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Review article

Opportunities for science in touristic shark feeding aggregations – A review

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ABSTRACT

Shark tourism has been rising exponentially over the past decades. This is particularly true for dive operators that make use of artificial provisioning to attract the animals, increasing the likelihood of encounters for participants. However, this practice is often deemed controversial as previous research has pointed out positive as well as negative consequences of such activities which are often highly case-dependent. In this review, we investigate to which extent these anthropogenic-based activities have contributed to different disciplines within shark related science and discuss its potential future role. We demonstrate its scientific contribution especially in the fields of behavior and social dynamics of large shark species, which are usually elusive and difficult to access in the wild. Additionally, touristic shark feeding sites have benefitted the application and testing of novel methods and technologies. Recent research direction shows that one of the greatest benefits might be the regular access to the same individuals over time, allowing a shift from population-based towards individual-based research. This will advance our understanding of inter- and intra-individual differences and its underlying principles as we will be able to dive deeper into shark personalities, social interactions and their mechanisms.

1. Introduction

Research on elasmobranchs has received substantial attention since the beginning of this century (Parton et al., 2019). However, studying large, predatory sharks has proven very challenging as many species undertake long migrations, inhabit hard-to-access parts of the ocean and most of the time avoid interaction with humans. Hence, most of the available data is based on catch-and-release approaches in the wild or juveniles maintained in (semi-) captive environments that fail to provide information on the more intricate levels needed for a holistic understanding of a species ecology and behavior. There is an increasing awareness that the current gaps in our knowledge about sharks have contributed to their poor management in the past (Musick et al., 2000; Ferretti et al., 2010).

Today, around 70 % of oceanic sharks and rays are threatened with extinction (Pacoureau et al., 2021), while 59 % of reef-associated sharks and rays face a similar risk (Sherman et al., 2023). It is estimated that nearly all elasmobranch species (99.6 %) are exploited either directly or indirectly as bycatch (Dulvy et al., 2021) and persistent overexploitation remains the number one threat (Worm et al., 2013; Queiroz et al., 2019; MacNeil et al., 2020; Pacoureau et al., 2021; Sherman et al., 2023). Sharks are exploited for a

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multitude of reasons, with the extraction of meat being the main cause followed by bycatch and fins for species of large body size (Ripple et al., 2019). Besides the consumptive use of sharks, other non-consumptive anthropologic activities have evolved over the past decades such as the underwater observation of sharks.

1.1. Provisioned shark diving

Contrary to lethal relationships between humans and sharks (also including activities not related to commercial fishing such as sport fishing and culling campaigns) the commercial and non-consumptive exploitation of these animals in form of touristic wildlife encounters can be traced back to as early as the 1960s. However, it has been rapidly expanding over the last decades (Topelko and Dearden, 2005; Cisneros-Montemayor et al., 2013; Brena et al., 2015; Gallagher et al., 2015; Healy et al., 2020). Such activities are usually referred to as shark-ecotourism or shark-diving in the literature, both usually referring to the observation of sharks in their natural environment without the intention of harming them as well as including baited and non-baited experiences. It often includes other elasmobranch species such as rays and varying activities such as snorkelling, freediving or SCUBA-diving (Cisneros-Montemayor et al., 2013). In 2012, 590,000 tourists across 20 countries participated in such activities (Cisneros-Montemayor et al., 2013). Although recent global estimates are missing, the number of those operations around the world seems to continuously increase, especially as the global tourism is rapidly expanding again after the COVID-19 pandemic according to the United Nations World Tourism Organization.

The ocean's vastness and the elusive nature of most sharks generally make encounters a rare and short-lived experience. The increasing demand for shark-ecotourism activities has, therefore, led to an increase of dive operators utilizing some form of attractant, either consumable and/or non-consumable (purely olfactory stimuli in liquid form or inaccessible pieces of fish in boxes/bags) to increase the chances of sightings and customer satisfaction. However, this practice is often seen controversial to the extent that it became illegal in certain countries (e.g., French Polynesia in 2017 despite the potential as a touristic shark-feeding destination).

1.2. Potential negative outcomes of shark provisioning

Potentially fuelling a major portion of an animals energy requirements, artificial provisioning could prevent sharks from fully playing their roles in local ecosystems and food-webs (Brunnschweiler et al., 2018; Heim et al., 2021). Alterations of spatial distribution, diel-patterns and abundance may also occur resulting in potential negative consequences for the sharks energy budget or other vital biologic functions such as reproduction, although minimal or unclear (Clua et al., 2010; Fitzpatrick et al., 2011; Clarke et al., 2013; Jackson, 2020). Research on great white sharks (*Carcharodon carcharias*) from Australia indicates that attracting sharks through smell without feeding them results in sharks being less attracted over time and spending less time around operator boats due to the absence of a positive reward (Niella et al., 2024). However, such effects are arguably species dependent and in other, less migratory ones attraction without feeding may negatively affect an individual's fitness due to the repeated expenditure of energy without reward. Impacts on target-species have been researched quite early on, but they may also extend to non-target species, whole communities and ecosystems, and more research is needed in that area to fully understand those consequences (Vignon et al., 2010; Drew und McKeon, 2019; McKeon und Drew, 2019; Meyer et al., 2020). Interestingly, it has also been found that some shark species show high resilience to a stop of provisioning activities and conditioning prevailed after ceasing these activities (Séguigne et al., 2022). Further science-focused information about potential negative and/or positive impacts can be found in existing reviews (Brena et al., 2015; Burgin and Hardiman, 2015; Gallagher et al., 2015; Patroni et al., 2018).

