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First telemetry insights into the movements and vertical habitat use of megamouth shark (*Megachasma pelagios*) in the northwest Pacific

P.J. Clerkin [a,b,1], M.C. Arostegui [c,*,1], W.C. Chiang [d], S.J. Lin [d], C.D. Miller [b,e,f], C.D. Braun [c]

[a] *Virginia Institute of Marine Science, VA, USA*
[b] *Deep Blue Research Foundation, CA, USA*
[c] *Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA*
[d] *Eastern Fishery Research Center, Fisheries Research Institute, Taitung, Taiwan*
[e] *New York University, NY, USA*
[f] *School of Biological Sciences, Institute of Molecular Plant Sciences, The University of Edinburgh, UK*

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ABSTRACT

The megamouth shark (*Megachasma pelagios*) is one of the ocean's largest and most enigmatic elasmobranchs, with only a few hundred individuals ever recorded. Most of what is known about the species comes from rare fishery bycatch, stranding, or sighting events, precluding an in-depth understanding of its movement ecology. Here, we report the results from three megamouth sharks outfitted with pop-up satellite archival transmitting tags to assess the species' horizontal and vertical movement patterns. Deployments of 12, 58, and 244 d in duration provided the first direct evidence of multi-month fidelity to the waters east of Taiwan and seasonal movement out of the region. Depth and temperature data revealed a pattern of normal diel vertical migration, with the majority of the day spent in the mesopelagic zone and night in the epipelagic. Vertical habitat use suggests potential behavioral thermoregulation and was consistent with tracking of migrating mesopelagic prey across diel periods. We discuss the specialized analytical methods needed to reconstruct the spatial habitat use of deep-diving megamouth shark from tag sensor measurements of the magnetic field, as well as avenues for future research on this understudied megaplanktivore.

1. Introduction

Since the serendipitous discovery of a megamouth shark (*Megachasma pelagios*) tangled in the parachute sea anchor of a Hawaiian vessel in 1976 (Taylor et al., 1983), fewer than 300 individuals of this enigmatic species have been documented (Yu et al., 2021). The megamouth shark, one of three known filter-feeding sharks alongside the whale shark (*Rhincodon typus*) and basking shark (*Cetorhinus maximus*), occurs circumglobally in neritic and oceanic waters across tropical and subtropical latitudes (Watanabe and Papastamatiou, 2019). The species' depth range spans from the surface to at least the uppermost bathypelagic > 1200 m (Yu et al., 2021). This species is listed as Least Concern with an unknown population trend by the International Union for the Conservation of Nature (Kyne et al., 2019) due to its typically infrequent occurrence as fishery bycatch (e.g., Acuña-Perales et al., 2021; Diez et al., 2022). However, while there are currently no directed fisheries for this megaplanktivore, the species' large maximum body size (> 7 m and 1100 kg – Watanabe and Papastamatiou, 2019) is strongly suggestive of an intrinsically elevated extinction risk (Dulvy et al., 2014), and it occurs in many of the world's microplastic pollution hotspots that are known threats to other filter feeders (Germanov et al., 2018).

Given that what is known about megamouth shark is primarily derived from bycatch, stranding, and sighting occurrence data (Yu et al., 2021), there is a dearth of information on their horizontal and vertical movement ecology. There are no long-term tracking studies of megamouth shark, and their seasonal spatial habitat use is unknown. Currently, the paths, phenology, and ontogeny of the species' horizontal migrations in the Pacific are hypothesized from the aggregation of sparse sex- and size-specific occurrence data, the majority of which come from the waters east of Taiwan (Yu et al., 2021). One megamouth shark was tracked off of southern California (USA) for 2.1 days during which it exhibited a pattern of normal diel vertical migration (Nelson

* Corresponding author.
E-mail address: martin.arostegui@whoi.edu (M.C. Arostegui).
[1] Joint lead authors.

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et al., 1997). However, it is unknown if this represents typified behavior for the species or whether it is one of multiple vertical movement strategies. The species' broad depth range (Yu et al., 2021) and diet of vertically migrating zooplankton (e.g., Sawamoto and Matsumoto, 2012) suggest a greater potential reliance on the prey resources of the deep rather than near-surface ocean. A white band of denticles over the dark upper jaw, unique to megamouth shark, is thought to reflect bioluminescence emitted by deep ocean plankton and attract prey in dark pelagic ecosystems (Nakaya, 2001; Duchatelet et al., 2020).

