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To Madagascar and back: long-distance, return migration across open ocean by a pregnant female bull shark

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Abstract

A large, pregnant, female bull shark was tracked migrating from the Seychelles across open ocean to southeast Madagascar, approximately 2,000 km away, and back again. In Madagascar the shark spent a prolonged period shallower than 5 m, consistent with entering estuarine habitat to pup, and upon return to Seychelles the shark was slender and no longer gravid. This represents an unprecedented return migration across open ocean for a bull shark, and highlights the need for international collaboration to manage the regional bull shark population sustainably.

Keywords: geolocation, philopatry, PSAT, parturition, satellite telemetry

Animal migration and its underlying motivations are important factors in the understanding of population ecology. Where animal populations experience threats that jeopardise their sustainability, such as overfishing, an understanding is crucial for the development of informed management strategies. Although the study of movement behaviour in marine animals has traditionally lagged behind terrestrial species, increasing availability of remote telemetry is fuelling a growing literature on the spatial dynamics of marine species (Block *et al.* 2011). In particular several shark species have been shown to perform extensive migrations (Chapman *et al.* 2015), which is of particular concern given reports of severe declines in shark populations (Worm & Branch 2012), and the difficulties of managing species that traverse international boundaries and the high seas (Game *et al.* 2009).

In contrast to some areas of the Atlantic and Pacific, information on shark populations in the Indian Ocean remains comparatively limited. What information is available suggests the outlook is similarly poor. For example, in the Seychelles, from where large quantities of shark meat were exported during the 19th and 20th centuries, surveys of local fishermen suggest that shark populations have declined dramatically (Nevill *et al.* 2007), with sightings of larger sharks becoming exceptionally rare (Smith & Smith 1969). Yet in 2003–2005 shark fishing was intensified in the Seychelles, following the European Union ban on import of local swordfish, a principal target species, due to their high cadmium levels (Nevill *et al.* 2007). Declines have been further exacerbated by increased targeting of large sharks following two fatal attacks on tourists in 2011, at least one of which can be attributed to a bull shark *Carcharhinus leucas* (Müller and Henle, 1839) through genetic analysis of a tooth fragment (Seychelles Nation 2011). Thus even now there is intense fishing pressure on sharks in the Seychelles, putting populations at risk of severe declines. Consequently the movement behaviour of sharks, especially bull sharks, is now of particular interest in Seychelles, both from a fisheries management perspective and due to concerns of potential risks to human safety.

Apart from their presence in local waters, little is known about the ecology of bull sharks in the Seychelles. The bull shark is a large predatory shark (up to 4 m), found worldwide in tropical and warm temperate coastal waters, making seasonal appearances in cool temperate waters (Compagno 2001). They are assessed as Near Threatened on the IUCN Red List, mostly escaping targeted fisheries but kept as lucrative bycatch for their large fins (Simpfendorfer & Burgess 2009). Unlike other carcharhinids, they are able to tolerate fresh water, with females pupping in rivers or estuaries (Springer 1963), which the juveniles use as nurseries (Snelson, Mulligan & Williams 1984). Bull sharks have even been found thousands of kilometres inland up rivers (Thorson 1972; Thomerson 1977), but to date the majority of recorded movements have remained coastal. The present study set out to determine the movement patterns of bull sharks in the Seychelles to aid management efforts, and presents here an early result deemed of sufficient novelty to warrant communication.

A 3 m female bull shark was caught using a baited hand line and tagged with both an acoustic transmitter (V16, Vemco Ltd, Canada) and a pop-up satellite-linked archival transmitter (PSAT) (Mk 10 PAT tag, Wildlife Computers, Redmond, Washington, USA) on 21st August 2014 in the Amirantes, Seychelles (S 05°24’, E 053°17’). The PSAT was set to record depth every 10 seconds, with temperature and light levels being recorded every 5 minutes, and was attached to the shark via a monofilament tether through the first dorsal fin, set to pop-off after six months. The acoustic transmitter had a nominal delay of 60 –180 seconds, and was surgically implanted into the shark’s coelom to prevent any risk of tag loss, while the shark lay in tonic immobility alongside the research vessel. All field work was approved by, and conducted with the knowledge of the Environment Department, Seychelles. The shark handling and tagging methods were performed in accordance with the approved guidelines of the University of Plymouth, UK.

