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First insights into the vertical habitat use of young porbeagles in the north-western Atlantic with implications for bycatch reduction strategies

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ABSTRACT

Context. For threatened marine species, data on their vertical habitat use patterns can reveal risk of interactions with fishing gear and can inform bycatch avoidance strategies. Such data are lacking for young porbeagles (*Lamna nasus*), which are captured as bycatch in north-western Atlantic fisheries. **Aims.** We aimed to examine temporal patterns in diving and characterise vertical habitat use of young porbeagles during summer and autumn. **Methods.** We used data from short-term (28-day), high-resolution (5-min interval) pop-off satellite tags attached to 14 young (young-of-the-year and 1-year-old) porbeagles to model depth use. **Key results.** Occupied depths ranged from the sea surface to 679 m, with ambient water temperatures of −0.2 to 26°C. Diel period and season were factors related to depth use. **Conclusions.** Sharks exhibited a diel activity pattern characterised by more extensive use of the water column during the day while remaining primarily at the surface at night. Depth use differed between seasons, with summer characterised by greater affinity for surface waters (0–10 m) compared to autumn. **Implications.** Young porbeagles are at risk of interaction with active fisheries on the continental shelf, but interactions may be reduced by setting gear deeper at night or during summer.

Keywords: bycatch mitigation, diel migration, elasmobranch, fisheries, *Lamna nasus*, satellite tagging, shark conservation, wavelet analysis.

Introduction

Knowledge of movement patterns and habitat use is imperative to understanding species ecology and contributes to effective fisheries management for overexploited marine species (Heard *et al.* 2017; Hays *et al.* 2019; Andrzejaczek *et al.* 2022*a*). For example, information on vertical habitat use may be useful for understanding the risk of capture in fisheries and mitigating capture risk by adjusting the depths of fishing gear during temporal periods of high potential overlap (Cortés *et al.* 2010; Musyl *et al.* 2011*a*; Andrzejaczek *et al.* 2019; Bowlby *et al.* 2020*a*). Data on vertical movements have historically been difficult to obtain for highly mobile sharks that occupy wide geographic and vertical (depth) ranges (Carlisle *et al.* 2015; Queiroz *et al.* 2016, 2019). Fortunately, the advancement of satellite tagging technologies has revolutionised our abilities to monitor fine- and large-scale movements, behaviour, environmental preferences and habitat use of sharks (Hammerschlag *et al.* 2011; Renshaw *et al.* 2023). Studies using satellite telemetry have found the dynamics of shark movements and behaviour to be highly variable depending on a multitude of factors, including (but not limited to) time of day (Comfort and Weng 2015; Tyminski *et al.* 2015; Coffey *et al.* 2017; Andrzejaczek *et al.* 2022*a*), season (Shepard *et al.* 2006; Hoffmayer *et al.* 2021; Skomal *et al.* 2021), age or size (Afonso and Hazin 2015; Thorburn *et al.* 2019; Ajemian *et al.* 2020; Kock *et al.* 2022), sex (Campana *et al.* 2010; Stehfest *et al.* 2014), region (Santos *et al.* 2021; Bowlby *et al.* 2022) and changes to oceanic conditions (Vedor *et al.* 2021*a*; Hammerschlag *et al.* 2022). Research that considers multiple spatial and temporal scales, as well as different patterns by life stage, is most likely to appropriately describe the complex spatiotemporal dynamics of shark habitat use.

Despite technological advancements, the majority of studies to date have focused on adult or subadult life stages. Data on movement patterns for young individuals, especially young-of-the-year (YOY) sharks, are limited or absent for most highly migratory or pelagic species (Carlisle *et al.* 2015; Curtis *et al.* 2018; Nosal *et al.* 2019; Shaw *et al.* 2021). However, young individuals are generally the most vulnerable life stage to both natural (Smith *et al.* 1998) and fishing-induced mortality (Coelho *et al.* 2012; Bowlby *et al.* 2021). Moreover, there is often a strong relationship between YOY survival and population persistence for sharks (Kinney and Simpfendorfer 2009; Carlisle *et al.* 2015). These facts demonstrate the importance of understanding movement patterns and habitat use for early life history stages to help inform conservation and management decisions for highly mobile shark species (Carlisle *et al.* 2015). In particular, identifying critical habitats (i.e. pupping grounds, nursery grounds) that facilitate future recruitment of individuals into a stock has become a mandated priority for fisheries management (National Oceanic and Atmospheric Administration 1996; National Marine Fisheries Service 1999; Driggers *et al.* 2008; Kinney and Simpfendorfer 2009) and can be used as a basis for establishing spatial protection strategies for overexploited species (Heupel and Simpfendorfer 2005; Kinney and Simpfendorfer 2009).

The porbeagle (*Lamna nasus*) is a large, highly mobile and endothermic shark species that inhabits cold-temperate waters of the Atlantic, South Pacific and southern Indian Oceans (Francis *et al.* 2008). Similar to most large sharks, the porbeagle has conservative life history traits (i.e. slow growth, low reproductive output) that make this species particularly susceptible to overexploitation (Jensen *et al.* 2002; Natanson *et al.* 2002, 2019). The porbeagle was historically a commercially targeted species and has also been captured as bycatch throughout much of its range (Francis *et al.* 2008), which led to declines in multiple populations (Campana *et al.* 2002; Rigby *et al.* 2019). For example, following the introduction of a targeted pelagic longline fishery in the early 1960s (Aesen 1963), the north-western Atlantic population of porbeagles declined by an estimated 75–80%, and the population reached its lowest abundance in 2001 (Campana *et al.* 2013). The population was designated as endangered in Canada (Committee on the Status of Endangered Wildlife in Canada 2004) and retention of live porbeagles has been prohibited since 2014 (Campana *et al.* 2015). Additionally, petitions have been filed twice for the species to be protected under the United States (US) Endangered Species Act, although listing was ultimately deemed unwarranted given the stable or increasing stock numbers and the implementation of fisheries management strategies (catch limits, minimum size limits) designed to reduce fishing mortality (Curtis *et al.* 2016). Nevertheless, population recovery may take 100 years (National Oceanic and Atmospheric Administration 2022) and the porbeagle is still subject to capture as bycatch in pelagic longline, rod-and-reel, trawl and gillnet fisheries throughout the north-western Atlantic (Hurley 1998; Campana *et al.* 2015; Curtis *et al.* 2016; Haugen 2020; National Oceanic and Atmospheric Administration 2022). Although survival is reported to be high in rod-and-reel fisheries (Anderson *et al.* 2021), it is relatively low in pelagic longline fisheries (Campana *et al.* 2016), and an estimated 35.6% of captured porbeagles were discarded dead in the US otter trawl fishery in 2020 (National Oceanic and Atmospheric Administration 2022). In addition, although survival is unknown for gillnet fisheries, it is likely low due to suffocation in the net (Bendall *et al.* 2012; Cortés *et al.* 2020; National Oceanic and Atmospheric Administration 2022; B. Anderson and J. Sulikowski, unpubl. data).