The purpose of this study was to investigate the horizontal and vertical movement ecology of megamouth shark in the northwest Pacific. Using the first satellite telemetry dataset from adult megamouth shark, we developed specialized analytical methods to reconstruct the spatial habitat use of a species that largely avoids downwelling light in the near-surface that is typically used for geolocation (reviewed in Gatti et al., 2021). Estimated horizontal movements were used to identify patterns of seasonal residency and dispersal, and vertical movements indicated normal diel vertical migration extending into the mesopelagic zone. We present evidence for potential behavioral thermoregulation and discuss avenues for future research on this enigmatic species.

2. Methods

2.1. Tagging

In May 2018 (n = 4) and June 2022 (n = 1), five megamouth sharks were captured with the aid of commercial fishers active in the large-mesh driftnet fishery targeting ocean sunfishes (family Molidae) off the eastern coast of Taiwan (Fig. 1). Driftnet gear measured 100 m in height, approximately 2000 m in length, and had a mesh size of 90 cm. Nets were set before sunset and retrieved before dawn. Captured individuals were secured in minimal-stress conditions and remained submerged next to the vessel during measurement and tagging. The precaudal, standard, total, and first dorsal fin base lengths, as well as sex and maturity stage (based on external parameters and clasper length) were collected following standards set by Mostarda et al. (2016). Each individual was outfitted with a pop-up satellite archival transmitting (PSAT) tag from either Desert Star Systems LLC (Marina, CA, USA – model: SeaTag-6K; n = 4) or Wildlife Computers (Redmond, WA, USA – model: miniPAT; n = 1). Desert Star SeaTags were programmed to measure pressure (depth), temperature, light, salinity, and three-component geomagnetic intensity every 4 s and transmit those data at 4-min resolution, provide daily summaries of mean, minimum, and/or maximum values of the aforementioned variables, and release from the sharks after 18 months. The Wildlife Computers miniPAT was programmed to measure pressure (depth), temperature and light every 3 s and transmit summarized data products daily for the first 50 days of the deployment, after which the tag would duty-cycle off for one day and on for six days. The miniPAT also transmitted depth-temperature time series data at 5-min resolution for the duration of the deployment. The Desert Star SeaTags were attached with a stainless-steel dermal anchor via a stainless-steel split-tip applicator that was embedded into the basal cartilage of the first dorsal fin; two additional attachment points were positioned along the anterior margins of the first dorsal fin to minimize wear on the anchor from sharks' movements. The Wildlife Computers miniPAT was attached with a single, large titanium anchor embedded into the musculature at the base of the first dorsal fin. The entire tagging process lasted no longer than 15 min. All research was conducted under Institutional Animal Care and Use Committee or Panel (IACUC/IACUP) permission of the Fisheries Research Institute.

2.2. Geolocation

We conducted geolocations of the megamouth shark dataset from the Desert Star tags with HMMoce, a gridded hidden Markov model approach that compares diverse tag-based observations against grid-based representations of the ocean environment, such as remote sensing data and data-assimilating oceanographic model outputs, to generate likelihoods of a tagged individual's location at each time step of the deployment (Braun et al., 2018b). At 24-hr intervals, we calculated separate likelihoods for each shark's location based on all, or a portion, of the following inputs depending on their availability: (a) sea surface temperature (SST) generated from comparing tag-based SST values (<2 m depth) against the Multi-scale Ultra-high Resolution (MUR) SST dataset (NASA/JPL, 2015), (b) depth-temperature produced by comparing tag recorded profiles of depth and temperature against daily, 1/12° outputs of depth and temperature from the HYbrid Coordinate Ocean Model (HYCOM – Bleck, 2002; Chassignet et al., 2007), (c) geomagnetic main field total intensity calculated from comparing tag-based measurements of the three orthogonal strength components ($F = \sqrt{X^2 + Y^2 + Z^2}$) against the International Geomagnetic Reference Field (IGRF-13 – Alken et al., 2021), and (d) bathymetry calculated as a

Fig. 1. A tagged megamouth shark is released from a large-mesh driftnet off the eastern coast of Taiwan. Photo by Zola Chen.

binary likelihood surface that excludes areas shallower than the tag-recorded maximum daily depth (30-arcsecond resolution Global Topography SRTM30_PLUS dataset – Becker et al., 2009). The variance specification for the geomagnetic main field total intensity likelihood relied on the anomaly method (Nielsen et al., 2020) informed by the Earth Magnetic Anomaly Grid (2-arcminute resolution EMAG2v3 dataset, Meyer et al., 2017). All likelihood grids were resampled to match the geomagnetic anomaly grid in order to leverage the high-resolution anomaly field relative to the comparatively coarse resolution of the other environmental grids.

