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# Swimming Behaviour in Juvenile Smooth-Hammerhead Sharks (*Sphyrna zygaena*): Insights from UAV-Based Observations in a Coastal Nursery

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# Resumo

Predadores de topo, como os tubarões, desempenham papéis ecológicos fundamentais, mas as suas populações têm sofrido declínios severos a nível global. Entre os tubarões-martelo, o tubarão-martelo-liso (*Sphyrna zygaena*) permanece uma das espécies menos estudadas, sobretudo durante as fases iniciais do seu ciclo de vida. O presente estudo fornece a primeira descrição de referência (*baseline*) do comportamento de natação de *S. zygaena* numa zona de berçário costeira da Ilha do Faial, Açores, recorrendo a veículos aéreos não tripulados (UAV). Foram utilizados dois métodos de voo – transectos e voos a seguir o indivíduo alvo –, e este último provou ser o mais adequado para investigar o comportamento dos tubarões. A duração dos comportamentos, o tempo dos ciclos de batimento caudal (TBC) e as velocidades de natação foram quantificados e analisados sob diferentes contextos ecológicos (presença de “conspecíficos”, “presas potenciais” e “atividade antropogénica”).

Foram analisados 37 indivíduos, nos quais se identificaram 11 comportamentos distintos. Os comportamentos de natação “direcional” e “de cruzeiro” dominaram a utilização do tempo, comportamentos cujos gastos energéticos se preveem como dos mais baixos entre os diversos comportamentos. O TBC médio foi de 1,5 ± 0,3 s, apresentando correlação inversa com a velocidade de nado. Verificaram-se alterações comportamentais em contextos específicos: as taxas de atividade aumentaram significativamente na presença de “presas potenciais” e, sobretudo, de “atividade antropogénica”, sendo que este último contexto apresentou as maiores proporções de comportamentos “burst” e “zigzag”, previstos de se tratarem dos comportamentos com os maiores gastos energéticos entre os diversos identificados. Estes resultados demonstram que a presença humana pode impor um gasto energético adicional aos utilizadores deste berçário costeiro, com potenciais efeitos negativos sobre o crescimento e a sobrevivência dos juvenis.

Os resultados obtidos validam os UAVs como uma ferramenta eficaz, económica e não invasiva para estudos comportamentais de elevada resolução em habitats de berçário de tubarões, sublinhando a importância de avaliar e mitigar as perturbações de origem antropogénica em habitats críticos de berçário, como o existente nos Açores.

Palavras-chave: *Sphyrna zygaena*; Comportamento de natação; Berçário; UAV: Perturbação antropogénica; Custos energéticos

# Abstract

Apex predators such as sharks play key ecological roles, yet their populations have experienced severe global declines. Among the hammerhead sharks, the smooth hammerhead (*Sphyrna zygaena*) remains one of the least studied species, particularly during its early life stages. This study provides the first baseline description of the swimming behaviour of *S. zygaena* at a coastal nursery in Faial Island, Azores, using unmanned aerial vehicles (UAVs). Two UAV flight methods – transect and tracking flights – were employed, and tracking flights proved to be the most suitable to investigate shark behaviour. Behaviours' durations, tail beat cycles (TBC), and swim speeds were quantified and studied under varying ecological contexts (presence of "conspecifics", "potential prey", and "anthropogenic" activity).

A total of 37 individuals were analysed, revealing 11 distinct behaviours. "Directional" and "cruising" swimming dominated the time budget, behaviours believed to be associated with the lowest energetic costs. Overall mean TBC was 1.5 ± 0.3 s, inversely correlated with swim speed. Behavioural shifts occurred under specific contexts: activity rates increased significantly in the presence of "potential prey" and "anthropogenic" activities, with the latter's time budget evidencing the highest proportions of "burst" and "zigzag", the behaviours believed to be associated with the highest energetic costs. These results demonstrate that human presence may impose additional energetic expenditure on the juveniles using this coastal nursery, potentially affecting growth and survival.

These findings validate UAVs as a cost-effective, non-invasive tool for fine-scale behavioural studies in shark nurseries, and underscore the importance of assessing and mitigating anthropogenic disturbances in critical nursery habitats such as that of the Azores.

Key-words: *Sphyrna zygaena*; Swimming behaviour; Nursery; UAV; Anthropogenic impacts; Energetic costs

# General index

# List of figures

# List of tables

# List of equations

# List of abbreviations

**AMX** – Sampling area code: Praia de Almoxarife

**BORIS** – Behavioural Observation Research Interactive Software

**BRUV** – Baited Remote Underwater Video

**CED** – Sampling area code: Cedros point

**cm** – centimetres

**cm/pixel ratio** – centimetre per pixel ratio

**COT** – Cost of Transport

**CSV** – Comma-Separated Values (file format)

**CWT** – Continuous Wavelet Transformation

**DJI** – Da-Jiang Innovations

**DJI Mavic 3 Classic / DJI Mini 3** – Specific UAV DJI models

**EIR** – Sampling area code: Porto da Eira

**FL** – Fork Length

**fps** – frames per second

**GPS** – Global Positioning System

**Hz** – Hertz (Cycles per second)

**IQR** – Interquartile Range

**IUCN** – International Union for Conservation of Nature

**KS test** – Kolmogorov–Smirnov test

**m** – metres

**m/s** – metres per second

**NPE** – Sampling area code: Norte Pequeno

° – degrees

**°C** – degrees Celsius

***p* –** Test Probability Value

**PDN** – Sampling area code: Praia do Norte

**R** – R Statistical Programming Language

**$R^2$** – Coefficient of Determination

**RStudio –** R Integrated Development Environment

**ROV –** Remotely Operated Vehicle

**s** – seconds

**SAL** – Sampling area code: Porto do Salão

**SD** – Standard Deviation

**SD card –** Secure Digital card (memory card)

**TBC** – Tail-Beat Cycle

**TBF** – Tail-Beat Frequency

**T-test –** Student’s t-test

**TL –** Total Length

**UAV** – Unmanned Aerial Vehicle

**V –** Version (software version)

# 1. Introduction

Apex predators exert a top-down control on the distribution and abundance of their prey, and their removal from the ecosystems due to inexistant or ineffective management strategies can lead to extensive cascading effects, including disease and invasive species outbreaks, biodiversity loss, and changes to the ecosystem (Myers *et al.*, 2007; Estes *et al.*, 2011, Lennox *et al.*, 2018). The global decline of chondrichthyan populations has been widely recognized (Stevens et al., 2000; Jacques, 2010). Over the last half century, sharks and rays have experienced severe declines due to overfishing (both targeted and as bycatch) rendering them one of the most threatened vertebrate groups (Dulvy, 2014; Pacoureau *et al.*, 2021). Large-bodied hammerhead sharks in particular – category which includes the great (*Sphyrna mokarran*), the scalloped (*Sphyrna lewini*), and the smooth hammerhead (*Sphyrna zygaena*) – have suffered dramatic population declines of over 90% in some of their distribution ranges (Gallagher *et al.*, 2014; Gallagher & Klimley, 2018). These species, like many other elasmobranchs, faces difficulties in population recovery due to its life-history traits, including slow growth, late maturity, and long lifespan (Miller, 2016). Furthermore, misreporting and underreporting of catches further obscure the true population status of hammerhead sharks, hampering effective conservation (Rigby *et al*., 2019).

Among the three large hammerhead sharks, the smooth hammerhead shark (*Sphyrna zygaena*) is the least studied species (Gallagher & Klimley, 2018). This species is listed as Vulnerable on the IUCN Red List of Threatened Species (Rigby *et al*., 2019), but in the specific case of the European population conservation status is classified as Data Deficient (Ferretti *et al*., 2015). Even its basic biological traits remain poorly understood (Gallagher & Klimley, 2018). Size at birth varies considerably among authors, ranging between 42 and 61 cm of total length (TL) (Compagno, 1984; Coelho *et al.*, 2011; Nava & Márquez-Farías, 2014; Francis, 2016; Miller, 2016). During their early life stages, growth is believed to be relatively fast, with juveniles increasing approximately 25–28 cm in fork length (FL) per year (Coelho *et al.*, 2011; Bezerra *et al*., 2017). Males and females reach sexual maturity at around 210–250 cm TL and 250–270 cm TL, respectively (Miller, 2016; Nava Nava & Márquez-Farías, 2014). Longevity estimates remain uncertain, ranging between 18–28 years for males and 21–32 years for females (Huynh & Tsai, 2023). Parturition is thought to occur during summer, when pregnant females have been identified in the shallower nearshore habitats utilized by the juveniles (Félix-López *et al*., 2019).

The protection of immature individuals – neonates, juveniles, and subadults – has been highlighted as a critical measure for the long-term sustainability of hammerhead populations (Huynh & Tsai, 2023). A nursery is characterized as an area with higher frequencies and higher residency of a species juveniles, exhibiting repeated use by them year after year, representing critical habitats for the early life stages of such species, guaranteeing a later contribution to support the adult populations (Heupel *et al.*, 2007, Heupel *et al.*, 2019). In the Azores, one nursery has been classified under those criteria (Afonso *et al.*, 2022). Adult pregnant female smooth hammerhead sharks are thought to migrate to coastal nurseries to pup, with juveniles residing in these habitats for several years until they transition to a more oceanic life (Afonso *et al*., 2014; Das & Afonso, 2017; Afonso *et al.*, 2022). Seasonal aggregations of juveniles have been consistently documented along the north shore of Faial, particularly at locations such as Salão, Cedros point, and Praia do Norte, typically over transition zones between rocky and sandy substrates (Afonso *et al*., 2022). The particular functions of this nursery area are still not ascertained, but must be related with providing shelter from predators or facilitated access to food sources, and ultimately contribute to the individual's fitness, as hypothesized for nurseries in general (Heupel *et al.*, 2019).

However, the functions of this nursery may be at risk, as human activities in coastal zones are constantly increasing, and diving centres operating in this particular nursery area are emerging, offering encounters with juvenile hammerheads, which raises conservation concerns. Aggregations are particularly vulnerable to anthropogenic disturbance, with evidence showing that human activities such as boating, fishing, and diving can disrupt or even prevent aggregation behaviours (Mucientes *et al.*, 2009; Hueter *et al*., 2013; Cubero-Pardo *et al*., 2011; Apps *et al*., 2015; Cattano *et al*., 2021; López *et al.*, 2023). In the case of scalloped hammerheads (*Sphyrna lewini*), non-extractive recreational activities have been pointed out to possibly increase stress levels, alter swimming behaviour, or even provoke abandonment of aggregation sites (Smith *et al*., 2010; Barker *et al*., 2011; Cubero-Pardo *et al*., 2011; Trave *et al*., 2017; Cattano *et al*., 2021; López *et al.*, 2023) and such impacts may not only reduce population resilience but also heighten the risk of negative interactions between sharks and humans.

Analysing shark behaviour offers a window to understand the effects of human activities on sharks. From an ecological perspective, the act of locomotion spends a big slice from most of the mobile species energetic budget (Lawson et al., 2019; Waller *et al.*, 2023). Therefore, the selection of movement strategies that allow the most effective use of the energy acquired – including speed adjustments, power output, and activity duration – directly influences growth, foraging success, and the individual's overall fitness (Weihs & Webb, 1983; Sims, 2003; Papastamatiou *et al*., 2018; Waller *et al.*, 2023). As a result, any additional energetic costs from anthropogenic disturbance may significantly affect growth and survival. To study how sharks optimise their movements strategies to maximize energy efficiency, kinematic parameters like tail beat frequency (TBF) and swim speed have been reliably used predictors of shark's oxygen consumption and metabolic rates (Lowe, 2001; Lowe, 2002). Examining swimming behaviour, including tailbeat frequency and movement patterns, thus provides valuable insight into the well-being and ecological strategies of sharks within nursery habitats (Lowe, 2001; Lowe, 2002; Waller et al., 2023), particularly across contexts such as foraging, social interactions, predator avoidance, and ontogenetic changes in body size.

In recent years, unmanned aerial vehicles (UAVs) have emerged as powerful tools to study the abundance and fine-scale behaviour of a diverse range of megafauna species, including sharks (Porter *et al*., 2020; López *et al*., 2023). Previous studies have also employed UAVs for a broad spectrum of ecological and environmental monitoring purposes in both marine and land ecosystems (Lu & He, 2017; Kattenborn *et al*., 2019; Liao & Juang, 2022). Transect-based UAV surveys have been used to estimate abundances and habitat use (Hodgson *et al*., 2013; Barasona *et al*., 2014), while flights hovering above the study subjects have become a preferred approach for studying animal behaviour, allowing continuous, non-invasive observation of individuals and groups. For instance, UAV tracking flight observations have provided insights into fine-scale movement parameters, general behaviours, social interactions and courtship and mating behaviours of several aquatic species (Bevan *et al*., 2016; Torres *et al*., 2018; Oleksyn *et al.*, 2020; Lauridsen *et al*., 2025). In the specific case of sharks, UAVs enable non-invasive, high-resolution monitoring of surface-associated aggregations (Butcher *et al*., 2021; López *et al*., 2023). Not even for size estimation is physical handling required, as photogrammetry techniques allow shark length measurements using pixel-to-centimetre conversion ratios calibrated for each UAV model (Oleksyn *et al*., 2020), although optical distortion by the water surface may be a factor influencing the length estimation, especially during days with stronger wind conditions. Compared to biologgers or manned aircraft, UAVs are cost-effective, portable, and capable of providing orthogonal footage that facilitates accurate kinematic and photogrammetric analyses, with minimal underwater noise impacts that reduce the likelihood of altered behaviours (Christiansen *et al*., 2016; Rieucau *et al*., 2018; Porter *et al*., 2020). These attributes make UAVs particularly well suited for studying juvenile hammerhead shark behaviour during daytime in coastal nurseries like the one in Faial, where traditional approaches may not be as practical, cost-effective, or minimally invasive.

As a case study illustrating why UAVs are well suited to fine-scale movement ecology in coastal systems, a recent study on short-tail stingrays used UAVs to obtain non-invasive, high-resolution video and synchronized flight logs (10 Hz GPS, altitude, speed) while manually maintaining the UAV directly above the individual so that the UAV's GPS track served as a proxy for the ray's trajectory. From the footage collected, photogrammetric and movement metrics capturing complementary aspects of behaviour were extracted (mean speed, speed variability, sinuosity, total distance/duration, step length). Methodologically, this workflow shows how UAVs can: 1) standardize focal shark tracking's over hundreds of metres; 2) pair video-verified behaviour with kinematic proxies at fine temporal resolution; and 3) embed calibration and quality-control steps to convert imagery into morphometrics and movement parameters - providing an operational template that links observable behaviour to environmental context without handling animals, and that is directly transferable to nursery-area studies like the present one.

Considering the lack of knowledge on the fine-scale behavioural baselines of the smooth hammerhead sharks in nursery areas and the importance of establishing such baselines to anticipate how disturbance may ultimately alter survival during early life stages, this study provides the first quantitative baseline of juvenile smooth hammerhead shark behaviour in a natural nursery, forming a reference for future comparisons under varying conditions. Specifically, this study aimed to: 1) characterize baseline swimming behaviour of the Faial's nursery *Sphyrna zygaena* using UAV-derived kinematics; 2) assess behavioural differences across biotic contexts ("conspecifics", "potential prey", and "anthropogenic" presence); and 3) evaluate the potential effects of "anthropogenic" presence on activity rates as a proxy for energetic cost, with a view to informing practical conservation measures in a designated nursery habitat.

# 2. Materials and methods

## 2.1. Study Species

The smooth hammerhead shark, *Sphyrna zygaena*, is a semi pelagic species which aggregates in shallow water habitats in the first years of life. They can be identified mainly by the four indentations in the anterior ledge of their slightly arched anterior margin of the cephalofoil head, with no median indentation and their dark-grey brown dorsal part of the body (Ebert *et al.*, 2021; Figure 1). This species is known to use the north shore of Faial Island, Azores, as a nursery ground (Afonso *et al.*, 2022), but the lack of further information on their behaviour and ecology prevents us from knowing their habits and therefore prevents us from creating measures to adequately protect the younger portion of this species, according to the IUCN Red List (Rigby *et al*., 2019), "Endangered" species. The time of the year they are most commonly sighted near the surface is during summer and that is why most of the sampling for this thesis occurs during that period, in daytime.

**FIGURE 1 –** Smooth-hammerhead shark, *Sphyrna zygaena*, photograph (photography by Robert Priester).

## 2.2. Study site

The north waters of Faial Island, Azores, Portugal, have been classified as a nursery area for the focal species (Afonso *et al*., 2022), although the specific functions of this nursery are still not clear. The place has plenty of boat traffic from fishing boats and also some maritime tourism operators, especially since some of the maritime tourism operators started bait attracting hammerhead sharks as a new activity for tourists. The reasons behind the formation of this aggregation of juvenile hammerheads still lacks deeper understanding. Juvenile sharks are usually found in nearshore habitats with depths between 10 and 50 m, but during day hours in the summertime sharks seem to use the waters close to the surface, in a depth of 0-2 m and a lot of the times with the dorsal and the upper lobe of the caudal fin breaking the water surface into the air. These factors, together with the clear visibility around the archipelago, make this kind of aggregation a good scenario to study these specimens' behaviour through UAV surveys. The specific locations for the employment of the flights were chosen based on this previous knowledge of where the nursery occurs and restricted to areas where the land access to the coast line was achievable, while simultaneously guaranteeing a good deployment spot and clear visibility to the sampled area. Six different deployment sites – Norte Pequeno (NPE), Praia do Norte (PDN), Cedros point (CED), Porto da Eira (EIR), Porto do Salão (SAL), Praia de Almoxarife (AMX) – were used and are illustrated in Figure 2.

**FIGURE 2 –** Satellite picture of Faial Island with the deployment locations pinpointed on the map labelled with the respective code name for the local (Retrieved and adapted from Google Maps; https://www.google.com/maps/@38.5895293,-28.7020231).

## 2.3. Tracking method

To access the best way to sample the data to fit the proposed objectives, footage from two different sampling methods were analysed, pre-programmed standardized UAV transect flights and UAV tracking flights, tracking individual sharks manually while hovering above them. Before any of the flight types, weather conditions were carefully assessed. Wind speed, rain and swell were especially important factors, with low-wind, dry conditions, low swell and clear sky preferred to ensure safety and flight stability as well as to minimize glare from the water surface. Intermittent rain, high winds and big swells occasionally prevented flights from being carried out. Flights were performed between 9h and 20h, depending on the weather conditions. Besides, take-off altitude was manually entered for any flight type to reduce the effect of the barometer's underestimation of the UAV flight altitude and, consequently, to improve the accuracy of size estimations (Rex *et al*., 2024).

