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High fidelity of sea turtles to their foraging grounds revealed by satellite tracking and capture-mark-recapture: New insights for the establishment of key marine conservation areas

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ABSTRACT

Movement ecology studies are essential to protect highly mobile threatened species such as the green turtle (*Chelonia mydas*), classified as an endangered species by the IUCN. In 2019, the South Atlantic subpopulation has been downlisted to 'Least Concern', but the maintenance of this status strongly relies on the pursuit of research and conservation, especially on immatures, which contribute to the demographic renewal of this subpopulation. Identifying marine areas used by immatures is therefore crucial to implement efficient measures for the conservation of sea turtles in the Caribbean. We analysed data of capture-mark-recapture of 107 (out of 299) immatures recaptured at least once in Martinique, and satellite tracked 24 immatures to investigate their site fidelity and habitat use. Our results revealed a strong fidelity to foraging grounds, with mean residence times higher than 2 years, and with a high degree of affinity for specific areas within the coastal marine vegetation strip. Home ranges (95% kernel contour) and core areas (50% kernel contour) varied from 0.17 to 235.13 km^2 (mean ± SD = 30.73 ± 54.34 km^2) and from 0.03 to 22.66 km^2 (mean ± SD = 2.95 ± 5.06 km^2), respectively. Our findings shed light on a critical developmental area for immature green turtles in the French West Indies, and should help to refine Regional Management Units and reinforce the cooperative network aiming at ensuring conservation of the species at international scale.

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1. Introduction

Studying animal movements is required to understanding their ecology and interactions with human activities (Maxwell et al., 2013). For marine vertebrates such as sea turtles that are distributed over large extents, investigating migratory patterns, habitat use and site fidelity is crucial to implement effective conservation actions in sites heavily used throughout their life cycle.

The green turtle (*Chelonia mydas*) has a complex life cycle involving the use of several habitat types, where the species is exposed to different threats at different life stages (Lutcavage et al., 1997; Musick and Limpus, 1997). The annual number of nesting females is estimated to have decreased by 48 to 67% in three generations (Seminoff, 2004). Despite the classification of the South-Atlantic subpopulation as 'Least Concern' in 2019, due to a simultaneous increase in nesting abundance in the South-Western Atlantic Ocean and Caribbean Sea regions (Broderick and Patricio, 2019; Seminoff, 2004), green turtles fully deserve their status of endangered species on the International Union for Conservation of Nature (IUCN) Red List. Indeed, due to their late maturity (26–36 years; Seminoff, 2004), the state of reproductive females does not reflect current life circumstances and pressures experienced by younger individuals (Bjorndal et al., 2005, 1999). Because reliable data on sex ratios and survival rates across life stages are missing, it is also difficult to derive male and non-reproductive female abundances from breeding female abundances (Broderick and Patricio, 2019), so that current findings may not be representative of the entire regional entity (Seminoff and Shanker, 2008).

One of the greatest issues in implementing effective conservation and management measures of sea turtles at different spatio-temporal scales certainly comes from the difficulty of studying their at-sea behaviour (Wallace et al., 2010). Most studies on sea turtle in natura have focused on females while nesting on land (Bjorndal, 1999). Accordingly, legislation and conservation programmes have widely targeted nesting beaches to protect females, eggs, and hatchlings. Yet, stage-based population models on long-lived turtle species have highlighted the importance of reducing mortality in immatures and subadults to promote population recovery (Crouse et al., 1987; Heppell et al., 1996). While scientists have tried to resolve the mystery of the 'lost years' (i.e. the first 3–5 years spent in the open ocean by juveniles up to 25–35 cm long) using environmental modelling, stable isotopes and satellite tracking (Dalleau et al., 2014; Putman et al., 2012; Reich et al., 2007), there are still major uncertainties concerning the behaviour of immature green turtles once they enter neritic habitats and coastal feeding grounds, which represent key marine habitats for their growth.

After centuries of overharvesting in the Caribbean, the current threats sea turtles face in neritic habitats in this region are incidental captures by local fishing gears, which kill hundreds of individuals each year in their nesting and developmental areas (Dow et al., 2007). Artisanal fishing in the French West Indies, involving more than 2000 fishing boats in Guadeloupe and Martinique, is mainly concentrated on the continental shelf because of its accessibility and the presence of commercially interesting species. Representing 20% of the gear used, bottom nets such as trammel nets and conch fishing gears (non-selective and deployed for long times) are the main cause of bycatch for numerous species, including sea turtles (Louis-Jean, 2019; Louis-Jean et al., 2008). Other prevalent threats to at-sea turtles are vessel collisions, marine debris, pollution and degradation of marine habitats (Dow et al., 2007; Seminoff et al., 2015).

The literature remains scarce about foraging aggregations of immature green turtles in the Lesser Antilles, despite occurrences of such individuals around these islands (Chevalier, 2006; Meylan, 1983). In Martinique, Chambault et al. (2018) evidenced the presence of immatures originating from different rookeries, among which some individuals departed in migration when approaching sexual maturity. However, much less is known regarding immatures that have not undertaken post-developmental migration and to date, their site fidelity and habitat use remain unknown. To fill this gap, we performed the first long-term at-sea study focusing on a green turtle aggregation of immatures in the Lesser Antilles. We collected Capture-Mark-Recapture (CMR) data on immatures along the western coast of Martinique to investigate their habitat use over the long-term and satellite tracked 31 of them to assess their degree of site fidelity. As juvenile green turtles coming back from pelagic waters to neritic foraging grounds (when they are longer than 25–35 cm; Reich et al., 2007) are known to switch gradually from a carnivorous to an omnivorous diet containing generally a substantial proportion of plants (Bjorndal, 1997; Bjorndal et al., 2000; Howell, 2012), we paid particular attention to the use of seagrass meadows. Godley et al. (2003) found that some Brazilian immatures performed medium to long-range movements. Accordingly, we hypothesised that those observed in Martinique may move between the neighbouring islands, where foraging aggregations of immature green turtles have already been reported (Dow et al., 2007).

2. Materials and methods

2.1. Ethics statements

This study meets the French legal and ethical requirements. The protocol was approved by the Conseil National de la Protection de la Nature and the French Ministry for Ecology (permit numbers: 2013154-0037 and 201710-0005) and followed the recommendations of the Police Prefecture of Martinique.

