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RESEARCH

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Depth-based geolocation processing of multi-year striped marlin archival tag data reveals residency in the Eastern Pacific Ocean

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Abstract

Background: The first successful application of implanted archival tags on striped marlin showed great potential in obtaining long-term tracks for an improved understanding of movement ecology, which is important for informing fisheries management decisions. Ten tags were physically recovered from fish tagged in the Eastern Pacific between 2008 and 2016, but unfortunately due to the failure of the external sensor stalk which houses the light sensor, full records of daily fish position could not be attained.

Results: Depth-based geolocation, which exploits the diel swimming patterns of striped marlin, was applied to derive position estimates for archival tagged fish up to 7.7 years. Reconstructed tracks revealed tagged striped marlin remained in the Eastern Pacific throughout the tracked duration. Trans-equatorial movements were also documented for the first time for striped marlin in this region, as were extended occupancy of > 1 year in pelagic waters.

Conclusions: Striped marlin connected both coastal and offshore habitats with seasonal runs, likely in fulfillment of their life history requirements from foraging to reproduction. Circadian rhythms in billfish and other pelagic fishes are well-established, and could provide a viable, alternative means to position an individual in a low or no light environment, and situations with sub-optimal or limited bio-logging capabilities. Depth-based geolocation, however rudimentary, has revealed variability in striped marlin horizontal movements over the multi-year observation period, and offered a unique spatiotemporal perspective that was unavailable to scientists and fisheries managers until now.

Keywords: Billfish, Archival tagging, Dispersal, Eastern Pacific, Biological clock, Trans-equatorial movement

Introduction

Striped marlin, *Kajikia audax*, is the first istiophorid successfully tagged with archival tags [1]. Ten recoveries out of 99 implanted tags, with days at liberty ranging from 400 to 2795 days, demonstrated the possibility of long-term tracking of billfish beyond the 1-year limit that is currently attainable with popup archival satellite tags (PSATs). However, obtaining tracks for these recovered tags remained a challenge due the eventual loss of the external sensor stalks that housed the light sensor. Without ambient light measurements, light-based geolocation, the main methodology for geo-positioning archival tags and PSATs, cannot be employed. If location data could be determined, these first archival datasets for striped marlin with multi-year time at liberty have the potential to detail species dispersal and refine stock definitions in fisheries management. This is important as stock structures derived from tagging and genetic studies do not always agree and will require reconciling. Recent genetic work identified at least three distinct Pacific populations, and the presence of basin-wide migrants connecting aggregations off Australia and Ecuador [2], which

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in combination, have shown complexities in striped marlin movement ecology. PSAT tracks of striped marlin tagged in the Central North Pacific also documented the frequent crossing of management boundaries defined by different regional fisheries management organizations for conducting stock assessments and devising conservation and management measures [3], highlighting an emerging need to move towards an integrated, Pacific-wide management [4]. Delineating longer-term movements will be critical to our understanding of how fishing fleets interact with this species throughout the Pacific Ocean in times of changing climate and ecosystems.

Prior to the successful recovery of archival tags, movements of striped marlin off Mexico were elucidated with a total of 46 PSAT deployments [5], at liberty for up to 259 (mean 98) days. PSAT-tagged fish aggregated year-round off Baja California, and no individual went south of 10°N. Baja California is also a mixing area between October and January during which striped marlin tagged off Southern California traveled south [6]. PSAT tagging data showed that no fish tagged off Mexico ventured north of 31°N [6], despite conventional tag recaptures indicating that return trips to Southern California were undertaken by some individuals [7]. Such movement patterns, together with historical conventional tag recaptures and fisheries catch patterns, have led to the characterization that striped marlin were regionally aggregated, and localized to productive, coastal waters [8, 9]. A published track obtained from the archival tagging of striped marlin [1], however, has challenged this established view. Fish 990317 showed directed movement from coastal Mexican waters to offshore areas south of 10° N, covering > 2200 km over a 9-month period instead of remaining in the vicinity of productive coastal waters. This fish was eventually captured by an Ecuador-based fisherman 6.6 years after its release [1]. The long time at liberty of archival-tagged striped marlin hence provides a rare opportunity to investigate inter-annual variations in their movement.

The inability to acquire positional data for these archival tags due to the damaged light stalks represented a huge loss given the resources and effort invested in tag deployment and recovery and a disappointing waste of this valuable long-term dataset. Therefore, we developed a protocol to position tagged fish based on their logged depth data and provide the first, full set of multi-year tracks on striped marlin in the Eastern Pacific. This is based on the fact that striped marlin, like many pelagic billfish and tuna species, have been documented to exhibit diel swimming activities [6, 10]. Striped marlin are typically observed to utilize deeper depths near the base of the mixed layer or in the thermocline during the day, and occupy the top 5 m at night, and the transition between these depth strata is effected by descents or ascents around sunrise and sunset. This innate circadian rhythm has provided us a means to capture times of sunrise and sunset daily throughout a tag's deployment, as long as the depth sensor was functional. Similar approaches that utilize diel depth behavior for geolocation have been previously applied to bigeye tuna [11], silver eels [12], blue and shortfin mako sharks [13]. Despite our lack of understanding of the physiological mechanisms underpinning biological rhythms, perceptions of the environment and navigation, we present a systematic approach to utilize striped marlin's diel swimming patterns to estimate their inter-annual movements in the Eastern Pacific Ocean.

Materials and methods

Archival tagging

Detailed methodologies were previously published [1], so only a brief summary is presented here. Ninety-nine striped marlin were captured off Magdalena Bay, Baja California, Mexico (24.698° N, 112.228° W) in November of 2008–2010 using rod and reel, live bait, and circle hooks. Lower jaw fork length (LJFL) was measured from 150 to 228 (mean 187) cm. Archival tagging was performed on deck during which a seawater hose was attached to the mouth of the fish throughout the surgery. An incision was made in the epidermis, just off center of the ventral midline and forward of the anal fin, approximately in line with the posterior tip of the pectoral fin when laid along the side of the fish. A Wildlife Computers Mk9 archival tag (Redmond, WA, USA) was inserted into the peritoneal cavity, and the incision was then closed with Vicryl sutures (Ethicon, Inc., Somerville, NJ, USA). The archival tag is comprised of the logger (pressure and temperature sensors, clock, and memory) that was implanted inside the fish, and the external sensor stalk (light and temperature sensors) that protruded out of the fish body. To reduce drag, the sensor stalk was bent at 90° from its original manufactured configuration to allow it to lay flat against the body of a fish. Prior to release, a tagged fish was lowered into the water and restrained alongside the boat as the boat moved forward to aerate its gills.

Data retrieval

Ten archival tags were recaptured after tagged fish were at liberty between 400 and 2795 (mean 1569) days (Table 1). All tags had their external sensor stalk broken off from the logger after 32–286 (mean 83) days post-release.

