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Characterising the behaviour of bait-attracted blue sharks *Prionace glauca* using pelagic drift video

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ABSTRACT: Baited pelagic underwater videos are increasingly being used to assess ecological indices but they can also be effective in recording the behaviour of pelagic species attracted to the bait. In this study, the behaviour of 79 blue sharks *Prionace glauca* was recorded using drifting pelagic baited remote underwater video system (BRUVS) rigs, deployed outside the Professor Luiz Saldanha Marine Park, Portugal. Juveniles were more frequently sighted over epipelagic (depth between 60 and 200 m) and mesopelagic zones (200–1000 m), while adult sightings were more common further offshore, particularly over canyons (1200–2000 m). Importantly, juvenile sightings were more frequent in spring (breeding season), suggesting that the study area is likely an important nursery habitat. Blue sharks primarily exhibited inspection activities around the BRUVS. Generalised linear models indicated that visibility, distance to the shore, bathymetry and temperature influenced their behavioural patterns. Moreover, juveniles interacted with the BRUVS for a longer time (mean duration: 0.4 min) than adults (0.2 min). A preliminary analysis of blue sharks' reaction to boat presence suggests that boat noise decreased both the duration of interaction with the BRUVS and the range of observed behaviours. This study provides valuable insights into the behaviour of this species in its natural environment, which is relevant for management and conservation efforts.

KEY WORDS: Baited remote underwater video systems · BRUVS · Blue shark · Foraging behaviour · Noise pollution

1. INTRODUCTION

Underwater videos are a commonly used non-invasive and non-extractive tool for monitoring marine environments and species *in situ* (Mallet & Pelletier 2014, Vaudo et al. 2023). One such technique, the baited remote underwater video system (BRUVS), is widely used for underwater sampling of invertebrates (Jones et al. 2020) and fish assemblages (Cappo et al. 2007), including elasmobranchs (Osgood et al. 2019, Bruns & Henderson 2020). Globally, BRUVS are implemented for estimating biodiversity, abundance, species richness, community assemblages and their dynamics, individual identification and biomass (Wraith et al. 2013, Griffin et al. 2016, Letessier et al. 2022).

Pelagic BRUVS are commonly used worldwide to study top predator assemblages in offshore areas

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(Bouchet & Meeuwig 2015, Fukuba et al. 2015, Letessier et al. 2019, Cambra et al. 2021, Leonetti et al. 2024). More specifically, they have been used to study pelagic sharks in their natural environment, providing insights into their foraging behaviour (Lester et al. 2022), predator–prey interactions (Loiseau et al. 2016), social behaviour (Sabando et al. 2020) and responses to anthropogenic pressures (Roberts et al. 2016, Chapuis et al. 2019). Although the behaviour of species observed around BRUVS may not be entirely natural, as these are anthropogenic structures, BRUVS provide an effective tool to study animal behaviour in the natural marine environment.

Studying the distribution and behaviour of sharks is crucial, as many pelagic shark species play a vital role in the stability and functioning of marine ecosystems (Bornatowski et al. 2014, 2018). Commercial longline fisheries are depleting pelagic shark populations worldwide (Queiroz et al. 2019, Pacoureau et al. 2021), causing an imbalance in the ecological network that impacts both the environment and coastal livelihoods (Grubbs et al. 2016, Jaiteh et al. 2017, Shiffman et al. 2021).

The blue shark *Prionace glauca* is a pelagic carcharhinid distributed globally in temperate and tropical waters. In the North Atlantic Ocean, blue sharks exhibit highly migratory behaviour (Veríssimo et al. 2017, Coelho et al. 2018) and can be found in the water column from the surface to a depth of 1000 m (Lessa et al. 2003, Megalofonou et al. 2009, Weigmann 2016). This species is one of the most predominantly caught shark species worldwide (FAO 2023), and in 2019, it was classified as Near Threatened on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Rigby et al. 2019). Data from Portuguese landings also revealed that the blue shark is the most frequently caught species in pelagic longlines (Alves et al. 2020).

In addition to fisheries, other anthropogenic activities, such as noise pollution, may pose a threat to blue shark populations. Noise pollution has increased from coastal areas to the deep sea due to shipping, harbour development, fishing activities, marine traffic, wind farms and wave energy generation (Erbe et al. 2018, Duarte et al. 2021, Vieira et al. 2021). Underwater sound can lead to significant alterations in fish behaviour (Holles et al. 2013, Simpson et al. 2016), cause auditory masking and increase stress levels among other impacts (Erbe et al. 2019). Due to its deleterious effects, anthropogenic sound is included in the United Nations Convention on the Law of the Sea (United Nations 1994) and in European legislation such as the Marine Strategy Framework Directive 56/2008 CE (Tasker et al. 2010). Shark hearing relies on the detection of the particle-motion component of an acoustic field (Nedelec et al. 2016, Popper & Hawkins 2018). Their hearing range varies from 40 to 1500 Hz, which overlaps with low-frequency anthropogenic sounds like vessel sound (Myrberg 2001, Chapuis & Collin 2022, Nieder et al. 2023). Although elasmobranchs are one of the least studied groups of animals in terms of the effect of anthropogenic sound, there is evidence that noise pollution causes changes in their behaviour (Chapuis et al. 2019, de Vincenzi et al. 2021, Rider et al. 2021).

A previous study using pelagic drift BRUVS around the Professor Luiz Saldanha Marine Park (PLSMP), Portugal, showed that the blue shark was the most frequently observed megafauna species in the water column (Serrão et al. 2021), offering a unique opportunity to observe and investigate the foraging behaviour of this species in its natural habitat. This study thus aimed to (1) describe the behavioural patterns of blue sharks when attracted to bait; (2) evaluate whether differences in the occurrence and duration of behaviours are independent of temporal (spring, summer and autumn), spatial (bathymetric profile), biological (sex and life stage) and oceanographic factors (temperature, visibility, distance from shore and wind direction); and (3) provide a preliminary assessment of the effects of boat noise on this species' behavioural patterns.

2. MATERIALS AND METHODS

2.1. Study area

The study area is located on the west coast of Portugal, 10 nautical miles (nmi, ~18 km) outside the limits of PLSMP, a marine park that extends for approximately 38 km of the coastline (Fig. 1). It is also located near the fishing town of Sesimbra, whose fish market has one of the highest elasmobranch landings in the country, including the blue shark (Henriques et al. 2021).

One important characteristic of the study area is the topographic variability provided by the Lisboa-Setúbal submarine canyon. The canyon is divided into the Lisbon branch, west of the PLSMP, with the canyon head extending along a south–north axis, and the Setubal branch, south of the PLSMP, which extends from west to east (Fig. 1). In this area, bathymetry ranges between 60 and 2500 m (Lastras et al. 2009). The Sado estuary significantly impacts the area's physical and chemical conditions (Reid & Wood

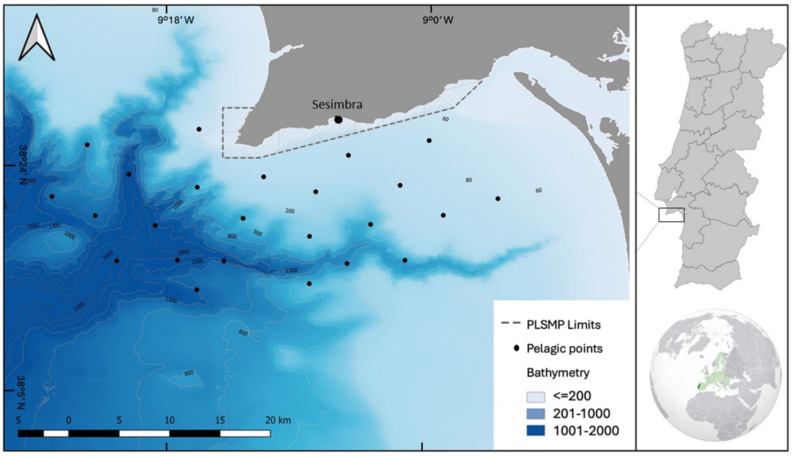

Fig. 1. Study area, showing the Lisboa-Setúbal submarine canyon system around Professor Luiz Saldanha Marine Park (PLSMP) in Portugal. Sampling points (black dots) and bathymetric levels (epipelagic: ⩽200 m; mesopelagic: 201–1000 m; bathypelagic: 1000–2600 m) are represented around the 10 nmi (~18 km) surrounding the park

1976), and the region is also affected by the coastal current, which moves southward due to prevailing northern winds that promote upwelling conditions during the spring and summer along the coast (Peliz et al. 2002). During autumn and early winter, the prevailing winds invert, affecting the coastal current and ceasing upwelling conditions (Ambar & Fiúza 1994).

