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Dissertação de Mestrado

**Loggerhead and green turtle population dynamics in the
western South Atlantic: insights from stranding patterns**

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Porto Alegre, abril de 2019

**Loggerhead and green turtle population dynamics in the western South
Atlantic: insights from stranding patterns**

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*“Às vezes me sinto um E.T.
Ao descrever a existência humana
Mas sei que sou muito humano
Quando eu me sinto só*

*E isso tudo sem perceber
O quanto a mente se engana
Me lembro de me sentir bicho
Quando sinto em mim o sol”*

pedroluz

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Resumo

Populações de tartaruga-cabeçuda (*Caretta caretta*) e de tartaruga-verde (*Chelonia mydas*) declinaram ao longo do tempo devido ao impacto de atividades humanas. Medidas de conservação foram tomadas em diversos países e, enquanto algumas populações mostram sinais de recuperação, outras continuam a declinar. Na costa do estado do Rio Grande do Sul, no sul do Brasil, que é usada como área de alimentação por tartarugas-cabeçudas e verdes, foi observado um aumento na quantidade de encalhes dessas duas espécies entre 1995 e 2014. Estudos anteriores reportam o crescimento populacional graças à proteção das praias de desova, bem como o aumento da mortalidade por atividades pesqueiras como possíveis explicações para este aumento na quantidade de encalhes de tartarugas-cabeçuda e verde. Nossos objetivos foram testar quais preditores tiveram um maior efeito sobre os encalhes de tartaruga-cabeçuda e verde, e analisar variações no tamanho corporal como reflexo da dinâmica dessas populações. Nós usamos modelos lineares generalizados (GLM) para modelar os padrões de encalhe e modelos lineares (LM) para modelar os comprimentos curvilíneos de carapaça (CCL) em relação à variáveis preditoras. A quantidade de encalhes das duas espécies aumentou enquanto o tamanho corporal diminuiu ao longo do tempo. Vento e temperatura foram as variáveis com maior influência sobre a quantidade de encalhes. Encontramos evidência de que crescimento populacional e ingestão de debris estão causando o aumento nos encalhes de tartaruga-verde, enquanto a captura acidental pela pesca parece ser a principal causa por trás do aumento nos encalhes de tartaruga-cabeçuda. Apresentamos evidências do aumento da mortalidade de juvenis que considerando o longo ciclo de vida das tartarugas-marinhas, pode levar décadas para ter um efeito em áreas reprodutivas e portanto deve ser considerado em futuras avaliações populacionais e de estado de conservação.

Palavras-chave: *tartaruga-cabeçuda, tartaruga-verde, ecologia populacional, encalhes, conservação.*

Abstract

Loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) populations have declined over time due to anthropogenic activities. Conservation measures have been taken in several countries and while some populations show signs of recovery, others continue to decline. The coast of the State of Rio Grande do Sul (RSC), in southern Brazil, is used as foraging ground by loggerhead and green turtles, where an increase in strandings of these two species has been observed between 1995 and 2014. Previous studies reported population growth resulting from nest protection as well as increased mortality from fisheries as possible explanations for the increase in loggerhead and green turtle strandings. Our objectives were to test which predictors had a greater effect over loggerhead and green turtle strandings and to analyze variations in body size reflecting these populations' dynamics. We used generalized linear models (GLM) to model number of strandings and linear models (LM) to model turtles' body size in response to predictors. Strandings for both species generally increased and body size decreased throughout time. Wind and temperature were the variables with greater influence over loggerhead and green turtle strandings. We found evidence that population growth and debris ingestion are causing green turtle strandings to increase, while bycatch from fisheries seems to be the main cause behind loggerhead turtle strandings increase. We present evidence of increasing juvenile mortality, which may take decades to have an effect on reproductive areas, considering sea turtles' long-life cycles, and thus should be considered on future population assessments and statuses reviews.

Keywords: *loggerhead turtle, green turtle, population ecology, strandings, conservation.*

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Introduction

Loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) populations have declined due to human exploitation (Conant et al. 2009; Seminoff et al. 2015). Indeed, marine animals have been an important resource for humans for millennia, but with the development of industrial fishing by the end of the 18th century, the exploration of marine resources greatly increased in scale and consequently so did its negative impacts on wildlife (Pitcher and Lam 2014). Several commercial and non-commercial marine species have declined due to exploration and bycatch, some almost to extinction such as cods (Myers et al. 1997), groupers (Sadovy de Mitcheson et al. 2013), and tunas (Safina and Klinger 2008). Life history traits such as large body mass, slow growth and high age at maturity make some species particularly vulnerable and less likely to recover from overexploitation (Denney et al. 2002; Hultchings and Baum 2005). Besides direct exploitation, bycatch in fisheries also affects species on the slow-end of the life history spectrum, including invertebrates (e.g. king crab *Lithodes santolla*, Varisco et al. 2017), fish (e.g. Pacific halibut *Hippoglossus stenolepis*, Kaimmer and Trumble 1998; sharks, rays and chimaeras, Stevens 2000), marine mammals (e.g. cetaceans and pinnipeds, Read et al. 2006), birds (e.g. albatrosses, petrels and shearwaters, Anderson et al. 2011) and all seven species of sea turtles (Lewison et al. 2004b).

Management policies have been widely discussed over the past century to mitigate the negative impacts of fisheries on populations and ecosystems as a whole (Jennings and Kaiser 1998). However, human global population continues to grow and fishing trade is currently widely globalized, with the increasing demand for seafood from three major markets – the EU, Japan and USA – pressing for ever higher fishing efforts (Swartz et al. 2010; Anticamara et al. 2011). Continued heavy fishing will necessarily limit population recoveries of threatened marine species (Myers et al. 1995).

A paradigmatic example of overexploitation and conservation refers to the great whales, whose populations were greatly reduced due to whaling, even to the point of extinction (i.e. Atlantic population of gray whales *Eschrichtius robustus*).

And yet, as result of conservation efforts, populations of some species show clear signs of recovery, although others remain threatened (Perry 1999). On the other hand, all sea turtle species, with the exception of the data-deficient flatback turtle (*Natator depressus*), are still classified as threatened (IUCN 2018), but, like for whales, efforts towards sea turtle conservation and research increased over time (Hamann et al. 2010). Studies relying on long-term surveys of nesting beaches reported growing numbers of nests and nesting females, especially of green turtles, presumably due to intensive monitoring, associated with greater protection from poachers (Balazs and Chaloupka 2004; Troëng and Rankin 2005; Richardson et al. 2006; Weber et al. 2014).

Other turtle species however, such as the leatherback (*Dermochelys coriacea*) and loggerhead turtles, showed population declines or presented steady numbers of nests and nesting females, despite intensive nest protection (Reina 2000; Witherington et al. 2009; Nel et al. 2013). It has been argued that focusing conservation efforts towards at-sea strategies, primarily by reducing fisheries impact, would be far more effective than protecting nesting beaches (Crowder et al. 1994; Crouse and Crowder 2013). Considering the ongoing increase of at-sea threats, such as fisheries bycatch (Lewison et al. 2004b; Lewison and Crowder 2007; Anticamara et al. 2011), and anthropogenic debris ingestion (Nelms et al. 2016) it is important to question whether current conservation strategies, often focusing on nesting beach protection, are well-suited for achieving long-term population recovery of sea turtles.

While sea turtle aggregations in foraging grounds usually mix individuals from various rookeries, sea turtles have a strong tendency to reproduce on the same area where they hatched, a phenomenon known as natal homing or philopatry (Bowen and Karl 2007). It follows that populations are structured around reproductive areas, and population assessments were usually based on data from nesting beaches (Seminoff and Shanker 2008). Even though nesting beach monitoring is still the most reliable and affordable way to assess long-term population trends, it may not be sensitive to recent events of increased at-sea mortality, considering sea turtles may take well over 20 years to mature (Miller 2017).