The resulting observation likelihoods were convolved with a one-state diffusive movement kernel. Parameter estimation of behavior state movement speed used the Genetic Algorithm (Scrucca, 2013). Daily posterior probabilities for both sharks were generated with the expanding kernel method (n = 25 "mini-expansions" per time step), which maintains realistic movements in areas with complex island topography and improves posterior probability surfaces (Nielsen et al., 2023). The most probable track for each deployment was generated with the Viterbi method, a global decoding solution that improves daily location estimates derived from the posterior probability surfaces (Nielsen et al., 2023). Overall spatial utilization distributions for each shark were generated by integrating daily posterior probability surfaces over the whole deployment.

The short duration of the miniPAT deployment (~12 days) precluded the use of HMMoce to infer any meaningful movement from that individual. Therefore, the geolocation analysis for this tag used GPE3, a state-space hidden Markov model (developed by Wildlife Computers) that is functionally similar to HMMoce but less customizable. GPE3 computes posterior probability distributions to estimate the most likely state (position) at each time point using only light level, sea surface temperature (SST) and bathymetric constraints. Tag based observations were compared to NOAA's 1/4° daily Optimum Interpolation Sea Surface Temperature (OISST) product and bathymetric constraints were implemented relative to ETOPO1 (Amante and Eakins, 2009). The speed parameter in the model was fixed *a priori* at 0.5 m s^{-1} and is used to build daily diffusion kernels that are convolved with light and SST-based likelihoods as described for HMMoce above. Given the short deployment, data for this individual was not included in most analyses but is retained for visualization purposes. This tag transmitted the only high-resolution depth-temperature time series and was thus primarily used for characterizing vertical habitat use.

2.3. Movement behavior

The straight-line distance between deployment start and end, as well as the displacement rate between daily location estimates, were calculated using Great Circle distance (sf package for R – Pebesma, 2018). Time series data of depth and temperature were classified into daytime and nighttime periods based on times of sunrise and sunset determined by National Oceanic and Atmospheric Administration (NOAA) algorithms (maptools package for R – Bivand et al., 2023). Any negative depth readings from the daily summaries or time series were set to a value of 0 m.

3. Results

Three of the five PSAT tags deployed on megamouth shark reported data. Two deployments (with Desert Star SeaTags) on sharks #1 (605 cm female) and #2 (410 cm male) lasted 58 and 244 days, respectively, both of which yielded limited data transmission. One deployment (with a Wildlife Computers miniPAT tag) on shark #3 ended prematurely after 12 days. For sharks #1 and #2, only 53.4 and 12.7% of daily summaries and 2.5 and 0.0% of time series were transmitted, respectively. Input likelihood coverage for geolocation as a proportion of deployment days was 10.3% SST, 65.5% depth-temperature profiles, 15.5% magnetic, and 86.2% bathymetry for shark #1. Shark #2 only reported daily summaries (no time series data) of min/max/mean depth and magnetic measurements that resulted in 12.3% (30 of 244) deployment days being informed by total magnetic field intensity and bathymetry likelihoods.

Spatial utilization distributions from geolocation indicated that both sharks that were at liberty for >30 days exhibited core-use areas in the Huatung Basin and western Philippine Sea south of the Ryukyu Islands (Fig. 2). Shark #1 remained in these waters east of Taiwan throughout its deployment from May to July, and the most probable track suggested a months-long movement away from and back to the vicinity of the Taiwanese coast. Shark #2 similarly remained in the waters east of Taiwan from May to October before moving into the South China Sea from November to January; the most probable track suggested a brief foray into the East China Sea and that the fall southwestward movement largely followed the continental slope. Straight-line displacements from deployment start to end were 90 and 836 km. Mean (maximum) displacement rates estimated from geolocation were 11 (59) and 19 (45) km/d for sharks #1 and #2, respectively. Data for shark #3 were not

