Newly Discovered migratory corridor and foraging ground for Atlantic green turtles, *Chelonia mydas*, nesting on Bioko Island, Equatorial Guinea

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Abstract

This study is the first to use satellite telemetry to track post-nesting movements of endangered green turtles (*Chelonia mydas*) in the Gulf of Guinea. Satellite transmitters were attached in 2018 to six Atlantic green turtles nesting on Bioko Island, Equatorial Guinea, to track their post-nesting movements and locate their foraging grounds. Track lengths of 20-198 days were analyzed, for a total of 536 movement days for the six turtles. Migratory pathways and foraging grounds were identified by applying a switching state space model to locational data, which provides daily position estimates to identify shifts between migrating and foraging behavior. Turtles exhibited a combination of coastal and oceanic migrations pathways that ranged from 957 km to 1,131 km. Of the six turtles, five completed their migration and maintained residency at the same foraging ground near the coastal waters of Accra, Ghana until transmission was lost. These five resident turtles inhabit heavily fished and polluted waters and are vulnerable to a variety of anthropogenic threats. The identification of these foraging grounds highlights the importance of these coastal waters for the protection of the endangered Atlantic green turtle.

Introduction

After entering the ocean as hatchlings, sea turtles spend the majority of their lives in the water, only emerging to lay eggs and or in some cases to bask [1] [2] [3]. Because of this, research on sea turtles has been largely restricted to nesting females, which has led to conservation efforts primarily focused on nesting beaches, rather than in-water habitat. Since in water habitats come with a variety of unique threats, including resource mining, fishing, and anthropogenic pollution, understanding oceanic habitat use and migration patterns is imperative to designing effective marine conservation strategies [4][5],[6],[7]. For example, endangered leatherback turtle populations in South Africa as well as Gabon have been unable to recover without in-water habitat protection, despite protection at nesting beaches, in
part because of intensive long-line fishery operations off the coast of both countries with high rates of
turtle bycatch [8],[9].

In West Africa, the Gulf of Guinea has experienced an increase in anthropogenic disturbances,
putting the turtle population at risk from many threats including ship traffic, pollution, commercial and
small-scale fishing operations [33], [5], and oil and gas development [7], [34]. Marine and coastal
pollution in the waters of the Gulf of Guinea has caused a host of environmental threats, including oxygen
depletion, faunal die-offs, and heavy metal and hydrocarbon accumulation in marine consumers [6], [35].

While sea turtles are protected under international and national law in most West African nations,
incidental bycatch in fisheries operations is a major threat in the Gulf of Guinea. Green turtles are
common bycatch in both gillnet and pelagic longline fishing operations [36], [37], [5]. Oil and gas
development has also rapidly intensified in the Gulf of Guinea in recent years [34], and poses diverse, but
difficult to measure, threats to sea turtle populations, with an increase in channel dredging, ship traffic, oil
leaks, and chemical pollution, which can affect adult turtles that forage or travel close to offshore
platforms [7]. These threats highlight the need to study migration patterns and foraging ground locations
of sea turtles to better understand their vulnerabilities.

Adult green sea turtles have been known to migrate hundreds to thousands of kilometers between
nesting seasons [38], [39], [40]. Generally post-nesting migrations are direct movements to foraging
habitats, and turtles spend little energy on detours [41]; however, a number of studies have shown that in
some cases individuals take indirect routes, including both open ocean and coastal pathways [42]. At
foraging grounds green turtles generally maintain localized, near shore home ranges near sea grass beds
[43], [44], [23]. Green turtles feed primarily on sea grass and other shallow water plant material; as such,
there is limited food in the open ocean and direct migration to foraging grounds is thought to be
advantageous by minimizing migration time and energy expenditure [45]. Just as green turtles show
fidelity to nesting beaches [46], they also show fidelity to foraging grounds and post-nesting migratory
routes are the same year after year [20]. Consequently, protecting migratory corridors and foraging grounds could have huge benefits for populations [40].

Little is known about the in-water movements and behavior of green turtles in the Gulf of Guinea. Green turtles that were flipper tagged on Bioko Island, Equatorial Guinea, in 1996-1998 have been recaptured in waters off the coast of Ghana, at least 1250 km from the nesting beaches of Bioko, in Corisco Bay, Gabon, about 280 km from Bioko, and off the coast of southern Gabon, at least 760 km from Bioko [47]. Since then, there have been no studies on post-nesting migration routes of green turtles from Bioko, and only one in the Gulf of Guinea, in which satellite telemetry was used to track green turtles nesting in Guinea-Bissau to their foraging ground off the coast of Mauritania [48].

