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Satellite tracking and field assessment highlight major foraging site for green turtles in the Banc d'Arguin, Mauritania

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ABSTRACT

There is a remarkable paucity of estimates of the numeric importance of sea turtles at foraging grounds. The Banc d'Arguin (BA) is a vast shallow marine area off the coast of Mauritania, known as a site of world importance for coastal migratory birds and other biodiversity, including extensive seagrass beds. We sampled foraging green turtles on the BA, and extensively tracked adult female green turtles from the Bijagós archipelago, the only significant nesting aggregation within 3000 km of the BA, to estimate the abundance of this foraging aggregation. Additionally, we used a demographic simulation to support our findings. Based on satellite tracking of adult females (n = 46), we estimate that 50 % of the nesting population from the Bijagós migrate to the BA post-nesting. We combine data on numbers nesting in the Bijagós with information on proportion migrating to the BA in the same years to conservatively estimate that 8285 adult female green turtles forage at this site. We also estimate that adult females represent only 5.6 % of the green turtles in the BA, implying that the number of turtles there is of the order of 150,000 individuals. Most of the BA enjoys effective protection as part of the Parc National du Banc d'Arguin where significant fisheries regulations are well enforced by a marine surveillance program. We show that the BA is one of the major foraging sites for green turtles nesting in the Bijagós and a site of critical importance for immature and adult green turtles in a global context.

1. Introduction

Assessing wildlife population abundance is fundamental for understanding ecosystem roles (Heithaus et al., 2008; Hammerschlag et al., 2019) and supporting conservation processes (Johnston et al., 2015; García-Barón et al., 2019). For instance, IUCN Red List assessments are highly dependent on population abundance estimates (IUCN, 2001). Baseline abundance estimates are also key to detect change in the face of threats or as a response to conservation efforts. Yet, for many groups of species obtaining such information is challenging, particularly for highly vagile marine animals, due to cryptic life-stages (e.g. Péron and Grémillet, 2013; Dalleau et al., 2014) and the additional demands associated with surveying marine habitats.

Sea turtles are species of conservation concern (Godley et al., 2020). Most of their main sites of reproduction are known and surveyed (Mazaris et al., 2017). Hence, assessing the numerical importance of nesting beaches and populations is relatively easy for most species, which is relevant for conservation and monitoring (e.g. Mazaris et al., 2017). In contrast, sea turtles are difficult to survey at sea, resulting in major gaps regarding important areas for foraging and growth (Rees et al., 2016). As sea turtles can take decades to mature, remaining mostly out of sight for the greater part of their life cycle, overall there is a poor knowledge of their abundance, distribution and various aspects of their ecology (Wildermann et al., 2018). Documenting important foraging sites and the composition and numerical importance of foraging aggregations is critical for management, for example for marine spatial planning or to put bycatch or other recorded mortality values into context (Seminoff et al., 2014; Shimada et al., 2016). Such information is

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also relevant to better understand the population dynamics of sea turtles and the role of these animals in marine ecosystems (Hamann et al., 2010).

Some abundance estimates at foraging sites have been obtained by counting turtles at or near the sea surface during transects from boats or from the air (Epperly et al., 1995; Benson et al., 2007; Lauriano et al., 2011), which provide absolute densities when analyzed in conjunction with data on turtle detectability (Seminoff et al., 2014; Fuentes et al., 2015; Sykora-Bodie et al., 2017). Alternatively, surveys over smaller areas can be carried out by divers or snorkellers (Roos et al., 2005; Mancini et al., 2015; Becker et al., 2019), or using drones (Robinson et al., 2020). Capture-mark-recapture methods are also possible, albeit challenging to use (Mancini et al., 2015). Each of these methods has advantages and limitations, resulting from various factors, such as the species-assemblage present, the existence of accurate knowledge of diving patterns, water turbidity, the size of the areas to survey and the numbers of turtles present.

In theory, for any area containing adult females originating from a known nesting population(s), it should be possible to estimate the total number of turtles in the foraging aggregation (Nt) based on three known/estimated quantities:

(a) number of adult females laying at the relevant nesting grounds,
(b) proportion of the number of adult females from the relevant nesting grounds that migrate to the target foraging ground,
(c) proportion of adult females amongst all the turtles present on the foraging grounds.

Multiplying (a) and (b) gives the number of adult females at the target foraging ground (Nf = a × b). The total number of turtles at the foraging ground is Nt = Nf × (1/c).

The Banc d'Arguin is a shallow marine area, including vast intertidal flats and channels, on the northern coast of Mauritania, West Africa. A large proportion of the area is protected by the Parc National du Banc Arguin (PNBA), which was created in 1976 in recognition of its exceptional biodiversity values, in particular as one of the major world wintering sites for migratory shorebirds (Araújo and Campredon, 2016). The Banc d'Arguin is also known to include extensive seagrass beds (Chefaoui et al., 2021; Trégarot et al., 2021) and to be a migratory destination for green turtles *Chelonia mydas* nesting in Guinea-Bissau (Godley et al., 2010; Patrício et al., 2022), but before this study little systematic work on sea turtles had been conducted in the region (but see Cardona et al., 2009; Monteiro et al., 2021). In particular, nothing was known on the size of the feeding aggregation or on the demographic structure of green turtles using this site.

