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Basking sharks of the Arctic Circle: year-long, high-resolution tracking data reveal wide thermal range and prey-driven vertical movements across habitats

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Abstract

Background Understanding the movement ecology of marine megaplanktivores is essential for conserving these ecologically significant species and managing their responses to environmental change. While telemetry has advanced our knowledge of filter-feeding mammal migrations, the annual movement patterns of large filter-feeding sharks, such as basking sharks (*Cetorhinus maximus*), remain poorly understood. This is particularly the case near their high latitude range limits where climate impacts are intensifying. In this study, we deployed pop-up satellite archival tags (PSATs) on *C. maximus* in northern Norway to investigate individual movement patterns and possible environmental drivers over an entire annual cycle.

Results Geolocated tracks from two females revealed contrasting migration strategies: one shark performed a return migration spending boreal winter close to the Azores, while the other resided north of the Arctic Circle until January before moving to the North Sea in spring. Across these diverse habitats, both sharks utilized a wide thermal range. This included previously unrecorded short-term exposures to sub-zero temperatures, extending the known thermal tolerance of the species. High-resolution time series data from recovered PSATs enabled the use of advanced signal processing and gradient-based filtering techniques to investigate vertical movement patterns in relation to the physical and biological environment. In oceanic habitats, elevated use of the mesopelagic was observed together with diel vertical migration, whereas in shelf areas depth-use patterns were confined by topography and more variable, reflective of more dynamic hydrographic conditions and prey distributions. With zooplankton distributions being structured by ambient light, density gradients, and local topography, the alignment of frequented depths with isolumes, mixed layer depths, bathymetric contours, and bioluminescence events suggests these sharks actively track prey layers across diverse habitats.

Conclusions Recorded eurythermy and behavioural plasticity suggest *C. maximus* to be well-adapted to dynamic ocean conditions. These traits may be critical for responding to the rapid climate-driven changes in the abiotic

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and biotic environments in high-latitudes, providing insights into how these endangered filter-feeders might navigate shifting ecosystems.

Keywords Satellite telemetry, DVM, Zooplankton, Thermal niche, Bioluminescence, Isolume, Wavelet analysis, Elasmobranchs, Lamniformes

Graphical Abstract



Background

Marine megafauna, including large sharks, whales, and sea turtles, are essential components of ocean ecosystems, serving as top predators and keystone species that shape the structure and function of marine communities [1-3]. Their wide-ranging movements often span thousands of kilometres across ocean basins, including dives to meso- and bathypelagic depths, to seek suitable habitats for foraging and reproduction [4, 5]. As such, these movements are intricately linked to the dynamic ocean environments, which in turn raises concerns about how populations may be impacted by the rapid pace of climate change. Climate-driven changes, such as longerterm ocean warming, deoxygenation, and abrupt extreme events such as marine heatwaves, have already altered ocean habitats, affecting the behaviour, habitat use, and distributions of apex marine predators [6-9]. These changes can have consequences for threatened species, by altering survival, reproductive success, and humaninduced mortality from increased spatial overlap with threats such as fishing and shipping [7, 10-12]. However, without an understanding of individual species' movements and behavioural responses to present-day environments across the broad range of habitats they occupy within their geographic range, predicting future distributions accurately will be difficult [12].

As a filter-feeder, the world's second largest fish, the basking shark Cetorhinus maximus (Gunnerus, 1765) exemplifies this intricate link between movement behaviour and the physical and biological environment. Feeding at the end of a short food chain (phytoplankton-zooplankton-shark), the movement patterns of C. *maximus* reflect the extreme heterogeneity in secondary production that is present in the oceans across a broad range of spatial and temporal scales [13-16]. Circumglobally distributed in tropical to subpolar waters, this species is highly mobile and known to inhabit a wide range of marine environments, from coastal waters to the open ocean, and from the surface to bathypelagic depths below 1000 m (e.g., [16–18]). In summer, C. maximus typically exploits the shallow depths of shelf habitats at higher latitudes to forage on dense aggregations of zooplankton [14, 19]. In the post-summer period, C. maximus has been shown to spend extended periods in adjacent epipelagic shelf and shelf-edge habitats, or to make large-scale movements to lower latitudes whilst increasingly occupying the mesopelagic zone [17, 18, 20-23]. Previous studies demonstrate that their horizontal and vertical movements are closely tied to habitat features such as thermal fronts, stratification (mixed layer depths), and the distribution and movements of their planktonic prey (e.g., [23-26]). In stratified oceanic waters, C. maximus has been observed to perform normal diel vertical migration (nDVM), characterized by dusk ascents and dawn descents, likely driven by the light-evading behaviour of their zooplankton prey [23, 25, 27]. Conversely, in coastal shelf habitats influenced by tidal fronts, sharks have been recorded to display reverse diel vertical migration (rDVM), with nocturnal descents after daytime surfacing behaviour, suggested to reflect anti-predatory behaviour of their copepod prey in response to larger invertebrates that undertake nDVM [25]. Tidal rhythms in vertical behaviour of *C. maximus* have also been recorded in inner shelf areas with complex topography and strong tidal streams, presumably as a result of sharks responding to tidally induced vertical displacements of zooplankton prey [27].

This underscores the diverse horizontal and vertical movement patterns *C. maximus* employs to locate and exploit resources in dynamic ocean environments [28], highlighting the need for comprehensive movement analyses across the wide range of abiotic and biotic habitats utilized. Previous telemetry studies in the Northeast Atlantic have been tracking C. maximus primarily in temperate waters between boreal spring to autumn and often had to rely on intermittently transmitted satellite data (e.g., [18, 25, 29]). Whilst fine- to meso-scale movements have been linked to local prey abundances using net sampling or acoustic data [14, 25], fine-scale, in situ habitat characterization over extended timescales have not been investigated due to the scarceness of highresolution data across seasons. Monitoring C. maximus movements across diverse habitats is essential for understanding its response to climate change and identifying regions that may require targeted conservation efforts. This is particularly critical in climate-sensitive regions like the Barents Sea, where the northernmost occurrences of C. maximus have been reported [30] and climate-driven range shifts and increased anthropogenic activity are predicted [12, 31].

To address these gaps, this study tagged three *C. maximus* individuals with pop-up archival tags (PSATs) in northern Norway, to track their horizontal and vertical movements over 365 days. Recovered PSATs provided continuous, high-resolution data on swimming depth, water temperature, and light levels at 5-s intervals, enabling detailed analysis of depth-use patterns across one of the broadest environmental ranges studied for this species.

