

## Article

# Evidence of Non-Random Social Interactions between Pairs of Bait-Attracted White Sharks in Gansbaai (South Africa)

Primo Micarelli <sup>1,2,\*</sup> , Francesca Romana Reineri <sup>1</sup> , Riccardo D'Agnese <sup>1</sup>, Antonio Pacifico <sup>1,3</sup> , Gianni Giglio <sup>4</sup> and Emilio Sperone <sup>4</sup> 

<sup>1</sup> Sharks Studies Center—Scientific Institute, 58024 Massa Marittima, Italy

<sup>2</sup> Department of Physical Sciences, Earth and Environment DSFTA, University of Siena, 53100 Siena, Italy

<sup>3</sup> Department of Economics and Law, University of Macerata, 62100 Macerata, Italy

<sup>4</sup> Department of Biology, Ecology and Earth Sciences DIBEST, University of Calabria, 87027 Rende, Italy

\* Correspondence: primo.micarelli@unisi.it

**Abstract:** Knowledge about the social behavior of sharks is a growing research field, but not many observations are available on the social interactions between pairs of sharks in the presence of passive surface bait and mainly related to aggregations. Between 2009 and 2018, in Gansbaai, South Africa, 415 white sharks were sighted, and 525 surface-generated social interactions were identified, exhibited by 169 different white sharks. The mean sighting rate was 0.91 (range 0.18–1.53) white sharks per hour. Eight patterns of social interaction were exhibited: swim by, parallel swim, follow/give way, follow, give way, stand back, splash fights, and piggyback. Non-random interactions occurred when pairs of specimens approached the passive surface bait, confirming that the white sharks made a real choice, showing a dominance hierarchy during the ten years of data collection. Evidence of non-random social interactions in the surface behavior of bait-attracted white sharks *Carcharodon carcharias* in Gansbaai's transient population was the goal of this research.

**Keywords:** social behavior; elasmobranchs; behavior; *Carcharodon carcharias*



**Citation:** Micarelli, P.; Reineri, F.R.; D'Agnese, R.; Pacifico, A.; Giglio, G.; Sperone, E. Evidence of Non-Random Social Interactions between Pairs of Bait-Attracted White Sharks in Gansbaai (South Africa). *Diversity* **2023**, *15*, 433. <https://doi.org/10.3390/d15030433>

Academic Editor: Bert W. Hoeksema

Received: 6 February 2023

Revised: 1 March 2023

Accepted: 7 March 2023

Published: 15 March 2023



**Copyright:** © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Social interactions occur when the behavior of an individual specifically modifies that of another of the same species [1]. Social behavior consists of interactions among conspecifics and results in relationships of variable form, duration, and function. It provides a broad array of behavioral phenomena, including many of the complex forms of cooperation and conflict that are of particular interest to behavioral biologists [2]. Social behavior is usually composed of a wide range of modules that affect different contexts of the individual's life, including reproduction, sexual segregation, game behavior, schooling or grouping, cooperation, aggression, and predatory activity; it consists of both genetic bases and precise behavioral units that constitute an intraspecific code that can be instinctive or learned during life [3].

The most observed social modules are those related to aggression [4–7]. Intraspecific competition occurs when two or more organisms of the same species have simultaneous access to a limited resource [8], and the access is commonly established through competitive events that rarely take the form of a direct confrontation. The signalman thus gains an advantage should the recipient decide to withdraw [9]. Intraspecific aggression, in addition to being instinctive, is one of the greatest nuances of sociality: threats, skirmishes, and fights have such a low intensity as to rarely reach harmful consequences for the contenders, thus revealing the presence of any braking mechanisms that promptly interrupt hostilities [3].

Such behaviors can be considered social, as sociability involves several individuals living and/or interacting together, which can lead to the formation of complex social structures [10–13] were the first to conduct research on the social behavior of elasmobranchs, carrying out the first quantitative analyses of domination and subordination in captive

specimens of the dogfish *Mustelus canis*. Subsequently, Myrberg and Gruber (1974) [14] identified a dominance hierarchy among scalloped hammerhead sharks *Sphyrna tiburo* depending on size and an apparent predominance of males over females. The direct observations and the passive acoustic tracking of the scalloped hammerhead shark also showed a social behavior that involved the grouping of specimens in a small area, the so-called home range [15].

Social interactions among white sharks, however, have received little attention, but increasing evidence suggests that this species is socially complex [16–19]. Some studies have reported that white sharks often congregate near whale or seal carcasses, and several discrete categories of social interactions have been defined [16,20,21].

As far as white sharks are concerned, the ranking mechanism seems to be represented by the establishment of a dimensional hierarchy: the large specimens are dominant compared to the smaller ones, which are identified as subordinate specimens [22,23]. The size, however, is not the only factor influencing the establishment of the hierarchy, but the direction of some relationships of dominance is typically determined by an asymmetry in the competitive behavior of individuals towards each other [24]; in the case of the Gansbaai (South Africa), white shark population, it particularly occurs among specimens of similar sizes. Sperone et al. (2010) [17] suggested that, in the case of sharks of similar lengths, animals need to adopt rituals to establish the social hierarchy: the individuals that manifest all or most aggressive attitudes is considered dominant, while the individual who receives them or initiates most of the acts of submission is considered subordinate. These dominance relationships form the hierarchical structure of the specimens [10,25]. In this study, the long-term observation of the multiple social-interaction patterns exhibited by white sharks with the help of video recordings proved to be useful to evaluate their frequency and priority in establishing the hierarchical relationships between pairs of sharks in the presence of passive prey.

Knowledge about the social behavior of sharks is growing, based on the data that researchers are collecting in different areas of the world. Findlay et al. (2016) [26], in Mosselbay (South Africa), who tried to evaluate whether the white shark forms non-random associations with conspecifics in coastal environments or whether the simultaneous presence of several specimens at the same time and space is entirely due to chance, indicated that the aggregations formed by a very conspicuous number of specimens during certain periods of the year are of an asocial type and due to the presence of external factors, such as the availability of prey, or for reproductive purposes. Subsequently, Schilds et al. (2019) [19] stated that white sharks in the Neptune Islands (South Australia) did not randomly co-occur with their conspecifics but formed four distinct communities or “social groups” in areas where large numbers of white sharks can be sighted throughout the year, including during periods of low seal abundance. Schilds et al. (2019) [19] hypothesized that the observed sex-dependent variations in co-occurrence were linked to intraspecific competition for resources, providing new insights into the aggregatory behavior of white sharks at a seal colony.

Gansbaai is a white shark aggregation site recognized worldwide, and it is the only location in the world where cage-diving trips operate daily, weather permitting [27]. White sharks frequently prey on Cape fur seals (*Arctocephalus pusillus pusillus*) at rookeries off southern Africa and particularly during autumn and winter, when juvenile seals leave to forage offshore for the first time, making them vulnerable to predation by white sharks [28–31]. Gansbaai is a white shark hotspot because the white sharks predate on the resident seals, but the diet also includes fishes and other elasmobranchs. It is an important seasonal feeding ground among individual sharks rather than an adult aggregation site, or a pupping or nursery area [32].

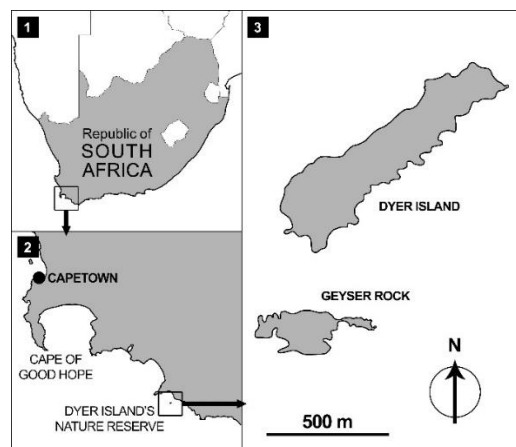
In the present study, we aimed to confirm whether the social interactions that occurred between pairs of white sharks’ specimens, when they approached surface bait in the Dyer Island Nature Reserve in Gansbaai, South Africa, were non-random events, and that such

interactions were not linked to chance but linked to choice, which aimed at establishing a dominance hierarchy.