2.2. Structure setup and experimental design of BRUVS

The BRUVS setup was composed of 3 individual stereo BRUVS rigs mounted in series, connected by a 250 m nylon floating string and deployed adapting the scheme of Bouchet & Meeuwig (2015). BRUVS were suspended with a large buoy at a depth of ~12 m, and one tracking buoy (WAMBLEE, W880 Longline HF Radio Buoy) was connected to each end of the setup to provide information about its location (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m753p137_supp/). This setup, adapted from Letessier et al. (2013), consisted of a stainless-steel frame with 2 GoPro HERO 5 Black cameras, set to 1080 p resolution, 60 fps (frames per second) and a medium FOV (field of view) for video recording. Concerning acoustic recordings, each GoPro is equipped with 3 internal microphones that can register sound with a sampling rate of 48 kHz. Following Chapuis et al. (2021), we disabled the automatic audio adjustments on the GoPro cameras and recorded raw audio files in WAV format using the protune settings instead of automatic gain and advanced audio coding. The acoustic characteristics of all cameras were tested with white noise and showed similar results (Fig. S2). The 2 GoPro cameras were mounted in stereo, approximately 80 cm apart, with an inward convergence angle of 4°, allowing for an optimal field of view up to 10 m. GoPro cameras were encased in SeaGIS waterproof housings (https://www.seagis.com.au/). A bait canister was placed 1.5 m at the cross-section in front of the cameras. We used 2–3 kg of chopped mackerel *Scomber* spp. as bait in every structure, according to standard BRUVS practices of 1 kg of bait per 60 min sampled (Harvey et al. 2013), for deployments between 160 and 180 min.

We used a stratified random sampling design based on the bathymetry sampling area, obtained from the European Marine Observation and Data Network portal (EMODnet Bathymetry Consortium 2018). Bathymetry was classified into 3 levels: epipelagic (60–200 m), mesopelagic (201–1000 m) and bathypelagic (1001–2600 m) (Fig. 1). At each bathymetric zone, 8 random points were generated, forming a total of 24 sample sites at a minimum distance of 5 km, using the Accuracy Assessment of Thematic Maps of QGIS software (QGIS Development Team 2020). The samples included 24 data points from 3 stereo BRUVS over 2 seasons in 2019 and 2020 (accounting for potential camera failures or material loss). The BRUVS sets were deployed during the day, at least 1 h after sunrise and recovered no later than 1 h before sunset to avoid fish crepuscular behaviour (Axenrot et al. 2004). The BRUVS deployment was oriented perpendicular to the surface current direction and drifted freely with local currents. The research boat maintained a safe distance of 150–250 m from the BRUVS setup in accordance with guidelines for observing marine fauna in the wild (Lewis & Walker 2018). For safety reasons, we chose not to turn the engines on and off multiple times a day while drifting 10 nmi (~18 km) offshore.

2.3. Video analyses

Videos with the presence of blue sharks were analysed to identify individuals and behaviour patterns and to estimate distribution. Pictures suitable for photo identification (photo ID) were extracted from the video footage for each individual during every BRUVS deployment. Identification was based on sex (female, male or not defined), size and body marks. Animals were sexed by verifying the presence or absence of claspers (present only in males).

The size of the animals was calculated with Event Measure software using the stereo-camera recordings (SeaGIS; https://www.seagis.com.au/event.html). The age of each individual was estimated based on total length (TL; length of a fish as measured from the tip of the snout to the tip of the tail), following the length–age data of Skomal & Natanson (2003) for the North Atlantic region considering adult animals older than 3 yr (>140 cm). The accuracy of length measurements was verified using the data set from Skomal & Natanson (2003), which is the largest database in the North Atlantic region, accounting for regional variations. A length growth model was developed to assess the animals' life stage. Age classes were classified as: 0+ yr (size: 50–96 cm), 1+ yr (97–125 cm), 2+ yr (126–142 cm), 3+ yr (143–170 cm), 4+ yr (171–200 cm), 5+ yr (201–225 cm) and 6+ yr (up to 240 cm).

Body marks were also used for photo ID. Scar markings (wounds, nicks, scratches and other marks) can change over time in elasmobranchs, but it typically takes around 6 mo for them to recover from injuries (Marshall & Bennett 2010, Anderson et al. 2011, Marshall & Pierce 2012). Therefore, body marks were used for individual identification within a single season. The maximum number of distinct individuals photo-identified in a single video or season (MaxID) was used during the analysis of social interactions (see Section 2.5).

2.4. Observation of behavioural patterns

To establish behavioural categories for analysis, 10% (2.8 h) of video footage was observed ad libitum, using the behavioural categories defined in other shark studies (Sperone et al. 2010). The videos were analysed and annotated using BORIS software (Friard & Gamba 2016) to estimate the number of occurrences and duration of behavioural patterns. In total, 9 behaviours within 4 broader categories were described (Table 1). The categories considered were swimming, BRUVS interaction, social behaviour and feeding; we also considered out of frame (when animals are out of view) (see Video S1 at www.int-res.com/articles/suppl/m753p137_supp/)

Videos were analysed using focal analysis with instantaneous sampling (annotating observed behaviours from each individual at a regular interval) (Martin & Bateson 1993). The occurrence of each behaviour was scored at 10 s intervals since the time at first sighting. Inter-observer reliability (between 2 observers) was assessed by calculating the mean percentage of agreement, ensuring concordance above 90%.

2.5. Social interactions and effects of boat sound

2.5.1. Social interactions

To study intraspecific interactions during bait attraction, we analysed 8 videos, each with a group of 2 or more individuals (MaxID ⩾ 2) engaging in different interactions. Focal analysis with continuous

Table 1. Ethogram of blue shark *Prionace glauca* with 5 behavioural categories and 9 behaviours. Notice that the 'out of frame' category was included to account for the periods when the animal is not visible in the baited remote underwater video system (BRUVS); it encompasses 2 behaviours based on the duration of absence

Behavioural category	Behaviour	Description
Swimming	Approach	Shark swims slowly, approaching the BRUVS at a considerable distance (5–10 m from the BRUVS). The animal passes by without any interaction
BRUVS interaction	Structure inspection	Shark swims around the BRUVS, closely observing the structure, camera and/or bait. Usually with frequent eye movements
	Vertical swimming	Shark swims vertically to the BRUVS
	Physical contact	Shark makes physical contact with the BRUVS with different parts of the body (but principally the head). Usually accelerates after contact
Feeding	Biting	Shark bites the bait box or pole
Social interaction	Parallel swimming	Two sharks swim parallel in the same or opposite direction
	Following	One shark follows the other
	Chasing	One shark follows the other while accelerating aggressively
	Being chased	One shark is chased and swims away
Out of frame	No visual	Shark is not in frame but is assumed to be close by
	Time out	Shark is not in frame for a long period (more than 30 s)

sampling was used to observe and record these interactions (Martin & Bateson 1993).