1.3. Potential positive outcomes of shark provisioning

In opposition to the above, in regions where this form of wildlife tourism occurs, direct and indirect business revenues, governmental taxes and job creation provide substantial benefits to local and national economies (Topelko and Dearden, 2005; Vianna et al., 2011; Huvneers et al., 2017). In the Bahamas, shark-diving contributed at least 113.8US\$ million annually to the Bahamian economy in the past (Haas et al., 2017). In Fiji, this contribution totalled at 42.2US\$ million in 2010 (Vianna et al., 2011) and in Australia, the total expenditures for shark-diving equalled 25.5US\$ million between 2013 and 2014 (Huvneers et al., 2017). Other regional estimations were calculated for the Maldives (Zimmerhackel et al., 2019), the Azores (Torres et al., 2017), Brazil (Pires et al., 2016) and French Polynesia (Clua et al., 2011). This stands in direct contrast to the traditional consumptive-use of sharks. The development associated with shark diving is therefore argued to play a fundamental role in the paradigm-shift towards perceiving sharks as a non-consumptive, socio-economically valuable and sustainable resource (Vianna et al., 2010; Gallagher and Hammerschlag, 2011; Vianna et al., 2011; Gallagher and Huvneers, 2018).

Besides the above-mentioned benefits, shark-diving has also proven to ease, and sometimes initiate, the implementation of marine protected areas and specific shark conservation actions around the world. By 2017, 17 countries had implemented shark-related marine protected areas, many of which are renowned shark-diving destinations (Ward-Paige, 2017). Based on the concept of "Relational Values" (Chan et al., 2016), positive interaction between humans and sharks in the form of diving could foster stewardship values directly impacting conservation efforts (Apps et al., 2018). Specific examples where these activities have directly supported the facilitation of marine protected areas include the Bahamas (Bahamas Shark Sanctuary), Palau, Philippines (e.g., Malapascua) and Fiji (Shark Reef Marine Reserve) (e.g. Brunnenschweiler, 2010; Haas et al., 2017). In return, those MPAs may prove beneficial not only for the conservation of sharks, but for entire ecosystems within and also in close proximity to MPAs borders (Balmford et al., 2009; Zupan et al., 2018; Jacquemont et al., 2022). Shark-based tourism can serve as a valuable tool in promoting a shift from an animal-centered to a people-centered conservation approach, integrating communities that heavily rely on these animals as a resource, both

consumptively and non-consumptively. However, the extent of its potential positive impacts is highly context-dependent, and to date, assessments of success are often lacking due to limited capacity for measurement and evaluation (Siddiqi et al., 2024).

Overall, whether such activities are “acceptable” from an ethical and ecological standpoint depends on different factors including but not limited to geographic location, species involved, practice of provisioning, regulatory frameworks, best practices, number of involved operators, public safety concerns and conservation outcomes (Dubois and Fraser, 2013; Meyer et al., 2022).

1.4. Aims and objectives

In this article we review how scientists may have benefitted from artificial shark-feeding aggregations for touristic purposes in the past. We aim to understand potential opportunities arising from such a unique and regular access to otherwise elusive animals and discuss potential challenges in that context. As it could significantly strengthen our capacity to study sharks in the wild, our findings have the potential to support the co-development of sustainable and science-informed shark provisioning activities.

2. Materials & methods

This review focusses on studies that utilized and exploited already existing touristic shark-feeding aggregations for scientific purposes. To enhance our understanding of potential opportunities and benefits in elasmobranch research, we restricted our review to articles that primarily explored aspects of shark biology, conservation, or related economic considerations, excluding those that focused mostly on provisioning effects (such as Hammerschlag et al., 2012; Heim et al., 2021; Esposito et al., 2022). While not being the focus of this study, we acknowledge that understanding negative and positive consequences of interaction with wildlife is critical to reduce and avoid harm to marine species and ecosystems. A number of complementary reviews have addressed the balance between the positive and negative effects of such provisioning (Brena et al., 2015; Burgin and Hardiman, 2015; Gallagher et al., 2015; Patroni et al., 2018), while other authors provide frameworks aiding informed decision-making whether or not such activities are justifiable (Dubois and Fraser, 2013; Meyer et al., 2022).

2.1. Literature review

A literature review was conducted to compile information on the state-of-the-art research regarding the potential benefits of studying predatory sharks in the context of touristic shark provisioning. The search was performed using the databases and terminologies (individual and in combination) outlined in Table 1, with the temporal scope ranging from 1960 to 2024. Shark species commonly targeted by touristic shark-feeding operations were additionally included in the search.

Publications were included in the review if they met the following criteria:

- 1) The study utilized an artificial shark-feeding aggregation for tourists, where the aggregation likely exists due to habituation effects. To be included, it had to be evident that the research would not have been possible to the same extent without the presence of such activities (e.g., bull sharks in the Fiji Shark Marine Reserve or Fuvamulah in the Maldives). Studies that could have been conducted using a “science-only” approach (e.g., at a natural aggregation site using common chumming practices) were excluded unless,
- 2) the publication mentioned direct collaboration with shark diving tourism operators (e.g., utilizing existing infrastructure such as tourist boats) and employed consumable or non-consumable stimuli to attract sharks. While this approach may not necessarily

Table 1
Inclusion criteria.