Methods

Tagging and data processing

Three individuals of Cetorhinus maximus were tagged with pop-up satellite archival transmitting tags (mini-PAT-348, Wildlife Computers, Inc., WA, USA) around Lofoten and Vesterålen (~68°N) in northern Norway in June and July 2022. Each tag was fitted with a titanium anchor (64 mm×16 mm×1 mm, Wildlife Computers, Inc., WA, USA) fixed to a custom-made 15-cm tether consisting of fluorocarbon monofilament line (220 lbs, 1.66 mm, Seaguar, Blue Label, NY, USA) covered with heat-shrunk plastic tubing. Sharks were approached and tagged from behind from the bow of a 10-m aluminium boat (Arronet 30 surprise, Arronet Teknik AB, Sweden). Total length was visually estimated relative to the length of the boat and underwater video was taken to obtain photo-identification images and to identify the sex by the absence (female) or presence (male) of claspers. A 3-m tagging pole was used to insert the anchor and entire tether connected to the tag below the left posterior base of the first dorsal fin. This procedure allowed the PSATs

to be attached as close to the body as possible with a fixed point at its cone (Figure S1).

With PSATs programmed to detach after 365 days, they sampled ambient light level, temperature, pressure (depth), and triaxial acceleration at 5-s intervals. Following their pop-up in 2023, tags were retrieved at sea using an Argos goniometer (CLS RXG-234, CLS, France).

Processing and analysis of archival PSAT data was performed in R (version 4.3.2, R Core Team, 2023). Archival data were visually inspected and truncated to remove the first day post-tagging and post-pop-off data. Data visualization was performed with the *ggplot2* package [32]. Obtained 5-s time series were aggregated into 1-min, 1-h, and 1-day intervals. Due to non-normal distributions of depth, temperature, and light level, these variables were aggregated using the median, while derived covariates from depth such as vertical velocity were summarized using the mean.

Habitat characterization

Annual depth-temperature envelope

To visualize annual depth-temperature envelopes of the sharks, kernel density estimation was applied to hourly data using the *MASS* package [33]. The *bandwidth.nrd* {*MASS*} function was applied to depth and temperature to calculate a suited smoothing bandwidth for both parameters. Analogous to conventions to define home ranges in geographical space [34], the 95% and 50% isopleths were calculated for the depth-temperature space.

Biogeographic provinces, bathymetry, and light regime

Biogeographic provinces were extracted from the Marine Ecoregions and Pelagic Provinces of the World based on Spalding [35, 36] that have been integrated into a single product [37]. Bottom depth was extracted from the GEBCO grid as a weighted average of the daily 99% utilization distribution kernel associated with each daily position.

The continuum of light regimes from polar night, and diel regimes, to midnight sun was based on the length of daylight between sunrise and sunset. Daylight hours as well as sun angles (α) were extracted with the *suncalc* package [38] for the daily coordinate obtained via geolocation (for details see Sect. "Horizontal movements"). Two covariates of sunlight phases were constructed, *daynight* (day: $\alpha \ge 0^{\circ}$) and *daynighttwilight* (day: $\alpha \ge 6^{\circ}$, night: $\alpha \le -6^{\circ}$, twilight: $-6 < \alpha < 6^{\circ}$).

Thermocline

To determine the thermal structure of the water column utilized by the sharks, we used the exponential leap-forward gradient (ELG) method [39], which had previously been used for identifying and characterizing the mixed layer and thermocline across global temperature profiles [40, 41]. Before identifying the thermocline, daily temperature profiles were generated by averaging sharkborne temperature measurements across 10-m-depth bins within a 3-day sliding window, followed by linear interpolation at 1-m-depth intervals to mitigate noise effects. To identify key characteristics of the thermocline, including its intensity (gradient), upper $z_{(0 1 \wedge T)}$, and lower $z_{(0.7\Delta T)}$ limit, the ELG method was applied to respective temperature profiles using MATLAB (Math-Works). Upper and lower limits marked depths at which the temperature difference between the mixed layer and deeper ocean layers was 10% and 70%, respectively. Quality control procedures were applied to flag low-quality temperature profiles prior to the application of the ELG algorithm. These included: (i) > 5 °C change between consecutive depth values; (ii) profiles not extending beyond 20 m depth (no access to the thermocline layer); and (iii) profiles not including the upper 50 m of the water column (no possibility of identifying the mixed layer) (see 41 for details).

Isolumes and bioluminescence

To highlight differences in light attenuation across habitats and identify depth strata preferable to putative lightevading prey, the average depth of a single isolume was determined for each shark and day for sun angles $\alpha > 6^{\circ}$. Values were only considered if they contained more than 20 datapoints and a sliding average (k=3 d) was applied to smooth depths for visualization. We chose a light level value around 30, $(29 \le LL \ge 31)$, hereafter LL30, as this corresponds to light intensities of approximately 10⁻¹¹ Wcm⁻², which lies within the preferred range reported for potential C. maximus prey (i.e. mesopelagic crustaceans) in the North Atlantic as well as global deep scattering layer (DSL) averages [42, 43]. However, we are aware that both higher (up to 10^{-7} W cm⁻²) and lower (down to 10^{-13} W cm⁻²) intensities for light comfort zones have been reported for the migratory fraction of the DSL [44–47]. Note that light level is a measure specific to the Wildlife Computers product and is a relative measurement of light primarily in the blue band (415-460 nm), with light level values of 25–225 presenting approximate end points on a logarithmic scale (Wildlife Computers, pers. comm.). While it does not permit direct conversion to light intensity, light levels of 150, 110, and 70 correlate to light intensities of approximately 10^{-5} Wcm⁻², 10^{-7}

 Wcm^{-2} , and 10^{-9} Wcm^{-2} , respectively [48]. Light level values are not directly comparable between tags.

Mesopelagic organisms, including for example euphausiids, ostracods, and copepods, are not only associated with preferred isolumes but many can also emit light, so-called bioluminescence [49]. To gain in situ insights into the presence of such potential prey within the shark's immediate environment, we analysed the archival light level time series for bioluminescence events, adapting the approach from Braun et al. [50]. Briefly, multiple filters were applied to peaks in relative light level to discern putative bioluminescent flashes from other sources of ambient light variation in the time series. First, events were excluded if they occurred in waters at least two orders of magnitude brighter in light intensity than the tag light sensor's sensitivity floor (light level 12 for both tags); these subsurface optical conditions represent shallower daytime waters where bioluminescent fauna are less likely to occur and harder to detect. In addition, potential peaks were not considered bioluminescence if they occurred >1 m shallower than the previous time step, thereby excluding increases in light potentially caused by a shark ascending into brighter water. Peaks were only included if the relative light intensity at the moment of potential bioluminescence at least 2 light levels higher than the measurement in the preceding two time steps and less than or equal to the peak value plus the measurement precision in the following two time steps. This ensured that all light-level increases putatively caused by bioluminescent flashes were greater than the measurement precision of the tag's light sensor. Lastly, to account for varying measurement noise across diel periods and depths, the increase in relative light level from the time step preceding the light-level peak to the peak itself had to be more than two times higher than the standard deviation in relative light level from 15 to five timesteps prior to the potential bioluminescent event. Given that the filtering steps exclude portions of the time series from consideration, this detection approach is inherently presence-only. All putative bioluminescence events identified by this approach were manually inspected and classified as true or false positives (or uncertain), based on comparison to previously defined flash characteristics measured with the same photodiode [51, 52].

