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# Spatial distribution of sea turtles on South Atlantic subtropical reefs

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ABSTRACT: Environmental conditions have a strong influence on sea turtle population dynamics. Sea turtles spend most of their lives in foraging areas; however, there is a lack of information on how oceanographic and biological parameters determine habitat use and density. Here, we estimated density of green turtles *Chelonia mydas* and hawksbill turtles *Eretmochelys imbricata* in a South Atlantic foraging area (Arraial do Cabo, Brazil). We also investigated the influence of environmental variables (wind fetch, temperature, depth, and visibility) and benthic composition on the distribution of turtles. Surveyed sites were split between a colder, more wave-exposed location (western), and a warmer, more sheltered location (eastern). To ensure that these mobile and sparsely distributed species were adequately surveyed, underwater visual censuses (timed transects) were conducted. Sea turtle densities were significantly different between warm/sheltered and cold/wave-exposed locations. *C. mydas* were almost 10 times more frequently sighted than *E. imbricata*. The local distribution of *E. imbricata* mirrored large-scale latitudinal patterns, where this tropical species is dominant on warmer reefs (similar to habitat conditions found at the eastern location). It was not possible to assess the environmental influence on *E. imbricata* sightings due to their low density. *C. mydas* were frequently sighted in the cold/exposed sites and negatively correlated with depth. Overall, the density of *E. imbricata* and *C. mydas* suggests that Arraial do Cabo is an important feeding ground in the western Atlantic Ocean. This study highlights that visual census can produce reliable density estimates of sea turtles in foraging areas.

KEY WORDS: Density estimates · Foraging area · Cheloniidae · Underwater visual survey



## 1. INTRODUCTION

The historical population declines of sea turtles affect the extent to which they fulfil their roles in maintaining the structure and function of marine ecosystems (Jackson et al. 2001, Bjorndal & Jackson 2003). Identifying a reliable baseline to assess trends in sea turtle populations is challenging because, in the Atlantic Ocean at least, the declines are generally believed to extend back prior to the pre-Columbian era (Frazier 2003). However, setting pre-human-exploitation levels as baselines for assessing population trends is perhaps an unsustainable recovery goal (Bjorndal & Bolten 2003). Existing and ongoing degradation of marine habitats means that it could be difficult to maintain sea turtle populations at historical abundance levels (León & Bjorndal 2002, Christianen et al. 2014). There are certainly reports of populations increasing at some nesting sites (Mazaris et al. 2017, Broderick & Patricio 2019), while the condition of key foraging grounds (e.g. seagrass fields and coral reefs) used by these recovering nesting populations is often unknown or declining (Jackson et al. 2001, Duarte et al. 2020). Hawksbill *Eretmochelys imbricata* and green turtles *Chelonia mydas*, for instance, inhabit mangroves, rocky, and coral reef systems throughout their life, yet density or abundance data are largely unknown, which hampers further

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studies of population status (Hamann et al. 2010, Goatley et al. 2012).

Estimating population density is a necessary baseline to inform appropriate management and conservation initiatives (Rees et al. 2016, Becker et al. 2019). Sea turtles are long-lived marine species with complex spatial population structures. Their vast geographical ranges and delayed sexual maturity require large-scale monitoring efforts (Rees et al. 2016). Most sea turtle population studies have focussed on breeding females in nesting beaches, biasing holistic ecological understanding (Bjorndal & Bolten 2000). This represents a major limitation for understanding sea turtle ecology, for which juveniles are the most abundant individuals of a population (Wildermann et al. 2018). There are fewer in-water studies of sea turtle density most likely due to logistical challenges, for instance, widely dispersed habitats and the propensity of sea turtles to spend most of their time underwater (Hamann et al. 2010). Long-term studies in foraging areas have advanced the knowledge on foraging ecology, recruitment, residency time, home range size, and maturity estimates (e.g. Bjorndal et al. 2000, Bellini et al. 2019). However, there is still a need for a better understanding of habitat use and dynamics of juvenile foraging aggregations (Wildermann et al. 2018).

A variety of techniques have been used to survey sea turtles in foraging areas (Herren et al. 2018). These in-water methods can be grouped into 3 general categories: catch per unit effort (CPUE), capture–mark–recapture (CMR), and line/strip transects (see Bjorndal & Bolten 2000). Once a question or aim of the survey is established, the ratio between costs and benefits of the techniques should be the primary concern when deciding on a technique (Mancini et al. 2015). CMR is the most commonly applied method to obtain information on demographic parameters (e.g. growth and survival rates), migration, and population size (see Bellini et al. 2013, 2019, Bjorndal et al. 2016) because it enables individuals to be followed over time. Captures (CPUE and CMR) allow identification and sampling of individual animals. However, most CPUE and CMR methods involve physically capturing an animal, and thus can be invasive and time-consuming (Mancini et al. 2015). Boat-based and aerial line/strip transects can cover a larger spatial area, but both methods can suffer from species misidentification, unknown values for sex, and high costs (Bjorndal & Bolten 2000). Strip transects by means of underwater visual census (UVC) is a widespread non-destructive technique largely used to assess reef fish assemblages (e.g. Brock 1982), but it has been rarely applied to sea turtles (e.g. Mancini et al. 2015, Becker et al. 2019). UVC implies visual identification instead of manipulative approaches, which in some habitats can reduce sampling time and costs. Timed transects (a UVC method) are appropriate for large-bodied and highly mobile species (Hill & Wilkinson 2004), which generally show sparse distributions and may occupy large areas (Choat & Pears 2003).

Knowledge of the distribution, movement, and habitat use by sea turtles is fundamental to identify key foraging areas for protection. Thus, it is essential to understand what environmental variables determine turtle spatial ecology within foraging habitats (Hamann et al. 2010). Environmental conditions have a strong influence on sea turtle populational parameters (e.g. population size, birth rates, mortality, and sex ratio) (Christiansen et al. 2017). Sea turtles have particular requirements regarding environmental conditions for their productivity (i.e. somatic growth and reproduction) (Bjorndal et al. 2016). Changes in the surrounding temperature and salinity, for instance, could affect metabolic rates and consequently influence growth rates (Diez & van Dam 2002). Additional environment features include food availability and quality, resource competition, and predator pressure (León & Bjorndal 2002), influencing resource acquisition and energy allocation (Williard 2013, Bjorndal et al. 2016). The interplay between density and local environmental conditions can help define how space is used and what defines 'optimum' foraging habitats, in terms of both their biological value and their importance for population viability of resident sea turtles (Hamann et al. 2010).