Data from nine of the ten tags recovered were successfully downloaded after the tags had been physically recovered off Mexico ($n=8$) and Ecuador ($n=1$).

Table 1 Tagging and data summary for striped marlin, *Kajikia audax*

Fish identifier	Lower jaw fork length (cm)	Release date	Release latitude (°N)	Release longitude (°W)	Recapture date	Recapture latitude (°N)	Recapture longitude (°W)	Days at liberty (DAL)	Light geolocation (no. of days)	Depth geolocation (no. of days)	Increase in DAL coverage by depth
890271	183	2008–11-02	24.35	111.93	2011-12-25	19.11	104.6	1148	56	515	40%
890272	181	2008–11-02	24.35	111.92	2015-05-15	24.35	109.2	2386	85	519	18%
890289	174	2008–11-08	24.33	111.95	2016-07-03	24.33	109.6	2794	81	2794	97%
890295	173	2008–11-08	24.32	111.95	2010-03-02	N/A	N/A	479	Firmware error		
890381	201	2008–11-06	24.22	111.87	2015-12-13	24.22	110.1	2594	66	266	8%
990317	163	2010–11-12	24.1	111.37	2017-06-17	1.96	80.86	2410	286	298	0.5%
990333	180	2010–11-08	24.17	111.55	2011-12-12	24.17	105.9	400	32	105	18%
990339	201	2010–11-12	24.1	111.33	2016-03-15	24.1	108.5	1951	45	1942	97%
990357	173	2010–11-12	24.1	111.35	2012-09-02	N/A	N/A	660	47	461	63%
990363	185	2010–11-12	24.1	111.38	2013-04-01	24.1	112.6	872	52	464	47%

Swimming depths were recorded for the entire deployment in two tags (1951 and 2794 days), but logging was terminated in the others after 102–530 (mean 447) days post-release due to saltwater intrusion following the loss of the external sensor stalk (Table 1).

Track reconstruction

Normally, positional data from implanted archival tags can be calculated using the logged light data by a variety of light-based geolocation routines, e.g., Wildlife Computer's GPE3 (static.wildlifecomputers.com/Location-Processing-UserGuide.pdf). However in this case, the external sensor stalks on all recovered tags were broken off at some point during the deployment (Fig. 1a), resulting in GPE3-derived tracks lasting only between 32 and 286 days [1]. To determine geolocation for these multi-year deployments, a depth-based geolocation method that exploits the diel swimming behavior of striped marlin was applied to the 1-min archival depth records with coverage from 102 to 2795 days (Table 1).

To determine times of sunrise and sunset (TSS), we relied on the identification a daily depth threshold that distinguishes nighttime and daytime depth occupancy by a tagged striped marlin (Fig. 1b), in the same manner that a light level threshold was used by Hill and Braun [14] in developing the first-generation light-based geolocation algorithms. Specifically, a histogram of depth values was built using 5-m bins every day during which a tagged fish was at liberty. Additionally, monthly depth histograms were constructed for all calendar months (e.g., 2008 March, 2009 March) for each fish. These histograms typically featured a bimodal depth distribution, indicative of the diel swimming behavior of striped marlin as described earlier. A search routine was then applied to a depth histogram to select the 5-m bin that was equidistance between the two modes as the depth threshold. This threshold was generated daily, but in any day during which the bimodal distribution was absent, i.e., diel swimming behavior was not observed, we substituted the threshold with that derived from the corresponding monthly histogram. Supplied with daily depth thresholds, a scanning algorithm then ran through the archival time series to identify the timestamps that a daily depth threshold was crossed during crepuscular periods, forming the TSS. We then applied a 5-day moving average (i.e., 2-d before and after) to the TSS. Such a smoothing technique has shown to reduce local variability and improve overall track reconstruction in swordfish [15]. Smoothed TSS (Additional file 2), along with a tagged fish's release date and position, were then input into the R package '*GeoLight*' [16] which used standard astronomical equations [14, 17] to calculate longitude and latitude. Longitude-latitude pairs (XYS) were then passed through a state-space Kalman-filter model, *kftrack* [18] to estimate a depth-only track (Fig. 1c).

A depth-only track (ZON) could be improved by incorporating portion of the light-based Wildlife Computer's GPE3-estimated track. To do so, we removed all XYS during which the external sensor stalk was still intact. Utilizing the last position of the GPE3-estimated track as the starting location, the remaining XYS were then refitted with *kftrack*. To identify this start was an estimate, rather than a known position e.g., site of fish release, the option "*fixed.first = FALSE*" was specified in *kftrack*'s main function call. The resulting positions were then appended to the GPE3-estimated portion to form a combined track (Fig. 1d).

From a combined track and its associated errors, positions were regularized to daily resolution using the R package '*crawl*' [19]. This regularization step was most noticeable in periods around the March and September equinoxes, during when TSS-based geolocation cannot estimate any positions as inherently limited by physics [17]. Interpolated waypoints would appear linear around the equinoxes. As a last step, bathymetric correction was applied to positions that were placed on land following the protocols in Galuardi et al. [20].

Horizontal movement

A utilization distribution (UD) was generated with all pooled positions on a bimonthly basis, with UD values between 0 and 50% representing high use areas [21]. To aid the interpretation of fish dispersal, bathymetric values from Smith & Sandwell Topography (0.0167° resolution, version 11.1) were obtained from the Copernicus Marine Service Global Monitoring and Forecasting Centre (CMEMS; marine.copernicus.eu). Surface temperature isotherms at 24 and 18.5 °C were also obtained from World Ocean Atlas 2013 monthly dataset [22]. The 24 °C isotherm has shown a strong association with fisheries catch distribution [23–25] and tagged fish [10]. The 18.5 °C isotherm is approximated to be the lower thermal boundary above which accounted for 90% of water temperatures occupied by striped marlin [6]. Dissolved oxygen at 100 m was also extracted from World Ocean Atlas 2013 monthly dataset [26], and contoured at 2 ml L^{-1} to denote the extent of the oxygen minimum zone (OMZ) in the Eastern Pacific.

Management boundaries of the Inter-American Tropical Tuna Commission (IATTC) were accessed through RAM Legacy Stock Boundary Database (marine.rutgers.edu/~cfree/ram-legacy-stock-boundary-database). These boundaries allow determination as to whether a tagged fish had left the management jurisdiction at any time over the course of the tracked period.