The presence/absence of the acoustic tag was recorded across the Amirantes by an array of 88 acoustic receivers (VR2W, Vemco Ltd, Canada). Underwater visual surveys were also performed at various locations in the Amirantes, whereby scuba divers released chum and recorded the abundance and diversity of shark species encountered, along with estimated size, sex, distinguishing marks, and notable behaviour. The tagged shark was encountered during one such survey on 19/01/2015 and came close enough for the divers to remove the PSAT, allowing retrieval of the raw archival data for analysis.

While the acoustic data reveals when the shark was recorded at particular receivers, reconstructing movements based on the PSAT archival data relies on light-based geolocation. The light-based geolocation was performed with Wildlife Computers' Global Position Estimator, which uses tag recorded light levels to estimate local time at midday and midnight and day length to provide approximate longitudes and latitudes respectively. However, these Global Position Estimates (GPE) have large error fields and perform poorly in estimating latitude near the equator or close to equinoxes. The GPE longitude outputs had a mean error of 107.46 km (range 25.30–798.12 km), while the GPE latitude outputs had a mean error of 493.90 km (range 27.80–3,333.68 km). Consequently, to improve on these raw estimates, the locations were filtered and refined by using a swim speed (diffusivity) filter and by matching sea surface temperature pixels and bathymetry. The process involves two steps. The first is to generate a 'cloud' of possible waypoints at each reachable location; the second is to select the 'best' waypoint at each location to produce a final, most probable path.

The process begins at the known deployment location by attempting to route to the first (target) GPE location. A swim speed of 2 ms^{-1} together with the time to the target location is used to define a circle representing the theoretically reachable area. This circle is intersected with the ellipse defined by the position error estimate at the target location. If no intersection is possible then the target location is considered unreachable and is rejected. The process then continues with subsequent locations until a valid intersection is achieved. Pixels within the intersection where the bathymetry (from GEBCO, 30 second resolution) is deeper than the maximum depth recorded on that day from the tag archive data and where the daily Sea Surface Temperature estimate (from OSTIA) is within 0.5°C of the recorded tag temperature, are selected as possible ‘waypoints’. If no matching pixels are identified then the location is rejected.

The process then continues by attempting to route in the same manner from each waypoint at the prior location to the next location, generating a collection of potential waypoints at each reachable location, until all locations have been processed. Any known, rather than estimated, locations, such as those from the acoustic array, the deployment and pop-up locations are considered to be ‘locked’, are always routed to and have a single waypoint.

To determine the ‘best’ path through the reachable locations the process again begins at the first location, which being known and locked comprises a single waypoint. Waypoints at the next reachable location are scored according to the distance to the estimated location coordinates, the SST difference and the distance to the prior waypoint. A ‘best’ waypoint is selected by choosing a waypoint at random using a distribution constructed from the waypoint scores to bias the selection to the higher scoring waypoints. Note, that if there is a large spread of points at the two locations, that it is possible for no way point at a given location to be reachable, given the 2 ms^{-1} swim speed, from the selected waypoint at a prior location. In these cases the location is rejected from this path. Waypoint selection is repeated in his way at each reachable location. The result is a path which is then assigned a score equal to the sum of the scores of the waypoints.

