Behavioural Processes 229 (2025) 105216

Contents lists available at ScienceDirect

Behavioural Processes

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

First insights into social behavioral patterns between pairs of bait-attracted mature female tiger sharks from Fuvahmulah Island, Maldives

Francesca Romana Reinero [a], Filippo Bocchi [b], Nathan Perisic [c], Jamie Crouch [c], Antonio Pacifico [d], Luca Asshauer [e], Consuelo Vicariotto [a], Primo Micarelli [a,f,*]

[a] Sharks Studies Center-Scientific Institute, Massa Marittima 58024, Italy
[b] Nature Friends of Maldives, NGO. Pelagic Divers Fuvahmulah, Fuvahmulah 18011, Maldives
[c] Fuvahmulah Dream, NGO. Fuvahmulah Dive School, Fuvahmulah 18011, Maldives
[d] Department of Economics and Law, University of Macerata, Macerata 62100, Italy
[e] Department of Biology and Chemistry, University of Bremen, Bremen 28359, Germany
[f] Department of Physical Sciences, Earth and Environment, University of Siena, Siena 53100, Italy

ARTICLE INFO

Keywords:
Galeocerdo cuvier
Tourism-based feeding
Behavioral ecology
Shark diving
Dominance hierarchy

ABSTRACT

Tiger sharks are predominantly known as solitary animals, yet their opportunistic and generalist predatory nature can drive interactions with conspecifics, including artificial provisioning sites. Underlying social dynamics may influence such instances of grouping behavior. Despite social behavior being an expanding niche in shark science, little is known about the social behavioral patterns of the tiger shark worldwide. Between 2023 and 2024 in Fuvahmulah Island, Maldives, 36 pair-wise non-random social interactions were observed at the provisioning site via video recordings by 40 photo-identified mature female tiger sharks. Social behaviors previously identified in white sharks and tiger sharks across multiple locations, such as *give way*, *swim by*, *parallel swimming*, *follow give way*, and *stand back*, have also been documented in tiger sharks from Fuvahmulah Island. Furthermore, this study presents two newly observed antagonistic social behaviors — *submission* and *push away* — described here for the first time. Within the mature female tiger shark aggregation in Fuvahmulah, a size-based hierarchy was observed, with certain individuals displaying the majority of dominance and social interactions. The asymmetry in the monthly display of social behaviors suggests an intra-specific variability of tiger shark movements to different home ranges. These findings deepen our knowledge of the tiger shark social behavior, highlighting data gaps in Maldives and ensuring effective conservation measures for this species. Recommendations for future research work at this site are also presented in this paper.

1. Introduction

Social behavior has become a focal point of research across various shark species (Allee and Dickinson, 1954; Myrberg and Gruber, 1974; Weihs et al., 1981; Klimley and Nelson, 1984; Ebert, 1991; Sims et al., 2000; Guttridge et al., 2009; Jacoby et al., 2010; Guttridge et al., 2011; Jacoby et al., 2021; Micarelli et al., 2023). Shark aggregations can arise as a result of external ecological factors – such as food availability, specific habitat requirements, or predictable temporal activity patterns on daily or seasonal scales (Johnson et al., 2002; Guttal and Couzin, 2010; Schilds et al., 2019), although they may also be shaped by social attraction (Clua et al., 2013; Jacoby et al., 2021; Micarelli et al., 2023). Understanding the balance between these ecological and social drivers is key to interpreting the structure and function of shark grouping behavior across species and environments.

Grouping can be socially derived when the behavior of one individual influences that of another of the same species, involving a wide range of behavioral modules that affect various contexts of an individual's life (Burghardt, 1970; Hinde, 1976; Baldaccini et al., 1990; Lorenz, 1996; Krause and Ruxton, 2002). Intraspecific competition arises when two or more individuals simultaneously seek access to a limited resource, with resource acquisition typically resulting in

* Correspondence to: Department of Physical Sciences, Earth and Environment, Strada Laterina 8, University of Siena, Siena 53100, Italy.
E-mail addresses: ricerca@centrostudisquali.org, stage@centrostudisquali.org (F.R. Reinero), fil.bocchi@gmail.com (F. Bocchi), nathan.perisic@gmail.com (N. Perisic), j.crouch125@googlemail.com (J. Crouch), antonio.pacifico@unimc.it (A. Pacifico), asshauerluca@gmail.com (L. Asshauer), primo.micarelli@unisi.it (P. Micarelli).

https://doi.org/10.1016/j.beproc.2025.105216
Received 3 January 2025; Received in revised form 18 May 2025; Accepted 18 May 2025
Available online 24 May 2025
0376-6357/

agonistic behaviors rather than direct physical confrontation (Wilson, 1975). These behaviors may foster social interactions, forming complex relationships and structures among individuals (Hinde, 1976; Krause and Ruxton, 2002). Pair-wise dominance can be assessed based on asymmetries in agonistic interaction between individuals (Chase, 1980): the dominant one performs most or all aggressive acts, attaining a higher hierarchical status and preferential access to resources, while the subordinate primarily receives these acts (Brena et al., 2018). Such dominance relationships form the hierarchy structure (Hinde, 1976).

Dominance relationships are often associated with asymmetries in competitive interactions among individuals of similar size. In these interactions, sharks that exhibit the most aggressive responses are typically considered dominant (Guttridge et al., 2009; Sperone et al., 2010; Brena et al., 2018; Micarelli et al., 2023). Factors such as sex and/or size can affect the relationship between pairs of individuals, although morphological traits alone cannot predict the outcome of an agonistic event (Brena et al., 2018). In large sharks, individual personality traits may also shape behavioral responses (Vignaud et al., 2023). Although "boldness" is often associated with size, where larger individuals generally exhibit greater dominance, body size alone may not reliably predict the behavior at a provisioning site (Sèguigne et al., 2023). In this context, sharks may show different patterns of interaction and unique personalities that likely play a crucial role in establishing dominance within individuals.

Social behaviors lead to a reduction in foraging efficiency, and the general fitness of an individual in a group varies as a function of group size, composition, and context (Jacoby et al., 2012).

Shark aggregations and environmental drivers of these events are well documented in literature (Heupel and Simpfendorfer, 2005; Weng et al., 2007; Jorgensen et al., 2010; Riley et al., 2010; Jacoby et al., 2012; Micarelli et al., 2024), as well as the occurrence of social behaviors and groups in both wild juvenile and adult sharks (Klimley and Nelson, 1984; Klimley, 1987; Ebert, 1991; Sims et al., 2000; Guttridge et al., 2009; Guttridge et al., 2011; Mourier et al., 2012; Mourier et al., 2017; Brena et al., 2018; Papastamatiou et al., 2020; Labourgade et al., 2020). Additionally, sharks have been observed displaying social non-random interactions and/or groups both in a controlled environment (Allee and Dickinson, 1954; Jacoby et al., 2010) and scavenging/baiting (Papastamatiou et al., 2022; Micarelli et al., 2023) and/or direct feeding (Mourier et al., 2012; Bouveroux et al., 2021). Some species may display both aggregation and social grouping, and aggregation may be an important prerequisite for the development of social interactions and networks (Jacoby et al., 2012; Clua et al., 2013; Bouveroux et al., 2021).

Social behaviors and groups are well documented in the scientific literature for sharks belonging to the Carcharhiniforms order (Allee and Dickinson, 1954; Myrberg and Gruber, 1974; Klimley, 1987; Guttridge et al., 2009; Jacoby et al., 2010; Guttridge et al., 2011; Mourier et al., 2012; Mourier et al., 2017; Papastamatiou et al., 2020; Labourgade et al., 2020), although information is scarcely available on the social behavior of the tiger shark *Galeocerdo cuvier* (Pèron & Lesueur, 1822).

The behavior of the tiger shark is often difficult to study due to the low density of individuals at one location, solitary habit, the large marine environments it occupies, and its potentially dangerous nature (Clua et al., 2013). However, it is largely known that *G. cuvier* is an opportunistic predator and dietary generalist who follows the theory of optimal foraging (Clua et al., 2013). Thus, solitary predators are compelled to socially interact with conspecific or heterospecific individuals in natural scavenging or provisioning conditions (Dudley et al., 2000; Clua and Sèret, 2012; Clua et al., 2013; Brena et al., 2018; Jacoby et al., 2021), and the observation of social behavioral patterns displayed by large sharks can also be helpful to identify animals (Clua et al., 2013).