Here, we combine satellite-tracking data with information of nesting

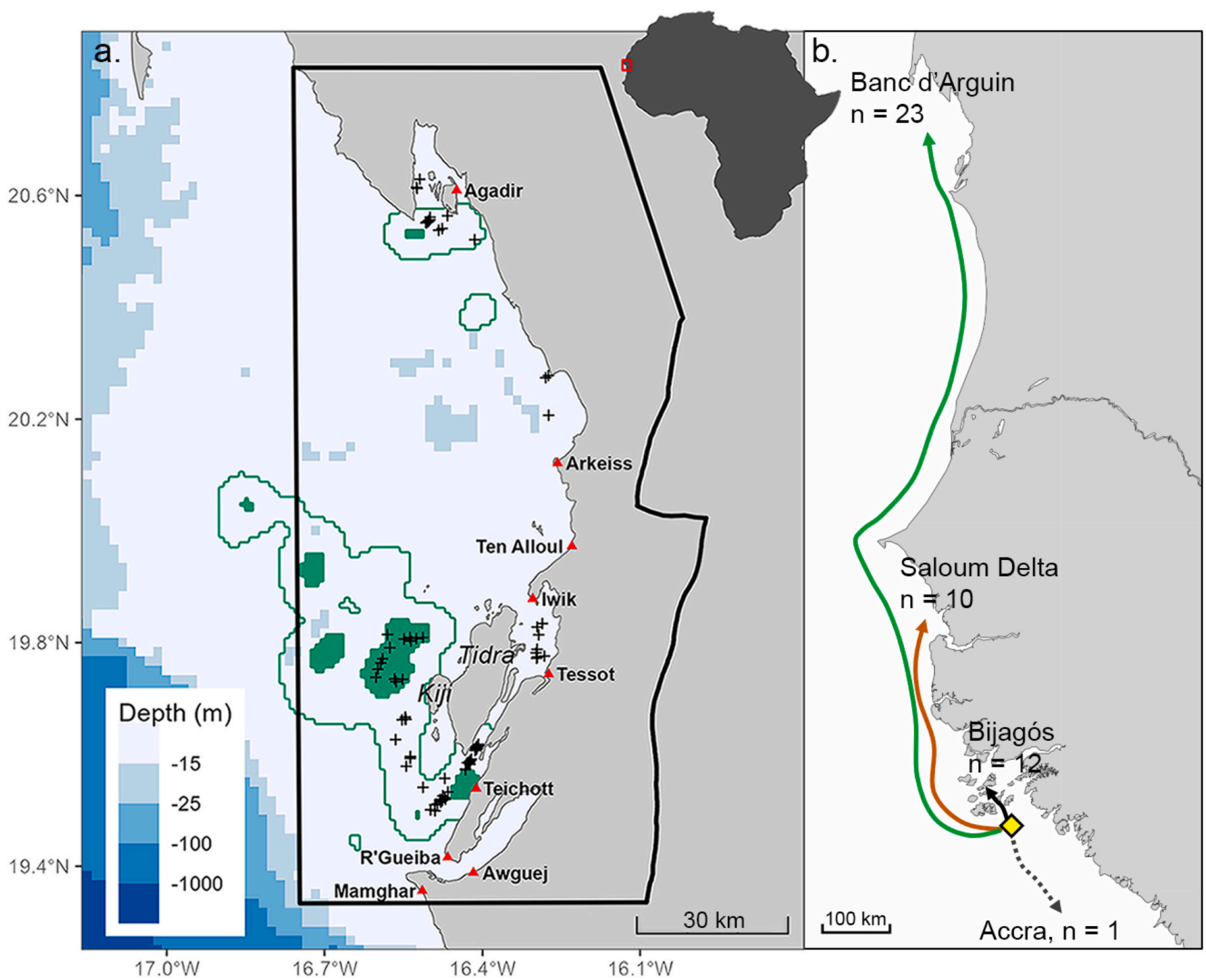

Fig. 1. Study sites and green turtle migrations - a. Inset map of Africa indicates the location of the study area, large map shows the Banc d'Arguin with capture locations of foraging green turtles (black crosses), Imraguen villages (red triangles) and estimated utilization distribution (UD) areas of adult female green turtles tracked from Poilão Island, Guinea-Bissau, to the Banc d'Arguin, in Mauritania: green line shows home range - 95 % UD – and filled in green are the core use areas - 50 % (UD). The bold solid black polygon indicates the limits of the National Park of the Banc d'Arguin (PNBA). The UD areas were taken from Patrício et al., 2022; b. representation of migratory routes displayed by post-nesting green turtles tracked from Poilão Island (yellow diamond), and number of turtles migrating to each foraging area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

numbers at the main source rookery and with at-sea captures of turtles to estimate the number of green turtles at a major foraging site, the Banc d'Arguin, and present a demographic simulation to further support our findings, while also providing information on the size-structure of this foraging aggregation.

2. Methods

2.1. Study areas

The Banc d'Arguin (Fig. 1a) covers a marine area located along the northern third of the Mauritanian coast, roughly between the Cap Blanc (20°46′N, 17°02′W) and the Cap Timiris (19°23′N, 16°32′W), at the western edge of the Sahara Desert. Most of the very shallow marine areas and the intertidal banks, in an area covering approximately 6000 km^2, are protected by the PNBA. Extensive seagrass beds composed of three species (the intertidal *Zostera noltei* and the subtidal *Cymodocea nodosa* and *Halodule wrightii*) are found here. The waters in the BA are mostly turbid, and seagrasses only grow in waters shallower than ~4 m (Chefaoui et al., 2021).

While the surface of the intertidal areas (and of the shallower subtidal zones) is readily evaluated through satellite imagery, the spread of seagrasses underwater is uncertain, with the overall extension of the beds being variedly estimated at 674 km^2 (Trégarot et al., 2021) or at 4295 km^2 (Chefaoui et al., 2021). The difference between estimates is in part justified by a different domain, the second study covering vast areas outside the PNBA. In addition, there are macroalgae present, which green turtles are known to forage upon in the region (Díaz-Abad et al., 2022).

The Bijagós Archipelago, in Guinea-Bissau, contains nearly one hundred islands. Green turtles nest on several of those islands, with the majority being concentrated in the João Vieira and Poilão Marine National Park, and particularly on the island of Poilão (Catry et al., 2009). Turtle nesting on this island has been closely monitored by the Institute of Biodiversity and Protected Areas (IBAP) of Guinea-Bissau since 2000 (Barbosa et al., 2018). Nesting females from this area regularly migrate to forage in the Banc d'Arguin (Godley et al., 2010; Patrício et al., 2022).

2.2. Turtle sampling in Mauritania

We sampled turtles throughout the Banc d'Arguin (Fig. 1a) in order to obtain an estimate of the size distribution of foraging individuals at this site and to infer the proportion of adult females amongst those individuals. Based on sizes of both reproductive female ($n = 409$) and male ($n = 12$) green turtles from the breeding site at Poilão, we considered turtles with CCL > 80 cm to be potential adults and, within this size-class, turtles were classified as males if they presented a thick elongated tail and large recurved claws on the front flippers (Miller, 1997).

Sampling of turtles in the Banc d'Arguin occurred from May 2018 to November 2021 and was based on directed captures for scientific purposes, complemented with surveys of remains of stranded turtles. Directed captures were carried out with the support of local fishers, the "Imraguen". We used one or two *lanches* (traditional sailing boats, Fig. 2) from which nets were deployed either on a seine action encircling an area where turtles were spotted when surfacing to breathe or simply deployed as a straight line across a channel in an area with detected turtle activity. Nets were 300–500 m long, 4 m deep and 32 cm mesh size. Nets were retrieved as soon as deployment finished, with no waiting soaking time, and entangled turtles were hauled-up to the boats.

The broad locations of the experimental fishing sessions (Fig. 1a) were defined mostly by asking fishers from various villages (Agadir, Arkeiss, Iwik, Teichott) spread-out along the Banc d'Arguin to take us to known areas with good numbers of sea turtles, and also by going to locations where turtles tracked from the nesting grounds were known to forage. There was a very high concordance between the locations informally gathered from the fishers and the locations indicated by

Fig. 2. Traditional sailing boat - ('lanche') used in the Banc d'Arguin by Imraguen fishers, and used to capture foraging green turtles for scientific purposes (all turtles were released at capture location after measurement and sampling).

satellite tracking.