2.2. Environment

Since 2010, we have conducted a Passive Integrated Transponder (PIT)-based monitoring programme in Martinique. Immatures were captured along the coast by freedivers (Bonola et al., 2019; Nivière et al., 2018) at various sites with depths up to 25 m (Fig. 1). Grande Anse (75 ha), Anse du Bourg (25 ha), Anse Chaudière (34 ha) and Petite Anse (42 ha) are large bays where grow algae and the three main phanerogams found in Martinique, i.e. two native species (*Syringodium filiforme* and *Thalassia testudinum*) and one exotic invasive species (*Halophila stipulacea*) (Hily et al., 2010). Anse Noire (6 ha) and Anse Dufour (6 ha) are covered by algae and *H. stipulacea* only. Joras is a shallow rock plate with corals and algae, with a generally strong current at the surface. Le Carbet (11 ha) and Saint-Pierre (88 ha) are two sites with wide beaches, covered mainly with *H. stipulacea.* Le Prêcheur (56 ha) contains seagrass meadows and algae. Distances between capture sites are shown in Table S1.

2.3. Site fidelity analysis using CMR data

The probability to change of residence area, as well as the mean residence time in a bay, were fitted using a multi-state continuous-time hidden Markov model as implemented in the *msm* R package (Jackson, 2011). This type of model assesses the different 'states' of an individual based on observations at arbitrary times that usually do not correspond to the actual times at which the states changed (Meira-Machado et al., 2009). We considered 10 possible states, corresponding to the 10 bays of capture. Our model included the capture probability by session (0.66 to 0.77) and the annual survivorship (0.30 to 0.43, including both true survival and size dependent departure from Martinique). Transition rates were modelled on a daily basis. Two categories of individuals were considered depending on the Curved Carapace Length (CCL) was smaller or larger than 30 cm. Complementary analyses based on other thresholds (40, 50, 60, and 70 cm) were also performed. The CCL was used as a direct or log-transformed (to normalise the data distribution) covariate in a proportional hazards model (Marshall and Jones, 1995). A comparison of models, with or without covariate, was performed using the Akaike Information Criterion (AIC) and Akaike weight. The distributions of distances between the locations of two successive

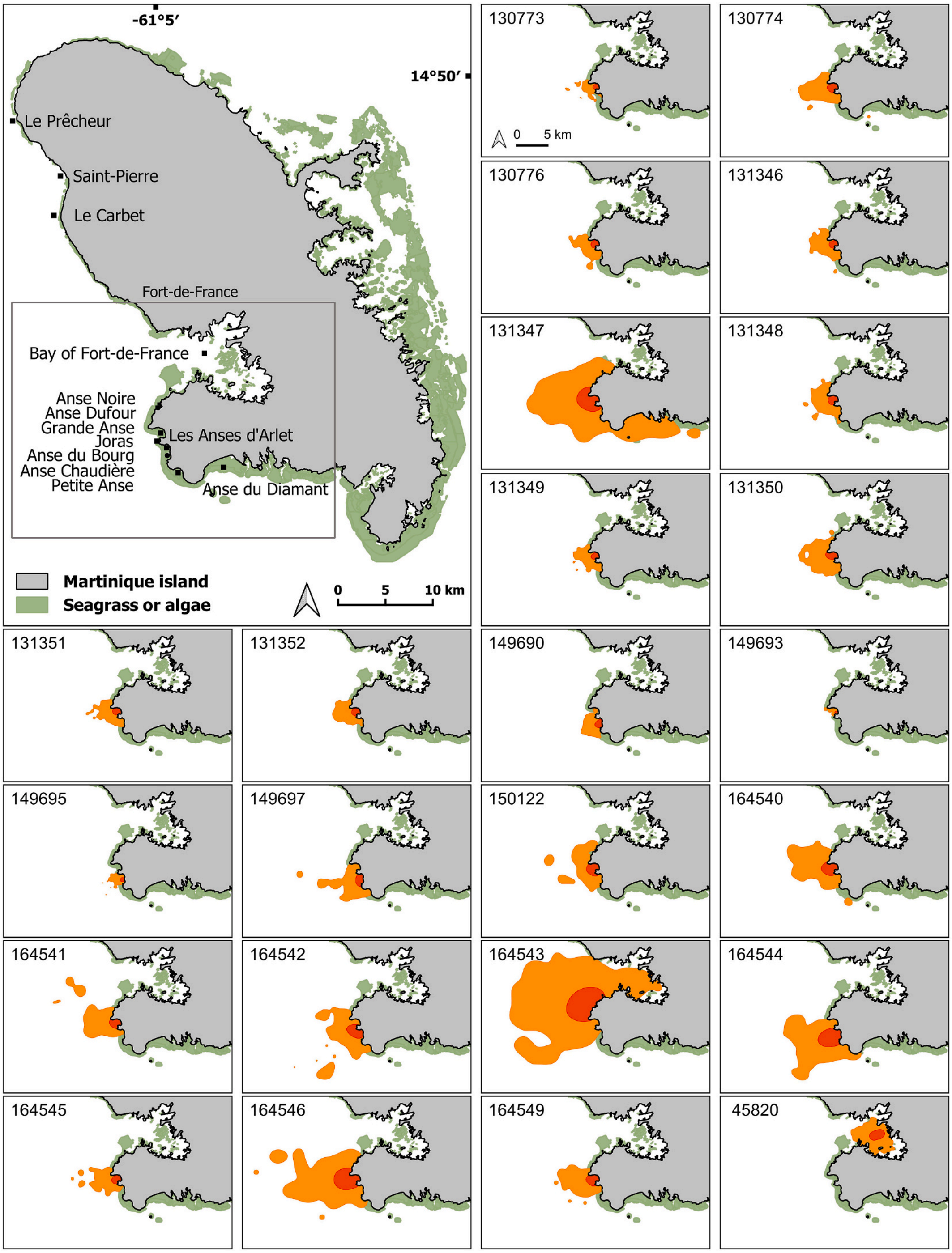

Fig. 1. Main panel: Map of Martinique surrounded by coastal marine vegetation, with capture locations and sites used by satellite-tracked turtles. The frame encompasses the area represented on the small panels. Small panels: Home ranges (areas within 95% UD in orange) and core areas (areas within 50% UD in red) computed using KDE for 24 immatures satellite-tracked between 2013 and 2018. The capture site of each individual is indicated in Table S2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

captures were estimated within 12 months and over the entire study period. The null distribution was built by random permutations involving 10,000 replicates based on the relative capture frequencies and was used to determine the mean distance (± SE) expected if turtles moved at random from one bay to the other.