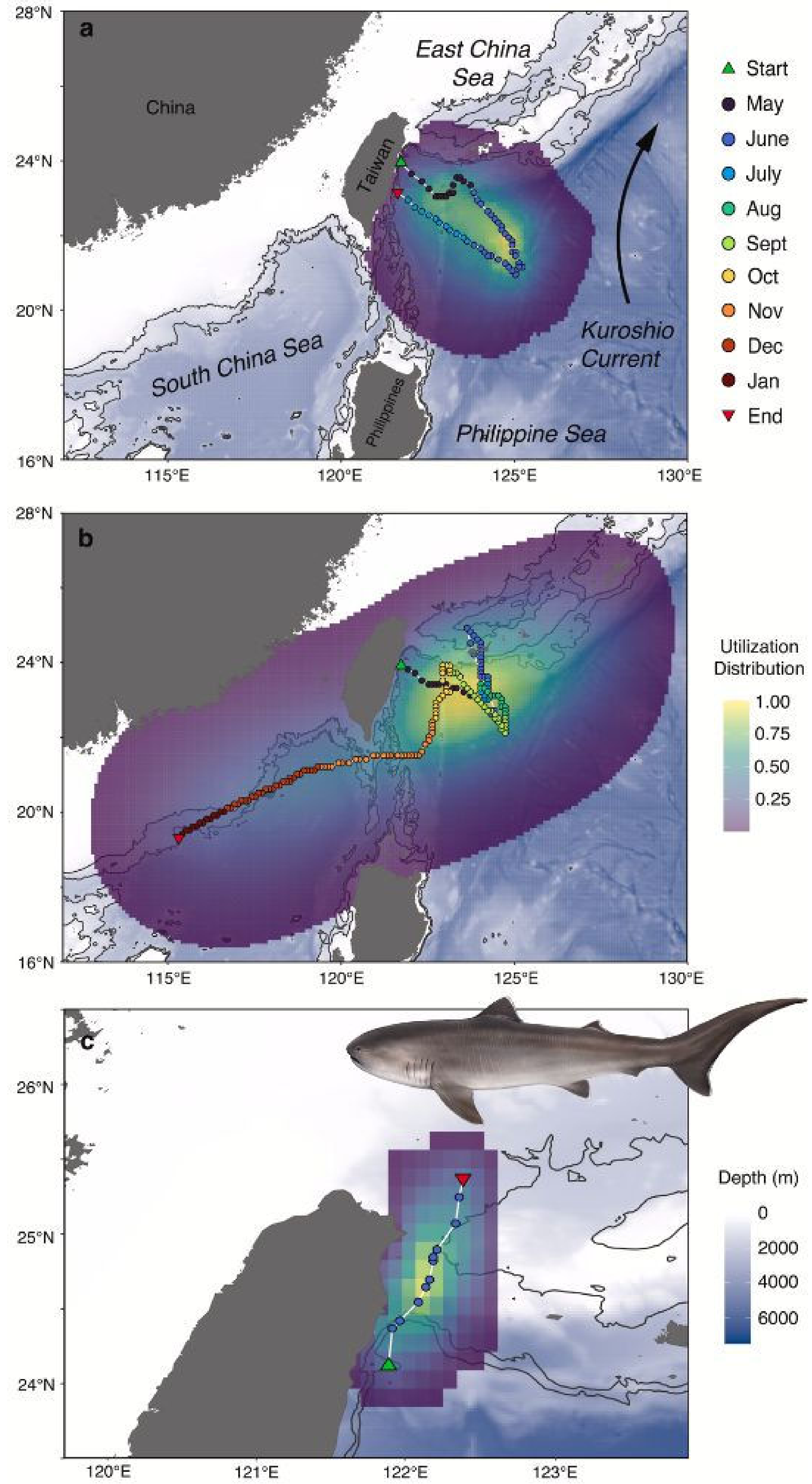

Fig. 2. Time-integrated spatial utilization distributions and corresponding most probable tracks for megamouth sharks a) #1, b) #2 and c) #3. Artwork by Les Gallagher (Fishpics® & IMAR-DOP, University of the Azores).

included in horizontal movement analyses due to the short deployment.

Daily minimum and maximum depths across the three sharks ranged from 0 to 142 and 194–733 m, respectively (Fig. 3a). Averaged across individuals, daily minimum depths occurred in the 0–50 m depth range on 85% of days and daily maximum depths occurred in the 400–700 m depth range on 80% of days (Fig. 3a). For the shark with only 2.5% transmitted time series data (#1), hourly depths summarized across the deployment exhibited crepuscular transitions between primarily epipelagic (< 200 m) nighttime and mesopelagic (> 200 m) daytime distributions (Fig. 4a). Similarly, for the shark with high quality transmitted time series data (#3), normal diel vertical migrations between the epipelagic in the nighttime and mesopelagic in the daytime were apparent on each calendar day of the deployment (Fig. 4b). This typified pattern was, however, interrupted during the daytime by one or more short-duration vertical movements ~200–500 m upward in the water column before returning to the target depth. These individuals experienced daytime (nighttime) median temperatures of 8.9 (20.6) and 13.2 (21.6)°C, respectively, from an overall temperature range of 6.5–29.2°C (Fig. 3b) that, within each 24-hr period, typically consisted of maximum temperature changes > 14.8 and 18.9°C, respectively. Averaged across these two sharks (those with transmitted temperature data, see Fig. 3b), 86% of the daytime was spent in waters < 18°C and 72% of the nighttime was spent in waters > 18°C.