Criteria	Specification
Years	1960–2022
Search terms	“Shark provisioning” “Shark feeding” “Shark bait attracted” “Shark diving” “Shark citizen science” “bull shark” “tiger shark” “white shark” “great hammerhead shark” “blue shark” “mako shark” “specific locations identified in this paper + specific species targeted at this location”
Databases	Web of Science Google Scholar Scientific literature journals
Inclusion criteria	Studies utilizing touristic shark-feeding aggregations & contributing to our general knowledge and understanding of sharks outside the scope of provisioning activities; Peer reviewed publications and PhD-theses Published in English;

enhance the aggregation of certain species through conditioning effects to same extent as above, it provides logistical advantages and consistent access over extended periods, which are often beyond the scope of purely scientific endeavors.

Any additional potentially relevant literature cited within the included studies was also considered for inclusion if it met the specified criteria (Table 1). Studies primarily focused on assessing the impacts of shark feeding were excluded. To ensure comprehensive coverage, further hand-searching was conducted based on expert recommendations. This also included researching websites of operators at identified shark-ecotourism locations (see 2.2) as some of those provide sections on scientific publications.

Data on study focus, location, species, and the involvement of non-scientists (e.g., recreational divers, non-scientific dive personnel) were extracted and compiled into a table for comparative analysis and subsequent conclusions.

2.2. Geographic distribution of shark-provisioning sites

Available literature (Brena et al., 2015; Healy et al., 2020) as well as personal knowledge from the authors was used to identify shark-provisioning locations. This information was coupled with expertise from a network of experts. Additionally, individual online-searches were carried out using the terms “shark diving/baited shark diving + country of interest” with information taken directly from the homepages of operators or hosted scientists. Information on location, target species, activity and form of provisioning (whenever available) were extracted allowing for the analysis of geographical distribution.

In our approach we included not only SCUBA-activities, but also snorkelling and freediving operations, referring to all three of them as shark-diving within this article.

3. Results

3.1. Geographic distribution of research-linked shark provisioning activities

In total 15 touristic shark-provisioning locations were identified in nine different countries that were used by scientists in the past to carry out research improving the scientific knowledge on sharks beyond the scope of provisioning impacts. Sites are found circum-globally and on most continents, except South America, Europe and Antarctica. The in-water activities strongly depend on the target species, with the presence of *Carcharodon carcharias* (great white sharks) usually resulting in the use of cages for protection. Certain locations however still offer cage diving without the regular presence of Great White Sharks, such as Hawaii. Snorkelling/freediving is offered mostly for experiences with pelagic species, whereas SCUBA-diving is regularly offered for both, pelagic and reef-associated species.

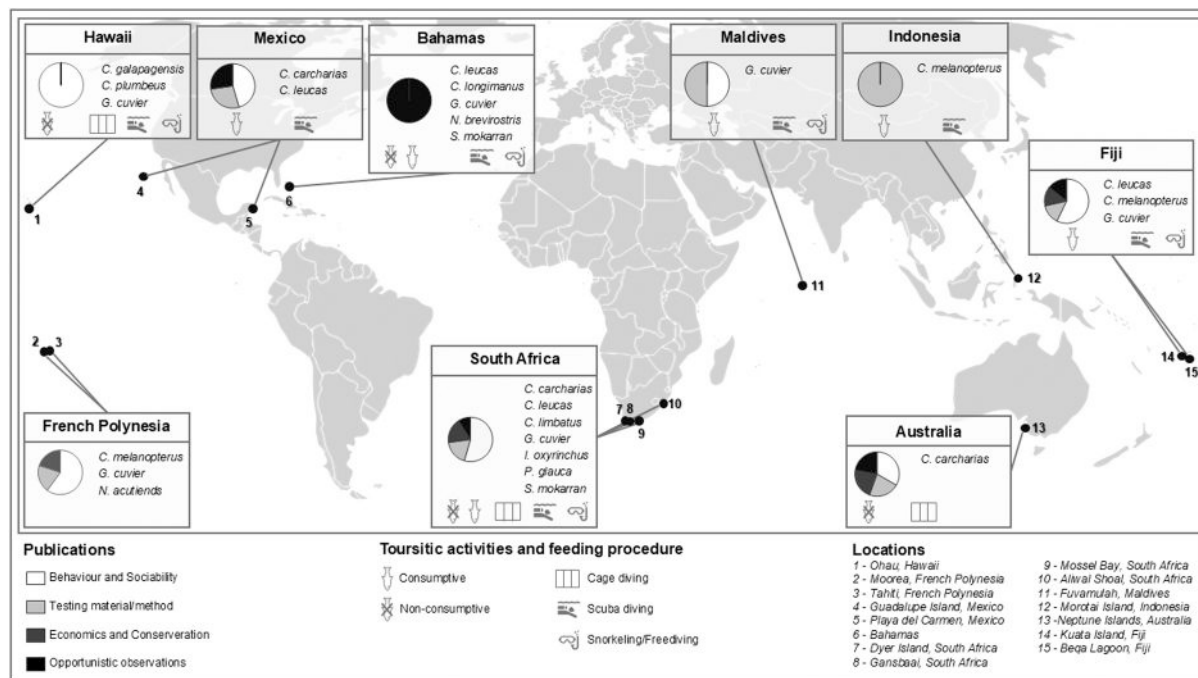


Fig. 1. Map of touristic shark feeding sites that produced peer-reviewed publications improving scientific knowledge of sharks (excluding provisioning impacts). Pie-charts represent the categories of carried out research.

