Ocean and Coastal Management 269 (2025) 107782

Contents lists available at ScienceDirect

Ocean and Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

Long-term multitracking reveals contrasting yet highly resident movement ecologies of two sympatric and endangered deep-sea sharks

Miguel Gandra [a,*], Jorge Fontes [b,c], Bruno C.L. Macena [b,c], Carl G. Meyer [d], Pedro Afonso [b,c]

[a] *Centro de Ciências Do Mar Do Algarve (CCMAR/CIMAR LA), Campus de Gambelas, Universidade Do Algarve, 8005-139, Faro, Portugal*
[b] *Institute of Marine Sciences (OKEANOS), University of the Azores, 9901-862, Horta, Portugal*
[c] *Institute of Marine Research (IMAR), University of the Azores, 9901-862, Horta, Portugal*
[d] *Hawaii Institute of Marine Biology, University of Hawaii at Manoa, Kaneohe, HI, USA*

ARTICLE INFO

Keywords:
Biotelemetry
Hexanchus griseus
Dalatias licha
Spatial ecology
Site fidelity
Sexual segregation
Deep-sea conservation

ABSTRACT

Studying shark movement ecology is vital for understanding their ecological roles and supporting sustainable management and conservation strategies. However, such information remains scarce for deep-sea sharks. We used biotelemetry to investigate the spatial behaviour and movements of two endangered deep-sea predators, the kitefin (*Dalatias licha*) and bluntnose sixgill (*Hexanchus griseus*) sharks, in the Azores, northern Mid-Atlantic Ridge. We tagged a total of 21 kitefin sharks with acoustic transmitters (some including depth sensors) and seven sixgill sharks with different tag configurations: three were fitted exclusively with acoustic transmitters, two were double-tagged with both acoustic transmitters and pop-up satellite archival tags (PSATs), and two were tagged exclusively with PSATs deployed via a speargun-equipped submersible. Both species exhibited diel vertical migrations and unexpected high site fidelity (up to 4 years), using habitats that inter-connect seamounts, slopes, and island shelves. Sixgill sharks exhibited more extensive and diverse individual home ranges and vertical diel activity patterns than kitefin sharks. Sexual segregation was evident in kitefin sharks, with males and females displaying distinct differences in depth distribution and habitat use, supporting earlier hypotheses based on fisheries data. These behavioural patterns suggest that sixgill sharks function as wide-ranging, deep-sea opportunistic foragers and predators, traversing interconnected habitats in search of prey – including kitefin sharks, which occupy a more slope-associated mesopredator niche. Our novel findings support ecological theory suggesting that deep-sea sharks exhibit far more contrasting spatial ecologies than previously thought, driven by their life histories. These differences may have implications for their high vulnerability to fisheries and climate change-induced habitat degradation.

1. Introduction

The deep sea is Earth's vastest ecosystem and holds vital ecological significance. It encompasses multiple ecological zones, each with its own distinct biodiversity. The bathypelagic zone is one of the largest biomes and spans depths from 1000 m down to 4000 m (Armstrong et al., 2012; Ramirez-Llodra et al., 2010). This zone extends from the continental shelf edge to the upper boundary of the abyssal zone and is characterised by the complete absence of sunlight. Above it lies the mesopelagic zone (approximately 200–1000 m), where partial sunlight penetration creates a transitional "twilight zone" between the epipelagic and bathypelagic zones. The twilight zone alone accounts for up to 20 % of the global ocean volume and covers over 60 % of the Earth's surface (Proud et al., 2017).

Despite the lack of sunlight, low temperatures and extreme pressures, these deep-sea biomes sustain extraordinary biodiversity (Ramirez-Llodra et al., 2010). They play a pivotal role in nutrient and carbon cycling and profoundly influence global marine ecosystems and climate. Although estimates vary, recent studies suggest that the global meso- and bathypelagic fish biomass may significantly exceed earlier projections (Braun et al., 2022; Hernández-León et al., 2020), potentially constituting a substantial portion of the world's total fish biomass (Irigoien et al., 2014). Consequently, these biomes serve as critical habitat for a diverse array of marine predators, including pelagic and demersal sharks and fishes, sea turtles and marine mammals, which drive bentho-pelagic coupling and biochemical flow through the water

---

* Corresponding author.
E-mail address: m3gandra@gmail.com (M. Gandra).

https://doi.org/10.1016/j.ocecoaman.2025.107782
Received 14 February 2025; Received in revised form 11 April 2025; Accepted 28 May 2025

column (Braun et al., 2022; Naito et al., 2013).

However, the biology of many species inhabiting these remote realms remains poorly understood. Deep-sea exploration is an ongoing and evolving endeavour requiring advanced technologies and interdisciplinary collaborations. Recent advances in marine telemetry and biologging have begun to reveal insights into the movement and behaviour of deep-sea species (Edwards et al., 2019), but substantial knowledge gaps persist (Braun et al., 2022). With marine ecosystems facing increasing threats from climate change, pollution, habitat loss and overexploitation, understanding key deep-sea species and habitats has become an urgent priority. Shark populations, in particular, are declining rapidly worldwide, necessitating effective, knowledge-based management strategies (Pacoureau et al., 2021). This includes addressing the overexploitation of threatened deep-water shark (DWS) species, driven by demand for liver oil and bycatch in deep-water fisheries (Finucci et al., 2024).

The kitefin shark, *Dalatias licha* (Bonnaterre, 1788), and the bluntnose sixgill shark, *Hexanchus griseus* (Bonnaterre, 1788), are cosmopolitan DWS predators inhabiting tropical and temperate oceans. Both species primarily dwell on continental and insular shelves, upper slopes and seamounts, typically in close association with the seafloor (Carey and Clark, 1995; Comfort and Weng, 2015; Compagno, 1984). The kitefin is a medium-sized squaliform shark usually found at depths of 200–600 m. Females can reach 1.8 m, and males grow to 1.2 m in length (Mallefet et al., 2021). It is ovoviviparous, producing litters of 10–20 pups (Compagno, 1984). Although fisheries data suggest high levels of sexual segregation in certain habitats (e.g., Silva, 1987), its pupping grounds and juvenile habitats remain unknown. Dietary studies suggest it is a mesopredator, consuming a variety of prey including benthic and demersal fishes, crustaceans, cephalopods and polychaetes (Capapé et al., 2008; Dunn et al., 2010; Navarro et al., 2014). In the Mediterranean, stomach contents and stable isotope analyses revealed a high prevalence of small demersal sharks in its diet (Navarro et al., 2014). However, little is known about the trophic ecology of kitefin shark populations inhabiting offshore deep-sea habitats, such as those in the Azores Archipelago on the Mid-Atlantic Ridge. In these and other regions, the species was heavily targeted for liver oil extraction between the 1970s and the 90s, leading to a drastic stock depletion (Perrotta, 2004). Due to its vulnerability to overexploitation and its k-strategy life history traits, the species is now listed as "Vulnerable" globally (Finucci et al., 2018b) and "Endangered" in European waters (Walls and Guallart, 2015) by the IUCN Red List.

The bluntnose sixgill (hereinafter referred to as sixgill) shark is a Hexanchiform and one of the largest extant sharks, growing up to 5.5 m. It is believed to have one of the longest life spans of any vertebrate (Dunbrack and Zielinski, 2003). Its bathymetric distribution ranges from 0 to 2500 m, though it is typically captured below 100 m (Ebert, 1994). Juveniles are found inshore in shallower waters (King and Surry, 2017), and females and sub-adults occasionally occur in these areas (Dunbrack and Zielinski, 2003; Griffing et al., 2014; King and Surry, 2017). It is viviparous and produces large litters of up to 108 pups (Ebert, 1986), with sexual maturity reached at approximately 3.1 m in males and 4.2 m in females (Ebert, 2002). It feeds on a wide range of species at a higher trophic level than the kitefin shark, including other sharks and rays, bony fishes, cephalopods, crustaceans, and the carcasses of marine mammals and other large animals (Ebert, 1994; Reum et al., 2020). Despite multiple attempts to reduce deep-water shark mortality in demersal fisheries, sixgill sharks are still commonly caught as bycatch throughout their range, including by bottom longline fisheries, bottom and mid-water trawlers, and trammel nets (Fauconnet et al., 2019; Nuez et al., 2023). Due to its slow growth and late maturity, it is highly vulnerable to overharvesting and is classified as "Near Threatened" by the IUCN (Finucci et al., 2020).

Despite their ecological importance and vulnerability (e.g., Finucci et al., 2024), ecological studies on these species remain scarce and geographically biased. Knowledge of their spatial behaviour and movement ecology is fragmented across population segments, with rudimentary (sixgill) or absent (kitefin) data on interannual patterns and limited outside the Pacific and Mediterranean regions (e.g., Andrews et al., 2009; Celona et al., 2005; Coffey et al., 2020; Comfort and Weng, 2015; Dunbrack and Zielinski, 2003; Griffing et al., 2014; King and Surry, 2017; Nakamura et al., 2015). For example, only two immature sixgill sharks were tracked for 2–4 days off Bermuda in the Northwest Atlantic (Carey and Clark, 1995). This knowledge gap hampers the development of effective conservation strategies, including marine protected areas (MPAs) to safeguard essential habitats and migration corridors for these keystone species. Addressing this gap aligns with global commitments to marine biodiversity conservation, including the UN Sustainable Development Goal 14 and the 30x30 marine protection target.

Here, we present the first electronic tracking study of kitefin and sixgill sharks in the Atlantic Ocean, aimed at investigating: (I) long-term residencies and site attachment to essential habitats, (II) vertical movement patterns to identify critical habitat envelopes, and (III) intra and interspecific interactions to contextualize their movement ecology within their contrasting ecological roles.

2. Materials and methods

2.1. Study area

This study was conducted in the Azores, a remote Portuguese archipelago located on the northern Mid-Atlantic Ridge. The archipelago comprises nine volcanic islands spanning over 600 km with an Exclusive Economic Zone (EEZ) of approximately one million km^2 (Das et al., 2022). The region is characterised by very narrow continental shelves, steep slopes, and a highly complex, deep seafloor with numerous seamounts and ridges. This diverse seascape hosts Vulnerable Marine Ecosystems, including hydrothermal vent fields, cold-water and mesophotic black coral gardens, and deep-sea sponge aggregations (Abecasis et al., 2015; Das and Afonso, 2017). It also contains one of the largest marine protected area networks in the Atlantic, covering coastal, oceanic and deep-sea habitats (Afonso et al., 2020).

The waters surrounding the Azores form an ecological transitional zone (ecotone), lying between the southern boundary of cold-water species and the northern boundary of tropical and subtropical species. The southern branch of the warm Gulf Stream and its eddies and filaments, influence the warm-temperate region with a dynamic subtropical effect (Afonso et al., 2020; Santos et al., 1995). This transition zone is particularly important for many elasmobranch species, as it may serve as a migratory corridor or provide feeding, mating, pupping and resting grounds (Afonso et al., 2020).

This study focused on the shelves and slope habitats of Faial and Pico islands, and the surrounding seamounts (Fig. 1). The islands are separated by a shallow channel up to 250 m deep and 8 km wide, and are surrounded by a narrow island shelf ranging from 1 to 3 km in width, which descends steeply to depths of 1200 m. The substrates are a mix of sedimentary (biogenic and lithogenic) bottoms and basaltic rocky reefs, resulting from volcanic activity and the erosion of the steep shores (Afonso et al., 2022).