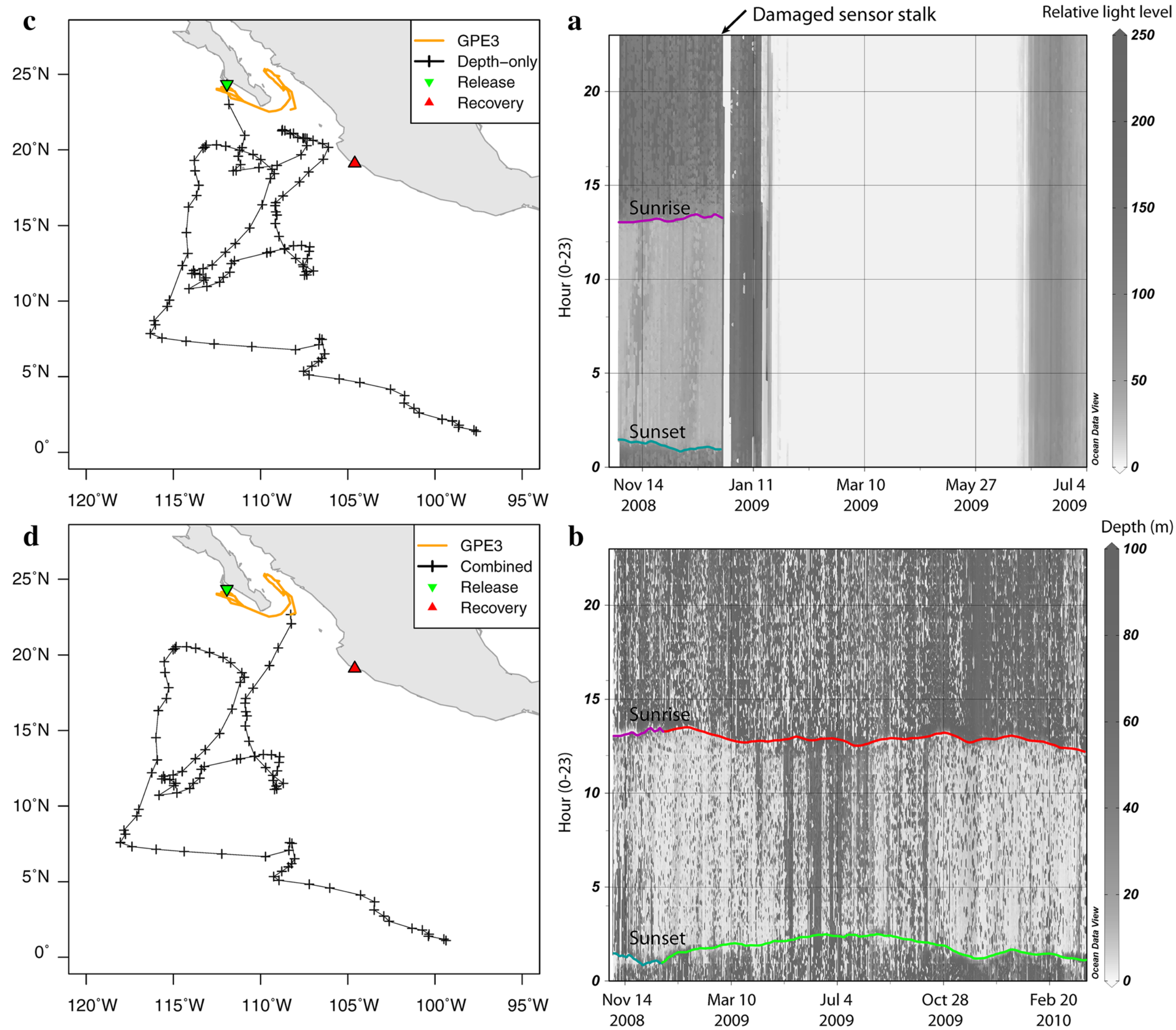

Fig. 1 Positioning of archival-tagged striped marlin (Fish 890271) using depth records. Clockwise from top left. **a** Light level data were properly sampled by sensor embedded in the external sensor stalk until the stalk was damaged less than two months post-release. Rise and fall in logged light levels corresponded to changes in ambient light throughout a 24-h day (*y*-axis, hours in UTC), with times of sunset and sunrise outlined in turquoise and purple, respectively. As soon as the sensor stalk was damaged, and eventually fell off, logged light level no longer reflected changes over the course of a day. **b** Depth data were still available many months after the external sensor stalk was damaged, as the pressure sensor was housed inside the main logger implanted in the fish's body cavity. Diel swimming activities, including deeper during daytime and shallower at night, coupled with crepuscular ascents and descents have allowed an estimation of times of sunset (red line) and sunset (green line) in UTC. These solar events could then be used in the astronomical derivation of longitude and latitude estimates. **c** Track estimates obtained with logged light via Wildlife Computer's GPE3 model (orange line), and with depth via our depth-based geolocation strategy (black line, crosses). Release (start) location is denoted by a green triangle, and tag recovery location by a red triangle. Note depth-logging terminated 626 days prior to physical tag recovery, which accounts for the apparently large discrepancy between the last track position and recovery location. **d** Final reconstructed track utilizing both light-based and depth-based positions

Results

Track reconstruction

Depth-only positions (ZON) were successfully derived for all nine tags, and extended overall geolocation coverage (Table 1). Fish 990317 logged a similar number of data days for both light and depth, and therefore provided the opportunity to evaluate ZON relative to those of GPE3. Without double-tagging the same animal with a radio-linked (Argos or GPS) tag, there is no accurate reference to "ground-truth" geolocation methods [27].

Therefore, the only option was to compare GPE3 and ZON positions, with the goal of finding convergence in their track solutions.

Absolute distance between GPE3 and ZON positions for Fish 990317 was 307 ± 181 km (mean ± sd; Additional file 2). GPE3 and ZON tracks followed each other throughout most of the deployment (Fig. 2), particularly in their longitudinal spread. Their alignment was strongest around 13° N 95° W where the tracked marlin spent extended time, and along ~ 109°W where the fish traveled south. Some ZON positions, derived in the absence of any constraint, were placed on land in parts of the Mexican coastal waters. In contrast, GPE3, utilizing both bathymetric and temperature constraints, kept all positions off land. Overall, there was good agreement between GPE3 and ZON trajectories, and demonstrated depth-based geolocation is a valid approach for reconstructing broad-scale movements of striped marlin.

Horizontal distribution

Archival depth data allowed the reconstruction of nine tracks for a total of 7364 daily positions (Additional file 3). Detailed analysis of individual waypoints requires an investigation in combination with vertical movement data and environmental features, thus cannot be adequately covered in the current work. Instead, horizontal movement patterns are characterized with reference to local places, bathymetric and oceanographic features.