Monitoring of populations in foraging grounds may thus fill an important knowledge gap by providing information on mortality and survival of juvenile turtles. Some examples are studies reporting impacts from fisheries' bycatch (Poiner et al. 1990; Lewison et al. 2004a; Báez et al. 2019), anthropogenic debris ingestion (Bjorndal et al. 1994; Bugoni et al. 2001; Wilcox et al. 2018), and estimates of turtle survival probabilities (Chaloupka and Limpus 2002; Bjorndal et al. 2003; Campbell and Lagueux 2005; Casale et al. 2007). Several studies demonstrated a relationship between at-sea mortality and sea turtle strandings (Vélez-Rubio et al. 2013; Monteiro et al. 2016; Domènech et al. 2019), indicating that strandings are a valuable source of empirical information about sea turtle populations. The motivation behind the present study was the increase in the number of stranded sea turtles from 1995 to 2015, mainly green and loggerhead turtles, reported on the coast of the Rio Grande do Sul state (RSC), in southern Brazil (Scherer et al. 2014; Monteiro et al. 2016). Scherer et al. (2014) were the first to suggest that the observed increase in sea turtle strandings was due to anthropogenic impact causing an increase in mortality and a consequent decline in species populations. In addition, Monteiro et al. (2016) proposed an alternative explanation to this increasing pattern in sea turtle strandings, at least for green turtles: a higher abundance of turtles, due to population growth.

Green turtles are long-lived animals that may take over 40 years to reach maturity (Goshe et al. 2010). They spend their first years in oceanic habitats, recruiting to coastal habitats upon reaching a certain age (usually three to five years old), when they shift from a carnivorous to an herbivorous diet (Reich et al. 2007). Green turtles found stranded in RSC and adjacent regions are mostly small juveniles, between two to seven years old, in this transitional phase (Vélez-Rubio et al. 2016; Lenz et al. 2017). These juveniles come from various rookeries across the Atlantic, forming a genetic mixed stock (Figure 1). Studies on genetic composition demonstrated that Ascension Island's rookery is the main source for green turtles that forage in RSC, followed by Aves Island/Surinam's and Trindade Island's populations (Proietti et al. 2012). Ascension is South Atlantic's largest green turtle rookery, where a steep increase in the number of nests was observed from 1980 to 2013, in response to protection from poaching (Weber et

al. 2014). Aves Island's population has also reported an increase in the number of nests (García-Cruz et al. 2015), while Trindade Island appears to be stable (Almeida et al. 2011). In this context, an increase in the number of juveniles coming from the source rookeries could be driving the increasing pattern in green turtle strandings in Southern Atlantic coasts (Monteiro et al. 2016).

Loggerhead turtles are also long-lived animals and their age at maturity in the western South Atlantic Ocean (WSAO) is around 32 years (Petitet et al. 2012). Like green turtles, they also spend their first years in oceanic habitats and recruit to coastal habitats upon reaching a certain age, although this shift occurs later, and not as marked as in green turtles (Ramirez et al. 2015). Loggerhead turtles foraging in RSC are mostly large juveniles, between 10 and 29 years old (Lenz et al. 2016). The average age at transition from oceanic to neritic habitat for loggerhead turtles in RSC is 13 years old, although there is high variability between individuals, with ages ranging from eight to 18 years (Lenz et al. 2016; Monteiro 2017). These individuals also exhibit a high plasticity in habitat use: some spend most of the year in coastal waters, while others present seasonal displacement between coastal and oceanic habitats (Barceló et al. 2013; Monteiro 2017). Loggerhead turtles foraging in RSC are likely to come exclusively from Brazilian rookeries, as those foraging in the Argentine coast (Figure 1; Prosdocimi et al. 2015). Loggerhead reproductive populations in Brazil have shown some signs of recovery, thanks to the protection of nesting beaches by Projeto TAMAR (Marcovaldi and Chaloupka 2007). Monteiro et al. (2016) argued that the increase in the number of nests reported in Brazil would not be sufficient to explain the marked increase in loggerhead strandings, and suggested instead fishing-related mortality as the main cause for this increase.

In order to understand the process of stranding, our first objective in this study was to test which predictors have higher influence over loggerhead and green turtle strandings. We expect positive correlations between the number of strandings and fisheries activity, hatchling emergences, frontal winds and sea surface temperature due to the effect of these predictors on sea turtles' mortality, abundance, or stranding rates.

Strandings however, are influenced by a great number of ecological, physical and sampling factors, which are not all accountable for and may add noise or biases to our conclusions. Therefore, our second objective was to analyze variations in loggerhead and green turtle body sizes from 1996 to 2018, which are presumably influenced by fewer factors and may reveal important aspects of these populations' dynamics. Since the production of hatchlings in reproductive areas is increasing for both species, we expect a higher proportion of small juveniles throughout the study period, and a consequent decrease in the average body size of turtles found stranded. The number of green turtle hatchlings emerged in Ascension has increased six-fold from 1977 to 2013 (Weber et al. 2014), therefore we expect a negative correlation between the numbers of hatchlings born in Ascension and the sizes of green turtles found stranded. For loggerhead turtles, pelagic longline fishing might also have an influence on the body sizes of turtles found stranded. Since individuals captured by pelagic longline fisheries are often oceanic juveniles and smaller than the average of turtles found stranded (Monteiro et al. 2016), high pelagic longline fishing effort might result in more small loggerhead turtles found stranded. Therefore, we expect a negative correlation between pelagic longline fishing activity and body sizes of loggerhead turtles found stranded.

Material and methods

Beach surveys and specimens' data

The specimens of loggerhead ($N=6199$) and green turtles ($N=4476$) as well as their data analyzed in this study were recorded in beach surveys conducted between 1996 and 2018 in the coast of the state of Rio Grande do Sul (RSC). Three different institutions conducted the beach surveys: Núcleo de Educação e Monitoramento Ambiental (NEMA-RS, from 1996 to 2018), Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul (GEMARS, from 1996 to 2011), and Centro de Estudos Costeiros e Limnológicos of Universidade Federal do Rio Grande do Sul (CECLIMAR-IB-UFRGS, from 2012 to 2018). Hundreds of carcasses were collected by the institutions and deposited in their scientific collections as voucher material.

The study area comprehends the 620 kilometres of coastline of RSC. NEMA-RS surveys were conducted in the southern region of RSC, covering 355 km from Lagoa do Peixe (31°21'S; 051°02'W) to Chuí (33°44'S; 053°22'W), while GEMARS and CECLIMAR-IB-UFRGS surveys were conducted in the northern region of RSC, covering 265 km from Lagoa do Peixe (31°21'S; 051°02'W) to Praia da Guarita (29°21'S; 49°44'W). Beach surveys were conducted on average every 18 days by each group, though sampling effort was uneven through time. The distance covered in each survey was registered as a measure of sampling effort. We obtained data from 959 beach surveys, 583 of which were in the southern area and 376 in the northern. A total of 107.870 km were covered, between 1996 and 2018.

All beach surveys applied the same methodology: the study area was covered using a four-wheel drive vehicle at an approximate driving speed of 30 km/h, with two to four observers scanning the beach, from the wash zone to the base of the sand dunes in search of large stranded vertebrates. In this study we recognized as “stranding” any sea turtle or its remains washed ashore, dead or alive, whose species could be identified (as described in Pritchard and Mortimer 1999). We analyzed only loggerhead and green turtle strandings, which account for over 90% of sea turtle strandings in the region. For each stranded sea turtle found, we recorded date, species and curved carapace length (CCL) taken from notch to tip (Bolten 1999). Each dead stranded turtle was collected and/or spray painted in order to avoid multiple counting; live turtles were transported to the closest rehabilitation centre for veterinary care.

