

RESEARCH ARTICLE

The surface behaviour of white sharks during ecotourism: A baseline for monitoring this threatened species around Guadalupe Island, Mexico

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Abstract

1. Cage diving is the most important activity for the sustainable use of white sharks (*Carcharodon carcharias*). However, information related to their behaviour during ecotourism is scarce.
2. This study provides useful information for monitoring *C. carcharias* during cage-diving activities around Guadalupe Island, Mexico. Surface behaviour of 106 white sharks was recorded for 87 days on-board six cage-diving boats in 2012, 2013, and 2014.
3. Of the observed sharks, 63% were immature specimens ($n = 67$) and 37% were considered mature ($n = 39$). Seventy-one per cent were males ($n = 75$) and 29% were females ($n = 31$).
4. Interactions were classified into one of the 11 behaviours: parading, close inspection, horizontal attack, vertical attack, bait catching, feeding, not feeding, buoy catching, encounter, escape, and staying.
5. Parading, close inspections, and horizontal attacks were performed more often by mature males, whereas immature females performed more vertical attacks, with no differences between mature and immature males.
6. A total of 1,542 ethograms were registered. Each ethogram consisted on average of 6.3 ± 5.6 behaviours with a significant transitional pattern from horizontal attacks to parading and close inspections, and from vertical and horizontal attacks to bait being caught.
7. A pattern related to feeding in a simple stimulus response reflex was observed. The shark's length seems to play an important role in the efficiency of the attacks, presumably resulting from the experience of mature individuals. Intentional feeding should be avoided to prevent negative effects related to ecotourism.
8. This study constitutes a baseline for future research on white shark behaviour. It can be applied in other regions regardless of environmental conditions, quantity and size of the boats, and types of bait. Using this standard method could improve the monitoring, management, and conservation of this vulnerable species.

KEYWORDS

fish, marine reserve, ocean, protected species, recreation, sustainability

1 | INTRODUCTION

The white shark (*Carcharodon carcharias*, Linnaeus, 1758) is a vulnerable and protected species in countries such as South Africa, New Zealand, Australia, and Mexico (Fergusson, Compagno, & Marks, 2009; Torres-Aguilar et al., 2015). Fishing bans, trade regulation, the reduction of bycatch, and ecotourism are some of the most important measures for global conservation of white sharks (Fergusson et al., 2009). In Mexican waters, the cage-diving industry has been developing since 2001 and contributes to the education of tourists, vigilance against illegal fisheries, and scientific research in Guadalupe Island Biosphere Reserve (Torres-Aguilar et al., 2015). Local regulations for the conservation of white sharks during ecotourism prohibit fishing for baits in the diving area, chumming, diving out of the cages, or the use of any other attractant, like electricity or sound, in order to not disturb the behaviour of the animals (Iñiguez-Hernández, 2008; Torres-Aguilar et al., 2015). However, the effect of tourism, legal or illegal, on white sharks is not currently evaluated (Iñiguez-Hernández, 2008).

Knowledge about *C. carcharias* around Guadalupe Island is derived from a limited number of studies related to migration (Domeier & Nasby-Lucas, 2008), ecology (Becerril-García, 2015; Bonfil & O'Brien, 2015; Hoyos-Padilla, Klimley, Galván-Magaña, & Antoniou, 2016; Jaime-Rivera, Caraveo-Patiño, Hoyos-Padilla, & Galván-Magaña, 2013), and local movements (Hoyos-Padilla et al., 2016; Skomal, Hoyos-Padilla, Kukulya, & Stokey, 2015). There is no ethological research describing the surface behaviour of white sharks related to cage-diving boats in Mexico or in the whole eastern Pacific, despite its importance for the Mexican authorities (Becerril-García, 2015; Torres-Aguilar et al., 2015). These ethological studies have proven to be useful for the description of behavioural events under baiting situations in South Africa (Sperone et al., 2012, 2010) and could be used for the monitoring of this species during ecotourism.

At continental aggregation sites, the ethology of *C. carcharias* has been used to describe hunting strategies (Klimley, Pyle, & Anderson, 1996; Martin, 2003; Martin, Hammerschlag, Collier, & Fallows, 2005; Tricas, 1985), effects of environmental factors on abundance and hunting strategies (Hammerschlag, Martin, & Fallows, 2006; Pyle, Klimley, Anderson, & Henderson, 1996), and local movements of white sharks around pinniped colonies (Goldman & Anderson, 1999; Klimley et al., 2001). Regarding the surface behaviour of bait-attracted white sharks, Sperone et al. (2012) observed eight behavioural responses that showed a complex tactical situation with multiple responses for the acquisition of baits, such as predatory and social behaviours previously observed for South African white sharks (Martin et al., 2005; Sperone et al., 2010). However, the study of the surface behaviour at other aggregation sites is poorly understood (Laroche, Kock, Lawrence, & Oosthuizen, 2007; Sperone et al.,

2012, 2010) despite the increasing demand of ecotourism (Cisneros-Montemayor, Barnes-Mauthe, Al-Abdulrazzak, Navarro-Holm, & Sumaila, 2013).