Depth of water at net-launching sites varied between 2 and 10 m. Successful captures took place on 55 different dates, with number of turtles captured varying between 0 and 40 per net set. For the calculation of the proportion of adult females in the population, we only consider capture sessions between December and June, when adult females are unlikely to be away from the Banc d'Arguin while engaged on reproductive migrations.

To obtain complementary information on the sizes of turtles present in the Banc d'Arguin, in March 2019 and April and May 2021 we walked ca. 20 km of beaches on the islands of Kiji and Agadir and along the coast around Teichott (Fig. 1a) and measured the curved carapace length (CCL) of all undamaged carapaces found. Each section of the coast was surveyed only once, to avoid repeatedly sampling the same turtles.

2.3. Turtle tracking from Guinea-Bissau

From 2018 to 2021, we used satellite tags to track 46 adult female green turtles nesting at the João Vieira Poilão Marine National Park, in the southeast of the Bijagós Archipelago, Guinea-Bissau (hereafter "Bijagós", Fig. 1b). Satellite tags were deployed on the island of Poilão ($n = 44$), where most of the green turtles in Guinea-Bissau reproduce (Catry et al., 2009, 2010), and on the neighbouring island of Meio ($n = 2$). See Patrício et al. (2022) for attachment procedure. The main green turtle nesting season at these rookeries extends from August to October (Catry et al., 2009), and we deployed tags throughout the season to obtain a representative sample of migratory destinations of this population. We used two models of Platform Transmitter Terminal (PTT) devices; SPOT-375B from Wildlife Computers, Seattle, Washington, which transmit Argos locations, and F6G - 376B from Lotek, Havelock North, New Zealand, which transmit both Argos and Fast GPS (hereafter 'FGPS') location information via the Argos satellite system. Both tag types were set to transmit a position every 15 s.

To estimate the proportion of adult females from the Bijagós that forage in the Banc d'Arguin, we assigned the tracked turtles to a foraging ground. Assignment was not possible when the PTTs stopped transmitting while the turtle was still around the nesting site or engaged in active migratory movement. Those turtles that were tracked for long completed post-nesting migrations to foraging grounds where they initiated restricted movements, typical of foraging behaviour (10 to 288 foraging days, see Patrício et al., 2022). No turtles displayed stopovers that might confound the assignment to a specific foraging ground.

2.4. Nesting numbers in Guinea-Bissau

Numbers of nests on Poilão are estimated based on daily track counts (corrected for laying success, Catry et al., 2009) on the nesting beaches during most of the nesting season, from early August to late November each year (Catry et al., 2002, Barbosa et al., 2018, IBAP, unpublished data).

We estimate that in Guinea-Bissau, 16 % of the green turtles nest outside Poilão, almost all on other islands of the Bijagós. Such estimate is based on published data (Catry et al., 2009, 2010; Barbosa et al., 2018), and on IBAP – Guinea-Bissau unpublished data.

Estimates of number of adult females using a specific nesting area are generally based on counts of nests, plus complementary data on clutch frequency and remigration intervals. Due to the massive size of the nesting aggregation on Poilão and other constraints, it has not been possible to obtain reliable data on such parameters.

Our data of clutch frequency per nesting season and per female on Poilão suffers from biases described in other populations that lead to a severe underestimation (Esteban et al., 2017). Number of clutches per season is better evaluated through telemetry studies. Limited satellite telemetry at Poilão suggest that females may lay 8 or more clutches per season, considering an interesting interval of 12.2 days (Catry et al., 2009), however tracking was not conducted from the beginning of the season such that recorded mean clutch frequency (mean = 4.5 ± 1.8 SD) is likely underestimated. Thus, we used instead the mean of the estimates from two detailed studies that tracked green turtles from the start of the nesting season, which have estimated 6.3 clutches per season on Ascension Island, Atlantic Ocean (Weber et al., 2013) and 6.0 clutches per season on the Chagos Archipelago, Indian Ocean (Esteban et al., 2017). Based on these, we used a value of 6.15 in our calculations.

Remigration interval is apparently highly variable in green turtles (Seminoff et al., 2015) and this parameter has a heavy weight in the estimation (from nest counts) of overall nesting females in a population. Furthermore, remigration intervals may potentially vary within a single population as a function of distance to foraging sites. Rather than making assumptions on this parameter, we opted to consider a reliable minimum number of turtles nesting in Guinea-Bissau. Green turtles only exceptionally nest in two consecutive seasons (and the few that do so are unlikely to be long-distance migrants, such as the ones migrating from the Bijagós to the Banc d'Arguin). Because we have good tracking data for 2020 and 2021, and concurrent data in the same years in the Banc d'Arguin, we took these two years to obtain a minimum number of turtles nesting in Guinea-Bissau on the assumption that all turtles nesting in these two years were different individuals.

2.5. Proportion of adult females in the Banc d'Arguin

Estimating the number of adult female turtles amongst the ones captured at the Banc d'Arguin is not straightforward. The size-distribution of adult females at the nesting grounds in Guinea-Bissau shows that, excluding rare outliers, the smaller reproducing turtles are in the 80–85 CCL class, but that there is a peak in sizes of CCL of 100–105 cm (Fig. 3c). Because there is no reason to believe that, in a growing population (Barbosa et al., 2018), there should be fewer turtles in smaller size classes than in larger ones (Hays et al., 2022), it is reasonable to admit that only a proportion of the turtles of sizes below 100 cm are sexually mature and laying. We used the relative frequency of different adult female size-classes to estimate the number of females that were actually already reproducing amongst those in the captured sample. Making the conservative assumptions that all turtles above 100 CCL are adult breeders and that there are as many female turtles alive in size class N_i (i = 80–85, 85–90, 90–95, 95–100 cm) as in size class $N_{100-105}$ ($n = 143$ turtles in our sample), we estimated the proportions of females reproducing in these size-classes as $PR_i = N_i/N_{100-105}$. So, in the 95–100 size-class ($n = 114$) we estimate that 80 % are reproducing (PRi = 114/143), in the 90–95 ($n = 40$) this value is 28 % (PRi = 40/143), and so on. We then used these values to estimate the proportion of female turtles that have recruited into the breeding population amongst the turtles sized between 80 and 100 cm CCL captured in the BA. For example, we captured 10 females in the size-class 95–100, but since we estimate that only 80 % of the turtles of this size class reproduce, we consider that only 8 of those 10 turtles are adult females.