None of the studies on the movement patterns and habitat use of porbeagles in the north-western Atlantic (i.e. Campana and Joyce 2004; Campana *et al.* 2010; Kohler and Turner 2019; Wang *et al.* 2020; Skomal *et al.* 2021) included tagging of YOY (<107-cm fork length, FL; Natanson *et al.* 2002) and 1-year-old juveniles (107–119 cm FL; Natanson *et al.* 2002). Only one study to date has focused its efforts on understanding the movement patterns of juvenile porbeagles in the north-western Atlantic (Skomal *et al.* 2021), yet tagged individuals ranged in size from 128 to 154 cm FL and were estimated to be 2–6 years old (Natanson *et al.* 2002). These older juveniles displayed wide-ranging horizontal and vertical movements that were seasonally dependent. Similar to mature females tagged by Campana *et al.* (2010), larger juvenile porbeagles migrated into more southern waters off of the continental shelf during late autumn, returning to shallower continental shelf waters in spring (Skomal *et al.* 2021). In the summer and early autumn, these larger juveniles primarily occupied water depths <200 m and spent the majority of their time in the top 25 m of the water column. When occupying deeper offshore habitat in late autumn and winter, these larger juvenile porbeagles displayed one of two diving behaviours, either predominantly remaining in colder epipelagic waters (0–200 m; termed 'non-divers') north of the Gulf Stream or making frequent deep dives and remaining in the mesopelagic zone (200–1000 m; termed 'divers') when occupying warmer waters within or south of the Gulf Stream (Skomal *et al.* 2021). Given the vulnerability of YOY and 1-year-old juveniles to fishing mortality (Cortés and Semba 2020; Cortés *et al.* 2020) and the potential for ontogenetic changes in movement patterns as individuals age (Afonso and Hazin 2015; Thorburn *et al.* 2019; Ajemian *et al.* 2020; Kock *et al.* 2022), research on early life stages remains a key knowledge gap for this species. Dive information would need to be at higher resolution than 6–12 h intervals (per Skomal *et al.* 2021) to identify diel patterns and seasonal changes in individual behaviour (e.g. Wang *et al.* 2020).

Pop-off satellite archival tags (PSATs) developed for studies on post-release mortality offer high-resolution data over shorter time scales, as compared to those typically employed for habitat use studies that are designed to monitor longer time periods, usually at the expense of resolution

(Musyl *et al.* 2011*b*). Accordingly, we analysed data from short-term (28-day), high-resolution (5-min interval) PSATs deployed on young (YOY and 1-year-old) porbeagles in the north-western Atlantic to assess fine-scale vertical movement patterns and to identify potential temporal trends (i.e. hourly, daily, seasonal scales) in their depth distribution.

Methods

Capture and tagging techniques

Young-of-the-year and 1-year-old porbeagles were opportunistically caught between August 2016 and October 2019 in the north-western Atlantic Ocean using rod-and-reel, research pelagic longline gear, or in the swordfish *Xiphias gladius* pelagic longline fishery as detailed in Bowlby *et al.* (2020*b*) and Anderson *et al.* (2021). All sharks were captured during the summer or autumn. Captured sharks were either left in the water or brought onboard the fishing vessel; length or estimated over the body FL (cm) and geographic location were recorded. The age of each shark was determined from a length-at-age relationship for this population (Natanson *et al.* 2002): individuals with FL <107 cm were considered YOY and individuals 107–119 cm FL were considered 1-year-old. Sex was recorded for the majority (13 of 14) of individuals. However, sex was unknown for one YOY shark that was captured in the swordfish pelagic longline fishery and tagged in the water with a pole. Prior to release, the hook was removed or the line was cut close to the hook for all animals brought onboard.

Sharks were equipped with a PSATLIFE manufactured by Lotek Wireless, Inc. Prior to release, tag attachment was done using a stainless-steel dart anchor (see https://hallprint.com/fish-tag-products/tag/Shark+Tags) inserted into the dorsal musculature, engaging the pterygiophores. The PSATs collected pressure (i.e. depth, hereafter referred to as 'depth') and ambient water temperature at 10-s intervals for the pre-programed 28-day deployment period, after which the tag is designed to release from the animal, float to the sea surface and transmit archived data. Owing to battery life and satellite throughput limitations, the full time series at 10-s intervals is not transmitted by the tags. Instead, a subset of the recorded time series, in 5-min rather than 10-s intervals, is sent to the satellites. All tags also had some further reduction of time-series resolution, where transmitted data were not at 5-min intervals for the entire time series, likely due to battery reduction over time or limited satellite coverage during the transmission period. Additionally, PSATs were programmed to release or transmit data prematurely if depth remained constant (±5 m) for 3 days, indicating a mortality or a shed tag floating at the surface or washed ashore. One tag (Shark 2) was recovered after pop-off and the full time-series dataset at 10-s resolution was available to download.

All protocols were approved by University of New England's Institutional Animal Care and Use Committee (protocol number 051518-001).

Data analyses

Minimum horizontal displacement of each porbeagle was calculated from the recorded tagging location and the first satellite-transmitted location after the tag pop-off (Fig. 1) and was plotted using the *R* package *ggmap* (ver. 4.0.0, see https://cran.r-project.org/package=ggmap; Kahle and Wickham 2013). Prior research has demonstrated that porbeagles can exhibit post-release recovery behaviour characterised by extended surface swimming following capture and handling (Hoolihan *et al.* 2011; Anderson *et al.* 2021; Bowlby *et al.* 2021). Any such post-release recovery behaviour was removed prior to analyses to eliminate potential biases on our understanding of natural diving behaviours. Recovery periods were identified using a breakpoint analysis of dive variance (Anderson *et al.* 2021; Bowlby *et al.* 2021). Any depth values <0 (i.e. above the sea surface, which can occur due to the error margin of depth readings) were converted to zero.

For each shark, dominant temporal periodicities of vertical movements (i.e. patterns of diving and ascending over a common temporal interval) were investigated using continuous wavelet analysis with a Morlet wavelet transform for the time series of swimming depths. This analysis has been previously used to examine temporal patterns in diving for elasmobranchs when high-resolution data were available (Thorburn *et al.* 2019; Burke *et al.* 2020). The continuous wavelet analysis decomposes a time series into time-frequency space to identify dominant temporal frequencies of cyclical functions, or the amount of time between successive peaks in a wave cycle (Cazelles *et al.* 2008). In this case, the wavelet analysis identifies time periods with organisation in diving behaviour such as repeated movement to similar depths, and the temporal trends in this behaviour, such as diel vertical migration occurring over a 24-h period (Thorburn *et al.* 2019; Burke *et al.* 2020). A benefit of the continuous wavelet analysis compared to traditional methods of addressing cyclical patterns in a time-series (e.g. fast Fourier transform) is that it does not assume stationarity of the periodicities (Cazelles *et al.* 2008). As such, the continuous wavelet analysis can detect variations in the dominant dive cycle periodicities across the time series (Cazelles *et al.* 2008), or intra-individual variability in the temporal patterns of diving behaviour. Moreover, another benefit of the continuous wavelet analysis is that it can be used to evaluate a customisable range of temporal periodicities, on the order of minutes to days depending on the length of the time-series intervals and the objectives (Rösch and Schmidbauer 2018).

The continuous wavelet analysis was completed using the *R* package *WaveletComp* (ver. 1.1, A. Rösch and H. Schmidbauer, see https://CRAN.R-project.org/package=WaveletComp). Based on the temporal resolution of our data, periodicities

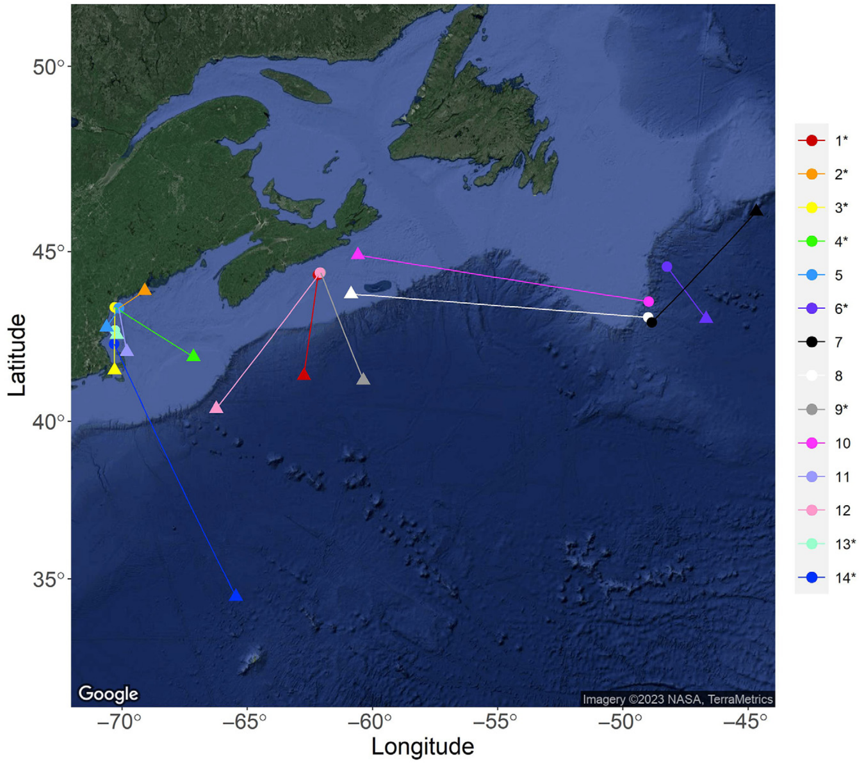

Fig. 1. Map of the study site with deployment location (circle) and the location of the first satellite transmission after pop-off (triangle) for pop-off satellite archival tags (PSATs) affixed to young-of-the-year (YOY) and 1-year-old porbeagles in the north-western Atlantic. Asterisks (*) indicate that the tag popped prematurely and the first satellite-transmitted location occurred 1–3 days after initial tag shedding.