2.4. Satellite tracking and data pre-processing

In 2013 and 2015, 19 immatures were equipped with Argos/GPS devices: 11 with Fastloc GPS tags (Wildlife Computers, Redmond, WA, USA) programmed to record a GPS-based location every 4 h (to save battery), but only Argos-based locations could be acquired, and 8 with GPS Satellite Relayed Data Loggers (SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) programmed to record a location every 15 min, which were able to acquire a few GPS-based locations in addition to Argos-based ones. The issue certainly came from the lower location of the GPS antenna with respect to the Argos antenna, which prevented the acquisition of GPS locations while individuals tend to breath in a mainly upward attitude. In 2016 and 2017, 12 additional individuals were equipped with Argos tags (SPOT, from Wildlife

Computers) (Table S2). GPS-based locations represented less than 3% of the whole dataset and were available only for four individuals. When both types of location were available for a particular time, only the GPS-based location was kept. The attachment procedure was described in Baudouin et al. (2015) and Chambault et al. (2015). Animals were released at their capture site. Unrealistic locations, as those occurring on land, involving a speed > 5 km·h^{-1}, or generating 'hairpin' shapes were removed (Hart and Fujisaki, 2010). Locations recorded after departure from Martinique and corresponding to a post-developmental migration were also excluded.

2.5. Home range and habitat use estimates

For each of the 24 satellite-tracked turtles that remained in the area for at least 40 days, we checked the stationarity of the distribution of locations using a new segmentation method (Patin et al., 2020; see Supplementary method S1). The corresponding Utilisation Distributions (UD) were estimated using the Kernel Density Estimation (KDE) method as implemented in the *adehabitatHR* R package (Calenge, 2006) with an ad hoc smoothing parameter (Kie, 2013). Home ranges (HRs) and core areas (CAs) were then computed as the areas within the 95% and 50% cumulative UD isopleths, respectively. However, such areas represent both the magnitude of animal movements and the location measure errors, which may be high when Argos-based. For the three individuals that had at least 50% of good quality locations (#149693, #149695, #149697, Table S2), we computed corrected HRs and CAs based on those locations only. For the other individuals, we estimated that the mean location error should be about 1 km, resulting in areas that tended to be overestimated by a factor of 1.8 on average, and which were therefore corrected accordingly (Supplementary method S2, Table S2). Habitat use was assessed by plotting UDs on the map of habitat types provided by the Observatoire du Milieu Marin Martiniquais (OMMM, 2009). The potentially favourable habitats (Fig. 1) were seagrass meadows (50 km^2), algal communities (142 km^2), and communities mixing seagrass and coral (15 km^2).

3. Results

3.1. Site fidelity from CMR data

Between 2010 and 2019, 488 green turtles were captured involving 299 individuals (mean ± SD CCL at first capture: 60.7 ± 14.1 cm): 192 individuals were captured only once, while 62 were captured twice, 30 three times, 7 four times, 1 five times, 4 six times, 1 seven times, and 2 nine times. The 189 recapture events (Table S3), involving 107 individuals, were used in the analysis of residency. We selected the model without covariate, as it had the lowest AIC and a very high Akaike weight (0.986) (Table S4). The fitted daily transition matrix for the selected model is shown in Table S5. For any bay, the probability of finding an individual in the same bay from one day to the next (> 0.998) was higher than finding it in another bay. Estimated residence times in the bays (mean ± SE) were 15 ± 7 years for Anse du Bourg, 2 ± 1 years for Anse Noire and 74 ± 53 years for Grande Anse (Table S6). The distance between two locations of the same turtle was 24 ± 24 m within 12 months, 158 ± 48 m over the entire study period, and 3986 ± 86 m for the null model (Fig. S1.a–b).

3.2. Habitat use and site fidelity from tracking data

Seven individuals (CCL: 86.9 ± 3.8 cm) migrated shortly after being tagged and never returned to Martinique during the tracking period, while 24 turtles (CCL: 77.1 ± 8.3 cm) established their HRs in its vicinity for 42 to 383 days (Figs. 1 & S2). The (corrected) HR and CA sizes varied from 0.17 to 235.13 km^2 (mean ± SD = 30.73 ± 54.34 km^2) and from 0.03 to 22.66 km^2 (mean ± SD = 2.95 ± 5.06 km^2), respectively (Table S2). Most individuals remained in nearshore areas and had a single CA (Figs. 1 & S2). Three of these 24 turtles eventually migrated. All individuals that undertook long-distance migration had a CCL > 78.5 cm (in agreement with Chambault et al., 2018). At least nine individuals did not migrate soon after the tracking period: they were recaptured in the following years.

4. Discussion

This study provides the first long-term at-sea study focusing on immature green turtles in the Lesser Antilles. Based on CMR data and satellite tracking, our results reveal strong fidelity to foraging grounds and high residence times with a high degree of affinity for specific areas within the coastal marine vegetation strip. These areas are concentrated on the seagrass beds of the southwest coast of Martinique. Our results contribute to improving our general understanding of immature sea turtle ecology in their critical developmental area to better define the regional conservation strategy of this endangered species.

4.1. Long-term and year-round residency

In our study as well as in Chambault et al.'s (2018) one, the individuals that performed post-developmental migrations were larger than the resident ones. This suggests they were subadults approaching sexual maturity, leaving Martinique towards adult foraging grounds or breeding sites. These migrants were unlikely to be in transit in Martinique when they were equipped for tracking because half of them had already been captured around the island during previous years (Table S2). No satellite-tracked turtles with a CCL < 78.5 cm undertook long-distance migration, and some larger individuals also stayed around Martinique. These turtles remained from one to twelve months south of Martinique, and for most of them, in a single bay (Table S2, Figs. 1 & S2). This was confirmed by the CMR analysis, which revealed that turtles were recaptured on average at 160 m from the previous capture site (Fig. S1.b). Pilcher (2010) and Colman et al. (2015) found similar, although somewhat larger figures (360–500 m) for Malaysia and Brazil, respectively. Contrary to our hypothesis, no individual moved to neighbouring islands. According to the literature, 0.1 to 9% of immature green turtles are recaptured in sites different from where they were marked (usually tens to hundreds of km apart), thus possibly using several foraging grounds (Bjorndal et al., 2005; Colman et al., 2015; Gallo et al., 2006; Godley et al., 2003; Moncada et al., 2006; Patrício et al., 2011; Senko et al., 2010). Foraging sites philopatry has been evidenced in several species of sea turtles and across lifestages, with some adults returning after breeding migrations to the foraging areas they already used as immatures (Shimada et al., 2020). Green turtles may maintain tight fidelity to foraging grounds for multiple reasons (Broderick et al., 2007; Moran and Bjorndal, 2007; Shimada et al., 2020). They seem to adopt a low-risk strategy, ensuring their long-term survival by staying in familiar environments (Schofield et al., 2010; Shimada et al., 2020).

