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Approche écologique, économique et socio-anthropologique de la conservation des requins en milieu récifo-corallien.

Ecologic, economic, and socio-anthropologic approach of shark conservation in coral reef ecosystems

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À mon Père,

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ABSTRACT

Sharks contribute to the balance and productivity of coral reefs. These animals provide a variety of ecosystem services to humans and, in addition to their major ecological function, support both profitable ecotourism and rich cultural beliefs. Unfortunately, these valuable roles are currently being undermined by a worldwide decline in shark populations, mainly due to overfishing. Conservation efforts are further hampered by a particularly negative modern perception of these animals, full of cognitive biases, compared with more positive ancestral perceptions, particularly in Oceania. The aim of this thesis is to optimize the effectiveness of shark protection measures by reconciling Nature, Humanity and Economy, the three pillars of sustainable development.

To do this, the state of the human-shark relationship in the world's largest sanctuary, French Polynesia, was studied (**Chapter 1**). It revealed a lack of understanding of the objectives of the protection measures in place, and a fear of the risk of being bitten. This Western-oriented vision is linked to a decline in traditional ecological knowledge and local culture (*Publication 1*). Furthermore, the major economic gains generated by shark ecotourism, directly promoting their significant non-consumptive value (*Publication 2*), are jeopardized by particularly negative perceptions of artificial provisioning, which led in 2017 to its ban (*Publication 3*).

However, our work in the Pacific (**Chapter 2**) demonstrates that shark feeding can be sustainable, if a well-defined code of conduct is followed. Indeed, although these animals demonstrate significant memory retention capacities, the conditioning resulting from this practice does not lead to food dependency in blacktip reef (*Publication 4), or bull* (*Publication 5*) sharks, and does not generate significant changes in abundance or fidelity index in tiger sharks at dedicated sites (*Publication 6*).

It is also important to understand the motivations behind shark bites, in order to change the perception of incidents and to be able to implement effective shark risk management (**Chapter 3**). It appears that only a small number of bites can be attributed to predation on humans (*Publication 7*). In addition, recent advances in animal personality allow us to assume the existence of individuality in sharks, and thus a high degree of variability in the level of risk between several animals belonging to the same species (*Publication 8*). As risk is no longer directly considered to be density-dependent, new guidelines for "problem individuals" could emerge, enabling more eco-sustainable management (*Publication 9*).

An accurate perception of sharks is a matter of communication and education (**Chapter 4**). The media - particularly effective tools of influence - could become a major ally for conservation, rather than a catalyst for popular fears (*Publication 10*). Furthermore, it would appear necessary to involve citizens directly, to increase their ownership of the conservation measures in place. Thus, citizen science could be a major tool to successfully change not only perceptions, but also knowledge, through a reconnection between science and the general public (*Publication 11*).

This PhD highlights the importance of a global approach, at the crossroads of disciplinary fields. Indeed, this work offers prospects to optimize conservation measures, and a hope for future coral reefs to see healthier shark populations and a de-demonized image in human society.

RÉSUMÉ

Les requins contribuent à l'équilibre et à la productivité des récifs coralliens. Ces animaux rendent à l'Homme des services écosystémiques variés et, outre leur fonction écologique majeure, servent de support tant à un écotourisme rentable qu'à des croyances culturelles riches. Malheureusement, ces rôles précieux sont actuellement remis en cause par une dégradation des populations de requins à l'échelle mondiale, principalement du fait de leur surpêche. Les efforts de conservation sont par ailleurs défavorisés par une perception moderne particulièrement négative de ces animaux, emplie de biais cognitifs, en comparaison avec des perceptions ancestrales plus positives, notamment en Océanie. L'objectif de cette thèse est d'optimiser l'efficacité des mesures de protection des requins en réconciliant Nature, Humain et Économie, qui représentent les trois piliers du développement durable.

Pour se faire, l'état de la relation homme-requin dans le plus grand sanctuaire du monde, la Polynésie française, a été étudié (**Chapitre 1**). Il a été mis en lumière une méconnaissance des objectifs des mesures de protection en place, ainsi qu'une crainte du risque de morsure. Cette vision, plutôt d'obédience occidentale, est en lien avec une déliquescence des savoirs écologiques traditionnels et de la culture locale (*Publication 1*). De surcroit, les gains économiques majeurs générés par l'écotourisme requin, promouvant directement leur importante valeur non-consommatrice (*Publication 2*), sont mis en danger par des perceptions particulièrement négatives du nourrissage artificiel qui ont conduit en 2017 à son interdiction (*Publication 3*).

Pourtant, nos travaux dans le Pacifique (**Chapitre 2**) démontrent que le *shark feeding* peut être durable, à condition de suivre un code de conduite bien défini. En effet, bien que ces animaux fassent preuve de capacités de rétention mémorielles importantes, le conditionnement découlant de cette pratique n'entraîne pas de dépendance alimentaire du requin pointes noires (*Publications 4)* ou bouledogue *(Publication 5)* et ne génère pas d'évolution significative de l'abondance ou de l'indice de fidélité du requin tigre sur les sites dédiés (*Publication 6*).

Il s'avère également important de comprendre quelles sont les motivations des morsures afin d'en changer la perception et de pouvoir instaurer une bonne gestion du risque requin (**Chapitre 3**). Il apparaît que seul un nombre minime d'entre elles peut être attribué à de la prédation sur l'Homme (*Publication 7*). De plus, de récentes avancées sur la personnalité animale permettent de supputer l'existence d'individualités chez les requins, et ainsi une forte variabilité du niveau de risque entre plusieurs animaux appartenant à une même espèce (*Publication 8*). Le risque n'étant plus directement considéré comme densité-dépendant, de nouvelles mesures de gestion des individus déclarés « à problème » pourraient voir le jour et permettre une gestion plus eco-durable (*Publication 9*).

Une juste perception des requins est affaire de communication et d'éducation (**Chapitre 4**). Pour cela, les médias, outils d'influence particulièrement efficaces, pourraient devenir un allier de taille pour la conservation plutôt qu'un catalyseur des peurs populaires (*Publication 10*). Enfin, pour développer l'appropriation par les citoyens des mesures de conservations en place, il apparaît nécessaire de les impliquer directement. À ce titre, les sciences participatives pourraient être un outil majeur dans la réussite de l'évolution des perceptions, mais également des connaissances via une reconnexion entre science et grand public (*Publication 11*).

Cette thèse met en valeur l'importance d'une approche globale, à la croisée des champs disciplinaires. Elle offre des perspectives d'optimisation des mesures de conservation, et un espoir pour les récifs coralliens de demain d'observer une meilleure santé des populations de requins ainsi qu'une lédiabolisation de leur image auprès de la société humaine.

INTRODUCTION

The threats faced by sharks

Class of Chondrichthyes includes sharks, rays and chimeras and is one of the oldest vertebrate taxa on Earth, surviving at least five mass extinctions during their 420 million years of existence (Cappetta 1987, Sibert & Rubin 2021). A first evaluation of the population threat status by the IUCN Red List in 2014 reported that over one quarter of the more than 1 000 species listed were at risk of extinction (Dulvy et al. 2014). Despite this warning, a global acceleration of the depletion of Chondrichtyes populations facing always more anthropogenic pressures has been observed. Indeed, more than a third of species is now endangered (Dulvy et al. 2021). Despite several causes might be pointed out, such as the loss and degradation of habitat, the climate change impact and the pollution, overfishing stays the major threat, mainly for shark populations (Dulvy et al. 2021, Parcoureau et al. 2021, Sherman et al. 2023). Indeed, sharks appear to be particularly vulnerable, as they generally display slow growth rates, low reproduction rates, long gestation time and a late sexual maturity, which explain the low resilience of their populations in front of fisheries (Barker & Schluessel 2005). Shark products used by humans include fins, meat, liver, skin, cartilage or jaws and teeth (Musick 2005), which can be used for various purposes such as for direct consumption (Chen et al. 1996, Camhi et al. 1998), textile industries (Vannuccini 1999), cosmetics (Kuang 1999), curios (Rose 1996) or for the pharmaceutical industry (Hallgreen & Larsson 1962, Broholt et al. 1986, Moore et al. 1993, Sills et al. 1998, Rao et al. 2000). Interestingly, meat and fins are respectively a particularly cheap source of protein and one of the most valuable food ingredients in the world, and both exploitations could lead to significant proportion of global shark fishing mortality (Vannuccini 1999).

Indeed, the continuing demand for human food, mainly in developing countries, led to very active small-scaled shark fisheries, often informal, unmonitored, and unmanaged in worldwide poverty-stricken coastal villages (Vannuccini 1999, McVean et al. 2006, Lestari et al. 2017, Glaus et al. 2018, Yulicanto et al. 2018, Booth et al. 2018, Prasetyo et al. 2021, Seidu et al. 2022). In such social communities, often poor and socio-economically vulnerable, local fishermen trade shark meat locally, while the fins are exported to the international market (Seidu et al. 2022). The interest of shark fins is their use as the key ingredient for shark fin soup, a traditional luxury meal in Chinese culture (Musick 2005, Clarke et al. 2007). Some first-grade fins, particularly expensive, can reach important prices, like for the dusky shark (*Carcharhinus obscurus*), usually sold between 400 and 500 USD per kilogram (Wu 2016, Hau et al. 2018). Such economical importance appears to directly influence the extinction risk for large-bodied shark species and is potentially the most important determinant of their future fate (Clarke et al. 2007, Davidson et al. 2016, McClenachan et al. 2016). Indeed, estimates from Hong Kong market suggest that between 26 and 73 million sharks could have been traded for their fins worldwide during the year 2000 (Clarke et al. 2006).

However, consumption of meat or fins may be very deleterious for human health. As predators, sharks can be strongly affected by metals and metalloids bioaccumulation, as well as the biomagnification of some. For instance, high rates of mercury (Hg) or arsenic (As), way above medical recommendations, have already been reported both in flesh and fins (Gilbert et al. 2015, Amorim-Lopes et al. 2020, Shipley et al. 2021). Furthermore, despite the strong economic importance of fisheries, sharks display a wide variety of ecosystem services to humans, contributing directly or indirectly to their well-being, and to substantial incomes linked to their potentially huge non-consumptive value.

The cultural & spiritual value of sharks

Although shark consumption shows tonicity, aphrodisiac, or prosperity proprieties in Chinese culture (Clarke et al. 2007, Fabinyi 2012), they may display a strong non-consumptive spiritual value, often observed in many Pacific cultures (Techera 2012). Indeed, despite shark products have been as well used for food, ceremonial, or utilitarian purposes, such as teeth to create weapons or cutting devices (Kirch 1985, Taylor 1993, McDavitt 2005, Drew et al. 2013), they were infrequently consumed. Sharks represent the link between Ocean and Earth, Gods and Humans, Living and Ancestors, and are seen as powerful, graceful, and respectable animals (McDavitt 2005, Gerhardt 2018, Torrente et al. 2018). In Anaa, a remote island of French Polynesia, the mythology even displays a shark called *Tumu-mago* (origin - shark) as the masculine origin of life, alongside *Tumu-rito* (origin - vegetal growth), the feminine origin. Sharks are considered as earth representations of gods in many traditional societies, as in Fiji (Techera 2012), Hawaii (Puniwai 2020), Polynesia (Torrente et al. 2018) or Tonga (Techera 2012), which made them *tapu*, not to be killed. According to ancestral cultures of Oceania, fishing a shark without following strict rules and conditions is punished by the gods through bites, sometimes fatal (McDavitt 2005, Clua & Guiart 2015, Torrente 2015). Furthermore, aboriginal societies are divided in family groups called clans. Each of them is portraying their ancestry through unique distinct group of totem animals (McDavitt 2005, Gerhardt 2018, Puniwai 2020). Sharks are generally depicting influential families, such as for the Australian clan Yolngu, where the strong *Mäṉa* is a powerful shark-totem, representing justified vengeance and strength to overcome obstacles (McDavitt 2005).

The encyclopedic knowledge displayed by traditional clans of Oceania has enabled them to generally develop a sustainable use of their marine resources (Friedlander 2018). However, the collapse of ancestral societies following Western colonization led to a significant decline in this precious cultural knowledge (Babadzan 1983, Alévêque 2009). In addition, centralized government structures, economic development and globalization are now holding back Pacific peoples from reappropriating their culture (Friedlander 2018). The modern Western perception of sharks has spread rapidly, and we currently may see the development of an unjustified fear of these animals, inherited from colonization. As an example, the result of interviews in Hawaii in a Christian children center shows that for most respondents, their guardian animal was forgotten or never knew (Pukui 1972, Taylor 1993). The Western view of these animals is particularly influenced by Peter

Benchley's bestseller *Jaws*, followed by the associated blockbuster released in 1975. The effects were immediate, since recreational "monster fishing" has never been as popular as it was after that date (Hueter 1991, Neff & Hueter 2013). Thus, the loss of traditional knowledge seems to have directly led to a loss of interest of non-consumptive cultural use of sharks, despite its previous strong spiritual importance.

The ecological value of sharks

Sharks also have an important indirect use value, as they play a vital role in the balance of coral ecosystems. Indeed, these animals, considered either as apex or large meso- predators, can strongly shape their ecosystem, by generating anti-predatory responses of their potential preys, and potentially influence the demography, growth, morphology and behavior of other animals (Heithaus et al. 2007, Wirsing et al. 2007, Asunsolo-Rivera et al. 2023). Some apex predators, such as tiger sharks (*Galeocerdo cuvier*) or great hammerhead sharks (*Sphyrna mokarran*), occupying the top trophic level, can even display profound top-down effects in case of reduction of their abundance, which may be strongly deleterious for ecosystem productivity and health (Friedlander & DeMartini 2002, Ferretti et al. 2010, Heithaus et al. 2012, Heupel et al. 2014, Frisch et al. 2016, Sherman et al. 2020). More recently, in situ studies have shown that for coral ecosystems exposed to severe stress, the presence of sharks favors high densities of herbivorous fishes, thanks to the predation of meso-predators. Thus, they contribute to coral survival and growth, helping to limit algal proliferation (Ruppert 2013, Ruppert 2016).

However, the negative perception of shark has led to a fear that wealthy populations of these animals may cause an increase of bite incidents. Furthermore, bite events, which are extremely rare, are reported with sensationalism in the written, audiovisual, or digital media. This phenomenon amplifies the need for media consumption, the main source of information for the human population, and greatly magnifies the real danger faced (Muter et al. 2012, Neff & Hueter 2013, Bombieri et al. 2018, Sabatier & Huveneers 2018, Hardiman et al. 2020). The stressful discourse about human-shark interactions and the personification of these animals, depicted as criminals, can be observed within metaphors and specific vocabulary such as "man-eater", "rogue shark", "attack" and anxiety-provoking photographs in many articles (Thomson & Mintzes 2002, Neff & Hueter 2013, McCagh et al. 2015, Neff 2015, Pepin-Neff & Wynter 2018, Sabatier & Huveneers 2018). This negative editorial strategy, also known in other predators (Bombieri et al. 2018), can generate significant cognitive biases in readers. In the case of sharks, this persistent fear, called the "Jaws effect", can even lead to a desire to eliminate these animals, to ensure the safety of humanity (Neff 2015). Interestingly, these culling campaigns exactly mimic the response shown in *Jaws*, and were replicated after bite clusters in Egypt, Russia, Seychelles, Mexico, Western Australia, and in the French overseas territories of Reunion Island (O’Connell et al. 2011, Ritter et al. 2013, Neff 2015, Chin et al. 2017), and more recently New Caledonia. As a result, hundreds of sharks are unnecessarily killed every year, including from endangered species, and a greater tolerance of the exploitation of shark populations is currently observed, paired with a strong passivity in front of conservation measures (Neff 2015, Hardiman et al. 2020, Dulvy et al. 2021).

The economic value of sharks

Instead of seeing sharks as simple catches or nuisances, they can be as well formidable business partners. Indeed, many adventure-seeking divers and snorkelers choose a specific destination because it offers the unique opportunity to observe charismatic, often rare, or large species (Orams et al. 2002, Topelko & Dearden 2005). Observations of emblematic animals, such as the whale shark (*Rhincodon typus*), globally endangered (Pierce & Norman 2016), have yielded profits of USD 3.7 million in Belize (Graham 2004), USD 4.99 million in Seychelles (Rowat & Engelhardt 2007), or USD 10.4 million in Indonesia (Anna & Saputra 2017). The tiger shark (*Galeocerdo cuvier*), near threatened (Ferreira & Simpfendorfer 2019), and the great white shark (*Carcharodon carcharias*), vulnerable (Rigby et al. 2022) generated USD 1.62 million and USD 4.99 million respectively for the South African economy (Dicken & Hosking 2009, Hara et al. 2003). In the Pacific, the sicklefin lemon shark (*Negaprion acutidens*), endangered (Simpfendorfer et al. 2021a), accounts for USD 5.4 million alone in French Polynesia (Clua et al. 2011), when all shark-watching tourism represented USD 25.5 million in Australia (Huveneers et al. 2017), USD 42.2 million in Fiji (Vianna et al. 2011) and even USD 18 million in Palau, which represents 8% of its gross domestic product (Vianna et al. 2012). Overall, more than 590 000 tourists and more than USD 314 million, supporting more than 10 000 jobs, have been generated worldwide, according to a 2013 study. This work also predicts a drastic increase in shark-watching tourism, and forecasts gains exceeding USD 780 million over the next 20 years, i.e., USD 150 million more than the profits generated by shark-fishing industry (Cisneros-Montemayor et al. 2013). This is not the only example where the economic value generated by shark ecotourism tends to be higher than the one of fisheries (Clua et al. 2011, Vianna et al. 2011, Vianna et al. 2012). Indeed, even though shark fishing is particularly active in Indonesia, it appears that shark watching locally exceeds the value of their annual exports by 1.45 times (Mustika et al. 2020). However, generating such incomes is largely dependent on the satisfaction of tourists, who expect to encounter their target species in optimal conditions of proximity or animal abundance (Orams et al. 2002, Topelko & Deaden 2005). To do so, a large majority of tourism operators are using provisioning to lure sharks (Orams et al. 2002, Gallagher & Hammerschlag 2011, Clua 2018), which includes various practices from chumming with blood and/or liquidized fish parts or feeding with large pieces of fish (Laroche et al. 2007, Clua et al. 2010, Gallagher et al. 2015).

These provisioning practices faced strong polemics in front of the idea it could cause potentially deleterious effects on targeted species biology, and create dangerous situations for the participants (Orams et al. 2002). Indeed, some negative effects have been highlighted on shark ecology, such as modification of the composition of elasmobranch communities (Meyer et al. 2009, Brunnschweiler et al. 2014), changes in mobility and habitat use (Clua et al. 2010, Bruce & Bradford 2013, Mourier et al. 2021), altered activity patterns (Bruce & Bradford 2013, Barnett et al. 2016), and on shark behavior, which may result in elevated intra- and inter- specific competition (Clua et al. 2010, Brunnschweiler et al. 2014). However, recent studies highlighted situations where provisioning does not significantly impact – if it does – shark ecology and behavior, such as for the great white shark (*Carcharodon carcharias*) in South Africa (Laroche et al. 2007), or in Mexico (Becerrill-Garcia et al. 2019, Becerrill-Garcia et al. 2020), the Caribbean reef shark (*Carcharhinus perezii*) in Bahamas (Maljković & Côté 2011), the tiger shark (*Galeocerdo cuvier*) in the Caribbean (Hammerschlag et al. 2012a), and the bull shark (*Carcharhinus leucas*) in Fiji (Brunnschweiler & Barnett 2013). Furthermore, the number of incidents involving sharks has not significantly increased close to provisioning sites, if strict regulations are followed by operators (Gibbs & Warren 2014, Clua 2018). Thus, it appears that shark provisioning displays differential effects depending on species and practices, and might potentially be considered as sustainable if a proper code of conduct is established (Clua 2018, Mourier et al. 2021). However, the current perception of these tourism practices has led to the ban of this activity, such as in 2017 in French Polynesia, and to a potential risk to reduce the importance of the non-consumptive value of sharks if tourists are unsatisfied.

Objectives

These statements show the urgent need to reassert the relevance of the ecosystem services provided by sharks, apart from their consumptive value. Indeed, their critical importance has been profoundly weakened by strong cognitive biases maintaining a visceral fear of these animals, based on popular beliefs rather than on proven scientific facts. However, the enhancement of cultural and spiritual values, of their contribution to ecosystem balance, and of ecotourism, could help human societies to be more aware of the benefits provided by shark conservation. Indeed, despite the existence of numerous preservation programs worldwide, ranging from simple fishing restrictions to total bans over vast areas (MacNeil et al. 2020), the initiatives for shark conservation do not show the same efficiency as for other taxa, such as marine mammals or sea turtles (Moore et al. 2009, Roman et al. 2013). Thus, an awakening of humans in front of the significance of healthy shark populations is necessary to a rise of the effectiveness of implemented protection measures.

The aim of this PhD thesis is to search paths that reconcile ecology, economics, and socio-anthropology, to optimize existing protection measures. Indeed, rethinking the management of shark populations at the crossroads of these disciplinary fields would enable a "sustainable development" approach of shark conservation, based on three pillars defined as nature, people and economy (Purvis et al. 2019). Thus, a triple objective has been determined: (i) To investigate the existing links between these disciplines in the context of shark conservation, (ii) To find answers that could reduce the current dominant negative perceptions of these animals by the general public, (iii) To provide reliable scientific information intended for decision-makers and tourism operators, to make reliable and wise decisions concerning human-shark relationship.

THESIS STRUCTURE

This work consists of 11 scientific publications submitted, under review or published in A-rank journals, in which I was either first author (n = 7) or co-author (n = 4) (*Table 1*). These articles are divided into 4 chapters, ensuring the structure of the thesis: (**Chapter 1**) Human-shark relationships in the world's largest shark sanctuary, (**Chapter 2**) On the potential effects of shark provisioning on behavior and ecology, (**Chapter 3**) Understanding why sharks are biting to help conservation ownership, (**Chapter 4**) Perspectives to improve shark conservation.

Chapter 1 focuses on French Polynesia, a Pacific region characterized by the sanctuarization of its waters since 2006 for all shark species, except for the mako (*Isurus oxyrinchus*), also protected from 2012. The entire French Polynesia's exclusive economic zone, covering 5.5 million km^2, bans all fishing and trade in shark products. Furthermore, this territory is one of the world's most emblematic destinations for elasmobranch observation. The aim of this chapter is to determine the current vision of shark protection measures on various Polynesian islands, different by their level of westernization and their distance to the capital, Papeete (*Publication 1*); to quantify the economic importance of shark-watching activities for local residents (*Publication 2*); but also, to determine the social perception of recreational practices associated with ecotourism (*Publication 3*). This work is also intended to determine the potential cognitive biases persisting in the Polynesian population, the state of local traditional ecological knowledge, and the most reluctant public to shark conservation initiatives.

In order to provide answers to the controversies surrounding artificial provisioning, **Chapter 2** seeks to answer two major questions: Can conditioned sharks become dependent on tourism feeding? Does it exist worrying ecological or behavioral impacts on a variety of target species? Two studies were carried out following the lockdowns associated with the COVID-19 pandemic, and thus the cessation of provisioning for two species, at two distinct sites, representing two different environments. The first focusses on the blacktip reef shark (*Carcharhinus melanopterus*), targeted by feeding in the lagoon of Moorea (French Polynesia), which was stopped for 6 weeks during the COVID-19 Anthropause (*Publication 4*). The second focuses on a species potentially dangerous to humans, the bull shark (*Carcharhinus leucas*), deprived of artificial food provisioning on Yakawe reef (Fiji) for an entire year (*Publication 5*). In addition, data previously collected in Tahiti (French Polynesia) were used to explore the impact of an outer reef artificial feeding on the site fidelity and abundance of tiger sharks (*Galeocerdo cuvier*) prior to its definitive stop in 2017 (*Publication 6*).

Chapter 3 aims to better understand the reasons why sharks bite humans, and what could be the best risk management strategy to apply. Using an extensive database of bite events in French Polynesia, various hypotheses for bite motivations are investigated. The objective is to understand the significant increase in the number of incidents that was registered following the reopening of the COVID-19 lockdown, even though the number of people in the water was considerably reduced (*Publication 7*). Investigations on the existence of personality traits among large shark species were as well performed, to contribute to the testing of the hypothesis whether the probability to observe a "predatory" bite would differ among conspecifics from a same population depending on the individual level of boldness and aggressiveness (*Publication 8*). We also propose the possibility to specifically identify a potential "problem shark" that has repeatedly bitten humans using different methods, and thus offering new perspectives for more responsible and effective shark risk management (*Publication 9*).

Chapter 4 focuses on potential paths to improve knowledge and perception of sharks, through media discourse and direct involvement of the public. The impact of the sanctuarization of 2006 on the media coverage in French Polynesia is studied to analyze the evolution of the image of sharks shared in newspapers, ahead of a positive conservation event (*Publication 10*). On the other hand, the potentially positive effect for conservation, but as well for knowledge gain, of citizen science initiatives is investigated thanks to a large project led by the Polynesian Shark Observatory (ORP), regrouping dive instructors along French Polynesia territory (*Publication 11*).

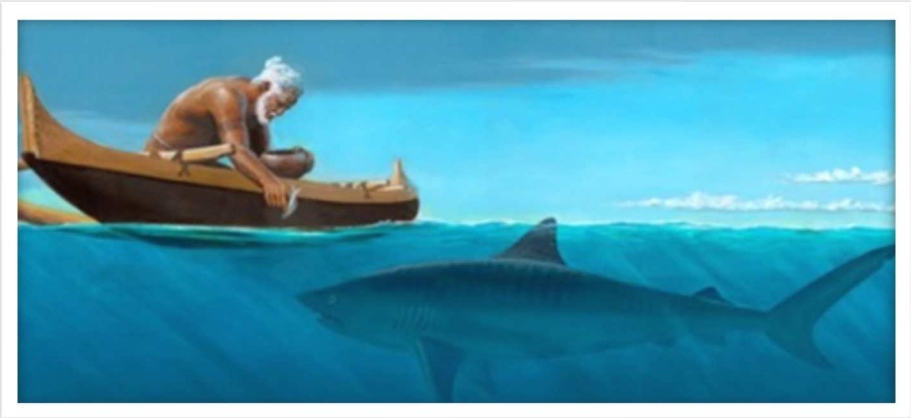
A synthesis of the results and findings provided by these papers, included in the following pages, is presented before the discussion.

Chapter	Publication	Title	Authors	Personal contribution	Journal	Journal IF	Status (Juil. 2023)
Chapter 1: Human-shark relationships in the world's largest shark sanctuary	*Publication 1*	Knowledge, perception and ownership by local stakeholders among the world's largest shark sanctuary a decade after its inception	**C. Séguigne**, M. Bond, A. Goyaud, M. Heithaus, G. Siu, Z. Rowe, F. Torrente, E. Clua	Data analysis, Data visualization, Original draft preparation, Review and editing	Humanities and Social Sciences Communications	2.731	First review
	Publication 2	Economic importance of elasmobranch ecotourism in French Polynesia prior to the cessation of provisioning activities and the COVID-19 pandemic	**C. Séguigne**, M. Ombrouck, N. Pascal, A. Brathwaite, E.Clua	Data collection, Data analysis, Data visualization, Original draft preparation, Review and editing	Tourism Economics	4.582	First review
	Publication 3	Human perception of sharks' dangerousness and vulnerability among the world's largest shark sanctuary: perspectives for improved coexistence and conservation	**C. Séguigne**, M. Bond, A. Goyaud, M. Heithaus, G. Siu, F. Torrente, E. Clua	Data analysis, Data visualization, Original draft preparation, Review and editing	Tourism Management	12.879	First review
Chapter 2: On the potential effects of shark provisioning on behavior and ecology	*Publication 4*	Effects of a COVID-19 lockdown-induced pause and resumption of artificial provisioning on blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*) in French Polynesia	**C. Séguigne**, J. Mourier, T. Vignaud, N. Buray, E. Clua	Data analysis, Data visualization, Original draft preparation, Review and editing	Ethology 128(2)	1.897	Published in 2022 (3 citations)
	Publication 5	Long-lasting memory of a free-ranging top marine predator, the Bull shark *Carcharhinus leucas*	**C. Séguigne**, T. Vignaud, C. Meyer, J. Bierwirth, E. Clua	Data collection, Data analysis, Data visualization, Original draft preparation, Review and editing	Behaviour	1.991	First review
	Publication 6	Provisioning ecotourism does not increase tiger shark site fidelity	**C. Séguigne**, M. Bègue, C. Meyer, J. Mourier, E. Clua	Data analysis, Data visualization, Original draft preparation, Review and editing	Scientific Reports 13(1)	4.997	Published in 2023
Chapter 3: Understanding why sharks are biting to help conservation ownership	*Publication 7*	Humans experience an increase in coastal shark bite frequency linked to the COVID-19 lockdown	E. Clua, C. Meyer, **C. Séguigne**, A. Wirsing	Data analysis, Data visualization, Review and editing	Global Ecology and Conservation	3.97	Second review
	Publication 8	Exploring personalities in wild adult Bull sharks, *Carcharhinus leucas*	T. Vignaud, C. Meyer, **C. Séguigne**, E. Clua	Data analysis, Data visualization, Review and editing	Behaviour	1.991	Second review
	Publication 9	Evidence of individual sharks repeatedly targeting humans.	E. Clua, C. Meyer, S. Baksay, M. Freeman, A. Haguenauer, J.D.C. Linnell, **C. Séguigne**, S. Surina, M. Vély, T. Vignaud, S. Planes	Data analysis (allelic frequencies), Review and editing	Scientific Reports	4.997	Second review
Chapter 4: Perspectives to improve shark conservation	*Publication 10*	The perception of sharks in French Polynesia in the written media from 1996 to 2006	Z. Rowe, E. Clua, A. Goyaud, **C. Séguigne**	Supervision of Z. Rowe, Original draft preparation, Review and editing	Oceans	0.6	First review
	Publication 11	Citizen science provides valuable data to evaluate elasmobranch diversity and trends throughout the French Polynesia's shark sanctuary	**C. Séguigne**, J. Mourier, E. Clua, N. Buray, S. Planes	Data analysis, Data visualization, Original draft preparation, Review and editing	PLOS ONE	3.752	Published in 2023

Table 1: Presentation of the papers on which the PhD thesis is based with indication of the status of the publication and authoring

CHAPTER 1

Human-shark relationships in the world's largest shark sanctuary



A strong human-shark link through ancestral culture...

...And through shark-watching ecotourism

List of publications:

1. *Knowledge, perception and ownership by local stakeholders among the world's largest shark sanctuary a decade after its inception.* **C. Séguigne**, M. Bond, A. Goyaud, M. Heithaus, G. Siu, Z. Rowe, F. Torrente, E. Clua. In review in Humanities and Social Sciences Communications.

2. *Economic importance of elasmobranch ecotourism in French Polynesia prior to the cessation of provisioning activities and the COVID-19 pandemic.* **C. Séguigne**, M. Ombrouck, N. Pascal, A. Brathwaite, E.Clua. Submitted in Tourism management.

3. *Human perception of sharks' dangerousness and vulnerability among the world's largest shark sanctuary: perspectives for improved coexistence and conservation.* **C. Séguigne**, M. Bond, A. Goyaud, M. Heithaus, G. Siu, F. Torrente, E. Clua. Submitted in Tourism management.

Knowledge, perception, and ownership by local stakeholders among the world's largest shark sanctuary a decade after its inception

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Keywords: *Protection and conservation; vulnerable species; enforcement gaps; Traditional Ecological Knowledge; French Polynesia; social science; fishing ban.*

Abstract

Shark sanctuaries can be an effective tool for maintaining relatively high abundances of reef-associated sharks. Legally protecting sharks within a sanctuary, however, may not be sufficient without adequate compliance and/or enforcement within the protected area. This may be especially true in large and remote areas. We evaluated the knowledge and perception of stakeholders within the world's largest shark sanctuary of French Polynesia. We also assessed the sand knowledge of traditional stories about sharks within stakeholder groups. We conducted 300 interviews with stakeholders on six islands representing a gradient of westernization. Overall, 74% of the people were aware of the shark sanctuary. There was, however, uncertainty about the specific rules of the sanctuary a little knowledge of the ecological and economic value of sharks. There was also little understanding of Traditional Ecological Knowledge. Taken together, these results suggest that the efficacy of the sanctuary might be improved through efforts to better educate stakeholders about the specific goals and protections afforded to sharks by the sanctuary and an connecting the broader population with cultural connections of Polynesians with sharks.

Introduction

Elasmobranchs (sharks, rays, and skates) are the second most threatened taxa globally, with an estimated 37% of species at risk of extinction (IUCN, 2022). Declining shark populations can primarily be attributed to fishing-induced mortality, both as targeted and incidental catch in a range of fisheries (Dulvy et al., 2021). In response to the shark conservation crisis, some governments have prohibited the commercial landing and trading of sharks and shark-derived products throughout their entire exclusive economic zone (EEZ). This management approach is commonly referred to as a 'shark sanctuary' (Ward-Paige, 2017). These large-scale shark specific, marine protected areas have been enacted as independent laws, amendments to domestic fisheries acts, or as government declarations (hereafter referred to as 'regulations'). Although the specifics of each sanctuary vary; the common theme is to make commercial shark fishing illegal and ban the sale of shark products. French Polynesia is a French overseas territory (collectivité d'outre-mer), benefiting from an extended autonomy regarding the management of its natural assets as defined by the statutory law of 27 February 2004 (Organic Law 2004-192). This legal framework allowed French Polynesia to designate its Economic Exclusive Zone (EEZ) as a shark sanctuary in 2006 in response to increasing local fishing pressure to supply a growing international demand for shark fins in the early 2000s (Anonymous, 2004; Anonymous, 2006; Rowe et al., subm.). Under article 3 of the Ministers' Council statement N°396 CM of 28 April 2006, all shark species, except for shortfin mako (*Isurus oxyrinchus*), were classified as protected. This prohibited their landing in commercial fisheries and their products from being traded domestically and internationally. The initial decision to exclude shortfin mako sharks from the 2006 regulation was due to local market and export sales for flesh consumption being considered sustainable. However, in 2012 the legislation was amended to also include shortfin makos, due to their low purchase price compared to the important volume required by its storage in boat slips (Ministers' Council statement N°1784 CM of 2012; ORP, 2012). The sanctuary regulations of French Polynesia fully prohibit the fishing and/or disturbing of protected animals (Art. LP 124-81). Penalties for non-compliance with environmental code regulations include monetary fines between F CFP 50,000 - 1,000,000 (US$ 460 - 9,190) for first-time offences, and F CFP 350,000 - 9,000,000 (US$ 3,215 - 82,690) or up to six months in prison, for repeat offenders (Art. D. 184-82).

Ensuring compliance and effective enforcement is a common challenge for marine resource managers (Keane et al., 2008; Collins et al., 2022). In French Polynesia, enforcing compliance with this the shark sanctuary is particularly challenging due to an EEZ covering approximately 5.5 million km^2 and limited enforcement resources. Artisanal fishermen in remote and small-scale communities of French Polynesia contribute to fishing-induced shark mortality, but its extent is poorly known. Therefore, understanding their perceptions and attitudes towards the sanctuary would provide valuable insight into the degree to which they comply with the regulation. If shark killing events are still occurring across the archipelago, it could be that significant numbers of sharks are killed in French Polynesia annually, potentially undermining the effectiveness of the sanctuary measures (Vianna et al., 2013; Espinoza et al., 2015; Clua & Millot, 2018). Indeed, given the generally low dispersal ranges of resident reef sharks (e.g., Vignaud et al., 2013; Osgood and Baum 2015; Chapman et al. 2022), localized fishing or lethal bycatch could affect local populations. Thus, adequate knowledge of the sanctuary in fishing communities throughout French Polynesia could be critical for meeting the goals of the sanctuary.

Historically, sharks have held a privileged position in Polynesian culture, where they were perceived as representatives of God and spiritual messengers. They acted as both guardian protectors and a potentially harmful threat to be feared (Clua & Guiart, 2015; Torrente et al., 2018). In most islands, only lagoonal and coastal sharks were occasionally fished and consumed through complex rituals. Pelagic species were feared and respected. They were considered as *tapu* (protected) animals which were not to be killed (Torrente et al., 2018). A lucrative shark-based tourism sector featuring interaction between sharks and people during snorkeling and diving tours began in the 1990's (Clua et al., 2011). Traditional beliefs combined with tourism might contribute to the robust reef shark populations in French Polynesia. Indeed, the relative abundance or resident reef sharks are among the highest (MacNeil et al., 2020). However, maintaining these populations depends on knowledge of the sanctuary, levels of voluntary compliance, and, if necessary, enforcement.

Here, we assessed the perceptions of the local community using semi-structured social science surveys. The objectives of this study were to (i) determine the level of awareness of the shark sanctuary across stakeholder groups, (ii) investigate willingness to comply with sanctuary regulations, and (iii) assess the proportion of the population aware of traditional knowledge on sharks. Ultimately, we aimed to provide insights that could help decision-makers in improving the efficiency and success of the sanctuary in achieving its long-term goals.

Material & Methods

Sampling design

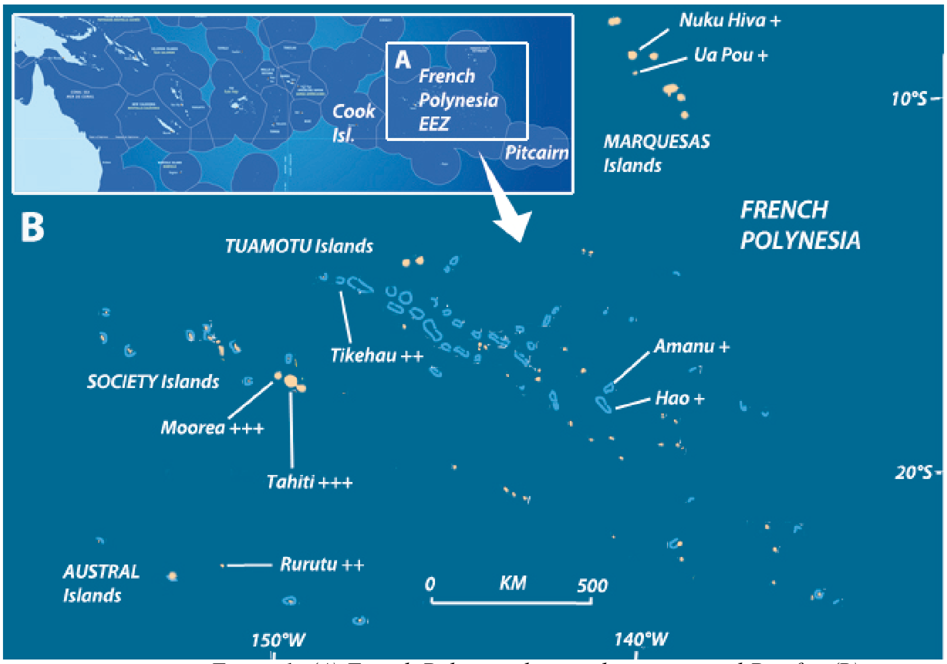

Figure 1: (A) French Polynesia lies, in the east central Pacific. (B) The six sampling areas were located on two westernized islands of the Society archipelago (Tahiti and Moorea, +++), two moderately westernized islands of the Austral and Tuamotu archipelagoes (Rurutu and Tikehau, ++) and two slightly westernized islands of Marquesas and Tuamotuan archipelagoes (Nuku Hiva/Ua Pou and Hao/Amanu, +).

French Polynesia encompasses 118 islands grouped into five different archipelagoes: (i) the Leeward Islands (which includes the capital of Papeete, on the island of Tahiti), (ii) the Austral Archipelago (iii), the Gambier Archipelago (iv) the Tuamotu Archipelago and (v) the Marquesas Islands composed of high islands without lagoons (*Figure 1*).

Six study sites based on estimates of the degree of their "westernization" (*Table 1*). Westernization was categorized based on the number of hotels (>5 rooms), the number of diving centers, and the extent of the French influence provided by expatriates and/or tourists. The latter was assessed qualitatively as high, moderate, or low. Tahiti and Moorea, from the Society archipelago, were the most westernized islands. Tikehau Island (Tuamotu Archipelago) and Rurutu Island (Austral Archipelago) were considered moderately westernized. Finally, Hao and Amanu (Tuamotu Archipelago), Nuku Hiva and Ua Pou (Marquesas Islands) were slightly westernized (*Figure 1; Table 1*).

At each site, 50 interviews were conducted directly with members of the local population. Surveys were conducted in French, the official language, by two trained interviewers. The minimum age of respondents was 18 years old, and the interviewers attempted to balance the surveys across age demographics. This was done by grouping individuals by age into four age categories: young adults (18-30 years old), adults (31-45 years old), late adults (46-55 years old) and seniors (>55 years old). Approximately two thirds of respondents at each study site were of Polynesian descent and one third were of European descent. We also aimed to obtain a cross section of different stakeholder groups at each location. This was accomplished by interviewing ten fishermen, five members of the administration (public service), five tourism operators, five people involved in conservation (through their work or NGOs), five ocean users other than fishers (e.g., surfers, SCUBA divers, kayakers) and 20 people without any specific profile.

	Archipelago	*Surface (emerged land) (km²)*	*Number of people*	*Number of hotels (> 5 rooms)*	*Number of diving centers*	*Indicator of westernization*
Tahiti	Society	1 040	180 000	> 20	8	High (+++)
Moorea	Society	134	16 000	> 10	5	High (+++)
Tikehau	Tuamotu	30	529	6	3	Moderate (++)
Rurutu	Austral	33	2 300	6	1	Moderate (++)
Nuku Hiva	Marquesas	339	3 000	5	1	Low (+)
Ua Pou		106	2 000	1	0	
Hao	Tuamotu	40	1 300	2	0	Low (+)
Amanu		17	200	0	0	

Table 1 – Parameters used to categorize the areas on a westernization continuum. Data from 2016 is presented and issued by the local statistical institute (ISPF)

Survey structure

The semi-structured interview survey consisted of 11 questions (*Table 2*). The surveys were conducted in Hao and Amanu (Tuamotu) in October 2017, in Tikehau (Tuamotu) and Rurutu (Austral) in November 2017, in Nuku Hiva and Ua Pou (Marquesas) in December 2017, and in Tahiti and Moorea in January 2018.

Statistical analysis

Chi-squared tests of independence were performed between the potential responses to the questionnaire and the factors; **nationality** (Polynesian descendants, European), **sex** (Male, Female), **age** (Young adults, Adults, Late adults, Seniors), **island** (Tahiti, Moorea, Tikehau, Rurutu, Hao/Amanu, Nuku Hiva/Ua Pou), **occupation** (Fisherman (Fish.), Tourism operator (TO), other sea user (OSU), conservationist (through their work with Non-Governmental Organizations) (NGO), administration (Admin.), and without specific relationship to the marine environment (WSR)). When significant, Pearson residuals (std res.) were calculated and categories presenting values beyond the range of ± 2 were considered as a major contribution to the Chi-squared value (Agresti, 2003). All relevant post-hoc analysis visualizations can be found in ESM1. All statistical analyses were performed using R software (V 4.2.3; R Core Team, 2023).

Questions	***Answers***	***Type***	***Target population***
(i) Are sharks protected in French Polynesia?	**3-levels:** Yes, No, I don't know	Single answer	All interviewees
(ii) What is the interest to protect them?	**6-levels:** For reef health, There is an extinction reef, They are overfished, None, For their economic value, For their cultural value	Multiple answer	Interviewees answering "Yes" for (i)
(iii) Do you know what "shark sanctuary" means?	**2-levels:** Yes, No	Single answer	All interviewees
(iv) Which area does the ban encompass?	**4-levels:** All French Polynesia EEZ, MPA only, Lagoons & islands surroundings, Lagoons	Single answer	Interviewees answering "Yes" for (iii)
(v) What is the risk to fish a shark?	**4-levels:** Getting a fine, Going to jail, God sanction, Nothing	Multiple answer	Interviewees answering "Yes" for (iii)
(vi) Would you kill a shark in French Polynesia?	**3-levels:** Yes, No, Maybe	Single answer	All interviewees
(vii) Why would you kill a shark?	**5-levels:** To protect catches, To eat it, It is dangerous, To sell it, For fun	Multiple answer	Interviewees answering "Yes" or "Maybe" for (vi)
(viii) Why wouldn't you kill a shark?	**6-levels:** It is forbidden, It harms the ecosystem, It holds my ancestors' soul, It is dangerous, It is not eatable, It brings more money alive	Multiple answer	Interviewees answering "No" or "Maybe" for (vi)
(ix) Do you know a myth/folk story involving sharks?	**2-levels:** Yes, No	Single answer	All interviewees
(x) How many French vernacular names do you know?	**7-levels:** None, One, Two, Three, Four to Five, Six to Ten, More than Ten	Single answer	All interviewees
(xi) How many Polynesian vernacular names do you know?	**7-levels:** None, One, Two, Three, Four to Five, Six to Ten, More than Ten	Single answer	All interviewees

Table 2 – Survey questions, possible answers, and target population.

Results

Profiles of interviewees

Of the 300 interviews were completed across the six sites (6 x 50), 77% of respondents were of Polynesian descent and 23% of European descent. The overall sex-ratio was 1.6:1 (63% males and 37% females) and 20% of interviewees were young adults, 32% adults, 24% late adults and 24% seniors. The sample included 20% fishermen/hunters, 13% administration, 9% tourism operators, 9% sea users other than fishermen, 7% as members of conservation NGOs and 41% with another profile.

Knowledge and opinions of shark protection in French Polynesia

Overall, three-quarters (74%); n = 222 of 300) of respondents knew that sharks are protected in French Polynesia, while 11% did not think that they were and 15% who were unsure of the protection status of sharks. The proportions of responses only varied with **island** (Chi-squared = 36.40, df = 10, p-value = 7.19×10^{-5}). Respondents on Rurutu were significantly more likely to be unsure if sharks were protected (std res. = 3.37) and those on Hao and Amanu were more likely to respond that sharks are not protected (std res. = 2.89).

Of the respondents (n = 219) who were aware that sharks are protected in French Polynesia, 50% cited coral reef health and 18% cited shark extinction risk as the most important reason for shark conservation. Only 7% of interviewees mentioned the economic value of sharks and 5% their cultural value as motivations for protections. Interestingly, only 12% of respondents worried about the risk of overfishing. Finally, there was 8% of respondents that did not see any interest in shark preservation. We did not detect significant variation in the proportions of responses across any tested factors.

Knowledge of the shark sanctuary

Despite almost three-quarters of the respondents being aware of the shark protection status, only 26% (n = 78 of 300) of interviewees knew of the existence and the significance of the Polynesian Shark Sanctuary. Furthermore, despite more than half of the respondents having heard the term "sanctuary", many of them were not able to correctly define it. Interestingly, two incorrect answers were consistently given, showing that for some people "shark sanctuary" was mainly linked to the concepts of "shark aggregation" or "shark cemetery". Responses given that were different from overall answers were to do with the factors **Nationality** (Chi-squared = 67.62, df = 1, p-value $< 2.2 \times 10^{-16}$), **Island** (Chi-squared = 22.52, df = 5, p-value = 4.17×10^{-4}) and **Occupation** (Chi-squared = 34.85, df = 5, p-value = 1.61×10^{-6}). Significantly fewer respondents of Polynesian descent knew the meaning of the term "sanctuary" (std res. = 2.02) and were able to define it (std res. = -3.44), compared to respondents of European descent (resp. std res. = -3.73 & std res. = 6.35). Respondents from Moorea (std res. = 2.00) along with Nuku Hiva and Ua Pou (std res. = 2.00) were more likely than expected to know the definition of sanctuary, while those from Rurutu were less likely than expected (std res. = -2.74). Also, fewer fishermen than expected knew what the shark sanctuary was (std res. = -2.90), while conservationists more likely to be able to define sanctuary (std res. = 3.94). Furthermore, fewer conservationists than expected were aware of it (std res. = -2.31).

Of the respondents who were aware of the sanctuary (n=220), 94% knew that killing sharks is prohibited throughout French Polynesia's EEZ. The 6% who did not know there were protections throught the EEZ thought protections were either restricted to lagoons only (1%), lagoons and waters around islands (1%), and MPAs only (4%). No specific factors were significant. For respondents aware of protections (n = 220), 75% were aware of financial penalties if caught fishing a shark. Only 12% of people aware of protections thought that there is no risk to killing a shark, while 10% thought jail time was a penalty. Divine punishment was cited by only 3% of respondents. Understanding of penalties varied only with **Island** (Chi-squared = 32.01, df = 15, p-value = 6.42×10^{-3}). Respondents from Nuku Hiva and Ua Pou were more likely to think that violators risked jail time (std res. = -2.05) and more people than expected from Hao and Amanu thought that a divine sanction might occur (std res. = 3.14).

Willingness to kill or fish a shark in French Polynesia

Overall, 55% (n = 165 of 300) of the surveyed individuals said they would not kill a shark, while 30% said that they would and 15% indicated they might kill a shark. Answers varied with **nationality** (Chi-squared = 21.80, df = 2, p-value = 1.84×10^{-5}), **island** (Chi-squared = 43.35, df = 10, p-value = 4.31×10^{-6}) and **occupation** (Chi-squared = 24.46, df = 10, p-value = 6.47×10^{-3}). Respondents of European descent were more likely to say they would not kill a shark (std res. = 2.76) and fewer indicated they would (std res. = -2.34). Interviewees from Nuku Hiva & Ua Pou were more likely than expected to indicate they were willing to kill a shark (std res. = 3.04), while less people than expected from Rurutu (std res. = -2.61) and Tahiti (std res. = -2.10) were willing to kill one. Less fishermen than expected said they would never fish a shark (std res. = -2.23) and the more indicated they might kill one in some situations (std res. = 2.33).

Of the 133 respondents who were willing, or might be willing, to kill a shark, 31% would kill them to protect their catch, 30% would kill a shark to consume it, and 29% would kill them because they were perceived as dangerous. The pleasure of catching a shark (5%) and the ability to sell a shark carcass (5%) were rarely mentioned. Responses only varied with **occupation** (Chi-squared = 36.90, df = 20, p-value = 0.012). Tour operators were more likely than expected to answer that they would kill a shark to eat it (std res. = 2.53) or to sell some part of it (std res. = 2.08).

Of the 200 respondents who were unwilling to kill sharks or only might kill a shark, 41% cited protections of sharks as the reason to not kill one. The importance of sharks to the marine ecosystem was cited as a reason they would not kill sharks by 31% of interviewees. The cultural value sharks, as a totem animal for some families (i.e., containing their ancestors' souls) received 13% of the overall answers. The economic value of a live shark (3%), the perception that they are not edible (4%), and the danger pose by shark fishing (8%) were other reasons respondents cited for not killing them. The reasons not to kill sharks vary with **nationality** (Chi-squared = 11.91, df = 5, p-value = 0.036), and **island** (Chi-squared = 55.31, df = 25, p-value = 4.48×10^{-4}). Interviewees of European descent were more likely to cite legal protections as a reason not to kill sharks (std res. = 2.06), And, on Rurutu more people than expected cited the danger of sharks as a reason not to kill them (std res. =

2.92) while fewer than expected cited legal reasons (std res. = -3.07). In contrast, interviewees on Nuku Hiva and Ua Pou were more likely to cite legal protections (std res. = 2.62).

Cultural knowledge about sharks

Overall, only 8% (n = 24 of 300) of respondents were able to recall a myth or a folk story involving sharks. Only 4% of respondents were unable to cite one or more shark species by its French common name, but 38% were unable to name at least one species using a Polynesian common name (*Figure* 2). In general, respondents were able to name more species in French than in Polynesian with most people being able to name four to ten shark species in French (Figure 2).

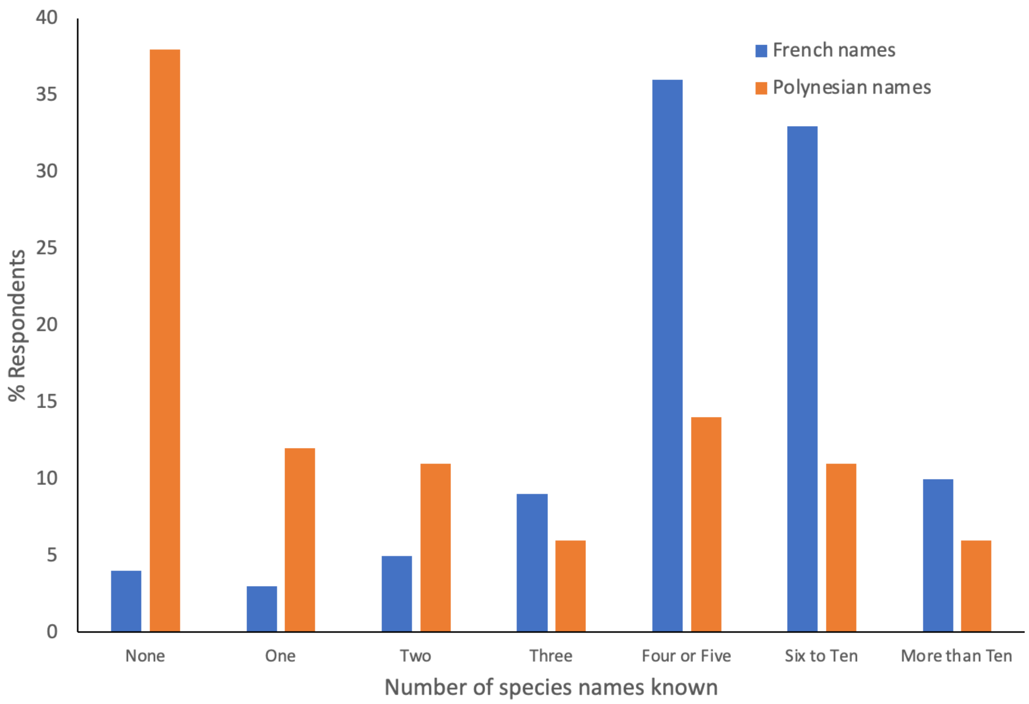

Figure 2 – Proportion of respondents who identified the number of shark species they could identify by name in French (blue bars) and Polynesian (orange bars).

The ability to recall a shark myth varied with **island** (Chi-squared = 20.64, df = 5, p-value = 9.47 x 10^{-4}) and **occupation** (Chi-squared = 22.51, df = 5, p-value = 4.19 x 10^{-4}). No respondents from Moorea were able to recall a local myth involving sharks, which is significantly less than expected (std res. = -2.04), whereas respondents from Hao & Amanu and from Nuku Hiva & Ua Pou were significantly more likely to know a myth for both std res. = 2.37), with 18% of individuals being able to recall one in both islands.

The ability to name species in French varied with **nationality** (Chi-squared = 36.45, df = 6, p-value = 2.25 x 10^{-6}), **sex** (Chi-squared = 24.31, df = 6, p-value = 4.58 x 10^{-4}), **island** (Chi-squared = 50.10, df = 30, p-value = 0.012) and **occupation** (Chi-squared = 49.81, df = 30, p-value = 0.013). Interviewees of European were more likely than expected to say that they knew "Six to Ten species" (std res. = 3.16) and "More than Ten species" (std res. = 2.25) and less than expected to answer "Four to Five species (std res. = -2.12). More women than expected cited the ability to name one species (std res. = 2.32). On Rurutu, more interviewees cited that they knew one species (std res. = 3.18), whereas on Tahiti, more interviews said they knew three species (std res. = 2.12), and on Moorea, respondents were more likely to say that they knew names of more than ten species (std res. = 2.13). More tour operators than expected answered "More than Ten" (std res. = 2.41), while without a specific relationship to the marine environment were more likely than expected to cite one species in French (std res. = 2.05) and less likely to cite more than ten species (std res. = -2.44).

The number of species names people said they knew Polynesian varied with the same factors: **Nationality** (Chi-squared = 23.70, df = 6, p-value = 5.94×10^{-4}), **Sex** (Chi-squared = 25.75, df = 6, p-value = 2.48×10^{-4}), **Island** (Chi-squared = 71.15, df = 30, p-value = 3.40×10^{-5}) and **Occupation** (Chi-squared = 99.28, df = 30, p-value = 2.42×10^{-9}). Respondents of European descent were more likely to cite that they knew "None" (std res. = 2.34) and "Four to Five species" (std res. = -2.80). Women were also more likely than expected to cite "none" (std res. = 2.15), and six to ten species (std res. = -2.09). On Moorea, fewer people than expected answered "Four to Five species" (std res. = -2.30), while people on Tikehau answered "Six to Ten species" more often than expected (std res. = 2.35) and those on Hao & Amanu showed significantly more "Four to Five species" answers (std res. = 2.55) and less "None" answers (std res. = -3.24). Fishers selected "More than Ten" answers more than expected (std res. = 5.48) and "None" less than expected (std res. = -2.50. Also, tour operators had significantly more "Six to Ten species" answers than expected (std res. = 2.80) and other sea users and conservationists working in NGO were more able likely than expected to cite only one Polynesian name (resp. std res. = 2.07 and std res. = 2.77). People without any specific relationship to the marine environment answered "None" more than expected (std res. = 2.02) and "Six to Ten species" (std res. = -2.05) and "More than Ten" (std res. = -2.72; no answer) less than expected.

Discussion

For marine management regulations to be effective, especially in areas where enforcement is challenging or limited, it is important that stakeholders are aware of the regulations and comply with their measures. We found that in the world's largest shark sanctuary of French Polynesia, almost three-quarters of respondents were aware that sharks are protected by law. This level of awareness, combined with the majority of individuals saying they would not kill a shark – often due to legal protections and deterrents – suggests that the sanctuary is largely effective even in the absence of comprehensive enforcement. There is, however, notable willingness to kill sharks and a quarter of the population that is not aware of regulations. Thus, while reef shark populations remain robust (MacNeil et al. 2020; Farabaugh et al. in review), there is room to improve the efficacy of the sanctuary by enhancing awareness of the sanctuary, increasing understanding of the scope and protections of the sanctuary, and better connecting residents to sharks and reasons they should be protected. Efforts to enhance understanding can further be targeted to specific areas and groups to improve the effectiveness of the sanctuary more efficiently.

