



OPEN ACCESS

EDITED BY

Nuno Queiroz,
Centro de Investigacao em Biodiversidade e
Recursos Geneticos (CIBIO-InBIO), Portugal

REVIEWED BY

Kesley Gibson Banks,
Texas A&M University Corpus Christi,
United States
Peter Gausmann,
Ruhr University Bochum, Germany

*CORRESPONDENCE

Brendan D. Shea
✉ bshea@vt.edu

RECEIVED 26 April 2024

ACCEPTED 08 November 2024

PUBLISHED 09 December 2024

CITATION

Shea BD, Chapple TK, Echwikhi K,
Gambardella C, Jenrette JF, Moro S,
Schallert RJ, Block BA and Ferretti F (2024)
First satellite track of a juvenile shortfin
mako shark (*Isurus oxyrinchus*) in the
Mediterranean Sea.
Front. Mar. Sci. 11:1423507.
doi: 10.3389/fmars.2024.1423507

COPYRIGHT

© 2024 Shea, Chapple, Echwikhi, Gambardella,
Jenrette, Moro, Schallert, Block and Ferretti.
This is an open-access article distributed under
the terms of the [Creative Commons Attribution
License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or
reproduction in other forums is permitted,
provided the original author(s) and the
copyright owner(s) are credited and that the
original publication in this journal is cited, in
accordance with accepted academic
practice. No use, distribution or reproduction
is permitted which does not comply with
these terms.

First satellite track of a juvenile shortfin mako shark (*Isurus oxyrinchus*) in the Mediterranean Sea

Brendan D. Shea^{1,2*}, Taylor K. Chapple³, Khaled Echwikhi⁴,
Chiara Gambardella^{1,5,6}, Jeremy F. Jenrette¹, Stefano Moro⁷,
Robert J. Schallert⁸, Barbara A. Block⁸ and Francesco Ferretti¹

¹Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA, United States, ²Beneath the Waves, Boston, MA, United States, ³Coastal Oregon Marine Experiment Station, Oregon State University, Newport, OR, United States, ⁴High Institute of Applied Biology of Medenine, Gabès University, Medenine, Gabès, Tunisia, ⁵Dipartimento di Ecologia Marina Integrata, Stazione Zoologica Anton Dohrn, Naples, Italy, ⁶Department of Life and Environmental Sciences, Università Politecnica delle Marche, Ancona, Italy, ⁷Dipartimento di Ecologia Marina Integrata, Stazione Zoologica Anton Dohrn, Rome, Italy, ⁸Hopkins Marine Station, Stanford University, Pacific Grove, CA, United States

KEYWORDS

telemetry, elasmobranchs, conservation, sharks, Central Mediterranean

1 Introduction

The shortfin mako shark (*Isurus oxyrinchus*) is a highly mobile, coastal littoral, and epipelagic oceanic species broadly distributed in tropical, subtropical, and temperate seas worldwide (Rigby et al., 2019). In recent years, there has been growing recognition of the impacts of overfishing on shortfin mako populations, and the species is now listed as Endangered by the International Union for the Conservation of Nature (IUCN) (Rigby et al., 2019). The species is listed as Critically Endangered in the Mediterranean Sea due to long-term and continuing exploitation coupled with inadequate management (Walls and Soldo, 2016). Of particular concern is the ongoing capture of juvenile mako sharks in the Central Mediterranean and the Strait of Sicily, which have been identified as potential nursery areas (Walls and Soldo, 2016; Cattano et al., 2023; Mancusi et al., 2023).

Even with significant declines in pelagic sharks regionally (Ferretti et al., 2008), sharks continue to be occasionally targeted in the Mediterranean Sea, though the most critical risk to shark populations in the region is bycatch in other fisheries (Bradai et al., 2018; Carpentieri et al., 2021). In the Mediterranean, most fishers typically retain their shark bycatch, with some estimates of shark discard rates as low as 1% (Megalofonou et al., 2005) even for protected species, though discard rates are likely to vary by season and gear (Carpentieri et al., 2021). Despite their imperiled status, shortfin mako sharks remain one of the region's commonly encountered sharks for fishers, especially for longlines (Carpentieri et al., 2021), and sharks are typically retained despite falling under regional protections such as the Bern Convention, Bonn Convention, and Barcelona Convention (Serena et al., 2014). Of additional concern is the relatively unmonitored recreational fishery, which may additionally encounter high numbers of shortfin mako sharks, many of

which are retained, but the scale of this fishery is not well known (Udovičić et al., 2019; Panayiotou et al., 2020). Concerningly, young-of-the-year (YOY) and juvenile specimens comprise the bulk of captured individuals reported in the Mediterranean (Saidi et al., 2019; Udovičić et al., 2019; Panayiotou et al., 2020; Cattano et al., 2023; Mancusi et al., 2023; Scacco et al., 2023). Given the life history of shortfin mako sharks, particularly their advanced age at maturity (Natanson et al., 2020), this frequent and ongoing capture of juvenile sharks represents a severe threat to regional populations, as many sharks will never reach maturity, let alone successfully reproduce. These losses highlight the need for more detailed information regarding the movement patterns and space use of juvenile shortfin mako sharks, for which little is known in the Mediterranean.

In recent years, a proliferation of telemetry studies has drastically improved our understanding of the movements and space use of large marine predators like shortfin mako sharks around the globe (Queiroz et al., 2019); however, virtually no study has focused on Mediterranean populations, especially sharks. Here, we report the satellite track from a pop-off archival tag (PAT) deployed on a juvenile shortfin mako shark in the Mediterranean Sea in May 2023. To our knowledge, this track represents the first satellite tag deployed on a shortfin mako shark in the Mediterranean Sea. We describe the horizontal and vertical movements the study shark performed over 54 days at liberty (DAL), discussing potential drivers for the observed movements and the implications of the track for the conservation of shortfin mako sharks regionally.

