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Movement ecology of black marlin *Istiompax indica* in the Western Indian Ocean

Christoph A. Rohner[1] | Roy Bealey[2] | Bernerd M. Fulanda[3] |
Jason D. Everett[4,5,6] | Anthony J. Richardson[4,5] | Simon J. Pierce[1]

[1]Marine Megafauna Foundation, Truckee, California

[2]Pelagic Fisheries Consulting Ltd, Grantham, UK

[3]Department of Biological Sciences, Pwani University, Kilifi, Kenya

[4]School of Mathematics and Physics, The University of Queensland, St Lucia, Queensland, Australia

[5]Commonwealth Scientific and Industrial Research Organisation, Oceans and Atmosphere, Biosciences Precinct, St Lucia, Queensland, Australia

[6]Centre for Marine Science and Innovation, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia

Correspondence

Christoph A. Rohner, Marine Megafauna Foundation, Truckee, CA 96161, USA.
Email: chris@marinemegafauna.org

Abstract

The black marlin *Istiompax indica* is an apex marine predator and is susceptible to overfishing. The movement ecology of the species remains poorly known, particularly within the Indian Ocean, which has hampered assessment of their conservation status and fisheries management requirements. Here, we used pop-up archival satellite tags to track *I. indica* movement and examine their dispersal. Forty-nine tags were deployed off Kenya during both the north-east (November–April) and south-west (August–September) monsoon seasons, providing locations from every month of the year. Individual *I. indica* were highly mobile and track distance correlated with the duration of tag attachment. Mean track duration was 38 days and mean track distance was >1800 km. Individuals dispersed in several directions: north-east into Somalian waters and up to northern Oman, east towards the Seychelles, and south into the Mozambique Channel. Their core habitat shifted seasonally and overlapped with areas of high productivity off Kenya, Somalia and Oman during the first half of the year. A second annual aggregation off the Kenyan coast, during August and September, did not coincide with high chlorophyll-*a* (chl-*a*) concentrations or thermal fronts, and the drivers of the species' presence and movement from this second aggregation was unclear. We tested their habitat preferences by comparing environmental conditions at track locations to the conditions at locations along simulated tracks based on the empirical data. Observed *I. indica* preferred cooler water with higher chl-*a* concentrations and stayed closer to the coast than simulated tracks. The rapid and extensive dispersal of *I. indica* from Kenya suggests that there is likely a single stock in the Western Indian Ocean, with individuals swimming between areas of high commercial catches off northern Somalia and Oman, and artisanal and recreational fisheries catches throughout East Africa and Mozambique.

KEYWORDS

billfish, fish movement, kernel utilization distribution, remote sensing, satellite telemetry

1 | INTRODUCTION

Black marlin *Istiompax indica* (Cuvier, 1832) are large, highly mobile predators distributed throughout the tropical Indo-Pacific (Collette & Graves, 2019; Nakamura, 1975). The species is primarily epipelagic (top 200 m), and has traditionally been associated with coastal waters (IOTC, 2017; Nakamura, 1985), although both mark-recapture (*i.e.*, conventional tagging) and electronic tracking studies have demonstrated that individuals also undertake extensive oceanic movements (Collette & Graves, 2019; Domeier & Speare, 2012; Ortiz *et al*., 2003). The application of conventional marker tags to recreationally fished marlin has demonstrated that individual *I. indica* can cross the Pacific Ocean and move between the Indian and Pacific Oceans (Ortiz *et al*., 2003). Satellite-linked archival pop-up tags (henceforth satellite tags) use light-level geolocation to estimate a series of intermediate animal locations and hence resolve a more detailed movement path, or 'track', for an individual. Studies using satellite tags have shown that the species' seasonal movements are often predictable (Collette & Graves, 2019). *I. indica* remained off north-east Australia in October and November, after which they dispersed widely into the Coral Sea and the South Pacific (Domeier & Speare, 2012). Individuals tagged off Taiwan swam north into the East China Sea in spring and summer, and south to the South China Sea in winter, dispersing ∼1200 km away from the tagging site (Chiang *et al*., 2015). *I. indica* also form relatively dense seasonal hotspots in several other locations, including in waters off Panama, Ecuador, and in the Arafura Sea between Australia and Indonesia (Nakamura, 1975).

Drivers of movements to some of these seasonal hotspots have been at least provisionally established: *I. indica* aggregate to spawn near the Great Barrier Reef (Domeier & Speare, 2012; Nakamura, 1975) and to feed off south-western Japan (Shimose *et al*., 2008). However, the movement ecology of billfishes is poorly known within the Indian Ocean, and no spawning areas for *I. indica* have yet been identified there (Collette & Graves, 2019; IOTC, 2017). Environmental preferences or tolerances may drive their movement in the absence of spawning, but these are not well understood, particularly in the Indian Ocean. In general, istiophorid billfishes prefer water of 22°C or warmer (Braun *et al*., 2015), with *I. indica* in the Coral Sea only dispersing southwards from northern Australia as temperatures of 26–27°C spread south (Domeier & Speare, 2012). Ocean temperature is arguably the best-understood and most influential environmental variable driving pelagic fish behaviour and distributions (Horodysky *et al*., 2016), and the location of thermal fronts is hypothesized to be an important driver of billfish distribution and seasonal movements (Braun *et al*., 2015; Rohner *et al*., 2020).

In the Western Indian Ocean (WIO), *I. indica* contributes to livelihoods and food security through artisanal fisheries, while recreational and charter sport-fisheries for the species, primarily catch-and-release, make significant contributions to the tourism industry in Kenya (Kadagi *et al*., 2020). *I. indica* are also caught in commercial fisheries, largely as a bycatch in gillnets and on longlines targeting tuna (Collette *et al*., 2011; Collette & Graves, 2019; IOTC, 2018). Their catches have increased in the Indian Ocean by an order of magnitude from the early 1990s, reaching over 20,000 tons in 2017 (Parker *et al*.,

2018). A paucity of data, however, has led to minimal management of commercial catches (Collette *et al*., 2011; IOTC, 2018).

Investigating the movements of *I. indica* in the WIO is an important start to guiding fisheries management. The species was once thought to be one single stock (Falterman, 1999), but more recently genetic data have delineated stocks that are geographically separated in the central Indo-Pacific, supporting the need for regional stock management (Williams *et al*., 2015). *I. indica* has been assessed as a single ocean-wide stock within the Indian Ocean (IOTC, 2017) based on preliminary genetic results (Williams, 2018). This Indian Ocean stock was classified as overfished in the 2016 stock assessments that used a Stock-Production Model Incorporating Covariates and a Bayesian State-Space Production Model (Andrade, 2016; Nishida, 2016). The Stock-Production model also suggested that even if catch was reduced by 40%, the species would still be at a high risk (70%) of being overfished. A more recent Bayesian state-space surplus production model found ambiguous results due to model misspecification, likely caused by erroneous input data for catch and catch per unit effort (Parker *et al*., 2018). Globally, too, *I. indica* is categorized as 'Data Deficient' on the IUCN Red List due to a lack of reliable stock assessments (Collette *et al*., 2011). These issues highlight the need for more information on the species to inform robust sustainable management, particularly as their habit of forming dense aggregations can leave the species vulnerable to impacts from even small-scale fisheries (IOTC, 2017).

I. indica are present biannually off Kenya during the north-east monsoon season, from December to March, and in the south-west monsoon from August to September. Their consistent seasonal presence indicates that predictable movement patterns may also exist in this region, similar to those in the Pacific Ocean (Collette & Graves, 2019). However, regional movement data are largely lacking, and no satellite tracks have been published for the species in the Indian Ocean. Some information is available from marker-tagged individuals from Kenya, which were largely recaptured off the Kenyan coast, with one fish recaptured off Yemen 159 days after release (Kadagi *et al*., 2011) and one recaptured off Manda Pam, India after 363 days at liberty. It is possible that *I. indica* largely stay in regional waters outside of the local fishing seasons, as indicated by marker tags. Alternatively, they may regularly move long distances, similar to striped marlin *Kajikia audax* (Philippi 1887) tagged off Kenya, which swam to northern Somalia and Yemen, as well as east to the Seychelles and the Maldives (Rohner *et al*., 2020).

Here we tagged 49 *I. indica* with pop-up archival satellite tags to examine their movements in the WIO. The study aimed to (a) map their short-term dispersal away from the tagging site in Kenya, (b) assess differences in movement patterns and characteristics between the two fishing seasons, and (c) examine potential environmental and biological drivers of their movements.

