



# Movement patterns of green turtles at a key foraging site: the Banc d'Arguin, Mauritania

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## Abstract

Interactions with fisheries is a major threat to sea turtles. However, space-use at foraging locations remains overlooked in many populations, preventing effective protection. We assess the space-use of 14 juvenile and 24 adult green turtles (*Chelonia mydas*) satellite-tracked in 2018–2022 within a foraging site of global importance for this species, the Banc d'Arguin in Mauritania, West Africa. Turtles exhibited a patchy distribution and used overlapping habitats irrespective of sexes and life stages. Mean individual home range was larger ( $151.5 \pm 160.5$  km<sup>2</sup>) than values reported in most green turtle populations. Individuals concentrated in two main areas used year-round. Inshore/offshore movements seem to occur within the central part of the Banc d'Arguin, with turtles moving to deeper areas during colder months. More than half of the turtles performed within-season range shifts and switched between up to four distinct areas, with some individuals returning to previously visited sites. Turtles mostly exploited shallow areas ( $4.30 \pm 3.42$  m) and seemed to use disproportionately more of the areas inside the Parc National du Banc d'Arguin, than areas of similar bathymetry outside this marine protected area. This suggests that foraging green turtles have been benefiting from the management of the Park since it was established in 1976. However, turtles' home range overlapped greatly with artisanal fisheries, which operate in the central shallow waters of the Park. The present study provides valuable ecological information that can be used to inform the planning of fisheries management zones, aiming to reduce the interactions between turtles and artisanal fisheries.

**Keywords** Satellite tracking · Bio-logging · Movement ecology · Foraging habitat · Sea turtle · West Africa

## Introduction

As anthropogenic pressures on the marine environment increase (Sequeira et al. 2019a), it becomes ever more important to understand the spatiotemporal distribution and habitat use of migratory marine megafauna (Sequeira et al. 2019b). Sea turtles are one group of megafauna threatened by human activities at sea, particularly through negative interactions with fishing activities (e.g., bycatch, Fuentes et al. 2023). Given the naturally elevated mortality of hatching sea turtles, the survival of older juveniles and adults is crucial to maintaining population stability in these long-lived animals (Richards et al. 2024). Sea turtles spend most of their lives in foraging areas, where individuals of different age groups may mix (Bell et al. 2019; Catry et al. 2023). Thus, understanding the space and habitat use of turtles at their foraging grounds can help direct efforts to manage threats and ultimately support their populations.

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Individual sea turtles of at least five species (loggerheads *Caretta caretta*, hawksbills *Eretmochelys imbricata*, greens *Chelonia mydas*, flatbacks *Natator depressus* and Kemp's Ridleys *Lepidochelys kempii*) have been shown to display fidelity to foraging sites after long-distance migrations from breeding sites, likely related to diet and predictability of prey resources (see Shimada et al. 2020 and references therein). However, habitat use and residency patterns at foraging grounds have long been considered a knowledge gap, with little known about the influence of age, body size, and sex on habitat preferences (Hamann et al. 2010). For example, green turtles display long-term residency and very high fidelity to their foraging areas at Ningaloo reef, Australia and Mayotte Island (Taquet et al. 2006, Pillans et al. 2022). On the contrary, green and loggerhead turtles from Queensland, Australia, tend to shift their foraging areas seasonally (Shimada et al. 2021). At some foraging sites, especially in the subtropics, sea-surface temperature (hereafter 'SST') has a significant effect on site fidelity (shifts to overlapping habitats of similar area or increase in home range size during summer months; Shimada et al. 2016).

Foraging green turtles have been found to segregate spatially according to body size in Chile (Álvarez-Varas et al. 2017), Florida (Bresette et al. 2010) and Australia (Pillans et al. 2022), with small juveniles generally found in shallower coastal waters. This spatial segregation appears to be driven by habitat preferences and food requirements, as shown at Mayotte Island (Ballorain et al. 2010), Australia (Pillans et al. 2022) and Florida (Welsh and Mansfield 2022). Bathymetry in combination with the tide cycle are important drivers of the distribution of green turtles, with individuals shown to avoid the shallowest areas at low tide (Pillans et al. 2021). Despite these insights, space use remains poorly understood at many key foraging sites, notably at one of the largest foraging grounds for green turtles globally: the Banc d'Arguin (hereafter 'BA') in Mauritania, West Africa.

Recent tracking studies have highlighted strong connectivity, established by both breeding females (Patrício et al. 2022) and males (Beal et al. 2022), between the BA and the largest green turtle rookery in the Eastern Atlantic, located in the Bijagós archipelago, Guinea-Bissau (Patrício et al. 2019; Broderick and Patrício 2019). Other foraging locations have been identified for this nesting population, namely the Bijagós archipelago in Guinea-Bissau, the Saloum Delta and Joal-Fadiouth in Senegal and the coastal waters of the Tanji-Bijol islands of The Gambia, but most of the tracked females migrated to the BA (50% on average from 2018 to 2021; Catry et al. 2023). Additionally, Catry et al. (2023) estimated that ca. 150,000 green turtles forage in the BA, including juveniles (8% of which originate from South America; Patrício et al. 2024) and adults of both sexes, further underlining the importance of this foraging

area. The eastern side of the BA is included within the Parc National du Banc d'Arguin ('PNBA' hereafter), the largest marine protected area in West Africa. Created in 1976, the PNBA spreads over 6,000 km<sup>2</sup> and coincides with an internationally recognized biodiversity hotspot. Besides sea turtles, the PNBA supports a key fish nursery (Guénette et al. 2014; Trégarot et al. 2020) and is a major feeding area for many local and migratory waterbird species (e.g. Oudman et al. 2020). The area is rich in vast seagrass meadows of three species (the intertidal *Zostera noltei*, and the subtidal *Cymodocea nodosa* and *Halodule wrightii*; van Lent et al. 1991, Chefaoui et al. 2021) that are potential food sources for green turtles (Esteban et al. 2020) and likely support the large foraging aggregation found there. Because green turtles are the only sea turtle species that are primarily herbivores as adults (Bjorndal 1997), we expect their habitat to overlap with the distribution of seagrass meadows. Previously, green turtles from 28 rookeries in tropical and subtropical areas (including the Pacific, Atlantic and Indian Oceans, as well as the Mediterranean Sea) have been found to aggregate in marine protected areas to forage (Scott et al. 2012). However, the fine-scale distribution of green turtles in relation to the PNBA boundaries remains unexplored.

Here, we characterize the movements and habitat use of green turtles in the BA. We satellite-tracked 38 turtles, including juveniles and sexually mature adults of both sexes. We describe their usage of the PNBA and investigate the possible effects of environmental parameters on the spatial distribution of turtles. Lastly, we describe seasonal variation in the turtles' spatial distribution and individual-level movements.

## Materials and methods

### Satellite tag deployments

From 2018 to 2021, tracking devices were deployed on green turtles at a breeding site on Poilão Island (10°52'N, 15°43'W) in the Bijagós archipelago, Guinea Bissau, and at foraging grounds within the PNBA, Mauritania. Twenty-two females were tagged on the nesting beaches, after oviposition had begun, to minimize disturbance. Two breeding males were captured at the Bijagós archipelago using a pirogue and net casts, operated by Bijagós fishers. Within the BA, 15 juveniles and two males were captured using nets deployed from a traditional sailing boat, operated by Imraguen fishers. Details on tag deployments are available in Table 1 and metadata related to the tracked turtles are presented in Tables S1 and S2 (Online Resource 1). Wildlife Computer tags recorded Argos locations, while Lotek tags recorded both Argos and Fast GPS locations.