Enhancing understanding of the sanctuary and its specific protections and consequences of infractions

Although 74% of people were aware of the protection of sharks, approximately 45% of them would potentially kill a shark. This suggests that a campaign to better communicate the reasons for the creation of the sanctuary and the consequences of killing sharks would be beneficial. Consequences of killing sharks is an important deterrent, with 41% of the 55% of individuals who would not kill sharks, or probably would not kill sharks, citing their primary reason as the legal protections. Other individuals cited the threats sharks face (possible extinction) and ecological importance of sharks as primary reasons not to kill sharks, suggesting that communication campaigns to disseminate information on ecological importance of sharks and the threats they face are making inroads among many user groups and across French Polynesia. Still, compliance is far from universal, and hundreds of reef sharks are yearly culled in the traditional fishing traps of the Tuamotu archipelago. This practice, while sporadic; it is not insignificant (Clua and Millot, 2018). In this specific case, fishermen are culling the shark to reduce the risk of being bitten (Klimley et al., 2023, Clua et al. subm.). Bites are not infrequent in fisheries in this area and mostly occur when sharks are captured in the labyrinth of fish traps that the fishermen use to trap teleost fish. Such occurrences likely explain why it is accepted in some places of French Polynesia that a fisherman should be allowed to kill potentially aggressive sharks. Indeed, *ca.* 29% of people willing to kill a shark cited the potential threat of being harmed as the primary reason they would do so. Local spearfishermen also purposely shoot reef sharks to kill because they might feed on fish stored on their spear. Of those willing to kill sharks, many (41%) people cited protecting catches as a motivation. Finally, 30% of the individuals who would kill sharks – or might kill sharks – said they would do so to consume them.

Leveraging reasons not to kill sharks

While legal protections were cited most commonly as a reason to not kill sharks, especially among those of European descent, 31% of referenced the importance of sharks to ecosystem health as a reason not to kill them. While this might indicate that the population still has not been adequately educated on the potentially important role of these species in coral reef ecosystem dynamics (see Chapman et al. 2022, Heithaus et al. 2008, 2022 for reviews), it may also be that many respondents who selected other primary reasons for not killing sharks are aware of these ecosystem dynamics. Further, individuals willing to kill sharks may still be willing to modify their behavior in ways that reduce overall shark mortality due to an understanding of potential ecological importance. Future surveys focused specifically on perceptions of ecological importance and how this relates to individual decisions about shark fishing or support of specific policies might help determine whether a campaign focused on public education would be beneficial.

Given that in French Polynesia shark-based ecotourism is well developed (Brena et al., 2016), it is surprising that only 3% of the respondents identified that sharks are more valuable alive than dead as the primary reason for not being willing to kill sharks. Islands such as Tahiti, Moorea and Tikehau (half of the sampling zone) have well-developed shark-based ecotourism that contributes substantial economic inputs to the local economy

(Clua et al., 2011). Responses suggest that either people are not aware of this dynamics, that other issues are more important to them in terms of protecting sharks (i.e., following legal mandates, the ecological importance of sharks), or they are working in sectors where there are not economic benefits of shark ecotourism. Future surveys designed to specifically determine understanding to the economic benefits, direct and indirect, of shark ecotourism and perceptions of the industry would benefit efforts to build public support of the sanctuary.

Traditional Ecological Knowledge

Stakeholders showed very limited knowledge of the local vernacular names of sharks. Despite *ca.* 75% of respondents being of Polynesian descent, more than 30 % of individuals not knowing a single Polynesian name for a shark (Fig. 5C). In contrast most interviewees (68%) were able to cite between six and ten French vernacular names (Fig. 5B). Furthermore, *ca.* 92% of the interviewees were unable to cite any myth or legend involving sharks. Given the importance that sharks had in the ancient cosmogony, culture, and religion (Torrente et al., 2018), these results are unexpected. Not surprisingly, tour operators were among the more informed occupations regarding names of shark species in French and Polynesian, as well as about the local myths. Therefore, they might be good ambassadors for the transmission of Polynesian traditions and knowledge, as is the case for aboriginal rainforest culture (Tropics, 2001). Cultural sustainability of the different islands of French Polynesia requires recognition of their traditional ecological knowledge (TEK). The merger of TEK with western traditions would help advance a shared sense of responsibility and synergy to preserve both ecosystem services and biodiversity, as highlighted in other locations (Tropics, 2001; Becker & Ghimire, 2003; Moller et al., 2004; Drew, 2005; Maine, 2020; Montgomery et al., 2020).

Understanding of the 'sanctuary' concept

Somewhat surprisingly, 94% of people who knew that the sanctuary encompasses the full Economic Exclusive Zone of French Polynesia 74% of respondents indicated that they were unsure of the meaning of the term “sanctuary”. This could reduce adherence to sanctuary guidelines and compromise diffusion of knowledge of the sanctuary through the population. This suggests that either the term “shark sanctuary” should be better explained, or it should be accompanied with a more locally understandable name, such as “Rahui” (traditional name of marine managed area in the Polynesian culture; see Fabre et al., 2021). The importance of developing a more collaborative dynamic between Polynesian and western culture is particularly highlighted by the situation in the Marquesas. Indeed, inhabitants of Nuku Hiva and Ua Pou islands expressed significantly more willingness to kill a shark despite their awareness of the fishing ban. This may be explained by people from remote and less westernized areas feeling that shark protection is a decision “made in Tahiti (the capital island)” by “people that don’t care about their traditional Polynesian culture” (F. Torrente & E. Clua, pers. com.).

Improving compliance and ownership

The observed willingness to kill a shark can be linked to a poor understanding of the importance of shark conservation in French Polynesia, even among people who are aware sharks are currently protected. Improved knowledge of stakeholders on what is not allowed and the motivation underpinning the measures, has results in improved compliance to regulations (Apps et al., 2015). Therefore, a public outreach and a local/national media campaign could be beneficial. Campaigns would be aimed at increasing awareness about shark conservation measures via posters, public service videos and educational visits to schools. This approach has already proven successful in French Polynesia for similar conservation campaigns for other threatened marine species (whales and turtles). These conservation initiatives appear to have benefitted greatly from repetitive TV campaigns, publications in local newspapers about convicted poachers, and success stories of efficient action by local NGOs, promoting the conservation of these animals (C. Séguigne, pers. obs.). Our findings are consistent with those from Hasting and Ryan, (2017), that also noted "a lack of clarity regarding the likely benefits of the Ngari Capes Marine Parks, implying a need to improve public communication and community engagement". As for Trenouth et al., (2012), the important involvement of stakeholders in the design and management of Marine Protected Areas is crucial to its success.

Conclusion

Our results highlight that social science interviews can be an effective tool to identify current gaps and areas to optimize compliance with, and effectiveness of, shark sanctuaries. Considering the current global priority of increasing spatial protections under the recent CBD and ABNJ treaties, surveys like the ones presented here could be replicated to ensure planned spatial protections are achieving their maximum conservation potential. Nevertheless, without (i) raising better awareness among the residents about its existence and goal, (ii) fighting against the strong cognitive bias anchored in the local population, and (iii) better involving the local people in the practice of shark conservation, the world's largest shark sanctuary may not reach its full potential.

Ethical approval

The protocol was approved by FIU under the number IRB-17-0345. All research was performed in accordance with relevant regulations applicable when human participants are involved.

Competing interests

The authors declare no competing interests

Data availability

The original dataset is available as a supplementary material.

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Economic importance of elasmobranchs ecotourism in French Polynesia prior to the cessation of provisioning activities and the COVID-19 pandemic

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Abstract

Tourism based on elasmobranch-watching can represent critical financial incomes for vulnerable island economies. In many places around the world, artificial provisioning is necessary to allow the observation of naturally shy animals. This activity is however controversial and was banned in French Polynesia in 2017. This study aims at (i) describing the specificities of the elasmobranch-watching operators in French Polynesia, as well as (ii) determining the part of provisioning in the local tourism industry before the cessation of provisioning activities in 2017. Our census gathered 146 ecotourism operators who were offering elasmobranch encounters which can be split into lagoon-based and outer reef slope activities, respectively. In 2016, the former ones were mostly concentrated in Society islands (n = 70 operators mainly in Moorea and Bora-Bora islands), focusing on target species such as the blacktip reef sharks and the pink whiprays. Differently, the outer reef tourism is mostly located in Tuamotu islands (n = 23 operators mainly in Rangiroa and Fakarava atolls), focusing on large and rare species such as the tiger shark, the great hammerhead shark, the sicklefin lemon shark or forming large aggregations such as the grey reef shark. From a financial point of view, elasmobranch-based tourism activities in 2016 weighed 24.2 MUSD per year, just above countries such as Canary islands (22.8 MUSD) or Indonesia (22 MUSD) that were also practicing artificial provisioning. The contribution of shark and ray feeding in French Polynesia could be assessed at 10.7 MUSD (57% of 24.2 MUSD), an income meant to vanish after the 2017 ban. This amount should be validated by a new study to be carried out, but it calls for reflection on the appropriateness of such a decision, with the potentially very deleterious economic repercussions that our study outlines. Furthermore, such a decision could lead certain local tour operators to continue artificial feeding illegally, particularly among lagoon-based activities, thereby putting themselves in legal jeopardy. This is more regrettable given that examples of tourism involving artificial feeding governed by strict codes of conduct show to be sustainable throughout the world.

Introduction

Around one-third of Chondrichthyans (i.e., sharks, rays & chimaeras) are considered as threatened according to IUCN Red List criteria due to targeted and incidental overfishing (Dulvy et al. 2021), with catches possibly exceeding the maximum sustainable yield levels for some species (Clarke et al. 2006). However, despite the elasmobranch products trade generating large profits (Dent & Clarke 2015), the fast growth of shark and ray ecotourism industry may allow a more sustainable use of these animals (Gallagher & Hammerschlag 2011, Gonzáles-Mantilla et al. 2021). Annual incomes from tourism at a global scale are significant (Cisneros-Montemayor et al. 2013, O'Malley et al. 2013), both at a country or region scale. Yearly revenues for shark watching compagnies are estimated at 113.8M USD per year in Bahamas (Haas et al. 2017), 51.4M USD per year in Maldives (Zimmerhackel et al. 2019), 42.2M USD per year in Fiji (Vianna et al. 2011), 25.5M USD per year in Australia (Huveneers et al. 2017) and 18M USD in Palau (Vianna et al. 2012). The elasmobranch contribution to the local economy is often larger than those generated by fisheries (Clua et al. 2011, Vianna et al. 2011, Vianna et al. 2012, Cisneros-Montemayor et al. 2013), reaching for instance 1.45 times the value of ('official') annual shark exports in Indonesia in 2017 (Mustika et al. 2020). Thus, the recognition and economic valuation of the non-extractive value of elasmobranchs ecosystem service can have important positive impact on their conservation (Laurans et al. 2013). In addition, the development of sustainable ecotourism may have additional benefits, such as supporting the livelihoods of local communities and supporting conservation strategies and management (Vianna et al. 2012, Vianna et al. 2018).

Shark and ray tourism includes various practices that range from passive observation from a boat to active feeding of the animals (Gallagher et al. 2015). Special areas, such as cleaning stations or natural foraging aggregations (Mourier et al. 2016, Zemah Shamir et al. 2019, Cattano et al. 2021), as well as some planktivorous species such as Manta rays (*Manta spp.*) (Venables et al. 2016, Kessel et al. 2017), basking sharks (*Cetorhinus maximus*) (Gore et al. 2018) or whale sharks (*Rhincodon typus*) (Catlin & Jones 2010, Valsecchi et al. 2021), are generally not targeted by provisioning. The latter represents the majority of tourism operations, based on the number of visitors (Orams et al. 2002, Gallagher & Hammerschlag 2011, Clua 2018). When these special areas are not available, the use of an attractant, which includes chumming with blood and/or liquidized fish parts (Laroche et al. 2007) or feeding with large pieces of fish (Clua et al. 2010), increases the probability of encounters with rare species, the number of individuals simultaneously present, and the proximity of animals to the participants (Gallagher et al. 2015, Clua 2018). Through this kind of activities, tourism operators expect to enhance the visitor experience (Orams et al. 2002, Topelko & Dearden 2005).

Provisioning practices is facing many controversies in terms of impacts. On one side, the following potentially deleterious effects on elasmobranch have been described on their biology, such as a modification of the composition of elasmobranch communities (Brunnschweiler et al. 2014, Meyer et al. 2009), changes in mobility and habitat use (Bruce & Bradford 2013, Clua et al. 2010, Corcoran et al. 2013, Huveneers et al. 2013, Mourier et al. 2021), altered activity patterns (Bruce & Bradford 2013, Corcoran et al. 2013, Barnett et al. 2016), transmission of ectodermal parasites (Semeniuk et al. 2009, Semeniuk & Rothley 2008), alteration of physiological characteristics (Semeniuk et al. 2009) and behavior, which may result in elevated intra- and inter- specific competition (Brunnschweiler et al. 2014, Clua et al. 2010, Newsome et al. 2004, Semeniuk & Rothley 2008), as well as potentially dangerous situations for the public (Orams et al. 2002).

On the other side, recent studies highlighted situations where some form of provisioning did not significantly impact -if at all - the ecology of the elasmobranchs targeted (Laroche et al. 2007, Maljković & Côté 2011, Hammerschlag et al. 2012, Brunnschweiler & Barnett 2013, Abrantes et al. 2018, Heinrich et al. 2021, Séguigne et al. 2022, Séguigne et al. 2023a), or participant safety (Gibbs & Warren 2014, Richards et al. 2015, Clua 2018). The use of a strict code of conduct and the implementation of local regulations for provisioning management such as avoiding hand and surface feeding (Clua 2018) are often determined to be the best trade-offs between the risk of negative human-elasmobranchs interactions and any economic and/or conservation benefits (Abrantes et al. 2018, Clua & Torrente 2015, Gallagher et al. 2015, Zimmerhackel et al. 2019, Healy et al. 2020).

French Polynesia is one of the top spots globally for their observation, with 20 species of sharks and 7 species of rays spotted by local tourism operators (Séguigne et al. 2023b). This includes some critically endangered species such as oceanic whitetip shark (*Carcharhinus longimanus*), and the great hammerhead shark (*Sphyrna mokarran*) (IUCN 2021). Tourism is one of the primary revenue generators in French Polynesia, with direct and indirect economic impacts respectively estimated at 360 million and 1 billion USD in 2013 (ISPF 2015). In 2014, the tourism sector represented 78% of the foreign trade and 6% of local GDP (ISPF 2015). Ecotourism activities have been shown to be particularly attractive, as discovering wild and abundant tropical nature, is the primary motivation for tourists to visit this territory (Kahn 2015). Indeed, interacting with animals in their natural ecosystem, whatever their taxon, produced a global turnover of 42 M USD in 2016, with more than 310,000 participants per year (Lagouy & Clua 2016). Elasmobranchs appear to be among the most fascinating for tourists, with tours advertising the opportunity to spot the animals being extremely popular (Lagouy & Clua 2016). This territory is characterized by the establishment in 2006, of the largest elasmobranch sanctuary in the world, covering the whole French Polynesia EEZ (Clua et al. 2018). It encompasses more than 4.7 million km^2, in which the fishing and sale of elasmobranchs is prohibited except for the mako shark (*Isurus oxyrinchus*), which was added to the species protected in French Polynesia in 2012. The willingness by the government to ensure complete protection of sharks and rays was reinforced in 2017, when provisioning activities were banned by way of the precautionary principle (Law of the Country 2017-25). No information is currently available on the economic and conservation implications of such a drastic decision.

This study aims to (i) describe the specificities of the elasmobranch-watching operators in French Polynesia, as well as (ii) determine the part of provisioning in the local tourism industry before the cessation of provisioning activities in 2017.

Material & Methods

Study area

French Polynesia is an overseas collectivity of France located in the South Pacific Ocean. Its wide territory is composed of 118 islands grouped in five archipelagoes, covering 5.5 million of km^2: Society, Austral, Gambier, Tuamotu, and Marquesas islands (*Figure 1*). The geomorphology of Polynesian islands allows for marine activities in the lagoon, the pass (that links the lagoon with the open ocean) and the outer slope of the reef barrier. The remoteness of Austral and Gambier islands, as well as the absence of lagoon in Marquesas are respectively limiting factors for a larger development of tourism for these three archipelagos.

Elasmobranch-watching tourism activity

Among the 258 businesses involved in animal watching in French Polynesia in 2016, whatever the taxon, 146 ecotourism operators (~57%) were offering elasmobranch encounters (Lagouy & Clua 2016). An elasmobranch operator is defined as a tourism business proposing at least one activity where sharks or rays might be present. Among the activity advertising elasmobranch encounter as part of their operations, we count the lagoon tour, which includes boating and/or snorkeling, scuba diving, jet ski, sliding sports, which includes paddle board, kayak and *vaa'a* (local pirogue), underwater discovery, which includes helmet diving and submarine tours, and whale watching which often combine the possibility to observe whales and dolphins with the possibility to observe pelagic sharks, or which promote finishing their tours with lagoonal elasmobranchs observation. All elasmobranch watching companies were contacted and bilateral interviews were conducted either in-person or by phone, via the use of semi-directed questionnaires. In addition, internet websites, social networks and company flyers were consulted to complete the information.

All shark and ray watching businesses were questioned about their tours, specifically: (i) the sites where they implement sharks and rays watching, (ii) the different species of elasmobranch targeted, (iii) whether provisioning is practiced. A company is considered as a feeding operator if provisioning is implemented at least once per week. Note that data presented within this paper relies on the declarations of the operators. No ground truthing has been done.

In Moorea island, information on the gross turnover for each company in 2016 was collected using direct interviews of operators. To reflect the importance of shark and ray watching tourism in French Polynesia, Moorea island was chosen as a case study due to its proximity with Tahiti and its strong tourism development in term of number of operators. The economic value of elasmobranch watching site was deduced from the the turnover of each structure per site. A differentiation within the turnover generated on a site with the activity proposed by the operator was also performed.

To quantify the part of provisioning elasmobranch ecotourism in the GDP of French Polynesia, we used the data from the local statistical institute (ISPF) website concerning the Polynesian Gross Domestic Product (GDP) as well as the turnover generated by animal watching and specifically by elasmobranch watching (Lagouy & Clua 2016). Then, an estimation of the turnover generated by provisioning was calculated, using the percentage of structures frequenting each site. This percentage is normalized to give a weight to the provisioning activity.

The average number of nights spent by tourists on each island was obtained on the ISPF website and used to adjust the weight of each site depending on its localization or a highly tourist island or contrarily on a less visited island. Then, the proportion of the provisioning profit among the different island is deduced and multiplied by the shark and ray tourism turnover to obtain specifically the provisioning turnover. In the specific case of Moorea, since we have data about turnovers, the provisioning part has been computed directly through turnovers and not only frequentation of provisioned sites. In other words, we have been able to be more precise in the case of Moorea and we have adjusted the final figure for the provisioning turnover in Polynesia accordingly.

Our approach to determine the economic weight of provisioning in French Polynesia is very conservative as it only consider the direct economic impact of wildlife tourism. In other words, we focus only on expenditures related to tourism activities, excluding ancillary expenditures such as meals, transportation, or hotel nights. Indeed, it is complex to define the impact of the activity practiced on the tourist attraction of the island. In the case of divers who come in French Polynesia only for elasmobranch watching, the ancillary expenses linked to this activity can be huge and much higher than the direct expenses. However, in the case where the client of the structure came to Polynesia for other reasons, there is no reason to attribute to the observation of sharks and rays the additional expenses. Thus, our approach is complementary to the one of Clua et al. 2011, assessing these ancillary expenses using questionnaires, for the more important outer-reef provisioning ecotourism site of Moorea island.

Statistical analysis

Statistical analyses were carried out using R software (V 4.0.5). Statistical significance was tested at the p-value < 0.05 level. Chi-squared contingency table tests were performed to examine the effect of location (lagoon or outer reef) on their willingness to declare if they use provisioning or not. If significant, post-hoc analyses based on residuals of Pearson's Chi-squared tests for count data were explored, using the **chisq.posthoc.test** R package (Ebbert & Ebbert 2019). Circular barplots and pie charts were displayed using **ggplot2** R package (Wickham et al. 2016).

Results

Geography of shark and ray watching

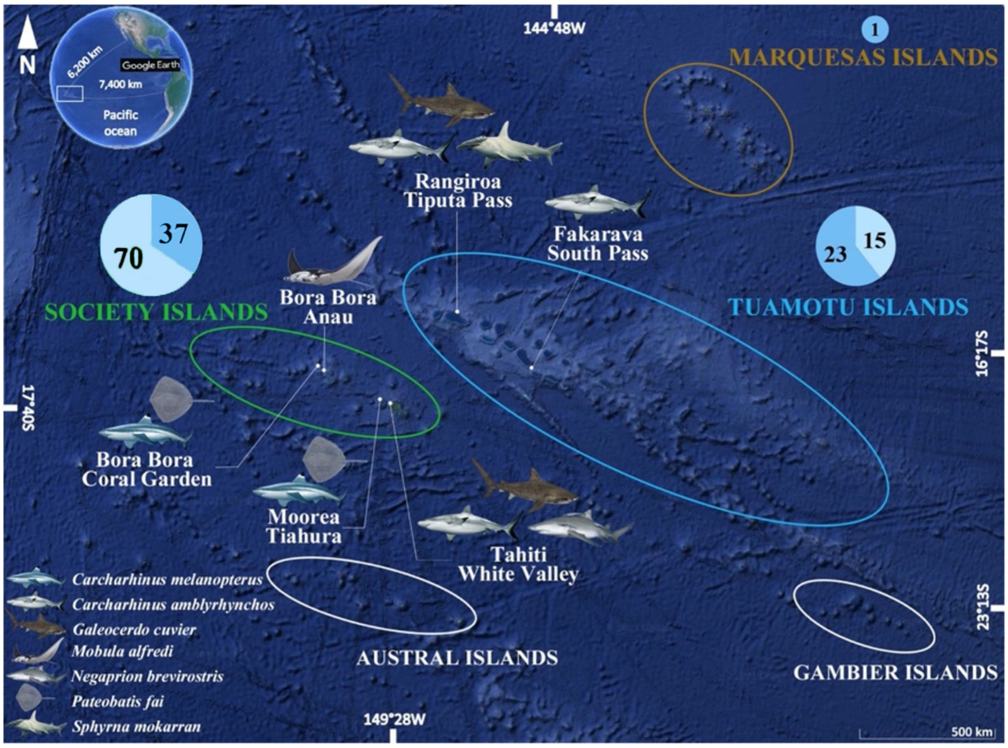

Figure 1: Distribution of elasmobranch-watchers in the different archipelagoes of French Polynesia. For each archipelago where shark and ray tourism occurs, a pie chart indicates the number of operators in lagoon-area (light blue) and outer reef (blue). The 6 sites are regularly visited by a minimum of 10 different companies. Each site is presented with their emblematic species.

The elasmobranch-watching operators were mostly concentrated in Society (n = 107 operators) and Tuamotu archipelagoes (n = 38 operators) in 2016. In Marquesas archipelago, one diving center in Nuku Hiva only promotes outer-reef exploration of sites where sharks and rays are usually present. In Austral and Gambier archipelagoes, despite several species being observed, no elasmobranch activity was reported, at least during this study. In total, 16 islands propose the opportunity to meet sharks and/or rays during tours (*Figure 1*).

The shark and ray watching activity in French Polynesia offer different locations and species, even in the same island. Two different types of tourism can be distinguished: the lagoon-based tourism and the outer-reef tourism. The lagoon-based tourism is mostly represented in Society islands (n = 70 operators), which represent 65% of the shark and ray tourism on this archipelago. Two islands are particularly representative, covering 77% of all the Society islands lagoon-based tourism structures: Moorea (n = 28 operators) and Bora Bora (n = 26 operators). In Tuamotu islands, lagoon-based activities represent 15 operators, located in Rangiroa (n = 6 operators), Tikehau (n = 5 operators) and Fakarava (n = 4 operators). Lagoon-based tourism is characterized by an important panel of activities proposed, with snorkeling, scuba diving, sliding, or jet ski activities. Target species are mainly blacktip reef sharks (*Carcharhinus melanopterus*, Vulnerable and decreasing worldwide, IUCN 2020) and the pink whiprays (*Pateobatis fai*, Vulnerable and decreasing worldwide, IUCN 2016). Six lagoon sites are recognized as regularly fed by different operators in Bora Bora (n = 2 sites), in Rangiroa (n = 2 sites), in Moorea (n = 1 site) and in Tahaa (1 site). Among them, two are considered as the most popular sites in all French Polynesia, in term of number of operators frequenting them: Tiahura in Moorea (n = 27 operators) and Coral Garden in Bora Bora (n = 16 operators). Reef manta ray (*Mobula alfredi*, Vulnerable and decreasing worldwide, IUCN 2018) watching tourism is also generally located in the lagoon but did not require any provisioning to attract the animals, as they are observed in natural cleaning or feeding stations. The most popular manta ray site is in Anau, in Bora Bora, and regroups 11 operators (*Figure 1*).

The outer reef tourism is mostly located in Tuamotu islands where it represents 60% of the operators (n = 23 operators), in Society island the outer reef represent 35% of the number of operators (n = 37 operators). The only experience offered in these outer reef sites is scuba diving. The most popular species targeted in this area are generally large and rare species, such as the tiger shark (*Galeocerdo cuvier*, Near Threatened and decreasing worldwide, IUCN 2019), the great hammerhead shark (*Sphyrna mokarran*, Critically Endangered and decreasing worldwide, IUCN 2018), or the sicklefin lemon shark (*Negaprion acutidens*, Endangered and decreasing worldwide, IUCN 2020) or forming large aggregations such as the grey reef shark (*Carcharhinus amblyrhynchos*, Endangered and decreasing worldwide, IUCN 2020). In Tuamotu islands, no regular feeding operations are implemented, but traditional fishing techniques, such as fishing traps aggregating fishes inside, or large natural aggregation of potential preys, may play a strong role in promoting the sighting of rare animals. This is for instance the case of the Tiputa pass in Rangiroa, attracting 11 operators or the Tumakohua South pass in Fakarava, attracting 10 operators. In Society archipelago, such fishing activities with increased probabilities of sighting are not existing. Thus, three main sites (2 in Moorea and 1 in Tahiti) are daily fed to favor encounters. One of these sites is considered as one of the most popular of French Polynesia: the White Valley, located in Tahiti and frequented by 10 of the 11 diving centers of the island (*Figure 1*).

On the provisioning practice

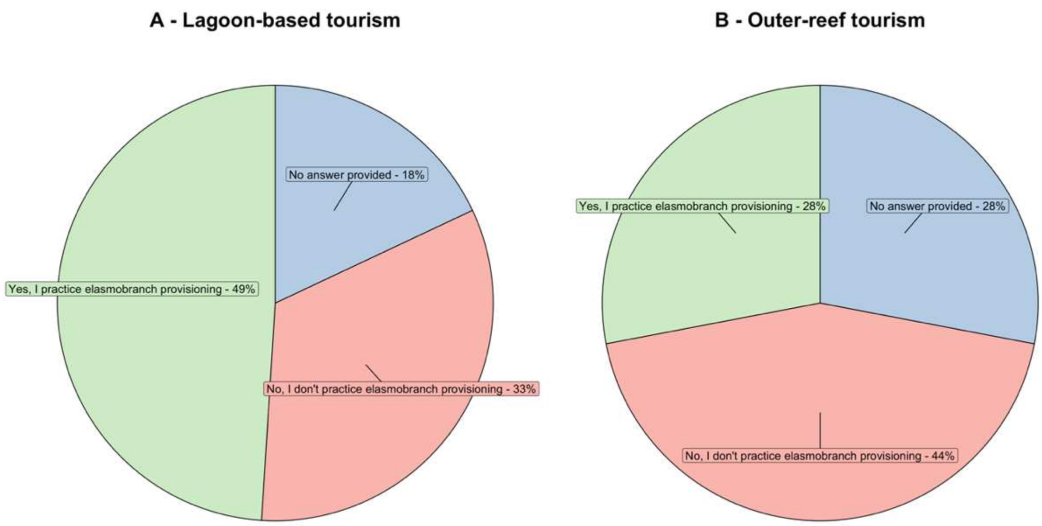

Figure 2: Pie chart showing the repartition of answers provided by tourism operators concerning their provisioning practice A – in the lagoon and B – outer reef.

The most cited answer for lagoon-based operators concerning provisioning was that almost half of them (49%) were admitting practicing provisioning regularly. Outer reef, the opposite pattern is remarked, with a main answer (44%) displaying a non-use of provisioning in the ecotourism sites frequented. Interestingly, 18% of lagoon-based operators and 28% of outer reef operators decided not to give information on if they were feeding or not, which, if they did not assume performing this controversial activity, could mean that more than half of the operators were provisioning in the lagoon (67%) and outer-reef (56%). The chi-squared test revealed a significant difference in the results obtained between the lagoon-based and the outer reef operators (chi-squared = 6.68, df = 2, p-value = 0.035) despite post-hoc tests didn't show any difference between the categories of answers.

Gross annual turnover generated by tourism sites in Moorea Island

The main result show that the great majority of the turnover is concentrated in the lagoon (87.5%), with most of it (81.4%) localized specifically in Tiahura, a lagoon-based provisioning site targeting blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*). This site generated more than 788 M XPF per year (*Figure 3*). Tiahura realize many activities to sensitize the general public on shark conservation, as it regroups all the activities proposing elasmobranch watching in Moorea. Differently, other lagoon-based sites, non-provisioned, only proposed either snorkeling and boating through lagoon tours or scuba diving.

Out of all sites, the three provisioned spots gather 86.6% of the turnover of Moorea island (*Figure 3*). Outer reef, the two sites where feeding is practiced, mainly to attract sicklefin lemon sharks (*Negaprion acutidens*) and grey reef sharks (*Carcharhinus amblyrhynchos*), are part of the three most important sites in term of economic input outer reef. They generated a turnover estimated at 33 M XPF for Lemon Shark Valley and 17 M XPF for Tiki (*Figure 3*).

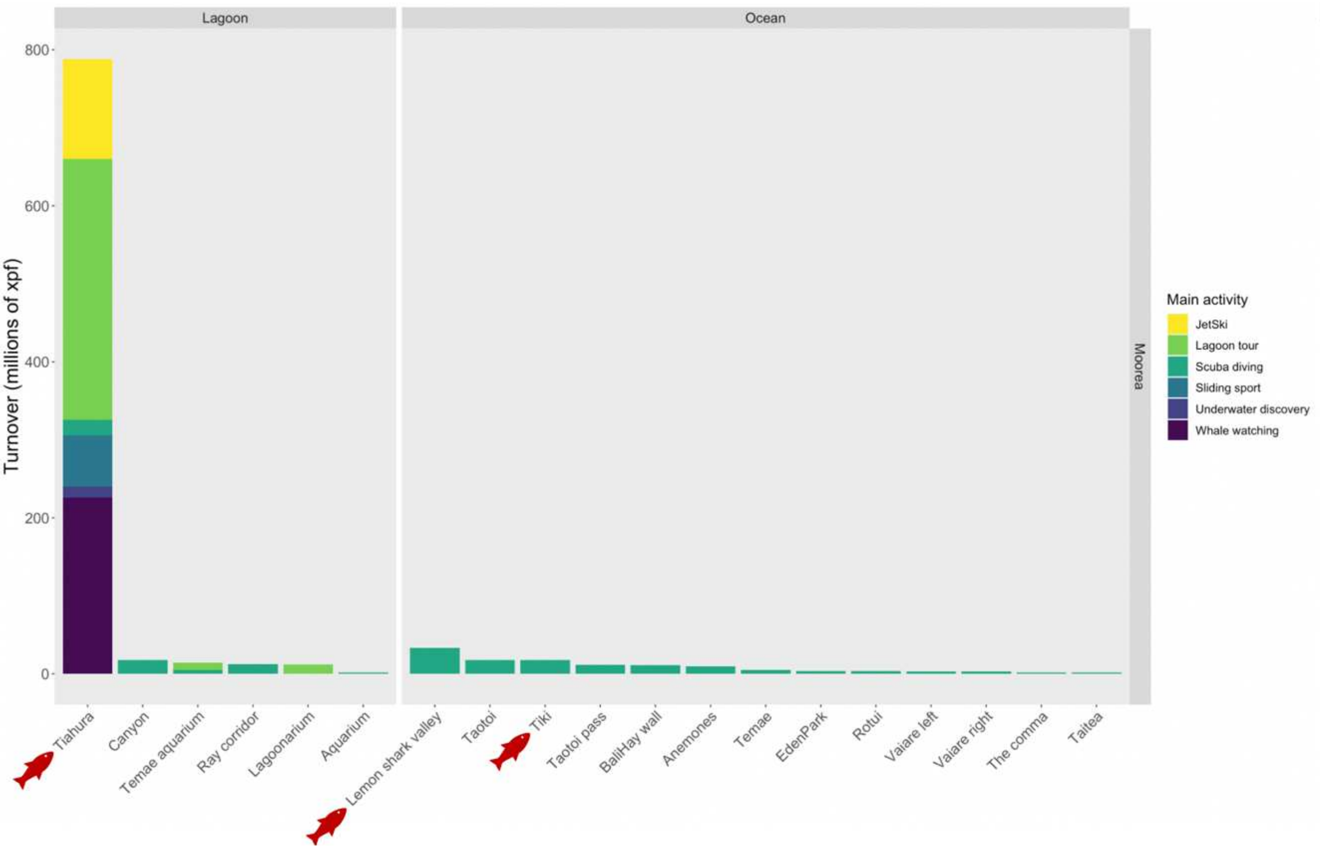

Figure 3: Distribution of the turnover generated by tourism operators depending on the elasmobranch watching spots of Moorea island. Left part of the histogram represent lagoon-based sites and right part of the graph represent outer reef sites. Each bar gives the total turnover generated by each site and details about the types of activities generating the turnover. Red fishes in x-axis represent regularly provisioned sites, open to all operators.

Extrapolation of the gross turnover generated by provisioning in all French Polynesia

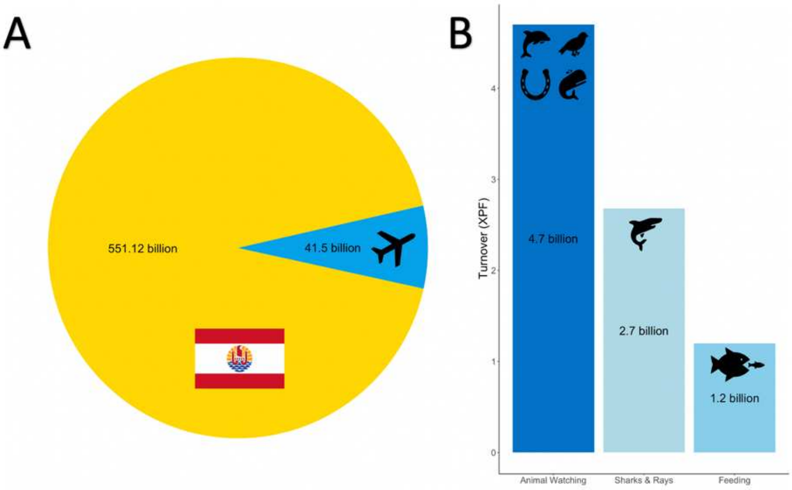

Figure 4: A- Pie chart representing the part of tourism (in blue) in the French Polynesia's Gross Domestic Product (GDP) (in yellow) in 2016 (ISPF); B- Gross turnover generated by animal tourism (Lagouy & Clua 2016), elasmobranch watching and shark and ray provisioning in French Polynesia in 2016.

The tourism is an important part of the GDP of French Polynesia, as it represents 13.28% of the generated wealth of this territory, reaching 41.5 billion XPF (*Figure 4A*). One of the most important economic parts of local tourism concerns animal watching operations, with a turnover of 4.7 billion XPF, which account for 11.33% of the economic input. Among these activities, one of the most popular and occurring year-round is the shark and ray watching tourism, representing more than half (57%) of the revenue of the animal watching tours, reaching 2.7 billion. Despite controversies around the practice, shark provisioning in French Polynesia reaches a turnover of 1.2 billion and represents 44% of the revenue generated by shark and ray operators, and 25.53% of the total of the one of the animal-watching industry, which represents a very conservative measure.

Discussion

Using the interviews of animal-watching operators of French Polynesia in 2016, we identified a total of 146 elasmobranch operators, spread out between 3 archipelagoes and 16 islands. Two main types of sharks and rays' tourism where defined: the lagoon-based tourism where target species are usually small species with low-risk of incidents on participants, and the outer-reef tourism where target species are usually large and rare, but requiring a diving certification to be involved in. Part of these activities, shark provisioning, principally used to maintain target species on lagoon-based sites, is estimated to generate more than 1.2 billion XPF (~10.7 M USD) per year in French Polynesia prior to its ban, which represent 57% of the 2.7 billion XPF (~24.2 M USD) generated by all elasmobranch watching activities.

The observation of sharks and rays is similar to Canary islands which total 22.8 M USD (De la Cruz Modino 2011) and Indonesia 22 M USD (Mustika et al. 2020). Bahamas displayed an annual income estimated at 113.8 M USD for shark-watching only, but this value consider as well indirect expenses (Haas et al. 2017). The data collected in our study only includes direct expenses, as all different islands show potential strong differences in term of ancillary expenses. Thus, the value obtained to quantify both shark and ray tourism and specific provisioning tourism are very conservative and might be very underestimated. Bora Bora, with its 34 elasmobranch-watching operators, mainly lagoon-based, attracts many international visitors searching for a luxury tourism experience, with particularly high prices for accommodation in comparison to other islands (Lagouy & Clua 2016).

Another important result is that prohibition of provisioning activities would not probably have the same economic impact in the lagoon or outer reef. The visitor satisfaction is directly led to the probability to encounter animals, to the species diversity, the abundance of sharks and rays and the possibility to get close of them (Moscardo 2006). It has been observed that the prohibition has led to a strong rarefaction of encounters, with almost a quasi-desertion of the old baited sites either in the lagoon and outer reef (Séguigne et al. 2022, Séguigne et al. subm.)., During COVID-19 lockdown, even the very frequented and fed Tiahura site in Moorea was completely deserted by sharks and rays as soon as the provisioning stopped (Séguigne et al. 2022). This may explain why, despite the interdiction, several tourism operators are continuing the practice in lagoons to maintain the animal presence and abundance (Séguigne et al. 2022). Without the large revenues made by this important type of tourism, a subsequent number of people would lose their main source of revenues.

Such effects have also been observed in outer reef sites after legal ban, as for the White Valley dive site in Tahiti, where sighting of the rare and solitary tiger shark (*Galeocerdo cuvier*) became hugely scarce in the area (C. Séguigne, pers. obs.). In French Polynesia, due to fishing practices and "special places", outer reef shark tourism activity can maintain its potential without provisioning, especially in Tuamotu archipelago. Large aggregations can be naturally spotted, such as in Fakarava South Pass, where hundreds of grey reef sharks (*Carcharhinus amblyrhynchos*) are almost daily seen (Mourier et al. 2016). Large and rare species may also be commonly observed in the special environment created by the pass of vast atolls, that are predominant in these islands. Indeed, these reef passages are aggregating a subsequent number of bony fishes (Filous et al. 2022), which attracts rays and mesopredators, and then large sharks (Mourier et al. 2013). This is for instance the case of the emblematic great hammerhead shark (*Sphyrna mokarran*), critically endangered and seasonally observed in the Tiputa pass, when spotted eagle rays (*Aetobatus ocellatus*) are presenting the most important probability of presence (Séguigne et al. 2023b). This strong probability of popular species presence is strengthened by the traditional fishing techniques taking place in the area, such as fishing traps (Clua & Millot 2018) or spawning aggregation fishery, for instance on the longnose emperor (*Lethrinus olivaceus*) (Filous et al. 2022). Although this olfactive stimulus is not generated on purpose to attract sharks, it may play a strong role in the sighting of rare animals, such as in Tikehau or Rangiroa, with the regular presence of great hammerhead sharks (*Sphyrna mokarran*) and tiger sharks (*Galeocerdo cuvier*).

The public targeted is highly different between lagoon-based activities and outer reef activities, providing strong difference in term of perception. Indeed, scuba divers, mainly present outer reef, are expected to be more environmentally minded and educated to the potential threats faced by elasmobranchs, and then more susceptible to a "ceiling effect" (Sutcliffe & Barnes 2018). On the opposite, the lagoon-based activity, mainly jet ski or board sports, attracts a wide diversity of tourists, and potentially provide stronger gains for conservations for people displaying generally low willingness to protect elasmobranchs. This reduced level of knowledge often associated with strong negative cognitive bias generally characterize Western culture (Neff 2014). In this case, a "de-demonization" of these animals, as well a change of behavior and an emotional engagement, might be efficient to modify predominant perception. Indeed, more and more evidence are showing that increasingly people have increased knowledge, mainly by meeting elasmobranchs in their natural environment, which leads to better support for conservation (O'Bryhim & Parsons 2015, Apps et al. 2018, Sutcliffe & Barnes 2018).

Another problem between lagoon-based and outer reef tourism consists of the potential social conflicts between operators. The shark conservation regulations may have strong impacts in front of disparities caused, as it has already been demonstrated concerning shark fishing ban (Booth et al. 2021, Malpica-Cruz et al. 2021). Regarding shark provisioning, the turnover generated by provisioned sites in the lagoon is so important to the local economy that the authorities turn a blind eye to the practice. However, the fact that no standardized protocol is implemented for elasmobranch provisioning increases the level of bite risk, especially where some practices such as hand feeding are regularly used (Clua 2018). Thus, in addition to raise the level of negative perception if any incident occurs (Sabatier & Huveneers 2018), it creates strong differences in term of risk taken between lagoon-based operators, mainly led by Polynesians and outer reef operators, mainly managed by Europeans (C. Séguigne, pers. obs.). Indeed, the absence of any code of conduct concerning provisioning is a "slow-burning" legal issue, putting lagoon-based tourism operators in a negative position in the event of incidents, which might be another point in favor of a management instead of a ban.

Another conflict can be observed between operators sharing the same provisioning site. Indeed, some of them choose to promote non-provisioned responsible tours (C. Séguigne, pers. obs.). However, frequenting the same sites as the feeders allows these operators to benefit from the strong probability of presence and proximity of highly conditioned animals. Indeed, sharks and rays are both able to display a cognitive connection between two linked stimuli: an unconditioned, linked to a potential food reward, and a conditioned, with sound or visual stimuli (Pavlov 1927). Previous findings showed that the sound emitted by an engine can be sufficient to attract some elasmobranch individuals on a regularly provisioned site (Gaspar et al. 2008, Bruce & Bradford 2013, Vila Pouca & Brown 2018, Séguigne et al. 2022), and thus making them easily observable by non-provisioners.

Some of the operators are only targeting non-provisioned planktivorous species, such as the emblematic reef manta ray (*Mobula alfredi*), in dedicated cleaning or feeding stations. These animals particularly seduce tourists with its lack of potential danger despite its large size, with some rare individuals reaching up to 500 cm Disc Width (DW) (Marshall et al. 2009, Lawson et al. 2017). 317 of them have already been photo-identified, mainly in Maupiti and Bora Bora thanks to a local citizen science initiative (Carpentier et al. 2019). Nevertheless, initiate a real ban for provisioning activity in lagoons might lead to an increase of tourism pressure on this species. Snorkeling or scuba diving tours may be highly deleterious for the manta rays, as it has been observed locally that a large percentage of sublethal injuries on these animals have been caused by boat propeller strikes (Carpentier et al. 2019).

This suggests that damage to species targeted by tourism is not only caused by provisioning but is also a potential danger for participants. Indeed, even though shark feeding may result in elevated risks in unmanaged situations, they may be controlled with appropriate training for participants and staff and implementation of codes of conduct (Healy et al. 2020). Thus, all different tourism activities present different hazards depending on the environment explored, the potential species encountered, the public and the type of activity itself. Indeed, a predatory bite by an oceanic whitetip shark (*Carcharhinus longimanus*) has been suspected in the case of a snorkeler off Moorea island during a whale-watching tour (Clua et al. 2021). French Polynesia has strict regulations concerning cetaceans' approach, such as distance from animals and ratio of people per guide in water (***Art. A. 2213-1*** Code of Environment of French Polynesia). However, this statute law does not consider the other species which present a potential risk, such as oceanic whitetip shark, potentially sharing the pelagic environment, or often associated with the targeted animals (Clua et al. 2021). Even if this animal is not directly targeted by operators, its often highly inquisitive behavior promotes a risk to swimmers of being bitten (Compagno 1984). Thus, all activities where sharks might be found, whatever the species or environmental conditions, one must examine the risks they present, and develop a distinctive code of conduct with all the specific hazards, as every bite incident might result in reduced motivation to protect elasmobranchs (Neff 2014).

Despite the amazing potential for elasmobranch-watching without provisioning in Tuamotu islands, tourism is rarely developed beside Rangiroa, Fakarava and Tikehau, as shown by the low number of tourism operators. Furthermore, the accommodation capacities, considered as the basic element of the tourist economy material base (Nevena 2005), are much weaker than in Society islands. Indeed, 826 985 rooms were rented by tourists in Society archipelago in 2016, compared to 62 202 for all other archipelagoes, which represent less than 7% of the number of rooms rented in French Polynesia (ISPF 2016). On the other hand, Tuamotu islands are far from Tahiti, where international flights land, which make them expensive destinations compared to nearer islands of Society archipelago. Thus, to compensate potential financial loss linked to end of provisioning by reinforcing elasmobranch-watching in Tuamotu islands appear to be difficult, except if a strong tourism development take place.

Nowadays, the identification and tourism use of new natural elasmobranch-watching sites is strongly encouraged in scientific literature to help shark and ray conservation (Topelko & Dearden 2005, Cisneros-Montemayor et al. 2013, Gonzáles-Mantilla et al. 2021), primarily in regions where major declines of their population are observed due to overfishing (Gonzáles-Mantilla et al. 2021). Despite the standing of Sanctuary of French Polynesia, the fight against the illegal, unreported, and unregulated (IUU) fishing, which is estimated to represent approximately 20% of the world's reported catch (Agnew et al. 2009, Arias & Pressey 2016), might be a major challenge in an EEZ which covers approximately 5.5 million km^2. Furthermore, intentional shark killing occurs in some islands, as protection laws are still poorly known (Séguigne et al. subm.), or because sharks are targeted by small-scale fishers who view them as competitors (Clua & Millot 2018). Thus, despite the protection measures, hundreds to thousands of individuals might still be killed in French Polynesia annually, potentially undermining the effectiveness of the sanctuary measures and compromising local populations of reef sharks (Vianna et al. 2013, Vignaud et al. 2013). Thus, it could be interesting to extend the number of sites, as well as the species targeted, to develop tourism in other archipelagoes. The development of shark tourism in new islands has the potential to reinforce the non-consumptive value of elasmobranchs for the inhabitants strongly isolated from the most touristic islands. As previously observed in Palau (Vianna et al. 2012), shark and ray diving can economically benefit several sectors of the economy by generating incomes to tourism operators and supporting business such as hotels, restaurants, and local craft. It also leads to a stimulated development of remote islands and to high revenues generated for the government, while reinforcing the conservation inclination of the populations (Vianna et al. 2012). As ecotourism might be an important vehicle to changing the perception towards elasmobranchs, it can also be a way to promote traditional ecological knowledge, as has been observed for aboriginal rainforest culture (Tropics 2001). Indeed, sharing protection responsibility with indigenous people, preserving valuable ancient expertise, and better preserving both ecosystem services and biodiversity may directly lead to improved conservation potential based on sustainable development, as it links ecology, economy, and local community (Parris & Kates 2003).

This paper highlighted the economic importance of the ecosystem service of elasmobranch tourism. It provides strong argument for elasmobranch protection as well as indicates the importance for French Polynesia to support this industry. It informs about the benefits of potentially reopen sustainable provisioning activities. It gives a reliable baseline to assess the potential economic loss that could be linked to the prohibition of feeding activities. If provisioning should be again implemented, the main priority would be to re-authorize lagoonal baiting, due to the large potential profits and ability to raise public awareness in those, people being not often sensitized to shark conservation. Outer reef feeding is much more geared towards scuba diving aficionados, who are already convinced about non-consumptive value of sharks. However, re-opening this activity would generate high profits from the number of people involved, with a low impact – if any – on the species targeted (Séguigne et al. 2023b). Thus, the challenge would be to re-allow elasmobranch provisioning in a sustainable way, via new regulations and codes of conduct, to better manage the activity and prevent associated risks.

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Human perception of sharks' dangerousness and vulnerability among the world's largest shark sanctuary: perspectives for improved coexistence and conservation

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Abstract

Shark conservation can be achieved through a variety of approaches, including the establishment of sanctuaries or the development of sustainable ecotourism as an alternative to fishing. In both cases, the effectiveness of these approaches depends on the stakeholder's perception of the status of the animals targeted by the legislation. In 2006, French Polynesia became the first South Pacific territory to implement a shark sanctuary as well as provide regulations for artificial provisioning. A series of fifty interviews were conducted on six different islands (n=300) and thus represent a westernization gradient. The questions address a representative panel based on people's age, gender, ethnic origin and occupation. The aim of this study was to assess (i) the perception of the risk that sharks represent for humans (as a proxy for the legitimacy of their protection) and (ii) the perception of the practice of shark-feeding (as a lucrative but controversial ecotourism activity). Despite a very low rate of human bites in French Polynesia, about 50% of the people believed that sharks are potentially dangerous to humans. Furthermore, despite it generating important financial income, 74% of people held a negative opinion about shark provisioning as potentially being a facilitating factor of bites on humans and having deleterious effects on shark ecology. These results show how large the gap is between most people's perception and the reality described by scientific facts. The latter demonstrates a global innocuity for animals and the potential sustainability of shark-feeding-based ecotourism, if properly regulated. When crossed with the statement of lack of compliance with the regulations of the shark sanctuary and the feeding ban in French Polynesia, these results also suggest the importance of local political decision-making to better integrate internationally validated scientific data. This data would then have the potential to improve the co-existence between people and sharks and better ensure their conservation.

Introduction

Sharks are currently facing a high risk of extinction, as around one-third of Condrichthyans (i.e., sharks, rays & chimaeras) are currently threatened according to IUCN Red List criteria [1]. Their main threat essentially stems from targeted and incidental overfishing, compounded by climate change and habitat degradation [2]. Indeed, catches are possibly exceeding the maximum sustainable yield levels for some species [3]. However, sharks are of paramount importance to the balance of marine ecosystems, fulfilling important direct and indirect ecological roles [4]. Therefore, strong measures must be implemented promptly to ensure their conservation.

To tackle the threats faced by sharks, some territories decided to ban shark culling and fishing, as well as trading products from these animals. These protective measures led to the creation of "sanctuaries", covering huge areas of territory in the ocean [5,6]. Currently, one of the biggest active shark sanctuaries was implemented in French Polynesia in 2006. This was the first Pacific nation to protect its shark populations within its entire and vast Exclusive Economic Zone (EEZ) of 5.5 million km^2 (article 3 of the Ministers' Council statement N°396 CM of 28 April 2006). The shark-watching industry includes a large variety of activities, with an extensive target audience (from non-trained tourists and snorkelers to skilled scuba-divers) This activity takes place in both lagoon and outer reef environments and is a critical contributor to tourism revenues (Séguigne et al. subm.). Among these activities, shark provisioning was regularly used to attract several species of elasmobranchs to popular aggregation sites, until its ban in October 2017 (Law of the Country 2017-25). This measure was taken by precautionary principle in the face of possible deleterious effects on shark ecology and a potential increased risk of being bitten, despite there being no scientific evidence to validate these assumptions [7,8,9]. Regardless of the complete legal banning of artificial provisioning, this practice is still often used and tolerated in lagoon-based activities among the Society islands, such as in Moorea to continue to attract revenue generating tourism to the area.[10].

The effectiveness and local ownership of processes such as the creation of a sanctuary -to protect the totality of the sharks- and the legal banning of artificial provisioning -to protect sharks' health status and decrease conflicts with humans-, might have limited effects if the local population's perception of sharks is not more positive and they continue to be seen as dangerous and deleterious animals [11,12,13]. Historically, Polynesian descendants shared a special relationship with sharks, as they symbolized a link between the spiritual underworld and physical life on earth., They acted as both guardian protectors and a potentially harmful threat to be feared [14,15]. However, the prevailing public perception is generally still very negative [13], and there is currently no information available on the state of shark perception in French Polynesia.

To optimize the potential of the conservation measures put in place in French Polynesia, the perceptions of the community and stakeholders concerning the dangerousness of sharks, were assessed to evaluate the extent of cognitive bias in local populations. Thus, this study aims to fill a gap on (i) a potential human-shark conflict in one of the largest sanctuaries at a time and on (ii) the perception of provisioning ecotourism in French Polynesia.

Material & Methods

Sampling design

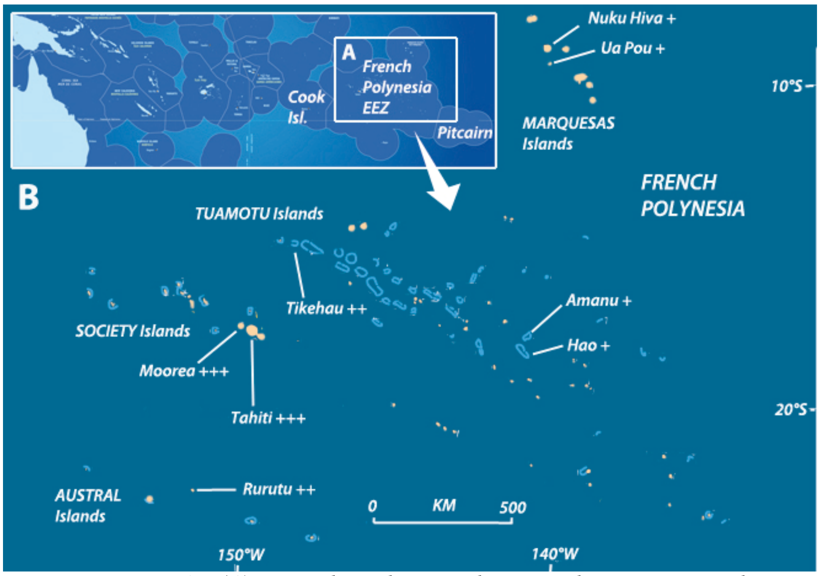

Figure 1: (A) French Polynesia lies, in the east central Pacific. (B) The six sampling areas were located on two westernized islands of the Society archipelago (Tahiti and Moorea, +++), two moderately westernized islands of the Austral and Tuamotu archipelagoes (Rurutu and Tikehau, ++) and two slightly westernized islands of Marquesas and Tuamotuan archipelagoes (Nuku Hiva/Ua Pou and Hao/Amanu, +).

French Polynesia is a highly recognized area for shark-watching tourism, with amongst the most popular diving spots in the world. Although sharks are present and can be observed throughout the entire EEZ [16,17], tourism is mainly divided between two archipelagoes: (i) the Leeward Islands (which includes the capital, Papeete, on the island of Tahiti) and (ii) the Tuamotu Archipelago that is mainly made up of atolls. Three more archipelagoes make up the entirety of French Polynesia, with (iii) the Austral and (iv) Gambier archipelagos, which are made out of high islands with lagoons and (v) the Marquesas Islands, made up of high islands without lagoons (*Figure 1*).

Six study sites were assessed and categorized depending on their low, moderate, or high level of "westernization" (*Table 1*). Westernization was delineated based on objective criteria linked to the extent of tourist development at each site., The number of hotels (>5 rooms), diving centers, as well as the extent of French influence provided by expatriates and/or tourists, were evaluated. Tahiti and Moorea, from the Society archipelago, were assessed as the most westernized islands. Tikehau Island (Tuamotu Archipelago) and Rurutu Island (Austral Archipelago) were considered to be moderately westernized. Finally, Hao, Amanu

	Archipelago	*Surface (emerged land) (km²)*	*Number of people*	*Number of hotels (> 5 rooms)*	*Number of diving centers*	*Indicator of westernization*
Tahiti	Society	1 040	180 000	> 20	8	High (+++)
Moorea	Society	134	16 000	> 10	5	High (+++)
Tikehau	Tuamotu	30	529	6	3	Moderate (++)
Rurutu	Austral	33	2 300	6	1	Moderate (++)
Nuku Hiva	Marquesas	339	3 000	5	1	Low (+)
Ua Pou		106	2 000	1	0	
Hao	Tuamotu	40	1 300	2	0	Low (+)
Amanu		17	200	0	0	

Table 1: Parameters used to categorize the areas on a westernization continuum. Data from 2016 is presented and issued by the local statistical institute (ISPF 2016).

(Tuamotu Archipelago), Nuku Hiva and Ua Pou (Marquesas Islands) were defined as slightly westernized (*Figure 1; Table 1*).

At each site, 50 interviews were conducted directly with members of the local population, between October 2017 and January 2018. Surveys were conducted in French, the official language, by two trained interviewers. The minimum age of respondents was 18 years old, and the interviewers attempted to balance the surveys across age demographics. This was done by grouping individuals by age into four categories: young adults (18-30 years old), adults (31-45 years old), late adults (46-55 years old) and seniors (>55 years old). Approximately two thirds of respondents at each study site were of Polynesian descent and one third were of European descent. We aimed to obtain a cross section of different stakeholder groups at each location. This was accomplished by interviewing ten fishermen, five members of the administration (public service), five tourism operators, five people involved in conservation (through their work or NGOs), five ocean goers other than fishermen (e.g., surfers, SCUBA divers, kayakers) and finally 20 people without any specific profile.

Survey structure

The semi-structured interview survey consisted of 6 questions (*Table 2*). The maximum number of answers for the multiple choice' questions was three. The surveys were conducted in Hao and Amanu (Tuamotu) in October 2017, in Tikehau (Tuamotu) and Rurutu (Austral) in November 2017, in Nuku Hiva and Ua Pou (Marquesas) in December 2017, and in Tahiti and Moorea in January 2018.

