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REVIEW

The elusive sex: satellite tracking contributions to male sea turtle spatial ecology

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ABSTRACT: Satellite tracking has revolutionized our understanding of the behavior and ecology of sea turtles. However, most satellite tracking of sea turtles has been performed on breeding females, leaving knowledge gaps with regard to males. To inform future studies, we examined the peer-reviewed literature to summarize the contribution that satellite tracking has made to the spatial ecology of male turtles and describe how the published research varies across time, species, life stages, seasonal cycle phases, regions, and research topics. We systematically reviewed 61 publications reporting tracking of male sea turtles across 6 species. Loggerheads emerged as the most studied species, featuring in 49% of the publications, with green turtles and loggerheads having the highest number of tracked males. The North Atlantic was the most represented region (39% of publications), followed by the Mediterranean (29%). Most tracking of males has been undertaken at foraging areas (77%), often providing information on home range residency. This is followed by migration publications (44%), which have revealed differences among populations and between sexes, with the breeding period being the least studied. We highlight differences in the spatial ecology of males and females (e.g. residency in breeding areas and migration distance) and identified unanswered research questions about male sea turtles. To overcome the lack of knowledge about this important demographic group, efforts should be undertaken to increase the sample size and geographic coverage of tracked males, with special focus on flatback and Kemp's ridleys, as well as studies in the Indian and Pacific Oceans.

KEY WORDS: Male marine turtle · Spatial ecology · Home range · Dive · Biologging · Distribution · Migration

1. INTRODUCTION

In recent decades, animal-tracking technologies (e.g. satellite and acoustic transmitters) have emerged as key tools for studying marine megafauna (Hussey et al. 2015). By providing a spatiotemporal record of an animal's movement and behavior, tracking devices deliver invaluable insights that may be difficult to obtain from direct observation (Ropert-Coudert & Wilson 2005). Satellite tracking has become a commonly used tool to study sea turtles at sea (Godley et al. 2008, Hart & Hyrenbach 2009). Since the first deployment of satellite tags on turtles in the 1980s (Stoneburner 1982, Timko & Kolz 1982), technological innovation has led to smaller, more robust, and longer-lasting tags that provide ever-improving sampling rates and spatial resolutions as well as additional behavioral (e.g. dive) and environmental data (e.g. temperature; Hays & Hawkes 2018, Roberts et al. 2022). These advancements have allowed the identification of key habitats (e.g. foraging, breeding), migratory corridors, critical resources, and hotspot

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areas where turtles aggregate, and have provided information on behavioral states (Santos et al. 2023), helped determine human impacts of sea turtles and their environment (Fuentes et al. 2020, 2023), and informed the conservation and management of sea turtles (Jeffers & Godley 2016, Hays et al. 2019). Despite the broad applicability of satellite telemetry in sea turtle research, it is widely recognized that biases exist with respect to geography, species, life stage (e.g. immature turtles), and sex (e.g. females) (Godley et al. 2008, Hart & Hyrenbach 2009, Hays & Hawkes 2018, Wildermann et al. 2018).

Most of the tracking work conducted on sea turtles to date has focused on tagging of nesting females due to their accessibility while laying eggs (Godley et al. 2008, Hart & Hyrenbach 2009). Therefore, our knowledge of the spatial ecology of sea turtles is biased towards the behavior of this demographic group during post-nesting, such as the identification of migratory routes to foraging areas (Godley et al. 2008). However, differences have been found between the spatial ecology of males and females, including differential migration distances, proximity of feeding areas to breeding grounds, breeding area residency, and breeding interval (Van Dam et al. 2008, Hays et al. 2010, Schofield et al. 2013a, Cuevas et al. 2020, Beal et al. 2022). Thus, tracking of adult males can help elucidate longstanding questions related to sex-specific breeding patterns, migratory behavior, and resource and habitat use (Beal et al. 2022). Despite recent efforts to track male sea turtles and analyze their movements and behavior, this segment of the population remains largely underrepresented (Godley et al. 2008, Hays & Hawkes 2018). To inform and prioritize future studies on this demographic, we collated and critically evaluated the published literature on male sea turtle satellite tracking. With this systematic literature review, we describe the variation in research published on male sea turtles across time, species, life stages, seasonal cycle phases, regions, and research topics. Based on this compiled information, we summarize current knowledge on male sea turtle spatial ecology, identify knowledge gaps, and provide suggestions for future research directions. Although this review focuses solely on satellite tracking data, it is worth noting that other methodologies can also provide valuable insights into male sea turtle ecology. For instance, molecular analyses can assess multiple paternity (Lee et al. 2018, Silver-Gorges et al. 2024), while direct observations, such as those from drone surveys, can help infer seasonal patterns of mating and occurrence (Schofield et al. 2019, Staines et al. 2022).

2. METHODS

Peer-reviewed literature on satellite tracking of male sea turtles was compiled by searching the Scopus Database on 1 April 2024 (https://www.elsevier.com/products/scopus) following the steps outlined in Grames et al. (2019) and using the graphic interface for litsearchr to generate and update search terms (https://elizagrames.shinyapps.io/litsearchr/). Our initial naive search used the following search string: TITLE-ABS-KEY ("Satellite telemetry" OR "satellite tag" OR "PTT" OR "platform transmitter terminal" OR "platform terminal transmit" OR "GPS" OR "track" OR "ARGOS" OR "Fastloc" AND "Male" OR "Masculine" AND "Sea turtles" OR "Marine turtles" OR "Chelonioid" OR "Green turtle" OR "Chelonia mydas" OR "Loggerhead " OR "Caretta caretta" OR "Hawksbill" OR "Eretmochelys imbricata" OR "Leatherback" OR "Dermochelys coriacea" OR "Flatback turtle" OR "Natator depressus" OR "Olive Ridley" OR "Lepidochelys olivacea" OR "Kemp's Ridley" OR "Lepidochelys kempii"), which resulted in 63 entries (Fig. 1). Using the results from the naive search, we looked for duplicate records and identified and extracted keywords to update our search, using the following search string: TITLE-ABS-KEY ("adult* femal*" OR "adult* male*" OR "adult* turtl*" OR "breed* popul*" OR "male* remain*") AND ("caretta* caretta*" OR "chelonia* myda*" OR "dermoch* coriacea*" OR "endang* leatherback*" OR "eretmoch* imbricata*" OR "green* turtl*" OR "hawksbil* turtl*" OR "leatherback* turtl*" OR "loggerhead* turtl*" OR "marin* turtl*" OR "marin* vertebr*" OR "turtl* caretta*") AND ("activ* pattern*" OR "anim* migrat*" OR "global* posit*" OR "kernel* densiti*" OR "migrat* pattern*" OR "migrat* rout*" OR "migratori* behavior*" OR "migratori* speci*" OR "movement* pattern*" OR "posit* system*" OR "satellit* imageri*" OR "satellit* telemetri*" OR "satellit* track*" OR "satellit* transmitt*" OR "spatial* distribut*" OR "spatial* ecolog*" OR "track* turtl*" OR "turtl* migrat*"); this Boolean search resulted in 425 entries (Fig. 1).