**Table 1** Site, year and month of satellite-tag deployments on juvenile green turtles and adults of both sexes captured at breeding and foraging grounds in West Africa. ‘-’ indicates that no tag was deployed for specific sexes or size class

Site	Year	Month	Females (n)	Males (n)	Juveniles (n)	Tag type
Breeding site, Poilão Island, Guinea-Bissau	2018	Aug.-Nov.	7	–	–	SPOT-375B (99×55×21 mm, 152 g, <sup>®</sup> Wildlife Computers, Redmond, Washington, USA)
	2020	Sep.	6	–	–	F6G 376 A Fast GPS (115×64×43.5 mm, 220 g, <sup>®</sup> Lotek, Havelock North, New Zealand)
	2021	Nov.	9	–	–	F6G 376B Fast GPS (115×64×44 mm, 240 g, <sup>®</sup> Lotek, Havelock North, New Zealand)
		Jul.	–	–	2	–
Foraging ground, Parc National du Banc d’Arguin, Mauritania	2020	Nov.	–	–	3	F6G 276 F Fast GPS (101×44×32 mm, 148 g, <sup>®</sup> Lotek, Havelock North, New Zealand)
	2021	Apr.-May	–	2	9	F6G 276 F Fast GPS (101×44×32 mm, 148 g, <sup>®</sup> Lotek, Havelock North, New Zealand)
		Nov.	–	–	–	3

Before tag deployments, the curved carapace length (‘CCL’ hereafter) of turtles was measured to the nearest millimeter with a flexible measuring tape (Bolten 1999). Individuals captured at foraging ground were assigned as juvenile or adult based on their CCL, using 85 cm as a threshold (Bresette et al. 2010). Adults were visually sexed using tail length, since males have disproportionately longer tails than females (Hendrickson 1958).

The carapace of each turtle was cleaned with sandpaper and acetone. A fiberglass cloth slightly larger than the base of the tag was applied on the dry carapace and glued with quick-setting epoxy (<sup>®</sup>Devcon 5 min Epoxy). A two-part steel resin (magic metal, <sup>®</sup>Loctite) was then modelled to fit the base of the tag and applied on the dry fiberglass cloth to fit the curvature of the carapace. Once the steel resin was dry, another layer of fiberglass cloth was added on the four lateral sides of the tag to ensure optimal adherence.

## Data processing

The tracks of turtles were truncated when a gap of recording reached one week and no meaningful data were available after this period. The tracking data were initially filtered by removing the Z and B location classes provided by the Argos service, considered as error (Witt et al. 2010) and lowest accuracy locations highly prevalent in the dataset (Beal et al. 2022). Fast GPS locations obtained from four or more satellites were retained in the dataset.

Unrealistic fixes with a horizontal traveling speed  $> 5 \text{ km h}^{-1}$  and a turning angle  $< 20^\circ$  were discarded (Metcalfe et al. 2020) using the *sdafilter* function from the *argos-filter* R package (Freitas 2012). The McConnell speed filter (McConnell et al. 1992) was then set at  $5 \text{ km h}^{-1}$  using the stricter *speedfilter* function from the *trip* R package (Sumner

et al. 2009) to remove remaining implausible locations (Patterson et al. 2010). Outlier locations that passed the previous filters were discarded using the *ctmm::outlie* function, based on the deviation of locations from the core distribution (Calabrese et al. 2016).

For turtles equipped at breeding grounds, the calculation and visual inspection of the net square displacement enabled the partition of the trips between breeding, migrating and foraging (Singh et al. 2016). Only the locations occurring at foraging grounds in the BA region were kept for analysis. The dataset contained 14,348 locations after filtering, including 8499 Argos locations (59%) and 5849 Fast GPS locations of high accuracy (41%).

A Kalman filter was then fitted with the *crwMLE* function from the *crawl* R package (Johnson et al. 2008; Johnson and London 2018), implementing error multiplication factors from the *foiegras* R package (Jonsen and Patterson 2019), to increase estimates of positioning accuracy (Patterson et al. 2010; Lopez et al. 2014). Locations were interpolated at a two-hour time step, the mean time interval between two raw consecutive locations, through the *crwPredict* function from the *crawl* R package (Johnson et al. 2008; Johnson and London 2018).

If a turtle shifted area and/or movement range over the course of the foraging period (i.e. present different home range phases characterized by a specific mean and variance of latitude and longitude), its locations were split into segments using the *segmentation* function from the *segclust2d* R package (Patin et al. 2019, 2020). We arbitrarily chose one week as the shortest segment duration in order to prevent over-segmentation. The optimal number of segments was automatically assessed using the Lavielle criterium (Lavielle 2005). If the number of segments automatically selected did not correspond to a clear break in the penalized

log-likelihood of the segmentation, the appropriate number of segments was assessed after visual inspection. Each segment was visually classified as stationary (movements restricted within a relatively small area and characterized by high tortuosity), transit (short, directed movement between two stationary phases) or erratic (a mix of the two aforementioned categories).

Environmental parameters were extracted at each turtle location, including the bathymetry, SST and the presence of two seagrass species, namely *C. nodosa* and *Z. noltei* (see Table 2 for details on dataset resolution and sources). Although *H. wrightii* is also present in the BA (Chefaoui et al. 2021) and green turtles are known to feed on this seagrass species in West Africa (Díaz-Abad et al. 2021), we did not assess turtles distribution according to this species because of a lack of detailed mapping. However, a recent study suggests that *H. wrightii* and *C. nodosa* share the same distribution (Chefaoui et al. 2021).

## Statistical analyses

The datasets were processed and analysed with the R v. 3.6.1 software (R Core Team 2019). All descriptive statistics are presented as means  $\pm$  S.D. We used the processed data to describe population-level and monthly distribution of the turtles. We explored the importance of the PNBA for green turtles and investigated individual movement patterns.

### Population-level distribution

The Kernel Utilization Distributions (KUDs) were computed for each turtle, using the *kernelUD* function from the *adehabitat* R package (Calenge 2006). First, we calculated the canonical reference bandwidth for each turtle. We then used the median reference bandwidth (1060 m) as the smoothing parameter for KUD calculations (Beal et al. 2021). KUDs of 50% and 95% were used to estimate the core areas and home ranges of turtles, respectively (e.g. Hamilton et al. 2021). Being aware of the difference in

precision for locations obtained from Argos and Fast GPS (Argos locations are known to be less accurate; Hays et al. 2024), we compared KUDs obtained from both types of devices. After rigorous data filtering, there was no bias in KUD estimates between tags recording Argos and Fast GPS locations (home range:  $152.1 \pm 175.9$  km<sup>2</sup>, core area:  $21.2 \pm 16.6$  km<sup>2</sup>,  $n=31$  turtles) and tags providing Argos locations only (home range:  $149.1 \pm 64.6$  km<sup>2</sup>, core area:  $21.7 \pm 8.9$  km<sup>2</sup>,  $n=7$ ), so we pooled the two datasets for population home range estimates. We averaged the individual utilization distributions (UDs) to estimate the population-level distribution for all turtles and for females, males and juveniles, separately.

We calculated the mean bathymetry and SST values experienced by turtles over the tracking period and estimated the amount of turtle locations overlapping with seagrass meadows. We finally investigated the distribution of bathymetry values under the locations of adult and juveniles separately.

### Seasonal distribution

We assessed the turtles monthly distribution (average of monthly individual UD, independently from the sex and life stage). We compared the monthly distribution of the depth values at turtle locations and fitted a Linear Mixed Model (LMM) using the *nlme* package (Pinheiro and Bates 2020) to assess whether turtles used areas with different depths according to the time of year. We explained the bathymetry according to the SST and the life stage of turtles (21 adult females versus 14 juveniles, males were discarded from this model because of limited sample size). Individual was included as a random effect to account for correlation between multiple observations from the same turtle and a first-order auto-regressive (AR1) structure was incorporated to account for temporal correlation.