Considering the gap of information about sea turtle ecology in foraging areas, we investigated the influence of environmental variables on turtle densities and spatial distribution on subtropical rocky reefs on the Brazilian coast combining free and autonomous diving sampling methods. We hypothesised that the majority of turtle sightings would occur at the warm/sheltered reefs, as higher temperatures would be more favourable for ectotherms and the lower hydrodynamics may offer better conditions for foraging. However, food abundance may play a significant role in the distribution of turtles, and we predicted that sites with higher resource availability would have higher densities. The results are expected to highlight the differences in aggregation structure between cold/exposed (western location) and warm/sheltered (eastern location) reefs and the need for incorporating standardized methods for estimating sea turtle densities.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study was carried out between January and August 2019 at Arraial do Cabo (22° 57′ S, 42° 01′ W) on the southeastern coast of Brazil, where sea surface temperatures are often cooler than nearby coastal and offshore waters (Fig. 1a). The region of Arraial do Cabo is part of a sustainable use conservation unit (Arraial do Cabo Marine Extractive Reserve, ICMBio 2020) where only local traditional fishers are allowed to exploit resources. Yet, no-take zones were not established, and many types of fishing gear are used, from nets to spearfishing, and enforcement is considered inefficient (Bender et al. 2014). Arraial do Cabo is formed by an isthmus and 2 islands where granitic rocky shores dominate. The region is also influenced by an asymmetrical and semi-diurnal microtidal regime (high: 1.0 m and low: 0.06–0.025 m) (Castro et al. 2014). Small-scale upwelling processes often occur as a result of the prevailing winds and coastal morphology, creating 2 main distinct locations within which sampling sites were allocated (Fig. 1b): the western location, with exposed shores, directly affected by upwelling waters (mean temperature: <18°C); and the eastern location, with shallower, sheltered coastlines reaching comparatively higher average temperatures (mean temperature: >22°C) (Valentin 1984, Cordeiro et al. 2016). The western location is also characterized by deeper reefs ranging from 5 to 25 m. The eastern location is formed by shallow reefs (0–12 m), averaging up to 6 m deep. These features favour the accumulation of species with both tropical and temperate affinities; hence, this region has ecological and biogeographic importance (Yoneshigue-Valentin & Valentin 1992, Ferreira et al. 2001, Aued et al. 2018). Habitat type differences are inherent to location (eastern and western) because of local geography and upwelling influence (Cordeiro et al. 2016). Sampling sites accounted for the gradient of upwelling exposure and isolation (accessibility from the mainland), consisting of 6 sites at the eastern location and 4 sites at the western location (Fig. 1b).

### 2.2. Wave exposure

Wave exposure was calculated using fetch as a proxy to quantify the differences in both locations and among sites (Garcon et al. 2010). Fetch was calculated as the unobstructed length of water over

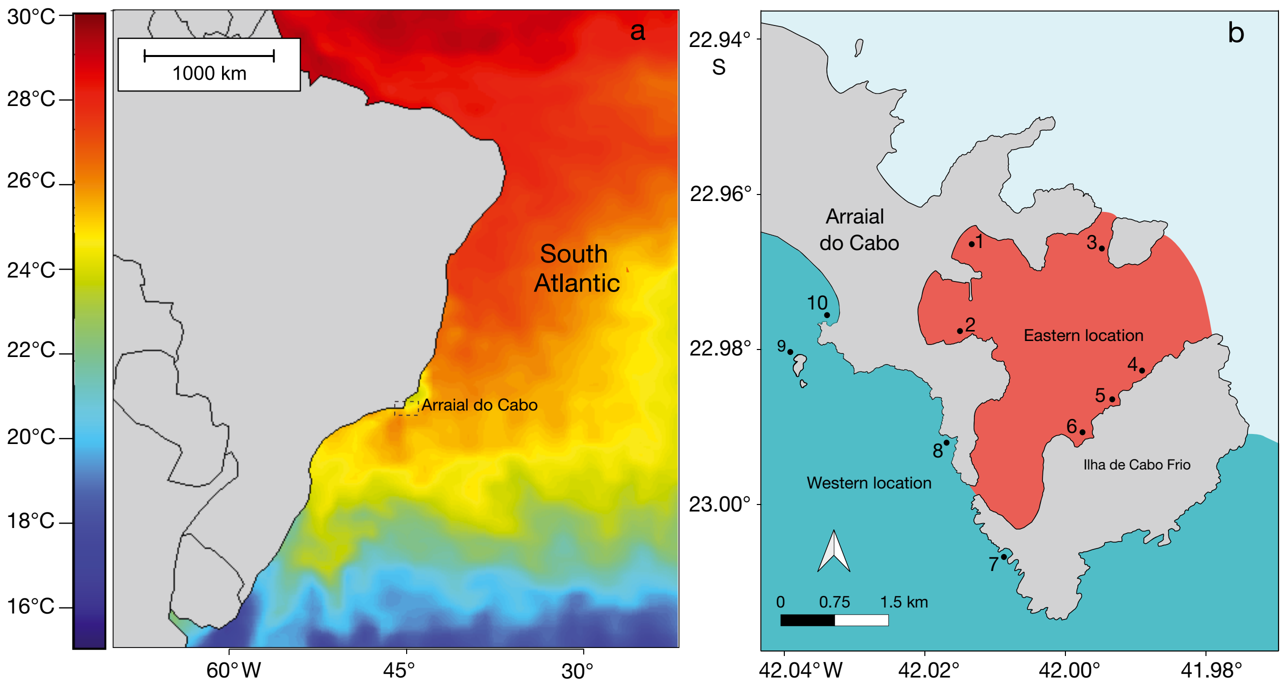


Fig. 1. (a) Sea surface temperatures in the South Atlantic. The location of Arraial do Cabo is indicated by the dashed square. (b) Arraial do Cabo region (Rio de Janeiro, Brazil), indicating the sampled sites. Red = eastern location, indirectly influenced by upwelling (>22°C); turquoise = western location, directly influenced by upwelling (<20°C). The maximum local depth at each site is shown inside parentheses: 1 = Praia do Forno (3 m); 2 = Praia dos Anjos (7 m); 3 = Porcos (12 m); 4 = Escadinha (8 m); 5 = Pedra Vermelha (6 m); 6 = Maramutá (6 m); 7 = Ingleses (25 m); 8 = Sometudo (15 m); 9 = Franceses (25 m); 10 = Praia Grande (5 m)

which wind from a certain direction can blow (see full details in Burrows et al. 2008). Briefly, a map of wave exposure for Arraial do Cabo was produced based on the total fetch as the distance to the nearest coast around any point on the map and 16 calculated equiangular fetch vectors with a maximum distance of 200 km (Burrows et al. 2008). The higher the fetch from a certain direction, the more energy is imparted onto the water surface, resulting in a lower wind shadow and larger wave exposure (Garcon et al. 2010). A site located at a straight open coast with no barriers for wind would have 8 out of 16 sectors with maximum fetch values (in this case 200 km). The final fetch values for each site were calculated as the mean fetch over all 16 vectors.