The process of path generation is continued, with better scoring paths being selected as the ‘best’ path until 500 new paths have been generated without improving on the score. The 'best' path points had reduced error fields, particularly for latitude: filtered latitude outputs had a mean error of 199.64 km (range 5.53–1,084.10 km), with filtered longitude outputs having a mean error of 147.52 km (5.34–798.65 km). The 'best' path locations also had low standard deviations, with +/- 34.14 km latitude and +/- 24.28 km for longitude. This ‘best’ path represented the final track used to plot the shark’s movements. Estimating where the shark was and when, also allowed time-at-depth profiles to be assigned to particular locations or portions of the track. Time-at-depth profiles were calculated as the proportion of time spent within a particular depth range, either on a daily basis or across a particular portion of the track (e.g. when migrating).

In total the movements of this large female bull shark (300 cm total length) were tracked for 151 days from 21/08/2014. The final track consisted of 263 locations, comprising the tagging location, 194 acoustic detections, 67 filtered light-based geolocations, and the location of tag retrieval. During tagging the shark was notably gravid, presenting with considerable girth, and the writhing movement of pups could be felt through the ventral surface. The shark was then encountered again on 17/01/2015 and 19/01/2015 during underwater visual surveys, appearing slender and with fresh bite marks on the left side.

Over the course of the track the shark is estimated to have travelled over 10,670 km at an average speed of 0.82 ms^{-1}. The shark is known to have remained within the Amirantes until at least 20/10/2014, which represents the last detection on the Amirantes acoustic array (at Marie-Louise). After this the shark's movements inferred from the light-based geolocation revealed a long-distance migration to the southeast coast of Madagascar (Fig. 1), approximately 1,960 km away from the tagging location in the Amirantes. Between 20/10/2014 and approximately 19/11/2014, the shark travelled south from the Amirantes and across open ocean to the northern tip of Madagascar, passing near the Farquhar group of islands. The majority of geolocations available around Madagascar are focused along the south-eastern coast. Around 29/12/2014 the shark started to head north again, reaching the tagging area around 17/01/2015, having completed a roundtrip migration of approximately 4,000 km.

The shark displayed relatively restricted vertical movements, with the deepest dive during the entire track being to 164 m (Fig. 2). The shark only experienced temperatures in excess of 20°C, ranging from 21°C at 164 m to 29°C at the surface, although the majority of time was spent around 26°C. Whilst in the Amirantes the shark's depth profile appears restricted by bathymetry. The Amirantes plateau barely gets deeper than 60–70m, and before leaving the Amirantes in mid-October the shark spent 86.3% of its time shallower than 50 m, with 56.6% of time spent at 30–50 m (Fig. 3). Despite this preference for deeper water, the shark did on occasion move up to the surface rapidly, sometimes at speeds of up to 4.3 ms^{-1}.

When migrating across open ocean (both to and from Madagascar), the shark displayed a much broader range of depth use and tended to stay deeper than when on the Amirantes (Fig. 2), spending over a third of its time below 100 m (Fig. 3). The shark regularly dived to depths of up to 164 m, often oscillating between 50 and 100 m. On several occasions the shark made some marked accelerations to the surface, including one from 130 m to the surface over the course of 60 s.

Once along the coast of Madagascar the shark displayed a marked change in depth use (Fig. 2), with 59.2% of time spent shallower than 5 m (Fig. 3). This is predominantly attributable to the latter half of December, once the shark was along the southeast coast and remained almost exclusively shallower than 5 m (Fig. 2).

This large, female bull shark travelled from a remote chain of islands in the Seychelles to southeast Madagascar, approximately 2,000 km away, before returning back to the Seychelles. Previous tracking studies on bull sharks have generally reported relatively restricted coastal movements (Kohler, Casey & Turner 1998; Brunnschweiler, Queiroz & Sims 2010; Hammerschlag *et al.* 2012), with juveniles often being perennial residents in estuarine nurseries (Heupel & Simpfendorfer 2008). Some large movements have been recorded, such as 1,500 km along the coast of the United States (Carlson *et al.* 2010), and 2,000 km along the coast of South Africa to Mozambique (Save Our Seas Foundation, 2011). Bull sharks have been recorded moving over deeper water for short periods in the Gulf of Mexico, the Gulf Stream, and Reunion Island near Madagascar (Carlson *et al.* 2010; Brunnschweiler *et al.* 2010; Soria *et al.* 2015), but sustained, directed migration across open ocean as presented here has not previously been reported. Consequently this return migration is believed to be the first reported of its kind for a bull shark, being long-distance across deep, open ocean, and also represents the longest known PSAT track of a bull shark (151 days, previously 85 (Carlson *et al.* 2010)).

