Check for updates

APPLIED ECOLOGY

Remote submerged banks and mesophotic ecosystems can provide key habitat for endangered marine megafauna

Graeme C. Hays[1]*, Jacques-Olivier Laloë[1], Jeanne A. Mortimer[2,3], Alex Rattray[1], Jared J. Tromp[1], Nicole Esteban[4]

Copyright © 2024 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).

The importance of some ecosystems remains poorly understood. We showed that mesophotic ecosystems (30 to 150 m) are a key habitat for a critically endangered species, with strong evidence that a globally important population of adult hawksbill turtles (*Eretmochelys imbricata*) almost exclusively foraged at these depths on remote submerged banks. This discovery highlights the need for such areas to be included in conservation planning, for example, as part of the United Nations High Seas Treaty. We equipped nesting turtles with Fastloc-GPS (Global Positioning System) satellite tags at an Indian Ocean breeding area and they all traveled to deep foraging sites (6765 days of tracking data across 22 individuals including 183,921 dive-depth measurements) rather than shallow coral reef sites. Both chart depths and depth data relayed from the tags indicated that turtles foraged at mesophotic depths, the modal dive depths being between 35 and 40 m. We calculate that 55,554 km^2 of the western Indian Ocean alone consists of submerged banks between 30 and 60 m.

INTRODUCTION

Across the world's oceans, key habitats and the species they support are under various anthropogenic threats, including climate change, fishing pressure, and pollution (*1*). Given these threats, there is an urgent need to triage key areas for protection, and yet for some habitats, there remains a lack of information to allow informed evidence-based conservation and management decisions. Knowledge of mesophotic ecosystems is very scant, prompting calls for more studies to investigate their ecology (*2*–*5*). Mesophotic ecosystems are logistically challenging to explore because their depths are largely beyond the limits of routine scientific SCUBA diving and further these ecosystems may often be distant from land, which adds to their inaccessibility (*5*). Yet, some studies have suggested that mesophotic ecosystems can have rich biodiversity [e.g., (*6*, *7*)] with abundant fish (*8*, *9*), corals and sponges (*5*) with benthic invertebrates sometimes at such high densities that they are described as "marine animal forests" (*3*).

While there are a few anecdotal observations, it is largely unknown how important mesophotic depths and submerged banks are for foraging marine megafauna, such as sharks, turtles, and marine mammals. For these groups, one important route to identify key areas for conservation is through satellite tracking, which allows animals to be followed regardless of where they move and so helps avoid logistical challenges of having to directly visit inaccessible habitats (*1*). Given this importance of assessing the megafauna use of mesophotic ecosystems, we attached high-accuracy satellite tags to nesting hawksbill turtles (*Eretmochelys imbricata*), a critically endangered species, and then tracked them to their distant foraging grounds with state-of-the-art Fastloc-GPS (Global Positioning System) satellite tags, some linked to depth sensors. In this way, we avoided the biases associated with only sampling accessible sites and were able to identify the relative importance of foraging sites on shallow coral reefs close to land versus deeper remote areas. Through high-accuracy satellite tracking, we both (i) triage key high seas areas for conservation for a critically endangered species and (ii) highlight an approach that will have broad utility across species and regions. Our work is timely given the recently signed United Nations High Seas Treaty (4 March 2023), which aims to improve the conservation of remote ocean areas as part of the goal of protecting at least 30% of the world's oceans by 2030 (*10*), meaning that informed evidence-based decisions to identify key areas for protection are urgently needed.

[1]Deakin Marine Research and Innovation Centre, School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia. [2]Department of Biology, University of Florida, Gainesville, FL 32611, USA. [3]PO Box 1443, Victoria, Mahé, Seychelles. [4]Department of Biosciences, Swansea University, Swansea SA2 8PP, Wales, UK.
*Corresponding author. Email: g.hays@deakin.edu.au

RESULTS

Twenty-two turtles were tracked to their foraging grounds in the Chagos Archipelago. Turtles traveled from their nesting beaches on Diego Garcia to foraging grounds on submerged banks within 200 km, the Great Chagos Bank, Centurion Bank, and Pitt Bank with a total of 6765 days of tracking data from the foraging areas (Fig. 1). No turtles traveled to foraging sites on shallow reefs associated with islanded atolls in the Chagos Archipelago.