The list of publications from each search was combined and duplicates were removed. We then identified publications that were published in peer-reviewed academic journals and that analyzed tracking data from male sea turtles, as indicated in the paper. As such we did not consider studies where the sex of tracked individuals was not stated, but recognize that these studies may still contain data from males. An additional backwards and forwards search was conducted on all publications that fit the inclusion criteria and on previous literature reviews on spatial ecology of sea turtles (Godley et al. 2008, Hays & Hawkes 2018).

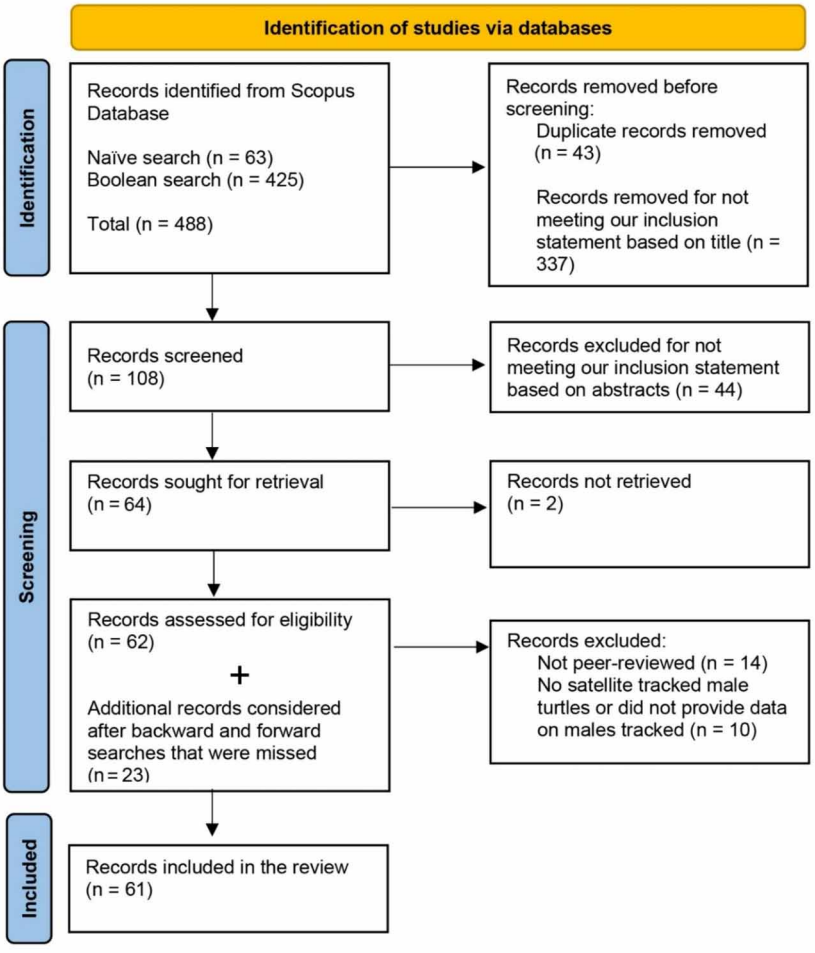

Fig. 1. PRISMA flow diagram indicating the number of publications at different steps of the systematic review

Finally, we identified 61 peer-reviewed publications containing information on the spatial ecology of male sea turtles as determined by satellite telemetry.

The following information was extracted from each publication: date of study and publication, study location, number of individuals tracked, species, life stage (i.e. adult or immature), seasonal cycle stages covered (i.e. breeding, foraging, migration), type of satellite telemetry device, morphometrics (curved carapace length or straight carapace length), duration of tracking, whether the publication also analyzed tracking data from females, and how sex was determined (Table S1 in the Supplement at www.int-res.com/articles/suppl/n057p273_supp.xlsx). We also collected information on the research topic (see Table 1), and major findings related to foraging and breeding site fidelity, and the distance covered on reproductive migration (Table S1). The term 'site fidelity' has been variably applied across the sea turtle tracking literature, so to be consistent we use this term to describe when an individual turtle returns to a previously used area after spending time away. In addition, the term 'residency' was used to refer to an individual turtle remaining within a localized area. Lastly, we extracted available estimates for minimum convex polygon, size of the 50% core use areas and 95% home range areas, and home range analysis type. However, differences in methodological approaches, seasonal life cycle stages, and unreported details (e.g. specific analyses used to estimate home ranges, smoothing parameters, etc.) limit the comparability of these estimates across studies. When summarizing sample sizes across studies, we calculated 2 values: 'tracks', which refers to the number of tracking events, including potential duplicates across studies, and 'individuals', which refers to the number of uniquely tracked male turtles, both in total and per year.

3. OVERVIEW OF MALE-TRACKING PUBLICATIONS

3.1. Temporal, technological, and sex-composition trends

We identified 61 peer-reviewed publications which contained a total of 595 male sea turtle tracks from 309 individual males from 1996 to April 2024. The first male sea turtle was tracked in 1996 in Kushimoto, Japan (Sakamoto et al. 1997; Table S1). Following the initial 2 yr of peer-reviewed publications on male sea turtle tracking, 4 gaps in publication were noted: between 1998 and 2000, from 2002 to 2004, in 2011, and in 2019. The annual number of publications from 1998 to 2024 ranged from 0 to 5 (Fig. 2A). The near-exponential increase in publications analyzing sea turtle tracking data reported by Hays & Hawkes (2018) is not reflected in publications featuring male tracking data (Fig. 2A). Although the mean number of tracks analyzed per study increased since the first publication, there was substantial interannual variability (Fig. 2B). Additionally, of 7002 sea turtle tracking records — including both sexes and all ages — analyzed between 1982 and 2017 by Hays & Hawkes (2018), only 322 (4.6%) corresponded to male sea turtles (Fig. A1 in the Appendix). A total of 39% of publi-

