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SPATIAL DISTRIBUTION OF SEA TURTLES ON A SOUTH ATLANTIC SUBTROPICAL ROCKY REEF

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Spatial distribution of sea turtles on a South Atlantic subtropical rocky reef

Dissertação apresentada ao Programa de Pós-Graduação em Dinâmica dos Oceanos e da Terra, da Universidade Federal Fluminense, como requisito parcial para obtenção do grau de Mestre em Ecologia Marinha.

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A todas as meninas que sonham em ser cientistas.

AGRADECIMENTOS

RESUMO

As tartarugas marinhas são espécies de vida longa e com estruturação populacional complexa. Embora tenha havido um aumento substancial nos esforços de pesquisa e conservação de tartarugas nas últimas décadas, muito sobre abundância e distribuição de populações permanece por resolver. Apesar da grande extensão da costa brasileira, a maioria dos estudos subaquáticos sobre tartarugas marinhas em áreas de forrageamento são qualitativos, carecem de estimativas de densidade e têm restrições geográficas. Neste trabalho, produzimos estimativas de abundância e investigamos padrões de distribuições de tartarugas marinhas em locais direta (oeste) e indiretamente (leste) influenciados por eventos de ressurgência em um recife rochoso subtropical brasileiro (23°S, 42°W). A fim de garantir que essas espécies móveis fossem adequadamente amostradas, foram realizados transectos subaquáticos cronometrados. Observamos apenas duas espécies de tartarugas, sendo que a tartaruga-verde (*Chelonia mydas*) foi quase 10 vezes mais abundante do que a tartaruga-de-pente (*Eretmochelys imbricata*), o que já era esperado dada a preferência geral de *C. mydas* em se alimentar de algas e dos extensos bancos de macroalgas na região. A distribuição das tartarugas-de-pente espelha padrões latitudinais observados ao longo da costa brasileira, onde essa espécie tropical é dominante nos recifes do nordeste (semelhante aqui à localização leste). Embora amplamente distribuída, a abundância de tartarugas-verdes variou significativamente com as características de profundidade e localização em uma escala de poucos quilômetros. As tartarugas-verde foram mais abundantes na localização mais fria e exposta (oeste) e nos primeiros metros da coluna d'água. No geral, a abundância de tartaruga-de-pente e tartaruga-verde foi relativamente maior em comparação a outros recifes subtropicais, o que confirma a importância regional de Arraial do Cabo. Este estudo destacou que métodos simples e análise básicas podem produzir estimativas confiáveis da abundância e densidade relativa de tartarugas marinhas em áreas rasas de forrageamento, quando as limitações são consideradas. O entendimento da abundância e distribuição nos recifes brasileiros contribuirá para esforços nacionais de planejamento de conservação, como estratégias de manejo e a priorização espacial de áreas críticas de forrageamento.

Palavras-chave: abundância populacional, área de forrageamento, tartarugas marinhas, monitoramento subaquático.

ABSTRACT

Sea turtles are long-living marine species with complex spatial population structures. Although there was a substantial increase on sea turtles' research and conservation efforts in recent decades, much about abundance and distribution of populations remains unsolved. Despite the large extension of the Brazilian coast, most underwater studies regarding sea turtles in foraging areas are qualitative, lack density estimates, and are geographically restricted. We produced estimates of sea turtle density and investigated their distribution patterns in locations directly (western) and indirectly (eastern) influenced by upwelling events on a brazilian subtropical rocky reef (23°S, 42°W). To ensure that these mobile and sparsely distributed species were adequately surveyed, underwater timed strip transects were conducted. We observed two species, with green turtle (*Chelonia mydas*) being almost 10 times more abundant than hawksbill turtle (*Eretmochelys imbricata*), driven by the presence of large macroalgae beds, which represent the primary food for *C. mydas*. The distribution of hawksbill turtles mirrored large-scale latitudinal patterns observed along the entire Brazilian coast, where this tropical species is dominant on north-eastern reefs (similar to the eastern location). Although widely distributed, the density of green turtles varied significantly with depth and local features on a scale of a few kilometres. Green turtles were more abundant in the colder-exposed location (western) and in the first few meters of the water column. Overall, the density of hawksbill and green turtles were higher compared to other subtropical coastal sites, which confirms the regional importance of Arraial do Cabo. This study highlighted that simple methods and basic data analysis can produce reliable estimates of relative abundance and density of sea turtles in shallow foraging areas when limitations are considered. Moreover, understanding the distribution patterns of sea turtles along brazilian reefs will contribute to national conservation efforts, such as management strategies and the spatial prioritization of critical foraging areas.

Keywords: population abundance, foraging area, sea turtles, underwater survey.

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Introduction

Sea turtles are long-living marine species with complex spatial population structures. Despite the substantial increase in sea turtle research and conservation efforts in recent decades (Frazier, 2003), much about their demographics, abundance, and population distribution remains unsolved (Rees et al., 2016; Hamann et al., 2010). This knowledge gap is inherent to logistical challenges while studying sea turtles; for instance, foraging and breeding habitats are often widely dispersed in geographically distinct sites (Luschi et al., 2003). Additionally, sea turtles may take several decades to mature, with variable intervals between successive nesting years (Bjorndal et al., 2010). Their vast ranges and lengthy life histories require unusually large-scale monitoring efforts (Musick & Limpus, 1997).

Estimating population abundance and density is a necessary baseline to inform appropriate management and conservation initiatives (Rees et al., 2016; Becker et al., 2019). Most sea turtle population studies have focused on breeding females while in nesting beaches, biasing ecological understanding (e.g. Balazs & Chaloupka, 2004; Marcovaldi et al., 2007). This represents a major limitation for sea turtles, for which juveniles and subadults are the most abundant individuals of a population (Heppel et al., 1996; Casale & Heppell, 2016). A complementary approach to assess demographic patterns is the use of underwater visual surveys (UVC) (Becker et al., 2019), which may assess different life stages than beach surveys (Mancini et al., 2015; Becker et al., 2019). However, limitations of UVC included intensive field effort and potentially altered turtle behaviour due to the presence of divers.

Underwater visual census is a widespread non-destructive technique largely used to assess reef fish populations and assemblages (e.g. Brock, 1982); however, it was rarely applied to sea turtles (e.g. Mancini et al., 2015; Fernandes et al., 2017; Cardona et al., 2020). UVC implies visual identification instead of manipulative approaches, reducing sampling time and costs. Large and timed transects are the most appropriate methods for large-bodied and highly mobile species (Hill & Wilkinson, 2004), which generally show sparse distributions and may occupy large areas (Choat & Pears, 2003). The use of large UVC, although limited by the size of the sampled areas, increases the probability of detecting individuals, hence robustness of the estimates (Hill & Wilkinson, 2004; Mancini et al., 2015).

Sea turtles play a fundamental ecological role on the marine systems they inhabit, balancing food webs, providing substrates for epibionts, transporting nutrients, and in green

and hawksbill turtles' case, as modifiers of the landscape by feeding on algae and sessile invertebrates (Goatley et al., 2012). Yet, data about the densities of sea turtles in reef habitats is incipient, and little is known about their contribution to the total biomass of herbivores and invertivores (Goatley et al., 2012). Both green and hawksbill turtles (*Chelonia Mydas* and *Eretmochelys imbricata*) spend most of their lives in the same foraging area and experience seasonal fluctuations in local environmental conditions (Southwood et al., 2006). The responses of sea turtles to changes in abiotic and biotic factors can have profound effects on energetic and possible survival consequences (Musick and Limpus, 1997). Fluctuations in ambient temperature, for instance, directly affects the physiology of sea turtles which may, in turn, influence individual's ability to acquire resources and allocate energy to critical activities (i.e. somatic growth and reproduction) (Williard, 2013; Bjorndal et al., 2016).