2.6. Structure of virtual green turtle populations

To assess whether our estimate of the proportion of adult females in the BA was plausible, and not stemming from a potential sampling bias, we built simulations to estimate the structure of virtual green turtle populations based on different sets of realistic biological parameters based on published literature (Bolten et al., 1992; Chaloupka, 2002; Seminoff et al., 2002; Balazs and Chaloupka, 2004; Patrício et al., 2011, 2014; Eguchi et al., 2012; Omeyer et al., 2017; Pfaller et al., 2018). Annual survival rates and growth rates of individuals of each age-class of green turtles reported in different studies are highly variable and contain important sources of uncertainty. There are no estimates for such demographic rates in West Africa. So, we opted to produce simulations using a broad range of parameter values simply to assess whether our results are realistic according to at least some of the scenarios that may potentially apply to our study population whose demography is

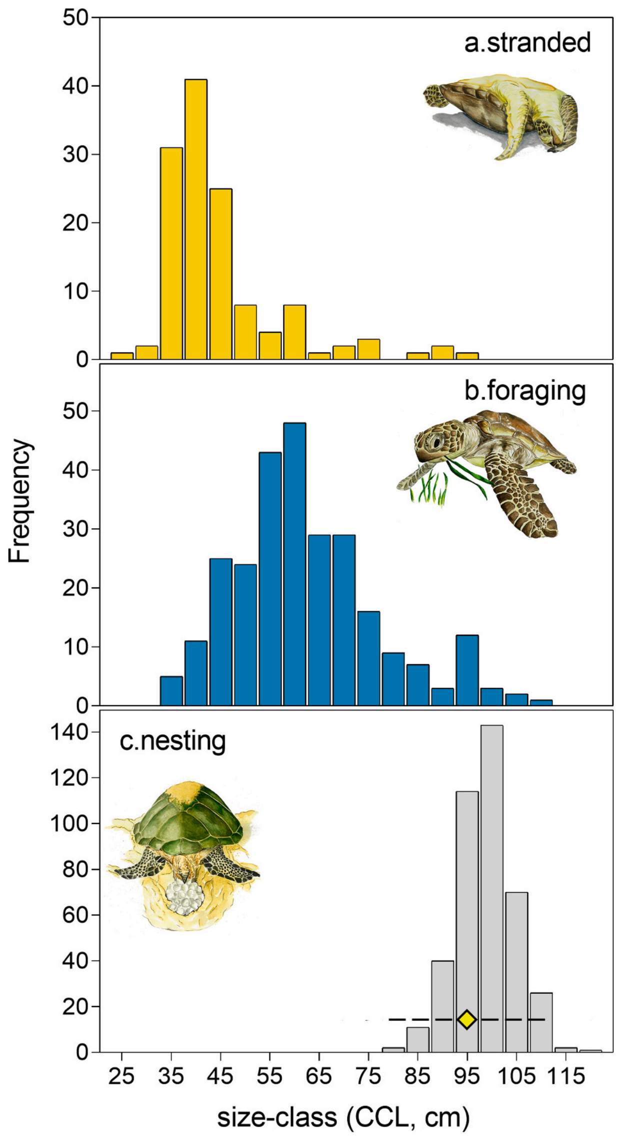

Fig. 3. Size distributions of green turtles - a. found stranded along the shore of the PNBA, Mauritania, b. caught during experimental fishing at the PNBA and c. nesting at Poilão Island, in Guinea-Bissau. In panel c., dashed line shows the size range of breeding males at Poilão and yellow diamond indicates their mean size-class. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

unknown (see electronic Supplementary methods 1 for details on the methodological approach).

3. Results

3.1. Adult females migrating to the Banc d'Arguin

Of the 46 adult females nesting in Guinea-Bissau that were successfully tracked to a foraging ground from 2018 to 2021, exactly half ($n = 23$) migrated to the Banc d'Arguin. However, this proportion varied from year to year ($\chi 2 = 24.85$, $P = 0.003$, Table 1). Weighing these proportions by the number of females estimated to nest in each of these years (IBAP, unpublished data) coincidentally still gives almost the same result: 50.3 % of the adult females migrating from Guinea-Bissau to the Banc d'Arguin.

The number of estimated clutches on Poilão was 59,676 and 14,260 in 2020 and 2021, respectively. Assuming that Poilão represents 84 % of the national population (see Methods), we have estimates of 71,042 and 16,976 clutches for Guinea-Bissau in 2020 and 2021, respectively. Assuming 6.15 clutches per females per season, this yields 11,552 females in 2020 and 2760 females in 2021. Multiplying these numbers by the proportions indicated in Table 1 and summing the two years, we reach a value of 8285 adult females migrating to the Banc d'Arguin.

Table 1
Post-nesting migratory destinations of female green turtles laying in the Bijagós Archipelago, Guinea-Bissau, from 2018 to 2021, as assessed by satellite tracking. The proportion of tracked turtles per year migrating to the Banc d'Arguin is given in parenthesis.

Foraging destination	2018	2019	2020	2021
Bijagós Archipelago, Guinea-Bissau	4	6	2	0
Senegal and The Gambia	4	2	4	0
Banc d'Arguin, Mauritania	7 (47 %)	0 (0 %)	6 (50 %)	10 (91 %)
Off Accra, Ghana	0	0	0	1
No. turtles tracked to foraging ground	15	8	12	11

3.2. Turtles foraging at the Banc d'Arguin

We captured 323 turtles in the PNBA, all of which were green turtles. Furthermore, out of 157 turtles (carapaces) recorded on the beaches on the PNBA, all but one (a loggerhead *Caretta caretta*) were green turtles. For the following size structure analyses, we only consider 267 live turtles captured from December to June (see Methods).

The mean CCL of foraging turtles was 65.2 ± SD 14.9 cm ($n = 267$, range: 36.5–115 cm CCL), while the corresponding value for stranded turtles was 47.9 ± SD 12.3 cm ($n = 130$, range: 29–96 cm CCL). There was a statistically significant difference ($\chi^2 = 127.88$, $P < 2.2 \times 10^{-16}$) between the size distributions of the two groups (Fig. 3a and b). Turtles ≤50 cm CCL represent 77 % of the stranded turtles but only 15 % of the ones we captured.

We measured 409 turtles laying in Poilão in 2020 and 2021. Excluding an outlier with 81.6 cm CCL, the smallest females had a CCL ≥ 85 cm (Fig. 3c). Turtles with a CCL ≥ 85 cm represented 10.5 % of our captures in the PNBA, and 9.0 % if we exclude individuals clearly assigned as adult males ($n = 4$, mean tail length = 45.3 cm ± 1.6 cm SD, range: 43.5–46 cm). Using the probability of breeding per size-class (Table 2), we estimate that from the turtles captured between December and June with CCL ≥ 85 cm, 15 were breeding females, giving an estimate of 5.6 % adult female green turtles in this foraging aggregation. Combining adult females and adult males, we estimate a value of 7.1 % (19/267) adult turtles in the foraging aggregation.

Using the estimates of 8285 adult females migrating to the BA and assuming that adult females represent only 5.6 % of the turtles foraging there, we reach an estimate of 147,946 green turtles present in this foraging aggregation. It is also interesting to note that we only captured 4 adult males compared to an estimated 15 adult females, giving a 1 to 3.75 male to female adult sex-ratio in the BA.