Statistical analysis

Chi-squared tests of independence were performed between the factors **Nationality** (Polynesian descendants, European), **Sex** (Male, Female – as the sex assigned at birth), **Age** (Young adults, Adults, Late adults, Seniors), **Island** (Tahiti, Moorea, Tikehau, Rurutu, Hao/Amanu, Nuku Hiva/Ua Pou), **Occupation** (Fisherman (Fish.), Tourism operator (TO), Other sea user (OSU), Conservationist (through their work with Non-Governmental Organizations) (NGO), Administration (Admin.), and Without specific relationship with the marine environment (WSR)), and the potential responses to the questionnaire. When significant, Pearson residuals (std res.) were calculated and categories presenting values beyond the range of ± 2 were considered as a major contribution to the Chi-squared value [18]. All relevant post-hoc analysis visualizations can be

Questions	*Answers*	*Type*	*Target population*
(i) Are sharks dangerous animals?	**3-levels:** Yes, No, I don't know	Single answer	All interviewees
(ii) How many adults bitten by a shark do you know?	**6-levels:** None, One, Two, Three, Four to Five, Six to Ten	Single answer	All interviewees
(iii) How many children bitten by a shark do you know?	**3-levels:** None, One, Two	Single answer	All interviewees
(iv) Do you think shark provisioning is a good practice?	**3-levels:** Yes, No, I don't know	Single answer	All interviewees
(v) If yes, why?	**5-levels:** It feeds sharks, It pays tourism operators, It reuses food wastes, It keeps away sharks from fishermen, It dedemonize sharks	Multiple answer	Interviewees answering "Yes" for (iv)
(vi) If no, why?	**5-levels:** It may facilitate attacks, It is bad for shark health, It is dangerous for fishermen, It is dangerous for other sea users, It is dangerous for watchers	Multiple answer	Interviewees answering "No" for (iv)

Table 2: Survey questions, possible answers, and target population

found in ESM1. Significance was tested at the p-value < 0.05 level, and all statistical analyses were performed using R software (V 4.2.3) [19]. Pie charts were created using **ggplot2** R package [20], and mosaic plots were generated for all factors showing a significant Chi-squared test.

Results

Profiles of interviewees

A total of 300 interviews were completed across the six sites (6 x 50) which produced a demographic breakdown of 77% Polynesian and 23% European descendants, with an overall sex-ratio of 1.6:1 (63% males and 37% females). The age distribution was 20% young adults, 32% adults, 24% late adults and 24% seniors. The sample included 20% fishermen/hunters, 13% administration, 9% tourism operators, 9% sea users other than fishermen, 7% as members of conservation NGOs and 41% with another profile.

Perception of the danger posed by sharks to humans

The interviewee perspective on the risk posed by sharks to humans was globally balanced even if the "No" answer was slightly favored (52% "No" answer vs. 46% "Yes" answer). Interestingly, the "I don't know" answer was only given by 2% of respondents, showing most of them have a clear-cut opinion about their dangerousness (*Figure 2A*). Three factors displayed significantly different answers given depending on categories: **Nationality** (Chi-squared = 18.86, df = 2, p-value = 8.05 x 10^{-5}), **Island** (Chi-squared = 39.73, df = 10, p-value = 1.89 x 10^{-5}) and **Occupation** (Chi-squared = 25.83, df = 10, p-value = 3.98 x 10^{-3}). Indeed, more European descendants than expected think that sharks are not dangerous (std res. = 2.63), while fewer of them think they are (std res. = -2.76). Concerning islands, Rurutu is the only one presenting significantly more people answering that they don't know about the dangerousness of sharks (std res. = 2.48). Tahiti displays more respondents than expected thinking that they are not dangerous (std res. = 2.55) and fewer thinking they are (std res. = -2.52), which is the opposite pattern observed in Hao and Amanu (resp. std res. = -2.16 & std res. = 2.26). Surprisingly, the only profession showing different results than expected was the one of tour operators, with more people

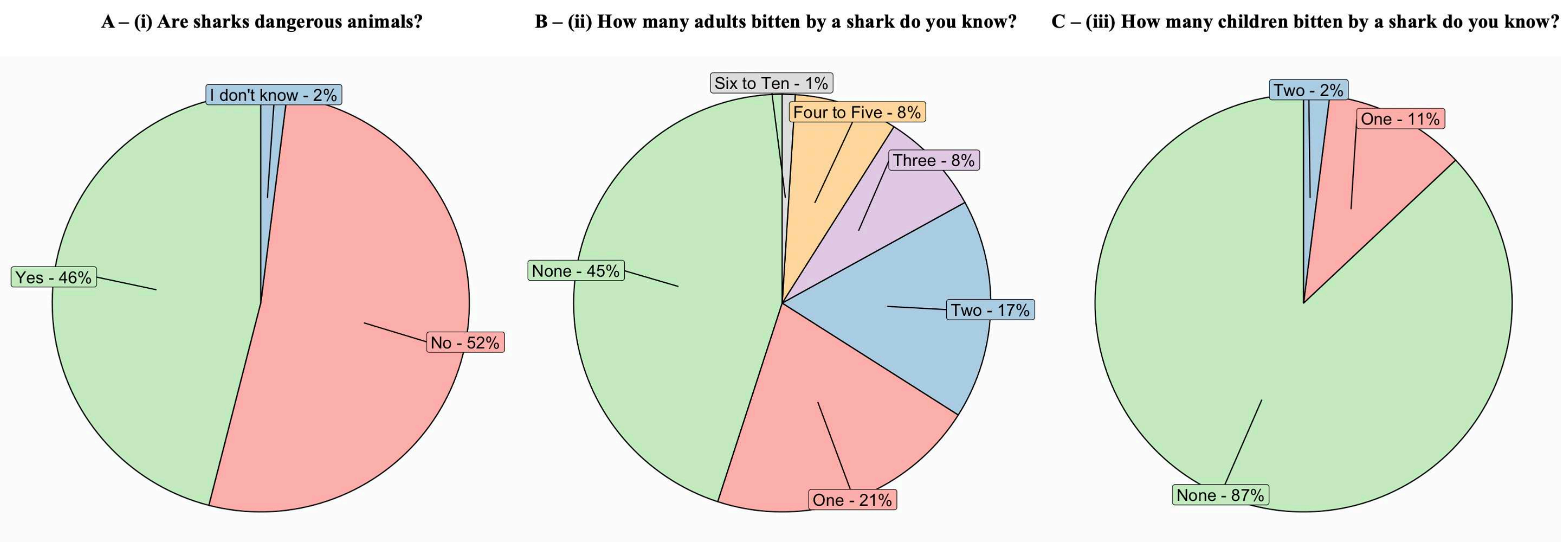

Figure 2 – Answers to questions (i) to (iii) about the perception of the human danger posed by sharks. A- Answers to question (i), asked to all interviewees (N = 296); B- Answers to question (ii), asked to all interviewees (N = 292); C- Answers to question (iii), asked to all interviewees (N = 290).

than expected having chosen the “I don’t know” answer (std res. = 2.29).

Remarkably none of the interviewees knew more than 10 adults or more than 2 kids bitten (*Figure 2A & 2B*). Interestingly, none of the respondents knew of more than 2 people killed by a shark, thus the incidents were mainly non-lethal bites. For all questions concerning the knowledge of a bite of an acquaintance of the interviewee, the main answer was “None”, reaching 45% of adults, even if most people were aware of at least one bite in this age category (55%) (*Figure 2B*), and 87% on children (*Figure 2C*). Regarding bites on adults, two factors were displaying significant differences with the overall answers: **Nationality** (Chi-squared = 23.26, df = 6, p-value = 3.01 x 10^{-4}) and **Island** (Chi-squared = 81.24, df = 25, p-value = 7.29 x 10^{-8}). Indeed, it appears that significantly more European descendants than expected do not know anybody bitten by a shark (std res. = 2.80), and even less of them know a total of two people (std res. = -2.15) or of four or five victims (std res. = -2.25; no answer for this category). Regarding the location, Tahiti shows significantly more people that don’t know any victims of shark bites (std res. = 2.27), while it is significantly less for Tikehau (std res. = -2.02). However, the latter island shows significantly more respondents than expected knowing one adult that was bitten by a shark (std res. = 2.65). Similarly, Hao & Amanu displayed fewer people than expected answering “None” (std res. = -3.07) when more of them knew a high number of victims with significantly more “Four to Five” (std res. = 4.57) and “Six to Ten” (std res. = 2.00) answers.

Concerning bites on children, only the factor **Island** was significant (Chi-squared = 40.47, df = 10, p-value = 1.40 x 10^{-3}), with significantly more people than expected knowing one person bitten in Hao & Amanu (std res. = 2.33) and in Nuku Hiva & Ua Pou (std res. = 3.27). Furthermore, the Marquesas Islands were showing more people aware of two bites on children (std res. = 2.34).

Perception of shark provisioning

Most respondents, (73%), are strongly opposed to shark provisioning. This is a practice generally used to attract animals close to the participants and potentially increase the probability of encounters. Whereas, only 18% of interviewees support this activity (*Figure 3A*). Interestingly, the overall answers given are similar for all the different factors studied, with no Chi-squared tests presenting a p-value exceeding 0.05.

Among the people agreeing to the practice of shark provisioning, less than one quarter (24%) justify their answer by "generating income for tourism operators", the preferential choice remaining that this activity provides easy food for sharks (34%) (*Figure 3B*). The only factor presenting significant differences from the overall answers was the **Nationality** (Chi-squared = 18.02, df = 4, p-value = 1.23 x 10^{-3}) with more European descendants than expected in favor of provisioning because it helps to de-demonize sharks in the face of their bad reputation (std res. = 3.28).

The respondents opposed to this practice equivalently worry about a potential impact on the overall health of the shark or on it's potential to increase the risk of shark bites (37%) (*Figure 3C*). As for the "pro-provisioning" respondents, only the factor **Nationality** displays significant results (Chi-squared = 11.16, df = 4, p-value = 0.025). However, the analysis of Pearson residuals did not reveal any categories showing strong differences between the expected and the observed values.

Discussion

This study highlighted a surprisingly evenly mixed perception of shark dangerousness, even though there were only a low number of bites reported and it took place in a territory where a shark sanctuary is enforced. Furthermore, shark provisioning is deeply rejected in spite of the fact that the practice is still running in lagoon-based activities. It is generally associated with a potential increase of aggressivity in sharks as well as appearing deleterious for targeted species.

Surprisingly, European descendants were the ones who significantly displayed a more optimistic view of these animals. This result differs from the traditional western perception, often characterized by a perpetually strong fear of sharks, called the "*Jaws effect*", which encourages a strong cognitive bias toward this predator [11,21]. This result might reflect a contemporary shift in the public's perception of sharks due to a better general knowledge of these animals, as has already been observed in other studies from westernized countries [11,22,23]. Interestingly, although Polynesian descendants had a more positive and balanced image of these animals in traditional

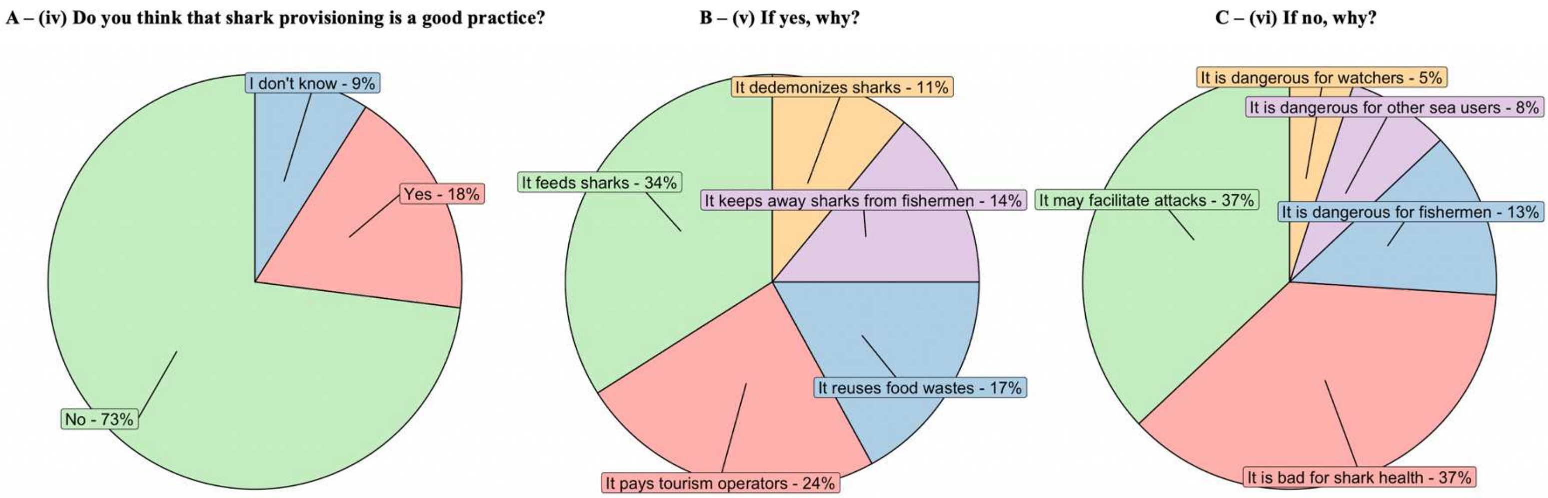

Figure 3 – Answers to questions (iv) to (vi) about the perception of the shark provisioning activity. A- Answers to question (iv), asked to all interviewees (N = 295); B- Answers to question (v), asked to interviewees choosing "Yes" to question (iv) (N = 53); C- Answers to question (vi), asked to interviewees choosing "No" to question (iv) (N = 200).

ancient societies, they might have developed a more Western-attributed fear of sharks, inherited from colonization [24,25]. Additionally, neither age nor gender appears to influence the perception of the dangerousness of these animals, which differs from the current tendency where younger people exhibit a reduced fear of sharks [11].

European descendants and people living in Tahiti are also characterized by a significantly lower number of people who know a person bitten among their acquaintances. Reversely, the islands of Hao and Amanu cumulated the most negative perception of shark dangerousness and the highest number of people knowing the most victims of shark bites. This might be explained by the different degrees of westernization of the different islands, and thus the difference in popularity of activities. Indeed, spearfishing, which is an activity where Polynesian descendants are generally highly involved, displayed more risks of incidents than scuba diving, which is more popular with expatriates (C. Séguigne, pers. obs.). The sensory perception of sharks may be very different when confronted by these two disciplines. This is emphasized due to the difference in their behaviour regarding a scuba diver compared to a spearfisherman. Indeed carrying freshly wounded fish is potentially much more attractive, thus unintentionally creating a situation of human-shark competition [26,27]. Coherently, aside from a few rare events, most shark bites recorded in French Polynesia are on spearfishermen, whereas bites on scuba divers are extremely rare (Clua et al. subm.). The differences in perception between the interviewees may largely explain why our results differed from those mentioned in Ward-Paige & Worm (2017) [28]. Indeed, they found that conservation awareness was "low in Micronesia and high in Honduras and French Polynesia". These results may be the outcome of a methodological bias. The study is based on the questioning of scuba divers, both professional and amateur, that are considered to be part of a more "shark-enthusiast" group and mainly composed of European descendants.

SCUBA diving has the capacity to increase people's awareness and support of shark conservation. The increase of non-threatening encounters with these animals canonizes them [29,30,31]. In many worldwide destinations, shark provisioning is used to increase the probability of encountering rare or large sharks [32,33]. However, this activity remains very controversial in French Polynesia, where most respondents were against the practice. In spite of the banning, provisioning remains a daily and intentional occurrence in French Polynesian waters, as it is mainly linked to lagoon-based activities. Indeed, lagoon-based shark-watching appeared to be strongly dependent on provisioning to ensure a sustainable amount of encounters. This was demonstrated by the complete desertion of sharks and rays on one of the most important feeding sites in Moorea during the COVID-19 lockdown and closure of the borders to foreign tourists. [10]. Furthermore, outer-reef targeted species, such as lemon sharks (*Negaprion acutidens*) showed a drop in their sightings by scuba divers in the same island after the provisioning ban [16]. Nevertheless, French Polynesia is characterized by natural or indirect (or passive) artificial provisioning areas of aggregations, mainly located in the pass. Indeed, large schools of fish have the potential to strongly lure predators, such as for the famous Tumakohua pass, attracting hundreds of grey reef sharks (*Carcharhinus amblyrhynchos*) [34] or traditional fishing techniques, such as fishing traps [35], possibly playing an important role in escalating their sighting. This could favour a strong disparity in the perception of the public who gets access to sharks by hindering the spread of awareness among those who are not scuba divers. This is because scuba divers are automatically more likely to know their importance and the threats that they are currently facing.

Furthermore, the consequences of the shark provisioning ban are unbalanced between those that exploit the lagoon, essentially Polynesians and those that exploit the outer reef, mainly Europeans. The inequity of these measures might create unnecessary conflicts between parties as it is the lagoon-based operators who suffer economically from the ban. Such conflicts between sea users in the face of disparity caused by shark conservation regulations have already been demonstrated. Researchers have therefore incited governments to take into consideration, local communities, before making drastic decisions to protect the ecosystem [36,37]. To not disrupt the local economy, the authorities turn a blind eye to Polynesians who are still provisioning, yet these individuals are still at legal risk if any incident occurs. This tendency to illegally continue to practice shark feeding in French Polynesia is contrary to what is promoted elsewhere in the world. Feeding is regulated by a strict code of conduct to maximize the safety of animals, operators, and tourists [38,39,40,41,42,43]. The fact that no standardized protocol is implemented to feed the sharks increases the level of bite risk, especially where some practices such as hand feeding are regularly used [7]. This has the potential to raise the level of bad perception if any incident occurs [44].

There was no significant difference between the origins of respondents concerning the perception of provisioning. However, amongst those who are in favour of provisioning, the main explanation that was given was for the purpose of "feeding the animals". This aligns with the traditional vision of Polynesians where it was normalized to do this in some rituals. On the contrary, respondents against provisioning mainly criticized the practice for facilitating the occurrence of attacks, attracting potentially dangerous sharks such as tiger shark (*Galeocerdo cuvier*), as well as the risk of deteriorating their ecological balance. Nonetheless, there is no reported significant increase in the number of incidents involving sharks and humans in a controlled provisioning activity [7,8,9]. Furthermore, even though the effects of shark provisioning appear to significantly vary between species and practices [7,45], an increasing number of studies shows that there is a limited – if any – effect on the targeted specie's ecology in a well-managed context [40,46,47,48,49,50]. In French Polynesia, the only two predation-motivated bites in the last century that have happened to our knowledge (see database on Clua et al., subm.), were by an oceanic whitetip shark (*Carcharhinus longimanus*) in a whale-watching context after the shark provisioning ban was introduced [51] and by a tiger shark (*Galeocerdo cuvier*) in the context of aquaculture farming [52].

Provisioning does not appear to be in conflict with conservation measures, as this practice is used in other sanctuaries such as The Bahamas or Palau, where shark-watching activities provide an attractive economic alternative to shark fishing It gets the local population involved, generating high revenues, all the while ensuring the ecological sustainability of shark populations [48,53]. As tourism is one of the primary generators of revenue for French Polynesia (ISPF 2015), ecosystem services provided by sharks should be highlighted. Indeed, the survey shows that only a few of the respondents were thinking about the economic potential of sharks as a booster for their conservation. Thus, it would be interesting to increase the awareness of people about these advantages to favour the dualism between economy and ecology that are often segregated [54].

To help French Polynesia's shark sanctuary obtain its optimal efficacity, it is critical to communicate more about the importance of sharks for the coral ecosystem, as well as the ecosystem services they render. Indeed, knowledge appears to be one of the main drivers of positive public attitudes towards conservation measures [55]. Important cognitive bias on shark dangerousness, mainly attributed to westernized cultures, strongly persist throughout the entire population, including those of Polynesian descent. The implementation of appropriate regulations on shark provisioning, first and foremost for lagoon-based activities, must be deliberated to protect the local operators from legal issues, as well as the animals and humans from malpractice. Furthermore, implementing a strict code of conduct would not necessarily be bad for sharks and would help to develop a strong associated economy. It would also encourage the development of research programs that are only possible thanks to shark aggregation spots [10,56,57], and citizen science programs. These programs can be an important tool to involve people in science and conservation [16,58].

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CHAPTER 2:

On the potential effects of shark provisioning on behavior & ecology

Is shark provisioning dangerous for the participants?...

...Or does it show an impact on the ecology of targeted species?

List of articles:

4. *Effects of a COVID-19 lockdown-induced pause and resumption of artificial provisioning on blacktip reef sharks (Carcharhinus melanopterus) and pink whiprays (Pateobatis fai) in French Polynesia.* **C. Séguigne**, J. Mourier, T. Vignaud, N. Buray, E. Clua. Published in Ethology (128(2), 119-130, 2021).

5. *Long-lasting memory of a free-ranging top marine predator, the Bull shark Carcharhinus leucas.* **C. Séguigne**, T. Vignaud, C. Meyer, J. Bierwirth, E. Clua. In review in Behaviour.

6. *Provisioning ecotourism does not increase tiger shark site fidelity.* **C. Séguigne**, M. Bègue, C. Meyer, J. Mourier, E. Clua. Published in Scientific Reports (13(1), 7785, 2023).

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RESEARCH ARTICLE

ethology WILEY

Effects of a COVID-19 lockdown-induced pause and resumption of artificial provisioning on blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*) in French Polynesia (East-Pacific)

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Abstract
The tourism activities linked to artificial provisioning of blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*) on a specific site in French Polynesia were suddenly and completely stopped due to a COVID-19 lockdown that lasted 6 weeks from March 20 until April 30, 2020. Using both drone footage and underwater counting, we were able to track the abundance of those two species before, during, and after reopening and thus investigate the impact of provisioning on wild shark populations. The absence of any stimulus during this long period resulted in almost total desertion of the site by the elasmobranchs. However, 1 day prior to reopening, some individuals of both species positively reacted to the single acoustic stimulus of an engine boat, showing the resilience of conditioning, and some elasmobranchs reacted to acoustic and olfactive stimuli linked to the provisioning practice from the first day after reopening. During the first 2 weeks after reopening, the abundance of both species remained at reduced levels comparable to those observed between 2008 and 2010 for sharks; i.e., around 9 animals in the presence of local tourists. Pre-lockdown abundance levels, reaching approximatively 15 individuals for sharks and 10 for rays, were considered restored 1 and 2 months after reopening for blacktip reef sharks and pink whiprays, respectively. These findings improve our capacity to better understand the potential effects of artificial provisioning tourism on the abundance of elasmobranchs by showing that conditioning is resilient for several weeks, suggesting that intermittent interruption of elasmobranchs feeding would not really help to decrease its impact on animal welfare.

KEYWORDS
anthropause, conditioned behavior, feeding, memory retention, reconditioning delay

1 | INTRODUCTION

Tourism based on elasmobranchs, whereby participants seek contact with sharks and rays in their natural environment, is a fast-growing activity (Clua et al., 2011; Gallagher & Hammerschlag, 2011; Zimmerhackel et al., 2019). To maximize the chances of encounters or to aggregate animals at the same location, many tour operators use provisioning, a practice that includes simple attraction by olfactory stimulus (chumming) and active feeding of elasmobranchs (see review by Gallagher et al., 2015). Shark and ray tourism, attracting more than 500,000 participants expending around USD 314 million per year globally, has clear economic benefits and may lead to greater willingness to conserve these animals by governments and the general public (Cisneros-Montemayor et al., 2013; Clua et al., 2011; Vianna et al., 2012; Zimmerhackel et al., 2018). Accordingly, it may help to meet the urgent need for measures to preserve shark and ray populations, many of which have declined at a worldwide scale and, in some cases, become functionally extinct (Dulvy et al., 2014; Macneil et al., 2020). This conservation application is particularly important because many elasmobranchs are considered keystone species (Stevens et al., 2000).

The provisioning of sharks and rays also raises concerns regarding the potential ecological effects on the animals. Indeed, previous studies highlighted some negative impacts such as modification of the composition of elasmobranch communities (Brunnschweiler et al., 2014; Meyer et al., 2009), reduced mobility or habitat shifts (Bruce & Bradford, 2013; Clua et al., 2010; Corcoran et al., 2013; Huveneers et al., 2013; Mourier et al., 2021), altered activity patterns (Barnett et al., 2016; Bruce & Bradford, 2013; Corcoran et al., 2013), the transmission of ectodermal parasites (Semeniuk et al., 2009; Semeniuk & Rothley, 2008), alteration of physiological characteristics (Semeniuk et al., 2009), and elevated intra- and interspecific competition (Brunnschweiler et al., 2014; Clua et al., 2010; Newsome et al., 2004; Semeniuk & Rothley, 2008). However, other studies did not show any significant negative impacts on ecology and behavior of targeted elasmobranchs species including white sharks (*Carcharodon carcharias*) (Laroche et al., 2007), Caribbean reef sharks (*Carcharhinus perezii*) (Maljković & Côté, 2011), tiger sharks (*Galeocerdo cuvier*) (Hammerschlag et al., 2012), bull sharks (*Carcharhinus leucas*) (Abrantes et al., 2018; Brunnschweiler & Barnett, 2013), and juvenile lemon sharks (*Negaprion brevirostris*) (Heinrich et al., 2021). Thus, shark provisioning appears to have differential effects depending upon practices, with hand or surface feeding facilitating the development of agonistic behavior in sharks for instance (Clua, 2018), and species, with resident species potentially more affected than highly mobile species (Mourier et al., 2021).

Wildlife provisioning also creates unprecedented opportunities for scientific data collection, aggregating animals that are difficult to study without baiting due to their low density, solitary behavior, or pelagic environment (Bègue et al., 2020; Brena et al., 2015,2018; Gallagher & Hammerschlag, 2011; Meyer et al., 2009). Flourishing shark and ray watching also promotes the development of participatory science, involving tourists in the production of scientific research and raising their awareness on elasmobranch conservation (Gallagher et al., 2015; Mieras et al., 2017; Ward-Paige et al., 2020). Finally, the ecological and economic importance of elasmobranchs for local communities has the potential to enhance the creation of protected areas to better conserve these often highly threatened species and potentially benefit the entire ecosystem (Govan et al., 2008; Jupiter et al., 2014; Ward-Paige et al., 2020).

While some effects of chronic feeding on shark and ray populations have been studied, responses to a sudden prolonged break of this stimulus have rarely been observed in the wild (but see Huveneers et al., 2021). In fish, long-term retention of information for activities such as food retrieval is traded-off with the benefits of discarding memory in favor of reduced energy expenditure and flexibility (Fuss & Schluessel, 2015). Thus, elasmobranchs are hypothesized to exhibit memory windows that vary with task and the behavioral ecology of the species considered. Some sharks exhibit considerable information retention capacities ranging from 24 h to more than 40 days in juvenile Port-Jackson sharks (*Heterodontus portusjacksoni*) (Guttridge & Brown, 2014), more than 10 weeks in some adult lemon sharks (*Negaprion brevirostris*) (Clark, 1959), more than 12 weeks in juveniles of the same species (Heinrich et al., 2021), and more than 50 weeks in some juvenile grey bamboo sharks (*Chiloscyllium griseum*) (Fuss & Schluessel, 2015). However, little information, if any, is available on the memory capacities of wild pink whiprays (*Pateobatis fai*) and blacktip reef sharks (*Carcharhinus melanopterus*). These two species are highly targeted by lagoon-based provisioning in French Polynesia, particularly at the touristic site of Tiahura in Moorea. From March 20 to April 30, 2020, a total break of provisioning was observed at the Tiahura site due to a COVID-19 lockdown, as in multiple tourist spots worldwide (Bates et al., 2021). This historic event induced the first globally considerable slowing of human activity, termed "anthropause" (Rutz et al., 2020), where short- and long-term effects on biodiversity are currently being evaluated worldwide (Bates et al., 2020,2021; Corlett et al., 2020). Thus, this 6-week complete break of provisioning activities offered a unique opportunity to contribute to an unprecedent global research effort (Bates et al., 2021).

In elasmobranchs, the deconditioning process (i.e., the decline of response) following cessation of provisioning can manifest as (i) a lower reaction to the noise of boat engines associated with baiting; (ii) augmentation of the distance to human-feeders and tourists; (iii) an increase in the time before contact with a familiar attractant and a reduction in speed of approach when food is released; and (iv) a reduction in the number of individuals seen simultaneously on the site. The reconditioning processes, characterized by a return to usual behavioral responses, have been only described once for wild provisioned white sharks (*Carcharodon carcharias*) in a similar COVID-19 context (Huveneers et al., 2021). Conditioned elasmobranchs targeted in this study were mainly lagoon-resident and may present highly differential behavioral responses relative to those of white sharks. Thus, this situation offered a unique opportunity to investigate the effects of cessation of provisioning and the resumption of touristic activities on the behavior and ecology of elasmobranchs.

2 | MATERIALS AND METHODS

2.1 | Study area and description of provisioning activity

The study was carried out on the Tiahura Marine Reserve, located in the North-West of the island of Moorea (17°30′S; 149°51′W), belonging to the Society Archipelago in French Polynesia (Figure 1a).

This lagoon site is surrounded by a central channel, with depths between 2 and 7 meters, and shallow coral reefs (Kiszka et al., 2016) (Figure 1b). The provisioning site in Tiahura shows a total surface area of approximately 4470 m^2, with a very shallow water area (<1.5 meters) covered by sand where people can easily stand. This convenient access allowed the development of touristic activities on the area, targeting two elasmobranchs species: blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*). These two species share their habitat in the lagoons of French Polynesia, although blacktip reef sharks are also present in the fore-reef area (Gaspar et al., 2008; Mourier et al., 2013). Both species are globally declining in numbers and are listed on the IUCN Red List as "Near threatened" and "Vulnerable", respectively (Heupel, 2009; Manjaji Matsumoto et al., 2016). Daily and year-round provisioning of both sharks and rays has been carried out on Tiahura since the 1980s (and inconsistently before), usually with fish discards and frozen squids (Clua et al., 2011; Mourier et al., 2021). Both professional operators who can bring up to 50 tourists per boat and individual users can share the area, which receives an average daily human attendance of around 100 people and up to almost 500 for special occasions such as Polynesian holidays when locals mix with tourists (Buray, 2015). Overall, animal-based tourism in French Polynesia attracts around 420,000 participants every year, and shallow water (lagoon) feeding of elasmobranchs accounts for 145,000 tourists per year (35%) through six different islands; Moorea island accounts for an average of 40,000 people per year (9.5%) (Lagouy & Clua, 2016).

Both species are strongly conditioned to people, displaying strong attenuation of their fear of humans when in the presence of an unconditioned stimulus (US) that is related to food and smell and associated as a reward. Consequently, they react positively to a conditioned stimulus (CS, Pavlov, 1927), i.e., the noise of boat motor, increasing their speed, and swimming in a circle. Additionally, sharks and rays are usually fed regularly during the day and consequently anticipate the arrival of boats one or 2 h before feeding hours (Gaspar et al., 2008).

2.2 | Pre-lockdown abundance assessment

Pre-lockdown abundances of elasmobranchs were defined previously in the study site in Tiahura in three studies: Study 1: Mourier et al., 2012; Study 2: Kiszka et al., 2016; Study 3: Buray, 2015 (Table 1). Abundance data from studies 1 and 3 were collected similarly, using in-water sampling, whereas Study 2 used UAV overflights to estimate the number of animals in the area.

Comparisons between data of blacktip reef shark abundances were explored from the original data sets for all three studies. Due to the suddenness and the impossibility to anticipate the lockdown decision, no data were collected right before the closure of the provisioning activity. Nevertheless, according to experts and professional touristic operators, the average abundance of sharks and rays appears to be similar and maximal since Studies 2 and 3. Thus, we defined these values as "Business As Usual" (BAU) and considered them as the pre-lockdown reference for abundance.

2.3 | Lockdown abundance assessment

Following the worldwide spread of the COVID-19 pandemic, an official lockdown was implemented on March 20, 2020, in French Polynesia, which carried out complete removal of human presence and activity in the feeding spot of Tiahura for a 6-week period.

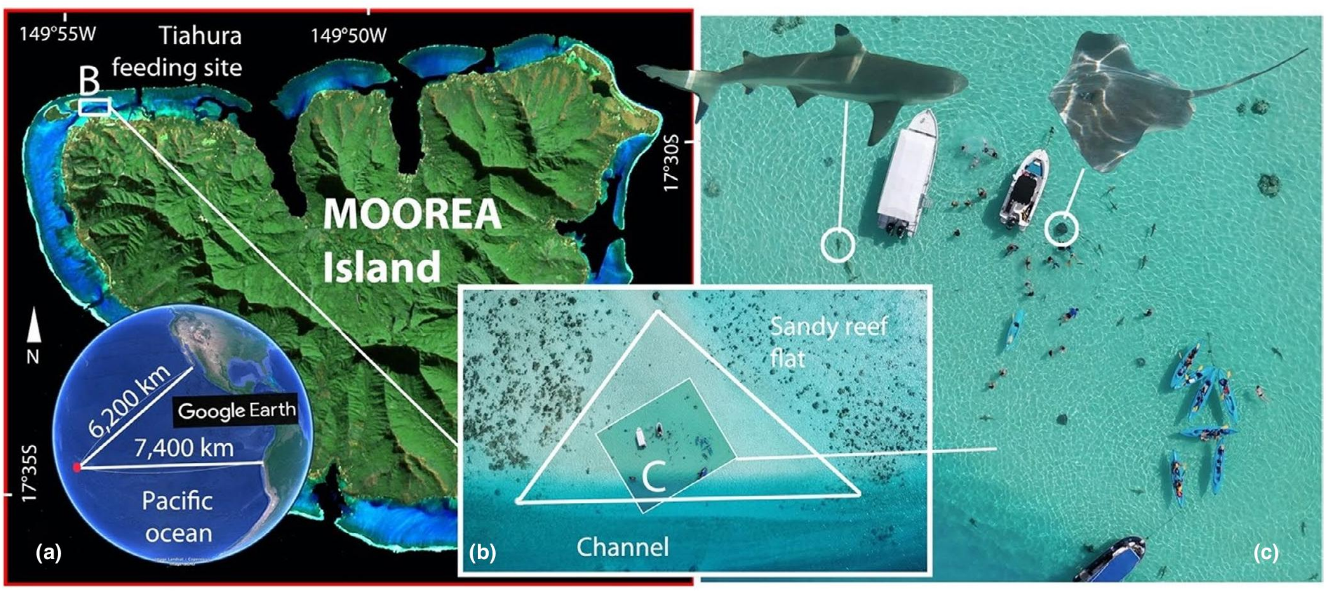

FIGURE 1 Study area. a: Localization of Moorea, French Polynesia. b: Unmanned Aerial Vehicle (UAV) overflight of the Tiahura marine reserve. C: UAV overflight of a provisioning session involving different tour operators and swimmers interacting with blacktip reef sharks (Cacharhinus melanopterus) and pink whiprays (Pateobatis fai)

TABLE 1 Overview of the publications used as references for pre-lockdown assessment in the present study

Study description	Data collection period	Blacktip reef shark abundance	Pink whipray abundance	Reference
Study 1: Evidence of social communities in a spatially structured network of a free-ranging shark species	From March 2008 to June 2010	8.97 ± 0.72 (SD)	NA	Mourier et al., 2012
Study 2: Using unmanned aerial vehicles (UAVs) to investigate shark and ray densities in a shallow coral lagoon	July 2014	15.1 ± 2.77 (SD)	10.00 ± 4.59 (SD)	Kiszka et al., 2016
Study 3: Étude comportementale des requins sur le site touristique du « ray feeding» de Tiahura à Moorea en Polynésie Française.	From July to August 2015	15.4 ± 7.8 (SD)	NA	Buray, 2015

Nevertheless, there remained very marginal sound stimuli emitted by passing boats (around 1 to maximum 3 per day) in the small channel neighboring the feeding site driven by some fishermen on their way to the reef passage. An expert observer was confined in her house right in the front of the Tiahura site at a distance of 200 meters with a direct and exhaustive view facilitated by the water clarity, allowing her to: (i) Confirm the absence of elasmobranchs in the area during the usual peak periods of provisioning and regularly during the daylight hours and (ii) confirm the absence of any significant olfactory or sound stimulus on the Tiahura site itself (C. Gaspar, Pers. Comm.).

In order to confirm the expert observer results and to record the number of sharks and rays simultaneously present, a 10-min UAV survey session was implemented at 10 a.m. on 29 and April 30, 2020. The drone flights were conducted using a DJI Mavic 2 Pro UAV quadcopter equipped with a Hasselblad L1D-20c camera, allowing us to capture 20-megapixel aerial shots and 4K HDR video. The Mavic 2 Pro includes a multi-axis flight controller, GPS, and compass that allow for stable flight, maintenance of a consistently chosen altitude of 60 meters, wind compensation, station holding, and reliable user control.

2.4 | Post-lockdown abundance assessment

The data collection focusing on elasmobranch abundances was carried out 1–3 times a day from May 1, 2020, the day of reopening after lockdown, to May 15, 2020, totaling 31 dives, in the presence of favorable climatic conditions (unaltered visibility, moderate current). Three additional dives were conducted in June 2020 at 10 a.m. in order to record elasmobranch abundance in the area 1 month after reopening. Despite the low amount of data collected in June, samplings sessions were separated into two groups—"early post-lockdown" with May data and "late post-lockdown" with June data—in order to highlight the possible differences in terms of elasmobranchs abundance. Diver results (see below) were compared to UAV data, collected at the beginning (4 days, between 1 and May 5, 2020) and at the end of the post-lockdown period (3 days, during late post-lockdown dives). During lockdown, a 10-min stationary UAV survey was performed with the same equipment, at the same height.

The underwater diver surveys were conducted by a qualified and trained freediver from an independent boat, who counted and identified individual blacktip reef sharks and pink whiprays over 30-min sessions at up to three different times of the day overlapping with provisioning sessions of most professional touristic operators; i.e., at 10 a.m., 12 a.m., and 4 p.m.. During each count, the diver recorded the number of people present in the water, boats with (tour operators, jet skis, private boats) or without motors (standup paddle, kayak, pirogue), and whether provisioning occurred or not. The presence/absence of the sharks and rays targeted was evaluated four times: at the entrance of the diver in the water, after 10 min, after 20 min, and at the end of each session.

The counting of the sharks was carried out with the help of photo-identification techniques such as the identification of individual shape of margins separating black, white, and brown color patterns on both sides of the dorsal fin as well as other distinctive body marks such as scars, notches, and dots (Mourier et al., 2012; Porcher, 2005). Similarly, rays can be differentiated using the dorsal and ventral color shapes and patterns. Sex was determined by the presence or absence of claspers for both species. Such information about shark and ray individual discrimination allowed us to avoid counting them twice and thus to generate more accurate measures of abundance. Identification was facilitated by the excellent visibility of the site (Figure 1), allowing photos and videos to be taken to confirm the identity of the animals observed.

2.5 | Statistical analysis

Statistical analyses were completed using R software (V 2.0.4; R Core Team, 2020). Statistical significance was tested at the *p*-value <.05 level. Anthropogenic variables, including information on boats, and people present on the site, were tested for collinearity using the variance inflation factor (VIF). Low multicollinearity, expressed by a VIF < 5 was revealed, suggesting low collinearity between predictor variables for the abundance of the two species of elasmobranchs. Pearson correlations were performed between the number of sharks and rays and the anthropogenic variables in order to detect possible associations between animal and human presence. Comparisons between drone and observer data were performed using χ^2 tests

FIGURE 2 Photographs from drone surveys showcasing representative abundance of sharks (red circles) and rays (yellow circles) at the Tiahura feeding site on (a) 04/29/2020 (2 days before re-opening) showing the presence of one shark; (b) 04/30/3030 (1 day before re-opening) showing the presence of four sharks and three rays; (c) 05/02/2020 (1 day after re-opening) showing the presence of eleven sharks and five rays; (d) 06/01/2020 (31 day after re-opening), showing the presence of 20 sharks and 9 rays. All images were taken at 10 a.m. and have been adjusted to optimize shark and ray counts

of independence. Comparisons between counts were done using Kruskal-Wallis rank-sum tests and pairwise comparisons post hoc tests. Given the reduced sample size for the late post-lockdown data, a power analysis was used to ensure sufficient power and reliability (power = 0.99; "kwpower" function, R-package "MultNonParam", Kolassa & Jankowski, 2021).

A site fidelity index (SFI), obtained by dividing the number of samplings where the individual was present by the total number of sessions, was calculated for all the elasmobranchs seen at least one time in the Tiahura site. Animals with SFI > 0.5 were considered as residents during the post-lockdown period sampled and thus frequently seen from the reopening of tourism activities. In order to control if the individuals responding to auditory and olfactory cues were consistent post-lockdown and to explore the potential intra-specific difference of presence pattern, the response curve of presence/absence observed during the sampling was fitted with a Loess smoother for all the photo-identified elasmobranchs. Furthermore, an accumulation curve was performed in order to estimate the number of dives needed to observe all the individuals listed.

2.6 | Ethical note and STRANGE statement

This study was conducted under a special permit issued by the Ministry of Culture and Environment of French Polynesia (ref: N°011492/MCE/ENV) from October 16, 2019, and was designed to minimize the disturbance and stress. The following statements on sampling biases are made with reference to the STRANGE framework (Rutz & Webster, 2021; Webster & Rutz, 2020). All individuals photo-identified were in their natural environment where they could interact freely with all the other animals and tourists frequenting the Tiahura site (Social background). In order to take into account the variability of daily energy expenditure of animals in such conditions, three different sessions were sampled, as explained in the "Post-lockdown abundance assessment" section (Natural changes in responsiveness). The elasmobranchs monitored had been targeted by ecotourism practices for years as described above in the "Study area and provisioning activity description" section and thus were highly conditioned to provisioning practices, minimizing the bias that might cause novelty in such a study (Rearing history, Experience). Furthermore, bias linked to potentially higher detectability of bold individuals may exist given that tourists may be perceived as a threat (Biro & Dingemanse, 2008). However, the long-term conditioning phenomenon likely decreased the natural vigilance of the focal animals being fed and viewed by humans and thus likely allowed shyer individuals to be present simultaneously (Bejder et al., 2009). Moreover, the excellent visibility at the site may have allowed the detection of individuals positioned more distantly in the visual field of the diver, and potentially displaying lower levels of boldness (Trappability and self-selection, Genetic make-up). According to the above statements, the STRANGEness of the sampling may be considered as low. All potential biases related to the STRANGE framework that could be due to inter-specific and inter-individual differences are discussed in the "**Discussion**" section.

3 | RESULTS

3.1 | Lockdown abundance assessment

The observer confined at home did not observe any significant presence of sharks during the lockdown duration. A maximum of one animal quickly crossing the area was observed in the absence of any stimulus. Nevertheless, on April 30, 2020, the observer spotted 9 elasmobranchs (6 sharks and 3 rays) aggregating after the arrival of a motorboat at the provisioning site, potentially stimulating the animals acoustically but without any food release. This was the only event where a boat was anchored in the area during the lockdown period.

The UAV videos recorded during the lockdown confirmed these observations with 1 shark and 0 rays counted on April 29, 2020 when no boats were crossing the area (Figure 2a). The shark seen was traveling without any visible change in swimming speed and only stayed for a few seconds in the UAV frame. By contrast, analysis of drone data recorded April 30, 2020 with a motorboat arriving and anchoring in the area highlighted 6 sharks and 3 rays (Figure 2b). Both species remained for several minutes in the area and noticeably increased their speed quickly after the arrival of the boat, with a trajectory directed toward the boat, and circled the boat when it stopped despite the fact that no provisioning occurred.

3.2 | Post-lockdown abundance assessment

UAV data and diver data were considered as independent using χ^2 tests during the mutual surveys (*p*-value >.05). For subsequent statistical analysis, only freediver counts were used, as they provided more samples. Data collected revealed a significant increase in anthropogenic activity between early and late post-lockdown with an intensification of the number of the motor and non-motorboats, the number of boats feeding and the number of people present on Tiahura (Kruskal–Wallis tests: *p*-value <.05 for all anthropogenic parameters) (Table 2).

From the first day of reopening, numbers of sharks (10 a.m.: 8, 12 a.m.: 11, 4 p.m.: 10) and rays (10 a.m.: 7, 12 a.m.: 9, 4 p.m.: 4) were sufficient to allow for tourist activity to resume as normal, despite being about half of the pre-COVID levels (Figure 2c). Mean abundance levels of both species for the early post-lockdown part of the survey were 7.82 ± 3.04 sharks and 4.77 ± 2.24 rays, showing some variation between days and time of the day (Table 2). Shark abundance recorded at early post-lockdown was only comparable to the one measured in Study 1, 10 years before (*p*-value = .667) and was significantly lower than the abundances measured in other two previous studies (*p*-values <.05) (Figure 3). Early post-lockdown ray abundance was comparable to late post-lockdown ray abundance (*p*-value = .372), but was significantly lower than the one measured in Study 2, 6 years before (*p*-value = .041) (Figure 3).

Both species showed an increase in abundance during late post-lockdown compared to early post-lockdown; this increase was significant for sharks (*p*-value = .040) with a mean of 19.92 ± 2.07 individuals but non-significant for rays (*p*-value = .372) with a mean of 6.58 ± 1.31 animals (Table 2, Figure 3). One month after reopening, in June 2021, shark abundance appeared fully recovered to pre-COVID levels and comparable to the ones obtained in Study 2 and Study 3, with a minimum of 17 individuals simultaneously present (Figure 3a). Concerning ray abundance, no significant difference was either observed between early and late post-lockdown data or between late post-lockdown and Study 2 counts. This result suggests a return to BAU for rays since June 2020, but with a slower abundance increase than for sharks and a complete recovery fully achieved 1 month later in July 2020 according to tourist operators' estimation (Figure 3b).

Results of the Pearson correlations between elasmobranch abundance and anthropogenic parameters show significant and positive relationships between all the variables and numbers of sharks and rays. Indeed, the increase of the number of provisioning boats, offering both olfactory and acoustic stimuli, was linked to a significant increase in the number of individuals in the area for both species (Pearson correlation: *p* = .45; *p*-value <.001). Furthermore, the increase of the total number of boats, with or without an engine, appeared to attract elasmobranchs and showed a significant positive relationship with shark and ray presence (Pearson correlation: *p* = .64; *p*-value <.001).

A total of 31 different blacktip reef sharks, including 16 females and 15 males, and of 10 individuals pink whiprays, with 7 females and 3 males, were photo-identified (Appendix S1). Six individuals reached a SFI > 0.5, with 4 female rays and 2 male sharks. No significant correlation between SFI value and species was observed (KW: *p*-value = .21). Furthermore, no significant link between sex and higher SFI was highlighted for either species (KW: *p*-value = .053 for sharks and *p*-value = .73 for rays). The maximal SFI was 0.82 for a

TABLE 2 Description of the data collected on elasmobranch abundance and anthropogenic parameters

Variable		Minimum	Maximum	Mean	SD
Number of blacktip reef sharks	Early post-lockdown	1	16	7.82	3.04
	Late post-lockdown	17	23	19.92	2.07
Number of pink whiprays	Early post-lockdown	0	10	4.77	2.24
	Late post-lockdown	5	9	6.58	1.31
Number of boats provisioning	Early post-lockdown	0	4	1.50	0.81
	Late post-lockdown	1	4	2.83	0.94
Number of motorboats	Early post-lockdown	0	10	2.45	2.09
	Late post-lockdown	3	14	7.33	3.14
Number of non-motorboats	Early post-lockdown	0	6	0.84	1.19
	Late post-lockdown	3	9	6.58	1.83
Number of people	Early post-lockdown	1	45	8.48	8.35
	Late post-lockdown	24	119	60.17	35.70

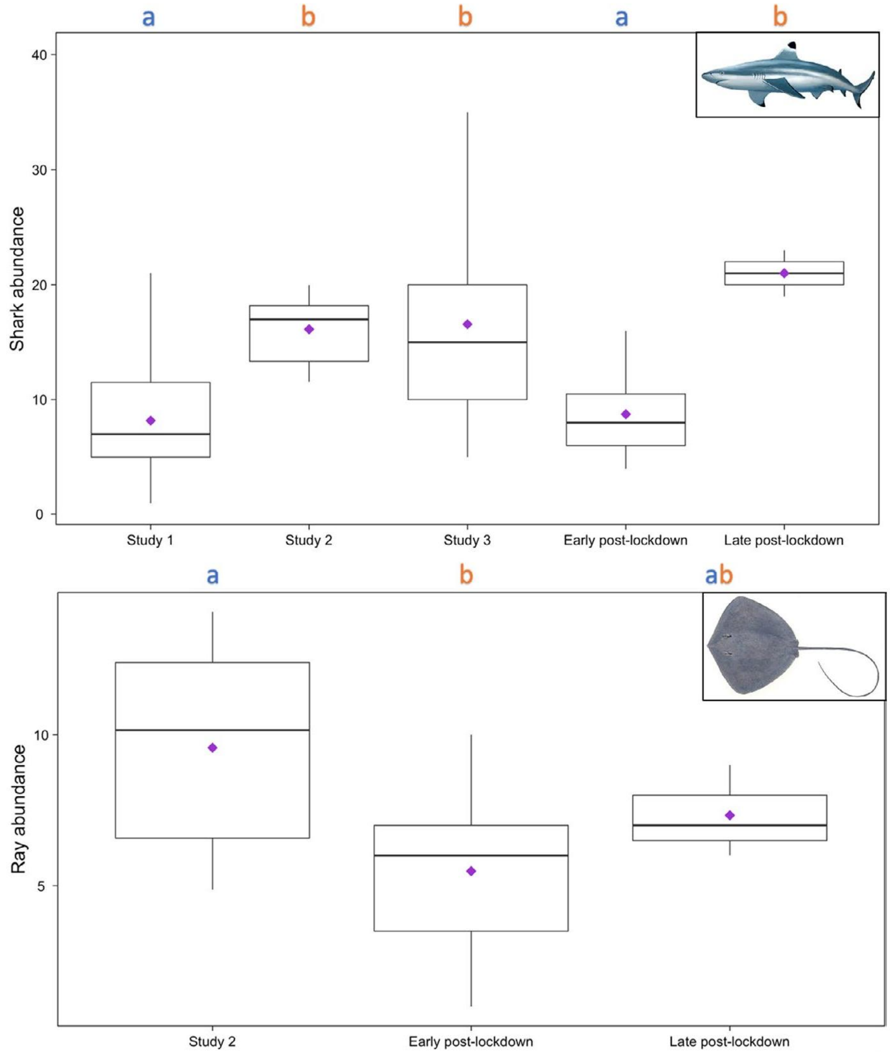

FIGURE 3 Abundance of blacktip reef sharks (Carcharhinus melanopterus) and pink whiprays (Pateobatis fai) furnished by several studies completed in Tiahura. Boxplots not sharing the same letter are significantly different in pairwise comparisons (p-value <.05). Purple dots represent mean values of the abundance for the study considered. Note that the y-axis varies with species

female ray. Nine individuals displayed a SFI < 0.1 (6 sharks and 3 rays) and 2 of them were seen only once (2 female rays).

The probability of individual presence varied among the individuals observed (Appendix S2). Indeed, despite the majority of the animals showing an increase in their presence probability with time, it is interesting to note an inflection of the presence probability during the second week for the majority of individuals present since the beginning, before increasing again at late post-lockdown. Furthermore, 12 individuals from both species (29% of the total number of individuals targeted) showed a maximum in their probability of presence during early post-lockdown, with a reduced probability during late post-lockdown. Among the six individuals spotted from the first day after reopening of tourism activities, only one of them displayed a SFI > 0.5.

Accumulation curves showed a strong increase in the numbers of individual sharks and rays spotted after reopening of the Tiahura site and then asymptotes after half the first week. Indeed, 90% of the animals were seen after 97 samples (beginning of the second week after reopening) for blacktip reef sharks and 63 (end of the first week after reopening) for pink whiprays, both during early post-lockdown. All the rays identified visited Tiahura after 86 samples, and then during early post-lockdown (beginning of the second week after reopening), but three individuals among the sharks we photo-identified were only spotted after 129 samples, from June 1, 2020, during the late post-lockdown (Figure 4).

4 | DISCUSSION

Using drones and underwater observations, we were able to accurately monitor the presence and abundance of two elasmobranch species at a specific feeding site for ecotourism purposes after a 6-week break in provisioning. Based on the reaction of several animals from both species to a single acoustic stimulus (a motorboat) 1 day prior to the re-opening of the site, our findings suggest that sharks and rays can remember stimuli for periods exceeding 6 weeks (i.e., we observed a positive reaction to a CS in both species). This result confirms the resilience of conditioning as described following deliberate cessation of artificial stimuli in previous studies for other elasmobranch species (Clark, 1959; Fuss & Schluessel, 2015; Guttridge & Brown, 2014; Heinrich et al., 2021). The fact that both species were attracted with a single sound stimulus supports previous findings on Pink whipray (Gaspar et al., 2008), white sharks (*Carcharodon carcharias*) (Bruce & Bradford, 2013), and Port-Jackson sharks (*Heterodontus portusjacksoni*) (Pouca & Brown, 2018), showing a possible cognitive connection of two linked stimuli (food being the US). In this study, the noise of the engine appears to be an important stimulus that attracts highly conditioned blacktip reef sharks and pink whiprays. Further studies could explore a potential cognitive association between food reward and splashes (as CS) made by tourists practicing snorkeling or paddling in a highly frequented area. It has been already observed that human-induced noises caused avoidance behavior for whale sharks (*Rhincodon typus*) in the touristic site of Panaon island (Philippines) in 39% of the cases (Araujo et al., 2017). By implication, elasmobranchs may be able to associate other sound stimuli like splashes to negative events (i.e., disturbance to the animals) or positive events (i.e., food reward). Such noises linked to provisioning participants should be, therefore, considered in future codes of conduct to improve the quality and safety of the experience. Indeed, even if all paddling noises cannot be avoided, tour operators could raise awareness about reducing splash entry in the water from boats and loud fin kicking when swimming. Notably, the number of provisioning boats in our study area was significantly higher for late post-lockdown than for early post-lockdown, and the amounts and types of food and the duration of exposure were not standardized and sometimes difficult to assess, possibly biasing our results. Nevertheless, a recent study suggests that the reward magnitude has a limited effect on learning rates (Heinrich et al., 2020) when it is hypothesized that CS could play an important role in associations made by sharks with the presence of baits. Thus, the bias potentially caused by the possible differences in provisioning effort between early and late post-lockdown may be considered as minimal, as CS was present since the first day of reopening.

Previous studies have shown that in some places, focal species, such as bull sharks (*Carcharhinus leucas*) and whitetip reef sharks (*Trianodon obesus*), are not dependent on the provisioning activities as a significant food source (Abrantes et al., 2018). However, heavy dependence has been observed in some other species, such as southern stingrays (*Dasyatis Americana*) (Semeniuk et al., 2007). This could be a sign of potential differential effects of artificial feeding depending on species and practices, which may as well occur at an intraspecific level (Brunnschweiler et al., 2017). Thus, it is expected that elasmobranchs that are fully dependent on daily provisioning activities continue to regularly visit the site, anticipating being fed. Given that the sharks and rays in Tiahura completely deserted the area during the lockdown, they may not depend on this feeding activity to sustain and satisfy their nutritional needs. However, further studies focusing on food intake would be needed to confirm this observation.

The differences observed in presence-absence patterns and return to BAU between sharks and rays could be linked to the different ecologies of these two species. Indeed, blacktip reef sharks are ram ventilators that must remain continuously swimming (Bernal et al., 2012). By contrast, pink whiprays spend most of their time motionless, sitting on (or in) the sand to save energy and avoid predation. Such a difference in their behavioral ecology and respective capacities to explore their environment could explain the slower response of rays compared to sharks to relocate to the provisioning site in spite of the return of daily olfactory and acoustic stimuli. Another explanation could be linked to differences in auditory capacities for sharks relative to rays, with the former being more efficient.

Despite the majority of photo-identified individuals displaying an increased probability of being present at the feeding site with time, strong inter-individual differences were highlighted. This intra-specific variation could be linked to physiological differences. A sudden restart of artificial provisioning could lead to a feeling of satiety owing to important and unexpected food intake. A physiological shift may be needed from natural levels of eating to chronic artificial feeding (Leigh et al., 2017; Papastamatiou et al., 2007). Sharks fed first after the reopening, still in a slow metabolism and slow digestion state, may feel "full" quickly and abandon the feeding site a few days after unnatural levels of eating, leaving space for others.

Another explanation could be linked to competition among individuals due to a rapid increase in the number of elasmobranchs

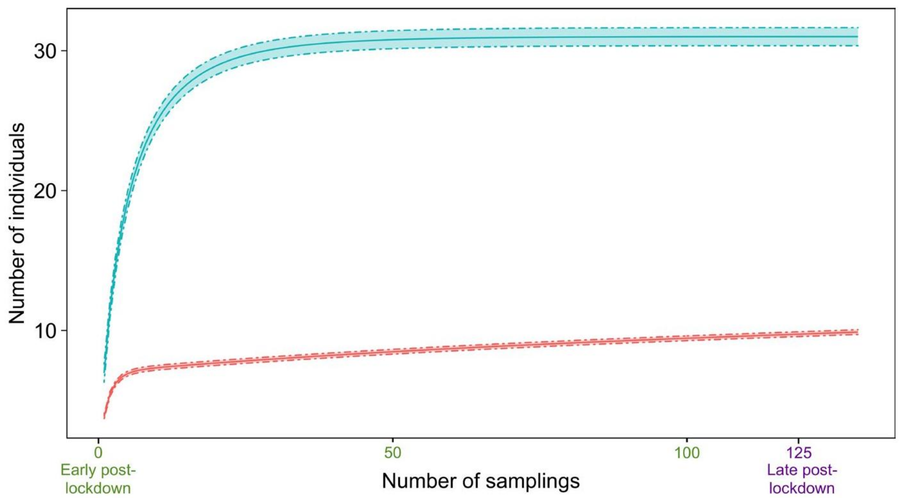

FIGURE 4 Accumulation curve of the individuals photo-identified at the Tiahura site. The blue line represents the accumulation curve for blacktip reef sharks and the red line for pink whiprays. Colored values on the x-axis represent samplings collected during early post-lockdown in green ($n = 124$) and samplings collected during late post-lockdown in purple ($n = 12$). 95% confidence intervals are highlighted for each curve

foraging in the area. Such negative interactions have already been observed for sicklefin lemon sharks (*Negaprion acutidens*) in another feeding site in Moorea, located on the outer reef, where some animals were displaying wounds inflicted during fights for dominance (Clua et al., 2010). Particularly strong dominance interactions could have occurred after reopening, but then progressively attenuated with time, allowing coexistence of different individuals in the same area of interest, as has already been shown for tiger sharks (*Galeocerdo cuvier*) around a blue whale carcass (Clua et al., 2013).