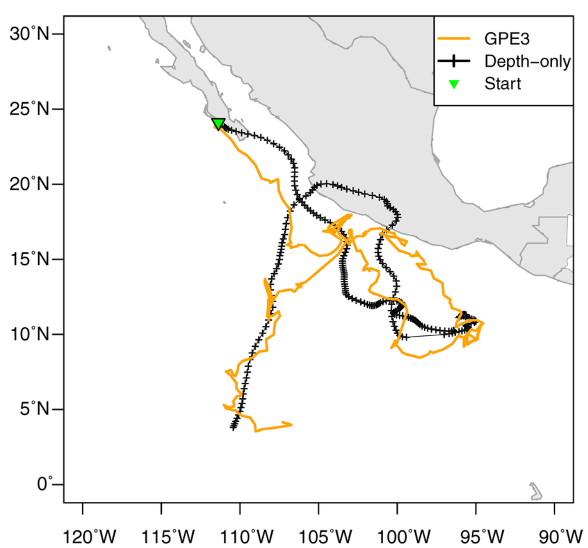

Fig. 2 Relative track estimates of Wildlife Computer's light-based geolocation model, GPE3 (orange line) and our depth-only geolocation (black line and crosses) for Fish 990317. GPE3 is a hidden-Markov model incorporating light-based geolocation with sea surface temperature (SST) and bathymetric covariates. Release (start) location is denoted by a green triangle

Available tracks showed all tagged fish remained in the Eastern Pacific, spanning 93–132° W and 16° S to 31° N (Fig. 3). With respect to the IATTC management, only 1.7% of fish positions occurred outside of its jurisdiction, and 71% were found in statistical area A3. Striped marlin concentrated (UD < 50%) around 105–119° W and 13–28° N, and off the tip of Baja California over the course of a year. Core use areas for striped marlin changed seasonally (Fig. 4). In the winter months (November–February), striped marlin aggregated off the southern tip of Baja California in both the Pacific Ocean and the Gulf of California, and north of Islas Marías off the Mexican coast (Fig. 4a, f). By March, key habitat expanded over a broad area southeast and southwest of Baja California (Fig. 4b). Fish concentrated around the Revillagigedo Islands, and were potentially associated with various seamounts located between the Revillagigedo and waters north of 10°N, to the west of Clipperton Island. This association remained through June (Fig. 4c). Occupancy of oxygen-depleted waters west of the Galápagos Islands was prominent from March to June. In the summer months (July and August), core area was in pelagic waters between 10 and 19°N, and centered south of the Revillagigedo Islands (Fig. 4d). The majority of their habitat had sea surface temperatures ≥ 24 °C. By September, striped marlin headed north towards Baja California. Their core habitat remained pelagic, north of 19°N along the 24 °C SST isotherm, just outside of the OMZ (Fig. 4e). Striped marlin then returned to the Magdalena Escarpment off Baja California and coastal Mexican waters (Fig. 4f). Few fish were found in waters with SST < 18.5 °C throughout the year.

Temporal variations in individual movement

Two individuals (890289 and 990339) were tracked for seven and five full calendar years respectively, and displayed year-to-year variations in their horizontal movement (Additional file 1: Fig. S1). Fish 890289 utilized the southern tip of Baja California and the Mexican coastal waters in winter and early spring over six out of nine tracked years (Fig. 5). Throughout mid-2012 to September 2013 and 2015 to mid-2016, this individual remained offshore between 0 and 20° N, away from the coastal aggregations. During May to August across all tracked years, this individual was found farthest away from the coast, and south of 18° N. This fish covered the largest latitudinal reach (27° N to 11° S) in 2010, and visited waters southwest of the Galápagos Islands in spring. Similarly spring or summer forays to pelagic waters east of the Galápagos occurred in 2013 and 2014.

Fish 990339 was more restricted to the longitudinal band between 110 and 125° W and its variations in movement were primarily in the north–south

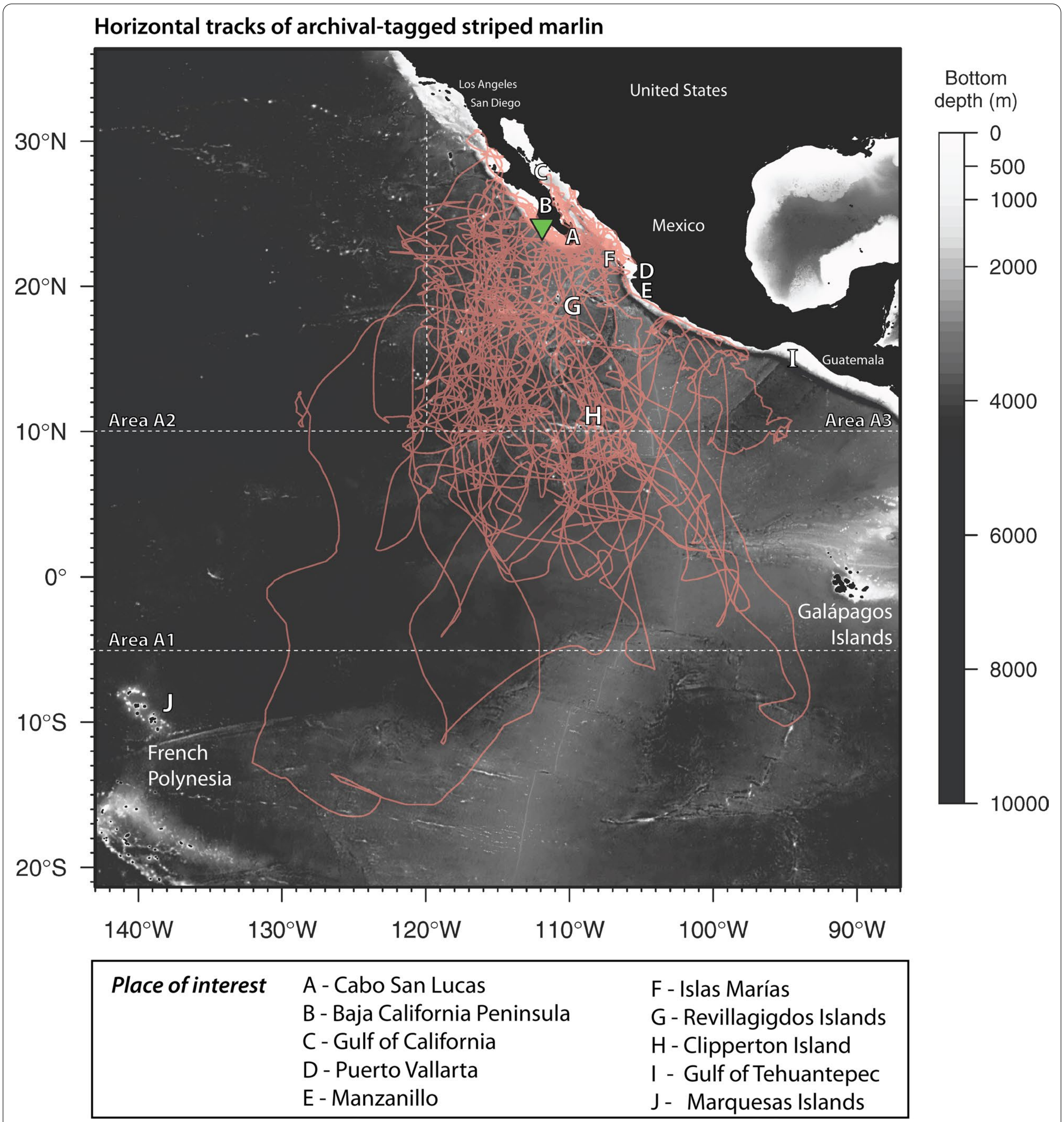

Fig. 3 Horizontal tracks of archival-tagged striped marlin. Tracks are outlined in red, and tagging site is denoted with a green triangle. Selected locations are labeled (**A**–**J**). Bottom depth is represented in greyscale. Management boundaries of the Inter-American Tropical Tuna Commission are outlined by dotted white lines