2 Methods

2.1 Tagging

We opportunistically tagged a juvenile female shortfin mako shark (estimated size = ~120 cm total length; estimated age: 1-4 years) while observing longline fishing operations on the Tunisian plateau (Figure 1). The shark was tagged on the 17th of May 2023, in the early morning, after being captured at approximately 40 meters (m) depth. The shark was captured via bottom longline in an area of the plateau characterized by seagrass meadows. The longline was deployed over a 3-hour period from 19:30-22:30 on the night of the 16th of May 2023, and was left to soak for 90 minutes before longline retrieval commenced at midnight. The shark was observed on the line and brought to the boat at approximately 03:15 in the morning, roughly halfway through the longline retrieval. The shark was quickly brought on board and tagged with a PAT (Model: MiniPAT, Wildlife Computers, Redmond, WA, USA), which was attached to the shark using a monofilament tether wrapped in heat shrink tubing and a stainless-steel dart anchor that was implanted in the dorsal musculature (Jorgensen et al., 2010). The PAT tag was programmed to sample light, depth, and temperature every 3 seconds for 180 days and was deployed with the auto-detect mortality and depth threshold release (DTR) settings activated. Immediately after tagging, the hook was removed, and the shark was quickly released. All research was conducted under Virginia Tech Institutional Animal Care and Use Committee Protocol 22-094.

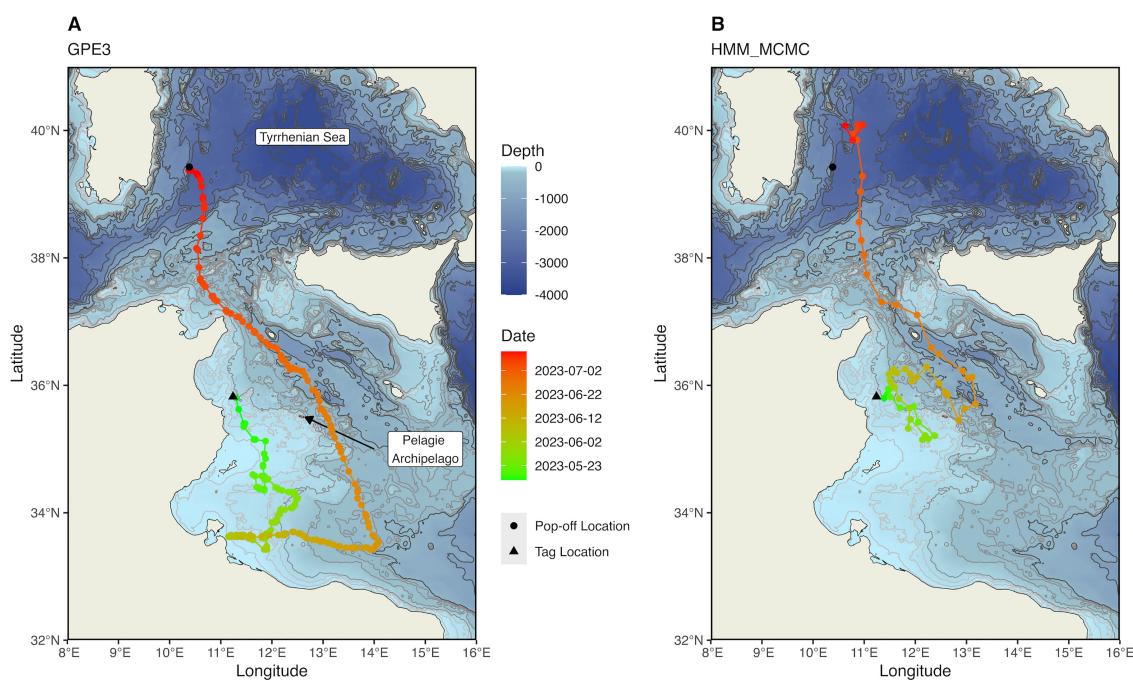


FIGURE 1

Figure shows model-estimated track of the tagged shark as estimated by (A) GPE3 and (B) the HMM_MCMC model. 25-meter contour lines are displayed for the uppermost 100m in light gray; 100-meter contour lines from 100-500m are displayed in medium gray; 500-meter contour lines are displayed in dark gray.

2.2 Statistical analysis

We reconstructed the animal's most probable movements via two frequently used models for interpreting light-level position estimates from PATs. We did not omit any tag days immediately after tagging due to the limited track length. We first estimated the animal's movements using GPE3, a location processing framework using a Hidden Markov model (HMM) provided by the tag manufacturer using published methods (Pedersen et al., 2011). Initial position estimates are derived algorithmically using light curves generated during twilight events to create estimates of latitude and longitude, which are further constrained by comparing tag-derived sea surface temperatures (SSTs) with remotely sensed SSTs (obtained from NOAA Optimum Interpolation SST V2 High Resolution Dataset) at the estimated location. These position estimates are then processed within the HMM to estimate the hidden state (i.e., the animal's true location) by incorporating observation error, estimated animal speed, and the application of a bathymetric mask (from NOAA ETOPO1 1 Arc-Minute Global Relief Model) to further constrain estimated locations daily. A posterior probability distribution is generated for the most likely animal position at every time step, consisting of two estimated locations per day. We iteratively ran the HMM model with different diffusion speeds (i.e., the speed parameter controlling the hypothetical distance an animal could travel between observations) ranging from 0.75 meters per second (m/s) to 2 m/s (in intervals of 0.25 m/s) and selected the speed that resulted in the highest model score (model scores provided by the manufacturer; selected speed was 1.75 m/s). The minimum diffusion speed at which the model would converge was 0.9 m/s, so the 0.9 m/s run was used instead of the 0.75 m/s run. The range of speeds tested was selected according to the manufacturer's recommendation of 1.5–2x the average sustained swimming speed of the animal; recent studies using animal-borne biologgers have estimated mean cruising speeds for shortfin mako ranging from 0.53 m/s (Saraiva et al., 2023) to 0.91 m/s (Waller et al., 2023). Plots of tracks from all GPE3 model runs are included as [Supplementary Figure S1](#).

We additionally estimated animal positions using the methods developed in Block et al. (2011) and Wilson et al. (2015). This model also uses an HMM framework, yet there are key differences. Most notably, the latter framework incorporates a Markov chain Monte Carlo (MCMC) sampling approach to further refine the posterior probability distribution, and as such, we refer to this model as the HMM_MCMC model for the duration of the manuscript. Furthermore, the HMM_MCMC model only estimated one position per day.

The tag was physically recovered on the 17th of July 2023, while drifting 20 meters from a beach in central-eastern Sardinia, and returned to us, allowing us to access the raw, 3-second interval data records for depth and temperature rather than relying on the time-binned data that is transmitted via satellite. We analyzed the raw data to characterize time-at-depth (TAD) and time-at-temperature (TAT) distributions according to diel period. All analyses were conducted using R version 4.3.1 (R Core Team, 2023) using RStudio version 2023.09.1 + 494 (RStudio Team, 2023). Data manipulation was performed using packages within the *tidyverse* (Wickham et al.,

2019), as well as the package *suncalc* (Thieurmel and Elmarhraoui, 2022) for assigning local sunrise and sunset times. Data visualization was performed using the following packages: *ggplot2* (Wickham, 2016), *marmap* (Pante et al., 2023), *viridis* (Garnier et al., 2024) and *scales* (Wickham et al., 2023).