2 | MATERIALS AND METHODS

2.1 | Tagging location

I. indica were tagged off Watamu on the coast of Kenya (Figure 1). The Kenyan coast is a hub for billfish sport-fishers, with over
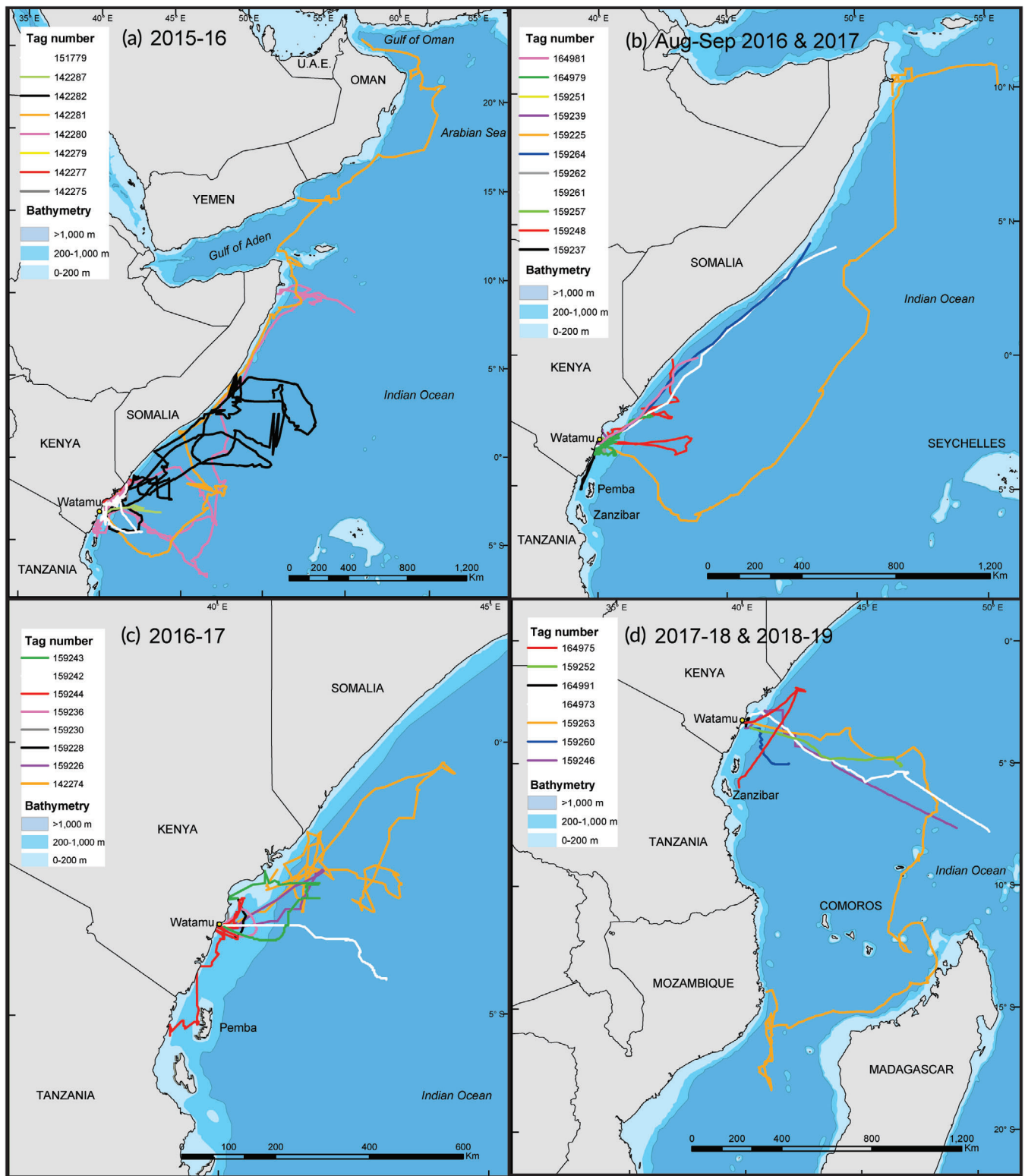
FIGURE 1 Most likely tracks of black marlin *Istiompax indica* tagged off Watamu, Kenya, with fish tagged in (a) the 2015/2016 season, (b) the two August–September mid-year seasons of 2016 and 2017, (c) the 2016/2017 season, and (d) the 2017/2018 and 2018/2019 seasons

30 recreational boats operating during the peak fishing seasons. The main fishing season runs from October to April, when *I. indica*, *K. audax*, blue marlin *Makaira nigricans* Lacepède 1802, broadbill swordfish *Xiphias gladius* and sailfish *Istiophorus platypterus* (Shaw 1792) are all regularly caught and released by recreational fishers.

Unlike other marlin species, *I. indica* are also caught during the shorter August–September fishing season. When targeting *I. indica*, recreational fishing boats typically operate in coastal waters within 40 km from shore. Water depths at tag deployment locations ranged from 8 to 687 m (mean ± S.D. = 205 ± 153.3 m).

2.2 | Tagging procedures

Experienced skippers, scientists, or trained crew of recreational fishing boats deployed 49 miniPAT satellite tags (dimensions 124 × 38 mm, 60 g; Tagware versions 2.04e, 2.04k & 2.04n) from Wildlife Computers (Redmond, Washington, USA). *I. indica* were tagged over 5 years, with 37 tags deployed between November and April during the main fishing season (2015–2019), and 12 tags deployed during the shorter August–September fishing season (2016–2017; Table 1). Tags were set to detach from the animal and start transmitting data *via* the ARGOS satellite system (www.argos-system.org) under three circumstances: (a) after the 180-day programmed deployment period; (b) if the tag exceeded its floatation crush depth at 1700 m; or (c) if the tag stayed at a constant depth for >24 h due to either tag shedding or a presumed mortality event. Tags also recorded depth and temperature time-series, and provided data on the sea surface temperature (SST) and time in the mixed layer.

The tagging procedure and tag attachment techniques followed methods outlined in Rohner *et al.* (2020) for *K. audax*. Briefly, *I. indica* were hooked by sport-fishers using live baits or artificial lures and brought to the boat ('fight time') while being kept in the water at all times. Drag settings and line strength varied among fishers depending on their preference. Only active, healthy individuals were tagged. The tag anchor was inserted between the dorsal pterygiophores using a handheld applicator ('handling time'). Most fish (86%) were then revived prior to release ('revive time'). Structural tag attachment setups varied over the course of the study in an attempt to improve tag retention. The tagging initially started with a single 'Domeier' umbrella dart, then a second dart was added to the tether, and later the second attachment was removed and the main dart was replaced with a nylon 'flopper' dart, as described by Rohner *et al.* (2020). Individuals were tagged during the day, between 7:45 and 17:00 h, and their weights were estimated by experienced skippers. Males and females are visually indistinguishable (Collette & Graves, 2019), so sex was not assessed.

2.3 | Ethical statement

This study and tagging process were conducted in line with ethical guidelines as provided for under University Research and the Ethics Review Committee (ERC) of Pwani University, and conditions of sport-fisheries licensing under the Fisheries Management and Development Act No 35 of 2016. All fish were tagged from licenced recreational fishing boats. The study was conducted under Kenyan research permit NACOSTI/P/19/2101 covering the Malindi-Watamu Biosphere.

2.4 | Movement analyses

We used state-space model GPE3 from Wildlife Computers to estimate fish positions from received tag data of light levels, SST, dive depth, GPS coordinates of the tagging location and the first reliable ARGOS location (class 1 or better) where the tag popped-up (Pedersen *et al.*, 2011). This approach uses a gridded hidden Markov model that calculates posterior probability distributions to estimate the most likely position at each time point based on constraints from light level, SST and bathymetric data. Input variables were tag deployment GPS locations and the pop-up location from ARGOS when transmissions started. Two tags detached from their respective fish and floated at the surface, but did not start transmitting data on time due to a clock error failing to initiate the constant depth release sequence (Wildlife Computers, pers. comm.). Depth data from these tags were used to identify when the tag detached from the fish and to truncate the horizontal track at that point. Swim speed (horizontal straight-line) is a required input variable for the GPE3 model and represents the standard deviation of a normal distribution of diffusion rate for the animal. *I. indica* in the Pacific Ocean had a maximum swim speed of 122 km day^{-1} (Chiang *et al.*, 2015). Following those results, we set the maximum swim speed in the GPE3 model to 200 km day^{-1} for the present study to not constrain the tracks if our fish swam faster. The GPE3 model was restricted to locations in the ocean. The model ideally estimated two locations per day (dusk and dawn) based on light levels, two additional locations per day (noon and midnight), and several locations when SST data were recorded. Duplicate locations recorded to store SST data were removed from spatial analyses. Not all location information was available on all days, but there were no gaps, and we estimated a mean of 5.8 locations per day of tracking. Model outputs included 50% and 95% confidence area ellipses on 0.25° grid cells, as well as the most likely location, multiple times per day. Up to 50 confidence area ellipses were plotted per track, allowing a robust assessment of the error in location estimates. We calculated track length as the sum of the shortest Euclidean (straight-line) distances between estimated locations of the most likely track. The daily distance covered considered these horizontal movements only and was calculated as track length divided by track duration. The estimated nature of light-level based locations means that track lengths and daily distances covered are approximations, even after applying a hidden Markov model using additional SST and depth data (GPE3). The maximum dispersal distance was calculated as the longest straight-line distance between the tagging location and the fish's position. We mapped the most likely tracks using ArcMap 10.4 and displayed the 200 and 1000 m bathymetry, since the species is unlikely to dive deeper than 1000 m (Williams *et al.*, 2017).