Movement behaviour characterization Horizontal movements

Geolocation of the PSAT data was conducted using the R package *HMMoce* [53]. This gridded hidden Markov model approach compares diverse tag-based observations against remote sensing and data-assimilating oceanographic model outputs to generate likelihoods

of a tagged individual's location and behaviour at each time step of its deployment. At 24-h intervals, we calculated five separate likelihoods: (a) bathymetry calculated by excluding areas shallower than the tag-recorded maximum depth in the SRTM30 PLUS dataset [54]; light-based (b) latitude and (c) longitude determined by a threshold-based algorithm ([55]; GPE2 software); (d) sea surface temperature (SST) generated from comparing tag-based SST values (<10 m depth) against the National Oceanic and Atmospheric Administration 0.25° Daily Optimum Interpolation SST (OISST) climate data record [56, 57]; and (e) ocean heat content [58] generated from comparing integrated tag-based profiles of depth and temperature against those from the 1/12° Global Ocean Physics Reanalysis (GLORYS; [59]). All likelihood grids were resampled to 0.25° spatial resolution. The light-based latitude and longitude likelihoods were visually checked and filtered to exclude spurious location estimates. The resulting observation likelihoods were convolved with a diffusive movement kernel for a single behaviour state. Parameter estimation of behaviour state movement used bound-constrained optimization [60]. Parameter bounds and the initial value for the movement kernel were informed by the daily displacement rates (km d^{-1}) estimated from previous telemetry studies of *C*. maximus (e.g., [17]) and Rhincodon typus (e.g., [61]). The daily posterior likelihood surfaces were summed for each shark to yield their time-integrated, spatial utilization distributions (UDs) throughout the overall deployment as well as for each month. The most probable track for each deployment was calculated with the Viterbi method, a global decoding solution that improves daily location estimates derived from the posterior probability surfaces [62].

Geographical distances were calculated as a straight line between the tagging location and daily geolocated coordinates to obtain the distance to tagging location across the track. To estimate the distance covered by each shark over the deployment, geographical distances were calculated between each geolocated position and summed across the entire track. To visualize bathymetry, the GEBCO 2023 grid was used providing elevation data, in metres, on a 15 arc-second interval grid [63]. An equidistant conic projection centred to the midpoint of the track was used that preserves distance along meridians.

Periodicity in vertical movements

To investigate the periodicity and the presence of diel patterns in the depth signal, a continuous wavelet analysis was performed on hourly aggregated year-long depth time series using the *WaveletComp* package [64], following methods similar to those described in Klöcker et al. [65]. Briefly, we used the Morlet (x_0 =6) wavelet function



Fig. 1 Annual horizontal migration and depth-temperature envelope for shark 1 (red) and shark 2 (blue) over 365-day deployments. **a** Most probable tracks with daily positions, tagging locations (downward triangles) and pop-up locations (upward triangles). **b** Depth-temperature envelopes based on hourly median depth and temperature data for each shark ($n = 2 \times 8760$ h). Isopleths encompass 50% (solid lines) and 95% (dashed lines) of the data. Marginal densities for depth and temperature are displayed along the respective axes. For visualization purposes, the plot was restricted to 0 °C and 1000 m depth, excluding 13 datapoints

and assessed the significance of the wavelet spectrum by generating 1000 simulated time series per shark with a lag-1 autoregressive AR [1] model using p = 0.5 and the mean of the data [66]. Values exceeding the bootstrapped 95% confidence levels were considered statistically significant and were used to identify non-random vertical migratory behaviour within the time series. Prevalent periods in the depth signal were displayed over time as a scalogram for each shark. To determine if an individual showed diel vertical migration (DVM), the p-values for the 24-h period were examined for significance (p < 0.05). While a pure sinusoidal depth signal generates a single 24-h component in the frequency spectrum, depth time series that deviate from the sine curve due to U-shaped dives with quick descents or ascents, as well as deviations from a 12:12 h up-and-down regime due to a seasonal light regime of higher latitudes, will in addition to the 24-h period result in a series of harmonics, with the magnitude of harmonics reducing with increasing frequency [27, 65, 67]. Comprising ecologically uninterpretable signals, harmonics of a 24-h period (e.g., 12 h, 6 h) were thus ignored.

Dive behaviour

To differentiate dive phases (ascent, descent, level swimming), the rolling sum of vertical velocity was calculated for the 5-s time series over a 30-s window (ascent: $\nu > 0.5$ m, descent: $\nu < -0.5$ m, level: $-0.5 \text{ m} \le \nu \le 0.5$ m). Consecutive data points classified as the same dive phase were considered as one coherent ascent, descent, or level swimming event. The dive amplitude was calculated as the difference between the last and first depth recorded of the respective event. Ascents and descents with an amplitude <5 m were reclassified as level swimming (Figure S2).

To compare performance between ascents and descents, vertical velocity was calculated per dive phase from the raw timeseries. Mann–Whitney *U* tests were used to determine if performance differences between ascents and descents were statistically significant.

The occurrence of U and V-shaped dives was inspected visually: V-shaped dives were characterized as those showing level-swimming at depth (bottom phase) for no longer than one minute, while dives with level swimming for longer time intervals were considered U-shaped dives.

To facilitate the description and visualization of finescale vertical movement behaviour, four focal periods (F1–F4) were chosen across each deployment based on



Fig. 2 Habitat encountered across the year-long deployment by shark 1 (**a**–**c**) and shark 2 (**d**, **e**). **a**, **d** Most probable track with daily positions coloured by date and corresponding time-integrated utilization distributions from the geolocation model (UDs; grey polygons). Triangles indicate tagging (downward) and pop-up locations (upward). Focal periods (F1–F4) are indicated as boxes. **b**, **e** Light regime and thermal structure of the water column encountered by the shark. Time intervals for F1–F4 are highlighted at the bottom. Upper bar marks number of daytime hours. Lower bar denotes stratification strength quantified as the gradient of the thermocline. **c**, **f** Temperature profiles recorded by the tag across each focal period F1–F4 (mean±s.d.). Note that the *y*-axis was limited to 250 m. Thermocline limits in **b**, **c**, **e**, **f** mark the upper (10%) and lower (70%) extent of the thermocline

representativeness of behaviour in a given habitat. Associated habitat characteristics were aggregated using the mean of numeric and the mode of categorical variables with exclusion of any missing values.