2.5.2. Effect of boat sound on behaviour patterns

During field operations, the sound emanating from our boat was captured in the video footage from a significant number of samples that also showed the presence of blue sharks. This allowed for a preliminary analysis of the potential impact of boat sound on blue shark behaviour around BRUVS. Furthermore, we verified the proximity of other boats to the structure by annotating and calculating their positions. The distance from our boat to the structure was determined using data from the WAMBLEE W880 Longline HF Radio Buoy and the boat navigation system (http://www.wamblee.it/w880; Fig. S1). During video recordings containing sharks, no other boats were in the vicinity. Hence, the only source of boat sound was our research vessel, which was present during fieldwork to prevent interference between the BRUVS setup and fishermen's buoys or from boats crossing. Our boat was making either continuous sound, which occurred when we were moving steadily, or intermittent sound, which occurred when we were manoeuvring the boat. Sound spectrograms of continuous and intermittent boat sounds are shown in Fig. S3.

Soundtracks were extracted from the videos and inspected both aurally and visually (using spectrograms and oscillograms) for the presence of boat sound, using Raven Pro software (v.1.6) (Cornell Laboratory of Ornithology 2023). The boat sounds were characterised in the frequency and time domains to evaluate their duration and whether they were continuous or intermittent. The boat sound was typically between 500 and 1500 Hz (Table S1).

To assess the impact of boat sound on shark behaviour, 15 videos with the presence of sharks (23 individuals) and boat sound were inspected. The observation was divided into 3 periods: before noise (BN; the period before any boat sound was captured), during noise (DN; when boat sound was detected by the camera microphone) and after noise (AN; once boat sound was no longer detectable). Only video segments in which a shark was visible were considered. The available duration of each of the 3 periods varied greatly per video, with most videos not including all 3 periods (Table S2).

An analysis was performed to compare the number and average duration of behaviours between experimental (with boat sound, and only considering the DN period) and control animals (without boat sound). From the experimental group, we selected 12 videos with a minimum DN duration of 2 min (range: 0:02:02—0:17:25 min) for further analysis. We also considered another 12 videos for the control group (range: 0:04:04—0:31:30 min) from which we selected random clips of similar duration to the considered DN videos (Table S2). Each video segment featured only one visible shark, allowing us to study individual responses to boat sound. All individuals (12 experimental + 12 control) in the selected videos were thus different animals.

To further explore the reaction of sharks to boat sound, a within-individual comparison was conducted. As very few individuals were visible in all 3 periods (Table S2), only BN and DN were used to compare the number of behaviours between periods. From the individuals with BN and DN periods available for analysis, only 6 met the minimum time length criteria of 2 min in each of these 2 periods. A 2 min subsample from both the BN and DN periods was used to compare the behaviour within these individuals (selected individuals are shown in Table S2). When possible (i.e. when longer periods were available), a random 2 min subsample was chosen. In all videos, shark behaviour was measured by focal analysis with continuous sampling. For these analyses, only foraging behaviours were considered: approaching, structure inspection, vertical swimming, physical contact and biting.

2.6. Statistical analysis

To assess which variables (temporal, spatial, biological and oceanographic) influence the behaviour of blue sharks, the average of the total number of behaviours per minute was calculated for every individual. Generalised linear models (GLMs) (McCullagh & Nelder 1989) were used to investigate which parameters could explain the variability in the observed behaviour. For each response variable (behaviour), a set of categorical and continuous explanatory variables were used. The categorical explanatory variables were bathymetric zones (bathypelagic, mesopelagic and epipelagic), seasons (autumn, spring and summer), the sex of the individuals (male, female or not defined) and life stage (juvenile or adult). We also considered duration (the length of time when the animals were visible) as a continuous variable. Biogeochemical oceanographic attributes, such as sea surface temperature (SST), were obtained from the EU Copernicus Marine Service Information platform as NetCDF files (https://resources.marine.copernicus.eu/). Other considered variables were visibility measured with a Secchi disc (depth, m), distance to the shore (m) obtained from EMODnet (https://emodnet.ec.europa.eu/en) and wind intensity (knots) obtained from the Portuguese Institute for Sea and Atmosphere (IPMA) database (https://www.ipma.pt/en/oipma/quem/ipma/). The response variables were the selected behaviour patterns: structure inspection, physical contact, vertical swimming, approach and biting (Table 1). Social interactions such as parallel swimming, following, chasing and being chased were not considered in the analyses as the sample size was too low.

All response variables were analysed using a Poisson distribution (McCullagh & Nelder 1989). The Poisson density function is expressed in terms of a dispersion parameter $\varnothing = 1$ and a canonical link $\theta = \log(\mu_i)$; therefore, the Poisson variance $V(\mu_i) = \mu_i$, and a logarithmic-link function $\log(\mu_i)$ was used for these variables. Stepwise procedures were performed by backward elimination to provide a set of comparable models from the full ones. Akaike's information criterion was used to check which model best fit the data (Akaike 1973, Burnham et al. 2011). Normal probability plots of the residual components of the deviance versus quantiles as well as the null and residual deviances were also evaluated for the selected models. Analysis of deviance was performed to evaluate the significance of the variables and interactions for all selected models. Note that although each longline had 3 BRUVS, the same blue shark individual was never observed on more than one camera. As such, behavioural data obtained from videos of different BRUVS and used in statistical tests were considered independent, as they were collected from different individuals. Furthermore, Bouchet et al. (2018) indicated that data from pelagic BRUVS are independent when the devices are deployed 200–500 m apart.

We compared the total number of behaviours per minute and the average duration of all behaviours of each shark, for individuals exposed to boat sound (DN, n = 12) and control individuals (sharks from videos without boat sound; control, n = 12), using unpaired 2-sample Wilcoxon tests. Additionally, we compared the total number of behaviours per minute exhibited by each of 6 blue sharks between the BN and DN periods with a paired Student's *t*-test. Note that we did not consider the average duration of all behaviours observed per shark because the considered periods were only 2 min long, rendering duration less informative.

All statistics were carried out using R (v.4.2.2) (R Core Team 2022) with the packages 'devtools' (Wickham et al. 2022) and 'ggpubr' (Kassambara & Mundt 2020).

3. RESULTS

A total of 248 BRUVS deployments (24 sets of 3 BRUVS in 2 seasons) were conducted within the scope of the INFORBIOMARES project (108 BRUVS in 2019 and 140 BRUVS in 2020; https://www.lpn.pt/pt/conservacao-da-natureza/projetos-cofinanciados-pela-ue/inforbiomares), resulting in 374 h of video footage from 84 samples. From these, 45 videos (21 epipelagic, 16 mesopelagic and 8 bathypelagic) recorded the presence of blue sharks, resulting in 28 h of video analyses.