Transect flights were carried out in eleven different days between June and December of 2024, summing a total of nineteen aerial transects across 5 different locations (AMX, CED, EIR, NPE, PDN). These were designed as three separate and parallel 1,500 m legs separated 500 m apart, which were perpendicular to the coast line, thus covering the continuous habitat gradient from shallow inshore waters to deeper shelf waters (Figure 3). Thus, a total distance of 4,500 m was covered on each transect flight. The DJI Mavic 3 Classic was used to fly the pre-programmed transect legs at a constant speed of 5 m/s, at a height of 30 m from the surface of the water, while video recording with the camera angle pointing vertically to the water, at 90º from the horizontal plain, and an attached polarized filter to reduce glare (video settings: 4K, 60 fps). The UAV was always deployed with a fully charged battery to allow the 25-minute flight time necessary to cover a full transect continuously.

**FIGURE 3 –** Satellite view from an example of a transect flight path from Cedros point, the three long legs are the actual segments that correspond to the transects and where the video recording occurred (Retrieved from: www.airdata.com).

Tracking flights were carried during the late spring and summertime, June to October, of two consecutive years (2023 and 2024). Throughout that period, flights were done in a total of 11 days, summing a total of 26 flights flown in three different locations (CED, EIR, SAL). For these flights, the UAV hovered directly above the target individual tracking the shark trajectory while recording. A DJI Mini 3 and a DJI Mavic 3 Classic, with polarized filters, were used to spot, record and track the specimens, hovering above them for as long as the shark was visible or the battery of the UAV allowed it – usually 25-30 minutes of usable flight battery before returning to the home point of that flight. Random flight patterns were used to scan coastal waters between 50 – 500 m from the coast for sharks (Figure 4).

Once a shark was located, the pilot manoeuvred the UAV to centre the individual in the viewing screen and guaranteed it was in an altitude between 5 and 35 m. No lower than 5 m because at such low altitudes even small altitude errors could cause large size estimation errors, due to the logarithmic behaviour of the calibration curve. Also, lower flights would make the shark body occupy a larger portion of the field of view, making it more likely to reach the frame edges, where the convex lens provoked radial distortion is exacerbated (Rex *et al.*, 2024). Additionally, maintaining higher altitudes helped to reduce the likelihood of the UAV's visual presence or noise provoking behavioural disturbances to the animals (Bourke *et al.*, 2023). On the other hand, 35 m was the highest altitude allowed because with much higher altitudes image resolution would decrease and a "blooming" effect that obscures fine anatomical details, such as the tip of the caudal fin, would become more noticeable and make it difficult to distinguish the actual structure from surrounding coloured pixels (Bierlich *et al.*, 2021; Rex *et al.*, 2024). The tracking altitude was selected based on visibility conditions, wind strength, and the ability to safely maintain that height over time, avoiding hazards such as boats or seabirds. Recordings were started as soon as the individual was centred in the frame, using the following video settings: 4K, 60 fps for DJI Mavic and 30 fps for the DJI Mini; and made with the camera oriented directly downward or as close to vertical as possible if adjustments of the angle were needed to attempt to avoid some directional glare, to allow to expand sample size across a broader range of light and daytime conditions. Flight parameters including GPS location, altitude, video angle and velocity were recorded in the UAV storage SD card, stored and accessed later. Tracking flight duration was determined by UAV autonomy, and tracking flights were stopped at 20% battery. If the focal shark was lost from view, the recording was also terminated, as it was not possible to confirm that any shark reappearing seconds later was the same individual. If more than one shark was sighted before starting the recording, the first sighted shark was the one to be tracked. It is important to consider that there is still a chance that the same shark may have been sampled twice, in two different moments, although it is not likely due to the usual amount of days between consecutive sampling days and the effort to avoid flying in the same place in two different times of the same day, and also due to the high mobility of the species. The general tracking methods were adapted from the methods of Oleksyn *et al.* (2020) and Raoult *et al.* (2018).

Tracking flights were operated both from boat or from land stations, depending solely on logistical factors. The mode of deployment was not considered to affect the results, as it only related to whether sea-based activities were already scheduled. When tracking flights were flown from the boat the vessel-shark distance was kept at 100 m or more, and when this was not possible the presence of the boat was registered to be kept in consideration.

**FIGURE 4 –** Satellite view from an example of a tracking flight path from Cedros point (Retrieved from: www.airdata.com).

Additionally, there was still a more specific type of tracking flight employed. With the aim of recording and understanding the behavioural response of sharks to a simulated boat passage, an experimental boat approach was employed to some of the individuals during the tracking flight. These flights were operated from the boat and started in the eastern part of the north coast of the island, and the UAV began the search towards the west with the boat following behind it with a distance always greater than 100 m, to avoid disturbing hammerhead sharks that would later be sampled. The distance from the coast was approximately 100-500 m. After identifying an individual with the UAV at a distance at least 100 m away from the boat, the recording started and the rigid-hulled inflatable boat of approximately 5 m was kept on neutral for the duration of one minute. After one minute, the boat moved forward at a constant speed of approximately 5 knots while moving in the direction of the UAV. Then, when closer to the UAV adjustments of boat heading were kept to a minimum. This was made to attempt to pass close to the shark while still simulating a boat passage, where direction is not constantly adjusted. After the passage, the boat kept the same heading until it was further than 100 m away from the UAV and the video kept being recorded for an additional minute, or until the shark disappeared.

## 2.4. Data processing

The transect flights videos were watched at original speed and the number of hammerhead sharks found in each transect was recorded. Due to the markedly shorter time of identifiable tail beat cycles (TBC) per individual (5.58 s on average for transect flights VS 354 s on average for tracking flights – almost the entire duration of the video for each shark being tracked) and the similar number of individuals sampled with the two methods (36 for transect flights VS 37 for tracking flights), transect flights were subsequently excluded from behavioural and TBC analyses.

Tracking flight videos were watched three times using the software BORIS V8.27.10 (Friard & Gamba, 2016) to annotate the different behaviours and variables of study: First, videos were watched at original velocity annotating the periods where tail beats were sufficiently visible for annotation as a state event. Then, tail beat duration was quantified by inspecting the videos at 0.4x speed and adding a point event every time the tail tip reached the rightmost point in that tail beat (Figure 5). The velocity of 0.4x was identified as the best because it was the fastest speed visibly allowing the proper identification of the tail beats. A paired Wilcoxon signed-rank test showed no significant differences between the TBCs annotated at the velocities 0.4x and 0.1x, the slowest visualization velocity ($p > 0.05$; Appendix II). During a last observation, different behaviours were annotated as different state events, based on a compiled ethogram of the identified behaviours (Table I).

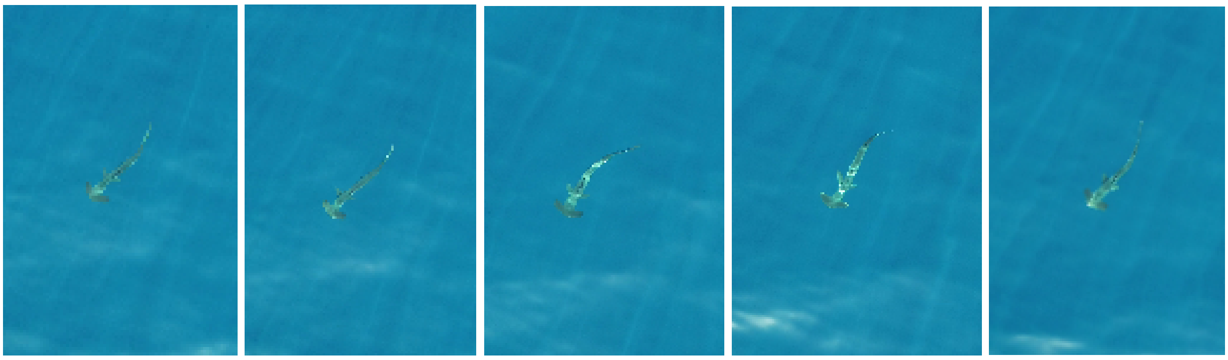


**FIGURE 5 –** Sequence of a full tail beat cycle, from left to right, starting when the tail tip reaches the right most point of the tail beat (picture in the left) and ending when the tail tip returns to the same position (picture in the right).

**TABLE I –** Ethogram with the descriptions of the observed behaviours.

| Behaviours | Description |
|---|---|
| Approach | Individual swimming towards another individual or floating object, adjusting direction towards it. |
| Ascent | Clear ascent from a deeper, less visible water layer to a shallower, more visible one. |
| Burst | Individual has a clearly identifiable sudden accelaration in swimming. |
| Circle | Individual completes a full circle, constantly adjusting direction to the same side, in an approximately constant angular velocity. |
| Cruising | Individual swimming at relatively slow speed without major direction (>45º) or depth changes. |
| Descent | Clear descent from a shallower, more visible layer of water to a deeper, less visible one. |
| Directional | Individual swimming without direction or depth changes, at constant speed and throughout at least 30 seconds. |
| Follow | Focus individual follows a second individual head to tail with a distance no bigger than two body lengths, adjusting direction in the same way as the second individual. |
| Parallel | Focus individual swims parallel to a second individual, both facing the same direction and next to each other, with a distance between them no bigger than two bodylengths and adjusting the direction in the same way as the second individual. |
| Surface | Individual breaking the surface of the water with the dorsal fin, the upper lobe tip of the caudal fin or both. |
| Zigzag | Individual swimming with frequent, major (> 45º) and irregular changes of direction. |

As there was no previously established ethogram for juvenile smooth hammerhead sharks (*Sphyrna zygaena*) under natural conditions, the behavioural categories used in this study were developed directly from the analysis of the video footage and before any statistical analysis were performed. Each behaviour was defined and named based on consistent visual differences in body posture, swimming orientation, apparent tail beat pattern, and interaction with different contexts within the field of view. Some of the behavioural descriptions were conceptually informed by the general behavioural framework for elasmobranchs presented by Klimley *et al.* (2023), although the terminology and specific definitions used here were independently developed to suit the species and the observational context of this study. The aim of this classification was to create an operational framework to quantify and later compare measurable parameters such as TBCs, swim speed and behaviour durations across several biotic contexts, as well as to establish a descriptive behavioural baseline for future reference and comparative studies. These parameters were selected not only because they can objectively describe individual activity but also because they have been identified as reliable predictors of relative energy expenditure in fish and elasmobranchs (Lowe, 2001; Lowe, 2002; Oleksyn *et al.*, 2020), allowing for subsequent inferences on the relative energetic costs associated with the behaviours.

Besides the annotated behaviours, three other types of state events were added to describe possible biotic contexts present in the field of view (Figure 6). State event “conspecific” was added for the periods during which other hammerhead sharks were present in the field of view. State event “potential prey” was created when a school of small fishes or potential prey for the hammerhead sharks was sighted in the recording. State event “anthropogenic” was also created to register the time intervals at which any kind of anthropogenic activity was observable in the field of view, namely the presence of boats passing, boats with the engine off or even bait and free divers in the water in a tourism operation like scenario. Whenever none of these three contexts were present, data was processed under a fourth context, “none”. These four contexts’ behaviours were then subjected to analysis. No potential predators of the hammerheads were identified, otherwise those moments would have been registered under another state event.

Finally, a state event named “subject in frame” was selected for all the duration of the video at which the shark was visible, to allow for better estimations of the time budget of each behaviour than it would be possible had the total video time been used in the analyses instead.

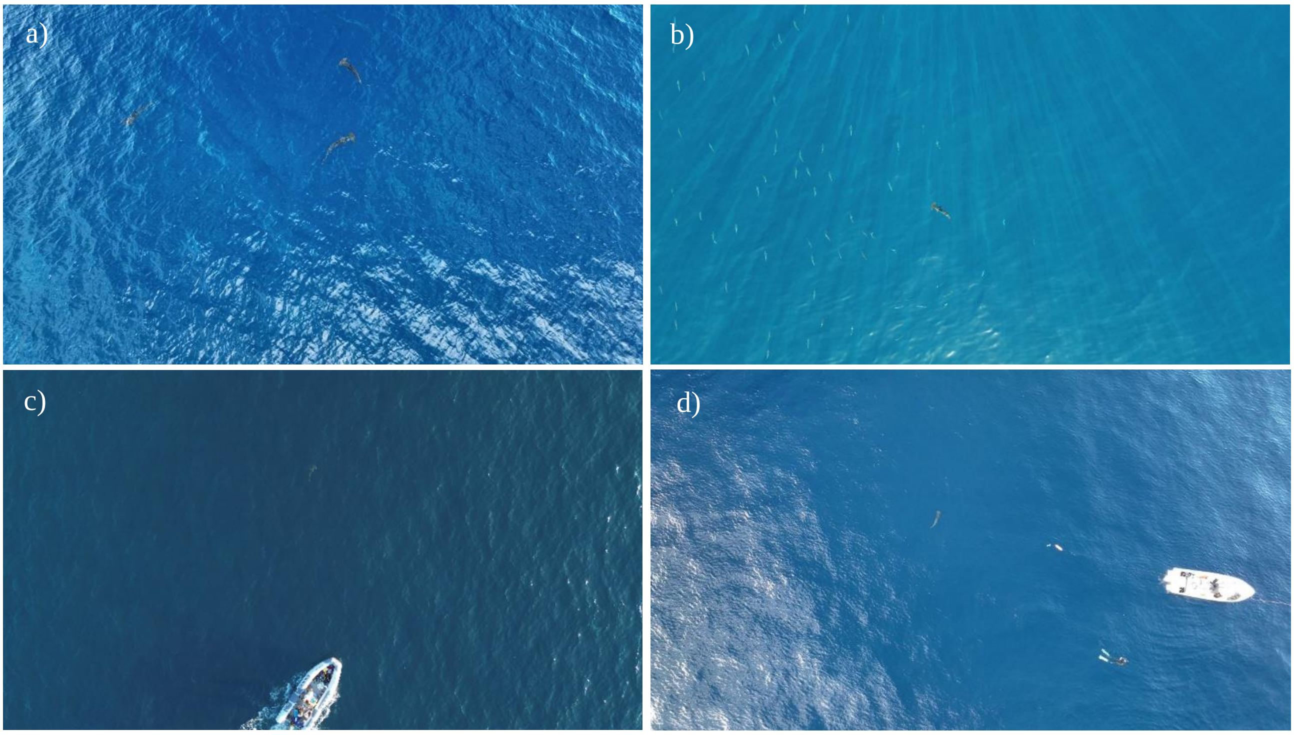


**FIGURE 6 –** Examples of each of the biotic contexts identified: a) “Conspecific” present; b) “Potential prey” present; c) and d) represent two different scenarios included in the “anthropogenic” presence context (c) represents an example of a boat passage and d) represents the example of the tourism operation scenario with bait and divers in the water, and the boat with the engine off.

Time line data for each shark annotations was extracted with the behaviours and respective video times. These files were processed in two different ways: To facilitate behaviour time budget, data was extracted at a frequency of 10 Hz (10 rows for each second) with one binary column for each of the recorded behaviours and contexts identifying their presence/absence throughout time. To facilitate TBC and horizontal UAV velocity analysis, the same binary columns for each behaviour and context were added, but instead of using a frequency of 10 Hz, only the tail beat point events' and TBC state events' times were kept. Then, time differences between consecutive tail beats were calculated, leaving the first row of a sequence of tail beats empty to signalize the interruption of the interruption of the tail beats recording between the empty row video time and its previous row video time. In the end, in both the situations all the shark observation extracts were merged into a single running data base with the observation code names in a column identifying the rows of the respective observations. In addition, datetime in the YY/MM/DD hh:mm:ss.sss format, and the instantaneous horizontal UAV velocities corresponding to the tracking video, were extracted from the original flight data files, which were stored on the UAV's, and added to each database. However, in the case of the TBC database, to match the temporal resolution of TBC records, the mean horizontal UAV velocity over the duration of each TBC was calculated beforehand. These averaged UAV velocity values – representing the UAV's horizontal displacement during each TBC – were hereafter referred to as swim speed, and used as a proxy for the shark's actual swimming speed. In the flight data, the specific track data for each individual could be distinguished among the other tracks that may have been done during the same tracking flight through the time of the file of the saved media and through the total time of the videos. In the flight data file, the column "isVideo" identified the status of the video as on/off through binary code.

A time budget per behaviour table was transferred from BORIS to describe the general use of time for each of the behaviours through the cumulative duration for each behaviour, the number of individuals at which the behaviour occurred, the total number of occurrences across individuals and the relative frequencies of each behaviour in the total duration of time that the individuals were observed in the field of view.

## 2.5. Photogrammetry

To be able to measure the size of the sharks accurately through conversions from the number of pixels in the frame there was the need of making a curve of altitude to understand how the distance from the shark, which in most of the tracks corresponded to the altitude, influences the cm/ pixel ratio. To achieve this goal, two calibration flights were carried out, one for each UAV model. During the calibration flights, the UAV were flown with the camera pointing directly downwards (90º from the horizontal plane) and a rectangle-shaped polypropylene foam bar – measuring 100 cm in its biggest axis and 6 cm in the smallest) – centred in the middle of the screen (Figure 7). Video recording started when the UAV was above 30 metres, then the UAV descended and stopped at 6 different altitudes (5, 10, 15, 20, 25 e 30 metres), in each of which it made a full rotation (360 degrees) on the horizontal plane around its vertical axis. After that, the two videos were seen, and three screenshots of three different frames were taken at each stopping altitude. In the software ImageJ V1.54d (Schneider *et al.*, 2012), the biggest axis of the prototype was measured to obtain the respective size in pixels. Then, the values were divided by the actual size of the shark prototype (100 cm), to obtain the pixels/cm ratio for each of the measurements. Finally, the pixels/cm ratios of each of the measurements (Y cartesian axis) were plotted against the respective real altitudes (X cartesian axis; altitudes checked in the CSV or the SRT file) and a tendency line was added, to withdraw its equation to use for the estimations of the TL sizes from the shark pixels measurements (Figure 8).

**FIGURE 7 –** Screenshot of the DJI Mini 3 calibration flight, at 5 m of altitude, with the 100-centimeter-long bar in the centre of the camera field of view.