To investigate seasonal changes in the habitat use of *I. indica*, we mapped the activity hotspots binned by month of the year for all tracks combined. First, we temporally standardized tag locations by calculating centres of activity for each individual track at 12 h intervals (see Rohner *et al.*, 2020). Centres of activity are position estimates based on weighted means of location estimates over a time period (Simpfendorfer *et al.*, 2002). The monthly kernel utilization distribution (KUD) areas were then calculated based on the centres of activity, with href as the smoothing parameter, and a grid of 7000 using the *adehabitatHR* package (Calenge, 2006) in R version 3.6.1 (R Development Core Team, 2019). We calculated KUDs for each individual with >5 relocations (*i.e.*, >6 centres of activity) within a month and then took the mean of the individual KUDs to estimate the

TABLE 1 General tagging information for black marlin *Istiompax indica*

Tag number	Weight (kg)	Season	Deployment	Pop-up	Fate	Total distance (km)	Track duration (days)	Daily distance covered (km)	Maximum dispersal (km)
142275	55	NE	8 December 2015	31 December 2015	2	497.4	22.5	22.1	230.3
142277	70	NE	27 November 2015	26 December 2015	2	830.2	28.3	29.4	305.1
142279	73	NE	4 March 2016	15 March 2016	4	446.7	11.0	40.6	203.5
142280	65	NE	9 December 2015	6 June 2016	1	9505.2	180.2	52.7	2179.2
142281	60	NE	17 January 2016	19 July 2016	1	8187.2	184.2	44.5	3706.4
142282	109	NE	2 March 2016	16 August 2016	2	11,943.6	167.3	71.4	1598.3
142287	60	NE	12 January 2016	16 January 2016	2	920.0	4.1	225.5	427.6
151779	50	NE	25 January 2016	15 March 2016	3	1942.3	50.1	38.8	319.0
142278	60	NE	26 February 2016	No track	4				
142283	50	NE	24 December 2015	No track	4				
142289	90	NE	2 March 2016	No track	4				
142296	91	NE	7 March 2016	No track	4				
151778	110	NE	22 December 2015	Did not report					
159237	55	SW	24 August 2016	4 September 2016	3	416.3	10.8	38.4	213.6
159248	110	SW	12 August 2016	29 September 2016	2	1864.4	47.5	39.3	472.3
159257	150	SW	5 August 2016	13 August 2016	2	89.9	8.3	10.9	50.1
159261	70	SW	11 August 2016	27 August 2016	2	1393.9	15.5	89.8	1308.3
159262	40	SW	22 August 2016	30 August 2016	3	122.5	7.9	15.6	49.8
159264	80	SW	21 August 2016	2 September 2016	2	1258.7	11.7	107.7	1244.8
159254	70	SW	19 August 2016	No track					
142274	80	NE	23 December 2016	12 February 2017	3	2539.5	50.9	49.9	570.0
159226	50	NE	21 January 2017	1 February 2017	2	488.5	11.1	43.9	239.0
159228	150	NE	2 March 2017	8 March 2017	2	98.1	5.3	18.4	64.5
159230	80	NE	17 April 2017	22 April 2017	2	102.2	5.8	17.6	64.5
159236	90	NE	24 February 2017	27 February 2017	3	112.4	3.0	37.5	47.0
159242	70	NE	19 January 2017	26 January 2017	2	419.1	6.8	61.6	362.5
159243	160	NE	5 January 2017	20 February 2017	2	770.8	45.8	16.8	221.2
159244	120	NE	19 January 2017	12 February 2017	2	796.0	24.2	32.9	251.1
159227	85	NE	25 March 2017	No track	4				
159232	70	NE	14 February 2017	No track	3				
159245	110	NE	21 January 2017	Did not report					
159225	70	SW	13 August 2017	3 October 2017	2	4071.2	51.5	79.1	2312.0
159239	60	SW	15 August 2017	25 August 2017	2	158.5	10.3	15.3	64.5
159251	90	SW	8 September 2017	12 September 2017	2	30.0	4.0	7.5	31.6
164979	80	SW	27 August 2017	15 October 2017	2	1193.1	48.8	24.4	255.2
164981	100	SW	11 August 2017	17 August 2017	2	2473.4	6.3	390.5	644.5
159246	227	NE	13 February 2018	14 March 2018	2	1299.1	29.1	44.7	1079.7
159260	150	NE	23 March 2018	27 March 2018	2	340.8	3.7	92.7	282.6
159263	60	NE	29 December 2017	2 April 2018	2	4577.4	93.8	48.8	1697.5
164973	130	NE	13 February 2018	7 April 2018	2	1458.6	53.3	27.4	1204.3
164991	200	NE	20 March 2018	26 March 2018	2	100.8	5.4	18.6	31.7
164974	70	NE	14 March 2018	No track	4				
164980	70	NE	17 February 2018	No track	4				
164990	50	NE	2 March 2018	No track	4				
159252	80	NE	8 February 2019	22 February 2019	2	753.7	13.6	55.5	735.1
164975	75	NE	19 December 2018	14 January 2019	2	971.2	26.1	37.1	309.8

TABLE 1 (Continued)

Tag number	Weight (kg)	Season	Deployment	Pop-up	Fate	Total distance (km)	Track duration (days)	Daily distance covered (km)	Maximum dispersal (km)
164986	80	NE	15 March 2019	Did not report					
164988	90	NE	8 January 2019	No track	4				
164994	90	NE	2 February 2019	Mesopelagic predator					
Mean	88.9					1828.6	36.7	57.3	669.9
SD	38.6					2795.9	49.1	71.0	825.2
Min	40					30.0	3.0	7.5	31.6
Max	227					11,943.6	184.2	390.5	3706.4

Note. Fate categories: 1, pre-programmed end of 180-day tag mission; 2, premature detachment; 3, constant depth release at depth after 24 h, likely mortality; 4, mortality. Tags are grouped into deployment periods, with NE (north-east monsoon, November–April deployments) and SW (south-west monsoon, August–September deployments).

monthly distributions. This approach includes most tracks each month, even if the tags were only active for a subset of the whole month. The number of active tags and locations varied among months as tags detached over the course of the study (Supporting Information Figure S1). The 50% KUD represents the core habitat, and the 95% KUD area is the home range used during each month.

2.5 | Environmental conditions and simulated tracks

We investigated environmental conditions at marlin locations from the GPE3 model output to examine potential drivers of their movements. The estimated nature of the most likely locations from the GPE3 model output means that there is uncertainty in the environmental parameters that are extracted *post hoc*. SST was the main driver of marlin distribution in oceanic waters of the Pacific (Lien *et al.*, 2014), while it was chlorophyll-*a* concentration (chl-*a*) in the coastal waters of the Pacific (Acosta-Pachón *et al.* 2017). We examined both variables. We used tag-recorded (observed) SST from the GPE3 output, which resulted in a total of 9467 SST data points. Chl-*a* values for each location of all tags were extracted using the *rerddapXtracto* R package (Mendelssohn, 2019), with chl-*a* as a monthly composite level-3 data with a 4 km resolution obtained from the NASA MODIS Aqua satellites. Monthly means were chosen over 8-day means to reduce the number of missing values due to cloud cover, resulting in 12,170 data points, and only 1624 locations with a missing value. To assess whether *I. indica* frequented a vertically unrestricted habitat or stayed close to the coast, bathymetric values at marlin locations from the GPE3 output were extracted from the ETOPO1 dataset (Amante & Eakins, 2009) and the distance from the coast for each location was calculated using the *marmap* R package (Pante & Simon-Bouhet, 2013).

To assess the environmental preferences of tagged *I. indica* we then created 100 random tracks for each real track (Rohner *et al.*, 2018). These simulated tracks had the same overall track distance, the same step lengths, and the same angles between steps as the real tracks, but the order of the step lengths and angles was randomized.

Simulated tracks were restricted to locations at sea. We chose to randomize the observed angles, rather than taking random angles, to preserve the overall direction tagged *I. indica* took. We also chose to preserve the step lengths and overall track lengths to restrict the simulated tracks to the region of the real tracks (Supporting Information Figure S2). We then extracted SST, chl-*a*, bathymetry, and distance from the coast for the locations of the simulated tracks and compared the means to those of the real tracks with a *t*-test. We used the same procedures as described above for chl-*a*, bathymetry, and distance to coast, and for SST we used 8-day composite daytime level-3 data with a 4 km resolution from the NASA MODIS Aqua satellites.

To investigate seasonal variation in the wider region, monthly climatologies (*i.e.*, monthly means of SST and chl-*a*) were calculated using the same data product for chl-*a* as described above, and monthly composite daytime SST level-3 data with a 4 km resolution from the NASA MODIS Aqua satellites for SST. To represent *in situ* conditions for tagged marlin, we only used data from months that had at least one tag active, for example the January value incorporated mean data from 2016 to 2019, while for August we used data from 2016 to 2017.