3 Results

On the 10th of July 2023, after 54 DAL, the PAT's DTR was activated, causing the tag to release from its tether and float to the surface to begin satellite transmission of the binned data. MiniPAT tags are rated to withstand pressure to depths of 2,000 m; the DTR protects the tag by causing it to release at 1,800 m before it achieves crush depth. Given our knowledge of the vertical ecology of shortfin mako sharks (Vaudo et al., 2016; Andrzejczek et al., 2022) and the rapid, consistent speed at which the tag moved to depth, the juvenile shark likely suffered a putative mortality event and sank into deep waters, causing the DTR to activate ahead of the programmed 180-day deployment period. The tag surfaced approximately 64 kilometers (km) east of Sardinia, a total linear displacement of 408 km from the point of tagging, although the actual track was significantly longer according to both models (Figure 1).

There were differences in the model outputs between the GPE3 and HMM_MCMC models. The GPE3-estimated track was slightly longer (summed distance between points of 1405 km) than the HMM_MCMC track (summed distance of 1207 km), taking the shark south across the Gulf of Gabès and then east into the waters north of Libya during the second half of May and the first half of June (Figure 1A). In mid-June, GPE3 estimated that the shark began to swim consistently to the northwest, passing through the Strait of Sicily and into the Tyrrhenian Sea, covering more than 700 km in approximately three weeks. In contrast, the HMM_MCMC-estimated track suggested the shark performed much more constrained movements during the first part of its track (late May and early June), moving off the coastal shelf of the Tunisian plateau in early June into the deeper waters of the Strait of Sicily, but at a similar latitude to where it was tagged (Figure 1B). As with the GPE3-estimated track, the HMM_MCMC model also showed directed movements to the Tyrrhenian Sea beginning in mid-June, although the scale of this estimated movement was smaller given the more constrained movements in the first part of the track.

Notably, the depth-temperature profiles for the shark showed that for the four weeks post-tagging, the shark remained within the uppermost 50 m of the water column, primarily in the mixed layer and thermocline (Figure 2). In late May and early June, the shark made several dives in the 100 m range. By mid-June, the shark began a pattern of frequent diving to depths of 150–200 m, which continued for approximately two weeks (Figure 2A). From the start of July, diving depths were generally constrained within the uppermost 125 m of the water column; however, beginning on July 6, the mako shark began diving deeper than it had previously, reaching depths of approximately 400 m for several consecutive days, despite spending most of its time above 50 m (Figure 2B).

After a prolonged period at the surface in the early morning hours of July 10, the PAT experienced a pulse of light, after which it

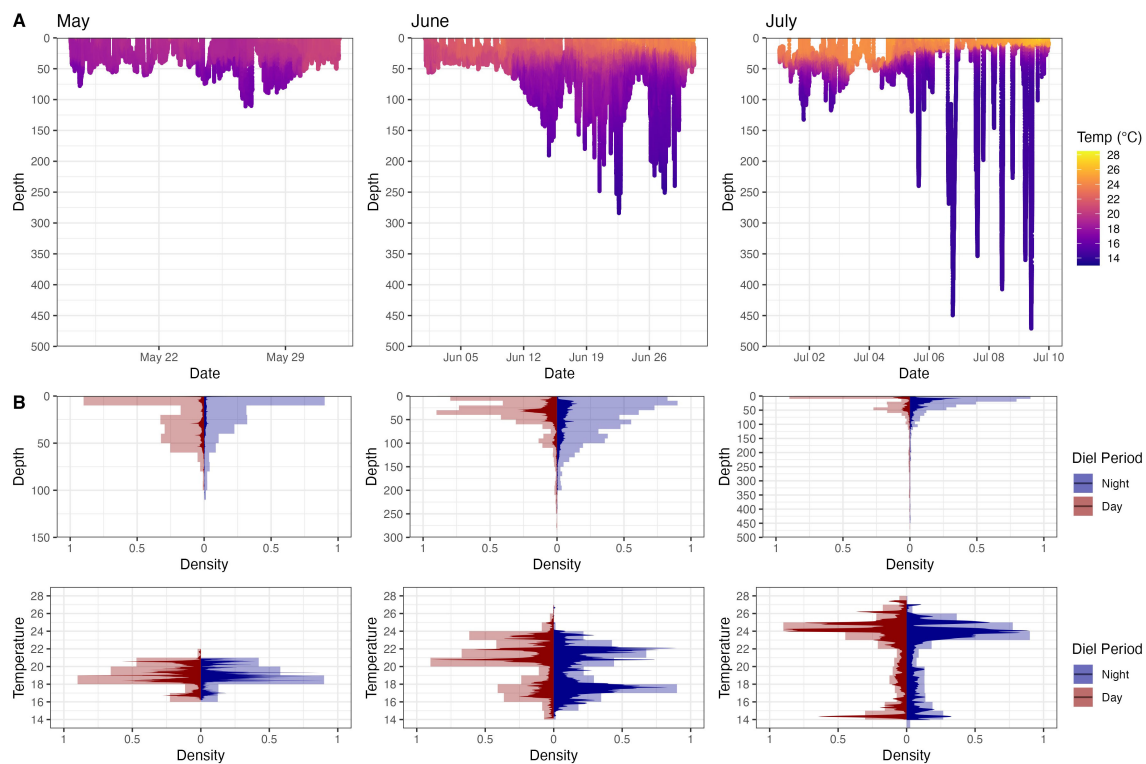


FIGURE 2

(A) Monthly depth-temperature profile summarizing the shark's vertical movements during its time at liberty, with depth indicated on the y-axis and temperatures indicated by color. Note that May and July do not reflect a complete month worth of data due to the timing of tagging and the premature tag release. (B) Monthly time-at-depth (TAD; top row) and time-at-temperature (TAT; bottom row) distributions, with daytime distributions in red and nighttime distributions in blue. Note that y-axes for TAD distributions vary between panels.

recorded a rapid descent from the surface to approximately 110 m, followed by a slightly slower but still rapid descent, to approximately 505 m, the deepest observations recorded up until this point (Supplementary Figure S2). Over the following approximately 8 hours, the tag recorded depths ranging between 500 m and 650 m, with a general pattern of slow descent observed. This was followed by a rapid ascent from 650 m to approximately 400 m. The tag then recorded a slow descent from 400 m to 475 m over approximately 3 hours before another period of ascent, after which the tag rapidly descended to 1,800 m, activating the DTR.