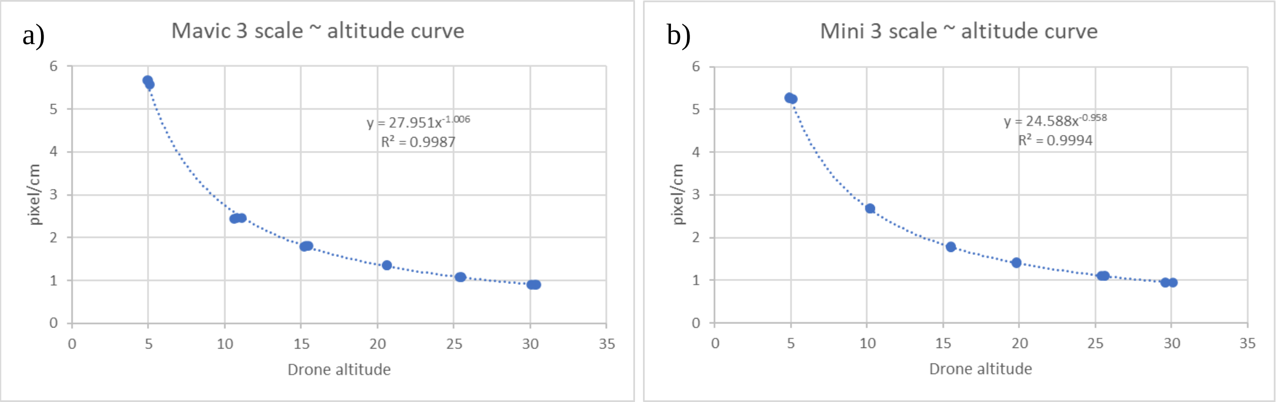
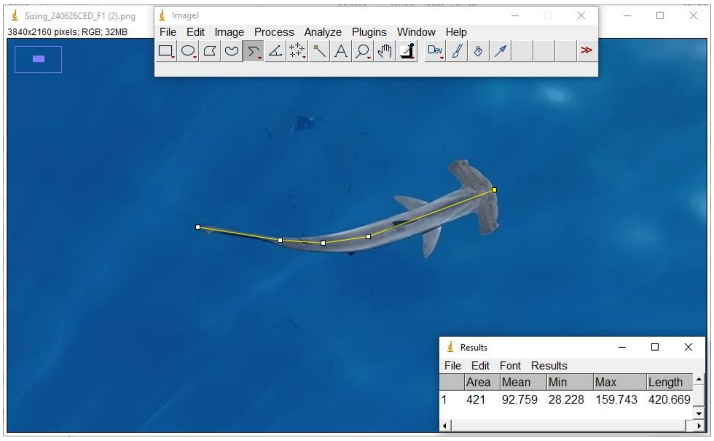


**FIGURE 8 –** Altitude curves calculated with the pixel/cm ratios and altitudes of each of the measurements made from the calibration flights screenshots for each of the UAV's: a) DJI Mavic 3 Classic size-altitude curve; b) DJI Mini 3 size-altitude curve.

To measure the individual shark's TL in pixels, three screenshots of three different frames were taken, with at least one tail beat apart from each other. The moments chosen for the screenshots followed an order of priority: 1) In the screenshot the shark had to be visible from the most anterior edge of the cephalofoil to the tip of the caudal fin to allow the measurement; 2) The gimbal angle in the moments of the screenshots was as close to vertical as possible for that video recording, preferably with the camera pointing directly downward (90 degrees); 3) The subject had to be close to the centre of the frame in the moment of the screenshots and, if the gimbal angle was different from 90 degrees, the shark's body had to be laterally oriented, to avoid differences in size due to changing focal distance to the different parts of the body; 4) The flight altitude variation in the interval chosen to take the screenshots could not exceed 0.5 m. 5) The altitude at the time of the screenshots had to be as low as possible, to achieve better resolution, provided that the above requirements were met. Once the time interval for the screenshots was found, the screenshots were taken and measured in the ImageJ software with the option "segmented line", by drawing a line with as many midpoints as needed to closely follow the imaginary longitudinal dorsal line that starts at the most anterior edge of the cephalofoil, runs aligned with the base of the dorsal fins and ends in the tip of the caudal fin (Figure 9). In the end, the sizes in pixels, the respective altitude of each of the screenshots measured and the gimbal angle were added to the respective equations to estimate the shark's real size (Equations 1 and 2). In the end, the mean of the three values measured for each shark was calculated.



|  | Area | Mean | Min | Max | Length |
|---|---|---|---|---|---|
| 1 | 421 | 92.759 | 28.228 | 159.743 | 420.669 |

**FIGURE 9 –** ImageJ screenshot example of an individual TL measurement with a segmented line.

$$TL\ in\ cm = \frac{Size\ in\ pixels}{27.951 \times \left[\frac{Drone\ altitude}{\cos\left(radianos\left(90^{\circ} - Gimbal\ angle\right)\right)}\right]^{-1.006}}$$

**EQUATION 1 –** Equation adapted from the DJI Mavic 3 Classic regression line equation to estimate the shark's total length by replacing Size in pixels with the measured TL in pixels, and UAV altitude and Gimbal angle with the altitude above the sea level and the recorded gimbal angle at the time of the screenshot, respectively.

$$TL\ in\ cm = \frac{Size\ in\ pixels}{24.558 \times \left[\frac{Drone\ altitude}{\cos\left(radianos(90^\circ - Gimbal\ angle)\right)}\right]^{-0.958}}$$

**EQUATION 2 –** Equation adapted from the DJI Mini 3 regression line equation to estimate the shark's total length by replacing Size in pixels with the measured TL in pixels, and UAV altitude and Gimbal angle with the altitude above the sea level and the recorded gimbal angle at the time of the screenshot, respectively.

## 2.6. Statistical analysis

To discard the possibility of the focal shark's size influencing the behaviour and consequently the TBC and the swim speed, the size distribution of the focal sharks was verified and then $R^2$ of the correlation between size and each of the response variables – mean TBC and mean swim speed per focal shark – was used to access the proportion of those variables that could be explained by the size of the individuals. To search for statistical evidence that there was any linear relationship between the individual's size, and the mean TBC and mean swim speed, the significance values for the regression were also investigated.

Similarly, after observing the general TBC distribution, for which a Kolmogorov-Smirnov test was used due to the large sample size ($n > 5000$), a linear regression was performed to model the relationship between the values of the TBC and swim speed, and the $R^2$ was used to investigate the relationship between swim speed and TBC. Significance values for the regression were also investigated

To characterize the amount of time spent in each behaviour by the hammerhead sharks, the proportion of the total time with subjects present in the field of view for each of the behaviours was estimated and described. To understand which behaviours may require more or less investment by the sharks, differences among behaviours in TBC and swim speed were evaluated using the non-parametric Kruskal-Wallis test. When significant global effects were detected, pairwise Dunn's post-hoc tests with Benjamini–Hochberg correction were used to identify which pairs of behaviours differed significantly.

For each of the biotic contexts' duration intervals, the percentage of time spent on each behaviour was calculated to identify the behaviours that were relatively more frequent in each of the situations, to describe the behaviour utilization for each context and compare them. Kruskal-Wallis test and pairwise Dunn's post-hoc tests with Benjamini–Hochberg correction were used to compare TBC between the different biotic contexts identified, including "none" as a control condition, to understand once more the differences in the energetic investment sharks may have to do in each one.

To further explore the effects of the anthropogenic presence in the hammerhead shark behaviour, the TBC and identified behaviours found throughout a focal shark video were observed for two different individuals. One of them as an example of what happened to the TBC times since the beginning until the end of the video in one of the boat approach attempts, keeping in mind the time interval at which the boat was present in the field of view. And the second as an example of what can happen in a tourism operation scenario, with bait, divers and the boat with the engine off in water.

All the values of the different variables in this analysis were raw-unrounded values, only the final results were rounded. Final results were rounded to different decimal places depending on the variable type: percentages were rounded to one decimal place as well as TL measurements (cm), distances (m) velocities (m/s) and time (s), whereas the statistical tests results and $R^2$ were rounded to three decimal places.

All data was processed and analysed using Microsoft® Excel© 2016 (Microsoft Corporation, 2016) and RStudio V2025.05.0+496 (Posit Team, 2025). Before the use of any non-parametric tests, data were inspected for normality and homogeneity of variances using the Shapiro-Wilk and Levene's tests, respectively, being only used in the cases where the assumptions of normality or homoscedasticity were not met. Results of any tests performed were considered significant if the *p* of the test was lower than 0.05 (<5%).

# 3. Results

## 3.1. Sampling effort

The 19 transect flights done through the 10 days of data collection lasted a mean of 26 min and 28 s per flight, covering the required 4,500 m per flight and summing to a total area of 4,223,700 m$^2$ (3 transect legs of 1,500 m per flight; Table II). In these transects, 36 individuals were recorded in 5 of the flights, while in the other 14 flights no individuals were visible. In addition to that, due to the constant movement of the UAV at a speed of 5.0 m/s and considering the height of the field of view as 27.9 m, each individual was visible on average for 5.6 s.

The 26 tracking flights carried out in the 11 different days of data collection, between 2023 and 2024, allowed the collection of 39 different videos tracking 39 smooth hammerhead sharks swimming near the surface in the nursery area in the north of Faial, Azores. From these 39 videos, 37 of them allowed for a clear identification of the focus subject and respective behaviours for the majority of the total video time (12,463.70 s from the 12,538.93 s total time of the 37 videos). The duration of those sharks' videos ranged from 19 s to 22 min and 25 s, with a mean of 5 min and 39 s per individual tracked. Through the totality of that time for the 37 individuals, 11 different behaviours were identified.

Within the tracking flights dataset, tail beat analysis was possible for 34 individuals, generating 8,989.78 s of footage with identifiable tail beats and resulting in the registration of approximately 5,985 tail beat point events. Photogrammetry was possible for 30 of the 34 individuals with identifiable tail beats. In two tracking flights, the use of optical zoom during recording went unnoticed, preventing accurate scaling of the images and, consequently, accurate TL estimation. For two additional tracking flights, the loss of flight logs made it impossible to retrieve the altitude and gimbal angle of the camera at the time of the screenshots, also precluding total length estimation.

**TABLE II** – Summary results of the effort and resulting usable data for the different flight types: a) transect flights; b) tracking flights.

| a) | **Transect flights** |
|---|---|
| Years of sampling | 1 |
| Days of sampling | 10 |
| Number of different locations | 5 |
| Number of transect flights | 19 |
| Number of transect legs | 57 |
| Total accumulated area (m$^2$) | 4,223,700 |
| Mean flight time (hh:mm:ss) | 00:26:28 |
| Mean time in the FOV (s) | 5.6 |
| Sharks counted | 36 |

| b) | **Follow flights** |
|---|---|
| Years of sampling | 2 |
| Days of sampling | 11 |
| Number of different locations | 3 |
| Number of follow flights | 26 |
| Total video time (s) | 12,607 |
| Mean follow time (s) | 354 |
| Sharks followed | 37 |
| Sharks with identifiable tail beats | 34 |
| Sharks possible to measure | 30 |

## 3.2. Shark size

Among the sharks tracked in the northern shore of Faial Island (Azores) with identifiable tail beats, the total length (TL) was possible to estimate for 30 of the sharks, distributed as shown in Figure 10. The most frequent size class was 140–150 cm, represented by seven sharks. The smallest measured 56.0 cm and the biggest measured 187.7 cm Overall, the mean TL was 128.7 cm (± 32.0 cm SD) and the median was 133.2 cm.

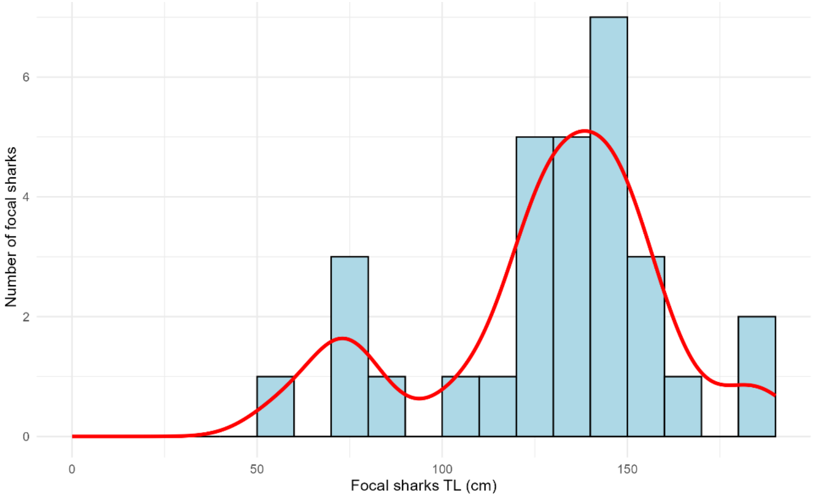


**FIGURE 10 –** Individuals size distribution histogram in 10 cm bins with kernel density line overlaid.

When TL was compared with mean TBC per individual and mean swim speed, both relationships were statistically non-significant ($p > 0.05$). TL had no effect on mean TBC ($R^2 = 0.061$, $p = 0.189$) and swim speed was also not correlated to body length ($R^2 = 0.052$, $p = 0.226$) (Figure 11 and 12).

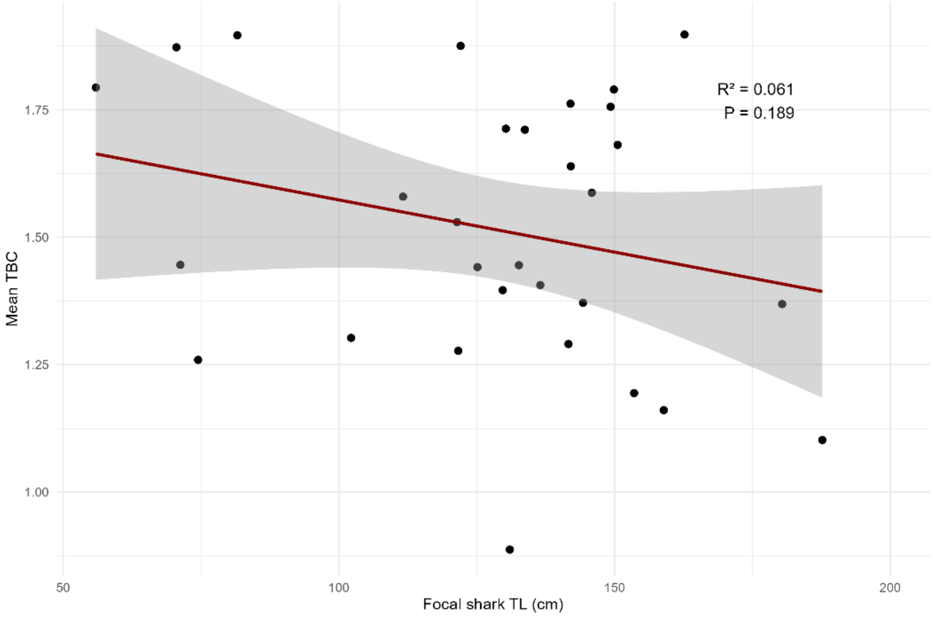


**FIGURE 11 –** Relationship between the smooth hammerhead shark (*Sphyrna zygaena*) TL (in cm) and mean TBC per shark with regression line and respective confidence interval, $R^2$ and *p* of the relation (n = 30).

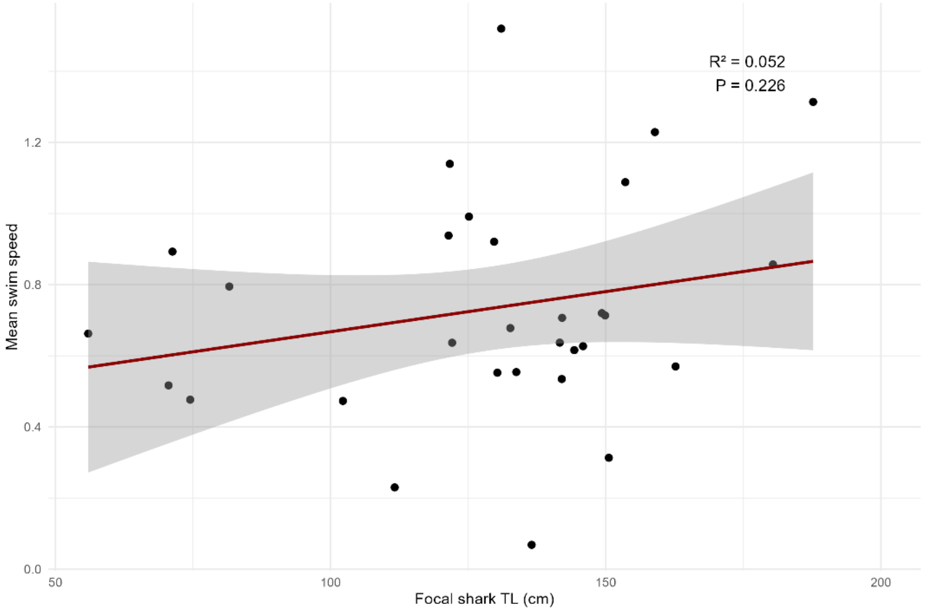


**FIGURE 12 –** Relationship between the smooth hammerhead shark (*Sphyrna zygaena*) TL (in cm) and mean swim speed per shark with regression line and respective confidence interval, $R^2$ and *p* of the relation (n = 30).

## 3.3. Tail beat cycles

From the total of 37 individuals tracked, 34 individuals had identifiable tail beats, summing a total of 5,985 tail beat events recorded through the course of 8,989.78 s. The distribution of all the recorded TBCs is shown in Figure 13. Data distribution was not considered normal (Kolmogorov-Smirnov test: $p < 0.05$), being visibly slightly skewed to the left. The mean TBC time was 1.5 s (± 0.3 s standard deviation), with a median of 1.6 s. The most frequent class was 1.6–1.7 s, with just under 800 occurrences. Observed values ranged from a minimum of 0.1 s to a maximum of 3.0 s.

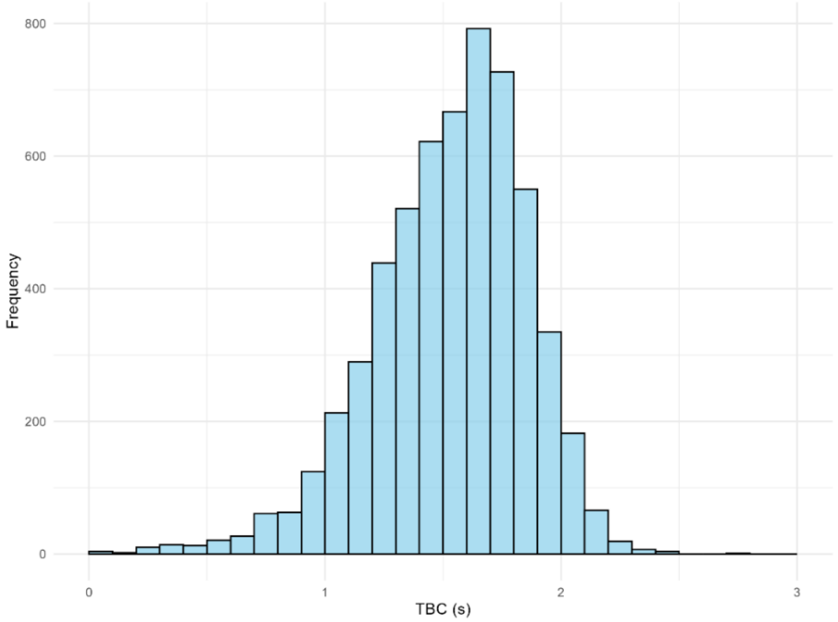


**FIGURE 13 –** General TBC histogram in 0.1 s bins.

When TBC was plotted against swim speed, the negative relationship explained only a small proportion of the variance in swim speed ($R^2 = 0.109$). Nevertheless, the fitted regression line was statistically significant ($p < 0.05$), indicating that, despite the weak explanatory power, the association between TBC and swim speed was not random. Importantly, the relationship between the TBC and swim speed was negative, with longer TBC associated with slower swim speeds (Figure 14).