direction (Fig. 6). The range of horizontal movements was similar in 2011 and 2012, and this individual only reached as south as 12°N during the summer months. In contrast, the fish went south of 12°N every summer in 2013–2015, and remained offshore for the entire 2014. Much like Fish 890289, this marlin spent its winter months either off Baja California or in pelagic waters between 10 and 20° N.

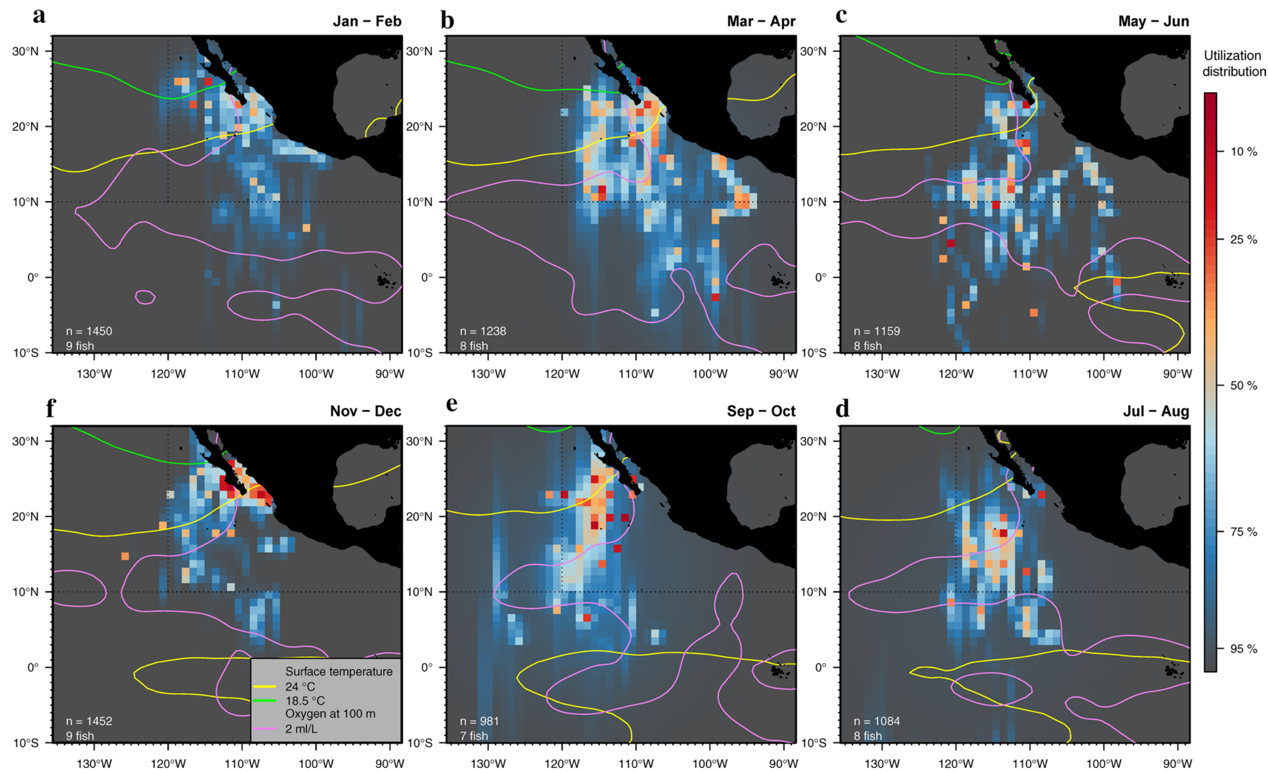

Fig. 4 Bimonthly spatial use of the Eastern Pacific by archival-tagged striped marlin. Utilization distribution (UD) is represented in false color. UD values of less than 50% signify high use areas. In each panel, monthly climatological surface temperature isotherms at 18.5 (green) and 24 °C (yellow) are contoured. Spatial extents are also shown for 2 ml L^{-1} dissolved oxygen at 100 m (lavender). For clarity, only isotherms and dissolved oxygen extents from the second month of each period are shown. The number of individuals and positions available are indicated. Management boundaries of the Inter-American Tropical Tuna Commission are outlined by dotted lines

Synchronicity of horizontal movement

Four individuals released within a week of each other in 2008 (Table 1) showed a broad agreement in seasonal occupancy of latitude ranges over the next two years (Fig. 7). For example, from January to March, tagged marlin remained mostly north of 10°N in 2009, and all traveled south of 10°N in 2010. Three fish (890271, 890272, 890289) took different trajectories since their release but were found together again among the various seamounts (~113°W 15°N) south of Isla Socorro, Revillagigedo Islands during July–August 2009.

Among five fish tracked in 2011, variations in individual movement were prominent (Fig. 8). Cyclic migrations were observed for three striped marlin, each of which departed to disparate destinations after wintering off Baja California. Fish 900363 reached an offshore area (132°W 13°S) to the east of the Marquesas Islands of French Polynesia, while Fish 900339 covered a shorter distance between Gulf of California and the Revillagigedo Islands. Fish 890289, as did 990317, undertook a southeasterly course along the coast to reach waters just north of the Gulf of Tehuantepec, where strong coastal eddies were known to contribute to a high productivity [28].