The fate of PIT-tagged immatures that were not recaptured (about 64% of them) remains perplexing. The most obvious answer – they have left the area – is at variance with the results obtained for tracked individuals, most of them (> 75%) remaining in the area for a long time. The assumption of PIT-tag loss is also unlikely, as the probability of losing one PIT-tag was estimated to 0.06 and 0.009 in studies of adult loggerheads (Pfaller et al., 2019) and leatherbacks (Chevallier et al., 2020), respectively. Thus, the non-recaptured individuals may rather have been present but missed, left offshore for their daily activities, or died. Coastal fisheries bycatch is estimated to affect about 800 green turtles annually in Martinique, with a mortality rate of 63.5% (Louis-Jean, 2019). To our knowledge, the only individual we tracked that died is #131347 after ingesting a fishing line. Almost half of the turtles that did not migrate were recaptured in the subsequent years in Martinique. For individuals captured several times, the probability of recapture in the same bay is strong, corroborating the strong site fidelity of immatures to specific bays, with residence times in a timescale of years or decades. Our results are in agreement with other multiple-year CMR studies. In the Bahamas and Malaysia, the longest residence period ranged from 7 to 15 years (Bjorndal et al., 2005; Pilcher, 2010). In Brazil, the longest time interval between first and last capture was estimated to reach 22 years when using fidelity estimation based on size at capture and growth rates (Colman et al., 2015). The high residence times and upper confidence intervals found in Grande Anse may sound surprising, but these figures are influenced by the exceptional presence of large immatures that complete their development and reproduce in Martinique. Moreover, these values are conditioned by the presence of the individuals in the neritic habitats. They do not include data about life expectancy and long-distance migrations observed in individuals approaching sexual maturity. Our results suggest that some foraging grounds may host multiple life stages up to adulthood and reproduction, in agreement with historical records of nesting females in Martinique. As no adults were sighted during monitoring, Martinique should nowadays mainly be used by immatures as temporary developmental habitats, similar to what is commonly observed in the Bahamas, Brazil, Malaysia or Mexico (Bjorndal et al., 2005; Gallo et al., 2006; Pilcher, 2010; Senko et al., 2010).

4.2. Habitat use

Once corrected to take the location measurement errors into account, the HR and CA sizes in Martinique are smaller than those found for immature green turtles in Florida (HR: 154 ± 136 km^2, CA: 22 ± 22 km^2; Hart and Fujisaki, 2010), and in North Carolina (HR: 85 ± 48 km^2; McClellan and Read, 2009) with Argos-based locations, but consistent with those found for immature and adult green turtles in the Indian Ocean, using Fastloc-GPS data (Chambault et al., 2020; Christiansen et al., 2017). The high use of nearshore areas likely results from foraging on seagrass. Most of the tracked individuals spent their time within Grande Anse and Anse du Bourg, where multi-species seagrass meadows are found (i.e. composed of *S. filiforme*, *T. testudinum*, and the invasive species *H. stipulacea*). Although green turtle's diet is not restricted to plants, immatures and adults can be considered the only herbivorous sea turtles (Bjorndal, 1997). The preference for seagrass or algae may be influenced by multiple factors, like plant biomass and availability (Ballorain et al., 2010; López-Mendilaharsu et al., 2008). *T. testudinum* is the main component of green turtles' diet in the Caribbean (Bjorndal, 1997), but the other two species are also occasionally consumed (Christianen et al., 2018; Mendonça, 1983; Whitman et al., 2019). Individual variability in diet preferences should reduce intraspecific competition for food resources, allowing numerous individuals to share the same foraging area (Svanbäck and Bolnick, 2005). Individuals inhabiting Anse Noire may use this particular area for a shorter period, and restrict less their activity to the bay itself due to the presence of monospecific stands of *H. stipulacea*. It is surprising that turtles concentrated so much in the specific area of 'Les Anses d'Arlet' (a series of five contiguous bays), whereas seagrass meadows are widespread all along the southern areas of the Caribbean coast. Prospecting along the coast further north and south of 'Les Anses d'Arlet' revealed very low to null densities of turtles. It likely indicates that other environmental factors (e.g. currents, swell, water depth, clarity and quality, predators, human disturbance) may have deterred turtles from establishing in these areas.

Some individuals appeared to use offshore areas sporadically. Although this behaviour may be linked to feeding on gelatinous animals in the water column (Bjorndal, 1997; Howell, 2012), we cannot exclude that this may just reflect the occurrence of erroneous Argos-based locations. Two turtles settled in the bay of Fort-de-France, which provides algae and seagrass and is fringed by a mangrove. Mangrove compounds have been regularly found in mouth and gut contents of green turtles, and juveniles have already been reported inhabiting mangroves (Chambault et al., 2020; Guebert-Bartholo et al., 2011). A few Martinican turtles may feed in this habitat, in relation with specific physiological adaptations (to digest fruits, algae, and highly energetic animal prey; Bjorndal et al., 2000).

Other factors such as body condition in relation to predation risk (review by Hays, 2008), intraspecific competition (Svanbäck and Bolnick, 2005), or behavioural plasticity (Chambault et al., 2020) may drive individuals to settle in various, including seldom-used, habitats. Site selection has been demonstrated to potentially affect size-specific growth rates, with individuals growing slowly moving from lower to higher quality habitats (Bjorndal et al., 2000). Individuals displaying exploratory behaviour may be disadvantaged by their body condition or low competitiveness, whereas turtles staying in a single site may have higher growth rates. On the other hand, variability in HR size may be attributed to resource availability, distribution, density, patchiness and nutritional quality, in relation to turtle body condition and energy requirements (Christiansen et al., 2017; Seminoff et al., 2002; Van De Merwe et al., 2009). A recent study highlighted that, in Martinique, immature green turtles caught in years associated with high net primary production were heavier than expected with respect to their size (Bonola et al., 2019). Individuals exploiting habitats with higher food quality and seagrass density should occupy smaller areas (Mendonça, 1983; Renaud et al., 1995; Seminoff et al., 2002; Whiting and Miller, 1998). Areas exploited by green turtles in the southwestern coast of Martinique, and especially in 'Les Anses d'Arlet', should therefore provide denser and more profitable resources than elsewhere.

Even though sea turtles are considered solitary, recent studies have evidenced the existence of social interactions, in the form of antagonistic behaviours in loggerheads (Schofield et al., 2007a, 2007b). In Martinique, we frequently observe immature green turtles resting or foraging in groups from two to six individuals. It is however unclear whether this correspond to simple aggregations (individuals attracted by the same sites) or to congregations (individuals attracted to each other). Gathering may be a way to decrease risk per capita and increase predator detection (Bednekoff, 2007) or vigilance towards humans. These individuals also occasionally come into contact with each other. These observations offer new perspectives on acoustic communication between sea turtles (Ferrara et al., 2014; McKenna et al., 2019). Like nest environments or arribadas of olive Ridley turtles, foraging hotspots offer an interesting context for investigating the sociality and communication in these species, and for trying to understand what the benefits of these groupings might be.