This large, female bull shark could have travelled to Madagascar for parturition. At the time of tagging the shark was notably gravid, and the area of Madagascar it travelled to near Manakara has several large rivers and estuaries nearby. As previously mentioned, female bull sharks preferentially pup in riverine and estuarine habitats (Springer 1963). Moreover, when in this area of Madagascar, the shark displayed a marked change in diving behaviour, remaining almost exclusively shallower than 5 m for several days, consistent with entering a river or estuary system. Immediately after leaving the shallower habitat, the shark resumed regular diving behaviour all the way back to the Seychelles, where it was observed as slender and no longer gravid. Consequently the shark must have pupped during the intervening absence from the Seychelles, and the shallow depth profile in the vicinity of estuarine habitats in Madagascar seems a plausible candidate for its pupping ground.

This result is particularly surprising given that juvenile bull sharks are encountered coastally around Mahe in the Seychelles (pers. obs.), just over 200 km from the Amirantes. This raises the question as to why this shark would migrate 2,000 km away if suitable habitat was much nearer. Elsewhere female bull sharks are suspected of high reproductive philopatry, as evidenced by highly restricted maternal gene flow between different nursery areas (Karl *et al.* 2011; Tillett *et al.* 2012). Some shark species even show natal philopatry, returning to their own place of birth for parturition (Feldheim *et al.* 2014). Consequently this shark may simply have exhibited strong, possibly natal, philopatry to a particular nursery area. Alternatively, individual condition and the associated cost/benefit ratio may play a role in migration propensity (Chapman *et al.* 2012). There is little suitable estuarine habitat around Mahe, so perhaps the estuaries of Madagascar offer more favourable nursery habitat, and this individual may have been of sufficient body condition to afford the costs of migration to seek better habitat and survival odds for its offspring.

These data suggest that bull shark life cycles in the southwest Indian Ocean may play out over large geographical scales that cross international boundaries and the high seas, perhaps constituting a single population. This highlights the need for international cooperation on potential management efforts. How such collaboration can be achieved is exemplified by the Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats in the Indian Ocean and South-East Asia (IOSEA Marine Turtle MoU), whereby signatory states have agreed to protect a network of sites important to marine turtles (Hays *et al*. 2014). We propose that southwest Indian Ocean states adopt a similar initiative for migratory sharks in the region, with signatories agreeing to share data and collectively manage areas deemed of particular importance to regional populations, such as potential nursery habitats for bull sharks in Madagascar. Madagascar may be an important pupping habitat for bull sharks regionally, with genetic analysis also indicating gene flow between Madagascar and Reunion Island 870 km to the east (Soria *et al*. 2015).

Further investigation incorporating genetics, shark condition and a larger sample size will be required to fully understand the migratory behaviour of bull sharks in the Seychelles. In the meantime, discovery of this novel, long-distance reproductive migration across open ocean highlights a potentially important pupping and nursery area for bull sharks regionally, and that management of this species will need to be considered across the ocean basin and not just locally. Finally, this also suggests that potential risks to beachgoers may also vary seasonally, and that southwest Indian Ocean states should collaborate on strategies to mitigate risk.

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References

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W. & Costa, D.P. (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature,* **475**, 86–90.

Brunnschweiler, J.M., Queiroz, N. & Sims, D.W. (2010) Oceans apart? Short-term movements and behaviour of adult bull sharks *Carcharhinus leucas* in Atlantic and Pacific Oceans determined from pop-off satellite archival tagging. *Journal of Fish Biology*, **77**, 1343–1358.