Discussion

This work presents the first, full reconstruction of multi-year tracks from archival-tagged striped marlin. Tracked fish showed consistent habitat use in the Eastern Pacific between 2008 and 2016, with core use areas off Baja California and offshore of the Revillagigedo Islands. Similar seasonal habitat for striped marlin had been identified in the Eastern Pacific using historical and recent fisheries catch records [7, 8, 29, 30], suggesting this habitat utilization is temporally stable. Many of these areas are likely ecologically dynamic, as they are characterized by complex bathymetric features (e.g., coastal shelves, seamounts, ridges and fracture zones), a mean mixed layer depth of 20–60 m [31], and dissolved oxygen at 100 m less than 2 ml L^{-1}. A subsurface chlorophyll maximum at 60–90 m also extended from 10°S to 20°N across the longitudinal band of 110–120°W [32]. Sea surface temperature fronts often persisted from 3 months to years, especially within the region of 102–121° W and 18–35° N

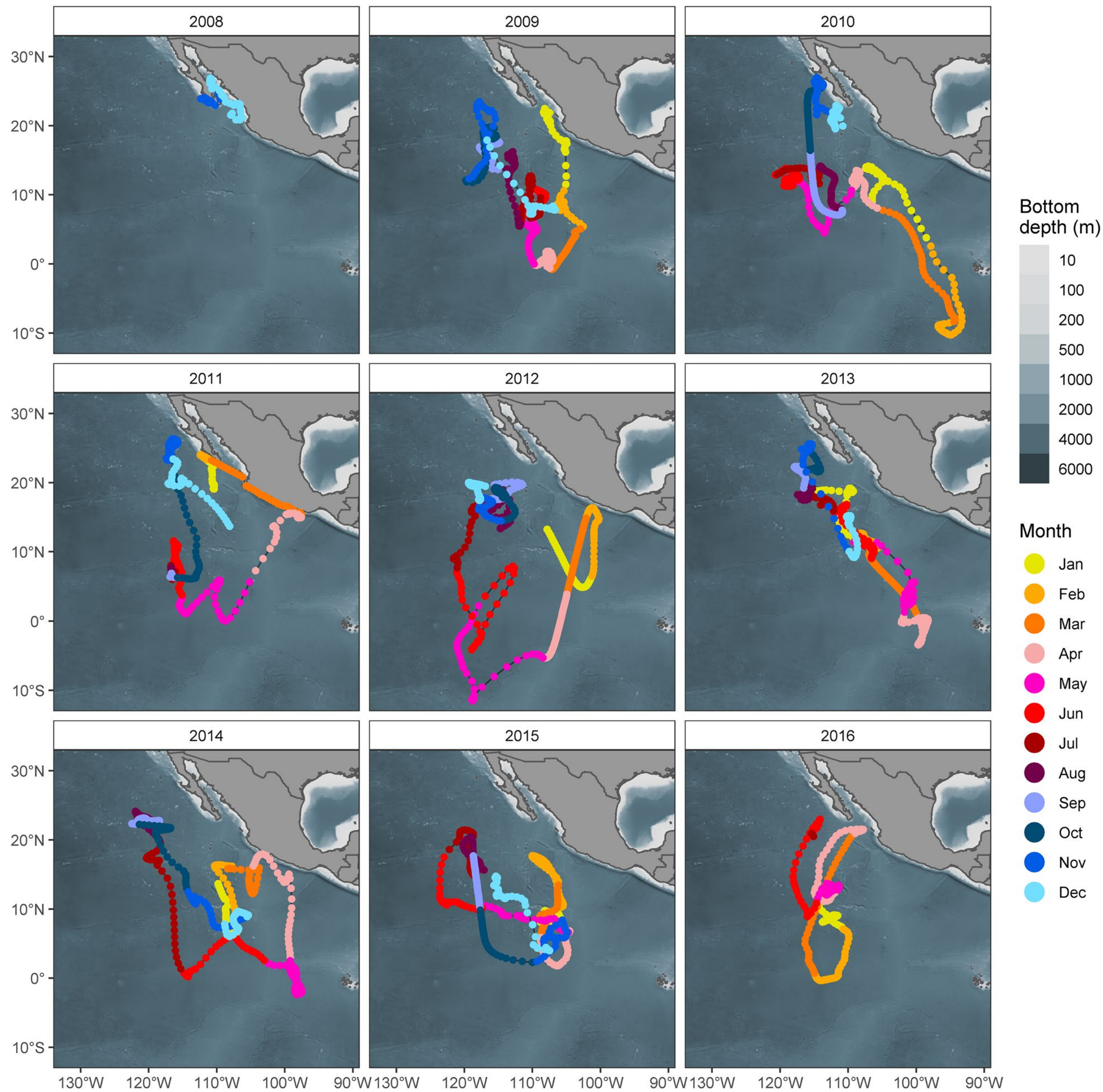

Fig. 5 Movement track of Fish 890289 between 2008 and 2016. Positions are color-coded by months and each panel represents a single tracking year. Bathymetry is plotted as false color

[33]. It is conceivable striped marlin dispersed to exploit the changing dynamics of regional productivities.

Archival-tagged striped marlin were found to spend at least a year in pelagic waters and did not return to the coastal habitat off Mexico or Central America, contrary to all previous tagging results. Offshore movements signaled the potential connectivity between striped marlin aggregations off coastal Mexico and the Galápagos Islands. Striped marlin also exhibited trans-equatorial movements not previously documented, however, individual and inter-annual variations also mean such crossing may not occur on a regular, yearly basis. It is likely that changes in local oceanographic and foraging conditions provide the necessary impetus for a fish to transit through the Equator. Limited by the small sample size, it is unclear what impacts ENSO and other climatic oscillations had on striped marlin movements, despite an exceptionally high catch rate off Cabo San Lucas in 2008