The three turtles with depth-enabled tags traveled to the Great Chagos Bank. These three tags relayed dive data from the foraging grounds for a total of 1120 days ($n = 415$, 386, and 319 days for each tag, respectively), with a total of 183,921 raw 5-min depth values being relayed over this time. The 5-min depth values were further summarized into 1-hour intervals (n = 15,327, of which 8944 were either at night or day, i.e., local midday and midnight ± 3 hours) and 24-hour depth-use categories (n = 1091). The modal depth across all three tags was 34.3 m (SD: 6.2 m), derived from the 1-hour modal depths, with 95% of 1-hour modal depths lying between 33.5 and 56.5 m, between 28.5 and 67.5 m, and between 22.5 and 62 m for each of the turtles with depth-enabled tags. These mesophotic depths were used for many months, until the tags failed (Fig. 2).

When we compared the modal depths, calculated hourly from the 5-min records, these three turtles all showed a clear diel pattern in depth use with significantly deeper daytime dives ($t_{>1400} > 50$, $P < 0.001$ in all three cases). For example, the mean depth of the 1-hour modal depth summaries for day and night for these three

Downloaded from https://www.science.org on March 12, 2024

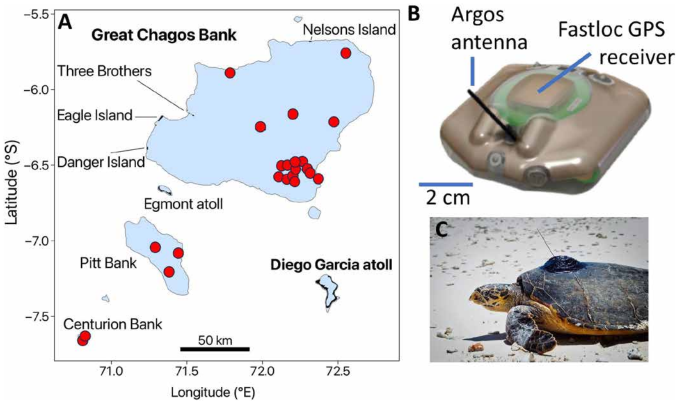

Fig. 1. Identifying the foraging sites of turtles. (**A**) The foraging sites (filled circles) in the Chagos Archipelago for 22 hawksbill turtles equipped with satellite tags on their nesting beach. Seventeen traveled to the Great Chagos Bank, three traveled to the Pitt Bank, and two traveled to the Centurion Bank. The blue shading represents water shallower than approximately 100 m. Islands on atolls are identified in black: Diego Garcia (where tags were attached), Egmont atoll, Danger Island, Eagle Island, Three Brothers, and Nelson Island. (**B**) The depth-enabled Wildlife Computer Fastloc-GPS depth tag used in this study. (**C**) A turtle equipped with a tag on the nesting beach on Diego Garcia.

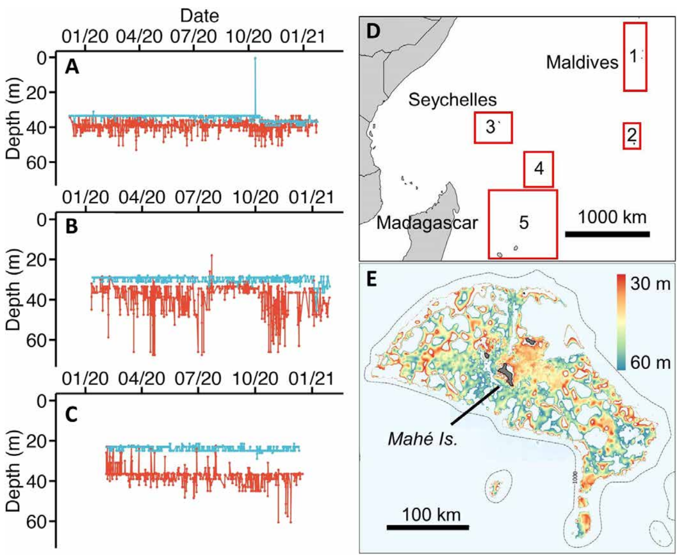

Fig. 2. Use of mesophotic depths on submerged banks. (**A** to **C**) For three depth-enabled tags, the modal depth every hour for daytime (red) and nighttime (blue), showing the diel variation in depth use. Frequency histograms of depth utilization showed the same pattern (fig. S1), reiterating the typical use of mesophotic depths. (**D**) Location of bathymetric analysis of mesophotic depths on submerged banks in the western Indian Ocean; 1, northern Chagos-Laccadive Plateau (Maldives Plateau); 2, southern Chagos-Laccadive Plateau (Great Chagos Bank, Speakers Bank, Pitt Bank, Centurion Bank, Wight Bank, Ganges Bank, and Diego Garcia Atoll); 3, northern Mascarene Plateau (Seychelles Bank, Amirante Bank, and Farquhar Ridge); 4, central Mascarene Plateau (Saya de Malha Bank and Ritchie Bank); and 5, southern Mascarene Plateau (Nazareth Bank, Cargados Bank, Soudan Bank, Rodriguez Ridge, Mauritius, and Reunion). (**E**) An example of distribution of mesophotic ecosystems from 30 to 60 m depth on the Seychelles Bank, western Indian Ocean. Depths are indicated by colors where red shows 30 m depth and blue shows 60 m depth.