Carlson, J.K., Ribera, M.M., Conrath, C.L., Heupel, M.R. & Burgess, G.H. (2010) Habitat use and movement patterns of bull sharks *Carcharhinus leucas* determined using pop-up satellite archival tags. *Journal of Fish Biology*, **77**, 661–675.

Chapman, D.D., Feldheim, K., Papastamatiou, Y. & Hueter, R.E. (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annual Review of Marine Science*, **7**, 547–570.

Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.-A. & Brönmark, C. (2012) Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, **81**, 456–478.

Compagno, L.J. (2001) *Sharks of the world: an annotated and illustrated catalogue of* *shark species known to date*. Food & Agriculture Org., Rome.

Feldheim, K.A., Gruber, S.H., Dibattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., Pikitch, E.K., Ashley, M.V. & Chapman, D.D. (2014) Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Molecular Ecology*, **23**, 110–117.

Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P. & Richardson, A.J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology and Evolution*, **24**, 360–369.

Hammerschlag, N., Luo, J., Irschick, D.J. & Ault, J.S. (2012) A comparison of spatial and movement patterns between sympatric predators: bull sharks (*Carcharhinus leucas*) and Atlantic tarpon (*Megalops atlanticus*). *PLoS ONE* **7**, e45958

Hays, G.C., Mortimer, J.A., Ierodiaconou, D. & Esteban, E. (2014) Use of long-distance migration patterns of an endangered species to inform conservation planning for the world's largest marine protected area. *Conservation Biology*, **28**, 1636–1644.

Heupel, M.R. & Simpfendorfer, C.A. (2008) Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology*, **1**, 277–289.

Karl, S.A., Castro, A.L.F., Lopez, J.A., Charvet, P. & Burgess, G.H. (2011) Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. *Conservation Genetics*, **12,** 371–382.

Kohler, N., Casey, J. & Turner, P. (1998a) NMFS cooperative shark tagging program, 1962-93: An atlas of shark tag and recapture data. *Marine Fisheries Review*, **60**, 1–87.

Nevill, J., Robinson, J., Giroux, F. & Isidore, M. (2007) *Seychelles National Plan of Action* *for the Conservation and Management of Sharks*. Seychelles Fishing Authority, Victoria, Seychelles.

Smith, J.L.B. & Smith, M.M. (1969) *The Fishes of Seychelles*. J.L.B. Smith Institute of Ichthyology.

Snelson, F.F., Mulligan, T.J. & Williams, S.E. (1984) Food habits, occurrence, and population structure of the bull shark, *Carcharhinus leucas*, in Florida coastal lagoons. *Bulletin of Marine Science*, **34**, 71–80.

Springer, S. (1963) Field observations on large sharks of the Florida-Caribbean region. *Sharks and survival* pp. 95–113. D. C. Heath Co., Boston.

Thomerson, J.E. (1977) The bull shark, *Carcharhinus leucas*, from the upper Mississippi River near Alton, Illinois. *Copeia*, **1**, 166–168.

Thorson, T.B. (1972) The status of the bull shark, *Carcharhinus leucas*, in the Amazon River. *Copeia*, 601–605.

Tillett, B.J., Meekan, M.G., Field, I.C., Thorburn, D.C. & Ovenden, J.R. (2012) Evidence for reproductive philopatry in the bull shark *Carcharhinus leucas*. *Journal of Fish Biology*, **80**, 2140–2158.

Worm, B. & Branch, T.A. (2012) The future of fish. *Trends in Ecology and Evolution*, **27**, 594–599.