of interest and related previous work (Thorburn *et al.* 2019; Burke *et al.* 2020) parameters were set as follows: a loess span of 0, a sampling resolution of 0.5 h, a frequency resolution of 1/250, a lower period for the wavelet function of 1 h, an upper period for the wavelet function of 128 h, and the number of simulations of 100 (details in Rösch and Schmidbauer 2018). The continuous wavelet analysis returns a plot of the wavelet power spectrum, which identifies dominant dive periodicities (h; *y*-axis) over the duration of the tag deployment (*x*-axis). The wavelet power level (colour) in the fitted plot reflects the strength of the cyclical pattern detected.

To overcome discontinuities in the datasets associated with PSAT transmission and to standardise temporal resolution, each time series was binned into 30-min windows to calculate a mean depth prior to wavelet analyses. Missing values were interpolated from the nearest average depth values in the binned time series. Interpolated values represented a range of 0.3–42.9% (median = 10.5%) of the data. A period of 30 min represented the optimal tradeoff to reduce discontinuities in the dataset while maintaining high-resolution information on dive periodicity for use in the wavelet analysis (Thorburn *et al.* 2019). We evaluated sensitivity to the binning interval using data from the recovered tag (Shark 2). The wavelet power spectrum for the satellite-transmitted time series (5-min interval) was compared to the high-resolution downloaded time series (10-s interval) for Shark 2, where both were binned into 30-min windows. Of values from the satellite-transmitted series, 42.6% needed to be interpolated prior to this comparison. Additionally, we analysed and plotted the wavelet coherence of the downloaded and transmitted time series, where both were binned into 30-min windows. The wavelet coherence provides a measure of correlation in oscillatory behaviour between two time series, in this case identifying how similar the transmitted time-series wavelet analysis is to the downloaded time-series wavelet analysis.

Although the continuous wavelet analysis identifies high-resolution temporal patterns of cyclical diving throughout each individual track, it does not provide information on environmental covariates with depth. As such, linear mixed models (LMMs) with Gamma distributions and log link functions were used to investigate the influence of diel period (day *v.* night) and season (summer *v.* autumn) and their interaction on the depth distribution of YOY and 1-year-old porbeagles. The response variable was either the average depth (an indicator of overall depth preference) or the standard deviation (s.d.) of depth (an indicator of vertical activity levels), where the raw depth data were used for calculating averages and standard deviations over each diel period (i.e. 2 averages and s.d.s of depth per day per shark). Additionally, the corAR1 function was used to account for temporal autocorrelation. Categorical predictors were diel periods (day and night) and season (summer and autumn). The *R* package *suncalc* (ver. 0.5.1, B. Thieurmel and A. Elmarhraoui, see https://cran.r-project.org/package=suncalc) was used to determine the times of sunrise and sunset at the tagging and pop-off locations for each shark and subsequently categorise PSAT data into diel periods. Diel periods were categorised based on the time of sunrise and sunset at the tagging location for the first half of the deployment and the pop-off location for the second half of the deployment. The summer and autumn seasons were differentiated based on the equinoxes of the tagging year (2016 and 2017: summer, 20 June–21 September; autumn, 22 September–20 Decemeber; 2018: summer, 21 June–21 September; autumn, 22 September–20 December; 2019: summer, 21 June–22 September; autumn, 23 September–20 December) to align with Skomal *et al.* (2021) and allow the most appropriate comparison with this study. Models were fitted using the *R* package *glmmTMB* (ver. 1.1.9, M. Brooks *et al.*, see https://cran.r-project.org/package=glmmTMB; Brooks *et al.* 2017). Akaike information criterion (AIC) and backward selection were used to determine the most parsimonious model (Akaike 1973).

Results

Data from a total of eleven YOY porbeagles measuring (mean ± s.d.) 93.9 ± 6.7 cm FL and three 1-year-old porbeagles measuring 111.3 ± 2.3 cm FL tagged in the north-western Atlantic were used for our analyses (Table 1). The sex ratio was female-biased with 11 females, 2 males and 1 individual of unknown sex tagged. Six of the PSATs transmitted after completing the entire programmed deployment period (28 days), whereas eight others transmitted early with deployments ranging from 8 to 27 days in duration. Premature tag transmissions were due to tag shedding rather than mortality, as the time series of depth and temperature data indicated all sharks were alive immediately prior to tag pop-off (Anderson *et al.* 2021). Regarding seasons, four tag deployments occurred exclusively in the summer, five exclusively in the autumn and five spanned portions of both seasons; overall, ~40% of depth and temperature data were from summer and ~60% were from autumn. For sharks whose PSAT transmitted after completing the entire programmed deployment period, the minimum horizontal displacement ranged from 75 to 962 km (mean ± s.d. = 527 ± 377 km) (Fig. 1, Table 1). For sharks whose PSAT popped early, estimated minimum horizontal displacement ranged from 15 to 975 km (Fig. 1, Table 1). However, it is important to note that for these tags that detached prematurely, the first satellite transmission occurred 1–3 days after initial shedding from the shark. Sharks tagged in this study moved in multiple directions from the tagging to pop-off location and one individual (Shark 14), a 114-cm 1-year-old male, appeared to move as far south as 35°N. All other porbeagles appeared to remain north of 40°N based on tagging and tag pop-off locations, although locations used by sharks between tagging and tag pop-off were unknown.

Vertical and thermal habitat use

Following the removal of behavioural recovery periods, which ranged in length from 0 to 282 h (median = 30 h), depth and ambient water temperature data were available for time periods ranging from 8 to 28 days. Collectively, young porbeagles occupied a wide range of depths (Fig. 2 and

Table 1. Summary of results from pop-off satellite archival tags (PSATs) deployed on young-of-the-year (YOY) and 1-year-old porbeagles in the north-western Atlantic.

Shark number	Sex	FL (cm)	Tag date	DAL	Maximum depth (m)	Minimum temperature (°C)	Maximum temperature (°C)	Temperature range	Distance travelled (km)
1	F	80	8 October 2018	8	283	9.0	20.1	11.2	332[A]
2	F	88	9 July 2018	27	117	5.9	21.2	15.3	100[A]
3	F	90	30 August 2018	10	72	9.0	20.6	11.7	207[A]
4	F	90	23 September 2018	24	145	7.2	17.6	10.4	304[A]
5	F	94	10 September 2016	28	104	4.9	18.4	13.5	74
6	F	95	5 September 2016	22	389	3.1	20.4	17.3	209[A]
7	M	95	19 September 2016	28	236	−0.2	16.1	16.3	482
8	F	96	19 September 2016	28	238	1.8	20.6	18.8	962
9	F	100	9 October 2018	23	542	6.2	21.4	15.2	379[A]
10	F	102	13 September 2016	28	218	1.3	17.9	16.5	938
11	F	103	13 July 2019	28	141	5.7	22.7	17.0	145
12	U	110	9 October 2018	28	565	5.7	26.0	20.3	562
13	F	110	27 June 2019	27	121	5.2	21.7	16.5	15[A]
14	M	114	1 October 2019	27	679	5.7	25.7	20.0	975[A]

F, female; M, male; U, unknown; DAL, days at liberty.