This study is a general description of the surface behaviour of bait-attracted white sharks during ecotourist activities around Guadalupe Island, Mexico. This paper aims to provide practical information regarding the behavioural responses and their frequency, ethograms for sex and age, and a size-based hierarchy observed in this marine protected area. The ethological approach could be used for the monitoring of white sharks regardless of the country, environmental factors, or potential changes in the ecotourism regulations, which will allow the detection of changes of their behaviour, in relation to human activity, and other potential negative effects, such as conditioning to the presence of boats.

2 | METHODS

2.1 | Study area

Guadalupe Island Biosphere Reserve (29°00'N, 118°26'W) is located 240 km off Baja California's coast, Mexico (Gallo-Reynoso & Figueroa-Carranza, 2005). This oceanic environment is characterized by the abundance of macroalgae, invertebrates, bony fishes, elasmobranchs, cetaceans, and pinnipeds, such as the California sea lion *Zalophus californianus*, the northern elephant seal *Mirounga angustirostris*, and the Guadalupe fur seal *Arctocephalus townsendi* (Gallo-Reynoso & Figueroa-Carranza, 2005; Hoyos-Padilla et al., 2016). Abundance of prey has been suggested as one of the main reasons for the seasonal presence of white sharks in this aggregation site during July to January of each year (Domeier & Nasby-Lucas, 2008; Hoyos-Padilla et al., 2016; Jaime-Rivera et al., 2013).

The presence of white sharks has allowed the development of a cage-diving industry since 2001, with a tourist season lasting from July to November that occurs exclusively in the north-east bay known as Rada Norte, which is the location of the present study (Iñiguez-Hernández, 2008; Torres-Aguilar et al., 2015; Figure 1). Sea surface water temperature ranged from 19.1 to 24.5°C and underwater visibility was recorded from 9 to 30 m by Secchi disc for the duration of the study period.

2.2 | Data collection

Data collection was performed on-board six ecotourism boats that visited the island in the seasons of 2012, 2013, and 2014, for a total of 87 days at sea and 4–11 hr of observation per day. All boats in this study were equipped with two surface cages and were anchored at 200–250 m off the coast at a depth of 70–80 m. The sharks were

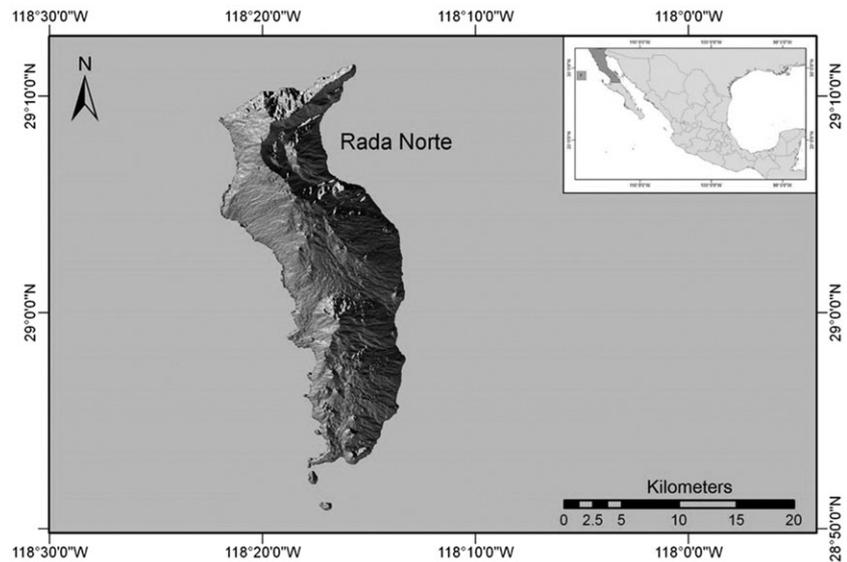


FIGURE 1 Location of Guadalupe Island, Baja California, Mexico

attracted to the boat using yellow fin tuna (*Thunnus albacares*) attached to a buoy by a rope for flotation, with the instruction to the crew of not feeding the sharks intentionally, as indicated by local regulations (Torres-Aguilar et al., 2015).

The total length (TL) of each shark was estimated by the comparison of the length of the cages with the length of each shark when they approached horizontally, parallel, and close to the cage. Each observation was carried out by the same observer (EEBG). The sex of the shark was determined by the presence or absence of claspers and confirmed with underwater photographs. Males with a TL > 3.5 m and females with a TL > 4.5 m were considered mature specimens, according to the data published by Compagno, Dando, and Fowler (2005).