3.2. Focus of studies and involved species

The search resulted in the compilation of 48 articles (Table A1) that fulfilled the inclusion criteria. The studies were organized into four different categories based on their focus (possibility of inclusion in multiple categories) as followed: 1.) Behaviour and Sociability, 2.) Economics and Conservation, 3.) Testing material/method, 4.) Opportunistic observations.

The highest number of articles was obtained for “Behaviour and Sociability” with $n = 23$ (48 %) followed by “Testing method/material” with $n = 11$ (23 %) and “Opportunistic observations” with $n = 8$ (17 %). Only six publications (13 %) were found addressing “Economics and Conservation” in sharks. Noteworthy is the recent increase of publications in the fields of “Behaviour and Sociability”. The distribution of publications across different categories is displayed in Fig. 2 as well as the evolution over time.

In total, eight different species were involved across included publications with the majority focussing on either on *Carcharhinus carcharias* (white sharks), *Carcharhinus leucas* (bull sharks) or *Galeocerdo cuvier* (tiger shark) with 52 %, 14 % and 10 % respectively. Other species were assessed less frequently such as *Negaprion acutidens* (sicklefin lemon sharks) and *Carcharinus melanopterus* (black tip reef sharks). *Carcharhinus plumbeus* (sandbar sharks), *Carcharhinus galapagensis* (galapagos sharks) and *Sphyrna mokarran* (great hammerhead sharks) were least frequently assessed only occurring in one study each.

Comparing the different locations, Mexico and South Africa produced the highest number of publications ($n = 11$), followed by Australia ($n = 9$) and Fiji ($n = 7$). Highest diversity of related categories was found for South Africa, Australia and Fiji (all four categories). So far, Hawaii, Bahamas and Indonesia produced only one publication each matching the inclusion criteria. It is to mention, that touristic shark provisioning in French Polynesia as well as in Guadalupe Island (Mexico) are currently (September 2024) banned, but some articles were published based on data collected while these activities were still allowed.

3.2.1. Behaviour & sociability

This category represents the largest group including 22 publications with most of them either addressing abundance or social behaviours. Scientists have benefitted from natural aggregations used by ecotourism operators (e.g., Guadalupe Island) as well as artificially created ones through attraction (e.g., Fiji) to understand different aspects of population dynamics, social behaviour among individuals of the same species as well as hunting behaviour. Individual photoidentification and sighting data from scientists collaborating with operators or obtained from operators directly, have allowed multiple of such studies. In a 6-year study, co-occurrences of white sharks in Mossel Bay (South Africa) were found to be mostly random supporting the theory of solitary animals (Findlay et al., 2016). Although a weak level of spatio-temporal stratification based on ontogenetic factors was detected, the authors hypothesize this might be due to preferred kind of prey at certain life stages or other benefits of proximity with conspecifics and that white sharks most likely do not form social groups with strong interactions. Opposed to the above mentioned study, first

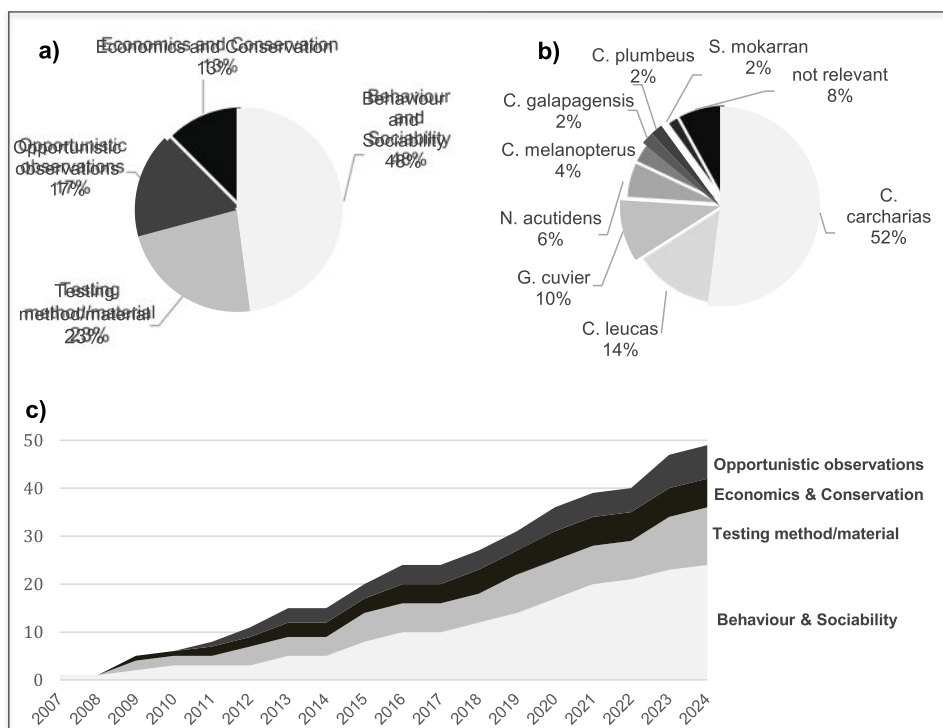


Fig. 2. (a) Distribution of publications within each category. (b) Distribution of species assessed across publications. (c) Development of the number of publications over time according to each category.