Knowledge about local oceanographic and biological parameters coupled with sea turtle density can help define how the space is used and what defines an "optimum" foraging habitat, in terms of both their biological value and their importance for population viability (Hamann et al., 2010). As proper sampling techniques result in accurate estimates to monitor populations effectively, this study aimed to produce estimates of sea turtle density from visual assessment on a feeding area, as well as investigate distribution patterns of sea turtles in environmental gradients of water temperature and wave exposure on a subtropical rocky reef in the Brazilian coast. To our knowledge, this is one of the few studies available that estimate sea turtle in-water abundance using snorkelling and SCUBA transects. All results generated here are aligned with the National Action Plan for sea turtles, which are necessary for a better understanding of the population dynamics, and to establish trends to inform local and regional management actions (Marcovaldi et al., 2011b).

Materials and methods

Study area

The region of Arraial do Cabo (Rio de Janeiro, Brazil) is part of a sustainable use conservation unit where only local traditional fishers are allowed to exploit resources. Despite some fishing restrictions, no-take zones were not established, and many types of fishing gear are used, from nets to spearfishing, while enforcement is considered inefficient (Bender et al., 2014). Arraial do Cabo is formed by an isthmus and two islands where rocky shores dominate (Figure 1). Small-scale upwelling processes often occur as a result of the prevailing winds and coastal morphology, creating two main distinct locations: the western

location, with exposed shores, directly affected by upwelling waters (average temperature: < 20°C); and the eastern location, with shallower, sheltered coastlines reaching comparatively higher average temperatures (average temperature: > 22°C) (Valentin, 1984; Cordeiro et al., 2016). The western location is also generally characterized by deep reefs ranging from 5 to 25 m. Moreover, the eastern location is formed by shallow reefs (0-12 m), with the majority reaching only 6 m. These features favour the existence of two main realms a few kilometres apart: one with tropical affinity fauna, and another with typically subtropical and temperate components (Yoneshigue-Valentin & Valentin, 1992; Ferreira et al., 2001). This accumulation of species from different climatic domains characterizes Arraial do Cabo as a biodiversity hotspot (Aued et al, 2018).
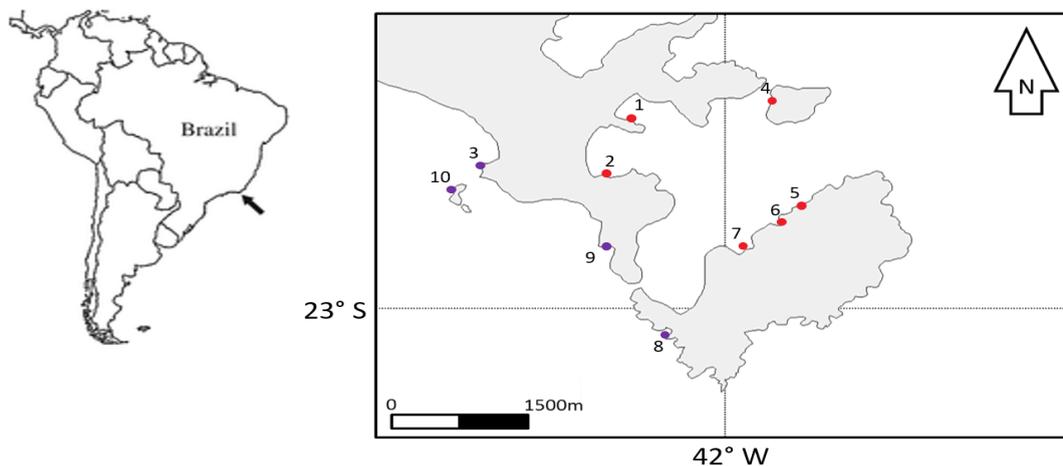
Figure 1: Map of the Arraial do Cabo region (Rio de Janeiro, Brazil) indicating the sampled sites. Red = eastern sites indirectly influenced by upwelling (>22 ° C); purple = western sites directly influenced by upwelling (<20 ° C). The maximum local depth of each site is shown inside parenthesis: 1 = Praia do Forno (3 m); 2 = Praia dos Anjos (7 m); 3 = Praia Grande (5 m); 4 = Porcos (12 m); 5 = Escadinha (8 m); 6 = Pedra Vermelha (6 m); 7 = Maramutá (6 m); 8 = Ingleses (25 m); 9 = Sometudo (15 m); 10 = Franceses (25 m).

Wave exposure

The wave exposure at each site was calculated using fetch as a proxy (see full details in Burrows et al., 2008) to quantify the differences in wave exposure on both locations and among sites. Fetch were calculated as the unobstructed length of water over which wind from a certain direction can blow over (Burrows et al., 2008). A map of wave exposure for Arraial do Cabo was produced (Sup. Figure 1), based on total fetch as the distance to the nearest land around any point on the map, and sixteen equiangular fetch vectors calculated with a maximum distance of 200 km. The higher the fetch from a certain direction, the more energy is imparted onto the surface of the water, resulting in a larger

wave exposition. The final fetch values for each site were calculated as the mean fetch over all vectors.

Sea turtle survey

Surveys were conducted, from January to August 2019, in ten sites (Figure 1) through snorkelling (water depth ≥ 5 m) and SCUBA (water depth ≤ 6 m). During surveys, two observers swam along the transect length, yet only one fixed diver was responsible for data collection. Sea turtle density was evaluated at each site by underwater timed strip transects (10 min x 6 m) using underwater scooters (Sea-Doo® Pro Scooter) to maintain constant speed (~ 5 km.h⁻¹); thereby, decreasing the likelihood of double counting (Hill & Wilkinson, 2004; Cordeiro et al., 2016). A pilot survey was performed to check sea turtles' responsive behaviour to diver/scooter. Despite the possible noise generated by the propeller, which could scare some individuals, such behaviour was not observed.

The study area suffers great interference from anthropogenic noises, especially at the daytime, which corresponds to periods of intense touristic and fishing activities (Campbell et al., 2019). All sighted sea turtle individuals were identified by species and classified within size classes. Size was estimated considering carapace length intervals of 5 cm to minimize possible errors. Green turtles were classified as new recruits (< 45 cm), juveniles (≥ 45 – 60 cm), subadults (≤ 60 – 90 cm) and adults (≥ 90 cm) (Almeida et al., 2011). The size classes for hawksbill turtles are slightly smaller with new recruits (< 35 cm), juveniles (≤ 35 – 60 cm), subadults (≤ 60 – 80 cm) and adults (≥ 80 cm) (Sanches, 1999).

All transects were georeferenced at the beginning and end of the counts. Thus, the length of transects was estimated based on the distance between the start and ends, following the contour of the coast (Cordeiro et al., 2016). Areas with maximum depths of < 8 m were divided in two strata, shallow (1 – 6 m) and mid-depth (6 – 12 m), totalling a minimum of six replicates per stratum and site. As the total length of transects differ, density was calculated as the number of turtles per total transect area standardized by individuals per 100 m². Visibility was measured as the distance between divers using a 20 m tape measure, and temperature was based on dive computer readings (Mares® Puck Pro).

Benthic community characterization

Benthic surveys were conducted to quantitatively describe the spatial distribution of potential food resources to foraging sea turtles. At each site, surveys were conducted at two depth strata: 1 – 6 m (shallow), and 6 – 13 m (mid-deep), unless only one-depth stratum was

found. The benthic community was characterized using ten 25 cm² photoquadrats along 200 m transects on each depth stratum and site. All images obtained from the photoquadrats were analyzed using *photoQuad* software (Trygonis & Sini, 2012) by laying thirty stratified points on each image and identifying the organism underneath. Benthic organisms were classified in morpho-functional groups as: articulated coralline algae (ACA), crustose coralline algae (CCA), epilithic algal matrix (EAM), macroalgae, cyanobacteria, Anthozoa, Hydrozoa, coral, other invertebrates, octocoral, sponge and zoanthid (adapted from Cordeiro et al., 2016; Aued et al., 2018).