Overall, the shark spent 26.6% of its time within 10 m of the surface and 73.9% within the uppermost 50 m, although this pattern varied slightly by month. It was more surface-oriented during May and July, spending 40.5% and 37.5% of its time in the upper 10 m, respectively, while that figure dropped to 16.9% during June. Although the tag recorded dives to depths > 250 m and 450 m, respectively during the months of June and July, the shark spent > 90% of its time in the epipelagic (upper 100 m) both overall and within each individual month (Figure 2B).

4 Discussion

The satellite track reported here represents the first documented fine-scale movements of a shortfin mako shark in the

Mediterranean, and despite representing the movements of only one animal, it reveals that juvenile mako sharks in the region can be highly mobile even at early life stages. Although the Tunisian plateau and Pelagie Islands are hypothesized to play a nursery role for mako sharks (Walls and Soldo, 2016; Cattano et al., 2023) and other lamnids regionally (Fergusson, 2002; Moro et al., 2020), the juvenile shark in our study made highly directional movements away from this area even at a very young age. Although no age-growth curves are available in the Mediterranean, based on data from other populations, the study shark was likely between one and four years old (Ribot-Carballal et al., 2005; Natanson et al., 2007). Such rapid and highly directional movement (408 km minimum displacement in 54 days) at an early life stage may have important conservation implications, particularly when considering the multiple hypothesized shortfin mako nurseries within the Mediterranean Sea.

Various studies have documented the repeated captures of YOY and juvenile shortfin mako sharks to hypothesize potential nursery areas in numerous locations around the Mediterranean Sea, including the coastal waters of Turkey (Tunçer and Kabasakal, 2016; Bengil et al., 2019; Ergüden et al., 2021; Akyol and Capapé, 2024), the Pelagie Archipelago (Cattano et al., 2023), the Ligurian and northwest Tyrrhenian Seas (Mancusi et al., 2023), the Asinara Gulf (Scacco et al., 2023), and the Adriatic Sea (Udovičić et al., 2019). The track we present here, while only for one shark, provides evidence that even early life stage shortfin mako sharks are capable

of long-range movements across the Mediterranean over short time scales, demonstrating their potential to move between and potentially connect the variously hypothesized nursery areas. Broad-scale movements by juveniles in the Mediterranean, if confirmed with additional telemetry datasets, would not be unique to the region. Juvenile shortfin mako sharks tagged in New Zealand and Australia commonly displaced >1000 km after tagging, and demonstrated varying and complex individual movement strategies that included long periods of both residency and travel, with presumptive migration patterns commonly but not always observed (Rogers et al., 2015; Francis et al., 2018). In general, there is a relatively high degree of intraspecific variation in shortfin mako shark movements across all life stages. A suite of studies in the Northwest Atlantic has documented a host of disparate movement strategies in both juveniles and adults, ranging from primarily resident animals with high site fidelity to individuals who performed long-range movements and migrations of varying magnitude and direction (Casey and Kohler, 1992; Gibson et al., 2021; Santos et al., 2021). This variation underscores the need for further tagging studies in the Mediterranean, as we show here that even at early life stages, the hypothesized nursery areas for shortfin mako sharks in the region may not be entirely discrete, a notion that would have important conservation implications given the historical focus on using catch records of juveniles to delineate nursery areas as candidates for spatial protection.

Although both model's tracks demonstrate directed movements toward the Tyrrhenian Sea, the different model outputs differ considerably in the early part of the track. While not substantially different in total length, the tracks do have potentially differing conservation implications. The GPE3-estimated track takes the shark south across the Tunisian plateau before moving east into Libyan waters, effectively traversing the coastal waters of the two Mediterranean nations with the highest levels of shark catches (Bradai et al., 2018; Milazzo et al., 2021). In contrast, the movements estimated by the HMM_MCMC model during the first portion of the track were more resident at the northern portion of the Tunisian plateau and the shelf edge. In both tracks, the shark was estimated to have quickly crossed multiple jurisdictions, highlighting the need for international cooperation in any conservation efforts (Daly et al., 2023). Given the lack of data on the spatial ecology of the species regionally, the deployment of additional tags across a wide range of life stages should be prioritized. Where possible, future tagging studies in the region should implement double-tagging to help constrain light-level geolocation model estimates and to help refine the use of GPE3/HMM_MCMC and other similar HMM models in the Mediterranean basin.

Of note during the study period is the increased vertical movements by the tagged shark during its time at liberty. While precise linkages between the shark's horizontal position and dive profiles are challenging given the inherent uncertainty in light-level geolocation, the relative lack of diving during the early part of the track is likely due to the bathymetric constraints of the shark's position on the Tunisian plateau, where bottom depths less than 50 meters are common. Indeed, in June and July, the shark spent close to 10% of its time at depths greater than 100 m, while in May, this figure was less than 1%. As the tagged shark moved away from

Tunisia into deeper waters, it began to increase its vertical activity, and notably, during the last days of the track, the shark expanded its vertical range even further, achieving daily depths of ~400 m in the days leading up to the presumed fishery interaction. Potential drivers for the increased vertical activity throughout the track include thermoregulation, foraging, and behavioral mode (Abascal et al., 2010; Rogers et al., 2015; Francis et al., 2018; Santos et al., 2021; Braun et al., 2023; Vaudo et al., 2024).

Temperature may have influenced not just vertical activity but also the observed movement toward the Tyrrhenian Sea at the end of the track. SSTs on the Tunisian plateau frequently approach 30°C in the summer months, and while thermal preferences of shortfin mako are likely to vary geographically, juvenile makos in other parts of the world have been shown to preferentially occupy waters with ambient temperatures closer to 20°C (Rogers et al., 2015; Santos et al., 2021). As SSTs increased regionally heading into the summer, the tagged shark moved northward and began diving deeper and more frequently. Additionally, diel TAD profiles showed an increased tendency to spend time in the mixed layer (where temperatures are warmest) during cooler nighttime than during the day. However, it should be noted that in our study, as the tagged shark dove more frequently in June and July, it often continued its dives far beyond the mixed layer and thermocline, continuing to dive to depths of 150 meters or more despite experiencing relatively constant temperatures below ~75 meters depth (Figure 2A), even at the end of the track when the animal began diving to depths of 400 m or more. Furthermore, TAD profiles during the daytime and nighttime were highly similar (Figure 2B, bottom row), challenging the notion that any diel variation in diving was directed toward occupying a preferential thermal band. However, the increasingly warm surface waters experienced in early July may have allowed the shark to increasingly probe deeper waters for longer periods of time, given the increased capacity to re-warm at the surface following a dive (Carey et al., 1981; Klimley et al., 2002; Loefer et al., 2005). Though additional dive profiles are needed to better elucidate drivers of vertical activity for juvenile shortfin mako sharks regionally, ambient temperature does indeed influence both horizontal and vertical movements to some degree (Abascal et al., 2010; Vaudo et al., 2017; Francis et al., 2018; Santos et al., 2021). Thermoregulation likely played at least a partial role in driving both the northward movements during June and July as SSTs warmed, as well as the increase in vertical activity. Additional tagging studies to resolve the thermal preferences of shortfin mako sharks regionally are key given the rapid increase in SST in the Mediterranean over recent decades (Marriner et al., 2022) and potential alterations in species distributions that may result from such changes (Parravicini et al., 2015).