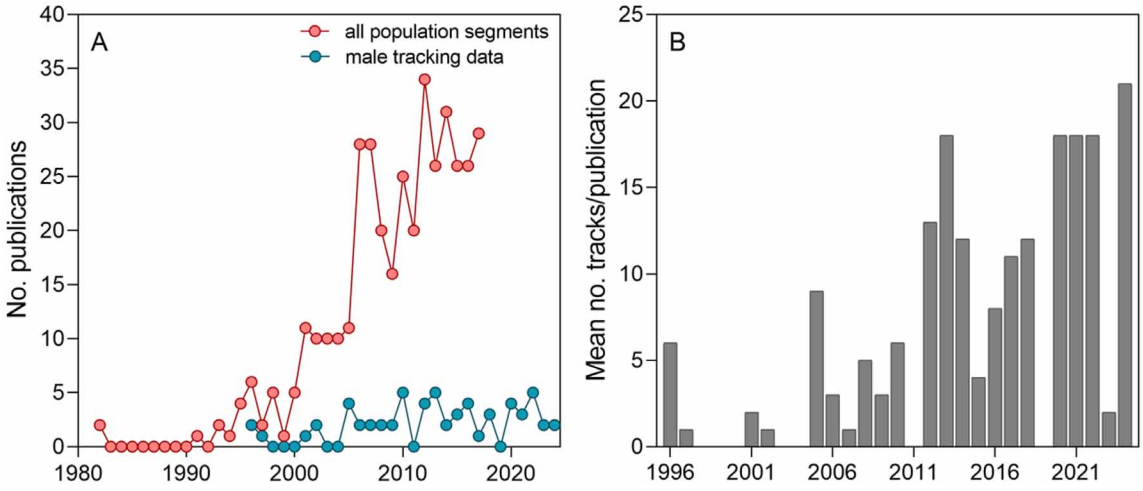

Fig. 2. (A) Annual number of peer-reviewed publications analyzing sea turtle tracking data for all population segments from Hays & Hawkes (2018) (red) and for males (blue). (B) Mean number of male sea turtle tracks analyzed per peer-reviewed publication per year

cations considered (24 of 61 publications) analyzed tracking data from male sea turtles previously included in earlier studies. Of these, 10 also incorporated new males in addition to reanalyzing existing data. Notably, 28 (46%) of the publications had a low sample size (⩽3 males tracked). Argos devices were used in 34 (55%) of the publications, 27 (44%) used Fastloc-GPS, and 13 (21%) used both Argos and Fastloc-GPS. The first publication that deployed Fastloc-GPS to track male turtles was published in 2009 and was conducted on loggerheads *Caretta caretta* in the Mediterranean (Schofield et al. 2009). Of the publications analyzed, 69% (n = 42) also included tracking data from females. Of these, however, 33% (14 of 42 publications) did not report results by sex, impeding our attempt to draw conclusions about sex-specific differences in spatial ecology. In 26 of 42 publications, more females were tracked than males, suggesting that in some cases, the tracking of males could have been more opportunistic rather than a primary research objective. However, given that most sea turtle populations are female-biased, this trend can also partially reflect the lower abundance of males and the fact that they are more difficult to locate and capture.

3.2. Species

The analyzed tracks of male sea turtles (n = 595 including replicates) showed a similar species representation pattern as reported by Hays & Hawkes (2018), with loggerheads being the most common species, followed by leatherbacks *Dermochelys coriacea* and green turtles *Chelonia mydas* (Fig. 3A). The remaining species had fewer tracks and, notably, no tracks have been published from male flatback turtles *Natator depressus* (Fig. 3A). Green turtles and loggerheads were the most tracked species, representing 37% (114 of 309 individuals, excluding replicates) and 35% of tracked males (107 of 309 individuals), respectively (Fig. 3B). Hawksbills *Eretmochelys imbricata*, Kemp's ridley *Lepidochelys kempii*, and olive ridley *L. olivacea* turtles were the least represented, with <10% of tracked males for each species, with male flatback turtles yet to be satellite tracked (Fig. 3). With respect to the total number of scientific publications, loggerheads were the most studied species, featuring in 49% of publications (30 of 61 publications, Fig. 3C). Green turtles and leatherbacks followed, with 24% and 21%, respectively. Next were hawksbills (12%), Kemp's ridleys (7%), and olive ridleys (3%, Fig. 3C). It should be noted that the number of publications per species exceeds the total number analyzed, as 6 report data on multiple species; 4 of these publications include data on 2 species each, and 2 of the publications provide data on 4 species each (Fig. 3C, Table S1).

3.3. Life stage

In 79% of the publications (48 of 61), the tracked male turtles were classified as adults. Four publications included both adult and immature male turtles, 3 included exclusively immature male turtles, and 3 did not specify life stage. To identify the sex of the

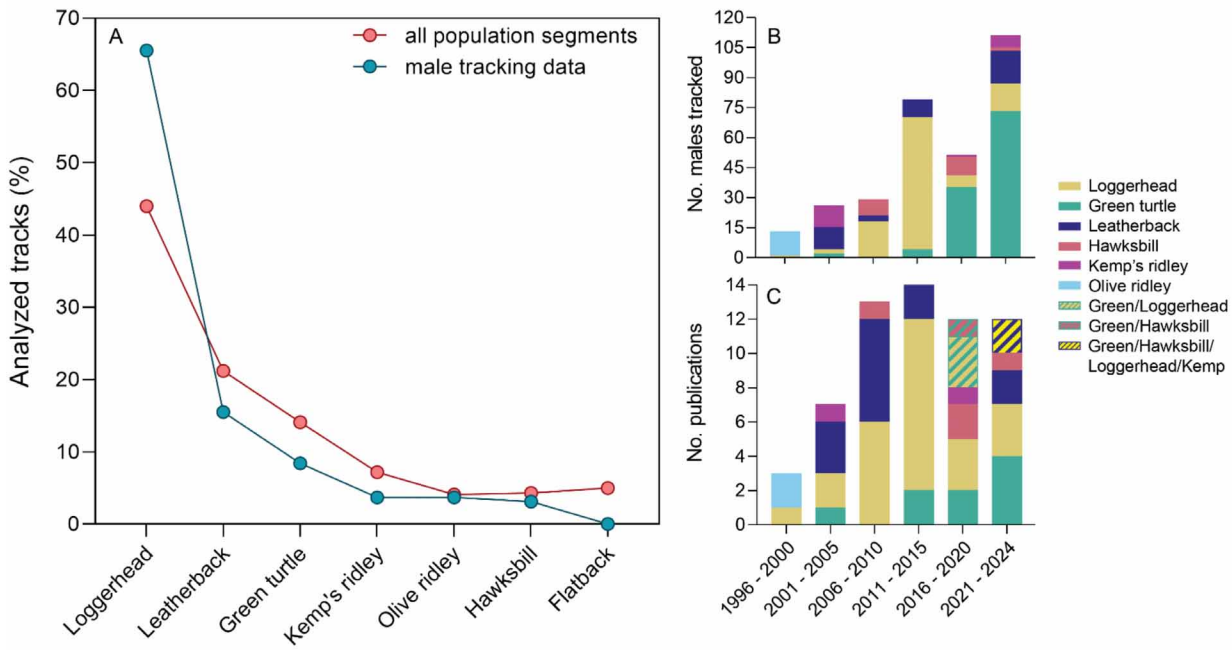

Fig. 3. (A) Percentage of analyzed tracks by species for all population segments from Hays & Hawkes (2018) (red) and for males (present study) (blue). (B) Number of individual male sea turtles tagged with satellite tags and (C) the number of peer-reviewed publications analyzing male sea turtle tracking data by species, each grouped into 5 yr intervals

tagged turtles, 3 publications used the carapace and tail length, while all others employed laparoscopy (n = 8) or observed mating behaviors (n = 6) (Table S1). Some publications (n = 14, 23%) did not specify the methods used for sex identification, or provided vague descriptions, such as 'external characteristics' without further details (Table S1).