Data analysis

The eastern and western locations portray meaningful differences, with high wave exposure to the west and calmer water to the east (Table 1; Sup. Figure 3). The western outer location coastline has the highest mean fetch values (50 to 63 km), with Praia Grande's coast forming a small embayment, presenting lower fetch value (37 km). Sites at the eastern location had much lower mean values (0.6 to 13 km), reflecting their much more sheltered conditions as result of Ilha de Cabo Frio position (Sup. Figure 2). However, the eastern location still has wind-facing sites with higher mean values for Praia dos Anjos and Porcos (25 and 38 km, respectively). For clarification, a site located at a straight open coast with no blocks for wind blow would have 8 out of 16 sectors with maximum fetch values (in this case 200 km). To capture the fetch effect on the abundance of sea turtles, categories were created following natural breaks of mean fetch values (1 – 5, being 1 the most sheltered site). Differences in environmental characteristics (fetch, temperature, and depth) were assessed between locations by Nonmetric Multidimensional Scaling analysis (NMDS) with Euclidean dissimilarity using the function metaMDS within the "vegan" package (Oksanen et al., 2011).

Table 1: Summarised values of fetch data calculated with a maximum distance of 200 km using sixteen equiangular fetch vectors in Arraial do Cabo.

Site	Location	Fetch value (km)
Maramutá	eastern	0.67
Pedra Vermelha	eastern	0.73
Forno	eastern	0.86
Escadinha	eastern	13.13
Anjos	eastern	25.99
Porcos	eastern	37.82
Praia Grande	western	37.90

Ingleses	western	50.07
Sometudo	western	62.57
Franceses	western	62.78

Prior to benthic community composition exploration, percent cover data were transformed by arcsine-square root, to reduce the influence of abundant and rare organisms. The mean macroalgae percentage cover between locations (eastern/western) was tested via t-test.

A Generalized Linear Model (GLM) specification with a log link function was built to investigate the potential relationship of explanatory variables on the total number of green turtle individual sightings per transect. To adequately deal with the zero-inflation in the data, the Hurdle regression was performed using the "glmmTMB" package (Magnusson et al., 2020). The Hurdle count model is a two-component model with a truncated count component for positive counts and a hurdle component that fit the zero counts. The independent variables were location, fetch, temperature, visibility, and depth. As there are intrinsic variability, site was included as a nested variable to the general model. To balance the uneven survey effort, we used the log area of transects as an offset in the negative binomial model to account for sampling intensity.

After a visual inspection of the response variable against each explanatory variable (Sup. Figure 4), it was noticed some relationships were curvilinear. However, afterwards, the inclusion of a polynomial term (quadratic) to fetch and temperature did not improve model performance. Multicollinearity was evaluated using a Variance Inflation Factor (VIF) applied to the explanatory variables of the model using the "performance package" (Lüdecke et al., 2020). Variables with high correlation were identified and removed from the analyses, as was the case for fetch in the zero inflated component. Model selection was performed by comparing all possible subsets of the full model using Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002). To ensure model assumptions were met, residuals were checked. Finally, a hierarchical partitioning analysis was used to estimate the contribution of each variable using the hier.part package (Walsh & MacNally 2013). All analyses were performed in R software (R Development Core Team; www.r-project.org).

Results

A total of 167 timed transects were conducted in 10 sites with median length of 232.5 m (Q1 = 175.0, Q3 = 286.00, minimum = 107.0, maximum = 352.0). The mean length of

transects varied significantly only between locations (Wilcoxon rank test = 23099, p < 0.05). In all surveyed sites, 304 sea turtles of two species were observed. Green turtles represented 90.79% of total observations, while hawksbills had a lower contribution of 8.3% (Figure 2; Table 2). Despite the low incidence of hawksbills individuals, sighting hotspots for hawksbill turtles overlapped with high abundance areas for green turtles at Praia do Forno and Sometudo (Figure 2; Sup. Figure 5).
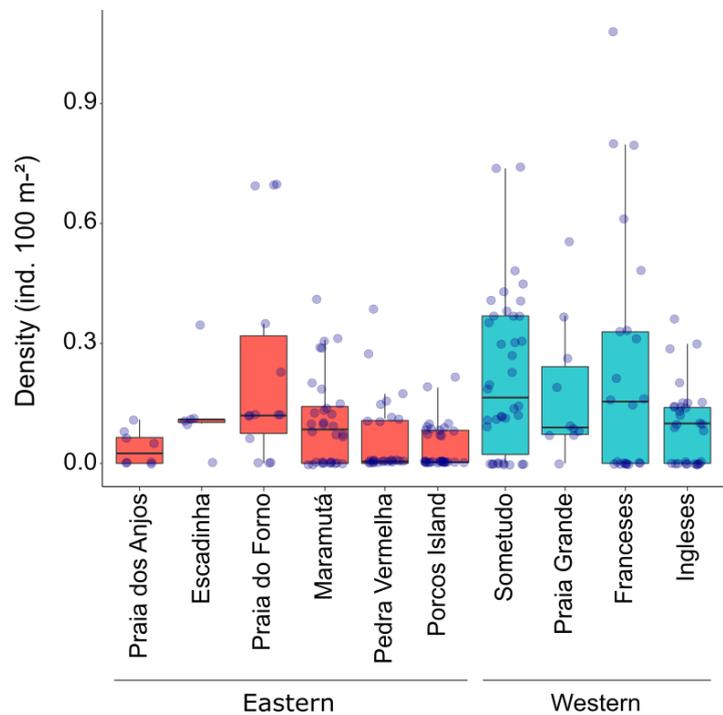
Figure 2: Comparative density of *Chelonia mydas* among sampled sites and locations. Boxplots represent the median, Q1 and Q3. Whiskers represent largest and smallest values removing outliers. Each dot represents standardized density from each underwater visual census and black dots outliers.

Large-sized hawksbills (≥ 70 cm) were only observed at eastern location, and small individuals found mainly at western location (Sup. Figure 5; Sup. Figure 6). As hawksbills have low overall abundance, they were not included in further analyses.

The best Hurdle model indicated that green turtles' sightings were influenced by location and depth (Table 2). The density of green turtles in the eastern location was significantly smaller than in the western (Figure 3a). Differences in green turtle density and habitat characteristics among sites were observed, and samples from western and eastern locations were distributed into two groups (Figure 3b). The fetch negative effect on green turtles' abundance highlights the importance of some sheltered sites to the overall green turtle abundance. Sites with minimum values of fetch (e.g. Praia do Forno and Maramutá) had mean standardized abundance similar to more exposed sites (e.g. Praia Grande). The

model also showed a negative effect of depth on the density of green turtles; thereby, turtles are predominantly associated with shallow waters (1 – 6 m) (Figure 4). For the binomial model, no variable was correlated with the density of sea turtles (Table 2). The hierarchical partitioning analysis indicated that depth contributed most to the explanation of the model (Sup. Figure 7).

Table 2: Zero Altered Model (negative binomial distribution) for the relationship between the abundance of *Chelonia mydas* and environmental drivers (location, fetch, and depth). * = significantly different ($p < 0.05$).