2.6 | Mortality assessment

To infer post-release mortality, we used depth data transmitted prior to the tag floating. There were four scenarios to define the end of a track (Supporting Information Figure S3): (a) the tag detached as programmed after 180 days on the fish; (b) the tag detached prematurely and floated at the surface for 24 h before initiating data transfer due to the constant depth release; (c) the tag sank to a constant depth (the sea floor) and detached from the tether after 24 h due to the constant depth release being initiated, whereupon it floated to the surface to transmit data; and (d) the tag sank to a constant depth, but floated back to the surface after less than 24 h and initiated data transfer after floating at the surface for 24 h. We classified all tags in scenario 1 as having reached the programmed duration, and all tags in scenario 2 as having detached prematurely because the tether broke or was dislodged while still attached to the tag. The

inference from scenario 3 was complicated because we used a double tether on tags deployed in the August–September 2016 season (*n* = 7), which rendered that set-up negatively buoyant. Tags with only one tether floated. Four of the tags with a double tether dislodged and floated as per scenario 2, presumably due to tether failure, and only two sank as per scenario 3. Therefore, scenario 3 likely indicated a mortality event for tags with one tether, but it was ambiguous for tags with two tethers attached and we did not classify those as a mortality event. We classified scenario 4 as a post-release mortality because the tag did not remain at depth for 24 h to initiate the release, but rather floated to the surface early, suggesting dislodgement by predators at depth. The alternative, that the live fish directly dived to and stayed at a constant depth for hours to presumably recover from capture-related stress (Pepperell and Davis 1999), before vertically ascending to the surface and losing its tag there immediately, was deemed highly unlikely. We plotted Kaplan–Meier curves to estimate the survival probability over up to 180 days. This analysis incorporates missing data (Kaplan & Meier, 1958), which is useful here as few tracks completed the whole 180-day study period. We correlated the post-release mortality outcome with fish weight and with fight-, handling-, and revive times to examine potential influences. Other factors can also play a role and our assessment is not exhaustive, nor is it a dedicated study of mortality rates (Musyl *et al.*, 2015). We also correlated fish weight with fight, handling, and revive time. Before comparing groups, we tested the data for normality and used a Mann–Whitney test for non-normally distributed data. The normality of residuals of the dependent variable in linear regressions was tested, and the Siegel method of the Kendall–Theil nonparametric regression for non-normally distributed data was used in the package *mblm* (Komsta, 2019).

3 | RESULTS

Tagged *I. indica* ranged from 40 to 227 kg in estimated weight (mean ± S.D. = 88.9 ± 38.59 kg; Table 1). Fight times ranged from 5 to 75 min (23.95 ± 13.12 min), handling times from 1 to 6 min (3.44 ± 1.52), and revive times from 0 to 20 min (3.2 ± 4.09). Fish weight was correlated with fight time (Siegel nonparametric regression, *P* < 0.001) and revive time (*P* = 0.004), but not handling time (*P* = 0.9). Heavier fish took longer to be brought in and required longer revival times.

3.1 | Tag performance and mortality

Tag retention was the main challenge in this tracking study. Early tag loss was the largest factor contributing to a reduced data set, with 10 of 49 tags (20.4%) producing no track due to <1 day of data collection (Table 1). Most tags dislodged prematurely (end-of-track scenario 2; 57% of all tags). Likely mortalities were from scenario 3 (9%, excluding the ambiguous two tags with a double tether) and scenario 4 (22%), resulting in an overall mortality rate of 31.8%. Although there was no difference in weight between individuals suffering post-

release mortality (72.8 ± 15.6 kg) and those that survived (95.9 ± 46.2 kg, *W* = 255, *P* = 0.26), there were no post-release mortalities identified among the 11 individuals weighing ≥100 kg (Supporting Information Figure S4). Overall survival probability had the biggest drop on the first day, reflecting post-release mortality, although the 95% confidence intervals were large throughout the study period (Supporting Information Figure S4). There was no correlation between mortality event and fight time (*W* = 162, *P* = 0.86), handling time (*W* = 137, *P* = 0.84), or revive time (*W* = 127, *P* = 0.93). Ten of these mortality events occurred within a day of tagging, resulting in no track. Additionally, one tag (#159254) was lost off the fish immediately post-tagging, and one tag (#164994) may have been ingested by a mesopelagic predator, with depth readings consistently below 270 m depth over a month before the tag reached the surface and began transmissions. Three tags (6.1%) did not report any data. The remaining 34 tags were used for analyses and had a mean track duration of 36.7 days (± 49.1 days), ranging from 3 to 184 days (Table 1). Eleven tags (32.4%) stayed on for <10 days, while two tags stayed attached for the full programmed 180-day deployment duration (scenario 1).

3.2 | Horizontal movements

Tagged *I. indica* dispersed widely within the WIO (Figure 1). Their mean track length was 1818 km, with a range of 30 to 11,944 km. The large variation in track length was primarily explained by the variation in track duration, with shorter duration tracks having shorter track lengths (*P* < 0.001). Overall, they spent most of their time off Kenya and Somalia. Almost half (45.5%) of the individuals recording longer tracks (>40 days at liberty, *n* = 11) also stayed within Kenyan and southern Somalian waters. Some of the longer tracks extended further north to the Horn of Africa, into the Gulf of Oman, and south into Tanzanian and Mozambican waters. On the other hand, some shorter duration tracks also dispersed long distances. For example, two individuals with 12- and 16-day tracks (#159264 and #159261) swam over 1200 km north-east along the coast into Somalia. Both fish were tagged during the shorter August season. Easterly movements were restricted to shorter distances, not reaching the main islands of the Seychelles (Figure 1). Maximum dispersal from the tagging location ranged from 32 km to over 3700 km, with a mean of 667.4 ± 825.4 km (Table 1).

3.3 | Individual movements

I. indica tracks showed high variation among individuals. Tag #142281 had the longest dispersal distance, with the tag popping up in the Gulf of Oman, a >3700 km straight-line distance from the tagging location (Figure 2a). This individual swam east into offshore waters initially, returned to coastal waters off southern Somalia, and followed the coast northwards before crossing the Gulf of Aden and continuing north into the Gulf of Oman. The total track length for that individual
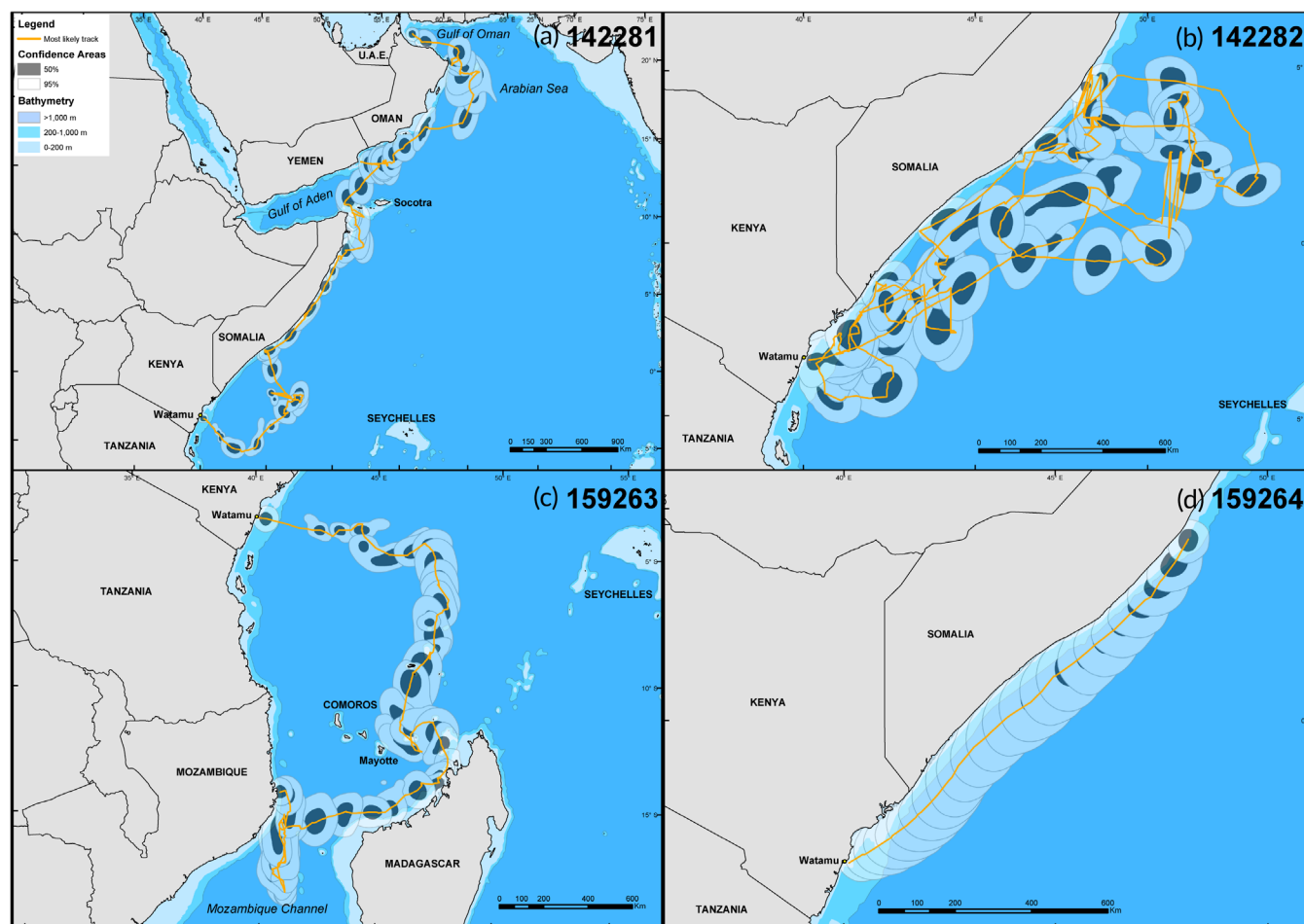
FIGURE 2 Most likely tracks and the 50% and 95% confidence areas of four individual black marlin *Istiompax indica*, with (a) tag #142281 that had the largest dispersal, (b) tag #142282 that had the longest track, (c) tag #159263 that went the furthest south, and (d) tag #152264 that dispersed widely in a short time