### 2.3. Benthic community characterization

Benthic habitat surveys were conducted at each site between May and June 2019 to quantitatively describe the spatial distribution of potential food resources for foraging sea turtles. Sites were surveyed according to their maximum depth: 1–6 m (shallow) and 6–12 m (mid-deep), unless only 1 depth stratum was available. The benthic community was characterized using 25 $cm^2$ photoquadrats (n = 10) along 200 m transects at each depth stratum and site. All images obtained from the photoquadrats were analysed using photoQuad software (Trygonis & Sini 2012) by laying 30 stratified points on each image and identifying the organism underneath. Benthic organisms were classified in morpho-functional groups as articulated coralline algae, crustose coralline algae, epilithic algal matrix, macroalgae, cyanobacteria, scleractinian coral, octocoral, sponge, zoanthid, or other invertebrates (anemone, ascidian, Cirripedia, echinoderms, Gastropoda, Hydrozoa) (adapted from Cordeiro et al. 2016, Aued et al. 2018).

### 2.4. Sea turtle survey

The sea turtle survey was carried out between January and August 2019 independently from benthic surveys but at the same sites and depths. This period was chosen to avoid cold front-associated high wave surge, taking advantage of the best water visibility. Sampling was conducted by snorkelling (water depth ≤5 m) and SCUBA diving (water depth ≥6 m). During surveys, 2 observers (for safety reasons) swam along a transect, but only 1 diver (J. Mello-Fonseca) was responsible for data collection. Sea turtle density was evaluated at each site using data from underwater timed strip transects (10 min long, 6 m wide) 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 determined that sea turtles did not respond negatively to divers or scooters. This method was already tested for fish species and did not show negative effects on fish behaviour (Cordeiro et al. 2016). Despite the possible noise generated by the propeller, which could scare some individuals, such behaviour was not observed for sea turtle species within our transects. It must be considered that the study area suffers high interference from anthropogenic noises, especially during the daytime, which corresponds to periods of intense tourism and fishing activities (Campbell et al. 2019).

All transects were georeferenced at the beginning and end of the survey. Thus, the length of transects (6 m width) was calculated based on the distance between the start and endpoints, following the contour of the coast (Cordeiro et al. 2016). Surveys were conducted during the daytime between 09:00 and 14:00 h. Vertically replicated censuses were continuously performed for a better understanding of the turtle vertical distribution. Maximum depth differs among sites, thus, transects were conducted by stratum. At reefs with maximum depths of ≤8 m, only 1 depth stratum was surveyed (i.e. shallow). For areas with depths >8 m, 2 strata were surveyed: shallow (1–6 m) and mid-depth (6–12 m). At least 6 transects were surveyed at each depth stratum at each site. The number of transects (eastern = 112 and western = 81) per site was proportional to the maximum area of each site (i.e. a higher number of transects to cover the larger areas): Praia do Forno (7); Praia dos Anjos (7); Porcos (34); Escadinha (6); Pedra Vermelha (26); Maramutá (32); Ingleses (30); Sometudo (29); Franceses (16); Praia Grande (6).

All sighted individual sea turtles were identified by species, and their sizes (straight carapace length, SCL) were visually estimated in intervals of 5 cm to minimize possible errors. All data were recorded on a PVC slate while the diver followed the transect. Green turtles were classified as recent recruits (≤40 cm SCL), juveniles (41–65 cm SCL), subadults (66–90 cm SCL), and adult-sized (>91 cm SCL) (Almeida et al. 2011). The size classes for hawksbill turtles are slightly smaller: recruits (≤35 cm SCL), juveniles (36–60 cm SCL), subadults (60–80 cm SCL), and adults (>81 cm SCL) (Sanches & Bellini 1999). As the length of each transect differed, density was calculated as the number of turtles per total transect area standardized to individuals per 100 $m^2$. Visibility was measured as the horizontal distance at which 2 divers could see each other using a 20 m tape measure, while depth and temperature were based on dive computer readings (Mares® Puck Pro). All samplings were performed under permit SISBIO #64976-1(Instituto Chico Mendes de Conservação da Biodiversidade, https://sicae.sisicmbio.icmbio.gov.br/usuario-externo/login).

### 2.5. Data analysis

To capture the fetch effect on the occurrence of sea turtles, categories were created following natural breaks of mean fetch values, varying from 1 to 5, with the lowest values (1) associated with the most sheltered site. Differences in environmental characteristics (fetch, temperature, and depth) were assessed between locations by metric multidimensional scaling analysis (MDS) with Euclidean dissimilarity using the function 'metaMDS' within the R package 'vegan' (Oksanen et al. 2011). Before benthic community composition analysis, percent cover data were transformed by the arcsine-square root to linearize distance relationships. The mean macroalgae relative cover differences between locations (eastern/western) were tested with a *t*-test.

A generalized linear model (GLM) with negative binomial distribution and a log link function was built to investigate the potential relationship of environmental variables on the total number of green turtle individual sightings per transect. To adequately deal with the zero-inflation in the data, a Hurdle model was performed using the 'glmmTMB' package (Magnusson et al. 2017). The Hurdle model is a 2-component model with a truncated part for positive counts and a hurdle part that models the zero counts. The independent variables were location, fetch, temperature, visibility, and depth (used here as a continuous variable). As there is intrinsic variability among sites, this factor (i.e. site) was nested within the location in the models. To balance the uneven survey effort, we used the log-transformed area of transects as an offset to account for sampling intensity.

After a visual inspection of the response variable against each explanatory variable (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m678p125_supp.pdf), it was clear that some relationships were nonlinear. However, the inclusion of quadratic terms for fetch and temperature variables did not improve the model performance and were not retained in the final models. Multicollinearity was evaluated using a variance inflation factor applied to the explanatory variables of the model using the 'performance' package (Lüdecke et al. 2019). 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 (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 v. 3.6.1 (R Core Team 2016).