Another explanation could be the existence of clustering in the subpopulation of the elasmobranchs in the Tiahura site, with preferred associations between individuals that did not frequent the site simultaneously, as has been already suggested in the full population of blacktip reef sharks around Moorea island (Mourier et al., 2012). Residency patterns could also be different between identified individuals with resident, semi-resident, or opportunistic individuals as has been observed in sicklefin lemon shark on a provisioning site (Clua et al., 2010). The drop of in the probability of the presence of some sharks after 2 weeks could be linked to individual choices, linked to life-history traits (Mourier et al., 2013) or to individual personality (Finger et al., 2017), with shyer individuals avoiding competition or displaying higher exploratory behavior encouraging foraging on new sites.

Even if it is still too early to evaluate the long-term effects of the COVID-19 pandemic, the present study on the Tiahura provisioning site in Moorea suggests a limited impact on elasmobranch tourism in the area due to the fast recovery to before-lockdown abundances of blacktip reef sharks and pink whiprays. Regarding the sustainability of tourism practices, the near desertion of the site during the Anthropause and the decrease in abundance observed at early post-lockdown provide more evidence that feeding elasmobranchs may not necessarily lead to drastic ecological change that cannot be reversed. Whatever their level of conditioning, our results suggest provisioned sharks and rays can adapt when provisioning stops, and then return when provisioning resumes. Those findings are in line with a growing number of studies showing minimal (if any) negative effects of shark feeding on the biology and ecology of some species (Abrantes et al., 2018; Brunnschweiler & Barnett, 2013; Hammerschlag et al., 2012; Heinrich et al., 2021; Laroche et al., 2007; Maljković & Côté, 2011). Nevertheless, precautionary approaches should be taken to limit the potential negative impact of tourism on species with the high level of residency such as blacktip reef sharks (Mourier et al., 2021), with a necessity to redesign the activity with sustainable management practices if impacts are documented. It is, however, important to place the potential impacts of these tourism activities in the context of the threats faced by sharks and rays (Healy et al., 2020). Indeed, fishing and habitat loss remain the main causes of elasmobranch declines, and addressing these threats should remain the priority of conservation efforts for these species (Dulvy et al., 2014; Healy et al., 2020). Furthermore, the use of codes of conduct standardizing ways to bait animals and to behave in the water during provisioning should help to minimize the potential impacts of this tourism activity on wildlife and on the safety of participants (Abrantes et al., 2018; Clua, 2018; Clua & Torrente, 2015; Gallagher et al., 2015; Healy et al., 2020; Newsome et al., 2004; Zimmerhackel et al., 2019) while increasing the ecological and economic benefits (Semeniuk et al., 2009; Zimmerhackel et al., 2018). Evidence in the wild, including from this study, reveals strong levels of conditioning in sharks and rays strengthens the need for these codes of conduct to be adopted, implemented, and enforced in every provisioning site around the world. Our study reveals that conditioning stability is so strong that a cessation of the activity, even for several weeks (up to six in this case), has no significant impact on the conditioning of the animals. Therefore, efforts to reduce potentially deleterious effects of provisioning on animals should not rely on temporary feeding stoppages and instead focus on standardizing and optimizing both provisioning practices, which currently vary considerably among operators, as well as human behavior in the water.

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DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Evidence of long-lasting memory of a free-ranging top marine predator, the bull shark *Carcharhinus leucas*

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Abstract

Recent studies suggest sharks cognitive abilities are comparable to other vertebrates such as mammals and birds, but we still know relatively little about the long-term memory capacity of sharks. We took advantage of the COVID-19 anthropause to determine whether bull sharks conditioned at a provisioning ecotourism site in Fiji would remember the site after an 18-month hiatus in shark feeding activities. We hypothesized that if bull sharks remembered the food rewards associated with divers at the site, they would return to the reactivated site more rapidly than the original recruitment process that occurred when the site was first established in, 2015. We assumed that original recruitment to the newly established site represent a period of learning and conditioning, whereas a significantly faster recolonization of the site would imply memory recall of the original conditioning. We monitored bull shark abundance at the site for three years (1018 dives) from its original establishment in 2015 until all feeding and diving activities were ceased for 18 months in December, 2020. When shark feeding resumed, we documented bull sharks returning to the site over a three-week period (45 dives beginning June 22, 2022) and compared observed abundances with modelled predictions assuming no interruption to provisioning. Results revealed a rapid return

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to ‘business as usual’, suggesting that bull sharks still remembered the food reward conditioning despite an 18-month hiatus in provisioning. This supports the existence of long-lasting cognitive capacities in this species and highlights their relevance for managing activities that could disrupt their natural ecology.

Keywords
anthropause, conditioned behaviour, elasmobranch cognition, memory retention, provisioning.

1. Introduction

Elasmobranchs cognitive abilities have been recently recognized as comparable to most other vertebrates, including mammals and birds (Brown & Schluessel, 2022). However, conducting experiments to assess their cognition is very challenging, particularly on free-ranging adult sharks (Schluessel, 2015, Finger et al., 2017, Brown & Schluessel, 2022). Of particular interest is the sharks’ ability to form and retain memories because this capability can confer strong fitness advantages (Fuss & Schluessel, 2015, Brown & Schluessel, 2022). Previous captive studies suggest that the memory capacity of sharks may be linked to their behavioural ecology and can vary between individuals of the same species. For example, memory retention has been estimated to vary from 24 hours to more than 40 days in juvenile Port-Jackson sharks (*Heterodontus portusjacksoni*) (Guttridge & Brown, 2014), over 12 weeks in juvenile lemon sharks (*Negaprion brevirostris*) (Heinrich et al., 2021), and even over 50 weeks in some juvenile grey bamboo sharks (*Chiloscyllium griseum*) (Fuss & Schluessel, 2015).

Shark provisioning (i.e., artificially feeding wild sharks) is a practice used to aggregate sharks at specific sites for tourism purposes, and thus generally leads to the conditioning of targeted animals (Gallagher et al., 2015). Shark provisioning sites provide valuable opportunities for longitudinal studies of shark behaviour, biology, and movement patterns because of the predictable long-term presence of target species and individuals at these locations (Brunnschweiler & Barnett, 2013, Bègue et al., 2020). The COVID-19 pandemic lockdown shut down tourism and created unique opportunities to study the effect of the cessation of these activities on wildlife (Bates et al., 2020, Rutz et al., 2020). To date, two studies have explored the effect of COVID-19 pandemic interruption of provisioning on shark biology and behaviour. Huveneers et al. (2021) found no significant effect of a 51-day cessation of provisioning on the biology and movements of free-ranging great white sharks (*Carcharodon carcharias*). Séguigne et al. (2022) found that wild blacktip reef sharks (*Carcharhinus melanopterus*) returned to 'business as usual' behaviour and abundance at an ecotourism site within one month after a 6-weeks shutdown of shark feeding despite completely deserting the site during the pandemic lockdown. However, no study to date has specifically evaluated long-term memory retention in large wild sharks.

Fiji is renowned for shark diving, notably within the Shark Marine Reserve established in, 2002 at the Beqa Lagoon area (Brunnschweiler, 2010), where four companies currently operate shark feeding sites. In September, 2015, a new shark feeding site was established by a single operator on a remote reef in Western Fiji. The main target species is the bull shark (*Carcharhinus leucas*), a large (>3 m total length), primarily coastal marine apex predator. This species is in global decline and is listed as 'Vulnerable' to extinction on the IUCN Red List (Rigby et al., 2021). The COVID-19 lockdown shut down daily shark feeding at the provisioning site for 18 months (December, 2020 to June, 2022). Provisioning resumed in June, 2022, offering the opportunity to study the return of adult bull sharks to the site.

We hypothesized that strong retention of conditioning would result in a rapid return to 'Business as usual' (BAU) bull shark behaviours and pre-COVID abundances at the ecotourism site once daily provisioning resumed, whereas weak memory retention would require conditioning to restart from baseline levels.

2. Material and methods

2.1. Study area and description of provisioning activity

The study was carried out off Kuata island (17°23′21″ S, 177°4′52″ E) in the Yasawa archipelago in Western Fiji (Figure 1A). Twice-daily provisioning to attract bull sharks (*Carcharhinus leucas*) occurs at two co-located dive sites at depths of 22 and 12 m (Figure 1B). Other species such as tiger sharks (*Galeocerdo cuvier*), lemon sharks (*Negaprion acutidens*), nurse sharks (*Nebrius ferrugineus*), whitetip reef sharks (*Triaenodon obesus*) and blacktip reef sharks (*Carcharhinus melanopterus*) also visit the site sporadically. A single dive operator uses this site resulting in carefully controlled and monitored provisioning carried out according to a sustainable code of conduct to minimize disturbance and avoid overfeeding.

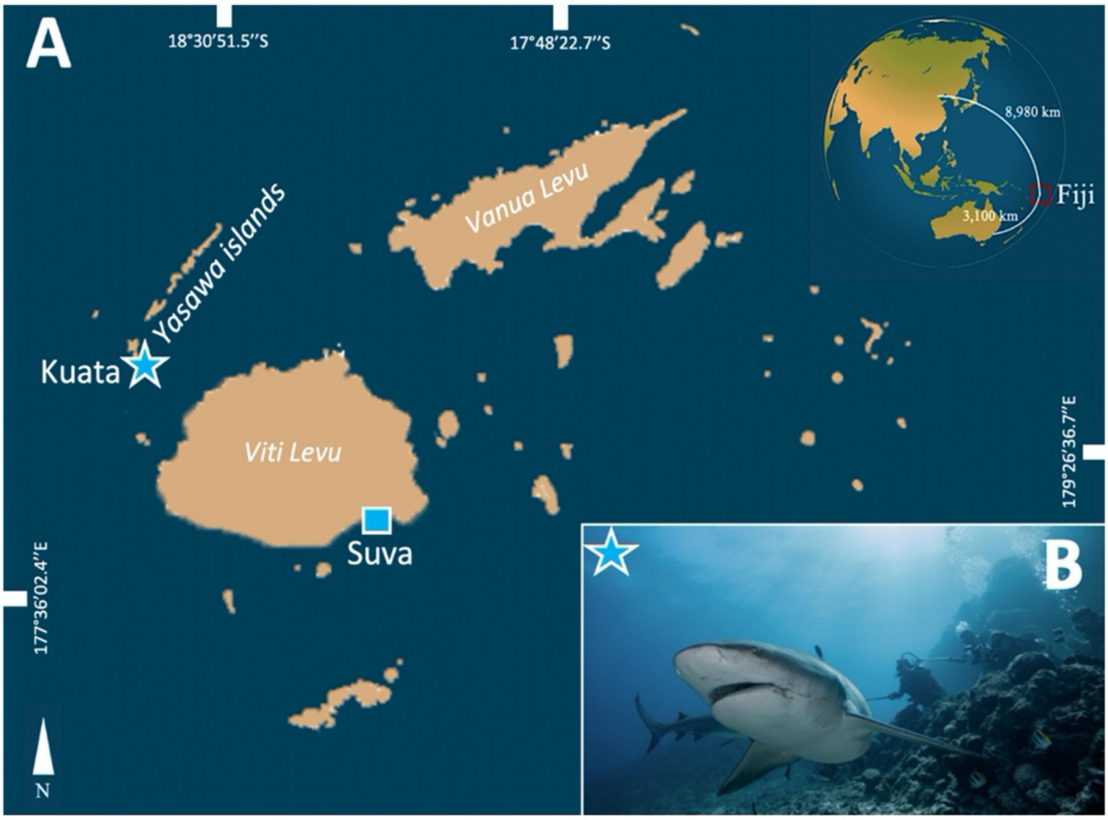

Figure 1. Study area. (A) Location of Kuata (Western Fiji). (B) View of a provisioning session at the 12-m depth ecotourism site from the feeder and bodyguard perspective (Photo credit: T. Vignaud).

From September 13, 2015 to December 17, 2020, sharks were fed near daily when weather conditions were suitable for safe diving and accurate data collection (i.e., stable visibility, moderate currents). Each 30–45-min dive utilized 5–10 fish heads (mainly yellowfin tuna, *Thunnus albacares*) sourced from commercial fisheries waste. Over time, several individuals became highly conditioned to diver presence, and were reliably present at the provisioning site during feeding hours but not at other times (T. Vignaud, pers. obs.). We quantified changes in bull shark abundance over time at the provisioning site during 1018 dives spanning from the first day of provisioning on September 13, 2015 to January 13, 2018.

All provisioning ceased during COVID-19 lockdowns between December 18, 2020 and June 2, 2022, and then resumed using pre-lockdown protocols on June 3, 2022. To quantify the impact of the long hiatus in provisioning activity on the bull shark presence, we monitored their abundance and behaviour at the dive sites for 4 weeks following resumption of shark feeding (45 dives from June 3, 2022 to July 4, 2022). Pre-COVID data were recorded by T. Vignaud, and post-COVID data were recorded by T. Vignaud and C. Séguigne.

2.2. *Data collection*

Bull shark abundance and presence of known individuals were recorded every 15 min during dives conducted before and after the lockdown. Accuracy of counts and individual identifications was further enhanced by reviewing photos and/or videos taken during every dive. Individual bull sharks were uniquely identified using a combination of traits including sex, size, colours pigmentation and patterns, body shape, and unique marks and nicks, previously used to identify individual bull and sicklefin lemon sharks (*Negaprion acutidens*) in other studies (Buray et al., 2009, Brunnschweiler & Baensch, 2011, Bouveroux et al., 2021).

2.3. *Time series analysis and forecasting*

Data analyses were conducted using R (V 4.2.2, R Core Team, 2022) with a significance level set to 0.05. We examined both skewness, reflecting distribution asymmetry, and kurtosis, measuring deviation of distribution tails from a normal distribution. To assess normality, we sought skewness values between -2 and $+2$, combined with kurtosis values between -7 and $+7$, as recommended by Hair et al. (2010). Following these criteria, the number of bull sharks reported per dive pre- and post-cessation of provisioning demonstrated normality: $\text{Skewness}_{\text{before}} = -0.050$, $\text{Kurtosis}_{\text{before}} = 2.20$; $\text{Skewness}_{\text{after}} = -0.53$, $\text{Kurtosis}_{\text{after}} = 2.87$.

Because we collected data almost every day, except during unfavourable conditions, we chose to use a weekly time scale to show the abundance of bull sharks over time. We employed Seasonal Trend decomposition using Loess (STL) to visualize the variations in weekly bull shark abundance across the data collection period preceding the lockdown. This facilitated the identification of potential trends, seasonal patterns and residual variations, representing the data variability not accounted for by trends and seasonality (Cleveland et al., 1990). We employed a Signal-to-Noise Ratio (SNR) metric that gauges a signal's strength against background noise in a time series. SNR helped to assess the importance of trend and seasonal components obtained from the STL decomposition. A SNR exceeding one denoted significance, while a value below one implied observed variability ascribed to noise (Hyndman & Athanasopoulos, 2018).

We employed forecasting methods to predict the future trajectory of weekly mean bull shark abundance per dive following the initial sampling period. Those previsions enabled the modelling of a 'Business as usual' (BAU) abundance, subsequently compared with actual post-lockdown data. This approach facilitated a precise assessment of the impact of provisioning interruption on observed bull shark abundance during dives. Given the pronounced trend and seasonal patterns in the time series data, we opted for forecasting methods that accounted for these components. Thus, we utilized the forecast R package (Hyndman & Khandakar, 2008) to conduct a seasonal AutoRegressive Integrated Moving Average (ARIMA) and a Seasonal Trend decomposition using Loess and Forecasting (STLF) models. Both methods are widely recognized for their effectiveness in time series forecasting, adept at handling intricate seasonal patterns and trend shifts, even within extensively segmented data.

We assessed model accuracy using Root Mean Squared Error (RMSE), Mean Absolute Error (MAE) and Mean Absolute Squared Error (MASE). RMSE calculates the square root of the average squared difference between forecasted and actual values. MAE computes the average absolute difference between forecasted values and actual values. MASE evaluates the mean absolute error of the forecast relative to the mean absolute error of a simple naïve forecast, which uses the last observed value as the next period's forecast. A value below 1 indicates superior prediction compared to a naïve forecast (Hyndman & Athanasopoulos, 2018). The chosen forecast for comparison with post-lockdown data was the one displaying the lowest values across these measures.

We employed a Kruskal–Wallis test to determine whether there were significant differences in bull shark abundance values collected after provisioning interruption based on the sampling week. In case of significance, pairwise comparisons were conducted using the Dunn post-hoc test from the dunn.test R package (Dinno & Dinno, 2017).

2.4. *Accumulation curves*

We generated accumulation curves using the vegan R package (Oksanen et al., 2013) to visualize the number of dives required to observe all photo-identified sharks. To compare the rate at which *C. leucas* individuals accumulated before and after the lockdown periods, we used a standardized sample size of $N = 45$ dives for each period. This evaluation focused exclusively on sharks that had been identified previously.

We predicted that if bull sharks remembered the food rewards associated with divers at the site, they would return to the reactivated site more rapidly than the original recruitment process that occurred when the site was first established in 2015. Conversely, if sharks had forgotten about the provisioning site then their accumulation rates would mirror the original recruitment to the newly established site in 2015.

3. Results

3.1. Description of bull sharks' presence before lockdown

The first recorded sighting of a bull shark at the site occurred on October 11, 2015, after a series of 20 provisioning dives starting on September 13, 2015. Over the course of 1026 dives, the number of bull sharks observed per dive ranged from 0 to 19 individuals (mean $= 7.14 \pm 4.4$). A notable upward trend persisted throughout the study ($SNR_{trend} = 3.94$), characterized by a strong increase in the weekly mean number of bull sharks per dive until February, 2017, when the pace slowed, signalling the start of a stabilization phase. However, the data collection did not reach a stable plateau by its conclusion on January 13, 2018, prompting additional forecasting analysis (Figure 2B).

Although a consistent upward trend in the weekly number of bull sharks per dive was evident as time progressed, notable fluctuations due to seasonality emerged ($SNR_{seasonality} = 1.59$) starting from 2016. The peak abundance of *C. leucas* at the site occurs between April and September, followed by a decline until the subsequent cycle, except for February, which registers a distinct peak in bull shark abundance (Figure 2C).

Forty-eight individual bull sharks (40 females and 8 males, see Appendix at 10.6084/m9.figshare.24063942) were uniquely photo-identified between September 13, 2015 and January 13, 2016. Ninety dives over four months were required to observe 90% of the photo-identified animals (by January 13, 2016). These four months likely encompassed the time needed to expose most potentially identifiable animals to provisioning stimuli (Figure 3).

3.2. Forecasting of the evolution of bull sharks' abundance with time

The optimal seasonal ARIMA model, ARIMA $(3,1,0)(0,1,0)_{52}$, aligns with the weekly data's annual seasonality. This model incorporates 3 autoregressive terms to account for historical values, one non-seasonal difference for

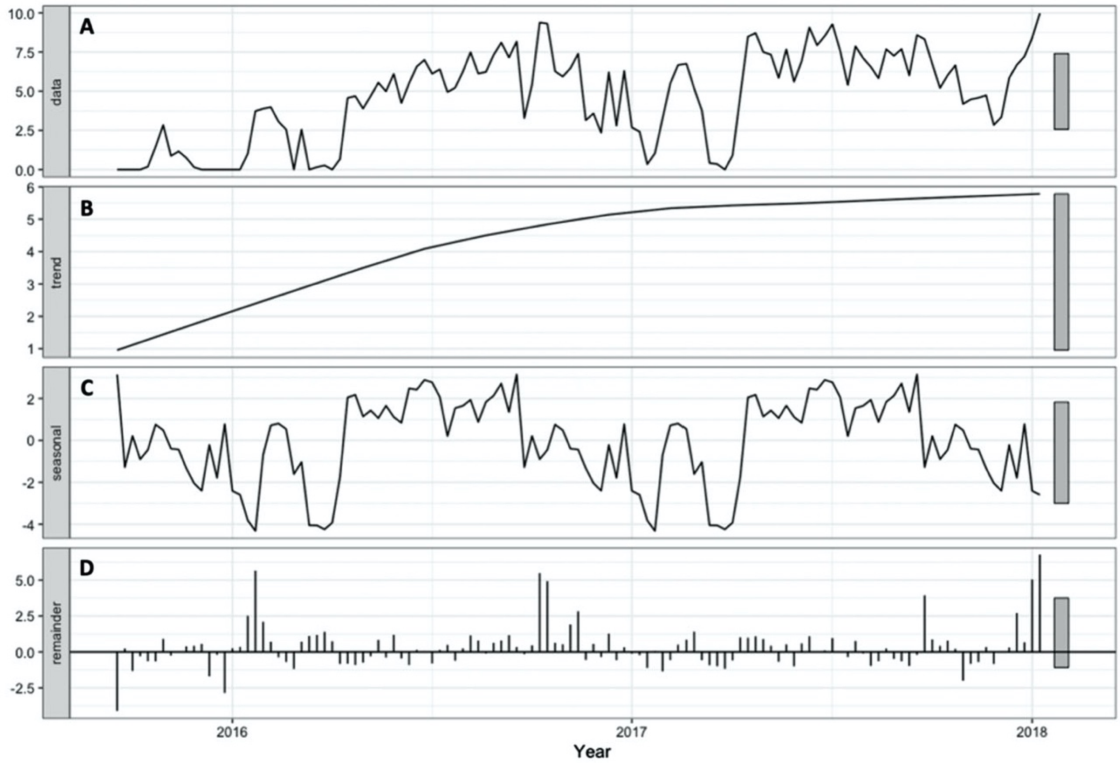

Figure 2. Weekly mean number of bull sharks per dive between September 13, 2015 and January 13, 2018 (A) Seasonal Trend decomposition using Loess (STL) was used to decompose the series into its trend (B), seasonal (C) and remainder (D) components.

time series stationarity, and no moving average terms. While it lacks seasonal autoregressive terms, it employs a seasonal difference to accommodate seasonal variations, without involving seasonal moving average terms. The ARIMA's accuracy measurements were RMSE = 2.48, MAE = 1.56 and MASE = 0.45. In contrast, the STLF forecast yields superior outcomes, with all accuracy measures showing improvement (RSME = 1.82, MAE = 1.46 and MASE = 0.37). As a result, the STLF forecast was selected for further analysis.

3.3. Comparisons between predicted and observed data

No bull sharks were initially present when provisioning resumed on June 3, 2022. However, on the following day, two bull sharks appeared, including a previously identified individual (Cl13F, see Appendix at 10.6084/m9.figshare.24063942). Bull sharks were present on all subsequent dives with the number of individuals sighted per dive fluctuated between 0 (only on the first day) and 26 (mean = 16.54 ± 6.2). Shark abundance exhibited significant weekly variations (Kruskal–Wallis test: $\chi^2 = 30.9$; df = 5;

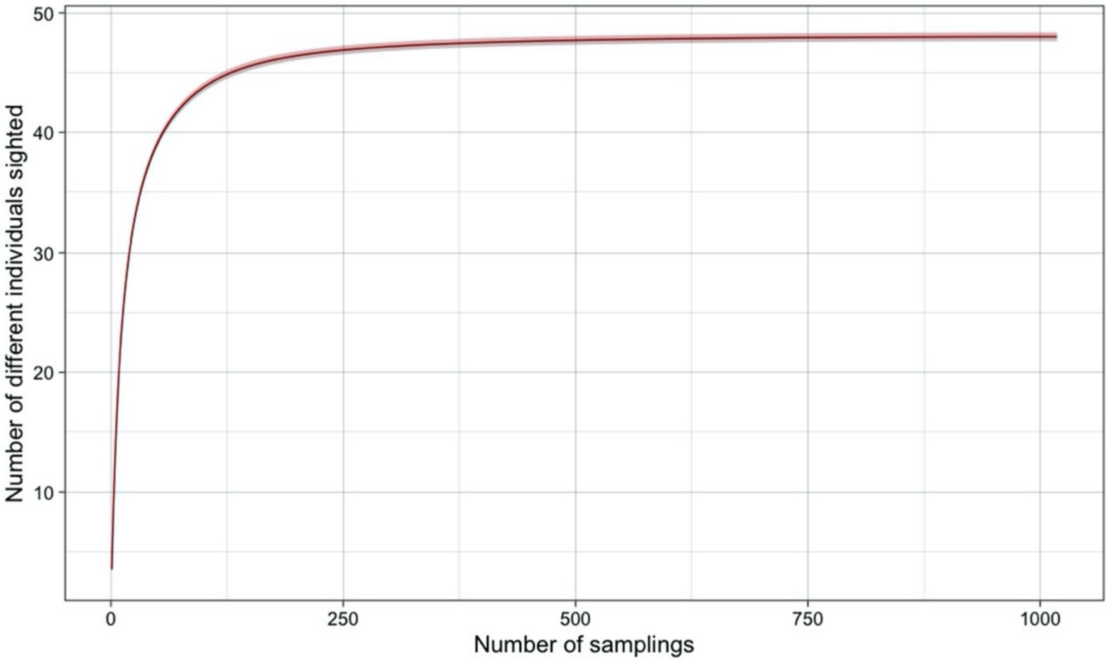

Figure 3. Accumulation curve of photo-identified individuals at the Kuata provisioning site during the data collection campaign anterior to lockdown ($N = 1026$ dives). 95% confidence interval is highlighted.

$p < 0.00001$). Bull sharks were significantly less abundant at the provisioning during the first week of post-lockdown sampling compared to all subsequent weeks (Dunn post-hoc test: p-values < 0.05). Bull shark abundance appeared stable from the fourth week onward, with the last three sampled weeks exhibiting no significant difference based on the Dunn post-hoc test (p-values > 0.05).

All weekly mean numbers of observed bull sharks per dive fell within the 95% confidence interval of the STLF forecast except the first week of sampling which lay outside the 30% confidence interval. According to our model, from the second week onwards observed bull shark abundance mirrored what would be anticipated if shark provisioning had continued uninterrupted by the COVID-19 lockdown (Figure 4).

3.4. Comparison of the shape of accumulation curves before and after the lockdown

During post-lockdown dives, a total of 29 individuals (13 males, 16 females) were photo-identified including 13 (45%) bull sharks previously observed before the lockdown (see Appendix at 10.6084/m9.figshare.24063942). Only 9 dives were needed to observe 90% of the sharks identified during the post-

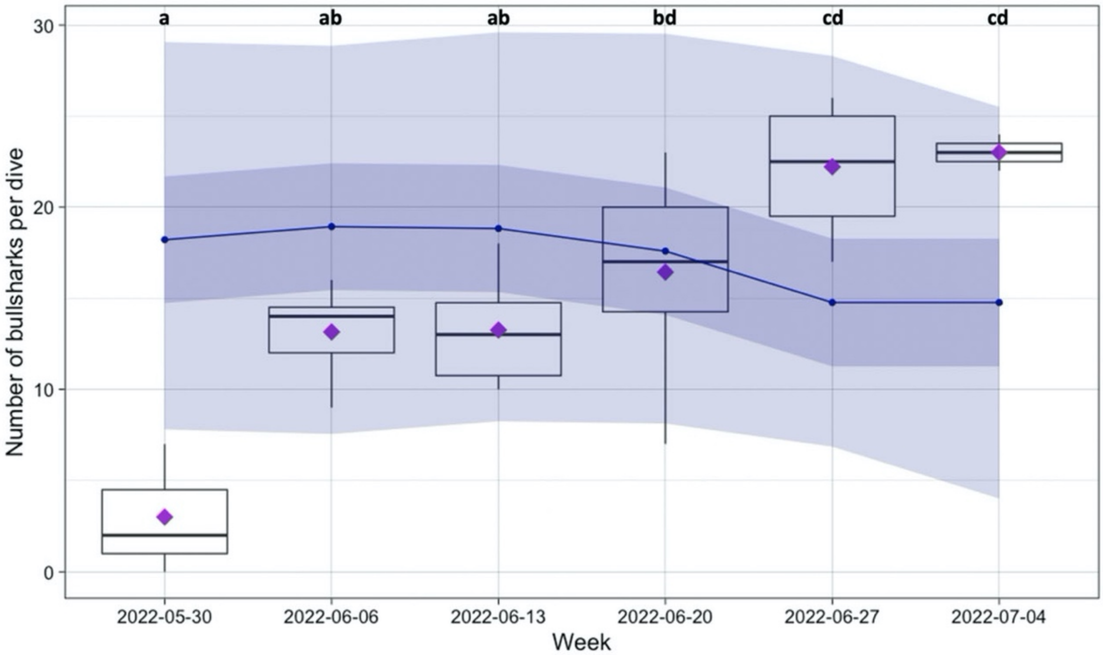

Figure 4. Boxplots represent the number of bull sharks per dive collected from June 3, 2022 to July 4, 2022. Boxplots not sharing the same letter are significantly different in pairwise comparisons ($p < 0.05$). Purple dots represent the mean values of the abundance for the study considered. The blue line shows the predictions of the STLF with light blue ribbon for a 30% confidence interval and darker blue ribbon for a 10% confidence interval.

lockdown period. In contrast, during the initial provisioning phase, which also occurred during the peak sighting season, only 5 animals were spotted in the same number of dives and a total of 25 dives were needed to observe 90% of the known bull sharks, which is more than twice the effort required during the post-lockdown period (Figure 5).

4. Discussion

When shark feeding resumed after an 18-month hiatus, bull sharks quickly returned to the feeding site and resumed the 'Business As Usual' (BAU) behaviour. This result is best explained by bull sharks remembering the association between divers and food at this location for 18 months despite no on-going reinforcement of this conditioning. Thus, sustained provisioning may lead to long-lasting conditioning in this species. Other elasmobranch species also remember conditioning (Clark, 1959, Guttridge & Brown, 2014, Fuss & Schluessel, 2015, Heinrich et al., 2021, Séguigne et al., 2022) but our study demonstrated retention of memories over a longer period than previous studies (18 months).

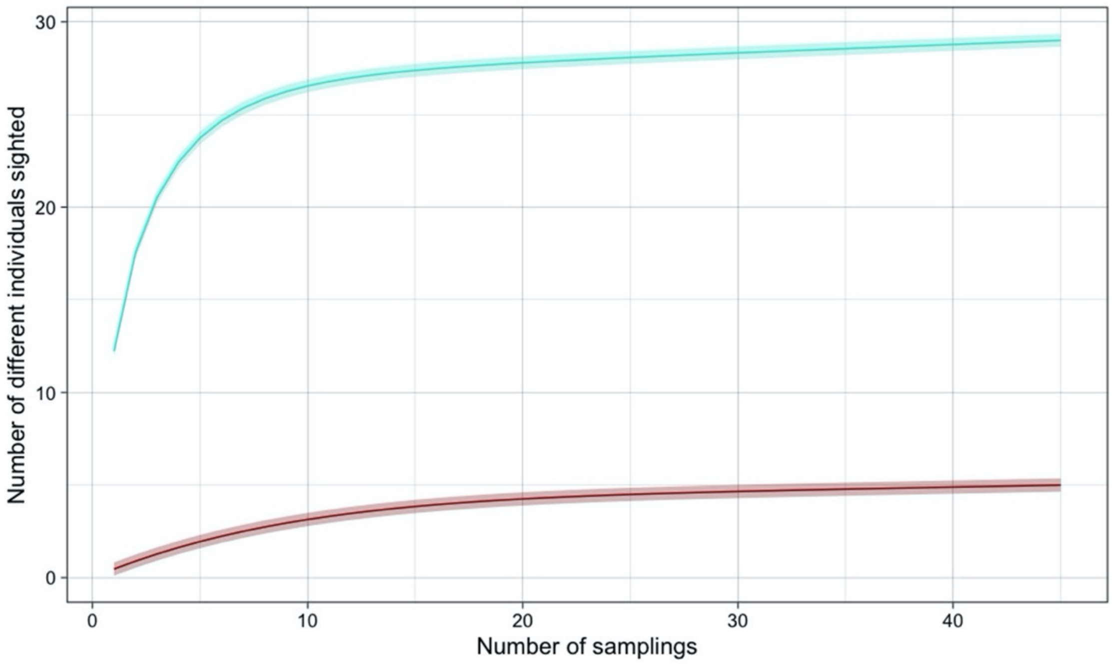

Figure 5. Accumulation curves of the photo-identified individuals at the Kuata provisioning site during the data collection campaign. The red line shows the accumulation curve obtained at the beginning of provisioning process and the blue line shows the results of the reopening of tourism activity, both considering the same sampling scale ($N = 45$ dives). 95% confidence intervals are highlighted.

Bull shark abundance at the shark feeding site returned to pre-COVID levels only one week after resumption of provisioning, markedly quicker than blacktip reef sharks (*Carcharhinus melanopterus*) which took one month to return to BAU levels at a provisioning site in French Polynesia (Séguigne et al., 2022), despite their high site fidelity to small home ranges and a shorter cessation of shark feeding (6 weeks). One possible explanation for this disparity lies in species ecology: blacktip reef sharks are mesopredators, whereas bull sharks are apex predator (Roff et al., 2016). This ecological distinction likely shapes the trade-offs they encounter, from preserving information vital for foraging to conserving energy through memory erasure. The blacktip reef shark faces potential predation, primarily from larger sharks, possibly necessitating increased energy expenditure for anti-predation measures. Such trade-offs are evident in mesopredators like tarpons (*Megalops atlanticus*), which balance food assimilation risks against energy-intensive osmoregulation for reduced predation (Hammerschlag et al., 2012). Consequently, apex predators like bull sharks may allocate more energy to foraging activities compared to mesopredators, potentially explaining their memory retention compared with blacktip reef sharks. Additionally, factors like bull sharks' multi-decades lifespans, access to high-energy food and larger brains could enable them to develop strategies akin to long-lived creatures such as elephants, with associated benefit of enhanced memory (Hart et al., 2008, Yopak, 2012, Yopak & Lisney, 2012).

The faster recruitment of bull sharks to the feeding site on resumption of feeding in, 2022 compared to the initial establishment of the site in, 2015 also suggests that these sharks remembered their conditioning for 18 months. The number of unique individuals observed after 45 dives increased five-fold following resumption of shark feeding, and the time required to identify 90% of the known sharks halved. This disparity in accumulation patterns between the two sampling periods implies a significant shift in the way animals recruited to the site. The post-COVID recruitment was probably faster simply because it was facilitated by prior conditioning. The rapid reappearance of certain specific individuals probably reflects the natural overlap between the provisioning sites and limited coastal home ranges (about 5–6 km daily on average; Carlson et al., 2010) of those individuals.

Only 45% of sharks observed during the post-lockdown period had been previously identified, although this value is likely an underestimate. Our initial scientific data collection ended in January, 2018, but provisioning continued until the COVID-19 lockdown. Consequently, some conditioned sharks may have been excluded from our original dataset and/or the one-month post-lockdown sampling period was insufficient to cycle through all previously conditioned sharks. Sharks exhibit inter-individual variability in activity patterns and movements potentially leading some to be naturally absent during post-lockdown sampling (Meyer et al., 2009, Papastamatiou et al., 2010, Brunnschweiler & Barnett, 2013, Séguigne et al., 2023). Previously documented individuals may also have been caught by fisheries or attracted to alternate provisioning sites in Pacific Harbor and Beqa Island (Southern Viti Levu) that reopened 12 months before Kuata island. Bull sharks were observed moving between distant Fiji provisioning sites before lockdown (Vignaud pers. obs.; Bouveroux et al., 2021).

Post-lockdown sightings revealed an influx of new sharks starting with the first bull sharks observed at the feeding site. This could result from the species' preference for associations with conspecifics (Bouveroux et al., 2021) leading to naïve sharks being guided to the site by experienced individuals. Many newcomers were young and occasionally immature and could be juvenile sharks expending their home range (Werry et al., 2011) until they overlap with the provisioning site and thus become new 'recruits'.

Despite resilient conditioning due to provisioning practices, bull sharks did not become permanent residents at the shark feeding site. High turn-over was consistently observed among the individuals present on the site, with most individuals staying only a few days before disappearing, sometimes for over 6 months. This phenomenon has been previously noted in bull sharks (Brunnschweiler & Barnett, 2013), as well as blacktip reef sharks (Séguigne et al., 2022) and whitetip reef sharks (*Triaenodon obesus*) (Abrantes et al., 2018), reaffirming the limited impact of artificial feeding on their natural behaviour. Seasonal patterns of bull shark abundance suggest a limited impact of artificial provisioning on natural movements. For instance, these bull sharks vanish during the *Lutjanus bohar* spawning aggregation, suggesting that they opt for natural feeding events over artificial one (Vignaud, pers. obs.). Similar patterns of natural prey aggregations have been observed for tiger sharks (*Galeocerdo cuvier*) (Meyer et al., 2010, Hammerschlag et al., 2015).

This study provides initial insights into the memory retention of wild bull sharks, suggesting that information about potential food availability could be retained for over a year and half, possibly even longer. This challenges the efficacy of intermittent feeding interruptions as a management strategy, not to mention the economic drawbacks of such an approach (Séguigne et al., 2022). Instead, a well-monitored and scientifically supported provisioning site enables close observation and detection of any adverse impacts on sharks or ecosystems. Moreover, while further research is necessary, the benefits of provisioning tourism for shark conservation might extend beyond the already recognized advantages, including sustainability, promotion of non-consumptive value, support for scientific research, enhancement of tourist knowledge, and positive effects on shark conservation (Clua et al., 2011, Cisneros-Montemayor et al., 2013, Gallagher et al., 2015, Sutcliffe & Barnes, 2018, Bègue et al., 2020, Mustika et al., 2020).

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Provisioning ecotourism does not increase tiger shark site fidelity

Clémentine Séguigne[1,2]✉, Michel Bègue[1], Carl Meyer[3], Johann Mourier[4] & Éric Clua[1,2]

A perennial criticism of provisioning ecotourism is that it alters the natural behavior and ecology of the target species by providing an artificial food source. Here we evaluate its impact on the long-term site fidelity patterns of tiger sharks in French Polynesia. We hypothesized that a significant impact of provisioning would lead to (1) increases in individual site fidelity over time, and (2) an increase in the number of resident individuals over time. Of 53 individuals photo-identified and monitored during > 500 dives over five years, 10 individuals accounted for > 75% of all sightings, whereas 35 sharks were sighted very infrequently. Even the most frequently observed tiger sharks exhibited overall low fidelity at the site and showed no increase in site fidelity over time. Furthermore, the number of tiger sharks sighted during each dive did not increase. The observed patterns of tiger shark sightings were best explained by natural movements, including general roaming within home ranges along the coastline and seasonal migrations. Despite the apparent lack of impact of provisioning ecotourism on tiger shark ecology in Tahitian waters, it would be prudent to implement a strict code of conduct during any future provisioning activities to maximize the safety of participants and animals involved.

The tiger shark *Galeocerdo cuvier* (Péron & Lesueur 1822) is a large (up to 550 cm Total Length)[1] apex predator in tropical and temperate waters[2]. Although routinely present in coastal shelf, reef and slope habitats[2], tiger sharks are typically rarely encountered by scuba divers in the wild, excepted under baited conditions[2,3]. This species is currently near threatened[2] with population declines evident in several locations including Northeast Australia[4] and the Arabian Seas Region[5]. Their large size and reputation as a potentially dangerous apex predator make tiger sharks a popular target species for shark ecotourism in locations such as Fiji, South Africa and the Bahamas, where in the latter it has contributed to a shark watching industry that has generated $800 million over a 20 years period[6–8]. The economic viability of shark tourism depends on predictable and sustainable sightings of the target species[9] which in the case of tiger sharks typically requires the use of attractants ranging from simple olfactory stimulus (chumming) to active feeding of individuals present in the area[10].

Shark feeding for ecotourism purposes is a controversial activity[11,12]. A primary concern is that provisioning may teach sharks to associate humans with food and thereby increase the risk of shark bites[13,14]. However, to date no demonstrable increase in shark bites has been observed at or around provisioning sites many of which have shark feeding regulations that strictly limit the amount of food that can be consumed[15–17]. A further criticism is that artificial provisioning (i.e. humans deliberately feeding wildlife) alters the natural ecology and behavior of the target species by increasing site fidelity (i.e. time spent at provisioning sites) at the expense of wider-ranging movements[18,19]. This effect is inherently difficult to assess because shark site fidelity naturally varies both inter- and intra-specifically[15,20,21]. For example, significant intraspecific variability in site fidelity is naturally present in silky sharks *Carcharhinus falciformis* (Bibron 1839)[22], sicklefin lemon sharks *Negaprion acutidens* (Rüppel 1837)[23], and bull sharks *Carcharhinus leucas* (Valenciennes in Müller & Henle 1839)[24] with some individuals showing high fidelity at specific sites while others are only occasional transient visitors. The limited evidence available to date suggests that tiger shark movement patterns are not significantly affected by provisioning[25]. Despite these inherent challenges, it is important for us to understand how provisioning activities impact shark behavior and ecology in order to effectively manage shark ecotourism activities to ensure adequate protection of these iconic species[10,26].

The major concerns surrounding provisioning ecotourism are particularly pertinent to tiger sharks because they are one of the three main shark species routinely implicated in unprovoked bites on humans (second only to white sharks *Carcharodon carcharias* (Linnaeus 1758))[27] and show considerable natural variability in movement patterns, often showing fidelity to a specific "home" island, but also able to roam thousands of kilometers

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into open-ocean[28]. Tiger sharks variously show high site-fidelity to core use areas (CUA) and wide-ranging movements in coastal habitats, and wide-ranging movements and multi-month residence times in open-ocean in both the Indo-Pacific and Atlantic regions[29–32]. Seasonal migrations by tiger sharks have been documented in the Atlantic, Indian and Pacific Oceans[31,33,34], and appear to be linked to sea surface temperature (SST), especially in more temperate regions toward the latitudinal limits of tiger shark distribution[31,34]. Tiger sharks occur in SSTs ranging from 18 to 33 °C but coastal abundance and swimming performance of tiger sharks are both highest at ~ 22 °C, suggesting thermal constraints on performance may regulate this species' distribution[35–37].

Tiger sharks were a focal species at the "Vallée Blanche" (VB) shark ecotourism dive site in Tahiti (French Polynesia) where shark provisioning activities occurred from 2011 until October 2017 when shark feeding was officially banned (Law of the Country 2017–25). The regular ecotourism activities at the VB site from October 7, 2012 to October 9, 2017 provided an opportunity to study the long-term impacts of provisioning on tiger shark abundance and site fidelity. We hypothesized that an impact of provisioning on tiger shark movement patterns would result in (i) increased fidelity of individual tiger sharks over time (i.e. visiting on more days and being present for longer periods), and (ii) an increase in the number of individuals observed per dive over time.

Results

Tiger shark relative abundance. A total of 1027 tiger shark sightings were recorded at the VB site during 544 dives conducted between 7 October 2012 and 9 October 2017. Among the 1027 sightings, 855 (84%) were of individuals previously documented by Bègue et al.[38]. The total number of individuals observed simultaneously during each dive ranged from 0 to 8 (mean = 1.87 ± 1.30 SD). The relative abundance of tiger sharks per dive had a non-normal, non-homoscedastic distribution (Shapiro–Wilk normality test & Bartlett test of homogeneity of variances, p-values < 0.05). The number of bait drums present per dive ranged from 0 to 4 (mean = 1.38 ± 0.80 SD). Bait drum numbers had a non-normal (Shapiro–Wilk normality test, p-value < 0.0001) but homoscedastic (Bartlett test of homogeneity of variances, p-value = 0.86) distribution. No significant correlation was found between the relative abundance of tiger sharks observed per dive and number of bait drums simultaneously present (Spearman correlation, $S = 9.48 \times 10^5$, p-value = 0.17, rho = 0.10; Supplementary Fig. S1). The relative abundance of tiger sharks observed per dive did not change significantly across the years sampled (Spearman correlation, $S = 2.71 \times 10^7$, p-value = 0.66, rho = 0.019, Supplementary Fig. S2). However, within years the relative abundance of tiger sharks observed per dive was significantly higher during austral winter than austral summer (Kruskal–Wallis rank sum test, $\chi^2 = 24.95$, df = 1, p-value < 0.0001, Supplementary Fig. S3).

Site fidelity & use. Tiger sharks (n = 53) observed at the VB site were predominantly (94%) female and primarily sexually mature (64% of females, 100% of males). The sex ratio did not display any significant variation between years (Spearman correlation, $S = 2.28 \times 10^7$, p-value = 0.13, rho = – 0.068) or between seasons (Kruskal–Wallis rank sum test, $\chi^2 = 0.52$, df = 1, p-value = 0.47). The total number of sightings of each individual ranged from 1 to 109 with a mean value of 16.11 ± 28.17 (Table 1). The maximum overall SFI (SFI_g) value for any photo-identified individual was 0.2 (Fig. 1, Table 1), and the overall mean SFI_g value was 0.03 ± 0.05. Five female tiger sharks with $SFI_g > 0.1$ accounted for > 55% of the total sightings at VB despite collectively representing less than 10% of 53 photo-identified tiger sharks (Fig. 1, Table 1). The ten most frequently sighted ($SFI_g > 0.05$) individuals were all females and collectively accounted for more than 76% of the total sightings (Fig. 1, Table 1). Thirty-five (66%) of 53 photo-identified tiger sharks were sighted 5 times or less and 18 (34%) of sharks were sighted only once (Fig. 1, Table 1).

Individual annual site fidelity (SFI_a) varied with no consistent patterns evident across years (Spearman correlation, $S = 2.15 \times 10^6$, p-value = 0.76, rho = – 0.020, Supplementary Fig. S4) or between individuals (Kruskal–Wallis rank sum test, $\chi^2 = 134.14$, df = 52, p-value = 3.48×10^{-9}, no pairwise comparisons were significant with Dunn's test, Supplementary Fig. S5). Some tiger sharks were sighted during every year of the 6-year survey whereas others were absent for up to a year between sightings (Fig. 1, Table 1). The maximum annual SFI_a value was 0.413, obtained for TF01M during the first year of study, and the minimum annual SFI value was 0. The 10 most frequently sighted individuals ($SFI_g > 0.05$) did not show any significant variation in SFI_a between years (Spearman correlation, $S = 1.61 \times 10^4$, p-value = 0.66, rho = 0.067, Supplementary Fig. S6).

Despite a general trend of more frequent tiger shark sightings during the austral summer, some intra-specific variation in seasonal patterns of tiger shark sightings was also evident (Fig. 3). For example, sightings of 8 of the 10 most frequently sighted tiger sharks ($SFI_g > 0.05$, 28–109 occurrences), peaked during austral summer and were lowest during austral winter, whereas TF03M was present most frequently between January and September and TF22nM between December and June (Table 1, Fig. 3). All sharks except TF04M showed a strong intra-individual variability in presence pattern depending on the month of the year. Furthermore, 7 sharks were rarely present (presence probability < 0.05) or completely absent from the ecotourism site for several months. Other individuals (e.g. TF04M) showed less seasonal variation in presence, or had a high year round probability of presence (e.g. TF13nM) (Fig. 2). No significant difference in presence between the number of non-mature and mature individuals was observed between austral winter and austral summer (χ^2 test: $\chi^2 = 0.32$, df = 1, p-value = 0.57).

Discussion

We found no evidence of either increasing site fidelity or established resident behavior (SFI > 0.5)[39] by tiger sharks at the VB ecotourism site despite over 6 years of regular provisioning at this location. Overall site fidelity (SFI_g) of each of the 53 uniquely identified tiger sharks was low (⩽ 0.2) and the maximum annual site fidelity (SFI_a) for any individual was 0.413 and declined over time. Furthermore, no significant rise in the number of tiger sharks sighted simultaneously during each dive was apparent. This observed lack of significant impact of regular provisioning on tiger shark fidelity in French Polynesia is consistent with the results of previous studies

Shark ID	Date of 1st occurrence	Nb of occurrences	SFIg	SFIa				
				Year 1	Year 2	Year 3	Year 4	Year 5
TF02M	21/10/2012	109	0.200	**0.326**	0.305	0.125	0.168	0.181
TF01M	07/10/2012	101	0.186	**0.413**	0.219	0.227	0.114	0.087
TF03M	18/12/2012	83	0.153	0.152	0.029	0.227	0.074	**0.284**
TF13nM	31/08/2013	94	0.173	0.065	0.0343	0.133	0.087	**0.216**
TF19M	03/11/2013	80	0.147	NA	0.143	0.172	**0.188**	0.129
TF22nM	23/04/2014	53	0.097	NA	**0.248**	0.195	0.013	0
TF14M	05/09/2013	47	0.086	0.022	0.057	0.055	**0.114**	0.078
TF30nM	23/09/2014	41	0.075	NA	0.010	0.078	**0.128**	0.095
TF15M	10/09/2013	37	0.068	0.043	0.029	0.055	**0.114**	0.069
TF04M	14/03/2013	28	0.051	0.043	0.029	0.055	0.034	**0.095**
TF06nM	23/05/2013	23	0.042	0.065	0.048	**0.070**	0.013	0.034
TF11M	10/08/2013	22	0.040	0.065	0	0.055	0.020	**0.078**
TF24M	29/06/2014	15	0.028	NA	0.010	0	**0.094**	0
TM02M	22/08/2013	14	0.026	**0.043**	0.019	0.039	0.027	0.009
TF40nM	19/05/2015	11	0.020	NA	NA	0.023	**0.040**	0.017
TF34M	13/11/2014	9	0.017	NA	NA	0.008	**0.054**	0
TF17M	24/09/2013	8	0.015	0.022	0	0.023	0	**0.034**
TF21M	20/12/2013	6	0.011	NA	**0.019**	0	0.013	0.017
TF12nM	29/08/2013	5	0.009	0.022	0	**0.023**	0	0.009
TF20M	21/11/2013	5	0.009	NA	**0.019**	0.008	0.013	0
TF38M	14/04/2015	5	0.009	NA	NA	**0.039**	0	0
TF47nM	20/07/2016	5	0.009	NA	NA	NA	**0.034**	0
TF29M	12/09/2014	4	0.007	NA	0.010	**0.023**	0	0
TF45M	02/06/2016	4	0.007	NA	NA	NA	**0.027**	0
TF31nM	30/09/2014	3	0.006	NA	0.010	**0.016**	0	0
TF32M	23/10/2014	3	0.006	NA	NA	**0.016**	0	0.009
TF39nM	21/04/2015	3	0.006	NA	NA	0.008	0.007	**0.009**
TF44M	24/05/2016	3	0.006	NA	NA	NA	0.007	**0.017**
TF49M	14/08/2017	3	0.006	NA	NA	NA	NA	**0.026**
TF10M	23/07/2013	2	0.004	**0.022**	0	0.008	0	0
TF28M	31/08/2014	2	0.004	NA	**0.019**	0	0	0
TF43nM	05/04/2016	2	0.004	NA	NA	NA	**0.013**	0
TF46M	15/07/2016	2	0.004	NA	NA	NA	**0.013**	0
TF48nM	18/08/2016	2	0.004	NA	NA	NA	**0.013**	0
TF50nM	09/09/2017	2	0.004	NA	NA	NA	NA	**0.017**
TF05nM	11/04/2013	1	0.002	**0.022**	0	0	0	0
TF07M	23/05/2013	1	0.002	**0.022**	0	0	0	0
TF08nM	04/07/2013	1	0.002	**0.022**	0	0	0	0
TM01M	04/07/2013	1	0.002	**0.022**	0	0	0	0
TF09M	23/07/2013	1	0.002	**0.022**	0	0	0	0
TF16M	18/09/2013	1	0.002	**0.022**	0	0	0	0
TF18M	03/10/2013	1	0.002	**0.022**	0	0	0	0
TF23M	15/05/2014	1	0.002	NA	0.010	0	0	0
TF25M	08/07/2014	1	0.002	NA	**0.010**	0	0	0
TF26nM	10/07/2014	1	0.002	NA	**0.010**	0	0	0
TF27nM	28/08/2014	1	0.002	NA	**0.010**	0	0	0
TF33M	03/11/2014	1	0.002	NA	NA	**0.008**	0	0
TF35M	27/11/2014	1	0.002	NA	NA	**0.008**	0	0
TF36nM	26/02/2015	1	0.002	NA	NA	**0.008**	0	0
TF37nM	09/04/2015	1	0.002	NA	NA	**0.008**	0	0
TF41M	24/09/2015	1	0.002	NA	NA	**0.008**	0	0
TM03M	29/10/2015	1	0.002	NA	NA	NA	**0.007**	0
TF42M	25/11/2015	1	0.002	NA	NA	NA	**0.007**	0

Table 1. Site Fidelity Indices calculated from sightings of uniquely identifiable G. cuvier at the Vallée Blanche ecotourism site between the 7 October 2012 and the 9 October 2017. Bold values indicate the year of maximum SFI_a for the each individual. Individuals are ordered by decreasing SFI_g.

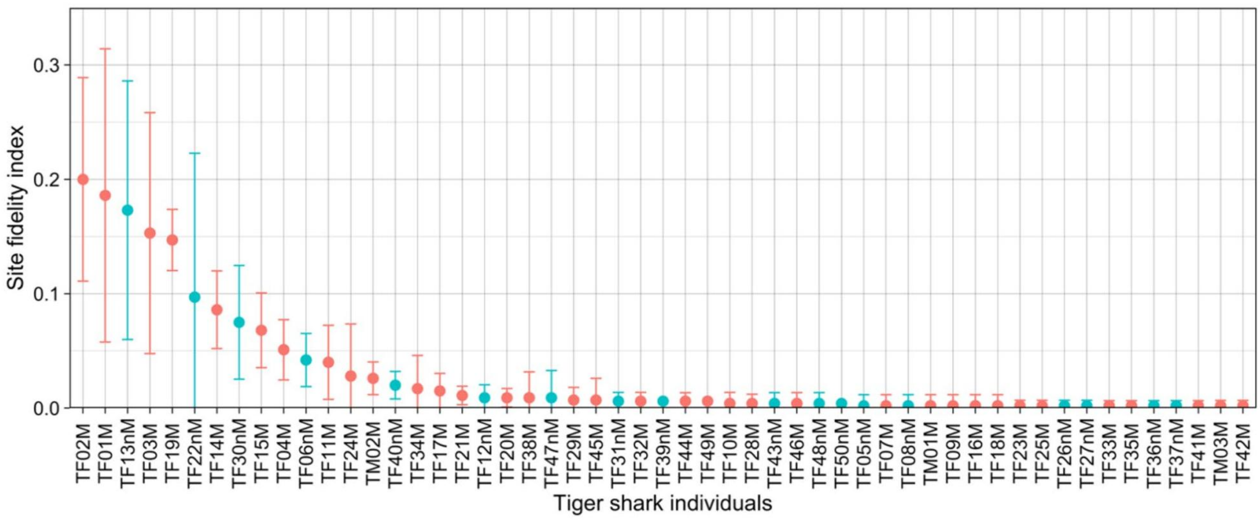

Figure 1. Site Fidelity Indices calculated from sightings of uniquely identifiable G. cuvier at the Vallée Blanche ecotourism site between the 7 October 2012 and the 9 October 2017. Individuals are ordered by decreasing SFI_g. Standard Deviation (SD) represents variation between years. Mature individuals are represented in red and non-mature in blue.

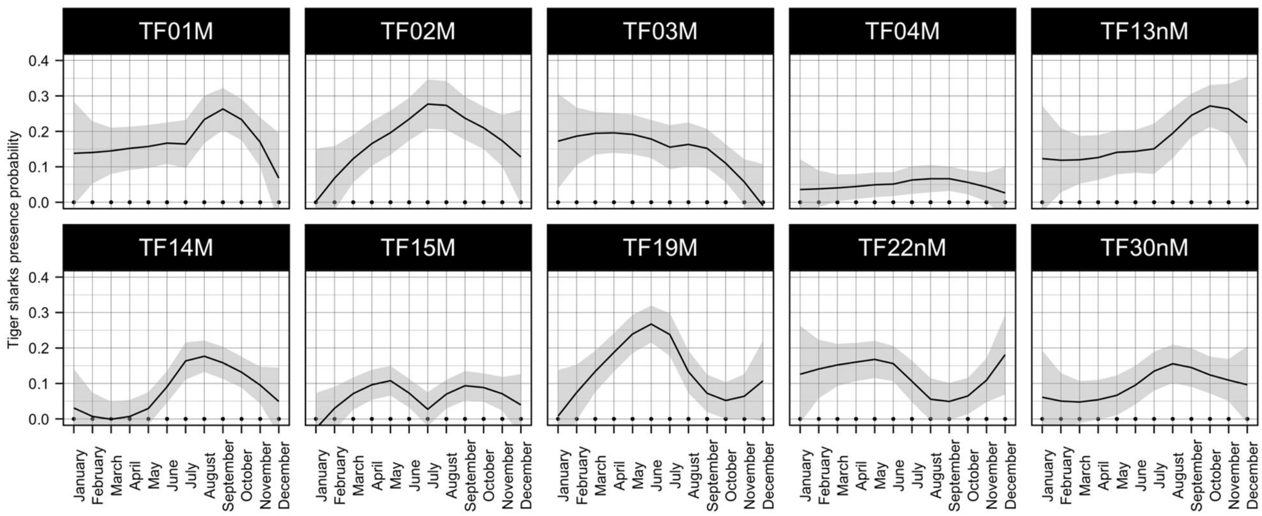

Figure 2. Inter-individual differences in seasonal probability of presence for the ten most frequently sighted ($SFI_g > 0.05$) tiger sharks. Shaded areas represent 95% confidence intervals.

on highly migratory sharks including tiger sharks in the Caribbean[25], white sharks *Carcharodon carcharias* at cage diving sites in South Africa[40] and Mexico[41,42], and bull sharks *Carcharhinus leucas* in Fiji[24], none of which found any demonstrable influence of provisioning on site fidelity. By contrast, previous studies of less mobile species such as sicklefin lemon sharks *Negaprion acutidens*[16,23] and blacktip reef sharks *Carcharhinus melanopterus* (Quoy & Gaimard 1824)[19] did detect increasing fidelity over time at other Polynesian provisioning sites. These interspecific differences in susceptibility to provisioning effects on fidelity may stem from fundamental differences in the spatial ecology of these various species. Species displaying naturally high levels of mobility and strong variability in movement patterns (e.g. tiger sharks) may simply be harder to retain at provisioning sites than highly reef-associated sharks (e.g. blacktip reef sharks).