4. Discussion

4.1. Spatial movements

Residence of the tracked megamouth sharks from late spring to fall in the waters east of Taiwan highlight the importance of this habitat in the Northwest Pacific. Of the limited megamouth shark records globally, the majority come from the east coast of Taiwan (Yu et al., 2021) in spring and summer (Lee and Shao, 2009; Liu et al., 2018; Watanabe and Papastamatiou, 2019). Based on occurrence records, previous research hypothesized a general migration pattern in which megamouth sharks occur east of Taiwan from April to August. In fall, movements are believed to follow the Kuroshio Current northeast towards Japan where some adults remain while others migrate to the Eastern Tropical Pacific. Adults are assumed to return to the western Pacific the following spring (Yu et al., 2021). In contrast to this hypothesized migration, the adult female megamouth shark tracked for > 200 days in this study started moving southwest into the South China Sea in the fall (Fig. 2b). This occurred at the time of year when the South China Sea western boundary current, which switches directions seasonally, is flowing to the southwest along the continental shelf and slope (Fang et al., 2012). While it is unknown if this observed movement route for megamouth sharks is common or an exception, the transpacific migration cycle proposed by Yu et al. (2021) seems unlikely given the sustained swimming speeds required. A megamouth shark migrating in a straight line from Japan to the Eastern Tropical Pacific and back to Taiwan – starting in October and ending in March (as suggested by Yu et al., 2021) – would require an average daily displacement rate > 140 km/d, more than twice the maximum rate estimated from the geolocations in this study and previous acoustic tracking of megamouth shark (Nelson et al., 1997) and far exceeding the mean displacement rates observed for the other highly migratory, filter-feeding sharks (i.e., whale shark – Rohner et al., 2018; basking shark – Dewar et al., 2018). While megamouth shark migration dynamics remain largely unresolved, these satellite telemetry results provide the first direct evidence of this species exhibiting multi-month fidelity to the waters east of Taiwan and seasonal departure from the region.

4.2. Vertical habitat use

The megamouth sharks transitioning from a shallower nighttime distribution to deeper daytime distribution, and associated large daily depth ranges (Figs. 3 and 4), is consistent with the normal diel vertical migration pattern observed in the lone megamouth shark tagged previously (Nelson et al., 1997) as well as many other elasmobranchs for which this is the primary vertical movement paradigm (Andrzejaczek et al., 2022). A notable difference is that the previous tracking study on megamouth shark in California documented an exclusively epipelagic depth range < 170 m even in waters with a bottom depth > 400 m (Nelson et al., 1997). In contrast, the sharks in this study descended into