[A] Tag popped prematurely and the first satellite transmitted location occurred 1–3 days after initial tag pop-off.

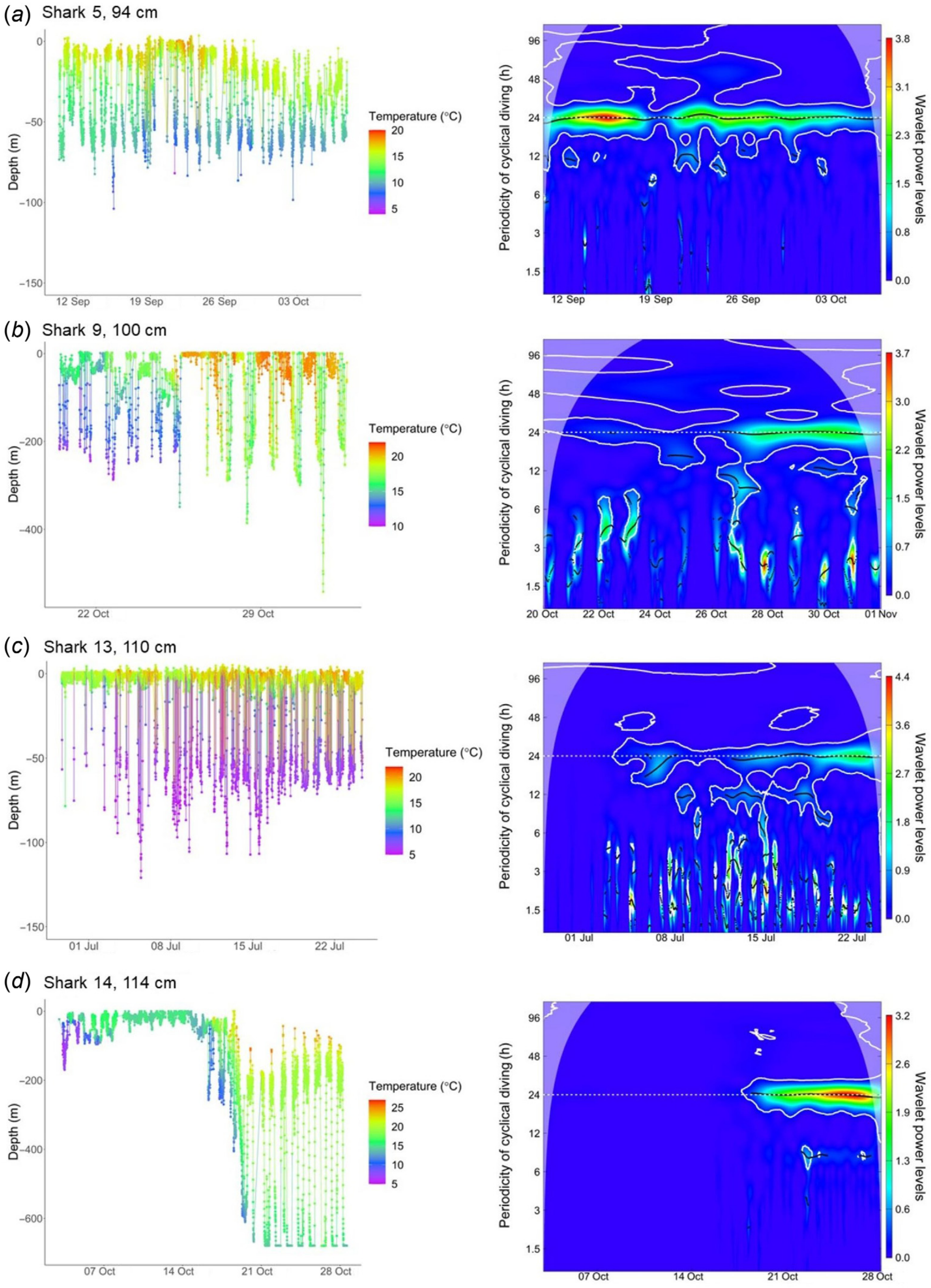

Fig. 2. Representative time series of temperature-integrated dive profiles (left) and corresponding continuous wavelet power spectra (right) for four young-of-the-year (YOY; $n = 2$; *a*, *b*) and 1-year-old ($n = 2$; *c*, *d*) porbeagles over the duration of the tag deployment. For the wavelet power spectra, areas encircled in white represent time periods with significant cyclical patterns ($P < 0.05$). Within the white encircled areas, the wavelet power level (colour) reflects the strength of the cyclical pattern detected, with red representing the strongest cyclical pattern. The black lines represent wavelet power ridges, or the local maxima of wavelet power. The periodicity (*y*-axis) reflects the time interval over which a cyclical diving pattern is detected. The white dashed reference line identifies the periodicity of 24 h. Shaded areas outside of the cone of influence should not be interpreted. Note the differences in scales of axes and legends among individual plots. Temperature-integrated dive profiles and continuous wavelet power spectra for all 14 individuals can be found in Fig. S1 of the Supplementary material.

Supplementary Fig. S1) from the sea surface to a maximum of 679 m by a 114-cm 1-year-old male (Shark 14). Associated water temperatures ranged from –0.2 to 26°C (Fig. 2, S1). Porbeagles reached an average maximum depth of 275 ± 194 m (range = 72–679 m) during the tag deployments (Table 1). Collectively, tagged sharks spent ~95% of time in the epipelagic zone (0–200 m) and 5% in the mesopelagic zone (200–1000 m).

Young porbeagles displayed rapid oscillatory dives, repetitively descending and ascending through the water column, for the majority of the tag deployments (Fig. 2, S1). However, there appeared to be underlying diel and seasonal patterns in the relative depths of these oscillations and in overall vertical habitat use. Deep oscillatory dives occurred most frequently during the day (Fig. 3); average depth was deeper and s.d. of depth was greater during the day than night (Fig. 4). On average, ~15% of the day was spent at depths >100 m, whereas ~5% of the night was spent at depths >100 m (Fig. 5). In comparison, oscillatory diving in surface waters was more common during the nighttime (Fig. 3); on average, ~39% of nighttime was spent at depths of 0–10 m and ~28% of daytime was spent at depths of 0–10 m (Fig. 5). Accordingly, the diel time at temperature profile showed that young porbeagles also spent more time at warmer ambient water temperatures during the night than during the day (Fig. 6). On average, ~69% of the night was spent in ambient water temperatures of 15–21°C, whereas ~47% of the day was spent in ambient water temperatures of 15–21°C (Fig. 6). In regard to season, young porbeagles exhibited a more restricted depth distribution in the summer (Fig. 4, 7). They displayed a clear affinity for surface waters during the summer, with over 50% of their time spent at 0–10 m (Fig. 7). In comparison, young porbeagles spent less than 20% of their time at 0–10 m and spent more time at deeper depths during the autumn (Fig. 7). For example, dives into the mesopelagic

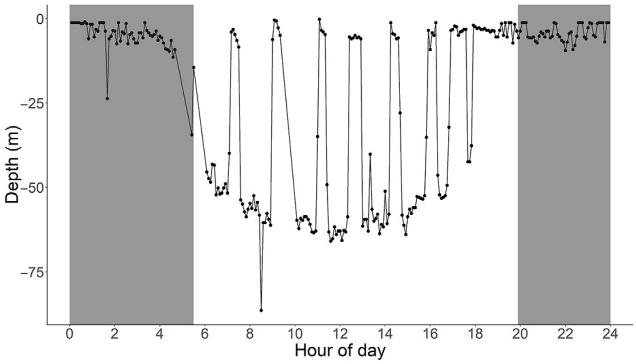

Fig. 3. Example of a diving profile over a 24-h period (5 August 2019) for Shark 11, a 103-cm young-of-the-year (YOY) female, showing a representative diel activity pattern of surface-oriented oscillatory diving during the night (shaded region) and deeper oscillatory diving during the day (unshaded region).