Inter-individual differences in tiger shark SFI_g observed at VB may also simply reflect natural variability in movement patterns and home range locations. Previous telemetry studies in Hawaii have shown tiger sharks occupy core-structured home ranges around oceanic islands[15,28,30,43,44]. Although their entire home range may span multiple oceanic islands and extend into open-ocean, individual tiger sharks spend most of their time within a smaller Core Use Area (CUA) often associated with one stretch of coastline, and multiple individuals routinely occupy highly overlapping CUAs within the same general area[28]. Similar tiger shark home range characteristics may exist around the oceanic Windward Islands of French Polynesia. Thus, the most frequently sighted tiger sharks in this current study may have CUAs that include VB but still exhibited overall low fidelity at the ecotourism site because they continually roam back and forth within a CUA that may be as large as the entire North coast of Tahiti, similar to the observations made in Hawaii's oceanic islands[28]. Conversely, tiger sharks that were only

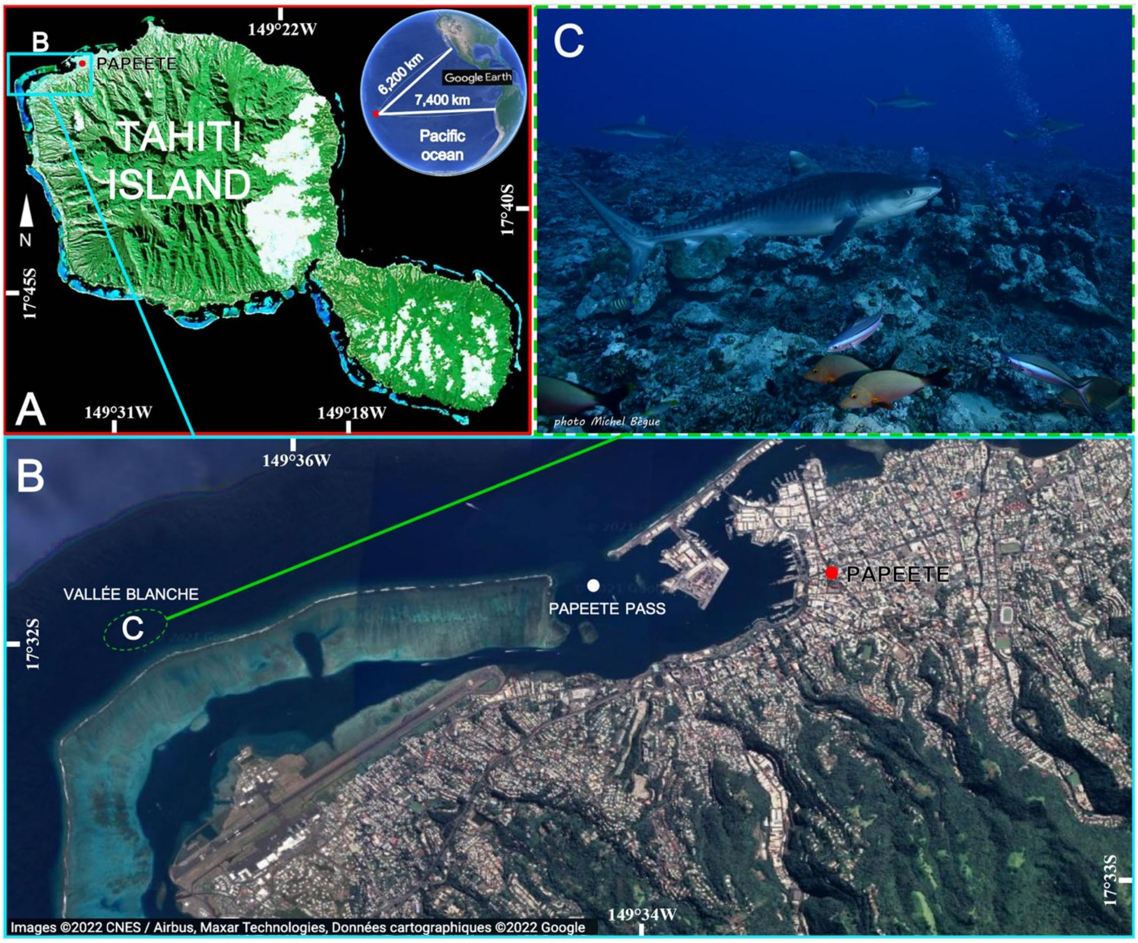

Figure 3. Map of the study area with (**A**) Its location off Tahiti, French Polynesia; (**B**) Its satellite view (Google Earth); (**C**) An underwater view of shark provisioning (photo credit: Michel Bègue). White circle: location of the Papeete pass, when red circle represents the city of Papeete, capital of Tahiti island.

occasionally sighted may occupy CUAs that do not include VB and their sporadic appearances at the ecotourism site reflect less-frequent wider-ranging movements outside their CUAs. Thus, the observed patterns of tiger shark sightings at provisioning ecotourism sites could be entirely explained by natural home range structure and there is no evidence that provisioning is significantly modifying their movement patterns or CUA locations. Satellite tagging could be used to empirically define tiger shark CUAs around Tahiti island to evaluate this hypothesis.

Although home range structure alone could reasonably explain observed SFI patterns it is important to consider a potential confounding effect of individual shark "boldness" on those patterns. We cannot rule out the possibility that bolder sharks willing to come closer to divers were seen most frequently whereas other more timid tiger sharks were also attracted to the site by provisioning activities but simply remained out of sight for most of the time. Previous studies with juvenile bull sharks showed some individuals being detected in riskier locations more often than others[45] reinforcing the possibility that variable boldness among individuals could be contributing to the observed patterns of tiger shark use of the VB site. Boldness can be related to body size in sharks with larger animals generally dominant at feeding aggregations and smaller sharks excluded until larger individuals are satiated[46,47]. However, at the VB site three subadult tiger sharks were among the 10 most frequently sighted individuals and overlapped in presence with large adults indicating that body size alone does not explain observed SFI patterns. Additional telemetry studies of tiger shark movements around Tahiti could help to clarify whether individual boldness influences diver-based surveys of tiger shark presence. Furthermore, a recent study suggests that individual tiger sharks displaying high levels of testosterone or plasma steroids may be correlated with longer time spent at the provisioning site[48]. Thus, impact of physiological state on site occupancy must be further explored in future studies.

The significant and consistent seasonal fluctuations in tiger shark abundance at the VB ecotourism site are a further indication that their natural movement patterns are not significantly influenced by provisioning. The distinctive high-low winter-summer pattern of tiger shark abundance at VB is consistent with seasonal migrations of the kind previously documented in tiger sharks in other locations without artificial provisioning[29,33], and also in tiger sharks and other species at other provisioning ecotourism sites[15,22–24,49,50]. The drivers of these seasonal movements could include reproduction or seasonal prey abundance. For example, the VB site is predominantly frequented by adult females, similar to Tiger Beach in Bahamas[51], which may migrate seasonally for mating or pupping purposes. Seasonal variations in tiger shark abundance in other areas have been related to foraging on seasonal prey-aggregations such as fledging albatross *Phoebastria spp.* in Hawaii[30] or loggerhead turtles *Caretta caretta* (Linnaeus 1758)[52] in the North Atlantic ocean. Although the drivers of seasonal cycles of tiger shark abundance at the VB site are unknown, their continued manifestation despite consistent provisioning demonstrates that artificial feeding does not overwhelm these natural patterns.

Wildlife provisioning is controversial largely because it can be deleterious to animals and people[53]. Examples of wildlife provisioning leading to negative outcomes include the death of a 9-year old boy resulting in the culling of 31 Australian dingoes *Canis lupus dingo* (Linnaeus 1758) in the Fraser Island National Park[54], a dangerous increase in the number of Indonesian Komodo dragons *Varanus komodoensis* (Ouwens 1912) in provisioning areas[55], and provisioned Thai macaques *Macaca fascicularis* (Raffles 1821) showing more aggressive behaviours than non-provisioned individuals towards humans[56]. Thus, potential impacts of shark provisioning must be carefully considered in order to avoid negative consequences to sharks and people. Our current results support those of other recent studies suggesting a general lack of chronic or irreversible impacts of feeding activities on sharks[24,25,40,50,57–59]. In fact the positive experiences of participants in these activities leads to important economic benefits and increased support for shark conservation[60–62]. However, careful management and adherence a strict code of conduct are essential to keep shark provisioning ecotourism safe and ecologically sustainable[10,13,16,58,63,64]. For example, regulations restricting shark provisioning permits to certified operators, might be a way to penalize non-compliance with management plans. Such measures are intended to increase the safety of participants and target species and are already successfully applied in Australia with the endangered whale shark *Rhincodon typus* (Smith 1828) as well as with the critically endangered sand tiger shark *Carcharias taurus* (Rafinesque 1810)[65–67]. Our results suggest that provisioning ecotourism at the VB site did not significantly influence tiger shark site fidelity and we suggest that this practice can be kept safe and sustainable through appropriate regulations including prohibiting risky practices such as hand feeding[16,63].

Methods

Study area. The study was carried out at the "Vallée Blanche" (VB) dive site (S 17.542°; W 149.624°), located on the outer slope of the barrier reef close to the Papeete pass on North-West coast of Tahiti (French Polynesia) (Fig. 3A,B). This site covers an area of approximately 40,000 m^2 characterized by a central valley of sand and coral debris at a depth of between 15 and 20 m, surrounded by pinnacles of hard corals, and adjacent to a steep drop-off and exposed to strong and variable currents[38]. Diving centers initiated shark feeding activity in 2011 in order to concentrate sharks in a particular area and to increase the probabilities of sighting six different species: blacktip reef sharks *Carcharhinus melanopterus*, grey reef sharks *Carcharhinus amblyrhynchos* (Bleeker 1856), whitetip reef sharks *Triaenodon obesus* (Rüppel 1837), tawny nurse sharks *Nebrius ferrugineus* (Lesson 1831), sicklefin lemon sharks *Negaprion acutidens* and tiger sharks *Galeocerdo cuvier* (Fig. 3C). Overall, 53 tiger sharks (50 females and 3 males) were individually photo-identified using unique characteristics, including skin pattern such as stripes or deep scars, wounds, or damaged dorsal or pectoral fins[38,47]. Individual identities were carefully validated via a thorough cross comparison of different body areas.

Data collection. Shark feeding activity occured year-round at VB, with almost daily provisioning sessions during Polynesian austral winter (May to October) but more sporadic provisioning during austral summer due to frequently unfavorable ocean conditions (high swell) and fewer tourists, but did occur whenever sea conditions were suitable. Sharks were attracted to the site using 4–6 yellowfin tuna heads *Thunnus albacares* (Bonnaterre 1788) contained in metal washing-machine drums (to prevent bait consumption) placed on the seabed at a depth of 18 m. The attraction process began each day at 8 AM on the first dive of the day. A second dive usually took place at 11 AM without food release, followed by a third dive at 2 PM, where the bait was released (head by head) at the end of the dive and fed to the waiting sharks. This schedule was based on the typical activity schedules of local dive centers. Dives were typically 45 min in duration. During the sampling period, VB was visited by 10 dive centers of which up to 4 attracted sharks at the same time with multiple bait drums distributed across the dive spot[68]. There was no coordination of these activities among dive operators but all dive centers involved in provisioning sharks visited VB almost daily for at least one dive. Due to the difficulty in evaluating the exact amount of tuna heads provided when several diving operators were sharing VB, the bait quantity was evaluated using the number of visible drums present. All dives were considered as independent in the following analysis.

Relative abundance, defined as the number of tiger sharks sighted per dive, identity, and size were recorded by an expert diver (M. Bègue) with more than 500 dives on the site. All the sharks identified in a previously developed database, were individually recognizable by based on their unique markings[38]. The size was assessed visually by the expert, and confirmed with the use of stereo-laser photogrammetry on several animals ($n = 12$), which showed an acceptable error $< 5\%$ of the estimated size. This non-invasive technique consists of two perfectly parallel laser dots calibrated at a specific distance apart, allowing the total length of the animal to be calculated from pictures[69,70]. ImageJ was used to compare the number of pixels between the two dots and the number of pixels for the total length of the shark. The sexual maturity status of each individual was estimated from their total lengths, with females > 3.30 m TL and males > 2.92 m TL considered to be sexually mature[71]. Each individual was assigned an alphanumeric identification code consisting of "T" for the species (Tiger), "F" (Female) or "M" (Male) for the sex, a two-digit number linked to the ranking of the first observation at VB (first tiger observed = 01, second observed = 02 etc.), and "M" (Mature) or "nM" (non-Mature) indicating the sexual maturity of the animals.

Evaluation of potential deleterious effects of provisioning. Data analyses were conducted in R (V 4.2.2)[72] with the significance level set to 0.05. Shapiro–Wilk tests were used to check the normality and

Bartlett tests to check the homoscedasticity of the distributions of different variables studied, resulting in non-parametric tests being selected for the data analyses. We used a Spearman correlation test to compare baiting level, quantified as the number of drums simultaneously present during the dive, with tiger shark relative abundance. We used Kruskal–Wallis rank sum tests to evaluate yearly and seasonal variations in tiger shark relative abundance with relative abundance as response variable and the year of sampling or the season as potential explanatory variables. Wilcoxon tests were used to make pairwise comparisons of significant results in order to identify periods of the year where tiger sharks were sighted significantly more frequently by divers at the VB site.

We calculated the global site fidelity index (SFI_g) and the annual site fidelity index (SFI_a) for each photo-identified individual by dividing the number of dives where the shark was seen by the total number of dives conducted during the respective sampling period. SFI values range from 0 to 1, with low values characterizing tiger sharks with a low site fidelity at VB and vice versa. An individual was considered as "resident" for a given year if the calculated SFI_a was equal to or higher than 0.5, and as "inter-annual resident" when it showed a SFI_a equal or higher than 0.5 over consecutive years[40]. To explore potential intra-specific differences in site use during the sampling period, we used Durbin Watson tests to examine the autocorrelation in sightings of individuals with > 25 total observations during the 5 years of sampling. For the 10 most-frequently sighted photo-identified tiger sharks, we generated response curves of monthly probability of presence deduced from the binomial presence/absence (1/0) data and fitted with a Loess smoother. χ^2 tests were used to evaluate whether presence patterns of the most frequently sighted sharks was significantly associated with either maturity status (mature and non-mature) or season (austral summer or austral winter). If significant, post hoc analysis based on residuals of Pearson's χ^2 test for count data were used to further characterize the relationships. For the 10 most-frequently sighted tiger sharks, we used Kruskal–Wallis tests to evaluate the influence of study year on SFI_a. Significant results were further assesses using Wilcoxon tests paiwise comparisons.

Data availability

The datasets used and analyzed during the current study are available from the corresponding author upon reasonable request.

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Author contributions

E.C. designed the experiment. M.B. collected the data. C.S., J.M., C.M. & E.C. performed analysis. C.S. and C.M. wrote the main manuscript text. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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CHAPTER 3:

Understanding why sharks are biting to help conservation ownership

Understanding the motivational classification of bites…

…To better deal with problem individuals

List of articles:

7. *Humans experience an increase in coastal shark bite frequency linked to the COVID-19 lockdown.* E. Clua, C. Meyer, **C. Séguigne**, A. Wirsing. Submitted in Global Ecology and Conservation.

8. *Exploring personalities in wild adult Bull sharks, Carcharhinus leucas.* T. Vignaud, C. Meyer, **C. Séguigne**, E. Clua. In review in Behaviour.

9. *Evidence of individual sharks repeatedly targeting humans.* E. Clua, C. Meyer, S. Baksay, M. Freeman, A. Haguenauer, J.D.C. Linnell, **C. Séguigne**, S. Surina, M. Vély, T. Vignaud, S. Planes. Submitted in Scientific Reports.

Humans experience an increase in coastal shark bite frequency linked to the COVID-19 lockdown

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Abstract:

The effects of the COVID-19 lockdown on wildlife aggression toward humans have not been studied. Using records of shark bites on humans in French Polynesia between 2009 and 2021, we show that from an annual average of about five over the decade 2009-2019, bites were significantly higher in 2020 (n=15), despite the virtual absence of humans from the marine environment during a six-week curfew in April-May 2020, and then returned to pre-Anthropause baseline levels (n=3) in 2021. A qualitative analysis of bite motivations revealed that the majority of bites in 2020 occurred just after the lockdown and were carried out by the gray reef shark, *Carcharhinus amblyrhynchos*, and that the primary motivation for most of these bites was dominance/territoriality rather than anti-predatory or predation behaviours. This phenomenon of increased biting suggests that the Anthropause triggered the return of dominance/territoriality behavior in coastal sharks that is normally suppressed by the spatiotemporal omnipresence of humans and thus sheds new light on the risks sharks pose to ocean users and the management of agonistic interactions between humans and marine predators.

1. Background

The 2020 global lockdown of human populations to mitigate the SARS-Cov-2 (COVID-19) pandemic resulted in an "Anthropause" where human presence in natural environments was dramatically reduced for several weeks resulting in both positive and negative impacts on wildlife [1-4] Positive impacts included increased reproductive success of birds and decreased roadkill of reptiles and amphibians [2]. Negative effects included an increase in invasive species [2] and decreased reproductive success of some avian species in urban areas [4]. However, the possibility that the Anthropause also modified impacts of wildlife on humans remains largely unexplored. For example, no study to date has quantified Anthropause effects on agonistic interactions between predators and people.

Concerning shark bites on humans, the only triggering factor shown to date is a positive correlation with the number of human-shark interactions (through the number of sea users), as has been demonstrated in the USA (Balbridge

1974, Ferretti et al. 2015) and Australia (West 2011). It would be interesting to explore other avenues, in particular those related to the behavioral characteristics of these marine predators. Whether it is the immemorial link between the native Oceanian people and the omnipresent ocean (Torrente et al. 2018) or the development of a significant ocean-linked tourism industry in recent decades, French Polynesia is a privileged place on a global scale to observe and analyze shark-human interactions. During the resumption of activities at sea following the COVID lockdown19, the main author of this article anecdotally noted a resurgence of bites on sea users, which suggested that this unexpected phenomenon should be analyzed in perspective with the pre- and post-COVID periods.

In the present study, we analyzed the frequency of shark bites on humans in French Polynesia over a thirteen-year span (2009-2021) that bracketed the 2020 COVID-19 lockdown. Crucially, this interval allowed us to contrast shark bite rates before, during, and after the lockdown curtailed human use of the ocean in our study region. We hypothesized that shark bites are primarily byproducts of spatiotemporal overlap with humans, that reduced use of the ocean during the Anthropause would thus result in fewer bites, and that subsequent resumption of more normal ocean activity in 2021 would yield bite rates similar to those seen before the lockdown. We also evaluated the behavioral explanations for the observed bites to determine whether they were best explained as competitive, defensive, dominance-territorial or feeding attempts [5-8].

2. Material and methods

a) Data collection

The Centre de Recherche Insulaire et Observatoire de l'Environnement (CRIOBE) located on the island of Moorea (French Polynesia) maintains a database of shark bites on humans in French Polynesia, a 4.5 million km^2 Exclusive Economic Zone (EEZ) encompassing 118 islands (Fig1). Data concerning each victim's profile, their ocean activity, and the conditions surrounding the incident are collected from media articles (written and televised) and the register of medical evacuations from remote islands compiled by the Central Hospital of the capital Tahiti. Although the data go back to the 1940s, the accuracy of this database has improved significantly since 2009 when CRIOBE researchers began systematic interviews of shark bite victims and witnesses. In parallel, a study focusing on shark bites on humans was conducted in 2012-2015 through an online questionnaire sent to all diving professionals involved in the French Polynesian Shark Observatory. A specific form to report a bite (see ESM 1) was also distributed to several medical clinics in the Tuamotu islands (80 islands) and Marquesas archipelago (7 islands); this form as well as all interviews conducted directly with the victims included the investigation of the presence or absence of agonistic behavioral displays [9] before the bite. This three-pronged approach allowed for a more exhaustive collection of data during the last decade, including less-severe bites not reported in the media. For the purposes of our study, we focused on humans who have a high probability of coming into contact with sharks, namely on one hand scuba divers or snorkelers (far mostly foreign tourists) and on the other hand spearfishermen (strictly indigenous) who fish for their subsistence or to supply hotels, in an unprofessional way (which is tolerated by the local government). To put it in quantitative terms, the former represented around 370,000 dives in 2016 (Lagouy and Clua 2016) and the latter around 206,000 fishing sessions per year between 2015 and 2019 on the basis of an average weekly session for an average of 4,300 indigenous fishers (ISPF 2022).

We chose the decade 2009-2019 as the reference period for the average annual incidence of shark bites on humans in French Polynesia, which we then compared with 2020, the year in which lockdown occurred for 6 weeks (from March 20 until April 30), and 2021, by which time baseline ocean use was presumed to have resumed. Note that the 2020 lockdown resulted in a curfew that was strictly enforced with fines and broadly respected [10-11]. For example, four aerial surveys between 20 March and 5 April 2020 revealed the cumulative presence of three large fishing vessels (longliners) and 12 small vessels (sailboats and motorboats) over the entire EEZ (BAEM 2022). All recreational diving clubs in French Polynesia were closed and only professional fishermen (who fish from a boat) were allowed to go out to sea (DPAM 2020); however, this derogation did not apply to non-professional spearfishermen who are the ones likely to interact with sharks underwater. Thus, we are confident that use of the coastal ocean during this period was markedly reduced across French Polynesia. The resumption of activities at sea in June 2020 could only be lower in overall intensity than before the lockdown. Indeed, the level of intensity of use of the maritime space in French Polynesia is strongly correlated to the presence of tourists, whose annual attendance is close to the total Polynesian population (around 280,000 people). As such, the number of international flights fell from 244 flights between January and February 2020, down to 97 flights in March, then to only ten flights in the following three months (April, May and June). Commercial rotations resumed in mid-July, with activity three times less than the previous year. At the end of the year, 120,000 passengers landed in Tahiti compared to 240,000 in 2019 (ISPF 2020). The absence of tourists in hotels has reduced demand of edible fishes - that is partially met by spearfishermen - and there is then no reason to believe that their activity in the months following the lockdown had any legitimacy to increase over normal levels. Thus, we are confident that there was not any surge of people at sea after the lockdown which could explain a significant increase in shark-human interactions, which in turn could be responsible for an increase in the number of bites as shown in other situations such as Australia (West 2011) and USA (Ferretti et al. 2015). We are also confident in our assumption that ocean use was back to an acceptable baseline in 2021, given that subsistence fishing plays a paramount role in the French Polynesian way of life [12], particularly in the remote islands where shark bites tend to occur, and thus there would have been strong incentive to return to the ocean once restrictions were lifted. Also, the markets for French and American (US) tourists were re-open in December 2020 and June 2021, respectively (ISPF 2021).

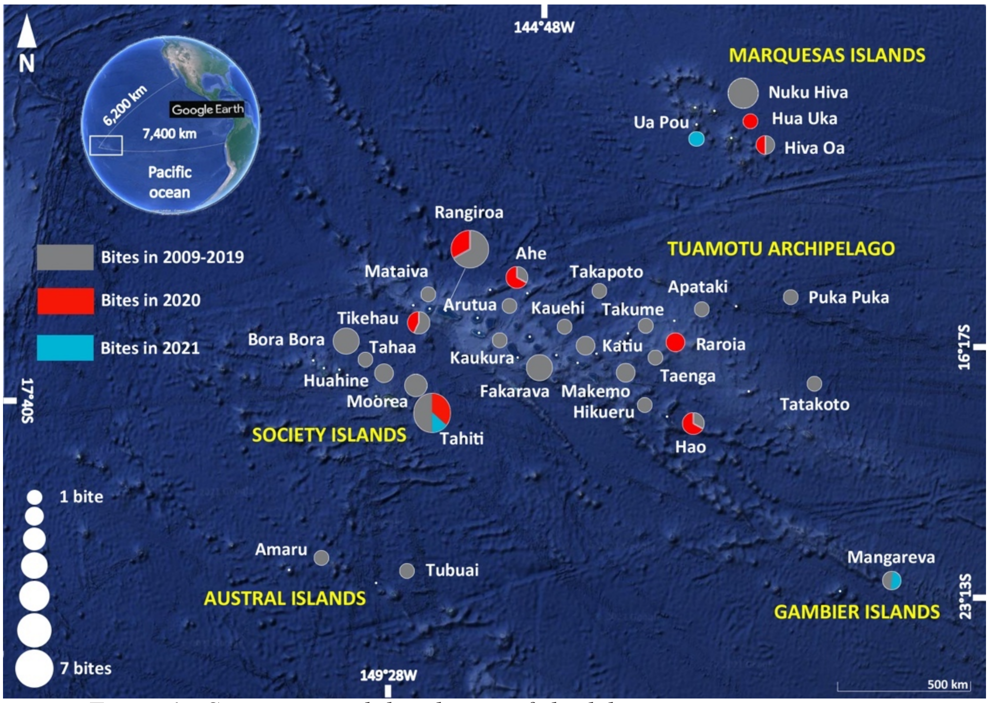

Figure 1 - Spatiotemporal distribution of shark bites among the five archipelagos of French Polynesia between 2009-2019 (black), 2020 (red) and 2021 (blue) periods.

b) Characterization of shark bites on humans in French Polynesia

The widespread presence of sharks in French Polynesia combined with a large number of in-water human activities results in numerous superficial and non-fatal bites every year [13] but fatal bites are rare with only 4 occurring over the last 80 years. Overall, most bites in this region occur on recreational scuba-divers (42%) and underwater spearfishers (33%) [14] and fall into several behavioral categories (Table 1). First, bites may be the result of reflexes or clumsiness when a confused shark bites a diver who is holding bait [15]; these types of bites have always been a risk to ecotourism professionals and tourist divers but became more prevalent after 2005 when ecotourism based on artificial provisioning of sharks significantly increased (until 2017 when it was officially banned). Second, spearfishers are often victims of competition/food access bites by sharks that are targeting wounded prey. Third, when these same spearfishers intentionally or unintentionally spear a shark, or a shark is the victim of another type of human attack, the aggressor may be subjected to retaliation through a self-defense/fear bite (Table 1). Predation as the main motivation for sharks has only been observed in Polynesia on two recent occasions. The first one in 2019 was off Moorea (Society islands) with multiple non-fatal bites on a snorkeler involved in cetacean watching [16] and the second one in 2021 off Mangareva (Tuamotu archipelago) with a non-fatal bite on a snorkeler involved in pearl farming (E. Clua, unpublished data). In both cases, the victims suffered major tissue loss as a direct proof of predatory motive.

Non predatory shark bites may be proceeded by specific agonistic 'warning' behaviors such as swimming with a jerking motion and body twisting or "hunching" [5, 17]. This warning behavior has been found most frequently in the gray reef shark *Carcharhinus amblyrynchos* but also exists in several other species of Carcharinidae and Sphyrnidae around the world [9, 18]. It was studied intensively in the 1970s-80s and has been attributed either to an attitude of dominance/territoriality (whereby the shark seeks to evict an intruder from a space where it is in close contact with the shark), or to an anti-predatory strategy (leading the shark to anticipate a potential threat and to defend itself proactively) [6] (Table 1). While this second explanation has been favored by some authors [7, 8], others [19, McNair 1975] promoted "territoriality" as follows "The same shark might be aggressive on one piece of a reef while half a mile away the same individual may be docile or shy……territoriality seems the only logical conclusion.". Nevertheless, "no conclusive findings have been made to date and evidence for territorial-like behaviors such as site-related dominance… needs confirmation" [7]. Hence, we merged them and, for the purposes of this analysis, all shark bites were classified according to five possibilities: (i) predation/investigation; (ii) reflex/clumsiness; (iii) competition/food access; (iv) self-defense/retaliation; and (v) dominance-territoriality/anti-predatory (see ESM2). In all cases, the presence/absence of an agonistic display by the shark prior to the bite was also addressed.

Table 1 - Descriptions of potential motivations for a shark to bite a human. For each motivating mechanism, we provide the main triggering factors: A: Close spatial proximity between shark and human; B: Non-voluntary biting on human (at least one); C: Feeding motivation on natural prey; D: Deliberate biting on human (at least one); E: Deliberate repeated bites on human; F: Characterized (actual) aggression on shark by human; G: Anticipated (not actual) aggression on shark by human; H: Behavioral agonistic display by shark; I: Feeding motivation on a human being.

Bite motivation	Main triggering factors	Feeding trigger	Swimming display	Characteristics of the aggression	References (not exhaustive)
Reflex / Clumpsiness	ABC	Yes	No	Bite (most often not repeated) on a human that is the result of poor judgment in the context of the animal's feeding behaviour (not directed against humans). No warning signs. The main trigger is based on a state of haste, often exacerbated by competition between sharks for access to a food resource (sometimes leading to feeding frenzies); e.g., a human observer bitten during a feeding frenzy in the context of shark artificial provisioning or in natural conditions.	[7, 15, 19]
Self-Defense / Retaliation	DEF	No	No	Bite on a human that voluntarily or involuntarily constitutes a danger to the shark. No warning signs. The main trigger is based on previous or imminent aggression of humans toward the shark; e.g., a person angling for a shark, a speafisher shooting a spear at a shark, or a diver attempting to grab a shark.	[20, 21]
Dominance-Territoriality / Anti-predatory	DAGH	No	Yes	Dominance: Bite on a human who has voluntarily or involuntarily penetrated the shark idiosphere (sensu Martin 2007). Anti-predatory: Bite on a human who voluntarily or involuntarily appears as a potential threat to the shark. In both cases, the shark may instinctively display a specific agonistic behavior (lowering pectoral fins, shaking its body, as well as accelerating its jerky swimming). For dominance, the main trigger is spatial; e.g., a surfer, swimmer or diver who gets too close to a shark (can be eaxcerbated by physiological status linked to breeding season or pregnancy). For Anti-predatory, the distance between the shark and the human is a determining factor in the attack, especially if the human swims quickly toward the shark or reduces its range of escape by pressing it against the substrate; e.g., a scubadiver approaching a shark quickly with an underwater scooter pr along a rock face.	[7- 9, 17, 18 21-29]
Competition / Resource access	DEC	Yes	No	Bite on a human who represents, voluntarily or involuntarily, a direct competitor for the access to a food resource. No warning signs. The main trigger is the presence of this food stimulus; e.g., a spearfisher who tries to defend or remove a speared and wounded fish from th grasp of a shark.	[7, 26, 28, 30]
Predation / Investigation / Mistaken identity	DEI	Yes	No	Biting (most often repeated except for an investigative bite) that is part of a feeding process on human prey, motivated by hunger but only concerning individuals among large shark species (in particular *Carcharodon carcharias, Galeocerdo cuvier, Carcharhinus leucas, C. longimanus*). No warning signs. In this case, the behavior of the human contributes minimally to the genesis of aggression.	[16, 24, 28, 31-35]

c) Data analysis

We performed Kruskal-Wallis tests to determine if: (A) monthly bite rates during any of the years studied differed significantly than the others; (B) at least one of the pre-, during-, and post-Anthropause periods presented significantly different numbers of monthly Dominance/Anti-predatory bites than the others for all shark species involved; (C) at least one of the pre-, during- and post-Anthropause periods exhibited a significantly different R-ratio, defined monthly over the sampling period as the number of bites preceded by agonistic behavior divided by the total number of bites. For the first question (A), we considered the years 2009-2019 to represent the baseline period pre-Anthropause, the year 2020 to represent the during-Anthropause interval, and the year 2021 to represent the post-Anthropause period. For the second (B) and third (C) questions, to test for differences within 2020 before and after the lockdown was lifted and because of lower sample sizes, we combined the years 2009-2019 (including January and February 2020) to represent the baseline period pre-Anthropause, combined the months March-April in 2020 to represent Anthropause, combined the months May-December in 2020 to represent the post-Anthropause (reopening) interval in that year during which residual effects of the lockdown could still be manifesting, and used the year 2021 to represent the post-Anthropause period. In cases of significance, a Dunn's test (R package **dunn.test**; [37] was performed to make pairwise comparisons. From the matrix of p-values resulting from this test, a set of letters is then assigned to each of the factors, with each shared letter representing a result considered similar with respect to the response variable (R package **multcompView** [38]). For all analyses, we set the threshold for statistical significance (α) at 0.05. Graphs were displayed using the **ggplot2** R package [39].

3. Results

During the years assessed (2009-2021), we documented a total of 66 bites comprising 48 bites between 2009-2019 (yearly mean of 5.08 +/- 3.78 SD) distributed across 31 islands, 15 bites in 2020 distributed among eight islands, and three bites in 2021 across three islands (ESM2, Fig. 1). Most (62%) bites occurred in the large Tuamotu archipelago, followed by the Society islands (23%), Marquesas (14%), and Austral islands (1%). The culprit species were the Gray reef shark (50%), followed by the Blacktip reef shark *Carcharhinus melanopterus* (21%), Blacktip shark *Climbatus* (14%), Sicklefin lemon shark (10%), Tiger shark (3%), Oceanic Whitetip shark (1%) and Scalloped hammerhead *Sphyrna lewinii* (1%). The most common documented bite motivation was Dominance-Territoriality/Antipredatory (32%), followed by Reflex (27%), Competition (24%), Self-Defense (14%), and Predation (3%)All bites were linked to the following activities: spearfishing (36%), shark feeding (20%), snorkeling and swimming (18%), surfing (11%), working with fishing traps (6%), scuba-diving without feeding (5%), *vaa* or canoe (3%), and shark handling (1%) (ESM2). Regarding victim's profile, one foreigner was bitten in 2020 (6.6%) while an average of 10 foreigners (18%) were bitten per year during the two pre-COVID period.

(A): ***Higher number of bites in 2020:*** Results of the Kruskal-Wallis showed that the monthly number of bites for at least one year differed significantly from the others (p-value = 0.024). Post-hoc tests and pairwise comparisons revealed that the bite rate for 2020 was significantly elevated (p-value < 0.05) relative to all other years save 2016 (p-value = 0.085). Notably, 2016 was statistically indistinguishable from 2010, 2014, 2015, 2017, 2018, 2019, and 2021 in terms of bite quantity (p-value > 0.05). Overall, then, 2020 featured more bite incidents than all but one of the other years, and the one year from which it was not significantly different (2016) was comparable to the majority of the other years in the baseline (pre-) period (Fig2). Furthermore, the bite rate during the post-Anthropause year (2021) was not significantly different from those during the pre-Anthropause interval (Fig. 2).

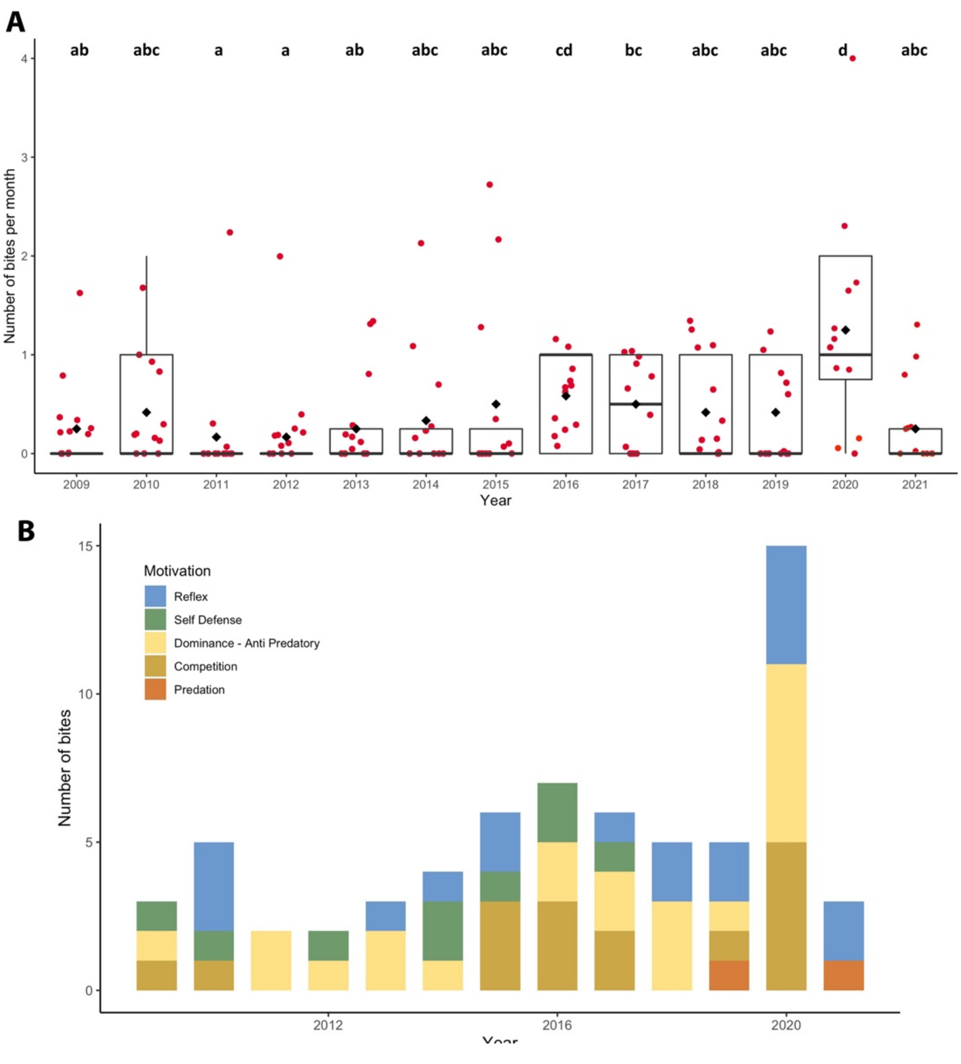

Figure 2. A: On the boxplot, the red dots represent the bites per months and per year; note, one dot combines four bites in 2020 that occurred in the single month of May 2020, the month of reopening. The black diamonds represent the average number of bites for each year. Post-hoc tests revealed significantly more bites in 2020, with the exception of 2016 (also shares the letter d, but by contrast 2016 also has the letter c and is therefore comparable to six other years). B: Bite motivations by year, showing in 2020 a prevalence of Dominance/Anti-predatory bites (53%), followed by Competition bites (40%) and Reflex/Clumsiness bites (7%).

(B): ***Higher number of Dominance / Anti-predatory bites in 2020***: There were no Dominance-Territoriality / Anti-predatory bites recorded during Anthropause (only two bites linked to competition, Tab. 2), and the global Kruskal-Wallis test indicated that at least one of the times periods we evaluated differed significantly from the others in terms of the frequency of these types of bites (p-value = 0.001). Post-hoc pairwise comparisons showed that the monthly number of 2020 Dominance-territoriality / Anti-predatory bites during the post-Anthropause period of 2020 (May-December) was significantly higher than that observed during either the earlier years (p-value = 0.005), the Anthropause period in 2020 (p-value = 0.026), and 2021 (p-value = 0.011). All other pairwise comparisons were non-significant (p-value ≥ 0.270).

(C): ***Higher numbers of pre-bite agonistic displays in 2020***: Only two pre-bite agonistic displays were documented during the 10-year pre-Anthropause period; the first preceding a bite on a snorkeler cleaning pearl lines in the Tuamotu (C35 in Tab. 2, described in [29]), and the second preceding a bite on a scuba diver on a scooter chasing a shark at a depth of 80 m (see C42 in Tab. 2). In May 2020, just following the lockdown, two Dominance-Territoriality/Anti-predatory bites on spearfishermen in Rangiroa and Ahe, respectively, were preceded by agonistic behaviors (see C54 and C56 in Tab. 2). A third bite, also preceded by such agonistic behavior, took place in Ahe in November 2020 on a snorkeler who was accompanying spearfishers just arriving at the fishing spot (see C61 in Tab. 2). For all these cases, the culprit species was identified as a gray reef shark. The Kruskal-Wallis test was significant (p-value = 0.00063), indicating at least one significant difference among the times periods being compared. Post-hoc tests showed that agonistic displays preceded bites significantly more frequently during the post-Anthropause period in 2020 than during the earlier years (p-value < 0.001), the post-Anthropause period in 2020 (p-value = 0.022), and 2021 (p-value < 0.001) Anthropause. All other pairwise comparisons were non-significant (all p-value ≥ 0.380).

Table 2 – Partial results of the study showing the details for 2020 cases and cases involving pre-bite agonistic display (grey lines). GRS stands for Grey Reef shark Carcharhinus amblyrhynchos; BRS for Blacktip Reef Shark C. melanopterus; LS for Lemon Shark Negaprion acutidens; HS for Hammerhead Shark Sphyrna spp.

Case #	Year	Month	Archipelago	island	Shark species	Bite motivation	Display	Activity	Victim profile	Description of context
C35	2017	April	Tuamotu	Mangareva	GRS	Dominance-Territoriality / Antipredatory	Yes	Snorkelling	Local polynesian	Snorkeller bitten on a foot as he was ascending to the surface after cleaning pearl oysters.
C42	2018	September	Society	Bora-Bora	GRS	Dominance-Territoriality / Antipredatory	Yes	Scuba-diving	Caucasian foreigner	Scuba diver bitten on the head as he was pursuing the shark with an underwater scooter
C49	2020	February	Marquesas	Ua Huka	Unknown	Clumsiness / reflex	No	Canooing	Local polynesian	Adult male canoying when the hull of his pirogue was bitten 'by a large shark'
C50		March	Tuamotu	Raroia	GRS	Competition / Food access	No	Spearfishing	local polynesian	Spearfisherman at the surface bitten on the calf while loading an arrow-wounded tuna G. unicolor onto a boat
C51		April	Tuamotu	Rangiroa	BRS	Competition / Food access	No	Spearfishing	local polynesian	Spearfisherman at the surface bitten on the hand while holding a bigeye fish Priacanthus spp. he had just speared
C52			Tuamotu	Rangiroa	BRS	Competition / Food access	No	Spearfishing	local polynesian	Spearfisherman at the surface bitten on the hand while holding a parrot fish Scarus spp. he had just speared
C53		May	Tuamotu	Raroia	BRS	Dominance-Territoriality / Antipredatory	No	Spearfishing	local polynesian	Spearfisherman at the surface bitten on the wrist while getting into the water without having started hunting
C54			Tuamotu	Rangiroa	GRS	Dominance-Territoriality / Antipredatory	Yes	Spearfishing	local polynesian	Spearfisherman at the surface bitten on the ankle by a shark coming straight from the bottom while holding in the hand a surgeon fish that he had just speared - Victim mentioned 'no interest in the fish'
C55			Society	Tahiti	BRS	Clumsiness / reflex	No	SharkFeeding	Local polynesian	Surface female swimmer bitten on the calf while at the surface in the vicinity of a feeding frenzy caused by discarded fish pieces thrown away by an ecotourism operator
C56			Tuamotu	Ahe	GRS	Dominance-Territoriality / Antipredatory	Yes	Spearfishing	local polynesian	Spearfisherman at the surface bitten on the hand while observing his companion below in the water column in hunting action (no fish injured)
C57		July	Tuamotu	Tikehau	LS	Dominance-Territoriality / Antipredatory	No	Swimming	local polynesian	Young boy bitten on the calf while swimming with his mother in < 1m of water, attacked without warning
C58			Society	Tahiti	HS	Clumsiness / reflex	No	Surfing	local polynesian	Kite surfer whose foil was bitten several times while sailing offshore
C59		August	Marquesas	Nuku Hiva	BTS	Dominance-Territoriality / Antipredatory	No	Swimming	local polynesian	Young man bitten on the thigh while swimming on the surface, no warning signs
C60		October	Society	Tahiti	GRS	Competition / Food access	No	Spearfishing	local polynesian	Spearfisherman bitten on the foot while getting back to the surface and holding in the hand a speared fish
C61		November	Tuamotu	Ahe	GRS	Dominance-Territoriality / Antipredatory	Yes	Snorkelling	Caucasian foreigner	Snorkeller bitten on the shoulder as it was at the surface observing spearfishers about to start the fishing session
C62			Tuamotu	Hao	GRS	Competition / Food access	No	Spearfishing	Local polynesian	Speafisherman bitten on the hand as he was at the surface after spearing a fish
C63		December	Tuamotu	Hao	GRS	Clumsiness / reflex	No	Fishing	Local polynesian	Fisherman standing on the reef flat bitten on the thigh as he was holding a bag with dead fish between his leg

4. Discussion

The frequency of wildlife attacks on humans often correlates positively with the amount of human exposure to species that might cause harm [40, 41] thus we expected the 2020 Anthropause to depress shark bite rates throughout French Polynesia. However, we found that annual shark bite rates in French Polynesia actually increased significantly during the 2020 Anthropause despite lower numbers of people in the water. The fact that there was only one bite on a tourist in 2020 (i.e. a percentage of 6.6% vs. the usual 18%), is consistent with the fact that the number of tourists in French Polynesia collapsed in 2020, making it difficult for sharks to interact with this type of potential victim. Moreover, Dominance/Anti-predatory bites on native spearfishermen and pre-bite agonistic displays by sharks occurred significantly more often immediately after the lockdown than in any prior or subsequent study intervals suggesting a transient change in shark behavior resulting from the total absence of humans in the ocean.

Dominance/Anti-predatory behavior (agonistic lowering of pectoral fins, hunching of the body and exaggerated swimming, biting; [20]) by gray reef sharks in response to human presence was commonly observed in French Polynesia and Micronesia in the 1970-80s [6,7, 20] but then diminished considerably with only two cases documented between 2009-2019 and in 2021 in French Polynesia. However, three such instances resulting in bites occurred in 2020 in French Polynesia immediately after the Anthropause. Furthermore, changes in gray reef shark behavior were also observed at the 'Vallée Blanche' ecotourism site off Tahiti This site, which is used regularly by several dozen individual blacktip reef sharks, Gray reef sharks, and lemon sharks, has been intensively studied since 2012 (see [42]). In more than 1,200 dives during which grey reef, blacktip reef and lemon sharks were routinely present, no hunching agonistic behavior was observed from any species (M. Bègue, Pers. Obs.). When divers returned to the site after the Anthropause in 2020, however, this type of behavior was frequently observed in gray reef sharks and filmed in May 2020 (see ESM3-1). The post-Anthropause reemergence and appearance of these agonistic behaviors in conjunction with reports of bites across French Polynesia and at the Vallée Blanche site, respectively, suggests that, rather than occurring in proportion to human presence, shark bites were made more likely by humans disappearing from and then returning to particular ocean locations. More specifically, it appears that the absence of humans from certain locations altered shark Dominance/Anti-predatory behavior in a way that predisposed these predators to exhibit agonistic displays, and subsequently to bite, once humans returned to these areas under otherwise identical conditions.

Because shark agonistic behaviors were common before the 1980s and then slowly vanished (E. Clua, pers. obs.), becoming almost absent between 2009 and 2019, it is appropriate to ask why they disappeared. After the 1980s, human presence at ocean depths between 0 and 40 m increased dramatically because of the rising popularity of free and scuba diving. It is possible that sharks – in particular resident coastal species such as the gray reef shark – became habituated (*sensu* [43]) to humans regularly penetrating their idiosphere (*sensu* [9]), leading them to decrease both their apprehension and their instinctive management of such confrontation with agonistic behavior. Though this hypothesis has yet to be tested, there is indirect evidence for such a process. In 2019 closed circuit (rebreathers) divers at a depth of 80 to 120 m approached a gray reef shark with an underwater scooter, despite clear signs of agonistic behavior on the part of the shark (see ESM3-2 ref. C42 in ESM2). The shark turned around and bit the head of one of the divers, who survived the incident. It is likely that this shark had never encountered a diver at this depth, which is inaccessible to the majority of Polynesian ocean users, and thus reacted with an instinct unaltered by the recurrent presence of humans, as had congeners closer to the surface prior to the 1980s. Some authors [7] came to the same conclusion of probable habituation of sharks to humans, noting "the reef sharks in the study area -Rangiroa reef passage- to be shy of divers. This shyness might be due to previous experiences with the native divers. In more remote areas rarely visited by divers, the sharks (especially grays) were noticeably bolder, at least initially." This hypothesis of habituation would explain why sharks, whatever their dominance or anti-predation motivations, had stopped trying to deter humans from entering their idiosphere prior to the Anthropause. Namely, such attempts at deterrence, if repeatedly deployed in the face of human omnipresence, would be energetically costly [44]. Accordingly, sharks forgoing this behavior in areas experiencing increased human use would have accrued a fitness benefit, promoting the progressive disappearance of agonistic interactions with humans beginning in the 1980s.

When the 2020 lockdown ended, there are two behavioral mechanisms that could have led sharks to respond agonistically and aggressively to humans reentering the water. First, Anthropause may have allowed sharks to reclaim their space and resources, particularly the fish on which they prey. The return of fishermen – as direct competitors for these same fish – would have then constituted an intrusion and a threat of competition for resources, triggering hunching agonistic behavior and dominance bites. Second, the Anthropause may have led at least some sharks to become unaccustomed to humans, whose return would have then constituted a new perceived threat capable of eliciting anti-predatory behavior. This latter anti-predatory mechanism would require sharks, over the course of six weeks, to have lost any learned responses to humans, including habituated responses, causing them to react aggressively in anticipation. However, a recent study conducted in French Polynesia showed that conditioned reef sharks still responded to the same conditioning six weeks after its temporary cessation owing to Anthropause [45]. By implication, it is unlikely that sharks became naïve to humans as a result of Anthropause. Instead, whereas agonistic behavior can precede an antipredatory bite, as when a diver creates a threat by approaching a shark rapidly or by limiting its escape space [7], our study suggests that, outside of these very specific cases, hunching and other agonistic movements are motivated primarily by dominance, linked to territoriality and/or access to a resource, and thus that dominance behavior drove the increase in shark bites after the lockdown ended.

Our results are also germane to the “mistaken identity” hypothesis, whereby sharks bite humans because of confusion with natural prey when conditions reduce visual acuity [36]. This hypothesis is typically applied to situations where sharks are delivering predatory bites, which were rare during the period of record for the present analysis. It also downplays other senses in sharks, in particular hearing and mechanoreception, which provide valuable real-time information to limit confusion during predator-prey interactions. It is nevertheless possible that certain environmental conditions (e.g, light levels, turbidity) could elevate the likelihood of any sort of shark bite by inhibiting visual discrimination. Yet, this hypothesis predicts a positive correlation between bites and the probability of an encounter between the predator and humans, with more humans in the water providing more opportunities for mistakes, rather than the drastic increase in bites observed for 2020, when human presence in the ocean was either reduced or recovering to normal levels. By implication, bites by sharks in French Polynesia, including predatory bites, are probably more a matter of shark behavior [46].

It is possible that, because of sharpened focus during the early stages of the pandemic, our vigilance in compiling bite accidents in 2020 contributed to the observed increase in shark bites during that year. There are four reasons to believe that this was not the case, however. First, there is no reason to suspect that our sampling effort between 2009 and 2019 was heterogeneous or deficient, as data from this period yielded an average around five bites per year and low inter-annual variance (Fig2a). Second, the same effort was maintained in 2021 and resulted with only three documented bites, a level close to that previous average. Third, the data collected between 2009 and 2019 confirm the prevalence of bites in places such as Rangiroa and Tahiti (Fig. 1), with most bites on underwater spearfishermen and scuba divers involved in artificial provisioning and with the gray reef shark as principal perpetrator, in line with previous studies [14]. Fourth, the difference in bite rate between 2020 and the other years is marked, making it unlikely to have arisen from sampling error alone. The drastic increase in bite rate during 2020, particularly because it was driven by a surge after the lockdown ended, also renders it unlikely to have derived from another, unmeasured, factor that varied over the same timescale, though we acknowledge that the correlative nature of our investigation leaves open such a possibility.

Most sharks are predators, and this fact likely contributes to overestimating the food component in the motivation of human bites. Our findings, on the other hand, suggest that Anthropause triggered the return of an instinctive response in coastal sharks – dominance behavior – that is probably masked in normal times by the spatiotemporal omnipresence of humans. By implication, even when sharks have abandoned the deployment of warning signs via the process of habituation, they may retain the reflex to potentially attack an intruder for 'territorial' reasons that they judge to be too close [21]. Such an understanding of coastal shark behavior should allow for better management of human behavior in the marine environment, especially when diving, in order to minimize negative interactions with these predators, which in turn often result in retaliatory actions that may harm their reputation and conservation. It is interesting to note that, unlike terrestrial predators such as pumas (*Puma concolor*) that have adapted to humans by minimizing encounters at the cost of expending greater energy [47], the shark species that perpetrate bites in French Polynesia seem to have dealt with the same problem by becoming accustomed to the presence of humans. This approach undoubtedly results in energy savings; however, it also results from the fact that humans generally do not show any systematic hostility when encountering most reef sharks in the water, whereas the potential for a negative outcome following an encounter with people for pumas and other large terrestrial carnivores provides strong incentive for avoidance, which can carry serious physiological consequences for wild animals [44]. Accordingly, our study also strengthens the notion that potentially conflicting relationships between sharks - as marine predators - and humans are more complex than those between land predators – such as big cats and bears - and humans [43] and thus warrant efforts to better understand them.

Ethics. Methods were observational and analytical only and adhered to local guidelines

Data accessibility. Data are available via the Open Science Foundation (https://XXX).

Authors' contributions. EEGC designed the study and implemented the acquisition and interpretation of data as well as drafting of the article. CS conducted the analysis of the data. CS, CGM, and AW made substantial contributions to the improvement of the draft article and its editing. All authors approve the final version of the manuscript and agree to be held accountable for its content.

Competing interests. We declare we have no competing interests.

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Special Issue on Elasmobranch cognition and behaviour

Examining individual behavioural variation in wild adult bull sharks (Carcharhinus leucas) suggests divergent personalities

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Abstract

Although many animal species demonstrate individual personalities, studying these traits in wild sharks has proven challenging. Past research focused mainly on captive or juvenile sharks. Our ethological study of 31 wild adult bull sharks (*Carcharhinus leucas*) utilized an artificial provisioning site, amassing 2813 observations over 651 dives from October 2015 to January 2018 (27 months). Behavioural traits, including boldness-shyness and aggressiveness-placidity, were assessed using an ad hoc ethogram and an influencing factors table. This innovative approach not only allowed us to characterize individual shark behaviours but also to quantify their changes over time. Our findings suggest that adult bull sharks likely possess distinct personalities, spanning from extreme shyness to pronounced boldness, with varying levels of plasticity among individuals. Further exploration of shark personalities holds promise for advancing our comprehension of human–shark interactions and refining the management of potential aggressive behaviours exhibited by large shark species toward humans.

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artificial provisioning, behavioural plasticity, behavioural traits, boldness-shyness, ethogram, feeding, human–wildlife interaction, individualities, temperament.

1. Introduction

Animal personality refers to variations in behaviour among individuals observed repeatedly (Sih et al., 2004; Réale et al., 2007; Ogden, 2012; Dingemanse & Wright, 2020). Initially, research centred on captive animals with high cognitive abilities, like chimpanzees, then expanded to other species and wild populations (reviewed in Gosling, 2008). Although captive fish were included, studying personality in wild fish remains rare (Castanheira et al., 2013; Kohda et al., 2022). Thus far, shark personality studies focused on small wild species or captive juvenile large species (e.g., Jacoby et al., 2014; Byrnes & Brown, 2016; Finger et al., 2017; Dhellemmes et al., 2020) due to the challenges posed by studying large, elusive sharks in the complex oceanic environment (see Brena et al., 2015; Bakker et al., 2017; Finger et al., 2017).

Understanding shark personalities carries significant implications for their conservation and management (Ogden, 2012; Clua & Linnell, 2018). For example, ‘boldness’ may increase vulnerability to fisheries interactions and ocean user encounters (Clua et al., 2020). Shark bycatch significantly contributes to population decline (Queiroz et al., 2019). Rare shark-human encounters garner disproportionate media attention, harming local economies and triggering ineffective shark culling campaigns (Clua et al., 2020). Shark personality insights can enhance mitigation efforts, but safely studying wild adult shark behaviour is challenging. One context in which individual large wild sharks can be successfully and repeatedly studied are provisioning ecotourism sites where bait or chum are used to attract sharks close to divers (Gallagher et al., 2015). For example, Brena et al. (2018) revealed complex social interactions and dominance hierarchies among sicklefin lemon sharks (*Negaprion acutidens*) in French Polynesia through artificial provisioning. Similarly, Becerril-García et al. (2018), characterized specific behaviours by great white sharks during cage-diving activities.

Bull sharks (*Carcharhinus leucas*, Müller & Henle, 1839) are among the largest shark species (adult TL > 3 m) frequently encountered at provisioning ecotourism sites in Fiji, South Africa and the Caribbean (Brena et al., 2015; Healy et al., 2020). Their distinct morphology, behaviour, remarkable jaw force (Habegger et al., 2012), ability to prey on large animals, and frequent presence in coastal waters (Lea et al., 2015) make them a potential threat to humans. They are the primary culprits behind shark bites in regions like Northern Brazil and La Reunion Island (Chapman & McPhee, 2016; Lagabrielle et al., 2018). Matich et al. (2011) noted significant variations in feeding habits among juvenile bull sharks from the same estuarine population, hinting at the existence of individual personality traits. This observation prompted us to investigate whether similar patterns persist among adult individuals in their natural habitat.

In this study, we documented the long-term behavioural patterns of wild adult bull sharks at a provisioning ecotourism site in Fiji. Our goal was to uncover disparities in their behaviours, explore the potential influences of external factors, and gain insights into their individual personalities.

2. Methods

To meet our objective to assess shark behavioural variations through their repetitive presence at the feeding site, we successively (1) used preliminary behavioural observations to create a table of key factors influencing individual shark behaviours (2) created an ad hoc ethogram, and (3) rated the behavioural attributes of each shark to then generate a global personality and plasticity score that enables comparison between individuals. In the discussion, we finally (4) explored the ecological and conservation implications that could be impacted by the observed bull shark personality spectrum.

2.1. Study context

Bull sharks were closely observed by a team of scuba divers, led by the main author and supported by other expert divers, at two adjacent provisioning ecotourism dive sites in western Fiji (Kuata Island, Yasawa Group) over a span of 27 months, from October 2015 to January 2018. During artificial provisioning activities (as depicted in Figure 1), the sharks were individually identified, and their behaviour meticulously documented. We adhered to a standardized protocol for diver placement and feeding procedures, ensuring consistency in timing and the quantity of food released (a detailed description can be found in Appendix A at 10.6084/m9.figshare.24204501). Despite a group of approximately 50 to 80 sharks identified, our analyses focused

Figure 1. Plan of the dive sites and photography illustrating the underwater setup. Left: Description of the two shark feeding sites from above, (A) at 24 m and (B) at 12 m. In both sites, divers are positioned behind a wall, and the feeder and his/her bodyguard are in front of the wall behind a feeding box and a metal grid. Right: photo of the 24 m site with observers (left) and feeder and bodyguard (right, in the back) in the presence of a bull shark (here Cl-24). The shark feeder actively deploy tuna heads up in the water column with a long stick before backing off, so that the fish heads is released at least 3 meters away from any scuba diver.

on the 31 individuals, consisting of 4 males and 27 females, which could be easily distinguished due to distinct markings. This cautious approach aimed to prevent any mistaken identity issues that might have otherwise complicated our interpretation of individual behaviours.