Table 2
For six size-classes of female green turtles, number (No.) measured in a sample while nesting at Poilão Island, Guinea-Bissau in 2020 and 2021, estimated proportion of female turtles reproducing and no. captured at the Banc d'Arguin, Mauritania.

CCL size-class (cm)	No. green turtles nesting at Poilão	% reproducing (PR_i)	No. green turtles captured in the BA
80.01–85	2	1.4	9
85.01–90	11	7.7	7
90.01–95	40	28	1
95.01–100	114	79.7	10
100.01–105	143	100	3
>105	99	100	3

3.3. Structure of virtual green turtle populations

Amongst the 12 simulations using plausible scenarios of survival and growth rates of green turtles of different size-classes, 5 resulted in stable populations where the percentage of adult turtles was smaller than our estimated percentage of adult turtles in the BA foraging aggregation (7.1 %). Further, amongst the turtles we captured, 8.6 % were larger than 90 cm CCL, while 6 of the 12 simulations resulted in percentages smaller than this (Table S1).

4. Discussion

By extensively tracking adult females nesting from the Bijagós Archipelago, Guinea-Bissau, we show that approximately 50 % of the individuals laying at this site of major global importance for green turtles migrate to the Banc d'Arguin, Mauritania. Furthermore, sampling at the Banc d'Arguin indicates that the site harbours highly abundant juvenile and subadult turtles, with their numbers likely being of the order of 150 thousand individuals. Although this last estimate contains several significant sources of uncertainty, there can be little if any doubt that the Banc d'Arguin is a foraging area of global importance for green turtles.

From 2017 to 2021, the mean annual number of green turtle clutches on Poilão was approximately 25,000 (peak of 60,000 in 2020, IBAP, unpublished data). This means that Poilão is currently only surpassed as a rookery for green turtles by Raine Island (Australia), Tortuguero (Costa Rica), Oman and Seychelles (SWOT, 2011; Broderick and Patrício, 2019). Poilão and neighbouring sites in Guinea-Bissau are likely the only significant contributors of adult turtles to the Banc d'Arguin, as no other sizeable rookeries are known within a radius of 3000 km from this site, and tracking from more distant rookeries within the South Atlantic Regional Management Unit does not indicate movements to Mauritania (Hays et al., 2002; Mettler et al., 2019). Still, as the Banc d'Arguin sustains half of the females nesting on Poilão, this indicates, by itself, a major foraging ground of great conservation value. Note that this estimate of the proportion of turtles migrating from Poilão to the Banc d'Arguin is based on 46 successfully tracked adult females, which according to the simulations presented by Sequeira et al. (2019) is a robust sample size for this type of evaluation. We estimate that in excess of 8000 adult female green turtles forage in the Banc d'Arguin, which is by any standard a large foraging aggregation.

Size frequency data from stranded turtles suggest that green turtles recruit to the Banc d'Arguin foraging area when mostly between 35 and 40 cm CCL. This size is within the typical values recorded elsewhere (Seminoff et al., 2015) and suggests that green turtles may potentially use the Banc d'Arguin for most of their development after the pelagic offshore phase of the so-called lost years. Note, however, that there are known development sites where green turtles seem to recruit at even smaller sizes (e.g. Foley et al., 2007). From in-water captures, we estimate that immature turtles in the Banc d'Arguin may exceed 90 % of the total number of individuals, likely representing over 100 thousand individuals. The simulations performed on the size structure of virtual populations of green turtles using plausible demographic rates support these findings. We recognise that the simulations of the size-structure of the virtual green turtle populations are crude, due to uncertainties in parameters such as growth and survival rates, which may vary considerably in time and space (Patrício et al., 2014; Bjorndal et al., 2017; Pfaller et al., 2018). Nevertheless, the conclusion that adult females represent only a very small proportion of green sea turtle populations seems to hold for a range of plausible demographic rates, supporting our empirical findings.

The proportion of mature females in foraging grounds can be directly assessed with laparoscopy, a mildly invasive surgery which allows the observation of the developmental stage of gonads (Limpus et al., 1994; Chaloupka et al., 2004). However, this procedure is challenging to implement in the field and it must be practiced by trained veterinarians. Alternatively, ultrasonography has been suggested as a substitute of laparoscopy, being easier and practical for fieldwork use, and less stressful for turtles (Blanvillain et al., 2008). Such method could potentially be used to obtain an independent estimate of the proportion of adult females amongst green turtles in the Banc d'Arguin.

Although the sample size of male green turtles was not sufficiently large to allow for robust statistical comparisons, we found that, amongst adults present around Poilão, males were on average smaller (mean CCL = 93.2 cm ± 6.2 cm SD, range: 83.0–106.3 cm, n = 12) than females (mean CCL = 101.7 cm ± 5.8 cm SD, range: 81.6–121.5, n = 409; own unpublished data), similarly to what was found for other green turtle populations (Godley et al., 2002; Mortimer et al., 2022). It is thus unlikely that turtles classified as adult females are prepubescent males. It is also interesting to note that we captured 4 adult males and estimate 15 adult females amongst our samples captured at the Banc d'Arguin. This female-biased sex ratio may result from the fact that most males from Guinea-Bissau migrate shorter distances than females, stopping short of Mauritania and the Banc d'Arguin (Beal et al., 2022) and hence the data presented here cannot provide an indication of the true population adult sex-ratio.

The comparison of the size-classes of captured and stranded turtles reveals marked differences and strongly suggests that our experimental fishing with the Imraguen largely missed the smaller turtles, particularly those of CCL ≤ 50 cm. We believe such large discrepancy may result from size-related differences in habitat selection (Bresette et al., 2010; Welsh and Mansfield, 2022) with small turtles concentrating in very shallow waters where the Imraguen were reluctant to venture with their sailing boats, and possibly some small turtles also being able to escape through the large mesh of the nets. Further, mortality rates of very small turtles could be higher, yielding an over-representation amongst stranded turtles. In any case, the combined evidence strongly suggests that our estimate of a population composed of 5.6 % adult females based on captures at sea may be reasonable or even above the actual value, in which case the total number of green turtles in the Banc d'Arguin might largely exceed the value of 147,946 calculated above.

Given the unknowns of turtle demographic traits and the numerous assumptions that were needed for obtaining the estimates presented in this paper, it would be interesting to attempt an independent confirmation of numbers, for example by estimating densities using boats, aircraft or drones (Epperly et al., 1995; Lauriano et al., 2011; Schofield et al., 2019) combined with information on turtle detectability, e.g. time near surface (Seminoff et al., 2014; Fuentes et al., 2015; Sykora-Bodie et al., 2017).