3.4. Seasonal cycle phase

Seventy-seven percent of the publications tracked males at their foraging areas (47 of 61 publications). The second most studied phase (e.g. breeding, migration, foraging) was migration, appearing in 44% (27 of 61) of publications, with reproductive migrations appearing in 50% (13 of 26) of the publications covering the movements from breeding to foraging sites, and half tracking movements from foraging to breeding areas (Fig. 4). Only 34% of publications tracked animals during the breeding period (21 of 61). A total of 32 publications focused on a single phase, 10 analyzed male sea turtle tracks across all 3 phases, 11 examined both foraging and migration periods, 5 focused on breeding and migration, and 1 publication assessed both breeding and foraging periods (Fig. 4). Tracking deployments on males extended across consecutive years in 2 publications on loggerheads (Hays et al. 2010, Varo-Cruz et al. 2013), 1 on leatherbacks (James et al. 2005a), 1 on hawksbills (Van Dam et al. 2008), and 1 on green turtles (Webster et al. 2022), providing insights into their remigration intervals and fidelity to breeding and foraging sites.

3.5. Geographic distribution

The northwest/northern Atlantic region was the most represented, comprising 39% of the total number of publications, those in the Mediterranean accounting for 29%, those in the western Pacific representing 15%, the southwest/southern Atlantic accounted for 5% of the publications, the East Atlantic, East Pacific, and Indian Ocean accounted for 3% each, and the Central Pacific for 2%. When considering sea turtle regional management units (RMUs), (Wallace et al. 2023), the loggerhead Mediterranean RMU had the most male-tracking publications, followed by the leatherback Northwest Atlantic RMU, each with 17 and 11 publications and 48 and 38 males tracked respectively (Fig. 5). These significant geographic biases in the effort to track male sea turtles are similar to those found in satellite tracking studies across all population segments (Godley et al. 2008), which likely result from disparities in the availability of research funding across different regions and logistical support (e.g. boats) (Robinson et al. 2022).

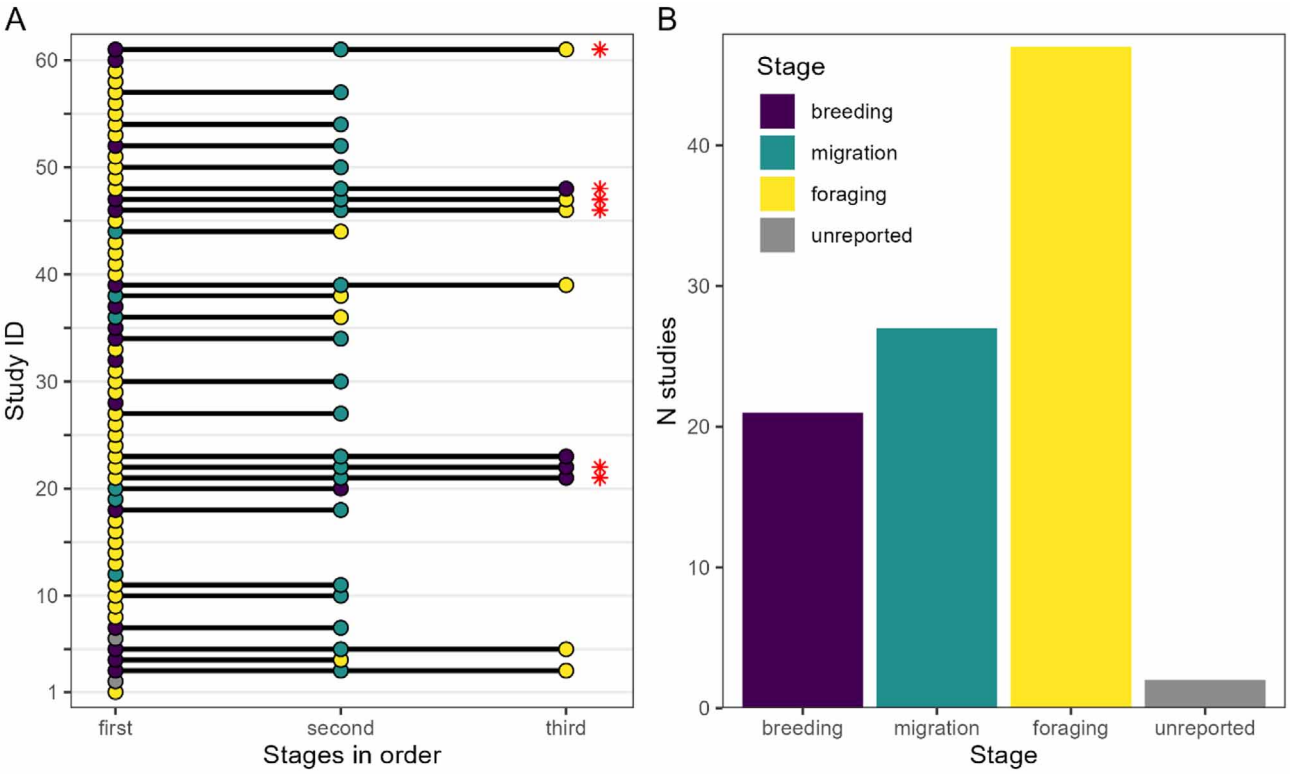

Fig. 4. Seasonal cycle stages covered by 61 satellite tracking publications of male sea turtles. (A) Seasonal stages covered in order, from the tagging stage (first) to the last stage analyzed or tag failure (third). Circle colors: stage type (as in B); red stars: publications in which ⩾1 male turtle was tracked throughout several reproductive migration cycles (partially or entirely, n = 6). (B) Number of publications covering each seasonal cycle stage, if reported

3.6. Research topics

The most studied research topic (as described in Table 1) for male-turtle tracking focused on reproductive migration—whether from breeding to foraging sites or vice versa — and on residency patterns at foraging or breeding sites (Figs. 4 & 6). The third-most explored topic was habitat use (i.e. spatial distribution in relation to environmental parameters, Table 1). Despite the importance of understanding breeding patterns — particularly in the face of climate change and its effect on the sex ratios of sea turtle populations (Patrício et al. 2021) — only 6 publications focused on this topic, making it the least studied topic (Fig. 6).

4. CURRENT KNOWLEDGE

4.1. Breeding

Research on male turtle behavior during breeding has been conducted on few species, with limited spatiotemporal scope and sample sizes (Rees et al. 2016). Publications suggest reproductive intervals of male loggerhead and green turtles in the Mediterranean may be shorter than those of females, with males potentially breeding twice as frequently as females (Hays et al. 2010, 2014, Wright et al. 2012). This difference may relate to the fact that males likely need to accumulate less energy reserves than females before subsequent reproductive events and as such spend less time at breeding grounds. There is also evidence that male turtles often travel shorter distances to foraging grounds, allowing them to re-build their energy reserves more quickly (Schofield et al. 2013a,b). However, longer remigration intervals, exceeding 1 yr, have also been observed in some populations (Wright et al. 2012, Casale et al. 2013, Naro-Maciel et al. 2018).