turtles was 39.2 m and 34.5 m ($n = 3632$ 1-hour modal dive summaries), 39.1 m and 30.0 m ($n = 2861$ 1-hour modal dive summaries), and 37.9 m and 24.0 m ($n = 2451$ 1-hour modal dive summaries), respectively (Fig. 2 and fig. S1). Associated with this diel pattern of diving, there was usually a clear horizontal movement between daytime and nighttime areas (fig. S2), with turtles generally transiting 1 to 2 km between their mean day and night locations.

For the other 19 turtles with location-only tags, the mean value of the nearest chart depth to each turtle was not significantly different from for the three turtles with depth-enabled tags ($t_{14} = 1.97$, $P > 0.05$); i.e., the implication is that across all 22 turtles, there was a tendency to occupy deep habitats. The mean GEBCO depth of the areas occupied by turtles in the day was 36.8 m.

We calculated the combined area of mesophotic ecosystems on submerged banks in the western Indian Ocean as 55,554, 77,054, and 90,039 km^2 for depth ranges of 30 to 60 m, 30 to 80 m, and 30 to 100 m, respectively. The majority (43,086 km^2) of mesophotic ecosystems occurring between depths of 30 and 60 m were identified on the Mascarene plateau with the remainder (12,469 km^2) on the Chagos-Laccadive Plateau, mainly the Great Chagos Bank and surrounding banks.

DISCUSSION

Our findings reveal the importance of mesophotic ecosystems and submerged banks for a critically endangered marine vertebrate and our approach may have broad applicability both across taxa and across other regions. Our approach of tracking a marine vertebrate also informs on the distribution of its prey and points to an abundance of benthic invertebrates at mesophotic depths, since hawksbill turtles are thought to feed primarily on sponges and other invertebrates (*11*). This conclusion adds to the growing evidence that mesophotic depths and submerged banks might support rich benthic biodiversity, including sponges [e.g., (*3*, *12*, *13*)] with, for example, both sponge growth rates and biomass reported to increase with depth (*14*). Furthermore, fishing fleets are known to target submerged banks, such as the Saya de Malha Bank, suggesting high fish abundance. Submerged banks in the Indian Ocean are also used by foraging green turtles [e.g., (*15*)] as well as several species of sharks and other large fish (*7*, *16*). The diel movements of hawksbills that we recorded are consistent with reports for other species of hard-shelled marine turtles (*17*), with turtles likely selecting nighttime resting areas with structure (rocks, caves, etc.) so that they are protected, to some extent, from predators such as sharks [e.g., (*18*)]. The picture that our evidence helps complete is that submerged banks and mesophotic depths may support an abundance of both benthic invertebrates and marine megafauna. This conclusion is very timely given the recently signed United Nations High Seas Treaty that aims to improve protection of remote areas (*10*), with global interest in now triaging the most important high seas areas in need of protection. While we show the importance of mesophotic depths for hawksbill turtles on submerged banks in the Chagos Archipelago, our work also highlights that more work is needed to document the specific areas within mesophotic ecosystems globally that are most in need of protection.

Our finding of an almost exclusive use of mesophotic foraging depths is made even more important by the global significance of the population we worked with. An estimated 6300 hawksbill clutches are laid annually in the Chagos Archipelago (*19*), which likely translates to a total population of several thousand adult females and possibly an equal number of adult males (*20*) foraging at mesophotic

Downloaded from https://www.science.org on March 12, 2024

depths on the Great Chagos Bank and surrounding banks. Sub-adult hawksbills also likely forage in those areas, making the region globally important for this critically endangered species.

There is good evidence that our conclusions likely apply more broadly across the Indian Ocean and beyond. For example, in the Seychelles, postnesting hawksbill turtles have been satellite tracked to foraging sites across the Seychelles Bank located at distances of 13 to 139 km from land (*21*). Examination of the approximate depths of their core foraging sites from available bathymetric charts (Admiralty 740 The Seychelles Group) indicates the following depth ranges for each of four of the turtles, respectively: 13 to 60 m, 14 to 70 m, 36 to 51 m, and 26 to 34 m. Furthermore, while the granitic Seychelles hosts large numbers of breeding hawksbills, during the nonbreeding season (March to August), adult hawksbills are rarely seen, and capture records from 1980 to 1983 show that few hawksbills >60 cm carapace length were captured in the vicinity of the granitic islands (*22*). In contrast, juvenile hawksbills were found year-round near the same islands. These observations again point to adult hawksbills generally living in deep waters distant from land outside the breeding season in other parts of the Indian Ocean.