was the third-longest in our dataset, at ∼8200 km over 184 days, with an average of 44.5 km travelled per day (Table 1). The longest track in our dataset was tag #142282, with a total track length of almost 12,000 km in 167 days (Table 1). Confidence areas show the error margin associated with light-level based geolocations (Figure 2b), but the overall pattern of the track displayed intensive movements in waters off Kenya and Somalia. Perhaps the most unusual track was recorded by tag #159263, which extended a long-distance southwards, in contrast to most others that swam largely east or north-east. This individual initially swam ∼700 km east, then turned south to reach the north-west coast of Madagascar before spending extended time in the Mozambique Channel. The tag popped up just off the Mozambican coast (Figure 2c). One individual tagged in the August season (tag #159264) quickly dispersed north-east, covering an average of 107.7 km per day (Table 1). It followed the coastline north-east before the tag was shed off the central coast of Somalia after just 13 days (Figure 2d). Errors associated with these locations show that we can have confidence in the overall patterns from the most likely tracks in this study, but underline the uncertainty associated with estimated locations. Tracks and confidence areas for all individuals are shown in Supporting Information Figure S5.

3.4 | Temporal patterns and activity hotspots

I. indica had similar post-tagging movement patterns during and following both the north-east monsoon (December–March; Figure 1a,c, d) and south-west monsoon (August–September; Figure 1b) seasons. Although the number of locations and active tags varied throughout the year (Supporting Information Figure S1), there were no significant differences in track distance ($W = 113$, $P = 0.64$) or duration ($W = 104.5$, $P = 0.43$) between the two tagging seasons. Fish tagged during the August–September season largely spent time near the tagging location, with five tracks extending north into Somali waters. These individuals experienced cooler surface temperatures (25.84 ± 0.51°C) than those tagged during the north-east monsoon (27.9 ± 1.47°C, $W = 163{,}927$, $P < 0.005$).

Activity hotspots varied through the year (Figure 3). At the start of the December season, the core habitat (50% KUD area) was small and largely restricted to coastal Kenya. The core use areas then expanded east- and northward from January to March, with an additional core habitat recorded in the Mozambique Channel in March due to one fish swimming south to that region. Core habitats were north of Kenya from May onwards, including around the Horn of
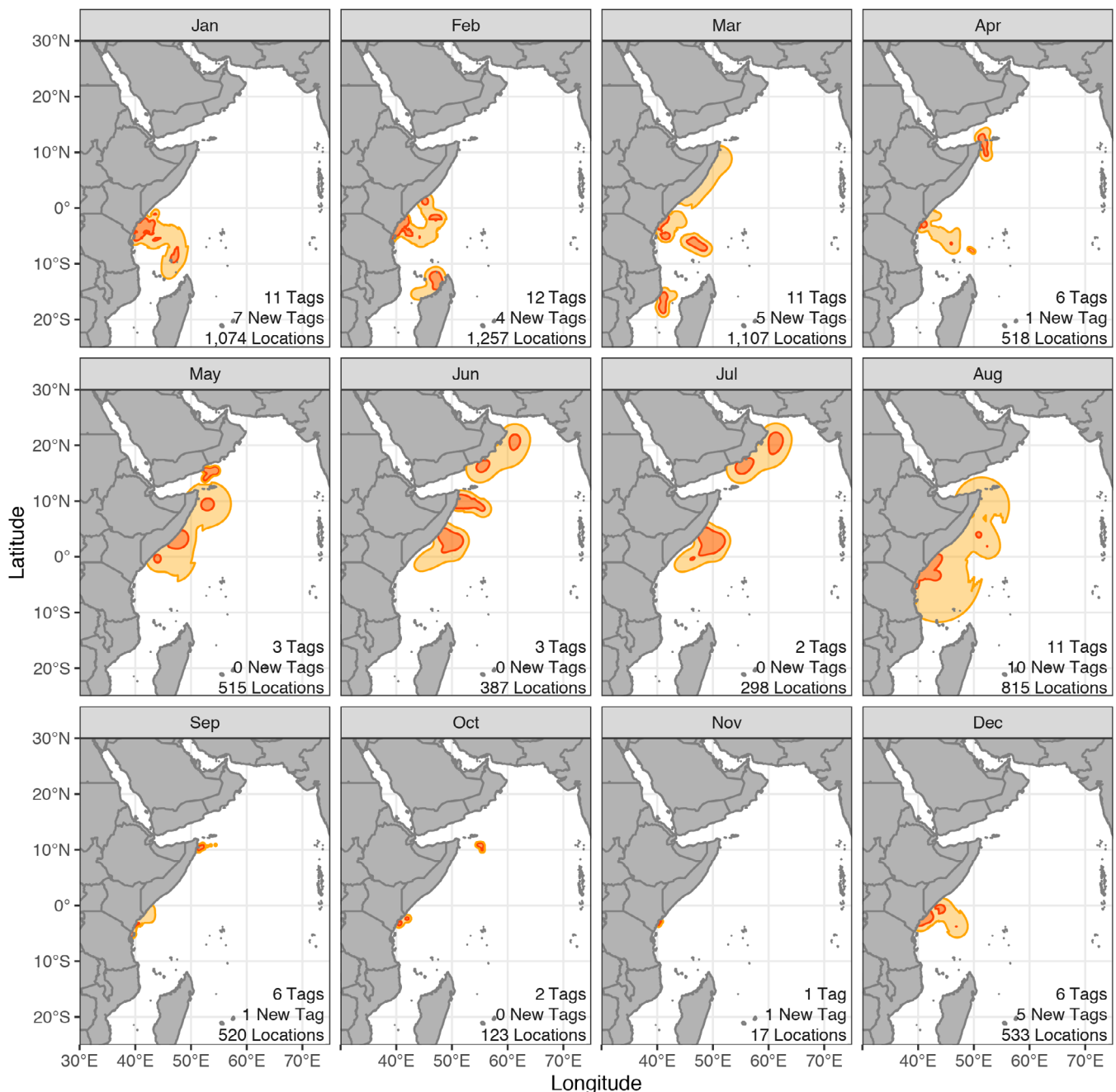
FIGURE 3 Map of the core habitat (red; 50% KUD) and the home range (orange; 95% KUD) for all black marlin *Istiompax indica* tracks combined and binned by month. The number of individuals tagged, the number of new tags deployed and the number of input locations (centres of activity) in each month are also shown

Africa and off Oman, before new tags were deployed off the Kenyan coast again in August and September. KUDs were smaller in the second half of the year when fewer tags were active (Figure 3 and Supporting Information Figure S1).

3.5 | Environmental variables

I. indica spent most of their time in areas with warm SSTs, with a mean of 27.4 ± 1.55°C. SSTs at marlin locations ranged from 20.3 to 30.9°C, but most (91.8%) were between 25 and 30°C (Figure 4a). September had the coolest mean surface temperature (25.3°C, n = 1371), while April was the warmest (29.7°C, n = 780). Tagged *I. indica* (mean = 27.4 ± 1.55°C) preferred cooler waters compared to simulated tracks (mean = 28.1 ± 1.77 °C, t = −20.7, d.f. = 2878, P < 0.001). Tag locations had a mean chl-*a* concentration of 0.7 ± 1.7 mg m^{-3} (n = 12,170). Most locations (79.4%) had low values <0.5 mg m^{-3} (Figure 4b). However, tagged *I. indica* preferred water with higher chl-*a* concentrations (t = 28.7, d.f. = 12,304, P < 0.001) than those from simulated tracks (mean = 0.27 ± 0.77 mg m^{-3}).