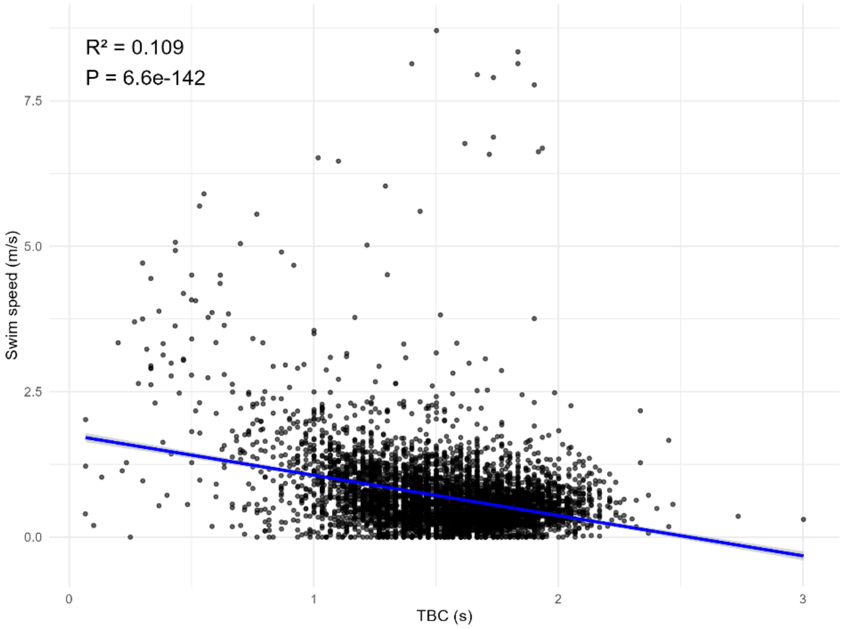


**FIGURE 14 –** Relationship between the smooth hammerhead shark (*Sphyrna zygaena*) TBC and swim speed, with regression line and respective confidence interval, $R^2$ and $p$ of the relation.

## 3.4. Behaviours

Through the entire tracking time at which the sharks were visible, a total of 11 different behaviours were identified according with Table I. The number of individuals presenting each of the behaviours identified varied from 21 sharks showing “descent” swimming to only 3 sharks showing “follow” behaviour, across the total of 37 sharks tracked (Table III).

From all the behaviours, “directional” swimming was the most frequent behaviour observed across individuals with 48.6% of the total duration of the tracks being employed in this behaviour. “Surface” was the second most common, identified for 14% of the observable time. Then, “cruising” was the third most common behaviour, with 11.7% of the duration of the tracks, and all the other swimming behaviours below 10% (Figure 15).

**TABLE III –** Behaviours summary statistics.

| Behaviour | Nº individuals | Occurences | Total duration (s) | Duration mean (s) | Duration SD (s) | % of time |
|---|---|---|---|---|---|---|
| Approach | 4 | 4 | 57.8 | 14.4 | 10.2 | 0.5 |
| Ascent | 12 | 19 | 350.7 | 18.5 | 14.4 | 2.8 |
| Burst | 10 | 13 | 75.4 | 5.8 | 4.7 | 0.6 |
| Circle | 5 | 8 | 184.9 | 23.1 | 8.1 | 1.5 |
| Cruising | 9 | 9 | 1454.5 | 161.6 | 98.9 | 11.7 |
| Descent | 21 | 35 | 633.9 | 18.1 | 14.2 | 5.1 |
| Directional | 19 | 81 | 6056.3 | 74.8 | 59.4 | 48.6 |
| Follow | 3 | 4 | 50.2 | 12.5 | 5.9 | 0.4 |
| Parallel | 4 | 10 | 148.7 | 14.9 | 14.9 | 1.2 |
| Surface | 14 | 45 | 1740.8 | 38.7 | 60.4 | 14 |
| Zigzag | 6 | 9 | 450.1 | 50.0 | 44.0 | 3.6 |

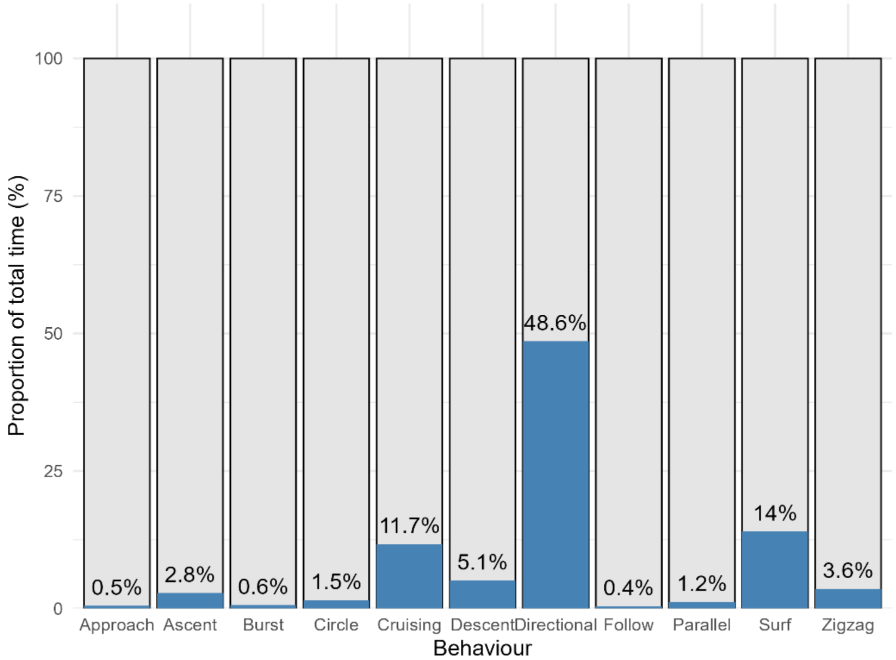


**FIGURE 15 –** Time budget (% time) by behaviour.

The sharks' TBC differed significantly between the different behaviours (Kruskal-Wallis: $p < 0.05$). Dunn's post-hoc test (Benjamini–Hochberg correction) revealed one major statistical grouping, "approach" (median TBC = 1.2 s, IQR: 1.1-1.4), "follow" (median TBC = 1.3 s, IQR: 1.1-1.5) and "zigzag" (median TBC = 1.2 s, IQR: 1.0-1.6), which showed significantly shorter TBC values than most of the other behaviours. "Burst" was the only exception (median TBC = 0.5 s, IQR: 0.36-0.68), presenting the smallest TBC values of all the behaviours, as expected based on its definition. In contrast, the TBC values of "circle" (median TBC = 1.9 s, IQR: 1.7-

2.0) and “cruising” (median TBC = 1.8 s, IQR: 1.6-2.0), were the longest among all the behaviours, with their median TBCs lasting more than three-fold the time of the ones in “burst” ($p < 0.05$). Observing the behaviours interquartile ranges for TBC, “zigzag” is the behaviour with the biggest variability (Figure 16).

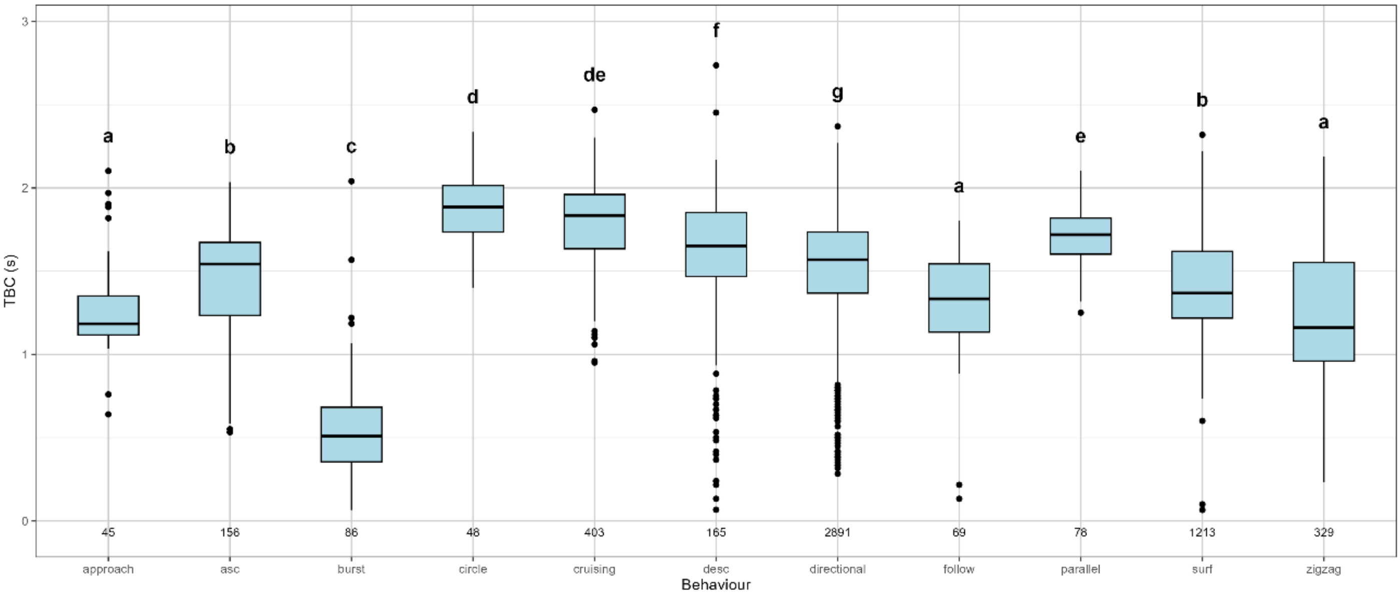


**Figure 16 –** TBC boxplots by behaviour. The central lines represent the medians, the boxes indicate the interquartile range (IQR), and the whiskers extend to 1.5 × IQR. Outliers are shown as individual points and the numbers below boxes indicate the TBC counts for the respective behaviour. Different letters above the boxes denote statistically significant differences according to Dunn post-hoc tests with Benjamini–Hochberg correction ($p < 0.05$). Groups sharing the same letter are not significantly different.

The sharks’ swim speeds also differed significantly between the different behaviours (Kruskal-Wallis: $p < 0.05$). From the Dunn’s post-hoc (Benjamini–Hochberg correction) statistical groupings identified, “approach”, “ascent”, “descent” and “parallel” formed the group with the slowest swim speeds, and although not significantly different from the other behaviours in the group “ascent” had the lowest median swim speed of all (median swim speed = 0.4 m/s, IQR: 0.3-0.6). On the other hand, “circle”, “cruising”, “follow”, “surface” and “zigzag” belonged to the group with some of the fastest swim speeds. However, “burst” swim speeds (median swim speed = 2.5 m/s, IQR: 1.3-3.6) are the ones that are the fastest among all the behaviours, significantly differing from all the other behaviours ($p < 0.05$). “Burst” was also the behaviour with the biggest interquartile swim speed variability (Figure 17).

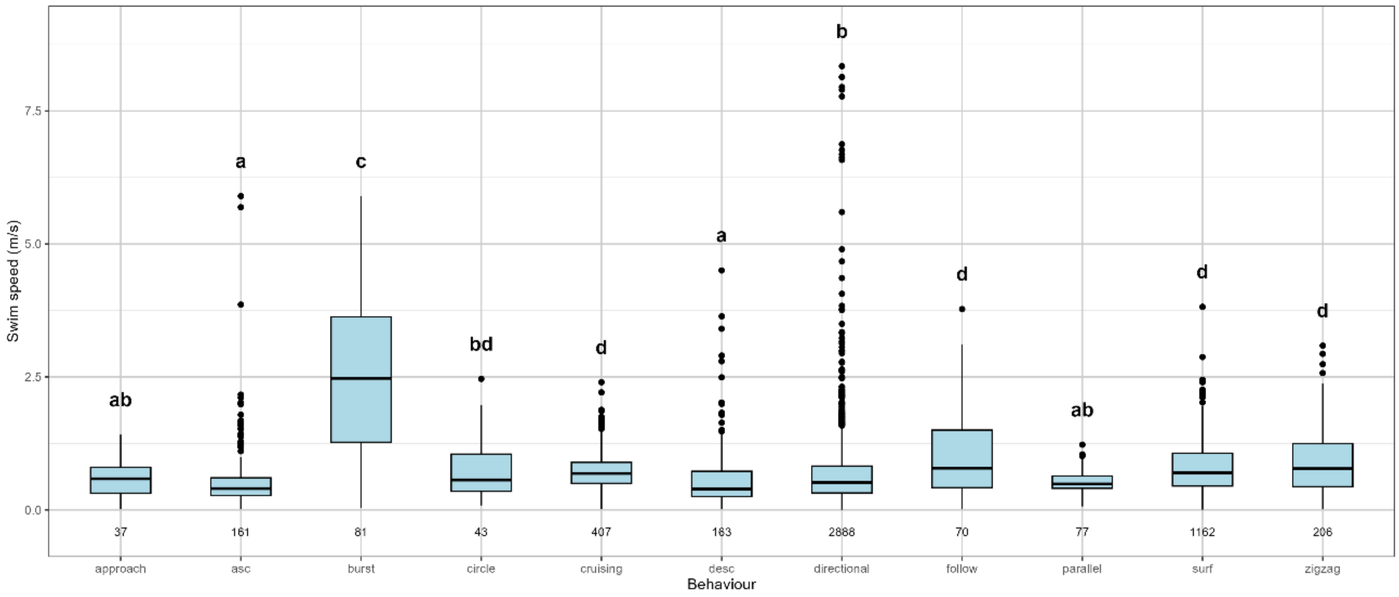


**FIGURE 17 –** Swim speed boxplots by behaviour. The central lines represent the medians, the boxes indicate the interquartile range (IQR), and the whiskers extend to 1.5 × IQR. Outliers are shown as individual points and the numbers below boxes indicate the swim speed counts for the respective behaviour. Different letters above the boxes denote statistically significant differences according to Dunn post-hoc tests with Benjamini–Hochberg correction ($p < 0.05$). Groups sharing the same letter are not significantly different.

## 3.5. Biotic contexts

During the tracking videos, four main biotic contexts that can potentially influence individuals' behaviour were identified – "conspecific", "potential prey" "anthropogenic" and "none", defined as the absence of any of the other biotic contexts. The number of sharks sampled under each context varied from 7 sharks in the presence of "anthropogenic" activities, summing a total duration of 264.69 s, to 27 sharks in the presence of "conspecifics", summing a total of 2653.12 s (Table IV).

**TABLE IV –** Biotic contexts summary statistics.

| Ecological context | Nº individuals | Occurences | Total duration (s) | Duration mean (s) | Duration SD (s) | % of time |
|---|---|---|---|---|---|---|
| Anthropogenic | 7 | 7 | 264.7 | 37.8 | 54.6 | 2.1 |
| Conspecific | 27 | 91 | 2653.1 | 29.2 | 33.0 | 21.3 |
| Potential prey | 11 | 15 | 672.5 | 44.8 | 51.6 | 5.4 |
| None | 37 | 124 | 9442.0 | 76.1 | 143.8 | 74.0 |

The proportions of time each behaviour occupied within the total duration of each of the contexts "none", "conspecific", "potential prey" and "anthropogenic" are represented in Figure 18. In the context "none", the most common identified behaviours were "directional" for 51.4% of the time, "surface" for 15.2% of the time and "cruising" for 12.7% of the time. Behaviours that required the presence of one of the contexts were completely absent –

"approach", "follow" and "parallel". Each of the rest of the behaviours occupied all a smaller portion of the time (less than 10%).

Similarly to "none", in the presence of "conspecific", the "directional" was the behaviour with the biggest presence (33.9%), despite the marked reduction in its presence in relation to "none". "Follow" and "parallel" were present in less than 10% of the total conspecific context duration – 1.9% and 5.6% respectively – but contrast with the other three contexts where they were completely absent. "Circle" swimming also contrasts from its presence in other contexts for being present in conspecific for more than twice the percentage of time it was present in any other context. The conspecific context presented the lowest percentage for the "surface" (4.3%) behaviour, with a reduction of at least three-fold in relation to the other three contexts. Each of the remainder behaviours also occupied less than 10% of the total recorded time with conspecifics.

In the context "potential prey", "directional" (32.3%) keeps the most common behaviour place, but with a similar percentage time occupied by the emergent "zigzag" behaviour (32.1%). "Surface" follows occupying 23.3% of the time. In contrast to the "none" and conspecific contexts, "cruising" was completely absent in the presence of potential prey. The rest of the behaviours had all presence percentages under 10%, yet, from those, "burst" had more than four-fold the presence time identified in "none" and conspecific.

Finally, when "anthropogenic" activities were identified, "zigzag" swimming shifted to the most common behaviour, occupying 57.5% of the context time and "directional" presence (2.9%) suffered a reduction by at least a factor of ten in relation to any of the other contexts. "Surface" swimming followed as the second most common behaviour occupying 26.6% of the context time, in similarity to the percentage of time it occupied in the presence of potential prey. Just like in the presence of potential prey, "cruising" was absent once again in the presence of anthropogenic activities. "Circle" swimming was only absent in this context. The rest of the behaviours occupied less than 10% of the duration of the anthropogenic context. However, "burst" and "approach" occupied more time from this context than from any other, with "burst" (8.8%) occupying four-fold the time it did in potential prey and substantially more than that when compared to the other two contexts, and "approach" (9.5%) occupying twice the time it did in potential prey and also substantially more than that in relation to the other two.

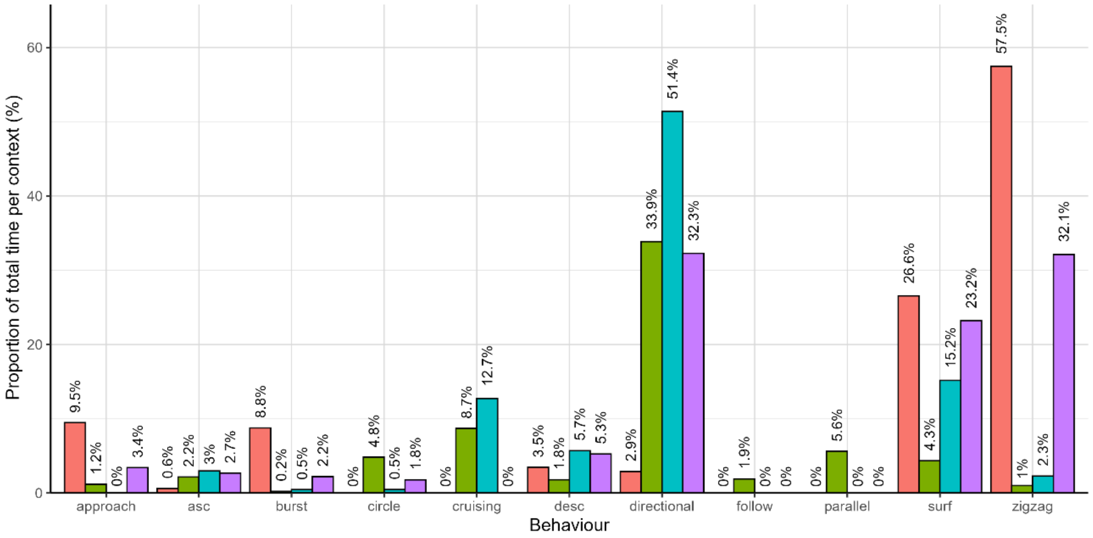


**FIGURE 18 –** Proportional time of each behaviour for the duration of each biotic context. Each column represents the proportion of total time of one behaviour as a percentage of the total time of the respective context. Here colour indicates the context (red – "anthropogenic", green – "conspecific", blue – "none" and purple – "potential prey") and the proportion is given at the top of each column.