The identification of individual sharks was made by analysing underwater photographs based on the observation of skin pigmentation patterns, scars, mutilations, and anatomical deformities (Domeier & Nasby-Lucas, 2007).

2.3 | Surface behaviour

The surface behaviour of white sharks was defined according to the types of display observed during ecotourism activities (Sperone et al., 2012, 2010). The frequency and sequence of these behaviours were registered and then used to create an ethogram. Each ethogram began when the shark approached the bait at an approximate distance of 10 m, and it ended when the shark was more than 10 m away for at least 5 min. For statistical analysis, the behaviour was correlated with the age and sex of the sharks using the frequency of behaviours in a chi-square analysis.

2.4 | Ethology during ecotourism

The ethograms of white sharks in the absence of other conspecifics were considered due to the possibility of social interactions which might affect their responses to the presence of the bait. The

behavioural analysis of the white sharks, based on frequency and event sequence, was made according to the methods published by Klimley et al. (1996), Martin et al. (2005), and Sperone et al. (2010, 2012). Transitional matrices showing the frequencies of transitions between one behaviour and another were analysed with the software Etholog (version 2.5 © E.B. Ottoni 1995–1999, Laboratory of Comparative Psychology and Ethology, Department of Experimental Psychology University of São Paulo, Brazil). These transitional matrices were used to describe the behaviour with flow charts, and their significance was determined using a chi-square test.

2.5 | Size-based hierarchy

Additional ethograms involving each white shark's interactions were considered for a size-based hierarchy analysis described by the frequency of these events. An interaction was defined as the encounter of two white sharks less than 3 m apart, caused by the arrival of a second shark to the bait zone. The reaction of the first shark to this interaction was recorded by its permanence or escape from the baiting area for more than 5 min. The frequency of these interactions was used to describe the significance of the behaviours using a chi-square analysis.

3 | RESULTS

One hundred and six individual white sharks were identified in this study (Table 1). The TL for both sexes ranged from 183 to 579 cm (mean: 358 ± 95 cm). Of the observed sharks, 63% were immature and 37% were considered mature specimens. The mean size for males was 331 ± 72 cm TL, and a mean size of 419 ± 113 cm TL was recorded for females (Table 1).

TABLE 1 Frequency of the 106 identified white shark's distribution according to sex, length, and maturity

Total length (m)	Mature males	Mature females	Immature males	Immature females
<2.4	0	0	11	2
2.5–3.4	0	0	43	11
3.5–4.4	15	0	0	0
4.5–5.4	6	12	0	0
>5.5	0	6	0	0
Total <i>n</i>	21	18	54	13

3.1 | Surface behaviour

The behaviour of the 106 individual white sharks was recorded in 5,783 events during 534 hr of direct observation. Each event was classified into one of 11 behaviours:

1. Parading (PAR): The shark swims slowly around the bait. The distance between shark and bait usually ranges from 1 to 10 m (Figure 2a). The end of the display occurs when the shark approaches within 1 m of the bait or moves to more than 10 m away. This behaviour was observed 1,120 times and represents 19.3% of all observed displays.
2. Close inspection (CLI): The shark swims close to the bait to a distance of <1 m, without opening its mouth for consumption (Figure 2b). The display ends when the shark moves away from the bait. This event was observed 1,391 times and represents 24% of all observed behaviours.
3. Horizontal attack (HA): The shark moves directly in the direction of the bait, with its mouth opening for capture at an angle <45° in relation to the surface (Figure 2c). This event was observed 1,744 times and represents 30.1% of all observed displays.
4. Vertical attack (VA): The shark moves from the deep, directly in the direction of the bait with its mouth open for capture, and at