	Estimate	SE	Z-value	*p* value
Counting model				
Intercept	2.313	0.766	3.019	0.002*
Location	3.022	1.320	2.289	0.022*
Fetch	-0.834	0.384	-2.172	0.030*
Depth	-0.139	0.056	-2.486	0.013*
Binomial model				
Intercept	-0.498	0.344	-1.447	0.148
Location	-0.488	0.340	-1.437	0.151
Depth	0.073	0.058	1.262	0.207
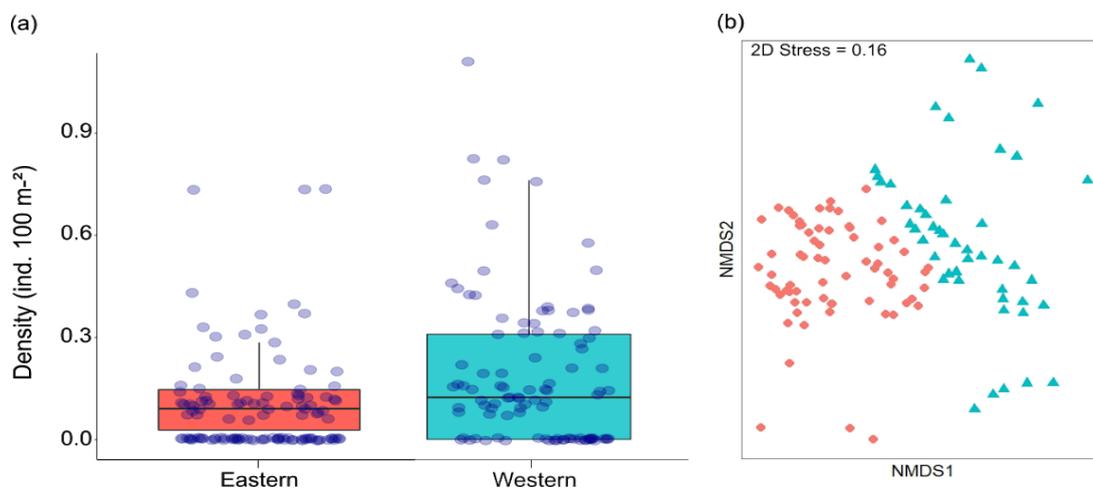
Figure 3: a) Density of *Chelonia mydas* according to location (eastern and western). Boxplots represent the median, Q1 and Q3. Whiskers represent largest and smallest values removing outliers. Each dot represents standardized abundance from each underwater visual census and black dots outliers. b) Nonmetrical multidimensional scaling showing the similarities between the environmental variables (fetch, temperature, depth and visibility) among locations. The data were standardized and

analyzed using Euclidean dissimilarity. Locations: eastern = protected/warm reef in red; western= exposed/cold reef in blue.
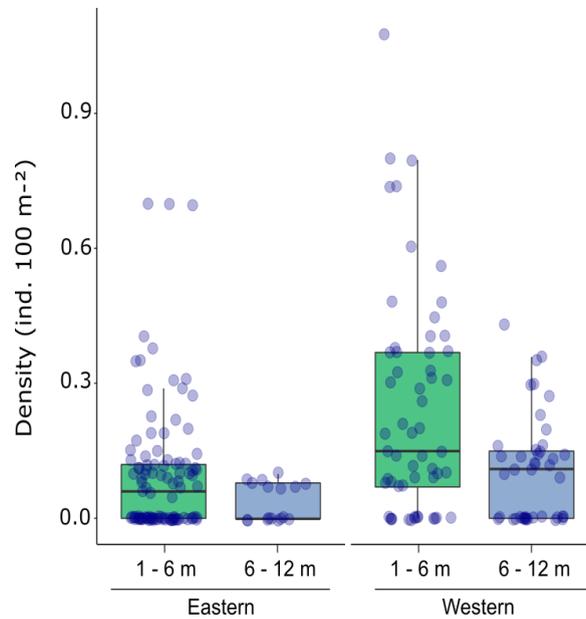
Figure 4: Density of *Chelonia mydas* according to depth strata and location. Boxplots represent the median, Q1 and Q3. Whiskers represent largest and smallest values removing outliers. Each dot represents standardized abundance from each underwater visual census and black dots outliers.

Observed life stage structure followed the commonly described pattern of mostly juvenile individuals (< 60 cm) for green turtle populations (67.03%; Figure 5a). Most of green turtles' individuals were small-sized (<40 cm; 27.53%), whereas sub-adults and adults represented only 5.44% (Table 2; Figure 5b). Small-sized individuals were more frequent at western location, and individuals with a larger size were slightly more abundant at eastern location.
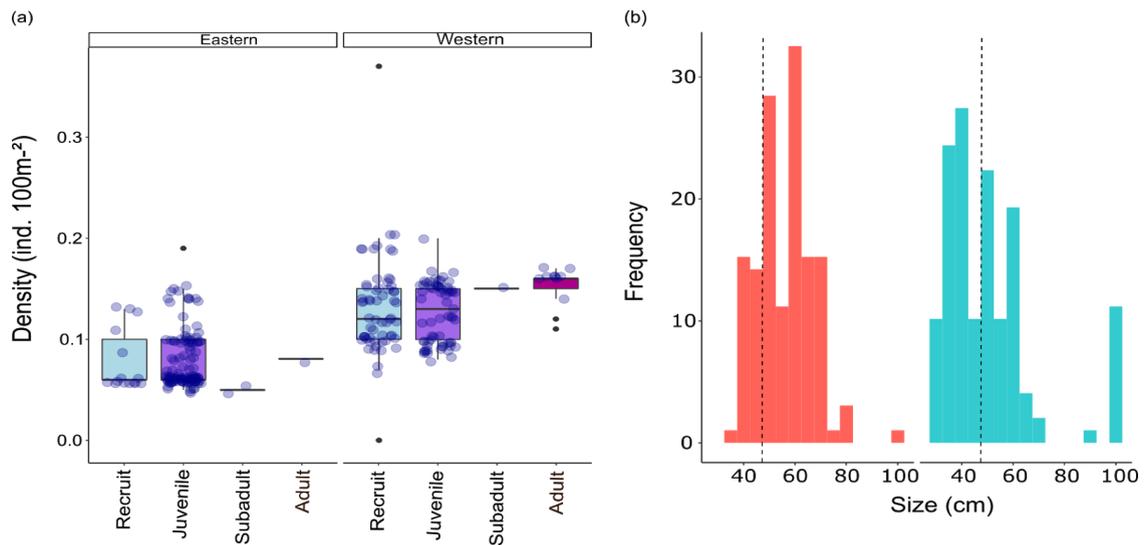
Figure 5: a) Comparative density of different life stages (recruit, juvenile, subadult and adult) of *Chelonia mydas* according to locations (eastern and western). Boxplots represent the median, Q1 and Q3. Whiskers represent largest and smallest values removing outliers. Each dot represents standardized abundance from each underwater visual census and black dots outliers. b) Frequency histogram of carapace length of *Chelonia mydas* according to locations (eastern = red, and western = blue). Dashed lines indicate recruits' maximum size.

Macroalgae had higher cover at the western location (t(162.82)= -2.1297, df = 162.82, p < 0.05). The class *Rhodophyceae* was dominant in both locations (eastern = 47%, western = 75%). The genus *Gelidium* were the most frequent taxa. In the western location, the genera *Ceramium* and *Asparagopsis* were also highly representative. The genus *Sargassum* was the second most abundant group of macroalgae at the eastern location. The species *Pterocladiella capillacea* were only detected at the western location. The coral species *Mussismilia hispida*, *Siderastrea stellata* and the hydrocoral *Millepora alcicornis* were found in the shallow habitats of the sheltered eastern location. The zoanthid *Palythoa caribaeorum* was the dominant species at the eastern location and ACA was the greater contributor for western benthic community (Figure 6). No corals or zoanthids were found at the western location.
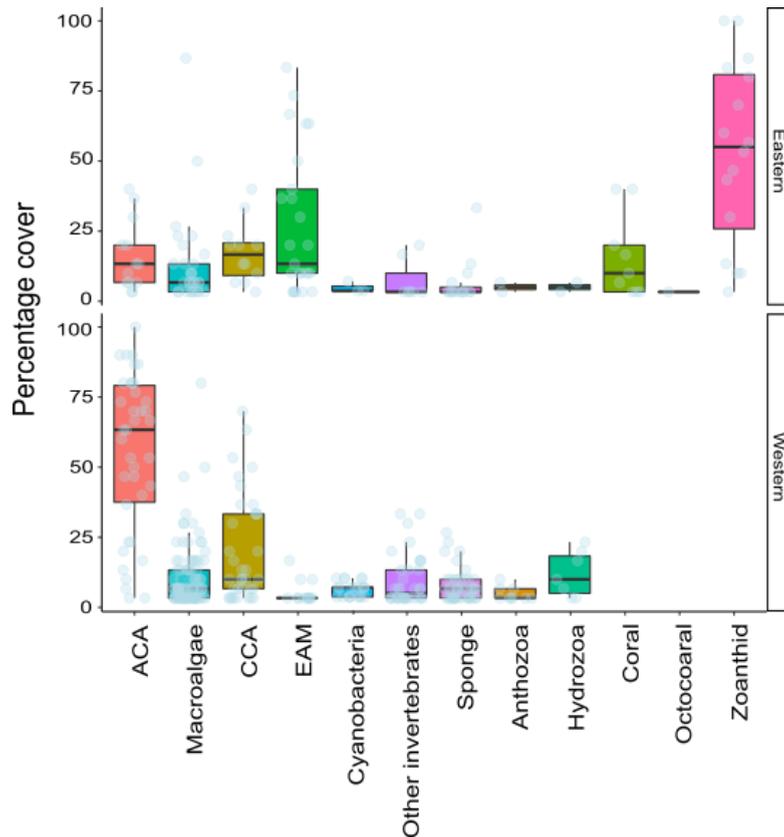
Figure 6: Comparative percentage cover of benthic morpho-functional groups between eastern and western sites. ACA - articulate coralline algae; CCA - crustose coralline algae; EAM - epilithic algal matrix. Boxplots represent the median, Q1 and Q3. Whiskers represent largest and smallest values removing outliers. Each dot represents percentage cover from each photoquadrat and black dots outliers.