To address the lack of knowledge on the post-nesting migratory routes of Atlantic green turtles in the Gulf of Guinea, we used satellite telemetry to track turtles from a nesting beach along the southern coast of Bioko Island, the second largest nesting rookery for green turtles within the Gulf [49], [50], [51]. Our specific objectives were to (1) map the post-nesting migration routes of green turtles from Bioko Island, (2) determine the directness of migratory routes and identify migratory corridors in the area, (3) categorize these migratory routes as coastal, open ocean, or both, and (4) locate coastal foraging grounds.

**Materials and methods**

**Ethics Statement**

This study was carried out in accordance with all federal, international, and institutional guidelines. All data was collected under the protocol approved by the Purdue Animal Care and Use Committee (PACUC Protocol Number 1410001142). Permissions to work within the protected area and with the study species were granted by the Instituto Nacional de Desarrollo Forestal y Gestión del Sistema de Áreas Protegidas (INDEFOR-AP permit #227), and the research protocol was approved by the Universidad Nacional de Guinea Ecuatorial (UNGE permit number 1011191091017).
Study site

Bioko Island, Equatorial Guinea (2027 km²) is situated 175 km Northeast of mainland Equatorial Guinea. The southern coast has approximately 20 km of black sand beaches suitable for sea turtle nesting, all of which are within the legally protected Gran Caldera and Southern Highlands Scientific Reserve (Fig. 1). The remainder of Bioko’s 150 km coastline is generally unsuitable for sea turtle nesting due to cliffs, rocky beaches, and proximity to villages and roads [49]. Four species of sea turtles (leatherback, *Dermochelys coriacea*; green, *Chelonia mydas*; olive ridley, *Lepidochelys olivacea* and, hawksbill, *Eretmochelys imbricata*) nest across the five nesting beaches (8°66’-8°46’ E and 3°22’-3°27’ N), with the largest numbers of green turtle nests on beaches A, B, and C [51]. This study was conducted on Beach C, chosen for its accessibility and high densities of green turtles (Fig. 1).

Figure 1: Map of the sea turtle nesting beaches on Bioko Island, Equatorial Guinea. Insert shows the five beaches (A-E) in relation to the nearest village, Ureca. Satellite transmitters were attached to green turtles nesting on Beach C, at the end of the nesting season in January-February 2018.

Turtle Selection

Nesting season for green turtles on Bioko spans October through February [49]. Satellite transmitters were attached at the end of the nesting season, in order to focus on tracking post-nesting migration and locational data from foraging grounds. Turtles that had laid their last nest, and therefore did not have developing vitellogenic follicles when scanned with a portable ultrasound (SonoSite 180 Plus; FUJIFILM SonoSite, Bothell, WA, USA), were preferentially selected as this generally indicates that the turtle is about to begin the post-nesting migration [13]. In addition, only turtles that had finished nesting and seemed to be in good health without any scarring or damage to the carapace where the transmitter...
would be attached were selected. Individuals were identified using a unique injectable passive integrated
transponder (PIT) tag (AVID Identification Systems Inc., Norco, CA).

**Satellite transmitters**

In January and February, 2018, six satellite transmitters (SirTrack, Kiwisat 202; Sirtrack, Havelock North, New Zealand) were attached to green turtles on Beach C, Bioko Island, after they had finished nesting. The transmitters were attached following the methods developed by Balazs et al. [52] modified by Luschi et al. [38], Troeng et al. [53], and Seminoff et al. [32]. Specifically, the carapace was cleaned, first with water, then with alcohol, and then scored with sandpaper to increase the strength of attachment. Transmitters were attached using Powers Pure50+ Two-Component Epoxy Adhesive (Powers, Brewster, NY, USA) to secure each transmitter to the second central scute of the carapace. Each turtle was restrained by a team of four or five researchers, and a wet cloth placed over the turtle’s eyes, to keep each turtle calm and in place while the epoxy hardened.

**Movement analysis**

Location data was relayed via the Argos satellite system, and location points were filtered using the “argosfilter” package for R (R statistical software, R 3.4.3, Vienna, Austria), which removed any point that required a travel speed >5 km/hr [38]. The filtered location data was fit with a state-space model using the ‘bsam’ package [54] for R to estimate the behavioral state of the turtles. Filtered locational data was used instead of raw data to enhance the accuracy of the state space model [55]. The ‘bsam’ package, based on the Bayesian switching state space model developed by Jonsen et al. [56] was applied to the turtle tracks, using a hierarchical switching first-difference correlated random walk model (hDCRWS). The model was fit with a total of 5,000 Markov Chain Monte Carlo (MCMC) samples after 5,000 were discarded as burn-in, and every 10<sup>th</sup> sample was retained. This model returns a behavioral
mode of 1 (MCMC mean values <1.5) or 2 (values >1.5). Behavioral mode 1 is considered transiting
behavior, and behavioral mode 2 is considered area restricted search (foraging) behavior.
Individual tracks were then mapped using ArcGIS 10.2 (Esri, Redlands, CA). Track length and daily
travel distance were calculated using R from total track distance. Tracks were overlaid with ocean current
data from the Ocean Surface Current Analysis Real-Time (OSCAR) from NASA [57].