**Table 2** Environmental covariates used as predictors of green turtle spatial distribution within the Banc d'Arguin, Mauritania

Variable	Description	Unit	Spatial resolution	Temporal resolution	Source
Bathymetry	Ocean depth	m	Raster obtained from a nautical chart. Values for southeast shallow unsurveyed waters were obtained from ETOPO1 arc minute dataset	–	Custom combination of a bathymetric map (see Fig. 1 in Aleman et al. 2014) and the ETOPO1 bedrock database (NOAA 2009)
Sea-surface temperature (SST)	Temperature of sea water near the surface	°C	$0.01 \times 0.01^\circ$	Daily	JPL MUR MEaSURES Project 2015 Chin et al. (2017)
<i>Cymodocea nodosa</i> and <i>Zostera noltei</i> meadows	Presence/absence	–	Individual shapefiles	–	Pottier et al. (2021)

## Importance of the Parc National Du Banc d'Arguin

We assessed the number of turtle locations falling inside the PNBA boundaries. We calculated the mean bathymetry at turtle locations and the PNBA mean bathymetry. Based on the bathymetry preferences observed, we estimated the area that appears suitable for green turtles within the PNBA. We used the rounded maximum bathymetry value that corresponded to 95% of the tracking locations as a threshold. We further assessed the areas potentially available for turtles within a 40 km buffer outside of the PNBA, encompassing the whole BA geographical area. To determine whether green turtles gather within the PNBA, we calculated the percentage of the apparently available habitat, within and outside the PNBA, overlapping with the 95% KUD for all turtles.

### Individual range shifts

We assessed patterns of individual variation and whether turtles displayed site fidelity by investigating the number of distinct areas they visited over the course of the foraging period. We tested the possible relationship between the number of areas visited by turtles and the recording duration of the tracking devices. We compared the CCL of turtles and time spent between stationary, transit and erratic phases.

We then discarded the last tracking segment (interrupted by tag failure) for all turtles and the first segment (that may be incomplete) for individuals captured at foraging ground. For complete stationary segments, we assessed the duration,

50% and 95% KUDs (using 587 m -median reference bandwidth of all segments- as smoothing parameter).

## Results

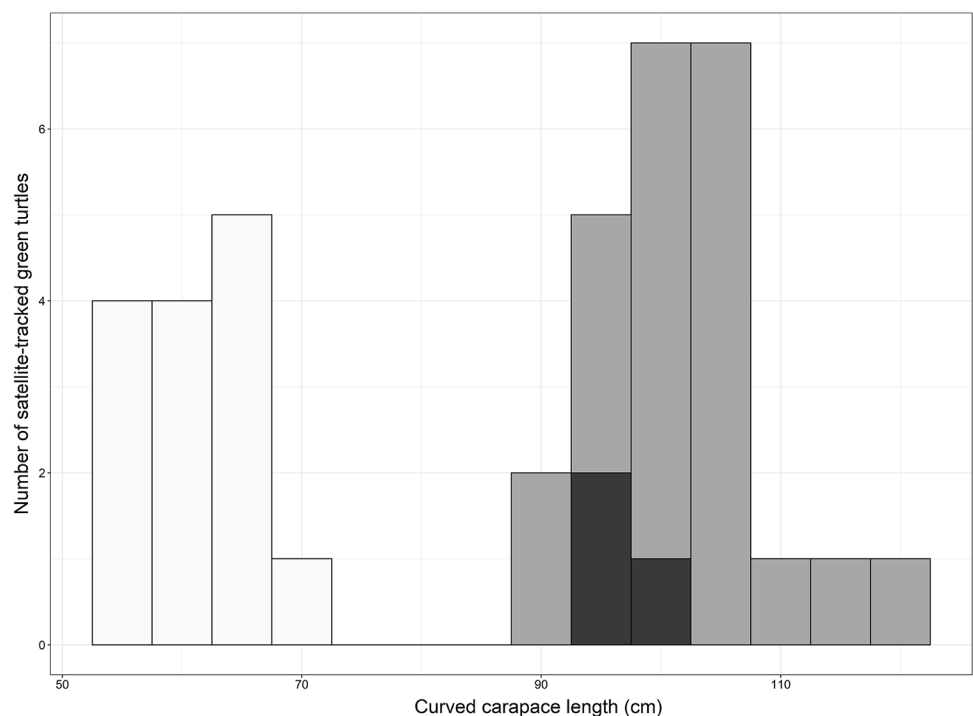
### Tracking parameters

We analysed the tracking data collected from 21 adult females, 3 adult males and 14 juveniles, totaling 38 individuals (one male, one female and one juvenile were discarded because of insufficient data). Turtles CCL ranged from 55 to 121.5 cm (Fig. 1). Tracking duration within the BA was  $135.5 \pm 94.8$  d (range: 9.1-305.5 d) for the 22 turtles equipped at Poilão, and  $78.8 \pm 34.7$  d (range: 26.8-175.5 d) for the 16 individuals fitted with tags within the PNBA.

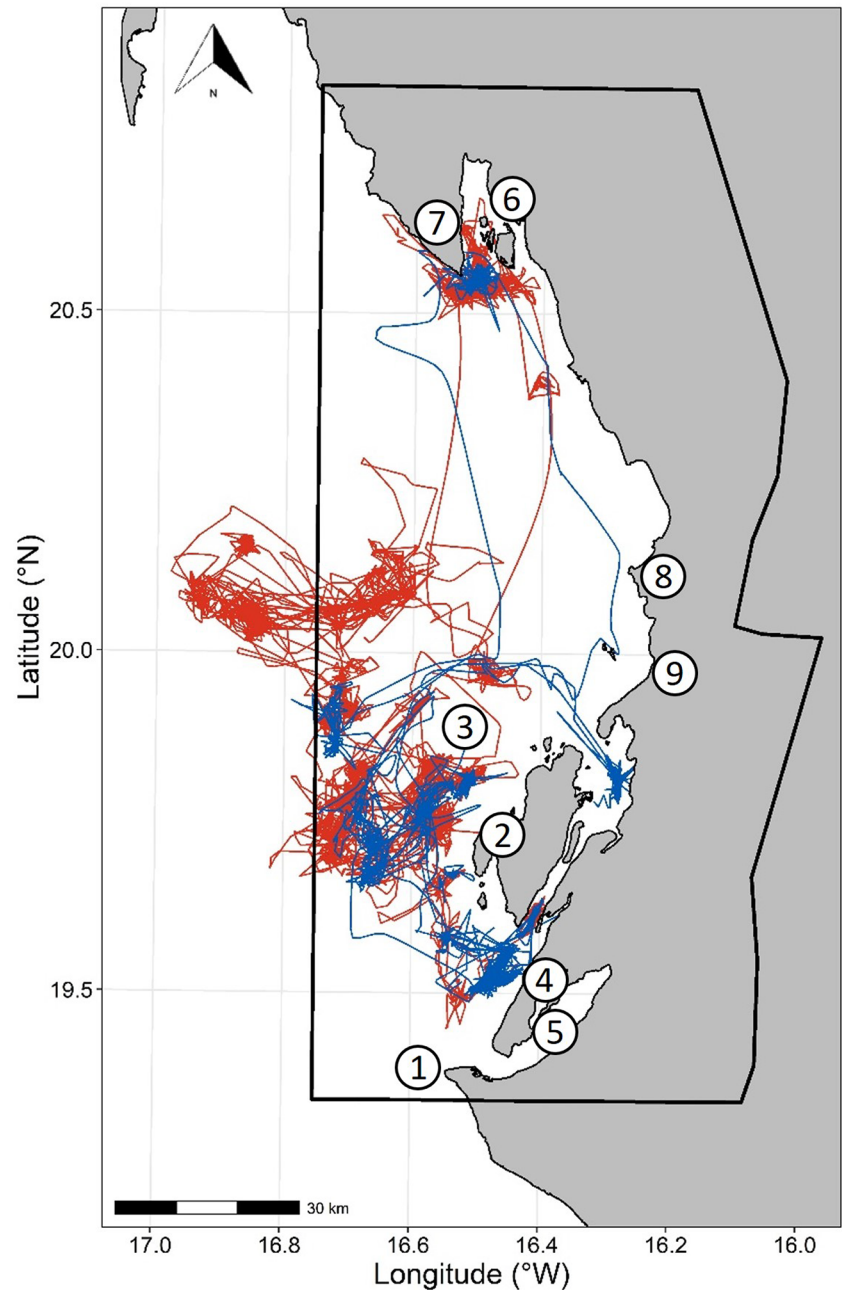
### Distribution at the population level