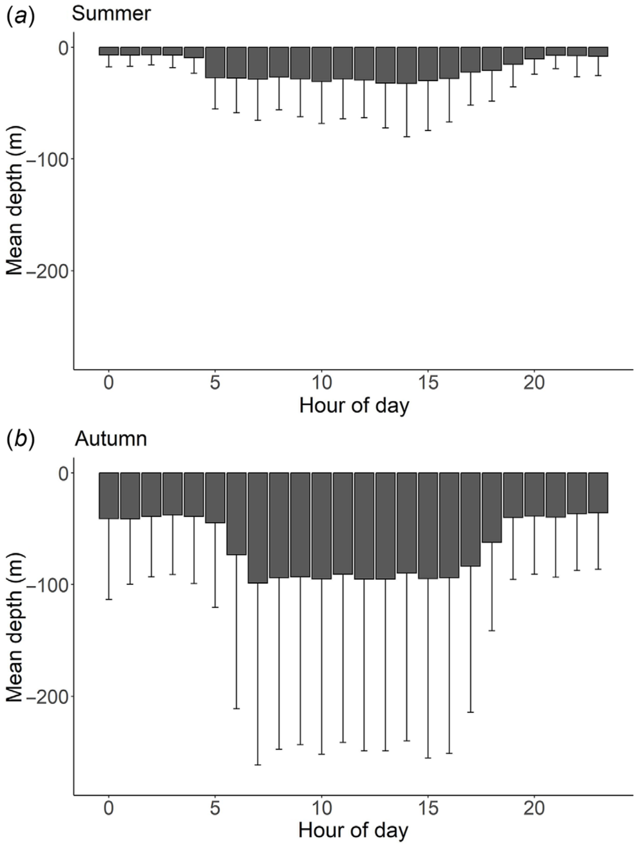

Fig. 4. Average depth (m) (+standard deviation) at each hour of day for all young-of-the-year (YOY) and 1-year-old porbeagles combined during the summer (*a*) and autumn (*b*).

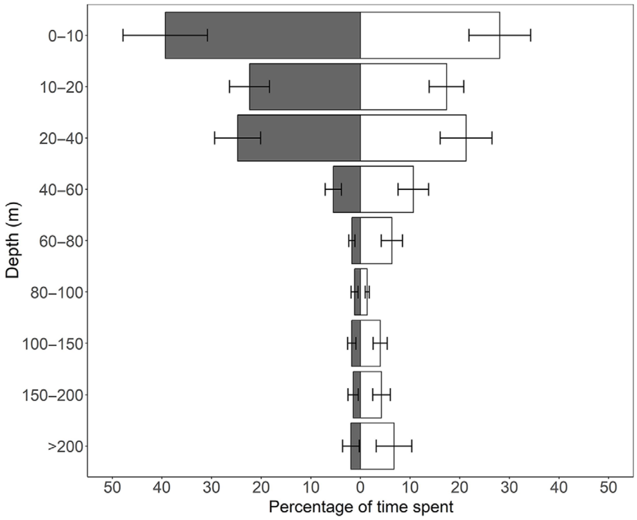

Fig. 5. The average percentage of time spent at depth (m) during the day (white bars) and night (grey bars) for young-of-the-year (YOY) and 1-year-old porbeagles. The error bars represent standard deviations.

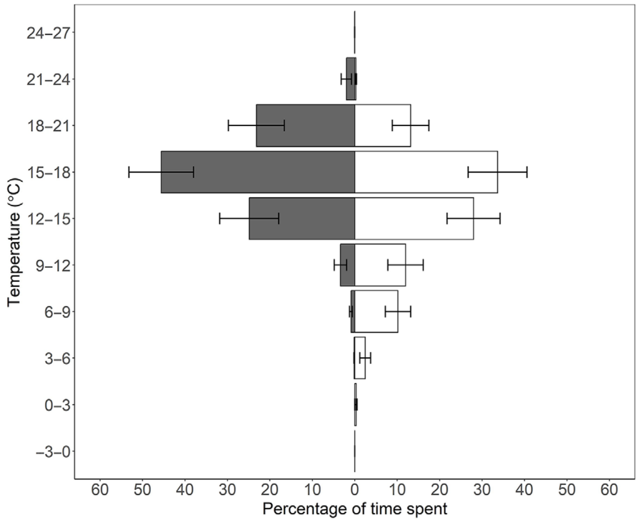

Fig. 6. The average percentage of time spent in ambient water temperatures (°C) during the day (white bars) and night (grey bars) for young-of-the-year (YOY) and 1-year-old porbeagles. The error bars represent standard deviations.

zone (200–1000 m) occurred almost exclusively in the autumn; only one individual, a 95-cm-YOY female (Shark 6) that was tagged offshore of the Grand Banks, made mesopelagic dives during the summer (Fig. S1F).

Continuous wavelet analysis

The sensitivity analysis for Shark 2 revealed that patterns in the diving time series (Fig. S2) as well as trends in diving periodicities determined by the wavelet power spectra were well preserved in both the satellite-transmitted time series (5-min intervals) binned and interpolated into 30-min windows and the downloaded time series (10-s intervals) binned into 30-min windows, with the downloaded data having slightly higher wavelet power (stronger cyclical pattern detected; Fig. 8). The use of satellite-transmitted time-series data for continuous wavelet analysis was further supported by the relatively high (>0.8) level of wavelet coherence between the satellite-transmitted and downloaded data throughout most of the time series (Fig. 8*c*). When considering all tagged sharks, there was substantial intra- and inter-individual variability in the periodicities of cyclical diving patterns throughout the tracks (i.e. how often individual sharks dove and ascended; Fig. 2, S1). However, the most prevalent periodicity in diving detected by continuous wavelet analysis was ~24 h (i.e. diel pattern; Fig. 2, S1). Shorter periodicities in cyclical diving (~1.5–8 h; i.e. 'yo-yo' diving) were also commonly observed in many tagged porbeagles (i.e. Fig. 2, S1). Taken together, the two dominant periodicities suggest diel activity patterns consisting of reasonably rapid cyclical diving occurring throughout both diel periods, but at differing depth distributions (i.e. deeper oscillations during the day, shallow oscillations during the night; Fig. 3).

Linear mixed models

The most parsimonious model of average swimming depth for young porbeagles included the fixed effects of both diel period and season, as well as their interaction (Table 2). Average depth was overall significantly deeper during the day compared to night for young porbeagles (Fig. 9). When considering their interaction, nighttime average depths were significantly deeper during the autumn compared to summer (Fig. 9). For the model

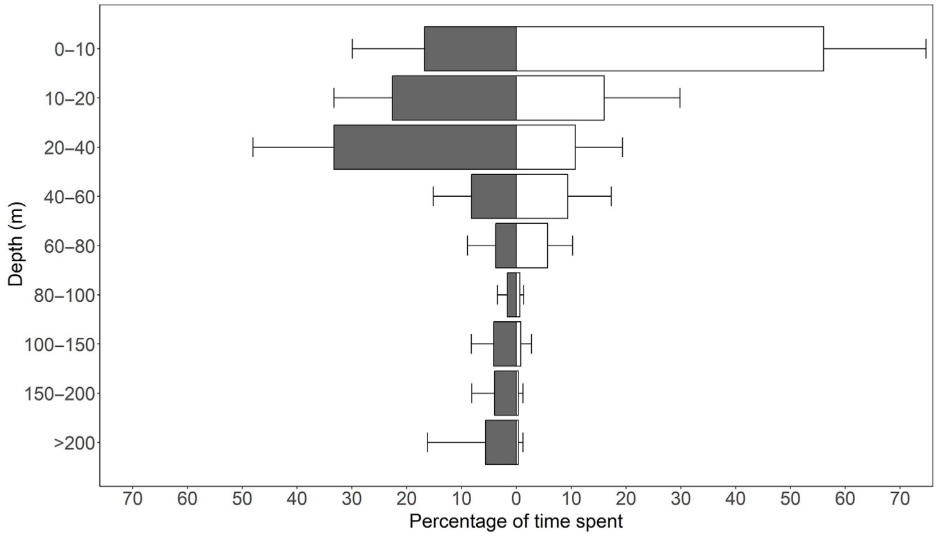

Fig. 7. The average percentage of time spent at depth (m) during the summer (white bars) and autumn (grey bars) for young-of-the-year (YOY) and 1-year-old porbeagles. The error bars represent standard deviations.