## 3. RESULTS

### 3.1. Environmental variables

Differences in environmental characteristics (fetch, temperature, and depth) among sites were observed and samples were divided into 2 groups (western and eastern locations) (Fig. 2a). The eastern and western locations showed differences, with high wave exposure to the west, and lower wave exposure to the east (Fig. 2b). The coastline of the outer western location had the highest mean fetch values (50–63 km), but the coast of Praia Grande forms a small embayment (lower fetch value 37 km). Sites at the eastern location had lower mean fetch values (0.6–13 km), because of shelter from the easterlies provided by Ilha de Cabo Frio (Fig. 2), but the eastern location still has wind-facing sites with higher mean fetch values (Praia dos Anjos: 25 km and Porcos: 38 km).

Macroalgae had higher cover at the western location (paired *t*-test, $t_{162.82} = -2.13$, $p < 0.05$). The class Rhodophyceae was dominant at both locations (eastern = 47%, western = 75%), and the genus *Gelidium* was the most frequent taxon. At 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* was only detected at the western location. The coral species *Mussismilia hispida* and *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 articulated coralline algae were the greater contributor for the western benthic community (Fig. 3). No corals or zoanthids were found at the western location.

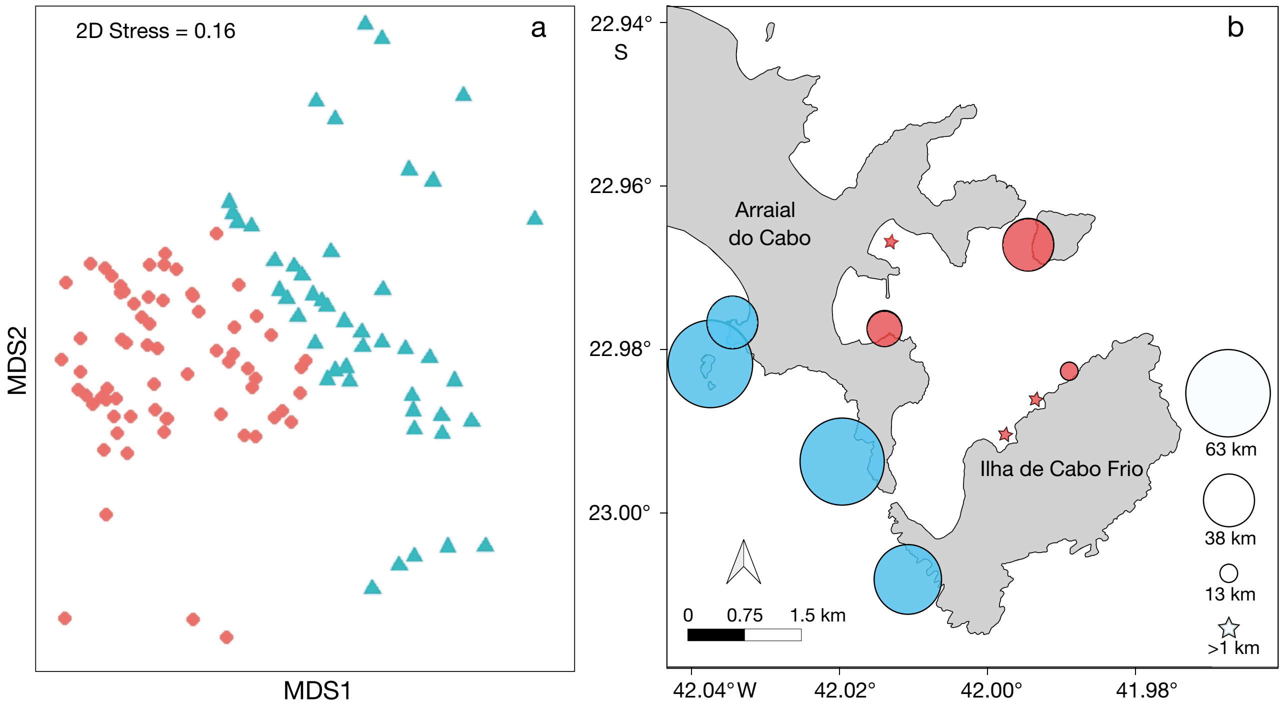


Fig. 2. (a) Multidimensional scaling (MDS) of environmental variables (fetch, temperature, depth, and visibility), showing the similarities between locations. Locations: eastern = warm/protected reef (red diamonds), western = cold/exposed reef (blue triangles). (b) Mean fetch values calculated with a maximum distance of 200 km using 16 equiangular fetch vectors in Arraial do Cabo. Blue (red) represents the western (eastern) location

### 3.2. Sea turtle density

A total of 193 timed transects (32.16 h) were conducted across 10 sites, with a median transect length of 232.5 m (Q1 = 175.0, Q3 = 286.0, minimum = 107.0, maximum = 352.0) covering 2261.33 m of the coastline. The mean length of transects varied significantly only between locations (western = 180.47 m vs. eastern = 246.20 m; Wilcoxon signed-rank test = 14 980, $p < 0.05$). Across all of the surveyed sites and all transect surveys, 305 sea turtles of 2 species were observed. Green turtles (90.81 % of total observations, n = 277) were nearly 10 times more frequently sighted than hawksbills (9.18 %, n = 28).

Green turtles occurred at all surveyed sites, at an average density of 0.10 ± 0.14 turtle 100 $m^{-2}$ (Fig. 4a), and a sighting rate of 8.61 turtles $h^{-1}$ in underwater surveys. Although hawksbill turtles were observed at almost all sites, their density was lower, averaging 0.01 ± 0.03 turtle 100 $m^{-2}$ (Fig. 5a). The sighting rate for hawksbill turtles was 0.87 turtle $h^{-1}$. As hawksbill turtles had low overall density, they were not included in further analysis. Sighting hotspots for hawksbill turtles overlapped with high-density areas for green turtles at Praia do Forno and Sometudo (Figs. 4a & 5a).

Most turtles sighted were in the immature size classes, with higher proportions of juvenile green turtles (45–60 cm SCL; Fig. 4b) and smaller-sized juveniles of hawksbill (<45 cm SCL; Fig. 5b). Subadult hawksbills (60–80 cm SCL) were observed only at the eastern location where waters are warmer. Although there was no statistical significance, large green turtles (≥60 cm SCL) were more frequently sighted at the eastern location, whereas small individuals (≤45 cm SCL) of both species were frequently sighted at the western location.

Green turtle density was influenced by location, fetch, and depth (Table 1), and they were less frequently sighted at the eastern location (Fig. 6a). Although the overall density was higher at the western location, the negative effect of fetch on green turtle density highlights the importance of some sheltered locations. Sites with minimum values of fetch (e.g. Praia do Forno and Maramutá) had mean standardized density similar to more exposed sites (e.g. Praia Grande). Depth was the most important variable to explain green turtle density (Table 2), with green turtles being predominantly sighted in shallower waters (1–6 m) (Fig. 6b). No variable was correlated with green turtle presence in the binomial model (Table 1).