The turtles exploited two main foraging areas (Fig. 2). The larger area (1303 km<sup>2</sup>), located in the southern part of the BA, is encompassed between the north of Cap Timiris and approximately 20.20°N. The turtles mostly concentrated west and south of Kiji and Tidra islands, with some individuals performing offshore forays, and around Arel island and close to Teichott, though some individuals traveled between the islands and the continent. No individual ventured in the Baie de Saint-Jean. The second area (180 km<sup>2</sup>) is located north of 20.35°N, mostly around the Arguin, Marguerite and

**Fig. 1** Curved carapace lengths of green turtles satellite-tracked at the Banc d'Arguin foraging ground, Mauritania, from 2018 to 2022. Light, midtone and dark grey correspond to juveniles ( $n = 14$ ), adult females ( $n = 21$ ) and adult males ( $n = 3$ ), respectively



**Fig. 2** Spatial distribution of green turtles satellite-tracked within the Banc d'Arguin, Mauritania, from 2018 to 2022. The movements of adult males and females fitted with tracking devices at Poilão Island breeding site, Guinea-Bissau, are represented in red ( $n=22$ ). The blue tracks correspond to juveniles and adult males equipped within the Parc National du Banc d'Arguin foraging ground ( $n=16$ ). The solid black line depicts the contour of the Parc National du Banc d'Arguin. The circled number correspond to ① Cap Timiris, ② Kiji and Tidra islands, ③ Arel island, ④ Teichott, ⑤ Baie de Saint-Jean, ⑥ Arguin, Marguerite and Ardent islands and ⑦ Cap d'Arguin. ⑧ and ⑨ denote Arkeiss and Ten Allou villages



Ardent islands and at the tip of Cap d'Arguin. At this latitude, no individual travelled west of  $\sim 16.6^{\circ}\text{W}$ .

### Influence of sex and life stage on distribution

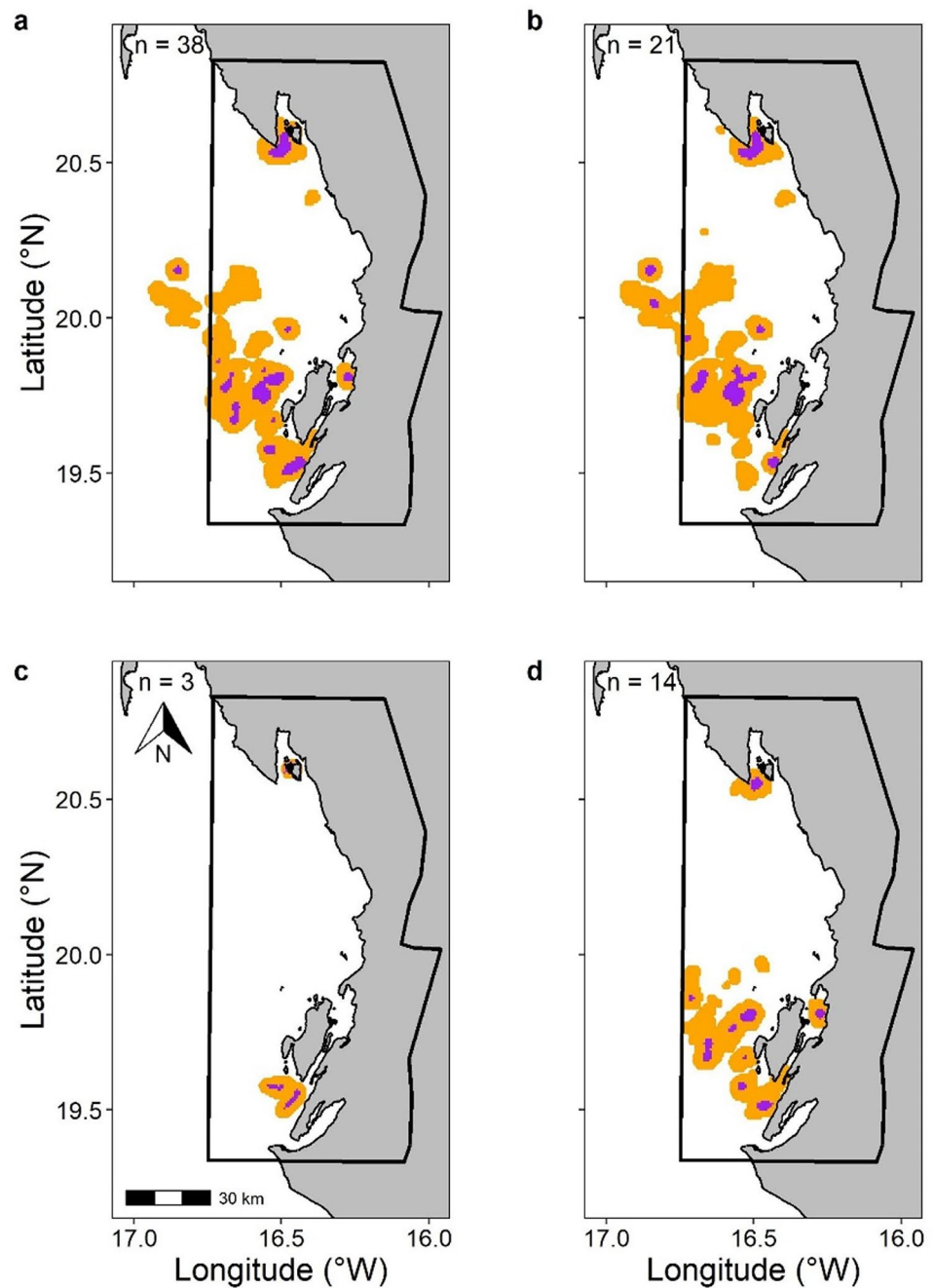
Adult females, adult males and juveniles mostly concentrated in overlapping areas, though juveniles tended to occur more inshore than females (Fig. 3). The mean core areas were  $23.4 \pm 16.1$  and  $17.6 \pm 13.7$   $\text{km}^2$  for adults ( $n=24$ ) and juveniles ( $n=14$ ) respectively. The home ranges were  $144.8 \pm 106.4$  and  $163.1 \pm 230.3$   $\text{km}^2$  for adults and juveniles respectively. There were no significant differences

in the core area ( $U=210$ ,  $P>0.2$ ) nor home range extents ( $U=191$ ,  $P>0.5$ ) between adults and juveniles. The mean individual core area and home range, irrespective of the life stage ( $n=38$ ), were  $21.3 \pm 15.3$  and  $151.5 \pm 160.5$   $\text{km}^2$  respectively.