Discussion

This study provides the first underwater assessment by means of visual census to estimate the densities of sea turtles on southeastern subtropical reefs of the Brazilian coast. The produced result adds important information on key life stages for which little demographic information is currently available (Hamann et al., 2010). The prevalence of juvenile sea turtles illustrates the importance of Arraial do Cabo as a development area. The distributional patterns of sea turtles vary among the studied sites within a few kilometres. These gradients result mainly from a combination of location (as exposure-temperature extremes), depth, and macroalgae cover, with the latter probably functioning as a proxy to food availability for green turtles. The main implication of this pattern of sea turtle distribution is the potential variation in behaviour exerted by low temperature on species (Southwood et al., 2006).

Arraial do Cabo gathered geological and oceanographic characteristics that represent a scale of considerable environmental variations, which promote the establishment

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of a rich marine biodiversity (Yoneshigue-Valentin & Valentin, 1992; Ferreira et al., 2001). Western sites are directly influenced by cold upwelling waters and higher wave exposure, while harbouring deeper reefs. In contrast, the eastern location presents warmer, calmer and shallower waters. The western location has a higher macroalgae cover as described here and elsewhere (Cordeiro et al., 2014; 2016). The biota in these exposed locations is linked directly to low temperature generated by upwelling events (Valentin, 1984; Yoneshigue-Valentin & Valentin, 1992). The upwelling system brings cold deep waters rich in nutrients to the surface, which are incorporated by phytoplankton, boosting primary production that propagates up the food chain (Valentin, 2001; Coelho-Souza et al., 2012). Upwelling zones are often cited as important grounds for sea turtle feeding, as these productive areas increase food availability (Amorocho & Reina, 2007).

Eretmochelys imbricata

Juvenile hawksbill turtles are distributed throughout the north-eastern Brazilian coastal waters and, less frequently, along the south and southeastern coast (Marcovaldi et al., 2011a). Underwater surveys on a tropical oceanic island, a tropical coastal coral reef, and a subtropical rocky reef in Brazil indicated densities of 2.05 turtles/hour, 2.02 turtles/hour and 0.09 turtles/hour, respectively (Proietti et al., 2012). Comparatively, Arraial do Cabo showed an encounter rate of 1.01 turtles/hour. The lower local frequency of hawksbill comparative to green turtles corroborates previous stranding monitoring in Arraial do Cabo and nearby regions where this species was the least observed (Reis et al., 2009; Reis et al., 2010; Reis et al., 2017). However, Tagliolatto et al. (2019) reported a relatively higher concentration of juvenile hawksbill stranding for Arraial do Cabo compared to other regions of the State, especially during intense upwelling (October to April).

In contrast to green turtle distribution, we found a higher abundance of juveniles and subadults of hawksbill at the eastern location. Hawksbill is the most tropical species of sea turtles; therefore, eastern location higher temperatures may favour the permanency of individuals. Moreover, this location has a rich tropical-like benthic community (Ferreira et al., 2001; Rogers et al., 2014), which is able to provide a valuable habitat for hawksbills, as they are closely tied to reef habitats on which they depend on sponges, zoanthids and corals (Pemberton et al., 2000; León and Bjorndal, 2002). The presence of hawksbills at Arraial do Cabo suggests they use the area for feeding, confirmed by intense foraging observations over *Palythoa caribbeorum* (CELF personal communication; Stampar et al., 2007).

Chelonia mydas

The distributional patterns of green turtles varied among the studied sites within the few kilometres temperature gradient. Herbivorous reef fish assemblages vary considerably along the same cold/warm water gradient, with species with more tropical affinity (e.g. parrotfishes, surgeonfishes) being more abundant in the eastern sites (Cordeiro et al., 2016), a pattern similar to large scale latitudinal variations found along the Brazilian coast (Ferreira et al., 2004; Longo et al., 2019). Green turtle individuals in the cold western location are susceptible to abrupt temperature changes, which may affect their behaviour. The mean water temperature in the eastern location is around 22°C, while in the western location, due to frequent upwelling events, mean temperature is about 18ºC, frequently reaching 13°C (Coelho-Souza et al., 2012). Studies with herbivorous fish at the same areas indicated that low temperatures were correlated with a decrease in feeding rates (Ferreira et al., 1998; Mendes et al., 2009). The inactivity threshold of green turtles is 15°C (Williard, 2003), albeit alteration in diving behaviour and foraging rates were also identified around 22°C (Southwood et al., 2003; Southwood et al., 2006). It is likely that in Arraial do Cabo, sea temperature acts in tandem with other site-specific environmental and ecological factors to determine habitat selection of green turtles.

Inspection of our model showed that green turtles were found more frequently at depths between 1 and 6 m. Indeed, routine dive depth for active juvenile green turtles at tropical areas reaches only 7.9 meters (Williard, 2013), with some populations spending a substantial amount of time at depths ≤ 5 m (Hazel et al., 2009). Their presence at these shallow depths may reflect the distribution of their prey (e.g. Seminoff et al., 2002; Fuentes et al., 2006). The range of depths at which green turtles were most frequently observed in the study area are consistent with macroalgae highest percentage cover (Cordeiro et. al, 2016), which is likely to enhance turtles' forage intake. Reisser et al. (2013) found a similar result for green turtles in a similar subtropical rocky reef, due to a longer time allocated to feeding in this zone, where selected food types were more abundant.

Arraial do Cabo presents one of the highest diversities of benthic organisms along the coast (Aued et al., 2018), with great contribution of macroalgae (Brasileiro et al., 2009), an important food resource for the local sea turtle population. Analysis of green turtle stomach contents from the Arraial do Cabo region reported predominance of the macroalgae *Sargassum vulgare*, *Ulva lactuca*, *Gelidiella acerosa,* and *Pterocladiella capillacea* (each species with more than 50% of frequency of occurrence and high visual predominance) (Awabdi et al., 2013). *Gelidium* was the most abundant genus throughout both locations, and

Sargassum was the second most abundant group at western location in our benthic community analysis. Moreover, *P. capillacea* was only detected at western location. The benthic characterization corroborated the presence of all macroalgae species targeted by green turtles described by previous studies (i.e. Awabdi et al., 2013; Di Beneditto et al., 2017). Nevertheless, food availability alone cannot explain the green turtles' preference for specific items. Further studies incorporating data from green turtle biomass and food selection will generate information on the trophic redundancy within the community of herbivores.