Satellite tracking, as well as parental analysis of clutches (Lee et al. 2007), indicated that males may have more relaxed breeding-site fidelity (Lee et al. 2007), often mating with females at multiple breeding grounds, and/or selecting breeding grounds that are different from their natal origin (Wright et al. 2012, Casale et al. 2013). These breeding patterns may play a critical role in buffering the impacts of climate change on sex ratios (Hays et al. 2022). However, it is unclear whether these patterns are consistent across species and locations, since our knowledge of breeding periodicity and breeding site fidelity are limited

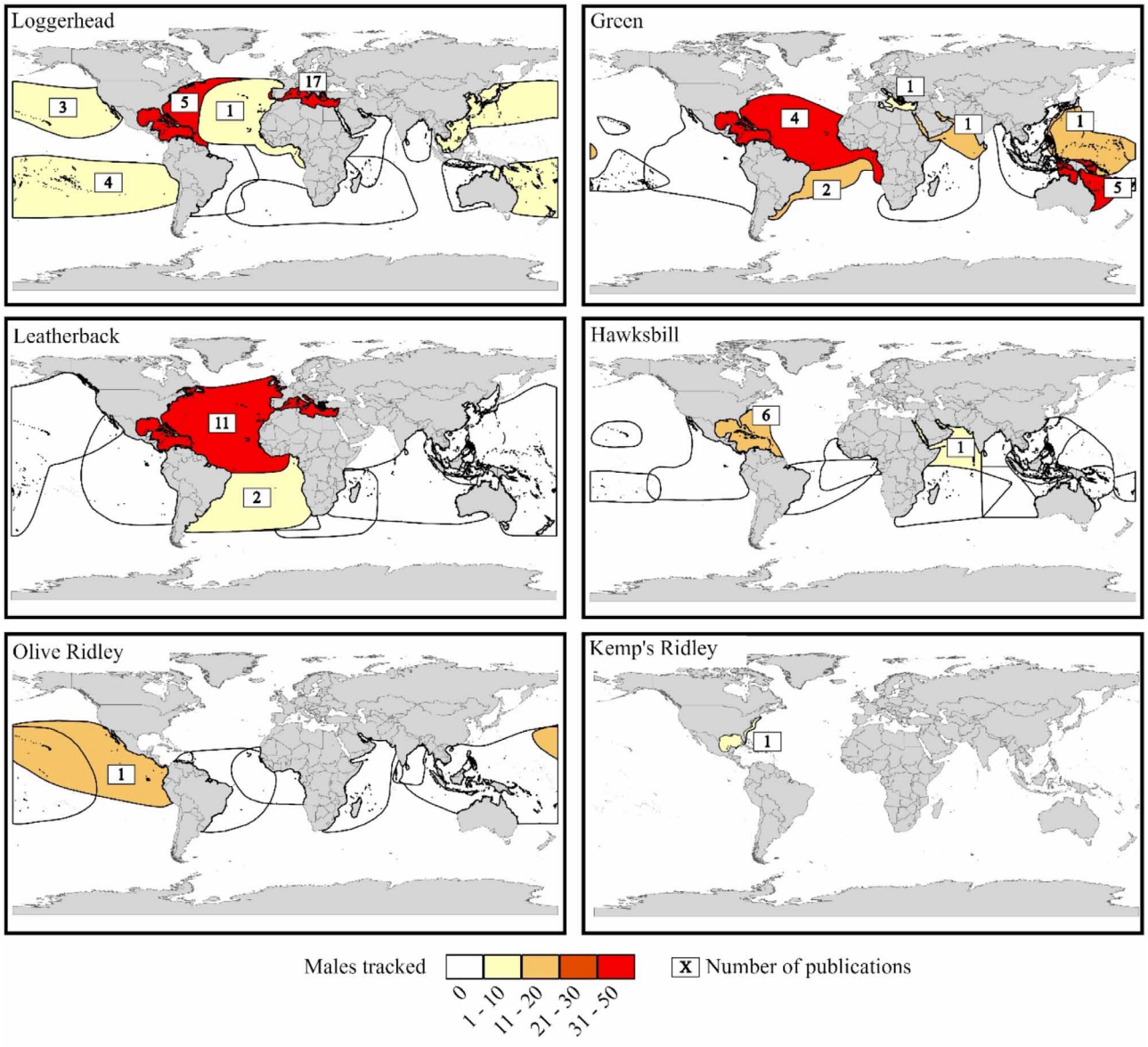

Fig. 5. Number of publications tracking male sea turtles and males tracked per species and regional management unit (as per Wallace et al. 2023)

to a few publications and species (see Hays et al. 2010, 2014, Wright et al. 2012, Casale et al. 2013). This might reflect geographic biases in tracking effort, but also the need to track males from their breeding grounds throughout an entire migration cycle to address these questions. Additionally, similar to some females (Whiting et al. 2008), some males may remain in the vicinity of breeding grounds year-round, as seen in Kemp's ridley in the Gulf of Mexico (Shaver et al. 2005); hawksbills in Puerto Rico (Van Dam et al. 2008); and loggerheads in the Mediterranean (Schofield et al. 2010b, 2020), Cabo Verde (Varo-Cruz et al. 2013), and Florida (Arendt et al. 2012b). This behavior seems to be more common among males and driven by individual-level differences, rather than a fixed population trait (e.g. sex, life stage). If food resources are available near the nesting beaches, this strategy may enhance mating opportunities, as resident males would increase their chances of being the first to access females as they arrive for nesting.

The spatial distribution of turtles at breeding sites can vary by sex. For example, male loggerhead turtles in Zakynthos, Greece had smaller home ranges and core use areas during breeding than females and were more concentrated near the nesting beach (Schofield et al. 2010b). This sex difference in space

Table 1. Description of main research topics appearing in 61 peer-reviewed publications analyzing tracking data from male sea turtles. MPA: marine protected area; SST: sea surface temperature

Topic	Description
Breeding patterns	Assessing operational sex ratios, frequency of breeding by males and mating events, duration of stay in breeding area
Conservation/ spatial planning	Assessing spatial distribution in relation to MPA limits, informing spatial conservation measures (e.g. MPA design, fisheries zones)
Foraging migration	Analyzing seasonal movements between distant foraging areas
Habitat use	Assessing the relationship between spatial distribution and environmental conditions (e.g. SST, bathymetry, distance to coastline)
Home range/residency	Estimating restricted space use within foraging and/or breeding grounds in space and/or time
Reproductive migration	Analyzing reproductive migrations (e.g. direction, distance, speed, duration) between foraging and breeding grounds (either direction)
Site fidelity	Assessing propensity to return to the same breeding/foraging site after migration
Technical/methods	Developing a methodology (e.g. to improve location data quality) or testing a technique (e.g. attachment of tracking devices)
Threats/impacts	Evaluating exposure to threats, assessing the impacts of threats
Vertical space use	Analyzing dive behavior/depth use data

use may be attributed to fertilized females dispersing farther during the internesting period to reduce the likelihood of male harassment and repeated mating attempts (Lee & Hays 2004).