Results

Two of the three PSATs were retrieved after 365 days of deployment, one deployed on 30 June (shark 1) and one on 1 July (shark 2) in 2022; the third tag did not report (Table S1). Both retrieved tags had been attached to females. Shark 1 was estimated 6–7 m total length $(L_{\rm T})$, and shark 2 was 5–6 m $L_{\rm T}$, suggesting both were

likely sub-adults [68]. The tag of shark 1 popped up on 1 July 2023, 83 km southwest from the tagging location at the western edge of the Lofoten peninsula (68.31° N, 12.83° E). The tag of shark 2 surfaced on 2 July 2023 in the central area of the North Sea at the northern edge of the Dogger Bank (55.70° N, 2.19° E), which was 1536 km direct distance from the respective tagging location (Fig. 1a). Throughout the deployment period, both sharks showed opposing seasonal horizontal migration strategies. During the deployment, also time at liberty, shark 1 spent July to September 2022 in the Norwegian Sea, migrated southwest towards the Azores in the North Atlantic by February 2023, before returning to the Norwegian Sea by June 2023 (Fig. 2a). Shark 2, by contrast, moved north from the tagging site and spent September 2022 to early January 2023 in the Barents Sea, north of the Arctic Circle, before heading south to arrive in the North Sea in June 2023 (Fig. 2d). Thus, both sharks inhabited diverse habitats characterized by a wide range of bottom depths, light regimes, water temperatures, and thermal stratification (Fig. 2). Habitat characteristics for the focal periods F1-F4 are summarized for both sharks in Table S2.

Habitats encountered

Annual depth-temperature envelope

Across both individuals and the entire deployment period, sharks used a median depth of 115 m (range: 0–1434 m, $q_{25}-q_{75}$: 15–266 m) and a median temperature of 7.9 °C (range: – 0.6 to 18.1 °C, $q_{25}-q_{75}$: 7.2–10.0 °C). Depth–temperature use varied between individuals. Both sharks spent most time in waters at 7–9 °C (mean±s.e.; shark 1: 45.7±1.8%; shark 2: 49.3±2.1%), but depth uses differed between individuals. Shark 1 primarily used mesopelagic depths (200–1000 m; 60.7±1.6%), while shark 2 favoured surface waters in the epipelagic zone (0–200 m; 84.5±1.6%, with 32.5±1.4% ≤ 10 m) (Figure S3).

Shark 1 spent 50% of its time in waters at around 170– 360 m and 7 °C (solid line, Fig. 1b). Its broader depth– temperature envelope (95% of time) included waters at 6-13 °C across distinct depths, such as the upper 80 m, 150-250 m, and 750-820 m (dashed line, Fig. 1b). In contrast, Shark 2's core depth use was confined to the top 80 m, with a broader core temperature range of 6-11 °C (50% of time, solid line, Fig. 1b). Its broader depth use extended to 350 m, covering water temperatures from 3-14 °C and 17 °C (95% of time, dashed line, Fig. 1b).

Shark 1 experienced the coldest temperatures but spent limited time in waters below 4 °C, with the longest consecutive period lasting 106 min (incl. 101 min < 2 °C). These cold-water exposures occurred mainly during transits past the Greenland–Scotland Ridge on 3–6 December 2022 and 11–13 May 2023, totalling 512 min below 4 °C. In contrast, shark 2 spent several months in the Barents Sea with average temperatures of 6.4 °C ($q_{25}-q_{75}$: 5.1–8.1 °C; 1 Sep 2022–15 Jan 2023), including two weeks consistently below 5 °C ($q_{25}-q_{75}$: 3.1–4.2 °C; 12–26 Dec 2022).

Shark 1

During the year-long deployment, shark 1 traversed three biogeographic provinces: 'Subarctic Atlantic' (235 days), 'North Atlantic Transitional' (127 days), and 'Northern European Seas' (3 days), spending 88.5% of its time (323 days) in waters with bottom depths exceeding 1000 m (Fig. 2a; Figure S4). After tagging, shark 1 remained near the shelf and shelf edge of the Lofoten peninsula and Vøring Plateau, including southern banks such as Røst Bank, Træna Bank, and Halten Bank, inhabiting moderately stratified waters with long days under the midnight sun. As the season progressed, a diel light regime reestablished, and the thermocline weakened and deepened, with an average (mean \pm s.e) gradient of 0.13 ± 0.01 °C m^{-1} spanning from $19 \pm 1 m$ to $51 \pm 7 m$ in July, compared to 0.03 ± 0.00 °C m⁻¹ at 53 ± 2 m to 110 ± 5 m in October. Until November, the light comfort zone of potential prey, centred around the LL30 isolume, was found at 288 ± 3 m.

By late November, shark 1 left the Norwegian shelf and migrated southwest, crossing the Iceland–Faroe Ridge, a barrier to the southward flow of cold Arctic water, into the weakly stratified oceanic waters of the 'North Atlantic Transitional' province. It continued southwest along the Lousy and Hatton Banks towards the West European Basin and Azores, reaching its south-westernmost point at 39 °N 23 °W in early February, around 4000 km from its tagging site. Shark 1 remained in this area until early March, with the thermocline extending from 272 ± 6 m to 567 ± 8 m in these weakly stratified waters.

On its return, shark 1 passed west of the Celtic Shelf and Porcupine Bank in mid-April, subsequently migrating through the Rockall Trough, and over the Wyville Thomson Ridge, and likely traversing the Greenland-Scotland Ridge via the Faroe-Shetland Channel (Fig. 2a; Fig. S4). Sunlight penetrated deeper in the oceanic waters (LL30 at 458 ± 3 m), but shallowed to around 303 ± 8 m beyond the sill. In late May, shark 1 re-entered 'Subarctic Atlantic' waters, gradually moving north along the Norwegian shelf edge. From June on, shark 1 was again exposed to a polar light regime and to increasingly stratified waters, with a simultaneous shallowing of LL30 to around 252 ± 3 m (Table S2). The tag detached on 1 July 2023, 83 km southwest of the tagging location, with a total track of 13,138 km and a median daily distance of 27.6 km.