The Banc d'Arguin is thus a major foraging site for growing green turtles, whose origins are currently being investigated using molecular methods. Many young turtles likely originate from the large rookery at Guinea-Bissau, similar to the adults, but there is one recovery in the Banc d'Arguin of a green turtle marked with a USA tag (of unknown exact origin; Campredon, 2000), supporting a more distant connectivity. This concurs with results from genetic studies in Cabo Verde (located 750 km southwest of the Banc d'Arguin), suggesting that many green turtles foraging there originate from the American continent (Monzón-Argüello et al., 2010). Our own preliminary genetic analyses indicate that green turtles growing in the Banc d'Arguin include individuals from the western board of the Atlantic (Patrício et al., unpublished data), and hence represent a diverse mixed foraging stock with connectivity at the scale of the Atlantic.

Most of the Banc d'Arguin is included in the PNBA and managed under strict fishing regulations. All fishing is carried-out from sailing boats without engines, of which less than one hundred (owned locally) are allowed to operate in the park (Patrício et al., 2022). Fisheries regulations are relatively well enforced. During fieldwork, for example, we never witnessed any motorboats travelling or fishing in the PNBA. Even though the Imraguen traditionally consumed sea turtle meat on a regular basis, turtle fishing is now strictly prohibited and there is no commercial capture. Some illicit local consumption is known to take place, but intentional or bycatch levels are currently unknown and hard to assess. The adult female population at Poilão, directly linked to this site, has been growing over the past two decades (Barbosa et al., 2018), which suggests that they are adequately protected at this and other foraging sites (Patrício et al., 2022), despite existing threats. There are however concerns that the extensive seagrass beds of the PNBA, which largely sustain the green turtle population, may face a severe decline over the next few decades as a result of climate change (Chefaoui et al., 2021). Notably, another green turtle foraging aggregation in West Africa was found to rely mostly on red algae as a food source (Díaz-Abad et al., 2022), and green turtles are also able to shift from seagrass to macroalgae feeding (Esteban et al., 2020), thus plasticity in foraging habits may contribute to the resilience of green turtles under climate change. Future work should focus on the diet of green turtles in this major foraging site and on their interactions with the local seagrass meadows.

Estimating the numerical importance of foraging aggregations of sea turtles remains challenging. The methods presented here, combining information of numbers on known nesting grounds, satellite tracking and the demographic structure present in the foraging grounds, clearly hold potential to be replicated at other sites. Such methods contribute to highlight regions of conservation value for sea turtles and sites where turtles, by their abundance, may likely play an important role in the dynamics of the marine ecosystems (Bjorndal and Jackson, 2003).

CRediT authorship contribution statement

Paulo Catry: Conceptualization; Investigation; Formal analysis; Methodology; Original draft preparation. Cheibani Senhoury: Project administration; Funding acquisition. Ebaye Sidina: Project administration; Funding acquisition. Nahi El Bar: Investigation. Abdallahi Samba Bilal: Investigation. Francesco Ventura: Methodology; Software. Brendan J Godley: Writing - Review & Editing. António J Pires: Investigation. Aissa Regalla: Project administration; Funding acquisition. Ana R. Patrício: Formal analysis; Investigation; Writing - Review & Editing; Visualization.

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.

Data availability

The tracking datasets analyzed herein are available on Movebank (www.movebank.org) under the studies "Chelonia mydas_bijagos_females_2021" [study ID: 2173907778], and "Chelonia mydas_bijagos_males_2021" [study ID: 2173900562].

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Ethical statement

This study was reviewed and approved by Orgão Responsável pelo Bem-estar Animal do ISPA (ORBEA - ISPA). Research permits were granted by the Instituto da Biodiversidade e das Áreas Protegidas, Dr. Alfredo Simão da Silva (IBAP), of Guinea-Bissau and by the Parc National du Banc d'Arguin, Mauritania. Fieldwork protocols involving sea turtles followed recommended guidelines (NMFS-SFC, 2008), to enhance efficiency and reduce possible disturbance to the turtles, and were conducted by trained personnel, in collaboration with national authorities for biodiversity management.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109823.

References

Araújo, A., Campredon, P., 2016. In: Banc d' Arguin (Mauritania). Wetl. Book. II. Distrib. Descr. Conserv. Springer, Dordrech, pp. 1319–1332.
Balazs, G.H., Chaloupka, M., 2004. Spatial and temporal variability in somatic growth of green sea turtles (Chelonia mydas) resident in the Hawaiian archipelago. Mar. Biol. 145, 1043–1059.
Barbosa, C., Patrício, R., Ferreira, B., Sampaio, M., Catry, P., 2018. Tartarugas Marinhas. In: Catry, P., Regalla, A. (Eds.), Parque Nacional Marinho João Vieira e Poilão: Biodiversidade e Conservação. IBAP – Instituto da Biodiversidade e das Áreas Protegidas, Bissau.
Beal, M., Catry, P., Regalla, A., Barbosa, C., Pires, A.J., Mestre, J., Senhoury, C., Sidina, E., Patrício, R., 2022. Satellite-tracking reveals sex-specific migration distance in green turtles (Chelonia mydas). Biol. Lett. 18, 20220325.
Becker, S.L., Brainard, R.E., Van Houtan, K.S., 2019. Densities and drivers of sea turtle populations across Pacific coral reef ecosystems. PLoS ONE 14, e0214972.
Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J.V., Dutton, P.H., 2007. Abundance, distribution, and habitat of leatherback turtles (Dermochelys coriacea) off California, 1990–2003. Fish. Bull. 105, 337–347.
Bjorndal, K.A., Jackson, J.B.C., 2003. Roles of sea turtles in marine ecosystems: reconstructing the past. In: Lutz, P., Musick, J., Wyneken, J. (Eds.), The Biology of Sea Turtles, Vol II. CRC Press, Boca Raton, FL, pp. 259–273.
Bjorndal, K.A., Bolten, A.B., Chaloupka, M., et al., 2017. Ecological regime shift drives declining growth rates of sea turtles throughout the West Atlantic. Glob. Chang. Biol. 23, 4556–4568.
Blanvillain, G., Pease, A.P., Segars, A.L., Rostal, D.C., Richards, A.J., Owens, D.W., 2008. Comparing methods for the assessment of reproductive activity in adult male loggerhead sea turtles Caretta caretta at Cape Canaveral, Florida. Endanger. Species Res. 6, 75–85.
Bolten, A.B., Bjorndal, K.A., Grumbles, J.A., Owens, D.W., 1992. Sex ratio and sex-specific growth rates of immature green turtles, Chelonia mydas, in the southern Bahamas. Copeia 4, 1098–1103.
Bresette, M.J., Witherington, B.E., Herren, R.M., Bagdley, D.A., Gorham, J.C., Traxler, S. L., Crady, C.K., Hardy, R., 2010. Size-class partitioning and herding in a foraging group of green turtles Chelonia mydas. Endang. Species. Res. 9, 105–116.
Broderick, A., Patrício, A., 2019. Chelonia mydas (South Atlantic Subpopulation). The IUCN Red List of Threatened Species 2019: e.T142121866A142086337. https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T142121866A142086337.en, 571pp.
Campredon, P., 2000. Entre le Sahara et L'Atlantique. Le Parc National du Banc d'Arguin. FIBA, La Tour du Valat, Arles, 124pp.
Cardona, L., Aguilar, A., Pazos, L., 2009. Delayed ontogenic dietary shift and high levels of omnivory in green turtles (Chelonia mydas) from the NW coast of Africa. Mar. Biol. 156, 1487–1495.
Catry, P., Barbosa, C., Indjai, B., Almeida, A., Godley, B.J., Vié, J.C., 2002. First census of the green turtle at Poilão, Bijagós archipelago, Guinea-Bissau: the most important nesting colony on the Atlantic Coast of Africa. Oryx 36, 400–403.
Catry, P., Barbosa, C., Paris, B., Indjai, B., Almeida, A., Limoges, B., Silva, C., Pereira, H., 2009. Status, ecology, and conservation of sea turtles in Guinea-Bissau. Chelonian Conserv. Biol. 8, 150–160.
Catry, P., Barbosa, C., Indjai, B., 2010. Marine Turtles of Guinea-Bissau. Status, Biology and Conservation. Instituto da Biodiversidade e das Áreas Protegidas, Bissau, 127p.
Chaloupka, M., 2002. Stochastic simulation modelling of southern great barrier reef green turtle population dynamics. Ecol. Model. 148, 79–109.
Chaloupka, M., Limpus, C., Miller, J., 2004. Green turtle somatic growth dynamics in a spatially disjunct great barrier reef metapopulation. Coral Reefs 23, 325–335.