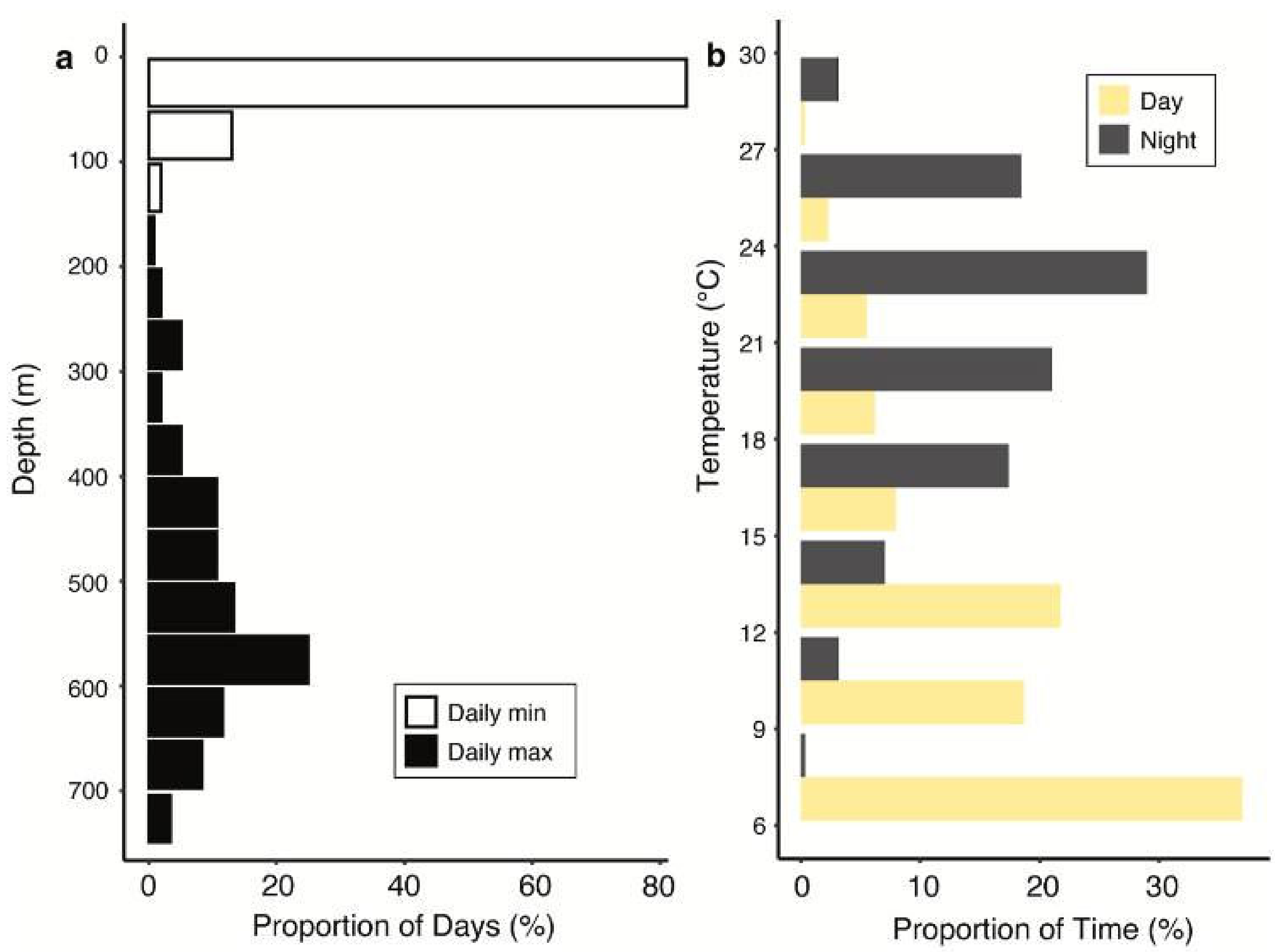

Fig. 3. a) Distribution of daily minimum and maximum depths for all three individuals and b) diel temperature distribution based on the deployment-wide time series data from megamouth sharks #1 and #3. Bin-specific values were calculated per individual (every 50 m or every 3°C) and then averaged across individuals.