Electronic References

Save Our Seas Foundation. (2011) Sensational findings on Breede river bull shark migration. URL http://saveourseas.com/press/sensational_findings_on_breede_river_bull_shark_migration [accessed 10 April 2015]

Seychelles Nation. (2011) Bull shark killed British honeymooner in Seychelles. URL http://sharkyear.com/2011/bull-shark-killed-british-honeymooner-in-seychelles.html [accessed 10 April 2015]

Simpfendorfer, C. & Burgess, G.H. (2009) *Carcharhinus leucas*. The IUCN Red List of Threatened Species. Version 2014.3. URL www.iucnredlist.org [accessed 10 April 2015] Soria, M., Jaquemet, S., Trystram, C., Chabanet, P., Bourjea, J., Jean, C., Ciccione, S., Dalleau, M., Bigot, L., Hemery, A., Blaison, A., Lemahieu, A., Dulau, V., Estrade, V., Magalon, H., Révillion, C., Pennober, G., Goutorbe, S., Cambert, H., Turquet, J., Cotel, P., Pirog, A. & Verlinden, N. (2015) Rapport scientifique final du programme CHARC (Connaissances de l'écologie et de l'habitat de deux espèces de requins côtiers sur la côte ouest de La Réunion).Technical Report, 130 pp. URL http://www.la-reunion.ird.fr/le-programme-charc [accessed 27 June 2015]

Figure 1: Map to show the 'best' path for the 3 m female bull shark tracked between 21st August 2014 and 19th January 2015. Points denote the processed track locations (red = receiver detections, white = PSAT geolocations), with a Bezier curve to illustrate the direction of travel (green = outbound, red = return). Map created in ArcGIS using ETOPO2v2 bathymetry data.