3.1. Sex–life-stage–age occurrence

In total, 79 blue sharks were identified in the 45 videos, varying from 1 to 4 MaxID per video. In terms of gender, nearly 48.1% were females, 29.11% were males and 22.78% were not defined. In terms of life stage, 81% (64 individuals) were classified as juveniles and 18.9% (15 individuals) as adults. A total of 40 juveniles were aged 0+ yr (50.6%), 21 were aged 1+ yr (26.6%) and 3 were aged 2+ yr (3.8%). Ten adults were aged 3+ yr (12.7%), 4 were aged 5+ yr (5.1%) and one was older than 6 yr (1.3%). Approximately 50.6% of the total individuals were juveniles and were observed during the spring in the epipelagic and mesopelagic zones (Fig. S4), whereas 10.2% of total individuals were adults and were more common in the autumn and in the offshore bathypelagic zone (near canyons) (Fig. 2). A total of 18 individuals could not be sexed either due to the low number of recorded frames, poor positioning relative to the cameras or their small size; 15 individuals were under 120 cm TL.

3.2. Observation of behavioural patterns

Of the 79 individuals observed, the average duration of individual presence in the videos was almost double for juveniles (0.38 ± [SE] 0.02 min throughout 25 h of footage) compared to adults (0.2 ± 0.04 min throughout 3 h 10 min of footage). The duration of the interaction ranged from a minimum of 10 s for both life stages to a maximum of 2 h 12 min for juveniles and 52 min for adults. The average of the total number of behaviours per life stage showed that juveniles interacted less (average [±SE] no. of behaviours min^{-1}: 1.84 ± 0.15) with the BRUVS rigs but they remained for longer periods around the structure than adults (average no. of behaviours min^{-1}: 2.87 ± 0.31). See Table S3 for the duration and number of behaviours per minute for all individuals.

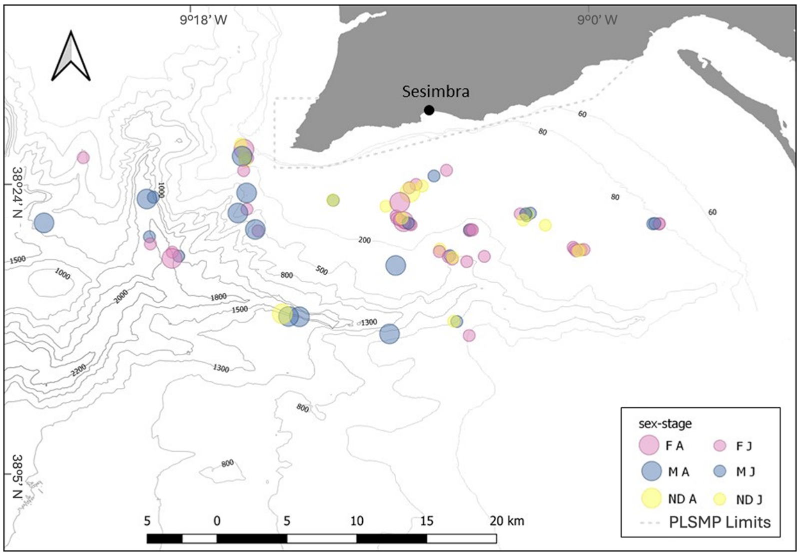

Fig. 2. Distribution of blue sharks in the study area in the surroundings of the Professor Luiz Saldanha Marine Park (PLSMP) determined by the coordinates of the radio buoy when sharks are detected. Dot size and colour indicate stage and sex: F: female; M: male; ND: not defined; A: adult; J: juvenile

Most of the observed behaviours were related to the BRUVS interaction category. Within this category, structure inspection (average no. of behaviours min^{-1}: 2.36 ± 0.44) was the most common behaviour, followed by physical contact (average no. of behaviours min^{-1}: 0.84 ± 0.03) and vertical swimming (average no. of behaviours min^{-1}: 0.066 ± 0.02) (Table 2, Fig. 3a–d). Sharks were more likely to interact with the BRUVS when in the epipelagic (depth: <200 m; distance to shore: 3113–13 464 m) and mesopelagic (depth: 201–1000 m; distance to shore: 6338–19 353 m) zones; note that BRUVS deployments were conducted at a depth of approximately 12 m over areas of these 3 ranges of bathymetry. A greater diversity of behaviours (average of the total number of behaviours per season) was observed during spring and summer, which corresponded with the seasons when animal occurrence was also higher (Fig. 4). In the epipelagic zone, BRUVS interaction was more frequent in spring for adults and in summer and early autumn for juveniles. However, in the mesopelagic zone, BRUVS interaction was more frequent for adults in autumn and for juveniles in the summer period. In the bathypelagic zone (depth: 1000–2000 m), adults exhibited a higher number of BRUVS interaction behaviours in autumn, whereas juveniles interacted more with the BRUVS in spring.

The GLMs (Fig. 5) showed that structure inspection was mostly influenced by north and south winds. Furthermore, structure inspection, physical contact and vertical swimming increased with visibility. In addition, physical contact and vertical swimming were influenced by season and sex. Physical contact and vertical swimming were more frequent during autumn and spring and less frequent during summer. Sex differences in behaviour were evident, with males exhibiting behaviours such as physical contact and vertical swimming more frequently than females. Nevertheless, vertical swimming was more frequent in juveniles than in adults. Biting was correlated with temperature; this behaviour was also more frequent in autumn and spring and more commonly observed in adult females. Table 3 shows the analysis of deviance for the GLMs.

3.3. Social interactions

From the 45 video recordings with shark presence, only 8 videos had a MaxID of more than one individual

Table 2. Average of total number of behaviours per minute, number of individuals presenting this behaviour and minimum and maximum occurrence of the behaviours observed over 28 h of video by instantaneous sampling (every 10 s scanning)

	Behaviour	Average ± SE	No. of individuals	Min.	Max.
BRUVS interaction	Structure inspection	2.366 ± 0.443	78	0	410
	Physical contact	0.084 ± 0.027	34	0	22
	Vertical swimming	0.066 ± 0.021	29	0	16
Feeding	Biting	0.012 ± 0.004	10	0	5
Social interaction	Being chased	0.002 ± 0.002	1	0	1
	Chasing	0.001 ± 0.001	1	0	1
	Parallel swimming	0.011 ± 0.006	7	0	2
Swimming	Approach	0.184 ± 0.077	48	0	12

Fig. 3. Examples of blue shark behaviours within the category of BRUVS interaction: (a) structure inspection, (b) vertical swimming, (c) physical contact, (d) biting and social interactions (e) parallel swimming and (f) following

(the number of individuals varied between 2 and 4). During the study, 19 individuals presented social interactions in 8 different interaction groups (Table S4). Of these individuals, only one was a female adult (life stage 3+ yr); the other 18 were juveniles (12 females, 6 males and 2 not defined). Furthermore, of the 18 juveniles, only one was 2+ yr, while the others were younger (0+ and 1+ yr). Some of the individuals in the group appeared at the same time but did not interact (Group 2; see Table S4). The highest proportion of social interaction (89%) was observed in spring due to the higher occurrence of sharks in this season, while a lower proportion (21%) was observed in autumn and summer.

Continuous sampling of these 19 individuals resulted in a total of 872 total behaviours, of which 149 were classified as social. The remaining behaviours included BRUVS interaction (structure inspection, vertical swimming and physical contact), swimming and biting (Fig. S5). Social interactions appeared only in the epipelagic and mesopelagic zones, which were areas with a higher number of shark observations. The average number of social interactions per minute in the 8 different interaction groups showed that parallel swimming and following were the most frequent social behaviours (Figs. 3e,f, & 6).

3.4. Noise-related behaviour

In this study, 23 sharks detected in 15 videos were exposed to boat engine sound. Of these, 7 individuals appeared only during boat sound exposure (i.e. DN) (ID1, ID10, ID11, ID12, ID27, ID 70 and ID2), while 8 individuals were present both before and after the boat sound (i.e. BN and AN) (ID20, UD21, ID26, ID39, ID56, ID74, ID58 and ID75) but not in the DN period (Fig. 7). Twelve individuals had a minimum duration of boat sound exposure of 2 min (ID10, ID12, ID18, ID27, ID30, ID58, ID63, ID66, ID64, ID70, ID4 and NID2) (see Table S2).