FIGURE 4 Histograms of environmental variables at black marlin *Istiompax indica* track locations (left) and at simulated track locations (right), with (a) sea surface temperature, (b) chlorophyll-*a* concentration, (c) bathymetric depth and (d) distance from the nearest coast. Dashed lines indicate the mean
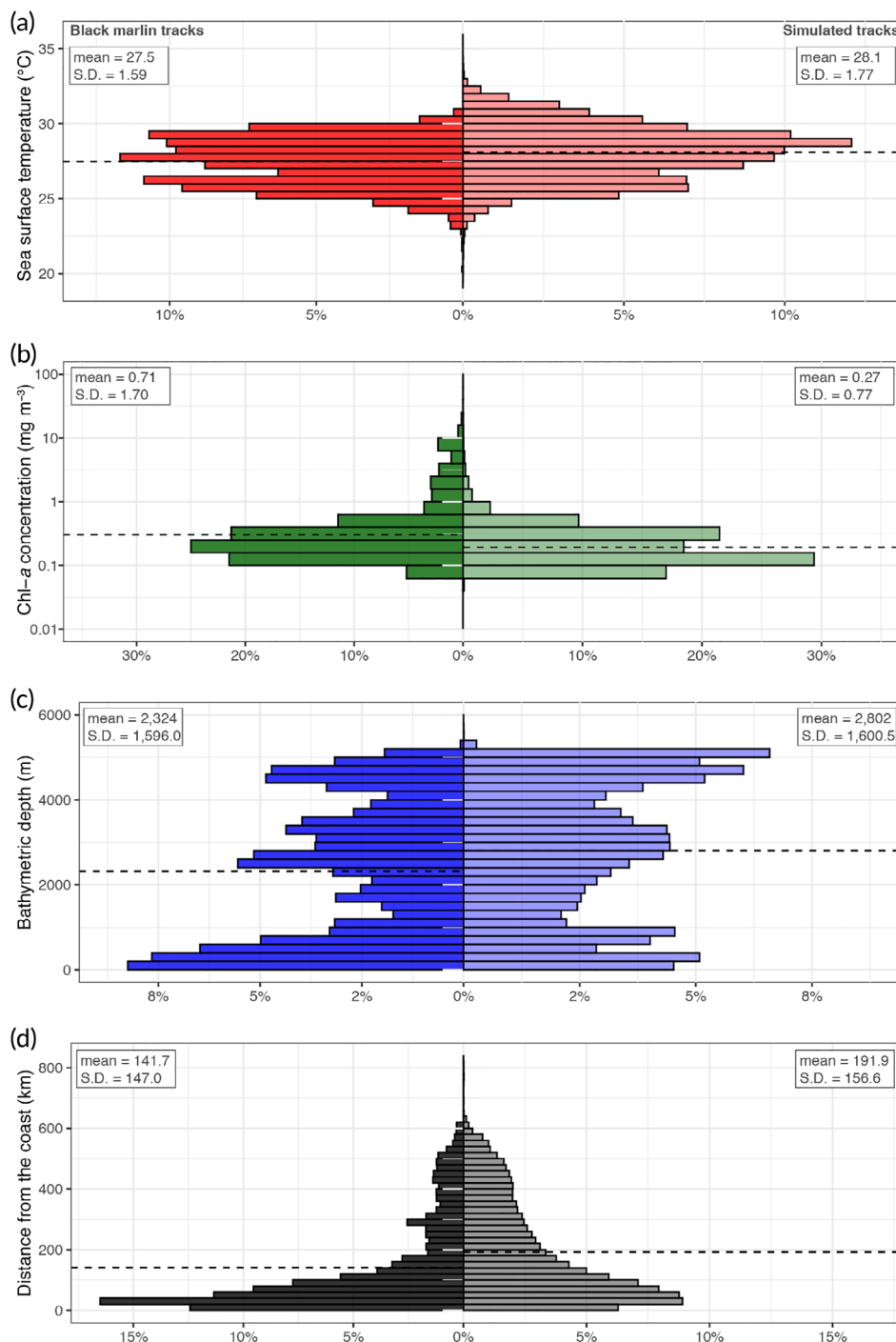
I. indica swam in waters with a large range of bottom depths (16–5278 m, $n = 11{,}576$), but preferred deep waters, spending only 3.9% of their time over continental shelf areas <200 m depth, 14.2% in waters <600 m depth and 28.6% in areas <1000 m depth (Figure 4c). Their mean depth (2324 ± 1596.0 m) was shallower than that of the simulated tracks (mean = $2{,}802 \pm 1600.5$, $t = 25.09$, d.f. = 7299, $P < 0.001$). Tagged *I. indica* spent 28.4% of their time within 40 km of the coast and over half (56.2%) of their time within 100 km of the coast (Figure 4d). They stayed closer to the coast (mean = 141.7 ± 147.0 km) than the simulated tracks (191.9 ± 156.6 km, $t = -28.66$, d.f. = 7389, $P < 0.001$).

3.6 | Oceanographic conditions

SST and chl-*a* concentrations varied spatially and temporally in the study region, reflecting the seasonal monsoon influence on this region. During the north-east monsoon (January–March), cooler waters of the southward-flowing Somali Current meet the warmer northward-flowing East African Coastal Current, resulting in a frontal zone that extends eastward (Figure 5). This frontal zone has relatively high chl-*a* concentrations, which overlapped with the core habitat of tagged individuals (Figure 6). In April, a core habitat area off the Horn of Africa coincided with the start of high seasonal
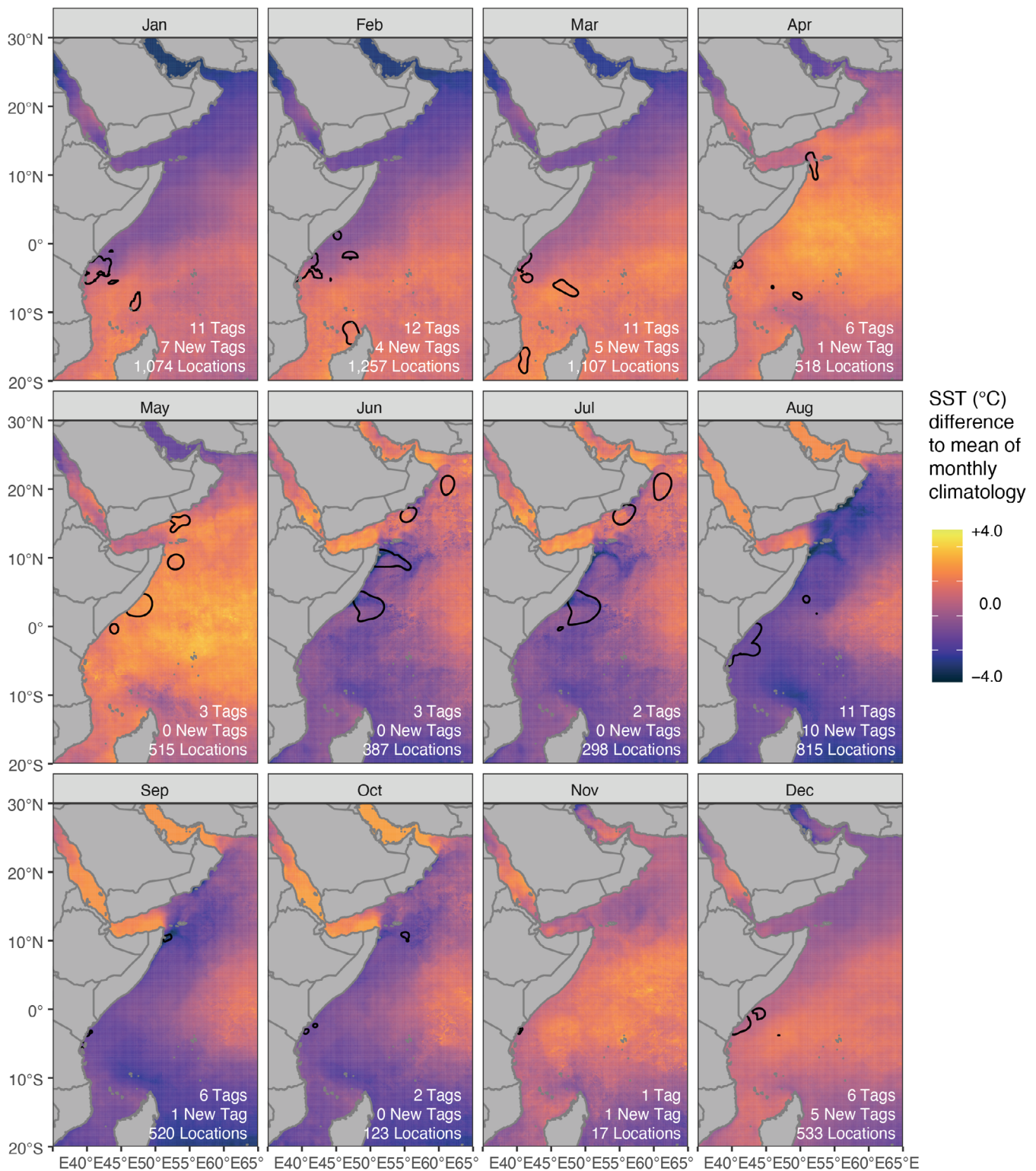
FIGURE 5 Monthly sea surface temperature climatology, calculated from data in months and years in which at least one tag was active, with the outline of the core habitat (50% kernel utilization distribution) overlaid in black. Note that the colour scale has a constant 8°C span relative to the mean temperature of each monthly climatology to visualize the thermal fronts. The number of individuals tagged, the number of new tags deployed, and the number of input locations (centres of activity) in each month are also shown