Chefaoui, R.M., Duarte, C.M., Tavares, A.I., Frade, D.G., Sidi Cheikh, M.A., Ba, M.A., Serrão, E.A., 2021. Predicted regime shift in the seagrass ecosystem of the Gulf of arguin driven by climate change. Glob. Ecol. Conserv. 32, e01890.

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, 1835–1849.

Díaz-Abad, L., Bacco-Mannina, N., Madeira, F.M., Neiva, J., Aires, T., Serrao, E.A., Regalla, A., Patrício, A.R., Frade, P.R., 2022. eDNA metabarcoding for diet analyses of green sea turtles (Chelonia mydas). Mar. Biol. 169, 1–12.

Eguchi, T., Seminoff, J.A., LeRoux, R.A., Prosperi, D., Dutton, D.L., Dutton, P.H., 2012. Morphology and growth rates of the green sea turtle (Chelonia mydas) in a northern-most temperate foraging ground. Herpetologica 68, 76–87.

Epperly, S.P., Braun, J., Chester, A.J., 1995. Aerial surveys for sea turtles in North Carolina inshore waters. Fish. Bull. 93, 254–261.

Esteban, N., Mortimer, J.A., Hays, G.C., 2017. How numbers of nesting sea turtles can be overestimated by nearly a factor of two. Proc. R. Soc. B 284, 20162581.

Esteban, N., Mortimer, J.A., Stokes, H.J., Laloë, J.O., Unsworth, R.K., Hays, G.C., 2020. A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. Mar. Biol. 167, 1–17.

Foley, A.M., Singel, K.E., Dutton, P.H., 2007. Characteristics of a green turtle (*Chelonia mydas*) assemblage in northwestern Florida determined during a hypothermic stunning event. Gulf Mexico Sci. 25 (2), 131–143.

Fuentes, M.M.P.B., Bell, I., Hagihara, R., Hamann, M., et al., 2015. Improving in-water estimates of marine turtle abundance by adjusting aerial survey counts for perception and availability biases. J. Exp. Mar. Biol. Ecol. 471, 77–83.

García-Barón, I., Authier, M., Caballero, A., Vázquez, J.A., Santos, M.B., Murcia, J.L., Louzao, M., 2019. Modelling the spatial abundance of a migratory predator: a call for transboundary marine protected areas. Divers. Distrib. 25, 346–360.

Godley, B.J., Broderick, A.C., Frauenstein, R., Glen, F., Hays, G.C., 2002. Reproductive seasonality and sexual dimorphism in green turtles. Mar. Ecol. Progr. Ser. 226, 125–133.

Godley, B.J., Barbosa, C., Bruford, M., Broderick, A.C., Catry, P., Coyne, M.S., Formia, A., Hays, G.C., Witt, M.J., 2010. Unravelling migratory connectivity in marine turtles using multiple methods. J. Appl. Ecol. 47, 769–778.

Godley, B.J., Broderick, A.C., Colman, L.P., Formia, A., Godfrey, M.H., Hamann, M., Nuno, A., Omeyer, L.C.M., Patrício, A.R., Phillott, A.D., Rees, A.F., 2020. Reflections on sea turtle conservation. Oryx 54, 287–289.

Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K.E., et al., 2010. Global research priorities for sea turtles: in forming management and conservation in the 21st century. Endang. Species Res. 11, 245–269.

Hammerschlag, N., Schmitz, O.J., Flecker, A.S., Lafferty, K.D., Sih, A., Atwood, T.B., Gallagher, A.J., Irschick, D.J., Skubel, R., Cooke, S.J., 2019. Ecosystem function and services of aquatic predators in the anthropocene. Trends Ecol. Evol. 34, 369–383.

Hays, G.C., Broderick, A.C., Godley, B.J., Lovell, P., Martin, C., McConnell, B.J., Richardson, S., 2002. Biphasal long-distance migration in green turtles. Anim. Behav. 64, 895–898.

Hays, G.C., Taxonera, A., Renom, B., Fairweather, K., Lopes, A., Cozens, J., Laloë, J.O., 2022. Changes in mean body size in an expanding population of a threatened species. Proc. R. Soc. B 289, 20220696.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23, 202–210.

International Union for Conservation of Nature, International Union for Conservation of Nature, Natural Resources, Species Survival Commission, IUCN Species Survival Commission, 2001. IUCN Red List Categories and Criteria. IUCN.

Johnston, A., Fink, D., Reynolds, M.D., Hochachka, W.M., Sullivan, B.L., Bruns, N.E., Hallstein, E., Merrifield, M.S., Matsumoto, S., Kelling, S., 2015. Abundance models improve spatial and temporal prioritization of conservation resources. Ecol. Appl. 25, 1749–1756.

Lauriano, G., Panigada, S., Casale, P., Pierantonio, N., Donovan, G.P., 2011. Aerial survey abundance estimates of the loggerhead sea turtle Caretta caretta in the pelagos sanctuary, northwestern Mediterranean Sea. Mar. Ecol. Prog. Ser. 437, 291–302.

Limpus, C.J., Couper, P.J., Read, M.A., 1994. The green turtle, Chelonia mydas, in Queensland: population structure in a warm temperate feeding area. Mem Queensland Mus 35, 139–154.

Mancini, A., Elsadek, I., Madon, B., 2015. When simple is better: comparing two sampling methods to estimate green turtles abundance at coastal feeding grounds. J. Exp. Mar. Biol. Ecol. 465, 113–120.

