*Chelonia mydas*), (b) loggerhead turtles (*Caretta caretta*), (c) leatherback turtles (*Dermochelys coriacea*), (d) hawksbill turtles (*Eretmochelys imbricata*), and (e) olive ridley turtles (*Lepidochelys olivacea*). Icons from phylopic.org. Blank spaces along the latitude plots represent the few gaps in the monitored area.

**Table 3.** Summary of selected unifying spatiotemporal GLMM1 (Table 2) describing the number of stranded green turtles (*Chelonia mydas*) per sampling unit (20 km band week<sup>-1</sup>), in which marginal  $R^2 = 0.3342$ , conditional  $R^2 = 0.4177$ , temporal random effect (week) variance =  $0.0242 \pm 0.156$  SD, and spatial random effect (mesoregion) variance =  $0.0409 \pm 0.202$  SD.

Stranding component	Independent variables (fixed effects) <sup>a</sup>	Parameter estimate	Standard error	Z-value	p-value
Time	Fall	8.6813	1.4558	5.963	<0.0001 <sup>b</sup>
	Spring	8.6815	1.4419	6.021	<0.0001 <sup>b</sup>
	Summer	8.4845	1.4572	5.822	<0.0001 <sup>b</sup>
	Winter	8.8583	1.4461	6.126	<0.0001 <sup>b</sup>
Space	Latitude	0.2468	0.0471	5.241	<0.0001 <sup>b</sup>
Occurrence	Sex proportion	0.4459	0.0345	12.94	<0.0001 <sup>b</sup>
	Body size	-0.0066	0.003	-2.17	0.0300 <sup>b</sup>
	Chlorophyll-a (20–50 km)	-0.0865	0.0178	-4.863	<0.0001 <sup>b</sup>
	Sea surface temperature (20–50 km)	-0.0238	0.0132	-1.8	0.0719
	Salinity (20–50 km)	-0.0346	0.0179	-1.933	0.0533
Death	Body condition	0.1344	0.0478	2.811	0.0050 <sup>b</sup>
	Pathology	-0.1957	0.0898	-2.181	0.0292 <sup>b</sup>
Drift	Decomposition state	0.2088	0.023	9.082	<0.0001 <sup>b</sup>
	Wave height (20–50 km)	0.1351	0.0414	3.268	0.0011 <sup>b</sup>

<sup>a</sup>The units of the variables are explained in Table 1.

<sup>b</sup>Statistical significance at  $\alpha = 0.05$ .

SD, standard deviation.

or temporal autocorrelation of the stranding data (Durbin–Watson test,  $DW = 1.7027$ ,  $p < 0.0001$ ) in the selected unifying model (Supplementary Figures S7 and S8).

The best-fitting unifying spatiotemporal model suggested a seasonal variation in green turtle stranding (Table 3, Figure 4a), with lower incidence in the austral summer in comparison to winter (Tukey Contrasts, winter–summer = 0.374,  $SD = 0.119$ ,  $Z = 3.145$ ,  $p = 0.0099$ ; the differences among all other seasons were not significant, Supplementary Tables S8 and S10). The model revealed a spatial variation in stranding incidence (Table 3; Figure 4b), indicating higher stranding incidence northward.