The different biotic contexts TBCs differed significantly among them (Kruskal-Wallis: $p < 0.05$). The Dunn's post-hoc test (Benjamini–Hochberg correction) revealed that sharks evidenced significantly longer TBCs in the presence of "none" (median TBC = 1.60 s, IQR: 1.37-1.77) and "conspecific" (median TBC = 1.59 s, IQR: 1.37-1.75), with no differences found between the latter two. "Potential prey" TBC values (median TBC = 1.07 s, IQR: 0.94-1.27) were in an intermediate position, being shorter than in the two contexts just mentioned but a little longer than in the presence of "anthropogenic". "Anthropogenic" TBC values were the shortest of all the contexts (median TBC = 0.98 s, IQR: 0.82-1.16) ($p < 0.05$; Figure 19).

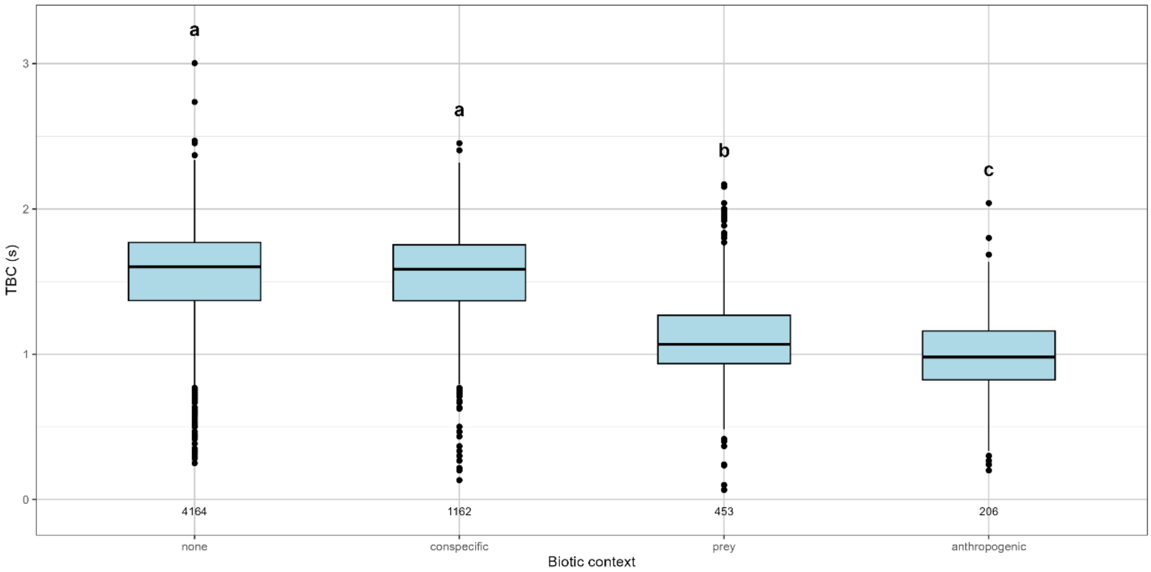


**FIGURE 19 –** TBC boxplots by biotic context, including "none" as the absence of identifiable biotic contexts. The central lines represent the medians, the boxes indicate the interquartile range (IQR), and the whiskers extend to 1.5 × IQR. Outliers are shown as individual points and the numbers below boxes indicate the TBC counts for the respective context. Different letters above the boxes denote statistically significant differences according to Dunn post-hoc tests with Benjamini–Hochberg correction ($p < 0.05$). Groups sharing the same letter are not significantly different.

## 3.6. Anthropogenic effects

To assess the response of the sharks to boats in more detail, TBC was visualized across time (Figure 20). In the single usable video, the boat approach triggered a marked response, with a fast drop in the TBC from a median of 1.5 s (IQR: 1.4-1.6), before the boat appeared, to a minimum of 0.2 s moments after the boat entered the field of view and stayed under 1.0 s for approximately 9.9 s. After the boat passed (duration of 54 s), TBC values increased gradually but never reached the initial state, with a median TBC of 1.4 s (IQR: 1.3-1.5). Behaviours observed before the appearance of the boat in the field of view included "cruising", "descent" and "ascent". While the boat was in the field of view, approximately for 7.5 s, the only behaviour possible to identify was "burst", starting when the distance between the front of the boat and the dorsal fin of the individual was 11.8 m. After the boat left the field of view no specific behaviours from those described in this study were possible to identify, with some direction changes but not sufficiently continuous and abrupt to fit the "zigzag" classification. The other individuals approached also changed the swimming behaviour, however, due to the changes of depth ("descent" behaviour), the individual was lost from sight even before the post-boat approach behaviours could be recorded, and data on the TBC of those individuals could not be extracted either due to the same reasons. Nonetheless, behaviours identified moments before the boat entered the field of view included "burst" and "descent", after which the individuals were lost from sight.

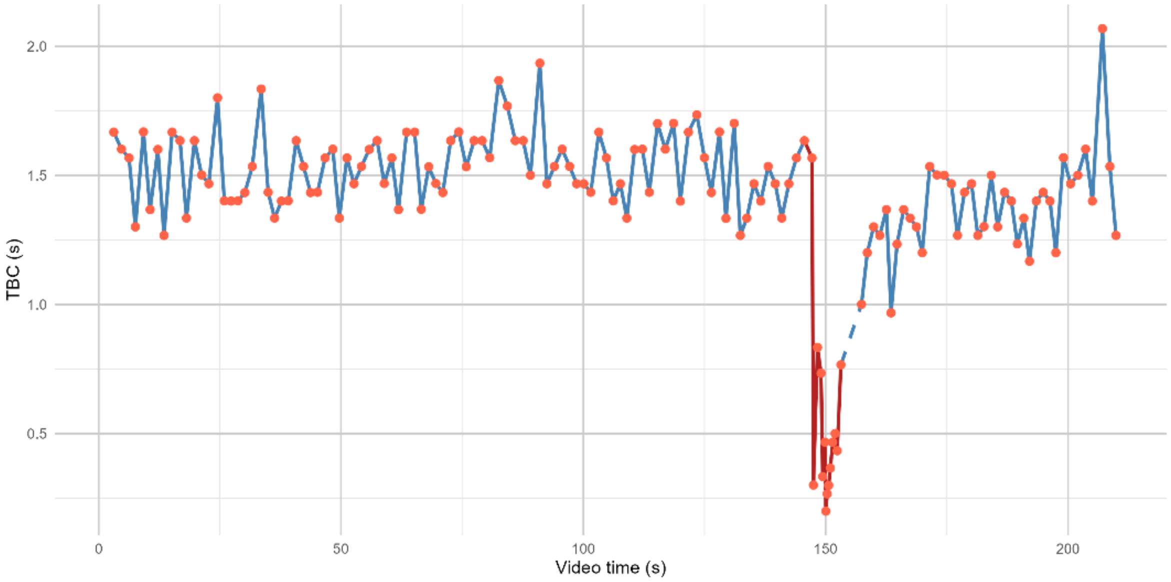


**FIGURE 20 –** Variation of TBC throughout time for one of the individuals approached by boat (Red line identifies the time in which the boat was in the frame of view; Dashed line indicates an interruption of the TBC counts due to loss of visual on the tail tip).

# 4. Discussion

These results offer the first insights into the juvenile smooth hammerhead shark behaviour near the surface, by means of UAV observations. Behaviours identified at the surface varied in frequency as well as between the overall kinematic parameters under different contexts, suggesting a possible optimisation of their movement strategies under specific ecological context.

## 4.1. Tracking vs transect flights

Comparison of the data output for the two observation methods, tracking and transect flights, indicated clearly that the tracking flights are a better method to characterize smooth hammerhead shark behaviour near the surface, since the much lower time in the field of view of the transect individuals makes it difficult to analyse TBC and identify the described behaviours. This is in conformity with previous UAV studies which utilized similar methods to investigate swimming kinematics and specific behaviours (Bevan *et al.*, 2016; Torres *et al.*, 2018; Oleksyn *et al.*, 2020; Lauridsen *et al.*, 2025). Nonetheless, transect flights would be more adequate to study species population parameters, like geographical distribution, size distribution and abundances (Hodgson *et al.*, 2013; Barasona *et al.*, 2014).

## 4.2. Size and age characterization

The pixel/cm ratio combined with the highly resolved UAV altitude data allowed for measurements of the tracked sharks, revealing size classes from neonates (56 cm) to immature juveniles. The smallest shark recorded in this study measured 56.0 cm total length, which within the size range reported at birth from previous studies, between 42 cm and 61 cm (Compagno, 1984; Coelho *et al*. 2011; Nava & Márquez-Farías, 2014; Francis, 2016; Miller, 2016). This suggests that the smallest individual recorded in this study most likely was a neonate. All the sharks sampled were smaller than 190 cm TL size, which is below the size at maturity, both for males (210-250 cm) and females (250-270 cm) (Miller, 2016), corroborating the previous reports that the area is an island nursery for the smooth hammerhead sharks (Afonso *et al*. 2022). The most common TL in this study was 140-150 cm, which is close to the most common sizes of 130-140 cm for the hammerheads described by Das *et al*. (2025) using experimental fishing and baited remote underwater video (BRUV) size estimations in the same area. This similarity among the size modes of this study and of Das *et al*. (2025) also supports the suitability of the size estimation method used in our study – UAV photogrammetry – to estimate the smooth hammerhead sizes in a coastal nursery. According to Francis (2016), if the sharks grow linearly in the first 4 years of life they should have approximately 85 cm, 115cm, 145 cm and 176 cm of TL in the first, second, third and fourth years of life, respectively, which means that the most common age in the sampled sharks should be 3 years-old. And since the maximum TL size registered was of 187.7 cm, the sharks sampled must have a maximum of 4 to 5 years-old.

No relationship was found between the shark's size and their kinematic metrics, TBC and swim speed. Changes in swimming speed and TBC across different sizes have been suggested for several elasmobranch species (*Carcharodon carcharias*, Anderson *et al*., 2022; *Bathytoshia brevicaudata*, Oleksyn *et al*., 2020). Because *Sphyrna zygaena* exhibits positive allometric growth in the weight–length relationship (Nava & Márquez-Farías, 2014) – individuals become proportionally heavier and more robust as they grow –, and given the potential for sharks with different body shapes to modulate their swimming kinematics to improve efficiency (Lowe, 1996), ontogenetic shifts in TBC or swimming speed were expected. However, the present results are more in line with the results of Porter *et al*. (2022), that also did not find any differences for the epaulette sharks, *Hemiscyllium ocellatum*, tail beat frequency at different life stages. A possible explanation for the inexistence of such relation in our study could be the lack of a better representation for each of the sizes sampled or maybe even the choice of the TL as the parameter to describe the individual's size. The cephalofoil is thought to influence hammerhead shark movement (Sternes & Higham, 2022), thus maybe the inclusion of the cephalofoil width would be a better method to reveal any relation between size and the kinematic parameters that may exist.

## 4.3. Tail beat cycle differences

This study presents the first approach to describe the smooth-hammerhead behaviours at the surface at a nursery and also the first to study TBC or swim speed for this species. Afonso *et al*. (2022) used acoustic telemetry to understand the long-term movement patterns and residency of these juveniles around the nursery across the year, as well as to investigate the diel patterns of habitat use and seasonal effect. However, until now, the surface swimming behaviour of this species had not been investigated.

Smooth hammerhead sharks exhibited a relatively slow swimming rhythm for hammerhead sharks, with a mean TBC of 1.5 s. Available data on juvenile scalloped hammerhead sharks suggests lower TBCs, with average TBCs typically below 1.0 s (Lowe, 2001; Lowe, 2002; Nieder et al., 2023 – values were converted to match the units used in this study). Given the morphologic similarities between the two hammerhead species (Gallagher & Klimley, 2018) and identical life stage in the two studies, such differences are unlikely to be exclusively driven by anatomy, suggesting that environmental or methodological conditions may be involved in shaping these values. Indeed, all these scalloped hammerhead observations were conducted in confined environments, whereas the smooth hammerheads in this study were recorded freely swimming in their natural habitat and without attached instruments. In a study of shortfin mako sharks (*Isurus oxyrinchus*) with biologgers in the wild (Waller *et al*., 2023), estimated TBC average was of 2.0 s (converted from Hz), closer to the results of this study. The relative proximity between the mean TBCs of these two morphologically very different species supports the idea that the differences between the results reported in this and those from the scalloped hammerhead studies may be mostly due to the differences in the environment of the study, although intrinsic species-specific differences cannot be excluded. These results highlight the importance of obtaining baseline data on natural behaviour through remote, non-invasive methods, such as the UAVs used in this study.

The minimum TBC recorded in this study (0.1 s) was exceptionally low compared with values reported for other shark species. For instance, Waller *et al*. (2023) documented minimum TBCs of approximately 0.2 s (correspondent to 6.49 Hz of TBF) for shortfin mako sharks (*Isurus oxyrinchus*), one of the fastest known sharks. Such discrepancies may be partly due to methodological differences, as TBF in most studies are estimated from tri-axial accelerometer data through continuous wavelet transformation (CWT) (Sakamoto *et al*., 2009; Saraiva *et al*., 2023; Waller *et al*., 2023). Low-amplitude oscillations, such as those recorded here, might not be detectable or considered by those methods. Moreover, the attachment site of biologgers, often on the dorsal fin (Waller *et al.*, 2023), can limit the detection of such subtle movements of the tip of the tail, as sensor placement has been highlighted as an important consideration to process accelerometer data (Williams *et al.*, 2019). Behaviourally, the very short TBCs observed here appeared to follow sharp turns and likely correspond to small corrective tail motions rather than full propulsive strokes, further explaining their low amplitude. Although this explanation is the most likely, it is also possible that the exceptionally low TBC value resulted from the limited temporal resolution of the video. The small number of frames between the start and end of this TBC may have led to an underestimation of its duration.

At the opposite extreme, the maximum TBC (3.0 s) also occurred during a sharp turn within a “zigzag” movement, where tail beat amplitude was considerably larger than usual. Together, the specific nature of these extreme TBC values and these findings underscore the importance of incorporating tail beat amplitude as a kinematic metric in future behavioural analyses, as demonstrated in blacktip sharks (*Carcharhinus limbatus*) by Porter *et al.* (2020), and underscores the unique capability of UAVs to identify and characterise brief or unusual behavioural patterns that could potentially be missed by other methods.

Despite the linear relationship between the sharks’ TBC and swim speed, the relationship could potentially improve if some methodology adjustments were made. Previous studies have also identified linear relationships between TBF and swim speed of scalloped hammerhead sharks, shortfin mako sharks and blacktip sharks (Lowe, 1996; Lowe, 2002; Porter *et al.*, 2020; Waller *et al.*, 2023). However, correlation was always stronger than in the present study ($R^2$ = 0.109). This difference likely reflects methodological limitations rather than biological differences. Therefore, the result could potentially improve if it was possible to compare the TBC with high resolution swim speed measurements from biologging for instance, instead of using the UAV swim speed data. The use of a small circle in the centre of the screen could potentially help maintaining the shark always in the centre of the field of view with even more precision, but the UAV would still be limited by the delayed response to rapid changes in shark swim speed. For this reason, summary statistics such as mean or median values are likely to provide more robust descriptors than instantaneous measures, and extreme values should be interpreted with caution.

## 4.4. Behaviour characterization

The behaviours identified and described in this study represent an important step towards understanding the behavioural patterns of this species. To date, no other study has provided such a description for the smooth hammerhead. Only a few studies have examined the behaviour of closely related species to the smooth hammerhead such as the bonnethead shark *Sphyrna tiburo* (Myrberg & Gruber, 1974), or focused on diving behaviour and long-term movements of juvenile smooth hammerheads (Afonso *et al.*, 2022). However, none has offered a detailed behavioural description of this species, nor attempted to quantify the frequency of each behaviour to understand how smooth hammerheads allocate their time and energy. Such information is crucial to determine how a species optimises its movement strategies, ultimately influencing individual growth and fitness (Papastamatiou, 2018; Weihs & Webb, 1983).

The predominance of behaviours such as "directional" swimming (48%) and cruising (11.7%) observed in *Sphyrna zygaena* likely reflects an energy optimization strategy. Behaviours which require frequent direction changes have been pointed out as energetic costly (Wilson *et al.*, 2013), and the "directional" and "cruising" were characterized exactly by the opposite, in contrast to behaviours such as "zigzag" or "circling". Besides, Lowe (2001) described the cost of transport (COT) net curve for juvenile scalloped hammerheads as a slightly U-shaped function of swimming speeds, where energy expenditure is minimized at intermediate swim speeds. Given the morphological similarities between that species and the smooth hammerhead, it is reasonable to assume a similar COT profile for both. In this study, "directional" swimming exhibited intermediate values of both TBC and swim speed compared to other behaviours, further supporting the idea that this behaviour optimizes energy use. Similarly, "cruising" showed some of the longest TBCs recorded and because TBC has been described to be inversely related to oxygen consumption (energetic cost) (Lowe, 2001), these long TBCs suggest that this behaviour, despite involving higher swim speeds, is also energetically efficient. Thus, the dominance of linear swimming behaviours like "directional" and "cruising" likely reflects an adaptive strategy for energy optimisation during sustained movement.

The "surface" swimming functions are more difficult to attribute, because although swimming close to the surface could be related to behavioural thermoregulation (Thums *et al.*, 2013), the functions of the specific case of swimming with the dorsal fin out of the water – which was considered as the "surface" behaviour – are more difficult to understand. However, the notable proportion of "surface" (14%) adds important methodological insights to the study of juvenile smooth hammerheads in this context. Since sharks swam with the dorsal fin out of the water during such a portion of the survey time, this behaviour may allow enough time of contact with satellites to collect data from fin-mounted biologgers (Eckert & Stewart, 2001) and accompany their positions throughout the day.