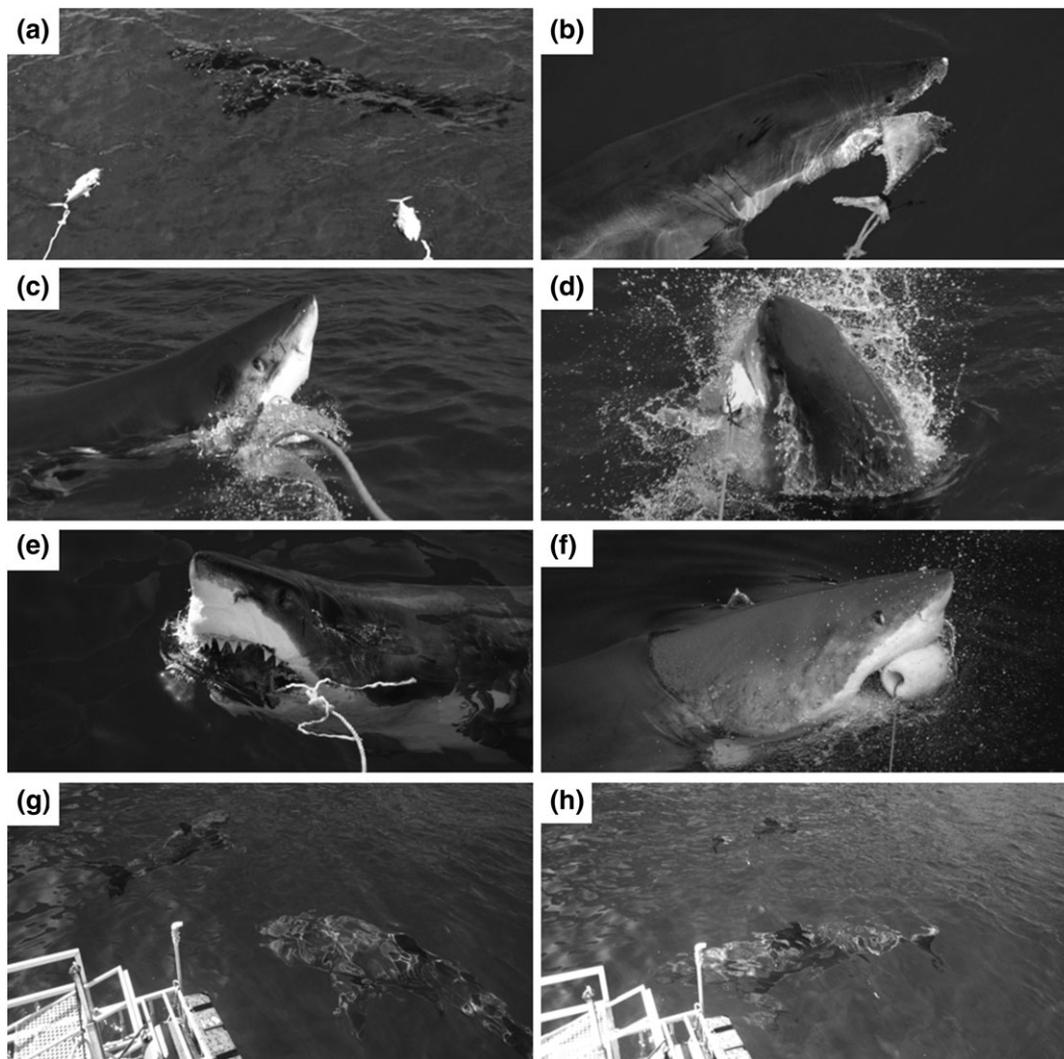


FIGURE 2 Surface behaviours observed among white sharks around Guadalupe Island, México: (a) parading (PAR); (b) close inspection (CLI); (c) horizontal attack (HA); (d) vertical attack (VA); (e) bait caught (BAC); (f) buoy caught (BUO); (g) encounter (EN); (h) reaction after the encounter—for example, a shark stays (STA) and the other escapes (ESC)

an angle of 46–90° in relation to the surface (Figure 2d). VA was observed 439 times and represents 7.6% of all observed behaviours.

5. Bait caught (BAC): The shark closes its jaws with the bait inside (Figure 2e). BAC was observed 419 times (7.2% of all observed displays).
6. Feeding (FE): The shark swallows the bait after catching it. FE was observed 256 times (4.4% of all observations).
7. No feeding (NFE): The shark bites at the caught bait but releases it without consuming it (Figure 2f). NFE was observed 144 times and represents 2.5% of all observed displays.
8. Buoy caught (BUO): The shark closes its jaws with the buoy inside (Figure 2g). BUO was observed 61 times and represents 1.0% of all observed displays.
9. Encounter (EN): The shark swims a distance of <3 m from another white shark during the second shark's interaction with the bait. EN was considered as social interaction and was observed 98 times. It represents 1.7% of all observed displays.
10. Escape (ESC): The shark moves more than 10 m away from the bait after an encounter. ESC was considered as a social interaction after EN and was observed 42 times and represents 0.76% of all observed displays.
11. Stay (STA): The shark remains near the bait (1–10 m) after an encounter. STA was considered as a social interaction after EN. STA was observed 56 times and represents 0.96% of all observed displays.

Independently, mature white sharks and male individuals were the groups with the highest efficiency in the attacks for the capture and consumption of baits, with success rates of 22% and 20% respectively for BAC, and 14% and 12% respectively for FE. The female and immature sharks showed a lower efficiency, with a success rate of 17% for both groups in the case of BAC and 10% for FE.