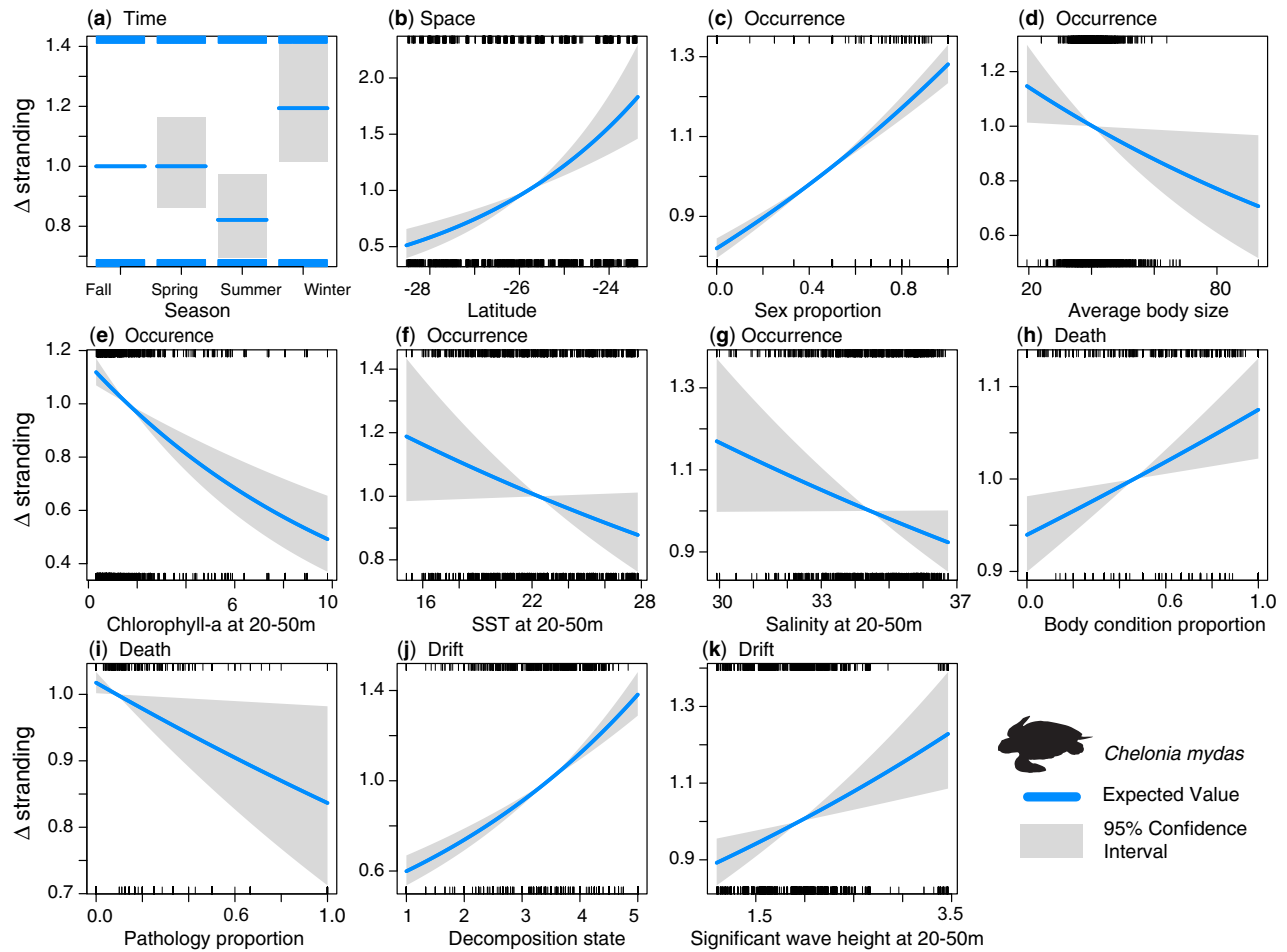
There was also influence of five descriptors of green turtle occurrence in the area: sex, body size, chlorophyll-*a* concentration, SST, and salinity at the 20–50 m isobaths (Table 3). Sex proportion had a positive effect on the stranding incidence (Figure 4c), likely due to the high proportion of females in our data (however, it remains unknown whether this proportion reflects the population sex ratio, or whether females tend to washed ashore more than males). All the other occurrence descriptors showed negative effects (Figure 4d–g); they suggested that the stranding incidence is higher for smaller individuals in waters with lower chlorophyll-*a* concentration, temperature, and salinity. Two descriptors of death probability influenced stranding (Table 3): there were a positive effect of body condition (proportion of good/bad condition; Figure 4h) and a negative effect of evidence of pathologies (proportion of presence/absence; Figure 4i). Taken together, these findings suggested that stranding incidence was more common for individuals of green turtle in poor health conditions but with lower incidence of macroscopic pathologies (N.B.: microscopic pathologies were not assessed and most of the animals were recorded in an advanced decomposition state). Finally, two descriptors of drift probability showed positive effects on stranding incidence (Table 3): the decomposition state of the carcass and the significant wave height at the 20–50 m isobaths (Figure 4j and k). A sensitivity analyses showed that all these trends were consistent with stranding incidence evaluated at finer (5 km week<sup>-1</sup>) and grosser (40 km month<sup>-1</sup>) spatiotemporal scales (Supplementary Figures S3 and S4).