2.2. *Implementing traits rating*

Given the highly dynamic feeding interactions and the frequent presence of multiple individuals at the provisioning site (sometimes up to 25 in a single session), we focussed on expert trait rating as the most effective approach to assess bull shark feeding behaviour. A comprehensive description of this method can be found in Appendix A at 10.6084/m9.figshare.24204501 and Drescher et al. (2013). Trait rating involves a focused assessment of specific behavioural traits and relies on the judgment of seasoned observers who possess an in-depth understanding of the species, its behavioural spectrum, the study site, and the influence of environmental factors. These experts are capable of distinguishing between inherent, long-term behavioural traits and short-term responses, enabling them to detect variations in behaviour over time (Fazey et al., 2006; Vazire et al., 2007; Drescher et al., 2013).

To characterize bull shark behaviours in this study, the first author and expert observer TV dedicated over 1000 h across multiple years to closely observe the same individuals during feeding interactions with conspecifics and human feeders, all under varying environmental conditions. TV's direct observations were complemented by photographic and video documentation, as well as observations of shark behaviour recorded by other trained divers at the feeding site.

2.3. Constructing the ethogram

Ethograms are highly species and context-specific, as emphasized by Koski (2014). Therefore, to design an appropriate ethogram, our initial step involved observing the behaviours of multiple bull sharks, including individuals not included in this analysis. This comprehensive observation allowed us to gain insights into the complete spectrum of potential behaviours and to fine-tune our characterizations. Creating an ethogram tailored specifically to wild bull sharks in artificial feeding scenarios provided us with a foundational understanding for analyzing bull shark behaviour within our unique context. Importantly, this approach did not supersede expert opinions on particular behaviours or actions. Instead, it incorporated various environmental and social factors (as detailed in Table 1 in the Results section) and relied on the tacit knowledge and extensive dive experience of the observers.

We then considered five distinct situations, formed by the combination of three factors: (a) whether the observed shark was feeding or not, (b) its proximity to scuba divers and (c) its proximity to other sharks. Within each of these five situations, our focus was on assessing personality traits that directly impact shark behaviour in the context of artificial provisioning. This context encompassed both positive stimuli, such as potential access to food, and negative ones, like the presence of competitors (conspecifics) and intruders (divers). Given the multifaceted nature of this complex situation, which involves elements like novelty, feeding incentives, potential threats, and social dynamics, we anticipated that individual shark behaviour would primarily be influenced by two key traits: 'boldness/shyness' and 'risk taking/risk avoidance' (Reale et al., 2007). However, it's worth noting that other traits, including 'aggression-passivity', 'dominance-submission', and 'level of activity' (as outlined in Finkemeier et al., 2018), may also interact with and contribute to individual behaviour. Importantly, the inclusion of these various traits does not undermine the validity of a composite and well-grounded behavioural assessment, especially when conducted over an extended period.

2.4. Evaluating shark's personalities over time

Based on the ethogram (Table 2), we systematically evaluated each individual, considering the various known influencing factors outlined in Table 1. To assess shark behaviours, we categorized them based on four distinct feeding scenarios:

- Potential reward without competition or risk (food, no other sharks, no divers)
- Potential reward without competition but with risk (food, no other sharks, divers)
- Potential reward with competition but without risk (food, other sharks, no divers)
- Potential reward with competition and risk (food, other sharks, divers)

In this context, 'no other sharks' signifies an individual approaching food without immediate competition from other sharks within a close range of approximately 5 m. Conversely, 'other sharks' denotes situations where direct competition for food was observed among individuals during the evaluation. 'No divers' implies that the feeding action took place at a distance greater than 5 m from the observer or any other divers, while 'divers' indicates that the feeding occurred in close proximity, within 5 m of scuba divers. These four scenarios were repeatedly observed during numerous dives, encompassing more than 15 distinct feeding events (each involving the release of food) per session.

Within each of these four scenarios, we utilized a 5-point scale, ranging from 'Timid' to 'Combative' (Table 2), to score the behaviour of each shark. This scale allowed us to document behavioural plasticity, where sharks exhibited various behaviours in similar situations, as described by Dingemanse et al. (2010). Each behavioural 'type' was weighted (see Table 2 for details) and averaged across the different situations to calculate a comprehensive feeding-behaviour score. It is important to note that a score of -5 is not represented here, as 'avoider' sharks were not observed closely or frequently enough to be rated. Additionally, we calculated a global plasticity score based on the averaged scores across behaviours and sessions.

3. Results

We collected data from 651 dives, with durations varying between 25 min (deeper sites) and 45 min (shallower sites), resulting in a total of 2813 individual observation sessions. For the purpose of assessing behaviour, we focused on 31 adult bull sharks, each identified by a unique number followed by either an F for female or an M for male (detailed scoring can be found in Appendix B at 10.6084/m9.figshare.24204501).

3.1. Table of key factors influencing shark behaviours

External and internal environmental factors influencing bull shark behaviour at feeding sites primarily included indicators of potential hunger (detected from clues such as body shape, skin texture, and documented shark feeding records), seasonal variations, pregnancy status, disturbances, interactions with other sharks, bait quality and placement, teleost activity, visibility, and swell conditions (as detailed in Table 1). It is important to note that we observed rapid learning abilities in sharks, including learning from the actions of other sharks (horizontal learning).

3.2. Ethogram

As this is the first ethogram for wild bull sharks in provisioning scenarios, we anticipate the necessity for future refinements tailored to specific local conditions. These adaptations might encompass adjustments to the shark feeding protocols or the development of distinct habituation methods. For instance, we noted that engine sounds, typically enticing on shark feeding dives, acted as repellents in our case if initiated during a dive. Our research enabled us to categorize and rate sharks along a continuum spanning from shy to bold, employing terminology that best corresponded to the observed behaviours during feeding encounters: Timid, Apprehensive, Confident, Bold, and Combative. Each category received a weighted score for personality assessment, ranging from −3 (indicating Timid) to +5 (indicating Combative). We considered five distinct situations at our specific site, providing a detailed description of underwater observations (Table 2).

3.3. Feeding-behaviour scores

Shark behaviour scores spanned a wide range, from −13.5 (indicating timid behaviour in individual 16F) to +22 (indicating combative behaviour in individual 46F). Plasticity scores exhibited similar variability, ranging from

Table 1.
Influence of various factors on the observed behaviour of sharks in artificial feeding situation at the studied site.

Influencing factors	Influence of ...	Leads to bolder behaviour	Leads to shyer behaviour
Satiety (level of hunger)	Natural feeding	No or low	Recently
	Artificial provisioning	No or low	Recently
	Seasonality	Return from mating season	Mating season
	Pregnancy (females)	Yes	–
Risk perception	Divers attitude	–	Agitated
	Number of divers	–	High
	Distance to divers	–	Close
	Space openness	–	Low
	Presence of bolder sharks	No	Yes
Extrinsic stimulation	Bait attractiveness	High (fat and fresh)	Low (rotten and/or low fat)
	Distance to bait	Close	Far
	Competition context (with sharks)	Depending on dominance	Depending on dominance
	Sounds triggers from teleost's bites on baits	High (e.g., snappers)	None or Low
Environmental factors	Water visibility	Good	Low
	Swell	–	High
	Boat activity (engine sound)*	–	Yes
	Presence of other large shark (e.g., large tiger shark)	–	Yes

Each factor can lead to the observed behaviour of a shark to be considered 'shyer' or 'bolder'. Influence can vary on other sites or for other species.

*In other sites, engine sounds can be used to attract and sometimes emboldens sharks as they associate it with feeding opportunities. This is not the case here.

2.5 (representing consistent behaviour in individual 50F) to 11.25 (indicating highly variable behaviour in individual 40F) (see Figure 2). It's worth noting that, outside the strict scope of our rating study, four sharks (among the 31 assessed) exhibited potentially hazardous behaviours towards humans, albeit very infrequently. These behaviours included reflexive bites on objects (individual 31), pushing against the feeder to obtain food (individuals 13

Table 2.
Ethogram for bull sharks at the artificial feeding sites.

Ethogram			Behaviour (weight)				
			Timid (−3)	Apprehensive (−2)	Confident (2)	Bold (3)	Combative (5)
Trying to get food	far from divers	alone	Slow foraging, regular backoffs, circle around food before final approach. Escape quickly after eating.	Shark displays slow foraging with regular pauses	Shark displays continuous foraging behaviour	Shark goes straight for the food at a fast pace	Shark rushes to the food at full speed or constantly occupies feeding area, occasionally bites on objects or in the water. Violent bite on food (jaw dislocation or sound).
Trying to get food	close to divers	alone	Shark stays away at a safe distance	Shark stays away but shows interest and occasional approaches, feeds as hit and run only if divers calm	Shark repeatedly approaches food and tries to feed but back off if overwhelmed, in proximity to diver or pole.	Shark does its possible to get the food while avoiding contact with divers. Backs off when touched or in close proximity to pole.	Same as above + May come to contact, try to steal food from feeder's hand, bump into feeding box, and push back against pole. Rapid turns, shacking eyes, random accelerations

Table 2.
(Continued.)

Ethogram			Behaviour (weight)				
			Timid (−3)	Apprehensive (−2)	Confident (2)	Bold (3)	Combative (5)
Trying to get food	far from divers	within group	Shark stays away at a safe distance	Shark stays away but shows interest and occasional approaches if other sharks smaller and shy too.	Shark repeatedly approaches food and tries to feed but back of if overwhelmed (too many or dominant other sharks)	Shark does not hesitate to compete with other sharks to get the food, including accelerations, but avoids contact.	Shark does not hesitate to compete with other sharks to get the food, including accelerations, and bump into other sharks. May bite objects or in the water. May accidentally bite other sharks when eating.
Trying to get food	close to divers	within group	Shark stays away at a safe distance	Shark stays away but shows interest and occasional approaches but almost never access the food	Shark repeatedly approaches food and tries to feed but back off if overwhelmed	Shark competes even close to divers, but will avoid contact.	Same as above + May come to contact, try to steal food from feeder's hand, bump into feeding box, and push back against pole. Rapid turns, shacking eyes, random accelerations

Table 2.
(Continued.)

Ethogram		Behaviour (weight)				
		Timid (−3)	Apprehensive (−2)	Confident (2)	Bold (3)	Combative (5)
No food	Behaviour toward diver(s)	Shark stays away at a safe distance and leaves the site within a few minutes	Shark stays away at a safe distance	Shark deviates around diver at same speed, but does not approach on purpose	Shark comes toward diver and shows interest but deviate and loses interest over time, or passes close to diver with minimum deviation	Shark comes toward diver and show interest, may come as close as possible, contact multiple times in a row. Curious.

The ethogram is designed for trait ratings in 5 different situations (rows), when the food is not directly given by the feeder (e.g., hand-feeding). Rare original behaviour observations should be noted separately. In this case, ‘safe distance’ or ‘far’ means $>$ 10 m, while ‘close’ means $<$ 3 m.

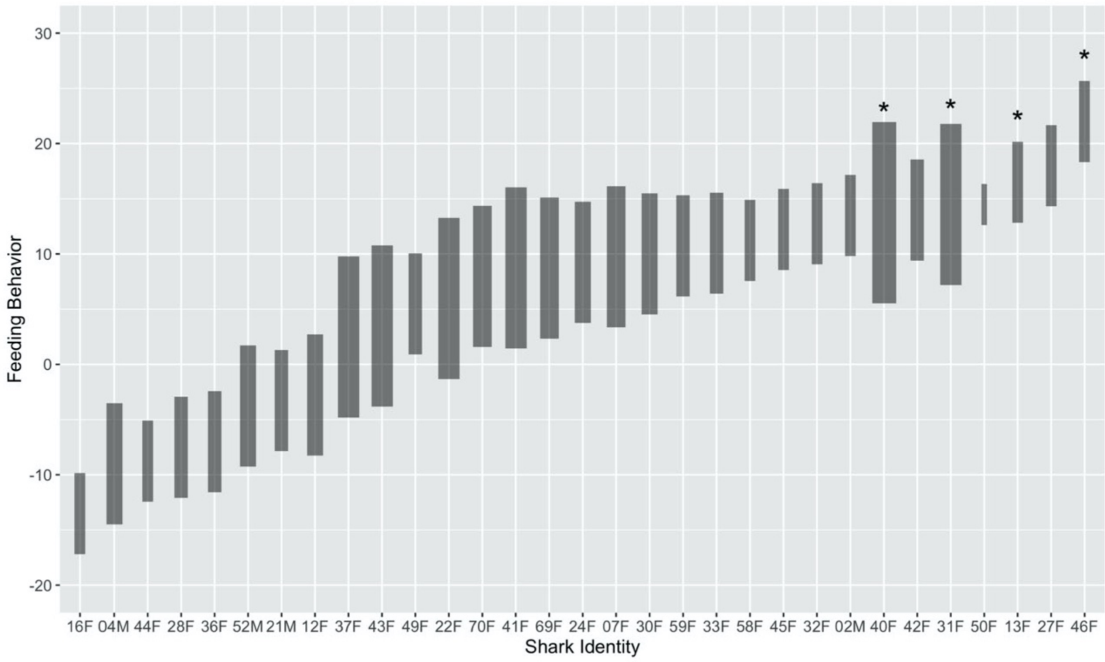

Figure 2. Inter individual variability in feeding behaviour ranked from lowest to highest values. Scores taken from Appendix B at 10.6084/m9.figshare.24204501. F: Female, M: Male. Height of the bar depends on the plasticity score. *Sharks that have been showing, although very rarely, repeated potentially dangerous behaviours toward humans (e.g. reflex bites on objects (31, 32), pushing for food against feeder (13, 46: potential accidental bite) or accelerating toward swimming diver (40: instinct triggers toward large objects)). Figure designed with the R package ggplot2 (Wickham, 2016).

and 46: potentially resulting in accidental bites), and accelerating towards swimming divers (individual 40: investigating even large objects) (refer to Figure 2 for further details).

4. Discussion

Expert trait ratings unveiled a spectrum of individual behaviours among bull sharks, ranging from timid to combative. Some sharks exhibited more behavioural plasticity across situations than others. Although our methods could be improved by additional coding data, we observed significant and consistent differences between individuals over time, which was the central focus of our study.

The presence of substantial, consistent differences in individual behaviour among wild adult sharks strongly suggests a wide range of personalities, corroborating the findings of Finger et al. (2017) who initially reported distinct personalities in juvenile sharks. Additionally, we identified key factors that may influence shark behaviour independently of underlying personality traits. These factors should be considered in potential studies in similar provisioning contexts. However, it is essential to acknowledge the adaptive nature of adult bull sharks, which could lead to rapid changes in how these factors influence behaviours. Personality assessments should be made with a comprehensive understanding of the history and broader context of the specific situation.

Our exploration of shark personality could be further enhanced by combining trait ratings with behaviour coding, along with extensive recording of environmental, contextual and social variables. Gathering this information is extremely challenging due to the chaotic and rapid nature of activities at the feeding site but remote underwater video cameras could serve as valuable supplementary tools for systematically recording and evaluating behaviours, helping to describe triggers and competition patterns for each individual (e.g., Brena et al., 2018). Cameras could also improve documentation of very shy individuals (often smaller) that avoid divers and were thus not included in this study, which inadvertently focused on bolder animals that are easier to observe.

It is also important to note that our study assessed the behaviour of sharks already habituated to provisioning activities rather than naive individuals visiting the provisioning site for the first time. Habituation is difficult to avoid when observing the same individuals in the same situation over time. Positive and negative reinforcement (e.g., giving, or withholding food rewards) at the site may have had an overall moderating effect on behaviours, with shy sharks becoming bolder and combative sharks becoming calmer over time. Consequently, although the observed bull sharks displayed a wide range of personalities, the divergence of behaviours might be even more pronounced with non-habituated animals in unfamiliar situations. In such cases, the strong influence of chance or random behaviour in new, sudden contexts may overshadow any underlying personality traits, highlighting the technical limits of interpretation.

The presence of distinct personalities in sharks may represent an Evolutionarily Stable Strategy (ESS) that maximizes their species' chances of survival by providing a hedge against variable environmental risks (Wolf & Weissing, 2012). Both boldness and shyness can be advantageous or disadvantageous depending on the context, as demonstrated in the work on juvenile lemon sharks' spatial behaviour (Dhellemmes et al., 2020, 2021).

For instance, bold bull sharks might excel in low-risk environments with scarce food and high competition, while shyer individuals could thrive in high-risk settings with abundant food and low competition. These personality differences likely stem from a complex interplay of factors, including instinct, genetics, epigenetics, personal experiences, and the ontogenetic environment. Exploring the origins of shark personalities presents an intriguing avenue for research, potentially involving genetic studies and hormonal analyses in known individuals (see Wilson et al., 2019). Similarly, comprehending the repercussions of personalities in terms of selection and evolution is a valuable field that can yield essential data for population management and conservation (Smith & Blumstein, 2008).

These personality differences may also influence which types of sharks, whether shy or bold, are captured by fishermen. Personalities are partially influenced by genetics (extensively studied in humans, see Zwir et al., 2020), hence they could tilt the average behaviour of a particular population in a specific direction. Traditional CPUE (Catch Per Unit Effort) analysis typically assumes that all individuals have equal chances of being captured and that capture probabilities are identical across populations. However, the existence of distinct personalities may challenge this assumption. Bold sharks might be more susceptible to capture in hook and line fisheries (see Arlinghaus et al., 2017 on timidity-syndrome driven by fisheries; and Hulthén et al., 2017). Additionally, we observed rapid learning abilities in sharks, including learning from the actions of other sharks (horizontal learning; TV, pers. obs.; and see Brena et al., 2018). Combined with their ability to detect metal hooks (Mourier et al., 2017), their personality traits and the influence of hunger (linked to prey availability), those learning capacities should prompt a re-evaluation of CPUE data, particularly when comparing populations or conducting temporal analyses.

Our scoring method consolidates various facets of each shark's personality to formulate an overall 'boldness' score, a technique employed in analogous studies (as observed in voles by Eccard et al., 2022). Bolder sharks are more inclined to explore novel prey and take risks, potentially increasing the likelihood of encounters with ocean users. In extreme cases, this propensity could give rise to what are referred to as 'problem individuals' (Clua & Linnell, 2018), which may repeatedly engage in biting incidents involving ocean users, resulting in clusters of such events (Clua et al., 2020). A recent example of a cluster occurred in Tanzania, where only one predatory shark bite was recorded before 2000 (in 1946). Subsequently, five fatal predatory bull shark bites were documented in the same area in June, July, August, and then twice in September 2000: leading to a ban on swimming in the area. No further shark bites have been reported in Tanzania since then (Shark Research Institute, Global Shark Attack File, 2020). Historical records also indicate clusters of shark bites, dating back to the late 19th century (Bryce, 1899), further supporting the premise that a single shark can be responsible for a series of predatory bites (Clua & Linnell, 2018).

Contrary to the assertions of some authors (Neff, 2019), these observations do not align with the 'rogue' shark hypothesis (Clua & Linnell, 2019). Instead, it suggests that a sufficiently bold shark, having successfully bitten a human and fed, may have a higher probability of repeating such behaviour than its conspecifics. The presence of 'problem individuals' among terrestrial predators is well-documented (Mukherjee & Heithaus, 2013; Blackwell et al., 2016), and there is no a priori reason to assume that such a phenomenon is absent among marine predators. A deeper understanding of the mechanisms and causes behind these events could lead to more effective and selective mitigation strategies than the widespread culling of large sharks, a practice still prevalent in several locations globally. It is important to note that not all shark bites on human would suggest a 'problem individuals', as this would only apply when the same individual displaying dangerous behaviours on several occasions.

4.1. Conclusion

Our research strongly indicates that adult wild bull sharks possess individual personalities that span a spectrum from timid to bold. Our findings carries substantial implications for conservation and management and should stimulate a re-evaluation of the common assumption that shark behaviour is uniform across individuals and populations.

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Evidence of individual sharks repeatedly targeting humans

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Abstract:

It is widely accepted that populations of terrestrial predators sometimes contain 'problem individuals' that occasionally but repeatedly attack humans, yet this phenomenon has never been demonstrated in sharks. Here, we present photographic and genetic evidence of problem individuals in populations of Tiger and Oceanic Whitetip sharks. These problem individuals exhibited: (1) Atypical behaviour compared to the rest of the population, (2) Repeated agonistic behaviour directed towards humans, and (3) Feeding or attempting to feed on humans. If such individuals account for a substantial proportion of shark bites on humans, then mass culling of sharks will have no effect unless the culprit individuals are captured. Although challenging in the marine environment, selective removal of these individuals would be a more effective, eco-responsible, cost-effective and ethical solution for vulnerable taxa than ongoing non-selective culling campaigns. (n=133)

Introduction:

Sharks are a perennial source of fear and fascination for humans, yet shark bites are actually very rare events with only approximately 100 incidents per year worldwide and less than 15% proving fatal (1). A slight increase in fatalities in recent decades is attributed to concomitant significant increases in the number of ocean users (2,3) combined with the emergence of new sports such as kite surfing that have extended human marine recreational activities into new, previously unused, and potentially dangerous, areas (4). Although rare, these human fatalities have a disproportionate media impact, with considerable psychological and economic repercussions, especially on island economies based on beach tourism (5).

The concept of a 'rogue' shark 'developing a taste for humans' resulting in multiple attacks first emerged in Australia in the early 1950s as a potential explanation for apparent clusters of fatal shark attacks (6). However, this concept has subsequently been widely criticized as anthropomorphic and improbable (7). The wildlife management response to fatal shark bites varies among geographic locations but is broadly divisible into culling or non-culling approaches. In locations where culling is utilized either in response to fatal bites, or as an ongoing risk mitigation strategy, the practice is typically very unselective with many individuals of multiple species being culled (8). Although shark culling campaigns remain a politically attractive response to shark bites in some locations there is no evidence that they actually reduce risk (3,9) and the tide of public opinion is turning against them (10) as the public learns more about the ecological importance of sharks and the conservation plight that they currently face from overfishing (11 - 13).

The original concept of 'rogue' individuals among predator species has been superseded in recent decades by the concept of 'problem individuals'. Although widely accepted as valid in terrestrial predators such as big cats (14, 15), there is greater reluctance to accept that this phenomenon may also exist among large shark species (16). In this study, we provide empirical evidence of individuals from two species of shark repeatedly targeting humans and thereby meeting the definition of 'problem individuals' as recognized in terrestrial predators.

Results:

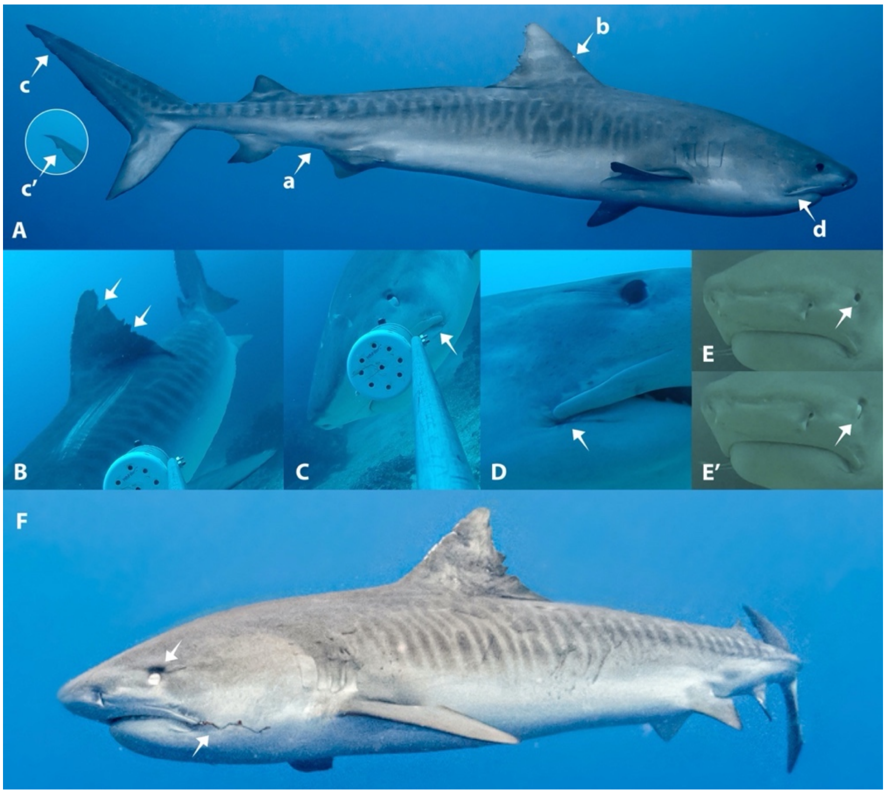
Genetic identification of a problem shark.

In December 2020, a female swimmer was fatally wounded in the left leg by a shark in Orient Bay on the French Caribbean island of St. Martin. One month later, another snorkeler survived having her left leg amputated by a shark in the coastal waters of St. Kitts and Nevis, 85 km away. In both cases, witnesses identified a tiger shark *Galeocerdo cuvier* of approximately 3 m in total length (TL) as the culprit (Fig. 1). In both cases, wound swabs were collected from victims in an attempt to collect transfer DNA from the culprit shark (see details in Methods and SI/CS1). Although degraded, sufficient nuclear DNA was recovered to permit fingerprinting through a Single Tandem Repeats (STRs) comparison (see Tab. S1) in order to test the hypothesis that a single shark was responsible for both incidents. This comparison was validated by calculating the allelic frequencies in a reference sample of 49 tiger sharks captured in the waters of Saint-Martin and St-Barth (n=35) and Saint Kitts and Nevis (n= 14). Of the 26 STRs examined, two could not be amplified, three were monomorphic (Tab. S1), 21 STRs were classified as identical in samples from both incidents, including nine STRSs that were very polymorphic (Tab. S2 and S3), resulting in an extremely low probability (8.15 x 10^{-11}) that two different individuals were responsible for these bites.

Photo-identification of problem sharks.

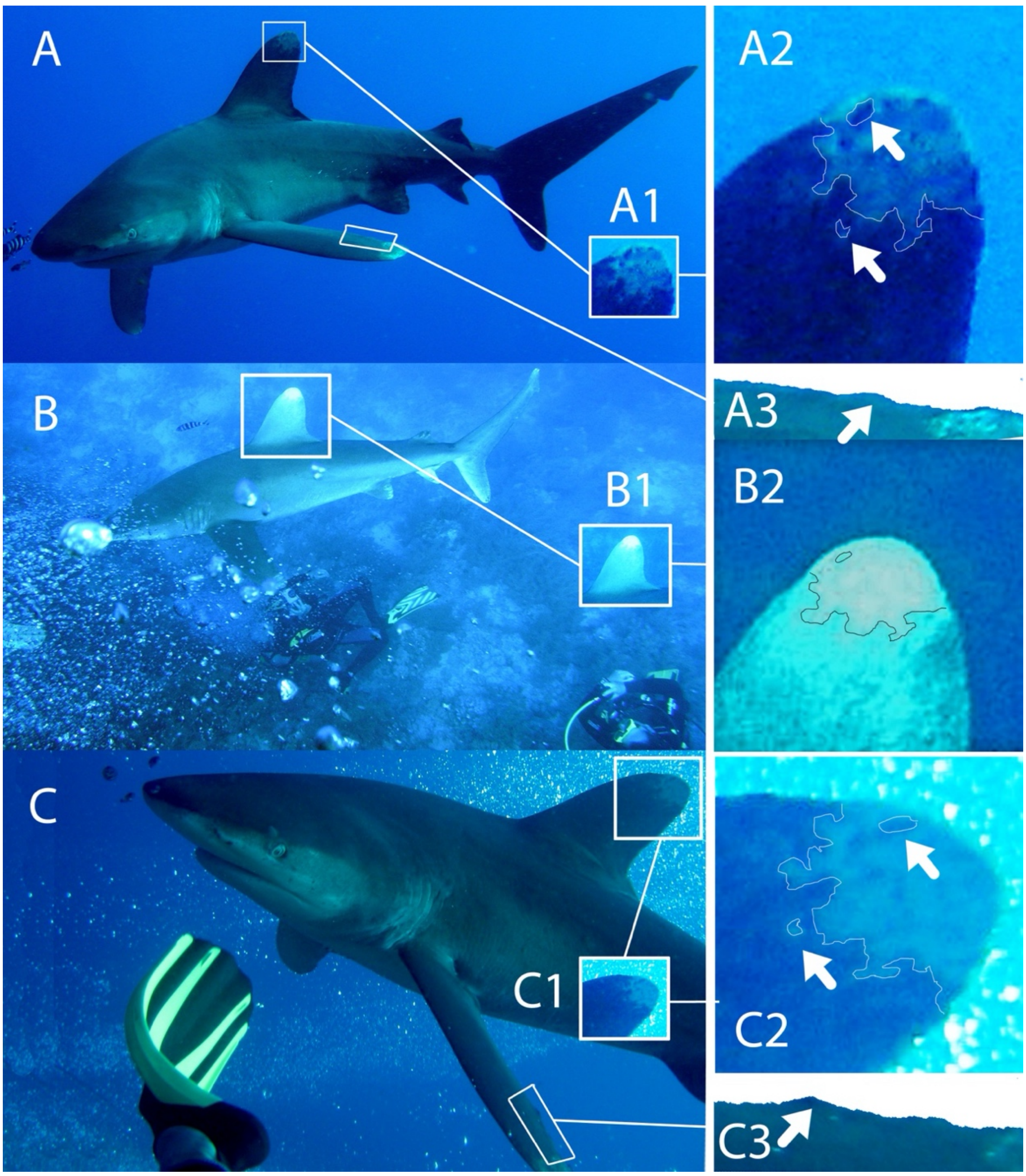
Between 2014 and 2018 in waters off the island of Cocos (Costa Rica, see Methods and SI/CS2, Fig. S1), a 3.5 m TL tiger shark (locally known as 'Lagertha') identifiable from unique markings (Fig. 1), was documented fatally biting a SCUBA diver in November 2017, injuring another diver in April 2018 (see details in Methods and SI/CS2, Fig. S2) and displaying agonistic behavior toward divers in nine other incidents (confirmed by video footage and eyewitness testimony) (Tab. S4 and Appendix S1 and S2).

Figure 1. Anatomic features of female tiger shark "Lagertha". *This individual was individually identified based on specific distinguishing marks such as A: (a) absence of claspers, (b) presence of a white spot on the right front edge of the dorsal fin, (c) absence of the subterminal notch on the back edge of the caudal fin (as in c' for another shark), and (d) a down-curving shape of the mouth (photo courtesy of M. Hunkel). B: the back edge of the dorsal fin also includes two specific cuts (probably mating wounds that have healed) (see white arrows). C and D: close up allowing the observation of healed wounds on both corners of the mouth (see white arrows), probably linked to fishing hooks that have disappeared (photos courtesy of J. Spaet through the use of a video recorded at a bait site on the 26th September 2018). E: chronological display of the shark head before a contact with a diver showing an open eye (E) before the closure (E') of the nictitating membrane for protecting the eyes during a bite (photo courtesy of C. De la Cruz) (see similar behaviour on C, before the contact with a cage enclosing bait on a Baited Remote Underwater Video device). F: Left flank displaying of Lagertha in September 2019 showing the closing of the nictitating membrane before a close encounter with a diver and the presence of an embedded hook on the left corner of the mouth (see white arrows) as well as a poor general condition (Photo courtesy of S. Boaz).*



In the Egyptian red sea, photo-identification revealed that three agonistic interactions, including one fatal, one non-fatal and one attempted bite, between oceanic whitetip (OWT) sharks *Carcharhinus longimanus* and divers were attributable to the same individual shark, a 3-m TL female with a specific dorsal fin markings and a skin excrescence on the left pectoral fin (Fig. 2, SI/CS3, Tab. S5 and Appendices S3).

Figure 2. Photo-identification of the 'problem' Oceanic Whitetip (OWT) shark from the red sea. Photographs of the large female Oceanic whitetip individual that was involved in agonistic behaviors toward humans. A: (photo courtesy of O. Rocchia): photo taken in the context of the fatal bites on a female swimmer on June 1st 2009 (see case 1 in Tab. S5), then B: (photo courtesy of D. Guillemet) in the context of the non-fatal bite on a diver on June 2nd 2009 at a distance of 1.5 km (see case 2 in Tab. S5) and finally C: (photo courtesy of Y. Eekout) again the same individual involved in an agonistic behavior 3 km away on June 3rd 2009 (case 3 in Tab. S5). A1, B1 and C1: Close-up of the dorsal fin (left side) with an amplification of contrast to better discriminate the margins of the terminal white spot. A2, B2 and C2: Close-up of A1, B1 and C1 in order to better observe the similarities of the white margins, in particular i) a small zone without a white coloration close to the proximal end (top arrow in A2 and C2) and ii) a small white spot, detached from the main white spot (lower white arrow in A2 and C2). In addition to the features of the white coloration of the dorsal fin, this shark has, in the last third of the posterior margin of its left pectoral fin, a skin excrescence (probably induced by the healing of an injury) which is clearly visible in close up A3 and C3.



Discussion:

To our knowledge, this is the first definitive evidence of individual sharks repeatedly targeting humans. The Caribbean tiger shark and the easily distinguishable Pacific female tiger shark nicknamed ‘Lagertha’ as well as the Oceanic whitetip shark (OWT) meet all three of the criteria that define a problem individual: (i) Atypical behavior compared to the rest of the population, (ii) Repeated agonistic behavior directed towards humans, and (iii) Feeding or attempting to feed on humans, including a human fatality attributed to each individual. Poor physical condition may have been a motivation for atypical aggressive behavior by the tiger shark ‘Lagertha’ at the Cocos Island (Fig. 1A and 1F) as has been noted in some terrestrial predators involved in predatory interactions with humans (17). However, the aggressive OWT shark, as well the tiger shark involved in the Caribbean attacks, appeared to be in normal physical condition, suggesting inherent personality traits such as boldness and risk-taking may be important drivers of agonistic encounters with humans. The presence of a subset of bold individuals in predator populations may be an evolutionarily stable state where the heightened propensity to try novel prey sometimes confers fitness advantages (18). There is certainly a growing body of evidence of different ‘personalities’ in large predatory sharks with some individuals being consistently bolder and more willing to investigate and bite unfamiliar objects that may be novel prey (19-23). Positive reinforcement to target humans could occur if investigative or direct predation bites are rewarded by the scent or taste of palatable tissue, thus encouraging naturally bold individuals to become problem individuals (such as the Caribbean tiger shark that struck in Saint-Martin and St Kitts and the Oceanic whitetip (OWT) shark from the Red Sea see SI/CS3 - Tab. S5). These incidents involved two of the primary shark species known to be responsible for human fatalities (1). Additionally, previous spatio-temporal clusters of shark bites have been associated with the other two species, namely the white shark and the bull shark, which account for a significant proportion of shark bite incidents. These clusters demonstrate a high level of consistency with the presence of 'problem individuals' (18) (Fig. 3).

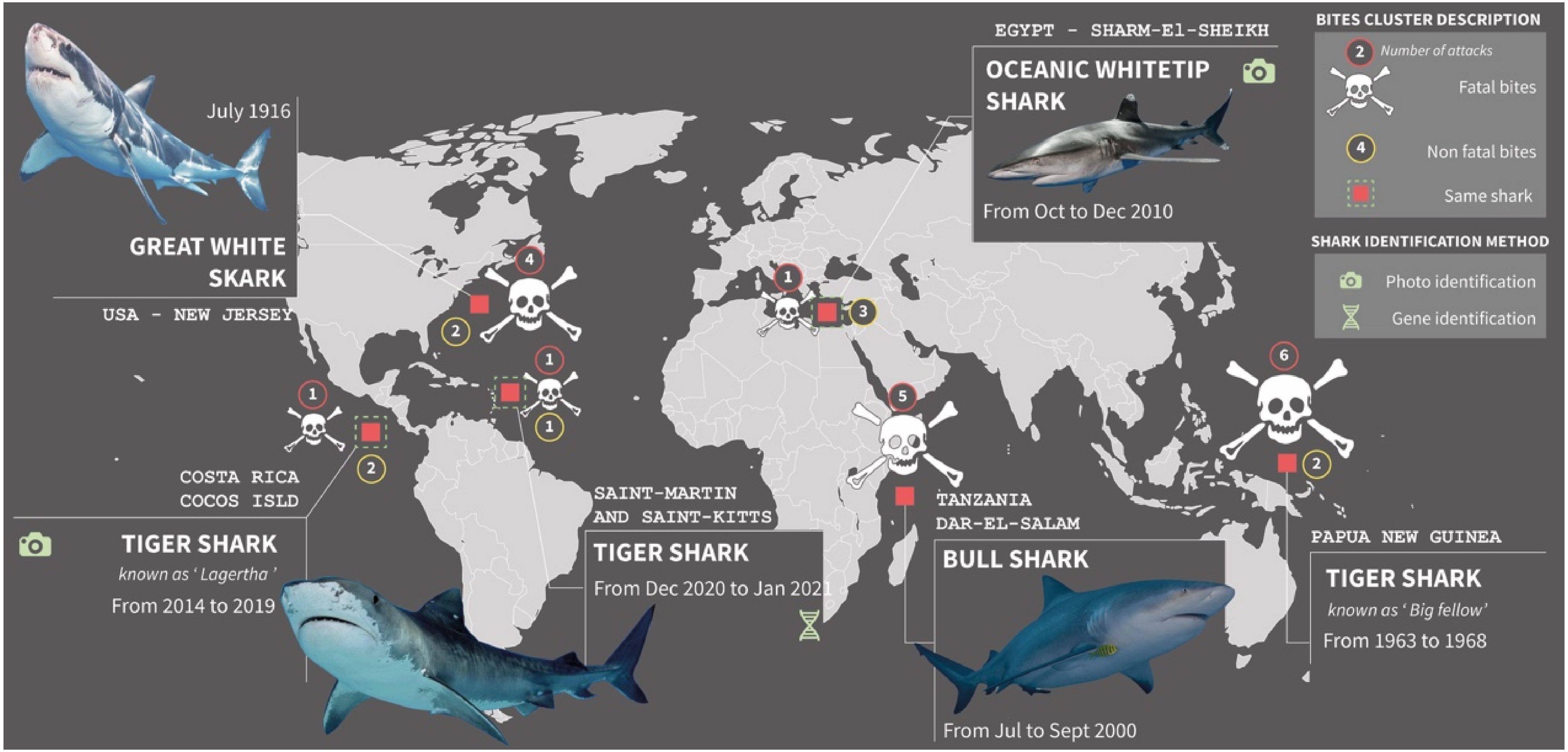


Fig. 3- Existing and potential shark bite clusters involving the four most traumatogenic species. Examples of spatio-temporal clusters of shark bites on humans that are consistent with the activities of problem Individuals. Great white shark: the summer of 1916 in New Jersey (USA) experienced a highly unusual series of fatal bites that occurred on swimmers (25). Bull shark: Tanzania experienced a fatal bite in May 1968 (unknown species), then no fatalities for more than 30 years until June 2000 when an initial fatality in Dar-Es-Salam, was followed by four additional fatalities within the next three months in the same area, involving this same species and until swimming was forbidden after death number 5. Oceanic Whitetip shark: the northern Red Sea experienced a cluster of several bites around the site of Sharm-El-Sheikh from October to December 2010, with a high probability of the same individual being involved (26). Tiger shark: in addition to the Costa Rica case study (tiger shark 'Lagertha'), Papua New Guinea experienced a total of 12 bites (possibly more), including 10 fatal, involving this species. Among these bites, six were believed to be perpetrated by a single individual nicknamed 'Big fellow' (24). Figure developed with the technical assistance of S. Roddier.

In this study we provide empirical evidence of individuals from two sharks species repeatedly biting or showing aggression toward humans. In a terrestrial setting, predators exhibiting this pattern of behavior would be classified as 'problem individuals'. Although this pattern is superficially similar to the original concept of a 'rogue' shark, there are important distinctions between these two concepts. The term 'rogue' implies an animal with savage or destructive tendencies' or 'a person or thing that behaves in an aberrant, faulty, or unpredictable way'. Thus 'rogue' anthropomorphizes the motivations of sharks that attack people in a way that 'problem individual' does not and implies that there is something 'wrong' with the animal. However, a perfectly normal healthy individual exhibiting normal foraging behavior could be a problem individual. For example, the OWT observed biting humans in the Red Sea appeared to be in good physical condition. Shark bites on humans are probably just a natural consequence of the shark's natural dietary plasticity and natural tendency to explore potential prey by biting. If a shark receives positive reinforcement from one of these encounters, then they may be more likely to try it again and thus become a 'problem individual' from a human perspective. There is nothing aberrant about this positive reinforcement mechanism, rather it is the normal process through which sharks learn to exploit prey and hence there is nothing 'rogue' about 'problem individuals'. We don't yet know the proportion of all shark bites that are attributable to 'problem individuals' but our results suggest that DNA fingerprinting samples obtained by taking swabs from bite wounds on people or equipment could answer this question. The existence of 'problem individuals' in shark populations would have obvious implications for management responses, opening for the potential of a shift from unselective culling to more targeted responses (27). In very practical terms, our results suggest that the medical protocols implemented in the context of shark bites on humans remain focused on the survival of the victims, but also systematically include the swabbing of wounds on the victims (27), before the use of any chemical medical treatment that could alter the DNA of the biting shark and jeopardize its identification. This action takes minimal time and can help save the lives of other people in the future.

Methods:

Caribbean problem tiger shark identified through genetics.

Single source and mixed forensic samples are prone to PCR inhibition and DNA degradation resulting in poor amplification and allele dropout (28). To account for possible transfer DNA washout and degradation at bite wound sites, we performed two separate and independent fingerprinting runs for each of the two sets of samples. First, DNA was extracted from the swab tips from St Martin (n=6 swabs) and St Kitts-and-Nevis (n=6 swabs) using the Gentra Puregene DNA Purification Kit (Qiagen) following manufacturer instructions, and the tooth splinter found in the victim's thigh from St Martin (CS1 - Fig. A), extracted using the DNA Wizard Purification Kit (Promega) following manufacturer instructions. DNA extraction quality was visualized on a 2% agarose gel.

Taxonomic identification (barcoding) was performed through a single run using the 250 bp CO1shark25F – CO1shark315R fragment (CO1shark25F -5' AGCAGGTATAGTTGGAACAGCCC 3' and CO1shark 315R -5' GCTCCAGCTTCTACTCCAGC 3')[37]. Mitochondrial sequences were amplified using Qiagen reagents kit, with 2.5µl Tampon TAQ 10X, 2µl MgCl2 25 mM, 2.5µl dNTPs 2 mM, 0.6µl of each primer (10µM), 0.1µl Taq polymerase (5u/µl), Ultra-Pure H2O, 5µl QSolution, for a final volume of 25µl. PCR programs consisted of an initial denaturing step at 95 °C for 3 min., followed by 35 cycles of 95 °C for 30 sec, 62 °C for 45 sec, and 72 °C for 30 sec, finished by 10 min at 72 °C and then held at 4°C (Thermocycler Eppendorf nexus gradient). PCR products were all ran on a 2% agarose gel. PCR products were sequenced by GenoScreen (Lille – France) using an Applied Biosystem's 3730xl DNA Analyzer. Sequence data were analyzed with BioEdit 7.2.5 and exported to the BLAST function (fasta format) from GenBank. CO1shark25F – CO1shark315R sequences were assigned allowing a best match score > 98%.

Individual identification (fingerprinting) was performed through two separate runs. In the first run genomic DNA Microsatellite markers were amplified using Type-it Microsatellite PCR kit (Qiagen, Hilden, Germany) in a final volume of 10 µL including 5 µL Type-it Multiplex PCR Master Mix (2X), 0.04 µL of each primer (25 µM forward and reverse primers diluted in TE pH 8 buffer) and 1 µL of DNA. PCR programs consisted of an initial denaturing step of 15 min at 95 °C, followed by 40 cycles of 1 min at 95 °C, 1 min at specified annealing temperature (53°C, 56° or 58°C – see table S1), 72 °C for 1 min, and a final elongation step at 72°C for 20 min. Due to the very low genomic DNA quantity, all loci were amplified in monoplex. PCR products were sequenced using an Applied Biosystems 3730 Sequencer, with GeneScan 500 LIZ (Applied Biosystems) for accurate sizing. (GenoScreen / Lille – France), allele sizes were scored and checked manually using GENEMAPPER 3.7 (Applied Biosystems). Special attention was paid to markers larger than 300 bp, due to the difficulty of obtaining correct amplifications for these loci (28,29). For markers yielding unreliable results (i.e. having low quality chromatograms with parasitic peaks, mis-amplifications, no or low amplification), PCR amplification was modified for the second run, increasing the stringency of the PCR conditions and limiting the effect of potential PCR inhibitors (28). A 2-step PCR amplification reduced the effect of PCR inhibitors, and consisted of an initial PCR reaction with an initial denaturing step of 15 min at 95 °C, followed by 20 cycles of 1 min at 95 °C, 1 min at specified annealing temperature (53°C, 56° or 58°C), 72 °C for 1 min, and a final elongation step at 72°C for 20 min. Subsequently, 1 µL of PCR product from the initial reaction was used as template for a second PCR reaction with same PCR conditions but increasing the cycle number to 30 cycles. Amplicons were sequenced and analyzed under the same conditions as described above.

As a quality control process, reading and analysis of the allele matching was performed independently by two different experts co-authoring this study (SB and SP).

A total of n=49 DNA samplings of individuals of *G. cuvier* were obtained for the genetic study of selected microsatellites. These animals were collected from three different sites in the Caribbean area where attacks took place, off the islands of St. Martin (n=34), St. Barth (n=1), and St. Kitts and Nevis (n=14). This number of tiger sharks has the potential to allow the calculation of allelic frequencies in a reliable and accurate manner, as 25-30 individuals are usually sufficient for this type of study (30). Genetic analysis (extraction, PCR) were conducted in the CRIOBE lab in Perpignan (France). Sequencing was subtracted to an exterior company.

A total of 26 microsatellites were sequenced for all sampled individuals (Tab. S1). Diversity indices such as number of alleles (na), allelic frequencies, expected and observed heterozygosity (Hexp and Hobs, respectively) were calculated for all markers using GenAlEx 6.5 (31, 32). This software also allowed the identification of possible deviations from Hardy-Weinberg equilibrium (HWE). The probability of identity (PId), the probability that two different randomly selected individuals share the same genotype, and the probability of identity in the presence of related individuals (PIdSibs) were also analyzed at each locus. The PIC (Polymorphism Information Content) was calculated for all polymorphic microsatellites studied using the following formula (33):

$$PIC = 1 - \sum_{i=1}^{k} {p_i}^2 - \left(\sum_{i=1}^{k} {p_i}^2\right)^2 + \sum_{i=1}^{k} {p_i}^4$$

After removal of the monomorphic microsatellites (CL12, CL14 and CL17), the selection of markers was made considering PIC > 0.5 in order to keep only the most informative loci (6). 11 microsatellites met this criterion, but only n=9 were retained for the calculation of allelic frequencies, as TIG12 and TIG15 could not be amplified for both samples due to the degradation of the collected DNA on both victims.

The number of alleles composing the selected microsatellites for the study varies between 4 for the TIG01 locus and 20 for the TGR891 locus, for an average of 9.556 ± 5.525 (SD). The average expected heterozygosity in the Caribbean tiger shark population is 0.746 ± 0.129 (SD) and the average observed homozygosity is 0.685 ± 0.172 (SD). None of the selected loci show a deviation from Hardy-Weinberg equilibrium (p-value > 0.05) and are thus marked by no significant difference between expected and observed genotype frequencies. The PIC value is lowest for the TGR1185 locus (0.504) and highest for the TGR348 locus (0.895), when the mean value of this parameter reaches 0.712 ± 0.150. The most polymorphic loci are TGR348, TGR891, TGR943 and TGR1157 due to the high values obtained for na, Hexp, Hobs and PIC. Moreover, the frequency of the most represented allele (FNA) for each of these loci is much lower than 0.5, marking their interest. The PId obtained for all loci combined, obtained by the product of the PId of all selected sequences, is extremely low: 8.73 x 10-11. Similarly, the PIdSibs obtained for all 9 loci reaches a value of 2.40 x 10-4. This result shows the very low probability of sharing the same genotype for two randomly selected individuals within the population studied, and thus underlines the relevance of the selected microsatellite loci for individual discrimination of tiger sharks evolving in the Caribbean area.

Allele frequencies for each of the 9 selected microsatellites were generated (Tab. S2). The genotypic frequency for each locus was calculated as the product of the two allele frequencies composing the genotype found on the two incidents from the information obtained after sequencing of the DNA collected from the two bites (Tab. S3).

The genotypic frequencies obtained on the bite incidents are particularly low for loci TGR943 (F(197/197) = 0.00689) and TGR348 (F(149/161) = 0.0123). The probability of matching (34) an individual to all these genotypic constraints on the 9 loci studied corresponds to the product of the genotypic frequencies and reaches 8.15 x 10-11. Thus, the probability of drawing two different individuals with the same genotype on these microsatellites is extremely low. This result supports the use of these microsatellites for individual identification of tiger sharks and supports the hypothesis that the same shark should have bitten both victims in the incidents considered. Nevertheless, this result could have been even more reliable given the potential value of the TIG12 and TIG15 markers, which were not used due to the lack of results obtained from the sequencing of the samples, because of the degradation of the residual shark DNA obtained from the victims' wounds.

Although the probability of two different individuals having the same genome decreases with the number of markers considered, the highly informative content of some microsatellites allows the number of loci studied to be reduced while maintaining a high degree of accuracy in individual identification. In the European wild boar (*Sus scrofa*), PId values similar to those obtained for the 14 microsatellites initially sequenced were obtained by combining results from 6 loci (35). A number less than or equal to the number of microsatellites used to discriminate the culprit individual from the bites-i.e., 9 markers-has previously been considered effective for individual identification in many taxa, although the probabilities obtained are higher than those obtained in the Caribbean tiger shark population. Indeed, a matching probability of 0.44 x 10^{-9} was obtained in a Korean breed of cattle (36) and 5.7 x 10^{-10} in the robust parrot (*Poicephalus robustus*) (37) at 9 loci, as well as a matching probability of 9.0 x 10^{-11} in a wild population of *Nerophis lumbriciformis syngnathus* at 8 loci (38). If it had been possible to obtain the genotype of the individual on markers TIG12 and TIG15, considered highly polymorphic with high degrees of heterozygosity, the probability of identity could nevertheless have been more precise, with slightly lower values of PId and PIdSibs, such as those obtained on 10 loci in snow leopard (*Panthera uncia*), reaching 2.1 x 10^{-11} for unrelated individuals and 7.5 x 10^{-5} for related individuals (39).

Cocos problem tiger shark identified through photo-identification

The island of Cocos (Costa Rica) (Fig. S1), listed as a World Heritage Site in 1997, is located in the Tropical Eastern Pacific, some 550 km off the Costa Rican mainland coast. This island is under the jurisdiction of a National Park (Cocos Island National Park - CINP) and the presence of a particularly diverse and abundant ichthyofauna (40) makes it one of the world's top recreational diving sites that brings around 7 million USD per year to the local economy (41). Chief attractions include the presence of large schools of hammerhead sharks *Sphyrna lewinii* and aggregations of whale sharks *Rincodon typus* (42). From 2000, the first tiger sharks *Galeocerdo cuvier* were observed in the wild without the use of attractants, with a steep increase in sightings after 2010 such that they are now typically observed on 12% of dives (43).

Tiger sharks were sometimes curious but never aggressive towards scuba divers until 2014 when a particular shark began to behave more aggressively. Following the two bites in November 2017 and the injury of another diver in April 2018, the first author EC visited Cocos in September 2018 to officially interview witnesses, examine photographic evidence and explore the incident locations. Interviews (n=7 corresponding to 1h 42 mn) were conducted with two boat captains, two diving supervisors and two dive masters from the two main dive companies working in the area as well as the CINP ranger diver directly involved in shark related issues. EC carried out 18 exploratory dives at both ecotourism (n=15) and non-ecotourism (n=3) locations. EC also examined photographs documenting sightings of Lagertha (n=18) and injuries from the two shark bite incidents (n=11). Finally, he was provided with another testimony of an agonistic encounter in November 2018 and photographs (n=2) from a recreational diver who experienced several close encounters with the shark in September 2019. The evidence collected was used to evaluate the hypothesis that a single problem individual was responsible for both bite incidents and other aggressive interactions with divers.

A 3 m female tiger shark with distinctive markings (named “Lagertha” by local divers, Fig. 1) began to show atypical curiosity towards divers as early as 2014 (Tab. S4). Whereas other tiger sharks always remained at a distance of several meters from divers, Lagertha would approach closely (sometimes <1 m), while closing the nictitating membranes (to protect its eyes during a potential strike – see SI Video 5) and pseudo-biting expressed by the jaw opening and closing with sometimes simultaneous sideways movement of the head (44) (see Fig. 1 and SI Video 1). Other visual evidence of aggressiveness also included flank displaying (see SI Video 2, SI Video 3 and SI Video 6: a sustained (>5 s) perpendicular bodily orientation of a signaler’s body toward a receiver, displaying its lateral surface) and pectoral fin depression (see SI Video 4: a sustained (>5 s), bilateral lowering of the pectoral fins from their usual position during swimming (45). Lagertha also consistently approached divers while they were in the water column (several meters above the bottom), on their way to the surface at the end of the dive (Tab. S4). In November 2017, a tourist scuba diver and dive-master ascending from a dive in the Manuelita Canal (Fig. S1B), were approached by the female tiger shark during their decompression safety stop. The shark was initially pushed away by the dive master but managed to hurt him. The captain rescued the diver master, whose foot was bleeding heavily, by hauling him aboard while the shark headed towards the other diver who had curled up on the surface. The boat rammed the shark on the surface as it was biting the remaining diver, allowing the captain to clearly identify the shark as Lagertha based on the white spot on the dorsal fin. The second diver died within a minute of her retrieval due to blood loss from major wounds to both thighs with a significant removal of tissue (Tab. S4, Fig. S2). In April 2018, an experienced underwater photographer diving on the outskirts of Manuelita Island (Fig. S1B) became separated from his group at the end of the dive. He was swimming at a few meters depth when he was struck from behind by what he identified as a large shark that grabbed the diving tank and buoyancy compensator in its mouth (Tab. S4, Fig. S2). The diver abandoned his diving equipment (that the shark kept in its mouth while swimming away), surfaced and took refuge on a rock, where he was able to observe and identify the shark as Lagertha patrolling at the surface while a boat was coming to pick him up. In September 2019, after no sightings for several months, Lagertha repeatedly approached a recreational diver who had separated from his group. During his ascent from 20m depth, the diver had to repel the shark three times by hitting its snout with his camera gear before being hauled aboard a boat. This diver photographed the shark enabling its identity to be confirmed (Fig. 1F).

Red Sea problem OWT sharks identified through photo-identification

The Red Sea and its reef ecosystems are a world-famous site for scuba diving with an annual average of >30,000 dives (46). This sea is home to many species of sharks, including the Oceanic Whitetip (OWT) shark which, although showing a strong affinity for pelagic waters, regularly frequents the coastal waters where it interacts with scuba divers (47). Although shark bites on humans by sharks in the Red Sea have been recorded for several decades, they have slightly increased between 2009 and 2020 (48). The possibility that some of the bites are from one and the same shark has been raised in a series of incidents between 2009 and 2013 but has not been clearly demonstrated (49). This increase in incidents has coincided with the generalization among recreational divers of underwater video systems that do not hesitate to put their films online, particularly when they have succeeded in capturing images of sharks' agonistic behavior towards humans. These images constitute a considerable sampling effort and the quality and resolution of the images in recent years allow the use of photo-identification to discriminate between different individuals within the OWT population. In addition to the size and sex of the animal, this discrimination is based in particular on the anatomical characteristics of the dorsal, pectoral or anal fins, bearing in mind that in this species, these appendages have terminal white spots specific to each individual (50).

One of the co-author (SS) acted as a dive master in Egypt from 2005 to 2020 (permit ref#(435) 21-5-2013), cumulating over 5,000 dives with recreational divers involved in dive-aboard trips that took place in all the main diving sites of the Egyptian Red sea. He had the opportunity to collect direct and indirect data (composed of detailed and agreed interviews of people and free use of photos or videos) documenting agonistic behaviours of OWT sharks toward divers, including himself. These data were analyzed in the perspective of identifying problem sharks.

On the June 1st 2009, a >3 m female OWT perpetrated several fatal bites on a 47-year old female swimmer in Gota Kebir (Saint-Johns reef) at 09:00 AM. On this day, only three OWT sharks were present at the diving spot, including two small sized individuals and the large female which was photographed (Fig. 2A) and clearly identified as the bite perpetrator (Appendix S03, T01). The day after on June 2nd, 2009, at 10:10 AM in Gota Soraya, 1.5 km from the previous location (Fig. S3), this same shark (Fig. 2B) attempted to bite the shoulder of a 36-year dive-master (T02). The day after, and 3 km away, in Habili Gafar it was again involved in a bite attempt at 10:30 AM on the fins and calf of a 21-year-old dive-master (SS) (Fig. 2C, T03) (Tab. S5). This individual was clearly identified through its size, gender and specific pattern of the white spot at the end of the dorsal fin as well as a skin excrescence at the end of the left pectoral fin (Fig. 2A, B and C).

Conformity of protocols and respect for guidelines:

All experimental protocols were approved by *Ad Hoc* institutions and/or licensing committees (details provided in acknowledgements and Supplementary Information). All methods were carried out in accordance with relevant guidelines and regulations with ARRIVE guidelines (https://arriveguidelines.org), the only interaction with the animals being underwater photographs.

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involving experimentation with humans referenced #no 980034BPC. All methods in the study were carried out in accordance with the Helsinki guidelines and declaration or any other relevant guidelines. Informed consent was obtained from all subjects and/or their legal guardian(s) for the publication of identifying information or images in an online open-access publication. Additional information regarding these case studies and fulfillment of ethics are provided in SI.

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Author contributions: EEGC designed the study and implemented the acquisition, analysis and interpretation of data and drafting of the article. AH suggested and designed the testing of fingerprinting on human wounds. MV and MF contributed to the field data (DNA) collection in the Caribbean case study. SB, CS and SP conducted the genetic analysis as well as the interpretation of results. SS and TV provided data on potential problem individuals among other species than tiger sharks and revised the article. JDCL and CGM made substantial contributions to refining the conceptual idea of problem individuals and revised the article. All authors approved the final version of the manuscript and agreed to be held accountable for its content.