Results

All turtles (n=6) migrated west from the nesting beach. Tracks were analyzed for a total of 536
days. Average daily distance traveled was 49.5km, and the average total distance traveled for the five
turtles that completed migrations was 1,055km. Two turtles exhibited oceanic migration routes and
remained in transit across the Bight of Benin until reaching the coast of Togo and Ghana, where the state
space model indicated a switch to foraging behavior (Fig. 2).

Figure 2. Post-nesting movements of six green turtles (Chelonia mydas) tracked from Bioko Island,
after the 2017-18 nesting season. Individuals traveled an average of >1,000km using a combination of
oceanic and coastal migratory routes. Two turtles exhibited oceanic migration routes (blue and dark green
tracks); two turtles remained closer to the continental shelf (light green and purple tracks); two turtles
migrated more directly across the Bight of Benin, to the coastal waters near Lagos, Nigeria, and then
maintained a coastal route (yellow and red tracks).

These two turtles migrated for an average of 15 days and 989 km. The remaining four turtles used
a combination of coastal and oceanic migratory routes, remaining closer to the continental shelf, a path
that took an average of 23 days and 1098 km. Two of these turtles remained closer to the continental
shelf, while two migrated more directly across the Bight of Benin, to the coastal waters near Lagos,
Nigeria, and then maintained a coastal route (Fig. 2). Both oceanic and coastal migration routes remained
in areas of weak currents for the duration of migrations (Fig. 3).
Figure 3. Ocean currents and daily locations (circles) of two green turtles tracked by satellite from Bioko Island across the Bight of Benin. A coastal and an oceanic migration route are overlaid onto ocean current data for the 5 day period from 15-20 Feb 2018. Green circles represent migrating behavior and red circles represent foraging behavior identified by the state-space model. Arrows represent current direction.

One turtle (Fig. 2: purple track) exhibited coastal migration and was in transit for 19 days until reaching the coastal waters of Lagos, Nigeria. Beginning on day 20, February 20th, all location transmissions were from land, in the Amuwo Odofin suburb of Lagos. Behavioral estimates provided by the state space model indicate that this turtle was still transiting, rather than foraging, when the transmissions from land began. As this turtle had no vitellogenic follicles remaining, there is no evidence that the turtle would have intentionally returned to land, and it is suspected that there was some human interaction that led to the transmitter being moved to land.

All five turtles ultimately began extended periods (>30 days) of residency and foraging behavior off the coast of Ghana, in a 50 km stretch east of Accra and west of the Volta River delta, after migration periods of 14-28 days (Fig. 4). Three turtles exhibited migrations interspersed with short (<3 days) periods of foraging off the coasts of Lagos, Nigeria, and Togo and Benin (Fig. 4). While the turtles exhibited both oceanic and coastal migrating behaviors, all exhibited near-shore foraging activity.

Figure 4. Daily locations (circles) of six turtles tracked from Bioko Island after the 2017-18 nesting season. Blue circles indicate transiting behavior and red circles indicate foraging behavior, as identified by the state space model. Three turtles exhibited migrations interspersed with short (<3 days) periods of foraging, while two exhibit direct migrations, followed by an extended period of foraging.

Discussion

All six turtles migrated westward from Bioko Island, and five turtles completed their migration, ending at a previously undocumented foraging ground in the coastal waters of Ghana (Fig. 1). Previous
recapture data suggested that some green turtles travel towards Ghana after nesting on Bioko, however the exact location of a foraging ground in the area was previously unknown [47].

Turtles exhibited both oceanic and coastal migration strategies, with two turtles traveling along a shorter route over deeper water (2000-3000m), and four traveling through shallower coastal waters (Fig. 1). Variations in migratory routes have been previously observed in green turtles nesting in Tortuguero, Costa Rica, as well as in the Galapagos [53], [32]. It has been hypothesized that these variations in migratory strategies may be linked to nutrient levels in post-nesting turtles, with more nutrient-depleted turtles taking the most direct route to a foraging ground, while turtle with higher nutrient levels may take a longer route [32].