## Discussion

We report a high incidence of stranded sea turtles within a relatively small area in the southwestern Atlantic Ocean during a short, 2-year period. This intensive field study not only sheds light onto the spatiotemporal occurrence and life-history of juvenile and adult sea turtles in an otherwise understudied area but also provides evidence for high mortality rates across RMUs (see Wallace *et al.*, 2010). The southwestern Atlantic waters provide important foraging grounds and migratory corridors for five sea turtle species (Almeida *et al.*, 2011; Santos *et al.*, 2011; González-Carman *et al.*, 2012a; Barceló *et al.*, 2013; Santos *et al.*, 2019; López-Mendilaharsu *et al.*, 2020). However, the same area also includes hotspots of multiple, cumulative threats for sea turtles (Fuentes *et al.*, 2020). Quantifying baseline stranding rates can inform the much-needed local and international conservation efforts (Hamann *et al.*, 2010), particularly for juvenile sea turtles (Wildermann *et al.*, 2018).

### Sea turtle occurrence in the southwestern Atlantic

Our findings reinforce that the southwestern Atlantic waters are used by five sea turtle species throughout the year (Marcovaldi and Marcovaldi, 1999; Santos *et al.*, 2011; Tagliolatto *et al.*, 2020), highlighting the relevance of the regional management units. Most sea turtle species occurred in more than one life stage, but the predominance of juvenile green turtles strengthens the results from few satellite-tagged individuals indicating that juveniles use, migrate through, and forage over more broadly the southwestern Atlantic (e.g. Almeida *et al.*, 2011; González-Carman *et al.*, 2012a; Santos *et al.*, 2019; Fuentes *et al.*, 2020). In our study, sea turtles were found slightly concentrated in some latitudes and times of the year, likely reflecting combination of biological factors (e.g. life stage, behavioural states) with variation in habitat quality in terms of resources and risks across space and time. While higher stranding incidence at a given location can be related to oceanographic and meteorological factors funnelling carcass drift, it is also plausible that the high number of stranded sea turtles can be associated with high and cumulative exposure to anthropogenic



**Figure 4.** Summary of the effects of predictors (fixed effects) on the weekly stranding of green turtles *Chelonia mydas* per 20 km latitude band as given by selected unifying spatiotemporal GLMM (Table 3), organized by components of the stranding probability (time, space, occurrence, death, drift). (a) Austral seasons, (b) latitude (degree), (c) sex (proportion of female/male), (d) body size (average curved carapace length, m), (e) average chlorophyll-a concentration ( $\text{mg m}^{-3}$ ) at the 20–50 km isobaths, (f) average sea surface temperature ( $^{\circ}\text{C}$ ) at the 20–50 km isobaths, (g) average salinity (practical salinity units) at the 20–50 km isobaths, (h) body condition (proportion bad/good), (i) pathology (proportion presence/absence), (j) decomposition state (mean decomposition code), (k) average Significant wave height (m) at the 20–50 km isobaths. Each variable is detailed in Table 1. The plots show the model parameters on the scale of the original variables by using the inverse link function; the x-axes show the effect on the expected value of the response variable (stranding) by moving the independent variable away from a reference point on the x-axis (i.e. the mean).

threats within the regional management units (Fuentes *et al.*, 2020; López-Mendilaharsu *et al.*, 2020).

Loggerhead turtles were the second-most frequent stranded species. Most of the stranded individuals were late juveniles and adults, and slightly more frequent during austral spring. For the olive ridley turtles, the strandings were considerably less frequent and distributed homogeneously throughout the year. These findings were in line with previous studies that used satellite tags to reveal how juveniles and adults of these two species use coastal waters and the continental shelf and slope of the southwestern Atlantic (Reis *et al.*, 2010; Barceló *et al.*, 2013; Santos *et al.*, 2019; López-Mendilaharsu *et al.*, 2020). Finally, stranding events of both hawksbill and leatherback turtles were rarer than all other species, with no apparent seasonal variation; this was different to results from Rio de Janeiro State just north of our study area (Tagliolatto *et al.*, 2020). The less frequent occurrence of these two species in our study area could be related to the wide-ranging

habits of these species. Hawksbill turtles are more distributed in tropical and temperate zones (e.g. Bowen *et al.*, 2006), and in our monitoring, only juveniles at the extremes of the study area were recorded. Leatherback turtles move over very large areas, and individuals from different stocks can mix in the southwestern Atlantic (see Vargas *et al.*, 2008; Colman *et al.*, 2019). For instance, they have been recorded between feeding grounds at the La Plata river (Argentina) to breeding grounds in the Gabon and southeastern Brazilian coasts (Billes *et al.*, 2006; López-Mendilaharsu *et al.*, 2009).