It is noteworthy that none of the tracked turtles traveled to shallow coral reefs associated with islands, which have long been considered as the primary foraging habitat for the species where they feed primarily on sponges and other invertebrates (*11*, *23–27*). There has been speculation that without the grazing of hawksbill turtles, coral reefs might become overgrown with demosponges (*11*). Yet, while extensive coral reefs border all the islanded atolls in the Chagos Archipelago, and many studies have shown the pristine nature of the reefs in this area [e.g., (*28*)], none of the tracked turtles foraged close to atolls. While it is without question that hawksbill turtles may forage at shallow depths on coral reefs in some parts of the world, there may be sampling biases in the general applicability of this finding. Many seminal pioneering studies that showed use of shallow water by hawksbills used either direct visual observations from snorkelers and divers in shallow water or data from loggers deployed and retrieved on turtles captured in shallow water [e.g., (*26*, *27*, *29*, *30*)]. Thus, by their very nature, such studies will shed light on shallow depth use as these were the areas sampled and will under-sample deeper areas. In contrast, deploying dive loggers linked to satellite tags on nesting turtles, as we have done, and then relaying the dive data from the foraging grounds, wherever they might be, helps avoid such biases. Such studies have shown that in some areas, adult hawksbills certainly use shallow depths, for example, in the eastern Pacific (*31*) and Red Sea (*32*). However, in other areas, there are indications that adult hawksbills may use deeper areas. Deep diving was shown by a female adult hawksbill turtle that was equipped with a depth-enabled satellite tag in the Caribbean (*33*), while other studies inferred use of depths >50 m by overlaying turtle locations on bathymetric charts (*34*). Similarly, Marshall *et al.* (*35*) tracked 18 postnesting hawksbills turtles in the Arabian Gulf with location-only satellite tags and inferred that turtles often traveled to foraging sites that were 30 to 50 m deep. A similar inference of use of mesophotic depths was made by tracking hawksbills with location-only tags on the west coast of Australia (*36*). There are further indications from disparate observations that our conclusion of mesophotic ecosystems being important for this species may apply broadly to many sites across the world. For example, off Puerto Rico (Caribbean), remote operated vehicles have been used to identify hawksbill turtles at depths between 25 and 40 m on seamounts (*37*), foraging at 65 m on a mesophotic coral ecosystem (*38*) and swimming at 87 m (*39*). In the Philippines, Quimpo *et al.* (*18*) observed hawksbill turtles at 30 to 40 m on mesophotic coral ecosystems. Thus, while few other studies have directly recorded foraging depths for adult hawksbill turtles after they have migrated to their foraging grounds, these observations complement our findings and suggest that hawksbills likely use mesophotic depths widely at sites around the world and, by implication, these depths can support a high abundance of benthic invertebrates globally. Across many thousands of adult hawksbill turtles in the Indian Ocean, it is likely that many are foraging deeper than the 60 m we routinely reported from turtles equipped with depth sensors. Thus, the total likely available foraging habitat on submerged banks might be better described by the 30- to 80-m or 30- to 100-m isobaths, with these areas encompassing 77,054 and 90,039 km^2, respectively. Regardless of this exact isobath limit for foraging, the available mesophotic areas accessible to hawkbills are clearly huge.

While the Great Chagos Bank lies within one of the world's largest Marine Protected Areas and so receives protection from industrial fishing [e.g., see figure 8a in (*40*)], there are ongoing negotiations about the future conservation management of this region (*41*). Management of the Saya de Malha Bank is difficult as it lies beyond waters of national jurisdiction and since 2012 has been jointly managed by Mauritius and the Republic of Seychelles as a Joint Management Area (*11*). Our findings suggest that these submerged banks, and likely those more broadly around the world, are key areas for conservation focus.

In summary, our findings highlight that submerged banks and mesophotic depths can be important foraging areas for critically endangered marine vertebrates and may support an abundance of benthic invertebrates. As such, these habitats should be considered important in conservation planning both in the Indian Ocean and globally, for example, as part of the United Nations High Seas Treaty. Our study also highlights the value of using satellite tracking to reveal key habitats for endangered marine megafauna.