Long distance migration is associated with high energy cost and all five complete migrations in this study were over 1,000 km. Turtles that used coastal migration routes exhibited short periods of foraging on the way to their final foraging ground (Fig. 2). Browsing behavior may decrease the overall energy cost of migration, and passing through suitable foraging habitat may be a benefit to a coastal migration pattern, mitigating the longer distance of coastal migratory routes. This behavioral plasticity has been documented in green turtles in the Caribbean and the coastal waters of Taiwan, in which turtles opportunistically utilized food sources that are available close to migratory routes [53], [42]. Similarly, turtles migrating from Bioko spent little time in areas that may have suitable foraging habitat, briefly foraging when advantageous and then continuing to a more distant foraging habitat, suggesting fidelity to a specific foraging ground. This could indicate that these stop over foraging habitats closer to Bioko cannot support sustained foraging of large numbers of turtles. It has also been reported that previously suitable coastal foraging habitat between Ghana and Nigeria has been compromised due to coastal erosion caused by sand mining and the development of harbors [33], which may necessitate longer migrations to more suitable habitat.

Green turtles often show fidelity to habitats, both nesting and foraging [46], [20]. Favoring specific foraging grounds, despite greater distances, may occur because of proximity to overwintering
locations, resource limitations, territorial defense, or long-term fidelity to foraging grounds selected due to juvenile dispersal patterns [20]. However, foraging ground selection among these turtles cannot be explained by oceanic conditions, as both coastal and oceanic migration paths were against prevailing currents (Fig. 3). Given the low speeds of the currents, it is unlikely that countercurrent migrations greatly increased energy cost in this case.

Given the existence of nesting populations of green turtles on the beaches nearby this foraging ground in Ghana, and the apparent habitat suitability, it is likely that this foraging ground is used by multiple rookeries within the East Atlantic, including those nesting on Bioko Island [33], [58]. Furthermore, genetic studies have shown that green turtles that nest on Bioko Island share haplotypes with turtles found nesting in Ascension Island, Sao Tome, Principe, Corisco Bay, and Poilao [58]. Genetic similarities between populations suggests there are multiple populations using the same foraging and breeding grounds as those that nest on Bioko Island [58].

The discovery of this foraging ground is of particular importance, as only one other foraging ground used by green turtles in the Gulf of Guinea has been documented and protected-- Corisco Bay in Equatorial Guinea and Gabon. Yet all five turtles that completed migrations maintained residency in this newly discovered Ghanaian foraging habitat, highlighting the need for protection of this area. Migration routes passed through the exclusive economic zones (EEZs) of five countries, all of which rely heavily on fisheries for economic activity, which poses challenges to regulation and protection of this area. Only one of these countries has a marine protected area (MPA), and it lies well outside the migration corridor used by these turtles (Equatorial Guinea designated Corisco Bay as an MPA). Migrations passed through no MPAs, meaning throughout the migration pathways and within foraging grounds fishing is unrestricted. Studies have shown that green turtles in the Gulf of Guinea are caught as bycatch in both artisanal and industrial fisheries, in gillnets, driftnets, and purse and beach seines [59]. Although the extent of bycatch is difficult to quantify, it is suspected that mortality is significant, and is frequently underestimated by studies [60]. One of the six turtles involved in this study had a suspected interaction with humans after
only 20 days of migrating, resulting in the transmitter being brought to land. While there is no way of knowing the nature of the interaction, turtles are consistently caught as bycatch in artisanal fishery operations in the area, and there is evidence that once caught, turtles are often transported to land and sold in markets [60].

Furthermore, this Ghanaian foraging ground lies near the outlet of a river that flows past the Kpone power plant as well as the Sakumo Lagoon, an important protected wetland heavily polluted by the inflow of industrial effluent, sewage, and domestic waste [61]. The Sakumo Lagoon has also been shown to have higher than average levels of Cadmium, Cobalt, Copper, Chromium, Nitrogen, and Zinc, which can have toxic effects on marine and aquatic wildlife [61].

**Conclusion**

These threats highlight the need for further research into effects of fishing and pollution on this population, as well as the need to protect this valuable foraging habitat. Both industrial and domestic pollution as well as extensive commercial fishing are important issues when considering the protection of this newly discovered foraging ground. The distinct coastal foraging behavior of green turtles lends itself well to protection by spatially-explicit management strategies, such as zonal regulation of fishing and industrial dumping. Protecting nesting beaches in combination with delineating and protecting coastal foraging habitat on a national and multinational level may be key in conserving this highly migratory endangered species.
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References