Predictor variables

Wind data was obtained from three meteorological stations along RSC (Torres, Rio Grande and Santa Vitória do Palmar; extracted from: <http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep>)(INMET 2018). This data included measurements every 6 hours on wind speed and direction. We combined wind speed s and direction d into a single variable w , assigning different values for d every 10° based on inclination relative to coastline (Fig. 1). The resulting variable *wind* had greater values for perpendicular winds, either

positive for onshore winds, which would carry carcasses to the coast, or negative for offshore winds, which would carry carcasses away, with a range of intermediate values in between. We then calculated the mean w for each day and summed the values for the last 10 days before each stranding survey.

Daily sea surface temperature was also obtained for a location in the centre of the study area (31° 30'S; 50° 30'S) from NOAA OISST.v2 (available in: <ftp://ftp.cdc.noaa.gov/Datasets/noaa.oisst.v2/sst.mnmean.nc>). We also extracted monthly values for the South Oscillation Index (SOI) from NOAA's database, in which prolonged series of negative values are associated with El Niño episodes and prolonged series of positive values with La Niña episodes (available in: https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/SOI/).

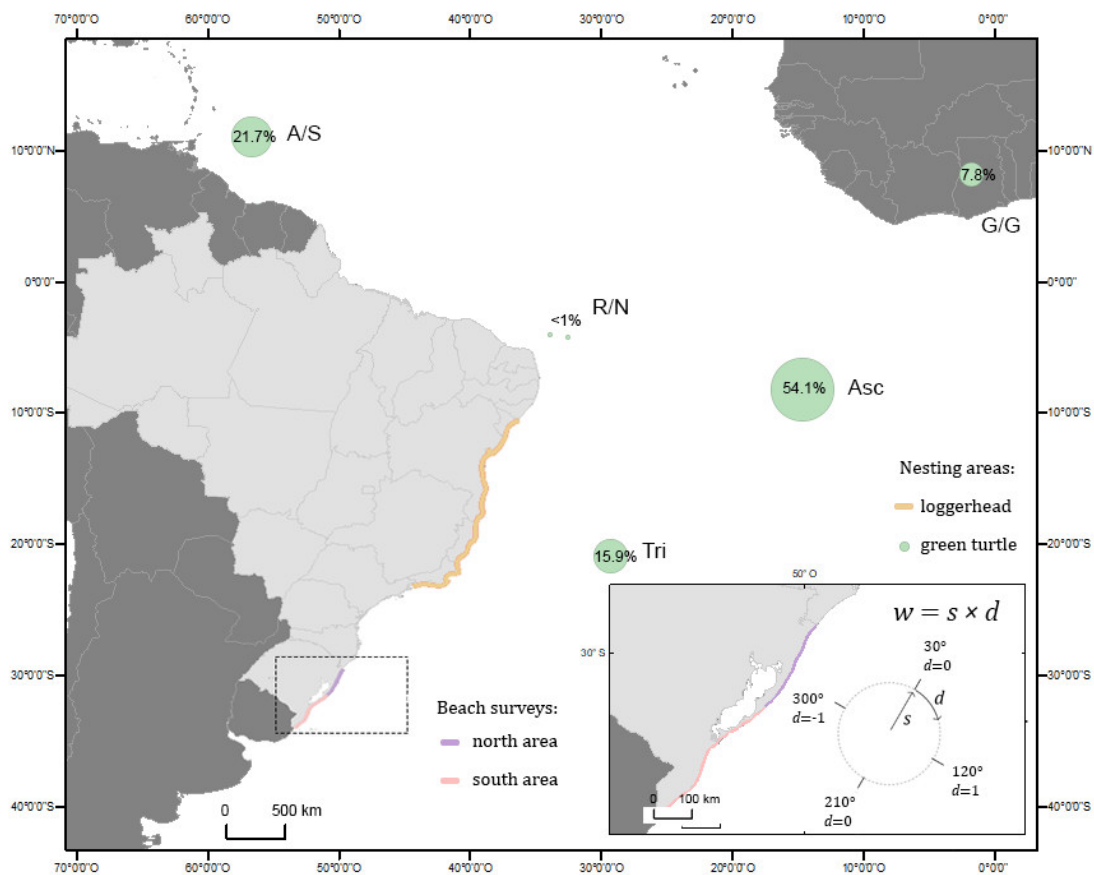


Figure 1. Study area and main nesting sites. Study area, representation of wind variable w , and main nesting sites for loggerhead (Brazil) and green turtles (Ascension, Aves Island/Surinam, Atol das Rocas/Fernando de Noronha, Trindade, Guiné

Bissau/Gulf of Guinea). Circle areas for green turtle represent relative contribution estimated from each rookery to the coast of the state of Rio Grande do Sul genetic mixed stock (Proietti et al. 2012)

Fisheries data in southern Brazil is scarce and no long time series of data on fishing effort is available. Therefore, we used landing counts as a measure of fisheries activity. Monthly number of landings from the industrial fisheries operating in waters adjacent to RSC were obtained from reports by Centro de Pesquisa e Gestão dos Recursos Lagunares e Estuarinos in Rio Grande do Sul (CEPERG 2001, 2003, 2012, 2004, 2005, 2006, 2007, 2008, 2009, 2011a, b), and by Universidade do Vale do Itajaí in Santa Catarina (UNIVALI/CTTMar 2001, 2003, 2013, 2004, 2006, 2007a, b, 2008, 2009, 2010, 2011). Monthly landing counts were available for both groups from 2000 to 2011, excepting 2001, which was not available for Rio Grande do Sul. We grouped fisheries into eight different categories: double-rig trawl, bottom otter trawl, bottom pair trawl, bottom longline, pelagic longline, gillnet, purseine and live bait. We only included fisheries with landing counts available for the whole monitored period (reports available in <http://www.icmbio.gov.br/cepsul/acervo-digital/37-download/estatistica/111-estatistica.html>). We also obtained longline annual catch in tons of tuna and tuna-like fish in the WSAO region between 1996 to 2017 from ICCAT's Task I statistical database (available in: <https://www.iccat.int/en/accesingdb.html>).

In order to represent the abundance of sea turtle juveniles in RSC, where they spend only a part of their life cycle, we created an index incorporating hatchling production and turtle ages. Since there is limited reproductive data available for loggerhead turtles in the WSAO this could only be done for green turtles. We used data from Ascension's hatchling emergences, between 1999 and 2013 (Weber et al. 2014), and age distribution of green turtles found stranded in RSC (Lenz et al. 2016). We gave different weights to the number of hatchlings born in prior years in Ascension based on ages of green turtles found in RSC (e.g.: the number of hatchling emergences in Ascension two years earlier is multiplied by the proportion of two-year-old turtles found stranded in RSC), as represented in the equation:

$$j_y = \sum_{a=2}^7 e_{y-a} \times p_a$$

where: j_y is the index calculated for each year y , e is the number of hatchling emergences in Ascension a years before and p is the proportion of juvenile green turtles found at age a . We used values of a between 2 and 7 years, representing most of the ages found in green turtles while maintaining a larger timespan and sample size.