chl-*a* levels in this area, while primary production was low off Kenya. The high productivity in coastal waters of northern Somalia continued over the next months, but the core marlin habitats were further north off Oman and off central Somalia. Both of these locations also had high chl-*a* from June to September during the southwest monsoon (Figure 6). During this time, the East African Coastal
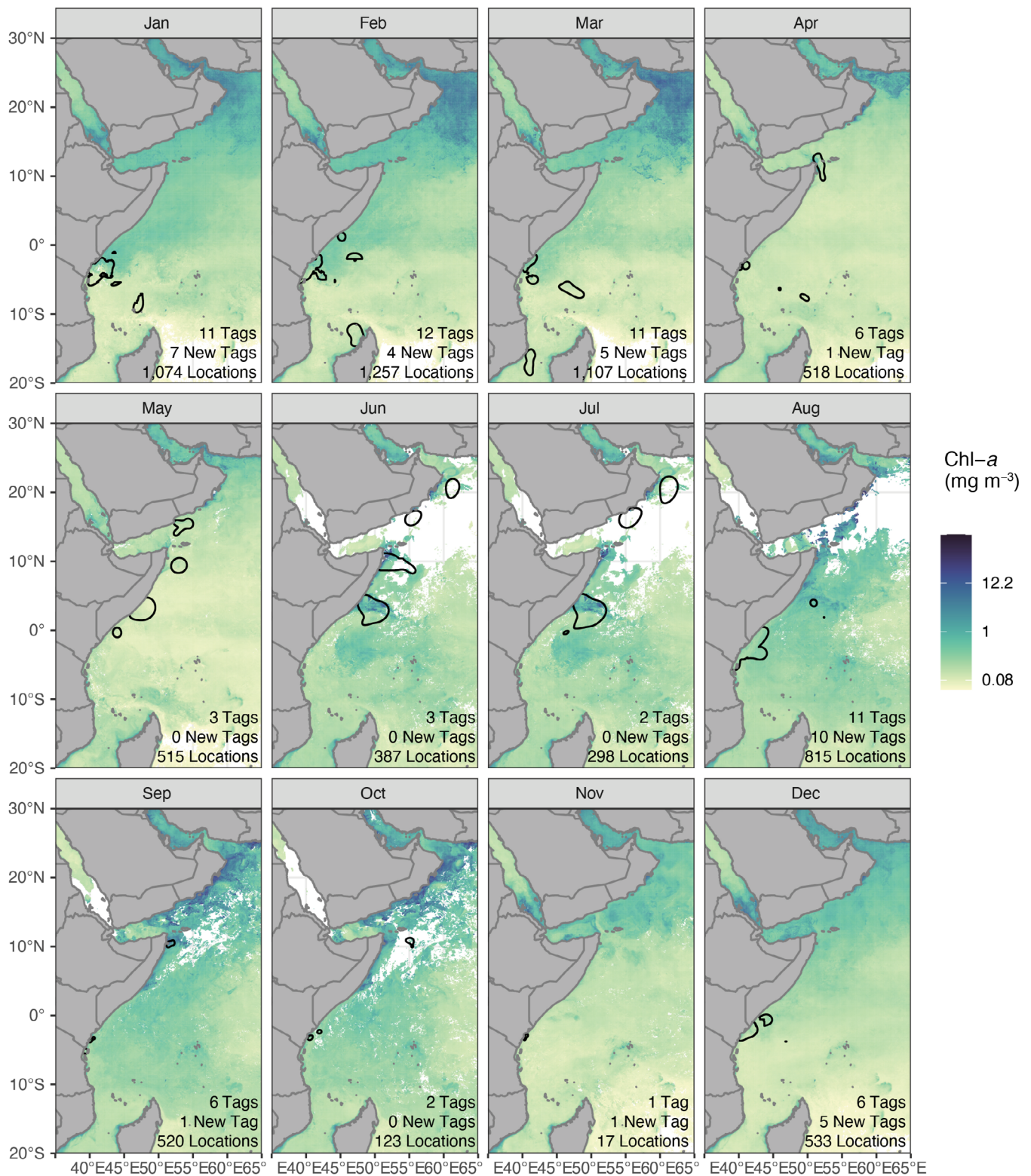
FIGURE 6 Monthly chlorophyll-*a* concentration climatology (log-transformed), calculated from data in months and years in which at least one tag was active, with the outline of the core habitat (50% kernel utilization distribution) overlaid in black. The number of individuals tagged, the number of new tags deployed, and the number of input locations (centres of activity) in each month are also shown

Current extended further north past Kenya, and upwelling was associated with the Great Whirl and the Southern Gyre in northern and central Somalia (Figures 5 and 6). The second fishing season

for *I. indica* off the Kenyan coast, and the associated core habitat in the same waters in August and September during the south-west monsoon, did not coincide with high chl-*a* at that time.

Furthermore, no clear long-duration thermal fronts were apparent in the area at that time.

4 | DISCUSSION

I. indica dispersed widely from the tagging location in Kenya, particularly to the north into Somalia, with one individual reaching the Gulf of Oman. Another individual moved south into the Mozambique Channel. The large sample size of 34 tracks, coupled with the biannual tagging season off Kenya, meant that we had tracking data covering all months, revealing seasonal changes in the location of their activity hotspots. *I. indica* encountered a variety of environmental conditions, but preferred cooler waters with higher chl-*a* levels compared to simulated tracks. The short mean track duration (∼37 days) was the main limitation of the results, as has been the case in previous billfish satellite tracking studies (Domeier *et al.*, 2019). Only two tags were retained for the full programmed 180-day deployment, while the others fell off prematurely. Post-release mortality may have also contributed to the short mean track duration, with individuals potentially more susceptible to capture- and tagging-related stress than *K. audax*, based on contemporaneous results from the latter species (Rohner *et al.*, 2020).

4.1 | Horizontal movements

I. indica swam far and fast, with a mean straight-line dispersal distance of 670 km from the tagging site, a mean track length of >1800 km, and an average daily horizontal distance of 57.3 km. While there was substantial variation among individuals, there was a predominant movement north-east into Somalian waters and east into oceanic waters. This pattern was broadly similar to that observed in *K. audax* tagged over the same period in the same general area, although they moved farther east past the Seychelles and to the Maldives (Rohner *et al.*, 2020). Other *I. indica* tagged in north-eastern Australia also dispersed widely (Domeier & Speare, 2012), suggesting that its movements away from high-density areas may be driven by environmental factors, along with local prey availability, rather than representing a distinct migratory pattern.

The activity hotspot off the Kenyan coast during December to March likely represents a feeding aggregation, since multiple species of billfish are successfully targeted by sport-fishers over this period (Kadagi *et al.*, 2020; Rohner *et al.*, 2020). Opportunistic macroscopic assessments of the gonadal development in landed fish do not suggest any spawning activity around Watamu to date (Supporting information Figure S6). During this study, the northward flow of the East African Coastal Current met the southward flow of the Somali Current off central Kenya, resulting in a strong thermal front that extended eastward, with associated high chl-*a* levels. This is a common pattern during the north-east monsoon (Schott & McCreary, 2001), but the upwelling location and intensity are variable (Jacobs *et al.*, 2020). From April to July, *I. indica* had activity hotspots off Somalia and

Oman. Their core habitat off the central Somali coast overlapped with the Southern Gyre, which was characterized by cold, high chl-*a* waters during the tracking years (and generally; Schott & McCreary, 2001). Notably, *K. audax* tagged off Kenya favoured an area further north off the Horn of Africa during May to July, where the Socotra Eddy and the Great Whirl result in strong upwelling, but the water is warmer than off central Somalia (Rohner *et al.*, 2020; Schott & McCreary, 2001). It appears that there is some partitioning between these two species in this region, with *I. indica* using slightly cooler surface waters than *K. audax* at that time, while the broader Somali waters are important for both species. The northernmost *I. indica* activity hotspot off Oman also overlapped with high chl-*a* waters, indicating potentially good feeding grounds. Large females have been reported from the Omani coast (RB, pers. obs.), indicating that this may also be a spawning area, but assessments of gonad development are needed to examine this hypothesis.

The biannual occurrence of *I. indica* off Kenya raises the question of what the drivers of their presence may be through the year. There were no clear differences in dispersal patterns between individuals tagged in the north-east monsoon *versus* the south-west monsoon. In contrast, *I. indica* movements off Taiwan showed a more defined seasonal pattern (Chiang *et al.*, 2015), with southward movements in winter coinciding with the onset of the spawning season (Sun *et al.*, 2015). During the second fishing season for *I. indica* off Kenya in the south-west monsoon, activity hotspots off Kenya and southern Somalia did not overlap with upwelling areas or thermal fronts. Oceanographic conditions during the south-west monsoon indicate that, similar to the preceding months, more productive conditions were available further north. Further investigation of this phenomenon is warranted.