2.2. Acoustic array

The acoustic telemetry array consisted of a total 83 listening stations equipped with acoustic receivers (models VR2W, VR2AR, VR2Tx and VR4UWM, Innovasea, CA), forming part of the Azorean Acoustic Telemetry Network (www.vliz.be/en/imis?module=dataset&dasid=5884). Receivers were deployed from July 2009 to November 2023 and grouped into three habitat categories: coastal shallow (<40 m deep; n = 28), deep slope (>40 m; n = 38), and seamount (88–724 m; n = 19). All receivers were suspended 3–5 m above the seabed using cable moorings with floats, except for a subset of shallow, diver-retrievable stations positioned up to

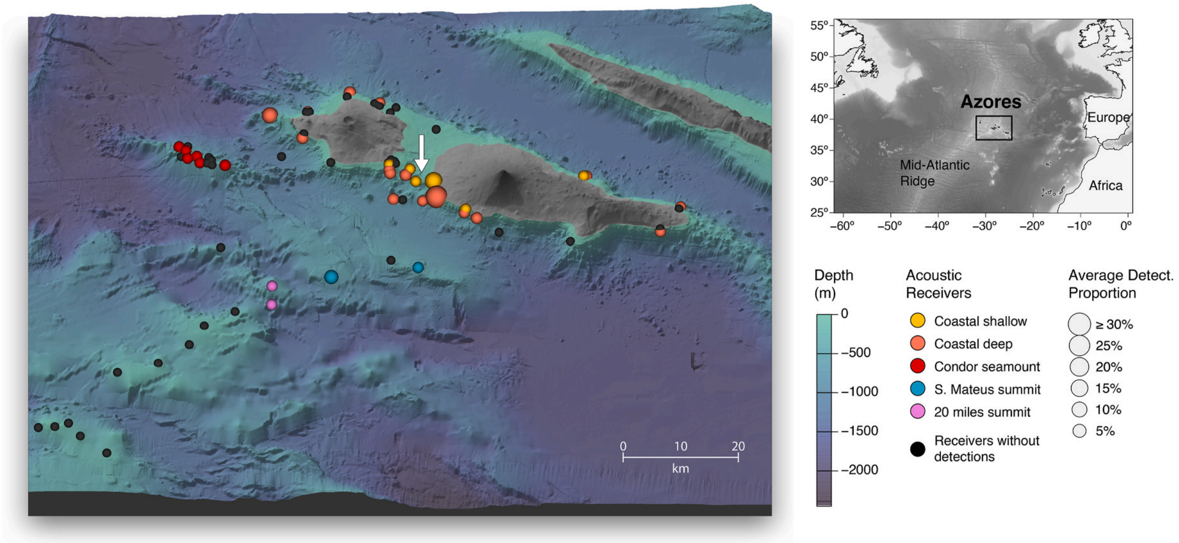

Fig. 1. Bathymetric map of the study area surrounding Faial and Pico islands (Azores, Portugal, North Atlantic Ocean) showing locations of acoustic monitoring stations comprising the listening array. Receiver stations are denoted by spherical markers: black markers indicate stations with no detections; coloured markers represent stations with detections (colour-coded by habitat type/site), with marker area scaled proportionally to the mean relative detection frequency (i.e., the mean across all individuals of each shark's detection proportion at that station). To enhance visualisation of spatial patterns, mean relative detection frequencies exceeding 30 % were truncated at this threshold, preventing disproportionate representation of the most frequently detected stations. The white arrow indicates the tagging location. Inset shows the geographic context of the Azores archipelago in the North Atlantic Ocean. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

20 m above the seafloor. Deeper stations were equipped with acoustic transponding releases (integrated VR2AR or independent devices such as AR50/60, Sub Sea Sonics, US; and PORT-MFE, EdgeTech, US) for surface retrieval. Receivers were serviced every 6–12 months for maintenance (cleaning, data offloading and battery replacement).

2.3. *Shark tagging*

Shark tagging was conducted during multiple campaigns targeting deep-sea sharks, with captures occurring in the channel between Faial and Pico Islands. A total of 21 kitefin sharks (102–158 cm total length; 10 females, 11 males) and 5 sixgill sharks (319–420 cm; 4 females, 1 male) were captured and tagged in a canyon southeast of the channel from November 2010 to July 2013 and August 2015 to October 2017, respectively. Sharks were captured at night using handlines baited with tuna at ca. 200–250 m depth and slowly hauled (approximately 0.2 m/s) to the surface to avoid barotrauma and decompression-related injuries. Only those individuals showing normal behaviour upon visual inspection (regular ventilation, horizontal positioning, and normal swimming) were tagged and released. Once at the surface, sharks were brought alongside the boat and turned upside down to induce tonic immobility. Following established protocols (e.g., Afonso et al., 2022), acoustic transmitters were surgically implanted into their peritoneal cavity via a 3–4 cm ventral incision, which was subsequently closed using absorbable sutures. Of the 26 tags deployed, 17 were continuous ID transmitters (VEMCO V16-4H/6H) and 9 were equipped with depth sensors (VEMCO V16P-4H). These transmitters had expected battery lives ranging from 351 to 2538 days (Table 1). Range tests conducted in these and similar environments demonstrated that V16 transmitters achieved a 50 % detection probability within a radius of approximately 800 m (Afonso et al., 2012).

Two of the 5 acoustically tagged sixgill sharks were double-tagged with pop-up satellite archival tags (PSATs) (MiniPAT, Wildlife Computers, US) implanted in the dorsal fin musculature using titanium darts and further secured using a keeper strap (Fig. S1). The PSATs were programmed for deployment periods of 130 and 150 days (Table 2), with sensor data recorded at 3-s intervals. They were also equipped with a programmed mortality release, triggering detachment if the tag remained at a constant depth (±3 m) for 48h. Two additional sixgill sharks were tagged with PSATs in June 2021 using a speargun-equipped submersible at ca. 250 m depth during a research expedition on the R/V OceanXplorer. These PSATs were programmed for 270-day deployments with a 3-s sampling rate, and a mortality release mechanism set to detach if constant depth (±3 m) was maintained for 72h. Of all the PSATs deployed, only the latter two were configured to collect accelerometry data, which was stored internally and accessible only upon tag recovery.

2.4. *Data analyses*

2.4.1. *Site fidelity and horizontal habitat-use*

Data processing and statistical analyses were conducted using the R programming environment (R Core Team, 2023). Before statistical analyses, potential spurious detections were identified and removed. False detections arise when signals from different transmitters collide within the range of the same receiver (Heupel et al., 2006). Detections were deemed spurious if they occurred in isolation within a 24-h window, with no preceding or subsequent detections from the same transmitter recorded during that period.

To assess site fidelity and overall detection patterns, time series for each individual were plotted across the monitoring period ("abacus plots"), and aggregated by day and hour to highlight seasonal and diel variations in the number of individuals detected throughout the study. Diel phase (day vs. night) was assigned to each detection based on daily sunrise and sunset times estimated for the study area using the "maptools" package (Bivand, 2023). Two residency indices were calculated: RI_A, defined as the number of days the animal was detected divided by the detection interval, i.e., the number of days between release and last detection (days at liberty); and RI_B, calculated as the number of days the animal was detected divided by the study interval, i.e., the total number of days between release and the tag expiration date. RI_A represents a maximum residency estimate, considering only the period when the animal was known to be alive and the tag was operational, whereas RI_B provides a minimum residency estimate, assuming the animal was alive and detectable throughout the entire study period (Kraft et al., 2023). Additionally, we calculated the quotient RI_B/RI_A, as suggested by Appert

Table 1

Summary data for tagged kitefin shark (*Dalatias licha*) and bluntnose sixgill shark (*Hexanchus griseus*). TL – total length; TP – total period of detection (days between first and last detection); DD – days with detections; RI_A – residency index based on the number of days the animal was detected divided by the detection interval (from release to last detection); RI_B – residency index based on the number of days the animal was detected divided by the study interval (from release to tag expiration date). Mean values ± SD are displayed below each species.

ID	Transmitter Code	TL (cm)	Sex	Transm. Model	Tag Duration (d)	PSAT	Tagging Date	Last Detection	N° Detections	N° Receivers	TP	DD	RI_A	RI_B	RI_B/RI_A
Dalatias licha															
#K01	200	112	male	V16P-4H	351	–	10/11/2010	18/12/2011	7245	2	404	77	0.19	0.22	1.00
#K02	53737	109	male	V16-4H	1472	–	10/11/2010	10/05/2014	4801	7	1278	214	0.17	0.15	0.87
#K03	201	110	male	V16P-4H	351	–	27/04/2011	26/05/2012	1074	4	396	21	0.05	0.06	1.00
#K04	53735	112	male	V16-4H	1472	–	27/04/2011	20/11/2014	3236	5	1304	185	0.14	0.13	0.89
#K05	53736	137	female	V16-4H	1472	–	21/06/2011	23/10/2012	411	3	491	29	0.06	0.02	0.33
#K06	55987	147	female	V16-4H	1472	–	21/06/2011	28/11/2011	78	1	161	5	0.03	0.00	0.11
#K07	210 | 33768	105	male	V16P-4H	822	–	06/06/2013	08/07/2014	2419	4	398	50	0.13	0.06	0.48
#K08	212 | 33770	102	male	V16P-4H	822	–	07/06/2013	27/07/2013	337	2	51	12	0.24	0.01	0.06
#K09	32930	109	male	V16-4H	1593	–	08/06/2013	29/07/2017	2220	4	1513	111	0.07	0.07	0.95
#K10	32931	116	male	V16-4H	1593	–	08/06/2013	02/10/2017	2692	10	1578	193	0.12	0.12	0.99
#K11	32932	110	male	V16-4H	1593	–	08/06/2013	19/09/2017	1265	6	1565	56	0.04	0.04	0.98
#K12	32933	121	male	V16-4H	1593	–	08/06/2013	14/08/2013	3132	1	68	55	0.81	0.03	0.04
#K13	32934	117	male	V16-4H	1593	–	08/06/2013	21/04/2017	406	6	1414	44	0.03	0.03	0.89
#K14	213 | 33771	127	female	V16P-4H	822	–	10/07/2013	08/07/2015	10522	4	729	267	0.37	0.32	0.89
#K15	211 | 33769	158	female	V16P-4H	822	–	11/07/2013	14/05/2014	793	1	308	158	0.51	0.19	0.37
#K16	32938	150	female	V16-4H	1593	–	11/07/2013	25/04/2014	266	2	289	88	0.30	0.06	0.18
#K17	32939	150	female	V16-4H	1593	–	11/07/2013	14/05/2014	334	2	308	80	0.26	0.05	0.19
#K18	59472	140	female	V16-4H	1625	–	11/07/2013	–	–	–	–	–	–	–	–
#K19	32935	144	female	V16-4H	1593	–	16/07/2013	24/12/2017	502	5	1623	123	0.08	0.08	1.00
#K20	32936	147	female	V16-4H	1593	–	16/07/2013	07/08/2014	1279	3	388	78	0.20	0.05	0.24
#K21	32937	141	female	V16-4H	1593	–	16/07/2013	–	–	–	–	–	–	–	–
Females Avg	–	144 ± 8	–	–	1418 ± 302	–	–	–	1773 ± 3325	3 ± 1	537 ± 440	104 ± 76	0.23 ± 0.16	0.10 ± 0.10	0.41 ± 0.32
Males Avg	–	111 ± 5	.	–	1205 ± 491	–	–	–	2621 ± 1938	5 ± 2	906 ± 604	93 ± 69	0.18 ± 0.21	0.08 ± 0.06	0.74 ± 0.35
Total Avg	–	127 ± 18	–	–	1306 ± 425	–	–	–	2264 ± 2647	4 ± 2	751 ± 571	97 ± 72	0.20 ± 0.19	0.09 ± 0.08	0.60 ± 0.38
Hexanchus griseus															

(*continued on next page*)

Table 1 (*continued*)

ID	Transmitter Code	TL (cm)	Sex	Transm. Model	Tag Duration (d)	PSAT	Tagging Date	Last Detection	N° Detections	N° Receivers	TP	DD	RI_A	RI_B	RI_B/RI_A
#S01	214 | 32282	–	female	V16P-4H	1540	–	18/08/2015	23/10/2019	1132	14	1528	81	0.05	0.05	0.99
#S02	215 | 32283	420	female	V16P-4H	1540	–	18/08/2015	29/06/2017	984	10	682	93	0.14	0.06	0.44
#S03	216 | 32284	385	female	V16P-4H	1540	–	18/08/2015	12/01/2017	2516	12	514	114	0.22	0.07	0.33
#S04	17182	319	male	V16-6H	2538	11P0127	18/05/2017	30/06/2018	4196	8	409	128	0.31	0.05	0.16
#S05	17180	410	female	V16-6H	2538	11P0136	11/10/2017	24/12/2021	4521	16	1536	238	0.15	0.09	0.61
#S06	–	400	female	–	–	20P1578	06/06/2021	–	–	–	–	–	–	–	–
#S07	–	400	female	–	–	20P1571	08/06/2021	–	–	–	–	–	–	–	–
Total Avg	–	383 ± 35	–	–	1939 ± 489	–	–	–	2670 ± 1482	12 ± 3	934 ± 496	131 ± 56	0.17 ± 0.09	0.06 ± 0.02	0.51 ± 0.28

et al. (2023), to quantify the extent of the gap between the last detection and the end of the monitoring period.