Statistical analysis

In order to understand which predictors have a higher influence on loggerhead and green turtle strandings, we used generalized linear models (GLM) to model strandings in response to the predictors described above. Each beach survey was treated as a sampling unit, and the distance covered in each survey was used as offset. The number of turtles found in each survey was used as response variable, modelling each species separately. We tested Pearson's correlations between predictors to prevent multicollinearity (using a threshold of 0,7); live bait landings were excluded from further analysis due to collinearity with sea surface temperature. Predictors used were wind(w), sea surface temperature, South Oscillation Index, fishing landings (bottom otter trawl, bottom pair trawl, double-rig trawl, gillnet, pelagic long-line, bottom long-line and seine, each included as a separate variable) and Ascension juvenile abundance(j) for green turtles. Models were fitted to the data using a negative binomial distribution. We applied a *post-hoc* Kolmogorov–Smirnov test to simulated residuals to test for overall goodness-of-fit in each model (Hartig 2018). The first model for loggerhead turtles was a poor fit according to the test, thus the model was refitted using the distance covered in each survey as a covariate instead of as an offset. We modelled green turtle strandings from 2006 to 2011 and loggerhead turtle strandings from 2000 to 2011, excepting 2001, according to the timespan available for the predictors used.

To search for trends in loggerhead and green turtle sizes throughout time we adjusted linear models (LM) to the data using curved carapace length (CCL) as

the response variable and year and month in which the turtle was found as predictors. One model was adjusted for each species. Year was included as a numerical variable to test for an overall increasing/decreasing pattern in turtles' CCLs and month was included as a categorical variable to test for differences between months separately. Linear models were also adjusted to test for correlations between loggerhead turtle' CCLs and longline catches in the WSAO and between green turtles' CCLs and Ascension juvenile abundance(*j*). For all tests, we set the significance level at $\alpha=0.01$. All statistical analyses were done in R statistical environment (R Core Team 2018),

Results

Green turtle

We obtained 4476 green turtle stranding records. Green turtle stranding rates (strandings per distance covered) were higher in warmer months of the year (austral spring and summer) than in colder months (austral winter) and showed an increase throughout time, particularly from 1996 to 2013, peaking in 2011 (Fig. 2a). Strandings showed a positive correlation with sea surface temperature (negative binomial GLM, $N=1437$, $z=6.675$, $P<0.001$; Fig. 2b), wind w ($z=9.509$, $P<0.001$; Fig. 2c), Ascension juvenile abundance j ($z=5.958$, $P<0.001$; Fig. 2d), and bottom pair trawl landings ($z=3.593$, $P<0.001$; Fig. 2e), and a negative correlation only with double-rig trawl landings ($z=-3.931$, $P<0.001$; Fig. 2f). All other correlations were non-significant (S.O.I., $z=1.336$, $P=0.181$; bottom otter trawl, $z=1.114$, $P=0.265$; gillnet, $z=-1.995$, $P=0.046$; pelagic longline, $z=1.456$, $P=0.145$; bottom longline, $z=-1.228$, $P=0.096$; seine, $z=-1.228$, $P=0.219$).

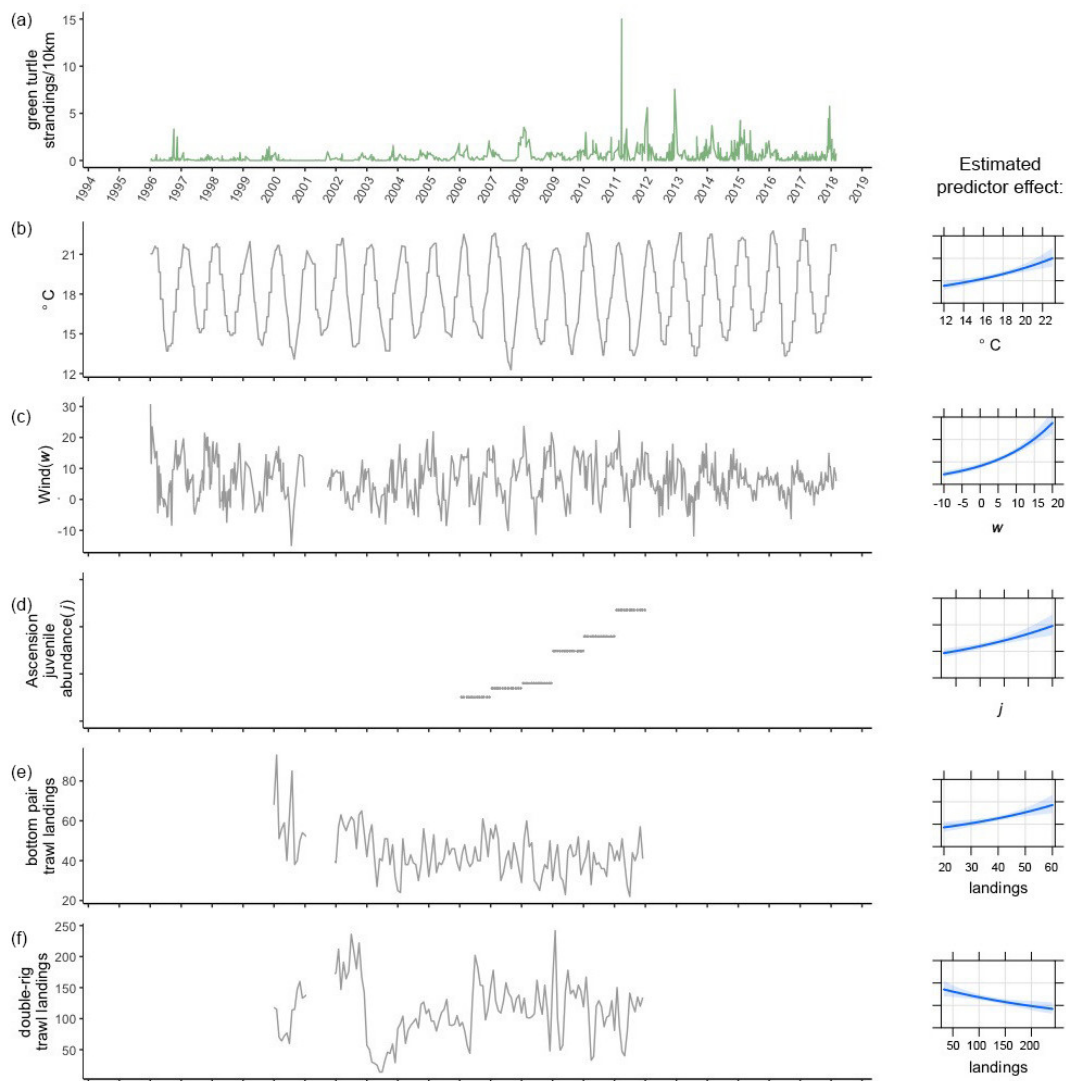


Figure 2. Green turtle strandings and predictors. Green turtle, *Chelonia mydas*, strandings between 1996 and 2018 along the coast of the state of Rio Grande do Sul (RSC), southern Brazil (2a). 2b-2f represent significant predictors over time (left) and effect of each predictor on strandings estimated by the GLM (right).

We obtained 3735 green turtles' curved carapace lengths (CCL), from specimens found in the study area between 1996 and 2018. In green turtles, there was an overall decreasing pattern in CCLs throughout time (LM, $N=3735$, adjusted $R^2=0.02869$, $t=-6.519$, $P<0.001$; Fig. 3a-b), with smaller CCLs reported in 2010, 2015 and 2017. Moreover, there was a seasonal pattern in green turtles' CCLs (Fig. 3c), with significant smaller turtles in April (month 4; $t=-1.78417$, $P<0.001$) and May (month 5; $t=-2.43585$, $P<0.001$). No correlation was found between

Ascension juvenile abundance (j) and green turtles' CCLs (LM, adjusted $R^2=0.001$, $t=-1.718$, $P= 0.085$).