### Monthly spatial and bathymetry distribution

Interestingly, the monthly turtles distribution revealed that the areas located at the tip of Agadir and west of the PNBA are used year-round, whereas inshore/offshore movements seem to occur within the PNBA, with turtles moving west

**Fig. 3** Estimated population-level distribution (average of individual Kernel Utilization Distributions; KUD) of green turtles satellite-tracked from 2018 to 2022 within the Banc d'Arguin, Mauritania. The purple and orange areas depict the core areas (50% KUD) and home ranges (95% KUD), respectively, for (a) all tracked turtles, (b) adult females, (c) adult males and (d) juveniles. The solid black line depicts the contour of the Parc National du Banc d'Arguin and sample sizes are indicated in the top left corner of each panel

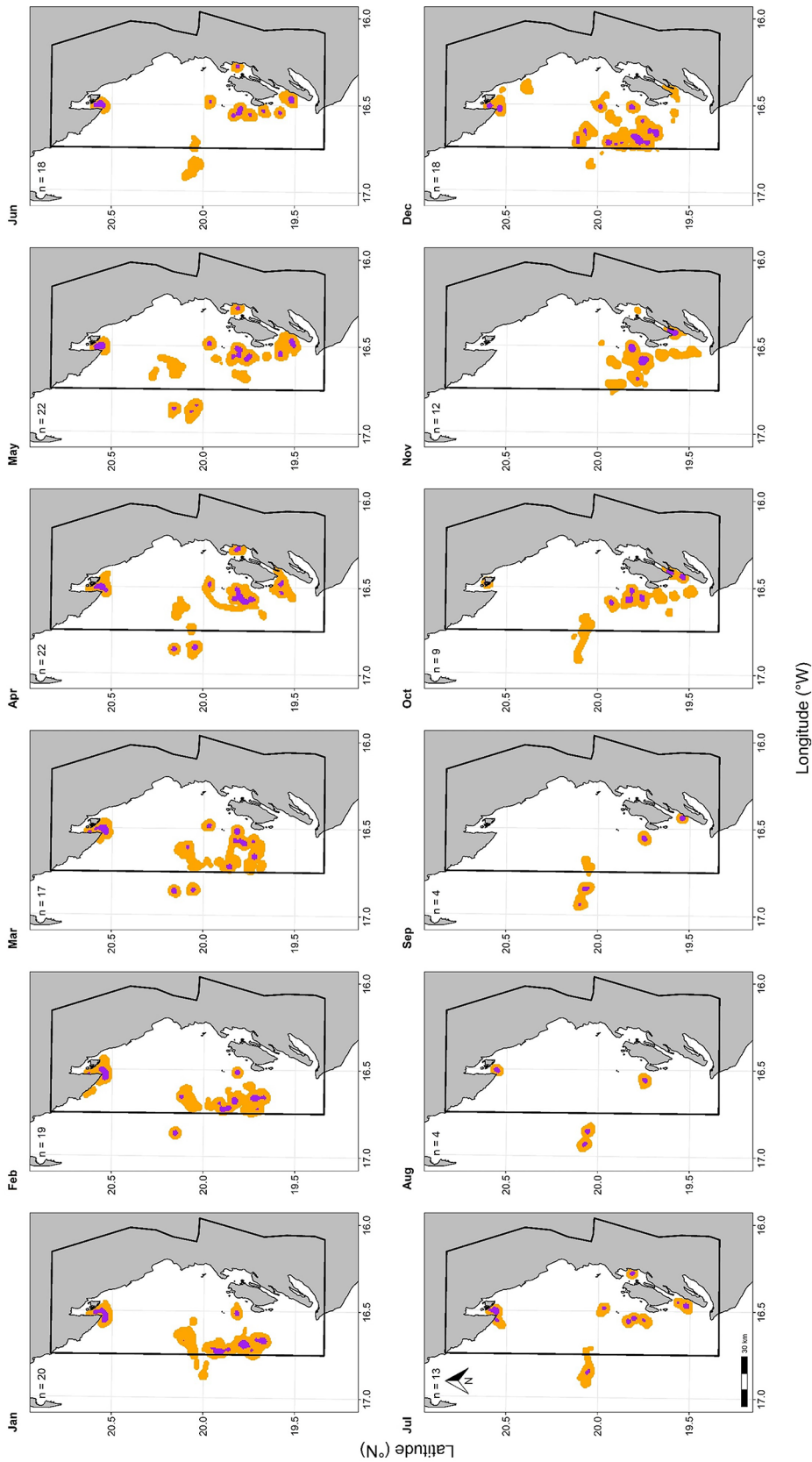


during the colder months (November–March; Fig. 4). The monthly distribution of bathymetry values at turtle locations revealed that they may use shallower waters in warmer months ( $2.9 \pm 2.8$  m; mid-April to mid-November) and deeper ones in colder months ( $5.5 \pm 3.4$  m; mid-November to mid-April) (Fig. 5).

### Sea-surface temperature and bathymetry

Turtles experienced SST values of  $21.2 \pm 2.1$  °C (range: 16.7–29.6 °C). No clear difference was observed between

the bathymetry values extracted at adults and juveniles' locations (Figure S1 in Online Resource 2) and the bimodal distribution observed for juveniles seems to be driven by individual variability and a smaller sample size (Figure S2 in Online Resource 2). Life stage was dropped from the LMM during the model selection process, confirming that life stage does not drive the bathymetric use of turtles and leaving SST ( $p < 0.05$ ) as the only explanatory variable. The model revealed that turtles use shallower areas when SST increases (estimate =  $-0.07 \pm 0.03$ ,  $F = 3.9$ ,  $t = -1.98$ ).



**Fig. 4** Monthly estimated population-level distribution (average of individual Kernel Utilization Distributions) of green turtles satellite-tracked from 2018 to 2022 within the Banc d'Arguin, Mauritania. The purple and orange areas depict the core areas (50% KUD) and home ranges (95% KUD) and home ranges (95% KUD) for all tracked turtles. The solid black line depicts the contour of the Parc National du Banc d'Arguin and sample sizes are indicated in the top left corner of each panel