After an initial developmental period in oceanic waters, green turtles with size ranging from 20 to 35 cm return to coastal environments (Musick & Limpus, 1997). These areas can be either shared with adults, which will be the adult residential foraging area, or be frequented only by juveniles, that will later migrate to an adult feeding ground (Musick & Limpus, 1997). There is evidence to support that the final development area used by juveniles are likely to be closer to the turtle's natal (and future nesting) beach than to their pelagic nursery habitats (Luschi et al.; 2003). Evidence from stranding monitoring indicated that green turtles washed up on Arraial do Cabo beaches are juveniles sizing < 42 cm (Reis et al., 2017; Lima et al, 2018). Although the green turtles observed here were larger than previous works reported (see Reis et al., 2017; Awabdi et al., 2013, Di Beneditto et al., 2017), they were predominantly juveniles, indicating that shallow marine habitats of Arraial do Cabo provide appropriate developmental habitat for juvenile green turtles. The major nesting areas for this species are the Brazilian oceanic islands (Almeida, et al., 2011; Bellini et al., 2013); thus, it is expected a lower occurrence of adults along the continental coast. For both hawksbill and green turtles, the average size at western colder location was smaller than at eastern warmer location. We hypothesise that the western location could be favoured by coastal geomorphology and hydrodynamic characteristics being more exposed to oceanic coastal currents.

Density estimates

Abundance estimates of sea turtles on their feeding grounds are essential for a better understanding of population dynamics and trends (Hamann et al., 2010; Seminoff & Shanker, 2008). Considering only timed surveys, it seems that the encounter rate of green turtles in Arraial do Cabo is greater than any other survey reported for Brazil (coast or island) (Table 4). However, these results must be examined with caution, as non-standardized methods are an obstacle to appropriately compare regions. In Table 4, comparison between tropical and subtropical areas highlight the variety of methods used. Surprisingly, the

majority of studies in foraging areas are qualitative, lack density estimates and are geographically restricted. Often, these non-standardized methods are simplistic and may generate dubious results due to low statistical power and bias. For instance, numerous in-water surveys use turtles' sightings per hour as a proxy of abundance and extrapolate it to the total surveyed site creating the illusion of an uniform distribution. However, the effective size of transects is not indicated, blurring any further density estimate. Managers could misguidedly use the resulting output to represent the total area of a marine protected area, leading to unrealistic local densities.

Table 3: Comparison of field methods to estimate population density of *Chelonia mydas* populations in their feeding grounds.

Foraging area	Region	Habitat	Method	Estimate	Author
Southern Great Barrier Reef, Australia	Tropical	Reef	Capture-recapture	4.5e-5 turtles m-²	Chaloupka & Limpus, 2001 apud Williams et al., 2017
Florida Keys, USA	Tropical	Reef	Vessel-based surveys	2.91e-5 turtles m-²	Herren et al., 2018
Tofo, Mozambique	Tropical	Reef	Dive logs surveys	0.28 turtles/dive	Williams et al., 2017
Fernando de Noronha, Brazil	Tropical	Reef	Underwater surveys	1.45 turtles/hour	Cardona et al., 2020
São Sebastião, Brazil	Subtropical	Rocky reef	Underwater surveys	0.53 turtles/hour	Fernandes et al., 2017
Ilha do Arvoredo, Brazil	Subtropical	Rocky reef	Underwater surveys	4.42 turtles/hour	Reisser et al., 2013
Arraial do Cabo, Brazil	Subtropical	Rocky reef	Timed strip transect	>0.1e-5 turtles m-² 9.92 turtles/hour	--

Recommendation for future use

The efficiency of monitoring sea turtles in their foraging areas depends on the selection of appropriate sampling techniques (Wallace et al., 2011; Mancini et al., 2015). The most common survey methods currently in use to estimate underwater sea turtle abundance are catch per unit effort, capture–mark–recapture, boat transects, and aerial surveys (see Bjorndal & Bolten, 2000). These methods are expensive, time-consuming, invasive (when capture is needed), and require specific training. Also, they are highly dependent on shallow waters or surfacing time of a sea turtle (Mancini et al., 2015). On the other hand, timed transects lead to high detection probabilities, producing robust values of abundance that are usually more precise than boat-based or aerial surveys (Roos et al., 2005; Schofield et al., 2007). Timed surveys allow for larger areas, depth strata, and more sites to be surveyed, producing detailed information on habitat use. Furthermore, with this method, density is

effectively calculated according to sampling size area (Mancini et al., 2015). We, therefore, suggest the replication of timed strip transects at coastal foraging areas used by sea turtles (see Table 5).

This document represents an attempt to develop survey guidelines that are specifically designed to in-water monitor sea turtles. Even though it is based on the best available information, it is important to remember that the science underpinning these methods were adapted from other organisms and is still developing. Thus, some limitations must be emphasised. The area that can be surveyed with this technique is relatively smaller than boat and aerial surveys, and external factors can negatively affect abundance estimates (e.g. Bjorndal and Bolten, 2000). Strip timed transects may be impossible to perform on reefs with complex habitat features, governmental restrictions, or intense interference from touristic activities. In addition, areas with turbid waters, strong current, and wave exposure will be hard to survey. Turtle sighting conditions must be the same during all transects. If a trap-shy effect exists in the population, it is likely that not all turtles within the surveyed area will be observed, creating a negative bias. The use of size categories reduces the power to detect small changes. Measuring the population structure of sea turtles requires experienced observers, or at least a previous repeated training for size estimation. When setbacks are considered, this method is advantageous to monitor abundance trends of sea turtles.

Management implications

Although the study area is located within a marine protected area, there is still no management plan that could be used to regulate the multiple uses. The eastern location, as being comparatively sheltered, is more affected by human use, including mariculture, fishing, sewage discharge, harbour activity, and intense tourism (Rogers et al., 2014; Giglio et al., 2017). The habitat use of sea turtles in the eastern location is a matter of concern as increasing tourism throughout the region has great potential to negatively affect local sea turtle populations through increased harassing, boat strikes, and acoustic and other pollution sources. The western location is less frequented by touristic operations, but it is likewise highly influenced by fishing (Silva et al. 2014). Currently, by-catch is considered the main threat to sea turtles worldwide (Wallace et al., 2010). Arraial do Cabo is a traditional artisanal fishing village (Giglio et al., 2017) but there is no monitoring for accidental catches of sea turtles, while reports on the web are numerous (authors, per. com.). While this MPA was not originally designed to protect sea turtles, the results indicate that the study area may be

important for green and hawksbill turtles and emphasize the need for government decision makers to include these species in future conservation plans.

The increasing abundance of juvenile turtles along the Brazilian coast is a result of 30 years of National Program for the Conservation of Sea Turtles success (Tamar, 2017). This means turtles are back to many coastal sites, and yet we do not understand their contribution as mega consumers to local food webs. Some modern populations of green turtles have already provoked substantial alterations in ecosystem functioning by controlling and even overgrazing some marine habitats (Christianen et al., 2014). This underscores that, even at low densities, turtles have the potential to play significant roles in marine ecosystems. While the general depletion of populations reduces the net benefits of size, sea turtle individuals can benefit ecological functioning in terms of mobility and dietary flexibility, and may complement the roles of herbivorous fishes and urchins on reef systems (Goatley et al., 2012; Cardona et al., 2020).

Differences in density across relatively close locations provide a valuable framework to understand how habitat drivers can regulate sea turtle distribution. We recommend additional studies to disentangle the possible effects of low temperatures on behaviour patterns, coupled with long-term species monitoring, to understand habitat use at both high and low temperatures. On a national scale, the results contribute to the understanding of sea turtles distribution, especially because these species are under constant pressure from anthropogenic impacts, particularly fishery and plastic pollution, which are common causes of mortality in Arraial do Cabo (Reis et al., 2017; Lima et al., 2018). This study highlights the scarcity of proper in-water surveyed areas along the Brazilian coast. Perhaps other algal dominated coastal areas might provide a quality habitat for sea turtle development, but are data deficient. Finally, we present recommendations for the sea turtles in-water monitoring (Table 4) based on methods applied here. These steps can be followed by independent research and conservation groups and are replicable in priority regions where information is needed, but resources are scarce.

Table 4: Summary of recommendations for in-water monitoring of sea turtles.