An alternative potential explanation for the increased diving activity is that the behavior was driven by foraging. Foraging has been posited as a primary driver for vertical activity in shortfin mako sharks (Abascal et al., 2010; Braun et al., 2023), with patterns in diving behavior often closely linked to the diel period. Shortfin mako sharks feed across multiple levels of the water column (Compagno, 2001), and have been observed to expand their vertical range during daylight hours (Loefer et al., 2005; Abascal et al., 2010), while spending nighttime hours closer to the surface,

where they can presumably feed on vertically migrating prey (Braun et al., 2023). We did not observe any consistent diel patterns in vertical habitat use during the study shark's time at liberty, though this is perhaps an artifact of the bathymetric limitation to diving during significant portions of the track where it traveled across the Tunisian plateau. Nonetheless, even if diving was not coupled with the movements of diel vertical migrators, the observed vertical activity is likely to have increased foraging opportunities for the study shark as it traveled, particularly toward the end of the track in the Tyrrhenian Sea, when it began diving to ~400 m or more. Achieving such depths potentially allowed the study shark to intersect with mesopelagic forage in deep scattering layers (DSLs), which have been identified at similar depths in other portions of the western Mediterranean (Peña et al., 2014; Peña, 2024). Many predators are thought to use DSLs as an important component of their energy budget (Andrzejczak et al., 2019, 2022; Braun et al., 2022, 2023), with shortfin mako sharks seemingly a species that may particularly exploit this resource (Braun et al., 2023).

A third possible driver for the observed increase in vertical activity may be associated with a switch in behavioral state as the study shark left the Tunisian plateau and began its comparably directed movements northward. Shortfin mako sharks have been shown to alter their diving patterns when they are in a travel state as opposed to a resident state, with traveling sharks diving deeper and more frequently, particularly in warmer waters (Vaudo et al., 2024) and when offshore (Santos et al., 2021). In doing so, shortfin mako sharks may attempt to maximize foraging opportunities while traveling to locate resources that are often more patchily distributed in offshore areas (Rogers et al., 2015; Vaudo et al., 2024). Since travel periods can last several weeks or months, sharks most likely must forage even during these relocation periods (Francis et al., 2018; Vaudo et al., 2024). Furthermore, diving while traveling may present opportunities for navigation (Rogers et al., 2015; Francis et al., 2018). Given the limited sample size and the inconclusive TAD/TAT patterns observed, we cannot determine any primary drivers for the observed vertical activity by the study shark; however, an animal's behavioral state and resulting vertical activity inherently comprises aspects of both foraging strategy and thermoregulation, and multiple partial drivers likely acted in concert to increase the study shark's use of deep waters.

Considering the depth profile recorded on the morning of the 10th of July, the shark likely experienced a mortality event near the surface in the early morning hours, after which the carcass rapidly sank to the seafloor. The nature of this mortality is impossible to discern from tag data alone; however, there is significant fishing pressure in the region (Kroodsmas et al., 2018; Paolo et al., 2024; Ferretti et al., 2024), and the tag recorded a spike of light right before its rapid descent, potentially suggesting the shark experienced an additional fishery interaction. The fate of the tagged shark emphasizes the risks faced by sharks regionally. The tagged shark was initially captured via longline, which results in animal retention >95% of the time (Megalofonou et al., 2005), and despite the fact that the study shark was alternatively tagged and released, it nonetheless suffered a mortality event after less than two months. Previous satellite telemetry work has shown that fisheries-dependent data can significantly underestimate fishing mortality in shortfin mako sharks (Byrne et al., 2017), and the mortality presented

here, presumably due to a fishing interaction, further underscores this threat. Though we cannot fully dismiss the possibility that this was a post-release mortality resulting from our own capture and tagging process, we do not believe the shark's extensive horizontal and vertical movements during its time at liberty reflect the movements of a physiologically compromised animal.

The successful deployment additionally highlights the value of collaboration with local fishers. Dozens of hours of directed shark fishing with rod-and-reel or handlines over two previous expeditions were unsuccessful in locating sharks for telemetry studies (Ferretti et al., 2024), while similar studies have reportedly encountered similar challenges (Micarelli et al., 2023), whereas the encounter rates increase with the increased scope of commercial fishing (e.g., this study, Cattano et al., 2023). Given the relatively low encounter rates outside of commercial fisheries, as well as the rate at which commercial fishers in Tunisia encounter sharks, including shortfin mako, sandbar (*Carcharhinus plumbeus*) (Echwikhi et al., 2014; Saidi et al., 2019), and white (*Carcharodon carcharias*) sharks (Bradai et al., 2018), collaboration with local fishers represents a promising avenue to increase animal encounter rates and promote the integration of local stakeholders into the planning and development of research and management plans that are urgently needed to protect the dwindling populations of large sharks in the region.