The association between the number of behaviours versus the sex and size of white sharks is shown in Figure 3. The actions of PAR ($\chi^2_{49} = 350.56$), CLI ($\chi^2_{49} = 428.67$), HA ($\chi^2_{49} = 624.25$), and FE ($\chi^2_{49} = 107.62$) were performed mainly by mature females with a

significant association ($P < 0.001$). Mature females showed a negative association with VA, BAC, and NFE. Immature males showed a high preference for PAR ($\chi^2_{49} = 156.02$), CLI ($\chi^2_{49} = 275.74$), and HA ($\chi^2_{49} = 139.91$), with negative association of VA and BAC. Immature females showed a significant ($P < 0.05$) preference of VA ($\chi^2_{49} = 70.27$), whereas a negative association was observed with PAR, CLI, and AH.

3.2 | Ethology during ecotourism

In total, 1,542 ethograms were registered during the 3 years of the study. The transitional matrix originating from these ethograms showed the transitions between the behavioural patterns recorded using a total of 4,823 behaviours (83.4% of all observed events). In this analysis, only the types of behaviour made by single white sharks in relation to the bait were considered. A general flow chart with the significant transitions was observed using all the registered ethograms (Figure 4). The most probable transitional pattern during an ethogram was from HA to PAR ($\chi^2_{49} = 78.8$) and from HA to CLI ($\chi^2_{49} = 159.6$), followed by HA or VA to BAC ($\chi^2_{49} = 170.28$; $\chi^2_{49} = 186.66$) with an obligatory FE or NFE ($\chi^2_{49} = 2,044.60$; $\chi^2_{49} = 1,338.62$) that was registered in all cases.

The significance of the transition was dependent on the size and sex of the sharks. The most probable transition was from HA or VA

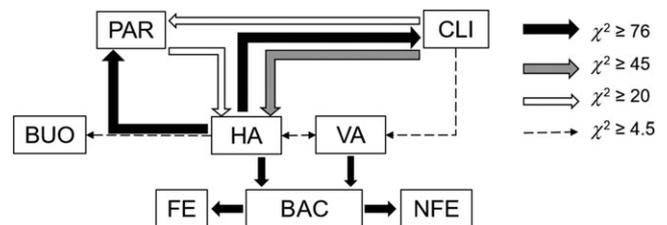
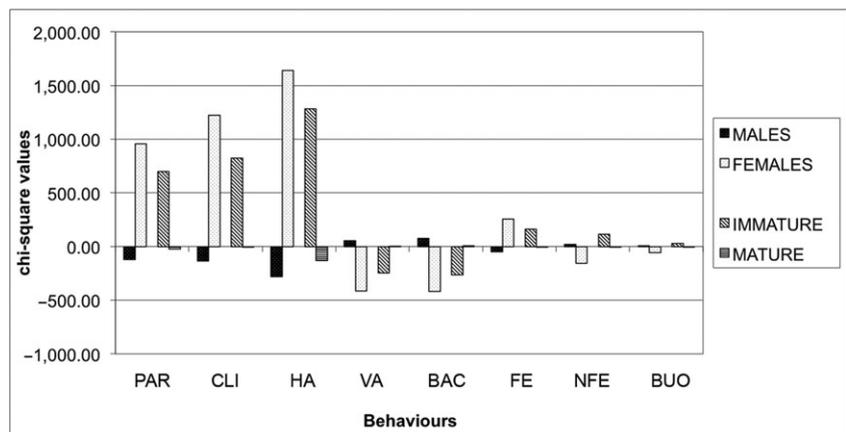


FIGURE 4 General flow chart of the significant behavioural transition of 106 individual white sharks under baiting situations: BAC, bait caught; BUO, buoy caught; CLI, close inspection; FE, feeding; HA, horizontal attack; NFE, no feeding; PAR, parading; VA, vertical attack

FIGURE 3 Association between number of behaviours with sex and size of observed white sharks: BAC, bait caught; BUO, buoy caught; CLI, close inspection; FE, feeding; HA, horizontal attack; NFE, no feeding; PAR, parading; VA, vertical attack