4.2. Post-breeding migration

To date, the movements of males from breeding grounds to foraging areas have been tracked and published for loggerheads breeding in Greece, Cabo Verde, East Australia, and USA (Florida), and green turtles breeding in Guinea-Bissau, Cyprus, East Australia, and Ascension Island (UK) (Table S1). The movements of males migrating to foraging grounds have further been identified for hawksbills breeding in Puerto Rico and Bonaire, and from multi-season tracking of leatherbacks tagged in Atlantic Canada (James et al. 2005a) and green turtles tagged in Florida (Ashford et al. 2022).

Tracking of males during post-breeding migrations indicates that male hawksbills (Van Dam et al. 2008), loggerhead (Schofield et al. 2020), and green turtles (Beal et al. 2022) tend to migrate shorter distances than females (Table S1). In the case of green turtles, this sex-specific difference in migration distance does not appear to be driven by differential habitat use (Beal et al. 2022). Tracking of different populations of the same species has shown that migration distances can vary widely, with e.g. 2 male hawksbills tagged at breeding grounds in Bonaire migrating 5–10 times further than post-breeding males from Puerto Rico (Van Dam et al. 2008, Becking et al. 2016). Additionally, migrant males generally leave breeding areas earlier than females, as seen for olive ridleys (Plotkin et al. 1996), loggerheads (Schofield et al. 2009, 2020, Arendt et al. 2012b), green turtles (Beal et al. 2022), and leatherbacks (Doyle et al. 2008), although exceptions exist (Becking et al. 2016).

If satellite tags transmit for at least a year, tracking may indicate the degree of fidelity that males have to breeding areas, as was shown for 3 loggerheads returning to breeding sites in Greece where they were tagged (Hays et al. 2010) and 1 male loggerhead re-

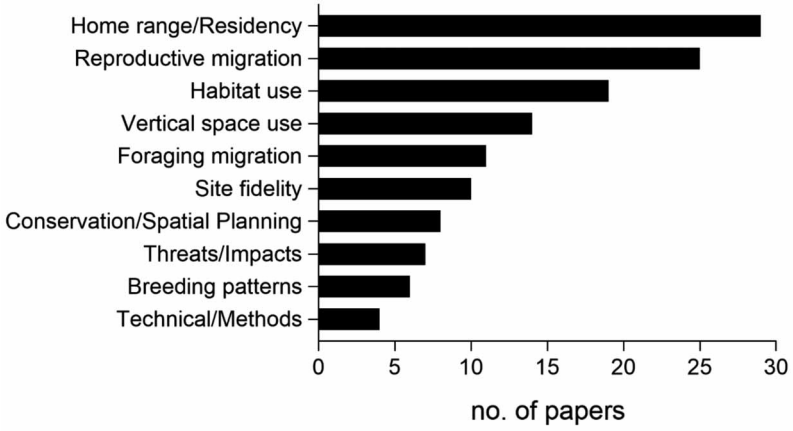

Fig. 6. Frequency of main research topics appearing in 61 peer-reviewed publications analyzing tracking data from male sea turtles (see Table 1 for description of the topics)

turning to the same breeding site in Cabo Verde (Varo-Cruz et al. 2013), as well as for 2 hawksbill males in the Caribbean (Van Dam et al. 2008). Tracking data from full migration cycles may be harder to get in some species, such as green turtles, which tend to have shorter transmission durations (Hart et al. 2021). Ultimately, the generality of male breeding site fidelity is difficult to characterize, given the low number of publications that have tracking data long enough to identify recursions, or a lack thereof (Shimada et al. 2020).

4.3. Foraging

The home ranges of male sea turtles during foraging vary across species and populations but do not appear to differ from females (e.g. see Shimada et al. 2016); it rather seems to be driven by a variety of factors (e.g. bathymetry, prey distribution, and mesoscale features) (Doyle et al. 2008, Schofield et al. 2010a). For instance, male sea turtle home ranges were found to vary depending on whether turtles were foraging in shallow neritic waters or oceanic regions (Schofield et al. 2010a). Flexibility in foraging strategy — such as neritic versus offshore foraging — has been demonstrated in male loggerheads from Cabo Verde (Varo-Cruz et al. 2013) and hawksbills in the Gulf of Mexico (Cuevas et al. 2020), similar to patterns observed in females (Hawkes et al. 2006, Schofield et al. 2010a). Yet, because of the shorter migration distances, males have been found to forage on average closer to breeding sites than females (Shaver et al. 2005, Van Dam et al. 2008, Schofield et al. 2010a, Nivière et al. 2018, Beal et al. 2022). While female sea turtles have also been observed foraging relatively close to breeding sites (within 100 km), e.g. in Cyprus (loggerheads; Broderick et al. 2007), Costa Rica (green turtles; Blanco et al. 2012), and Guinea-Bissau (green turtles; Patrício et al. 2022), males seem to do so more consistently. In contrast, one study by Pilcher et al. (2021) has indicated that males may remain at foraging grounds distant from nesting beaches throughout the breeding season, even if ready to mate (e.g. green turtles in the Arabian Gulf) and may eventually mate in these areas.

Foraging site fidelity appears to be a common feature among sea turtles (Shimada et al. 2020). To date, loggerhead and green male turtles have been found to return to the same foraging grounds after breeding (Schofield et al. 2010a, Shimada et al. 2020), although in some cases, males may switch foraging areas over time (Varo-Cruz et al. 2013, Webster et al. 2022), as has also been observed in females (Shimada et al. 2020, Pilcher et al. 2021). Leatherbacks, as they primarily foraging in pelagic habitats, may be less faithful to specific foraging locations, but at a regional level, male leatherbacks have still been shown to return to foraging areas (James et al. 2005a). In general, the sample sizes of males tracked over multiple migrations remain small, limiting the possibility of fully characterizing variability in foraging-site fidelity and making robust comparisons with females.

Sexual segregation at foraging grounds is not commonly reported, but male loggerheads in the Mediterranean have been found to forage closer to shore than females (Schofield et al. 2020) and juveniles (Casale et al. 2013), heightening their exposure to anthropogenic threats, such as boat strikes (Schofield et al. 2020). In the Caribbean, certain foraging grounds shared by adult male and juvenile hawksbills appear to be largely unused by adult females (Van Dam et al. 2008, Nivière et al. 2018). However, overlap between males and females at foraging areas seems more common elsewhere (e.g. Shimada et al. 2016, Naro-Maciel et al. 2018, Beal et al. 2022, Webster et al. 2022, 2024).