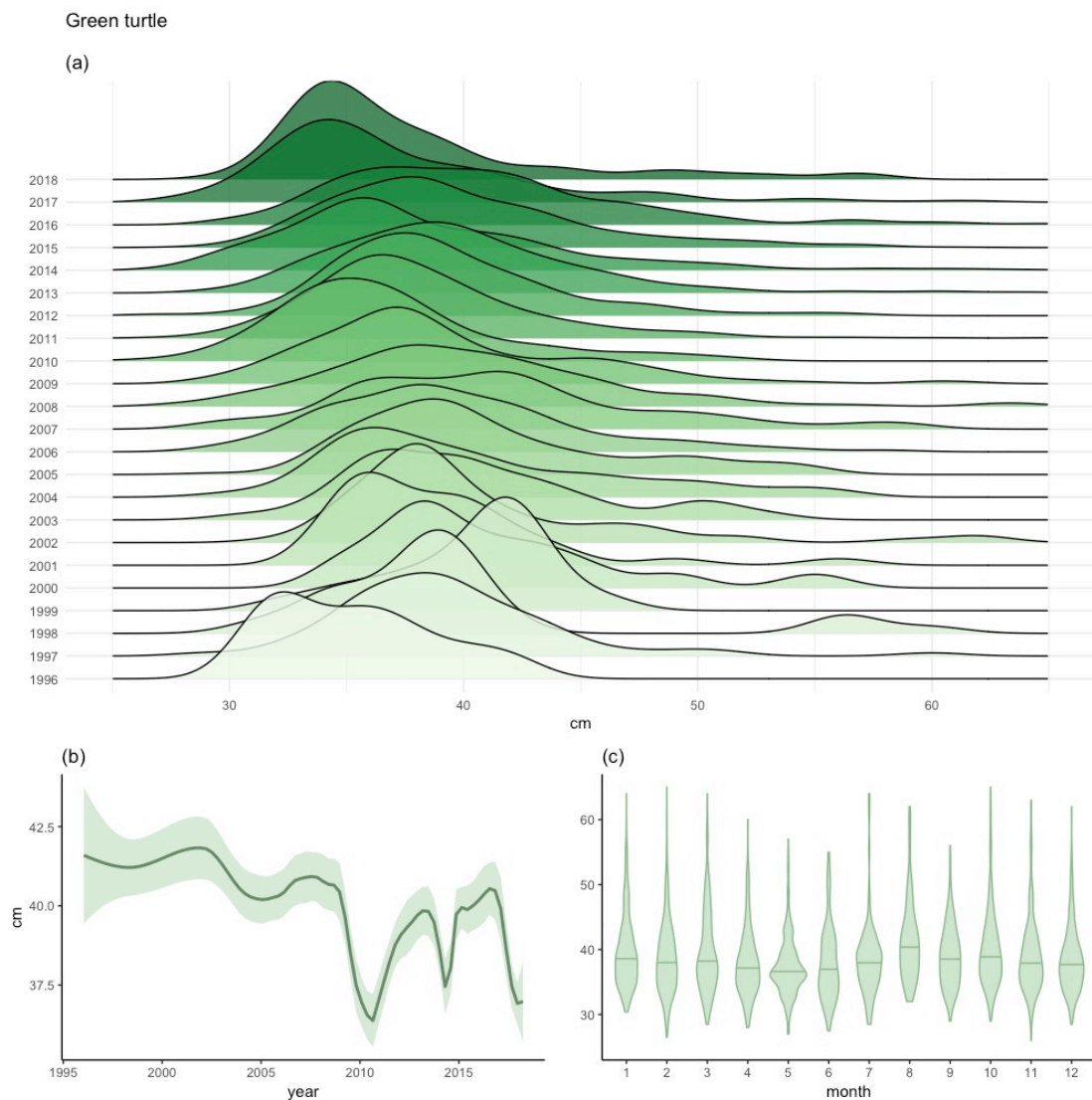


Figure 3. Green turtles' curved carapace lengths. Interannual distributions of curved carapace lengths (CCL) of green turtles, *Chelonia mydas*, found stranded between 1996 and 2018 along the coast of the state of Rio Grande do Sul, southern Brazil (3a). Locally estimated scatterplot smoothing of green turtles' CCL variation between 1996 and 2018, with a confidence interval of 95% (3b). Median and monthly distributions of green turtles' CCLs (3c).

Loggerhead turtle

We obtained 6199 loggerhead turtle stranding records. As in green turtles, loggerhead turtle stranding rates were higher in warmer months of the year

(austral spring and summer) than in colder months (austral winter) and generally increased throughout time (Fig. 4a). A positive correlation was observed between strandings and sea surface temperature (negative binomial GLM, $N=2524$, $z=8.752$, $P<0.001$; Fig. 4b), wind w ($z=6.189$, $P<0.001$; Fig. 4c), pelagic longline landings ($z=3.473$, $P<0.001$; Fig. 4d), double-rig trawl landings ($z=-3.118$, $P<0.001$; Fig. 4e) and distance covered ($z=7.651$, $P<0.001$; Fig. 4f). All other correlations were non-significant (S.O.I., $z=2.129$, $P=0.033$; bottom otter trawl, $z=-0.784$, $P=0.433$, bottom pair trawl, $z=-2.156$, $P=0.031$; gillnet, $z=0.791$, $P=0.428$; bottom longline, $z=-0.325$, $P=0.745$; seine, $z=-0.273$, $P=0.785$).