Some studies described the concurrent scavenging by white sharks (*Carcharodon carcharias*, Linnaeus 1758) and tiger sharks on a carcass of Bryde's whale in South Africa, reporting no significant inter- or intra-specific aggression (Dudley et al., 2000). A similar situation was also observed by (Clua and Sèret, 2012) on a sperm whale carcass in La Scarcelle Pass, in south New Caledonia. The only available studies in literature that describe both social behavioral patterns and networks of tiger sharks are those of Clua and Sèret (2012), Clua et al. (2013), and Jacoby et al. (2021), respectively. In Prony Bay, New Caledonia, (Clua et al., 2013) described the intra-specific interaction behaviors of tiger sharks in a scavenging condition on the carcass of a dead blue whale, highlighting individual biting and social antagonistic behaviors, along with three new social interactions that had never been described before for this species, but only for white sharks, such as *give way*, *stand back*, and *tail slapping* (Martin, 2003; Sperone et al., 2010; Micarelli et al., 2023). Jacoby et al. (2021) examined the impact of provisioning on the social behavior of tiger sharks at a dive tourism location called "Tiger Beach," in the Bahamas, documenting both random (7 networks) and non-random aggregations (5 networks) between non-provisioned and provisioned sites and highlighting the lower density of non-random social networks at provisioning sites. This suggests that sociality may occur naturally in "Tiger Beach," where there is an unusually high density of tiger sharks (Jacoby et al., 2021).

Scuba divers rarely encounter tiger sharks in the wild, and the use of attractants ranging from simple olfactory stimuli (chumming) to active feeding of individuals is required for shark ecotourism purposes (Bouveroux et al., 2021; Sèguigne et al., 2023). Provisioning is commonly associated with both active shark feeding and baiting activities (chumming), reproducing a scavenging situation based on olfactory stimuli (Jacoby et al., 2021; Bouveroux et al., 2021; Sèguigne et al., 2023). Granted the current debate of whether provisioning activity outweighs the negative impacts on sharks' behavior (Hammerschlag et al., 2017; Apps et al., 2018), shark ecotourism protects species, generating local income and employment, and raising public awareness of threatened species (Jacoby et al., 2021). Available data also suggests the lack of impact of provisioning ecotourism on tiger shark ecology (Hammerschlag et al., 2012; Sèguigne et al., 2023). Furthermore, understanding the behavioral response patterns to provisioning is important for social species and human safety, revealing the degree of resilience against anthropogenic impact (Gallagher and Huveneers, 2018).

Fuvahmulah Island, located in Gnaviyani Atoll in the southern part of the Republic of Maldives (western Indian Ocean), is a well-known provisioning site where both scavenging and baiting conditions are artificially recreated on a daily basis to attract tiger sharks for ecotourism purposes (Vossgaetter et al., 2024). Due to the individual's frequent use of the provisioning harbour area, Fuvahmulah hosts the world's largest known aggregation of tiger sharks within a geographically restricted site (Vossgaetter et al., 2024). The high density of individuals gathering at the harbour entrance provides the opportunity to observe potential social behavioral patterns.

Thus, the aims of this study are to: (i) describe the social behavioral patterns displayed by pairs of bait-attracted tiger sharks in Fuvahmulah; (ii) assess the presence of a dominance hierarchy; (iii) evaluate whether the dominance hierarchy and frequency of social interactions are influenced by individual maturity or identity; and (iv) examine the monthly occurrence of social interactions.

2. Materials and methods

2.1. Sampling area

Observations and behavioral data collection of the tiger shark aggregation were carried out in the waters at the entrance of the harbour of Fuvahmulah (0°17'35.56" S; 73°25'24.96" E), in the southern part of the Republic of Maldives. The harbour was built in 2004, and fish waste from the local traditional tuna fishery started accumulating around this area, which, since 2017, serves as a world-recognized dive site for tiger shark tourism (Vossgaetter et al., 2024). Both identification and behavioral data collection were conducted at Tiger Harbour (0°18'23.60" S; 73°26'28.54" E) (Fig. 1).

The study area is characterized by both a sandy bottom and biogenic rocks extending for 17 m in the longest side at a depth of 7 m. The area is surrounded by a shallow coral reef looking at the entrance of the harbour on the right side and by a deeper coral reef on the left that degrades towards a slope at a depth between 10 and 30 m and then flows into a drop off with a depth over 100 m (Vossgaetter et al., 2024; Sulikowski et al., 2024).

A scavenging/baiting condition is reproduced daily by the 11 diving centers by creating an odorous scent of fish blood and oil and hiding tuna heads under biogenic rocks (hereafter called Scavenging Point, SP). This activity is performed to make it difficult for tiger sharks to immediately access the prey, creating baiting conditions similar to those utilized by tiger sharks in more natural settings, and attracting them in front of the divers during every season. Occasionally, fish scraps and discards are used when tuna heads (either fresh or frozen) are unavailable.

Of the 239 tiger sharks identified to date in Tiger Harbour, most of them (84.5 %) are females with both large juveniles and adults present, and adult females displaying strong inter- and intra-annual site fidelity (Vossgaetter et al., 2024). Although the specific drivers of this large aggregation of tiger sharks remain unknown, this area likely serves as a gestation ground for pregnant females (Sulikowski et al., 2024). For instance, the lack of an internal lagoon, low-effort food source, and warm, shallow waters may reproduce ideal conditions to facilitate gestation for pregnant individuals (Sulikowski et al., 2024).

2.2. Data collection

Across one year and a half, from 01/01/2023–30/06/2024, about 25 ARA (self-contained air breathing apparatus) scuba dives of 40 minutes each were carried out for approximately 1000 minutes (~17 hours) monthly. Across 18 months of observations, approximately 18,000 minutes (~300 hours) of scuba diving were performed, between 8.00 AM and 4.00 PM. Diving activities were carried out at 7 m depth, and underwater temperature was recorded throughout the study period, ranging from 28° to 30°C (dive log data from dive computers). Several underwater video cameras with housing (GoPro Hero 7, 8, 10, 11, and 12) were used by researchers to collect underwater images of sharks and record their social behavioral patterns.

Tiger sharks were photo-identified based on unique, natural markings and pigmentation patterns, stable over time, enabling reliable distinction between individuals within the population (Pierce et al., 2018; Clua et al., 2013; Nakachi, 2021; Vossgaetter et al., 2024). Tiger sharks have seven unique and identifiable traits on each side: the countershading delineation on the head and body; the size, shape, and margins of the pectoral, dorsal, caudal, and rear fins, and the body stripe pattern, which result in a total of 14 potential unique and identifiable traits per individual (Nakachi, 2021). A new individual was considered when none of the aforementioned markings were present on another, and a code was assigned to each shark.

The females were recorded if the lack of claspers was verified, and their pelvic fin area was filmed (Vossgaetter et al., 2024).

Total length (TL) of tiger sharks at the provisioning site was measured by following (Vossgaetter et al., 2024). The size of tiger sharks (n = 29) was estimated at 3–4 m distance to the sharks using laser-photogrammetry, employing two adjustable, screw-mounted green lasers (520 nm, 5 mW) attached to PVC pipes spaced 60 cm apart. A distortion coefficient was calculated prior to the data collection using an underwater checkboard, and a linear regression model was applied to compare the observed and expected lengths. The regression equation obtained was then used to correct for lens distortion in all subsequent measurements. Calibration was conducted before each dive at distances of 3 m and 8 m from a calibration board with two markers spaced 60 cm apart to ensure accuracy and fixed laser alignment. Three individual frames were extracted from each video for subsequent measurements, and the TL measurement was based on the average of these frames.

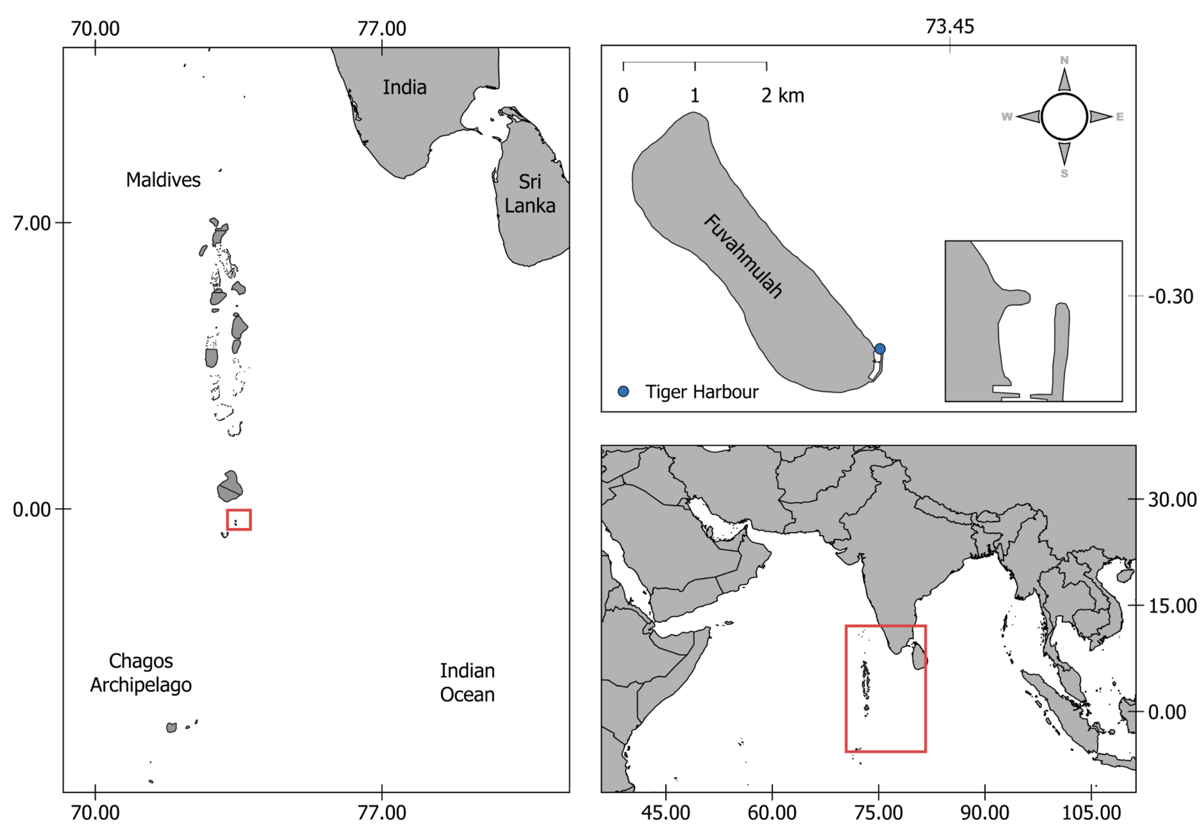

Fig. 1. Map of Fuvahmulah and Tiger Harbour sampling area.