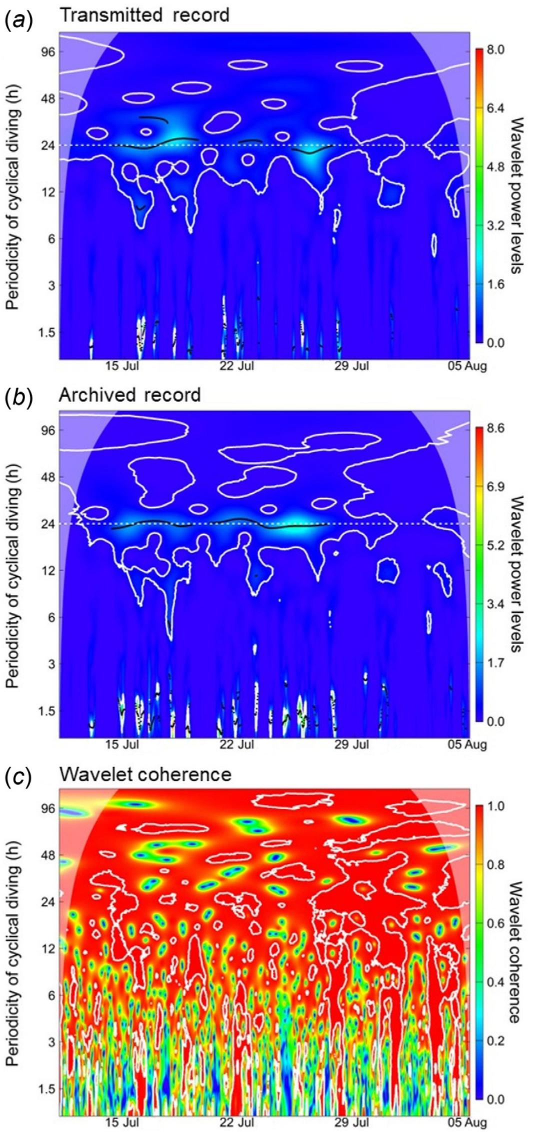

Fig. 8. Comparison of the wavelet power spectra for the satellite-transmitted data binned and interpolated into 30-min intervals (*a*) and the recovered, full archived data binned into 30-min intervals (*b*), and a plot of the wavelet coherence between both time series (*c*) for Shark 2. For the wavelet power spectra (*a*, *b*), areas encircled in white represent time periods with significant cyclical patterns ($P < 0.05$). Within the white encircled areas, the wavelet power level (colour) reflects the strength of the cyclical pattern detected, with red representing the strongest cyclical pattern. The black lines represent wavelet power ridges, or the local maxima of wavelet power. The periodicity (*y*-axis) reflects the time interval over which a cyclical diving pattern is detected. Shaded areas outside of the cone of influence should not be interpreted. Note the difference in scales of the wavelet power level legends between plots *a* and *b*. For the plot of wavelet coherence (*c*), areas encircled in white represent time periods with significant wavelet coherence ($P < 0.05$). The wavelet coherence (colour) reflects the level of similarity in the oscillatory patterns between the two time-series, with red representing the strongest similarity.

Table 2. Model comparison using Akaike's information criterion (AIC).

Model	DF	AIC	ΔAIC
1. Mean depth ~ diel period × season	575	4722.7	
Mean depth ~ diel period + season	576	4770.2	47.5
Mean depth ~ diel period	577	4773.3	50.6
Mean depth ~ 1	578	5741.7	1019
2. s.d. of depth ~ diel period × season	577	4343.5	
s.d. of depth ~ diel period + season	576	4360.2	16.7
s.d. of depth ~ diel period	575	4357.1	13.6
s.d. of depth ~ 1	578	4783.9	440.4

ΔAIC indicates difference between AIC scores and the top-ranked model. All models are linear mixed models with shark identity as a random variable and temporal autocorrelation.

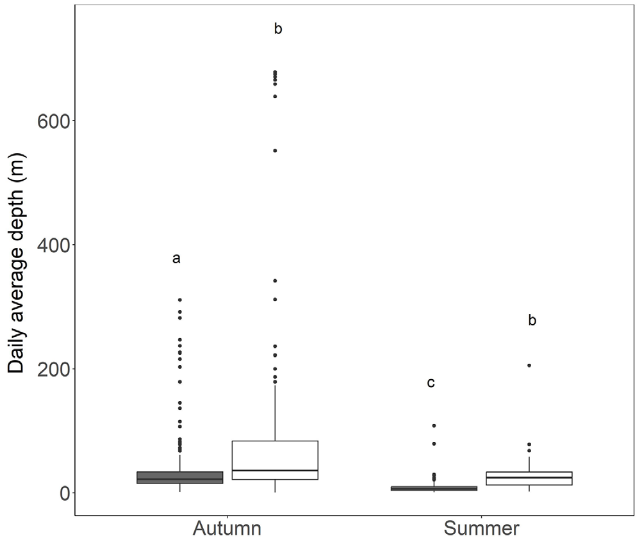

Fig. 9. Boxplots of daily average depth (m) by diel period and season for all young-of-the-year (YOY) and 1-year-old porbeagles. The circles represent outliers. Linear mixed models indicate overall daily average depth was deeper during the day (white boxplots) compared to night (grey boxplots). Additionally, nighttime average depth was deeper during the autumn compared to the summer. Different letters above the boxplots represent significant differences between groups ($P < 0.05$).

of s.d. of depth, the most parsimonious model included the fixed effects of both diel period and season, as well as their interaction (Table 2). s.d. of depth was overall significantly greater during the day compared to night (Fig. 10).

Discussion

Our analyses of short-term, high-resolution PSATs deployed on YOY and 1-year-old porbeagles provided the first insights into vertical habitat use of the youngest life stages

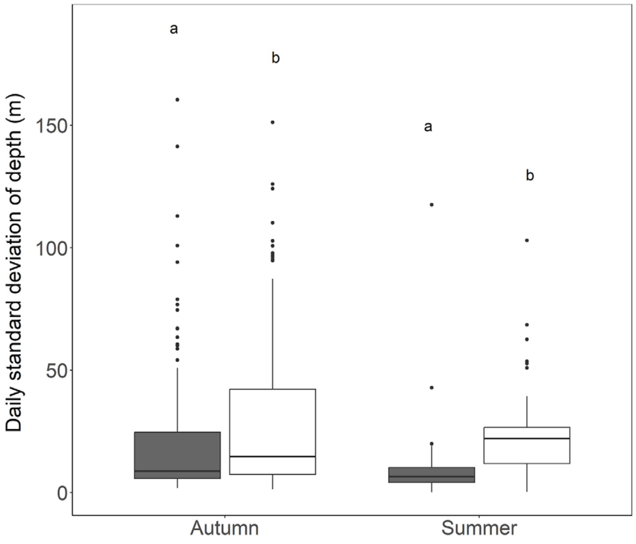

Fig. 10. Boxplots of daily standard deviation (s.d.) of depth (m) by diel period and season for all young-of-the-year (YOY) and 1-year-old porbeagles. The circles represent outliers. Linear mixed models indicate overall daily s.d. of depth was greater during the day (white boxplots) compared to the night (grey boxplots). Different letters above the boxplots represent significant differences between groups ($P < 0.05$).