Detections were pooled into 30-min bins, and centre of activity (COA) positions were estimated independently for each fish by weighting mean receivers coordinates by detection frequency, over each time bin (Simpfendorfer et al., 2002). These positions were converted into bivariate kernel utilisation distributions (KUDs; Worton, 1989) using the "adehabitatHR" package (Calenge, 2006). Core activity and home range areas were defined by the 50 % and 95 % KUDs contours, respectively. Distances travelled were estimated using a least-cost distance approach avoiding land intersections (Dijkstra's algorithm, "gdistance" package; van Etten, 2017). The rate of movement (ROM) and linearity index (LI) were also estimated to quantify individual variability in movement patterns. ROM was derived from distances interpolated between successive positions, while LI was calculated by dividing the distance between the first and last positions by the total travelled distance. LI values range from 0 (high site attachment) to 1 (strong directional movement) (Rechisky and Wetherbee, 2003; Villegas-Ríos et al., 2013). All statistical differences between species and sexes were assessed using a non-parametric Wilcoxon rank-sum test to account for skewed data and the limited sample sizes.

No geolocation based on the sixgill PSATs data was performed in the present study. However, movement tracks for two double-tagged sharks with acoustic transmitters were reconstructed in a separate study (Arostegui et al., 2024) by integrating depth-based bottom-contour constraints, acoustic detections, and three-dimensional temperature profiles within a Hidden Markov Model framework.

2.4.2. *Temporal patterns and vertical movements*

To investigate temporal shifts in behaviour using acoustic telemetry data, we averaged the number of detections and presences (i.e., binary values indicating each shark's presence or absence within each time interval) by month and hour, then generated colour-coded contour plots (i.e. heat maps) to visualise the patterns. Finer-scale rhythmicity in movement (detection) patterns was investigated using a Fast Fourier Transform (FFT) of hourly detections (individuals with >60 logged days) across the entire array. This algorithm decomposes data series into the frequency domain, enabling the identification of dominant spectral peaks that may indicate rhythmic patterns in habitat use, such as tidal (6–12 h) or diel (24 h) cycles (Afonso et al., 2009).

We used high-resolution data from PSATs to generate contour plots for sixgill sharks, visually summarising the depth and temperature time-series. Individual profiles were inspected by plotting depth and temperature time-series over the deployment period and calculating the percentage of time each shark spent in distinct depth and temperature intervals, separately for day and night. Depth data were pooled into 50 m bins, and temperature data into 1 °C bins. Depth and temperature data were obtained either from the archival time series of recovered tags or from subsampled data (provided at 300- or 450-s intervals) transmitted via Argos for tags that could not be retrieved. For the two recovered tags (#S04 and #S07), vertical displacement rates (i.e., vertical speeds) were calculated by determining the depth differences between consecutive measurements in the depth time-series. These differences were converted to metres per minute and then averaged over 5-min windows to provide a smoothed representation of vertical movement patterns. To quantify activity levels for the single sixgill shark for which accelerometery data was available (#S07), we quantified the magnitude of acceleration (MA) as the square root of the sum of squares of each acceleration axis ($MA = \sqrt{X^2 + Y^2 + Z^2}$). Following methods from Wright et al. (2021) and Gandra et al. (2024), we identified high-activity events (i.e., the upper 5 %) using the 95th percentile of MA values. The hourly frequency of these high-activity events was visualised and statistically tested with pairwise Wilcoxon signed-rank tests, with *p*-values adjusted using Bonferroni correction to reduce Type I errors. Significance groupings, represented by lowercase letters, indicate pairwise

Table 2

Summary data for bluntnose sixgill shark (*Hexanchus griseus*) tagged with satellite transmitters (PSATs). IDs with an asterisk indicate tags that were physically recovered. Mean temperature and depth values are reported with standard deviations (mean ± SD).

ID	Deploy Date	Pop-up Date	Programmed Deployment (d)	Deployment Duration (d)	Release Type	Tagging Location	Pop-up Location	Temp Range (°C)	Temp Mean (°C)	Depth Range (m)	Depth Mean (m)
#S04*	18/05/2017	25/09/2017	130	130	Interval	38.596°N, 28.533°W	40.150°N, 28.700°W	8.9–17.9	12.5 ± 1.7	56–807	445 ± 184
#S05	12/10/2017	11/03/2018	150	151	Interval	38.596°N, 28.533°W	38.482°N, 28.200°W	6.1–15.8	11.7 ± 1.9	125–1348	538 ± 245
#S06	06/06/2021	26/10/2021	270	148	Premature	38.486°N, 28.542°W	38.592°N, 28.215°W	8.8–16.7	13.1 ± 1.8	102–846	427 ± 204
#S07*	07/06/2021	24/01/2022	270	230	Floater	38.485°N, 28.542°W	38.583°N, 28.402°W	6.4–22.5	14.4 ± 2.5	7.5–1156	314 ± 225

comparisons where groups sharing the same letter are not significantly different at $p < 0.05$.

2.4.3. Individual interactions

To evaluate potential interactions among tagged sharks, we conducted two complementary analyses: (1) a spatiotemporal overlap assessment to detect associations or segregation in space and time, and (2) a spatial segregation test to explicitly examine habitat partitioning independent of temporal overlap.

For the spatiotemporal assessment, we estimated co-occurrences from detection data (using a 30-min bin interval) and constructed social networks. For each shark pair, we calculated a spatiotemporal overlap index analogous to the simple ratio association metric, representing the proportion of time two sharks were detected at the same receiver within the same time bin (ranging from 0 % for no overlap to 100 % for complete overlap). The index was calculated as $x/(x + y_A + y_B + y_{AB})$, where x denotes the number of time bins where a pair was detected at the same station, y_A and y_B the number of time bins where only one individual of the pair was detected, and y_{AB} the number of time bins where both were detected at different receivers. Following Gandra et al. (2020), we restricted pairwise comparisons to shared monitoring periods (from latest release to earliest last detection of each pair) to prevent biases due to transmitter failure or premature mortality. We assessed the statistical significance of the spatiotemporal overlaps using null model randomization tests. Simulated datasets were generated by randomly rearranging individual detections across time bins while preserving the total detections per shark and their distribution among receivers (pre-network permutation). To account for diel and seasonal patterns, permutations were restricted to time bins within the same diel phase and day (Castro-Arellano et al., 2010). For each shark, we generated 10,000 simulated datasets and tested for non-random associations by comparing observed overlap values to the randomized data. Empirical p-values were calculated as the proportion of randomized values greater or smaller than the observed mean overlap for each network.

To explicitly investigate spatial segregation, we employed a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) through the “vegan” R package (Oksanen et al., 2025). This approach tested whether species, and for kitefin sharks, sexes, exhibited significant differences in their use of monitored areas, independently of detection periods. We constructed a Bray-Curtis dissimilarity matrix based on the proportion of detections at each site per individual, accounting for variation in detection frequencies. PERMANOVA then evaluated differences in spatial use, potentially reflecting niche partitioning or sex-specific habitat preferences (Murray et al., 2024).

3. Results

Nineteen out of 21 acoustically tagged kitefin sharks and all five tagged sixgill sharks were successfully detected within the array. A total of 56,361 detections were recorded and validated during the study period, with an average of 2264 detections per kitefin and 2670 detections per sixgill shark (Table 1). Individual detection spans ranged from 51 to 1623 days for kitefin sharks (mean: 751 days or ~2.1 years) and 409 to 1536 days for sixgill sharks (mean: 934 days or ~2.6 years). Kitefin sharks exhibited lower average detection rates than sixgill sharks and were detected by significantly fewer receivers (range: 1–10 vs 8–16; $W = 1.5$, $p = 0.001$).

All four PSATs deployed on sixgill sharks either transmitted summary data through the Argos satellite system (two tags) or provided a full archive after successful recovery (two additional tags, yielding >10 million temperature and depth readings). Two tags remained attached for the entire programmed deployment (130 and 150 days), while the other two detached prematurely after 148 and 230 days instead of the programmed 270 days (Table 2). Deployments averaged 165 days, ranging from 130 to 230 days (~4.3–7.6 months).

3.1. Horizontal movements

Most detections occurred at the deep slope stations around Faial and Pico islands (Figs. 1 and 2; S2, S3), though female kitefin sharks were more frequently detected at shallow coastal stations (Figs. S2 and S3). Four of the five tagged sixgill sharks were detected at the neighbouring Condor - S. Mateus seamount line, while only three out of the 21 tagged kitefins were eventually detected at neighbouring seamounts (Fig. 3; S3). None of the tagged sharks were detected at the more distant stations in the regional acoustic network, including the Princess Alice seamount (ca. 85 km SE of Faial), the ridge seamounts (Gigante and 127, ca. 110 km W/NW of Faial) and the Formigas bank (ca. 370 km SE of Faial).

Both species exhibited relatively low average residency indices within the array. Kitefin sharks displayed slightly higher average residency indices compared to sixgill sharks ($RI_B = 0.09$ vs. 0.06), with individual values ranging from 0.00 to 0.32 for kitefin sharks and 0.05 to 0.09 for sixgill sharks (Table 1). Despite these low average residency values, many individuals were intermittently detected over long periods, as indicated by the average RI_B/RI_A quotient for kitefin (0.60) and sixgill sharks (0.51), indicating sporadic but repeated presence in the monitored area (Table 1). The more vagile behaviour of sixgill sharks was evident in their larger home range areas – over twice those of kitefin sharks – and their frequent movements across the contiguous Faial-Pico shelf, with occasional excursions to nearby seamounts (Table S1; Fig. 3). Sixgill sharks also exhibited lower linearity indices (0.03 vs. 0.40), indicative of minimal directional persistence and more tortuous paths, contrasting with the more oriented and spatially restricted movements

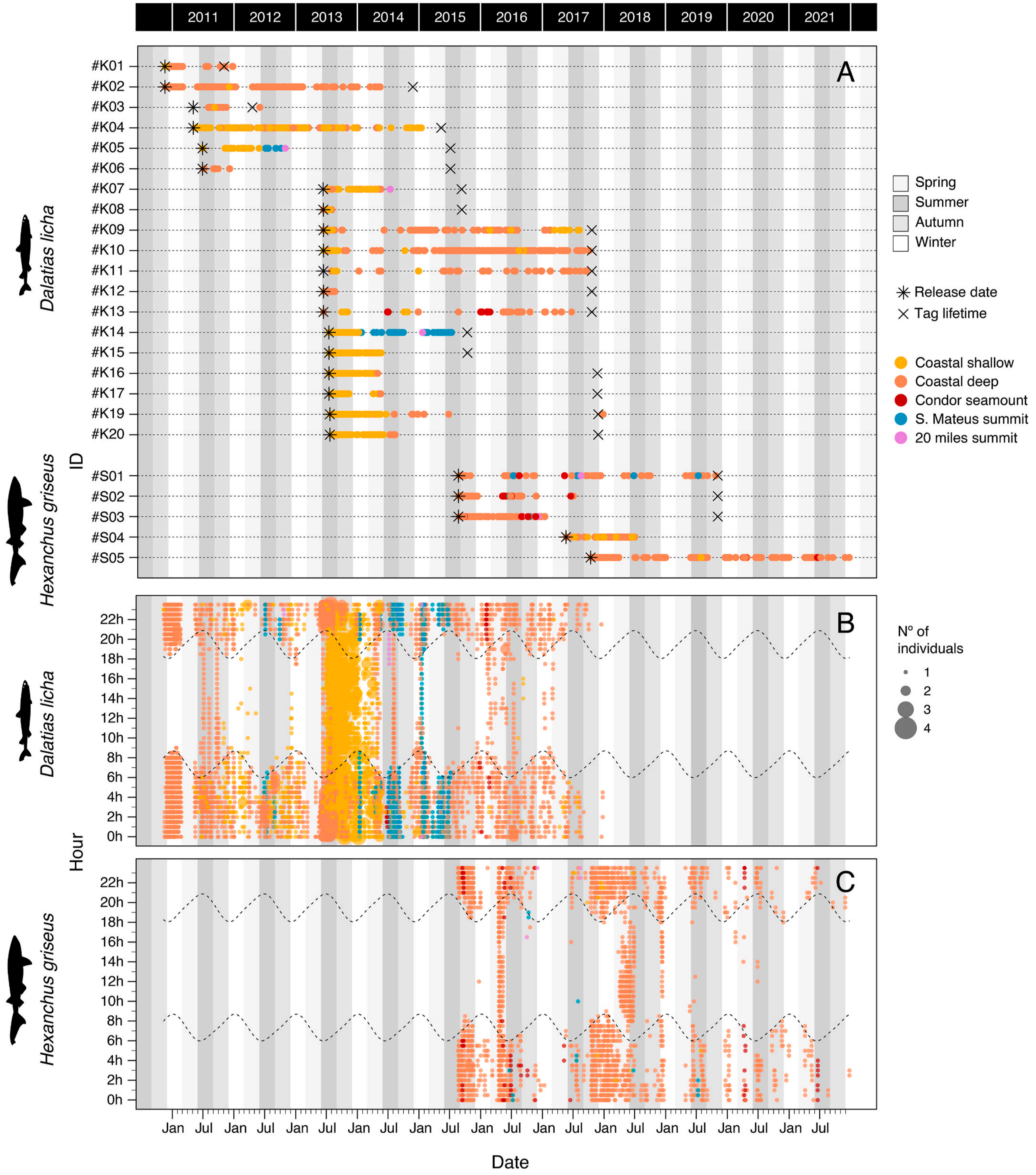

Fig. 2. Abacus plot of the monitored kitefin shark *Dalatias licha* and bluntnose sixgill shark *Hexanchus griseus* throughout the study duration (A). Detections are colour-coded by site; shaded areas illustrate different seasons; stars (*) depict release dates and cross marks (x) indicate the estimated lifetime of the tags. Number of kitefin (B) and sixgill (C) sharks detected per hour and day, colour-coded by site. Dashed lines indicate sunrise and sunset periods for the study region, illustrating the annual variation of daylight time. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