5. Conclusion & conservation implications

Our results suggest that immature green turtles in Martinique are long-term residents, which restrict their space use to a small developmental area along the southwestern coast, before emigrating towards foraging and reproduction areas used by adults (the Eastern Caribbean and in particular Surinamese and French Guianese beaches, but also the Northern Western Caribbean, Southwest Atlantic and Southeast Atlantic; Chambault et al., 2018). There are many examples where movement ecology studies of mobile species have induced changes in conservation practice, from grizzly bears to albatross, including sea turtles (Fraser et al., 2018; Hays et al., 2019). However, few studies have used both CMR and satellite-tracking to investigate site fidelity in sea turtles (e.g. Godley et al., 2003; Shimada et al., 2020). In Martinique, the year-round and restricted distribution of green turtles over the coastal region of 'Les Anses d'Arlet' combined with a high turtle abundance and intense tourism activity should foster the delineation of Marine Protected Areas in consultation with sea stakeholders, which would certainly be profitable for many other species. The presence of turtles benefits directly the development of ecotourism and fishing (Louis-Jean, 2019) because, as megaherbivores, green turtles are essential for maintaining ecosystem functions and specific diversity (Thayer et al., 1984). Nevertheless, they may be threatened by the arrival of *H. stipulacea* in the Caribbean (Ruiz and Ballantine, 2004), which takes over indigenous seagrass that originally constituted a substantial part of their diet. Studying small-scale habitat use, food selection, and activity budget is required to investigate the impacts of *H. stipulacea*, and the additional effects of turtle-watching and boating activities on habitat modification, turtle behaviour and growth. Priority zones with stronger legislation should be designed based on the areas preferentially used by green turtles, to reduce mortality caused by collisions with motorised vehicles, damages to seagrass meadows caused by boat chains and anchors, and prohibit turtle-watching by tour operators in order to limit the disturbance of sea turtles. Subsequently, it would be interesting to determine the reasons why turtles do not use other seagrass areas around Martinique to possibly define additional protected areas if the absence of turtles is linked to human activities that could be regulated.

Protecting green turtles of Martinique is vital for this species survival in this part of the world, in agreement with the recent recognition of *C. mydas* as Critically Endangered on the French Red List of threatened species in Martinique (UICN Comité français et al., 2020). As a major developmental area for immatures, this island represents a non-negligible source of future breeders for the Caribbean and South Atlantic basins (Chambault et al., 2018). Threat mitigation on these primary use areas appears essential for the conservation of this long-lived species exhibiting strong-site fidelity. Nevertheless, once subadults migrate, they are no more protected by the French legislation. Less than half of the Eastern Caribbean countries enforce complete protection of sea turtles, despite their international status of threatened species. Where turtle legal fisheries exist, there are no maximum size limits for at-sea stages, so that large immatures and adults – which have a high reproductive value (i.e. based on their future reproductive contribution to the population; Frazer, 1989) – remain at risk (Dow et al., 2007). On islands where turtles are under complete protection, exploitation and trade remain common, revealing failure in law enforcement or inadequate penalties.

Locating highly used mixed-stock developmental areas and describing connectivity between foraging grounds used by immatures, subadults and adults inside the Caribbean may help to refine Regional Management Units and improve their effectiveness (Wallace et al., 2010). Cooperation between countries and adequacy of management measures beyond borders, along with a strong collaboration between politics, scientists and sea stakeholders at the local and regional scales, is therefore required to ensure the survival of immature green turtles in the Caribbean.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Ballorain, K., Ciccione, S., Bourjea, J., Grizel, H., Enstipp, M., Georges, J.-Y.Y., 2010. Habitat use of a multispecific seagrass meadow by green turtles *Chelonia mydas* at Mayotte Island. Mar. Biol. 157 (12), 2581–2590. https://doi.org/10.1007/s00227-010-1520-7.

Baudouin, M., de Thoisy, B., Chambault, P., Berzins, R., Entraygues, M., Kelle, L., Turny, A., Le Maho, Y., Chevallier, D., 2015. Identification of key marine areas for conservation based on satellite tracking of post-nesting migrating green turtles (*Chelonia mydas*). Biol. Conserv. 184, 36–41. https://doi.org/10.1016/j.biocon.2014.12.021.

Bednekoff, P.A., 2007. Danger often depends on group size. In: Stephens, D.W., Brown, J.S., Ydenberg, R.C. (Eds.), Foraging: Behaviour and Ecology. University of Chicago Press, Chicago & London, pp. 319–324.

Bjorndal, K.A., 1997. Foraging ecology and nutrition of sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology of Sea Turtles. CRC Press, vol. I. Boca Raton, Florida, pp. 199–231.

Bjorndal, K.A., 1999. Priorities for research in foraging habitats. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), Research and Management Techniques for the Conservation of Sea Turtles. vol. 4. IUCN/SSC Marine Turtle Specialist Group, pp. 12–14.

Bjorndal, K.A., Wetherall, J.A., Bolten, A.B., Mortimer, J.A., 1999. Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: an encouraging trend. Conserv. Biol. 13 (1), 126–134. https://doi.org/10.1046/j.1523-1739.1999.97329.x.

Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2000. Green turtle somatic growth model: evidence for density dependence. Ecol. Appl. 10 (1), 269–282. https://doi.org/10.1890/1051-0761(2000)010[0269:GTSGME]2.0.CO;2.

Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2005. Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the Greater Caribbean. Ecol. Appl. 15 (1), 304–314. https://doi.org/10.1890/04-0059.

Bonola, M., Girondot, M., Robin, J.-P., Martin, J., Siegwalt, F., Jeantet, L., Lelong, P., Grand, C., Chambault, P., Etienne, D., Gresser, J., Hielard, G., Arqué, A., Régis, S., Lecerf, N., Frouin, C., Lefebvre, F., Sutter, E., Vedie, F., Barnerias, C., Thieulle, L., Bordes, R., Guimera, C., Aubert, N., Bouaziz, M., Pinson, A., Flora, F., Duru, M., Benhalilou, A., Murgale, C., Maillet, T., Andreani, L., Campistron, G., Sikora, M., Rateau, F., George, F., Eggenspieler, J., Woignier, T., Allenou, J.-P., Louis-Jean, L., Chanteur, B., Béranger, C., Crillon, J., Brador, A., Habold, C., Le Maho, Y., Chevallier, D., 2019. Fine scale geographic residence and annual primary production drive body condition of wild immature green turtles (*Chelonia mydas*) in Martinique Island (Lesser Antilles). Biol. Open 8, 1–10. https://doi.org/10.1242/bio.048058. bio048058.

Broderick, A., Patricio, A., 2019. *Chelonia mydas* South Atlantic subpopulation. In: The IUCN Red List of Threatened Species 2019, e.T142121866A142086337.