MATERIALS AND METHODS

Study site and tag deployments

The Chagos Archipelago lies in the western Indian Ocean and consists of discrete atolls with around 58 associated islands, surrounded by shallow-fringing coral reefs. While hawksbill turtles were ashore nesting during November 2018 and 2019 on the island of Diego Garcia, the largest atoll in the archipelago (7.428°S, 72.458°E), they were equipped with Fastloc-GPS Argos satellite tags (SPLASH10-BF, Wildlife Computers, Seattle, Washington, USA) [see (*42*) for attachment details]. From data relayed via the Argos system (http://www.argos-system.org/), Fastloc-GPS positions were determined. Only Fastloc-GPS positions obtained with a minimum of six satellites and a residual error value (a dimensionless unit produced in Fastloc-GPS processing) of ≤30 were used, producing locations that were generally within a few tens of meters of the true location (*43*). A speed filter was then applied to remove any GPS locations greater than 5 km/h. We identified each turtle's foraging grounds as the localized area they traveled to and remained in for several months before tags failed. Three of the tags additionally recorded depth every 5 min. Depth was measured (precision = 0.5 m) with a pressure transducer on the tag and relayed via Argos. Depth data were obtained in two main ways: (i) depth recorded every 5 min was relayed every time the turtle surfaces and (ii) all depth values recorded each 24-hour period were placed into depth histograms (2, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 60, 100, and >100 m) that were then relayed every

Downloaded from https://www.science.org on March 12, 2024

24 hours. These depth histograms were essentially a redundancy in case there were insufficient uplinks to obtain appreciable 5-min depth values. Depths recorded at 5-min intervals were summarized by the modal depth every hour. Where more than one mode was present within the hour, we derived the mean of those modal values. As turtles forage and rest on the seabed, their modal depth use likely reflects the seabed depth. When we estimated hourly modal depth, observations that had <8 records within the hour were removed. Turtles showed a clear diel pattern in movement, with defined nocturnal locations and a broader diurnal foraging pattern. To objectively quantify this movement, the average distance between the mean daily daytime and nighttime locations was calculated every 10 days, using daytime locations obtained at local midday ±3 hours and nighttime locations at local midnight ±3 hours. We used this same definition of day versus night to quantify day versus night dive depths. From a bathymetric chart (DM 61610 Chagos Archipelago), the depth sounding closest to each turtle's location (to the nearest 30 s) was noted.

Bathymetric analysis

Bathymetry data for the two largest shallow submarine features in the tropical Indian Ocean, the Chagos-Laccadive Plateau and the Mascarene Plateau, were extracted from the GEBCO 2023 15 arc-second grid (*44*). Bathymetry rasters were first cropped using extents corresponding to the 1000-m isobath for five study areas: northern Chagos-Laccadive Plateau (Maldives Plateau), southern Chagos-Laccadive Plateau (Great Chagos Bank, Speakers Bank, Pitt Bank, Centurion Bank, Wight Bank, Ganges Bank, and Diego Garcia Atoll), northern Mascarene Plateau (Seychelles Bank, Amirante Bank, and Farquhar Ridge), central Mascarene Plateau (Saya de Malha Bank and Ritchie Bank), and southern Mascarene Plateau (Nazareth Bank, Cargados Bank, Soudan Bank, Rodriguez Ridge, Mauritius, and Réunion). After reprojection of rasters to their local Universal Transverse Mercator (UTM) zones, vector masks encompassing three mesophotic depth ranges of 30 to 60 m, 30 to 80 m, and 30 to 100 m were derived and used to extract rasters for each depth range in the five study areas. The areas of each depth range were calculated by extrapolating pixel area across the full extents of each site. Data were analyzed in R v4.2.2 using RStudio v2023.03.1 (R Core Team, 2023) and maps were produced using QGIS v3.30.2.

Ethics statement

The study was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory Administration of the UK Foreign, Commonwealth, and Development Office. The study was endorsed through research permit nos. 0009SE18 and 0011SE19 from the Commissioner's Representative for British Indian Ocean Territory (BIOT), and the research complied with all relevant local and national legislation.