1. Lutz PL, Musick JW. The Biology of Sea Turtles Vol II [Internet]. Vol. 2, Mar Biol. 2002 [cited 2018 Oct 4]. 510 p. Available from: https://books.google.com/books?hl=en&lr=&id=9H_LBQAAQBAJ&oi=fnd&pg=PP1&dq=Lutz,+P.L.,+Musick,+J.A.+and+Wyneken,+J.+eds.,+2002.+The+biology+of+sea+turtles+(Vol.+2)+.+CRC+press.&ots=mdXEQUjGl&sig=4GfbefM_YA_Ito8GLNs72jpKUY

2. Maxwell SM, Jeglinski JWE, Trillmich F, Costa DP, Raimondi PT. The Influence of Weather and Tides on the Land Basking Behavior of Green Sea Turtles (Chelonia mydas) in the Galapagos Islands. Chelonian Conserv Biol [Internet]. 2014 [cited 2018 Oct 4];13(2):247–51. Available from: http://www.chelonianjournals.org/doi/abs/10.2744/CCB-1069.1

3. Van Houtan KS, Halley JM, Marks W. Terrestrial basking sea turtles are responding to spatio-temporal sea surface temperature patterns. Biol Lett [Internet]. 2015 [cited 2018 Oct 4];11(1). Available from: http://rsbl.royalsocietypublishing.org/content/11/1/20140744.abstract

4. Hamann M, Godfrey M, Seminoff J, Arthur K, Barata PCR, Bjorndal KA, et al. Global research priorities for sea turtles: informing management and conservation in the 21st century. Endanger Species Res [Internet]. 2010 [cited 2018 Oct 4];11:245–69. Available from: https://www.int-res.com/abstracts/esr/v11/n3/p245-269/

5. Tanner C. Sea Turtle Bycatch off the Western Region of the Ghanaian Coast. Mar Turt Newsl [Internet]. 2014 [cited 2018 Oct 22];(140):8–11. Available from: https://www.researchgate.net/profile/Claire_Tanner2/publication/293481488_Sea_Turtle_Bycatch_off_the_Western_Region_of_the_Ghanaian_Coast_Tanner_Claire_2014_Marine_Turtle_Newsletter_140_8-11/links/56b89bb108ae3c1b79b2e1a1.pdf

6. Mahu Edem; Nyarko EHSCKH. Distribution and enrichment of trace metals in marine sediments from the Eastern Equatorial Atlantic, off the Coast of Ghana in the Gulf of Guinea.
7. Witherington B, Pendooley K, Hearn GW, Honarvar S. Ancient mariners, ancient fuels: how sea turtles cope with our modern fossil fuel dependency. SWOT Report. 2009; 4.

8. Witt M, Broderick A, Coyne M, Formia A. Satellite tracking highlights difficulties in the design of effective protected areas for … Oryx [Internet]. 2008 [cited 2018 Oct 4]; Available from: https://www.cambridge.org/core/journals/oryx/article/satellite-tracking-highlights-difficulties-in-the-design-of-effective-protected-areas-for-critically-endangered-leatherback-turtles-dermochelys-coriacea-during-the-internesting-period/FAFBD27EEDA6F47A90FB49B572DF94A

9. Petersen SL, Honig MB, Ryan PG, Nel R, Underhill LG. Turtle bycatch in the pelagic longline fishery off southern Africa. African J Mar Sci [Internet]. 2009 Apr [cited 2018 Oct 4];31(1):87–96. Available from: http://www.tandfonline.com/doi/abs/10.2989/AJMS.2009.31.1.8.779

10. Godley BJ, Broderick AC, Glen F, Hays GC. Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking. J Exp Mar Bio Ecol [Internet]. 2003 [cited 2018 Oct 4];287(1):119–34. Available from: https://www.sciencedirect.com/science/article/pii/S0022098102005476

11. Shaver DJ, Rubio C. Post-nesting movement of wild and head-started Kemp’s ridley sea turtles Lepidochelys kempii in the Gulf of Mexico. int-res.com [Internet]. 2008 [cited 2018 Oct 4];4(January):43–55. Available from: https://www.int-res.com/abstracts/esr/v4/n1-2/p43-55/

12. Maxwell SM, Breed GA, Nickel BA, Makanga-Bahouna J, Pemo-Makaya E, Parnell RJ, et al. Using satellite tracking to optimize protection of long-lived marine species: Olive ridley sea turtle conservation in central Africa. Ropert-Coudert Y, editor. PLoS One [Internet]. 2011 May 11 [cited 2018 Oct 4];6(5):e19905. Available from: http://dx.plos.org/10.1371/journal.pone.0019905