evidence for non-random co-occurrences was found based on a similar study from Australia (Schildt et al., 2019). Using network-analysis, the authors found that some of the individuals co-occurred more frequently together and even formed co-occurrence communities than what would be expected by chance (random). Although both studies provide opposing results, these may stem from the difference in size/age groups that frequently visit the two locations as well as the different definitions of co-occurrence (appearing within two hours vs. appearing within a day). In another study, potential sexual segregation was discussed based on 14 years of sighting data, highlighting a strong seasonal gradient for female white sharks compared to male white sharks. No direct evidence of segregation by sex and size was found. However, the highly focussed seasonal appearance of female sharks compared to year-round males suggests differences in distribution and movements between sexes (Bruce and Bradford, 2015). For bull sharks, co-occurrences of specific individuals seemed to be non-random at a feeding site in Fiji, where the authors found proof for associations lasting between days up to multiple years. However, it is unclear whether this is a result of the spatio-temporal overlap of large numbers of bull sharks aggregating due to feeding activities or if it could reflect natural social interactions that would naturally be facilitated through non-artificial aggregations (e.g., prey aggregation) (Bouveroux et al., 2021). For smaller species, the benefits of stable grouping might be more obvious than for very large species and indeed, using social network analysis evidence has been found for black tip reef sharks (*Carcharhinus melanopterus*) to show signs of sociability through an active choice of association with conspecifics (Mourier et al., 2012). As mentioned above, different reason could lead to association, tolerance and avoidance and morphologic features are often discussed as explanation. Extending this view, sickle-fin lemon sharks' (*Negaprion acutidens*) interactions (tolerance/avoidance) at a feeding site in French Polynesia seemed to be driven less by morphological attributes but rather by individual behaviour, indicating the use of social cues in a non-gregarious species (Brena et al., 2018).

Additionally, a relatively large number of studies made use of touristic shark-feeding operations to gain valuable information on presence/absence of different species as well as potential movement patterns. Photographs collected over long-term periods helped to identify Guadalupe Island (Mexico) as an important white shark aggregation site in the Eastern Pacific and provided information on seasonal abundance. Site fidelity was high with 78 % of all individuals having been encountered in at least two out of five years (Domeier and Nasby-Lucas, 2007; Nasby-Lucas and Domeier, 2012). Building on these long-term data sets existing for Guadalupe Island, further studies investigated population characteristics and modelled spatial, temporal and environmental preferences of white sharks (Becerril-García et al., 2020a; Santana-Morales et al., 2021). In the Maldives, a similar approach has led to the discovery and characterization of the potentially largest tiger shark aggregations worldwide (Vossgaetter et al., 2024) and in Hawaii scientists used citizen science data to uncover long-term abundance trends and seasonal migrations in multiple species (Meyer et al., 2009). Long-term data collection has further helped to study population dynamics of white sharks in Gaasnbai, South Africa. Results there have shown a strong decline of shark presence during the last years of the study. The rate of re-sightings based on photo-IDs was very low indicating a highly transient population (Micarelli et al., 2021). Other studies have coupled available information to gain valuable knowledge on environmental drivers of shark movements (e.g., Towner et al., 2013a; Maycock et al., 2022) which might help to understand future impacts of climate change or improve public safety through non-lethal ways. Other focus topics included describing general behavioural displays (Becerril-García et al., 2019), cognition (Séguigne et al., 2023) and inter-/intraindividual differences (Vignaud et al., 2023), as well as the trophic ecology of different sex and size classes of white sharks (French et al., 2018) and hunting behaviour (Huveneers et al., 2015).

3.2.2. Testing method/material

Collaborating with touristic shark-feeding operations has provided a unique “stage” for experimenting on new technologies and approaches to study sharks. Being the second largest category in our analysis, 11 publications fell into it. Five of those focussed on the feasibility (Buray et al., 2009; Dureuil et al., 2015; Mukharro et al., 2019) and utilization of photographs and/or video material to study different aspects of shark biology such as abundance (Sosa-Nishizaki et al., 2012). Two of these further tested computer assisted recognition software (Dureuil et al., 2015; Maroen et al., 2024). Brunnenschweiler (2009) tested hand-feeding of intra-gastric transmitters to bull sharks as an alternative approach to obtain distribution and migration patterns of *C. leucas*. Albeit being successful, this method only offers the potential to provide short-term information compared with traditional acoustic-tagging approaches. A very recent study was carried out in Mexico at Playa del Carmen, successfully testing an underwater ultrasonography application on free swimming bull sharks during a feeding dive confirming the pregnancy of three individuals (Hoyos Padilla et al., 2023) which was further also successfully applied to tiger sharks in Fuvamulah (Sulikowski et al., 2024). Lastly, Huveneers et al., (2018) benefitted from available infrastructure of tourist operators in South Australia to carry out tests on multiple shark-deterrent devices and their effectiveness on white sharks.