## 2. Materials and Methods

### 2.1. Study Area

Observations were performed at Dyer Island's Nature Reserve, which is located on the continental shelf 7.5 km off Gansbaai, South Africa ( $34^{\circ}41' S$ ;  $19^{\circ}24' E$ ) and includes two islands (Figure 1): Dyer Island (the larger) is a low-profile island ca. 1.5 km long and 0.5 km wide, and it is characterized by the presence of different sea bird colonies; Geyser Rock (the smaller) is ca. 0.5 km long and 0.18 km wide, and it hosts a colony of Cape fur seals *Arctocephalus pusillus pusillus* (Schreber, 1775). The reserve is located in the Agulhas Bioregion, which is the meeting point between the Benguela Current, which is the meeting point between the Benguela Current (the eastern boundary current of the subtropical vortex located in the southern Atlantic Ocean) and the Agulhas Current (the current forming the western limit of the Indian Ocean). In summer, intensified south-easterly trade winds result in upwelling, causing the cold waters of Benguela origin to enter the bay (Jury, 1985). The upwelling along the coast results in high biological productivity, which in turn supports large fish stocks, including pilchard, anchovy, and hake [33]. A white shark population is regularly present between March and September in the waters off of the Dyer Island's Nature Reserve. Micarelli et al., 2021b, stated that the low number of resightings recorded in Gansbaai, five in 11 years, corresponding to 1.2% of the population, showed that the white shark population attending this area has a transient behavior. Towner et al. (2013a) [34], in Gansbaai, identified 532 unique individuals, resulting in an estimated super-population size of 908, mainly made up of immature females with a sex ratio of 1:2.2:0.8 for males, females, and unsexed, respectively [32].



**Figure 1.** Map of Dyer Island's Nature Reserve in Gansbaai, South Africa ( $34^{\circ}41' S$ ;  $19^{\circ}24' E$ ).

### 2.2. Data Collection

During ten scientific expeditions performed between March and May 2009–2018 in the study area, social interactions among white sharks were observed and recorded, and behaviors were later identified from the videos using social displays described by Martin (2003) [16]. White sharks are more abundant around the study area during the austral autumn because they feed on young cape fur seals [17]. During our activities, recorded water temperatures ranged from  $13.5^{\circ}$  to  $18^{\circ} C$ , and underwater visibility from 2 to 5 m (measured to the nearest 0.5 m with a Secchi disc). In total, there were nearly 420 hours of direct observation from the boat, including approximately 200 h from the diving cage. Observations occurred aboard the boat "Barracuda" (Shark Diving Unlimited owner), a 12 m long boat, between 2009 and 2013, and between 2014 and 2018 aboard "Slashfin" (Marine Dynamics), a 14 m long boat. A 4 m long, 3 m high, and 2 m deep rectangular floating cage made of galvanized steel was used for underwater observations; it housed up

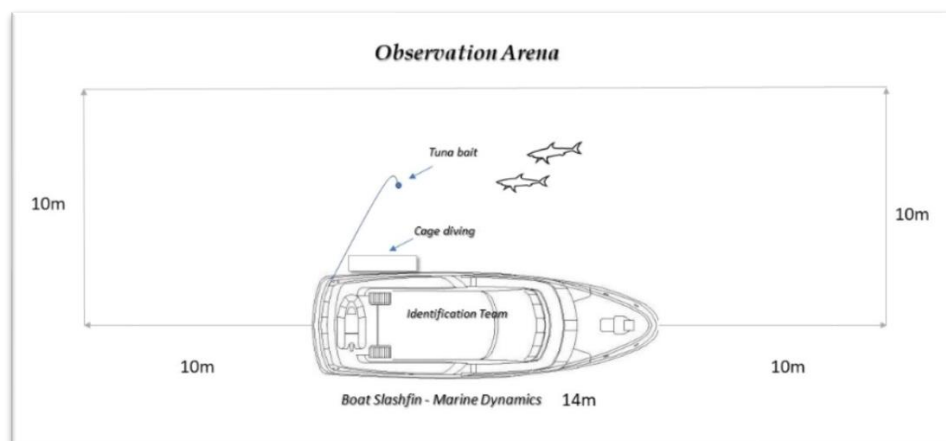
to three researchers at a time and was moored to the side of the boat. White sharks were sighted at two areas in Gansbaai, Geyser Rock, and Joubertsdam, as reported by Towner et al. (2013a) [34] and Micarelli et al. (2021a) [35], because sharks sighting areas in the Gansbaai gulf changed for unknown reasons, moving from the first area to the second area, and the boat was anchored in both locations at a depth of ~8–10 m, with similar bottom characteristics.

Sharks were attracted to the area around the boat by chumming, following methodologies of the Ferreira and Ferreira (1996) [36], Laroche et al. (2007) [37], and Sperone et al. (2010) [17]. The chum was a mixture of seawater, cod liver oil, fish blood, and pilchards, and an additional 2–3 kg of slices of tuna were used as bait, which were maintained at the sea surface by floats following the methods described by Sperone et al. (2010) [17] and Micarelli et al. (2021a) [35]. Observations from the boat lasted 6–8 h per day, whereas underwater observations lasted 2–4 h per day.

The sex and maturity of sharks were determined by underwater observations from the diving cage. Following Compagno et al. (2005) [38], males with total length (TL) <3.5 m and females with TL <4.5 m were considered immature specimens. Shark length was estimated to the nearest 0.5 m based on observations as sharks passed in front of the measured diving cage of 4.0 m length. Shark sex was determined based on the presence or absence of claspers by observing and filming the pelvic area. Identification of individuals was obtained through photo identification and compilation of specific identification cards, and it was also based on a larger pattern, including not only the different notches of the dorsal fin, but also the following characteristics: caudal fin features, pelvic fin patterns, presence or absence of claspers, gill slashes and body patterns, presence of scars, and/or presence of ectoparasites [32,39]. The identification of the specimens was necessary to verify the dominant and the recessive specimen, as reported in the identification forms compiled by the observers to optimize the analysis during each annual expedition. The surface behavior of white sharks was always recorded by the same team using digital photo cameras and digital video cameras and identified and confirmed from the video using social displays described by Martin (2003) [16].

All observations considered for this paper refer to interactions between two sharks. In our sampling model, aimed at identifying and recording the animals that exhibited social behaviors, a virtual “observation arena” with free-living sharks was drawn to optimize the team’s visual sightings from the boat.

This arena, defined as a function of the possibility of observing behavior on the surface up to a maximum depth of ~2–3 m depending on the daily visibility, was bounded in a rectangular area whose longest side was represented by the boat and by ~10 m from the boat’s aft and bow, while the shorter side corresponded to ~10 m of distance perpendicular to the boat (Figure 2). The surface area of the “observation arena” was approximately  $32 \times 10$  m (=320 m<sup>2</sup>) between 2007 and 2013 and  $34 \times 10$  m (=340 m<sup>2</sup>) between 2014 and 2018. The bait of floating tuna slices was placed inside the arena, with the aim of activating social behavior (occurring in competitive situations and including aggressive, submissive, and defensive behaviors) of an individual that qualifies, modifies, or otherwise alters the act of another individual of bait-attracted white sharks. As soon as the animals entered the “observation arena” in the direction of the bait, the observations began. An interaction began when two sharks approached each other within a distance of two body lengths, and it ended when two sharks were more than two body lengths apart, moving in different directions, and were not observed together again for at least 2 min, following methods described by Sperone et al. (2010) [17].