Unpaired Wilcoxon tests showed no effect of boat sound on either the total number of behaviours per minute or the duration of all behaviours between sharks exposed to noise (DN, n = 12) and those not exposed (control, n = 12) (no. of behaviours min^{-1}: $W = 69$, $p = 0.4$; duration: $W = 33$, $p = 0.012$; Fig. 8a, Table S2). However, when comparing behaviour between the BN and DN periods within individuals (paired *t*-tests), sharks exhibited a significantly higher number of behaviours per minute in BN than in DN periods ($n = 6$; $t = 6.52$, $df = 5$, $p = 0.001$; Fig. 8b).

4. DISCUSSION

Improved understanding of the distribution and behaviour of blue sharks is crucial for the conservation of these animals (Mas et al. 2024). However, studies focussing on the behaviour of sharks in their natural habitats are rare and challenging (Klimley et al. 2023). Our study highlights differences in the occurrence and behaviour of blue sharks in relation to seasonal, spatial, bathymetric, biological (sex and life stage) and oceanographic factors in a temperate coastal region adjacent to a marine protected area. Importantly, the high density of juveniles observed during spring suggests that the study area is likely a nursery, making it relevant for conservation. This study describes the behaviour of blue sharks in relation to BRUVS and suggests that anthropogenic sounds may influence their foraging behaviour, highlighting the potential impacts of noise pollution.

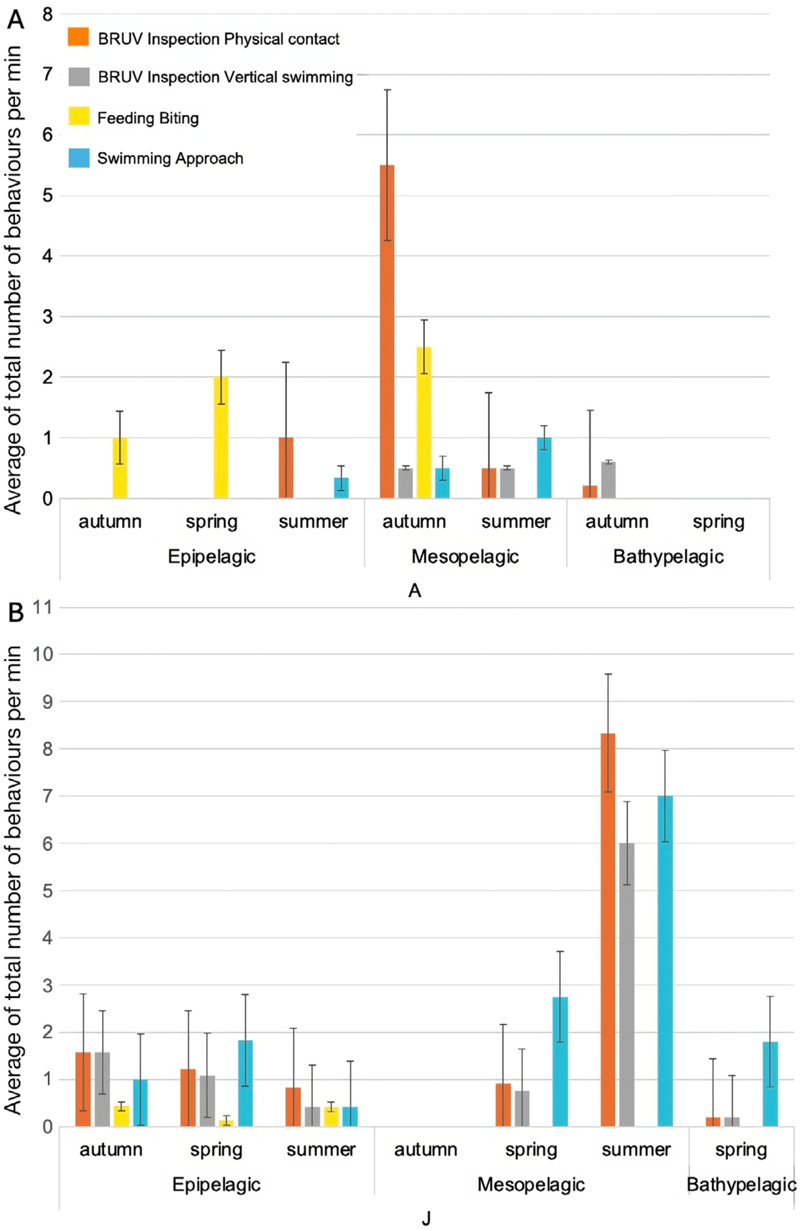

Fig. 4. Average (±SE) number of blue shark behaviours exhibited per minute by maturity stage ([A] adult; [B] juvenile) and season (autumn, spring, summer) per bathymetric area (epipelagic, mesopelagic, bathypelagic)

In sum, this study provides valuable insights relevant for the management and conservation of this species.

4.1. Sex–life-stage–age distribution

The spatio-temporal distribution of blue sharks in the study area exhibited certain trends in relation to the life stage and sex of the animals. Juveniles were more frequently observed in spring, while adults were more frequent in autumn. In addition, juveniles were sighted more frequently in the epipelagic and mesopelagic zones, and adults (mainly males) were mostly found in bathypelagic zones associated with the Lisbon and Setubal canyons.

Our results are consistent with previous distribution studies in the North Atlantic, which showed that the distribution of blue sharks in relation to water temperature varied by sex and life stage (Nakano & Stevens 2008). Data on blue shark landings in Europe (STECF 2015), the South Atlantic (Hsu et al. 2015) and several studies in the North Atlantic (Vandeperre et al. 2014, Howey et al. 2017, Coelho et al. 2018) suggest that larger blue sharks tend to prefer warmer regions, while smaller individuals are more commonly found in colder areas. In the North Pacific, blue shark distribution also seemed to be strongly influenced by SST (Maxwell et al. 2018).

Our data are also consistent with previous studies carried out in Portuguese waters. On the Portuguese coast, longlines mainly capture juvenile females, which comprise 61–77% of total blue shark catches (Queiroz et al. 2005). Moreover, juveniles and adult females are more frequent in shallow waters, whereas adult males prefer zones with active water dynamics, such as seamounts (Litvinov 2006). Spring is the breeding season for this species near Portuguese waters (Nakano & Stevens 2008), with nursery areas located off Portugal, north of Spain and near the Azores (Aires-da-Silva et al. 2008). Mature and pregnant females are found in African waters during winter, with mating and pupping likely occurring off the Portuguese coast (Nakano & Stevens 2008). Our 2 yr study identified a potential nursery area for blue sharks based on high shark density, especially juveniles, prolonged presence and frequent use over multiple years, meeting the criteria outlined by Heupel et al. (2018). Many sharks show site fidelity to specific areas, such as nurseries, mating grounds and feeding areas, but it remains unclear whether oceanic sharks exhibit long-term site fidelity to particular areas such