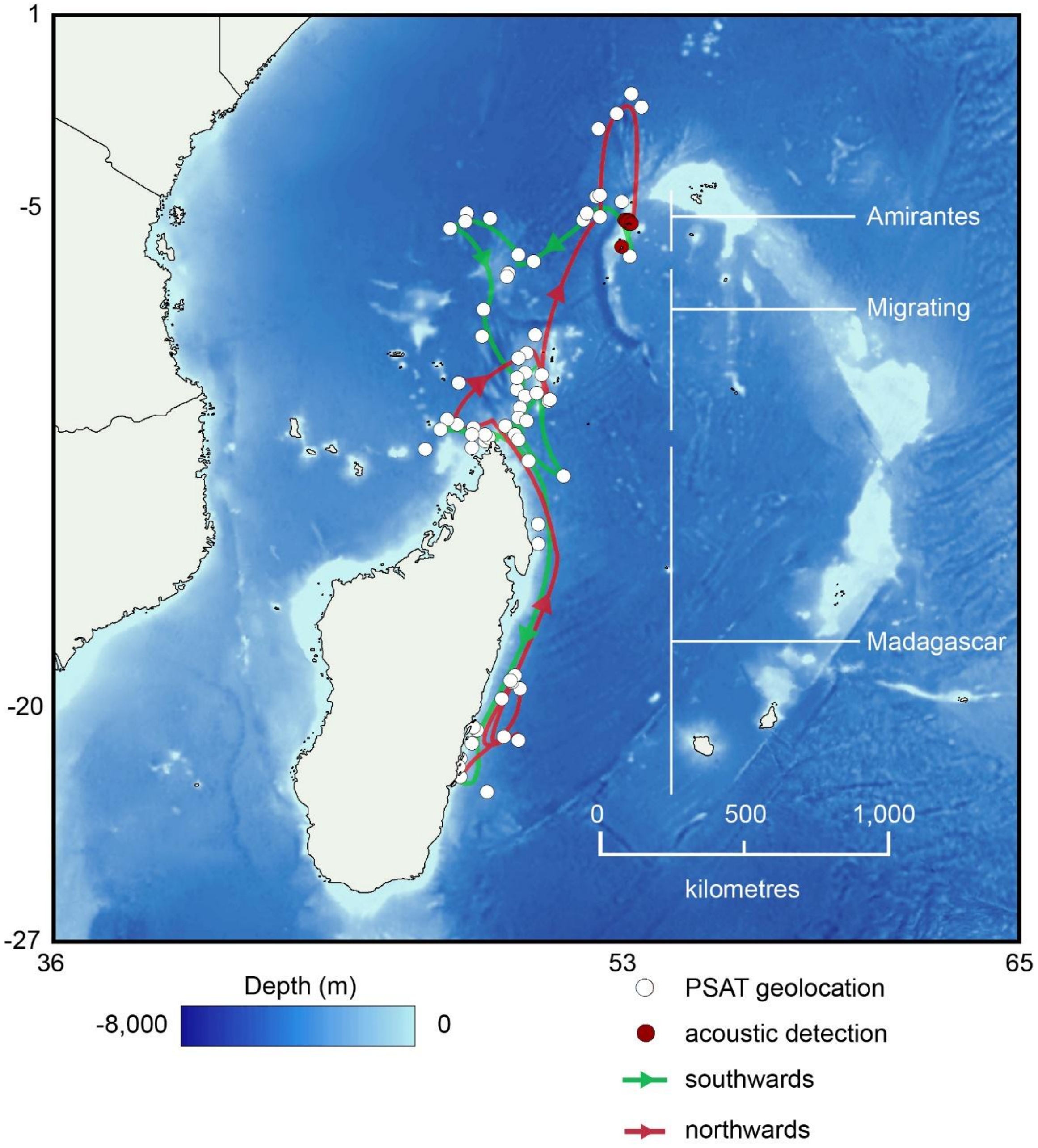

Figure 2: Plot of daily time-at-depth, overlaid with track latitude. Warmer colour denotes greater time spent at that depth. The string of detections around -5 degrees towards the start of the track are from the Amirantes acoustic array.

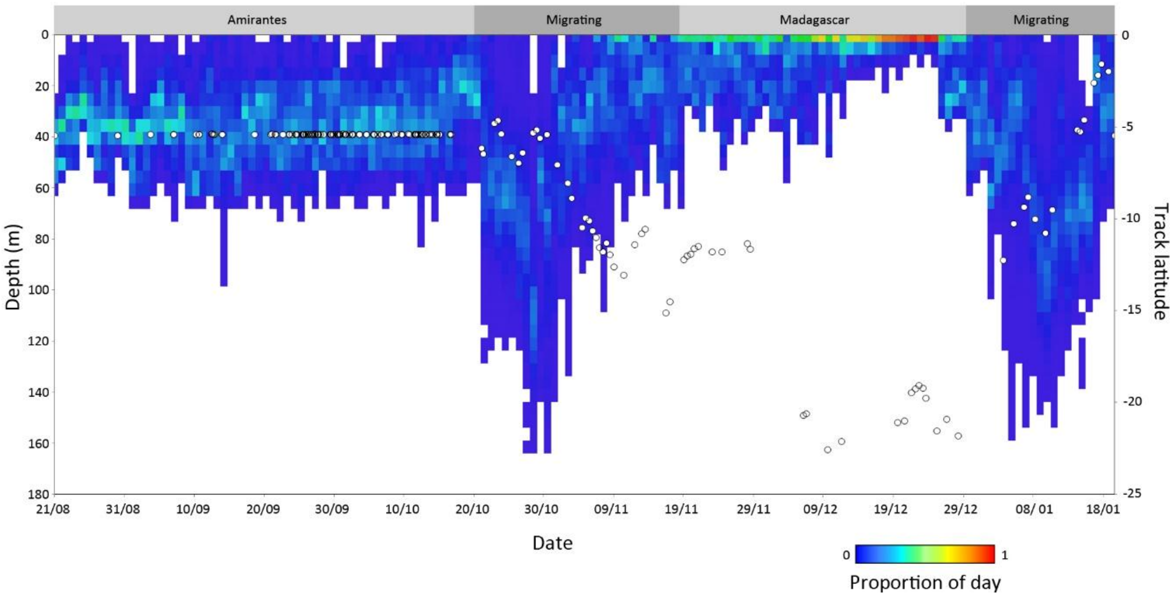

Figure 3: Time spent at depth while on the Amirantes plateau in Seychelles, during migration and at Madagascar.