**Figure 2.** Virtual “observation arena” based on “Slashfin”, the 14 m long boat (Marine Dynamics).

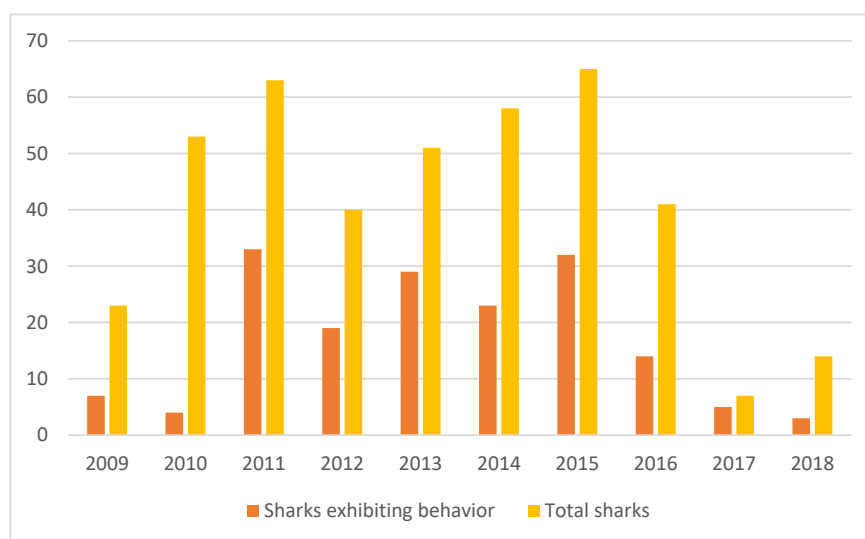
### 2.3. Statistical Analysis

Tests for the linear-independence hypothesis were carried out, through the use of chi-square statistics, to verify the independence between the variable pairs of sex/behavior exhibited, maturity/behavior exhibited, and sex/maturity on behavior exhibited.

To investigate the presence of causality between behavior and bait, we used Cochran’s Q test. Cochran’s Q test is based on the null hypothesis ( $H_0$ ), where there is no significant difference in the effectiveness of treatments (the choice is causal) and the alternative ( $H_1$ ), where there is a significant difference in the effectiveness of treatments (the choice is not causal). It is a non-parametric statistical test used to verify whether  $k$  treatments (or number of studies) have similar effects. Generally, the test statistic refers to two-way randomized block design, where the response variable takes only two possible outcomes, coded as 0 or 1, denoting failure or success, respectively. It is Often used to assess whether different observers of the same phenomenon have consistent results (interobserver variability). All statistics were made using Excel 16.44.

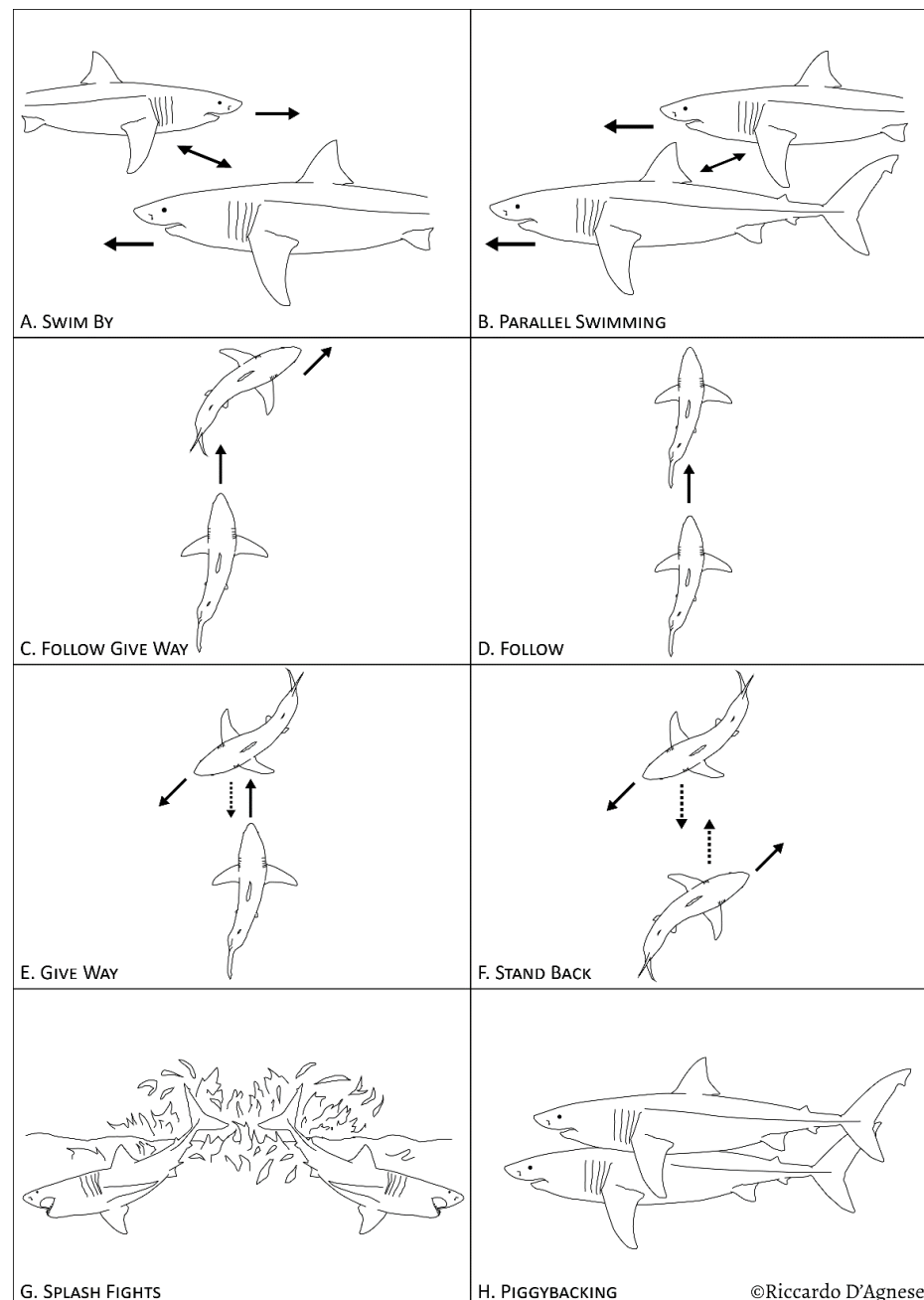
### 3. Results

In total, 415 sharks were sighted, and 525 surface-generated social interactions were identified and exhibited by 169 different white sharks (Figure 3).

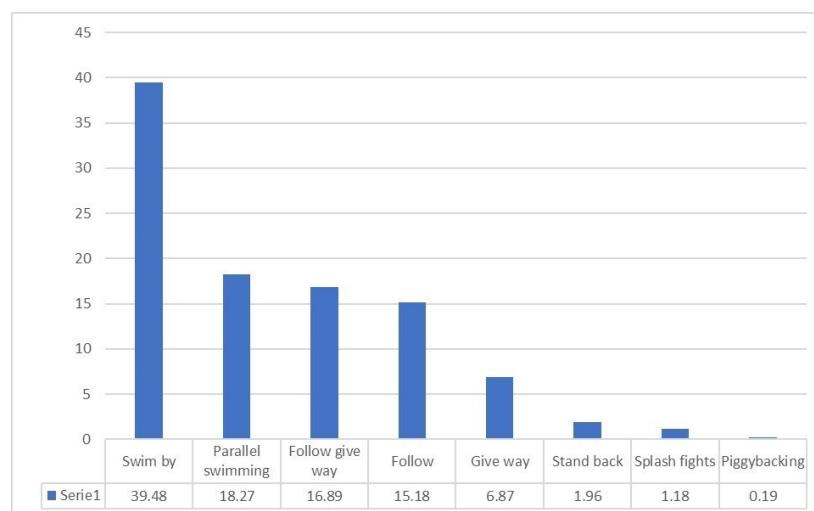


**Figure 3.** White sharks (*Carcharodon carcharias*) exhibiting social behavior each year and the total number of white sharks sighted per year.