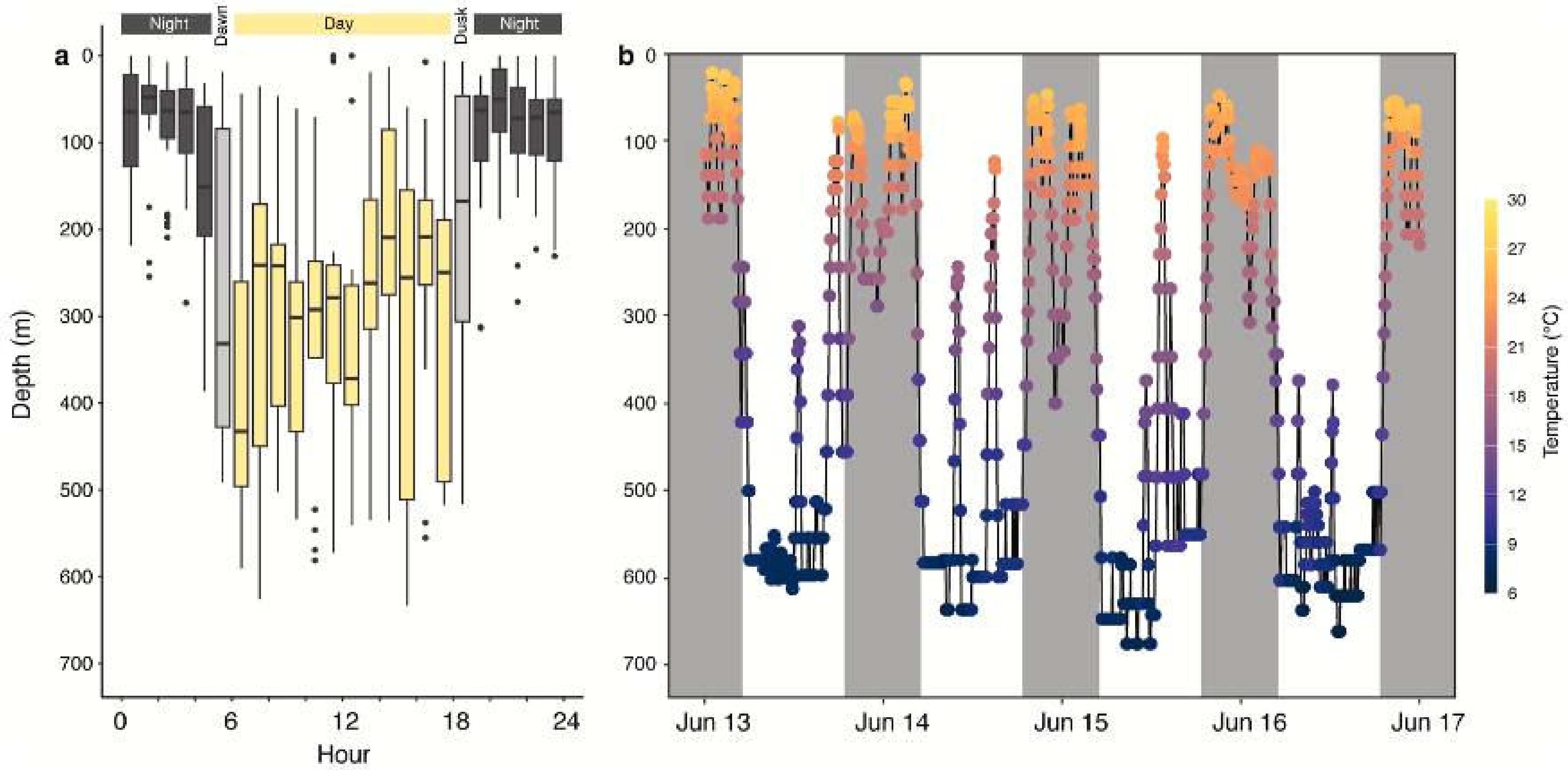

Fig. 4. a) Hourly depth distribution and b) depth-temperature time series (5-min resolution) for sharks #1 and #3, respectively.

the mesopelagic nearly every day. Vertical movements typically exceeded 400 m, consistent with depth- and time-specific sightings and capture records of the species (Yu et al., 2021).

For megamouth shark and certain other deep-diving predators, their depth distribution appears to follow changes in ambient light levels (Nelson et al., 1997; Arostegui et al., 2020; Abecassis et al., 2012) that drive diel vertical migration of acoustic scattering layers and determine modal daytime and nighttime depth distributions of the constituent prey (Røstad et al., 2016). Unlike other predators that target mesopelagic fishes and squids associated with scattering layers (e.g., Arostegui et al., 2020; Braun et al., 2023), the filter-feeding megamouth shark seemingly targets vertically migrating zooplankton (Taylor et al., 1983; Hays, 2003; Sawamoto and Matsumoto, 2012; de Moura et al., 2015). Offshore of eastern Taiwan, mesopelagic scattering layer depth and behavior vary with the underlying bathymetry. On the continental slope of 300 m bottom depth, a scattering layer predominantly comprised of crustacean zooplankton migrates from ~ 180–280 m during the daytime to ~ 10–150 m during the nighttime (Chou et al., 1999). However, farther offshore in waters of > 1000 m bottom depth, two deep scattering layers of unknown taxonomic composition occur from ~ 400–500 and 600–700 m during the daytime. A portion of these layers are non-migrant and remain at those depths across diel cycles while some undergo vertical migration, occupying the upper 200 m of the water column at night (Lee et al., 2011). While the spatial uncertainty of the megamouth sharks' daily positions does not permit clear distinction between periods of on- and off-slope occurrence, the observed maximum daily depths largely overlap with the daytime distribution of the two, off-slope deep scattering layers. Variation in the maximum daily depths of megamouth shark below 350 m may reflect changes in the upper boundary of the daytime depth distribution of these deeper organisms that are driven by overlying oceanography (Aksnes et al., 2017), such as those associated with mesoscale eddies in the region (Wang et al., 2024). However, one of the sharks exhibited instances where its daily maximum depths occurred from 200 to 300 m (Fig. 3a), consistent with daytime overlap of the comparatively shallower, on-slope scattering layer. Wide crepuscular depth ranges and the largely epipelagic nighttime depths of megamouth shark suggest that they likely track the migrant component of the scattering community upward into the near-surface at night to forage, rather than remaining in the mesopelagic to target non-migrant organisms.