3.2.3. Opportunistic observations

Regular access to sharks through tourism operators further offered unforeseen opportunities such as observations on wound healing, impacts of acoustic and or satellite tags and interspecies interactions. In South Australia, regular access to white sharks provided information on potential changes in white sharks pigmentation due to melanism which might have implications for the reliability of using such patterns for recognition (Robbins and Fox, 2012). Additionally, the same team of authors described first observations of proliferative lesions in white sharks as well as in bronze whalers (*Carcharinus brachyurus*) (Robbins et al., 2013). In South Africa, authors used the regular access to white sharks through tourist operators to assess potential negative impacts on SPOT-tag deployment. While longer deployment can lead to more severe causes of damage to the dorsal fin, it did not seem to compromise on animal's long term survival (Jewell et al., 2011). However, the sample size of the study was relatively low. A team of scientists studied the effects of fin-mounted geolocators on great hammerheads and observed strong wound healing capacities indicating that the risk of permanent damage to the fins seems low and the positive effects for species conservation may outweigh the

negative ones when applied with care (Heim et al., 2023). Collaborating with operators in Fiji, Brunnenschweiler et al. (2020) opportunistically documented interspecies interactions between shark suckers and bull sharks and the potential costs of cohabiting. Further evidence for interaction among different species was observed at Guadalupe Island. Scars and markings on the skin serve as evidence of white sharks interacting with large squids through predation (Becerril-García et al., 2020b) and, conversely, being targeted by the significantly smaller cookiecutter shark (*Isistius brasiliensis*) (Hoyos Padilla et al., 2013). Lastly, a team of scientists and medical doctors used a non-fatal accident inflicted by a shark bite that occurred during a cage dive at Guadalupe Island to describe their wound treatment process and provide recommendations for such cases (Popa and van Hoesen, 2016).

3.2.4. Economics & conservation

Although studies in these fields do not add new information on a biological or ecological level, they were included as they improve our understanding of the non-consumptive economic value of sharks (Dicken and Hosking, 2009; Vianna et al., 2011; Apps et al., 2018) as well as benefitting species protection (Towner et al., 2013b; Bègue et al., 2020). Interestingly, economic benefits were found not only on a local scale but may even translate into provincial and national scales (Dicken and Hosking, 2009). This is supported by findings from Fiji, where revenues of shark diving activities not only benefit local operators but are partly shared with adjacent communities as well as through taxation (Vianna et al., 2011). Besides socio-economic benefits the authors highlight the importance of further research on ecological impacts and challenges the industry may cause. The most recent studies conducted (Apps et al., 2016; Apps et al., 2018) focused on peoples' beliefs towards cage diving in Australia and how intended shark encounters may affect conservation perception and behaviour of participants. The authors stress that emotional engagement offers opportunities to cultivate conservational potential, if paired with meaningful education and awareness campaigns.

Using long-term observations from a shark feeding site in Tahiti, authors collected information on the prevalence of different types of hooks on tiger sharks and discussed potential impacts. Hooks were observed in 83 % of encountered sharks over the eight-year study period indicating at least one interaction with fisheries for each of these. Although growth of the sharks did not seem to be affected by the presence of hooks, the authors raised concerns about potential mortalities due to hooks stuck internally (Bègue et al., 2020). Additionally, fin-IDs taken on board of tourist operator boats served to estimate the population size of white sharks in South Africa. The study indicated that white shark numbers remained similar to previous estimates, which raised concerns about the lack of recovery rates despite the species being protected in adjacent waters since 1991 (Towner et al., 2013b).

4. Discussion

Our results highlight the potential of provisioned shark-diving as a unique opportunity for scientists. Studying large-bodied adult sharks in the wild is extremely challenging due to the elusive nature of these animals, the long-distance migrations of some species and the vastness of the ocean itself. Additionally, these species are often impossible to maintain in captive environments. Hence why, much of our knowledge about these animals is derived either from juvenile specimen held captive, smaller species or relatively invasive methods (e.g., catch-and-release). Of the eight different species assessed in included studies, six are threatened with extinction (CR: *S. mokarran*, EN: *C. plumbeus*, *N. acutidens*, VU: *C. carcharias*, *C. leucas*, *C. melanopterus*; according to IUCN Red List, assessed on 02/2025) highlighting the urgent need to improve their management and protection.

Building on already existing knowledge received through traditional methods, touristic shark-feeding sites provide regular access to the same individuals over large time scales. Instead of focusing on a population or species, it offers a new individual-based approach. We found that provisioned shark-diving has provided unique opportunities for scientists to advance our species-specific understanding in different fields such as sociability (Findlay et al., 2016; Schilds et al., 2019), behaviour (e.g., Sperone et al., 2010; Becerril-García et al., 2019; Vignaud et al., 2023) or cognition (e.g., Séguigne et al., 2023). Especially in the context of behavioural research it could lead to a much finer understanding of the diversity and differences between individuals of one or multiple species. However, feeding wildlife potentially changes the natural behaviour of studied species which may or may not have further cascading ecological consequences (Wilson et al., 2020). When utilizing such sites, it is therefore utmost important to understand these impacts. Not only for ecological reason, but also to understand limitations and challenges for sampling design within such a context. While science-based regulations can help reduce such impacts, scientists will need to develop context-specific protocols and sampling strategies. Given those criteria are fulfilled, research could, over time, further move from uncovering the potential existence/absence of social structures to potentially investigate the underlying mechanisms. This is not only paramount for other facets such as species evolution, ecology and management, but also for countering the “Jaws”-effect in political debates (Neff, 2015) as well as the general public perception of sharks as “all-the-same”, instinct-driven predators with low inter-species and inter-individual variability in ecology and behaviour.