Observed social interactions were classified into one of the following eight interaction patterns as described by Martin in 2003 [16] (Figure 4). Most of the sharks appeared individually in the “observation arena” during the expeditions. The reduced numbers of observations that occurred in 2017 and 2018 were linked to the decline in white shark sightings observed in Gansbaai since 2017 because of the presence of a pair of killer whales (Micarelli et al. 2021b) [35]. The displays are listed in descending order with respect to the performance percentages observed between 2009 and 2018 (Figure 5).



**Figure 4.** Eight social behaviors observed among white sharks (*Carcharodon carcharias*): swim by (A); parallel swim (B); follow/give way (C); follow (D); give way (E); stand back (F); splash fight (G); piggyback (H).



**Figure 5.** Percentage frequencies of social behavior modules observed between 2009 and 2018 in white sharks (*Carcharodon carcharias*).

**Swim by:** two sharks in parallel but not on collision courses swam slowly past one another at a close range, usually between 0.5 m and 2.5 m (Figure 4A). The end of the interaction occurred when the sharks passed each other. This display was exhibited during the observations in 39.48% of cases.

**Parallel swim:** two sharks swam close to one another and maintained a parallel course in the same direction (Figure 4B). The distance between the sharks ranged from 0.5 m to 2.0 m. The interaction usually ended when the followed shark moved away and did not reappear within 5 min. This display was exhibited during the observations in 18.27% of cases.

**Follow/give way** one shark followed another, causing the followed one to give way. The interaction ended when the followed shark turned left or right at an angle of about 45–90° and did not reappear within 5 min (Figure 4C). The distance between sharks usually ranged from 1 m to 2.5 m. This display was exhibited during the observations in 16.89% of cases.

**Follow:** one shark followed the other one, repeating its movements and usually with the jaw gaping (Figure 4D). The display ended when the followed shark moved away in a straight direction and did not reappear within 5 min. In this case, the distance between the sharks usually ranged from 0.5 m and 2 m. This display was exhibited during the observations in 15.18% of cases. (*The differences between follow/give way and follow consist in the fact that in the first case, the followed shark quickly moves away with a sharp angle of 45–90°, while in the second case, the following shark keeps its mouth open and repeats the movements of the followed one and this moves away fast without veering.*)

**Give way:** two sharks swam on a collision course, and the interaction ended when one shark turned left or right at an angle of ~45° and did not reappear within 5 min (Figure 4E). This display was exhibited during the observations in 6.87% of cases.

**Stand back:** simultaneous deviation of two colliding individuals with no established dominant (Figure 4F). This display was exhibited during the observations in 1.96% of cases.

**Splash fight:** this interaction began when one shark rolled onto its side at the surface and directed splashes towards the other one; the other could respond by returning similar splashes (Figure 4G). It ended when one of the sharks retreated. This display was exhibited during the observations in 1.18% of cases.

**Piggyback:** for this behavior, one shark descended onto the back of the other one, and the two animals swam in unison for several seconds (Figure 4H). It ended when the sharks separated. This interaction occurred only once, for 22 s, and between a male and a female shark of similar sizes. This display was exhibited during the observations in 0.19% of cases.

The Chi-square test of independence is a statistical hypothesis test used to determine whether two variables are likely to be related (dependency) or not (independency). This test is very useful when studying variables evaluated through frequency counts. More precisely, the statistic test is obtained by solving for the ratio between the mean squared error from the theoretical frequencies and their weights:

$$\chi^2 = \frac{\sum_i \sum_j (n_{(i,j)} - \hat{n}_{(i,j)})^2}{\hat{n}_{(i,j)}} \tag{1}$$

Here,  $n_{(i,j)}$  denote 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  $\chi^2$ 's test statistic).

In this study, we tested the independence between the following two pairs of variables: exhibited behavior/sex and exhibited behavior/maturity. As highlighted in Table 1, every variable (sex and maturity) shows  $p$ -values close to zero, leading to the rejection of the null hypothesis in favor of the alternative of dependency. According to the  $\chi^2$ 's test statistics addressed for every variable accounted for, the highest result is associated with females/immatures. Thus, immature female specimens would have significantly exhibited more social behaviors in 10 years of data collection (Table 1).

**Table 1.** Chi-square test. Table on the left refers to the test addressing the two pairs of variables. The  $\chi^2$ 's test statistics are 78.43 (Sex); 87.24 (Maturity); 63.69 (Sex/Maturity). The table on the right refers to the test addressed for every variable accounted for. The  $\chi^2$ 's test statistics are 63.21 (Males/Adults); 65.17 (Males/Immatures); 73.61 (Females/Adults); 84.19 (Females/Immatures). The significance codes stand for: \*\*\* significance at 1%, \*\* significance at 5%, \* significance at 10%.

Sex/Maturity (X)	Patterns/Behavior (Y)
Sex	$p$ -Value 0.00
Maturity	$p$ -Value 0.00
Sex/Maturity	$p$ -Value 0.00
Chi-Square on social behavior ( $p$ -Value)	
Total specimen	0.00 ***
Males	0.00 ***
Females	0.00 ***
Adults	0.00 ***
Immatures	0.00 ***

In this analysis, the random (casuality) or non-random (non-casuality) occurrence of the social interactions was tested using Cochran's Q test, where the treatments denote how the presence of the bait affects the sharks' behaviors. It is a non-parametric test applied to the analysis of two-way categorical variables (success = 1, unsuccess = 0). Thus, in technical terms, the test requires a binary variable of interest and assesses whether the proportion of causal links ("successes") is the same between the groups.

In this study, the nominal outcome is a causal and non-causal link according to shark's behavior, where the groups refer to the numerical indices  $i$  and  $j$  (raw data) of the nominal variable  $y_{(i,j)}$ . In this way, one would be able to test whether the effectiveness of the treatments is different between the groups. More precisely, we can investigate the



presence of heterogeneity between observations without incurring linear problems such as multicollinearity, heteroskedasticity, asymptotic distributions, and exogeneity.

Let the degrees of freedom be  $k - 1 = 1$ ; the resulting  $p$ -value is lower than the significance level ( $\alpha = 5\%$ ), so one should reject the null hypothesis in favor of the alternative (Table 2):

**Table 2.** Cochran’s test results: the “Test Statistic” refers to the Chi-squared distribution, the “critical value” is the threshold above which one should reject the null hypothesis, the “df” stands for the degrees of freedom, “ $p$ -value” denotes the probability of wrongly choosing the true hypothesis, and “significance level” denotes the probability of rejecting the null hypothesis when it is true (Type I Error).

Test Statistic	175,98
Chi-squared distribution (critical value)	3,840
df	1
$p$ -Value (one-tailed)	0,027
significance level	0,050

**H<sub>0</sub>.** *There is no significant difference in the effectiveness of treatments (the choice is casual).*

**H<sub>1</sub>.** *There is a significant difference in the effectiveness of treatments (the choice is not casual).*

#### 4. Discussion

Not many observations are available on the social behaviors of sharks, particularly about white sharks, and they are mainly related to aggregations. In fact, although sharks are often seen as solitary predators, it has been observed that some shark species can aggregate not simply in response to environmental changes, but in actual groups of mutually attracted individuals [40–42].