Frames were selected based on the criterion that the shark's fully extended total body was aligned close to a 90° angle relative to the camera to minimize parallax error (Rohner et al., 2011). Known sources of error include tailbeats that prevented full extension of the body in many instances (Klimley, 2013) and the contraction or movement of the caudal fin during swimming, which may affect TL measurements (Rohner et al., 2011). Therefore, precaudal length (PCL) was selected as the primary measurement parameter. When image quality permitted, fork length (FL) was also calculated. ImageJ software (version 1.53 t) was used for image analysis, while the distortion coefficient calculation and correction were performed in RStudio (version 2023.03.1 +446).

Tiger sharks whose size was not assessed using the laser-photogrammetry ($n = 11$), were measured visually by researchers based on objects of known lengths as a visual reference following (Vossgaetter et al., 2024), although these visual measurements were not considered in statistical analysis for a more accurate estimate.

Using photo-identification and measuring the TLs of the individuals was necessary to verify the dominant and the subordinate specimens during a social interaction.

The size at sexual maturity of female tiger sharks in Fuvahmulah Island is still unknown, and in several western Indian Ocean areas, it is comprised between 301 and 349 cm (Pirog et al., 2020). Thus, we used the size at sexual maturity of 300 cm suggested by Sulikowski et al. (2016) and adopted also by Vossgaetter et al. (2024) to establish the length at maturity in Fuvahmulah: TL < 300 cm corresponds to immature individuals; TL = 300–350 cm corresponds to recently mature individuals; TL > 350 cm corresponds to mature older individuals.

Social behavioral patterns refer to interactions between pairs of bait-attracted tiger sharks. A virtual free-swimming shark "observation arena," aimed at identifying and recording the sharks displaying social behaviors, was idealized following the method of (Micarelli et al., 2023). The rectangular 'observation arena', defined as a function to observe social behaviors in 7 m of water column, was bounded in the longest side by the sandy bottom and biogenic rocks at the entrance of the harbour extending 17 m from side to side, and the shorter side corresponded to 8 m of distance perpendicular from the entrance of the harbour to the beginning of the slope (Fig. 2). The SP (Scavenging Point) was placed inside the observation arena, positioned 3 m from the divers and 3.5 m from the dive guides, to facilitate the natural movement of tiger sharks and ensure competitive social interactions were displayed (Fig. 2).

Upon entering the observation arena and approaching the SP, aggressive, submissive, and dominant behavioral patterns were observed.

Social behavioral patterns were monitored by following the method described by Martin (2003), Sperone et al. (2010), and Micarelli et al. (2023) for white sharks: an interaction started when two sharks approached within two body lengths of each other and concluded when they moved more than two body lengths apart, heading in different directions. The duration of social behaviors was recorded in seconds and expressed as relative percentages.

2.3. Statistical Analysis

We used chi-square tests for the linear-independence hypothesis to verify whether two variables are likely to be related (dependency) or not (independency). The statistic test is obtained by solving for the ratio between the mean squared error from the theoretical frequencies and their weights:

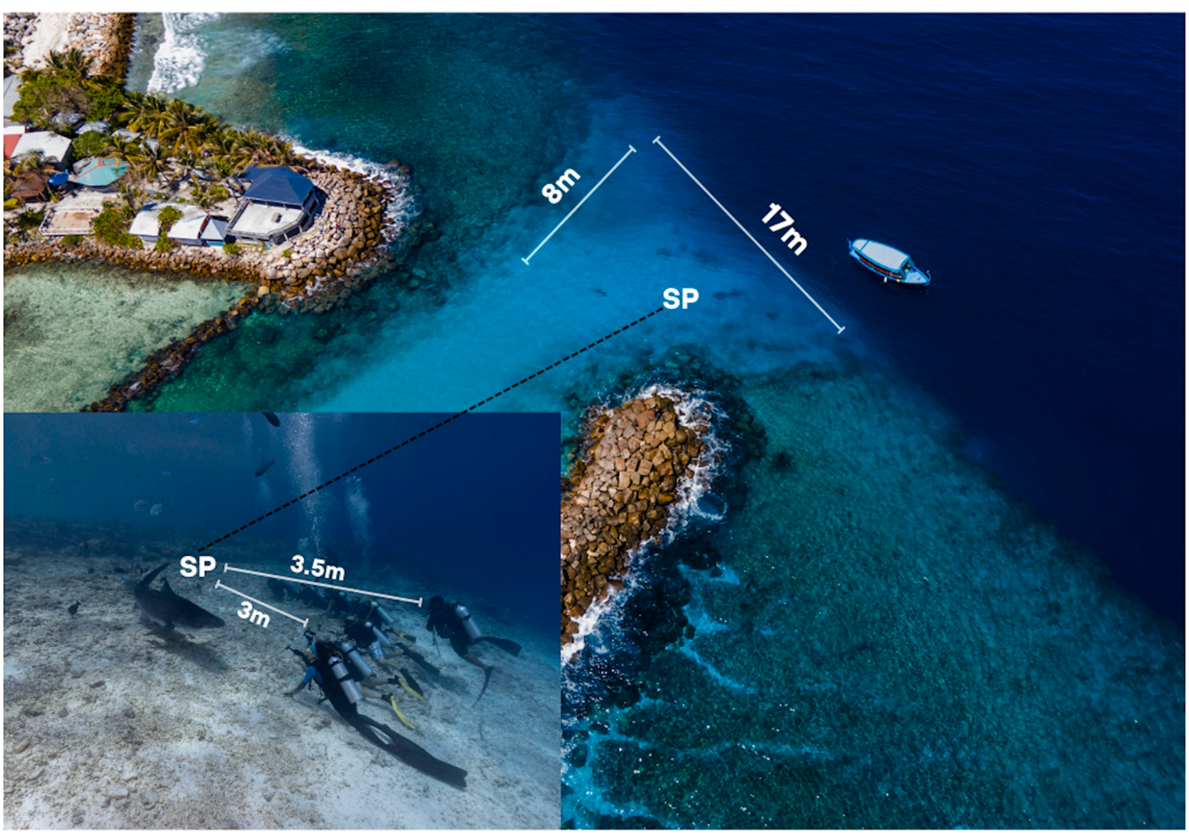

Fig. 2. Virtual "observation arena" for observing tiger shark social behavior at 7 m depth. The longest side (17 m) corresponds to sandy bottom and biogenic rocks at the entrance of the Fuvahmulah harbour; the shorter side (8 m) corresponds to the perpendicular distance from the entrance of the Fuvahmulah harbour and the beginning of the slope. SP (Scavenging Point) represents the place where the tuna's heads were hidden under the pile of biogenic rocks, at a distance of 3 m and 3.5 m from divers and diving guides, respectively.

$$\chi^2 = \frac{\sum_i \sum_j \left(n_{(i,j)} - \hat{n}_{(i,j)}\right)^2}{\hat{n}_{(i,j)}}$$

Here, $n(i,j)$ denotes the absolute joint frequency, where i and j are numerical indices (raw data) representing two random discrete variables and $\hat{n}(i,j)$ stands for the absolute joint frequency in case of independence. This latter, in the denominator, refers to the weights negatively related with the $n(i,j)$'s significance (dependency). Thus, in the case of a strongly causal (and then estimable) relationship between two variables, $\hat{n}(i,j)$ would decrease, improving the significance of the test (a higher chi-square test statistic).

We tested the independence between the variable pairs of *behavior frequency/behavior displayed*, *maturity/behavior displayed*, *individual frequency of interactions/number of behavioral interactions displayed*, *dominance of an individual/behavior displayed*, and *months/behavior displayed*.

To investigate whether social behavior is systematically associated with individual shark identity, we applied Cochran's Q test to assess differences in proportions across repeated measurements of a binary variable. The original variable, representing the number of social interactions per shark, was converted into a binary format: 1 if a shark exhibited more than one social interaction, and 0 otherwise.