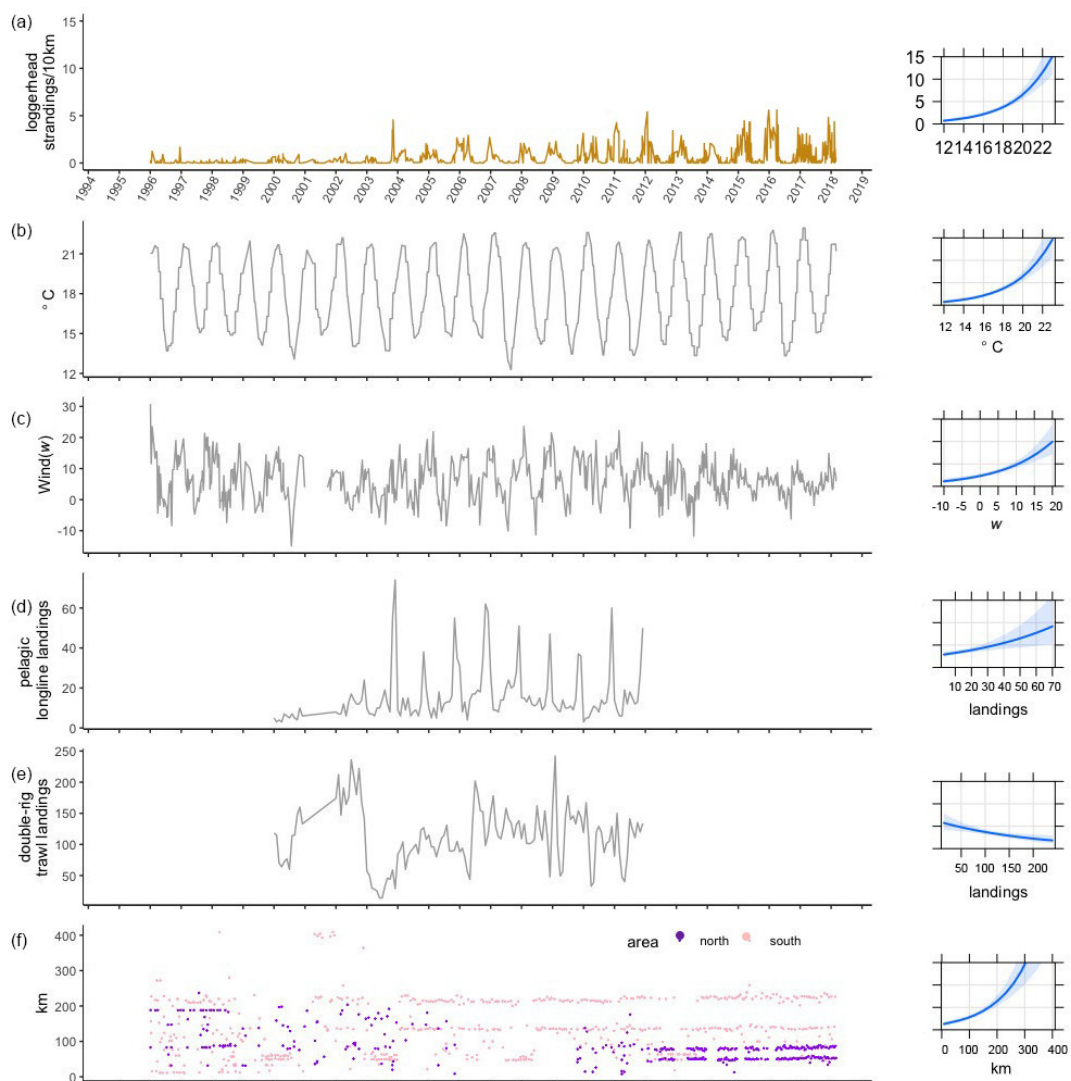


Figure 4. Loggerhead turtle strandings and predictors. Loggerhead turtle, *Caretta caretta*, strandings between 1996 and 2018 along the coast of the state of

Rio Grande do Sul, southern Brazil (4a). 4b-4f represent significant predictors over time (left) and effect of each predictor on strandings estimated by the generalized linear model (right).

We obtained 4353 loggerhead turtles' CCLs between 1996 and 2018. Loggerhead turtle's CCLs decreased from 1996 to 2012, and increased from 2012 onwards, resulting in an overall increasing tendency in loggerhead turtles' CCLs throughout time (LM, $N=4353$, adjusted $R^2=0.3285$, $t=-8.291$, $P<0.001$; Fig. 5a). There was a seasonal pattern in loggerhead turtles' CCLs (Fig. 5c, which were smaller in May (month 5; $t=-3.536$, $P<0.001$) and bigger in February (month 2; $t=2.869$, $P=0.004$) and March (month 3; $t=3.024$, $P=0.003$). A correlation was found between loggerhead turtles' CCLs and longline catches in the WSAO (Fig. 6c-d; LM, $N=4095$, adjusted $R^2=0.02052$, $t=-9.314$, $P<0.001$).

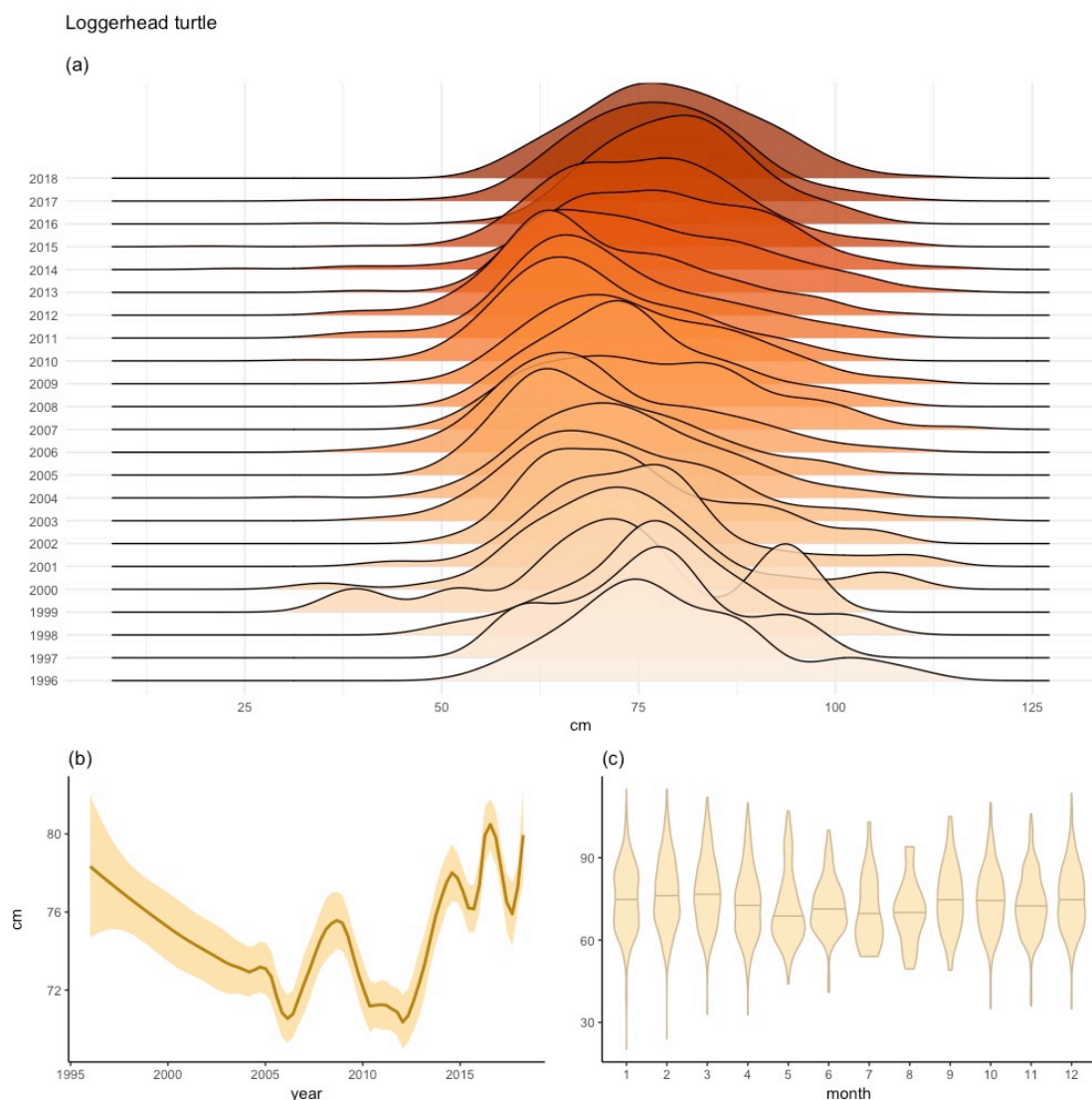


Figure 5. Loggerhead turtles' curved carapace lengths. Interannual distributions of curved carapace lengths (CCL) of loggerhead turtles, *Caretta caretta*, found stranded between 1996 and 2018 along the coast of the state of Rio Grande do Sul, southern Brazil (5a). Locally estimated scatterplot smoothing of loggerhead turtles' CCL variation between 1996 to 2018, with a confidence interval of 95% (5b). Median and monthly distributions of loggerhead turtles' CCLs (5c).

Discussion

Green turtles: population growth and impact from debris ingestion.

Wind and sea surface temperature were the variables with stronger effects over green turtle strandings. The correlation found between green turtle strandings and sea surface temperature reflects the seasonal pattern in green turtle strandings, with higher stranding rates during summer and lower stranding rates during winter. One explanation behind this seasonality might be a lower abundance of green turtles in RSC waters in the winter, as they are known to make seasonal migrations towards warmer waters during winter in WSAO, both northwards or offshore, to oceanic waters (González-Carman et al. 2012; Vélez-Rubio et al. 2016, 2018b). Another possible explanation might be the fact that green turtles in the region are less active during colder months (Reisser et al. 2013) and even exhibit dormancy (Felger et al. 1976; Hochscheid et al. 2007), which might decrease their chance of being caught in fishing gear. Furthermore, predominance of frontal winds was higher during austral spring and summer (Fig. 2c), which could drive carcasses to the coast and contribute to increased stranding rates in those parts of the year.