Such behaviors have been observed in the following orders: Heterodontiformes [43], Hexanchiformes [44], Squatiniformes [45], and Carcharhiniformes [46,47]. At the same time, evidence of social interactions has also been reported in planktophagous [48], in large predators [49], in coastal water species [46,50], and in reef sharks [47,51–53]. Several theories have been proposed for the reasons for these aggregations: the formation of groups could be attributed to communication, to the transfer of social information [46], to predation, to the protection of the group [52,54], and to reproduction [55–59].

In addition, the white shark, although mostly solitary, has been reported to aggregate at a number of sites worldwide: these include Seal Island, Gansbaai, and Mossel Bay in South Africa [60], Guadalupe Island in Mexico [61], the Chatham Islands in New Zealand [62], Cape Cod in Massachusetts, USA [63], and Neptune Islands in Australia [64]. Most aggregation sites have been suggested to provide important feeding grounds for white sharks [65], and aggregations have been shown to be driven by the seasonal availability and abundance of prey species [64,66,67]. At the same time, sharks have been observed to develop and maintain complex social behaviors such as dominance hierarchies [13,14] and stable social bonds [68], as well as to be able to learn social information [69,70]; these abilities are due to the fact that sharks are characterized by a high ratio between brain mass and body mass [71–73], comparable to that of mammals.

However, the highly mobile nature of sharks, combined with the difficulty of tracking their movements in the open sea, makes it difficult to study their social interactions.

The hypotheses of intraspecific associations and groupings are mainly based on direct observations in the field [52] and on some recent tracking data thanks to acoustic satellite telemetry [50] or the use of passive receivers [74–76]. By aggregating, individuals facilitate social interactions and mating [77].

Furthermore, some observations have revealed unusual adaptation mechanisms, particularly in some shark species [78]; among these, the seven-gill sharks *Notorynchus cepedianus* seem to use multiple feeding strategies depending on both size and type of prey, adopting strategies of social facilitation and hunting in packs to deal with larger prey such as Cape fur seals *Arctocephalus pusillus pusillus* [44].

The scientific literature has also begun to outline what the traits of the sociobiological background are of the elasmobranchs, and how this comes to structure itself beyond instinct [57,79,80]. Clues to this presumed influence are provided by the different forms of learning currently proven in elasmobranchs, such as those inherent in hunting: individuals can improve the techniques of searching and capturing prey over time, thus increasing their successes [79] and individual surface behavior of white sharks in the presence of bait is not a simple stimulus–response reflex, but rather a complex tactical situation with plastic responses [39].

Although for years the white shark has been considered a solitary species, some studies have led researchers to affirm that, in reality, it is a socially complex species [16,17]. For example [81], in southern California, hypothesized that juvenile white sharks form distinct communities during critical early phases of ontogeny and how a tendency to co-occur across life stages may originate from the formation of these communities in early ontogeny. Schilds et al. (2019) [19], in Australia in the Neptune Islands, found that white sharks did not randomly co-occur with their conspecifics, but formed four distinct communities. Off Guadalupe Island, Mexico, animal-borne telemetry receivers revealed that white sharks varied in the number of associations they formed and occurred most often when white sharks were swimming in straight paths or when they were turning frequently. While many associations were likely random, there was evidence of some stronger associations [82].

Klimley (2000) [83] defined the white shark as an “eavesdropper” species that is capable of interpreting and exploiting the successes of others during foraging; this feature is also called “social learning” or the possibility for some animals to extrapolate information gained from other individuals [79,84]. If it is true that juvenile white sharks form distinct communities, as claimed by Anderson et al. (2021) [81], the establishment of a hierarchy, in the presence of passive surface bait, is favorable for both individuals concerned, as it averts a direct confrontation and, therefore, the possibility of injury, presenting a gain both in terms of energy and the possibility of preserving themselves for future predation [17]. An example of the presence of a hierarchy in white sharks occurs during their scavenging activity, in which two possibilities of behavior are highlighted: either there is an approach to a carcass depending on the size order of the sharks present [23] or, in the event of numerous specimens intent on feeding, the larger ones have access to the portions with more fat and therefore energetically more beneficial, while the subordinate specimens feed on the remainder or pieces floating in the sea. This mechanism allows the reduction in collisions and life-threatening injuries. If there is no competition for a resource, aggression is minimal [85].

The analysis of the data collected in 10 years of observations showed how sharks did not form random social interactions and that this is not linked to chance but linked to choice to create a dominance hierarchy between them, and immature females were more inclined to do so. In Gansbaai, the white shark population is numerically dominated by females [32], probably explaining why females exhibit such behaviors.

Thus, despite having been regarded as a solitary species for many years [38], and if it is true that intraspecific competition ethogram occurs when two or more organisms of the same species have simultaneous access to a limited resource [8] and the access is commonly established through competitive events that rarely take the form of a direct confrontation, the white shark turns out to be an animal capable of exhibiting social behaviors in particular situations.

Specifically, the results of the social interactions exhibited by pairs of bait-attracted white sharks in the Dyer Island’s Nature Reserve show both competitive modules of follow and follow/give way, and “mild” observation modules [17], such as parallel swim and

swim by: the latter, in fact, as shown in Figure 5, was the most observed social behavior. As already noted in the study by Sperone et al. (2012) [40] in Gansbaai, these “mild” observation modules reflect a type of extremely calm approach and an initial hesitation, thus confirming the studies by Bromilow (2014) [86] and the observations made by Martin et al. (2005) [29], who argued that the white shark certainly has a more aggressive approach with natural prey rather than with passive ones, when the investigation period is of longer duration.

In particular, although this species was considered by many to be myopic [16,87,88], recently, Micarelli et al. (2021a) [36], in the Gansbaai population, stated that white sharks implement their predatory choices to energetically richer prey, thanks especially to their visual ability, which plays an important role in adults and immatures with dietary shifts in their feeding patterns and, as noted in juvenile white sharks in the study by Lisney et al. (2007) [89], the olfactory bulbs are relatively smaller and the optic roof relatively larger than in adults; for this reason, in Gansbaai, immatures tended to be more observant in the hunting area and confronted each other in capturing prey, exhibiting the social interactions with the modules described by Martin in 2003.

In the future, having highlighted and confirmed the presence of non-random social behaviors between pairs of sharks in Gansbaai in the presence of passive surface bait finalized to establish a dominance hierarchy, it would be interesting to apply network analysis methodologies to evaluate the possible presence in this area of distinct social groups, as already observed in the Neptune Islands in Australia [19], or in southern California [82], where non-random co-occurrence of juvenile white sharks at seasonal aggregation sites were recorded. Because Reiner et al. 2022 [90] stated that environmental factors influence the prey discrimination of white sharks in Gansbaai during their surface passive prey predatory behavior and that tide range is the most important factor that influences the white sharks’ prey choice, followed by underwater visibility, water temperature, and sea conditions, it will also be important to deepen the understanding of whether social behaviors of white sharks may also be affected by potential factors such as abiotic conditions, natural prey and competitor species, and interspecific interactions.

**Author Contributions:** P.M., conceptualization, formal analysis, investigation, methodology, writing—original draft and editing; F.R.R., formal analysis, investigation and writing—review; R.D., formal analysis and writing—review; G.G., investigation and writing—review E.S., conceptualization, formal analysis, investigation, methodology and writing—review; A.P., formal analysis and writing—review. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** The ethical review and approval were waived for this study because it did not intervene in the observed animals.