While only one track, we show here the broad movement capacity of juvenile shortfin mako sharks in the Mediterranean, adding important context to the previously reported captures of juveniles and YOY from disparate areas across the Mediterranean Sea by demonstrating the capability of even young sharks to travel long distances over short time scales. The study shark's subsequent mortality additionally highlights the elevated risk that shortfin mako sharks are exposed to regionally even at early life stages, which represents a grave threat to the population, yet can be underestimated using fisheries dependent data alone. While additional tagging efforts are sorely needed, here we provide evidence to shape deeper investigations into the movements and ecology of shortfin mako sharks in the Mediterranean Sea.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Virginia Tech Institutional Animal Care and Use Committee. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

BS: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. TC: Conceptualization, Formal

analysis, Methodology, Project administration, Writing – review & editing. KE: Conceptualization, Investigation, Project administration, Writing – review & editing. CG: Investigation, Writing – review & editing. JJ: Investigation, Writing – review & editing. SM: Investigation, Writing – review & editing. RS: Conceptualization, Methodology, Writing – review & editing. BB: Conceptualization, Formal analysis, Methodology, Project administration, Writing – review & editing. FF: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This work was conducted while on expedition for an ongoing research project researching white sharks in the region. Funding for the white shark project was provided by The Explorers Club, Discovery Channel, Sharkproject, the Augmentum platform, and individual donors. The individual donors were not involved in the study design, collection, analysis, interpretation of data, the writing of this article, or the decision to submit it for publication.

Acknowledgments

We would like to acknowledge Rosie O'Donnell and Yachts for Science for their support in fundraising and securing an expedition vessel, Frank Peeters, Jeff Doolan, and Romy Hunt for their in-kind support, Mike Castleton for analytical assistance, and Hani Berriche

and Chiheb Lemsi for assistance on the ground in Tunisia. BS acknowledges the monetary support of the Acorn Alcinda Foundation. FF acknowledges the monetary support of the Bertarelli Foundation. We would also like to thank Alessia Cirillo and Alessandro Langiu for help recovering the tag after deployment

Conflict of interest

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.

The handling editor NQ declared a past co-authorship with the authors BS, TC, FF.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1423507/full#supplementary-material>

References

- Abascal, F. J., Mejuto, J., Quintans, M., and Ramos-Cartelle, A. (2010). Horizontal and vertical movements of swordfish in the Southeast Pacific. *ICES J. Mar. Sci.* 67, 466–474. doi: 10.1093/icesjms/fsp252
- Akyol, O., and Capapé, C. (2024). Capture of a new-born shortfin mako shark *Isurus oxyrinchus* (Lamniformes: Lamnidae), with updated records from the Turkish marine waters. *Nat. Eng. Sci.* 9 (1), 1–9. doi: 10.28978/nesciences.1472086
- Andrzejczek, S., Gleiss, A. C., Pattiaratchi, C. B., and Meekan, M. G. (2019). Patterns and drivers of vertical movements of the large fishes of the epipelagic. *Rev. Fish Biol. Fish.* 29, 335–354. doi: 10.1007/s11160-019-09555-1
- Andrzejczek, S., Lucas, T. C. D., Goodman, M. C., Hussey, N. E., Armstrong, A. J., Carlisle, A., et al. (2022). Diving into the vertical dimension of elasmobranch movement ecology. *Sci. Adv.* 8, eabo1754. doi: 10.1126/sciadv.abo1754
- Bengil, E. G. T., Akalin, M., Tüney Kizilkaya, İ., and Bengil, F. (2019). Biology of shortfin mako shark (*Isurus oxyrinchus rafinesque* 1810) from the eastern mediterranean. *Acta Aquat. Turc.* 15, 425–432. doi: 10.22392/actaqua.545997
- Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., et al. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature* 475, 86–90. doi: 10.1038/nature10082
- Bradai, M. N., Saidi, B., Enajjar, S., Bradai, M. N., Saidi, B., and Enajjar, S. (2018). Overview on mediterranean shark's fisheries: impact on the biodiversity. *Mar. Ecol. - Biotic Abiotic Interact.* 211–230. doi: 10.5772/intechopen.74923
- Braun, C. D., Arostegui, M. C., Thorrold, S. R., Papastamatiou, Y. P., Gaube, P., Fontes, J., et al. (2022). The functional and ecological significance of deep diving by large marine predators. *Annu. Rev. Mar. Sci.* 14, 129–159. doi: 10.1146/annurev-marine-032521-103517
- Braun, C. D., Della Penna, A., Arostegui, M. C., Afonso, P., Berumen, M. L., Block, B. A., et al. (2023). Linking vertical movements of large pelagic predators with distribution patterns of biomass in the open ocean. *Proc. Natl. Acad. Sci.* 120, e2306357120. doi: 10.1073/pnas.2306357120
- Byrne, M. E., Cortés, E., Vaudo, J. J., Harvey, G. C. M. N., Sampson, M., Wetherbee, B. M., et al. (2017). Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator. *Proc. R. Soc B Biol. Sci.* 284, 20170658. doi: 10.1098/rspb.2017.0658
- Carey, F. G., Teal, J. M., and Kanwisher, J. W. (1981). The visceral temperatures of mackerel sharks (Lamnidae). *Physiol. Zool.* 54, 334–344. doi: 10.1086/physzool.54.3.30159948
- Carpentieri, P., Nastasi, A., Sessa, M., and Srour, A. (2021). *Incidental catch of vulnerable species in Mediterranean and Black Sea fisheries - A review* (Rome: FAO). doi: 10.4060/cb5405en
- Casey, J., and Kohler, N. (1992). Tagging studies on the Shortfin Mako Shark (*Isurus oxyrinchus*) in the Western North Atlantic. *Mar. Freshw. Res.* 43, 45. doi: 10.1071/MF9920045
- Cattano, C., Gambardella, C., Grancagnolo, D., Principato, E., Aglieri, G., Turco, G., et al. (2023). Multiple interannual records of young-of-the-year identify an important area for the protection of the shortfin mako, *Isurus oxyrinchus*. *Mar. Environ. Res.* 192, 106217. doi: 10.1016/j.marenvres.2023.106217
- Compagno, L. J. V. (2001). "Sharks of the world: an annotated and illustrated CAAtalogue of shark species known to date," in *Volume 2: Bullhead, mackerel and carpenter sharks (Heterodontiformes, Lamniformes and Orectolobiformes)* (Food and Agriculture Organization of the United Nations, Rome).
- Daly, R., Venables, S., Rogers, T., Filmler, J., Hempson, T., Murray, T., et al. (2023). Persistent transboundary movements of threatened sharks highlight the importance of cooperative management for effective conservation. *Mar. Ecol. Prog. Ser.* 720, 117–131. doi: 10.3354/meps14413
- Echwikhi, K., Saidi, B., and Bradai, M. N. (2014). Elasmobranchs longline fisheries in the Gulf of Gabès (southern Tunisia). *J. Mar. Biol. Assoc. U. K.* 94, 203–210. doi: 10.1017/S0025315413000726