Broderick, A.C., Coyne, M.S., Fuller, W.J., Glen, F., Godley, B.J., 2007. Fidelity and over-wintering of sea turtles. Proc. R. Soc. B Biol. Sci. 274 (1617), 1533–1538. https://doi.org/10.1098/rspb.2007.0211.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197 (3–4), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Chambault, P., Pinaud, D., Vantrepotte, V., Kelle, L., Entraygues, M., Guinet, C., Berzins, R., Bilo, K., Gaspar, P., De Thoisy, B., Le Maho, Y., Chevallier, D., 2015. Dispersal and diving adjustments of the green turtle *Chelonia mydas* in response to dynamic environmental conditions during post-nesting migration. PLoS One 10 (9), 1–19. https://doi.org/10.1371/journal.pone.0137340.

Chambault, P., de Thoisy, B., Huguin, M., Martin, J., Bonola, M., Etienne, D., Gresser, J., Hiélard, G., Mailles, J., Védie, F., Barnerias, C., Sutter, E., Guillemot, B., Dumont-Dayot, É., Régis, S., Lecerf, N., Frouin, C., Aubert, N., Guimera, C., Bordes, R., Thieulle, L., Duru, M., Bouaziz, M., Pinson, A., Flora, F., Queneherve, P., Woignier, T., Allenou, J.-P., Cimiterra, N., Benhalilou, A., Murgale, C., Maillet, T., Rangon, L., Chanteux, N., Chanteur, B., Béranger, C., Le Maho, Y., Petit, O., Chevallier, D., 2018. Connecting paths between juvenile and adult habitats in the Atlantic green turtle using genetics and satellite tracking. Ecol. Evol. 8, 12790–12802. https://doi.org/10.1002/ece3.4708.

Chambault, P., Dalleau, M., Nicet, J., Mouquet, P., Ballorain, K., Jean, C., 2020. Contrasted habitats and individual plasticity drive the fine scale movements of juvenile green turtles in coastal ecosystems. Mov. Ecol. 8 (1), 1–15. https://doi.org/10.1186/s40462-019-0184-2.

Chevalier, J., 2006. Plan de restauration des tortues marines des Antilles françaises. Office National de la Chasse et de la Faune Sauvage. Direction Régionale Outre Mer. Pointe-à-Pitre, Guadeloupe.

Chevallier, D., Girondot, M., Berzins, R., Chevalier, J., de Thoisy, B., Fretey, J., Kelle, L., Lebreton, J., 2020. Survival and breeding interval of an endangered marine vertebrate, the leatherback turtle *Dermochelys coriacea*, in French Guiana. Endanger. Species Res. 41, 153–165. https://doi.org/10.3354/esr01013.

Christianen, M.J.A., Smulders, F.O.H., Engel, M.S., Nava, M.I., Willis, S., Debrot, A.O., Palsbøll, P.J., Vonk, J.A., Becking, L.E., 2018. Megaherbivores may impact expansion of invasive seagrass in the Caribbean. J. Ecol. 107 (May), 1–13. https://doi.org/10.1111/1365-2745.13021.

Christiansen, F., Esteban, N., Mortimer, J.A., Dujon, A.M., Hays, G.C., 2017. Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. Mar. Biol. 164 (1), 1–11. https://doi.org/10.1007/s00227-016-3048-y.

Colman, L.P., Patrício, A.R.C., McGowan, A., Santos, A.J.B., Marcovaldi, M.Â., Bellini, C., Godley, B.J., 2015. Long-term growth and survival dynamics of green turtles (*Chelonia mydas*) at an isolated tropical archipelago in Brazil. Mar. Biol. 162 (1), 111–122. https://doi.org/10.1007/s00227-014-2585-5.

Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68 (5), 1412–1423. https://doi.org/10.2307/1939225.

Dalleau, M., Benhamou, S., Sudre, J., Ciccione, S., Bourjea, J., 2014. The spatial ecology of juvenile loggerhead turtles (*Caretta caretta*) in the Indian Ocean sheds light on the “lost years” mystery. Mar. Biol. 161 (8), 1835–1849. https://doi.org/10.1007/s00227-014-2465-z.

Dow, W., Eckert, K.L., Palmer, M., Kramer, P., 2007. An atlas of sea turtle nesting habitat for the Wider Caribbean region. In: WIDECAST Technical Report.

Ferrara, C.R., Vogt, R.C., Giles, J.C., Kuchling, G., 2014. Chelonian vocal communication. In: Witzany, G. (Ed.), Biocommunication of Animals. Springer, Dordrecht, pp. 261–274. https://doi.org/10.1007/978-94-007-7414-8.

Fieberg, J., Kochanny, C.O., 2005. Quantifying home-range overlap: the importance of the utilization distribution. J. Wildl. Manag. 69 (4), 1346–1359. https://doi.org/10.2193/0022-541x(2005)69[1346:qhotio]2.0.co;2.

Fraser, K.C., Davies, K.T.A., Davy, C.M., Ford, A.T., Flockhart, D.T.T., Martins, E.G., 2018. Tracking the conservation promise of movement ecology. Front. Ecol. Evol. 6 (150), 1–8. https://doi.org/10.3389/fevo.2018.00150.

Frazer, N.B., 1989. Management options: a philosophical approach to population models. In: Ogren, L. (Ed.), Proceedings of the Second Western Atlantic Turtle Symposium. NOAA Technical Memorandum NMFS-SEFC-226. U.S. Department of Commerce, Miami, pp. 198–207.

Gallo, B.M.G., Macedo, S., Giffoni, B. de B., Becker, J.H., Barata, P.C.R., 2006. Sea turtle conservation in Ubatuba, southeastern Brazil, a feeding area with incidental capture in coastal fisheries. Chelonian Conserv. Biol. 5 (1), 93–101. https://doi.org/10.2744/1071-8443(2006)5[93:stcius]2.0.co;2.

Godley, B.J., Lima, E.H.S.M., Åkesson, S., Broderick, A.C., Glen, F., Godfrey, M.H., Luschi, P., Hays, G.C., 2003. Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. Mar. Ecol. Prog. Ser. 253, 279–288. https://doi.org/10.3354/meps253279.

Guebert-Bartholo, F.M., Barletta, M., Costa, M.F., Monteiro-Filho, E.L.A., 2011. Using gut contents to assess foraging patterns of juvenile green turtles *Chelonia mydas* in the Paranaguá Estuary, Brazil. Endanger. Species Res. 13, 131–143. https://doi.org/10.3354/esr00320.

Hart, K.M.K., Fujisaki, I., 2010. Satellite tracking reveals habitat use by juvenile green sea turtles *Chelonia mydas* in the Everglades, Florida, USA. Endanger. Species Res. 11 (3), 221–232. https://doi.org/10.3354/esr00284.

Hays, G.C., 2008. Sea turtles: a review of some key recent discoveries and remaining questions. J. Exp. Mar. Bio. Ecol. 356, 1–7. https://doi.org/10.1016/j.jembe.2007.12.016.