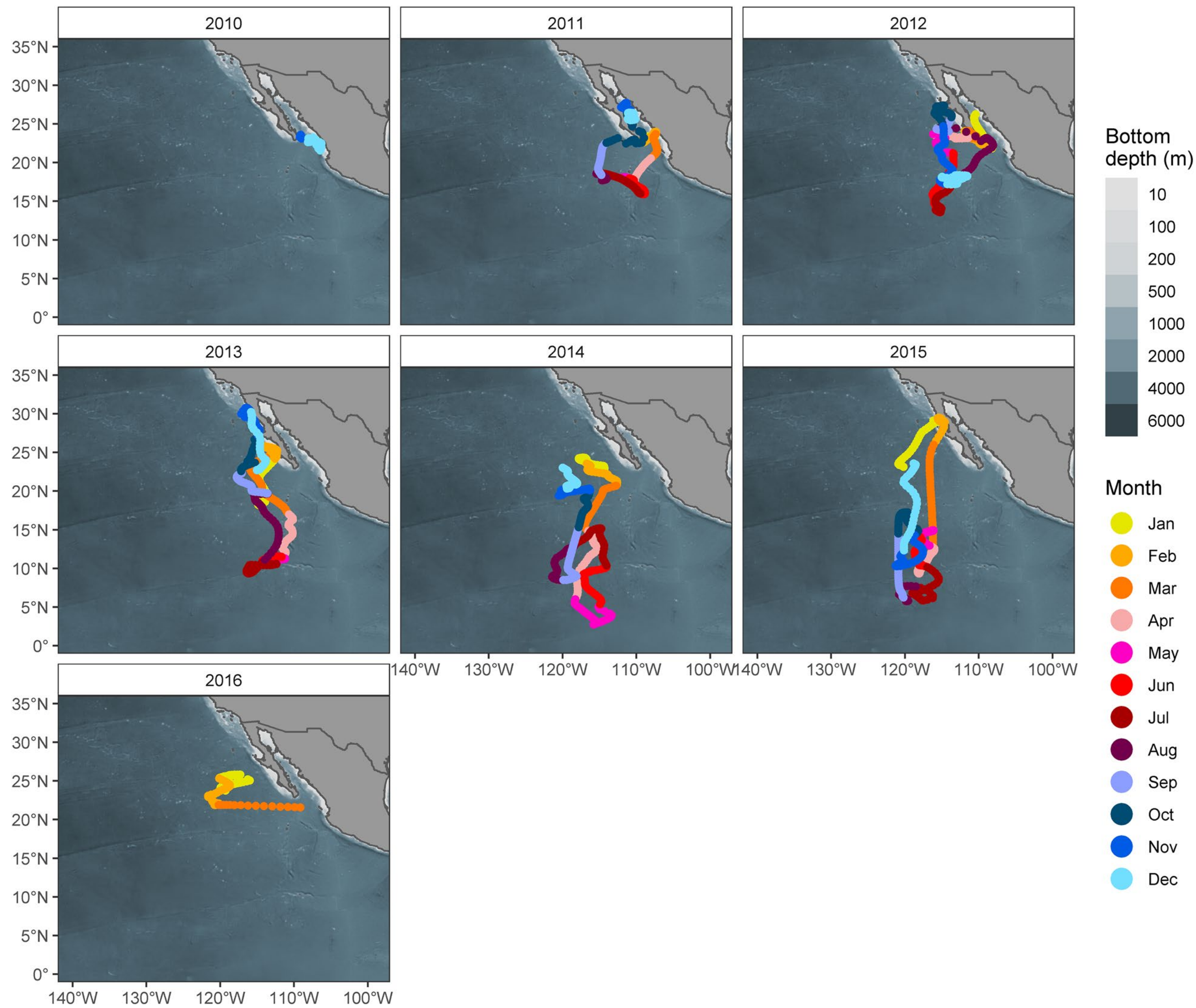

Fig. 6 Movement track of Fish 990339 between 2010 and 2016. Positions are color-coded by months and each panel represents a single tracking year. Bathymetry is plotted as false color

which coincided with a La Niña event [34]. It should be noted that Fish 890289 did not display marked differences in its yearly movement patterns between 2013 and 2016 (Fig. 5), despite 2015–2016 was considered a strong El Niño event [35]. A substantially larger collection of multi-year tracks will be needed to investigate possible influences of climate systems on striped marlin movements.

Movements and genetic populations

None of the archival-tagged striped marlin traveled to the Southern California, where a high availability of fish often occurs between September and October [7]. Tracked fish only ventured as far north as 31°N, and all of them tended to move southward. This general movement pattern is consistent with the overall genetic structuring of the Pacific: one distinct population composed of fish from Baja California, Ecuador and Peru (ECPO), and another with fish from Japan, Taiwan, Hawaii and California [2]. Our tracked fish were rarely present in the coastal waters of Ecuador or Peru, and instead occupied pelagic areas west of the Galápagos Islands, and as far west (132° W 16.5° S) as the Marquesas Islands. This same area in French Polynesia was reached by striped marlin tagged off New Zealand [5, 10, 36], indicating waters surrounding the greater French Polynesia could represent a mixing area for fish populations from both sides of the

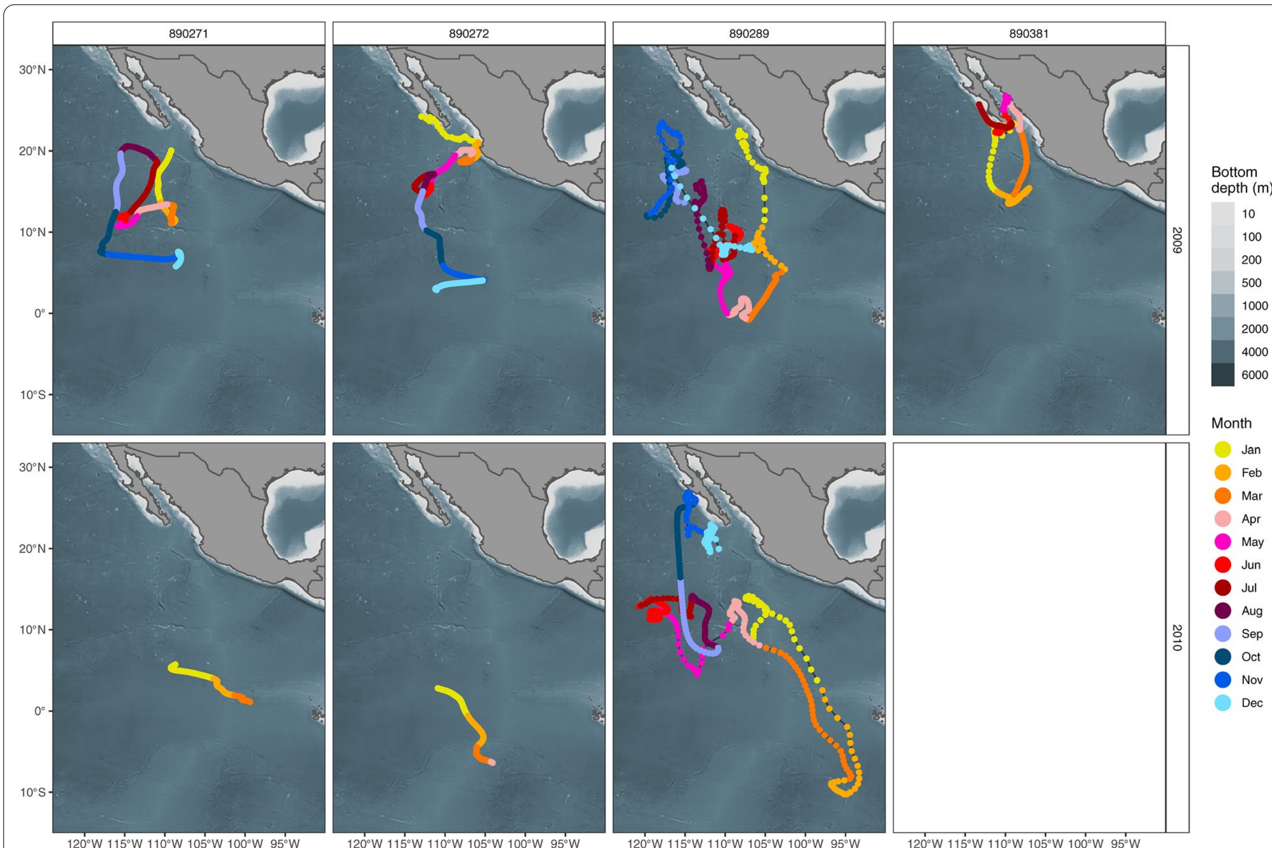

Fig. 7 Horizontal movement of striped marlin between 2009 and 2010. Vertical panels are organized by fish identifier, and horizontal panels represent tracking year. Positions are color-coded by months and each panel represents a single tracking year. Bathymetry is plotted as false color

Pacific. Mixing may be more commonplace than currently realized as genetic analyses detected migrants from Eastern Australia or New Zealand in 3 out of 35 samples collected from Ecuador [2].