Megamouth sharks undergoing diel vertical migration in the open ocean experience large ambient temperature changes (Fig. 3b and 4) that may necessitate behavioral thermoregulation. The sparse depth-time series data transmitted from the two DesertStar tag deployments in this study cannot clearly resolve whether these individuals typically remained at a particular depth or if they conducted sequential descents and ascents during the daytime on each deployment day. However, the depth-temperature time series data transmitted from the Wildlife Computers tag deployment indicated marked variability in depth distribution across daylight hours, especially midday near-surface outliers when the sharks would be expected to be at the deepest point of their diel vertical migration (Fig. 4a). Variability in vertical habitat use during the day suggests that they may periodically ascend above the thermocline to rewarm after prolonged cold exposure in the mesopelagic. Such behavioral thermoregulation during the daytime may manifest as infrequent basking events as has been observed in swordfish (*Xiphias gladius* – Dewar et al., 2011) or as repeated dive cycles as in bigeye tuna (*Thunnus obesus* – Holland et al., 1992).

4.3. Geolocation of midwater species

Geolocation of the megamouth sharks in this study was largely enabled by likelihoods based on total magnetic field intensity, a rarely used input in movement models for estimating horizontal movements of satellite-tagged fishes. Most archival tracking studies of pelagic fishes rely on light and sea surface temperature measurements (Gatti et al., 2021). Low availability of these inputs can significantly reduce the accuracy of geolocation model outputs, necessitating the incorporation of other inputs to better constrain location estimates (Braun et al., 2018b), particularly for species frequenting the mesopelagic (e.g., swordfish – Braun et al., 2019). The state-of-the-art approach for geolocation of midwater species, for which tag data typically yields limited or no light or sea surface temperature data, is to incorporate depth-temperature profiles in comparison to 3D ocean-resolving models (Braun et al., 2018a). Yet, the scarcity (or absence) of depth-temperature profile data from the PSAT tags used in this study necessitated additional reliance on magnetic intensity measurements to infer movement patterns.

Geolocation using magnetics combines three-component (*X, Y, Z*) magnetic intensity measurements that, when compared to a reference field map, can further constrain position estimates beyond traditional input likelihoods (Klimley et al., 2017; Nielsen et al., 2020). A major limitation of this approach is the spatial variability in the utility of magnetic field measurements. Positions can be better constrained in regions with steep total magnetic intensity gradients, such as the Northwest Pacific, compared to those with weak gradients, such as the South Atlantic (Klimley et al., 2017). A theoretical alternative to using a single input likelihood based on total magnetic field intensity is to use separate input likelihoods for the various permutations of magnetic components (Nielsen et al., 2020). However, while we found that the PSAT tags'

three-component measurements in combination yielded reasonable total magnetic field intensity likelihoods, they did not separately provide viable horizontal ($H = \sqrt{X^2 + Y^2}$) and vertical (Z) intensity nor declination ($D = \arctan(Y/X)$) and inclination ($I = \arctan(Z/H)$) likelihoods. This is, at least in part, reflective of how component magnetic measurements may be distorted by tag orientation (Nielsen et al., 2020). Regardless of how magnetic measurements are used to produce spatial likelihood fields, pervasive sensor bias and precision variability among magnetic-capable tags may limit their utility in geolocation without careful assessment (Nielsen et al., 2020).

5. Conclusion

Harvest of megamouth shark has been banned in Taiwan since 2020 (Yu et al., 2021), and data-limited stock assessment suggests the regional population is in a healthy state (Ju et al., 2020). However, recent work suggests the deep ocean will also likely face a number of climate-induced changes, including impacting scattering layer fauna (Ariza et al., 2022) that this species seemingly relies on, with major implications for the ecosystem services that the mesopelagic is thought to provide to marine predators (Braun et al., 2022, 2023). Future studies should investigate how physical and biological oceanographic conditions in the deep ocean east of Taiwan promote seasonal residency of megamouth sharks to this region and structure their connectivity to mesopelagic resources. As shown in this study, long-term satellite-tracking studies of megamouth shark, including predictably encountering this rare species, are viable and necessary to improve our understanding of their movement ecology. Given that the vertical movement behavior of this species limits the availability of traditional inputs to geolocation, highly specialized techniques are needed to reconstruct their spatial habitat use at finer scales.

CRediT authorship contribution statement

P.J. Clerkin: Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **M.C. Arostegui:** Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation. **W.C. Chiang:** Writing – review & editing, Resources. **S.J. Lin:** Writing – review & editing, Investigation. **C.D. Miller:** Writing – review & editing, Investigation, Funding acquisition. **C.D. Braun:** Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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