The null hypothesis (H_0) assumes equal proportions of binary outcomes across individuals (i.e., no significant differences in social behavior), and the alternative hypothesis (H_1) posits that at least one shark exhibits a significantly different pattern, indicating non-random behavior. The test statistic follows a chi-squared distribution with k - 1 degrees of freedom, where k is the number of sharks observed. Cochran's Q test is appropriate for two-way randomized block designs involving dichotomous outcomes. All analyses were conducted in RStudio (version 4.3.1, 2023–06–16), using a significance level of 0.05.

3. Results

In total, 40 different female tiger sharks were identified showing social interactions and displaying different dominance patterns (Table 1). The mean TL of the 29 measured interacting sharks was 376.7 ± 0.33 cm. The smallest specimen during the sampling period was 311 cm in TL (F-110) and the biggest one was 430 cm in TL (F-055). Overall, two were recently mature (TL = 300–350 cm), and 24 mature older (TL > 350 cm) individuals. The remaining three sharks were measured in TL with the laser-photogrammetric survey in 2021 and 2022 (F-164, 346 cm in 2022; F-167, 271 cm in 2022; F-138, 338 cm in 2021) and in the following years they probably became recently mature (F-167) and mature older individuals (F-164, F-138). No immature individuals and neonates (YOY) were observed during the sampling period (Table 1).

In total, 36 bait-generated social behavioral patterns were displayed, especially in the months of April and November 2023, and generally during autumn, spring, and winter periods. Conversely, there is a lack of social behaviors displayed during summer, with only one social interaction exhibited in August 2023 (Fig. 3).

Observed social interactions were classified into one of the following five interaction patterns as first described by (Martin, 2003) and then reported by (Micarelli et al., 2023) for white sharks in South Africa and by (Clua et al., 2013) for tiger sharks in Prony Bay, New Caledonia. In addition, two new social behaviors were described for the first time for tiger sharks, herein named *push away* and *submission* (Table 2, Fig. 4).

The displays in Table 2 and Fig. 4 are listed in descending order with respect to performance percentages observed between January 2023 and June 2024.

Submission was displayed during the observations in 27.78 % of cases and for 26.73 % of time; *give way* in 27.78 % of cases and for 25.25 % of time; *swim by* in 13.89 % of cases and for 16.34 % of time; *parallel swimming* in 13.89 % of cases and for 15.84 % of time; *push away* in 11.11 % of cases and for 10.89 % of time; *follow give way* in 2.78 % of cases and for 2.97 % of time; and *stand back* in 2.78 % of cases and for 1.98 % of time (Table 3).

Table 1
Overview of size, number of social interactions, hierarchical level, and number of dominance displays of each of the 40 tiger sharks identified at Tiger Harbour, Fuvahmulah (January 2023-June 2024). Total lengths (TL, cm) were obtained via laser-photogrammetry or through visual estimates when the size was not determined (nd).

Individual code	TL (cm) with laser and corresponding year	Number of social interactions	Dominance hierarchy	Dominance displays
F−011	400 (2024)	3	Dominant	1
F−173	nd (visually 300)	1	Subordinate	0
F−054	376 (2024)	3	Dominant	1
F−009	405 (2021)	4	Dominant	3
F−164	346 (2022)	2	Dominant	1
F−018	394 (2024)	2	Subordinate	0
F−140	418 (2024)	4	Dominant	3
F−110	311 (2024)	3	Dominant	1
F−167	271 (2022)	3	Subordinate	0
F−162	359 (2022)	1	Dominant	1
F−049	nd (visually > 350)	1	Subordinate	0
F−002	nd (visually > 350)	5	Dominant	2
F−053	390 (2024)	1	Subordinate	0
F−055	430 (2023)	1	Dominant	1
F−040	360 (2024)	2	Subordinate	0
F−051	416 (2023)	1	Subordinate	0
F−028	nd (visually > 350)	1	Dominant	1
F−021	368 (2024)	1	Dominant	1
F−080	411 (2024)	1	Subordinate	0
F−126	362 (2024)	1	Subordinate	0
F−038	376 (2024)	1	Dominant	1
F−127	nd (visually > 400)	1	Dominant	1
F−207	nd (visually 300–350)	4	Dominant	1
F−145	nd (visually 300–350)	1	Subordinate	0
F−128	370 (2024)	1	Subordinate	0
F−138	338 (2021)	1	Dominant	1
F−012	385 (2021)	1	Subordinate	0
F−059	341 (2024)	3	Dominant	2
F−007	391 (2024)	1	Dominant	1
F−108	nd (visually > 350)	1	Subordinate	0
F−076	385 (2024)	2	Subordinate	0
F−061	383 (2024)	1	Dominant	1
F−103	420 (2024)	1	Dominant	1
F−131	375 (2024)	1	Dominant	1
F−117	nd (visually > 350)	2	Dominant	2
F−159	nd (visually 300–350)	1	Dominant	1
F−016	409 (2024)	1	Dominant	1
F−067	360 (2022)	1	Subordinate	0
F−010	nd (visually 400)	1	Subordinate	0
F−099	377 (2021)	1	Subordinate	0

The chi-square tests indicate the extent of the difference between the observed frequencies and the expected frequencies, assuming no association between the variables (H_0). A higher chi-square statistic suggests a larger discrepancy between the observed and expected values.

Several variables (*behavior frequency*, *maturity*, *individual frequency of interactions*, and *dominance of an individual*) showed significant *p-values* at the 5 % significance level, leading to the rejection of the null hypothesis in favor of the alternative of dependency. However, the variable *months* shows a non-significant *p-value*.

Give way and *submission* were identified as the most frequently displayed social behaviors, each observed 10 times (chi-squared = 10.23, *p-value* = 0.037; Table 3). Mature older female sharks were significantly

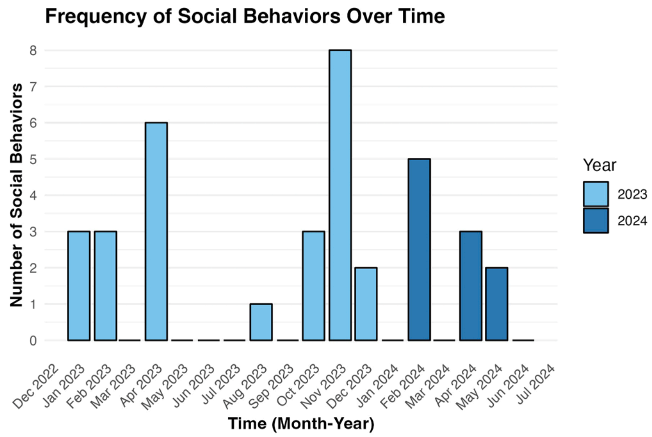

Fig. 3. Number of social behaviors displayed by tiger sharks each month, from January 2023 to June 2024.

more dominant in social interactions than recently mature females (chi-squared = 13.75, *p-value* = 0.032; Table 1). This indicates a statistically significant relationship between binned TL and social dominance, indicating that larger sharks are likelier to establish a hierarchy. Particularly, three mature older females (F-140, F-009, F-002) and a recently mature female (F-207) were involved in significantly more social interactions (4, 4, 5, and 4 respectively; chi-squared = 16.56, *p-value* = 0.039; Table 1), resulting in higher re-sighting rates than other individuals. Of these, F-009 and F-140, exceeding 4 m in TL, were most frequently dominant (3 times each), with significant competitive behaviors (chi-squared = 12.17, *p-value* = 0.041; Table 1).

Social behaviors were recorded in specific months (January, February, April, August, October, November, and December 2023; February, April, and May 2024) but were absent in others (March, May, June, July, and September 2023; January, March, and June 2024) (Fig. 3). However, this monthly variation was not statistically significant (chi-squared = 108, *p-value* = 0.323), suggesting that the absence of interactions in some months may occur randomly.

Cochran's Q test yielded a chi-squared value of 5.67 with 4 degrees of freedom (*p-value* = 0.058). Although the null hypothesis could not be rejected at the 5 % significance level, the result suggests marginal significance at the 10 % level, indicating potential differences in social interaction patterns among the observed tiger sharks.

4. Discussion

Tiger sharks are known to be solitary but also opportunistic and generalist predators (Matich et al., 2011); thus, they can aggregate and interact with conspecifics, tolerating each other when foraging opportunities arise (Heithaus, 2001; Meyer et al., 2010; Clua et al., 2013).

The reproduction of scavenging conditions in Fuvahmulah for shark ecotourism can enhance the level of sociality of tiger sharks at the provisioning site and allow for interesting insight into their social behavior, as demonstrated by our study. In this study, we suggest that mature female tiger sharks are capable of sociality and form bait-driven non-random social interactions in Tiger Harbour.