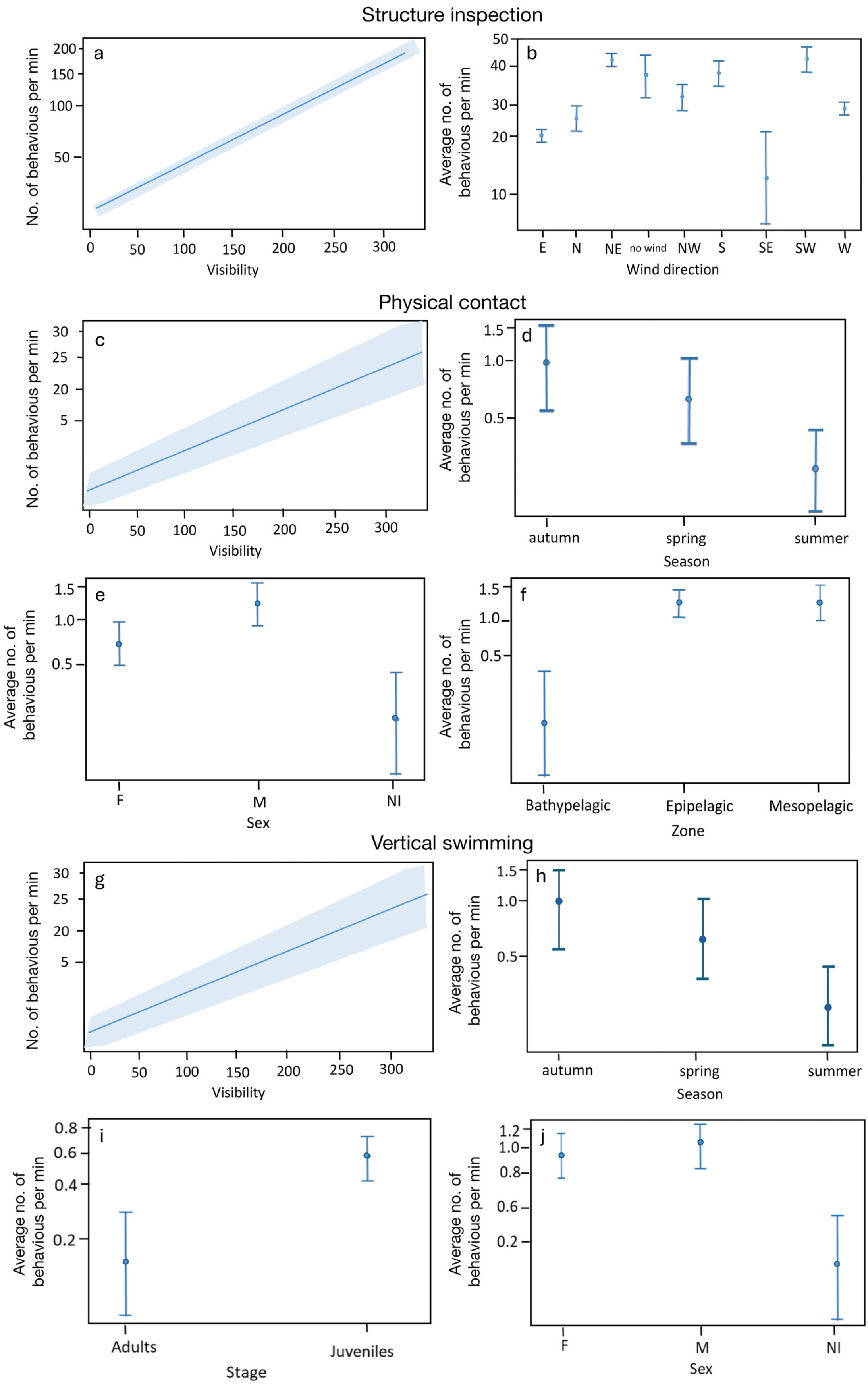

Fig. 5 continued on next page

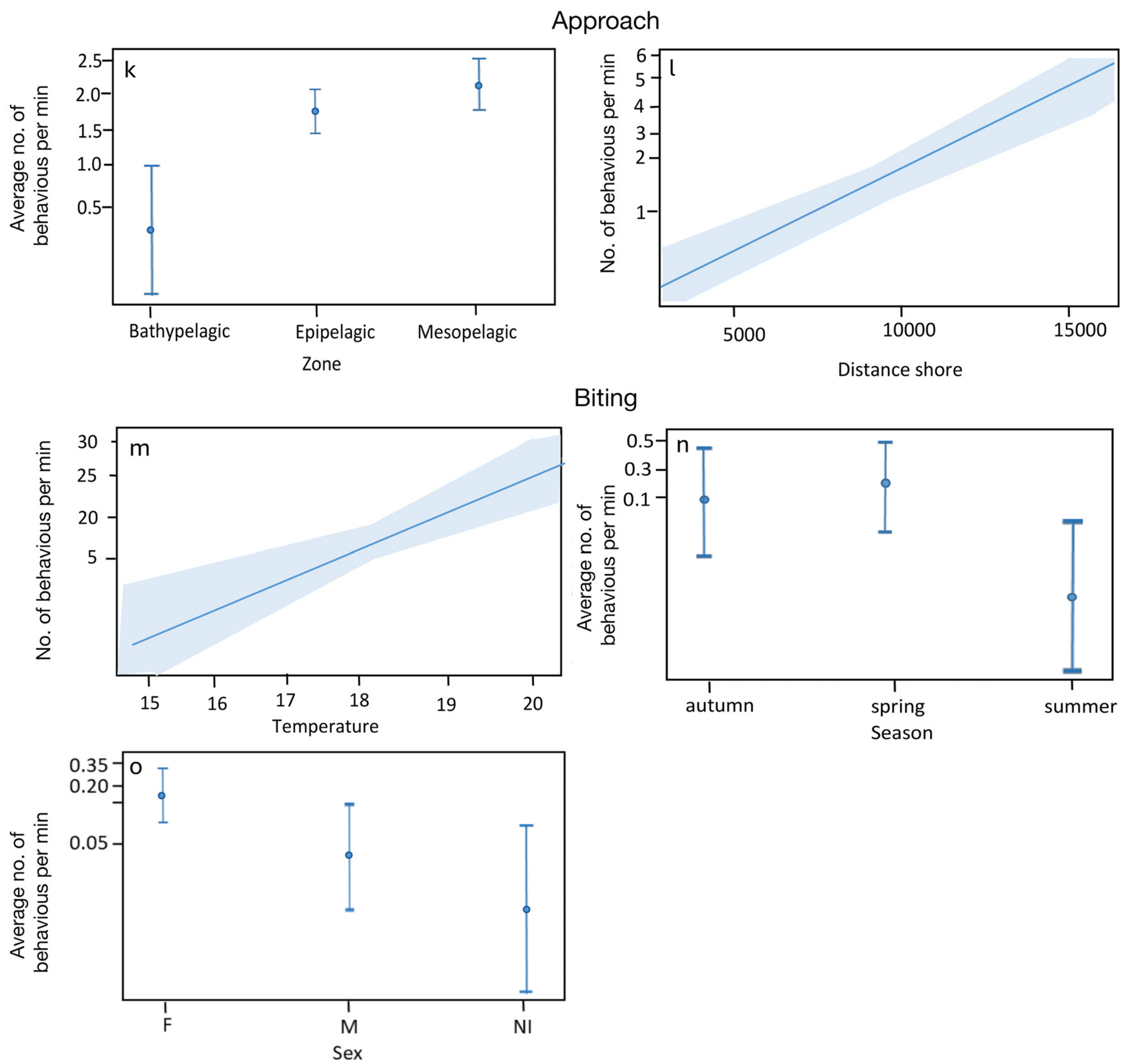

Fig. 5. General linear mixed model fitting the response of the average number of behaviours exhibited by blue sharks per minute in relation to continuous variables (depth, visibility, wind direction, distance to the coast, temperature) and categorical variables zone (epipelagic, mesopelagic, bathypelagic), season (autumn, spring, summer), sex (female: F; male: M; not defined: ND) and life stage (juvenile: J; adult: A). Shading and error bars: 95% confidence intervals. Number of structure inspections based on (a) visibility and (b) wind direction; physical contacts based on (c) visibility and (d) season; physical contacts by (e) sex and (f) zone; vertical swimming activities based on (g) visibility and (h) season; vertical swimming activities by (i) stage and (j) sex; approaches (k) by zone and (l) distance to shore; and biting incidents based on (m) temperature, (n) season and (o) sex

as nursery or feeding grounds (Hueter et al. 2005). Nevertheless, recent sightings of blue sharks in specific areas challenge the belief that they are purely oceanic wanderers, suggesting that blue sharks may exhibit residency or philopatry, returning to the same locations regularly (Fontes et al. 2024). If the study area is confirmed as a nursery area, this information could provide valuable insights for management, potentially supporting its designation as an Important Shark and Ray Area.