Fig. 3 Diving behaviour of shark 1 in the context of time of day **a** across the 365-day deployment and **b** for the focal periods (F1–F4). **a** Minutely depth use coloured by the time of day (day: $a \ge 6^\circ$, twilight: $-6^\circ < a > 6^\circ$, night $a \le -6^\circ$). Focal periods are highlighted at the bottom. Bar above shows *p*-values from the wavelet analysis testing the presence of a 24-h period in the hourly depth time series. **b** Behaviour during F1–F4 with, from left to right, histograms for time-at-depth and time-at-temperature, as well as a detailed depth time series in the context of time of day based on minutely data. Histograms show the average percentage of time spent per day in each of the nine depth and temperature bins, for day and night defined by sunset and sunrise. Error bars indicate standard errors across days within focal period. Note free *y*-axes for the depth time series in **b**

Shark 2

Shark 2 occupied four biogeographic provinces over the course of its 365-day deployment: 'Arctic' (166 days), 'Subarctic Atlantic' (112 days), 'Northern European Seas' (68 days), and 'North Atlantic Transitional' (19 days) (Fig. 2d; Figure S5). Shark 2 spent only 124 days (34%), in waters with bottom depths exceeding 1000 m, a marked difference to shark 1. After tagging, shark 2 remained along the shelf edge of the Lofoten Peninsula and Vøring Plateau until late July, encountering isolume LL30 at 268 ± 6 m and thermocline extending from 16.9 ± 0.9 to 52.9 ± 7.9 m similar to those experienced by shark 1 during the same period.

In contrast to shark 1's southwestern migration, shark 2 moved north, reaching the Barents Sea shelf and formally 'Arctic' waters by early August, where it remained until mid-January. The seasonal residence in the area included probable excursions as far north as 73.6 °N and east to 42.4 °E and exposure to polar-night conditions from November onwards. During this time, the water column was fully mixed, with uniform temperatures around 5 °C.

In mid-January, shark 2 left the southern Barents Sea, crossing the Lofoten Basin to move south along the Norwegian continental shelf. From February to mid-April, shark 2 likely remained along the shelf edge of the Norwegian Basin (Fig. 2d; Figure S5). In late April to early May, it utilized waters around the Shetland Islands, before entering the northern North Sea and its increasingly shallow and seasonally stratified waters. Thermal stratification was strongest in June, with gradients of up to $0.41 \,^{\circ}\text{C} \,\text{m}^{-1}$ and a shallow thermocline between 11.5 ± 0.2 and 25 ± 0.6 m (Table S2). The tag detached on 2 July 2023 north of the Dogger Bank, 1536 km from the tagging location. Over the year, shark 2 travelled approximately 14,262 km with a median daily distance of 32.2 km.

Vertical movement across habitats

Throughout the deployments, distinct differences in vertical movement patterns emerged between the two sharks. Across the deployment, a significant diel depthuse pattern was exhibited by shark 1 but not by shark 2 (Figure S6b, d). Continuous wavelet analysis identified a significant 24-h cycle in shark 1's depth time series between late December and early May, aligning with the shark's use of oceanic waters in boreal winter (Figure S6a). In contrast, shark 2 exhibited significant diel patterns only briefly in late August and early February (Figure S6c).

Both sharks engaged in a range of dive types, including predominant V- and U-shaped dives, prolonged swimming at both surface and depth, and oscillatory dives ranging from 24 h to 40 s cycles. Across both deployments, sharks spent the majority of their time (57%) engaged in level swimming. While this was almost consistently the case for shark 2, shark 1 diverged from this pattern between mid-December to early May, spending more time on ascents and descents (74%; Figure S7). Vertical velocities were significantly higher on descents compared to ascents for both sharks across the deployment (Mann–Whitney U-test; shark 1: $n_A = 44,101$, $n_D = 41,883$, U = 771,079,919, p < 0.0001; shark 2: $n_A = 23,946, n_D = 23,590, U = 184,152,054,$ p < 0.0001). Shark 2 showed more pronounced differences, with mean vertical velocities of $|\overline{v_A}| = 0.11$ m s⁻¹ and $|\overline{\nu_D}| = 0.15$ m s⁻¹, compared to shark 1 with $|\overline{\nu_A}|$ $|=0.14 \text{ m s}^{-1}$ and $|\overline{v_D}|=0.16 \text{ m s}^{-1}$. This smaller difference between shark 1's ascents and descents across the deployment likely reflects reversed vertical velocity trends associated with its diel vertical movement during winter (Figure S8).

Shark 1

During early and late periods of tag deployment (Julmid-Nov, mid-May-Jun; incl. F1, F2, F4), shark 1 exhibited vertical movement behaviour characterized by the absence of significant diel patterns, with time spent at depth evenly distributed between day and night (Fig. 3). Nevertheless, it showed bimodal depth use, spending considerable time in the upper 50 m and at specific depths of 200 m (July to August 2022; late June 2023) and 200-400 m (August to November 2022; May to June 2023). During boreal summer (incl. F1), shark 1 displayed surface-oriented behaviour with short dives from the surface to 20-50 m, interspersed with regular V-shaped and occasional U-shaped dives to deeper depths (e.g., 150-250 m; Figure S9a). From August to mid-November (incl. F2), shark 1 entered intermittent phases where it followed specific depth contours without spending time at the surface. These depths corresponded with an elevated number of bioluminescence events (Fig. 5a; Figure S9b).

The significant diel pattern in depth use observed between late December to early May (incl. F3) was associated with shallower depths occupied at night (100–500 m) compared to mesopelagic depth use during daytime (600–900 m), which together with dawn descents and dusk ascents characterize nDVM behaviour (Figures S10, S11). Between February and mid-April, shark 1 regularly spent 1–2 h in surface waters around dusk before descending to distinct night depths, e.g., 250 m (F3, Fig. S9c). In contrast to vertical velocities displayed on dives in other habitats, nDVM behaviour in shark 1 such as during F3 coincided with significantly higher absolute mean vertical velocities on ascents compared to descents (Mann–Whitney *U*-test, n_A =683, n_D =767, *U*=326,952,



Fig. 4 Diving behaviour of shark 2 in the context of time of day **a** across the 365-day deployment and **b** for the focal periods (F1–F4). **a** Minutely depth use coloured by the time of day (day: $a \ge 6^\circ$, twilight: $-6^\circ < a > 6^\circ$, night $a \le -6^\circ$). Focal periods are highlighted at the bottom. Bar above shows *p*-values from the wavelet analysis testing the presence of a 24-h period in the hourly depth time series. **b** Behaviour during F1–F4 with, from left to right, histograms for time-at-depth and time-at-temperature, as well as a detailed depth time series in the context of time of day based on minutely data. Histograms show the average percentage of time spent per day in each of the nine depth and temperature bins, for day and night defined by sunset and sunrise. Error bars indicate standard errors across days within focal period. Note free *y*-axes for the depth time series in **b**

p < 0.0001; Figure S8). Bioluminescence events were consistently detected by the shark-borne light sensor both day and night (Fig. 5a). During this period, shark 1 predominantly exhibited continued residence at depth

during the day, hereafter referred to as strict nDVM. These patterns were also observed in the time-at-temperature histograms, even though not as pronounced due to weak thermal stratification and occasional daytime



Fig. 5 Depth use in the context of the physical and biological environment for **a** shark 1 and **b** shark 2. Shades of red indicate percentage of time per day spent in each 10-m-depth bin based on minutely time series. Thermocline limits mark the upper (10%) and lower (70%) extent of the thermocline. Circles show presence of bioluminescence events coloured by time of day (day: $a \ge 6^\circ$, twilight: $-6^\circ < a > 6^\circ$, night $a \le -6^\circ$). Note free *y*-axes

surfacing (Figure S12). During these surfacing events, shark 1 spent 10 to 50 min (interquartile range) at the surface before descending at comparably high vertical velocities of 0.29 ± 0.14 m s⁻¹ to typical daytime depths (Figures S9c, S10).