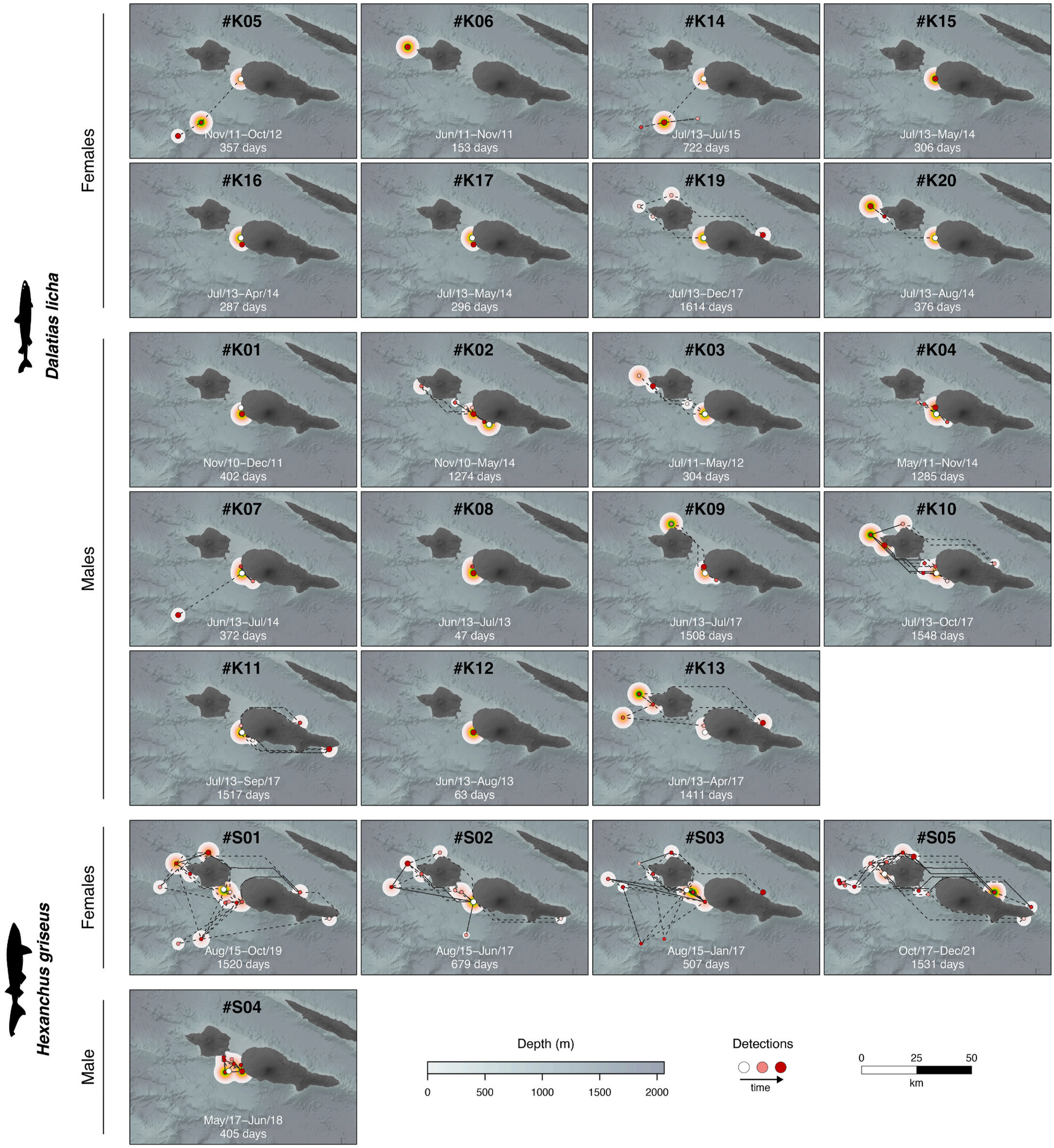

Fig. 3. Home-ranges (kernel utilisation distributions) and acoustic detections of monitored kitefin shark (*Dalatias licha*) and bluntnose sixgill shark (*Hexanchus griseus*). Least cost trajectory paths are indicated by dotted lines. Acoustic detections are coloured from white to red, respectively from the oldest (first position) to the most recent (latest) location. The monitoring period and the n° of days between first and last detection of each individual are indicated at the bottom of each plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of kitefin sharks.

Horizontal movements also differed significantly between male and female kitefin sharks. Males primarily used deeper slope stations, while females preferred shallow coastal stations (Fig. S3). Males showed significantly higher mobility than females, with average rates of movement nearly four times higher ($W = 1$, $p = 0.001$), and maximum rates over four times higher ($W = 4$, $p = 0.002$). They also had broader activity areas and lower linearity indices than females (Table S1).

3.2. Vertical movements

Acoustic transmitters with pressure sensors recorded depths of

116–690 m for sixgill sharks and 33–684 m for kitefin sharks. Both species exhibited patterns consistent with diel vertical migration (DVM), though the magnitude of depth shifts differed. Although high-resolution depth time series were unavailable for kitefin sharks, detection patterns and transmitter-derived depth data indicated modest DVM, with individuals occupying deeper waters during daylight hours (Fig. 4). However, significantly less depth transmissions – originated from acoustic tags with integrated pressure sensors – occurred during daytime period, reflecting the significantly higher nocturnal detection rates across most individuals (Fig. 4; $W = 82$, $p < 0.001$). Spectral analysis of detection frequencies via Fast Fourier Transform (FFT) reinforced these diel patterns, revealing distinct 24-h periodicity in sixgill sharks and male kitefin sharks, but not in most females (Fig. S4). Female kitefin sharks deviated from this trend, maintaining consistent detectability at coastal receivers both day and night for extended periods (up to one year; Fig. S2). Their depth distributions showed limited diel variation, averaging ~200 m during daytime and ~150 m at night (Fig. 4). In contrast, males exhibited stronger DVM, with nighttime detections clustered at 200–400 m and a few daytime records >500 m. This sexual segregation resulted in nearly non-overlapping depth distributions, though the sample size of individuals with depth-sensing transmitters was limited (females: $n = 2$; males: $n = 4$). Notably, one female (#K14) that migrated to a seamount displayed deeper occupancy (~450–550 m), suggesting a stronger depth shift associated with dispersal or seasonal movements rather than those associated with DVMs.

PSAT data from sixgill sharks revealed particularly robust DVM patterns. Maximum recorded depths ranged from 807 m to 1348 m (Table 2), with minimum depths typically between 56 m and 102 m, except for shark #S07, which often ventured closer to the surface, reaching depths as shallow as 8 m (Fig. 5). More than 85 % of daytime records occurred between 350 and 800 m, with distributions shifting markedly shallower at night (45–350 m; Fig. 6A; S5). High-resolution data from the two recovered tags (#S04, #S07) showed peak vertical displacement rates during crepuscular periods, with maximum ascent rates at dusk and descent rates at dawn (Fig. 6C). Shark #S07 exhibited especially pronounced high-activity peaks around sunset during the ascent phase (Fig. 6D).

For PSAT-tagged sixgill, temperature patterns closely followed depth distributions: daytime temperatures at 350–800 m ranged from 6.5 °C to 14.0 °C, while nighttime temperatures at 45–350 m ranged from 13.0 °C to 18.0 °C (Fig. 6B; S5). An exception was shark #S07, which ascended into unusually warm surface waters (22.5 °C) during dusk in August 2021 (Fig. 5; Table 2). Across all PSAT deployments, recorded temperatures ranged from 6.1 °C to 17.9 °C, with #S07 being the only individual experiencing temperatures above 18 °C (Table 2).

3.3. Individual associations

A total of 449 localized shark co-occurrence events were recorded during the entire monitoring period (Fig. S3). Nearly all of these

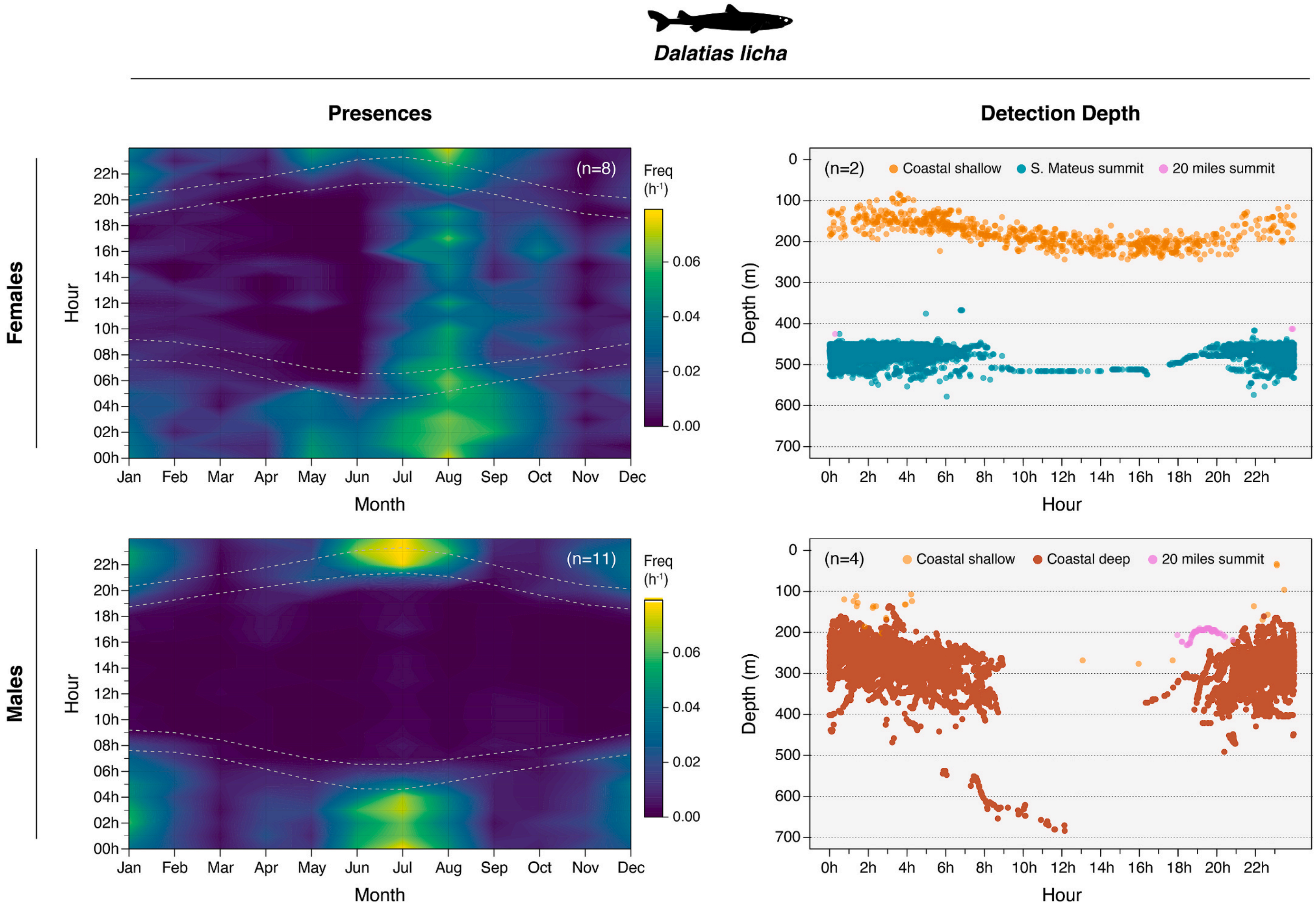

Fig. 4. Diel and seasonal patterns in presence and detection depth of kitefin sharks (*Dalatias licha*) by sex, from acoustic telemetry. The left panels show the hourly presence of individuals across months for females (top) and males (bottom), with colour intensity representing presence frequency (h^{-1}). The right panels depict detection depths by hour for individual sharks equipped with depth-sensing transmitters, with point colours denoting detection sites. Dashed lines indicate estimated dawn, sunrise, sunset, and dusk times. Sample sizes (n), indicated in parentheses in the top right corner of each panel, represent the number of individuals included in each plot. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