Much of the recent knowledge in the above-mentioned fields has already been the product of cooperation between shark feeding sites and scientists. In this review, we were relatively strict with the inclusion criteria as we wanted to investigate future research directions outside the field of negative or positive impacts of these activities. Although some of the excluded studies may provide information beyond these impacts, they were still excluded if it seemed to be the main scope of the research (e.g., Hammerschlag et al., 2012; Esposito et al., 2022). However, we do acknowledge the importance of those studies as they are a crucial part to monitor potential consequences and help develop safer and more sustainable practices, while potentially allowing new scientific discoveries.

Before the COVID-19 pandemic, global tourism numbers were rising continuously with predictions reaching 1.8 billion international visits in 2030 (according to the UNWTO). Although we may yet remain unsure of the long-term impacts on these predictions, the UNWTO indicated that tourist numbers are rising rapidly again. Wildlife tourism in particular has experienced continuous growth over the last decades pre-COVID19 (Balmford et al., 2009; Curtin and Kragh, 2014; Holden, 2016; Steven et al., 2020), driven by the growing desire for people to see wild animals in a natural environment and visit protected areas. It is reasonable to expect this trend to

continue post-COVID19.

Our findings are indicating a similar trend within the shark diving industry that uses provisioning to attract these animals, which is in agreement with earlier analyses (Topelko and Dearden, 2005; Cisneros-Montemayor et al., 2013; Gallagher et al., 2015; Healy et al., 2020). We are confident that this trend will continue and places such as Fuvamulah in the Maldives have demonstrated how fast this expansion can happen.

One limitation of this study are the conservative inclusion criteria, which may lead to an underestimation of the true extent of benefits derived from past, present, and future collaborations between industry and science. Additionally, the extent to which such collaborations are explicitly acknowledged in publications varies. While some cases are clearly documented, studies that do not explicitly mention these collaborations could not be included (e.g., Domeier and Nasby-Lucas, 2008; Papastamatiou et al., 2022). From a historical perspective, scientific research has often followed the development of tourism operations. While the shared interest in specific locations is expected, additional factors likely contribute to this trend. Notable examples include the Neptune Islands in South Australia, Guadalupe Island, and the emerging case of Fuvamulah. The first two locations have served as global hotspots for white shark research, generating numerous studies that were excluded from this analysis (e.g., Domeier and Nasby-Lucas, 2008; Watanabe et al., 2019; Aquino-Baleytó et al. 2021; Kanive et al., 2023), despite likely benefiting indirectly from tourism. These benefits may include access to funding (e.g., through operator supported/created trusts), personnel, and the expertise of individuals who engage with the marine environment daily. A similar dynamic exists in the Bahamas, where scientific expeditions and research stations are often closely linked to tourism operators. However, such associations are not always explicitly stated in publications (e.g., O'Connell et al., 2015; Guttridge et al., 2017; Gallagher et al., 2021).

Challenges for harnessing this potential may arise from relationship between the industry and scientists and different visions on the exploitation, code-of-conducts and the way of operating. "Pseudo-science-and-conservation" as marketing strategy, and the exploitation of early career scientists and/or paying volunteers (sometimes becoming a business) are serious problems that should not be neglected (Osiecka et al., 2021). Nevertheless, the number of good examples where operators are interested in good science arguably seems to increase which can lead to the development of a win-win strategy building on each other's strengths. Sustainability and code-of-conducts are a rising concern for tourists (Lund-Durlacher et al., 2019) and science can offer solutions that help operators to improve activities in this context. The Fiji Shark Marine Reserve is one example where a long-lasting relationship has resulted in benefits derived for operators, researchers as well as on species and ecosystem level. These include substantial economic gains to the national economy and local communities (Vianna et al., 2011) as well the increase in abundance and diversity in non-target species including even herbivorous and planktivorous reef fish (McKeon and Drew, 2019). Findings such as from Esposito et al. (2022), if confirmed, regarding reduced microbiome diversity in sharks' guts after eating a low-diversity food could further help operators to introduce higher diversity in provisioned food to keep sharks as healthy as possible. However, we cannot stress enough that also we, as scientists, need to stay humble, show understanding of the other side and anticipate potential conflicts to find common ground and harness synergies. Those challenges aside, science can help improving customers perception of sharks, make activities more sustainable and safer, and vice versa: tourist operators can offer scientists a unique access to sharks, data collection, provide naturalists' eyes insights, and participate in the dissemination of results. As often, working together is key, and we recommend to any present and future shark diving operation to reach out to a team of scientists and work together for the better.