Trawl and gillnet fisheries are known to strongly impact green turtles (Casale 2011), and WSAO is no exception to this pattern, as there is evidence of fishing related mortality from gillnet and trawl fisheries (Vélez-Rubio et al. 2013; Monteiro et al. 2016), therefore we expected to find positive correlations between these fisheries and green turtle strandings, as turtles killed by this

fisheries are often found stranded. This could explain the positive correlation found between bottom pair trawl landings and green turtle strandings. However, we found no significant correlation between gillnet and bottom otter trawl landings in the region and green turtle strandings, and even a negative correlation between double-rig trawl landings and green turtle strandings, for which we have no plausible explanation, and therefore believe to be spurious. Rather than actually reflecting the influence of trawl and gillnet fisheries on green turtle strandings, these results strongly suggest that landing counts are a very poor representation of fishing effort for those fisheries, which is expected, as the number of landings does not account for fishing gear size, capture rates and time spent at-sea, all of which have a high influence on bycatch rates. However, landing counts were the only long time series of data available on fisheries activity in the region, highlighting the need for better long-term fisheries monitoring programs and reports on fishing effort.

Again, wind and temperature were the best predictors of green turtle strandings, yet, neither of these environmental variables showed any signs of significantly increasing from 1996 to 2018, while green turtle strandings did increase during that time. The correlation found between Ascension's juvenile abundance (j) and green turtle strandings between 2006 and 2011 supports the idea that population growth does play an important role in the increasing pattern in green turtle strandings. But does that explain the decrease found in green turtles' CCLs? Despite the decreasing pattern found in green turtles' CCLs from 1996 to 2018 being compatible with the higher proportion of juveniles expected in a population growth scenario, we found no correlation between Ascension's juvenile abundance and green turtles' CCLs, which would be expected in that case. Furthermore, if increasing juvenile abundance was the cause behind decreasing CCLs, a decreasing pattern in green turtles CCLs should be consistent across the SWAO. There is no such consistence, as a study in Ubatuba, southeastern Brazil, reports an opposite increasing trend in green turtles's CCLs for green turtles caught in coastal fisheries from 1995 to 2016, while also reporting growing green turtle abundance (Silva et al. 2017).

We suggest an alternative explanation to the decreasing pattern found in stranded green turtles CCLs: increasing impact from debris ingestion. Since younger/smaller turtles are the most vulnerable to debris ingestion due to their specific diet at young ages (Vélez-Rubio et al. 2018a), as the concentration of plastic in the ocean increases (Cózar et al. 2014), we would expect an increase in small green turtles mortality and a consequent decline in the mean CCL of turtles found dead, as reflected by our data. This explanation is consistent with the increasingly number of green turtles found stranded with debris in their gut contents in southern Brazil and Uruguay (Bugoni et al. 2001; Monteiro et al. 2016; Vélez-Rubio et al. 2018a). Increasing green turtle juvenile mortality due to anthropogenic debris ingestion would also explain why an increasing pattern in CCLs was found for green turtles caught by coastal fisheries in Ubatuba since small turtles that die because of debris ingestion do not get caught in fishing gear, causing the average CCL of green turtles caught by coastal fisheries to increase. Therefore, this trend of smaller turtles found stranded and bigger ones caught in fishing gear appears to be further evidence of the impact of debris ingestion on juvenile green turtles and, since debris ingestion is a globally widespread threat, we expect this trend to be found elsewhere in similar developmental habitats.

But, what would explain the seasonal pattern found in green turtles CCLs? Research on green turtles caught by artisanal fisheries in Ubatuba (SP) also detected a similar seasonal pattern in green turtles' CCLs, with smaller turtles found before and during winter, suggesting that this seasonal pattern would be due to differences in juvenile recruitment, either from southern or from oceanic foraging habitats (Gallo et al. 2006; Silva et al. 2017). Green turtles in the WSAO seem to migrate northwards as they develop (Barata et al. 2011), and perform seasonal latitudinal migrations from south foraging grounds in the summer to north foraging grounds in the winter, presumably to escape from cold temperatures and thermal stress (González-Carman et al. 2012; Vélez-Rubio et al. 2016). There is no apparent reason why recruitment from oceanic to neritic habitats would increase just before winter in RSC, since coastal waters would be subject to colder temperatures than oceanic waters during winter due to the

predominance of Malvinas Current (Olson et al. 1988). Therefore, we believe that latitudinal migration or some other unknown factor is responsible for the seasonal pattern found in green turtles' CCLs in RSC and possibly in Ubatuba, in southeastern Brazil.

Loggerhead turtles: evidence of impact from pelagic longline fishing

As in green turtles, the variables with higher explanatory power over loggerhead strandings were sea surface temperature and predominance of perpendicular winds (w), also including explicitly the distance covered in each survey, implicit in the green turtle model. Loggerhead strandings were also more frequent during warmer periods of the year. Seasonal migrations might be causing this pattern, since offshore migrations during winter have been reported for loggerhead turtles in the region (Barceló et al. 2013; Monteiro 2017). Furthermore, loggerhead turtles exhibit some level of dormancy during winter (Hochscheid et al. 2007), which might decrease their chance of being caught in fishing gear and explain why strandings are less frequent in colder months. Additionally, there might be a higher mortality from fisheries during warmer months, since pelagic longline activity usually peaks in December (Fig 6b).

Impacts on loggerhead turtles have been reported from several different fisheries, such as gillnets, trawlers and longline (Casale 2011). Yet, as in green turtles, the absence of positive correlation between gillnet and trawlers and loggerhead turtle strandings, and the negative correlation between double-rig trawl landings and loggerhead turtle strandings suggests that landing counts are a very poor representation of fishing effort for those fisheries. For pelagic longline however, unlike other fisheries, number of landings might be a more accurate representation of this fishery's activity since there is a very clear seasonal pattern (Fig. 6b). Indeed, we found a clear correlation between pelagic longline landings and loggerhead turtle strandings. Effects of pelagic longline bycatch on loggerhead turtle populations have gained much attention (Lewison et al. 2004a; Lewison and Crowder 2007), and longline bycatch has been reported as the main cause of mortality for stranded loggerhead turtles in Spain (Tomás et al. 2008), and stranded turtles with direct evidence of longline related

mortality have also been found in RSC and Uruguay (Vélez-Rubio et al. 2013; Monteiro et al. 2016).

The patterns in loggerhead strandings and longline landings were quite similar (Fig. 6a-b), with longline activity peaks followed by loggerhead turtle stranding peaks. Such a pattern is consistent with loggerhead turtles being caught by longline fisheries, then dying and stranding some time later. This is quite worrisome considering we only included landings from the pelagic longline fleet from Rio Grande do Sul and Santa Catarina, while other longline fleets operate in the region, such as the Itaipava fleet (Bugoni et al. 2008; Fiedler et al. 2015), and that longline catches in the WSAO have greatly increased from 1990 to 2011 (Fig. 6d).