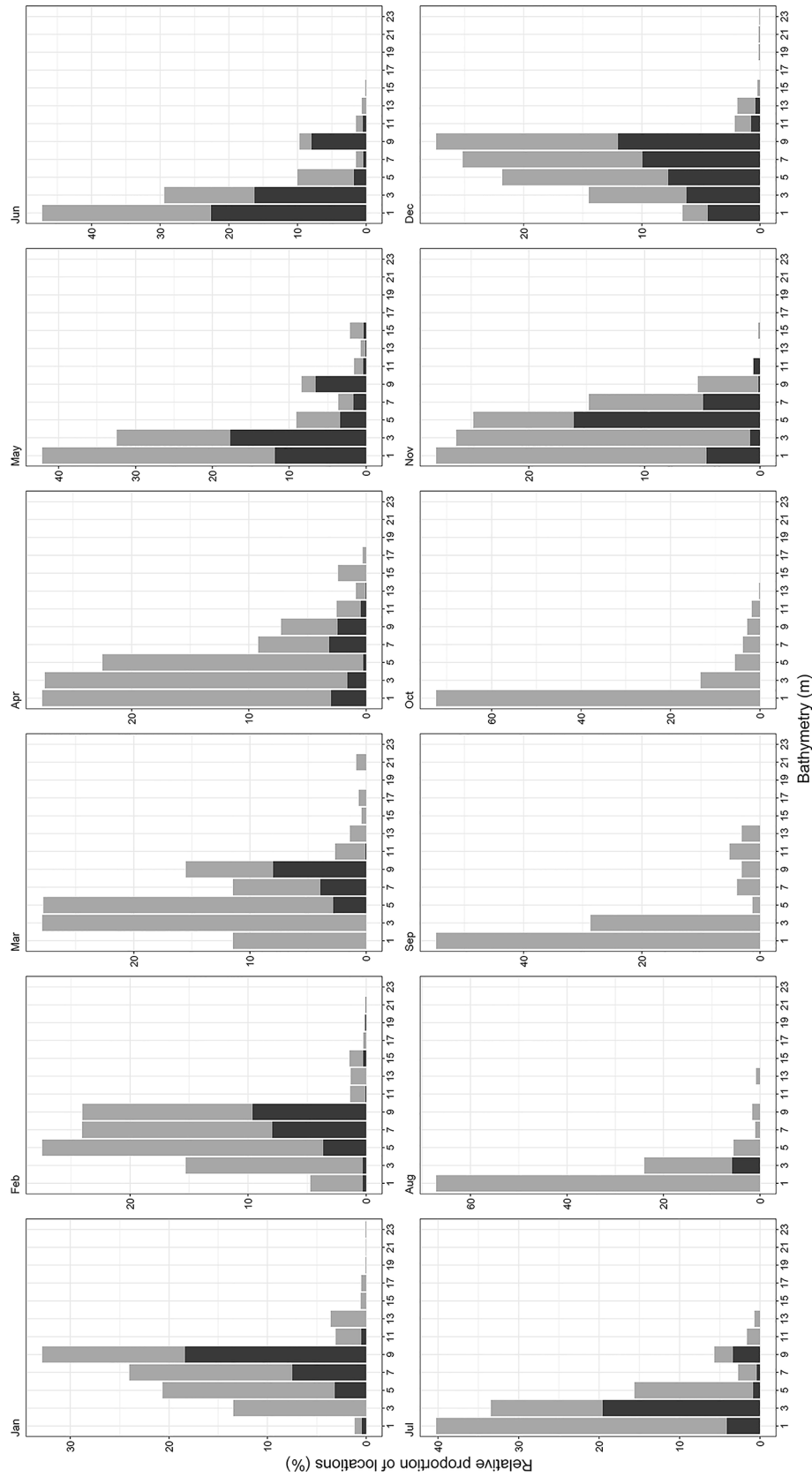


Fig. 5 Monthly distribution of bathymetry values at turtle locations. Light and dark grey correspond to adults and juveniles, respectively

## Sea turtle distribution relative to Park borders and seagrass beds

The mean bathymetry at turtle locations was shallower ( $4.30 \pm 3.42$  m [range: 0.01–22.98]) than the mean bathymetry available within the PNBA ( $6.46 \pm 4.15$  m [range: 0–23.46]) (Mann-Whitney U test,  $U = 143107938$ ,  $P < 0.001$ , see Figure S3 in Online Resource 2 for histograms of the range of depths available and depths used by the turtles). The turtles mostly stayed within the park limits (89.1% of locations), however, seven females and one juvenile explored the western part of the BA, outside of the PNBA (Figs. 2 and 3, Table S3 in Online Resource 3).

When using a 10 m threshold (95% of tracking locations occurred in areas shallower than 10 m depth) to estimate the habitat apparently available to turtles, these shallow areas spread over 5098 km<sup>2</sup> within the PNBA (i.e. 80% of the marine part of the PNBA) and 3805 km<sup>2</sup> within a 40 km buffer outside of the Park limits. By overlapping these apparently available habitats with the population-level 95% KUD of turtles, we estimated that green turtles used a much greater percentage (22.5%) of the apparently available habitats inside the PNBA than outside the park (4.1%). The distribution of turtles did not match closely the distribution of seagrass beds, as only 11.08 and 8.48% of turtle locations fall into *C. nodosa* and *Z. noltei* seagrass meadows, respectively. Considering that the estimated population-level distribution of turtles (Fig. 3a) extent is 1483 km<sup>2</sup>, when merging the distribution of *C. nodosa* and *Z. noltei* meadows, this means that 83% of the population-level home range (1233 km<sup>2</sup>) fell outside of the known seagrass distribution (as estimated per Pottier et al., 2021).

## Fine-scale movements and individual behavior

We identified from one to five movement phases per individual (Table S3 in Online Resource 3), totaling 81 tracking segments, including 71 stationary, four transit and six erratic phases. The tracked turtles exhibited a variety of movement patterns. While 14 out of 38 individuals remained faithful to their foraging site (Fig. 6a), more than half of the tracked turtles performed range shifts (i.e. changed area and/or movement scale through time; Fig. 6b) and switched between up to four distinct areas. The number of visited areas was strongly correlated to the tag recording duration ( $\rho = 0.75$ ,  $p < 0.001$ ). Seven turtles returned to previously visited sites (Fig. 6c).

We did not detect any difference in the CCL of the turtles that performed stationary, transit and erratic segments (Kruskal-Wallis test,  $H = 1.17$ ,  $df = 2$ ,  $P > 0.05$ ). The duration of the tracking segments significantly varied between tracking phases (Kruskal-Wallis test,  $H = 15.82$ ,  $df = 2$ ,

$P < 0.001$ ). Stationary segments ( $57 \pm 38$  days) were significantly longer than erratic segments ( $26 \pm 18$  days; Dunn post hoc test,  $P < 0.001$ ), that were significantly longer than transit segments ( $7 \pm 1$  days; Dunn post hoc test,  $P < 0.001$ ).

The 31 complete stationary segments had a mean duration of  $53 \pm 29$  days (median = 49) and KUDs of  $10.6 \pm 8.5$  and  $62.6 \pm 50.4$  km<sup>2</sup>, for core area and home range respectively.

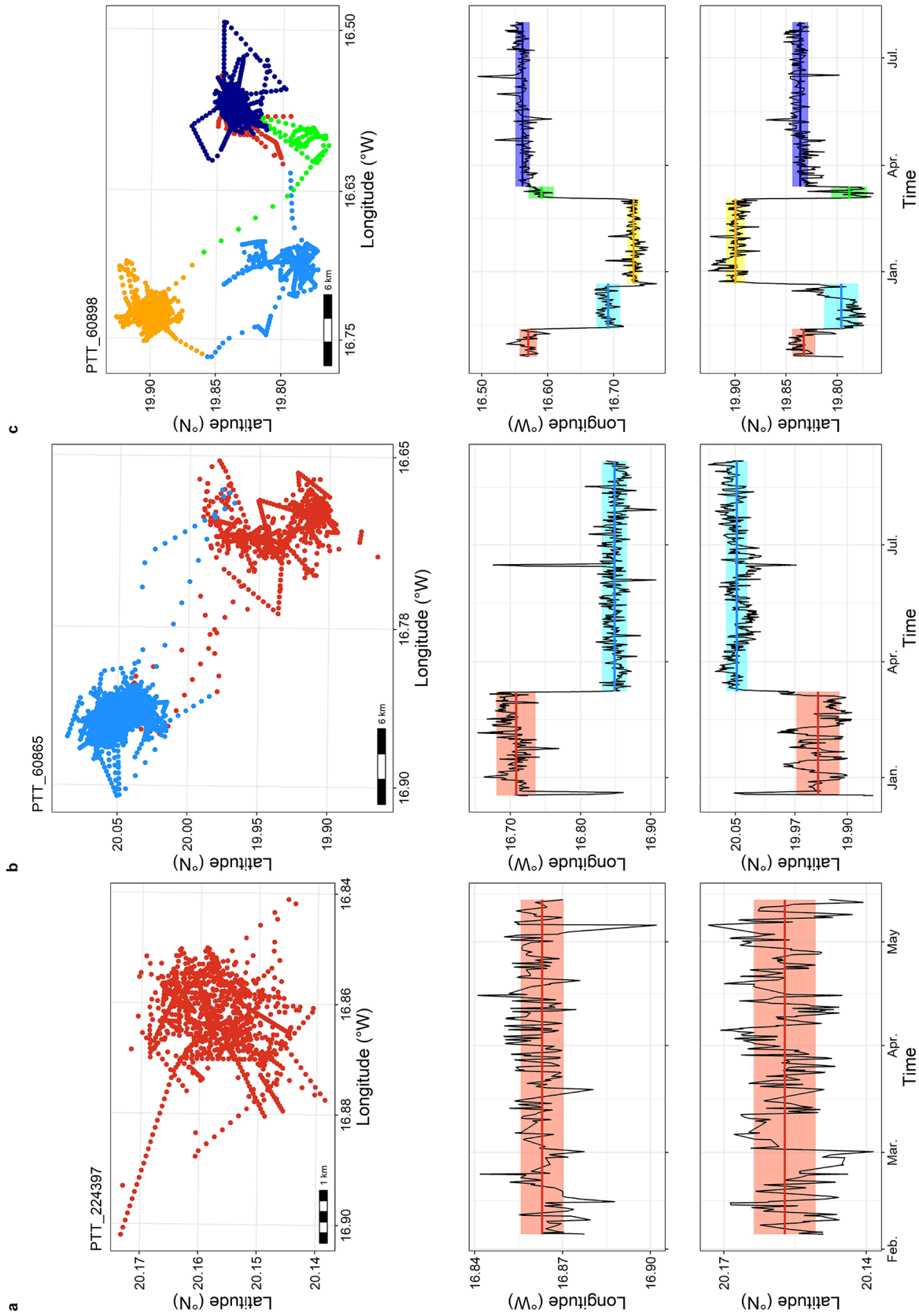
We did not find significant differences between the mean phase duration, 50% and 95% KUDs of the complete stationary segments of females that performed a switch and females that remained faithful to their fine-scale foraging habitat (did not perform a switch) (Table S4 in Online Resource 4).