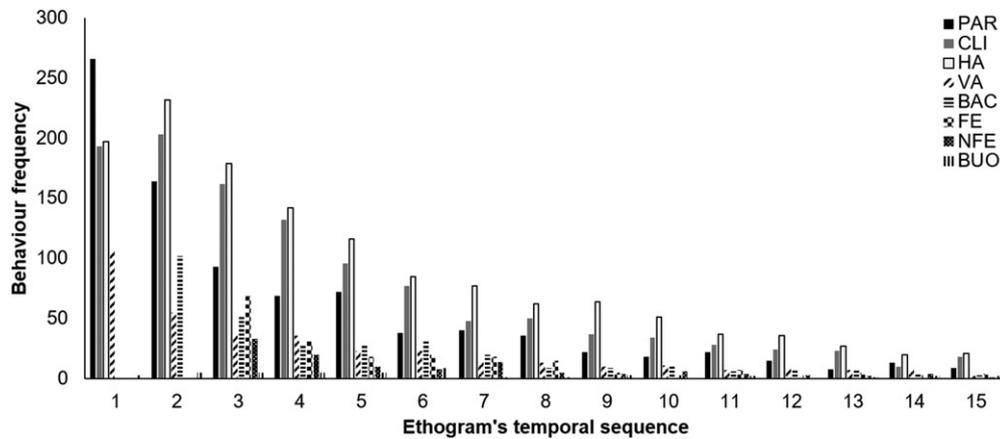


FIGURE 5 Sequential order of the first 15 observed behavioural events: BAC, bait caught; BUO, buoy caught; CLI, close inspection; FE, feeding; HA, horizontal attack; NFE, no feeding; PAR, parading; VA, vertical attack

to BAC ($\chi^2_{49} = 114.52$; $\chi^2_{49} = 109.93$) in the case of the mature sharks, and from HA to INT in immature individuals ($\chi^2_{49} = 95.69$). Regarding sex, a significant transition from HA or VA to BAC was observed in the males ($\chi^2_{49} = 119.93$; $\chi^2_{49} = 153.84$), without an evident pattern in the females.

The average number of behaviours per ethogram was 6.3 ± 5.6 with a minimum and maximum of 2 and 62 behaviours respectively. The beginning of an ethogram usually began with inspection or attack behaviours, with a subsequent capture of the bait (Figure 5). The most frequent initial behaviour was PAR, followed by CLI and HA in succession; however, these three behaviours were frequently registered in all the ethograms analysed in this study. The BAC was registered in the ethograms as the second behaviour, whereas FE occurred after the third display. BUO was registered sporadically, and it was determined as a confused reaction with the bait. There is a significant negative correlation (Spearman's coefficient $n = 773$, $r = -0.1762$, $P < 0.01$) between body size of sharks and the number of behaviours in ethograms, with smaller sharks having a higher number of behaviours.

3.3 | Size-based hierarchy

Social interactions of 47 individual white sharks were recorded 98 times in 94 ethograms ($n = 935$ episodes). The most frequent behaviour was EN with a small shark, occurring in 77.5% of all observed interactions. The EN of a small shark with a larger shark was observed in only 22.5% of all observed interactions (Table 2). In terms of proportion, the first shark remained in the area twice as many times as it left after the arrival of a second but smaller shark ($\chi^2_1 = 0.99$, $P > 0.05$). When the second shark was a larger specimen, the first shark escaped on three times as many occasions than it remained. This first shark moved away from the second and thereby completed its ethogram. This last reaction was considered significant according to the chi-square test ($\chi^2_1 = 4.58$, $P < 0.05$).

TABLE 2 Frequency of the reactions performed by the first white shark after an encounter, according to the situation observed

Situation	Reaction		Total
	Stay (STA)	Escape (ESC)	
Arrival of a smaller shark	50	26	76
Arrival of a bigger shark	6	16	22
Total	56	42	98

4 | DISCUSSION

This study constitutes the first ethological analysis of the behaviour of white sharks in an oceanic aggregation site. It provides a standardized method for the study of this species under baiting situations around Guadalupe Island, and constitutes a useful baseline for future ethological analyses during the seasonal monitoring of this species in the area (Torres-Aguilar et al., 2015). Despite the absence of ethological studies around Guadalupe Island, it was possible to compare the results with the behaviour of white sharks in other aggregation sites.

4.1 | Surface behaviour

The most frequently observed behaviours were HA, PAR, and CLI, considered as aggressions and visual inspections relating to the presence of bait. According to Martin (2003) and Sperone et al. (2012), PAR constitutes a search pattern for feeding, as an essential behaviour for the hunting strategies of white sharks in South Africa and based on calculated approximations for the capture of prey (Klimley et al., 1996; Martin, 2003; Sperone et al., 2012). In the clear waters of Guadalupe Island, PAR could be related to a distance inspection of the conditions for prey capture, the presence of competitors or conspecifics of the opposite sex, and the economization of energy (Hoyos-Padilla et al., 2016; Myrberg & Gruber, 1974; Sperone et al., 2012). CLI is similar to the 'visual inspection' reported by Martin (2003) and Sperone

et al. (2012). The similarity is based on the method of approach of the sharks to the bait, which has been linked to the choice of prey (Sperone et al., 2012). This approach gives information on the prey's reaction, so white sharks could evaluate the most efficient way to attack and catch the prey, or the bait. HA was the most frequent behaviour in this study. This is consistent with observations in Australia (Strong, 1996; Tricas, 1985) and South African waters (Sperone et al., 2012). The latter defines this behaviour as 'bait follow' and linked it to the inspection of bait, but without considering the action of an attack or consumption, due to the strict ban on feeding white sharks during cage-diving activities in South Africa (Laroche et al., 2007). However, this type of behaviour would be directly related to feeding, regardless of the handling of the bait, as was observed both in this study and by Strong (1996) and Tricas (1985).