of this species during summer and early autumn in the north-western Atlantic Ocean. Our data revealed common temporal patterns in vertical habitat use for these young porbeagles, ranging from rapid oscillatory (or 'yo-yo') diving to seasonal differences in water column usage. Although more detailed examination of dive shapes and individual dive durations was not the focus of this work, this represents another potential avenue for future research with these fine-scale data. Nevertheless, the results of this study underscore the benefits of using high-resolution PSATs to examine variability in swimming depths at a fine temporal scale. For example, these young porbeagles not only dove significantly deeper during the day compared to the night, but also had greater dive variability. None of the shorter periodicities in dive behaviour (1.5–8 h) would have been evident from data binned at 6- or 12-h intervals, neither would the behavioural tendency to exhibit greater dive variability during the day as compared to night. Such behavioural flexibility forms an important component to our understanding of vertical habitat use, and indicates these young sharks were not only shifting their average swimming depths from nighttime to daytime, but also their vertical activity levels (the amplitude or frequency of oscillatory movement). In most cases, young porbeagles tagged in this study maintained a degree of affinity for surface waters or near surface waters during both diel periods. However, they made repeated oscillatory dive excursions between surface (or near surface) waters and deeper depths during the day, whereas the amplitude of oscillatory diving was restricted to surface (or near surface) waters during the night. Collectively, these findings suggest young porbeagles were not often following the traditional definition of diel vertical migration, in which animals remain at deep depths during the day and shallow depths during the night (Francis *et al.* 2015; Andrzejaczek *et al.* 2019). Instead, young porbeagles were most commonly exhibiting a 'diel activity pattern' in which dive distributions had different variance during the day and the night, yet overlapped in depth (Arostegui *et al.* 2017). Although this diel activity pattern of shifting the depths and amplitudes of oscillatory dives is quite common in pelagic predators (e.g. Goodyear *et al.* 2008; Andrzejaczek *et al.* 2019, 2023; Nasby-Lucas *et al.* 2019; Vedor *et al.* 2021*b*), most other work characterising diving behaviour of porbeagles suggested the traditional diel vertical migration pattern was most common for larger life stages of the species (Campana *et al.* 2010; Francis *et al.* 2015). Only one previous study that had obtained high-resolution data from a recovered PSAT also found similar evidence of a diel activity pattern (greater average depth and dive variability during the day than night) during the summer for a mature female porbeagle tagged in the north-western Atlantic (Wang *et al.* 2020). Although it is possible that data resolution in previous studies (i.e. Pade *et al.* 2009; Campana *et al.* 2010; Francis *et al.* 2015; Skomal *et al.* 2021) restricted the calculation of dive variability over shorter time scales for larger porbeagles, we cannot rule out that this diel activity pattern is more characteristic of the earliest life stages.

Although tag deployments were short, sample size was low, and geolocation tracks could not be constructed, there appeared to be differences in habitat use and depth distributions of these young porbeagles between summer and autumn. Several young porbeagles in this study appeared to move into deeper waters off the continental shelf during autumn (based on dive depths >200 m and locations of tag pop-off), a migration that occurred earlier in our study compared to previously documented seasonal movements for larger porbeagles tagged in the north-western Atlantic (Campana *et al.* 2010; Skomal *et al.* 2021). The young porbeagles tagged in our study moved into deeper waters by late October, whereas mature females moved offshore in December to March (Campana *et al.* 2010) and larger juveniles in late November to December (Skomal *et al.* 2021). Young porbeagles in our study also exhibited greater use of surface waters in the summer and greater use of deeper depths in the autumn. For example, the most frequent depths used by young porbeagles was 0–10 m (~56% of time) during summer and 20–40 m (~33% of time) during the autumn. Moreover, some young porbeagles (i.e. Sharks 12 and 14) that moved into deeper waters off the continental shelf in the autumn completely avoided surface waters, remaining below 50–150 m and reaching maximum daytime depths of over 500 m. Similar transitions to deeper depths when occupying offshore habitat were also observed in larger porbeagles (Campana *et al.* 2010; Skomal *et al.* 2021), yet the maximum depth observed for young porbeagles tagged in this study (679 m) was much shallower than the maximum depth reported for larger conspecifics (~1300 m) (Campana *et al.* 2010; Skomal *et al.* 2021). Although this difference in maximum depth between studies could be due to the shorter tag deployments in our study, it is possible that the youngest life stages of porbeagles do not dive as deep as older life stages (Campana *et al.* 2010; Skomal *et al.* 2021), likely due to a reduced thermal inertia compared to larger conspecifics (i.e. Carlisle *et al.* 2015). Moreover, although the seasonal patterns observed in this study are fairly consistent with previous work on larger life stages (Campana *et al.* 2010; Skomal *et al.* 2021), it is important to consider that differences in habitat and depth use between seasons for young porbeagles in this study could at least partially be affected by the short deployment durations and tagging location. For example, most individuals with summer deployments were tagged in coastal waters where maximum dive depths may be constrained by bathymetry. We cannot discount the possibility that diving patterns or depth distributions may have differed if these individuals were tagged in deeper habitats; for example, Shark 6 was tagged offshore of the Grand Banks and did make mesopelagic dives during late summer. More regionally widespread tagging efforts and longer tag deployments would be needed to fully disentangle seasonal depth use patterns for the youngest life stage.

Shark diving behaviours are thought to be primarily related to prey distribution and availability within different habitats (Nakamura *et al.* 2011; Francis *et al.* 2015; Heard *et al.* 2017; Andrzejaczek *et al.* 2019). Thus, the diel vertical activity pattern and seasonal differences in depth distribution of young porbeagles in this study suggests a need for different prey search tactics (Pade *et al.* 2009) in different habitats as their distribution changes seasonally. Stomach sampling suggests that juvenile porbeagles <150 cm consume mainly groundfish, cephalopods and pelagic fishes during summer and autumn (Joyce *et al.* 2002). Given the opportunistic diet of young porbeagles during the summer and autumn, and varying distribution of these prey within the water column, we hypothesise that the diel activity pattern exhibited by young porbeagles likely functions as a foraging tactic that maximises the amount of prey that can be encountered (Sepulveda *et al.* 2004; Pade *et al.* 2009; Madigan *et al.* 2021; Santos *et al.* 2021). For example, the observed diel activity pattern (remaining in surface waters at night and yo-yo diving between the surface and deeper waters during the day) has also been documented in other pelagic species including Atlantic blue marlin (*Makaira nigricans*) (Goodyear *et al.* 2008), juvenile shortfin makos (*Isurus oxyrinchus*) (Sepulveda *et al.* 2004) and white sharks (*Carcharodon carcharias*) (i.e. Weng *et al.* 2007*a*, 2007*b*; Andrzejaczek *et al.* 2022*b*). These diel activity patterns were suggested to be related to daytime visual feeding in shortfin makos (Sepulveda *et al.* 2004), white sharks (Andrzejaczek *et al.* 2022*b*) and blue marlin (*Makaira nigricans*) (Goodyear *et al.* 2008). It is possible that searching an extensive portion of the water column for prey may be more advantageous during the day when light levels are highest (Sepulveda *et al.* 2004; Goodyear *et al.* 2008; Andrzejaczek *et al.* 2022*b*). At night, it may be more efficient to reduce the extent of the water column used while hunting under the cover of darkness (Andrzejaczek *et al.* 2022*b*), especially given many small pelagic species, including prey of porbeagles, migrate to shallow depths at night (Hays 2003; Francis *et al.* 2015; Andrzejaczek *et al.* 2019). The shift to deeper waters in the autumn by some individuals was also likely influenced by the seasonal shifts in prey distribution, as cephalopod and pelagic teleosts are known to migrate to or overwinter in offshore habitats in our study region (Hendrickson 2004; Van Beveren *et al.* 2023). Previous work suggested that the diet of juvenile porbeagles shifts to a higher proportion of cephalopods and pelagic teleosts during winter and spring (Joyce *et al.* 2002), and this diet shift likely coincides with the transition into deeper offshore habitat (Skomal *et al.* 2021). When the young porbeagles migrated offshore they may have begun to occupy deeper depths, at least in part, to follow the vertical movement patterns of their mesopelagic prey, as has been suggested for larger porbeagles occupying mesopelagic environments (Saunders *et al.* 2011; Francis *et al.* 2015; Skomal *et al.* 2021).