The 40 recently mature and mature older female tiger sharks identified in Fuvahmulah during social interactions ranged from 311 to 430 cm in TL, according to size ranges observed by (Vossgaetter et al., 2024) at this site. The absence of smaller juvenile tiger sharks and neonates (YOY) observed is probably due to the elevated predation risks possibly encountered with a large diversity of apex predators (Vossgaetter et al., 2024). The highest number of mature older females agrees with their inter- and intra-annual site fidelity, whereas smaller females probably tend to remain in close geographical proximity to the island (Vossgaetter et al., 2024). Additionally, the size-sex segregation

Table 2
Definition of the social behaviors displayed by tiger sharks from Fuvahmulah. Five of the seven identified behaviors (*give way*, *swim by*, *parallel swimming*, *follow give way*, and *stand back*) were based on the review by (Martin, 2003), whereas *submission* and *push away* were described for the first time in this study. Please see the article's Supplementary material tab to access the video: [a] Video Clips 1; [b] Video Clips 2; [c] Video Clips 3; [d] Video Clips 4; [e] Video Clips 5; [f] Video Clips 6; [g] Video Clips 7.

Term	Definition	Reference	Previously observed for tiger sharks
Submission[a]	Sudden and abrupt deviation of the trajectory of one shark literally escaping at the approach of another, rolling sideways showing partially or completely its underside, away from the prey, implying a social precedence of the undeviating individual (dominant species).	This study	No
Give way[b]	Deflection of the trajectory of one shark characterized by ~ 45° turn to either the left or right, typically observed as a response to another shark approaching, implying a social precedence of the undeviating individual (dominant specimen) to the prey	(Martin, 2003)	Yes
Swim by[c]	Opposite courses of the sharks close to the prey, without a collision, exhibiting slow, close-range movement, maintaining a distance of approximately 0.5 m to 2.5 m from one another. The interaction concluded as the sharks passed each other without further engagement	(Martin, 2003)	No
Parallel swimming[d]	Parallel course of two sharks in the same direction without a collision close to the prey. The sharks swam close to one another maintaining a distance between 0.5 m to 2.0 m	(Martin, 2003)	No
Push away[e]	Converging path of two sharks towards the prey, with the dominant individual voluntarily nudging the subordinate aside with a bump	This study	No
Follow give way[f]	The dominant shark follows the subordinate towards the prey, prompting the latter to exhibit an avoidance response, akin to a "give-way" behavior. The interaction concluded when the subordinate turned left or right at an angle of approximately 45° to 90°. Typical distance between the sharks ranged from 1 to 2.5 m	(Martin, 2003)	No
Stand back[g]	Simultaneous deviation of two colliding individuals towards the prey with no established dominance	(Martin, 2003)	Yes

in Fuvahmulah suggests reproductive needs (Vossgaetter et al., 2024; Sulikowski et al., 2024), as was proposed for the Tiger Beach area in the Bahamas (Sulikowski et al., 2016). Tiger Harbour, with calm, warm, and shallow waters, could facilitate females' gestation while avoiding male harassment, in contrast to the Tiger Beach area in the Bahamas, which seems absent (Sulikowski et al., 2016; Sulikowski et al., 2024; Jacoby et al., 2021; Vossgaetter et al., 2024).

The observed social interactions in this study are exclusively representative of mature females aggregating in the coastal waters of the Tiger Harbour site. As a consequence, we acknowledged that the

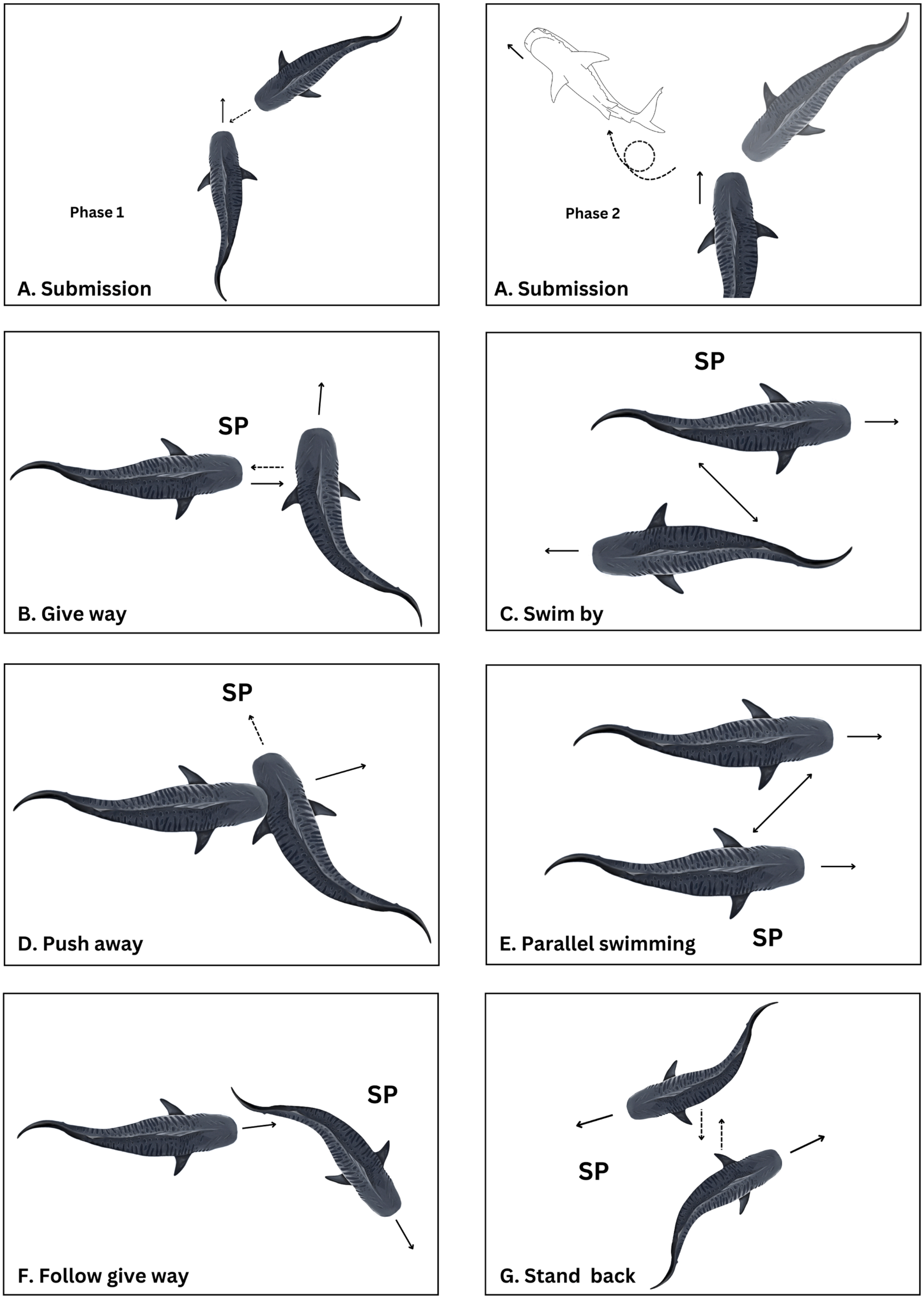

Fig. 4. Seven social behaviors displayed by tiger sharks: *submission* (A); *give way* (B); *swim by* (C); *push away* (D); *parallel swimming* (E); *follow give way* (F); *stand back* (G). SP (Scavenging Point) represents the area where the tuna heads were hidden under a pile of biogenic rocks.

Table 3
Total number, time (sec.), and relative percentages of social behaviors exhibited.

Social Behavior	Total number of displays and performance percentages	Total time (sec.) of displays and performance percentages
Submission	10 (27.78 %)	54 (26.73 %)
Give way	10 (27.78 %)	51 (25.25 %)
Swim by	5 (13.89 %)	33 (16.34 %)
Parallel swimming	5 (13.89 %)	32 (15.84 %)
Push away	4 (11.11 %)	22 (10.89 %)
Follow give way	1 (2.78 %)	6 (2.97 %)
Stand back	1 (2.78 %)	4 (1.98 %)
Total	36 (100 %)	202 (100 %)

observed social behavioral modules are limited to the individuals mentioned in this study, and not yet applicable to the entire population described previously by (Vossgaetter et al., 2024), including smaller males with an offshore distribution, nor the species in general. Furthermore, the evidence of a reduction in the number and social interactions of sharks with distance from the SP was not reported even though it would be necessary to test whether sociality may occur also in the absence of foraging opportunities.