The tendency of males to forage closer to breeding sites may be less pronounced in some populations, particularly among temperate populations, like some populations of loggerhead and leatherback turtles, which undertake seasonal foraging (i.e. non-reproductive) migrations (James et al. 2006, Doyle et al. 2008, López-Mendilaharsu et al. 2009, Arendt et al. 2012b, Dodge et al. 2014, Saito et al. 2015, Sasso et al. 2021). These migrations involve long-distance travel to higher latitudes during the summer in search of colder, nutrient-rich waters, returning to subtropical or tropical regions before winter (Southwood & Avens 2010). In the Mediterranean, loggerhead males have been shown to forage in the cooler western areas during the warmer months, then migrate eastward during colder periods (Bentivegna 2002). Females of the same populations perform similar seasonal foraging migrations (e.g. Bentivegna et al. 2007, Hawkes et al. 2011); however, the earlier departure of males from breeding sites may confer foraging benefits, e.g. potentially allowing male leatherbacks to reach higher-latitude foraging grounds during the warm months (Doyle et al. 2008). In contrast, as females stay longer at breeding sites to lay consecutive clutches, they may be limited to closer foraging grounds during reproductive years (Doyle et al. 2008). Additionally, by leaving earlier, males can potentially arrive at foraging grounds when prey availability is higher (Dujon et al. 2014). However, further tracking of male sea turtles and in-water observations are needed to test these hypotheses.

4.4. Post-foraging migration

Since only a portion of the males present at a foraging site will travel to breeding sites each year, and the duration of tag transmission is limited, many publications that tracked male turtles at foraging sites did not reveal subsequent migration nor breeding behavior (Casale et al. 2013, Naro-Maciel et al. 2018). Despite these difficulties, the tracking of foraging males has provided insights into their behavior during migration (James et al. 2005b) and helped determine links to breeding areas. We found publications reporting the migration of males from foraging grounds to breeding areas for leatherbacks in both the Northwest Atlantic (James et al. 2005a) and Southwest Atlantic (López-Mendilaharsu et al. 2009), loggerheads in the Mediterranean (Schofield et al. 2010a, Casale et al. 2013) and Northeast Atlantic (Varo-Cruz et al. 2013), and green turtles in the Gulf of Mexico (Ashford et al. 2022) and east Australia (Webster et al. 2022). Male leatherbacks tagged on foraging areas off the Atlantic coast of Canada showed that they likely breed in various locations in the Caribbean Sea (James et al. 2005b), providing insight into the longstanding mystery of where leatherbacks mate. Male loggerheads tagged on the Tunisian shelf revealed the importance of this foraging area for the breeding population in Libya and identified a key migratory corridor along the North African coast (Casale et al. 2013). Nevertheless, such information on foraging ground–breeding area connectivity for males is missing for most sea turtle populations worldwide.

4.5. Vertical space use

Previous work indicates that only 3% of publications on vertical space use in sea turtles considered male turtles (Hochscheid 2014). Of the publications examined in this study, 23% (14 of 61 publications) explored vertical space use of males. Half of these (8 of 14 publications) focused on the dive behavior during migration (James et al. 2005b,c, 2006, López-Mendilaharsu et al. 2009, Fossette et al. 2010, Rider et al. 2024), breeding (James et al. 2005b), and foraging in leatherbacks (James et al. 2006, Doyle et al. 2008, Fossette et al. 2010, Dodge et al. 2014, Rider et al. 2024). These publications were primarily focused on the Northwest Atlantic (6 of 8 publications), with 2 in the Southwest Atlantic (Table S1). The other publications focused on loggerhead (3 of 14 publications), and green, olive ridley, and hawksbill turtles (each with 1 publication) (Table S1).

Vertical space use by male turtles varies by season (migration, breeding, and foraging), between night and day, and across individuals (James et al. 2005b,c, 2006, Arendt et al. 2012a, Dodge et al. 2014, Nivière et al. 2018). Some publications also indicated sex differences in vertical space use. In one study, male green turtles were found to have shorter dives during the mating season than those recorded by females during internesting, and at the end of the mating season, males conducted longer dives than females (Hays et al. 2001). It is suggested that these patterns maybe be attributed to males maintaining higher activity levels during the mating season to locate and mate with as many females as possible, and that at the end of the breeding season, they rest before migrating (Hays et al. 2001). These interpretations should be viewed with caution due to the small sample size (n = 2), highlighting the need for further studies to confirm these patterns. Male leatherback turtles have been found to make deeper dives when compared to female leatherbacks in the North Atlantic Ocean (Dodge et al. 2014). The variability found in the vertical space use by males may reflect several additional factors, including occupying areas characterized by differences in bathymetry, currents, temperatures, proximity to coastal areas, as well as seasonal stratification and resource availability (James et al. 2006, Dodge et al. 2014); therefore, further research and larger sample sizes are needed to unravel these effects.

We found that most studies on male sea turtles' vertical space use analyzed dive data from preprogrammed depth bins at set intervals (e.g. 4–6 h, 5–10 m depth), a common approach across demographics (e.g. Sale et al. 2006). Higher-resolution data can be obtained using time-depth recorders (TDRs) combined with other sensors (e.g. animal-borne video, accelerometer, magnetometer), allowing for analyses of vertical bottom movement, descent rate, and post-dive surfacing time (Hounslow et al. 2022, Migneault et al. 2023). While not specific to males, these tools offer deeper insights into behavior, locomotion, posture, and energetics (Hounslow et al. 2022). Thus, ideally, researchers should select tracking devices that best match the scale and objectives of their study.

4.6. Threats and conservation

Satellite tracking has been used to explore human impacts on sea turtles by determining exposure to different threats (e.g. fisheries, Hays et al. 2003) and identifying the impacts of these threats (Fuentes et

al. 2023). Satellite tracking, in combination with environmental parameters (e.g. sea surface temperature, ocean circulation variables), has further been used to understand habitat use patterns, which can provide insight into how turtles may be impacted by climate change (Hays & Hawkes 2018, Patrício et al. 2021, Fuentes et al. 2023). Ultimately, information on the spatial overlap of turtles with threats can help guide their conservation and inform management by identifying areas to protect and by determining whether current management efforts are suitable and effective (e.g. Fuentes et al. 2019, Santos et al. 2021). Given that spatial data is key for threat assessments, and to inform conservation planning, it is crucial that differences between the spatial distributions of males and females are identified. Despite the paucity of information, some publications have found that males and females use different areas across a region (Schofield et al. 2010a, 2013a, Nivière et al. 2018), indicating that to adequately identify sites to protect sea turtle populations, it is necessary to track both sexes.