## Discussion

We provide here the first assessment of the habitat use of juvenile and adult green turtles in the BA developmental-feeding habitat. We showed that the turtles exploiting the central part of the BA perform seasonal movements, moving offshore during the winter months. Furthermore, we present the first evidence that a majority of green turtles (24 out of 38 tracked individuals) are not fine-scale residents but shift range at the intra-seasonal scale. We also provide evidence that they use more intensively the areas benefitting from protection by the National Park, with 89.1% of turtle locations falling within the PNBA.

## Distribution within the Banc d'Arguin

Several studies revealed a size-related spatial segregation of green turtles at foraging sites (e.g. Chile, Álvarez-Varas et al. 2017; Australia, Pillans et al. 2022; Florida, Welsh & Mansfield 2022). A very large overlap in the spatial distribution of adults and juveniles occurred in the BA, with a tendency for juveniles to be found more inshore. However, this tendency may result from juveniles having been captured within the PNBA – not at the most offshore sites – and remaining faithful to their foraging habitat, while adults were often tagged at the breeding site and hence suffered from no such bias. We did not detect any differences in core area and home range sizes between adult and juveniles, in contrary to what have been found for green turtles in Ningaloo reef, Australia (Pillans et al. 2022). Studies documenting size-related segregation and habitat extent often include smaller juveniles than the ones in our study (e.g. Pillans et al. 2022, Welsh and Mansfield 2022). We lack movement data on the smallest size classes (i.e. juveniles with CCL < 55 cm), even though they correspond to a large fraction of the population present within this developmental-feeding habitat (Catry et al. 2023).



**Fig. 6** Individual movement patterns of three green turtles satellite-tracked within the Banc d'Arguin, Mauritania. (a) PTT\_224397 kept the same range over the tracking duration. (b) PTT\_60865 performed range shifts and visited two different areas. (c) PTT\_60898 returned to a previously visited site

Sex does not seem to drive the distribution of the tracked adult turtles in the study area but we chose not to compare their home range sizes because of low sample size for males (3 males versus 21 adult females). A previous study conducted on green turtles in Mexico did not find an effect of sex on the home range size, but sample size for males was as low as in the present study (Seminoff et al. 2002). As reduced sample size does not enable strong inferences at the population level (Sequeira et al. 2019b; Shimada et al. 2021) we recommend future work to concentrate on the distribution and home range size of adult males.

Interestingly, some areas of the BA were used year-round, whereas turtles within the central part of the PNBA seem to move offshore during the colder winter months. This observation is amply corroborated by the testimonies received during conversations with the local Imraguen fishermen and a similar pattern has been observed at a larger spatial scale for green turtles in the Mediterranean Sea (Godley et al. 2002). These turtles may have stopped feeding and moved to different areas during the colder winter months, as cold water temperatures can lead to a decrease in seagrass production (Burkholz et al. 2019) and to a reduction of the metabolic rates and food intake in sea turtles (e.g. Godley et al. 2002). Our results further reveal that the tracked turtles used deeper waters in winter. Seasonal movements have been observed in green turtles in Australia, but are non-systematic and depend on study sites (Shimada et al. 2016) and individuals (Christiansen et al. 2016).

### Use of seagrass meadows and vulnerability to climate change

The tracked turtles exploited all known *Z. noltei* and *C. nodosa* meadows (Pottier et al. 2021), except the entrance of the Baie de Saint Jean, the coastline portion encompassed between Arkeiss and Ten Alloul and the contour of Tidra island. These seagrass patches may be poorly accessible to sea turtles because of coastal shallow depths combined with the tide cycle. The tide has been shown to influence the distribution of green turtles in Mexico and Australia (Brooks et al. 2009; Pillans et al. 2021), with turtles avoiding the shallowest areas at low tide. Imraguen fishermen report that turtles in the BA gather in deeper navigation channels at low tide, a behavior also observed in Australia (Pillans et al. 2021).

Interestingly, 83% of the population-level distribution of turtles fell outside of the estimated distribution of seagrass meadows (Pottier et al. 2021), suggesting that, potentially, the distribution of seagrass meadows is highly underestimated within the BA. We acknowledge that the seagrass distribution datasets currently available within the PNBA (Pottier et al. 2021) and higher estimate at the larger BA

scale (Chefaoui et al. 2021) rely on punctual in situ sampling and detections from satellite imageries that are still estimates and whose temporal coverage may not match the turtle tracking data. The extent of seagrass meadows was highly stable between 2003 and 2018 within the PNBA, despite variation in distribution (Pottier et al. 2021). This spatial variation is negligible compared to the extent of turtle movements, suggesting that this food source remained available for turtles over the last decades.

Satellite-tracked animals, including sea turtles, can be used as platforms to improve the mapping of seagrass meadows (Hays et al. 2018; Esteban et al. 2018; Gallagher et al. 2022). Camera tags have been deployed in a range of species, including sea turtles (e.g. Heaslip et al. 2012; Thomson & Heithaus 2014), to assess the fine-scale behavior of tracked individuals and identify their food sources (e.g. Yoshino et al. 2020; Tackaberry et al. 2020). The enhanced understanding of seagrasses distribution provided by animal-borne devices would be invaluable to interpret turtles tracking data.

A second non-exclusive hypothesis explaining the mismatch between turtle and seagrass distributions is that green turtles may exploit alternative food sources in the BA, including algae and invertebrates, as it has been shown in other populations (Lemons et al. 2011; Shimada et al. 2014; Sampson et al. 2018) and in juveniles from the same breeding population exploiting the Bijagós archipelago foraging ground (Díaz-Abad et al. 2021; Madeira et al. 2022). Recent work highlighted a relationship between SST and the level of omnivory of green turtles (Esteban et al. 2020) and the SST encountered by the tracked turtles in the BA suggests that they could present a mixed diet.

SST has been shown to increase at fast rate off Mauritania over the past three decades (Sweijd and Smit 2020) and is predicted to pursue a steep increase over the current century (Chefaoui et al. 2021). Species occurring at the limit of their range are supposed to be particularly vulnerable to environmental changes (Fraser et al. 2014) and Mauritanian waters are the Southern distribution limit of the temperate *Z. noltei* and *C. nodosa* and the Northern range limit of the tropical *H. wrightii*. A changing climate may drive a regime shift in the BA seagrass ecosystems (Chefaoui et al. 2021) and ultimately influence the distribution and energy budget of turtles through the availability and quality of food sources.