While crossing the Greenland–Scotland Ridge near the Faroe Islands during migrations in December 2022 and May 2023, shark 1 displayed clear transitions in depth use (Figure S13a–c). In November 2022, it followed the 300-m-depth contour in the Norwegian Sea, increasingly utilizing the upper 150 m and showing an emerging

but not yet significant nDVM trend. Before crossing the Iceland–Faroe Ridge, shark 1 made deep meso- and bathypelagic dives into sub-zero waters, transitioning to exclusive surface use during the ridge passage (8–11 December), interrupted only by a single U-shaped dive to 160 m. Thereafter, the shark adopted nDVM behaviour, diving to 500–700 m during the day in weakly stratified oligotrophic waters (Figure S13a). The reverse behavioural sequence was observed during its return migration in late April to early May 2023. Shark 1 displayed sinusoidal nDVM across the Rockall Trough and Wyville Thomson Ridge, with restricted depth use to 180 m on 25–26 April and 140 m on 4 May in the Faroe-Shetland Channel. Upon crossing, average daily temperatures dropped by 1 °C, and included waters below 1 °C encountered during deep dives (>500 m) on 11 and 13 May. From 18 May, shark 1 resumed consistent depth use at 300–350 m, interspersed with brief periodic ascents to the surface, with surface times of typically less than 15 min before descending again (Figure S13b). Between 10 and 23 June, shark 1 shifted from this seemingly bottomoriented behaviour to a surface-oriented pattern, characterized by regular V-shaped dives from the surface coccurring approximately at hourly intervals (F4, Figure S9d).

Shark 2

Before entering the Barents Sea shelf in late August, shark 2 displayed vertical movement behaviour comparable to that of shark 1 in the corresponding period (incl. F1; Fig. 4). Its time-at-depth distribution was bimodal, with elevated time spent in the upper 50 m and at distinct depths between 150 and 600 m. No significant diel depth-use pattern was detected. Shark 2 also followed distinct depth contours for several days, alternating with surface-oriented phases characterized by constant surface swimming, shorter dives to 30–100 m, and regular V-shaped or occasional U-shaped dives to greater depths, such as 500 m (Figure S9e).

Upon entering the Barents Sea under a diel light regime (incl. F2), shark 2 exhibited non-significant trends for nDVM, primarily occupying depths around 100 m during day and shallower depths above the thermocline (10–30 m) at night, the latter associated with bioluminescence events (Figs. 4, 5b). Daytime swimming at depth was interrupted by periodic ascents to the surface, with surface times typically < 30 min (F2; Figure S9f). During polar night (Nov–Jan; incl. F3), shark 2 spent almost no time in surface-layers, particularly in November and early December $(3.35 \pm 1.27\%)$; Figure S14). Vertical movement was variable, showing no consistent rhythms or dominant dive types (F3; Figure S9g). Bioluminescence, detected from mid-September to mid-January (incl. F2, F3), corresponded to depths where shark 2 spent most of its time (Fig. 5b).

During its southward migration from January to April, shark 2 displayed variable vertical behaviour, spending up to 61% of its time in the upper 10 m (Figure S14). A bimodal depth-use pattern emerged, particularly in late March, resembling behaviour observed in summer 2022, though less pronounced. In late February, shark 2 remained shallower than 40 m before diving to 500 m depth on 1 March. While few bioluminescence events were detected in this period, a marked peak was notable in mid-May as shark 2 entered the North Sea (Fig. 5b). In this phase, shark 2 typically resided near the surface during the day, executing numerous V-dives to depths of 15–35 m and, at night, diving to 70–80 m.

From 23 May onwards, shark 2 transitioned from surface-oriented behaviour to a more consistent use of 25-35 m beneath a strengthening thermocline, showing a non-significant tendency for rDVM (Figure S13d, e). At night, shark 2 remained in 8-9 °C waters at 25-35 m, while daytime behaviour was more variable, encountering 7–18 °C during surface-bound V-dives to depths of 5–90 m, with most dives not exceeding 20–30 m depth (F4; Figure S9h). These dives typically occurred at 15–45 min intervals. Bioluminescence events were frequently detected around the 30-m-depth contour at night (Fig. 5b).

Discussion

Year-long archival biologging data from two basking sharks *Cetorhinus maximus* tagged north of the Arctic Circle revealed opposing horizontal movement strategies, enabling the analysis of vertical behaviour across one of the widest habitat ranges studied for this species. These habitats included polar-night conditions in the Barents Sea, subarctic frontal waters along the Norwegian shelf under the midnight sun, seasonally stratified and shallow waters of the North Sea, and comparable warm, weakly stratified oligotrophic oceanic waters in the West European Basin close to the Azores. Continuous 5-s recordings of depth, water temperature, and light provided unprecedented insights into the annual movement cycle of *C. maximus* and its physical and biological drivers.

Annual habitat envelopes

Vertical habitats

Over the course of one year, the sharks utilized depths ranging from the surface to 1434 m, with notable differences in depth use between individuals. Shark 1 primarily inhabited mesopelagic depths (170–360 m) and spent 78% of the year off the continental shelf (>1000 m bottom depth), while shark 2 was largely found in the upper 80 m of the epipelagic zone, spending only 27% of its time in oceanic waters. These differences likely reflect the distinct habitats encountered, although individual preference cannot be ruled out.

On the shelf and shelf edges, depth use appeared constrained by bathymetry, as maximum depths closely matched bottom depths of respective shelfs. In areas with variable topography like the Norwegian shelf, mismatches between shark depth and extracted bathymetry likely stem from spatial uncertainties and nearshore biases inherent in the PSAT geolocation data [69, 70]. In oceanic waters, where bottom depths reach several thousand metres, depth use appeared unconstrained. Here, shark 1 spend 76% of the time below 200 m, aligning with the >60% recorded in the Northwest Atlantic (NWA) [17]. Increased mesopelagic depth use in oceanic habitat has previously been observed in *C. maximus* [17, 18, 20–22], as well as other pelagic megafauna (e.g., [71–73]).