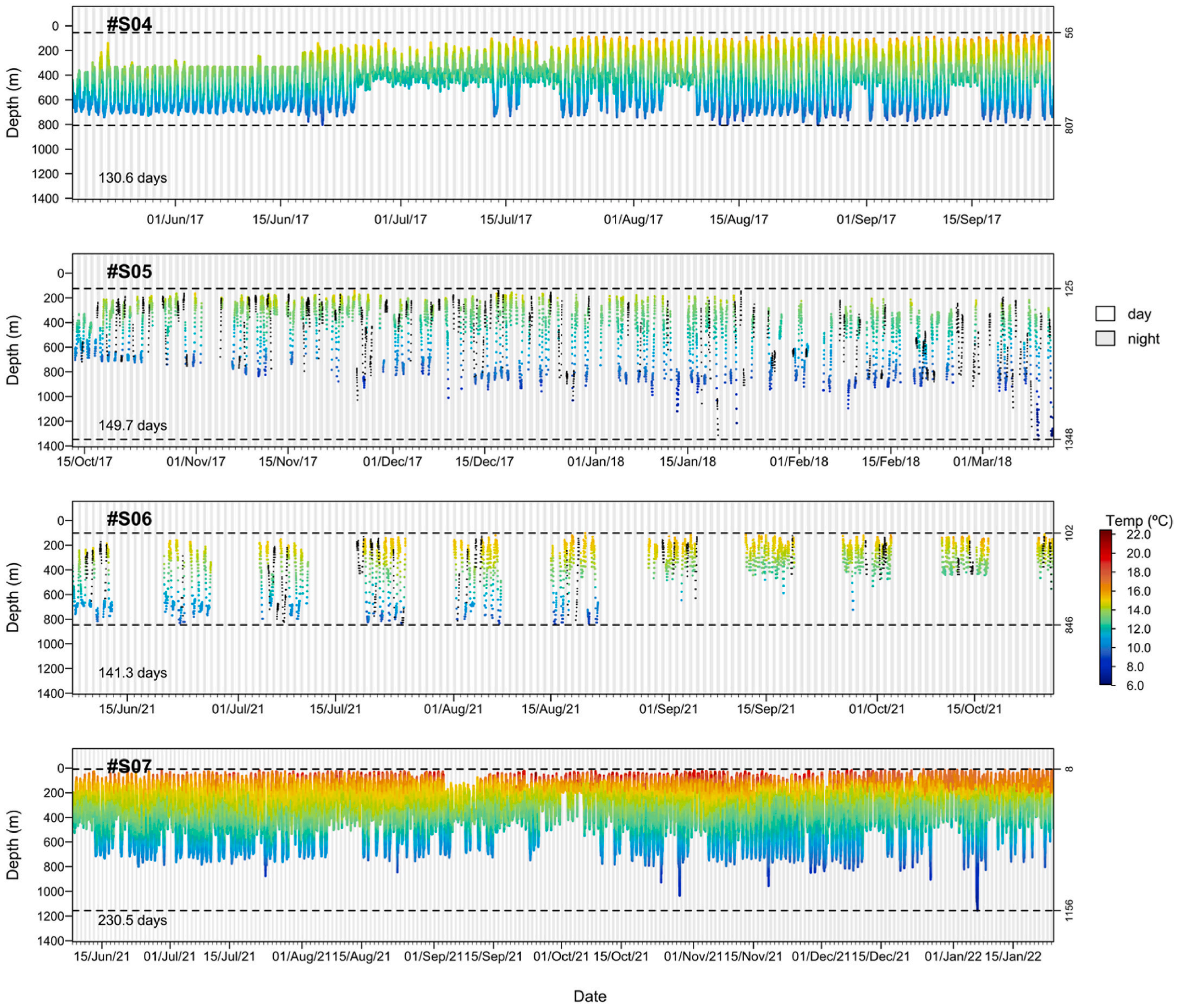

Fig. 5. Profiles of depth and temperature over time for bluntnose sixgill sharks (*Hexanchus griseus*) tagged with pop-up satellite archival tags (PSATs). Darker background bars indicate nighttime periods, lighter background bars indicate daytime periods. Horizontal dashed lines mark the shallowest and deepest recorded values for each shark. The deployment duration in days for each individual is shown at the bottom left of each plot.

involved intraspecific associations among kitefin sharks, with one sixgill intraspecific co-occurrence and two interspecific co-occurrences. Most co-occurrences occurred at receivers off southwest Pico, within the tagging area, at shallow (ca. 25 m) and deep (ca. 270 m) stations. The average spatiotemporal overlap (mean edge weight) was 0.91 % among kitefin sharks ($n = 119$ pairs), 0.02 % among sixgill sharks ($n = 7$ pairs), and 0.07 % among interspecific dyads ($n = 20$ pairs; Table 3). Only the average overlap within kitefin sharks was found to be significantly different from the random values generated by the null model simulations, indicating no significant associations in the other networks. Further analysis of intraspecific kitefin associations revealed an average spatiotemporal overlap of 3.21 % among females ($n = 16$ dyads), 1.23 % among males ($n = 41$ dyads), and 0.10 % between sharks of opposite sexes ($n = 62$ dyads; Fig. 7; Table 3). Female kitefin sharks exhibited significantly higher spatiotemporal overlap than expected by chance (3.21 %; null model: $p < 0.001$), while all other associations (male-male: 1.23 %; intersex: 0.10 %) were non-significant (Fig. 7). PERMANOVA confirmed significant habitat partitioning between male and female kitefin sharks ($p < 0.05$; Table S2).

4. Discussion

This study provides novel insights into the movement ecology and behaviour of two sympatric deep-sea predators, utilising over a decade of combined satellite and acoustic telemetry data collected across overlapping and distinct deployment periods. Few studies have investigated the long-term residency and movement patterns of deep-sea sharks, making this research a valuable contribution to understanding these elusive and threatened species. By integrating biologging techniques across multiple scales, we identified behavioural patterns with important implications for the ecological theory and conservation of deep-sea sharks in the north Atlantic and beyond.

4.1. Site fidelity and the use of essential habitat

Deep-sea sharks have traditionally been considered wide-ranging

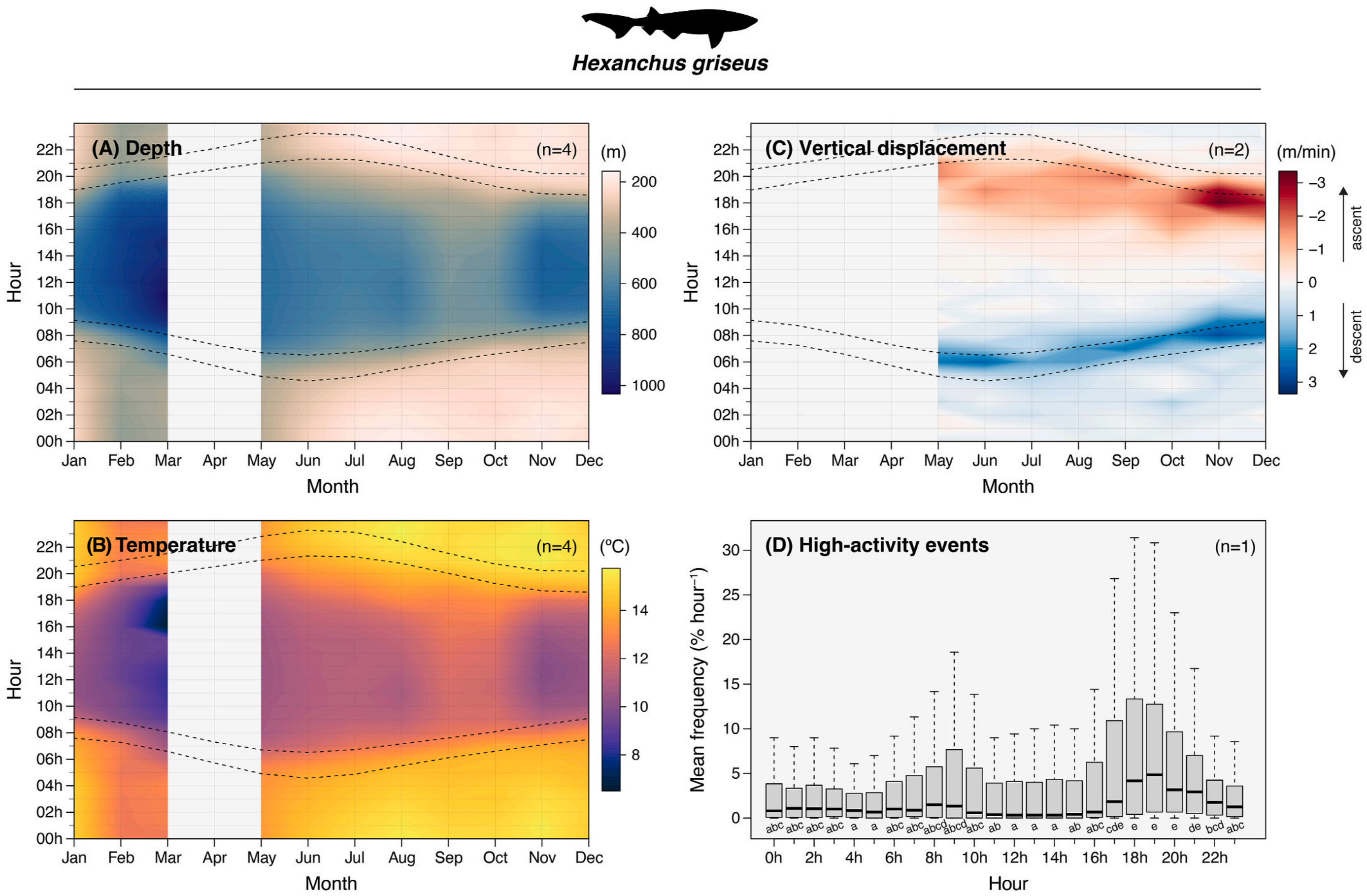

Fig. 6. Profiles of (A) depth and (B) temperature averaged per hour and month across all satellite-tagged sixgill sharks (*Hexanchus griseus*) (n = 4). No data were available from March to May. (C) Monthly hourly vertical displacement rates (m/min) of sixgill sharks with recovered tags (#S04 and #S07). Negative values correspond to ascent periods (decreasing depth), while positive values indicate descents (increasing depth). Dashed horizontal lines in A-C indicate estimated dawn, sunrise, sunset and dusk times at the study site, illustrating the annual variation in daylight period. (D) Mean percentage of high-activity events per hour, for the sixgill shark #S07. Boxes' upper and lower limits represent 75th and 25th quartiles, horizontal lines represent medians and whiskers represent values within 1.5 interquartile ranges. Outliers were excluded for clarity. Lowercase letters below the boxes represent significance groupings after a pairwise comparison (using Bonferroni correction) where groups sharing the same letter are not significantly different at $p < 0.05$.

Table 3
Social network statistics for acoustically tagged kitefin (*Dalatias licha*) and bluntnose sixgill sharks (*Hexanchus griseus*), as well as interspecific pairs. Number of dyads, mean shared monitoring period (days) and mean overlap for each network, together with summary results for the null model test (±SD) and significance. Significance codes: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Type	N° dyads	Mean shared period (d)	Mean overlap (%)	Mean null distribution (%)	*p*-value	
Dalatias licha	119	386	0.91 ± 2.03	0.71 ± 0.04	<0.001	***
Females - Females	16	326	3.21 ± 1.95	2.05 ± 0.03	<0.001	***
Males - Males	41	445	1.23 ± 2.73	1.12 ± 0.11	0.315	
Females - Males	62	362	0.10 ± 0.20	0.09 ± 0.02	0.596	
Hexanchus griseus	7	452	0.02 ± 0.05	0.07 ± 0.03	0.137	
Interspecific	20	513	0.07 ± 0.25	0.04 ± 0.02	0.231	

species due to their broad geographic and bathymetric ranges and the presumed scarcity of deep-sea food resources (Bird et al., 2018; Zeppilli et al., 2016). However, recent biotelemetry studies challenge this assumption, revealing long-term site fidelity and attachment to essential habitats. For example, Daley et al. (2015), documented resident behaviour in female southern dogfish sharks (*Centrophorus zeehaani*), and seasonal site fidelity was also observed in prickly sharks (*Echinorhinus cookei*; Dawson and Starr, 2009) and Greenland sharks (*Somniosus microcephalus*; Edwards et al., 2022) over multiple years. Our findings support this hypothesis, with kitefin and sixgill sharks exhibiting recurrent detections within a relatively small area for up to 4 years. Most individuals remained near the central component of the acoustic array for over 9 months, with absences likely reflecting short-range movements to unmonitored areas or depths rather than large-range migrations.