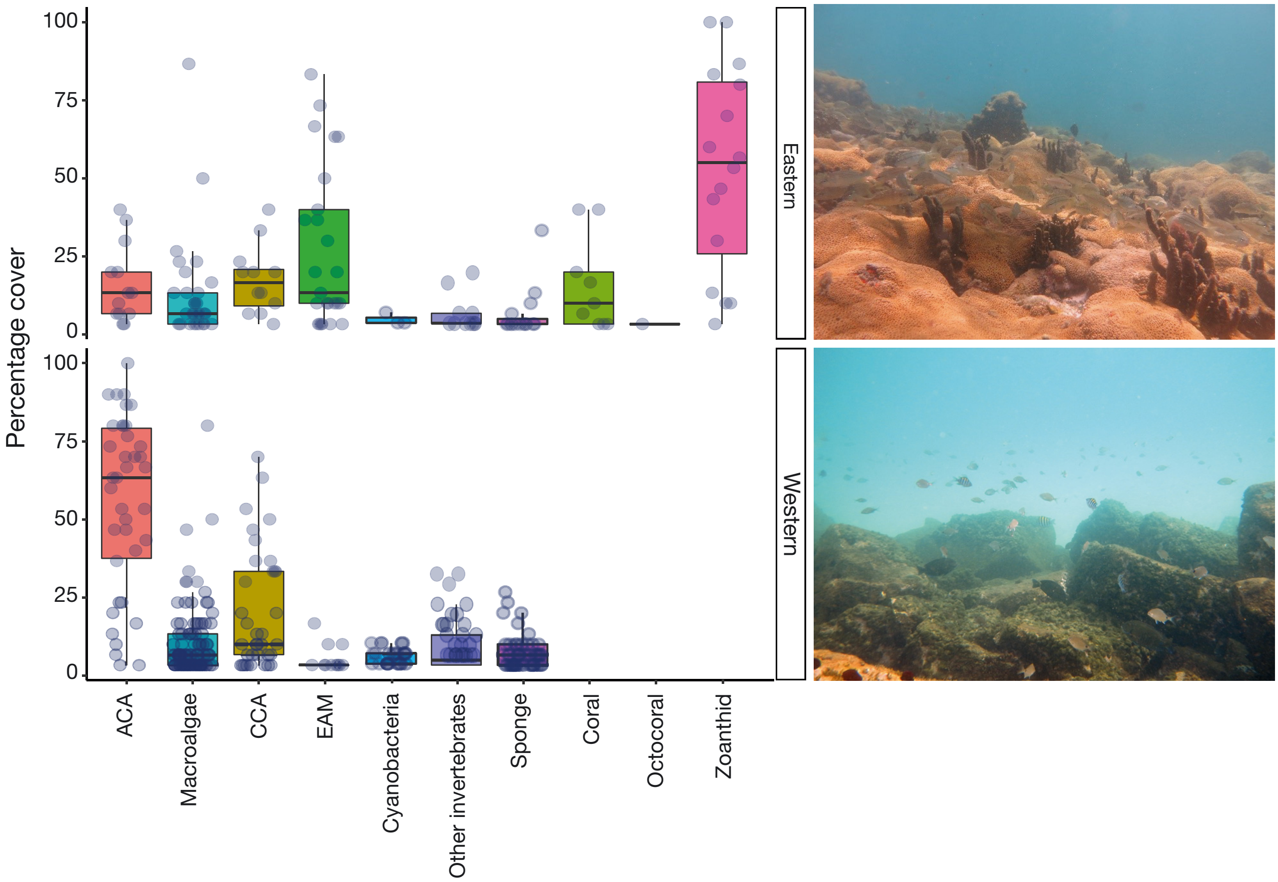


Fig. 3. Comparative percentage cover of benthic morpho-functional groups between eastern and western sites in Arraial do Cabo. ACA: articulated coralline algae; CCA: crustose coralline algae; EAM: epilithic algal matrix. Boxplots represent the median, Q1, and Q3, and whiskers represent the largest and smallest values when excluding outliers. Each dot represents standardized density from each underwater visual census

## 4. DISCUSSION

### 4.1. Spatial patterns

Herein, we provide the first assessment of environmental drivers of density and spatial distribution of *Chelonia mydas* and *Eretmochelys imbricata* in subtropical reefs of the Southwestern Atlantic. The distributional patterns of sea turtles are an effect of location (eastern and western), which are associated with gradients of temperature, wave exposure, and depth, plus benthic community composition. The latter functions as an important proxy of food availability. We found differences in size class distributions and overall density between eastern and western locations, suggesting a variation in habitat use, with recruits of both species approaching wave-exposed reefs (western location) and juveniles plus subadults occupying shallow warmer reefs (eastern location). Our results suggest that future comparative studies would benefit from standardized methods and replication to allow for foraging area comparisons, especially given the urgency of tracking habitat loss and pollution impacts worldwide.

The hawksbill is one of the most conservation-dependent sea turtle species (Mortimer & Donnelly 2008), and the reproductive area of the Brazilian hawksbill population (northern Brazil) is quite small compared to its historical distribution (Marcovaldi et al. 2011). Therefore, the reduced relative frequency of hawksbill turtle nesting may reflect its conservation status and its association with tropical reef habitats (Mortimer & Donnelly 2008). The hawksbill was also the least observed turtle species found in stranding monitoring at Arraial do Cabo (Reis et al. 2009, Tagliolatto et al. 2020); nevertheless, the Arraial do Cabo region has the highest hawksbill stranding concentration on the southern and southeastern Brazilian coast (Cantor et al. 2020, Tagliolatto et al. 2020). In our study, the western location had the low-