Within the feeding aggregation of mature female tiger sharks in Tiger Harbour, *submission* and *give way* were the most significant social behaviors displayed. In both interactions, the establishment of a hierarchy between two mature female tiger sharks to avoid a direct confrontation and, therefore, the possibility of injury is highlighted, with evident energetic gains (Sperone et al., 2010). For instance, tiger sharks displayed *give way* and *stand back* in the presence of a blue whale carcass in Prony Bay, New Caledonia, as reported by (Clua et al., 2013), demonstrating a tolerance of the dominant shark towards the subordinate. The authors also reported the presence of the *tail slapping* behavior occurring at the surface, mainly based on aggression between conspecifics. Unfortunately, *tail slapping* was not documented in Tiger Harbour due to the limitation of collecting data underwater as opposed to the surface. In our study, some of the behaviors displayed (*submission, give way, push away, and follow give way*) represent competitive modules, and others (*parallel swimming, swim by, and stand back*) display intimidation and mild observation modules (Sperone et al., 2010; Micarelli et al., 2023). Mature female tiger sharks in Fuvahmulah showed both elevated dominance and mainly *submission* and *give way* competition modules towards their conspecifics; thus, the SP could represent a "dominion place," and a crucial resource where dominant individuals try to chase away subordinates considered as competitor scavenger individuals (Clua et al., 2013). The opposite situation occurs for white sharks from Gansbaai (South Africa), where mild observation modules, such as *swim by* and *parallel swimming*, are more common, reflecting a calm approach and an initial hesitation of the animals (Micarelli et al., 2023). Hence, white sharks are mild observers in the hunting area, given their sophisticated visual acuity in confronting each other and in the prey selection when the investigation period is of longer duration (Martin et al., 2005; Bromilov, 2014; Micarelli et al., 2021; Micarelli et al., 2023; Reinero et al., 2022).

Conversely, tiger sharks displayed a more aggressive approach, considering their nature as pure generalists when the conditions allow (Clua et al., 2013). The two new social behaviors described here (*submission* and *push away*) indicate this higher aggression level. *Submission*, which occurred farther from the SP, involved a clear deterring response from the dominant shark towards the submissive one. This forced the submissive shark to rapidly escape, rolling sideways to partially or completely expose its underside, and causing an alteration of its trajectory. *Submission* has not been documented for sharks before, but a comparable behavior, where the submissive fish rolls sideways on its longitudinal axis to expose its underside, has been observed in daffodil cichlids (Reddon et al., 2024) and guppies (Gorlick, 1976). *Push away* likewise determined an aggressive response of the dominant shark, voluntarily repelling the submissive one far from the food source. (Clua et al., 2013) observed tiger sharks inflicting quick bites on a blue whale carcass in New Caledonia, resulting in short bumps between individuals. However, this scenario was documented during a *Feeding frenzies* event, not in Tiger Harbour, suggesting that such collisions may occur in that context, where bumps may be more frequent. Both these social behaviors contribute to established dominance in a real territory of dominion, following the concept developed by (Brown, 1975) and Wittenberger (1981).

Mature older female tiger sharks in Tiger Harbour exhibit greater dominance in social interactions than their recently mature counterparts. The existence of a size-based dominance hierarchy and the tendency of larger sharks to tolerate smaller ones have been documented in multiple shark species (Clark, 1963; Limbaugh, 1963; Myrberg and Gruber, 1974; Weihs et al., 1981; Parkes, 2021), including tiger sharks (Clua et al., 2013). Body markings seem to be visual signals enabling a shark to estimate the size of an approaching conspecific and, consequently, to maintain the size-dependent dominance hierarchy (Myrberg, 1991). Thus, larger sharks have priority access to the food source, while the smaller ones wait for their turn, avoiding collisions, aggression, and injuries between interacting parties (Fallows et al., 2013). In Fuvahmulah, (Vossgaetter et al., 2024) observed juvenile tiger sharks staying on the periphery of the dive site, waiting for mature females approaching the food source first, getting closer only when the larger sharks move away. Thus, the hierarchical patterns of tiger sharks in Fuvahmulah Island, as supposed by (Vossgaetter et al., 2024), seem to be assessed by the absence of immature sharks, with a clear size-based hierarchy between mature females during social behavioral interactions, as highlighted in this study. Similarly, (Parkes, 2021), in the Aliwal Shoal Marine Protected Area (South Africa), observed within the social behavior of oceanic blacktip sharks (*Carcharhinus limbatus*, Muller & Henle 1839) one of the largest female sharks to be remarkably more dominant than the others, with the highest level of re-sightings and dominance over the sample period.

The display of more interactions also by a recently mature tiger shark (F-207) in Tiger Harbour makes us speculate that size alone could not predict the outcome of an agonistic event, and sharks could rely on personality. For instance, (Vossgaetter et al., 2024) hypothesized that Tiger Harbour is dominated by a subset of the population that shows above-average dominance and aggression, and less dominant sharks can be chased away or avoid close interactions with larger dominants. Given that this study focuses on mature female tiger sharks in Tiger Harbour, dominance and personality dynamics may differ significantly in offshore natural or artificial feeding areas where male individuals are also present. In this context, animal personalities and repeatability in individual traits can be influenced by the interactive social strategies of individuals, such as inter-individual variation in aggression and boldness across different contexts (Jacoby et al., 2014). Thus, further studies could be conducted to test both personalities and the presence of tiger shark social networks in Fuvahmulah, the repeatability of individual network positions, and the coupling between individual preferences for specific group sizes and social network positions (Jacoby et al., 2014; Bouveroux et al., 2021).

Social behaviors were displayed mainly in April and November 2023, and generally during autumn, spring, and winter periods. Conversely, there is a lack of social behaviors displayed during summer, although not significant, probably due to the inconsistency of the sampling over time. Provisioning efforts in Fuvahmulah are the same throughout the year, and behaviors were recorded continuously during the study period. The absence of random interactions during certain months could be due to high levels of mobility and strong variability in movement patterns of tiger sharks to different home ranges (Meyer et al., 2018; Sèguigne et al., 2023) related to fulfilling life history requirements such as feeding, reproduction, and temperature (Lubitz et al., 2022). Thus, tiger sharks may show high sight-fidelity to core use areas (CUA) and wide-ranging movements in coastal and open ocean habitats (Meyer et al., 2018; Sèguigne et al., 2023). This could make it harder to retain this species at Tiger Harbour provisioning site than, for example, highly reef-associated sharks (Sèguigne et al., 2023). The monthly behavioral patterns of the tiger shark at Tiger Harbour could be explained by other natural focal areas around Fuvahmulah, where individuals could aggregate, establishing social interactions, such as Farikede, where tiger sharks are frequently observed unprovisioned (Vossgaetter et al., 2024). We recommend for future studies an investigation of the role of offshore conditions and fine-scale habitat on the entire spatial ecology of the species on the island that could potentially lead to unprovisioned social interactions with animal-borne cameras and/or acoustic telemetry.

5. Conclusions

Studying the social behavior of the tiger shark is challenging, especially given the scarce literature on the topic. First insights into the social behavioral patterns of this species highlighted the display of non-random social interactions between pairs of bait-attracted tiger sharks in Fuvahmulah, Maldives, and the establishment of a size-based dominance hierarchy in the context of a mature female coastal aggregation. However, several aspects related to tiger shark social interactions in other feeding areas, animal personalities that would trigger dominance patterns and distinct social networks, effects of the provisioning activity, and the intra-specific behavioral variability of tiger shark movements at different home ranges must be improved at this site. Moreover, it is recommended that further analyses with longer time series should be performed to investigate whether the social behavior of tiger sharks may also be affected by environmental factors and inter-specific interactions with competitor species. A deeper knowledge of intra-specific behavioral interactions and variations in behavior among individuals observed repeatedly is crucial for understanding tiger shark population dynamics in Fuvahmulah and ensuring protection plans and conservation measures for this near-threatened species within this area.

Ethical approval

All research was carried out through video recordings, and we did not intervene in the observed animals. We conducted this study under the research permit n. A280197 released by the Ministry of Fisheries, Marine Resources and Agriculture, Malè, Republic of Maldives.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

CRediT authorship contribution statement

Francesca Romana Reinero: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Filippo Bocchi:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. **Nathan Perisic:** Writing – review & editing, Resources, Data curation. **Jamie Crouch:** Resources, Data curation. **Antonio Pacifico:** Software, Formal analysis. **Luca Asshauer:** Software. **Consuelo Vicariotto:** Writing – review & editing, Methodology, Investigation. **Primo Micarelli:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We sincerely thank Mr. Ahmed Inah (Pelagic Divers Fuvahmulah), Ms. Tatiana Ivanova (Fuvahmulah Dive School), Mr. Hassan Sham (Fuvhamulah Scuba Club), and all the staff of these diving centers for their invaluable support with logistical arrangements, dive operations and boat support, and coordinating time schedules. Their dedication and assistance greatly contributed to the success of this research. Without their help this study would have not been possible. We further thank all the volunteers who took part in the Scientific expeditions carried out by the Sharks Studies Center-Scientific Institute, Mr. Max Kimble for his support with GIS and the production of the maps provided in this paper, and Mr. Ahmed Rameez, Mr. Aivan Mohamed Zahir, and Mr. Ibrahim Zihad for their contribution to fix underwater cameras and providing safety during the operations. Ultimately, we express gratitude towards all the dive guests that donate videographic equipment for the realization of this project.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2025.105216.

Data availability

Data will be made available on request.

References

Allee, W.C., Dickinson, J.C.J., 1954. Dominance and subordination in the smooth dogfish *Mustelus canis* (Mitchill). Physiol. Zool. 27 (4), 356–364.

Apps, K., Dimmock, K., Huveneers, C., 2018. Turning wildlife experiences into conservation action: can white shark cage-dive tourism influence conservation behaviour? Mar. Policy 88, 108–115. https://doi.org/10.1016/j.marpol.2017.11.024.