Thermal habitats

The 2-year-long deployments revealed both sharks to utilize colder thermal envelopes than previously reported, spending more than half of their time in 7.0 and 9.5 °C waters [17, 20, 74]. This downshifted envelope likely reflects the greater availability of cold-water habitats northeast of the Greenland–Scotland Ridge, for which no prior telemetry data exist. We acknowledge that the extended use of the Barents Sea until January observed in shark 2 is notably distinct from all but one *C. maximus* tracked in the Atlantic [17] and, in light of the low sample size, may not follow the typical migration pattern for this species. Nevertheless, together with shark 1, its data provide valuable insights into the range of physiologically tolerable temperatures in this species.

Overall, the sharks experienced ambient temperatures from – 0.6 to 18.1 °C, including sustained exposure below 5 °C (days to weeks) and brief periods below 2 °C (minutes to hours). This extends the minimum temperature limit for *C. maximus* (previously 4–7 °C; [17, 23, 74, 75]) and demonstrates that this species can occupy waters ranging from – 0.6 °C (this study) to 29.9 °C [17]. While capable of short-term exposure to sub-2 °C, long-term use of such cold waters seems to be constrained, with no extended use of these waters at depth or beyond the polar front, despite the relatively high biomass of lipidrich copepods associated with these Arctic water masses (<1 °C) [76–81].

In cold water, large-bodied fish benefit from a smaller surface area-to-volume ratio, reducing muscle temperature equilibration with the environment [82–84]. This high thermal inertia, along with partially internalized red muscle and counter-current heat exchangers associated with the viscera [85], likely facilitates both short- and long-term use of cold environments, contributing to the species' extended thermal range. Behavioural thermoregulation, for instance through rapid ascents to warmer surface waters (shark 1; Figure S9b), may also facilitate cold-water utilization, similar to the large ectothermic megamouth shark *Megachasma pelagios* [86] and other deep-diving pelagic fishes [5, 87].

Habitat-driven vertical movement

Our results suggest that vertical movement patterns in *C*. maximus are closely linked to their environmental context. Habitat-driven movements were particularly evident during transitions between different water masses, aligning with previous evidence [27]. The most notable behavioural shift was observed in shark 1 during its seasonal migration across the Greenland-Scotland Ridge. This sill separates the warm and saline Modified North Atlantic Water in the southwest from colder and fresher Norwegian North Atlantic Water and the even colder Arctic Intermediate Water prevailing at depth in the Norwegian Basin [88, 89]. On the Atlantic side, shark 1 consistently exhibited strict nDVM and used deeper depths and wider depth ranges. Conversely, on the Norwegian side, it displayed greater variability in dive and depth-use patterns, often remaining at confined depths irrespective of the time of day and spending more time in the upper 50 m in both 2022 and 2023. Similarly, shark 2's vertical behaviour transitioned upon entering the seasonally stratified waters of the North Sea in late May, shifting from surface-oriented depth use to increased time spent below the thermocline, particularly at night.

From a biological perspective, topography, depth (or pressure), and light affect marine megafauna indirectly by structuring for example temperature and prey distributions [87]. Given the species' extensive thermal range and morphological adaptations to cold-water environments, temperature may be a subordinate factor affecting C. maximus' movement behaviour throughout large parts of the habitat occupied [75]. As a megaplanktivore reliant on short food chains, prey distribution emerges as one of the most important factors influencing the sharks' movement [13, 14, 16]. Similar to other ram filter-feeders such as Balaenid whales [90, 91], C. maximus has been shown to target high density patches of energetically rich zooplankton, such as Calanus spp., in small-scale fronts and to forage only in waters where prey availability exceeds a critical threshold [14, 19, 25, 92]. Consequently, much of the observed plasticity in C. maximus is likely driven by variations in the abundance, distribution, and vertical movements of planktonic prey across different habitats. While this study lacked complementary net sampling or acoustic zooplankton data for the space and time occupied by the sharks, in situ proxies derived from tagrecorded temperature and light level timeseries, such as isolumes, bioluminescence events, and the strength and depth of the thermocline, combined with existing literature, provide valuable biological context for the sharks' movements.

Prey tracking in shelf habitats

In shelf and shelf-edge habitat, we found high plasticity in vertical movements consistent with the high variability in bathymetric and hydrographic conditions and light regimes affecting prey assemblages. Depth use appeared constrained and shaped by topography, particularly in the Norwegian and Barents Sea, where sharks tracked depth contours, likely reflecting bottom topography, as described for C. maximus in other regions [27]. In shelf regions, diel vertical migrators, in addition to light-driven structuring [93], are vertically restricted by topography. This so-called topographical blockage results in concentrated prey layers near the seafloor [94, 95], which are likely lucrative strata for the sharks to exploit as suggested by the close alignment between utilized depths and LL30 as well as the high number of associated bioluminescence events.

Similar to dynamic shelf areas around Cape Cod [96], no significant DVM patterns were observed in the Norwegian, Barents or North Seas. This contrasts with findings from the north European shelf (UK and Ireland) and the Bay of Fundy (Canada), were significant nDVM and rDVM have been reported [25, 26]. The absence of significant DVM in this study suggests that sharks were not following synchronized vertical prey movements, possibly disrupted by dynamic hydrographic conditions and the temporary absence of a diel light regime. The bimodal depth use, i.e. on the Norwegian Shelf, could indicate prey switching between surface-associated aggregations of Calanus spp. and vertically compressed mesopelagic prey layers, irrespective of the time of day. Additionally, we attribute the limited the detection of significant DVM behaviour to the restrictive DVM criterion used. Unlike common approaches for aggregated data which compare the mean depth at night and day (e.g., [97, 98]), the continuous wavelet analysis identifies intervals with significant 24-h periodicity, testing DVM sensu stricto [99]. For instance, shark 2 showed tendencies for nDVM during F2 and rDVM during F4, but these patterns lacked consistency to qualify as significant diel periods in the wavelet analysis.

Sharks frequently performed surface-oriented, U- and V-shaped dives both in frontally mixed and seasonally stratified waters of the Norwegian Shelf and North Sea. Prolonged bottom times are a common strategy for maximizing the exploitation of prey layers aggregated at a particular depth [72, 100, 101]. In the North Sea, for example, consistent night-time use of the mixed layer depth corresponded to the reported position of a deep chlorophyll maximum developing in summer, likely attracting zooplankton prey as suggested by associated bioluminescence detections [102–104].