Supplementary Materials

This PDF file includes:
Figs. S1 and S2
Legends for tables S1 and S2

Other Supplementary Material for this manuscript includes the following:
Tables S1 and S2

REFERENCES AND NOTES

1. A. M. M. Sequeira, G. C. Hays, D. W. Sims, V. M. Eguíluz, J. Rodriguez, M. Heupel, R. Harcourt, H. Callich, N. Queiroz, D. P. Costa, J. Fernández-Gracia, L. C. Ferreira, S. D. Goldsworthy, M. Hindell, M.-A. Lea, M. Meekan, A. Pagano, S. A. Shaffer, J. Reisser, M. Thums, M. Weise, C. M. Duarte, Overhauling ocean spatial planning to improve marine megafauna conservation. *Front. Mar. Sci.* **6**, 639 (2019).
2. L. A. Rocha, H. T. Pinheiro, B. Shepherd, Y. P. Papastamatiou, O. J. Luiz, R. L. Pyle, P. Bongaerts, Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science* **361**, 281–284 (2018).
3. M. D. O. Soares, T. C. L. Tavares, P. B. D. M. Carneiro, Mesophotic ecosystems: Distribution, impacts and conservation in the South Atlantic. *Divers Distrib.* **25**, 255–268 (2019).
4. G. Eyal, J. H. Laverick, P. Bongaerts, O. Levy, J. M. Pandolfi, Mesophotic coral ecosystems of the great barrier reef are understudied and underexplored. *Front. Mar. Sci.* **8**, 622856 (2021).
5. P. Bongaerts P, Mesophotic coral ecosystems. *Curr. Biol.* **32**, R345–R346 (2022).
6. S. E. Kahng, J. R. Garcia-Sais, H. L. Spalding, E. Brokovich, D. Wagner, E. Weil, L. Hinderstein, R. J. Toonen, Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* **29**, 255–275 (2010).
7. D. M. Tickler, T. B. Letessier, H. J. Koldewey, J. J. Meeuwig, Drivers of abundance and spatial distribution of reef-associated sharks in an isolated atoll reef system. *PLOS ONE* **12**, e0177374 (2017).
8. A. E. Pickard, J. J. Vaudo, B. M. Wetherbee, R. S. Nemeth, J. B. Blondeau, E. A. Kadison, M. S. Shivji, Comparative use of a Caribbean mesophotic coral ecosystem and association with fish spawning aggregations by three species of shark. *PLOS ONE* **11**, e0151221 (2016).
9. J. Asher, I. D. Williams, E. S. Harvey, An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago. *Sci. Rep.* **7**, 3905 (2017).
10. N. Jones, UN forges historic deal to protect ocean life: What researchers think. *Nature* **7**, 2023 (2023).
11. Y. M. León, K. A. Bjorndal, Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Mar. Ecol. Prog. Ser.* **245**, 249–258 (2002).
12. J. A. Turner, R. C. Babcock, R. Hovey, G. A. Kendrick, AUV-based classification of benthic communities of the Ningaloo shelf and mesophotic areas. *Coral Reefs* **37**, 763–778 (2018).
13. S. Ramah, G. Gendron, R. Bhagooli, M. Soondur, A. Souffre, R. Melanie, P. Coopen, L. Caussy, D. Bissessur, O. A. Bergstad, Diversity and distribution of the shallow water (23-50 m) benthic habitats on the Saya de Malha Bank, Mascarene Plateau. *WIO J. Mar. Sci.* **2**, 69–80 (2022).
14. M. P. Lesser, J. J. Slattery, Ecology of mesophotic coral reefs. *J. Exp. Mar. Biol. Ecol.* **375**, 1–8 (2009).
15. G. C. Hays, G. Cerritelli, N. Esteban, A. Rattray, P. Luschi, Open ocean reorientation and challenges of island finding by sea turtles during long-distance migration. *Curr. Biol.* **30**, 3236–3242.e3 (2020).
16. N. Esteban, R. K. F. Unsworth, J. B. Q. Gourlaya, G. C. Hays, The discovery of deep-water seagrass meadows in a pristine Indian Ocean wilderness revealed by tracking green turtles. *Mar. Pollut. Bull.* **134**, 99–105 (2018).
17. F. Christiansen, N. Esteban, J. A. Mortimer, A. M. Dujon, G. C. Hays, Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. *Mar. Biol.* **164**, 10 (2017).
18. T. J. R. Quimpo, P. C. Cabaitan, R. D. D. Olavides, E. E. Dumalagan, J. Munar, F. P. Siringan, Preliminary observations of macrobenthic invertebrates and megafauna communities in the upper mesophotic coral ecosystems in Apo Reef Natural Park Philippines. *Raffles Bull. Zool* **66**, 1–11 (2018).
19. J. A. Mortimer, N. Esteban, A. N. Guzman, G. C. Hays, Estimates of marine turtle nesting populations in the south-west Indian Ocean indicate the importance of the Chagos Archipelago. *Oryx* **54**, 332–343 (2020).
20. N. Esteban, J.-O. Laloë, J. A. Mortimer, A. N. Guzman, G. C. Hays, Male hatchling production in sea turtles from one of the world's largest marine protected areas, the Chagos Archipelago. *Sci. Rep.* **6**, 20339 (2016).
21. J.A. Mortimer, G.H. Balazs, Post-nesting migrations of hawksbill turtles in the granitic Seychelles and implications for conservation, in H. Kalb, T Wibbels, comps. *Proceedings of the 19th Annual Symposium on Sea Turtle Biology and Conservation, NOAA Tech. Memo, NMFS-SEFSC-443* (2000), pp. 22–26. NOAA.
22. J.A. Mortimer, *Marine Turtles in the Republic of Seychelles: Status and Management* (Publication of IUCN Conservation Library, 1984).
23. A. Carr, H. Hirth, L. Ogren, *The Ecology and Migration of Sea Turtles, 6, The Hawksbill Turtle in the Caribbean Sea* (American Museum Novitas, 1966).
24. A. Meylan, Spongivory in hawksbill turtles: A diet of glass. *Science* **239**, 393–395 (1988).
25. R. G. von Brandis, J. A. Mortimer, B. K. Reilly, R. W. M. van Soest, G. M. Branch, Taxonomic composition of the diet of hawksbill turtles *(Eretmochelys imbricata)* in the Republic of Seychelles. *WIO J. Mar. Sci.* **13**, 81–91 (2014).
26. R. P. van Dam, C. E. Diez, Diving behavior of immature hawksbill *turtles* (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs* **16**, 133–138 (1997).
27. J. D. R. Houghton, M. J. Callow, G. C. Hays, Habitat utilization by juvenile hawksbill turtles (*Eretmochelys* imbricata, Linnaeus, 1766) around a shallow water coral reef. *J. Nat. Hist.* **37**, 1269–1280 (2003).