Another potential driver of the diel and seasonal vertical movement patterns is the need to remain within an optimal temperature range and ontogenetic differences in thermal tolerance. Like other lamnid sharks, porbeagles are regionally endothermic and thus can maintain warmer internal temperatures relative to ambient water (Carey *et al.* 1985). However, given smaller sharks have a higher surface area to volume ratio than larger conspecifics (Carlisle *et al.* 2015; Shaw *et al.* 2021), it is likely that YOY and 1-year-old porbeagles have a reduced endothermic capacity compared to older individuals and prefer warmer temperatures than larger individuals, as has been suggested for YOY salmon sharks (*Lamna ditropis*) (Carlisle *et al.* 2015) and YOY white sharks (Shaw *et al.* 2021). Given the diel activity pattern observed in this study appears to be more prevalent in young porbeagles, this behaviour may be reflecting their need to return to the surface more frequently and for more extended periods to maintain their internal temperature when in colder waters on the continental shelf. For example, although there was no apparent size-based difference in the amount of time spent at cold temperatures (<12°C) for sharks in this study, these YOY and 1-year-old porbeagles spent less time at temperatures <12°C than larger juveniles tagged by Skomal *et al.* (2021). In particular, larger juveniles were observed to spend ~40–50% of the time during the summer and 50–60% of the time during the autumn at temperatures <12°C (Skomal *et al.* 2021), whereas the young porbeagles tagged in this study spent on average only 20% of the time during the summer and 15% of the time during the autumn at temperatures <12°C. That said, it is also possible that the difference in time at temperature found between studies could be due to differences in deployment durations, as

Skomal *et al.* (2021) had year-round data whereas our data were limited to late June through early November.

Although the tracking period was reasonably short, the young porbeagles did not seem to make use of water temperatures in excess of 22–26°C; collectively, less than 1% of their time was spent in water temperatures within this range. Moreover, the switch to submergence behaviour in deep habitats during autumn coincided with when maximum ambient water temperatures recorded by the tags were within this range. Submergence behavioural responses to sub-optimal water temperatures has previously been documented in larger porbeagles (Campana *et al.* 2010; Skomal *et al.* 2021), salmon sharks (Coffey *et al.* 2017), shortfin makos (Loefer *et al.* 2005) and a YOY white shark (Shaw *et al.* 2021). During periods in which young porbeagles primarily used deeper depths, ambient water temperatures at the sharks' minimum swimming depths approached the upper end of the species' known thermal tolerance (Francis *et al.* 2008, 2015; Campana *et al.* 2010; Saunders *et al.* 2011; Skomal *et al.* 2021). As such, it is possible that submergence behaviour observed in a few of the young porbeagles tagged in this study was at least partially associated with the avoidance of excessively warm surface waters (Campana *et al.* 2010; Skomal *et al.* 2021).

Predation risk and inter- or intra-specific competition could also be affecting dive behaviour (Andrews *et al.* 2009; Queiroz *et al.* 2012). For example, predation risk is a widely documented factor influencing ontogenetic shifts in habitat use of sharks (Morrissey and Gruber 1993; Grubbs 2010; Speed *et al.* 2010; Queiroz *et al.* 2012; Vianna *et al.* 2013; Carlisle *et al.* 2015). Competition has also been suggested to be mitigated by spatial, temporal or dietary partitioning among life stages or species (Weideli *et al.* 2023). The vertical movement patterns observed in young porbeagles in our study may be related to predation risk or competition given the diel activity pattern appears to be more common in YOY and 1-year-old sharks (Campana *et al.* 2010; Skomal *et al.* 2021). Moreover, young porbeagles tagged in our study spent more time at shallow depths during the summer and autumn compared to larger conspecifics (Campana *et al.* 2010; Skomal *et al.* 2021). Species that have the potential to be predators or competitors of young porbeagles include larger conspecifics and other large coastal and oceanic shark species (i.e. white shark, Curtis *et al.* 2016; tiger shark, *Galeocerdo cuvier*, Hammerschlag *et al.* 2022), although predation of porbeagles is currently undocumented. During the summer and autumn when our study occurred, larger porbeagles (Campana *et al.* 2010; B. Anderson and J. Sulikowski, unpubl. data), white sharks (Franks *et al.* 2021; Bowlby *et al.* 2022) and (to a lesser extent) tiger sharks (Hammerschlag *et al.* 2022) are known to inhabit the north-western Atlantic continental shelf, thus overlapping with young porbeagle habitat. Given this horizontal overlap, it is possible that the diel vertical activity pattern we observed in young porbeagles is a mechanism to reduce interactions with potential predators or competitors (Andrews *et al.* 2009; Speed *et al.* 2010; Queiroz *et al.* 2012; Vianna *et al.* 2013; Bond *et al.* 2015). It is also possible that the greater preference for surface waters and the transition into off-shelf habitats occurring earlier in the year in some young porbeagles compared to larger conspecifics could be beneficial for reducing intra-specific competition. However, understanding the role of predation and competition in shaping spatiotemporal movement patterns is challenging and more information (i.e. more high-resolution dive data for mature porbeagles) is needed to discern the influence of these factors on ontogenetic habitat use of this species.

Conservation implications

The tracking period of this study coincides with the most active US commercial and recreational rod-and-reel fishing season (summer and autumn), primarily targeting bluefin tuna (National Oceanic and Atmospheric Administration 2022), and also overlaps with commercial trawl and gillnet fisheries targeting benthic species (National Oceanic and Atmospheric Administration 2022). Reported porbeagle catches in the US recreational rod-and-reel fishery include an estimated 4.9 tonnes (Mg) of landings and 68 individuals discarded (National Oceanic and Atmospheric Administration 2022). Although porbeagle catch data for US trawl and gillnet fisheries are limited to observed sets, this species is one of the most frequently bycaught highly migratory shark in these fisheries in the northeast region (National Oceanic and Atmospheric Administration 2022). In 2020, 118 porbeagles were caught in 115 observed otter trawl sets and ~77 individuals were caught in 177 observed gillnet sets (National Oceanic and Atmospheric Administration 2022). Reported Canadian catches include an estimated 4.2 Mg in trawl fisheries and 1.4 Mg in longline fisheries in 2020 (www.iccat.int). In general, however, catches are predicted to be substantially underreported for this species (International Commission for the Conservation of Atlantic Tunas 2020).

Given the predicted slow rate of recovery and continued incidental capture in multiple fisheries in the region, the north-western Atlantic porbeagle population would benefit from reduced fisheries interaction. The data observed in this study suggest young porbeagles are most active during the day, when presumably feeding throughout the water column, yet primarily remain within surface waters at night. Based on these preliminary data, young porbeagles appear to be most at risk to rod-and-reel gear deployed in surface waters on the continental shelf during the night and summer, providing a potential avenue for adjusting the timing and depth of fishing gear for reducing interactions. Based on this diel depth distribution, setting rod-and-reel gear deeper during the nighttime as well as limiting bottom-oriented gear (trawls, gillnets) to night sets while young porbeagles appear to have an affinity for surface waters may reduce risk of interactions with this life stage, especially during the summer. When young porbeagles move off the continental shelf into deeper waters in the autumn, they would be less at risk to shallow water fisheries (rod-and-reel, gillnet, trawl). The pelagic longline fishery is the main fishery occurring in deeper waters off of the continental shelf. Given fisheries data suggest captures of porbeagles by pelagic longline gear have been minimal (12-kg reported catch in the US pelagic longline fishery in 2020; www.iccat.int) in recent years (National Oceanic and Atmospheric Administration 2022; www.iccat.int), current pelagic longline fishing techniques appear to successfully limit interactions with porbeagles.

Supplementary material

Supplementary material is available online.

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