For the ECPO population to remain reproductively isolated from others, striped marlin must utilize distinct spawning areas. Coastal Mexican waters between Mazatlan and Manzanillo (104–107° W, 18.5–23° N) could be one of such spawning locations, where larvae were found in June to September, and as late as November [37, 38]. At this location, two spawning seasons have been suggested, the latter of which coincided with the timing during when tagged striped marlin aggregated around the area (Fig. 4). Alternative spawning areas, as well as, spawning timing should also be revisited as year-of-young striped marlin (mean: 124 days old) were sampled across the Eastern Pacific, including at offshore locations [39].

Conclusions

We demonstrated the utility of obtaining coarse-resolution movement tracks from implanted archival tags in striped marlin using an unsophisticated depth-based geolocation method following the unfortunate happenstance of external sensor stalk breakage. Calculated tracks from archival tag data have documented seasonality and diversity in striped marlin movements in the Eastern Pacific, and the usage of coastal and offshore areas spanning the latitudes of 16°S to 31°N. Multi-year tracks revealed trans-equatorial movement not previously observed for striped marlin, challenging previous notions that striped marlin are only localized in their regional, coastal aggregations. Our work suggests that striped marlin could spend extended time in pelagic waters, a pattern which had not previously been captured by deployments of electronic tags. Continued striped marlin tagging efforts in concert with genetic profiling

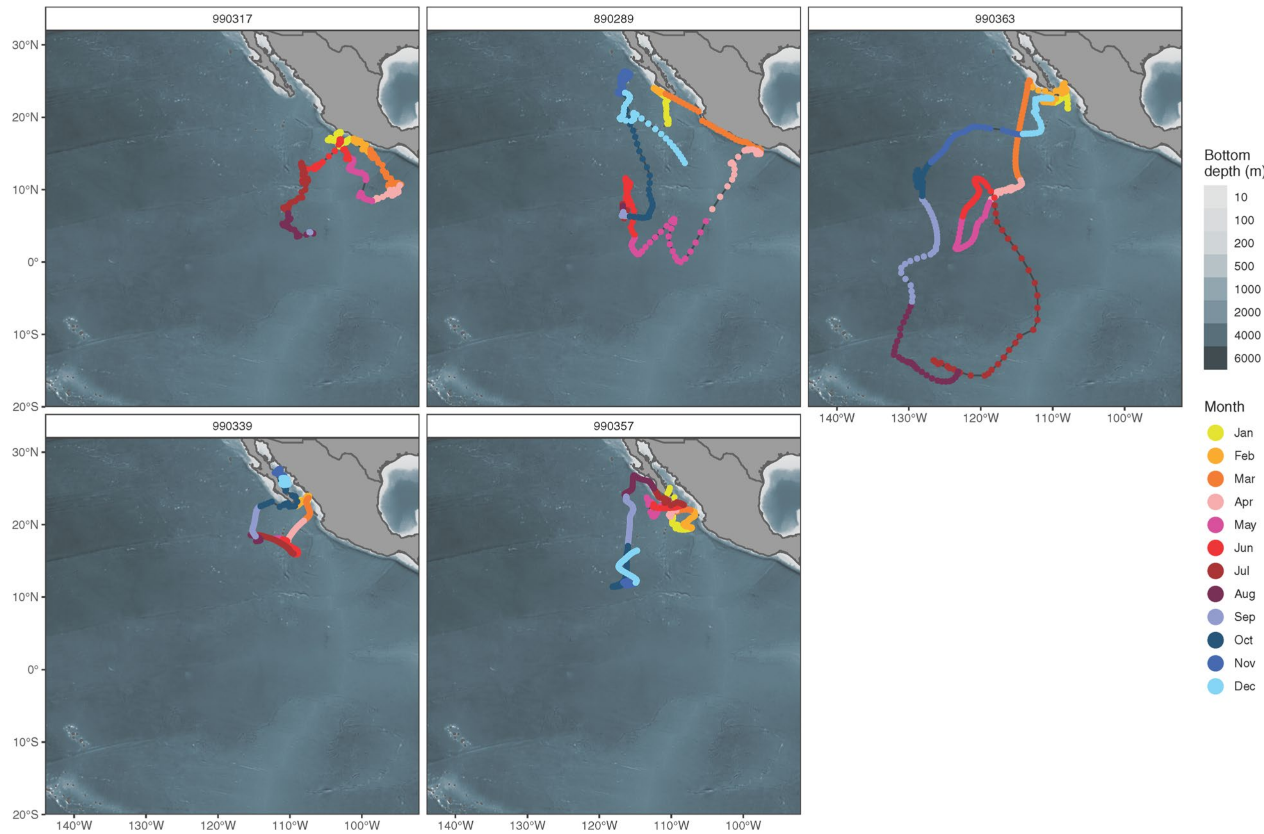

Fig. 8 Horizontal movement of striped marlin in 2011. Each panel contains the track of a tagged individual. Positions are color-coded by months and each panel represents a single tracking year. Bathymetry is plotted as false color

are highly encouraged. The use of archival tags that can deliver multi-year observations is recommended and will be critical to a more insightful understanding of billfish migration here and beyond.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-022-00294-y.

Additional file 1: Figure S1. Horizontal movement of striped marlin 890289 and 990339 between 2012 and 2016. Vertical panels are organized by tracking year, and horizontal panels by fish identifier. Positions are color-coded by months. Bathymetry is plotted as false color.

Additional file 2. Complete listing of smoothed times of sunset and sunset (TSS) identified for tagged striped marlin from their swimming depths.

Additional file 3. Relative distance between positions derived by depth-only geolocation (ZON) and Wildlife Computer's GPE3 algorithm for Fish 990317.

Additional file 4. Reconstructed tracks of tagged striped marlin. The confidence region along an estimated position is indicated by grey-shaded ellipses. Positions are color-coded by months. Tagging locations, green triangle; last known fish locations, red triangle.

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Author contributions

MD, PO, SOG and NL designed and executed the research; CL performed the analyses and prepared the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

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Consent for publication
Not applicable.

Competing interests
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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