	Details	Possible modi
Sampling design	Hierarchical or stratified sampling design	
Site selection	The surveyed area must be representative of the whole area of study with adequate space to conduct long transects (at least 300 m). Sites should be separated by a hundred meters and the exact location of each one should be recorded for future relocation.	If knowledge determine the
Survey timing	Daylight hours.	Sea turtles sig
Survey frequency	Rapid assessment: a single survey effort on one occasion (i.e. season). Long term monitoring: initiated by a rapid assessment followed by regular monitoring (yearly and in the same season) to monitor population status, threats, and management success for adaptive management.	
UVC methods	Each census consists of two observers swimming parallel to the reef at consistent depth for 10 mins (transect width 6 m). It is imperative to record the time accurately; the clock must be stopped if a short stop is needed and then restarted when swimming recommences. This is an important step because density measurements may be obtained from the sample time and swim speed. Observers should swim at a constant speed and be careful not to count the same individual twice, as they can move away from the diver along the transect. Care must also be taken to spend the same amount of time observing each part of the transect. The length of each timed transect should be measured by marking the beginning and end of each swim with a GPS, and measuring the distance between them. Surveys should be conducted through snorkelling (water depth ≥ 5 m) and SCUBA (water depth ≤ 6 m). Horizontal visibility should be measured as the distance between divers.	A GPS can be which can mo the boat drive a GPS is not a covered in 5 visibility, and average dista precise than census on sr more depth ra
Data	Record species identity, number of individuals, and size categories for each sea turtle sighted in the census area. Information on date/hour, water temperature, depth, and visibility should be recorded to each transect. Additional information on turtles' behaviour, number of divers or boats presented during the survey are highly recommended.	
Field personal	Two observers. One observer swims at shallower depths and the other swims at deeper depths. Divers should be able to visualize each other throughout the entire transect. If a boat is needed, include specific staff.	When visibilit should stay cl recommend o
Minimising disturbance	Observers should swim very quietly, waiting a few minutes to acclimate themselves before starting the survey. When possible, observers should avoid touristic presence peaks and driving the boat over survey areas prior to the survey.	
Training	Observers should be trained in underwater sea turtles' identification, counting and length estimation. Before commencing each survey, both observers should test the accuracy of their transect width and size estimates using a tape measure. It is also recommended calibration of swimming speed.	
Safety	Habitats should be surveyed in decreasing order of depth. When conducting SCUBA surveys, divers should have the assistance of a surface buoy for identification by boat drives.	
Equipment	Underwater slates, pencils and stopwatch. Tape measure to calibrate estimates of width. Full SCUBA equipment, including depth and temperature recorder. Surface buoy with a tow rope for safety. GPS to georectify survey tracks.	PVC pole to e
Data analysis	1. Calculate the area of each sampling unit: the area equals the distance covered in each transect multiplied by their width. 2. Calculate the total density (m²): density equals the number of turtles per total transect area standardized by individuals per 100 m². 3. Analyse the size structure of all species of sea turtles.	

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Supplementary Information
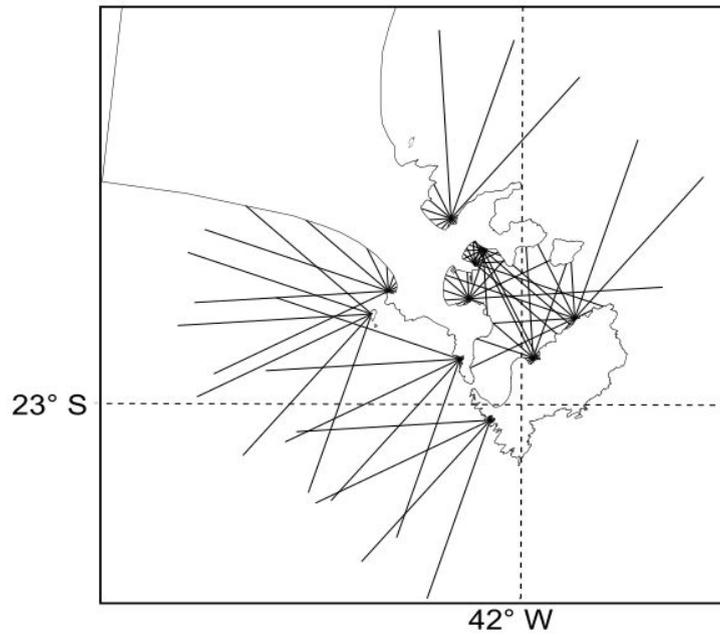
Sup. Figure 1: Map showing the fetch vectors with distance of 5 km (black lines) and coastline geography layer (filled grey polygons) for all the sites.
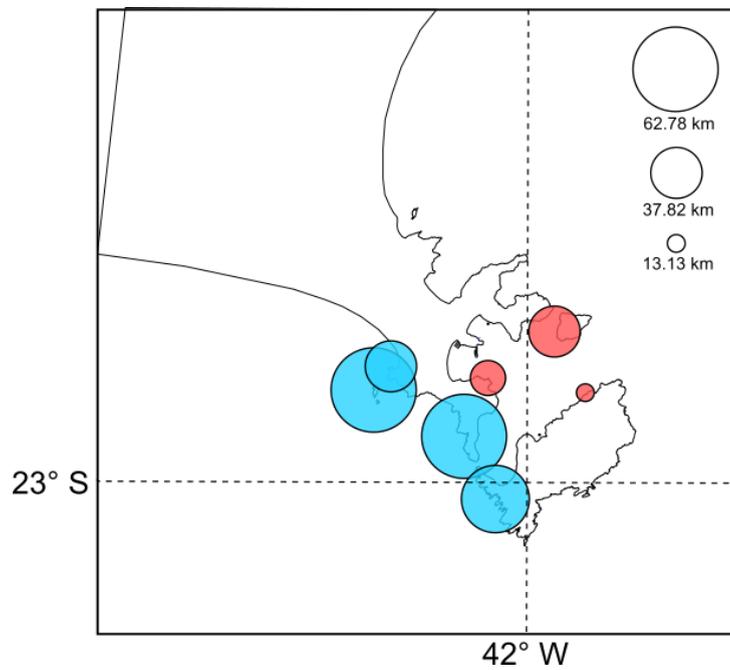