### Individual movement patterns

The mean individual core area calculated for green turtles in the BA ( $21.3 \pm 15.3$  km<sup>2</sup>,  $n=38$  including 24 adults and 14 juveniles) is very similar to what has been found for juvenile green turtles in Florida (mean = 22.5 km<sup>2</sup>,  $n=5$ , Hart and Fujisaki 2010) but approximately 9 times larger than

the mean core area reported for adult green turtles in the Western Indian Ocean (Hays et al. 2024). The mean individual home range found in this study ( $151.5 \pm 160.5 \text{ km}^2$ ) is much larger than the values reported in other studies, being approximately five (Siegwalt et al. 2020), 10 (Seminoff et al. 2002; Hays et al. 2024) and 30 times larger (Pillans et al. 2022). Comparisons among studies should be made with caution because of varying tracking devices (home range estimates tend to be higher for Argos tracking than for Fastloc GPS tracking; Hays et al. 2024), location accuracy (Dujon et al. 2014), home range calculation methods (see Hart and Fujisaki 2010 for an example of home range estimates using Kernel Density Estimator and Minimum Convex Polygon), size of the tracked turtles (e.g. Pillans et al. 2022) and foraging habitats specificities (e.g. turtles may exploit overlapping or distinct foraging and resting sites; Makowski et al. 2006; Ballorain et al. 2013). Furthermore, the size of the estimated habitat can vary a lot depending on whether the turtle is faithful to its fine-scale foraging habitat or switches between distinct areas. However, our results suggest that even in stationary phases, green turtles foraging in the BA have a larger habitat than overall home ranges reported elsewhere, suggesting that the comparison with other studies is conservative. To the best of our knowledge, the largest home range values reported in green turtles at foraging grounds have been attributed to turtles moving between isolated food patches (e.g. Whiting and Miller 1998) or commuting between distinct foraging and resting sites (e.g. Seminoff et al. 2002).

Green turtles shuttle between distinct feeding and resting areas at Mayotte Island (Ballorain et al. 2013), while turtles from Palm Beach, Florida, mostly exploit overlapping foraging and shelter sites (Makowski et al. 2006). It is unclear whether green turtles commute to distinct resting sites in the BA, however we did not notice regular movements suggesting such behavior. Turtles cannot perform assisted resting (i.e. under a rock, e.g. Reisser et al. 2013) within the shallow sandy-muddy BA. Green turtles probably bask or stay immediately below the surface to rest (Spotila and Standora 1985) and large individuals may not inspire fully to reach neutral buoyancy at depths regularly used in the BA (generally < 10 m, Hays et al. 2000). They hence would not need to move to specific resting sites. The deployment of time-depth recorders along with accelerometers will help assessing the behavioral states of turtles, including resting phases and feeding events (see Hounslow et al. 2022 for an example in flatback turtles).

Interestingly, we highlighted that more than half of the tracked turtles exploited several areas within the BA. Despite most studies report that green turtles display fidelity to a single fine-scale foraging area as shown in Ningaloo, Australia (Seminoff et al. 2002; Pillans et al. 2022), turtles

exploiting several areas have been reported in Mexico, where a minority of the tracked green turtles exploited up to three activity centers (Seminoff et al. 2002). Seasonal changes in movement patterns have been highlighted in three out of eight green turtles tracked in the Chagos Archipelago (Christiansen et al. 2016). Research conducted on other sea turtle species revealed that seasonal movements between distant foraging areas are observed more commonly in temperate than in tropical and subtropical waters (Shimada et al. 2016). While some of the tracked turtles moved between distinct areas in the BA, the shifts in habitat of some other turtles corresponded to changes in localized fidelity between overlapping areas, or to a contraction or expansion of habitat over time. Such patterns have also been observed in green turtles in Queensland, Australia (Shimada et al. 2016).

### Implication for conservation

The BA is thought to host the largest green turtle foraging aggregation in the eastern Atlantic (of the order of 150,000 individuals; Catry et al. 2023) and is hence invaluable for this species. Despite the fact that seven females and one juvenile performed westward excursions outside of the PNBA, the locations of most tracked turtles fell within the Park. Furthermore, the overlap between turtle home range and shallow waters (< 10 m; representing potentially suitable habitat) in the BA was 5.5 greater inside the PNBA than outside. This suggests that turtles preferentially use areas that are protected (characterized by a limited fishing effort, by sailing boats only) and that they may have been benefiting from the management of this protected area since it was established in 1976.

The Mauritanian waters are also a known foraging area for loggerhead turtles (off the 500 m isobath, south of the PNBA; Hawkes et al. 2006) from one of the world's largest nesting aggregations in Cape Verde (Laloë et al. 2019), which emphasizes their importance for sea turtles worldwide.

The tracked turtles exploited very shallow sites, even if deeper areas were available. This pattern is consistent with a previous study tracking four individuals in the same area (Godley et al. 2010) and has been observed in other green turtle populations (Gulf of California, Mexico, Seminoff et al. 2002; Queensland, Australia, Hazel et al. 2009; Mayotte Island, Ballorain et al. 2013). The habitat of the tracked turtles highly overlaps with artisanal fisheries in the central shallow waters of the Park (Trégarot et al. 2020) and it is known that some by-catch still occurs within the PNBA. A restriction of net casts in this area, if sustainable for local communities, would highly reduce ongoing interactions between turtles and artisanal fisheries. The present study

provides valuable ecological information that can be used to inform the planning of a fisheries zoning within the Park.

Though our study highlights the distribution of green turtles in relation to bathymetry, SST and seagrass meadows, we acknowledge that other factors including predation risk (Heithaus et al. 2007), currents and tide cycle (Brooks et al. 2009; Pillans et al. 2021) may drive the movements of turtles. Future work should investigate the effect of these parameters, as well as possible diel patterns in turtle behavior (Taquet et al. 2006; Ballorain et al. 2013; Enstipp et al. 2016; Christiansen et al. 2016), to further inform effective conservation strategies.

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**Author contributions** Paulo Catry, Ana Rita Patricio, Ebyte Sidina, Cheibani Senhoury and Aissa Regalla acquired fundings to enable this study. Ebyte Sidina, Cheibani Senhoury, Nahi El'bar and Aissa Regalla permitted fieldwork and provided logistical support. Paulo Catry and Ana Rita Patricio designed data collection and provided the dataset. Paulo Catry, Ana Rita Patricio, Julie Mestre and Nahi El'bar collected the data. Julie Mestre and Paulo Catry conceived the study. Julie Mestre analysed the data with substantial contribution from Martin Beal. Julie Mestre led the writing of the manuscript with significant input from Paulo Catry and Ana Rita Patricio. All authors contributed to the paper review, read and approved the final manuscript.

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**Data availability** The tracking datasets analysed during the current study can be requested from the authors on Movebank ([www.movebank.org](http://www.movebank.org)) under the study names ‘Chelonia mydas\_bijagos\_females\_2018’, ‘Chelonia mydas\_bijagos\_females\_2020’,

‘Chelonia mydas\_bijagos\_females\_2021’, ‘Chelonia mydas\_bijagos\_males\_2021’ and ‘Chelonia\_mydas\_Banc\_Arguin\_2020\_2021’.

## Declarations

**Compliance with ethical standards** Research permits and logistic support were provided by the Parc National du Banc d'Arguin (PNBA) in Mauritania and by the Instituto da Biodiversidade e das Áreas Protegidas, Dr. Alfredo Simão da Silva (IBAP) in Guinea-Bissau. The protocols were approved by the ethical committee of the Órgão Responsável pelo Bem-Estar Animal of Ispa - Instituto Universitário, Lisbon, Portugal (ORBEA-Ispa), which ensures the compliance of ethical standards and animal welfare rules. Field protocols were carefully performed by trained personnel following recommended guidelines to minimize disturbance to turtles (National Marine Fisheries Service Southeast Fisheries Center 2008) and handling time was reduced to the strictly necessary.

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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