Hays, G.C., Bailey, H., Bograd, S.J., Bowen, W.D., Campagna, C., Carmichael, R.H., Casale, P., Chiaradia, A., Costa, D.P., Cuevas, E., Nico de Bruyn, P.J., Dias, M.P., Duarte, C.M., Dunn, D.C., Dutton, P.H., Esteban, N., Friedlaender, A., Goetz, K.T., Godley, B.J., Halpin, P.N., Hamann, M., Hammerschlag, N., Harcourt, R., Harrison, A.L., Hazen, E.L., Heupel, M.R., Hoyt, E., Humphries, N.E., Kot, C.Y., Lea, J.S.E., Marsh, H., Maxwell, S.M., McMahon, C.R., Notarbartolo di Sciara, G., Palacios, D.M., Phillips, R.A., Righton, D., Schofield, G., Seminoff, J.A., Simpfendorfer, C.A., Sims, D.W., Takahashi, A., Tetley, M.J., Thums, M., Trathan, P.N., Villegas-Amtmann, S., Wells, R.S., Whiting, S.D., Wildermann, N.E., Sequeira, A.M.M., 2019. Translating marine animal tracking data into conservation policy and management. Trends Ecol. Evol. 34 (5), 459–473. https://doi.org/10.1016/j.tree.2019.01.009.

Heppell, S.S., Crowder, L.B., Crouse, D.T., 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecol. Appl. 6 (2), 556–565. https://doi.org/10.2307/2269391.

Hily, C., Duchêne, J., Bouchon, C., Bouchon-Navaro, Y., Gigou, A., Payri, C., Védie, F., 2010. Les herbiers de phanérogames marines de l’outre-mer français, écosystèmes associés aux récifs coralliens.

Howell, L., 2012. Ontogenetic Shifts in Diet and Habitat by Juvenile Green Sea Turtles (*Chelonia mydas*) along the Middle and Lower Texas Coast. Texas A&M University.

Jackson, C.H., 2011. Multi-state models for panel data: the msm package for R. J. Stat. Softw. 38 (8), 1–28. https://doi.org/10.18637/jss.v038.i08.

Kie, J.G., 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. Anim. Biotelem. 1 (13), 1–12. https://doi.org/10.1186/2050-3385-1-13.

López-Mendilaharsu, M., Gardner, S.C., Riosmena-Rodriguez, R., Seminoff, J.A., 2008. Diet selection by immature green turtles (*Chelonia mydas*) at Bahía Magdalena foraging ground in the Pacific coast of the Baja California Peninsula, México. J. Mar. Biol. Assoc. United Kingdom 88 (3), 641–647. https://doi.org/10.1017/S0025315408001057.

Louis-Jean, L., 2019. Étude de la pêche artisanale côtière aux filets de fond aux Antilles françaises afin de réduire les captures accidentelles de tortues marines et obtenir une activité plus durable. (EPHE Paris).

Louis-Jean, L., Lenfant, P., Galzin, R., Marechal, J., 2008. Crossing fishery statistics with marine turtle bycatch data and habitat mapping in Martinique, FWI. In: Proceedings of the 61st Gulf and Caribbean Fisheries Institute. Gosier, Guadeloupe, French West Indies, pp. 375–379.

Lutcavage, M.E., Plotkin, P., Wintherington, B., Lutz, P.L., 1997. Human impacts on sea turtle survival. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology of Sea Turtles. vol. I. CRC Press, Boca Raton, Florida, pp. 387–409.

Marshall, G., Jones, R.H., 1995. Multi-state models and diabetic retinopathy. Stat. Med. 14, 1975–1983. https://doi.org/10.1002/sim.4780141804.

Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B., Teutschel, N.M., Crowder, L.B., Benson, S., Dutton, P.H., Bailey, H., Kappes, M.A., Kuhn, C.E., Weise, M.J., Mate, B., Shaffer, S.A., Hassrick, J.L., Henry, R.W., Irvine, L., McDonald, B.I., Robinson, P.W., Block, B.A., Costa, D.P., 2013. Cumulative human impacts on marine predators. Nat. Commun. 4 (2688), 1–9. https://doi.org/10.1038/ncomms3688.

McClellan, C.M., Read, A.J., 2009. Confronting the gauntlet: understanding incidental capture of green turtles through fine-scale movement studies. Endanger. Species Res. 10 (1), 165–179. https://doi.org/10.3354/esr00199.

McKenna, L.N., Paladino, F.V., Tomillo, P.S., Robinson, N.J., 2019. Do sea turtles vocalize to synchronize hatching or nest emergence? Copeia 107 (1), 120–123. https://doi.org/10.1643/ce-18-069.

Meira-Machado, L.F., de Uña-Álvarez, J., Cadarso-Suárez, C., Andersen, P.K., 2009. Multi-state models for the analysis of time-to-event data. Stat. Methods Med. Res. 18, 195–222. https://doi.org/10.1177/0962280208092301.

Mendonça, M.T., 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Am. Soc. Ichthyol. Herpetol. 4, 1013–1023. https://doi.org/10.2307/1445104.

Meylan, A., 1983. Marine turtles of the Leeward Islands, Lesser Antilles. Atoll Res. Bull. 278, 1–24. https://doi.org/10.5479/si.00775630.278.1.

Moncada, F., Abreu-Grobois, F.A., Muhlia-Melo, A., Bell, C., Tröeng, S., Bjorndal, K.A., Bolten, A.B., Meylan, A.B., Zurita, J., Espinosa, G., Nodarse, G., Márquez-millán, R., Foley, A., Ehrhart, L., 2006. Movement patterns of green turtles (*Chelonia mydas*) in Cuba and adjacent Caribbean waters inferred from flipper tag recaptures. J. Herpetol. 40 (1), 22–34. https://doi.org/10.1670/39-05A.1.

Moran, K.L., Bjorndal, K.A., 2007. Simulated green turtle grazing affects nutrient composition of the seagrass *Thalassia testudinum*. Mar. Biol. 150 (6), 1083–1092. https://doi.org/10.1007/s00227-006-0427-9.

Musick, J.A., Limpus, C.J., 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz, P.L., Musick, J.A. (Eds.), The Biology of Sea Turtles. CRC Press, pp. 137–163.

Nivière, M., Chambault, P., Pérez, T., Etienne, D., Bonola, M., Martin, J., Barnérias, C., Védie, F., Mailles, J., Dumont-Dayot, É., Gresser, J., Hiélard, G., Régis, S., Lecerf, N., Thieulle, L., Duru, M., Lefebvre, F., Milet, G., Guillemot, B., Bildan, B., de Montgolfier, B., Benhalilou, A., Murgale, C., Maillet, T., Queneherve, P., Woignier, T., Safi, M., Le Maho, Y., Petit, O., Chevallier, D., 2018. Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle. Biol. Conserv. 223, 170–180. https://doi.org/10.1016/j.biocon.2018.05.002.