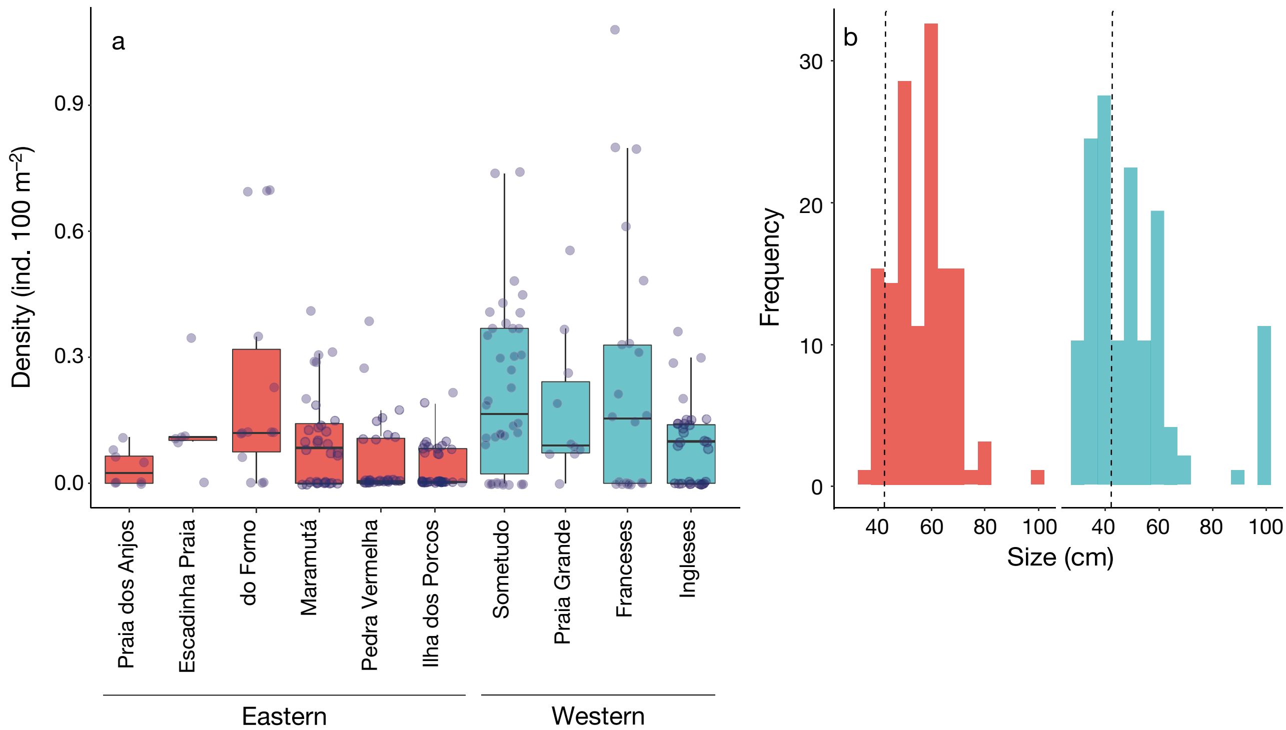


Fig. 4. (a) Comparative density of *Chelonia mydas* among sampled sites and locations in Arraial do Cabo (see Fig. 1). Boxplot parameters as in Fig. 3. (b) Frequency histogram of straight carapace length (SCL) of *C. mydas* according to location (eastern = red, western = blue). Dashed lines indicate maximum recruit size (≤40 cm SCL). Size was visually estimated

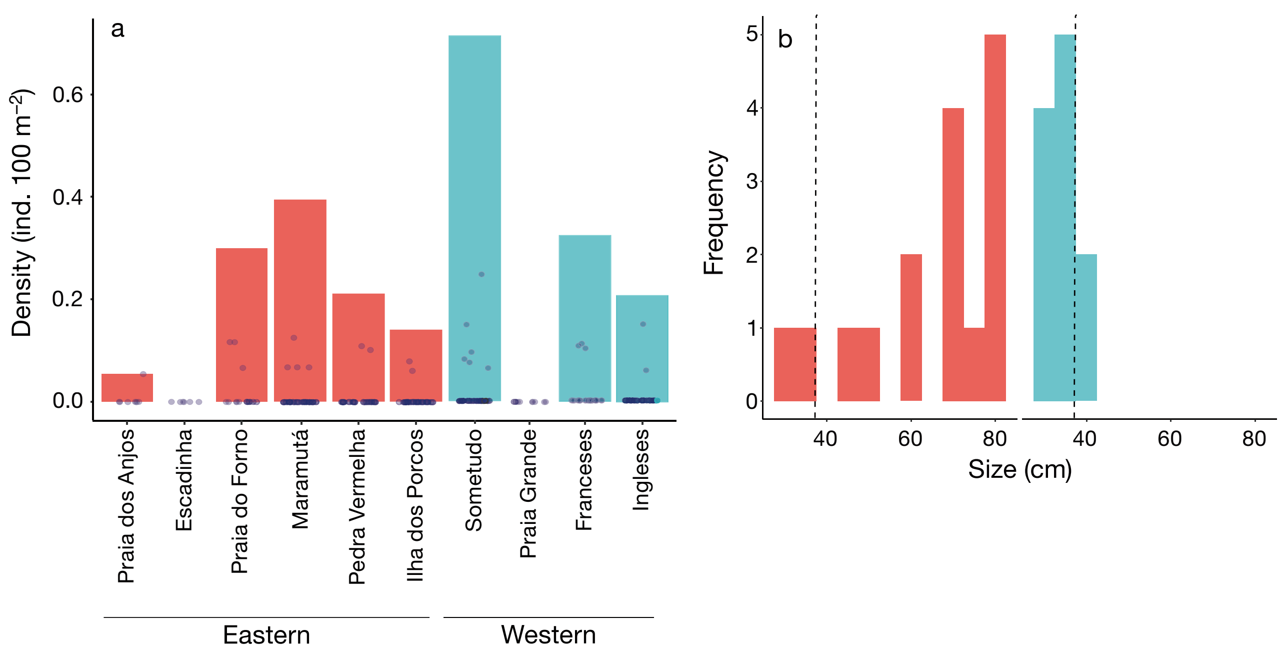


Fig. 5. (a) Comparative density of *Eretmochelys imbricata* among sampled sites and locations in Arraial do Cabo (Brazil). Each dot represents standardized density from each underwater visual census. (b) Frequency histogram of straight carapace length (SCL) of *E. imbricata* according to locations (eastern = red, western = blue). Dashed lines indicate maximum recruit size (≤35 cm SCL). Size was visually estimated

Table 1. Zero-altered model (negative binomial distribution) for the relationship between the sightings of *Chelonia mydas* and environmental drivers (location, fetch, and depth). Significant at 95% confidence

| | Estimate | SE | *Z* | p |
|---|---|---|---|---|
| Counting model | | | | |
| Intercept | 2.255 | 0.783 | 2.881 | 0.004* |
| Location | 3.067 | 1.343 | 2.285 | 0.022* |
| Fetch | −0.855 | 0.390 | −2.192 | 0.028* |
| Depth | −0.129 | 0.059 | −2.182 | 0.029* |
| Binomial model | | | | |
| Intercept | −0.542 | 0.344 | −1.578 | 0.115 |
| Location | −0.499 | 0.339 | −1.474 | 0.141 |
| Depth | 0.083 | 0.058 | 1.430 | 0.153 |