Conclusively, the advantages for science have been of a manifold ranging from direct benefits (e.g., the access to cage-diving boats) to more indirect contributions such as funding through operator created or supported trusts or the access to local knowledge. For the future, one of the biggest scientific advantages may further arise from the regular access to individual specimen of large-bodied, adult sharks that would otherwise be impossible to study in the wild on such an intrinsic level. Provided strong and trusted relationships between operators and scientists are built, new approaches addressing questions such as personality, sociability, cognition and the development of new less/non-invasive sampling approaches will rise and unlock yet another secret door in understanding such complex animals.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

CRediT authorship contribution statement

Clémentine Séguigne: Writing – review & editing, Data curation. **Eric Clua:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Thomas Vignaud:** Writing – original draft, Validation, Supervision. **Jan Bierwirth:** Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix

Table A1 –
Publications included in the review

1	Domeier and Nasby-Lucas (2007)	Behaviour & Sociability	<i>C. carcharias</i>
2	Brunnschweiler (2009)	Testing Method/Material	<i>C. leucas</i>
3	Buray et al. (2009)	Testing Method/Material	<i>N. acutidens</i>
4	Dicken and Hosking (2009)	Economics & Conservation	<i>G. cuvier</i>
5	Meyer et al. (2009)	Behaviour & Sociability	<i>C. galapagensis</i>
			<i>C. plumbeus</i>
			<i>G. cuvier</i>
6	Sperone et al. (2010)	Behaviour & Sociability	<i>C. carcharias</i>
7	Jewell et al. (2011)	Opportunistic Observations	<i>C. carcharias</i>
8	Vianna et al. (2011)	Economics & Conservation	-
9	Mourier et al. (2012)	Behaviour & Sociability	<i>C. melanopterus</i>
10	Nasby-Lucas and Domeier (2012)	Behaviour & Sociability	<i>C. carcharias</i>
11	Robbins and Fox (2012)	Opportunistic Observations	<i>C. carcharias</i>
12	Sosa-Nishizaki et al. (2012)	Testing Method/Material	<i>C. carcharias</i>
13		Opportunistic Observations	<i>C. carcharias</i>
14	Mourier et al. (2013)	Behaviour & Sociability	<i>N. acutidens</i>
15	Robbins et al. (2013)	Opportunistic Observations	<i>C. carcharias</i>
16	Towner et al. (2013a)	Behaviour & Sociability	<i>C. carcharias</i>
17	Towner et al. (2013b)	Economics & Conservation	<i>C. carcharias</i>
18	Bruce and Bradford (2015)	Behaviour & Sociability	<i>C. carcharias</i>
19	Dureuil et al. (2015)	Testing Method/Material	<i>C. carcharias</i>
20	Huveneers et al. (2015)	Behaviour & Sociability	<i>C. carcharias</i>
21	Kocsis et al. (2015)	Behaviour & Sociability	<i>C. leucas</i>
22	Skomal et al. (2015)	Testing Method/Material	<i>C. carcharias</i>
23	Apps et al. (2016)	Economics & Conservation	-
24	Findlay et al. (2016)	Behaviour & Sociability	<i>C. carcharias</i>
25	Popa et al. (2016)	Opportunistic Observations	-
26	Apps et al. (2018)	Economics & Conservation	-
27	Brena et al. (2018)	Behaviour & Sociability	<i>N. acutidens</i>
28	French et al. (2018)	Behaviour & Sociability	<i>C. carcharias</i>
29	Huveneers et al. (2018)	Testing Method/Material	<i>C. carcharias</i>
30	Becerril-García et al. (2019)	Behaviour & Sociability	<i>C. carcharias</i>
31	May et al. (2019)	Testing Method/Material	<i>C. carcharias</i>
32	Mukharor et al. (2019)	Testing Method/Material	<i>C. melanopterus</i>
33	Schilds et al. (2019)	Behaviour & Sociability	<i>C. carcharias</i>
34	Becerril-García et al. (2020a)	Behaviour & Sociability	<i>C. carcharias</i>
35	Becerril-García et al. (2020b)	Opportunistic Observations	<i>C. carcharias</i>
36	Bègue et al. (2020)	Economics & Conservation	<i>G. cuvier</i>
37	Brunnschweiler et al. (2020)	Opportunistic Observations	<i>C. leucas</i>
38	Bouveroux et al. (2021)	Behaviour & Sociability	<i>C. leucas</i>
39	Micarelli et al. (2021)	Behaviour & Sociability	<i>C. carcharias</i>
40	Santana-Morales et al. (2021)	Behaviour & Sociability	<i>C. carcharias</i>
41	Maycock et al. (2022)	Behaviour & Sociability	<i>C. carcharias</i>
42	Heim et al. (2023)	Opportunistic Observations	<i>S. mokarran</i>
43	Hoyos Padilla et al. (2023)	Testing Method/Material	<i>C. leucas</i>
44	Séguigne et al. (2023)	Behaviour & Sociability	<i>C. leucas</i>
45	Vignaud et al. (2023)	Behaviour & Sociability	<i>C. leucas</i>
46	Maroen et al. (2024)	Testing Method/Material	<i>C. carcharias</i>
47	Sulikowski et al. (2024)	Testing Method/Material	<i>G. cuvier</i>
48	Vossgetter et al. (2024)	Behaviour & Sociability	<i>G. cuvier</i>

Data availability

No data was used for the research described in the article.

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