13. Blanco GS, Morreale SJ, Bailey H, Seminoff JA, Paladino F V., Spotila JR. Post-nesting movements and feeding grounds of a resident East Pacific green turtle Chelonia mydas population from Costa Rica. Endanger Species Res [Internet]. 2012 [cited 2018 Oct 4];18(3):233–45. Available from: https://www.int-res.com/articles/esr/v18/n3/p233-245/

14. Troëng S, Dutton PH, Evans D. Migration of hawksbill turtles Eretmochelys imbricata from Tortuguero, Costa Rica. Ecography (Cop) [Internet]. 2005 Jun [cited 2018 Oct 4];28(3):394–402. Available from: http://doi.wiley.com/10.1111/j.0906-7590.2005.04110.x

15. Whittock PA, Pendooley KL, Hamann M. Inter-nesting distribution of flatback turtles Natator depressus and industrial development in Western Australia. Endanger Species Res [Internet]. 2014 [cited 2018 Oct 4];26(1):25–38. Available from: https://www.int-res.com/articles/esr/v26/n1/p25-38/

16. Robinson NJ, Morreale SJ, Nel R, Paladino F V. Coastal leatherback turtles reveal conservation hotspot. Sci Rep [Internet]. 2016 [cited 2018 Oct 4];6. Available from: https://www.nature.com/articles/srep37851

17. Hughes G, Luschi P, Mencacci R. Marine FP-J of E, 1998 undefined. The 7000-km oceanic journey of a leatherback turtle tracked by satellite. Elsevier [Internet]. [cited 2018 Oct 4]; Available from: https://www.sciencedirect.com/science/article/pii/S0022098198000525

18. Nichols W, Resendiz A, … JS-B of M, 2000 undefined. Transpacific migration of a loggerhead turtle monitored by satellite telemetry. ingentaconnect.com [Internet]. [cited 2018 Oct 4]; Available from:
19. Morreale SJ, Standora EA, Spotila JR, Paladino F V. Migration corridor for sea turtles. Nature [Internet]. 1996 [cited 2018 Oct 4];384(28):p319-320. Available from: https://www.nature.com/articles/384319a0

20. Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ. Fidelity and over-wintering of sea turtles. Proc R Soc B Biol Sci [Internet]. 2007 [cited 2018 Oct 4];274(1617):1533–8. Available from: http://rspb.royalsocietypublishing.org/content/274/1617/1533.short

21. Hochscheid S, Bentivegna F, Bradai MN, Hays GC. Overwintering behaviour in sea turtles: Dormancy is optional. Mar Ecol Prog Ser [Internet]. 2007 [cited 2018 Oct 4];340:287–98. Available from: https://www.int-res.com/abstracts/meps/v340/p287-298/

22. Makowski C, Seminoff JA, Salmon M. Home range and habitat use of juvenile Atlantic green turtles (Chelonia mydas L.) on shallow reef habitats in Palm Beach, Florida, USA. Mar Biol [Internet]. 2006 Mar 11 [cited 2018 Oct 4];148(5):1167–79. Available from: http://link.springer.com/10.1007/s00227-005-0150-y

23. Hart KM, Fujisaki I. Satellite tracking reveals habitat use by juvenile green sea turtles Chelonia mydas in the Everglades, Florida, USA. Endanger Species Res [Internet]. 2010 [cited 2018 Oct 4];11(3):221–32. Available from: https://www.int-res.com/abstracts/esr/v11/n3/p221-232/

24. Jonsen ID, Myers RA, James MC. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Mar Ecol Prog Ser [Internet]. 2007 [cited 2018 Oct 4];337:255–64. Available from: https://www.int-res.com/abstracts/meps/v337/p255-264/

25. Shimada T, Limpus C, Jones R, Hazel J, Groom R, Hamann M. Sea turtles return home after intentional displacement from coastal foraging areas. Mar Biol [Internet]. 2016 [cited 2018 Oct 4];163(1):1–14. Available from: https://link.springer.com/article/10.1007/s00227-015-2771-0

26. Hays GC, Broderick AC, Godley BJ, Luschi P, Nichols WJ. Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. Mar Ecol Prog Ser [Internet]. 2003 [cited 2018 Oct 12];262:305–9. Available from: https://www.int-res.com/abstracts/meps/v262/p305-309/

27. Dobbs K, Fernandes L, Slegers S, … BJ-PC, 2007 undefined. Incorporating marine turtle habitats into the marine protected area design for the Great Barrier Reef Marine Park, Queensland, Australia. CSIRO [Internet]. [cited 2018 Oct 12]; Available from: http://www.publish.csiro.au/PC/PC070293

28. Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB, Ehrhart LM, Limpus CJ, et al. Encouraging outlook for recovery of a once severely exploited marine mega-herbivore. Glob Ecol Biogeogr [Internet]. 2008 Mar [cited 2018 Oct 12];17(2):297–304. Available from: http://doi.wiley.com/10.1111/j.1466-8238.2007.00367.x