**Data Availability Statement:** Data for this project are maintained by the Sharks Studies Centre—Scientific Institute, the University of Calabria, and the University of Siena, Italy. The data are available from the authors.

**Acknowledgments:** We are grateful to the CSS team members that carried out 11 expeditions for their indirect financial support of this research, and thanks are also due to Marine Dynamics (Hennie Otto, Wilfred Chivel) for their logistical assistance and all other field assistance with data collection.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Baldaccini, N.E.; Mainardi, D.; Papi, F. “Introduzione Alla Etologia” Book—by Editoriale Grasso, Bologna. 1990. Available online: [https://elearning.unite.it/pluginfile.php/247583/mod\\_resource/content/1/Testo\\_Didattica.pdf](https://elearning.unite.it/pluginfile.php/247583/mod_resource/content/1/Testo_Didattica.pdf) (accessed on 1 March 2023).
2. Nowak, M.A. Five rules for the evolution of cooperation. *Science* **2006**, *314*, 1560–1563. [CrossRef] [PubMed]
3. Lorenz, K. *On Aggression*; Psychology Press: London, UK, 1966.
4. Silber, G.K. The relationship of social vocalizations to surface behaviour and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*). *Can. J. Zool.* **1986**, *64*, 2075–2080. [CrossRef]

5. Higley, J.D.; King, S.T., Jr.; Hasert, M.F.; Champoux, M.; Suomi, S.J.; Linnoila, M. Stability of interindividual differences in serotonin function and its relationship to severe aggression and competent social behavior in rhesus macaque females. *Neuropsychopharmacology* **1996**, *14*, 67–76. [CrossRef] [PubMed]
6. Connor, R.C.; Mann, J.; Tyack, P.L.; Whitehead, H. Social evolution in toothed whales. *Trends Ecol. Evol.* **1998**, *13*, 228–232. [CrossRef] [PubMed]
7. Oliveira, R.F.; Simões, J.M.; Teles, M.C.; Oliveira, C.R.; Becker, J.D.; Lopes, J.S. Assessment of fight outcome is needed to activate socially driven transcriptional changes in the zebrafish brain. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, E654–E661. [CrossRef] [PubMed]
8. Wilson, D.S. A theory of group selection. *Proc. Natl. Acad. Sci. USA* **1975**, *72*, 143–146. [CrossRef]
9. Burghardt, G.M. Defining “communication”. *Commun. Chem. Signals* **1970**, *1*, 5–18.
10. Hinde, R.A. Interactions, relationships and social structure. *Man* **1976**, *11*, 1–17. [CrossRef]
11. Krause, J.; Ruxton, G. *Living in Groups*; Oxford University Press: Oxford, UK, 2002.
12. Wey, T.; Blumstein, D.T.; Shen, W.; Jordan, F. Social network analysis of animal behaviour: A promising tool for the study of sociality. *Anim. Behav.* **2008**, *75*, 33344. [CrossRef]
13. Allee, W.C.; Dickinson, J.C. Dominance and subordination in the smooth dogfish, *Mustelus canis* (Mitchell). *Physiol. Zool.* **1954**, *27*, 356–364. [CrossRef]
14. Myrberg, A.A., Jr.; Gruber, S.H. The behaviour of the bonnethead shark, *Sphyrna tiburo*. *Copeia* **1974**, *1974*, 358–374. [CrossRef]
15. Klimley, A.P. Social Organization of Schools of the Scalloped Hammerhead Shark, *Sphyrna lewini* (Griffith and Smith), in the Gulf of California. Scripps Institution of Oceanography Technical Report, San Diego, CA, USA, 1983. Available online: <https://escholarship.org/uc/item/2qg6s9t5> (accessed on 1 March 2023).
16. Martin, R.A. *Field Guide to the Great White Shark*; ReefQuest Centre for Shark Research: Vancouver, BC, USA, 2003; 185p.
17. Sperone, E.; Micarelli, P.; Andreotti, S.; Spinetti, S.; Andreani, A.; Serena, F.; Brunelli, E.; Tripepi, S. Social interactions among bait attracted white sharks at Dyer Island (South Africa). *Mar. Bio Res.* **2010**, *6*, 408–414. [CrossRef]
18. Becerril-García, E.E.; Hoyos-Padilla, E.M.; Micarelli, P.; Galván-Magaña, F.; Sperone, E. The surface behaviour of white sharks during ecotourism: A baseline for monitoring this threatened species around Guadalupe Island, Mexico. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2019**, *29*, 773–782. [CrossRef]
19. Schilds, A.; Mourier, J.; Huvneers, C.; Nazimi, L.; Fox, A.; Leu, S.T. Evidence for non-random co-occurrences in a white shark aggregation. *Behav. Ecol. Sociobiol.* **2019**, *73*, 138. [CrossRef]
20. Compagno, L. *Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date. Vol. 2 Bullhead, Mackerel, and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*; FAO Species Catalogue for Fishery Purposes, no. 1; FAO: Rome, Italy, 2001; Volume 2.
21. Klimley, A.P.; Le Bouef, B.J.; Cantara, K.M.; Richert, J.E.; Davis, S.F.; Van Sommeran, S.; Kelly, J.T. The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Mar. Biol.* **2001**, *138*, 617–636. [CrossRef]
22. Klimley, A.P.; Anderson, S.D. Residency Patterns of White Sharks at the South Farallon Islands, California. In *Great White Sharks. The Biology of Carcharodon carcharias*; Klimley, A.P., Ainley, D., Eds.; Academic Press: Cambridge, MA, USA, 1996.
23. Long, D.J.; Jones, R.E. White shark predation and scavenging on cetaceans in the Eastern North Pacific Ocean. In *Great White Sharks. The Biology of Carcharodon carcharias*; Klimley, A.P., Ainley, D., Eds.; Academic Press: Cambridge, MA, USA, 1996.
24. Chase, I.D. Cooperative and noncooperative behavior in animals. *Am. Nat.* **1980**, *115*, 827–857. [CrossRef]
25. De Vries, H.; Stevens, J.M.G.; Vervaecke, H. Measuring and testing the steepness of dominance hierarchies. *Anim. Behav.* **2006**, *71*, 585–592. [CrossRef]
26. Findlay, R.; Gennari, E.; Cantor, M.; Tittensor, D.P. How solitary are white sharks: Social interactions or just spatial proximity? *Behav. Ecol. Sociobiol.* **2016**, *70*, 1735–1744. [CrossRef]
27. Towner, A.V. Great White Sharks *Carcharodon carcharias* in Gansbaai, South Africa: Environmental Influences and Changes over Time, 2007–2011. Master’s Thesis, University of Cape Town (UCT), Cape Town, South Africa, 2012.
28. Martin, R.A.; Hammerschlag, N.; Collier, R.S.; Fallows, C. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. UK* **2005**, *85*, 1121–1135. [CrossRef]
29. Hammerschlag, N.; Martin, R.A.; Fallows, C. Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Arctocephalus pusillus pusillus*) at Seal Island, South Africa. *Environ. Biol. Fishes* **2006**, *76*, 341–350. [CrossRef]
30. Kirkman, S.P.; Oosthuizen, W.H.; Meyer, M.A. The seal population of Seal Island, False Bay. In *Finding a Balance: White Shark Conservation and Recreational Safety in the Inshore Waters of Cape Town, South Africa*; Nel, D.C., Peschak, T.P., Eds.; Proceedings of a Specialist Workshop. WWF South Africa Report Series–2006/Marine/001 Annexure 1; YUMPU: Diepoldsau, Switzerland, 2006; pp. 83–94.
31. Towner, A.V.; Underhill, L.G.; Jewell, O.J.; Smale, M.J. Environmental influences on the abundance and sexual composition of white sharks *Carcharodon carcharias* in Gansbaai, South Africa. *PLoS ONE* **2013**, *8*, e71197. [CrossRef] [PubMed]
32. Micarelli, P.; Bonsignori, D.; Compagno, L.J.V.; Pacifico, A.; Romano, C.; Reinero, F.R. Analysis of sightings of white sharks in Gansbaai (South Africa). *Eur. Zool. J.* **2021**, *88*, 363–374. [CrossRef]
33. Griffiths, C.L.; Robinson, T.B.; Lange, L.; Mead, A. Marine biodiversity in South Africa: An evaluation of current states of knowledge. *PLoS ONE* **2010**, *5*, e12008. [CrossRef] [PubMed]