Baldaccini, N.E., Mainardi, D., Papi, F., 1990. Introduzione Alla Etologia, first ed. Editoriale Grasso, Bologna. ⟨https://elearning.unite.it/pluginfile.php/247583/mod_resource/content/1/Testo_Didattica.pdf⟩.

Bouveroux, T., Loiseau, N., Barnett, A., Marosi, N.D., Brunnschweiler, J.M., 2021. Companions and Casual Acquaintances: The Nature of Associations Among Bull Sharks at Shark Feeding Site in Fiji. Front. Mar. Sci. 8, 678074. https://doi.org/10.3389/fmars.2021.678074.

Brena, P.F., Mourier, J., Planes, S., Clua, E.E., 2018. Concede or clash? Solitary sharks competing for food assess rivals to decide. Proc. R. Soc. B: Biol. Sci. 285, 20180006. https://doi.org/10.1098/rspb.2018.0006.

Bromilov, M., 2014. Feeding behaviour of white sharks Carcharodon carcharias around a cage diving vessel and the implications for conservation. Ph.D. Thesis, University of Michigan, Department of Ecology & Evolutionary Biology, Ann Arbor, MI, USA, pp. 6-8.

Brown, J.L., 1975. The evolution of behavior, first ed. WW Norton & Co Inc, New York.

Burghardt, G.M., 1970. Defining "communication". Commun. Chem. Signals 1, 5–18.

Chase, I.D., 1980. Cooperative and noncooperative behaviour in animals. Am. Nat. 115, 827–857.

Clark, E., 1963. The maintenance of sharks in captivity, with a report on their instrumental conditioning. In: Gilbert, P.W. (Ed.), Sharks and Survival. Health & Co, Boston, pp. 115–150.

Clua, E., Chauvet, C., Read, T., Werry, J.M., Lee, S.Y., 2013. Behavioural patterns of a tiger shark feeding aggregation at a blue whale carcass in Prony Bay, New Caledonia. Mar. Freshw. Behav. Physiol. 46, 1–20. https://doi.org/10.1080/10236244.2013.773127.

Clua, E., Sèret, B., 2012. Global Perspectives on the biology and life history of the great white shark. In: Domeier, M.L. (Ed.), New Caledonia as a potential wintering ground for the white shark (Carcharodon carcharias). CRC Press, Boca Raton, pp. 343–353.

Dudley, F.J.S., Anderson-Reade, D.M., Thompson, S.G., McMullen, B.P., 2000. Concurrent scavenging off a whale carcass by great white sharks, *Carcharodon carcharias*, and tiger sharks, *Galeocerdo cuvier*. Fish. Bull. -Natl. Ocean. Atmos. Adm. 98 (3), 646–649.

Ebert, D.A., 1991. Observations of the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. South Afr. J. Mar. Sci. 11 (1), 455–465. https://doi.org/10.2989/025776191784287637.

Fallows, C., Gallagher, A.J., Hammerschlag, N., 2013. White sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping of the ecology of an apex predator. PLoS ONE 8 (4), e60797. https://doi.org/10.1371/journal.pone.0060797.

Gallagher, A.J., Huveneers, C., 2018. Emerging challenges to shark-diving tourism. Mar. Policy 96, 9–12. https://doi.org/10.1016/j.marpol.2018.07.009.