Mazaris, A., Schofield, G., Gkazinou, C., Almpanidou, V., Hays, G.C., 2017. Global sea turtle conservation successes. Sci. Adv. 3, e1600730.

Mettler, E., Clyde-Brockway, C.E., Honarvar, S., Paladino, F.V., 2019. Migratory corridor linking Atlantic green turtle, Chelonia mydas, nesting site on Bioko Island, Equatorial Guinea to ghanaian foraging grounds. Plos one 14, e0213231.

Miller, J.D., 1997. Reproduction in sea turtles. In: The Biology of Sea Turtles. CRC Press, pp. 51–81.

Monteiro, J., Duarte, M., Amadou, K., Barbosa, C., El Bar, N., Madeira, F.M., Regalla, A., Duarte, A., Tavares, L., Patrício, A.R., 2021. Fibropapillomatosis and the chelonid alphaherpesvirus 5 in green turtles from West Africa. EcoHealth 18, 229–240.

Monzón-Argüello, C., López-Jurado, L.F., Rico, C., Marco, A., López, P., Hays, G.C., Lee, P.L.M., 2010. Evidence from genetic and lagrangian drifter data for transatlantic transport of small juvenile green turtles. J. Biogeogr. 37, 1752–1766.

Mortimer, J.A., Appoo, J., Bautil, B., Betts, M., Burt, A.J., Chapman, R., Currie, J.C., Doak, N., Esteban, N., Liljevik, A., Mahoune, J.T., Onezia, C., Pistorius, P., Richards, H., Samedi, U., Sanchez, C.L., Seabrook, W., Underwood, A., van de Crommenacker, J., von Brandis, R., Hays, G.C., 2022. Long-term changes in adult size of green turtles at aldabra atoll and implications for clutch size, sexual dimorphism and growth rates. Mar. Biol. 169, 1–10.

National Marine Fisheries Service Southeast Fisheries Center, 2008. Sea Turtle Research Techniques Manual. NOAA Technical Memorandum NMFS-SEFSC-579, 92 p.

Omeyer, L.C.M., Godley, B.J., Broderick, A.C., 2017. Growth rates of adult sea turtles. Endanger. Species Res. 34, 357–371.

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.

Patrício, R., Diez, C.E., van Dam, R.P., 2014. Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico. Endang. Species Res. 23, 51–62.

Patrício, A.R., Beal, M., Barbosa, C., Diouck, D., Godley, B.J., Madeira, F.M., Regalla, A., Traoré, M.S., Senhoury, C., Sidina, E., Catry, P., 2022. Green turtles highlight connectivity across a regional marine protected area network in West Africa. Front. Mar. Sci. 9, 812144.

Péron, C., Grémillet, D., 2013. Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. PLoS One 8 (8), e72713.

Pfaller, J.B., Chaloupka, M., Bolten, A.B., Bjorndal, K.A., 2018. Phylogeny, biogeography and methodology: a meta-analytic perspective on heterogeneity in adult marine turtle survival rates. Sci. Rep. 8, 5852.

Rees, A.F., Alfaro-Shigueto, J., Barata, P.C.R., Bjorndal, K.A., Bolten, A.B., Bourjea, J., Broderick, A.C., Campbell, L.M., Cardona, L., Carreras, C., Casale, P., 2016. Are we working towards global research priorities for management and conservation of sea turtles? Endanger. Species Res. 31, 337–382.

Robinson, N.J., Bigelow, W.F., Cuffley, J., Gary, M., Hoefer, S., Mills, S., Smith, A., Miguel Blanco, A., 2020. Validating the use of drones for monitoring the abundance and behaviour of juvenile green sea turtles in mangrove creeks in the Bahamas. Testudo 9, 24–35.

Roos, D., Pelletier, D., Ciccione, S., Taquet, M., Hughes, G., 2005. Aerial and snorkelling census techniques for estimating green turtle abundance on foraging areas: a pilot study in Mayotte Island (Indian Ocean). Aquat. Living Resour. 18 (02), 193–198.

Schofield, G., Esteban, N., Katselidis, K.A., Hays, G.C., 2019. Drones for research on sea turtles and other marine vertebrates – a review. Biol. Conserv. 238, 108214.

Seminoff, J.A., Resendiz, A., Nichols, W.J., Jones, T., 2002. Growth rates of wild green turtles (Chelonia mydas) at a temperate foraging area in the Gulf of California, Mexico. Copeia 2002, 610–617.

Seminoff, J.A., Eguchi, T., Carretta, J., Allen, C.D., et al., 2014. Loggerhead Sea turtle abundance at a foraging hotspot in the eastern Pacific Ocean: implications for at sea conservation. Endang. Species Res. 2, 207–220.

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

Sequeira, A.M.M., Heupel, M.R., Lea, M.A., Eguíluz, V.M., Duarte, C.M., Meekan, M.G., Thums, M., Calich, H.J., Carmichael, R.H., Costa, D.P., Ferreira, L.C., Fernandéz-Garcia, J., Harcourt, R., Harrison, A.L., Jonsen, I., McMahon, C.R., Sims, D.W., Wilson, R.P., Hays, G.C., 2019. The importance of sample size in marine megafauna tagging studies. Ecol. Appl. 29, e01947.

Shimada, T., Jones, R., Limpus, C., Groom, R., Hamann, M., 2016. Long-term and seasonal patterns of sea turtle home ranges in warm coastal foraging habitats: implications for conservation. Mar. Ecol. Prog. Ser. 562, 163–179.

SWOT, 2011. The state of the World`s Sea Turtles. SWOT Report VI. www.SeaTurtleStatus.org.

Sykora-Bodie, S.T., Bezy, V., Johnston, D.W., et al., 2017. Quantifying nearshore sea turtle densities: applications of unmanned aerial systems for population assessments. Sci. Rep. 7, 17690.

Trégarot, E., Catry, T., Pottier, A., El-Hacen, E.M., Sidi Cheikh, M.A., Cornet, C.C., Maréchal, J., Failler, P., 2021. Coastal protection assessment: a tradeoff between ecological, social, and economic issues. Ecosphere 12, e03364.

Weber, N., Weber, S.B., Godley, B.J., Ellick, J., Witt, M., Broderick, A.C., 2013. Telemetry as a tool for improving estimates of marine turtle abundance. Biol. Conserv. 167, 90–96.

Welsh, R.C., Mansfield, K.L., 2022. Intraspecific spatial segregation on a green turtle foraging ground in the Florida Keys, USA. Mar. Biol. 169, 1–13.

Wildermann, N., Gredzens, C., Barrios-Garrido, H., Bell, I., Blumenthal, J., Bolten, A., et al., 2018. Informing research priorities for immature sea turtles through expert elicitation. Endanger. Species Res. 37, 55–76.