Downloaded from https://www.science.org on March 12, 2024

28. C. T. Perry, G. N. Murphy, N. A. Graham, S. K. Wilson, F. A. Januchowski-Hartley, H. K. East, Remote coral reefs can sustain high growth potential and may match future sea-level trends. *Sci. Rep.* **5**, 18289 (2015).
29. J. K. Matley, J. Jossart, L. Johansen, P. D. Jobsis, Environmental drivers of diving behavior and space-use of juvenile endangered Caribbean hawksbill sea turtles identified using acoustic telemetry. *Mar. Ecol. Prog. Ser.* **652**, 157–171 (2020).
30. K. L. Stokes, N. Esteban, H. J. Stokes, G. C. Hays, High dive efficiency in shallow water. *Mar. Biol.* **170**, 45 (2023).
31. A. R. Gaos, R. R. Lewison, B. P. Wallace, I. L. Yañez, M. L. Liles, A. Baquero, J. A. Seminoff, Dive behaviour of adult hawksbills (*Eretmochelys imbricata*, Linnaeus 1766) in the eastern Pacific Ocean highlights shallow depth use by the species. *J. Exp. Mar. Biol. Ecol.* **432–433**, 171–178 (2012).
32. L. K. Tanabe, J. E. M. Cochran, C. T. Williams, F. Garzon, U. Langner, R. S. Hardenstine, L. A. Hawkes, R. E. Brainard, A. A. Eweida, P. A. Marshall, M. L. Berumen, Case report: Tracking data from foraging hawksbill turtles in the northern Red Sea. *Anim. Biotelemetry* **11**, 1 (2023).
33. M. Nivière, P. Chambault, T. Pérez, D. Etienne, M. Bonola, J. Martin, C. Barnérias, F. Védie, J. Mailles, E. Dumont-Dayot, J. Gresser, G. Hiélard, S. Régis, N. Lecerf, L. Thieulle, M. Duru, F. Lefebvre, G. Milet, B. Guillemot, B. Bildan, B. de Montgolfier, A. Benhalilou, C. Murgale, T. Maillet, P. Queneherve, T. Woignier, M. Safi, Y. Le Maho, O. Petit, D. Chevallier, Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle. *Biol. Conserv.* **223**, 170–180 (2018).
34. L. A. Hawkes, J. Tomás, O. Revuelta, Y. M. León, J. M. Blumenthal, A. C. Broderick, M. Fish, J. A. Raga, M. J. Witt, B. J. Godley, Migratory patterns in hawksbill turtles described by satellite tracking. *Mar. Ecol. Prog. Ser.* **461**, 223–232 (2012).
35. C. D. Marshall, J. A. Cullen, M. Al-Ansi, S. Hamza, M. A. R. Abdel-Moati, Environmental drivers of habitat use by hawksbill turtles (*Eretmochelys imbricata*) in the Arabian Gulf (Qatar). *Front. Mar. Sci.* **7**, 549575 (2020).
36. S. Fossette, L. C. Ferreira, S. D. Whiting, J. King, K. Pendoley, T. Shimada, M. Speirs, A. D. Tucker, P. Wilson, M. Thums, Movements and distribution of hawksbill turtles in the Eastern Indian Ocean. *Glob. Ecol. Conserv.* **29**, e01713 (2021).
37. J.R. García-Sais, R. Castro, J. Sabater-Clavell, M. Carlo, R. Esteves, Characterization of benthic habitats and associated reef communities at Bajo de Sico Seamount, Mona Passage, Puerto Rico. Final Report, Coral Grant 2004, NA04NMS4410345 (2007).
38. F.E. Pagan, R.S. Appeldoorn, Use of small ROV Systems to survey mesophotic ecosystems, in *Proceedings of the 63rd Gulf and Caribbean Fisheries Institute* (2010), pp. 543–546. Gulf and Caribbean Fisheries Institute (GCFI).