34. Towner, A.V.; Wcisel, M.A.; Reisinger, R.R.; Edwards, D.; Jewell, O.J.D. Gauging the threat: The first population estimate for white sharks in South Africa using photo identification and automated software. *PLoS ONE* **2013**, *8*, e66035. [[CrossRef](#)]
35. Micarelli, P.; Chieppa, F.; Pacifico, A.; Rabboni, E.; Reinerio, F.R. Passive Prey Discrimination in Surface Predatory Behaviour of Bait-Attracted White Sharks from Gansbaai, South Africa. *Animals* **2021**, *11*, 2583. [[CrossRef](#)] [[PubMed](#)]
36. Ferreira, C.A.; Ferreira, T.P. Population dynamics of white sharks in South Africa. In *Great White Sharks: The Biology of Carcharodon carcharias*; Klimley, A.P., Ainley, D.G., Eds.; Academic Press: San Diego, CA, USA, 1996; pp. 381–391.
37. Laroche, R.K.; Kock, A.A.; Dill, L.M.; Oosthuizen, W.H. Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. *Mar. Ecol. Prog. Ser.* **2007**, *338*, 199–209. [[CrossRef](#)]
38. Compagno, L.; Dando, M.; Fowler, S. *Sharks of the World*; HarperCollins Publishers Ltd.: London, UK, 2005; 368p.
39. Sperone, E.; Micarelli, P.; Andreotti, S.; Brandmayr, P.; Bernabò, I.; Brunelli, E.; Tripepi, S. Surface behaviour of bait-attracted white sharks at Dyer Island (South Africa). *Mar. Biol. Res.* **2012**, *8*, 982–991. [[CrossRef](#)]
40. Springer, S. Social organization of shark populations. In *Sharks, Skates and Rays*; Gilbert, P.W., Mathewson, R.F., Rall, D.P., Eds.; Johns Hopkins Press: Baltimore, MA, USA, 1967; 644p.
41. Jacoby, D.M.P.; Croft, D.P.; Sims, D.W. Social behaviour in sharks and rays: Analysis, patterns and implications for conservation. *Fish Fish.* **2011**, *13*, 399–417. [[CrossRef](#)]
42. Micarelli, P.; Pieraccini, F.; Reinerio, F.R.; Sperone, E. Influence of male presence on the social structure of lesser spotted dogfish (*Scyliorhinus canicula*) female groups. *Int. J. Oceanogr. Aquac.* **2020**, *4*. [[CrossRef](#)]
43. Powter, D.M.; Gladstone, W. The reproductive biology and ecology of the Port Jackson shark *Heterodontus portusjacksoni* in the coastal waters of eastern Australia. *J. Fish Biol.* **2008**, *72*, 2615–2633. [[CrossRef](#)]
44. Ebert, D.A. Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus*. *S. Afr. J. Mar. Sci.* **1991**, *11*, 455–465. [[CrossRef](#)]
45. Standora, E.A.; Nelson, D.R. A telemetric study of the behavior of free-swimming angel sharks *Squatina californica*. *Bull. South. Calif. Acad. Sci.* **1977**, *76*, 193–201.
46. Klimley, A.P.; Nelson, D.R. Schooling of the scalloped hammerhead sharks, *Sphyrna lewini*, in the Gulf of California. *Fish. Bull.* **1981**, *79*, 356–360.
47. McKibben, J.N.; Nelson, D.R. Patterns of movement and grouping of gray reef sharks, *Carcharhinus amblyrhynchos*, at Enewetak, Marshall Islands. *Bull. Mar. Sci.* **1986**, *38*, 89–110.
48. Meekan, M.G.; Bradshaw, C.J.A.; Press, M.; McLean, C.; Richards, A.; Quasnicka, S.; Taylor, J. Population size and structure of whale sharks *Rhincodon typus* at Ningaloo Reef, Western Australia. *Mar. Ecol. Prog. Ser.* **2006**, *319*, 275–285. [[CrossRef](#)]
49. Domeier, M.L.; Nasby-Lucas, N. Annual re-sightings of photographically identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Mar. Biol.* **2007**, *150*, 977–984. [[CrossRef](#)]
50. Heupel, M.R.; Simpfendorfer, C.A. Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Mar. Biol.* **2005**, *147*, 1239–1249. [[CrossRef](#)]
51. Stevens, J.D. Biological observations on sharks caught by sport fisherman of New South Wales. *Mar. Freshw. Res.* **1984**, *35*, 573–590. [[CrossRef](#)]
52. Economakis, A.E.; Lobel, P.S. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnson Atoll, Central Pacific Ocean. *Environ. Biol. Fishes* **1998**, *51*, 129–139. [[CrossRef](#)]
53. Speed, C.W.; Meekan, M.G.; Field, I.C.; McMahon, C.R.; Stevens, J.D.; McGregor, F.; Huvneers, C.; Berger, Y.; Bradshaw, C.J.A. Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Mar. Ecol. Prog. Ser.* **2011**, *429*, 261–275. [[CrossRef](#)]
54. Wearmouth, V.J.; Sims, D.W. Sexual segregation in marine fish, reptiles, birds and mammals: Behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* **2008**, *54*, 107–170. [[PubMed](#)]
55. Simpfendorfer, C.A. The Biology of Sharks of the Family Carcharhinidae from the Nearshore Waters of Cleveland Bay, with particular reference to *Rhizoprionodon taylori*. Doctoral Dissertation, James Cook University, Brisbane, Australia, 1993.
56. Hight, B.H.; Lowe, C.G. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? *J. Exp. Mar. Biol. Ecol.* **2007**, *352*, 114–128. [[CrossRef](#)]
57. Jacoby, D.M.P.; Busawon, D.S.; Sims, D.W. Sex and social networking: The influence of male presence on social structure of female shark groups. *Behav. Ecol.* **2010**, *21*, 808–818. [[CrossRef](#)]
58. Elisio, M.; Colonello, J.H.; Cortés, F.; Jaureguizar, A.J.; Somoza, G.M.; Macchi, G.J. Aggregations and reproductive events of the narrownose smooth-hound shark (*Mustelus schmitti*) in relation to temperature and depth in coastal waters of the south-western Atlantic Ocean (38–42 S). *Mar. Freshw. Res.* **2016**, *68*, 732–742. [[CrossRef](#)]
59. Perry, C.T.; Clingham, E.; Webb, D.H.; de la Parra, R.; Pierce, S.J.; Beard, A.; Henry, L.; Taylor, B.; Andrews, K.; Hobbs, R.; et al. St. Helena: An important reproductive habitat for whale sharks (*Rhincodon typus*) in the central south Atlantic. *Front. Mar. Sci.* **2020**, *7*, 576343. [[CrossRef](#)]
60. Kock, A.; O’Riain, M.J.; Mauff, K.; Meyer, M.; Kotze, D.; Griffiths, C. Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS ONE* **2013**, *8*, e55048. [[CrossRef](#)]
61. Becerril-García, E.E.; Hoyos-Padilla, E.M.; Micarelli, P.; Galván-Magaña, F.; Sperone, E. Behavioural responses of white sharks to specific baits during cage diving ecotourism. *Sci. Rep.* **2020**, *10*, 11152. [[CrossRef](#)]