- Ergüden, D., Ayas, D., and Kabasakal, H. (2021). Recent occurrence of shortfin mako shark, *Isurus oxyrinchus rafinesque* 1810 (Chondrichthyes: lamnidae), from the north-eastern mediterranean coast of Turkey. *J. Mar. Sci. Fish.* 4, 79–85. doi: 10.46384/jmsf.839454
- Fergusson, I. (2002). Occurrence and biology of the great white shark, *Carcharodon carcharias*, in The Central Mediterranean Sea: A review, in *Proceedings of the 4th European Elasmobranch Association Meeting*, Livorno, Italy. 7–23.
- Ferretti, F., Myers, R. A., Serena, F., and Lotze, H. K. (2008). Loss of large predatory sharks from the mediterranean sea. *Conserv. Biol.* 22, 952–964. doi: 10.1111/j.1523-1739.2008.00938.x
- Ferretti, F., Shea, B. D., Gallagher, A. J., Gambardella, C., Jenrette, J. F., Moro, S., et al. (2024). On the tracks of white sharks in the mediterranean sea. *Front. Mar. Sci.* 11, 1425511. doi: 10.3389/fmars.2024.1425511
- Francis, M. P., Shivji, M. S., Duffy, C. A. J., Rogers, P. J., Byrne, M. E., Wetherbee, B. M., et al. (2018). Oceanic nomad or coastal resident? Behavioural switching in the shortfin mako shark (*Isurus oxyrinchus*). *Mar. Biol.* 166, 5. doi: 10.1007/s00227-018-3453-5
- Garnier, S., Ross, N., Rudis, R., Camargo, A.P., Sciaini, M., and Scherer, C. (2024). *viridis(Lite) - Colorblind-Friendly Color Maps for R*. doi: 10.5281/zenodo.4679423
- Gibson, K. J., Streich, M. K., Topping, T. S., and Stunz, G. W. (2021). New insights into the seasonal movement patterns of shortfin mako sharks in the gulf of Mexico. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.623104
- Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R., et al. (2010). Philopatry and migration of Pacific white sharks. *Proc. R. Soc B Biol. Sci.* 277, 679–688. doi: 10.1098/rspb.2009.1155
- Klimley, A. P., Beavers, S. C., Curtis, T. H., and Jorgensen, S. J. (2002). Movements and swimming behavior of three species of sharks in la jolla canyon, california. *Environ. Biol. Fishes* 63, 117–135. doi: 10.1023/A:1014200301213
- Kroodsmá, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., et al. (2018). Tracking the global footprint of fisheries. *Science* 359, 904–908. doi: 10.1126/science.aao5646
- Loefer, J. K., Sedberry, G. R., and McGovern, J. C. (2005). Vertical movements of a shortfin mako in the western north atlantic as determined by pop-up satellite tagging. *Southeast. Nat.* 4, 237–246. doi: 10.1656/1528-7092(2005)004[0237:VMOASM]2.0.CO;2
- Mancusi, C., Serena, F., Neri, A., Scacco, U., Bains, R. T., Voliani, A., et al. (2023). Unexpected records of newborn and young sharks in ligurian and north tyrrhenian seas (North-western mediterranean basin). *Diversity* 15, 806. doi: 10.3390/d15070806
- Marriner, N., Kaniewski, D., Pourkerman, M., and Devillers, B. (2022). Anthropocene tipping point reverses long-term Holocene cooling of the Mediterranean Sea: A meta-analysis of the basin's Sea Surface Temperature records. *Earth-Sci. Rev.* 227, 103986. doi: 10.1016/j.earscirev.2022.103986
- Megalofonou, P., Yannopoulos, C., Damalas, D., De Metrio, G., Deflorio, M., de la Serna, J. M., et al. (2005). Incidental catch and estimated discards of pelagic sharks from the swordfish and tuna fisheries in the Mediterranean Sea. *Fish. Bull.* 103, 620–634.
- Micarelli, P., Reinero, F. R., Marsella, A., Vernelli, E., Vittorini, E., Monteleone, L., et al. (2023). Attempts to locate and sample the white shark, *Carcharodon carcharias* (Lamniformes: Lamnidae), along the Italian coasts in the Mediterranean Sea. *Acta Adriat.* 64, 181–186. doi: 10.32582/aa.64.2.6
- Milazzo, M., Cattano, C., Al Mabruk, S. A. A., and Giovos, I. (2021). Mediterranean sharks and rays need action. *Science* 371, 355–356. doi: 10.1126/science.abg1943
- Moro, S., Jona-Lasinio, G., Block, B., Micheli, F., De Leo, G., Serena, F., et al. (2020). Abundance and distribution of the white shark in the Mediterranean Sea. *Fish. Fish.* 21, 338–349. doi: 10.1111/faf.12432
- Natanson, L. J., Kohler, N., Ardzzone, D., Cailliet, G., Wintner, S., and Mollet, H. (2007). Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. *Environ. Biol. Fishes - Environ. Biol. FISH.* 77, 367–383. doi: 10.1007/978-1-4020-5570-6_16
- Natanson, L. J., Winton, M., Bowlby, H., Joyce, W., Deacy, B., Coelho, R., et al. (2020). Updated reproductive parameters for the shortfin mako (*Isurus oxyrinchus*) in the North Atlantic Ocean with inferences of distribution by sex and reproductive stage. *Fish. Bull.* 118, 21–36. doi: 10.7755/FB.118.1.3
- Panayiotou, N., Biton Porsmoguer, S., Moutopoulos, D.K., and Lloret, J. (2020). Offshore recreational fisheries of large vulnerable sharks and teleost fish in the Mediterranean Sea: first information on the species caught. *Mediterr. Mar. Sci.* 21, 222. doi: 10.12681/mms.21938
- Pante, E., Simon-Bouhet, B., and Irissou, J.-O. (2023). *marmap: Import, Plot and Analyze Bathymetric and Topographic Data*. Available online at: <https://CRAN.R-project.org/package=marmap>.
- Paolo, F. S., Kroodsmá, D., Raynor, J., Hochberg, T., Davis, P., Cleary, J., et al. (2024). Satellite mapping reveals extensive industrial activity at sea. *Nature* 625, 85–91. doi: 10.1038/s41586-023-06825-8
- Parravicini, V., Mangialajo, L., Mousseau, L., Peirano, A., Morri, C., Montefalcone, M., et al. (2015). Climate change and warm-water species at the north-western boundary of the Mediterranean Sea. *Mar. Ecol.* 36, 897–909. doi: 10.1111/maec.12277
- Pedersen, M. W., Patterson, T. A., Thygesen, U. H., and Madsen, H. (2011). Estimating animal behavior and residency from movement data. *Oikos* 120, 1281–1290. doi: 10.1111/j.1600-0706.2011.19044.x