29. Christianen MJ a, Herman PMJ, Bouma TJ, Lamers LPM, Van MM, Heide T Van Der, et al. Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. Proc R Soc [Internet]. 2014 [cited 2018 Oct 12];281. Available from: http://rspb.royalsocietypublishing.org/content/281/1777/20132890.short

30. Hart CE, Blanco GS, Coyne MS, Delgado-Trejo C, Godley BJ, Todd Jones T, et al. Multinational tagging efforts illustrate regional scale of distribution and threats for east pacific green turtles (Chelonia mydas agassizii). Reina R, editor. PLoS One [Internet]. 2015
31. Shimada T, Limpus C, Jones R, Hamann M. Aligning habitat use with management zoning to reduce vessel strike of sea turtles. Ocean Coast Manag [Internet]. 2017 [cited 2018 Oct 12];142:163–72. Available from: https://www.sciencedirect.com/science/article/pii/S0964569116303957

32. Seminoff JA, Zarate P, Coyne M, Foley DG, Parker D, Lyon BN, et al. Post-nesting migrations of Galapagos green turtles Chelonia mydas in relation to oceanographic conditions: Integrating satellite telemetry with remotely sensed ocean data. Endanger Species Res [Internet]. 2008 [cited 2018 Oct 12];4(1–2):57–72. Available from: https://www.int-res.com/abstracts/esr/v4/n1-2/p57-72/

33. Formia A, Tiwari M, Fretey J, Billes A. Sea turtle conservation along the Atlantic coast of Africa. Mar Turt Newsl [Internet]. 2003 [cited 2018 Oct 22];(100):33–7. Available from: http://www.seaturtle.org/mtn/archives/mtn100/mtn100p33.shtml

34. Brownfield M, Charpentier R, Schenk C, Klett T. Assessment of undiscovered oil and gas resources of the West African Costal Province, West Africa. 2011 [cited 2018 Oct 22]; Available from: https://pubs.er.usgs.gov/publication/fs20113034

35. Scheren PA, Ibe AC, Janssen FJ, Lemmens AM. Environmental pollution in the Gulf of Guinea – a regional approach. Marine Pollution Bulletin [Internet]. 2002 [cited 2018 Oct 22];44(7):633–41. Available from: https://www.sciencedirect.com/science/article/pii/S0025326X01003058

36. Carranza A, Domingo A, Estrades A. Pelagic longlines: A threat to sea turtles in the Equatorial Eastern Atlantic. Biological Conservation [Internet]. 2006 [cited 2018 Oct 22];131(1):52–7. Available from: https://www.sciencedirect.com/science/article/pii/S0006320706000565

37. Wallace BP, Lewison RL, Mcdonald SL, Mcdonald RK, Kot CY, Kelez S, et al. Global patterns of marine turtle bycatch [Internet]. Vol. 3, Conservation Letters. 2010 [cited 2018 Oct 22]. p. 131–42. Available from: http://doi.wiley.com/10.1111/j.1755-263X.2010.00105.x

38. Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. Proceedings of the Royal Society of London B: Biological Sciences. 1998 Dec 7;265(1412):2279-84. 1. [cited 2018 Oct 22]; Available from: http://rspb.royalsocietypublishing.org/content/265/1412/2279.short

39. Benson SR, Dutton PH, Hitipeuw C, Samber B, Bakarbessy J, Parker D. Post-Nesting Migrations of Leatherback Turtles ( Dermochelys coriacea ) from Post-Nesting Migrations of Leatherback. Chelonian Conserv Biol [Internet]. 2007 [cited 2018 Oct 22];6(1):150–4. Available from: http://www.chelonianjournals.org/doi/abs/10.2744/1071-8443(2007)6[150:PMOLTID]2.0.CO;2

40. Stokes KL, Broderick AC, Canbolat AF, Candan O, Fuller WJ, Glen F, et al. Migratory corridors and foraging hotspots: critical habitats identified for Mediterranean green turtles. Richardson D, editor. Divers Distrib [Internet]. 2015 Jun [cited 2018 Oct 22];21(6):665–74. Available from: http://doi.wiley.com/10.1111/ddi.12317

41. Hays G, Broderick A, Godley B, Lovell P, Behaviour CM-A, 2002 U. Biphasal long-distance migration in green turtles. Elsevier [Internet]. [cited 2018 Oct 22]; Available from: https://www.sciencedirect.com/science/article/pii/S0003347202919755