4.2. Observation of behavioural patterns

Foraging behaviour patterns indicated that juveniles exhibited greater curiosity towards the bait than adults. This could be due to their foraging instinct and/or limited experiences, causing them to linger near the stimuli for longer periods. Adults were less likely to stay near the bait for extended periods, given that the food-related cues did not lead to actual prey (the bait box only released

Table 3. Generalised linear models analysing the response of the average number of behaviours to the continuous variables duration, depth, visibility, wind direction, distance to the coast and temperature, and the categorical variables zone, season, sex and stage. Significant results are indicated by asterisks (*p < 0.05; **p < 0.01; ***p < 0.001)

	df	Deviance	Residual df	Residual deviance	p
Structure inspection					
NULL			71	3584.6	
Duration	1	1582.29	70	2002.3	<0.001***
Depth	1	155.95	69	1846.3	<0.001***
Visibility	1	800.39	68	1045.9	<0.001***
Wind direction	8	181.21	60	864.7	<0.001***
Physical contact					
NULL			76	265.18	
Duration	1	48.416	75	216.76	<0.001***
Visibility	1	63.864	74	152.90	<0.001***
Season	2	4.676	72	148.22	0.097
Zone	2	19.090	70	129.13	<0.001***
Sex	2	12.777	68	116.36	0.0017**
Vertical swimming					
NULL			76	203.63	
Duration	1	34.930	75	168.70	<0.001***
Visibility	1	46.932	74	121.77	<0.001***
Season	2	7.731	72	114.04	0.021*
Stage	1	3.656	71	110.38	0.056
Sex	2	7.930	69	102.45	0.019*
Approach					
NULL			78	192.99	
Duration	1	88.244	77	184.17	0.0030**
Distance to shore	1	259.712	76	158.20	<0.001***
Zone	2	160.463	74	142.15	<0.001***
Biting					
NULL			78	86.201	
Duration	1	77.547	77	78.446	0.0054**
Temperature	1	163.384	76	62.108	<0.001***
Season	2	80.838	74	54.024	0.018*
Sex	2	73.666	72	46.657	0.025*

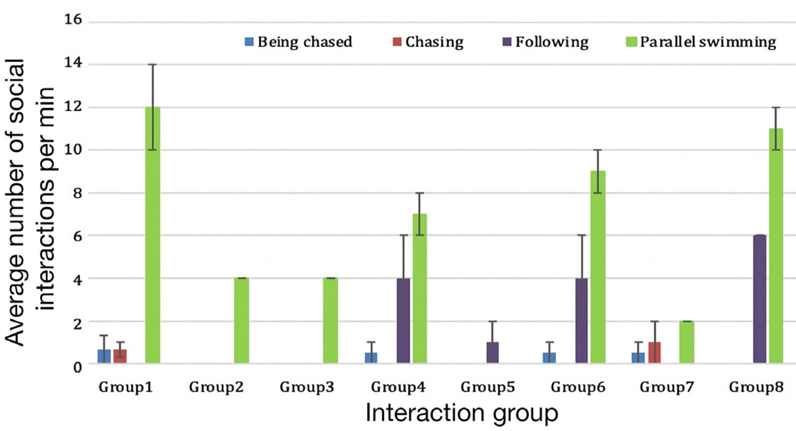

Fig. 6. Average (±SD) number of social interactions per minute exhibited by 8 groups of blue sharks. Group 1: 3 females (1 adult, 2 juveniles); Group 2: 3 juvenile females; Group 3: 2 juveniles (1 female, one not defined); Group 4: 2 juveniles (1 male, 1 female); Group 5: 2 juvenile females; Group 6: 2 juveniles (1 female, 1 male); Group 7: 2 juveniles (1 male, 1 not defined); Group 8: 2 juveniles (1 female, 1 not defined). For more details about time of interactions, see Table S2

scent and blood, not food). Despite spending less time around them, adults tended to bite the structures more frequently. Most behaviours were in the BRUVS interaction category, which indicates sharks were attempting to acquire information through visual (structure inspection), touch and electromagnetic senses (vertical swimming and physical contact). Naturally, olfactory cues are often the first utilised by aquatic animals searching for food (Gardiner et al. 2014). After olfactory attraction, visual stimuli also provide important information, followed by touch and electroreception (Lorenzini organs; Fields 2007). Indeed, sharks can follow multiple sensory cues simultaneously or alternate between them as they hunt or forage (Gardiner & Atema 2007, Gardiner et al. 2014).

Physical contact and vertical swimming were more frequent in autumn and spring. Furthermore, physical contact, vertical swimming and structure inspection behaviour increased with visibility. These observations are likely linked to the importance of visual cues for these pelagic predators. Structure inspection decreases and physical contact increases slightly with lower visibility and bathymetric zone. This could be explained by the fact that high turbidity impairs the use of vision as the main source of information, forcing sharks to rely more on tactile cues and electroreception (McFarland 1989).

Biting was significantly related to temperature, mostly at lower (15–16°C) and higher (>19°C) temperatures, and occurred more frequently in autumn and early spring. Biting was also more frequent in adults than in juveniles. This may be correlated with coastal upwelling conditions in late spring and summer, which impact SST, and, in turn, create ideal feeding conditions for pelagic fish schools such as sardines and mackerel (Santos et al. 2002). As a result, this can trigger foraging behaviour in sharks.

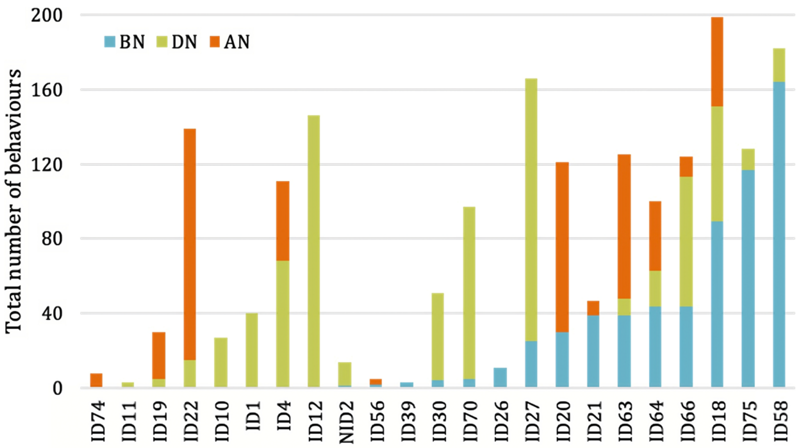

Fig. 7. Number of behaviours for 23 individual blue sharks (individual IDs are shown) observed in videos with boat sounds representing 3 periods: before (BN), during (DN) and after (AN) boat noise

4.3. Social interactions

Most of the social interactions observed in the study area were exhibited by juveniles. Juveniles tended to remain longer in response to food-related olfactory cues, which led to increased social interactions, especially in the spring when juvenile sharks were more abundant. None of the observed social interactions were considered aggressive, but rather intra-specific curiosity and exploratory behaviour. Although sharks are often seen as solitary predators, it has been observed that some shark species form aggregations when attracted to food stimuli or for reproductive purposes, often in response to environmental changes (Jacoby et al. 2012, Micarelli et al. 2020). In these cases, they can be observed to show intraspecific interactions. For example, although focussing on a different species, social studies based on direct observation and video footage of white sharks attracted to bait suggest that they exhibit repeated, specific behaviours in interactions with conspecifics (Micarelli et al. 2023).