- Peña, M. (2024). Atlantic versus Mediterranean deep scattering layers around the Iberian peninsula. *Prog. Oceanogr.* 221, 103211. doi: 10.1016/j.pcean.2024.103211
- Peña, M., Olivar, M. P., Balbín, R., López-Jurado, J. L., IglesiasM., and Miquel, J. (2014). Acoustic detection of mesopelagic fishes in scattering layers of the Balearic Sea (western Mediterranean). *Can. J. Fish. Aquat. Sci.* 71, 1186–1197. doi: 10.1139/cjfas-2013-0331
- Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., Da Costa, I., Sequeira, A. M. M., et al. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature* 572, 461–466. doi: 10.1038/s41586-019-1444-4
- R Core Team (2023). *R Version 4.3.1*.
- Ribot-Carballal, M. C., Galván-Magaña, F., and Quiñónez-Velázquez, C. (2005). Age and growth of the shortfin mako shark, *Isurus oxyrinchus*, from the western coast of Baja California Sur, Mexico. *Fish. Res.* 76, 14–21. doi: 10.1016/j.fishres.2005.05.004
- Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., et al. (2019). *Isurus oxyrinchus* (The IUCN Red List of Threatened Species). doi: 10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en
- Rogers, P. J., Huveneers, C., Page, B., Goldsworthy, S. D., Coyne, M., Lowther, A. D., et al. (2015). Living on the continental shelf edge: habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia. *Fish. Oceanogr.* 24, 205–218. doi: 10.1111/fog.12103
- RStudio Team (2023). *RStudio Version 2023.09.1 + 494*.
- Saidi, B., Enajjar, S., Karaa, S., Echwikhi, K., Jribi, I., and Bradai, M. N. (2019). Shark pelagic longline fishery in the Gulf of Gabes: Inter-decadal inspection reveals management needs. *Mediterr. Mar. Sci.* 20, 532. doi: 10.12681/mms.18862
- Santos, C. C., Domingo, A., Carlson, J., Natanson, L. J., Travassos, P., Macias, D., et al. (2021). Movements, habitat use, and diving behavior of shortfin mako in the atlantic ocean. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.686343
- Saraiva, B. M., Macena, B. C. L., Solleiet-Ferreira, S., Afonso, P., and Fontes, J. (2023). First insights into the shortfin mako shark (*Isurus oxyrinchus*) fine-scale swimming behaviour. *R. Soc. Open Sci.* 10, 230012. doi: 10.1098/rsos.230012
- Scacco, U., Gennari, E., Di Crescenzo, S., and Fanelli, E. (2023). Looking into the prevalence of bycatch juveniles of critically endangered elasmobranchs: a case study from pelagic longline and trammel net fisheries of the Asinara Gulf (western Mediterranean). *Front. Mar. Sci.* 10. doi: 10.3389/fmars.2023.1303961
- Serena, F., Mancusi, C., and Barone, M. (2014). *MEDiterranean Large Elasmobranchs Monitoring. Protocollo di Acquisizione Dati* (Roma, Italy: SharkLife Program). Available online at: <https://www.sibm.it/public/document-files/SIBM-SERENA-F-MANCUSI-C-BARONE-M-2014-MEDiterranean-Large-Elasmobranchs-Monitoring-.pdf> (Accessed June 5, 2024).
- Thieurmell, B., and Elmarhraoui, A. (2022). *suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase*. Available online at: <https://CRAN.R-project.org/package=suncalc>.
- Tunçer, S., and Kabasakal, H. (2016). *Capture of a juvenile shortfin mako shark, Isurus oxyrinchus rafinesque 1810 (Chondrichthyes: Lamnidae) in the Bay of Edremit, northern Aegean Sea (Turkey)*. 31–36.
- Udovičić, D., Ugarković, P., Madiraca, F., and Dragičević, B. (2019). On the recent occurrences of shortfin mako shark, *Isurus oxyrinchus* (Rafinesque 1810) in the adriatic sea. *Acta Adriat.* 59, 237–243. doi: 10.32582/aa.59.2.10
- Vaudo, J. J., Byrne, M. E., Wetherbee, B. M., Harvey, G. M., and Shivji, M. S. (2017). Long-term satellite tracking reveals region-specific movements of a large pelagic predator, the shortfin mako shark, in the western North Atlantic Ocean. *J. Appl. Ecol.* 54, 1765–1775. doi: 10.1111/1365-2664.12852
- Vaudo, J., Dewar, H., Byrne, M., Wetherbee, B., and Shivji, M. (2024). Integrating vertical and horizontal movements of shortfin mako sharks, *Isurus oxyrinchus*, in the eastern North Pacific Ocean. *Mar. Ecol. Prog. Ser.* 732, 95–99. doi: 10.3354/meps14542
- Vaudo, J., Wetherbee, B., Wood, A., Weng, K., Howey-Jordan, L., Harvey, G., et al. (2016). Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature. *Mar. Ecol. Prog. Ser.* 547, 163–175. doi: 10.3354/meps11646
- Waller, M. J., Queiroz, N., Da Costa, I., Cidade, T., Loureiro, B., Womersley, F. C., et al. (2023). Direct measurement of cruising and burst swimming speeds of the shortfin mako shark (*Isurus oxyrinchus*) with estimates of field metabolic rate. *J. Fish Biol.* 103, 864–883. doi: 10.1111/jfb.15475
- Walls, R. H. L., and Soldo, A. (2016). *Isurus oxyrinchus (Mediterranean Assessment)*. *The IUCN Red List of Threatened Species*. Available online at: <https://www.iucnredlist.org/species/39341/16527941> (Accessed October 6, 2023).
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag New York). Available at: <https://ggplot2.tidyverse.org>.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., et al. (2019). Welcome to the tidyverse. *J. Open Source Software* 4, 1686. doi: 10.21105/joss.01686
- Wickham, H., Pedersen, T. L., and Seidel, D. (2023). *scales: Scale Functions for Visualization*. Available online at: <https://CRAN.R-project.org/package=scales>.
- Wilson, S. G., Jonsen, I. D., Schallert, R. J., Ganong, J. E., Castleton, M. R., Spares, A. D., et al. (2015). Tracking the fidelity of Atlantic bluefin tuna released in Canadian waters to the Gulf of Mexico spawning grounds. *Can. J. Fish. Aquat. Sci.* 72, 1700–1717. doi: 10.1139/cjfas-2015-0110