39. R. Appeldoorn, D. Ballantine, I. Bejarano, M. Carlo, M. Nemeth, E. Otero, F. Pagan, H. Ruiz, N. Schizas, C. Sherman, E. Weil, Mesophotic coral ecosystems under anthropogenic stress: A case study at Ponce, Puerto Rico. *Coral Reefs* **35**, 63–75 (2016).
40. G. C. Hays, H. J. Koldewey, S. Andrzejaczek, M. J. Attrill, S. Barley, D. T. I. Bayley, C. E. Benkwitt, B. Block, R. J. Schallert, A. B. Carlisle, P. Carr, T. K. Chapple, C. Collins, C. Diaz, N. Dunn, R. B. Dunbar, D. S. Eager, J. Engel, C. B. Embling, N. Esteban, F. Ferretti, N. L. Foster, R. Freeman, M. Gollock, N. A. J. Graham, J. L. Harris, C. E. I. Head, P. Hosegood, K. L. Howell, N. E. Hussey, D. M. P. Jacoby, R. Jones, P. S. Sannassy, I. D. Lange, T. B. Letessier, E. Levy, M. Lindhart, J. M. McDevitt-Irwin, M. Meekan, J. J. Meeuwig, F. Micheli, A. O. M. Mogg, J. A. Mortimer, D. A. Mucciarone, M. A. Nicoll, A. Nuno, C. T. Perry, S. G. Preston, A. J. Rattray, E. Robinson, R. C. Roche, M. Schiele, E. V. Sheehan, A. Sheppard, C. Sheppard, A. L. Smith, B. Soule, M. Spalding, G. M. W. Stevens, M. Steyaert, S. Stifel, B. M. Taylor, D. Tickler, A. M. Trevail, P. Trueba, J. Turner, S. Votier, B. Wilson, G. J. Williams, B. J. Williamson, M. J. Williamson, H. Wood, D. J. Curnick, A review of a decade of lessons from one of the world's largest MPAs: Conservation gains and key challenges. *Mar. Biol.* **167**, 159 (2020).
41. P. Loft, in *British Indian Ocean Territory: UK to Negotiate Sovereignty 2022/23* (UK Parliament House of Commons Library 9673, 2022), pp. 1–17.
42. N. Esteban, J. A. Mortimer, G. C. Hays, How numbers of nesting sea turtles can be over-estimated by nearly a factor of two. *Proc. R. Soc. B* **284**, 20162581 (2017).
43. A. M. Dujon, R. T. Lindstrom, G. C. Hays, The accuracy of Fastloc-GPSlocations and implications for animal tracking. *Methods Ecol. Evol.* **5**, 1162–1169 (2014).
44. GEBCO Compilation Group, GEBCO 2023 Grid (doi: 10.5285/f98b053b-0cbc-6c23-e053-6c86abc0af7b) (accessed 06/10/2023) (2023).

Acknowledgments: We thank A. N. Guzman for invaluable help in the field and K. Stokes for input with initial data screening. We are grateful for logistical support provided by personnel in the BIOT in patrolling the beach in Diego Garcia and attaching satellite transmitters. **Funding:** This work was supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (grant numbers BPMS-2017-4 and 820633). **Author contributions:** G.C.H. and N.E. conceived the study. G.C.H. led the writing to which all authors contributed. G.C.H., A.R., and J.J.T. completed the data analysis. N.E., J.-O.L., and J.A.M. completed the fieldwork. J.J.T. compiled the raw data tables. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

Submitted 9 October 2023
Accepted 18 January 2024
Published 21 February 2024
10.1126/sciadv.adl2838

Downloaded from https://www.science.org on March 12, 2024