Sup. Figure 2: Map showing the mean fetch values calculated with a maximum distance of 200 km using sixteen equiangular fetch vectors in Arraial do Cabo. Blue circles represent western location, and red circles, eastern location.
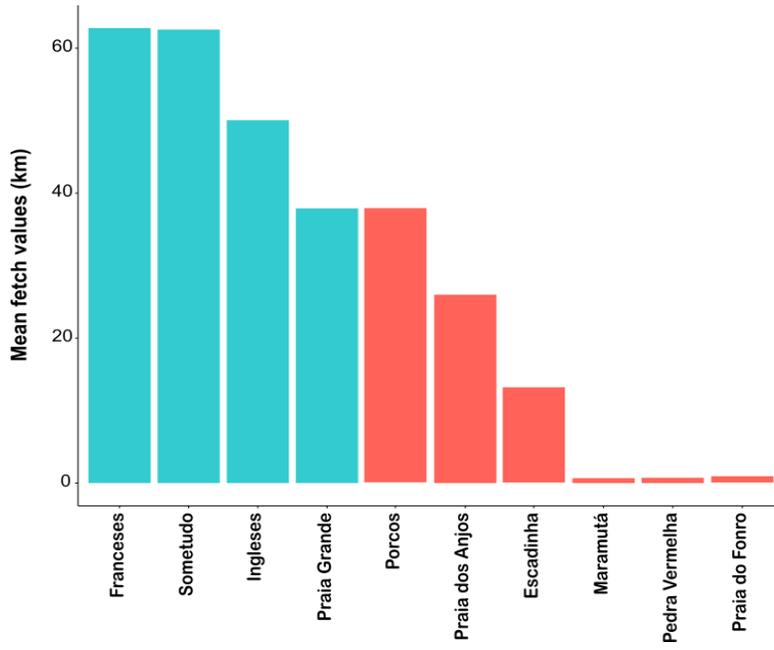
Sup. Figure 3: Fetch values calculated with a maximum distance of 200 km using sixteen equiangular fetch vectors in Arraial do Cabo. Blue bars represent western location, and red bars, eastern location.
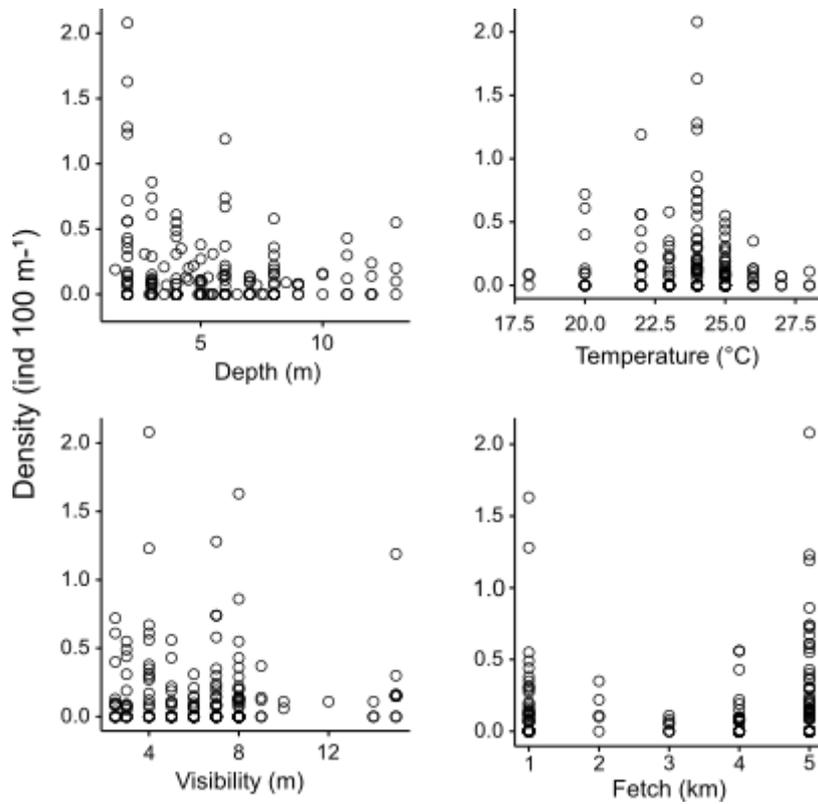

Sup. Figure 4: Relationship between abundance of *Chelonia mydas* and explanatory variables (depth, temperature, visibility and fetch) retained for the GLM model.
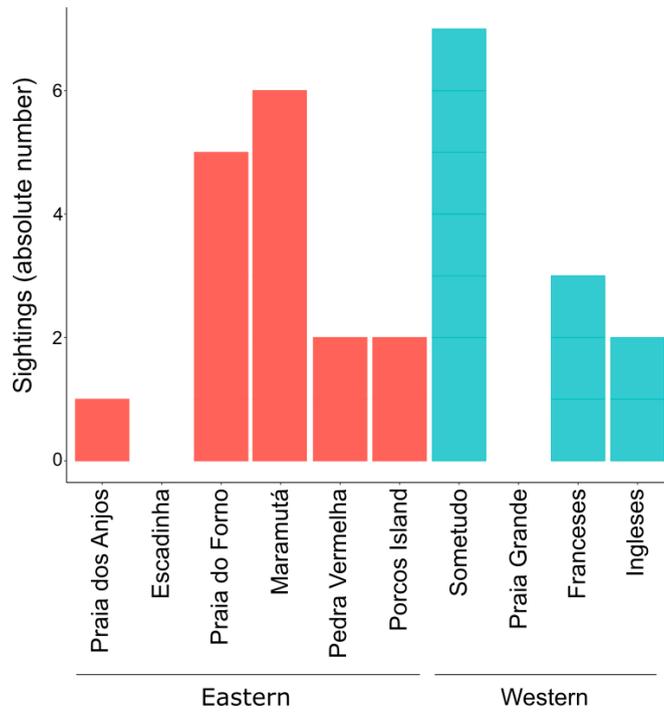
Sup. Figure 5: Comparative sightings of *Eretmochelys imbricata* among sampled sites and locations.
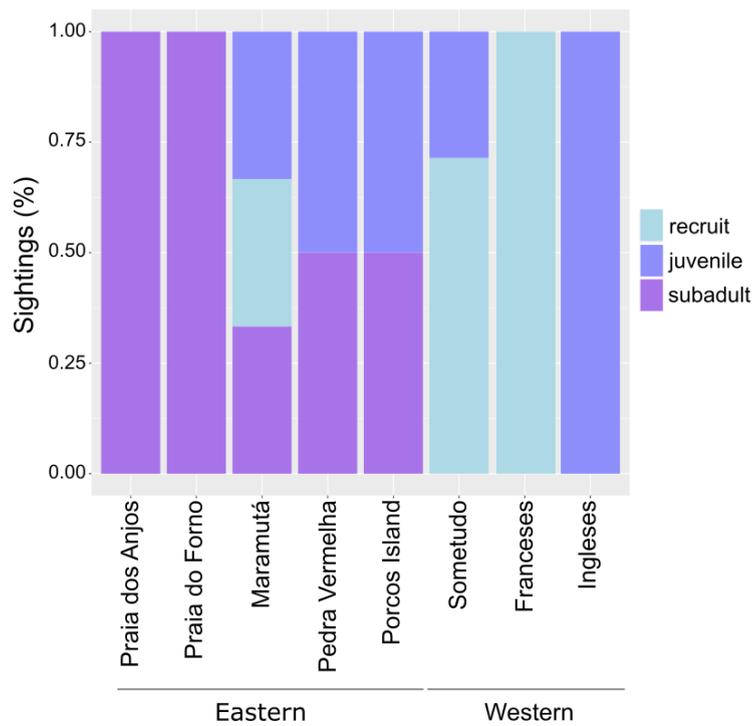
Sup. Figure 6: Comparative percentage sightings of different life stages (recruit, juvenile and subadult) of *Eretmochelys imbricata* according to locations (eastern and western).
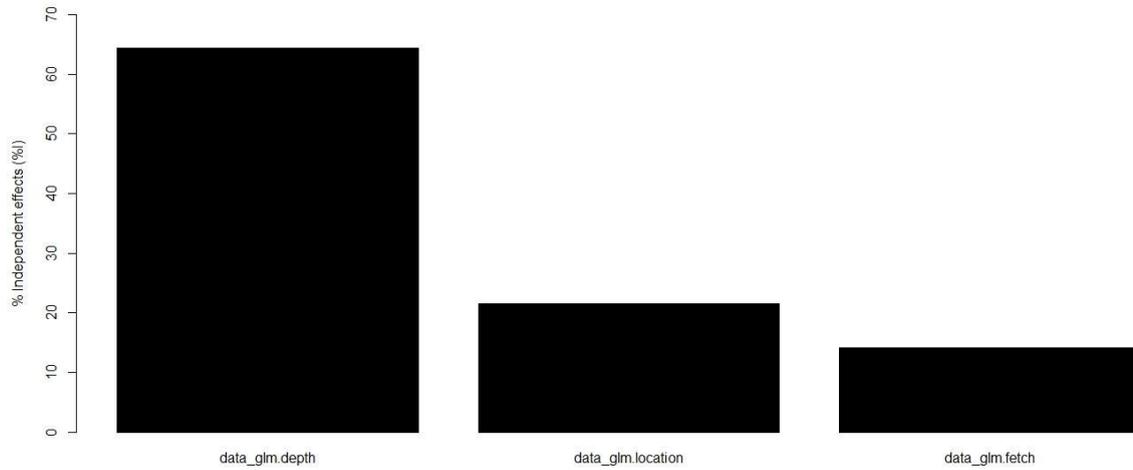
Sup. Figure 7: Relative importance of each statistically significant variable from the best generalized linear model for *Chelonia mydas*. Independent effects: percentage likelihood, ascertained by hierarchical partitioning, that each habitat variable contributes to variation in the presence of green turtles.