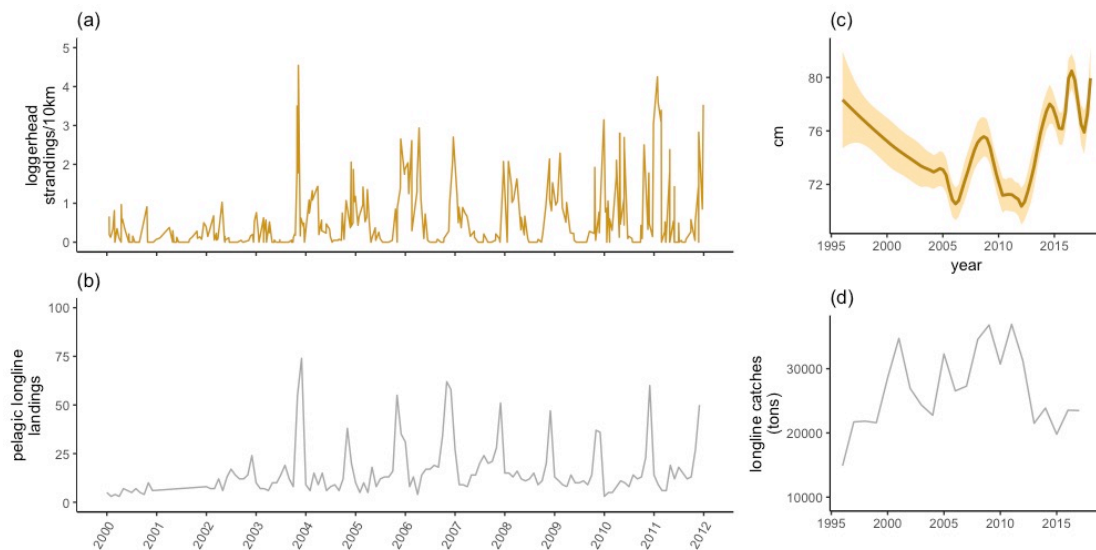


Figure 6. Pelagic longline fisheries and loggerhead strandings. Loggerhead turtle, *Caretta caretta*, strandings between 2000 and 2012 along the coast of the state of Rio Grande do Sul, southern Brazil (6a). Number of pelagic longline landings in southern Brazil between 2000 and 2012 (6b). Locally estimated scatterplot smoothing of loggerhead turtles curved carapace length variation between 2000 to 2012, with a confidence interval of 95% (6c). Tons of tuna and tuna-like fish caught by longline fisheries in the western South Atlantic Ocean between 1996 to 2017 (6d).

Body sizes of loggerhead turtles found stranded gives us further insight. Although unlikely, on the one hand, the decreasing trend on loggerhead turtle CCLs from 1996 to 2012 could be a positive sign, representing an increase in

juvenile abundance. Projeto TAMAR started protecting nesting beaches in Brazil in 1982 (Marcovaldi and dei Marcovaldi 1999); hence, considering that loggerhead turtles found stranded in RSC are in average 13 years old, juvenile loggerhead found stranded in 1996 onwards would have been born during the first years of nesting beach protection from poaching. However, the reported increase in the number of nests is still relatively small and recent compared to that of green turtles and thus, probably, unable to explain such an abrupt shift in turtles' CCLs and strandings.

Pelagic longline fishing provides better explanation for the variation in loggerhead turtles CCLs. We found a negative correlation between pelagic longline catches in the WSAO and stranded loggerhead turtles' CCLs (Fig. 6c-d). This supports the idea that the decreasing trend in stranded loggerhead turtles' CCLs from 1996-2012 was due to a higher mortality of small loggerhead turtles caused by pelagic longline fishing. This is particularly serious, because loggerhead turtles in the WSAO reach maturity around 32 years old (Petitet et al. 2012), so high juvenile mortality would take years or even decades to be noticed in reproductive areas.

As for green turtles, the seasonal pattern found in loggerhead turtles' CCLs, might be due to seasonal movements or migrations. Loggerhead turtles tracked from Rio de la Plata performed overwintering migrations northwards to waters off Uruguay and RSC (González-Carman et al. 2016). Loggerheads tracked from RSC and adjacent regions migrate northwards during winter and southwards during summer (Barceló et al. 2013), and some individuals perform offshore overwintering movements. These studies have demonstrated a high individual variability in loggerhead turtles' habitat usage making this seasonal pattern complex and difficult to explain. Furthermore, few adult loggerheads were found stranded in southern Brazil (Monteiro et al. 2016; Lenz et al. 2016), and satellite tracking of post-nesting females in the Brazilian coast showed high fidelity of adults to foraging grounds in the northernmost part of the Brazilian coast (Marcovaldi et al. 2010), showing that loggerheads foraging in the waters along RSC also migrate northwards at some point during their development.

Conclusions

Our results indicate both population recovery and impact from debris ingestion as important factors behind the increase in green turtle strandings in RSC from 1995 to 2018. Whereas for loggerhead turtles mortality from bycatch, particularly from longline fisheries, seems to be the main cause behind strandings increase. Our study highlights the importance of monitoring populations and impacts: due to the lack of data on fishing effort, the influence of several fisheries known to impact both loggerhead and green turtles could not be addressed. But most important, our study shows the urgent need for management policies aiming to mitigate both impact from plastic pollution and from fisheries. Despite current encouraging numbers of hatchlings from some nesting beaches, these numbers might return to decline if the impact from fisheries and debris ingestion is not reduced. Furthermore, here we presented evidence of increasing juvenile mortality, which might take decades to have an effect on reproductive populations, considering sea turtles' long life cycles and should, therefore, be carefully considered in future population assessments and conservation status reviews.

There are several studies from sea turtles' reproductive areas reporting number of nests, and indicators of sea turtle mortality due to human impact are also fairly common. However, mortality and natality should be put into perspective and interpreted as rates in a population. Because sea turtles have such long and complex life cycles, we lack studies integrating data from natality and mortality rates in these species. However, this is exactly the kind of approach we need if we ought to understand sustainability of sea turtle populations, predict long-term response to threats, and to propose adequate management measures. An integrative approach based on statistical modelling should be applied to sea turtle population ecology, using data from several different sources, accounting for all sea life stages, to model and predict populations' response to different possible scenarios. One interesting example in that direction is a recent study which estimated loggerhead and green turtle populations' sustainability in response to fisheries bycatch in the Mediterranean Sea (Casale and Heppell 2016). Relying population assessments and status reviews mostly on the number

of nests and hatchlings from nesting beaches may lead to over-optimistic or precipitated assumptions of population recovery.

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Supplementary material

	Green turtles			Loggerhead turtles		
	number of strandings	average CCL(cm)	SD	number of strandings	average CCL(cm)	SD
1996	36	40.98	14.26	50	78.92	12.42
1997	78	41.15	10.55	32	76.38	11.01
1998	37	40.71	8.55	42	77.56	11.61
1999	36	40.31	3.34	14	72.25	16.76
2000	18	41.13	5.29	51	73.22	13.72
2001	50	43.42	12.5	65	74.88	12.75
2002	73	41.3	8.86	66	74.64	12.44
2003	45	40.29	5.11	105	72.73	13.28
2004	167	40.56	6.58	318	73.29	11.76
2005	160	40.89	5.46	290	70.66	11.63
2006	154	40.02	6.89	318	70.3	12.9
2007	134	41.28	6.31	138	76.26	13.61
2008	193	40.37	6.52	186	74.62	11.57
2009	159	39.06	5.66	237	75.14	12.36
2010	315	36.65	4.65	360	70.35	11.8
2011	482	38.17	4.85	455	71.28	13.06
2012	239	39	4.62	280	70.77	12.82
2013	295	39.99	6.86	219	75.99	13.38
2014	439	38.31	6.8	405	77.61	13.52
2015	632	40.21	9.85	817	75.9	11.58
2016	196	40.54	6.12	582	79.85	9.72
2017	414	37.12	5.97	802	77.27	10.71
2018	124	38.12	8.09	367	78.88	10.76
total	4476	39.26	7.11	6199	74.91	12.3

Table 1. Loggerhead and green turtle's numbers of strandings and curved carapace lengths. Loggerhead turtle, *Caretta caretta*, and green turtle, *Chelonia mydas*, number of strandings and average curved carapace lengths per year,

between 1996 and 2018 along the coast of the state of Rio Grande do Sul, southern Brazil.