### Sea turtle mortality

Our 2-year beach monitoring shows that the mortality of sea turtles in the southwestern Atlantic Ocean is very high. Previous studies in this region have recorded considerably less stranding records—in the order of tens (e.g. Poli *et al.*, 2014), hundreds

(e.g. Monteiro *et al.*, 2016; Vélez-Rubio *et al.*, 2013), or few thousands of animals per year (Tagliolatto *et al.*, 2020)—but never close to the numbers we report here: over 6000 turtles per year, nearly 7 individuals stranded per kilometre. The beach monitoring effort in some of these previous studies was not daily, suggesting that such larger sampling intervals could have underestimated turtle mortality.

Assessing sea turtle mortality and health can also inform about the quality of the marine ecosystems more broadly, given that their health can be associated with immunosuppression resulting from habitat degradation (Domiciano *et al.*, 2017). Determining the precise *causa mortis* in stranded sea turtles can be complicated by the carcass drift time and decomposition state (Hart *et al.*, 2006; Peltier *et al.*, 2013), but in our study a considerable number of stranded cases (25.5%) were suggestive of the death causes—plastic ingestion, entanglement in fishing gears, boat collision, chronic illness, and other diseases. Nearly half of the animals were found stranded in poor body or health conditions (48.4%), many of which not easily associated with human interactions (22.9%) suggesting death of natural causes. The low percentage of stranded animals with pathologies (at least in macroscopic analyses) could be masked by the advanced decomposition stage of the carcasses—in most cases, hampering a thorough necropsic evaluation that could otherwise reveal subtler lesions in soft tissue.

Mortality was particularly high for juvenile green turtles. Green turtles are considered endangered worldwide (IUCN, 2019). Although regionally the IUCN specialist group proposed that the species may be reclassified as “least concern”, our study presents one of the highest numbers of green turtle mortality and stranding reported in such a short period (only 2 years) in the world (e.g. Vélez-Rubio *et al.*, 2013; Seminoff *et al.*, 2015; Monteiro *et al.*, 2016; Tagliolatto *et al.*, 2020). Considering that stranding data only reveal about 5–20% of the actual mortality (e.g. Epperly *et al.*, 1996; Hart *et al.*, 2006; Peltier *et al.*, 2012; Koch *et al.*, 2013), it is tempting to speculate about the rapid, massive removal of green turtle juveniles in the southwestern Atlantic. This feeding ground comprises a mixed-genetic stock from multiple origins such as Ascension Island, Caribbean, African, and Brazilian coasts (e.g. Naro-Maciel *et al.*, 2012; Proietti *et al.*, 2012; Prosdocimi *et al.*, 2012; Coelho *et al.*, 2018), where reproductive stocks are apparently stable (e.g. Wallace *et al.*, 2010, 2011; Santos *et al.*, 2011; IUCN, 2019), but within a global population that is in decline (Seminoff, 2004). Considering the long-life cycle of sea turtles, a large-scale mortality of juveniles can feedback into lower nesting rates that would have negative impacts on the conservation status green turtles in 10–20 years (see Hamann *et al.*, 2010; Wildermann *et al.*, 2018).

Our data also point a considerable mortality of loggerhead turtles in the southwestern Atlantic Ocean, which—although lower in absolute numbers than green turtles—involved both late juveniles and reproductive adults. Due to their direct contributions to recruitment, population that loses disproportionately more often adults and subadults may take longer than, or not recover as well as, populations losing only juveniles (see also Wallace *et al.*, 2008; Bolten *et al.*, 2011). In the southwestern Atlantic, fisheries bycatch is a major cause of mortality for loggerhead turtles. Immature loggerheads in oceanic waters are threatened by pelagic longline fisheries (e.g. Pons *et al.*, 2010; Barceló *et al.*, 2013), while for neritic juveniles and adults, the highest impact is caused by trawl fisheries (López-Mendilaharsu *et al.*, 2020). Considering that

most of the loggerhead turtles in southern and southeastern Brazil come from the northeastern Brazilian rookeries (Shamblin *et al.*, 2014), our findings highlight the importance of integrating conservation approaches over large areas, so the efforts in reproductive areas are not offset by intense mortality in the feeding areas.