62. Duffy, C.; Francis, M.P.; Manning, M.J.; Bonfil, R. Chapter 21: Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. In *Global Perspectives on the Biology and Life History of the White Shark*; Domeier, M.L., Ed.; CRC Press: Boca Raton, FL, USA, 2012; pp. 301–318.
63. Skomal, G.B.; Chisholm, J.; Correia, S.J. Implications of increasing pinniped populations on the diet and abundance of white sharks off the coast of Massachusetts. In *Global Perspectives on the Biology and Life History of the White Shark*; Domeier, M.L., Ed.; CRC Press: Boca Raton, FL, USA, 2012; pp. 405–418.
64. Robbins, R.L. Environmental variables affecting the sexual segregation of great white sharks *Carcharodon carcharias* at the Neptune Islands South Australia. *J. Fish Biol.* **2007**, *70*, 1350–1364. [[CrossRef](#)]
65. Semmens, J.; Payne, N.; Huvneers, C.; Sims, D.W.; Bruce, B. Feeding requirements of white sharks may be higher than originally thought. *Sci. Rep.* **2013**, *3*, 1471. [[CrossRef](#)]
66. Goldman, K.J.; Anderson, S.D. Space utilization and swimming depth of white sharks, *Carcharodon carcharias*, at the South Farallon Islands, central California. *Env. Biol. Fish.* **1999**, *56*, 351–364. [[CrossRef](#)]
67. Weng, K.C.; Boustany, A.M.; Pyle, P.; Anderson, S.D.; Brown, A.; Block, B.A. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Mar Biol* **2007**, *152*, 877–894. [[CrossRef](#)]
68. Dunbar, R.; Shultz, S. Evolution in the social brain. *Science* **2007**, *317*, 1344–1347. [[CrossRef](#)]
69. Clark, E. Instrumental conditioning of lemon sharks. *Science* **1959**, *130*, 217–218. [[CrossRef](#)]
70. Guttridge, T. The Social Organization and Behaviour of the Juvenile Lemon Shark *Negaprion brevirostris*. Ph.D. Thesis, University of Leeds, Institute of Integrative and Comparative, Leeds, UK, 2009.
71. Northcutt, R.G. Elasmobranch central nervous system organization and its possible evolutionary significance. *Am. Zool.* **1977**, *17*, 411–429. [[CrossRef](#)]
72. Yopak, K.E.; Lisney, T.J.; Collin, S.P.; Montgomery, J.C. Variation in brain organization and cerebellar foliation in chondrichthyans: Sharks and holocephalans. *Brain Behav. Evol.* **2007**, *69*, 280–300. [[CrossRef](#)]
73. Striedter, G.F.; Northcutt, R.G. Head size constrains forebrain development and evolution in ray-finned fishes. *Evol. Dev.* **2006**, *8*, 215–222. [[CrossRef](#)] [[PubMed](#)]
74. Holland, K.N.; Meyer, C.G.; Dagorn, L.C. Inter-animal telemetry: Results from first deployment of acoustic ‘business card’ tags. *Endanger. Species Res.* **2009**, *10*, 287–293. [[CrossRef](#)]
75. Guttridge, T.L.; Gruber, S.H.; Krause, J.; Sims, D.W. Novel acoustic technology for studying free-ranging shark social behaviour by recording individuals’ interactions. *PLoS ONE* **2010**, *5*, e9324. [[CrossRef](#)] [[PubMed](#)]
76. Krause, J.; James, R.; Croft, D.P. Personality in the context of social networks. *Philos. Trans. R. Soc. B Biol. Sci.* **2010**, *365*, 4099–4106. [[CrossRef](#)]
77. Klimley, A.P.; Nelson, D.R. Diel movement pattern of the scalloped hammerhead shark *Sphyrna lewini* in relation to el Bajo Espiritu Santo: A refuging central position social system. *Behav. Ecol. Sociobiol.* **1984**, *15*, 45–54. [[CrossRef](#)]
78. Sims, D.W.; Southall, E.J.; Quayle, V.A.; Fox, M. Annual social behaviour of basking sharks associated with coastal front areas. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **2000**, *267*, 1897–1904. [[CrossRef](#)] [[PubMed](#)]
79. Guttridge, T.L.; Gruber, S.H.; Gledhill, K.S.; Croft, D.P.; Sims, D.W.; Krause, J. Social preferences of juvenile lemon 543 sharks, *Negaprion brevirostris*. *Anim. Behav.* **2009**, *78*, 543–548. [[CrossRef](#)]
80. Jacoby, D.M.P.; Fear, L.N.; Sims, D.W.; Croft, D.P. Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behav. Ecol. Sociobiol.* **2014**, *68*, 1995–2003. [[CrossRef](#)]
81. Anderson, J.M.; Clevestine, A.J.; Stirling, B.S.; Burns, E.S.; Meese, E.N.; White, C.F.; Logan, R.K.; O’Sullivan, J.; Rex, P.T.; May, J., III; et al. Non-random Co-occurrence of Juvenile White Sharks (*Carcharodon carcharias*) at Seasonal Aggregation Sites in Southern California. *Front. Mar. Sci.* **2021**, *8*, 688505. [[CrossRef](#)]
82. Papastamatiou, Y.P.; Mourier, J.; TinHan, T.; Luongo, S.; Hosoki, S.; Santana-Morales, O.; Hoyos-Padilla, M. Social dynamics and individual hunting tactics of white sharks revealed by biologging. *Biol. Lett.* **2022**, *18*, 20210599. [[CrossRef](#)]
83. Klimley, A.P.; Le Boeuf, B.J.; Cantara, K.M.; Richert, J.E. Automated tracking of white shark *Carcharodon carcharias* by radio-acoustic positioning system. *Mar. Biol.* **2000**, *4*, 182–193.
84. Hsu, Y.; Earley, R.L.; Wolf, L.L. *Modulating Aggression through Experience. Fish Cognition and Behaviour*; Blackwell: Oxford, UK, 2006; pp. 96–118.
85. Fallows, C.; Gallagher, A.J.; Hammerschlag, N. White sharks (*Carcharodon carcharias*) scavenging on whales and its potential role in further shaping the ecology of an apex predator. *PLoS ONE* **2013**, *8*, e60797. [[CrossRef](#)]
86. Bromilov, M. 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, 2014; pp. 6–8.
87. Strong, W.R.; Murphy, R.C.; Bruce, D.B.; Nelson, D.R. Movements and associated observations of bait attracted white sharks *Carcharodon carcharias*: A preliminary report. *Mar. Freshw. Res.* **1992**, *43*, 13–20. [[CrossRef](#)]
88. Strong, W.R. Repetitive aerial gaping: A thwart-induced behaviour in white sharks. In *Great White Sharks*; Academic Press: Cambridge, MA, USA, 1996; pp. 207–215.

89. Lisney, T.J.; Bennet, M.B.; Collin, S.P. Volumetric analysis of sensory brain areas indicates ontogenetic shifts in the relative importance of sensory systems in elasmobranchs. *Raffles Bull. Zool.* **2007**, *55*, 7–15.
90. Reinero, F.R.; Sperone, E.; Giglio, G.; Pacifico, A.; Mahrer, M.; Micarelli, P. Influence of Environmental Factors on Prey Discrimination of Bait-Attracted White Sharks from Gansbaai, South Africa. *Animals* **2022**, *12*, 3276. [[CrossRef](#)] [[PubMed](#)]

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.