Kitefin sharks displayed smaller home-range areas and were much less transient than sixgill sharks, with over 80 % of kitefin detections recorded off the southwest coast of Pico, near their release site. In contrast, sixgill sharks used broader areas across more diverse habitats, including the Mid-Atlantic Ridge near the Azores, as supported by bathymetric and temperature data and reconstructed tracks (Arostegui et al., 2024). This interspecific contrast likely reflects differences in their ecological roles and physiological adaptations. Adult kitefin sharks, being more benthic and occupying shallower depths (Das et al., 2022),

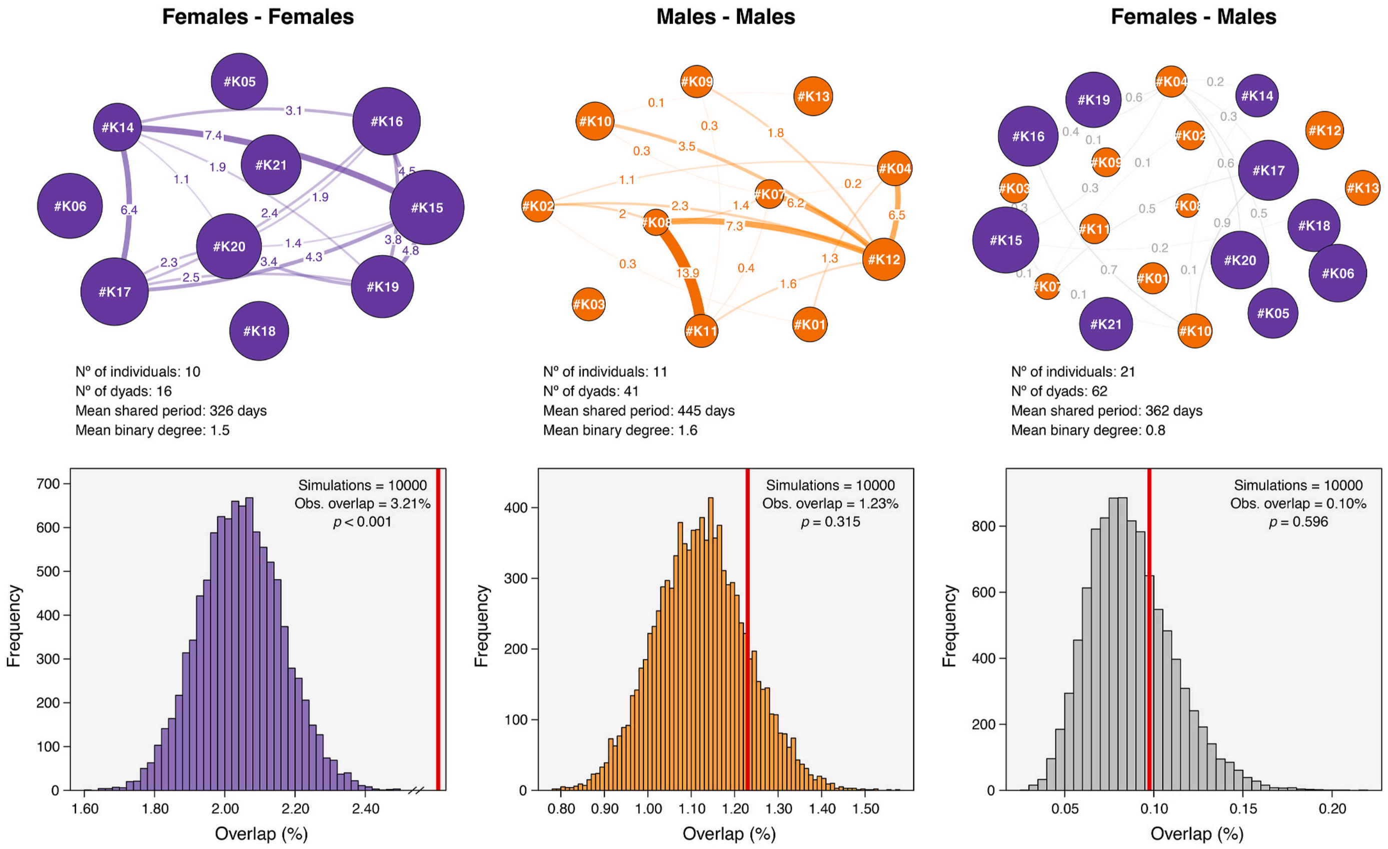

Fig. 7. Sex-specific social networks of acoustically tagged kitefin sharks (*Dalatias licha*). Node size is proportional to the body size of each shark (females indicated in purple and males in orange). Edges represent the extent of spatial overlap between each shark dyad (i.e. greater thickness indicates a higher overlap). Histograms show the distribution of the random overlaps obtained using 10,000 random permutations. The vertical red lines represent the empirically observed values (note the breaks in the x-axes). *p*-values were calculated as the proportion of randomized values higher or lower than the observed mean overlap. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

have limited suitable habitat and slower movement rates (Pinte et al., 2020). Sixgill sharks, as apex predators, exploit a wider range of habitats and prey types, including mesopelagic and epipelagic species (Ebert, 1994; Reum et al., 2020). These behaviours suggest sixgill sharks are more mobile apex predators, while kitefin sharks are intermediate-level, site-attached predators.

Seasonal movement patterns were also evident. Sixgill sharks performed pendular movements between island slopes and seamount habitats, often disappearing from the array during winter months. For example, sixgill shark #S01 alternated between habitats over four years, suggesting recurring seasonal use (Fig. 2). Kitefin sharks exhibited less distinct seasonal patterns but still showed intervals of absence, such as kitefin #02, which remained around Faial and Pico for 3.5 years but went undetected during winter and spring periods (Fig. 2). Such movement patterns, may influence genetic structure and population dynamics, as suggested by the high genetic differentiation observed in sixgill sharks (Vella and Vella, 2017).

4.2. Diel vertical movements

Vertical movements are fundamental for deep-sea organisms, connecting shallow productivity with meso- and bathypelagic habitats (Bianchi et al., 2013; Kelly et al., 2019). Our study provides evidence of diel vertical migration (DVM) in both kitefin and sixgill sharks, though the strength of evidence differs between species, and, in the case of kitefin sharks, between sexes.

Sixgill sharks exhibited pronounced DVM, with high-resolution PSAT data revealing consistent shifts from daytime depths of 350–800 m (6.5–14.0 °C) to shallower nighttime ranges (45–350 m; 13.0–18.0 °C). This behaviour aligns with previous studies in the Pacific (Andrews et al., 2009; Coffey et al., 2020; King and Surry, 2017). Notably, one individual (#S07) entered surface waters reaching 22.5 °C, exceeding the previously recorded maximum of 20.6 °C in Hawaii (Comfort and Weng, 2015), highlighting their thermal tolerance. Their large body mass likely provides considerable thermal inertia, allowing them to foray into colder or warmer waters for short periods while maintaining relatively stable intramuscular temperatures (Coffey et al., 2020).

Kitefin sharks tagged with depth-sensing acoustic transmitters exhibited more restricted vertical shifts (typically under 150 m day–-night difference), though these findings should be interpreted cautiously due to methodological constraints. Acoustic detection ranges may vary with environmental noise, and depth-transmitted data were sparse. However, the consistent patterns of (1) higher nighttime detection rates (when acoustic range is typically reduced; Afonso et al., 2012), (2) sequential detections across depth-stratified receivers, and (3) depth transmitter records collectively provide the first empirical evidence of circadian-linked movements in this species (cf. Pinte et al., 2020), marking an important addition to the existing knowledge on their ecological traits.

Although both species exhibited diel vertical migration (DVM) behaviour, their orientation to the seabed differed markedly. Depth-sensing acoustic tags and estimated seafloor depths revealed that DVM in sixgill shark is not solely driven by following bottom contours. Consistent with evidence from animal-borne cameras (Nakamura et al., 2015), active tracking (Carey and Clark, 1995), and fisheries data (Forster et al., 1970), our results suggest sixgill sharks remain closely associated with the seabed during the day but adopt more pelagic behaviour during crepuscular and nighttime hours. In contrast, kitefin sharks showed a stronger correlation between measured animal depth and estimated bottom depth (Fig. S6), indicating a persistent association with the seabed. This observation aligns with indirect evidence from underwater baited cameras and ROV footage, which consistently recorded kitefin sharks near the seafloor rather than in the water column (e.g., Morato et al., 2019; Morato et al., 2020).

Previous studies have suggested that sixgill sharks may be positively buoyant. Nakamura et al. (2015), using high-frequency tri-axial accelerometers, observed faster ascent rates and higher acceleration amplitudes during descents, consistent with the increased tailbeat effort required to counteract buoyancy. Similarly, Coffey et al. (2020) reported elevated overall dynamic body acceleration (ODBA) during dawn descents compared to dusk ascents, further supporting these findings. In our study, acceleration data were obtained from only a single individual (#S07) over a limited timeframe. As such, caution is warranted when extrapolating these findings to the broader population. Nevertheless, the significant peak in high-activity events during dusk ascents suggests that these sharks may exploit positive buoyancy as a stealth-based foraging strategy, gliding upward passively before initiating burst swimming to ambush prey, which is consistent with the hypothesis proposed by Nakamura et al. (2015). Stomach content analyses further support this behaviour, with prey items such as swordfish and marlin – species capable of high-speed swimming – likely representing predation events. However, opportunistic feeding on fishery deadfall cannot be ruled out (Celona et al., 2005; Compagno, 1984).

4.3. Sexual segregation and individual interactions

Although passive acoustic telemetry has limitations in resolving animal interactions and overlaps due to uncertainties in the precise positions of tagged animals (Mourier et al., 2017), network analyses are increasingly being used to uncover social and spatial dynamics in marine ecosystems. Coupled with null models hypothesis testing, these frameworks have proven effective in discerning social structures and resource utilisation across diverse spatial scales, from high-precision tracking systems (e.g., Aspillaga et al., 2021) to extensive arrays of non-overlapping acoustic receivers (e.g., Gandra et al., 2020; Jacoby et al., 2016). In our study, the large detection range allowed insights into movements across habitats despite limiting high-resolution positioning data, yet revealed sexually mediated and interspecific patterns with ecological significance.

Our findings indicate that adult kitefin sharks exhibit sexual spatial segregation along a depth gradient. Males were predominantly detected at deeper, offshore sites during the night, whereas females favoured shallower coastal areas with limited diel variation – except for two females that swam to nearby summits, showing increased nighttime detections. The low spatiotemporal overlap (0.10 %) among male-female pairs, along with significant PERMANOVA results for sex-based space-use differences, corroborates sexual segregation though habitat partitioning, as observed in both Azores (Perrotta, 2004; Silva, 1987) and Mediterranean fisheries data (Bottaro et al., 2023). This separation clearly reflects differences in vertical habitat use and potentially active habitat selection by one or both sexes. Such segregation could arise from differences in body size, physiological requirements, environmental preferences, or social behaviours (Sims, 2005). For instance, females may avoid males to reduce harassment associated with aggressive courtship, as hypothesized for other elasmobranchs (Finucci et al., 2018a; Jacoby et al., 2012).

Interestingly, more than 50 % of female-female kitefin shark pairs showed spatial overlap, suggesting possible joint habitat use or affiliative behaviour. This pattern aligns with observations in other deep-sea shark species, including the Portuguese dogfish (*Centroscymnus coelolepis*), the leafscale gulper shark (*Centrophorus squamosus*) and the birdbeak dogfish (*Deania calcea*) (Moura et al., 2014). Although kitefin sharks have traditionally been regarded as mostly solitary (Kiraly et al., 2003), ROV observations in the Azores have documented female aggregations (Morato et al., 2019), possibly driven by specific environmental or nutritional requirements, or conditions that may favour embryonic development, as suggested for other species (Moura et al., 2014). Growing evidence indicates such social-like spatial associations may be widespread among deep-sea elasmobranchs and holocephalans (e.g., Finucci et al., 2018a).