In general, the sea turtles in the southwestern Atlantic Ocean are exposed to several threats (e.g. Bugoni *et al.*, 2001; Kotas *et al.*, 2004; Sales *et al.*, 2008; Pons *et al.*, 2010; Goldberg *et al.*, 2015; Monteiro *et al.*, 2016; Wildermann *et al.*, 2018; Fuentes *et al.*, 2020; López-Mendilaharsu *et al.*, 2020). Absolute mortalities have not been effectively estimated for most species (and life stages), and only few studies consider the cumulative or synergistic effects of multiple threats (Monteiro *et al.*, 2016; Silva *et al.*, 2017; Fuentes *et al.*, 2020; López-Mendilaharsu *et al.*, 2020). Our study corroborates the convenience of using stranding events as proxies for the occurrence of animals that are hard to observe and track over large spatiotemporal scales (e.g. ten Doeschate *et al.*, 2018; Tagliolatto *et al.*, 2020). The accumulation of stranding data allows for the investigation of trends and inference on baseline stranding rates.

Given the large number of stranded animals recorded, our study provides an initial mapping of critical areas in the southern Atlantic Ocean that could be integrated with the threat hotspots identified for green turtles (Fuentes *et al.*, 2020) and the other species (e.g. Sales *et al.*, 2008; López-Mendilaharsu *et al.*, 2020). Still, despite the intensive fieldwork, it is likely that many individuals have not been recorded for not being washed ashore. While stranding records are highly informative for revealing threats faced by the turtles in oceanic and coastal waters through the evaluation of primary causes of injury, illness, and death, stranding data have limitations. The number of animals washed ashore represents the minimum mortality; thus, it likely underestimates the population mortality rates and the extent of anthropogenic disturbance offshore (Epperly *et al.*, 1996; Monteiro *et al.*, 2016). Marine habitat disturbance tends to intensify and ecosystem quality to decrease; the future picture may be more alarming than currently perceived. Our findings echo the urgency for effective conservation actions—including strategic marine spatial planning, community engagement, and government aid—to mitigate anthropogenic impacts and to reduce risks for sea turtle populations in southern Atlantic Ocean (see Wallace *et al.*, 2011; Wildermann *et al.*, 2018).

### Closing remarks

Sea turtles are indicators of environmental quality (Domiciano *et al.*, 2017; Gaus *et al.*, 2019). Developing baseline information on endangered species that are migratory, threatened, and protected by various national and international laws and conventions is an international priority for conservation. Our systematic monitoring relies on very high sampling effort that yields comprehensive data on the occurrence of sea turtles along a relatively understudied area. The simultaneous beach monitoring over >1000 km for two full years produces a reliable snapshot of the use of southwestern Atlantic Ocean by five species of sea turtles, validating suggestive results from satellite tagging of few individual sea turtles within this area (e.g. Almeida *et al.*, 2011; González-Carman *et al.*, 2012a; Barceló *et al.*, 2013; Vélez-Rubio *et al.*, 2018; Santos *et al.*, 2019; Fuentes *et al.*, 2020). Such threatened species are involved in national and international

conservation plans, but they specifically depend on actions in developing countries that face many difficulties of management and mitigation of anthropogenic impacts.

For migratory species, it is necessary to identify the core habitats and the exposure to multiple threats to support the most effective conservation efforts (Shaver *et al.*, 2013). Such efforts are difficult to implement for sea turtles in the southwestern Atlantic Ocean because it is used by animals of different origin and life stages that depend on various environmental conditions and habitats for feeding and reproducing. These characteristics are likely to require the mitigation of threats at multiple levels and geographic scales (Bolten *et al.*, 2011; Fuentes *et al.*, 2015; Fuentes *et al.*, 2020). Despite its inherent limitations, beach monitoring, especially if maintained over long spatiotemporal scales, can generate large volumes of ecological and health data on the elusive sea turtle species—an invaluable tool to support conservation policies and decision-making.

### Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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