Table 2. Relative importance of each statistically significant variable from the best generalized linear model for *Chelonia mydas* in Arraial do Cabo. *I*: percentage likelihood, ascertained by hierarchical partitioning, that each habitat variable contributes to variation in the presence of green turtles

| Variable | Importance rank | *I* (%) |
|---|---|---|
| Depth | 1 | 64.13 |
| Location | 2 | 21.45 |
| Fetch | 3 | 14.42 |

est density value, composed of recruits and small juveniles (≤40 cm SCL), which may indicate that they are likely to be newly arrived from pelagic or developmental habitats. In contrast, the higher occurrence of larger juveniles and subadults hawksbill at the eastern location may represent individuals with higher residence time. Indeed, some individuals were confirmed by photo-ID monitoring to occupy the eastern location for over 5 yr with a very small home range (Ferreira 2020). Our study area, including the eastern and western locations, presents a gradient from tropical to subtropical habitats within a few kilometres, resembling the latitudinal variation found along the Brazilian coast (Ferreira et al. 2004). As hawksbills have an affinity toward tropical zones, the higher temperatures of the eastern locations may favour the permanent residence of larger individuals. Moreover, the eastern location has a rich tropical-like benthic community, such as sponges, zoanthids, and soft corals (Ferreira et al. 2001, Rogers et al. 2014), providing preferential feeding resources to hawksbill turtles (León & Bjorndal 2002, Martins et al. 2020). The presence of juvenile hawksbills at Arraial do Cabo indicate they use the area as a feeding ground, confirmed by intense foraging observations over *Palythoa caribaeorum* (Stampar et al. 2007, C. E. L. Ferreira unpubl. data)

Patterns of green turtle density were similar to the observed for subtropical, cold-affinity, herbivorous reef fish species. For instance, although species like *Diplodus argenteus* and *Kyphosus* spp. were present at the eastern location, their abundance is higher at colder western location, reflecting their wider distribution on subtropical zones. In contrast, reef fishes with tropical origins (parrotfishes and surgeonfishes) were also found in both locations but had lower biomasses at the western location (Cordeiro et al. 2016). The mean water temperature in the eastern location

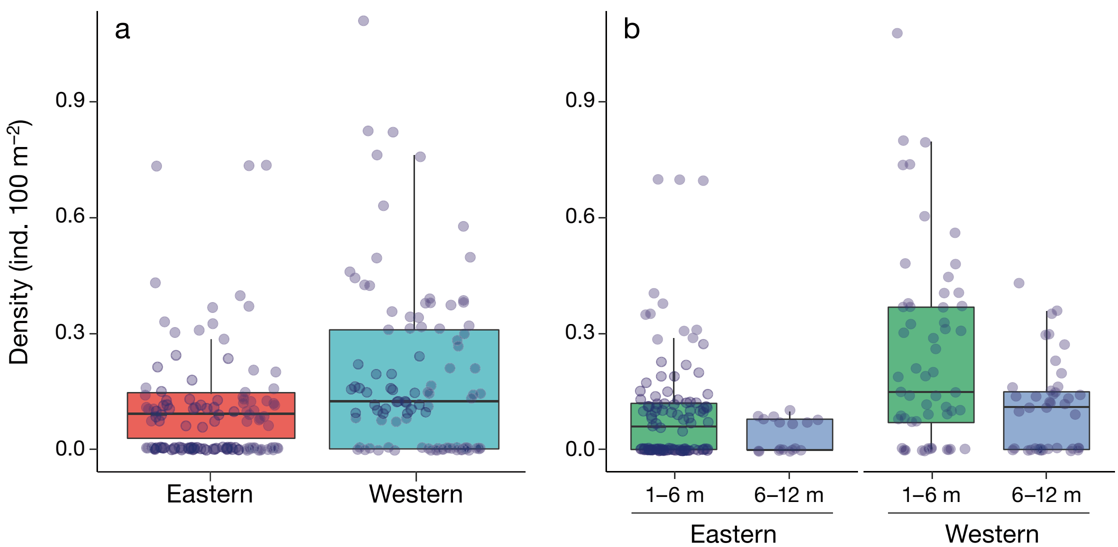


Fig. 6. Density of *Chelonia mydas* according to (a) location (eastern and western) and (b) depth stratum and location in Arraial do Cabo (Brazil). Boxplot parameters as in Fig. 3

is around 22°C, while in the western location mean temperature is about 18°C, frequently reaching 15°C in shallow depths (Coelho-Souza et al. 2012). Green turtles may be vulnerable to abrupt temperature decreases in the western location due to frequent upwelling events. This species has numerous physiological responses to cold water, such as a decrease in feeding rate (Southwood et al. 2003) and digestive efficiency (Bjorndal 1980). The inactivity threshold of green turtles is 15°C (Williard 2013), but changes in diving behaviour and foraging rates may occur at higher temperatures (around 22°C) (Southwood et al. 2003, 2006). Similarly, herbivorous fish from the eastern and western locations have reduced bite rates in response to the low temperature (18°C) (Ferreira et al. 1998, Mendes et al. 2009, Longo et al. 2014). During sampling, only temperatures above 18°C were recorded, thus additional local studies are required to investigate the thermal constraints in green turtle behaviour and habitat use.

Green turtles were associated with shallow sheltered areas with abundant food resources. Our model showed that turtles were more frequently sighted at depths between 1 and 6 m. The local rocky shore structural complexity could potentially influence the sighting of turtles hiding under hanging rocks or small caves, but the general complexity decreases with depth (Cordeiro et al. 2014) and shelter availability is lower at deeper sites. Indeed, routine dive depth for active juvenile green turtles in tropical areas reaches <8 m (Williard 2013), with turtles from some populations known to spend most of their time at depths ≤5 m (Hazel et al. 2009). Individuals occupying shallow areas may spend less energy in respiratory intervals and take advantage of warmer waters (Christiansen et al. 2017). Moreover, the use of shallow areas could enable longer feeding times (e.g. Seminoff et al. 2002, Fuentes et al. 2006, Reisser et al. 2013). Green turtle distribution overlaps with the stratum of the highest macroalgae cover at the study area, where potential selected food types were more abundant (Cordeiro et. al 2016). Foraging at these shallow but wavy habitats is energetically costly. Thus, green turtles are probably benefiting from the better nutritional composition and/or digestibility of this macroalgae community.