Although sexual segregation in sixgill sharks could not be fully evaluated, limited observations suggest it may occur. Only one male individual was captured during multiple fishing events, and no males were observed during submersible surveys at the tagging site (unpublished data). No significant spatiotemporal overlap was detected among sixgill females in this study, suggesting limited social interaction.

Interspecific co-occurrences between kitefin and sixgill sharks were rare, observed on only two occasions, with no significant overlap during the shared monitoring period. This likely reflects distinct ecological niches but warrants further investigation. Opportunistic feeding, such as scavenging on carrion, may explain these occasional interspecific interactions. Predation of kitefin sharks by sixgill sharks in the Azores is plausible given their differing trophic levels and global reports of chondrichthyan prey in sixgill shark diets (Ebert, 1994). Notably, one sixgill shark in this study consumed a hooked kitefin shark, supporting this potential predatory relationship. The high kitefin shark abundance (Das et al., 2022) and extensive sympatric habitat overlap in the region likely facilitate such interactions.

Our findings highlight the limited understanding of elasmobranch segregation and social networks, particularly in deep-sea species, for which data remain scarce (Jacoby et al., 2012). Further research is needed to clarify the drivers and ecological implications of these behaviours in the Azores and beyond.

4.4. Implications for the conservation and management of deep-water sharks

The significant gaps in our understanding of deep-sea species underscore the pressing need for focused research efforts and conservation measures. Our findings highlight the pivotal role played by oceanic islands and remote seamounts as biodiversity hotspots (Afonso et al., 2020), providing essential habitats for various marine organisms, including deep-sea species. Their complex topography and hydrodynamics foster higher productivity and biomass, attracting and supporting predators across trophic levels. These regions offer extensive seafloor habitats at optimal depths, aligning with observations that deep-sea sharks are typically absent beyond 2000 m (Priede et al., 2006) and that many shelf-dwelling elasmobranchs, including kitefin and sixgill sharks, likely depend on benthic prey or food falls (Aguzzi et al., 2018; Pethybridge et al., 2011).

The persistent bycatch in hook-and-line fisheries, particularly in deepwater regions like the Azores, highlights the urgent need for sustainable management practices tailored to deep-sea shark populations (Fauconnet et al., 2019, 2023). Our results demonstrate long-term residency and site attachment of deep-sea sharks to specific (essential) mid-Atlantic ridge habitats, challenging the traditional view of these species as nomadic and emphasizing their reliance on predictable food resources. This suggests that even conventional spatial management measures, including fishery closures and marine protected areas, may meaningfully benefit their conservation.

Our findings also reveal complex ecological dynamics, including sexual segregation in kitefin sharks. Understanding such patterns has critical implications for management and conservation, as differing spatial distributions or sizes may lead to sex-selective fishing, disproportionately impacting population structure. Addressing these challenges through spatially managed fisheries is essential to mitigate differential exploitation.

Advancements in biotelemetry and biologging technologies are revolutionising ecological research, enabling unprecedented insights into deep-sea species' behaviour and habitat use. Collectively, these findings highlight the applicability of cutting-edge tools but also underscore the urgency of continued research and conservation efforts to safeguard these deep-sea predators and their ecosystems. Our experimental design effectively tracked long-term movements of tagged deep-sea sharks around the Azorean islands and nearby seamounts, identifying key habitats and ecological traits. These results highlight the potential for broader application of such methodologies in monitoring deep mesopelagic species. Collectively, they reinforce the importance of sustained long-term research and conservation efforts to protect deep-sea predators and their ecosystems.

CRediT authorship contribution statement

Miguel Gandra: Writing – review & editing, Writing – original draft, Visualization, Software, Investigation, Formal analysis, Data curation. **Jorge Fontes:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Bruno C.L. Macena:** Writing – review & editing, Investigation, Data curation. **Carl G. Meyer:** Writing – review & editing, Resources. **Pedro Afonso:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used OpenAI's GPT-4 model to improve language and readability. The final manuscript was carefully reviewed and revised by the authors, who assume full responsibility for the accuracy and integrity of the work.

Funding

This study was funded by Portuguese national funds through the FCT – Foundation for Science and Technology through the projects UIDB/05634/2020, UIDB/04326/2020, and LA/P/0101/2020, as well as the fellowship UI/BD/151309/2021. Additional support was provided by the Azorean Regional Government through projects M1.1.A/FUNC.UI&D/003/2021–2024, M1.1.A/REEQ.CIENTÍFICO(UI&D/2021/010) and MoniCO – Azores Coastal Resources and Environmental Monitoring Program (SRMCT/DRP). Support was also provided by the proWIN proNature Foundation through the EcodivePWN project. Further funding was received from the European Commission under the H2020 framework through the Mission Atlantic (grant no. 862428), MEESO (grant no. 817669), and NAUTILOS (grant no. 101000825) projects. JF was co-financed by the Operational Program AZORES 2020 via the Fund 01-0145-FEDER-000140 ("MarAZ Researchers: Consolidate a body of researchers in Marine Sciences in the Azores of the European Union") and supported by the Regional Fund for Science and Technology of the Government of the Azores through the research grant M3.1.a/F/062/2016.

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.

Acknowledgements

We would like to thank the Dalio Foundation, OceanX, and the crew of the R/V OceanXplorer for their operational and logistical support during field operations. Special thanks to Dean Grubbs and the submersible team for their invaluable contributions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2025.107782.

Data availability

Data will be made available on request.

References

Abecasis, R.C., Afonso, P., Colaço, A., Longnecker, N., Clifton, J., Schmidt, L., Santos, R. S., 2015. Marine conservation in the Azores: evaluating marine protected area development in a remote island context. Front. Mar. Sci. 2, 104.

Afonso, P., Fontes, J., Giacomello, E., Magalhães, M.C., Martins, H.R., Morato, T., Neves, V., Prieto, R., Santos, R.S., Silva, M.A., 2020. The Azores: a mid-Atlantic hotspot for marine megafauna research and conservation. Front. Mar. Sci. 6, 826.

Afonso, P., Fontes, J., Holland, K.N., Santos, R.S., 2009. Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. Mar. Ecol. Prog. Ser. 381, 273–286.

Afonso, P., Gandra, M., Graça, G., Macena, B., Vandeperre, F., Fontes, J., 2022. The multi-annual residency of juvenile smooth hammerhead shark in an oceanic island nursery. Front. Mar. Sci. 9, 844893.

Afonso, P., Graça, G., Berke, G., Fontes, J., 2012. First observations on seamount habitat use of blackspot seabream (*Pagellus bogaraveo*) using acoustic telemetry. J. Exp. Mar. Biol. Ecol. 436, 1–10.

Aguzzi, J., Fanelli, E., Ciuffardi, T., Schirone, A., De Leo, F.C., Doya, C., Kawato, M., Miyazaki, M., Furushima, Y., Costa, C., 2018. Faunal activity rhythms influencing early community succession of an implanted whale carcass offshore Sagami Bay, Japan. Sci. Rep. 8, 11163.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Andrews, K.S., Williams, G.D., Farrer, D., Tolimieri, N., Harvey, C.J., Bargmann, G., Levin, P.S., 2009. Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. Anim. Behav. 78, 525–536.

Appert, C., Udyawer, V., Simpfendorfer, C.A., Heupel, M.R., Scott, M., Currey-Randall, L. M., Harborne, A.R., Jaine, F., Chin, A., 2023. Use, misuse, and ambiguity of indices of residence in acoustic telemetry studies. Mar. Ecol. Prog. Ser. 714, 27–44.

Armstrong, C.W., Foley, N.S., Tinch, R., van den Hove, S., 2012. Services from the deep: steps towards valuation of deep sea goods and services. Ecosyst. Serv. 2, 2–13.

Arostegui, M.C., Afonso, P., Fauconnet, L., Fontes, J., Macena, B.C.L., Meyer, C., Morato, T., Braun, C.D., 2024. Advancing the frontier of fish geolocation into the ocean's midwaters. Deep-Sea Res., Part A Oceanogr. Res. Pap. I 212, 104386.

Aspillaga, E., Arlinghaus, R., Martorell-Barceló, M., Barcelo-Serra, M., Alós, J., 2021. High-throughput tracking of social networks in marine fish populations. Front. Mar. Sci. 794.

Bianchi, D., Stock, C., Galbraith, E.D., Sarmiento, J.L., 2013. Diel vertical migration: ecological controls and impacts on the biological pump in a one-dimensional ocean model. Glob. Biogeochem. Cycles 27, 478–491.

Bird, C.S., Veríssimo, A., Magozzi, S., Abrantes, K.G., Aguilar, A., Al-Reasi, H., Barnett, A., Bethea, D.M., Biais, G., Borrell, A., 2018. A global perspective on the trophic geography of sharks. Nat Ecol Evol 2, 299–305.

Bivand, R., 2023. maptools: tools for handling spatial objects. R Package Version 1, 1–8.

Bottaro, M., Sinopoli, M., Bertocci, I., Follesa, M.C., Cau, A., Consalvo, I., Scarcelli, F., Sperone, E., Vacchi, M., Marsili, L., 2023. Jaws from the deep: biological and ecological insights on the kitefin shark *Dalatias licha* from the Mediterranean Sea. Front. Mar. Sci. 10, 1155731.

Braun, C.D., Arostegui, M.C., Thorrold, S.R., Papastamatiou, Y.P., Gaube, P., Fontes, J., Afonso, P., 2022. The functional and ecological significance of deep diving by large marine predators. Ann. Rev. Mar. Sci 14, 129–159.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Capapé, C., Hemida, F., Quignard, J.-P., Ben Amor, M.M., Reynaud, C., 2008. Biological observations on a rare deep-sea shark, *Dalatias licha* (Chondrichthyes: dalatiidae), off the Maghreb coast (south-western Mediterranean). Pan Am. J. Aquat. Sci. 3, 355–360.

Carey, F.G., Clark, E., 1995. Depth telemetry from the sixgill shark, *Hexanchus griseus*, at Bermuda. Environ. Biol. Fish. 42, 7–14.

Castro-Arellano, I., Lacher Jr, T.E., Willig, M.R., Rangel, T.F., 2010. Assessment of assemblage-wide temporal niche segregation using null models. Methods Ecol. Evol. 1, 311–318.

Celona, A., De Maddalena, A., Romeo, T., 2005. Bluntnose sixgill shark, *Hexanchus griseus* (Bonnaterre, 1788), in the eastern north Sicilian waters. Boll Mus Civ St Naz Vec 56, 137–151.

Coffey, D.M., Royer, M.A., Meyer, C.G., Holland, K.N., 2020. Diel patterns in swimming behavior of a vertically migrating deepwater shark, the bluntnose sixgill (*Hexanchus griseus*). PLoS One 15, e0228253.

Comfort, C.M., Weng, K.C., 2015. Vertical habitat and behaviour of the bluntnose sixgill shark in Hawaii. Deep Sea Res II 115, 116–126.

Compagno, L.J.V., 1984. FAO species catalogue. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes. FAO Fish Synop 125 4, 1–258.

Daley, R.K., Williams, A., Green, M., Barker, B., Brodie, P., 2015. Can marine reserves conserve vulnerable sharks in the deep sea? A case study of *Centrophorus zeehaani* (Centrophoridae), examined with acoustic telemetry. Deep Sea Res II 115, 127–136.

Das, D., Afonso, P., 2017. Review of the diversity, ecology, and conservation of elasmobranchs in the Azores region, mid-north Atlantic. Front. Mar. Sci. 4, 354.

Das, D., Gonzalez-Irusta, J.M., Morato, T., Fauconnet, L., Catarino, D., Afonso, P., Viegas, C., Rodrigues, L., Menezes, G., Rosa, A., 2022. Distribution models of deep-sea elasmobranchs in the Azores, Mid-Atlantic Ridge, to inform spatial planning. Deep-Sea Res., Part A Oceanogr. Res. Pap. I 182, 103707.

Dawson, C.L., Starr, R.M., 2009. Movements of subadult prickly sharks *Echinorhinus cookei* in the Monterey Canyon. Mar. Ecol. Prog. Ser. 386, 253–262.

Dunbrack, R., Zielinski, R., 2003. Seasonal and diurnal activity of sixgill sharks (*Hexanchus griseus*) on a shallow water reef in the Strait of Georgia, British Columbia. Can. J. Zool. 81, 1107–1111.