Interestingly, on 2 occasions during the present study, a mako shark *Isurus oxyrinchus* was observed near blue sharks, but smaller individuals of both species avoided interaction by leaving the area. Indeed, it has often been observed that animals avoid interspecific or intraspecific interactions with larger individuals when competing for a common resource (Thompson 1988).

While social interactions are poorly understood in sharks, this study provided a good opportunity to gain some preliminary insights. However, more targeted behavioural studies are needed.

4.4. Boat sound effect on behaviour

The comparison between the animals exposed to boat sounds and the control animals showed no significant difference in the duration of foraging behaviours, although the duration was on average 20%

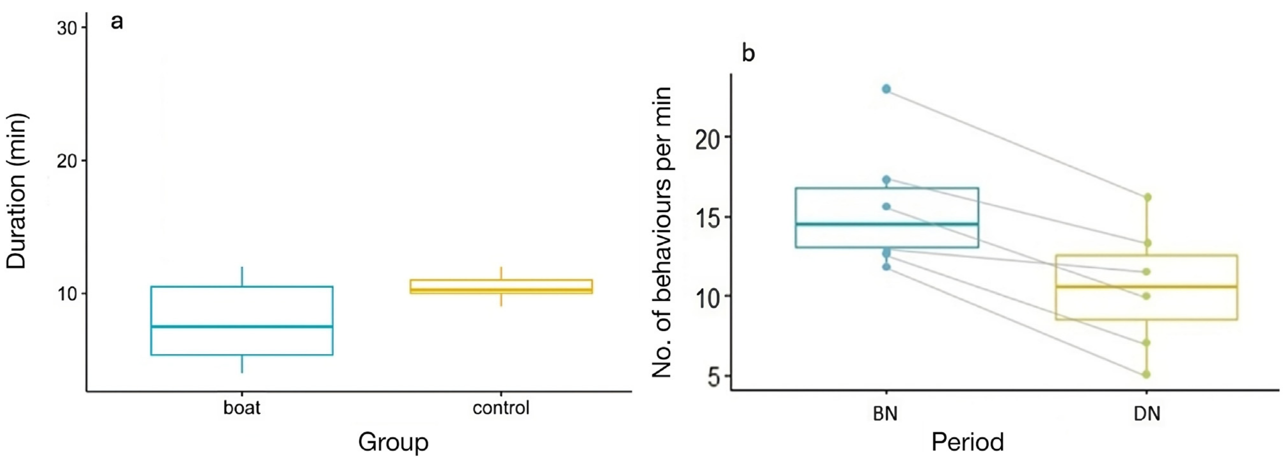

Fig. 8. (a) Total duration of behavioural states (approach, structure inspection, vertical swimming, physical contact, biting) exhibited by blue sharks either exposed to boat noise (boat) or not (control). (b) Number of behaviours (approach, structure inspection, vertical swimming, physical contact, biting) per minute and per individual before (BN) and during (DN) boat noise. Boxes represent interquartile range (IQR), encompassing the 25th to 75th percentiles of data; horizontal lines within the boxes indicate medians; whiskers extend to the minimum and maximum values, excluding outliers. Outliers are displayed as individual dots beyond the whiskers

longer in the control group than in noise-exposed sharks. However, when comparing the number of behaviours per minute performed by the same animal before and during sound exposure, we found a significant decrease in behaviour frequency in the presence of boat sound. These observations should be considered preliminary and interpreted with caution due to the small sample size and constraints faced in this study, namely the differences in available time periods and the duration of observable footage. Future studies on the effects of boat noise on this species should thus attempt to minimise or eliminate these constraints by using larger observation areas, complementary methods or *ex situ* experimental trials.

Although our results are preliminary, they suggest that anthropogenic sounds can affect the behaviour of this species. This could have potential implications for their distribution and/or foraging activity and deserves further investigation. Boat sounds are within the hearing range of sharks (Chapuis & Collin 2022) and other aquatic animals (Kasumyan 2005) and are known to cause measurable impacts (Chapuis et al. 2019, Alves et al. 2021, Amorim et al. 2022). Boat sounds other than those from our research vessel were not observed through direct observation of the spectrograms. However, this does not necessarily mean that other disturbances were not heard by the sharks. Nevertheless, nearby sounds are more likely to be perceived as a threat and therefore to impact behaviour (Myrberg et al. 1978, Rider et al. 2021). Research focussing on elasmobranchs has found mixed results in terms of noise effects. For example, some studies have exposed captive and wild elasmobranchs to artificial sounds without observing changes in their feeding behaviour (Ryan et al. 2018). By contrast, escape behaviour was observed in stingrays during exposure to anthropogenic sounds (Mickle et al. 2022). Consistent with our study, a BRUVS-based study in a coastal reef showed that sharks decreased in number of individuals and interactions within the video structure when artificial sound (with 95% of its energy below 1 kHz) was continuously played (Chapuis et al. 2019). Furthermore, alterations in swimming behaviour have been observed in small-spotted catsharks *Scyliorhinus canicular* exposed to loud sounds at 80 and 200 Hz (de Vincenzi et al. 2021). Together, these studies suggest that anthropogenic noise has the potential to negatively impact elasmobranch behaviour.

Despite the numerous reports on behavioural alterations in sharks exposed to short-term sounds, habituation may occur when exposure is recurrent. A study comparing the presence and abundance of 3 shark species with variable boat density and boat traffic (Rider et al. 2021) suggested habituation of sharks to high levels of recurrent boat activity within the study area. Boat noise may even attract sharks, particularly when sharks associate boat noise with food (Mitchell et al. 2018). Nevertheless, habituation or attraction to boat noise may still have negative consequences, such as increased physiological stress (Amorim et al. 2022, Di Franco et al. 2023), increased probability of bycatch (Mitchell et al. 2018) and reduced foraging success due to masking of auditory cues produced by prey (Codarin et al. 2009, Nedelec 2023).

5. CONCLUSIONS

Juvenile sharks were observed more frequently around BRUVS in the study area, and both juveniles and adults presented distinct seasonal occurrence patterns. Juveniles were more abundant in spring, coinciding with the breeding season, which hints at a potentially important nursery habitat in the study area. Results provided some insights into the spatial preferences and distribution of this species as well as the influence of the environment on behavioural patterns. Despite the aforementioned constraints related to observation times and sample sizes, which are difficult to avoid in a field study, our results support the use of BRUVS for studying foraging and social behaviours in pelagic predators such as blue sharks. This study also demonstrated that boat noise seems to disturb behavioural patterns in blue sharks, potentially affecting their foraging efficiency. There is a significant lack of acoustic and behavioural studies on sharks, yet such research is critical to strengthening our understanding and predictive capacity regarding the effects of anthropogenic stressors on sharks. Filling knowledge gaps on the behaviour of this threatened species is key to better planning and predicting the outcome of targeted conservation measures.

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