The macroalgae *Sargassum vulgare*, *Ulva lactuca*, *Gelidiella acerosa*, and *Pterocladiella capillacea* are common food items in the diet of green turtles (Awabdi et al. 2013, Di Beneditto et al. 2017). Here, Gelidiales (e.g. *G. acerosa* and *P. capillacea*) were the most abundant macroalgae throughout eastern and western locations, and *Sargassum* sp. was the second most abundant at the western location. Nevertheless, food availability alone cannot explain the preference of green turtles 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.

### 4.2. Density estimates

Nesting sites and primary foraging areas of hawksbill turtles are located in tropical northeastern Brazil (Marcovaldi et al. 2007). However, there is little knowledge on foraging turtles on the southeast and south coast (Marcovaldi et al. 2011). Most studies in foraging areas are qualitative, lack density estimates, and/or are geographically restricted (Bjorndal & Bolten 2000, Proietti et al. 2012, Fernandes et al. 2017). Considering only CPUE (sea turtle sightings per hour), it seems that the encounter rate of hawksbill turtles decreases towards higher latitudes (Table S1). However, these results must be examined with caution, as CPUE estimates from observational surveys may be interpreted as an indirect qualitative index rather than a quantitative variable (Bjorndal & Bolten 2000). As CPUE estimates are often not standardized by area and are usually biased towards searching effort and success, it is not recommended to compare the measurements with other methods such as sightings per transect (Krebs 1999). Associating standardized techniques to the assessment of spatial distribution and habitat preferences provides scientific bases to select key areas for the conservation of the Critically Endangered hawksbill turtle.

The global increasing population trends of green turtles are a result of global and national conservation action success (Almeida et al. 2011, Mazaris et al. 2017, Duarte et al. 2020). Population recovery is reflected in the recent IUCN downlisting of the South Atlantic subpopulation to Least Concern (Broderick & Patricio 2019). This means turtles are back to residing at many coastal sites, but we do not yet understand their contribution as mega consumers to local food webs. Our study presents what seems to be one of the highest comparative numbers of green turtles for a foraging area in the world (Table S2). Arraial do Cabo is similar in density (ca. 10 turtles $ha^{-1}$) to other locally dense aggregations, such as the Lakshadweep Archipelago, India (11.13 turtles $ha^{-1}$ in 2007) (Gangal et al. 2021), Mayotte Island, Mozambique Channel (24 turtles $ha^{-1}$) (Ballorain et al. 2010), and Derawan Island, Indonesia (20.6 turtles $ha^{-1}$)

(Christianen et al. 2014). Green turtles have the potential to play significant positive and negative roles in marine ecosystem restoration (Bjorndal & Jackson 2003, Christianen et al. 2021, Gangal et al. 2021). In Arraial do Cabo, large-bodied herbivorous fishes (parrotfishes) have been severely overfished, with some species being considered functionally extinct (Bender et al. 2014). In this scenario, green turtles at the densities detected can play a unique functional role in terms of mobility and dietary flexibility, complementing or even compensating the role of herbivorous fishes and urchins on reef systems (Goatley et al. 2012, Cardona et al. 2020, Cordeiro et al. 2020). Thus, it is crucial to understand the potential effects of green turtles as macroalgae consumers over different spatial scales for the effective management of habitats and their ecosystem services.

Underwater censuses are selective in size, appearance, and behaviour of target species, and density estimates are based on sightings (Brock 1982). In consequence, the effectiveness of sighting an animal along a transect is highly influenced by its availability to the observer (i.e. animals present in the search area but not seen) and perception bias of the observer (i.e. animals potentially visible but missed by observers) (Fuentes et al. 2015). For instance, the habitat type (e.g. availability of shelter) could influence turtle sightings (e.g. Williams et al. 2017). Moreover, shy/resting turtles are more likely to be missed, as they might hide or remain cryptic and therefore be less detectable (Mancini et al. 2015). However, the local habitat in our study has structural complexity which decreases with depth, and sea turtles usually rest in the sand and rocky reef interface or over bare rocks (Cordeiro et al. 2014, J. Mello-Fonseca unpubl. data), making them easier to be sighted. Furthermore, larger and longer transects generate less bias for highly mobile species, and fast swimming speeds of the observer should increase the precision of detections through reduced potential for double counting (Hill & Wilkinson 2004, Pais & Cabral 2018). Because our method is advantageous and statistically reliable for monitoring sea turtles at coastal foraging areas, we recommend the addition of an extra observer and transect video recording to reduce bias. The great practical advantage of timed in-person or video transects is the simultaneous assessment of turtle density and characteristics (e.g. species, sex, behaviour, size, health conditions) across spatial scales and the ability to cross check or have 2 observers score data from the recordings. Here, we provide a survey framework to aid in-water sampling methods and facilitate replication in monitoring programmes (see Table S3).

### 4.3. Management implications

The study area is located within a marine protected area with a recently elaborated management plan in which turtle species management was included but no specific monitoring activities or regulations were set yet. The eastern location, which is comparatively sheltered, is more affected by human activities, including mariculture, fishing, sewage discharge, harbour activity, and intense aquatic tourism (Rogers et al. 2014, Giglio et al. 2017, Sarmento et al. 2020). Habitat use by sea turtles in the eastern location is a matter of concern, as increasing tourism throughout the region has been negatively affecting local sea turtle aggregations through increased harassment, boat strikes, and acoustic and other pollution sources (Giglio et al. 2017, Lima et al. 2018, Campbell et al. 2019, Tagliolatto et al. 2020). The western location is less frequented by touristic operations, but it is likewise highly influenced by fishing (Silva et al. 2014). Bycatch is the main threat to sea turtles worldwide (Wallace et al. 2010). Arraial do Cabo is a traditional artisanal fishing village (Bender et al. 2014), but there is no monitoring of incidental catches of sea turtles, while reports on social media are numerous (J. Mello-Fonseca unpubl. data) and interaction is common (Awabdi 2019). The data included in our study are important as a baseline but also as a proposed method potentially applied for such species monitoring locally and other similar marine protected areas where CMR studies are not possible.

Quantifying the density of sea turtles in foraging areas is much-need information to support local and international conservation efforts (Hamann et al. 2010), particularly for juvenile sea turtles that are under constant pressure from anthropogenic impacts (Lima et al. 2018, Wildermann et al. 2018). We highlight the scarcity of in-water surveyed areas along the Brazilian coast. With almost 8000 km of coastline, from tropical to subtropical realms, including 4 oceanic islands, the Brazilian province (Aued et al. 2018) provides quality habitat for sea turtle development but is still data deficient. When financial resources are insufficient, low-cost methods like freediving transects can produce accurate estimates of density in shallow foraging areas. The survey recommendations provided here can be replicable by independent researchers or conservation groups in priority regions where information is needed and resources are scarce.

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