In general, all the smooth hammerhead sharks in this study were swimming close to the surface, which may serve thermoregulatory functions, as thermoregulatory behaviours have been described for several species (Speed et al., 2012; Thums et al., 2013; Watanabe et al., 2021). In fact, even the smooth hammerhead close relatives, scalloped hammerhead sharks, have been found to ‘hold their breath’ as a thermoregulation strategy during deeper dives (Royer *et al.*, 2023). Blacktip reef sharks, *Carcharhinus melanopterus*, have also been described to use shallow water during daytime periods to potentially regulate their temperature to maximize ingestion rates through the increased digestion rates it may provide (Papastamatiou *et al*., 2015). This could well be the case for these juvenile smooth hammerheads, potentially allowing individuals to absorb solar radiation in warmer surface waters before descending into cooler depths.

The vertical transitions observed – “descent” (5.1%) and “ascent” (2.8%) – could serve many functions, including small foraging dives to investigate clues initially detected from the surface. “Ascent” and “descent” belonged to the group of behaviours that had the slowest swim speeds. Increased capability of hammerhead sharks to adjust their head angle when compared to other carcharhiniform sharks has been described by Nakaya (1995) to possibly increase the shark manoeuvrability acting as an anterior rudder, and Gaylord *et al.*, (2020) confirmed that it is possible that the adjustment of the cephalofoil angle could create dynamic lift, but at an increased drag and high energetic cost. Therefore, the slower swim speeds identified for “ascent” and “descent” may be caused by the increased drag that occurs on the cephalofoil surface if the smooth hammerheads adjust their head angle to assist with the upward and downward direction changes, respectively.

Behaviours like “zigzag” (3.6%), “circle” (1.5%), “parallel” (1.2%), and “follow” (0.4%) are more complex and their low duration might mean they have more specific functions. “Follow” and “parallel” swimming have been documented in other elasmobranchs as social behaviours, such as courtship and may be involved in mechanisms of social learning (Harvey-Clark *et al.*, 1999; Martin, 2007, Guttridge *et al.*, 2013). Due to the young age of the individuals studied, courtship related functions can be excluded, leaving the social learning mechanism as the most likely function. “Circle” swimming has not been described in any juvenile individuals. A similar behaviour to a “follow” has been described for multiple basking sharks organized in a circular follow formation, assigned to courtship behaviour (Sims *et al.*, 2022). “Zigzag” has been previously described as manoeuvring and is associated to foraging or hunting (Myrberg &Gruber, 1974). Besides these potential functions and “zigzag” inherent requirement of direction changes, it has among the shortest TBCs and fastest swim speeds of all behaviours. Therefore, it must be one of the behaviours associated with the highest energetic costs, concurring with “burst” and contrasting with “directional” and “cruising”.

Although rare (0.6%), “burst” events may reflect high-arousal states, such as predator evasion, prey pursuit or even withdrawal from social encounters (Klimley, 1985; Moyano, 2023; Sayama *et al.*, 2024). In fact, despite not presenting constant changes of direction like “zigzag”, “burst” TBC values are the shortest of all behaviours and swim speeds values are the fastest of all the behaviours. These bursts of speed are energetically costly due to the increased muscular effort and elevated oxygen consumption (Williams *et al.*, 2020). In predators, such anaerobic bursts are typically followed by recovery periods (Williams *et al.*, 2020), which combined with its low frequency occurrence suggests that these behaviours are reserved for critical moments.

## 4.5. Context-dependent swimming behaviour

Diverse biotic factors have been described to influence fish and shark behaviour (Dill, 1983; Schlaff *et al.*, 2014). This study suggests that factors like the presence of “conspecifics”, “potential prey” or “anthropogenic” activity may drive behaviour shifts, but also the duration and frequency of each behaviour, with implications in the general swimming parameters.

In the context “none”, low-cost behaviours were dominant. The most common behaviours were “directional”, “surface” and “cruising”, from which “directional” and “cruising” are expected to be energetically low-cost behaviours. In its ethogram, Klimley *et al.* (2023) included, under the category “maintenance behaviours”, the behaviour “slow straight-line swimming”, which is the closest match to the described “directional” and “cruising” in our study.

Similarly, with “conspecific” presence, the sharks also engaged in low-cost behaviours, prioritizing the same two energetically low-cost behaviours, “directional” and “cruising”, and social behaviours emerged – “follow” and “parallel”. Besides the presence of the low-cost behaviours, the overall low-cost of the shark’s activity in the presence of “conspecific” could be further supported by its grouping with the context “none” as being the two contexts with the longest TBCs. When comparing the presence of “circle” behaviour between contexts, its higher occurrence in the “conspecific” context suggests that it may serve a social function, although its exact nature remains unclear. However, the small number of sharks observed exhibiting this behaviour adds some uncertainty to such interpretations, as such a rare and sporadic occurrence limits the strength of any conclusions that can be drawn.

When in the vicinity of “potential prey”, sharks showed a clear shift in behaviour towards more energetically costly activities. Compared with the “none” and “conspecific” contexts, this situation was marked by the appearance of “zigzag”, an increase in “burst”, and the disappearance of “cruising”, a low-cost behaviour. These changes were reflected in the significant differences between the TBCs of the pairs “potential prey”-“none” and “potential prey”-“conspecific”, indicating a higher activity rate near prey. As predators, sharks are expected to increase activity (shorter TBCs) and swim speed when close to potential prey to enable pursuit and capture (Lowe, 1996; Williams *et al*., 2020). This increased effort involves greater energetic expenditure but represents an adaptive trade-off that enhances feeding success. The stronger expression of “zigzag” and “burst” in the “potential prey” context further supports their interpretation as predation-related behaviours, consistent with observations in other species (Myrberg & Gruber, 1974; Ebert, 1991; Sayama *et al*., 2024)

Finally, in the “anthropogenic” context the sharks also engaged in high energetic-cost behaviours, with the shortest TBC indicating the highest energy expenditure of all four biotic contexts. The most common behaviours observed were “surface”, “approach”, and “zigzag” swimming, the latter being the most frequently observed behaviour, and possibly one of the most energetically costly behaviours identified in this study. Besides those behaviours, the fact that “burst” occupied at least four-fold the proportion of the total context time it did in any other context also deserves its attention on this context, especially when considering that it is the second of the two behaviours considered to require the highest energetic expenditures. In addition to serving predatory functions (Ebert, 1991), “burst” behaviour in this context may be related to an escape response from a perceived threat, which has been pointed out to happen in presence of predators or something perceived as such (Moyano, 2023). The higher relative time allocation to such behaviours in the “anthropogenic” context likely explains why its TBC values were significantly lower than in any other context. This pattern indicates that energetic expenditure under “anthropogenic” influence may even exceed that of the “potential prey” context, yet without any of the potential benefits that come with it.

The frequent use of energetically demanding behaviours such as “burst” and “zigzag” in response to “anthropogenic” indicates that human interactions may impose significant energetic costs. Considering that animals develop strategies to optimize energy use and that not even in predatory situations – which may have the reward of food intake – they spend such a proportion of time in those behaviours, then these behavioural responses may have potentially significant detrimental effects on the individual fitness and growth. According to Williams *et* *al*. (2020) predators respond differently to threats from how they would behave while hunting, because the offsets of being hunted down are way bigger than the offsets of losing an opportunity to hunt prey, leading individuals to push beyond their energetic limits to avoid potentially hazardous situations. The TBC differences (energy use) observed between the contexts "potential prey" and "anthropogenic" support this hypothesis.

Overall, these patterns suggest that "potential prey" and "anthropogenic" presence tends to elicit a relatively more frequent use of energetic costly behaviours such as "burst" and "zigzag", while "conspecific" presence and the absence of identifiable external stimuli, "none", are more associated with low-cost behaviours like "cruising" and "directional". This highlights the potential influence of human activities and prey availability on the behavioural strategies and energy expenditure of the studied individuals.

## 4.6. Anthropogenic effects

Although the major perturbation caused by the boat approach does not last more than 10 s, the decrease of the TBC to 0.2 s reveals the extreme behavioural impact that a perceived threat may have on a surface swimming juvenile shark. This is in line with the expected response to "anthropogenic" disturbance, considering the metabolic differences between hunting and hunted responses described by Williams *et al*. (2020). Despite the TBC and swim speed having returned to levels closer to the baseline, the metabolic rate is expected to stay high even hours after the activity decrease (Gleeson & Hancock, 2001). As a consequence, a realistic estimation of the boat approach effect on the shark's energetic expenditure is difficult to achieve from quantifying anthropogenic activity alone, calling for a need to be wary of the number of boats passing that may cause a chronic elevated metabolic rate, even if boat traffic, or other human disturbances, are not continuous or persistent.

Additionally, the fact that the behaviours that were being carried out before the boat approaches were interrupted and substituted by a different and possibly higher energetic cost behaviour, or by no identifiable behaviour at all, requires caution since each behaviour has its function and the interruption of any behaviour will prevent the benefits of that behaviour from being collected, independently if the behaviour has to do with maintenance, predation, socialization or other (Martin, 2007; Davies *et al*., 2012, Klimley *et al*., 2023).

Moreover, juvenile scalloped hammerheads have been pointed out for having a very slow growth in the summer season in a nursery in the Hawaiian archipelago, with many exhibiting slow growths and even weight loss (Bush & Holland, 2002; Lowe, 2002). If the smooth hammerhead sharks of the Azores happen to face similar problems, which is not that unlikely due to the morphological similarities between these two species (Gallagher & Klimley, 2018), then the extra pressure exerted by the human activities may be enough to affect the individual's fitness and consequently its survival, especially when summer coincides with the increased tourism and boat traffic around the island.

However, the description of a single observation has limitations to allow extrapolation to a larger scale as it is subject to interindividual variations. Further studies focusing on these and other kinematic variables of the behaviours and other energetic parameters of this species are still needed to be able to understand to what extent the impacts from the human pressures may threat this juvenile sharks' growth and fitness.

## 4.7. Implications for conservation and management

The present findings highlight the potential sensitivity of juvenile smooth hammerhead sharks to human activity, exacerbated by the fact that the sharks and human activities overlap in a nursery area – an especially vulnerable life stage in a critical habitat that requires special conservation and protection. Closing this area to fisheries was proposed by Afonso *et al*. (2022) to prevent the juvenile sharks from being captured. However, these findings show that measures to prevent the effects caused by the human activities, other than fishing, may also be needed.

Since boat cruising was one of the identified activities that impacts shark behaviour, to limit the presence of boats in the nursery area during the peak of their activity at the surface should be considered. Furthermore, limiting boat speed – in the area 0-500 m from coast and during the summer – may help minimizing the effects on the behaviour, since speed of the perceived threat, which in this case was the boat, has been described to be directly related to the intensity of the behavioural response (Seamone *et al*., 2014). The implementation of a minimum allowed distance between boats and an individual or group of individual sharks identifiable from the surface, would also potentially contribute to mitigate the impact of human disturbance, similar to whale watching regulations.

As for the tourism operations – specifically the ones where costumers are in the water with the sharks – to limit the number of persons allowed in the water at one time would be a good compromise, especially if a limitation of the number of operation permits is also implemented, only licensing a specific number of boats and tourism operators through a public bidding process every other year, which is a measure widely implemented for whale watching (Chalcobsky *et al*., 2017). In addition, limiting the daily carrying capacity of the nursery area – for instance, establishing a maximum number of boats allowed per day regardless of the number of active licenses – is another example of measure to consider.

At the same time, it is important to acknowledge that further knowledge is still needed before defining or expanding these measures. From a conservation perspective, this study highlights the need to better understand how behavioural responses to human activities may translate into effects on individual fitness and, ultimately, on population resilience. Future work should aim to quantify the frequency and intensity of disturbances experienced by juvenile smooth hammerheads under current levels of human activity, and determine whether these behavioural responses result in measurable fitness costs. Such knowledge is essential to guide the design of effective mitigation strategies that ensure sharks are not disturbed to levels that threaten their survival, while still allowing the sustainable coexistence of local economic activities, such as tourism and navigation. After all, many livelihoods depend on these activities, and responsible ecotourism not only generates economic value but can also foster public and political support for shark conservation through positive human-wildlife interactions. Continuous monitoring of shark behaviour will therefore be fundamental to evaluate the effectiveness of management actions and to support adaptive conservation strategies as new information becomes available.

## 4.8. Lessons for future shark UAV monitoring surveys

The present study successfully demonstrated the applicability of UAVs for monitoring and quantifying the behaviour of juvenile smooth hammerhead sharks in a remote nursery area. Yet some methodological aspects could still be refined to improve the potential of this tool for future research. The experience gained throughout this work provided valuable insights into both the strengths and the limitations of the approaches used, allowing for the identification of practical adjustments that could enhance the reliability, representativeness, and overall efficiency of shark monitoring programs using aerial platforms.

Some protocol improvement for the transect flights could potentially increase the number of sharks surveyed and consequently the representability of the sample. Transect flights tend to be more appropriate for assessing population parameters (Hodgson *et al.*, 2013; Barasona *et al*., 2014) because of the usually bigger number of individuals sampled, and that expectation of a bigger sample was the reason for the selection of this method, to sample more individuals' behaviours with similar flight efforts. However, transect flights resulted in a small and disproportionate number of shark detections. This limitation probably stems from the patchy distribution of the species, the underrepresentation of certain habitat types, large distances between sampled areas, and the limited sampling effort – factors described to potentially provoke underrepresentation of the actual number of individuals in BRUV surveys (Asher *et al.*, 2017). Methodological alternatives, like rosette-shaped flight designs, proposed by Linchant *et al.* (2023), could increase the area covered in each flight and provide a more representative sample of the smooth hammerhead, but it is probably not a good fit because the high mobility of these sharks increases the probability of the same shark being sampled multiple times. Instead, future transect-based approaches could be improved by adjusting flight paths to run parallel rather than perpendicular to the coastline, and closer to shore, where most individuals seemed to be found. For broader coverage, the use of fixed-wing UAVs could also be advantageous, given their longer flight duration, in comparison to the multi-rotor ones used in this study, which would allow performing continuous transects along the Faial coastline (Butcher *et al*., 2021; Benavides *et al.*, 2019).

Likewise, despite yielding valuable behavioural data, tracking flights could also benefit from some protocol changes. For instance, maintaining a consistent flight altitude around 20 metres would ensure a sufficiently large field of view to capture tail-tip movements and other fine details, and maintain comparability between flights. Standardizing altitude would also minimize variation in the area covered by the camera and improve the accuracy in detecting contextual elements such as conspecifics, prey, or human activities. Additionally, the avoidance of lower than 10-metre-altitude flights would further minimize size estimation errors, since it would both reduce the variation of the pixel-centimetre ratio caused by small, unattained for, changes in height, and reduce the likelihood of big distortion effects from the convex lens that happens if the individuals approach the edges of the frame (Rex *et al.*, 2024). Another measure that could slightly improve measurement accuracy would be accounting for the subject's depth in the water column (Rex *et al.*, 2024), even when already selecting the frames where individuals are closer to the surface as has been done in this study.

For the flights in general, a more systematic and less opportunistic sampling design would also strengthen future monitoring efforts. Conducting flights at consistent times of day, for instance, would help reduce potential biases associated with uneven temporal sampling, although not always possible due to the weather variability. Nonetheless, the present work confirms that UAVs can be a powerful tool to study juvenile smooth hammerhead behaviour in a nursery, with meaningful ecological and behavioural insights obtainable even from relatively small datasets.

Expanding this data set to offer more detailed and robust analysis methods of the differences among behaviours and among contexts should also be considered. The fact that all the anthropogenic activities were englobed under the same context, as a result of the small sample size, complicates the specific attribution of the behavioural changes identified to each of the activities, since their proportions were not exactly the same. With a bigger sample size, the samples could be subdivided in the different anthropogenic activities and would allow differentiations between the effects that each activity has on the behaviour. Additionally, behaviours' and contexts' TBC sample dimensions were very heterogenous, needing bigger samples for the least represented categories to increase analysis strength. It could also be useful to add other kinematic parameters to describe the behaviours and the contexts. For instance, track tortuosity and tail beat amplitude could be objectively described (Oleksyn *et al.*, 2020; Porter *et al.*, 2020)

Further work on how the biotic contexts here explored may interact with diverse abiotic factors would be very useful, since such interactions have been mentioned to potentially drive fine-scale movements of marine animals (Oleksyn *et al.*, 2020). For that, complementary sampling methods would certainly be enriching, like the use of biologgers and ROVs (remotely operated vehicles), to study the sharks at the depths and times of day at which the UAVs' use is limited (Porter *et al.*, 2020).

These methodological considerations will be essential to increase data accuracy and to maximize the scientific and conservation value of future UAV-based shark monitoring programs. Altogether, the refinement of these methodological aspects would consolidate UAV surveys as a practical and cost-effective approach for the long-term monitoring of the local smooth hammerhead nursery, combining reliable abundance estimates from transect flights with high-resolution behavioural data from tracking flights.

# 5. Conclusions

This study provides the first in-situ baseline of juvenile smooth hammerhead (*Sphyrna zygaena*) swimming behaviour at a coastal nursery using UAV imagery. Across 37 sharks, 11 behaviours were identified, with “directional”, “surface” and “cruising” dominating the time budget. Although less represented, the other eight behaviours revealed diversified activity rates. Photogrammetry indicated sharks’ TL sizes ranged between 56.0 and 187.7 cm, with 140-150 cm as the most common size class, reinforcing the suitability of this nursery for early life stages of the smooth hammerhead. However, body size did not influence TBC or swim speed. Overall, mean TBC was 1.5 ± 0.3 s.

Behavioural expression depended strongly on the biotic context. Under “none” and “conspecific” contexts, low activity behaviours such as “directional” and “cruising” were the most common. In the presence of “potential prey”, sharks shifted toward a higher use of “zigzag” and “burst” behaviours, reducing TBC and increasing swim speed, as expected for foraging. “Anthropogenic” presence elicited an even stronger response, with “zigzag” becoming predominant, “burst” frequency quadrupling, and TBC reaching the lowest values among contexts (1.0 s vs. 1.6 s in “none”). These patterns indicate that human activities can impose acute energetic costs on smooth hammerhead sharks, while lacking the compensatory benefits of successful foraging.

From a conservation perspective, quantifying exposure rates and response magnitude to determine whether behavioural changes translate into fitness costs and, ultimately, population-level effects, would potentially be useful to enable proportionate mitigation measures that safeguard sharks while allowing the sustainable coexistence of local economic activities. Continued behavioural monitoring would also be key to evaluate the effectiveness of management actions and to inform adaptive conservation strategies.

UAVs proved to be a cost-effective, non-invasive platform to quantify fine-scale kinematics and behaviour in coastal nursery habitats. Tracking flights were better suited for behavioural analyses than transect flights. While limitations existed, such as modest samples for some behaviours and contexts, daytime bias, and the use of UAV speed as a proxy for swim speed, these do not detract from the main inferences and underscore priorities for future work. Integrating UAV observations with biologgers’ data will extend temporal coverage and refine energetic cost estimates, potentially revealing cumulative effects of repeated disturbance.