The large number of attacks with respect to the number of catches and consumptions was the cause of the low effectiveness of this behaviour. The group of adult sharks was the one that managed to capture and consume the bait more frequently when compared with immature individuals. This can be attributed to the greater experience of white sharks according to their age, since adults perform a better assessment of conditions before ambushing their prey to better manage their energy expenditure (Goldman & Anderson, 1999; Jewell, Johnson, Gennari, & Bester, 2013). Other variables may be related to the effectiveness of bait capture, such as the environmental conditions, the experience of the shark, hierarchy of larger individuals, and bait management (Becerril-García, 2015; Sperone et al., 2012). In this study, the observations were made during real ecotourism activities around Guadalupe Island, so it was not always the same person involved in the handling of the baits, and the effectiveness might have been affected by this factor and should be considered in future analyses. The results suggest a possible loss of energy related to the lack of rewards, which could lead to an energy imbalance that could affect the health of the white sharks (Guerrero-Ávila, 2011; Orams, 2000).

Negative effects resulting from tourist activities have been observed in other marine protected species, such as marine birds and cetaceans, where interruptions in foraging and breeding have been linked to a higher use of energy (Green & Giese, 2004). Nevertheless, intentional and supplementary feeding would not necessarily affect the energy balance or feeding ecology in elasmobranchs, as it has been observed in bull sharks (*Carcharhinus leucas*) during the ecotourism in Fiji (Abrantes, Brunnschweiler, & Barnett, 2018; Brunnschweiler, Payne, & Barnett, 2018). However, the energy expenditure due to a lack of food reward is beyond the scope of this study and should be assessed in future research regarding baits and white shark physiology during ecotourist activities. Additionally, the evaluation of negative effects related to the conditioning of white sharks at Guadalupe Island remains necessary for the improvement of the sustainable management and conservation of this species in Mexico.

Intraspecific interactions along with buoy attacks were the least frequent surface behaviours observed during the present study. BAC was interpreted as a confusion of the shark during its interaction with the boats, since the proximity of the buoy to the bait could have generated this error. The attack on floating objects, such as algae, buoys,

or birds, may be related to a mistaken identity of prey, as has been documented in South Africa by Hammerschlag, Martin, Fallows, Collier, and Lawrence (2012). This kind of interaction could provide information to the shark about the identity of the attacked object (Heithaus, 2004), which could also explain the recording of this unusual behaviour.

From our observations, it is possible to underline a significant difference in behaviour between males and females and between mature and immature sharks. The first difference to be considered is that between mature and immature females: The former showed a clear preference for surface behaviours such as PAR, CLI, and HA, whereas the latter preferred depth behaviours such as VA. This could be explained in light of the possible differences in habitat usage capacity that could serve to minimize food competition, as observed in other contexts (Harasti, Lee, Bruce, Gallen, & Bradford, 2017; Towner, Underhill, Jewell, & Smale, 2013).

Differences in behaviours were not apparent between mature and immature males: Both avoided behaviours like VA, and immature sharks showed significant preferences to surface behaviours as did mature females. This could suggest that there is no clear hunting strategy between males and females during ecotourism, as both utilize mainly surface behaviours for the consumption of bait. Nevertheless, this study does not evaluate the abundance of white sharks in deeper waters that could affect the behaviour of the sharks at the surface. Additionally, the measure of time of interactions in future research could provide more information about the feeding ethology of the species, considering the potential differences between sex and size of the sharks.

4.2 | Ethology during ecotourism

The cage-diving industry for white sharks exists in Mexico, South Africa, the USA, Australia, and New Zealand. However, the surface ethology of bait-attracted white sharks has only been analysed in South African waters, by Sperone et al. (2012, 2010). The ethograms presented in that study were mainly performed by immature white sharks (81% of all observed individuals) and included nine behaviours with an average of 20 ± 21.8 events per ethogram associated in a complex behavioural pattern. In the present study, the 11 behaviours were observed with an average of 6.3 ± 5.6 behaviours per ethogram with an evident pattern that began with inspections and attacks of the bait for feeding. Differences could be related to the higher proportion of juveniles observed at Dyer Island, South Africa, and the differences in habitat between oceanic and coastal environments. At both sites, immature sharks showed ethograms with a higher number of events, explained by the reduced experience, learning, or a hierarchy effect compared with mature sharks (Bres, 1993; Goldman & Anderson, 1999; Sperone et al., 2012). In the case of environmental conditions, the good visibility at Guadalupe Island is favourable for the rapid evaluation of a situation, so sharks can inspect the bait and other competitors to perform its actions and ethograms in fewer events.