Gorlick, D.L., 1976. Dominance hierarchies and factors influencing dominance in the gruppy *Poecilia reticulata* (Peters). Anim. Behav. 24 (2), 336–346. https://doi.org/10.1016/S0003-3472(76)80041-3.
Guttal, V., Couzin, I.D., 2010. Social interactions, information use, and the evolution of collective migration. Proc. Natl. Acad. Sci. 107 (37), 16172–16177. https://doi.org/10.1073/pnas.1006874107.
Guttridge, T.L., Gruber, S.H., DiBattista, J.D., Feldheim, K.A., Croft, D.P., Krause, S., Krause, J., 2011. Assortative interactions and leadership in a free-ranging population of juvenile lemon shark *Negaprion brevirostris*. Mar. Ecol. Prog. Ser. 423, 235–245. https://doi.org/10.3354/meps08929.
Guttridge, T.L., Gruber, S.H., Gledhill, K.S., Croft, D.P., Sims, D.W., Krause, J., 2009. Social preferences of juvenile lemon sharks, *Negaprion brevirostris*. Anim. Behav. 78 (2), 543–548. https://doi.org/10.1016/j.anbehav.2009.06.009.
Hammerschlag, N., Gallagher, A.J., Wester, J., Luo, J., Ault, J.S., 2012. Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. Funct. Ecol. 26 (3), 567–576. https://doi.org/10.1111/j.1365-2435.2012.01973.x.
Hammerschlag, N., Gutowsky, L.F.G., Gallagher, A.J., Matich, P., Cooke, S.J., 2017. Diel habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high use area exposed to dive tourism. J. Exp. Mar. Biol. Ecol. 495, 24–34. https://doi.org/10.1016/j.jembe.2017.05.010.
Heithaus, M.R., 2001. The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environ. Biol. Fishes 61, 25–36. https://doi.org/10.1023/A:1011021210685.
Heupel, M.R., Simpfendorfer, C.A., 2005. Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar. Biol. 147, 1239–1249. https://doi.org/10.1007/s00227-005-0004-7.
Hinde, R.A., 1976. Interactions, relationships and social structure. Man 11, 1–17.
Jacoby, D.M.P., Busawon, D.S., Sims, D.W., 2010. Sex and social networking: the influence of male presence on social structure of female shark groups. Behav. Ecol. 21 (4), 808–818. https://doi.org/10.1093/beheco/arq061.
Jacoby, D.M.P., Croft, D.P., Sims, D.W., 2012. Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish Fish 13, 399–417. https://doi.org/10.1111/j.1467-2979.2011.00436.x.
Jacoby, D.M.P., Fairbaim, B.S., Frazier, B.S., Gallagher, A.J., Heithaus, M.R., Cooke, S.J., Hammerschlag, N., 2021. Social network analysis reveals the subtle impacts of tourism provisioning on the social behavior of a generalist marine apex predator. Front. Mar. Sci. 8, 665726. https://doi.org/10.3389/fmars.2021.665726.
Jacoby, D.M.P., Fear, L.N., Sims, D.W., Croft, D.P., 2014. Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. Behav. Ecol. Sociobiol. 68, 1995–2003. https://doi.org/10.1007/s00265-014-1805-9.
Johnson, D.D.P., Kays, R., Blackwell, P.G., Macdonald, D.W., 2002. Does the resource dispersion hypothesis explain group living? Trends Ecol. Evol. 17 (12), 563–570. https://doi.org/10.1016/S0169-5347(02)02619-8.
Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P., Block, B.A., 2010. Philopatry and migration of Pacific white sharks. Proc. R. Soc. B: Biol. Sci. 277 (1682), 679–688. https://doi.org/10.1098/rspb.2009.1155.
Klimley, A.P., 1987. The determinants of sexual segregation in the scalloped hammerhead shark *Sphyrna lewini*. Environ. Biol. Fishes 18, 27–40. https://doi.org/10.1007/BF00002325.
Klimley, A.P., 2013. The Biology of Sharks and Rays. The University of Chicago Press, USA.
Klimley, A.P., Nelson, D.R., 1984. Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav. Ecol. Sociobiol. 15, 45–54. https://doi.org/10.1007/BF00310214.
Krause, J., Ruxton, G.D., 2002. Living in Groups. Oxford University Press, New York.
Labourgade, P., Ballesta, L., Huveneers, C., Papastamatiou, Y., Mourier, J., 2020. Heterospecific foraging associations between reef-associated sharks: first evidence of kleptoparasitism in sharks. Ecology 101 (11), e03117. https://doi.org/10.1002/ecy.3117.
Limbaugh, C., 1963. Filed notes on sharks. In: Gilbert, P.W. (Ed.), Sharks and Survival. Health & Co, Boston, pp. 63–94.
Lorenz, K., 1996. On Aggression. Psychology Press, London.
Lubitz, N., Bradley, M., Sheaves, M., Hammerschlag, N., Daly, R., Barnett, A., 2022. The role of context in elucidating drivers of animal movement. Ecol. Evol. 12 (7), e9128. https://doi.org/10.1002/ece3.9128.
Martin, R.A., 2003. Field Guide to the Great White Shark, first ed. ReefQuest Centre for Shark Research, Vancouver.
Martin, R.A., Hammerschlag, N., Collier, R.S., Fallows, C., 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. J. Mar. Biol. Assoc. U. Kingd. 85 (5), 1121–1135. https://doi.org/10.1017/S002531540501218X.
Matich, P., Heithaus, M.R., Layman, C.A., 2011. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J. Anim. Ecol. 80 (1), 294–305. https://doi.org/10.1111/j.1365-2656.2010.01753.x.
Meyer, C.G., Anderson, J.M., Coffey, D.M., Hutchinson, M.R., Royer, M.A., Holland, K.N., 2018. Habitat geography around Hawaii's oceanic islands influences tiger shark (*Galeocerdo cuvier*) spatial behaviour and shark bite risk at ocean recreation sites. Sci. Rep. 8, 4945. https://doi.org/10.1038/s41598-018-23006-0.
Meyer, C.G., Papastamatiou, Y.P., Holland, K.N., 2010. A multiple instrument approach to quantifying the movement patterns and habitat use of tiger (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) at French Frigate Shoals, Hawaii. Mar. Biol. 157, 1857–1868. https://doi.org/10.1007/s00227-010-1457-x.
Micarelli, P., Chieppa, F., Pacifico, A., Rabboni, E., Reinero, F.R., 2021. Passive prey discrimination in surface predatory behaviour of bait-attracted white sharks from Gansbaai, South Africa. Animals 11, 2583. https://doi.org/10.3390/ani11092583.
Micarelli, P., Pireddu, M., Persia, D., Sanna, M., Vicariotto, C., Pacifico, A., Storelli, P., Mahrer, M., Venanzi, E., Reinero, F.R., 2024. Observations on an aggregation of grey reef sharks (*Carcharhinus amblyrhynchos*) in the Mozambique Channel off the coast of Nosy Be (Madagascar) and tools for photo-identification-A new aggregation nursery site? Biology 13, 661. https://doi.org/10.3390/biology13090661.
Micarelli, P., Reinero, F.R., D'Agnese, R., Pacifico, A., Giglio, G., Sperone, E., 2023. Evidence of non-random social interactions between pairs of bait-attracted white sharks in Gansbaai (South Africa). Diversity 15, 433. https://doi.org/10.3390/d15030433.
Mourier, J., Brown, C., Planes, S., 2017. Learning and robustness to catch-and-release fishing in a shark social network. Biol. Lett. 13, 20160824. https://doi.org/10.1098/rsbl.2016.0824.
Mourier, J., Vercelloni, J., Planes, S., 2012. Evidence of social communities in a spatially structured network of a free-ranging shark species. Anim. Behav. 83 (2), 389–401. https://doi.org/10.1016/j.anbehav.2011.11.008.
Myrberg, A.A., 1991. Distinctive markings of sharks: ethological considerations of visual function. J. Exp. Zool. 5, 156–166. https://doi.org/10.1002/jez.1402560520.
Myrberg, A.A., Gruber, S.H., 1974. The behavior of the bonnethead shark, *Sphyrna tiburo*. Copeia 358–374. https://doi.org/10.2307/1442530.
Nakachi, K.I., 2021. Heeding the history of Kahu Mano: developing and validating a pono photo-identification methodology for tiger sharks (*Galeocerdo cuvier*) in Hawai'i. Master's thesis, University of Hawai'I at Hilo, Tropical Conservation Biology and Environmental Science Graduate Program, USA, pp. 18-24.
Papastamatiou, Y.P., Bodey, T.W., Caselle, J.E., Bradley, D., Freeman, R., Friedlander, A. M., Jacoby, D.M.P., 2020. Multiyear social stability and social information use in reef sharks with diel fission-fusion dynamics. Proc. R. Soc. B: Biol. Sci. 287, 20201063. https://doi.org/10.1098/rspb.2020.1063.
Papastamatiou, Y.P., Mourier, J., TinHan, T., Luongo, S., Hosoki, S., Santana-Morales, O., Hoyos-Padilla, M., 2022. Social dynamics and individual hunting tactics of white sharks revealed by biologging. Biol. Lett. 18 (3), 20210599. https://doi.org/10.1098/rsbl.2021.0599.
Parkes, C.J., 2021. Behavioural ethograms & social hierarchy of Carcharhinus limbatus (blacktip) during a simulated-feeding scenario within South African MPA. Master Thesis, University of Algarve, Faculty of Sciences and Technology, Faro, Portugal, pp. 23-26. 〈https://sapientia.ualg.pt/server/api/core/bitstreams/165b4f1b-64d1-4739-bb94-aca8b10939d0/content〉.
Pierce, S.J., Holmberg, J., Kock, A.A., Marshall, A.D., 2018. Photographic identification of sharks. In: Carrier, J.C. (Ed.), Shark Research: emerging technologies and applications for the field and laboratory. CRC Press, Boca Raton, pp. 219–234.
Pirog, A., Magalon, H., Poirout, T., Jaquemet, S., 2020. New insights into the reproductive biology of the tiger shark *Galeocerdo cuvier* and no detection of polyandry in Reunion Island, western Indian Ocean. Mar. Freshw. Res. 71 (10), 1301–1312. https://doi.org/10.1071/MF19244.
Reddon, A.R., Richardson, C., Jose, A., Frommen, J.C., Swaney, W.T., 2024. Social fish use different submission signals depending on spatial distribution. Behaviour 161, 523–534. https://doi.org/10.1163/1568539X-bja10271.
Reinero, F.R., Sperone, E., Giglio, G., Pacifico, A., Mahrer, M., Micarelli, P., 2022. Influence of environmental factors on prey discrimination of bait-attracted white sharks from Gansbaai, South Africa. Animals 12 (23), 3276. https://doi.org/10.3390/ani12233276.
Riley, M.J., Hale, M.S., Harman, A., Rees, R.G., 2010. Analysis of whale shark *Rhincodon typus* aggregations near South Ari Atoll, Maldives Archipelago. Aquat. Biol. 8, 145–150. https://doi.org/10.3354/ab00215.
Rohner, C.A., Richardson, A.J., Marshall, A.D., Weeks, S.J., Pierce, S.J., 2011. How large is the world's largest fish? Measuring whale sharks *Rhincodon typus* with laser photogrammetry. J. Fish. Biol. 78, 378–385. https://doi.org/10.1111/j.1095-8649.2010.02861.x.
Schilds, A., Mourier, J., Huveneers, C., Nazimi, L., Fox, A., Leu, S.T., 2019. Evidence for non-random co-occurrences in a white shark aggregation. Behav. Ecol. Sociobiol. 73, 138. https://doi.org/10.1007/s00265-019-2745-1.
Sèguigne, C., Bègue, M., Meyer, C., Mourier, J., Clua, E., 2023. Provisioning ecotourism does not increase tiger shark site fidelity. Sci. Rep. 13 (1), 7785. https://doi.org/10.1038/s41598-023-34446-8.
Sims, D.W., Southall, E.J., Quayle, V.A., Fox, A.M., 2000. Annual social behaviour of basking sharks associated with coastal front areas. Proc. R. Soc. B: Biol. Sci. 276 (1455), 1897–1904. https://doi.org/10.1098/rspb.2000.1227.
Sperone, E., Micarelli, P., Andreotti, S., Spinetti, S., Andreani, A., Serena, F., Brunelli, E., Tripepi, S., 2010. Social interactions among bait attracted white sharks at Dyer Island (South Africa). Mar. Biol. Res. 6, 408–414. https://doi.org/10.1080/17451000903078648.
Sulikowski, J.A., Perisic, N., Askin, A., Vossgaetter, L., Bocchi, F., Ali Didi, H.H., Inah, A., Ivanova, T., 2024. Identification of the first gestational ground for tiger sharks (*Galeocerdo cuvier*) in the Central Indian Ocean using a high-definition submersible ultrasound. Front. Mar. Sci. 11, 1500176. https://doi.org/10.3389/fmars.2024.1500176.
Sulikowski, J.A., Wheeler, C.R., Gallagher, A.J., Prohaska, B.K., Langan, J.A., Hammerschlag, N., 2016. Seasonal and life-stage variation in the reproductive ecology of a marine apex predator, the tiger shark *Galeocerdo cuvier*, at a protected female-dominated site. Aquat. Biol. 24 (3), 175–184. https://doi.org/10.3354/ab00648.
Vignaud, T.M., Meyer, C.G., Sèguigne, C., Bierwirth, J., Clua, E.E.G., 2023. Examining individual behavioural variation in wild adult bull sharks (*Carcharhinus leucas*)

suggests divergent personalities. Behaviour 160, 1283–1301. https://doi.org/10.1163/1568539X-bja10244.

Vossgaetter, L., Dudeck, T., Crouch, J., Cope, M., Ivanova, T., Siyan, I., Niyaz, A., Riyaz, M., Araujo, G., 2024. Non-invasive methods characterise the world's largest tiger shark aggregation in Fuvahmulah, Maldives. Sci. Rep. 14, 21998. https://doi.org/10.1038/s41598-024-73079-3.

Weihs, D., Keyes, R.S., Stalls, D.M., 1981. Voluntary swimming speeds of two species of large carcharinid sharks. Copeia (1), 219–222. https://doi.org/10.2307/1444062.

Weng, K., Boustany, A., Pyle, P., Anderson, S., Brown, A., Block, B., 2007. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Mar. Biol. 152, 877–894. https://doi.org/10.1007/s00227-007-0739-4.

Wilson, D.S., 1975. A theory of group selection. Proc. Natl. Acad. Sci. 72 (1), 143–146. https://doi.org/10.1073/pnas.72.2.143.

Wittenberger, J.F., 1981. first ed. Animal social behavior. Duxbury Press, Boston.