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# 7.Appendices

## Appendix I – State of the art

### *S. zygaena* biology and ecology:

Currently described sharks are distributed among eight orders, from which Carcharhiniforms – the order of the ground sharks – comprises the biggest species diversity (Compagno, 1984; Ebert *et al.*, 2021). Within this order, the family Sphyrnidae – the hammerhead shark – is considered to be one of the most recent in evolution, with nine known species characterized by lateral expansions at each side of the head, a structure termed the cephalofoil (Ebert *et al.*, 2021; Miller, 2016).

The smooth hammerhead shark, *Sphyrna zygaena* (Linneaus, 1758), is one of those nine species (Compagno, 1984). Smooth hammerhead sharks can be identified by its broad, narrow-bladed head with a rounded, broadly arched anterior margin of the cephalofoil, and a mouth with a similar arching profile (Saldanha, 2003; Ebert *et al.*, 2021). Unlike its close relative, the scalloped hammerhead shark (*Sphyrna lewini*), *S. zygaena* presents four distinct notches on the cephalofoil but lacks a median indentation (Bezerra *et al.*, 2017; Ebert *et al.*, 2021; López *et al.*, 2022). The species also exhibits a moderately high first dorsal fin, while the second dorsal, pelvic and pectoral fins are considerably short, with the latter showing dark blotches on their underside tips (Bezerra, 2017; Ebert *et al.*, 2021). In general, smooth hammerheads display an olive-grey to brownish colouration dorsally, contrasting with a white ventral surface (Saldanha, 2003; Ebert *et al.*, 2021). Other distinctive features from the close looking *Sphyrna lewini* include the similar size of the base of the second dorsal and the base of the anal fin identified in the *Sphyrna zygaena*, and also the further distance of the free rear tip of the second dorsal fin from the upper caudal fin in *S. zygaena* when compared to *S. lewini* (López *et al.*, 2022). Additional diagnostic traits include well-developed prenarial grooves and a relatively short snout measuring one-fifth to less than one-third of the head width (Ebert *et al.*, 2021).

The smooth hammerhead shark, *Sphyrna zygaena* (Linnaeus, 1758), exhibits the typical K-selected life-history traits of elasmobranchs, characterized by slow growth, late sexual maturity, long generation times, and low fecundity (Stevens *et al.*, 2000; Miller, 2016). Reproduction in *S. zygaena* is viviparous, with embryos developing within the mother’s uterus and being nourished through a yolk-sac placenta. Litter sizes vary considerably, from 20 to 50 pups per gestation, with an average of about 33 (Miller, 2016). At birth, individuals measure approximately 49–64 cm TL, corresponding to roughly 29–39 cm fork length (FL) (Compagno, 1984; Coelho *et al.*, 2011; Miller, 2016). Early growth is relatively fast, estimated at around 25–28 cm FL per year during the first years of life (Coelho *et al.*, 2011; Bezerra *et al.*, 2017), before slowing considerably in later stages (Rosa *et al.*, 2017). Estimates indicate that *S. zygaena* may reach ages of 18–28 years in males and 21–32 years in females, with sexual maturity being achieved between 7–9 years and 9–11 years, respectively (Huynh & Tsai, 2023). Size at maturity varies geographically, generally ranging from 210–260 cm total length (TL) in males and 247–288 cm TL in females (Stevens, 1984; Castro & Mejuto, 1995; Muus & Nielsen 1999; Hayes 2007; Miller, 2016). This slow growth, combined with late maturity, underscores the vulnerability of the species to intensive fishing pressure and environmental change (Stevens *et al.*, 2000).

Smooth hammerhead sharks are a cosmopolitan semipelagic species with distribution across warm-temperate and tropical seas, occurring both in continental shelf waters and around oceanic islands and seamounts (Compagno, 1984; Coelho *et* al., 2011; Santos & Coelho, 2018; Ebert *et al.*, 2021). Neonates, juveniles and subadults are more frequently found in shallow coastal habitats (<40 m depth) that serve as nurseries, whereas adults are more pelagic, occupying offshore regions and sometimes descending to depths exceeding 200 m (Francis, 2016; Santos & Coelho, 2018; Afonso *et al.*, 2022). Maximum depths recorded have been 260.9 metres in a study from Santos & Coelho (2018) in the North Atlantic and 144 metres in a study from Francis (2016) in northern New Zealand. Nevertheless, both life stages spend a large proportion of time in the upper 50 m of the water column, generally in waters warmer than 23°C (Santos & Coelho, 2018). Juveniles tend to prefer slightly higher temperatures, around 28–29°C during the day, moving into slightly cooler layers (26–27°C) at night. Ontogenetic shifts in depth use are also observed, with juveniles exhibiting strong site fidelity to specific nearshore habitats such as the north coast of Faial Island, Azores, where a nursery area has been identified (Afonso *et al.*, 2022). Sharks there show a distinct reversed diel vertical migration pattern, remaining near the surface (0–20 m) during the day and diving to greater depths (>60 m) at night, a behaviour possibly related to prey availability or predator avoidance (Afonso *et al.*, 2022). Similarly, Francis (2016) also recorded occasional dives during the summer, but with an additional increase to deeper and longer dives just after summer.

Dietary analyses indicate that *S. zygaena* is a specialized top predator with a relatively narrow trophic niche and high trophic position (Gonzalez-Pestana *et al.*, 2017). In Peru, juvenile sharks predominantly consumed small teleost fish and cephalopods such as whip-lash squid, *Mastigoteuthis dentata,* and patagonian squid, *Doryteuthis (Amerigo) gahi*, while larger individuals progressively shift to larger cephalopod prey including jumbo flying squid, *Dosidicus gigas,* and sharpear enope squid, *Ancistrocheirus lesueuri* (Gonzalez-Pestana *et al*., 2017). This ontogenetic dietary shift likely reflects energetic optimization and prey availability across habitats. The species is considered an intermittent feeder, as evidenced by the high proportion of highly digested stomach contents observed in examined specimens (Gonzalez-Pestana *et al*., 2017). As an apex predator, the smooth hammerhead plays a key role in regulating cephalopod populations, potentially influencing broader trophic interactions and fisheries dynamics in pelagic ecosystems (Gonzalez-Pestana *et al*., 2017). Known natural predators include the killer whale (*Orcinus orca*), which has been documented preying upon juvenile smooth hammerheads (Visser, 2005), but there likely is other undocumented predators, especially in their early life stages.

Globally, *S. zygaena* populations have undergone substantial declines over recent decades, following the general trend of many oceanic sharks. Between 1970 and 2018, the abundance of oceanic sharks and rays declined by more than 70% globally (Pacoureau *et al*., 2021), driven mainly by overfishing and bycatch mortality. *S. zygaena* is caught both as target and bycatch species in commercial longline, purse seine, and gillnet fisheries (Rigby *et al*., 2019). Particularly high mortality rates have been recorded in pelagic longline fleets, with at-vessel mortality reaching up to 71% in Portuguese Atlantic waters (Coelho *et al*., 2012, Rigby *et al*., 2019). Additionally, juveniles are frequently caught in coastal fisheries and even in beach protection programs, where mortality rates are exceedingly high (Reid *et al*., 2011, Rigby *et al*., 2019). The meat, liver oil, skin, cartilage, and jaws are commercially utilized but the primary driver of population declines remains intensive exploitation for the shark fin trade. Hammerhead fins are among the most valuable in the global market, with smooth hammerhead fins accounting for approximately 1.7% of Hong Kong imports and ranking as the fourth most abundant fin type in trade records from 2014 (Fields *et al*., 2018, Rigby *et al*., 2019). Given its slow growth and low fecundity, such extraction rates are unsustainable, Their K-selected life history traits features make this species inherently susceptible to overexploitation and slow to recover from population declines (Pacoureau *et al*., 2021; Dulvy *et al*., 2014), leading to its current classification as “Vulnerable” on the IUCN Red List (Rigby *et al*., 2019).

Conservation efforts have advanced over recent decades but remain uneven in implementation and effectiveness. Since 2010, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has prohibited the retention, transshipment, or sale of any hammerhead shark (except *Sphyrna tiburo*) taken in association with ICCAT fisheries (Santos & Coelho, 2018). Furthermore, in 2013, the smooth hammerhead was listed in Appendix II of the Convention on International Trade in Endangered Species (CITES), convention regulating the international trade of vulnerable species (Bezerra *et al*., 2017). Similar listings under the Convention on the Conservation of Migratory Species (CMS) have sought to coordinate cross-jurisdictional management actions (López *et al*., 2022). However, the success of these frameworks largely depends on domestic implementation and enforcement, which remain limited in many regions (Rigby *et al*., 2019).

Recent population modelling indicates that reducing fishing mortality by at least 50% is essential to reverse current declines and ensure long-term sustainability (Huynh & Tsai, 2023). These findings also emphasize the disproportionate importance of juvenile survival to population recovery, with elasticity analyses showing that immature individuals have a greater impact on population growth rates than adults. Consequently, conservation strategies should prioritize the protection of nursery areas, such as those identified around oceanic islands like Faial (Afonso *et al*., 2022), where juveniles display multiannual residency and site fidelity. Establishing fishing closures or marine protected areas encompassing these nurseries could represent a precautionary and highly effective measure for safeguarding early life stages and maintaining population viability (Afonso *et al*., 2022; Chapman *et al*., 2015).

In conclusion, *Sphyrna zygaena* exemplifies a species whose ecological and biological traits render it especially vulnerable to human impacts. Understanding the species' habitat use, movement ecology, and population dynamics is therefore crucial to inform evidence-based management. The persistence of this species will likely depend on a combination of effective fisheries regulation, international cooperation, and local conservation initiatives targeting key habitats such as coastal nurseries and aggregation sites.

## UAVs in shark science:

Unmanned aerial vehicles (UAVs, commonly named "drones") have rapidly emerged as an important tool to marine ecological research and, in particular, shark-ecology studies, enabling fine-scale, non-intrusive observations of aggregations, behaviour, abundance, and habitat use across shallow and coastal systems where visibility allows detection (Kiszka *et al*., 2016; Rieucau *et al*., 2018; Doan & Kajiura, 2020; Ayres *et al*., 2021; López *et al*., 2023). The broader integration of behaviour, movement and habitat – once unachievable via a single method – is now enabled through calibrated UAV datasets that link spatial use to environmental context (López *et al.*, 2023; Rieucau *et al.*, 2018; Butcher *et al.*, 2021). As an alternative platform to manned aircraft and in-water methods, UAVs reduce both logistical and financial constraints, and minimise observer effects (Christiansen *et al.*,2016; Porter *et al.*, 2020; Butcher *et al.*, 2021). They have also been used for habitat mapping and species classification in terrestrial and coastal systems (Lu & He, 2017; Kattenborn *et al.*, 2019), and even for detecting marine debris (Liao & Juang, 2022).

UAV’s have been employed across two broad methodological families. First, transect-based surveys quantify distribution, relative density and habitat associations, mostly for population-level and ecosystem-level studies. Examples include ungulate aerial counts (Barasona *et al.*, 2014), dugongs (Hodgson *et al.*, 2013), and reef elasmobranchs (Kiszka *et al.*, 2016). Innovations in flight-path geometry - such as rosette or circular patterns – seek to optimise spatial coverage and detection while accounting for endurance and environmental variability (Linchant *et al.*, 2023). Second, UAVs have also been used to track individual animals, capturing fine-scale kinematic data such as swimming trajectories, velocity, and tail-beat frequency (Porter *et al.*, 2020; Oleksyn *et al.*, 2020) to analyse marine megafauna’s swimming kinematics, general behaviours, social structures reproductive behaviours, etc. In reef and coastal habitats, UAVs have been used to track rays, sharks, and other species in shallow clear waters, linking movement data to habitat structure at sub-metre spatial resolution (Kiszka *et al.*, 2016; Afonso *et al.*, 2022). In both flight types, flights can be preprogrammed and automated or manually controlled (Raoult *et al.*, 2018; Colefax *et al.*, 2019; Butcher *et al.*, 2021; Park *et al.*, 2021). Analyses can be done in real-time or after the flight, observing recorded video and flight data (Colefax *et al.*, 2019; Butcher *et al.*, 2021). From the video, one can extract photogrammetry estimations, photo identification of individuals, behaviour identification and description, to track predator-prey interactions, and to document natural predation and avoidance events (Doan & Kajiura, 2020; Butcher *et al.*, 2021; Álvarez-González *et al.*, 2023; López *et al.*, 2023). Relative positions and nearest-neighbour distances are other parameters possible to extract from the video that have also been described (Rieucau *et al.*, 2018). In the flight data, GPS positions, UAV instantaneous speed, flight altitude, time and video status can be checked for any moment of the flight (Oleksyn *et al.*, 2020). Species of marine megafauna studied with tracking flights include sharks (Rieucau *et al.*, 2018), rays (Oleksyn *et al.*, 2020), dolphins (Lauridsen *et al.*, 2025), whales (Torres *et al.*, 2018) and turtles (Bevan *et al.*, 2016).

Platform and sensor choice reflect the spatio-temporal scope of the study, data type and regulatory context. A standard operation couples the aircraft, a ground control station with live video and data feeds, and a communication link. Operational base platforms may include boats and coast points near the planned flight area (Colefax *et al.*, 2019). Two UAV types often used are fixed-wing and multi-rotor systems: fixed-wings enable longer transects (12-40 minutes) and greater endurance, requiring assisted launch/landing in clear areas – suitable for extensive transects or open-water surveys; multi-rotors (quadcopters or hexacopters) allow vertical take-off/landing and hovering with precise manoeuvrability albeit with shorter endurance, making them ideal for behavioural and aggregation studies (Colefax *et al.*, 2018; Benavides *et al.*, 2019, Butcher *et al.*, 2021). Flight duration in these systems typically ranges from 20 to 30 minutes depending on battery capacity and environmental conditions (Butcher *et al.*, 2021). UAVs combining both fixed-wing endurance and multi-rotor stability are also known, although they introduce greater cost (Butcher *et al.*, 2021).

Flight feasibility is strongly shaped by site conditions and regulatory constraints. Survey success is highly dependent on environmental conditions such as light, turbidity, wind, and wave height (López *et al.*, 2023; Bourke *et al.*, 2023; Butcher *et al.*, 2021). Telecommunications and access logistics may limit operations (Butcher *et al.*, 2019; Butcher *et al.*, 2021). Protected-area altitude caps, no-fly zones and visual-line-of-sight (VLOS) rules further restrict flight design (Butcher *et al.*, 2021). Practically, surveys are often timed to morning/early-afternoon under low-wind (<15–18 knots) windows, when glare is minimal and water clarity is high, as afternoon winds increase and low-light conditions before sunrise and after sunset hinder visibility (Bourke *et al.*, 2023; López *et al.*, 2023).

Methodological considerations are essential to ensure accuracy in UAV-based data collection. Flight altitude, camera resolution, and animal depth are primary determinants of measurement quality. Lower altitudes provide finer spatial resolution but increases the likelihood of the individual being tracked occupying the edges of the frame, where the convex lens induced distortion is bigger, while simultaneously presenting higher risk of provoking behavioural disturbances, whereas higher altitudes reduce that distortion effect on the individual only to increase a “blooming” effect that blurs the edges of fine traits and degrade pixel resolution (Rex *et al.*, 2024; Bierlich *et al.*, 2021). For orthomosaic and linear metrics, overlap and sidelap optimisation reduce error (Putch, 2017). Barometric altimeters and GNSS GPS trilateration systems introduce systematic errors – barometers may bias altitude estimation, while GPS trilateration becomes unreliable below ~70 m altitude (Albéri *et al.*, 2017; Rex *et* *al.*, 2024). Correcting for launch height and incorporating target depth markedly improves accuracy (Rex *et al.*, 2024). Studies consistently recommend intermediate altitudes around 40 m to balance resolution, distortion, and animal response (Rex *et al.*, 2024; Bierlich *et al.*, 2021). For behavioural and morphometric analyses, a practical approach is to record 4K video (3840×2160) at 30 frames per second, which captures dynamic information while allowing extraction of high-quality frames for measurements and maintaining manageable file sizes (Rex *et al.*, 2024), although still images typically yield lower uncertainty than video frames when measuring morphometric parameters (Bierlich *et al.*, 2021). If using video frames, there is a special need to be wary of possible underestimation errors for targets bigger than 2 m. If using still images, altitudes bigger than 40 m are the best option to reduce underestimation errors. This setup represents an effective compromise between spatial resolution, temporal detail, and manageable data volume.

Accurate morphometric estimation relies on pixel-to-real-world calibration using objects of known dimensions photographed across multiple altitudes, which typically yields centimetre-level precision (<5 cm error) (Oleksyn *et al.*, 2020). Depth beneath the surface introduces optical refraction and underestimation biases unless explicitly corrected, adding an approximate 1 m offset when animals swim near the surface substantially reduces this bias (Rex *et al.*, 2024). Similarly, correcting for the UAV’s launch altitude further refines total length estimates. Lens distortion and “blooming” effects at higher altitudes can blur edges and degrade pixel resolution (Bierlich *et al.*, 2021), underscoring the need for standardised flight parameters and image-processing protocols across studies (Ferreira *et al.*, 2024). Photogrammetry – particularly aerial photogrammetry – has become a key tool in ecological monitoring, complementing stereo-BRUV and laser photogrammetry techniques for assessing abundance, behaviour, and morphometrics of sharks and rays (Oleksyn *et al.*, 2020; Setyawan *et al.*, 2022; Ferreira *et al.*, 2024). When altitude and depth are corrected and ground-sample distance (GSD) calculators are applied, overall measurement accuracy can reach within 5% of true dimensions (Rex *et al.*, 2024).

Recent research has explored the integration of additional sensors and analytical frameworks. Green-laser LiDAR offers potential for estimating depth and bathymetry, enabling correction of submerged target distortion (Rex *et al.*, 2024). Combining LiDAR with high-resolution RGB imagery could reduce measurement error to within 1% (Rex *et al.*, 2024). Now, artificial intelligence (AI) and machine learning (ML) also allow automating image analysis, enabling automated detection, tracking, and even species identification from aerial video (Butcher *et al.*, 2021), reducing the duration of some of those time-consuming processes

UAV have significant advantages over traditional monitoring platforms. Compared with manned aircraft, they are cheaper to operate, require less training, and are quieter and less intrusive (Watts *et al.*, 2010). They can be deployed from beaches, small vessels, or remote field sites, with minimal logistical constraints (Porter *et al.*, 2020). In contrast to telemetry methods – such as satellite, archival, or acoustic tagging (Afonso *et al.*, 2022) – UAV observations do not require animal capture or tagging, thus avoiding physiological stress and behavioural alteration (Martins *et al.*, 2020). At altitudes above 5–10 m, noise from small UAVs is undetectable underwater, allowing non-invasive observations of undisturbed behaviours (Christiansen *et al.*, 2016). This advantage is critical in studying gregarious or easily disturbed species such as sharks, rays, and dolphins. UAVs complement biologgers by providing higher spatial resolution for short-term fine-scale movement and behavioural data, while biologgers are more effective for long-term, large-scale movement studies (Porter *et al.*, 2020).