4.3 | Size-based hierarchy

Although the number of encounters could represent a limitation for the reliability of the results, its low frequency is also a sign of the conflict avoidance behaviour previously reported for white sharks (Sperone et al., 2012, 2010). Like other species, intraspecific aggressions are rare and avoided through visual contact with other competitors (Martin, 2003; Sperone et al., 2010). Guadalupe Island is characterized by crystal clear waters with more than 30 m of visibility (Becerril-García, 2015; Hoyos-Padilla et al., 2016), so detection among sharks can occur without the need for close encounters. Therefore, the avoidance of conflict could be taken before approaching the bait or another shark, which respects the space of larger individuals. This was also observed with the low frequency of arrivals of larger individuals, as a small shark can detect the presence of other sharks and move away from the bait zone to avoid the possibility of aggression. On the contrary, a small shark could enter the bait zone with the presence of a larger shark after assessing the behaviour and tolerance of such a shark towards the other individuals (Sperone et al., 2010).

Size-based hierarchy was observed with the behaviour of the small sharks that escaped from the baiting area when larger individuals arrived. This reaction can be attributed to the inherent risk that exists in the social interactions between white sharks, since it compromises the survival of the smallest individuals (Martin, 2003). The escape (ESC) could allow the smaller shark to evaluate the behaviour and tolerance of the larger individual; or, as observed in other studies, it could take turns in the attack and consumption of the prey as an opportunistic predator (Curtis et al., 2006; Martin, 2003; Sperone et al., 2012).

In South African waters, environmental factors, such as low visibility and a higher proportion of juveniles, could be a reason for an elevated frequency of social interactions, as the white sharks are able to react behind other conspecifics in a shorter distance (<4 m; Sperone et al., 2012, 2010). The comparison of social interactions between different environments in oceanic and continental aggregation sites could be an opportunity to describe interactions during competition situations, along with the effect of the environmental and human factors on the frequency and types of behaviour. These comparisons could be useful for future conservation actions in these aggregation sites, as agonistic interactions can be detected and avoided; for example, if a higher frequency of encounters, aggressions, or accidents with the cages are observed during certain environmental conditions (Green & Giese, 2004; Hammerschlag et al., 2006; Johnson & Kock, 2006; Laroche et al., 2007).

4.4 | Implications for conservation

Wildlife ecotourism is the main activity for the sustainable use of white sharks around the world. Despite the benefits in education, science, and local economy, cage diving has been related to negative effects, such as a decrease in natural predation, the conditioning to artificial feeding, diseases transmitted by the baits, and the potential increment of accidents between humans, cages, and sharks, as has

been observed around Guadalupe Island on several occasions (Becerril-García, 2015; Green & Giese, 2004; Johnson & Kock, 2006; Laroche et al., 2007). Although this paper constitutes a baseline for Guadalupe Island, the ethological approach is an opportunity to develop insights into the effect of ecotourism, feeding ethology, and social behaviour in other white shark populations.

This study provides ethological techniques that allow the evaluation of the behaviour of a vulnerable species during its interaction with humans. In terms of sustainable management, the implementation of a standard method for monitoring white sharks is needed to benefit the evaluation of its behaviour through time. This will allow future comparisons in the case of changes in ecotourism activity, such as the number and size of the boats, number of divers, type of baits, the use of different areas in the aggregation sites, or modifications in the regulations for cage diving. The generated knowledge will contribute to the conservation of the species through sustainable management decisions based on scientific evidence.

The behaviour of white sharks during ecotourism activities revealed a pattern related to feeding in a simple stimulus–response reflex that involves curiosity and aggressive behaviours. The size of the shark seems to play an important role in the efficiency of the attacks for the consumption of bait, resulting from the experience of mature individuals (Sperone et al., 2012). This should be of special interest for authorities and boat owners, as the feeding of individuals should be avoided to prevent other problems, such as the potential conditioning of white sharks to the boats (Green & Giese, 2004; Johnson & Kock, 2006; Laroche et al., 2007).

Regarding tourist activity, the methods in this paper could be used by authorities during citizen science programmes, specifically for the obtention of pictures for photo identification of individuals. As has been observed in other studies, the implementation of these kinds of programme could provide useful information related to the interaction with other species (Hoyos-Padilla, Papastamatiou, O'Sullivan, & Lowe, 2013), demography by a mark–recapture technique (Towner, Wcisel, Reisinger, Edwards, & Jewell, 2013), and ecological data if environmental factors are considered (Becerril-García, 2015; Hammerschlag et al., 2006).

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