OMMM, 2009. Base de données cartographique des fonds marins côtiers de la Martinique. Biocénoses benthiques, Fort de France.

Patin, R., Etienne, M.P., Lebarbier, E., Chamaillé-Jammes, S., Benhamou, S., 2020. Identifying stationary phases in multivariate time series for highlighting behavioural modes and home range settlements. J. Anim. Ecol. 89, 44–56. https://doi.org/10.1111/1365-2656.13105.

Patrício, A.R., Velez-Zuazo, X., Diez, C.E., Van Dam, R., Sabat, A.M., 2011. Survival probability of immature green turtles in two foraging grounds at Culebra Puerto Rico. Mar. Ecol. Prog. Ser. 440, 217–227. https://doi.org/10.3354/meps09337.

Pfaller, J.B., Williams, K.L., Frick, M.G., Shamblin, B.M., Nairn, C.J., Girondot, M., 2019. Genetic determination of tag loss dynamics in nesting loggerhead turtles: a new chapter in “the tag loss problem”. Mar. Biol. 166 (97), 1–17. https://doi.org/10.1007/s00227-019-3545-x.

Pilcher, N., 2010. Population structure and growth of immature green turtles at Mantanani, Sabah, Malaysia. J. Herpetol. 44 (1), 168–171. https://doi.org/10.1670/08-115.1.

Putman, N.F., Verley, P., Shay, T.J., Lohmann, K.J., 2012. Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. J. Exp. Biol. 215, 1863–1870. https://doi.org/10.1242/jeb.067587.

Reich, K.J., Bjorndal, K.A., Bolten, A.B., 2007. The “lost years” of green turtles: using stable isotopes to study cryptic lifestages. Biol. Lett. 3 (6), 712–714. https://doi.org/10.1098/rsbl.2007.0394.

Renaud, M.L., Carpenter, J.A., Williams, J.A., Manzella-Tirpak, S.A., 1995. Activities of juvenile green turtles, *Chelonia mydas*, at a jettied pass in south Texas. Fish. Bull. 93 (3), 586–593 doi:00900656 (ISSN).

Ruiz, H., Ballantine, D.L., 2004. Occurrence of the seagrass *Halophila stipulacea* in the tropical west Atlantic. Bull. Mar. Sci. 75 (1), 131–135.

Schofield, G., Katselidis, K.A., Dimopoulos, P., Pantis, J.D., Hays, G.C., 2007a. Behaviour analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. Endanger. Species Res. 2, 71–79. https://doi.org/10.3354/esr002071.

Schofield, G., Katselidis, K.A., Pantis, J.D., Dimopoulos, P., Hays, G.C., 2007b. Female–female aggression: structure of interaction and outcome in loggerhead sea turtles. Mar. Ecol. Prog. Ser. 336, 267–274. https://doi.org/10.3354/meps336267.

Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A., Hays, G.C., 2010. Fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers. Distrib. 16 (5), 840–853. https://doi.org/10.1111/

j.1472-4642.2010.00694.x.

Seminoff, J.A., 2004. *Chelonia mydas*. In: The IUCN Red List of Threatened Species 2004, e.T4615A11037468.

Seminoff, J.A., Shanker, K., 2008. Marine turtles and IUCN red listing: a review of the process, the pitfalls, and novel assessment approaches. J. Exp. Mar. Bio. Ecol. 356, 52–68. https://doi.org/10.1016/j.jembe.2007.12.007.

Seminoff, J.A., Resendiz, A., Nichols, W.J., 2002. Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Mar. Ecol. Prog. Ser. 242, 253–265. https://doi.org/10.3354/meps242253.

Seminoff, J.A., Allen, C.D., Balazs, G.H., Dutton, P.H., Eguchi, T., Haas, H.L., Hargrove, S.A., Jensen, M., Klemm, D.L., Lauritsen, A.M., MacPherson, S.L., Opay, P., Possardt, E.E., Pultz, S., Seney, E., Van Houtan, K.S., Waples, R.S., 2015. Status review of the green turtle (*Chelonia mydas*) under the U.S. Endangered Species Act. In: NOAA Technical Memorandum, NOAA-NMFS-SWFSC-539, 571 pp.

Senko, J., López-Castro, M.C., Koch, V., Nichols, W.J., 2010. Immature east pacific green turtles (*Chelonia mydas*) use multiple foraging areas off the Pacific coast of Baja California Sur, Mexico: first evidence from mark-recapture data. Pacific Sci. 64 (1), 125–130. https://doi.org/10.2984/64.1.125.

Shimada, T., Limpus, C.J., Hamann, M., Bell, I., Esteban, N., Groom, R., Hays, G.C., 2020. Fidelity to foraging sites after long migrations. J. Anim. Ecol. 89 (4), 1008–1016. https://doi.org/10.1111/1365-2656.13157.

Svanbäck, R., Bolnick, D.I., 2005. Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. Evol. Ecol. Res. 7, 993–1012.

Thayer, G.W., Bjorndal, K.A., Ogden, J.C., Williams, S.L., Zieman, F.C., 1984. Role of larger herbivores in seagrass community. Estuaries 7 (4), 351–376. https://doi.org/10.2307/1351619.

UICN Comité français, OFB, MNHN, 2020. La Liste rouge des espèces menacées en France - chapitres faune de Martinique. Paris, France.

Van De Merwe, J.P., Ibrahim, K., Lee, S.Y., Whittier, J.M., 2009. Habitat use by green turtles (*Chelonia mydas*) nesting in Peninsular Malaysia: local and regional conservation implications. Wildl. Res. 36 (7), 637–645. https://doi.org/10.1071/WR09099.

Wallace, B.P., Dimatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Alan, B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-grobois, F.A., Marcovaldi, M.A., Mortimer, J.A., Musick, J.A., Pilcher, N.J., Seminoff, J.A., Troe, S., 2010. Regional Management Units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS One 5 (12), 1–11. https://doi.org/10.1371/journal.pone.0015465. e15465.

Whiting, S.D., Miller, J.D., 1998. Short term foraging ranges of adult green turtles (*Chelonia mydas*). J. Herpetol. 32 (3), 330–337. https://doi.org/10.2307/1565446.

Whitman, E., Heithaus, M., García Barcia, L., Brito, D., Rinaldi, C., Kiszka, J., 2019. Effect of seagrass nutrient content and relative abundance on the foraging behavior of green turtles in the face of a marine plant invasion. Supplement. Mar. Ecol. Prog. Ser. 628, 171–182. https://doi.org/10.3354/meps13092.