4.2 | Environmental drivers of movement

Tagged individuals largely stayed in warm surface waters, with >90% of locations in the 25–30°C band. Similarly, individuals tagged in north-east Australia had an affinity for 26–27°C surface waters (Domeier & Speare, 2012). *K. audax* tagged off Kenya had a preference for slightly warmer surface waters, between 26 and 31°C (Rohner *et al.*, 2020). However, within those warm, subtropical surface temperatures, *I. indica* preferred cooler water and had a narrower distribution compared to simulated tracks in the same region. This may indicate that they seek out thermal fronts where prey is often concentrated (Braun *et al.*, 2015). We also found a seasonal difference in surface temperatures, with *I. indica* tagged during the north-east monsoon season spending more time in warmer water than those tagged during the south-west monsoon. The latter group also had access to warmer water in the region during the south-west monsoon, particularly off northern Oman and in the western Sea of Aden, but they did not frequent those areas. Their apparent shift to cooler temperatures suggests that other factors, such as prey availability or spawning, may be more important than SST in driving their distribution within this tropical to subtropical region. Chl-*a* concentrations at

tag locations were generally low, similar to that observed from *K. audax* tagging and fisheries data (Lien *et al.*, 2014; Rohner *et al.*, 2020). However, they were higher than the chl-*a* concentrations for simulated track locations, demonstrating a preference for productive waters. Some of the *I. indica* activity hotspots overlapped with regions of strong thermal and chl-*a* frontal systems, and had an even stronger affinity for high chl-*a* waters than may have been expected. However, considering that there is a temporal and spatial lag from chl-*a* to zooplankton blooms and an associated abundance of billfish prey species (Grémillet *et al.*, 2008), and also the temporal stability of high chl-*a* frontal zones in our study region, it might be unsurprising that *I. indica* were close to, but not directly within, areas of high phytoplankton abundance.

Frontal zones, with their concentrated productivity, are likely to be preferred billfish spawning areas (Braun *et al.*, 2015). *K. audax* tracks, and the location and timing of the appearance of their larvae, suggested that the area around northern Somalia and the island of Socotra may be a spawning area for that species (Pillai & Ueyandagi, 1978; Rohner *et al.*, 2020). It is plausible that *I. indica* also spawn in that area. However, the lack of data on their reproduction and larval distribution from this large region precludes a robust assessment of potential spawning locations.

Only one tagged individual swam south into central Mozambican waters, and no *K. audax* tagged off Kenya in a concurrent study swam into the Mozambique Channel (Rohner *et al.*, 2020). Low rates of movement between East Africa and southern Mozambican waters have been noted in other migratory megafauna, such as whale sharks *Rhincodon typus* (Smith 1828) and Indian Ocean humpback dolphins *Sousa plumbea* (Cuvier 1829), and this has been hypothesized to be a result of regional ocean currents creating a partial spatial barrier to dispersal (Mendez *et al.*, 2011; Prebble *et al.*, 2018). More tagging work from the Mozambique Channel would be useful for clarifying the connectivity with known *I. indica* aggregations off southern Mozambique and South Africa. Connectivity between East Africa and Mozambique is particularly interesting, as Bazaruto in Mozambique is a likely spawning area for the species; macroscopic examination of the gonads from two large (∼400 kg) individuals caught off Bazaruto in October 2017 showed that spawning was imminent for these fish (Supporting Information Figure S6).

Bathymetry appeared to have little influence on the distribution of either *I. indica* (here) or *K. audax* (Rohner *et al.*, 2020). We found >90% of *I. indica* locations were from waters deeper than 600 m, where their vertical movements are unconstrained (Williams *et al.*, 2017). As observed tracks remained closer to the coast than their simulated counterparts, *I. indica* prefer waters relatively closer to the coast, while still undertaking large-scale movements in deeper waters.

4.3 | Tag performance and mortality

Changing tag attachment mechanisms between seasons showed no clear ways to improve tag retention in either *I. indica*, as shown here, or in *K. audax* tagged over a similar period (Rohner *et al.*, 2020). We could not assess the many other factors influencing tag retention,

such as fouling, wound infection and variation in skill among different taggers (Musyl *et al.*, 2011), but the mean duration of 37 days was lower than for *I. indica* tagged elsewhere (Chiang *et al.*, 2015; Musyl *et al.*, 2011). Similarly, we could not assess all factors influencing post-release mortality (Musyl & Gilman, 2019) to conduct an in-depth mortality analysis. However, depth data provided evidence of mortality events that are worth reporting. While assigning the fate of individuals from short tag deployments can be challenging, tags that descended to depth soon after tagging and floated to the surface soon afterwards most likely represent post-release mortality events. For a small subset of the tags ($n = 7$), it was possible that these tags detached quickly and sank with double-tethers still attached, rendering the tag negatively buoyant (Rohner *et al.*, 2020). However, these tags stayed at depth for <24 h, as only after that period the programmed constant-depth release from the tethers would have been initiated. The shorter times at depth, as observed here, suggest that the tagged fish likely died or were predated upon by sharks, and sank to the bottom before predators or scavenging organisms caused the tag to detach and float to the surface. While seven tags did have two tethers, many other tags with a single tether were positively buoyant and would have floated immediately if shedding occurred as a result of the tag not anchoring firmly, incorrect placement, or if the fish itself ejected the tag by jumping or scraping on the substrate. It is possible that shark depredation following their release was a contributing factor in this biodiverse area (Barkley *et al.*, 2019; Mitchell *et al.*, 2018).

Assuming that these cases did indicate mortalities, the post-release mortality observed here for *I. indica* was relatively high (31.8%) compared to 14% for billfish in general (Musyl & Gilman, 2019), and 4% in *K. audax* tagged in a concurrent study in the same area (Rohner *et al.*, 2020). While we did not have a large enough sample size to conduct a dedicated mortality study (Musyl *et al.*, 2015), and the 95% confidence intervals of the Kaplan–Meier curve were too large to estimate survival probability, our results suggest that capture- and tagging-related stress could be an important mortality factor for *I. indica* in fisheries, even if they are subsequently released. None of the larger >100 kg individuals perished, but there was no correlation between size and mortality outcome here, as was also the case in a more detailed billfish mortality study (Musyl *et al.*, 2015). Mortality for the species has been reported in some previous satellite and acoustic tagging studies (Domeier & Speare, 2012; Musyl *et al.*, 2015), but not in others (Chiang *et al.*, 2015), although the latter study deployed tags on free-swimming individuals rather than employing catch-and-release sport-fishing techniques. Factors such as gear type and fight time did not influence mortality outcome in the meta-analysis study of Musyl *et al.* (2015), leading to the conclusion that these are likely to be stochastic events. It is thus unclear how to improve survival of *I. indica* in catch-and-release fisheries.

4.4 | Implications for fisheries management

I. indica are mainly harvested as a bycatch or secondary catch in commercial gillnet and longline fisheries throughout the WIO (Collette *et al.*, 2011; Collette & Graves, 2019; IOTC, 2018). There are two regional hotspots for billfish catches: the north-west area, east of the

Horn of Africa, and the south-west area off eastern South Africa and Mozambique (Yokoi et al., 2016). Long-time recreational fishing hubs for the species exist in Kenya, and in the Bazaruto Archipelago in Mozambique (Everett et al., 2008; Howard & Starck II, 1975). Our tagging data show that *I. indica* throughout the WIO could conceivably be part of the same stock, with tracking locations stretching over 5500 km along the coast from northern Oman to central Mozambique. Preliminary genetics result support connectivity in this region (Williams, 2018). Tagged individuals caught off Kenya routinely moved to the north-west hotspot of commercial catches, similar to *K. audax* that were tagged from the same area (Rohner et al., 2020). Commercial harvest of *I. indica* in the north-west Indian Ocean therefore influences their availability to artisanal and recreational fishers in Kenya. Further decline in their stocks is likely to lead to increased economic hardship among the local fisher groups in Kenya (Kadagi et al., 2020).

Our limited success with medium-term tag attachments means that the connectivity of *I. indica* populations across the Indian Ocean remains an open question. Further tagging work in the Eastern Indian Ocean, and basin-level genetics data, will be useful to further inform fisheries management of the species within the region.

4.5 | Conclusions

These first satellite tracks of *I. indica* from the Indian Ocean demonstrate rapid and broad dispersal from their dense seasonal aggregation off the Kenyan coast, and provide information on the environmental drivers that may influence the species' movement. Despite a relatively short mean tracking duration of 37 days, the tagged individuals reported here moved widely through the WIO, corroborating the long-distance movements seen previously from tracking studies in the Pacific Ocean (Chiang et al., 2015; Domeier & Speare, 2012). High connectivity with commercial fishing hotspots confirms that the current lack of defined fisheries management strategies for the species, and associated declines in their stocks, will negatively impact local fisheries, and effect the already hard socio-economic conditions evident in small-scale fisheries in Kenya.

AUTHOR CONTRIBUTIONS

S.P. and C.R. designed the study. R.B. and B.F. organized and conducted field work. C.R. analysed the data with assistance from A.J.R. and J.D.E. C.R. and S.P. wrote the draft manuscript, and all authors edited the manuscript.

ORCID

Christoph A. Rohner https://orcid.org/0000-0001-8760-8972
Jason D. Everett https://orcid.org/0000-0002-6681-8054
Anthony J. Richardson https://orcid.org/0000-0002-9289-7366
Simon J. Pierce https://orcid.org/0000-0002-9375-5175

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.