42. Cheng IJ. Post-nesting migrations of green turtles (Chelonia mydas) at Wan-An Island, Penghu Archipelago, Taiwan. Mar Biol [Internet]. 2000 Nov 15 [cited 2018 Oct 22];137(4):747–54. Available from: http://link.springer.com/10.1007/s002270000375
43. Christiansen F, Esteban N, Mortimer JA, Dujon AM, Hays GC. Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. Mar Biol [Internet]. 2017 Jan 29 [cited 2018 Oct 22];164(1):10. Available from: http://link.springer.com/10.1007/s00227-016-3048-y

44. Levy Y, Keren T, Leader N, Weil G, Tchernov D, Rilov G. Spatiotemporal hotspots of habitat use by loggerhead (Caretta caretta) and green (Chelonia mydas) sea turtles in the Levant basin as tools for conservation. Mar Ecol Prog Ser [Internet]. 2017 [cited 2018 Oct 22];575:165–79. Available from: https://www.int-res.com/abstracts/meps/v575/p165-179/

45. Godley BJ, Richardson S, Broderick AC, Coyne MS, Glen F, Hays GC. Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecography (Cop) [Internet]. 2002 Jun [cited 2018 Oct 22];25(3):352–62. Available from: http://doi.wiley.com/10.1034/j.1600-0587.2002.250312.x

46. Bowen BW, Meylan AB, Ross JP, Limpus CJ, Balazs GH, Avise JC. GLOBAL POPULATION STRUCTURE AND NATURAL HISTORY OF THE GREEN TURTLE (CHELONIA MYDAS) IN TERMS OF MATRIARCHAL PHYLOGENY. Evolution (N Y) [Internet]. 1992 Aug [cited 2018 Oct 22];46(4):865–81. Available from: http://doi.wiley.com/10.1111/j.1558-5646.1992.tb00605.x

47. Tomás J, Formia A, Castroviejo J, Raga JA. Post-nesting movements of the green turtle, Chelonia mydas, nesting in the south of Bioko Island, Equatorial Guinea, West Africa. Mar Turt Newsl [Internet]. 2001 [cited 2018 Oct 22];94:3–6. Available from: http://www.seaturtle.org/mtn/archives/mtn94/mtn94p3.shtml?nocount

48. Godley BJ, Barbosa C, Bruford M, Broderick AC, Catry P, Coyne MS, et al. Unravelling migratory connectivity in marine turtles using multiple methods. J Appl Ecol [Internet]. 2010 May 21 [cited 2018 Oct 22];47(4):769–78. Available from: http://doi.wiley.com/10.1111/j.1365-2664.2010.01817.x

49. Tomás J, Godley BJ, Castroviejo J, Raga JA. Bioko: Critically important nesting habitat for sea turtles of West Africa. Biodivers Conserv [Internet]. 2010 Aug 4 [cited 2018 Oct 22];19(9):2699–714. Available from: http://link.springer.com/10.1007/s10531-010-9868-z

50. Fitzgerald DB, Ordway E, Honarvar S, Hearn GW. Challenges Confronting Sea Turtle Conservation on Bioko Island, Equatorial Guinea. Chelonian Conserv Biol [Internet]. 2011 Dec [cited 2018 Oct 22];10(2):177–80. Available from: http://www.bioone.org/doi/abs/10.2744/CCAB-0889.1

51. Honarvar S, Fitzgerald DB, Weitzman CL, Sinclair EM, Echube JME, O’Connor M, et al. Assessment of Important Marine Turtle Nesting Populations on the Southern Coast of Bioko Island, Equatorial Guinea. Chelonia Conserv Biol [Internet]. 2016 Jun [cited 2018 Oct 22];15(1):79–89. Available from: http://www.bioone.org/doi/10.2744/CCB-1194.1

52. Balazs GH, Miya RK, Beaver SC. Procedures to attach a satellite transmitter to the carapace of an adult green turtle, Chelonia mydas. In: Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation [Internet], 1995 [cited 2018 Oct 22]. p. 21–26. Available from: https://ci.nii.ac.jp/naid/10022589615/

53. Troëng S, Evans DR, Harrison E, Lagueux CJ. Migration of green turtles Chelonia mydas from Tortuguero, Costa Rica. Mar Biol [Internet]. 2005 Dec 25 [cited 2018 Oct 22];148(2):435–47. Available from: http://link.springer.com/10.1007/s00227-005-0076-4

54. Jonsen ID, Flemming JM, Myers RA. Robust state-space modeling of animal movement data. Ecology [Internet]. 2005 Nov [cited 2018 Oct 22];86(11):2874–80. Available from: http://doi.wiley.com/10.1890/04-1852
Figure 2
Figure 3