In environments where prey is sparse and unpredictable, or where the water column is stratified and vertical diffusivity of olfactory clues is low, short V-shaped dives present a search strategy to probe numerous isolated water layers for prey [20, 67, 105]. This was exemplified by shark 2 in the stratified North Sea during daylight hours, where vertical dispersion may present a predator-evasion strategy for copepods in these shallow, sunlit waters [25, 106]. Interestingly, during polar night in the Barents Sea, when vertical structuring by temperature, primary productivity, and light was absent, no clear biological rhythms or dominant dive patterns were observed.

A detailed discussion of the vertical movement patterns of both sharks in relation to prey dynamics across the three occupied shelf habitats is available in the Supplement.

Prey tracking in oceanic habitats

In oceanic waters, greater light penetration and weaker light gradients compared to shelf habitats result in deeper, vertically more diffuse layers of zooplankton and small fish in the mesopelagic [43, 46, 47]. The shark's consistent use of mesopelagic depths and strict nDVM behaviour match previous observations in offshore habitats (e.g., [23, 25, 27, 50, 100]), suggesting continued tracking of vertically migrating prey. Homogenous water temperatures of approximately 9 °C at these depths appear not to constrain the shark, allowing for continuous exploitation of these layers. Similar behaviour has been observed in other mesopelagic predators, such as swordfish *Xiphias gladius* (e.g., [107]) and *M. pelagios* [86].

Daytime depths of 600-900 m and night-time depths of 200-500 m are slightly below acoustically detected primary deep scattering layers (DSL) near the Azores [108] but match seasonal DSL ranges in the Canary Basin and Bay of Biscay, extending to the lower mesopelagic [109– 111]. They may also indicate foraging on a secondary, deeper DSL, as proposed for NWA waters [50]. However, reliance on low-frequency ship-borne acoustics [112, 113], which are better suited for detecting mesopelagic fish and larger micronekton than mesoplankton, likely the primary prey of C. maximus [92], remains a challenge. Frequent tag-based bioluminescence detections during both day and night indicate the presence of bioluminescent biomass at the shark's depth. These observations further suggest diel migratory behaviour among putative prey and a vertically expansive prey field spanning several hundred metres.

In this oceanic habitat, shark 1 spent only 10.4% of its time in the upper 100 m, primarily during 1–2 h surfacing events around dusk. Similar behaviour has been observed in *C. maximus* in the Clyde Sea and whale sharks *Rhinco-don typus* at Ningaloo Reef, and is possibly linked to the synchronized ascents of vertically migrating prey into surface layers [25, 107, 114]. Following these surfacing events, descents to night-time depths may be explained by the phenomenon of 'midnight sinking', where certain mesoplankton assemblages, after ascending to surface layers around dusk, descend to deeper waters around midnight as a predator-evasion strategy [115].

During nDVM, shark 1 exhibited faster ascents (~0.32 m s⁻¹) compared to descents (~0.17 m s⁻¹), contrasting with the faster descents observed in both sharks in nonoceanic habitats. Its ascent velocities were around 4.5 times faster than those reported for global DSL layers (0.07 m s⁻¹) [116], suggesting the shark was not directly tracking prey layers on the ascent but instead optimizing time at specific depths through rapid vertical movement. Similar patterns observed in shark 2 during F2 indicate that this could be a characteristic feature of *C. maximus* nDVM behaviour. Yet, further data are needed to confirm these dynamics across individuals.

Conclusions

Obtaining high-resolution PSAT data from two female basking sharks *Cetorhinus maximus* tagged north of the Arctic Circle, this study provides unprecedented insights into annual movement patterns at the species' northernmost range. The two sharks exhibited contrasting migration strategies reflective of the behavioural plasticity of the species across a wide environmental envelope.

During the year-long deployment, shark 1 was observed diving into waters below 2 °C for up to 100 consecutive minutes in the Norwegian Basin, while shark 2 spent extended periods in the Barents Sea during the polar night, including 2 weeks in waters below 5 °C. This study expands the known thermal range of *C. maximus* to - 0.6-29.9 °C, one of the widest ranges reported for sharks, further suggesting that thermal constraints are a secondary driver of *C. maximus* movement across much of its horizontal and vertical range.

Rather than physical habitat structure itself, we propose environmentally modulated prey availability and distribution as a primary driver of the species' movement patterns. Vertical movement varied notably across habitats but seemed consistent within them, leading to three Page 16 of 20

conclusions: (1) across habitats, thermoclines and isolumes affect the sharks' depth use by vertically structuring mesopelagic prey; (2) in oceanic waters at lower latitude, sharks track prey at mesopelagic depths, exhibiting strict nDVM under a diel light regime; while (3) in shelf habitats, depth use is more variable and bathymetrically constrained. Foraging on surface-associated copepods and vertical compressed prey layers likely drives the sharks' bimodal depth use, which under a constant light regime and hydrographically dynamic conditions may not follow consistent diurnal rhythms.

The high behavioural plasticity observed in just two individuals across habitats suggests *C. maximus* to be well-adapted to dynamic ocean conditions. Yet, expanding long-term tracking efforts at high-latitudes will be crucial to gain a comprehensive understanding of *C. maximus* movement dynamics and its ability to respond to accelerating Atlantification and climate-driven shifts, both at present and in the future.

Abbreviations

DCM	Deep chlorophyll maximum
DSL	Deep scattering layer
DVM	Diel vertical migration
nDVM	Normal diel vertical migration
rDVM	Reverse diel vertical migration
ELG	Exponential leap-forward gradient
F1-F4	Focal periods 1-4 defined in this study
LL30	Tag-based light level value 30
LT	Total length
NEA	Northeast Atlantic
NWA	Northwest Atlantic
PSATs	Pop-up archival tags
SST	Sea surface temperature
UD	Utilization distribution
Supplementary Information	

The online version contains supplementary material available at https://doi. org/10.1186/s40317-025-00407-3.

Supplementary Material 1.

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Author contributions

CAK, DWS, CJ, and NQ conceived the research. OB, KF, and CAK performed fieldwork and collected the data. CAK analysed, visualized, and validated the data. MCA geolocated the tracks and applied the bioluminescence filter to the light data. IDC and TC applied the ELG algorithm to parameterize thermal stratification. CJ and NQ supervised. CJ acquired funding and coordinated

the associated project. CAK prepared the manuscript with contributions from DWS. All authors contributed to subsequent drafts.

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Availability of data and materials

The datasets used for the study are available from Claudia Junge on reasonable request.

Declarations

Ethics approval and consent to participate

Tagging procedures and complementary mucus sampling were approved by the Norwegian Food Safety Authority (FOTS ID 29672).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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