Competing interests: The authors declare no conflicts of interest in relation to the content of this article.

Data availability: The datasets generated and analyzed during the current study are available in The GENBANK, Bethesda, Maryland USA repository at: SUB12912314. Accession number(s) for the six nucleotide sequences are: OQ569456, OQ569457, OQ569458, OQ569459, OQ569460, OQ569461. Other GENBANK reference numbers and primer sequences used for the fingerprinting are available in Table S1.

Supplementary materials:

Figs. S1 and S2

Tables S1 to S5

Appendices S1 to S3

Videos (n=6).

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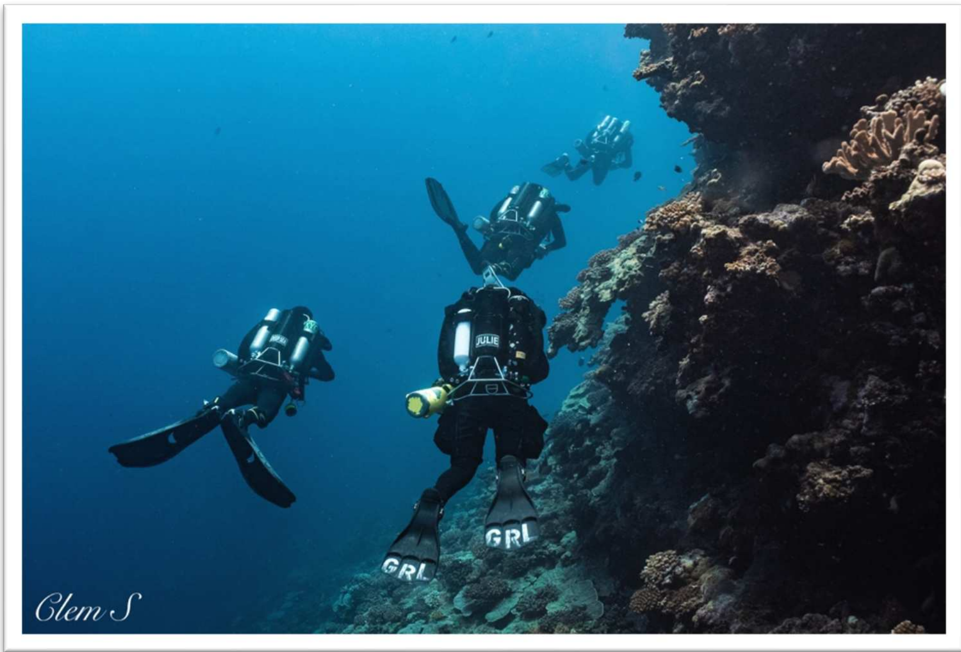
CHAPTER 4:

Perspectives to improve shark conservation



Improve knowledge through citizen science initiatives…

… Or thanks to the use of pedagogical aids

List of articles:

10. *The perception of sharks in French Polynesia in the written media from 1996 to 2006.* Z. Rowe, E. Clua, A. Goyaud, **C. Séguigne**. Submitted in Oceans.

11. *Citizen science provides valuable data to evaluate elasmobranch diversity and trends throughout the French Polynesia's shark sanctuary.* **C. Séguigne**, J. Mourier, E. Clua, N. Buray, S. Planes. Published in PLOS ONE (18(3), e0282837, 2023).

oceans

Article

The perception of sharks in French Polynesia in the written media from 1996 to 2006

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Abstract: This study consists of the evaluation of media portrayal of sharks in French Polynesia and its potential implication on their management based on review and analysis of ten years of media archives. Sharks appeared in the media a total of 82 times in "La Depeche de Tahiti" over the course of ten years, from 1996 to 2006, at an average of 8.2 articles per year. The portrayal of sharks in the media was generally positive, except for rare bite events and instances where sharks caused nuisance. An increase in the number of articles condemning shark finning and culling was observed from 2003, with a significantly higher representation of this subject one year before the implementation of the national shark sanctuary in French Polynesia. Thus, the threat to sharks from fishing as presented by newsreaders may have influenced policy, and improved receptivity of the public in favour of new protective action by the Government. These results highlight the importance of media discourse to positively predispose the public towards conservation measures in French Polynesia.

Keywords: Sharks; media; public perception; cognitive bias, shark sanctuary, conservation.

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1. Introduction

The media, by definition, is the primary means of mass communication and plays a major role in information dissemination, which is the spreading and distributing of facts to the public at large [1]. Moreover, media platforms are able to influence public perception, subjective and subject to manipulations, in a certain direction especially if there is a unified approach to a subject. [2,3]. Consequently, the media can obtain vast control in a society through their ability to sway perception and orientate what people think [4]. Additionally, public opinion may be fundamental in political decisions. The government are more likely to protect what the public cares about rather than what is feared, thus making the relationship between humans and apex predators a paradoxical topic in the media. [5]. Despite the importance of top predators for the balance of their ecosystems [6,7], significant cognitive biases still persist today among populations, giving them the worst reputation. The persistence of these cognitive biases, i.e. systematic error in judgment [8], may be due to the impressive features and abilities of predators, in regards to their morphological characteristics such as strength, a full mouth of teeth and precise hunting skills [9]. This is especially relevant to incidents with human beings. Although they are rare, they often get sensationalized by the media which increases newsreaders' perception of risk [10]. Sensationalism, allowing the media to generate more profits, is seen as a type of editorial bias in the mass media in which events and topics in news stories are over-hyped to increase viewership or readership figures [11,12]. Media being the primary information source for most people further amplifies cognitive bias and our initial fear of predators [13]. Studies have shown that media coverage increases after negative human-predators interactions, suggesting that extensive coverage and deleterious attitudes of the media may lead to a decrease in public tolerance for potentially dangerous animals [14,15]. However, human tolerance is a crucial aspect of predator conservation and calls for greater understanding of the factors that enhance or inhibit such tolerance [16,7].

In the case of sharks, the majority of beliefs and knowledge held by the general public were based on myths and legends [17]. Yet in the 20th century, as swimming became a more acceptable form of recreation, the amount of human-shark interactions increased, thus increasing the amounts of shark incidents. Even though they remained rare these accidents set a tone for "shark paranoia" and tapped into the primal fear of the unknown [18,19]. The publication of the book "Jaws" by Peter Benchley in 1974, and the subsequent release of its cinematic adaptation by Steven Spielberg in 1975, generated an unprecedented audience response of excitement and horror. The media exploited the public's reaction and fed the paranoia that the film generated [18, 20]. Awareness of sharks was raised to unprecedented levels, with both negative and positive repercussions. On one hand, it scared people out the water for years, and subsequently negatively impacted shark conservation [21,22]. On the other hand, the film generated world-wide public and scientific interest in shark biology [23]. This led to a better comprehension on the crucial role of sharks within their food webs and that reductions in the size of their populations can initiate trophic cascades through top-down effects [24,25, 26,27]. These animals are particularly vulnerable to fishing and over-exploitation due to their K-selected life history strategy [25]. Thus, understanding threats both direct and indirect is essential for their conservation. The leading direct threat is overfishing with bycatch and shark finning, defined as the practice of catching a shark to remove their fins and discard its body, often alive, at sea [28]. The market value of the fins used for traditional cooking is particularly high, and estimated to generate approximately $400 million for the fishing industry [29]. Whereas, an example of an indirect threat, is the perception of sharks in the media, and how these perceptions can influence governmental policies with their willingness to solve the problem using extreme management decisions, such as culling, which aims to kill problematic animals to end the threat [5].

This study was carried out in French Polynesia, where there are in the region of 33 shark species that may be encountered [30]. Indigenous natives belong to the cultures that respected and revered sharks [31]. They had strong spiritual connections with sharks as they are believed to be the "reincarnated souls of their deceased family members" and thus refused to kill them [32, 33, 31]. Research has shown that the recovery of anthropological "traditional ecological knowledge" (TEK) [33] has demonstrated these strong ancestral links that would likely strengthen the argument for the conservation of sharks in Polynesia [31]. Furthermore, in 2006, a major conservation measure has been voted in, protecting all shark species, except the Mako shark (*Isurus oxyrinchus*), which was added to the list in 2012 (Ministers' Council statement n°396, 28 April 2006). The implementation of laws that ban shark fishing within their Exclusive Economic Zone (EEZ) and prohibit the possession, sale or trade of sharks or shark parts has thus created this "shark sanctuary" [34].

This report is part of a larger study targeting the evolution of representation of shark in the media from French Polynesia between 1996 and 2016. This puts the shark sanctuary implementation at the barycentre of the period considered. This current work will particularly focus on how the mediation of sharks evolved in French Polynesia from 1996 to 2006. The aim of this study is to see if the media's discourse may have influenced, and or supported the creation of this large-scale protective measure, crucial for shark conservation in the South Pacific. Furthermore, unlike the link between indigenous culture and shark conservation, the perception of sharks in the local media has not yet been studied. This may fill a gap of knowledge crucial for the implementation of optimal protection measures for these essential predators.

The introduction should briefly place the study in a broad context and highlight why it is important. It should define the purpose of the work and its significance. The current state of the research field should be carefully reviewed and key publications cited. Please highlight controversial and diverging hypotheses when necessary. Finally, briefly mention the main aim of the work and highlight the principal conclusions. As far as possible, please keep the introduction comprehensible to scientists outside your particular field of research. References should be numbered in order of appearance and indicated by a numeral or numerals in square brackets—e.g., [1] or [2,3], or [4–6]. See the end of the document for further details on references.

2. Materials and Methods

2.1. Study area

French Polynesia is an overseas country of the French Republic in the southern Pacific Ocean. It is comprised of 118 geographically dispersed islands and atolls stretching over more than 2000 kilometres [35]. The 282,000 inhabitants are spread between five archipelagos (Australs, Gambier, Marquesas, Society and Tuamotu) (Figure 1). Most people live in the Winward group of the Society with 68,5% of the entire population living on Tahiti. The capital city of Papeete shows a population of 134,000 inhabitants, in accordance to the 2012 census [36].

The island of Tahiti is characterized by four types of local media such as broadcasts, the Internet, magazines and newspapers. "La Depeche de Tahiti", the most read daily newspaper, has been running since 1964. It has a daily circulation of more than 15 000 copies, which are distributed in Tahiti and circulated to the furthest islands in French Polynesia [37].

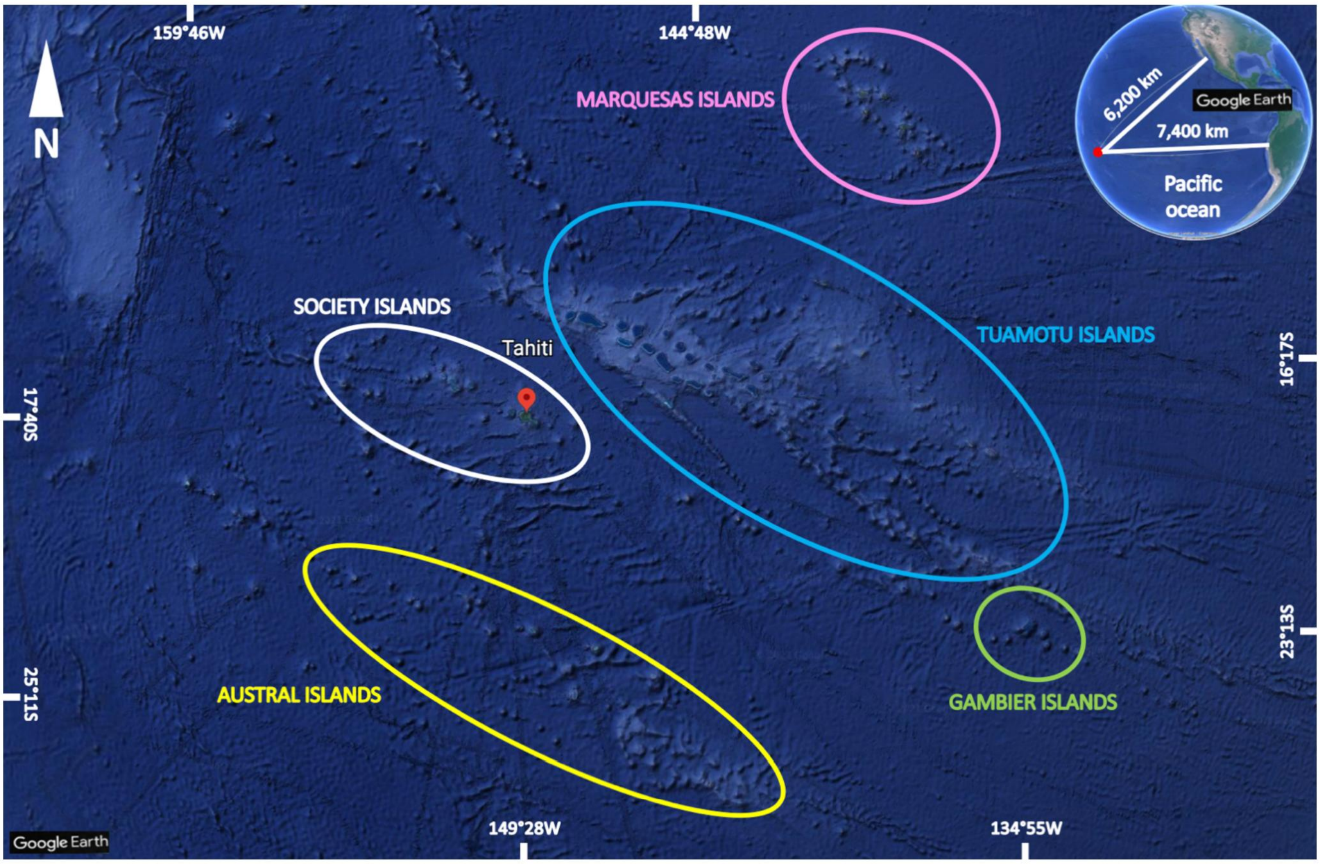

Figure 1. Map of Study Area with the five archipelagos covering the more than 7.5 million km^2 of the EEZ of French Polynesia. Red pin represents Tahiti island and its capital Papeete, where is printed "La Dépèche de Tahiti" newspaper.

2.2. *Transcription and characterization of the articles*

Substantial archival research from "La Dépèche de Tahiti" was made in order to select and assemble a file of all the articles dating from 1996 to 2006 where the keyword "shark" was mentioned at least one time. This strategy helped identify articles that were primarily about sharks (i.e., Chondrichthyes). Due to the fact that articles were only recently digitalised, all publications had to be researched by hand as the digital research for keywords was not yet available.

All articles were then transcribed from text in newspaper clippings to a digital format of Microsoft Word. A structured Excel spreadsheet was used for data collection from the articles in parallel with the transcription, in order to obtain information about possible media influences on public perceptions and to verify whether this perception can lead to impacts concerning the conservation of these animals

(*Table 1*). The date of publication was noted **(i)** as well as the shark portrayed in the article **(ii)**. Shark representation concerns their global depiction in the text and was defined as positive when they are either useful, aesthetic, or important, as neutral when their description is strictly biological and informative, and as negative when they are depicted as dangerous and cause accidents. The principal subject of the article was questioned in **(iii)** and seven categories were used after analysis of key words associated to all the articles. The topics cited 3 times, or more were subsequently chosen as main themes. The fact that the article mentioned a shark bite was pointed out **(iv)**, as well as it contains at least one time the words "shark finning" **(v)** and "sanctuary" **(vi)**.

Question	Type
(i) Is the shark the principal subject of the article?	**2-levels:** Yes, No
(ii) How is the shark portrayed?	**3-levels:** Positive, Negative, Neutral
(iii) What is the principal subject of the article?	**7-levels:** Economy/Tourism, Biology/Ecology, Importance in ecosystem, Bite, Culture, Nuisance, Sharkfinning
(iv) Does the article mention a shark bite?	**2-levels:** Yes, No
(v) Does the article contain the keywords "shark finning"?	**2-levels:** Yes, No
(vi) Does the article contain the keyword "sanctuary"?	**2-levels:** Yes, No

Table 1. Questions and possible answers used to characterize all the articles

2.3. *Statistical analysis*

The data collected in the Excel spreadsheet was later entered into R for statistical analysis [38]. Significance was tested at the p-value < 0.05 level. For R to be able to process the data, specific tables were made using excel to focus on the information collected relevant to the hypotheses of this paper.

Data was visualized with pie charts using ggplot2 [39] and with mosaic plots using ggmosaic [40] R packages. Chi-squared tests were performed to explore a possible link between the year and, (i) the perception of sharks as 'Positive', 'Negative' or 'Neutral', (ii) the theme 'shark finning', (iii) the presence of the keyword 'Sanctuary', and as well between the main theme of the article and the perception of sharks. When chi-squared tests were significant, post-hoc chi-squared tests were conducted, using the Bonferroni correction [41].

3. Results

A total of 82 articles from "La Dépèche de Tahiti" that met the search criteria described previously, were transcribed into Microsoft Word format. Between 1996 and 2006, an average of 8.2 articles were published per year, with a minimum of 1 article (1%) published in 1996 and 2002 and a maximum of 35 articles published in 2003, representing 43% of the total number of articles (*Figure 1A*). The perception of sharks in local media appeared to be globally positive, with only 1996 and 2000 displaying more negative than positive representations. During the period studied, bites were reported 9 times in "La Depèche de Tahiti", in 1996 (n=1, 100% of the yearly published articles), 1997 (n=1, 50%), 1998 (n=1, 7,7%), 1999 (n=1, 14,3%), 2000 (n=3, 42,9%), 2003 (n=1, 2,9%) and 2004 (n=1, 16,7%). Results of the Pearson's Chi-squared test displayed that at least one year showed different proportions of shark representations than the others

(Chi2 = 29.602, p-value = 0.0415). Post-hoc tests revealed that the only the articles published in 2000, which represents 9% (n=7) of articles released, effectively showed a significantly more negative image than other years (p-value = 0.004). Indeed, 85,7% (n=6) of negative articles were published, for 14,3% (n=1) of positive and 0% of neutral. Interestingly, this year displayed the highest number of bites incidents. The Year 2003, which showed the largest number of articles, is characterized by 77,1% of positive articles, 17,1% negative, 5,7% neutral (*Figure 1B*).

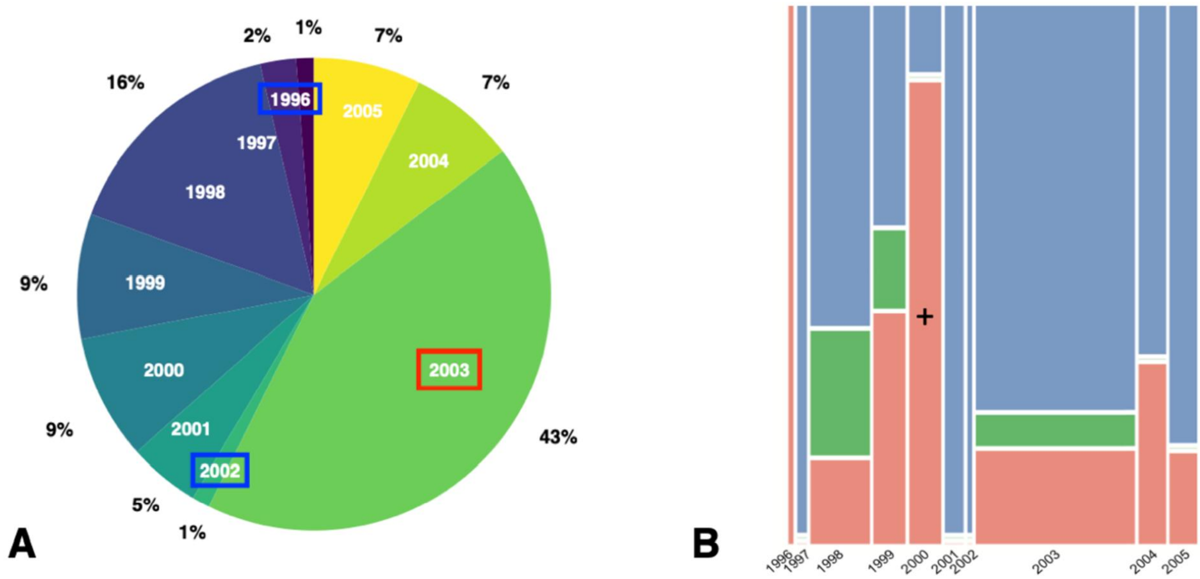

Figure 1. Evolution of media coverage of sharks from 1996 to 2006 with (A) the number of articles released by year, the red square representing the year where the number of articles published was maximal (n=35) and the blue squares representing the years where it was minimal (n=1) ; (B) The evolution of perception of sharks in media with years. Columns are representing the successive years of publication and horizontal parts showing the ratio of article carrying a positive (blue), neutral (green) or negative (red) image of sharks. "+" sign represents significant results (p-value < 0.05) displaying positive residuals to post-hoc tests.

Among the 7 different themes selected, the subject concerning shark finning was strongly covered, concerning 34% of all the articles published (n=28). The topic of tourism and the interest of sharks for local economy was the second most broached, with 32% of all the articles (n=26). The less discussed themes (5%) were culture (n=4) and the importance of sharks in ecosystems (n=4). Interestingly, shark bites was the third most covered article, although it only concerned 11% (n=9) of the articles (*Figure 2A*). Some themes were correlated with a significantly different perception to others (Chi2 = 90.015, p-value = 0.00377). The articles dealing with shark finning, economy & tourism, and importance in ecosystem showed a higher number positive representation of sharks. Nevertheless, only the subject of shark finning displayed a number of positive articles significantly more important than other themes (p-value = 0.00111) and a number of negative articles significantly less important (p-value = 0.0148). Bite and nuisance as the main subjects were linked to more negative shark views, as well as culture, surprisingly. However, this pattern was not significant for the culture, when it was for bites and nuisance, with significantly more negative articles than expected (p-value = 0.0020 ; p-value = 0.0033 respectively) and less positive articles than expected (p-value = 0.0036 ; p-value = 0.0238 respectively). Biology thematic was associated with significantly more neutral articles than the others (p-value < 0.001) (*Figure 2B*).

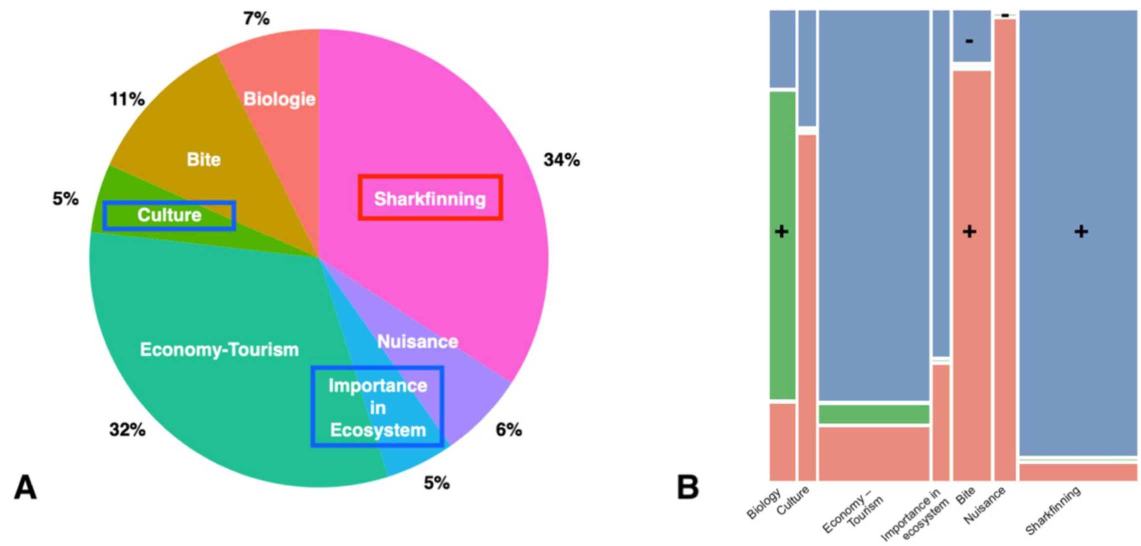

Figure 2. Public exposure to specific themes with (A) the number of articles released by Theme, the red square representing the themes where the publications was maximal (n=28) and the blue squares representing the themes where the amount of publications was minimal (n=4); (B) The perception of sharks in the media depending on themes. Columns are representing the different themes of articles and horizontal parts show the ratio of articles carrying a positive (blue), neutral (green) or positive (red) perception of sharks. "+" and "-" signs represents significant results (p-value < 0.05) displaying respectively positive and negative residuals to post-hoc tests.

Since the theme shark finning generated a significantly more positive perception of sharks in the media, the exploration of the representation of this subject over the years was performed. Before 2003, these particular fishing practices were almost never mentioned, except for 1 article in 1998. Nevertheless, this problematic has been more mediatized since 2003, with the majority of articles published on sharks, mentioning it in 2003 and 2005. Pearson's Chi-squared test showed that there were some years with significantly more articles speaking about shark finning than others (Chi2 = 33.339, p-value = 0.00012). Post-hoc tests revealed that significantly more articles were published overall on shark finning in 2003 (p-value = 0.0018) and in 2005 (p-value= 0.0082) (*Figure 3A*).

The concept of a shark sanctuary was only introduced in the studied period in 2003, but none of the years of publication displayed a number of articles speaking about Sanctuarization as more important than other type of articles. Pearson's Chi squared test showed that there were significantly more articles containing the key word "sanctuary" in at least one year of the study (Chi2 = 12.625, p-value= 0.1803). The post hoc tests revealed a significant increase of the number of articles containing this key word in 2005, one year before the implementation of the Polynesian Shark Sanctuary (p= 0.015529) (*Figure 3B*).

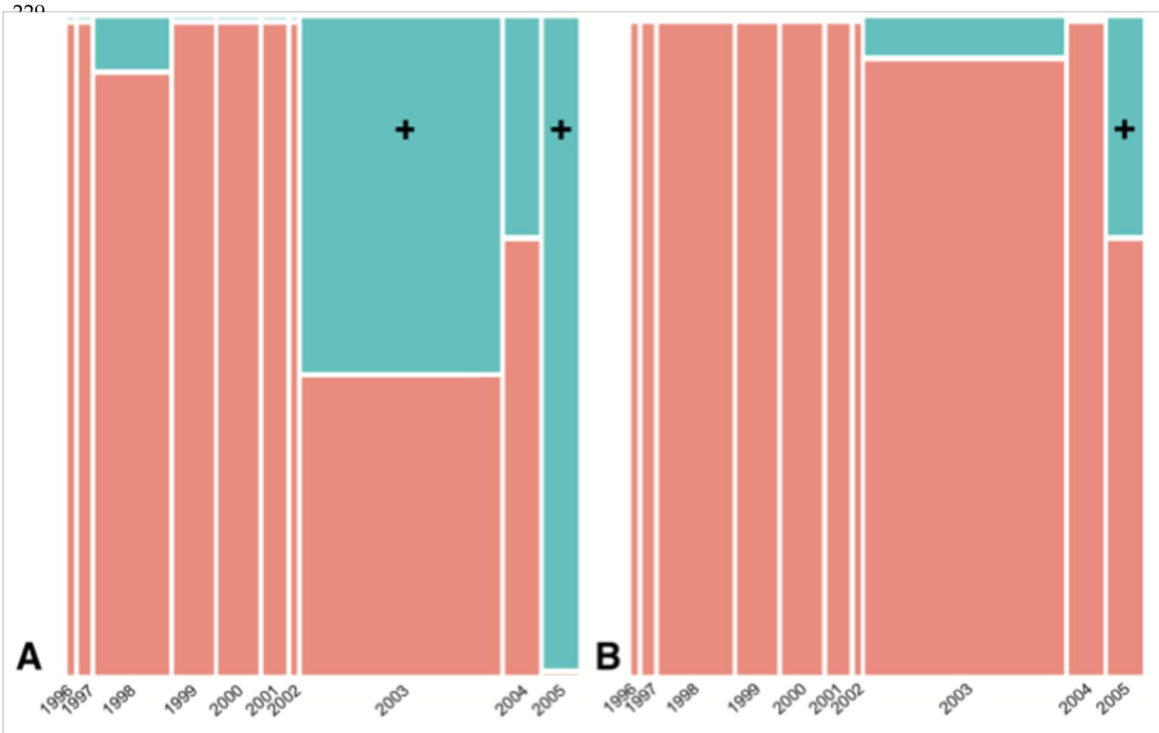

Figure 3. Representation of concepts related to conservation over time with (A) being the number of articles released specifically on shark finning by year, columns are representing the successive years of publication and rows indicating the ratio of articles concerned with shark finning (blue) compared to those not concerned with it (red) ; (B) The number of articles released containing the key word "sanctuary" by year with columns representing the successive years of publication and rows indicating the presence () or absence (pink) of the key word. "+" and "-" signs represents significant results (p-value < 0.05) displaying respectively positive and negative residuals to post-hoc tests.

4. Discussion

This study, conducted after the digitalization of ten years of archives of the most read newspaper of French Polynesia, provides elements that fill the current lack of information on the shark perception in local media. Furthermore, the strong increase in the number of articles describing the threats that faced sharks, mainly concerning finning and culling practices, may have eased the implementation of new protective measures banning shark fishing and selling of shark products in all the ZEE of French Polynesia.

Sharks were mediatized a total of 82 different times in La Depeche over the course of ten years, from 1996 to 2006, with an average of 8.2 articles per year. The number of articles published by this local newspaper does not appear to be particularly high in comparison to a similar study also made over a 10-year time frame in the United States (US) and Australia [42]. They found 3342 articles that matched their criteria, with an average of 342 articles per year and went on to analyse a random selection of n= 300. However, it must be taken into account that Australia and the US have a cumulative population of 407,56 million and are 2 of the most influential countries in global shark conservation policy [43]. Additionally, they are the countries where the most documented human-shark interactions occur compared to any other [44] thus making the two studies hard to compare. However, the perception of sharks in media of French Polynesia was found to be mostly positive. This is an opposite pattern to a consequent number of other studies performed in strongly westernized countries, such as the US and Australia, where the media discourse tend to be sensationalized, emotive, or fear mongering [45,5,42]. This may be explained by the more positive role that sharks display in Oceanian cultures, which does not appear as demonized [33, 31], and as well to the extremely low amount of negative human-shark interactions reported [44].

Positive perception was found to be mainly linked to the themes of shark finning, tourism, and the importance of sharks in the ecosystem. The large positivity of shark representation in articles speaking about shark finning appeared to have the potential to raise awareness to the threats sharks currently face, increasing evidence of the destructive impacts of human activities on the ocean. Indeed, regardless of personal attitudes towards sharks, it appears that large majority of people morally rejected finning [46]. This positive representation of sharks and the necessity to protect them in front of their risk of extinction in La Depeche may have influenced the political decision of shark sanctuary implementation in front of the public indictment against shark finning. Indeed, the media are susceptible to affect government decision-making, whether depiction of apex predators is negative [47] or positive [48]. Further studies on evolution of perception of sharks by Polynesian people have to be conducted in order to validate this hypothesis.

Furthermore, the discourse concerning the importance of sharks in the ecosystem, which was found to be one of the least discussed topics, may be an interesting subject to highlight in future articles. Indeed, repetitive exposure to such information may increase the collective consciousness about the ecological role of sharks and increase wide public knowledge, which is often linked with an increase of positive behaviours toward shark conservation, and may thus reinforce shark sanctuary efficiency and support by local population [49, 50].

Even though the economy and tourism did not generate a significantly more positive perception in the media compared to other themes, the articles on this subject were found to be mostly positive. Indeed, shark ecotourism is a global phenomenon which has the potential to benefits to local economies, generating important incomes [29, 51-53]. French Polynesia's economy already showed the attractivity of these animals with the example of scuba diving industry in Moorea island. Indeed, the 13 most sighted lemon sharks (*Negaprion acutidens*) were estimated to represent a potential contribution of USD 2.64 million during their life span [54]. Nevertheless, even if the activity is particularly lucrative and may generate positive attitudes towards sharks by promoting non-consumptive value of animals, it has to be strongly supervised with the implementation of code of conducts in front of the potential negative impact that may have incidents on participants [55].

Indeed, the negative representations of sharks portrayed in La Depeche were mainly linked to bites and to sharks being qualified as a "nuisance". Indeed, the year 2000, suffered from the highest number of bites being mediatized while also being the year where the perception of sharks was the most negative. Other studies obtained the same results in which the media's narrative had a tendency to demonize these apex predators after a bite occurred. This ensued a decreasing level of tolerance for sharks by the general public that is then sometimes used by the governments to alter their policies and take drastic measure, also known as the "Jaws Effect" [47]. However, this pattern of increase of the negative perception of sharks appeared to be possible to avoid as it has been demonstrated in some cases [56]. A clue for journalists may be linked to the use of a more prescriptive language. Indeed, avoiding terms such as "attack", presents in 100% of articles dealing about human-sharks negative interactions, could change the tone and emotional undercurrents in La Depeche de Tahiti. This may have implications for how the public interpret (and thus react to) human shark incidences [19].

The other major negative representation of sharks in the media was their portrayal as being a nuisance. Indeed, articles of La Depeche suggests that local fisherman often consider sharks to be a nuisance in front of shark depredation of their catches. However, Sandin et al. (2009) [57] showed that the presence of sharks was linked to an increase in biomass of commercial species, as fishes tend to allocate more energy to reproduction than in places where sharks were absent. Thus, fisherman and journalists should be informed of this indirect value of use of the shark. This would limit the potential illegal, unregulated and unreported (IUU) fishing that might occur even across protected areas [34] potentially by local fishermen, tired of depredation and therefore tempted to kill sharks.

The media have an extremely important potential to influence the perceptions of populations and the actions of public authorities, as they may have contributed to the Polynesian Shark Sanctuary implementation. Thus, to help to ensure optimal efficiency of this major protective measure, it is necessary that the local newspapers, although describing sharks in a generally positive manner as well as their economic and ecological interest, continue their efforts in the terms used and in the description of the different ecosystem services related to sharks. Indeed, other ecosystem services should be more treated, in particular to limit the legitimate cognitive biases of certain professions, such as those related to fishing, for example by promoting the indirect use value of animals (*sensu* Clua et al. 2010) [54].

Indeed, although killing sharks is currently punishable by heavy fines, an effective way to fight against the local IUU fishing in an area as large and difficult to monitor as the EEZ of French Polynesia may be to act directly on perceptions of the population with the help of local media.

Author Contributions:

All authors had significant contributions to this study. Conceptualization, E.C.; Methodology, Z.R., A.G., Software, Z.R., C.S.; Validation, C.S., E.C.; Formal analysis, Z.R., C.S.; Investigation, A.G., Z.R.; Resources, C.S., E.C. ; Data curation, Z.R., C.S. ; Writing – Original draft, Z.R., C.S.; Writing – review and editing, Z.R., C.S., E.C., A.G.,; Visualization, Z.R., C.S. ; Supervision, C.S., E.C., Project administration, C.S., E.C. All authors have read and agreed to the published version of the manuscript.

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The authors declare no conflict of interest.

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PLOS ONE

RESEARCH ARTICLE

Citizen science provides valuable data to evaluate elasmobranch diversity and trends throughout the French Polynesia's shark sanctuary

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Data Availability Statement: All the observation files are available from the ORP database (www.requinsdepolynesie.com). When you access the site, you can choose a dive and directly have the information of animals present. The full dataset used for the statistics is available on Dryad: https://doi.org/10.5061/dryad.z08kprrhm Seguigne, Clementine et al. (2023), Dataset about sharks in French Polynesia extracted from the ORP citizen science network, Dryad, Dataset, https://doi.org/10.5061/dryad.z08kprrhm.

Abstract

Observers of the Polynesian Shark Observatory (ORP), a citizen science network organized mainly through the Polynesian dive centers, collected an unprecedented amount of data from more than 13,916 dives spanning 43% of the islands of French Polynesia between July 8, 2011, and April 11, 2018. The objective for this type of data collection, which is not accessible within the standard research context, was to provide a unique dataset, and the opportunity to explore the specific diversity, distribution, seasonality and abundance of many elasmobranch species spread out throughout the territory of French Polynesia. Since the data are based on random citizen observations, the spatial distribution was biased toward the most frequented sites and islands where scuba diving is most developed. Overall, the increase in observed abundance of rays and sharks observed in French Polynesia, and the three most sampled islands as well as the high specific diversity recorded for the region, provide first evidence on the effectiveness of the French Polynesia's Shark Sanctuary, established in 2006. These data, collected randomly by the volunteers, also provide insights into potential movement patterns and site fidelity of some of the more commonly observed species. While no final conclusions can be drawn, it is clear that the network of volunteers that regularly contributes information to the Polynesian Shark Observatory plays a very important role in the delivery of much needed data for conservation and management action, as well as providing perspectives for new directions in research on sharks and rays in French Polynesia.

Introduction

Citizen science is defined as the collection and analysis of data relating to the natural world, mainly through data collection at large temporal and spatial scales, by members of the general

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public, typically as part of a collaborative project with professional scientists [1–7]. In this context, citizen science can be considered as an important additional tool for research, which can provide useful observations for large animals, such as sharks and rays, for which some species are both rare and difficult to observe. In addition, the involvement of volunteers in citizen science programs not only leads to a significant reduction in costs and logistical issues for tasks that would have been impossible to carry out through traditional research methods, but also covers time and spatial scales which can be orders of magnitude larger than those used in most research programs [2,7–9].

In elasmobranch research, some species are challenging when it comes to the collection of reliable data from fishery-independent sampling, due to their hard-to-access habitat, their low densities, their behavior or the need to follow them over a long period of time to provide conclusions about their biological habits [10–13]. The knowledge, skills and participation of some ocean users and stakeholders can be used, such as fishermen or scuba divers, to complement traditional data collection systems [5,14–22]. Volunteers can contribute to scientific research by counting all of the animals seen during a dive [17,23,24] or by forwarding photos or videos that allow for the photoidentification of animals, as a non-invasive capture-recapture technique [25–27].

The integration of the citizen science approach in research projects has enhanced data collections in many places around the world with respect to species richness [9,28,29], and has also contributed invaluable ecological data for many elasmobranch species such as manta rays (*Manta alfredi*) [27,30], whale sharks (*Rhincodon typus*) [25,31–34], grey reef sharks (*Carcharhinus amblyrhynchos*) [35] or different species of wobbegong sharks (*Orectolobidae*) [17]. Some websites have been developed to collate information on elasmobranchs at local or global scales, for single or multiple species, such as SharkPulse (www.sharkpulse.org) or eOceans (www.eoceans.org) [9,29,32–34,36,37]. To date, however, only a few scientific outputs have resulted from these datasets compared to datasets stemming from platforms used on other taxa [13].

Data collected from random processes are difficult to analyze since they are rarely area-based data, which are required for the calculation of density or biomass [12,28], and they present numerous observational biases, such as rounded values, species misidentification or inflation of estimates [8,23,24]. Overall, the quality of data can be affected by the difficulty associated with the coordination and management of volunteers in space and time [38]. Nevertheless, comparative studies have been conducted between the results of data collected by professionals and those obtained from divers or fishermen involved in citizen science programs, and have shown a significant reliability of these programs, despite the need for independent validation by a traditional approach [24,28,39–41].

French Polynesia, comprised of 118 islands spread over 5 archipelagos, has a vast Exclusive Economic Zone (EEZ) that spans 5.5 million km^2 and is known as one of the most important diving hotspots in the world. On April 28, 2006, its entire territory was declared as a shark sanctuary for all species except the mako shark (*Isurus oxyrinchus*), via legislation based on Article 3 of the Council of Ministers n°396. In 2012, the mako shark was added to this legislation, making the entire French Polynesia EEZ a complete sanctuary for sharks and rays. The sanctuarization of Polynesian waters represents a key step for shark conservation in the Pacific, as it places a ban on fishing and the trade of products from these animals [42–44]. In 2006, French Polynesia was the first country to establish a ban on shark fishing at the scale of the entire EEZ, and since this time, others countries in the Pacific have followed their lead, by also banning shark fishing.

The Polynesian Shark Observatory (ORP) (www.requinsdepolynesie.com) was created in 2011 by N. Buray with the assistance of the Centre for Island Research and Environmental

Observatory (CRIOBE) to improve survey techniques for elasmobranchs in French Polynesia, and to provide monitoring assistance at the scale of the Polynesian shark sanctuary. As a first action, the ORP developed a Web platform to centralize data and to allow for contributors to register their observations. This platform forms the core of ORP activities and proposes methods for data collection based on citizen sciences, allowing for large spatial and temporal scales to be covered. Data collected by the program participants were defined in collaboration with CRIOBE researchers, with the aim of analyzing them within the framework of a research strategy. Moreover, to limit species misidentification by inexperienced observers, highly experienced volunteers, such as member of the professional scuba diving and fishing communities, were targeted in order to meet the following objectives: (1) estimate the species richness at the scale of French Polynesia and the different archipelagos, (2) study the geographical distribution of the different species, (3) identify their presence patterns at different time scales, and (4) explore the variability of detected elasmobranch abundances and investigate the potential benefit of the sanctuary on shark populations.

The objective of the present study was to evaluate whether a citizen science program designed in conjunction with scientific research professionals could provide local knowledge via the valorization of data collected by the program's participants between July 8, 2011, and April 11, 2018. Species richness, patterns of distribution and seasonality of elasmobranchs and their abundances are largely undescribed in this region, yet some are critically endangered at a global scale, such as the great hammerhead shark (*Sphyrna mokarran*) [45]. Because of the unequal spatial distribution of the data collection, where heavily touristed sites were more sampled than others, a particular focus was placed on the Tiputa Pass site at Rangiroa in the present study, due to the larger number of observations collected in this place.

Materials and methods

Data collection & description

Observers were selected by ORP staff based on their underwater experience. It is important to note that not all citizens can immediately complete the forms in the ORP Web platform. Once the participant has been selected and registered within the ORP system, and once they have made their first observations, they then complete an online form (http://www.requinsdepolynesie.com; See attached dataset) which includes the characteristics of the dive such as date, time, site location and the presence/absence of provisioning activities (S1 and S2 Figs). Environmental parameters such as temperature and current direction are visually estimated by the observer. Next, information concerning the observed species is recorded, including number of individuals, sex and estimated size (S1 and S2 Figs). Abundance is defined as the number of sharks per dive reported by the observers. This counted value was reported directly for the number of individuals between 1 to 7 and then reported as intervals (7 to 10, 11 to 15, etc.), in order to facilitate the counting of animals by non-experts. For the remainder of the analyses, the median of each interval is considered as the abundance of the observed species.

To evaluate the bias associated with the tendence for observers to focus more on their observations of unusual species and to thus be less consistent in their reporting on common species, we classified three species as "common", namely the blacktip reef (*Carcharhinus melanopterus*), the grey reef (*Carcharhinus amblyrhynchos*) and the whitetip reef (*Trianodon obesus*) sharks, due to their high probability of occurrence at many sites. All other species were then considered as rare in French Polynesia.

The distribution of the data collected over time and throughout the Polynesian EEZ were explored to determine the reliability of the sampling. In the case of Rangiroa atoll, two contributors stood out for their significant participation in the program, accounting for the majority of dives in the ORP database, irrespective of the species and abundance observed. These contributors are therefore considered as "regular observers", as opposed to "non-regular observers" who provided observations from time to time. To determine whether the number of dives that contained at least one individual from a rare species depended on the quality of the observer, a $\chi 2$ test was performed.

Spatial analysis

For each island studied, the sampling effort was calculated as the ratio between the number of dives conducted at the site vs. the total number of dives in the database. These geographical data were also used for the species of higher sighting rate to determine areas where the probability of occurrence is particularly high. For each species, the number of sightings that included at least one individual at a given site was divided by the total number of dives reported in that same area to derive the occurrence.

Temporal analysis

To demonstrate the value of this citizen science program as an effective tool to describe the seasonal dynamics of elasmobranch assemblages over time, we targeted a dive site that was regularly monitored by observers across multiple years, which provided the most robust dataset based on almost constant sampling effort. Among several sites of interests, we chose the Tiputa Pass in the atoll of Rangiroa (14˚47′ S, 147˚05′ W) which is a renown diving site that provides the opportunity to observe a large number and diversity of elasmobranchs. The probability of presence for eight species of elasmobranchs was analyzed from the database because they were the most abundant one, namely the tiger shark (*G. cuvier*), the great hammerhead shark (*S. mokarran*), the silvertip shark (*C. albimarginatus*), the grey reef shark (*C. amblyrhynchos*), the whitetip reef shark (*T. obesus*), the blacktip reef shark (*C. melanopterus*), the ocellated eagle ray (*A. ocellatus*) and the reef manta ray (*M. alfredi*). The number of sightings of a species in each month is likely to be a function of not only the activity profile for that specific species, but also observer effort, which could vary with respect to time of year. In order to integrate this parameter in the analysis, we used the complete set of records for the focal species, including both presence and absence of records to generate a value of the total observer effort through time (i.e., the number of dives per month). We divided the monthly sum of the number of observations by the monthly sum of the observer effort to generate the probability of sighting the focal species per hour of observer effort.

We then used a permutation test to identify months in which observations of the focal species differed from the expectation by random variations. Because our measure of interest was the probability of observing the focal species in a given month, our aim was to generate a null distribution of the monthly probability of observation. We constructed the permutation test by randomly allocating the presence records for the focal species across all records in the dataset. Our input dataset contained one row representing each unique observation record, with a column containing the information on whether the focal species was observed in that record or not (a binary 0 or 1). The permutation test shuffled this "observed" column (thus maintaining both the number of observations of the focal species and the observer effort in time constant). After performing this reallocation of presence data, we recalculated the probability of sighting the focal species per month of observation effort (as above) for each month. We repeated this process 1000 times for each focal species and extracted the 95% range of the distribution for each month.

Variations and trends in abundance

Differences in total abundance and abundance of individuals belonging to species considered as rare were studied between the four most sampled islands: Rangiroa, Fakarava, Moorea and Tahiti. Kruskal-Wallis tests were performed, followed by post-hoc pairwise comparisons tests to identify significant differences between islands in term of abundance.

When the total abundances of elasmobranchs were used to determine their temporal evolution at the scale of French Polynesia, as well as for the four most sampled islands, a normalization of their skewed distributions was performed using Yeo-Johnson transformations, which are similar to Box-Cox transformations, but which deal with potential zero values [46,47]. The lambda values used for the Yeo-Johnson transformations were those which yielded the best combination of values of skewness, measuring the asymmetry of a distribution and kurtosis, defining how heavily the tails of a distribution differ from the tails of a normal distribution, confirming normality of data; specifically, 0.086 for all of French Polynesia territory and 0.14 for the dataset restricted to Fakarava, Rangiroa, Tahiti and Moorea. To evaluate the annual evolution of the number of rare animals observed by ORP contributors, a similar process was performed. This ratio was transformed using a Yeo-Johnson transformation with $\lambda = -0.24$ for French Polynesia, and $\lambda = -0.25$ for the four most sampled islands. Poisson GLMs were then fitted using total abundance of sharks, or the proportion of rare animals among all shark and ray observations, as the response variable, and the date, or date*Island, as the explanatory variable in the reduced dataset.

Statistics

All analyses were conducted using R software (V 4.0.5) [48]. Statistical significance was tested at the p-value < 0.05 level ($\alpha = 0.05$). Bathymetric data were imported from the NOAA server using **marmap** R package [49] and graphs were displayed using **ggplot2** R package [50].

Results

Database description

The dataset included a total of 13,916 dives made by 114 confirmed volunteers from 8 July 2011 to 11 April 2018. The sampling effort was consistent through time, from 2012 to 2017, ranging from 2,036 to 2,383 dives per year, except for 2011 and 2018, which had lower values as fewer months were included in the analysis (Fig 1). The sampling effort at the scale of French Polynesia showed a relatively homogeneous pattern through the years, with an average of 5.28 ± 1.23 dives reported in the database per day.

Noticeably, two volunteers, out of the 114, were particularly involved in the ORP program and conducted 2,152 and 1,646 dives at Rangiroa over the sampled period, equating to 30.9% and 23.6% of all data collected on the island (n = 6,970), respectively. Overall, data collected by these two participants account for more than 50% of the total observations.

Data were collected from 51 out of 118 of French Polynesia's islands, or 43.2% of the islands in the territory, distributed over the 5 archipelagos. In total, 311 dive sites, mainly in lagoons or on the outer reef, were recorded. The sampling effort according to the location appeared to be very unequal between the different archipelagos. A total of 9,033 observation dives were conducted in the Tuamotu archipelago, while only 4,771 were carried out in the Society archipelago, 76 in the Marquesas archipelago, 26 in the Australs archipelago and 10 in the Gambier archipelago. At the scale of the islands of an archipelago, the sampling was also not homogeneous, particularly in the Tuamotus and the Society. Only 4 islands had more than 1,000 dives over the sampling period, including Rangiroa (n = 6,970), Moorea (n = 3,287), Fakarava (n = 1,564) and Tahiti (n = 1,253) (Fig 2A and 2B).

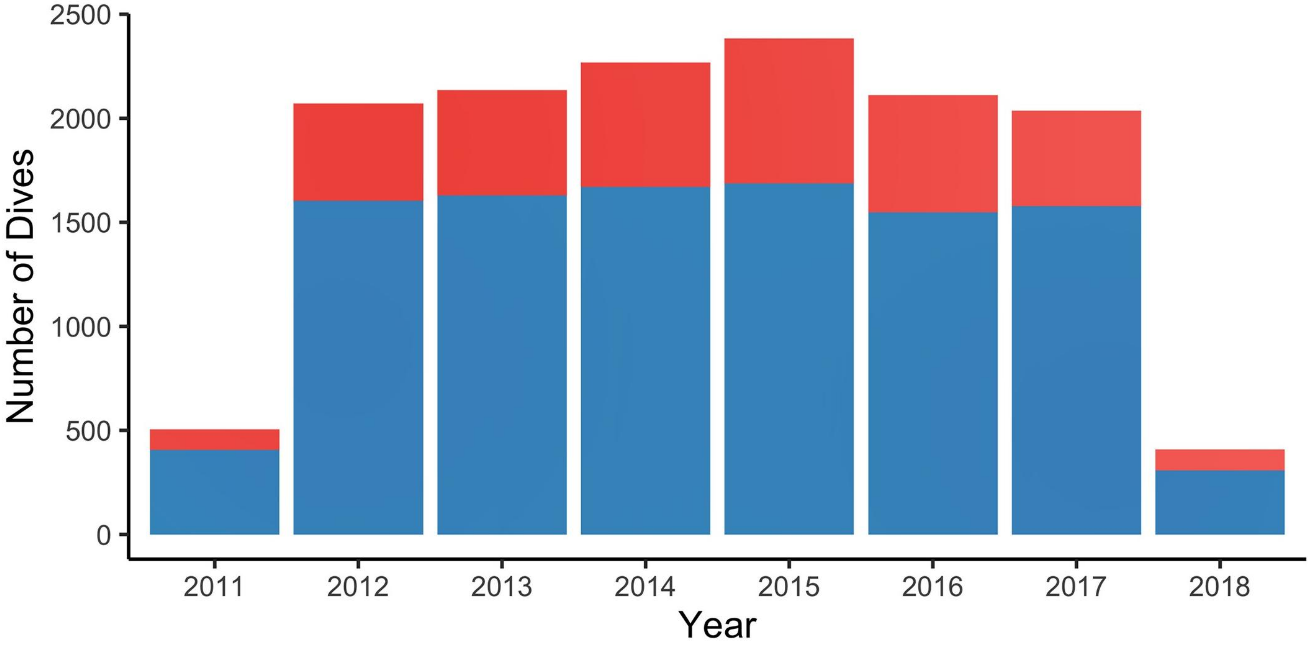

Fig 1. Evolution of the total number of dives reported by ORP observers between 8 July 2011 and 11 April 2018. The number of dives where at least one individual was qualified as "rare" is indicated in blue while the number of dives that only recorded individuals of "common" species is in red.

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While the sampling was considered homogeneous for the duration of the study for all of Polynesia's EEZ, not all islands presented regular and abundant observations. It is clear that Rangiroa, Moorea and Tahiti were intensively sampled over time. In contrast, while several other islands including Tikehau, Apataki, Bora-Bora, Raiatea, Huahine and Nuku Hiva were also sampled regularly through time, the number of observations made per year was low (Fig 3).

While investigating spatial and temporal distribution of the sampling effort, we also evaluated the quality of the sampling by looking at the ratio of observations of rare species vs common ones. Nearly 75% (n = 10,430) of the dives reported in the database included at least one individual that belonged to a species considered as "rare". The average annual ratio for the number of dives that only quantified common species but which ultimately included at least one rare species individual was 3.15 ± 0.50, a result that can be considered as homogeneous through time (Fig 1). A $\chi 2$ test indicated that there was an over-representation of the number of dives that included rare species as a function of the instructor's frequency of participation (p-value < 0.001). Thus, for dives conducted by non-regular observers, there was an over-representation of dives in which at least one individual from a rare species was recorded, whereas regular volunteers contributed more to the sampling of dives where only common species are observed on Rangiroa atoll. The proportion of dives which contained at least one individual belonging to a rare species varied substantially between islands. Of the four most sampled islands, Tahiti had the highest proportion of dives with a rare individual (84.7%), while Fakarava had the lowest proportion (59.3%) (Fig 2A).

Species diversity

Over the 13,916 observations, a total of 20 species of sharks and 7 species of rays, some of which are critically endangered, were described (Table 1). Among the most interesting recorded sightings, only known today because of the ORP, are the smooth hammerhead shark

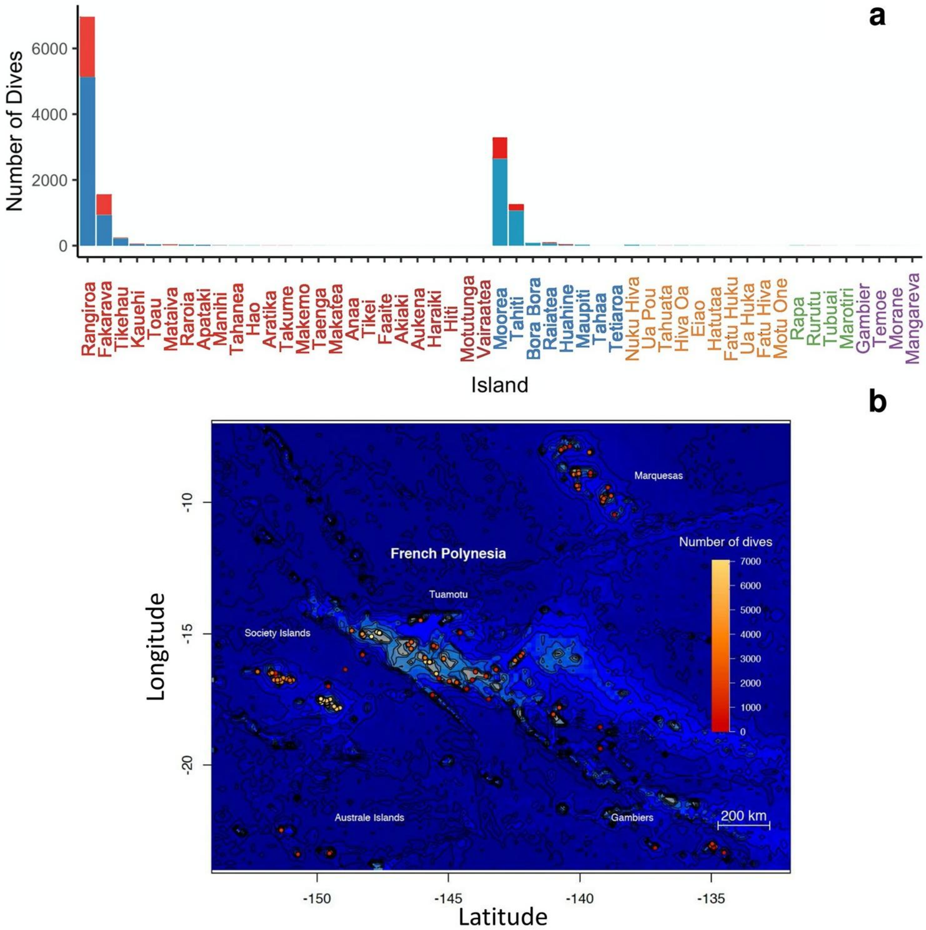

Fig 2. (a) Total number of dives reported according to the islands sampled. The blue part of the histogram corresponds to the number of dives where at least one individual of a species considered as "rare" is observed. The red part corresponds to the number of dives where only individuals of "common" species were counted. The archipelago to which the islands belong is represented by different colors along the x-axis: (1) red for the Tuamotu archipelago; (2) blue for the Society archipelago; (3) orange for the Marquesas archipelago; (4) green for the Australs archipelago; (5) purple for the Gambier archipelago. The islands are classified by decreasing number of dives within their archipelago. (b) Geographical distribution of the sampling effort.