A review by Jeffers & Godley (2016) indicates that conservation is a major focus for only a small number of publications that satellite-track sea turtles, with only a few documented examples where tracking data influenced conservation. Indeed, of the publications analyzed here, only 4 determined the exposure of male turtles to different threats (e.g. shipping, fishing, oil rigs, marine traffic) (Arendt et al. 2012a, Hart et al. 2015, Ashford et al. 2022, Pasanisi et al. 2022), and of these, just 2 publications (Arendt et al. 2012a, Ashford et al. 2022) focused solely on male sea turtles, and no publication compared how males and females are exposed to different threats in the same region. Such information would be valuable to calculate mortality rates for different sexes and improve population models. Similarly, more insights into whether survival rates differ for immature turtles of different sexes could be obtained with accurate sexing of tracked immature turtles. While advancements in tag-size reduction and improved capture methods have enabled tracking of immature turtles (Hays & Hawkes 2018), including head-started post-hatchlings (e.g. Mansfield et al. 2014), sex is often unreported for these younger individuals, as it typically relies on invasive techniques such as laparoscopy or blood samples (Wyneken et al. 2007, Tezak et al. 2020).

Satellite tracking data from male turtles has been used to determine how foraging and breeding areas overlap with protected areas (Schofield et al. 2010b, 2013a, Naro-Maciel et al. 2018, Pilcher et al. 2021, Abalo-Morla et al. 2022, Ashford et al. 2022) and to provide further suggestions for selecting areas to protect (Schofield et al. 2013a,b). Similarly, Shimada et al. (2017) determined the degree to which the 'Go Slow Zones' in Moreton Bay, Australia, provide protection to sea turtles, and the potential for improvement of current management initiatives. Publications often neglect to indicate what areas are critical to specifically protect males or do not investigate whether the design of marine protected areas (MPAs) should differ according to the sex of individuals being considered. Targeted protection of male turtles may become important if there is a reduction of males being produced, as projected with changes in climate (Patrício et al. 2021). Thus, identification of areas utilized by males, their exposure to threats, and level of protection may become key as climate change progresses.

4.7. Knowledge gaps and future directions

Although the existing literature offers valuable insights into male spatial ecology as described here, research on male sea turtles remains less comprehensive compared to females. To combat this knowledge bias, future studies should focus on species (e.g. flatback, Kemp's ridley, and olive ridley turtles) and regions (e.g. Indian and Pacific Oceans) that are underrepresented in tracking publications for both sexes — as indicated in this study and by others (Godley et al. 2008, Robinson et al. 2023). Future work should also aim to address the less-explored research topics identified here (e.g. breeding patterns), while prioritizing the translation and integration of data into conservation and management initiatives. We identified several cases where the methods used to determine sex or the seasonal life phase of tracked turtles were not reported. Additionally, differences in analytical approaches often made certain estimated parameters (e.g. home ranges) difficult to compare. To improve comparability, we emphasize the need for standardization in data collection, reporting, storage, and terminology (e.g. key terms as 'fidelity' and 'residency' were used interchangeably across studies). This will ensure studies are comparable and replicable, and that data can be combined to address more complex research questions and augment sampling size. Given the scarcity of male sea turtle tracking data, efforts should ensure tracks are accessible in centralized databases (e.g. OBIS, Seamap, Movebank) to facilitate data sharing, prevent duplication, and advance research (Grémillet et al. 2022). Additionally, capacity building in data analysis is crucial, which can be supported by sharing workflows and scripts among researchers.

5. FINAL REMARKS

Several notable differences between the behaviors of males and females were highlighted in our review. One key distinction is the relatively common occurrence of males remaining resident year-round, a behavior rarely observed in females. When males do migrate, they typically cover shorter distances than females. Males also tend to arrive earlier at foraging grounds after the breeding season, potentially giving them access to more resources when competition is reduced. Competition at foraging sites may drive sex-specific migratory patterns, with males securing closer sites and pushing females to travel farther — an aspect that remains relatively unexplored. In the case of temperate zone-foraging leatherbacks, males may reach more distant, seasonally available areas, than females — which stay longer at breeding areas. Differences in dive activity and profile of males and females was also observed by some studies, but require further investigation (e.g. using accelerometers, Hounslow et al. 2022) to determine if patterns are similar across species and populations. It is widely accepted that males experience lower energetic costs during the reproductive period, which may allow them greater flexibility in their migratory and foraging strategies. Consequently, behavioral plasticity may be common both between and within populations. This may involve staying in areas with variable food resources or exploring new foraging grounds.

Even though sex-based differences in the spatial ecology of sea turtles have frequently been found, 69% of publications (42 of 61 publications) reviewed here tracked male turtles concurrently to females, and of those publications, 67% compared the data obtained from both sexes, with 33% presenting the results from males and females together or not discussing any results from males. This highlights the need not only for more studies that explore the spatial ecology of male turtles but also for more comparative studies between the sexes. The fact that the tracking of male turtles is not increasing in line with what is seen for sea turtles in general may be due to adult males being captured and tagged opportunistically, particularly at foraging grounds, and the difficulties inherent in properly identifying non-mature males. The latter also biases our current knowledge of adult males, with only 10 studies identified as having tracked immature turtles identified as males (Table S1). Biases may also reflect the fact that typically, female turtles are more prevalent at foraging areas and easier to access at nesting grounds (Jensen et al. 2018). Ultimately, the scarcity of information on males restricts our ability to make robust, generalized conclusions, leaving several knowledge gaps, as highlighted in this review. Despite these challenges, it is encouraging to see a wider array of publications focusing on male sea turtles. Future research that addresses these gaps will undoubtedly provide crucial insights for more targeted conservation and management efforts, particularly in understanding how males and females differ in their spatial distributions.

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Appendix.

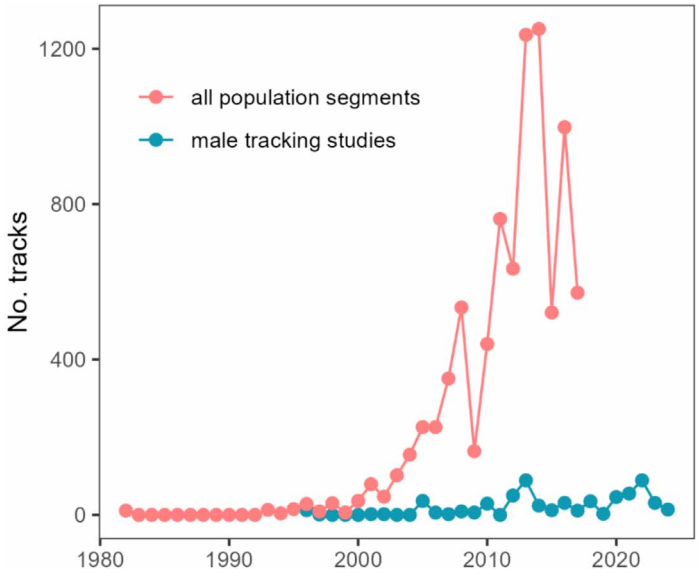

Fig. A1. Annual number of satellite tracks appearing in publications analyzing sea turtle tracking data for all population segments from Hays & Hawkes (2018) (red) and for males (current study) (blue)

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