Dunn, M.R., Szabo, A., McVeagh, M.S., Smith, P.J., 2010. The diet of deepwater sharks and the benefits of using DNA identification of prey. Deep-Sea Res., Part A Oceanogr. Res. Pap. I 57, 923–930.

Ebert, D.A., 1986. Biological aspects of the sixgill shark, *Hexanchus griseus*. Copeia 131–135.

Ebert, D.A., 1994. Diet of the sixgill shark *Hexanchus griseus* off southern Africa. S. Afr. J. Mar. Sci. 14, 213–218.

Ebert, D.A., 2002. Some observations on the reproductive biology of the sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) from South African waters. Afr. J. Mar. Sci. 24, 359–363.

Edwards, J.E., Hedges, K.J., Kessel, S.T., Hussey, N.E., 2022. Multi-year acoustic tracking reveals transient movements, recurring hotspots, and apparent seasonality in the coastal-offshore presence of Greenland sharks (*Somniosus microcephalus*). Front. Mar. Sci. 9, 902854.

Edwards, J.E., Pratt, J., Tress, N., Hussey, N.E., 2019. Thinking deeper: uncovering the mysteries of animal movement in the deep sea. Deep-Sea Res., Part A Oceanogr. Res. Pap. I 146, 24–43.

Fauconnet, L., Catarino, D., Das, D., Giacomello, E., Gonzalez-Irusta, J.M., Afonso, P., Morato, T., 2023. Challenges in avoiding deep-water shark bycatch in Azorean hook-and-line fisheries. ICES J. Mar. Sci. 80, 605–619.

Fauconnet, L., Pham, C.K., Canha, A., Afonso, P., Diogo, H., Machete, M., Silva, H.M., Vandeperre, F., Morato, T., 2019. An overview of fisheries discards in the Azores. Fish. Res. 209, 230–241.

Finucci, B., Barnett, A., Bineesh, K.K., Cheok, J., Cotton, C.F. Dharmadi, Graham, K.J., Kulka, D.W., Neat, F.C., Pacoureau, N., Rigby, C.L., Tanaka, S., Walker, T.I., 2020. *Hexanchus griseus*. The IUCN Red List of Threatened Species 2020 e. T10030A495630.

Finucci, B., Dunn, M.R., Jones, E.G., Valerio, B., 2018a. Aggregations and associations in deep-sea chondrichthyans. ICES J. Mar. Sci. 75, 1613–1626.

Finucci, B., Pacoureau, N., Rigby, C.L., Matsushiba, J.H., Faure-Beaulieu, N., Sherman, C. S., VanderWright, W.J., Jabado, R.W., Charvet, P., Mejía-Falla, P.A., 2024. Fishing for oil and meat drives irreversible defaunation of deepwater sharks and rays. Sci. Technol. Humanit. 383, 1135–1141.

Finucci, B., Walls, R.H.L., Guallart, J., Kyne, P.M., 2018b. *Dalatias licha*. The IUCN Red List of Threatened Species 2018 e.T6229A3111662. (Accessed 14 January 2025).

Forster, G.R., Badcock, J.R., Longbottom, M.R., Merrett, N.R., Thomson, K.S., 1970. Results of the Royal Society Indian Ocean deep slope fishing expedition, 1969. Proc. R. Soc. Lond. B Biol. Sci. 175, 367–404.

Gandra, M., Afonso, P., Fontes, J., 2020. Intra-and interspecific associations in two predatory reef fishes at a shallow seamount. Mar. Ecol. Prog. Ser. 654, 93–107.

Gandra, M., Winkler, A.C., Afonso, P., Abecasis, D., 2024. Long-distance migrations and seasonal movements of meagre (*Argyrosomus regius*), a large coastal predator, along the Iberian Peninsula coast. Mov Ecol Manuscript Accepted for Publication.

Griffing, D., Larson, S., Hollander, J., Carpenter, T., Christiansen, J., Doss, C., 2014. Observations on abundance of bluntnose sixgill sharks, *Hexanchus griseus*, in an urban waterway in Puget Sound, 2003-2005. PLoS One 9, e87081.

Hernández-León, S., Koppelmann, R., Fraile-Nuez, E., Bode, A., Mompeán, C., Irigoien, X., Olivar, M.P., Echevarría, F., Fernández de Puelles, M.L., González-Gordillo, J.I., 2020. Large deep-sea zooplankton biomass mirrors primary production in the global ocean. Nat. Commun. 11, 6048.

Heupel, M.R., Semmens, J.M., Hobday, A.J., 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar. Freshw. Res. 57, 1–13.

Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nat. Commun. 5, 3271.

Jacoby, D.M.P., Croft, D.P., Sims, D.W., 2012. Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish Fish. 13, 399–417.

Jacoby, D.M.P., Papastamatiou, Y.P., Freeman, R., 2016. Inferring animal social networks and leadership: applications for passive monitoring arrays. J. R. Soc. Interface 13, 20160676.

Kelly, T.B., Davison, P.C., Goericke, R., Landry, M.R., Ohman, M.D., Stukel, M.R., 2019. The importance of mesozooplankton diel vertical migration for sustaining a mesopelagic food web. Front. Mar. Sci. 6, 508.

King, J.R., Surry, A.M., 2017. Seasonal and daily movements of the bluntnose sixgill shark (*Hexanchus griseus*) in the strait of Georgia from satellite tag data. Environ. Biol. Fish. 100, 1543–1559.

Kiraly, S.J., Moore, J.A., Jasinski, P.H., 2003. Deepwater and other sharks of the U.S. Atlantic Ocean exclusive economic zone. Mar. Fish. Rev. 65, 1–63.

Kraft, S., Gandra, M., Lennox, R.J., Mourier, J., Winkler, A.C., Abecasis, D., 2023. Residency and space use estimation methods based on passive acoustic telemetry data. Mov Ecol 11, 12.

Mallefet, J., Stevens, D.W., Duchatelet, L., 2021. Bioluminescence of the largest luminous vertebrate, the kitefin shark, *Dalatias licha*: first insights and comparative aspects. Front. Mar. Sci. 8, 633582.

Morato, T., Carreiro-Silva, M., Taranto, G.H., Dominguez-Carrió, C., Ramos, M., Ríos, N., Laurence, F., Ocaña Vicente, O., Calado, A., Afonso, A., 2019. Cruise Report - Blue Azores Program Expedition 2018 on Board the NRP Gago Coutinho. Report. Zenodo. https://doi.org/10.5281/zenodo.3416898.

Morato, T., Dominguez-Carrió, C., Gomes, S., Taranto, G., Blasco, J., Ramos, M., Fauconnet, L., Zárate, C., Carreiro-Silva, M., 2020. MapGES 2019: Summer 2019 Cruise on Board of N/I Arquipélago. Report. Zenodo. https://doi.org/10.5281/zenodo.3727570.

Moura, T., Jones, E., Clarke, M.W., Cotton, C.F., Crozier, P., Daley, R.K., Diez, G., Dobby, H., Dyb, J.E., Fossen, I., 2014. Large-scale distribution of three deep-water squaloid sharks: integrating data on sex, maturity and environment. Fish. Res. 157, 47–61.

Mourier, J., Bass, N.C., Guttridge, T.L., Day, J., Brown, C., 2017. Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? R. Soc. Open Sci. 4, 170485.

Murray, T.S., Elston, C., Smale, M.J., Childs, A.R., Dicken, M.L., Cowley, P.D., 2024. Marine predators segregate interspecifically by space and time in a sheltered coastal bay. J. Fish. Biol. 1–15.

Naito, Y., Costa, D.P., Adachi, T., Robinson, P.W., Fowler, M., Takahashi, A., 2013. Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Funct. Ecol. 27, 710–717.

Nakamura, I., Meyer, C.G., Sato, K., 2015. Unexpected positive buoyancy in deep sea sharks, *Hexanchus griseus*, and a *Echinorhinus cookei*. PLoS One 10, e0127667.

Navarro, J., López, L., Coll, M., Barría, C., Sáez-Liante, R., 2014. Short-and long-term importance of small sharks in the diet of the rare deep-sea shark *Dalatias licha*. Mar. Biol. 161, 1697–1707.

Nuez, I., Giovos, I., Tiralongo, F., Penadés-Suay, J., Cetkovic, I., Di Lorenzo, M., Kleitou, P., Bakiu, R., Bradai, M.N., Almabruk, S.A.A., 2023. Assessing the current status of *Hexanchus griseus* in the Mediterranean Sea using local ecological knowledge. Mar. Pol. 147, 105378.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C.J.F., Weedon, J., Borman, T., 2025. Vegan: community ecology package. In: R Package Version 2.6-10.

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., 2021. Half a century of global decline in oceanic sharks and rays. Nature (London) 589, 567–571.

Perrotta, R.G., 2004. Kitefin shark *Dalatia licha* (Dalatiidae) fishery in the northeastern Atlantic and some recommendations for elasmobranchs explotation. Rev. Invest. Desarro. Pesq. 16, 97–101.

Pethybridge, H., Daley, R.K., Nichols, P.D., 2011. Diet of demersal sharks and chimaeras inferred by fatty acid profiles and stomach content analysis. J. Exp. Mar. Biol. Ecol. 409, 290–299.

Pinte, N., Parisot, P., Martin, U., Zintzen, V., De Vleeschouwer, C., Roberts, C.D., Mallefet, J., 2020. Ecological features and swimming capabilities of deep-sea sharks from New Zealand. Deep-Sea Res., Part A Oceanogr. Res. Pap. I 156, 103187.

Priede, I.G., Froese, R., Bailey, D.M., Bergstad, O.A., Collins, M.A., Dyb, J.E., Henriques, C., Jones, E.G., King, N., 2006. The absence of sharks from abyssal regions of the world's oceans. Proc R Soc B Biol Sci 273, 1435–1441.

Proud, R., Cox, M.J., Brierley, A.S., 2017. Biogeography of the global ocean's mesopelagic zone. Curr. Biol. 27, 113–119.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7, 2851–2899.

Rechisky, E.L., Wetherbee, B.M., 2003. Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ. Biol. Fish. 68, 113–128.

Reum, J.C.P., Williams, G.D., Harvey, C.J., Andrews, K.S., Levin, P.S., 2020. Trophic ecology of a large-bodied marine predator, bluntnose sixgill shark *Hexanchus griseus*, inferred using stable isotope analysis. Environ. Biol. Fish. 103, 147–162.

Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M., Isidro, E.J., 1995. Marine research, resources and conservation in the Azores. Aquat. Conserv. 5, 311–354.

Silva, H.M., 1987. An assessment of the Azorean stock of kitefin shark, *Dalatias licha* (Bonn, 1788). ICES Document CM 1987/G:66, 10pp.

Simpfendorfer, C.A., Heupel, M.R., Hueter, R.E., 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can. J. Fish. Aquat. Sci. 59, 23–32.

Sims, D.W., 2005. Differences in habitat selection and reproductive strategies of male and female sharks. In: Ruckstuhl, K.N.P. (Ed.), Sexual Segregation in Vertebrates: Ecology of the Two Sexes. Cambridge University Press, Cambridge, UK, pp. 127–147.

van Etten, J., 2017. R package gdistance: distances and routes on geographical grids. J. Stat. Software 76, 1–21.

Vella, N., Vella, A., 2017. Population genetics of the deep-sea bluntnose sixgill shark, *Hexanchus griseus*, revealing spatial genetic heterogeneity. Mar Genomics 36, 25–32.

Villegas-Ríos, D., Alós, J., March, D., Palmer, M., Mucientes, G., Saborido-Rey, F., 2013. Home range and diel behavior of the ballan wrasse, *Labrus bergylta*, determined by acoustic telemetry. J. Sea Res. 80, 61–71.

Walls, R., Guallart, J., 2015. Dalatias licha (Europe Assessment). The IUCN Red List of Threatened Species, 2015 e.T6229A48948357.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology (Bratisl.) 70, 164–168.

Wright, S.R., Righton, D., Naulaerts, J., Schallert, R.J., Griffiths, C.A., Chapple, T., Madigan, D., Laptikhovsky, V., Bendall, V., Hobbs, R., 2021. Yellowfin tuna behavioural ecology and catchability in the South Atlantic: the right place at the right time (and depth). Front. Mar. Sci. 8, 664593.

Zeppilli, D., Pusceddu, A., Trincardi, F., Danovaro, R., 2016. Seafloor heterogeneity influences the biodiversity–ecosystem functioning relationships in the deep sea. Sci. Rep. 6, 26352.