Despite these advances, several challenges persist. Flight duration, visibility, weather constraints, and legal limitations continue to restrict the temporal and spatial scale of UAV studies (Bourke *et al.*, 2023; López *et al.*, 2023). Measurement uncertainty due to altitude estimation, target depth, and image distortion remains a core methodological limitation (Bierlich *et al.*, 2021; Rex *et al.*, 2024) if the correct mitigation steps are not used. Environmental biases, including glare, turbidity, and surface reflection, can affect detection and quantification (López *et al.*, 2023). Moreover, the short battery life of multirotor UAVs (~20–30 minutes) limits the observation of prolonged social interactions (Butcher *et al.*, 2021). Also, while UAVs can aid beach safety and shark-hazard mitigation by detecting and alerting for large animals, they are not yet a substitute for trained human observers given species-identification limitations and weather/depth constraints. Nonetheless, rapid improvements in camera technology, battery capacity, automation, and AI-driven analytics are steadily enhancing reliability, resolution, and scope of UAV-based ecological monitoring. Besides, the availability and the perception bias described, that can affect abundance estimates, because of surface reflection, can be mitigated by flight timing, replicate surveys, and dual analyst review (López *et al.*, 2023), just like other mitigation measures may be employed to reduce uncertainty in other parameters.

In summary, UAVs have redefined methodological possibilities in marine ecology by providing high-resolution, low-disturbance, and cost-effective means of studying shark and ray ecology, as long as deployed under optimal conditions. From estimating abundance and mapping habitat use to quantifying swimming kinematics and documenting complex social interactions, UAVs enable a level of spatial and temporal precision that bridges the gap between observational and tagging approaches. Continued methodological refinement – particularly in calibration, automation, and sensor integration – will further increase the accuracy and scalability of UAV-based data, promising to expand our understanding of elasmobranch behaviour and ecology in their natural environments.

## Shark behaviour:

Understanding animal behaviour provides a window into the adaptive strategies that species employ to survive and reproduce within changing environments. Behaviour represents the dynamic link between physiology and ecology, shaping how individuals react according to fluctuations in predator presence, prey presence, conspecific presence and abiotic conditions, with learning playing a vital role in determining such reactions (Dill, 1983; Guttridge *et al*., 2009). For sharks, this capacity underpins their ecological success as apex or mesopredators and provides essential insight into the functioning of marine ecosystems. Examining behaviour therefore contributes not only to species-level knowledge but also to broader questions concerning cognitive evolution and environmental adaptation.

The scientific analysis of behaviour is grounded in the field of ethology, which formalises the observation and categorisation of animal actions through the construction of ethograms, catalogues discrete events and longer states of behaviour (Bateson & Martin, 2007; Klimley *et al.*, 2023), offering clarity and reproducibility across studies. Early ethological work focused on specific species, and were later expanded into multi-species ethograms (Klimley *et al*., 2023), instrumental in establishing consistent behavioural terminology. However, sharks were difficult to study under natural conditions and direct observation (Gruber & Myrberg, 1977). Modern tools such as acoustic telemetry, baited remote underwater videos (BRUVs), unmmaned aerial vehicles and biologging devices (Butcher *et al*., 2021; Jacoby *et al*. 2021; Waller *et al.*, 2023; Ríos *et al.*, 2025) have refined these approaches for the study of shark behaviour, allowing the collection of precise data on movement and social dynamics in wild populations.

The importance of studying behaviour lies in the need to understand the reasons behind it to be able to use that information in conservation or human-shark conflict management. Knowing how animals optimize their movement to maximize energetic efficiency

(Papastamatiou *et al.*, 2018) and considering that behaviour activity can be used to estimate relative energetic expenditure (Lowe, 2001), impacts of human activities can be measured by the behavioural responses presented to understand what mitigation practices may be efficient. By understanding habitat use and movement patterns, the areas where the conservation attempts would be more successful by creating time-area closures are revealed, such as frequent aggregation sites or migration corridors (Bond *et al.*, 2017; Afonso *et al.*; 2022). Instead of just being studied to understand its functions, behaviour observation can also be used as a method to study sharks physiology, as it has been used to understand sharks hearing capabilities, through operant conditioning, or to confirm if sharks possess colour vision (Van-Eyk *et al.*, 2011; Nieder *et al*., 2023). Ultimately, this physiology knowledge could potentially then be used to inform the development of visual-dependent shark deterrents, as other visual deterrents have already been successful (O'Connell *et al.*, 2014). Therefore, the study of behaviour transcends mere academic interest, becoming a crucial tool for applied research in shark conservation, conflict mitigation and technological innovation, but our understanding of their behaviours is dependent on our understanding of the factors that may shape it.

Abiotic factors are among the most powerful determinants of shark behaviour, shaping both fine-scale movement and long-term habitat use. Temperature, for instance, regulates metabolic rate, feeding frequency and growth in sharks such as *Sphyrna lewini* (Lowe, 2001). Moreover, deeper cooler waters can reduce metabolic efficiency, prompting behavioural thermoregulation, so scalloped hammerhead sharks are thought to "hold their breath" to try to maintain higher body temperatures in deeper foraging dives (Royer *et al*., 2023). Similarly, salinity and dissolved oxygen gradients drive rates of movement and movement patterns, as individuals seek physiologically optimal zones – a phenomenon described as behavioural osmoregulation (Carlson & Parsons, 2001; Hammerschlag, 2006; Dwyer *et al*., 2020). Tide based movements and the use of current updrafts have also been linked to energy conservation, with aggregating grey reef sharks, *Carcharhinus amblyrhhynchos,* adjusting swimming direction with current flow to reduce energetic expenditure (Papastamatiou *et al.*, 2021). Reversed diel movements described for smooth hammerhead sharks, *Sphyrna zygaena*, have been described by Afonso *et al.* (2022) to be seasonal dependent, possibly linked to foraging activity, showing how photoperiod may influence shark movement. Schlaff *et al.* (2014) also highlighted barometric pressure and pH as key variables influencing elasmobranch spatial ecology. Collectively, these findings demonstrate that environmental variability interact with physiological and behavioural repertoires, therefore species-specific movement strategies that optimise energy use and survival were developed.

Beyond the abiotic environment, biotic factors play pivotal roles in shaping shark behaviour. Schlaff *et al.* (2014) reported that prey availability and predator pressure are among the strongest biological drivers of spatial distribution and movement in elasmobranchs. For instance. White sharks, *Carcharodon carcharias,* abandonment of areas where they were previously abundant has been attributed to the predatory pressure of killer whales, *Orcinus orca*. Conspecific presence is another factor affecting shark behaviour, with sand tiger shark, *Carcharias taurus*, females using shallower waters when males passed by, possibly to avoid harassment (Gordon, 1993) and annual circle formation swimming of basking sharks, *Cetorhinus maximus,* for reproductive functions (Sims *et al.*, 2022). Besides, ontogeny-driven changes in smooth hammerhead shark habitat choice and depth use have also been reported, with juveniles using coastal shallower waters and engaging in shallower dives than adults (Francis, 2016; Santos & Coelho, 2018; Afonso, *et al.* 2022). Human disturbances, such as those provoked by ecotourism, also alter shark behaviour, by decreasing whale shark, *Rhyncodon typus*, avoidance when provisioned (Legaspi *et al.*, 2020), for instance, or the decrease in detections in areas where human presence increased (Afonso *et al.*, 2024). The interplay of biotic and abiotic factors thus determines not only where sharks move but also how and when they engage in essential behaviours, reinforcing the integrative nature of behavioural ecology.

According to Klimley *et al.* (2023), general shark behaviours can be broadly grouped into eight categories: maintenance, courtship, filter feeding, scavenging, predation**,** sociality, aggression and defensive behaviours. Maintenance behaviours encompass locomotion, resting, and self-care activities, crucial for sustaining physiological equilibrium. Courtship involves complex body postures, following displays and tactile contact, often associated with sexual dimorphism and mating readiness. Feeding-related behaviours, including filter feeding, scavenging and active predation, reveal ecological niche specialisation and energetic trade-offs. Sociality encompasses group formation, cooperative movements and hierarchical interactions, whereas aggression and defensive behaviours regulate social structure and survival. Klimley *et al.* (2023) emphasised that generalized behaviour descriptions and standardized terminology facilitates inter-studies and inter-species comparisons, as well as supports evolutionary interpretations of behavioural diversity. Within these frameworks, sharks in general exhibit very diversified behaviours, challenging the historical notion of them as instinct-driven predators. This classification also allows the study of how species balance the different behavioural categories maintenance, reproduction and survival in dynamic marine environments.

Members of the family Sphyrnidae, demonstrate a suite of distinct behavioural adaptations linked to their unique morphology and ecology. Myrberg & Gruber (1974) first described diverse behaviours for *Sphyrna tiburo* such as the recently renamed by Klimley *et al.* (2023) “Slow, straight-line swimming”, “Maneuvering”, “Follow”, “Follow formation” and “Give way”, highlighting size-dependent social hierarchies and interactions. Larger individuals dominated spatial interactions, while smaller conspecifics exhibited erratic swimming and avoidance responses, indicating the presence of social ranking rather than territoriality. Morphological traits, especially the cephalofoil, confer both hydrodynamic and sensory advantages. Nakaya (1995) and Gaylord *et al*. (2020) demonstrated that this wing-like head acts similarly to a rudder, promptly helping in the direction changes by changing its angle of attack, and not so much as a source of dynamic lift as previously hypothesized, actually increasing drag and energetic cost. Strong *et al.* (1990) also describes the *Sphyrna mokarran*’s cephalofoil advantage in predation behaviour, by allowing to control stingrays against the bottom. Collectively, these traits illustrate the behavioural and physiological specialisations that make hammerheads a model taxon for studying locomotor energetics, sensory ecology and social organisation.

Aggregation is a widespread behaviour among sharks, often linked to ecological optimisation and social structure. Aggregations can enhance feeding efficiency, reduce predation risk and facilitate reproduction (Heupel *et al.*, 2019; Sims *et al.*, 2022). Diel and seasonal aggregation patterns in juvenile *Carcharhinus limbatus* or *Sphyrna zygaena* have been identified (Heupel & Simpfendorfer, 2005; Afonso *et al.*, 2022). In juveniles, aggregations may serve as way of social learning to develop foraging skills (Guttridge *et al.*, 2009; Lowe, 2002). However, aggregation increases vulnerability to diverse human activities, which have the potential to disrupt or prevent such behaviours (Mucientes *et al.*, 2009; Hueter *et al*., 2013; Cubero-Pardo *et al*., 2011; Apps *et al*., 2015; Cattano *et al*., 2021; López *et al.*, 2023). Therefore, understanding the ecological and behavioural functions of aggregation is vital for assessing population resilience and species management.

Behavioural studies offer a window to the focal species energetics. Any animal spends energy with movement and behaviour (Lawson *et al*., 2019). Understanding behaviour changes through ontogeny, seasonal and environmental changes, as well as across different biotic factors, helps to understand how a species minimise the energy it expends to maximize growth, survival and ultimately its fitness (Papastamatiou *et al*., 2018; Oleksyn *et al*. (2020), Afonso *et al*., 2022). Swimming, in particular, is energetically costly for obligate ram-ventilating species like hammerheads, which must maintain constant movement to facilitate respiration (Lowe, 2001). Studies of juvenile *Sphyrna lewini* demonstrated that tailbeat frequency (TBF) and swimming speed can be used to estimate shark metabolic rates (Lowe, 2001; Lowe, 2002). Net cost of transport (COT) for scalloped hammerheads was described as a slight U-shaped curve, with the highest energetic costs at the fastest and slowest swimming speeds, and the lowest energetic costs at intermediate speeds (Lowe, 2001). Here, the cephalofoil-induced increased drag poses a disadvantage, requiring higher TBF and energy output to maintain forward motion (Gaylord *et al*., 2020; Lowe, 2001). Lowe (2002) highlighted the hammerhead pups' frequent loss of weight during summer, due to the higher metabolic rates and limited foraging efficiency. A comparative study has shown that hammerheads have among the highest TBF values of all sharks studied. (Watanabe *et al*., 2012; Waller *et al*., 2023). These findings underscore the coupling between morphology, swimming kinematics and energy expenditure, illustrating how behavioural strategies evolve to balance energetic efficiency and ecological function.

Behavioural studies provide indispensable insights for shark conservation, as behaviour directly mediates species' interactions with threats such as fishing, habitat loss and climate change. By elucidating habitat preferences, social dynamics and movement patterns, behavioural research informs the design of marine protected areas (MPAs) and time-area closures. For instance, the identification of the use of North Faial by smooth hammerheads as a nursery took Afonso *et al* (2022) to suggested the protection of that area. Moreover, identifying behavioural responses to anthropogenic stressors – such as avoidance of boats or divers (Cubero-Pardo *et al*., 2011; Cattano *et al*., 2021) – helps assess disturbance thresholds and guide sustainable ecotourism practices. Behavioural plasticity also serves as an indicator of adaptive potential (Dill, 1984; Júnior *et al*., 2022): species capable of modifying foraging or reproductive strategies in response to environmental change may exhibit greater resilience. In this way, behaviour acts as both a diagnostic and predictive tool in conservation biology, bridging the gap between physiology, ecology and management policy.

The behavioural ecology of sharks encompasses a diverse and complex array of adaptations, linking morphology, physiology and environmental interaction. From abiotic modulation of movement to social hierarchies and energy-optimised swimming, behaviour represents the dynamic expression of ecological strategy. The integration of ethological methods, such as ethograms and fine-scale tracking, has illuminated previously unseen aspects of shark life history, while advances in sensory and bioenergetic research continue to refine our understanding of these apex predators. Hammerhead sharks, with their distinctive cephalofoil and social tendencies, exemplify the intricate relationship between form, function and environment. Ultimately, studying shark behaviour not only advances biological knowledge but also underpins effective conservation.

## Appendix II – Annotation speed test

The purpose of this pre-test was to assess whether annotating tail beat point events of a random study shark at different playback speeds could lead to systematic differences in the estimation of TBCs. The comparison focused on two playback conditions: 0.1x, which represented the slowest playback speed available at the annotation software (BORIS), and 0.4x, which was the fastest speed that still allowed tail beats to be visually identified with confidence. The reason behind this test was to ensure that annotating at a higher playback speed (0.4x) to be more time-efficient would not compromise data accuracy or introduce measurable bias in the resulting TBC values.

Data were imported from an annotation file in CSV format and analysed in R. From the original annotation dataset, only rows corresponding to the tail beat point events corresponding to approximately 120 s of annotations were kept for analysis. Video times from the tail beat point events of the two different playback speeds were separated and paired in the same row with the correspondent tail beat point event from the other playback speed. TBCs were calculated as the difference between the video times of each two consecutive tail beat point events both for the 0.1x and the 0.4x speed. The resulting paired dataset thus contained, for each row, two directly comparable TBC values.

Prior to formal statistical comparison, the distributions of the TBCs for each of the playback speeds were observed to verify their normality. For this step, the Shapiro-Wilk test was used after visual inspection (Figure A1). Normality was not met for neither of the playback speeds' TBCs ($p < 0.05$), thus non-parametric paired Wilcoxon signed-rank test was used to compare the TBCs of 0.1x and 0.4x. In addition, a paired boxplot (Figure A2) summarizes the distribution of TBCs for each playback speed and connects paired observations from the same sequence, allowing an immediate visual assessment of potential differences between conditions. The total number of valid paired observations used in the analysis was 90. This test's result revealed there were no statistically significant differences between the TBCs annotated at the playback speeds of 0.1x (median TBC = 1.3 s, IQR: 1.2-1.4) and 0.4x (median TBC = 1.3 s, IQR: 1.3-1.4) ($p < 0.05$). Therefore, the use of a faster playback speed (0.4x) can be considered appropriate for subsequent analyses, as it decreases annotation time without compromising data reliability.

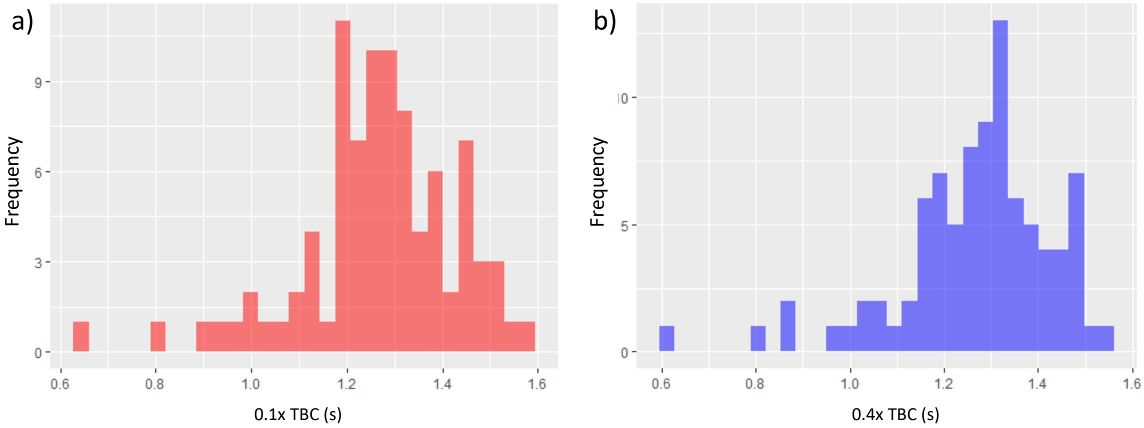

**FIGURE A1 –** Histogram of TBC distributions for the two different playback speeds: a) 0.1x and b) 0.4x.

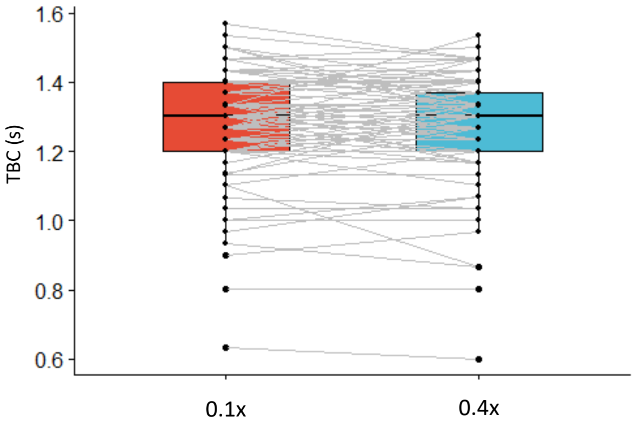

**FIGURE A2 –** Paired boxplot of TBC at 0.1x and 0.4x playback speeds.