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(*Sphyrna zygaena*) and the dogfish (*Squalus sp*.) which both appears to be very rare to detect, as they were observed only once in the Tuamotu and in Society islands, respectively. The *S. zygaena* sighting was made by a dive instructor in the Garuae Pass (Fakarava North), who reported 12 individuals swimming close to the surface. The *Squalus sp*. was seen in Opunohu Canyons (Moorea) by N. Buray after being caught and released during a demersal fishing effort at more than 80 meters. Both observations were confirmed with photos. Similarly, the shortfin mako (*Isurus oxyrinchus*), which is a pelagic species, was only reported twice: once in the Society islands and once in the Tuamotu islands. The sampling effort allowed for the maximum species richness to be approached for elasmobranchs in the Tuamotu Archipelago (24 species, 9,033 dives), Society Islands (23 species, 4,771 dives) and Marquesas Islands (11 species, 76 dives) as demonstrated by species richness cumulative curves (Fig 4). However, the low sampling effort in Gambier Islands (7 species, 10 dives) and Austral Islands (8 species, 26 dives) underestimated species richness as cumulative curves did not show an asymptotic shape

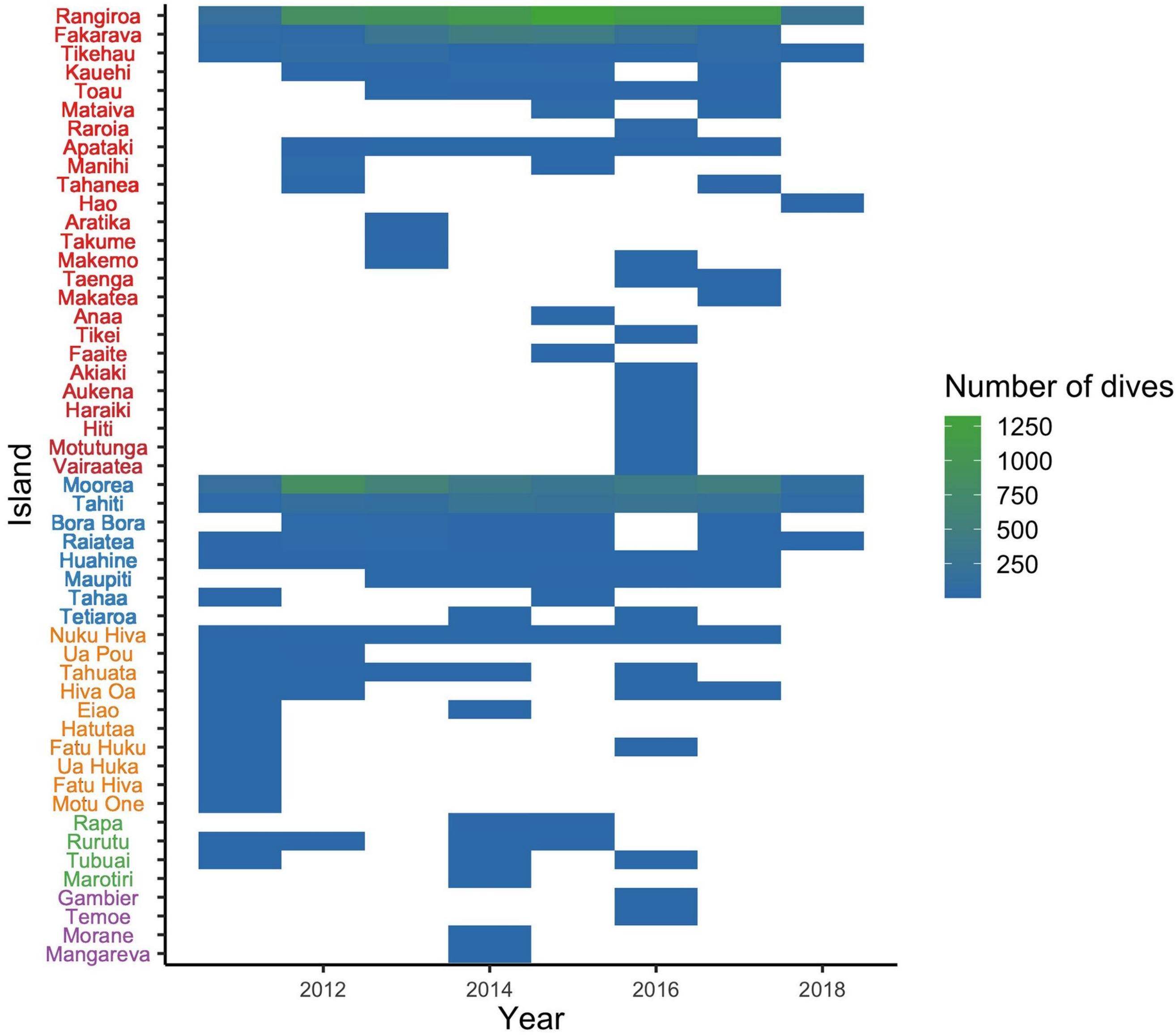

Fig 3. Heatmap of the distribution of sampling effort between July 8, 2011 and April 11, 2018 on the islands where ORP observers dove. The archipelago to which the islands belong varies with the color of the legend on the y-axis: (1) red for the Tuamotu Archipelago; (2) blue for the Society Archipelago; (3) orange for the Marquesas Archipelago; (4) green for the Australs Archipelago; (5) purple for the Gambier Archipelago. The islands are classified by decreasing number of dives within their archipelago.

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and indicated that the number of dives was too limited (Fig 4). The sampling effort in the Marquesas is interesting as it demonstrates that with 76 dives, the species richness cumulative curves reached a plateau, providing an estimate for the number of dives required to reach a plateau.

Distribution

The data collected through the ORP also provided information about the distribution of the different species of sharks (Fig 5) and rays (Fig 6) between the islands of French Polynesia.

Table 1. Species of sharks and rays reported by the ORP observations in French Polynesia.

Common name	Family	Genus	Species	Distribution	IUCN Global
Pelagic thresher shark	Alopiidae	*Alopias*	*pelagicus*	T	EN
Silvertip shark	Carcharhinidae	*Carcharhinus*	*albimarginatus*	S,T,M,G	VU
Grey reef shark	Carcharhinidae	*Carcharhinus*	*amblyrhynchos*	S,T,M,G,A	EN
Silky shark	Carcharhinidae	*Carcharhinus*	*falciformis*	S,T,G	VU
Galapagos shark	Carcharhinidae	*Carcharhinus*	*galapagensis*	G,A	LC
Bull shark	Carcharhinidae	*Carcharhinus*	*leucas*	S,T,A	NT
Common blacktip shark	Carcharhinidae	*Carcharhinus*	*limbatus*	S,T,M	NT
Oceanic whitetip shark	Carcharhinidae	*Carcharhinus*	*longimanus*	S,T,A	CR
Blacktip reef shark	Carcharhinidae	*Carcharhinus*	*melanopterus*	S,T,M,G	VU
Tiger shark	Carcharhinidae	*Galeocerdo*	*cuvier*	S,T	NT
Sicklefin lemon shark	Carcharhinidae	*Negaprion*	*acutidens*	S,T	VU
Whitetip reef shark	Carcharhinidae	*Trianodon*	*obesus*	S,T,M,G,A	VU
Tawny nurse shark	Ginglymostomatidae	*Nebrius*	*ferrugineus*	S,T	VU
Shortfin mako	Lamnidae	*Isurus*	*oxyrinchus*	S*,T*	EN
Smalltooth sandtiger shark	Odontaspididae	*Odontaspis*	*ferox*	T	VU
Whale shark	Rhincodontidae	*Rhincodon*	*typus*	S,T,A	EN
Scalloped hammerhead shark	Sphyrinidae	*Sphyrna*	*lewini*	S,T,M,G,A	CR
Great hammerhead shark	Sphyrinidae	*Sphyrna*	*mokarran*	S,T	CR
Smooth hammerhead shark	Sphyrnidae	*Sphyrna*	*zygaena*	T	VU
Dogfish	Squalidae	*Squalus*	*sp.*	S*	
Spotted eagle ray	Aetobatidae	*Aetobatus*	*ocellatus*	S,T,M	VU
Pink whipray	Dasyatidae	*Pateobatis*	*fai*	S,T,M	VU
Pelagic stingray	Dasyatidae	*Pteroplatytrygon*	*violacea*	S*,T	LC
Blotched fantail ray	Dasyatidae	*Taeniurops*	*meyeni*	M	VU
Reef manta	Mobulidae	*Mobula*	*alfredi*	S,T,M	VU
Oceanic manta	Mobulidae	*Mobula*	*birostris*	S,M	EN
Sicklefin devil ray	Mobulidae	*Mobula*	*tarapacana*	S,T	EN

The table is organized by Family, Genus, and Species, and includes distribution of sightings in the archipelagos, and global IUCN Red List[TM] conservation status [51]. Asterisks indicate a unique observation. Distribution categories: S, Society Islands; T, Tuamotu Islands; M, Marquesas Islands; G, Gambier Islands; A, Austral Islands. IUCN Global categories: LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically endangered.

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Most of species were observable at most sites throughout French Polynesian, but a few were only detected at the scale of an archipelago (Figs 4–6). This was the case for the blotched fantail ray (*Taeniura meyeni*), only observed in the Marquesas Islands, and the pelagic thresher shark (*Alopias pelagicus*) and the smalltooth sandtiger shark (*Odontaspis ferox*) which were only spotted in the Tuamotu Islands. Conversely, two species were observed throughout all of the archipelagos, including the grey reef shark (*Carcharhinus amblyrhynchos*) and the whitetip reef shark (*Trianodon obesus*) (Figs 5 and 6). Even if the Tuamotu had the highest species diversity and survey effort, some shark species that were observed multiple times in other archipelagos were never reported in the Tuamotu. This is true for the Galapagos shark (*Carcharhinus galapagensis*), only reported in the Gambier & Austral islands, of the blotched fantail ray (*Taeniurops meyeni*), only seen in the Marquesas archipelago, as well as the Oceanic manta (*Mobula birostris*), only observed in the Society and Marquesas islands (Figs 4–6).

Some specific sites could be particularly favorable for the observation of rare species, such as Maupiti island where the reef manta ray (*Mobula alfredi*) has been reported in a large proportion of the observations made in the area. In addition, the blacktip shark (*Carcharhinus*

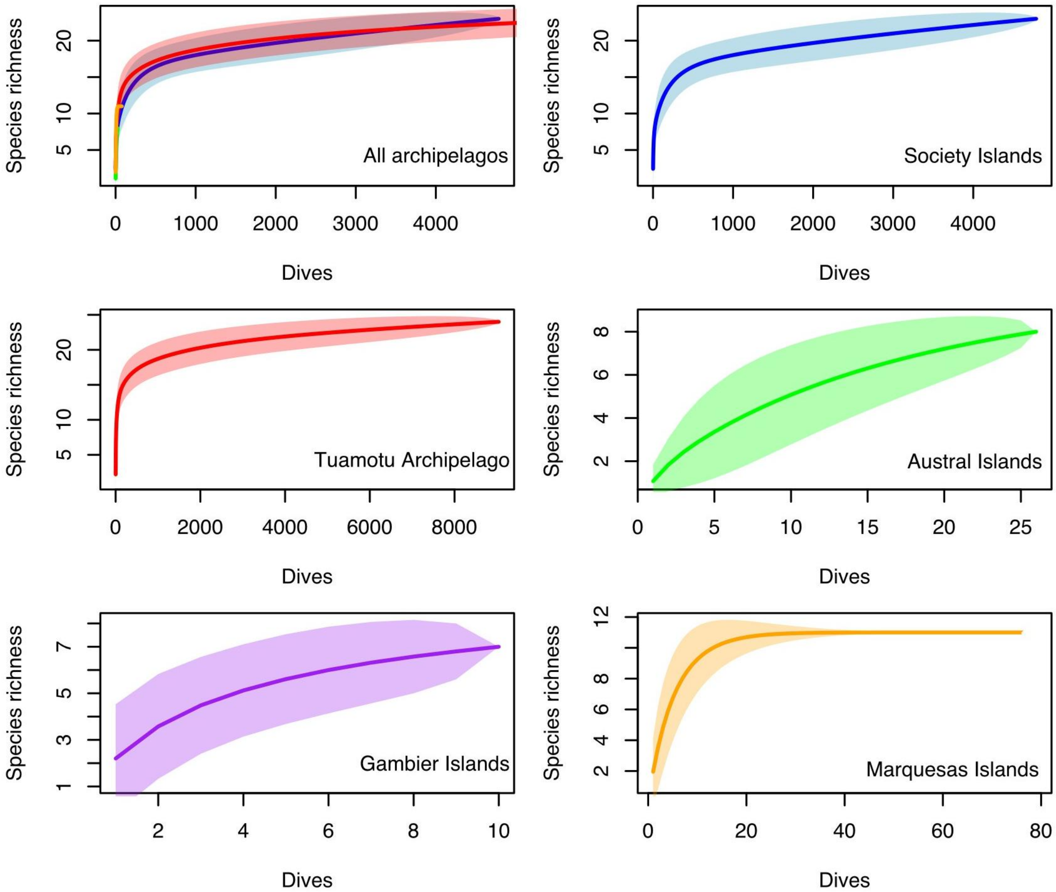

Fig 4. Evolution of species richness on the different archipelagos of French Polynesia as a function of the number of cumulative dives in the area. 95% confidence intervals are highlighted for each graph.

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limbatus) appeared to be difficult to detect by divers in most places in French Polynesia, though it was commonly observed in some parts of the Marquesas islands (Figs 5 and 6).

Temporal probability of presence

Among years, between 2011 and 2018, significant variations in the probability of sighting across species were found. A significant overall increase in the probability of observing tiger sharks (*Galeocerdo cuvier*), great hammerhead sharks (*Sphyrna mokarran*) and ocellated eagle rays (*Aetobatus ocellatus*) was observed as early as 2015, and from 2014, a similar increase was also observed for whitetip reef sharks (*Trianodon obesus*) and grey reef sharks (*Carcharhinus amblyrhynchos*). Conversely, the probability of sighting a silvertip shark (*Carcharhinus albimarginatus*) was significantly lower after 2014. Other species, such as the blacktip reef shark (*Carcharhinus melanopterus*) or the reef manta ray (*Mobula alfredi*) showed apparent fluctuations in their probability of occurrence, with a succession of years where occurrence in French Polynesia is significantly higher before a succession of years with higher and lower probabilities of occurrences (Fig 7). It is clear that 2011 and 2018 should not be considered in the analyses as data for each is incomplete, with only end-of-year data available for 2011 and only beginning-of-the-year data available for 2018. As such, seasonality may overly influence annual patterns for 2011 and 2018.

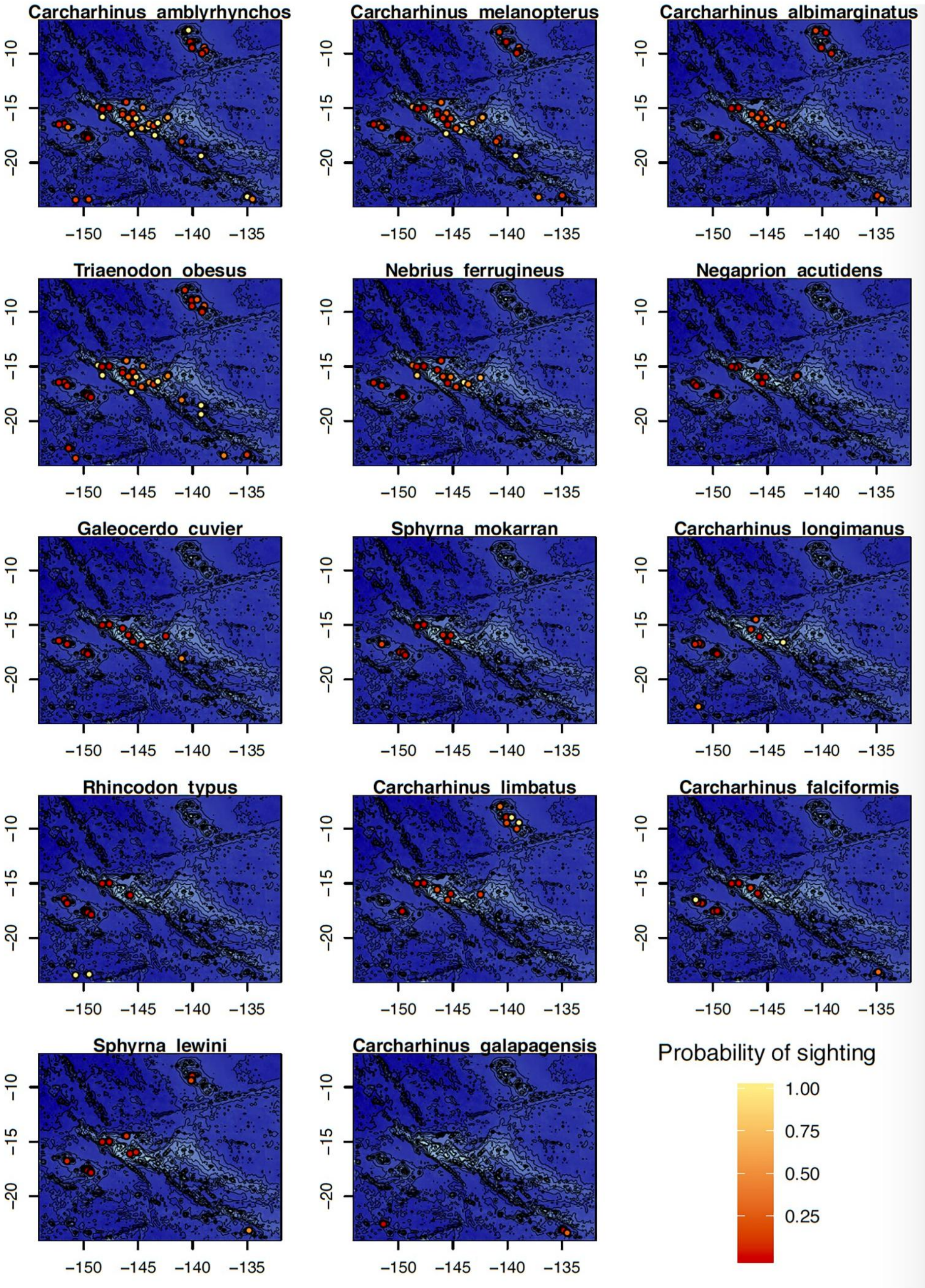

Fig 5. Distribution and probability of encounter of 11 shark species in French Polynesia.

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The detailed repeated observations made for the Tiputa site in Rangiroa allow for the seasonality of 8 frequently observed species to be determined. For the selected elasmobranchs, periods in which the probability of detection was significantly higher or lower than the probability of randomly observing these species during the year were determined (Fig 8). Two presence/absence patterns were of particular interest. The first concerned animals whose probability of presence was significantly higher or lower during short periods of the year, while for the rest of the year they were present in numbers comparable to a random temporal

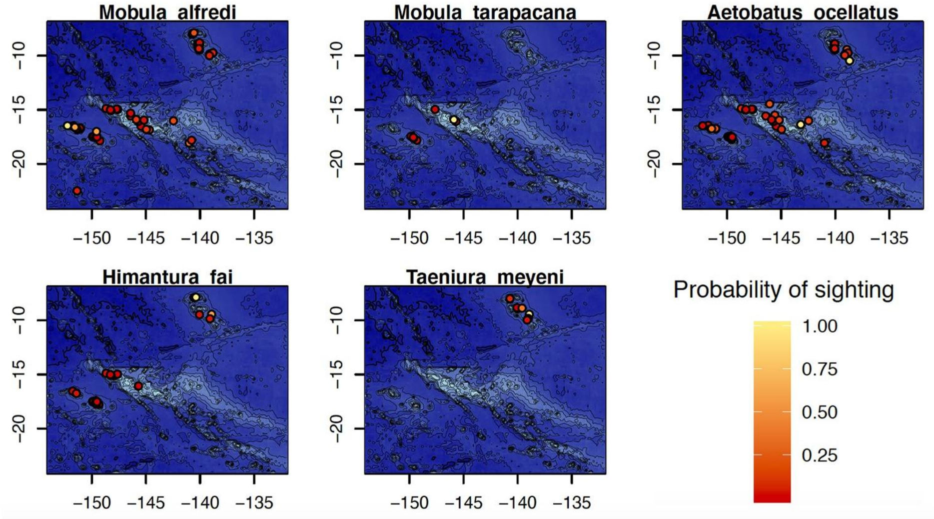

Fig 6. Distribution and probability of encounter of 5 ray species in French Polynesia.

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distribution, representing a seasonal presence of the species. This was the case for the tiger shark (*Galeocerdo cuvier*), which was frequently sighted in the Tiputa Pass in May, but was rarely observed from July to October. In contrast, other species had probabilities of presence that were rarely similar to the random distribution, and alternate periods of high and low probabilities of encounter. This is the case for the great hammerhead shark (*Sphyrna mokarran*), which is present in large numbers between November and April, but which is very rarely observed during the rest of the year (Fig 8).

Some patterns of presence for different species seemed to visually coincide. The ocellated eagle ray (*Aetobatus ocellatus*) and the great hammerhead shark (*Sphyrna mokarran*) showed some synchrony in their visitation patterns of the Tiputa Pass, with both more likely to be observed between December and April and less likely to be observed between August and November. This was also the case for the whitetip reef shark (*Trianodon obesus*) that showed higher probabilities of sightings in May, but was only slightly present between July and November, showing a similar seasonality pattern as the tiger shark (*Galeocerdo cuvier*) (Fig 8). Conversely, some species showed opposite presence patterns characterized by periods when one species was more frequently observed than the other, a pattern that could shift a few months later. This was the case for the grey reef shark (*Carcharhinus amblyrhynchos*), which was less frequently observed between January and May, when the great hammerhead shark (*Sphyrna mokarran*) was in greater numbers, but showed a significant increase in the probability of sightings between June and November when great hammerhead sharks disappeared (Fig 8).

Abundance trends

Total abundances differed significantly between the four most sampled islands (Kruskal-Wallis test: p-value < 0.05, pairwise test: p-value < 0.05 for all islands). The largest numbers of elasmobranchs seen simultaneously were recorded in Fakarava, followed by Tahiti, Rangiroa and Moorea; these being independent of the number of dives recorded in the database. Respectively, these data show a mean number (mean ± SD) of 66.31 ± 45.48; 48.57 ± 26.15; 34.57 ± 35.31 and 9.79 ± 5.62 (Fig 9A). Abundances of rare species were also significantly different between most islands (Kruskal-Wallis test: p-value < 0.05, pairwise test: p-value < 0.05), except for Moorea and Rangiroa, which had similar abundances for rare species

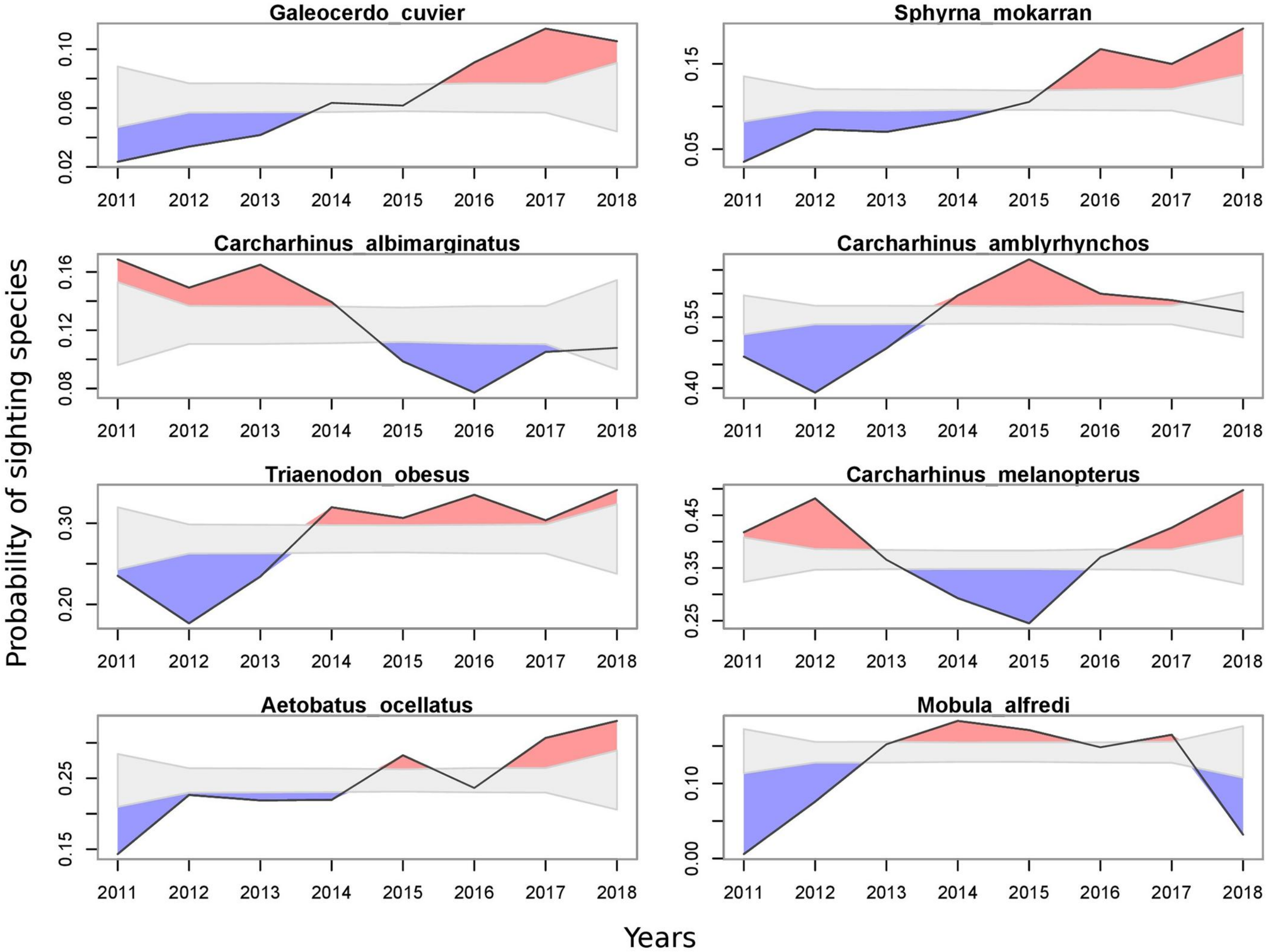

Fig 7. Probability of sighting for eight elasmobranch species frequently encountered throughout French Polynesia between 2011 and 2018. Solid black lines denote observed yearly sighting probability for each species. The gray-shaded polygon indicates the 95% range of the distribution of random sampling. Colored polygons highlight where the observed probability is above (red) or below (blue) the probability of observing that species if they were observed randomly.

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(pairwise test: p-value = 0.55), where both showed a median value of two animals. While Fakarava had the highest abundance for all species, it was also the island with the lowest median value of individuals that belonged to a remarkable species. Tahiti was the island with the highest median for the abundance of rare species, particularly at the White Valley ecotourism site. Rangiroa showed the maximal mean number of rare individuals, followed by Tahiti, Fakarava and Moorea, with respectively 5.78 ± 10.40; 5.50 ± 5.05; 3.22 ± 7.66; 3.13 ± 4.02 rare elasmobranchs, respectively, per dive (Fig 9B).

The Yeo-Johnson-transformed overall abundance detected by the ORP observers showed a very significant increase throughout French Polynesia, as well as on the islands of Rangiroa, Fakarava and Tahiti over the duration of the study (S3 Fig). Only Moorea showed a significant decrease in the abundance of sharks detected over time (S3B Fig). Among the islands where the number of elasmobranchs had significantly increased, Tahiti showed the steepest slope, with an estimated abundance close to the one obtained for Fakarava at the end of the study (S3B Fig). At the scale of French Polynesia as a whole, a significant increase in the Yeo-Johnson

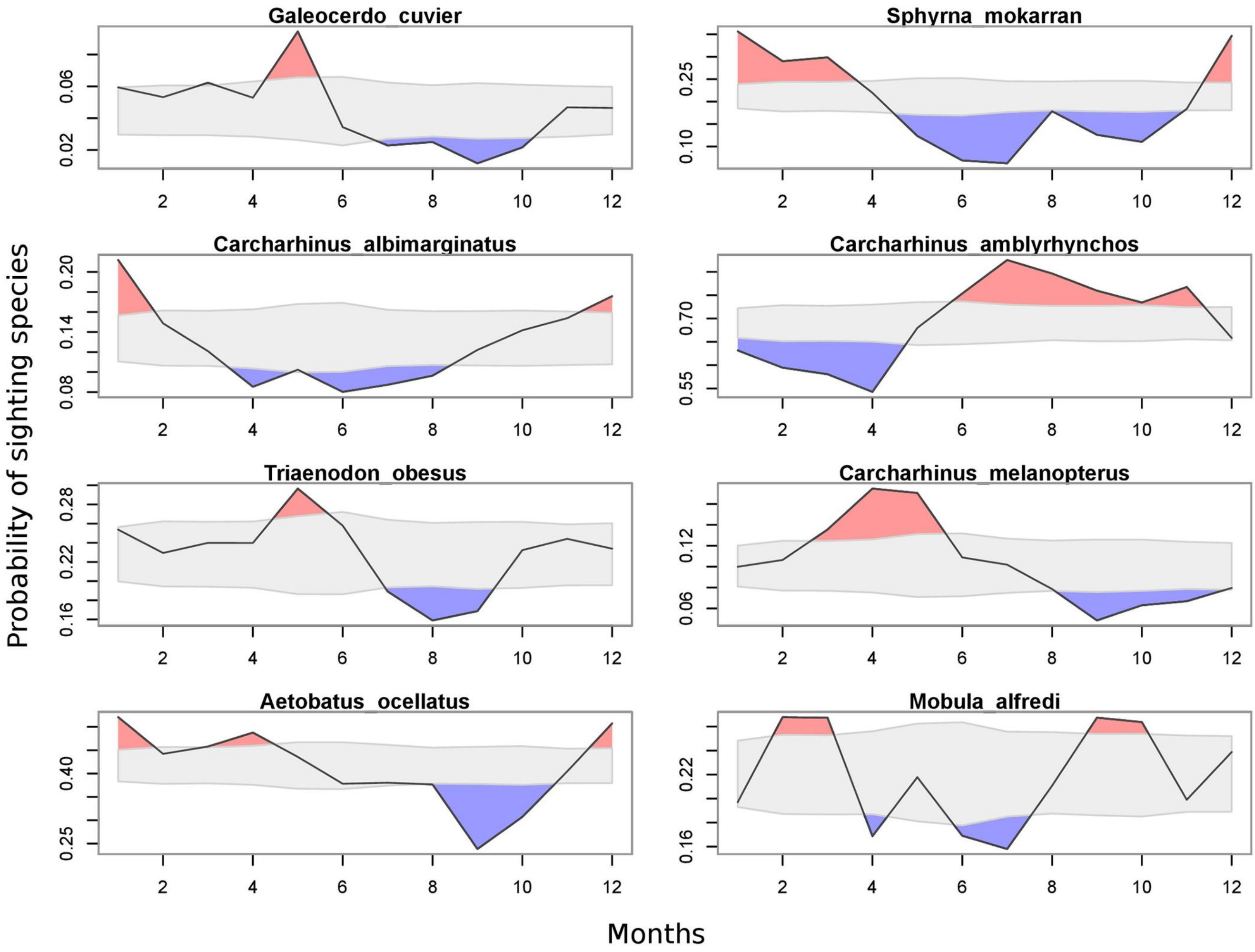

Fig 8. Yearly probability of sighting for eight elasmobranch species frequently encountered in the Tiputa Pass (Rangiroa). Solid black lines denote observed yearly sighting probability for each species. The gray-shaded polygon indicates the 95% range of the distribution of random sampling. Colored polygons highlight where the observed probability is above (red) or below (blue) the probability of observing that species if they were observed randomly.

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transformation for the number of rare animals observed per dive over time was revealed (S4 Fig). Tahiti, Rangiroa and Moorea all displayed a significant increase, which was particularly pronounced for Tahiti, in the number of individuals belonging to rare species reported per dive. In contrast, Fakarava showed a significant decrease in the number of rare sharks and rays, despite an increase in the total number of elasmobranchs in the area (S4B Fig).

Discussion

Thanks to the citizen science approach deployed by the ORP, we were able to analyze the elasmobranchs population at an unprecedented scale, both in space and time, throughout the entire EEZ of French Polynesia. This approach provided data for 43% of the islands of French Polynesia, from which we recorded 27 species of rays and sharks, including critically endangered and very rare species, and analyzed patterns of distribution and seasonality. In addition to these patterns, the analysis reported an overall significant increase in the observed abundance of elasmobranchs throughout the territory between July 8, 2011, and April 11, 2018,

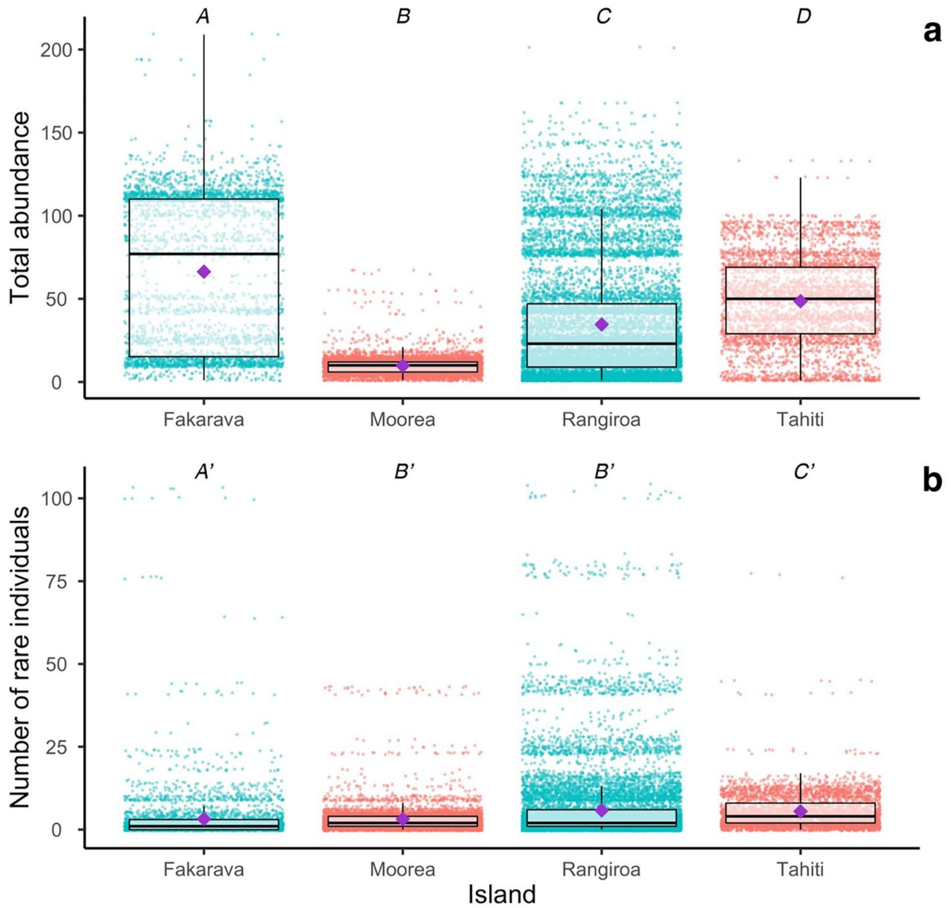

Fig 9. Difference of (a) total abundance; (b) elasmobranchs from rare species abundance between the four more sampled islands. Blue and red dots respectively represent dives conducted in Tuamotu and Society islands. Boxplots sharing different letters are significantly different in pairwise comparisons (p-value < 0,05). Purple dots represent mean values of the variable for the island considered. Note y-axis scale varies between graphs.

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likely a positive outcome of the sanctuary which was established in 2006 for the entire French Polynesian EEZ. Results from this study clearly indicate that the present citizen-science approach was extremely effective in helping to address important scientific questions.

The most significant result to come from the analysis of 13,916 dives made by 114 qualified volunteers, is the discovery of a significant increase in the abundance of elasmobranchs over time. This result suggests that since its establishment in 2006, the Polynesian shark sanctuary has been highly effective. This result is not surprising, as previous studies have demonstrated that placing a ban on shark fishing yields a higher density of sharks than in places where elasmobranchs are not protected [44]. At present, ORP volunteer observations, made on a daily basis, demonstrate an increase in the overall observation rate for elasmobranchs, including rare species, over time, across French Polynesia. Of course, such an approach (i.e., citizen science) is associated with a certain level of sampling bias, and in the present case, this bias is represented by the fact that diving hotspots (Tahiti, Moorea, Rangiroa and Fakarava) represent a disproportionally large number of the overall observations. Indeed, this geographic sampling bias, commonly found in citizen science initiatives, limits representativeness of the data at the global or low-sampled island scale, and this yields a value for true abundance that is much lower than expected [38,52].

In contrast, Rangiroa, Fakarava, Tahiti and Moorea benefited from regular data collection which led to an increase in the reliability of variability in abundance. In Rangiroa, Fakarava and Tahiti, a significant increase in elasmobranch abundance over the 8-year sampling period further confirms the effectiveness of the Polynesian sanctuary. Only Moorea showed a decrease in the number of animals detected in the area. This decrease could be related to the progressive drop followed by the complete cessation of shark feeding practices on the outer reef during the study. Although sharks were still present, they became more difficult to detect and formed smaller aggregations compared to the provisioning periods [53]. This decrease in abundance provides further evidence suggesting that the effect of feeding on elasmobranchs is not necessarily linked to a drastic ecological change without throwback. Similarly, the high abundance of rare elasmobranch species observed in Tahiti showed the value of baiting practices for the observation of remarkable species, such as the tiger shark (*Galeocerdo cuvier*), which was present on a very regular basis at the White Valley site until 2020, when the feeding activity was definitively stopped, and occurrences became extremely rare (C. Séguigne, pers. obs.).

The decrease in the number of rare species detected over time in Fakarava can be directly linked to an increase in the abundance of common species. It is clearly much more difficult to detect a rare individual within a group of common species, especially when the group contains more than a hundred individuals, as it is the case for grey reef sharks (*Carcharhinus amblyrhynchos*). A species which is described as "rare" in Fakarava, and which is typically found within large groups of other sharks such as silvertip sharks (*Carcharhinus albimarginatus*) and blacktip sharks (*Carcharhinus limbatus*). These shark species are morphologically quite similar and could be confused by non-experts under these conditions, though species detection errors remain rare among sharks [24]. In Moorea, however, despite the decrease in overall elasmobranch abundance in the area and the cessation of feeding activity, the increase in the proportion of rare species could be related to the presence of false negatives [52,54]. For example, divers may not report the presence of a common species if a sighting of a larger or rarer animal is made, such as the lemon shark (*Negaprion acutidens*). In addition, the ratio of the total number of dives with rare species is close to 75%, indicating that divers are more motivated to report their observations that are outside of the daily norm. On the other hand, few observers reported the complete absence of elasmobranchs during a dive. Absence data are those which are not directly described, but instead must be inferred from the non-presence of a species during a dive. Absence data and sampling on dive sites with low biodiversity are as important for statistical analyses and for the construction of presence/absence prediction models as data collected from sites with high biodiversity [55]. However, it is important to consider that in areas where biodiversity is low, volunteers may lack motivation and this could potentially have an important effect on the data collection [56].

After a total of 13,944 dives, 27 different species of elasmobranchs, including 20 sharks were recorded at least once in the ORP database, showing the relatively important specific diversity of French Polynesia, compared to other reefs at similar distances from the hotspot of diversity. Similarly, the eOceans participatory science initiative has listed a total of 12 species of sharks on 9,524 dives in Thailand and 11 species on over 30,000 dives in Fiji [9,29]. Nevertheless, "dark diversity", defined as species that should be present locally but which have not been detected, is high in these regions, where elasmobranch conservation measures are either less developed, or where they were implemented more recently [57–60]. Thus, the number of species that inhabit Polynesian waters is not necessarily greater than in Thailand or Fiji, but the high abundance of elasmobranchs allows for higher detection rate, including very rare species. Nevertheless, the geographical sampling bias also affected the results concerning the specific diversity. The total number of species detected increases very rapidly with the number of dives, and then stabilizes or increases marginally. It is difficult to observe rare species with limited sampling. Thus, the specific diversity obtained in this study for the Australs and Gambier archipelagos is most certainly underestimated. Additionally, only 11 species were recorded in the Marquesas Islands for a total of 76 dives. Despite the asymptotic appearance of the specific diversity curve, the fact that this archipelago is a true oasis of productivity within the very oligotrophic French Polynesian territory [61,62] suggests that observations for certain species were missed. In addition, a lack of detection does not necessarily mean an absence of the species and may be linked to low abundance, particular life history traits, and deep or pelagic habitat that hampers observations made by divers [58]. ORP observers tend to explore the outer reef primarily during the day and rarely exceed 50 meters depth, the limit for recreational diving in French Polynesia, despite occasional visits by technical divers to depths of 100 meters or more. Visual sampling methods thus remain limited for the estimation of specific diversity, which is why the use of environmental DNA is quickly becoming a preferred sampling method among researchers for species which are difficult to observe, as it allows for a much higher detection of the number of species present in the area, as has been demonstrated in New Caledonia [60].

The different species monitored by the ORP show differences in terms of geographical and temporal distributions. Some species are widely distributed throughout the year in French Polynesia, while others have only been observed in certain archipelagos, or have demonstrated a significant seasonality. The absence of some species in different geographical areas may also be biased by the low sampling in some islands. Nevertheless, the patterns of presence defined in Rangiroa, sampled throughout the year by very regular observers, can be considered robust and reliable. These variations can be explained by several biotic or abiotic factors. Among the abiotic factors, water temperature has been shown to potentially influence the migrations and movements of some ectotherm elasmobranchs [63–68]. French Polynesia's climate is punctuated by a cool dry season between April and November, and a warm wet season between December and March, where water temperatures can vary by several degrees, and which can potentially explain the seasonality of observations made at the scale of an archipelago or even an island. Among biotic factors, trophic interactions also seemed to play a significant role with respect to the presence of some animals, or even the co-occurrence between some species, in the context of predator-prey interactions [64–67]. These different factors can lead to episodes of horizontal migration, as observed for mako sharks (*Isurus oxyrinchus*) in the North Pacific, where seasonal movements follow increases in surface temperature [68], and for whale sharks (*Rhincodon typus*) in the Indian Ocean, whose movements are influenced by prevailing currents and where their habitat is generally restricted to their preferred temperature range [63]. Previous studies also demonstrated the existence of a vertical niche in space use for certain species of elasmobranchs, where depths of over a hundred meters could be reached, making these species virtually invisible to the eyes of ORP divers, and thus could explain why they were not recorded in the area. This is true for the scalloped hammerhead shark (*Sphyrna lewini*), which can even use the hypoxic zone to capture deep-water squids such as in the Gulf of California [64]. The silvertip shark (*Carcharhinus albimarginatus*), and the grey reef shark (*Carcharhinus amblyrhynchos*) exhibited significant vertical migrations in Fiji and Palau, respectively, which was attributed to both the search for optimal environmental conditions and prey distribution, as well as to the avoidance of certain large predators, particularly in juveniles [65,66]. Even if grey reef sharks are mostly observed in the shallow waters, where they often aggregate in channels to exploit the particular conditions of the current in order to save energy, they also occasionally venture into open water and reach depths up to 150 m [69].

In this study, important similarities were observed in the annual presence patterns of the great hammerhead shark (*Shyrna mokarran*) and the ocellated eagle ray (*Aetobatus ocellatus*), which may indicate that this species of ray could be a preferential prey of this apex-predator. Cases of predation by the great hammerhead shark have already been recorded on rays [70,71], including rays from the genus Aetobatus [72]. Conversely, the great hammerhead shark as well as the tiger shark (*Galeocerdo cuvier*) showed opposite presence patterns to those of the silvertip shark (*Carcharhinus albimarginatus*) and the grey reef shark (*Carcharhinus amblyrhynchos*). One explanation for this may be avoidance behavior, as the potential prey responded to a higher abundance in potential predators [65]. *Sphyrna mokarran* was directly observed preying on a grey reef shark (*Carcharhinus amblyrhynchos*) in Garuae Pass (Fakarava North) which could support this assumption [73]. An alternative hypothesis is that grey reef sharks did not actually leave the area during the seasonal presence of great hammerhead sharks but instead, shifted habitat, moving deeper along the slope of the drop off, and out of sight from most divers. The higher or lower probabilities of presence can also be linked to seasonal migrations or reproductive aggregations. Many shark species have been shown to have times of absence during the year, including within provisioning sites, such as for the sicklefin lemon shark (*Negaprion acutidens*) in Moorea [74] or the bull shark (*Carcharhinus leucas*) in Fiji [75]. In this scenario, it is also possible to observe a succession of breeding periods for different species on a given island, resulting in a strong seasonality in favorable sighting probabilities. Grey reef shark observations made at Rangiroa are similar to those made for Fakarava, where animals were often sighted aggregating in shallower waters from May, corresponding to their mating period [76], which could also contribute to the increase in detectability observed from June.

Citizen sciences are generally affected by bias which generate less reliable datasets than those collected by traditional scientific methods [55,77]. As part of the ORP program, the collection of data, mainly performed by dive instructors, was completely absent in places where there were no diving centers, which included many of the Polynesian islands which are uninhabited or are not developed for tourism. In addition, many of the observers were diving instructors with an interest in sharks and rays, which would drive them to focus their dives on sites of specific interest characterized by high elasmobranch abundances and higher sighting probabilities such as most reef passages and cleaning stations [27,69]. Thus, the sustained long-term collection of observations is complex for many sites, notably in the Marquesas, Australs and Gambier archipelagos that are remote and less accessible for divers. Another common bias which concerns the quality of data collected, is largely avoided in the case of the ORP because volunteers are selected according to their experience in the marine environment, similar to other terrestrial citizen science programs like STOC (Suivi Temporel des Oiseaux Communs; http://www.vigienature.fr/fr/suivi-temporel-des-oiseaux-communs-stoc), where only skilled ornithologists can contribute. The ORP invests in their volunteers, as they work to maintain the motivation of their participants in order to retain active members, which appears crucial to the success of such programs [78]. To do this, data are associated with the names of the individuals who collected them, a process which favors information exchange between participants. In addition, the more active and efficient individuals or dive centers are rewarded with gifts or ecolabels. Furthermore, this large investment in volunteers increases their knowledge of elasmobranch ecology and behavior, and consequently develops their awareness within a conservation context [6,9,13]. By strengthening the human-wildlife link, volunteers are more willing to implement good practices with respect to the observations they make on sharks and rays [9]. This may then create a strong interest in the citizen sciences, via the development of the increasingly popular domain of "scientific ecotourism", which is beneficial for both research and territories [9]. In the future, the ORP program could be improved through better representation of the five archipelagos whereby specific study sites would be selected prior to the start of data collection. Moreover, in response to the difficulty associated with the sampling of certain areas, mainly linked to the absence of diving centers, the development of a mixed network between professional scientists and ORP volunteers could be considered, with professionals filling the gaps in data collection [77].

This study demonstrates the major benefits of developing citizen science programs for the study of large areas such as French Polynesia EEZ, where monitoring with traditional scientific surveys is impractical, and whose vast territory hosts particularly rare species. The data collection carried out by the ORP observers represented a significant sampling effort and succeded in filing a data gap that traditional research resources were unable to provide. The sampling biases, notably linked to the geographical heterogeneity of the data collection, only provided a relative reliability for results at the global scale of Polynesia, although the initiative worked particularly well on the islands of Rangiroa, Fakarava, Moorea and Tahiti, and offered acceptable results at the local scale, where results were comparable to those of previous studies. This participatory science initiative can thus be considered as a preliminary approach to a research project on the themes addressed. The ORP should continue to build their network of qualified observers, and to collect regular data on dive sites throughout French Polynesia to improve the reliability of the data, such that these data can eventually be considered of a similar quality to those that are collected by professionals. These actions will help to maintain an ongoing monitoring effort of elasmobranch populations throughout the vast French Polynesian territory and will directly impact our ability to evaluate and improve efforts to protect them.

Supporting information

S1 Fig. Example of an online observation form from the ORP's citizen science program.
(TIF)

S2 Fig. Example of the data collected by a diving instructor and regular observer at the Tiputa Pass (Rangiroa) on the ORP's website.
(TIF)

S3 Fig. GLM summary outputs and graphs of the evolution of the Yeo-Johnson-transformed total abundance of elasmobranchs with time for French Polynesia and the four more sampled islands.
(TIF)

S4 Fig. GLMs summary outputs and graphs of evolution of the Yeo-Johnson transformation of the proportion of rare elasmobranchs among all the sharks and rays observed with time for French Polynesia and the four more sampled islands.
(TIF)

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SUMMARY OF RESULTS

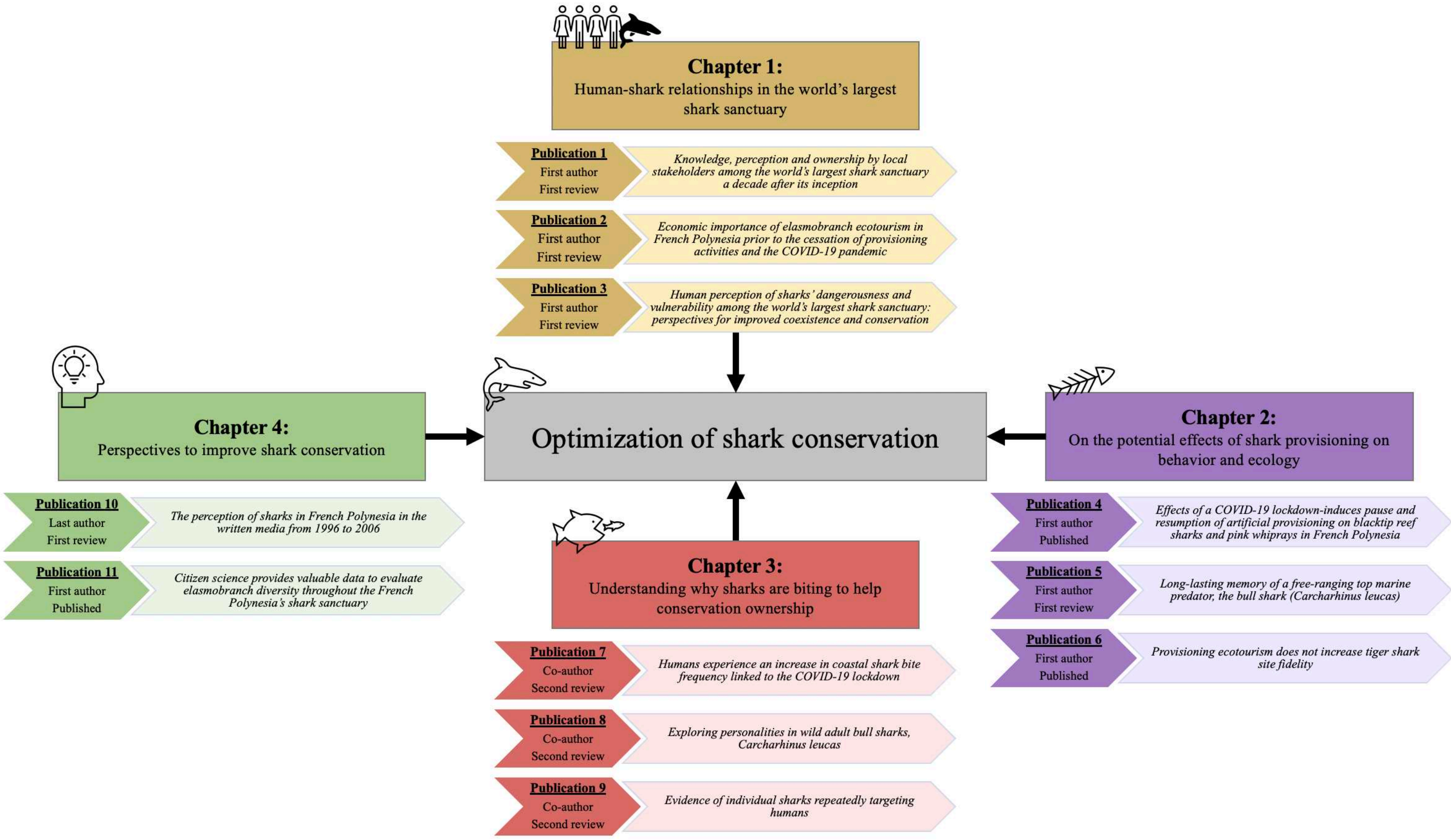

Figure 1: Summary of the PhD structure leading to an optimization of shark conservation through an approach mixing ecology, economy, and socio-anthropology

All the publications from this PhD thesis, at the crossroads of several disciplinary fields, have highlighted various obstacles encountered by shark protection measures, but also perspectives to improve their effectiveness (*Figure 1*).

Chapter 1 showed that even in the world's largest shark sanctuary, many people are displaying the willingness to kill a shark. This fact can be attributed to a lack of knowledge of the protection measures in place, to the vision of sharks as potentially dangerous competitors, and to the decay of traditional ecological knowledge. Furthermore, their major economic importance via the ecotourism of elasmobranch observation seems to be disregarded, and the associated artificial feeding practices are widely criticized.

However, the results presented in **Chapter 2** support the possibility to benefit from a potential sustainable feeding, or even from an “eco-feeding”. Indeed, despite the high resilience of the conditioning, explained by the sharks' high memory retention capacities, no dependence of the animals on feeding practices, nor any significant temporal evolution of their observed abundance or site fidelity index was demonstrated.

Chapter 3 provides practical reasons for bite incidents, most of which show no feeding motivation, but rather a response to a particular situation faced by the animal. Predatory bites could be mostly explained by the existence of strong differences in intraspecific personalities. Some sharks, particularly bold, could therefore be considered as "problem individuals" for humans. The use of photo-identification techniques and genetics via the collection of nuclear DNA from bite wounds offer important new opportunities for the eco-responsible management of these individuals.

The perspectives to improve Human-shark relationships proposed in **Chapter 4** allow to rethink the use of medias as a positive information dissemination tool for shark conservation. Citizen science is also particularly promising, as it enables the direct transmission of knowledge between science and society, and a reappropriation of the protection measures in place by the human populations themselves.

DISCUSSION

1. On the development of ecological and behavioral knowledge promoting a better human-shark relationship

1.1 On the impact of artificial provisioning practices: does an "eco-feeding" exist?

This work has highlighted the importance of further accumulating ecological and behavioral knowledge about sharks. It is crucial to understand which threats are primarily impacting their ecology. The results obtained in this thesis are in line with the growing scientific evidence that the polemics against artificial feeding should not be one of the priorities of shark conservation, given the extended damages generated by fisheries (Healy et al. 2020). However, it is imperative to consider the ecological characteristics of the target species, since the potential impacts of tourism practices could greatly depend on the mobility they naturally display. Highly migratory species may be more difficult to retain at provisioning sites than resident species. For instance, tiger sharks (*Galeocerdo cuvier*) (*Publication 6*, Hammerschlag et al. 2012a), great white sharks (*Carcharodon carcharias*) (Laroche et al. 2007, Becerill-Garcia et al. 2019, Becerill-Garcia et al. 2020) or bull sharks (*Carcharhinus leucas*) (Brunnschweiler & Barnett 2013), associated with high levels of mobility and variability in movement patterns, showed no significant temporal variability in their residency to feeding sites. Conversely, other species, such as the sicklefin lemon shark (*Negaprion acutidens*) (Clua et al. 2010, Clua 2018) or the blacktip reef shark (*Carcharhinus melanopterus*) (Mourier et al. 2021) showed an increase in their site fidelity index over time. However, it is important to notice that this same population of blacktip reef sharks showed no provisioning dependency, as they completely deserted the Tiahura site since the first day of the cessation of feeding activities following COVID-19 lockdown, as proved by drone flights (*Publication 4*). This result is in line with what has already been observed for another highly resident species, the whitetip reef shark (*Triaenodon obesus*), for which bait consumed at feeding sites does not represent its main food source (Abrantes et al. 2018). Thus, further research is required to deeply understand which provisioning techniques are minimizing the risk for a given target species, to promote a shark "eco-feeding".

The neutral or negative effects of shark artificial provisioning are often highlighted. However, potential positive effects remain to be considered, apart from the significant economic contributions generated, which is essential for the recognition of the non-consumptive value of these animals. Indeed, positive effects have already been observed for other species, as supplemental feeding even played a direct role in successful conservation programs, such as for the endangered Mauritius Kestrel (*Falco punctatus*) (Jones et al. 1995), or for the protected Northern Goshawk (*Accipiter gentilis*) (Ward & Kennedy 1996). Work carried out during this PhD on the Fijian bull sharks (*Carcharhinus leucas*), has led to the hypothesis that provisioning could deter them away from fisheries. Indeed, when tourist activities started again, after a one-year COVID-19 lockdown, a significant increase in the number of hooks was observed on photo-identified sharks beforehand (*Publication 5*, T. Vignaud & C. Séguigne pers. obs.). This might suggest that their interactions with fishermen intensified during the cessation of tourism practices. Sharks are particularly opportunistic animals, as many species appear to move depending on food availability or prey aggregations, as for the bull shark (*Carcharhinus leucas*) (Motta & Wilga 2001, Brunnschweiler & Barnett 2013, Espinoza et al. 2016), or the tiger shark (*Galeocerdo cuvier*) (Meyer et al. 2009). Furthermore, these animals have frequently been observed depredating on fishing boats and consequently are at risk of being caught on purpose or bycatch (Mitchell et al. 2018, Malara et al. 2021). Thus, the development of fixed and monitored artificial provisioning sites could help pull away the sharks from their main threat, particularly in areas where no protection measures are implemented.

French Polynesia is considered the world's largest shark sanctuary (Clua et al. 2018) and have led the way in such protection measures in the Pacific. However, the 2017 ban on artificial provisioning contributes to the stigmatization of shark-watching tourism (*Publication 3*). This also raises the risk of a major economic loss for the country, particularly concerning lagoon-based practices (*Publication 2*). This ban is in line with a modern ethical movement, generally more attributed to Westerners, which considers the protection of nature to be more effective if all links with Man are broken (Bruckner 2013). This ecologism rejects both capitalist and socialist doctrines, and shows humanity's deep disgust with itself, blamed for all the threats that faced an ideal vision of Nature (Bruckner 2013). This pathos is not a solution, as conservation measures can only be efficient if Humanity truly reconnects with Nature and restores a true harmony between Society and Environment, as promoted by sustainable development (Dogaru 2013, Dogaru 2021, Mikhno et al. 2021). Moreover, in the case of French Polynesia, such ban is finally in line with a profound decline in traditional cultural beliefs, whereas ancestral cultures from Oceania and nature are generally considered symbiotic (*Publication 1*, Kana'iaupuni & Malone 2006, Fisher 2015, Clua and Guiart 2020).

1.2 On biting events: how to better understand bites motivations?

It is interesting to report the lack of understanding of bite incidents worldwide, including in French Polynesia. Every bite reported locally since the 2017 ban on artificial provisioning has been systematically attributed as a direct consequence of this controversial practice by the population (C. Séguigne, pers. obs.). However, the only two predatory – that could have been fatal - bites in French Polynesia, attributed to an oceanic whitetip shark (*Carcharhinus longimanus*) during a whale-watching tour (Clua et al. 2021) and to a tiger shark (*Galeocerdo cuvier*) as part of the daily monitoring of an aquaculture structure (Clua et al. 2023), occurred after the ban, in contexts not involving any artificial olfactory stimulus and far from old feeding sites. Furthermore, the increase in dominance bites following the reopening of marine activities after the COVID-19 lockdown highlighted the importance of respectfully share the ocean with sharks to ensure our own safety (*Publication 7*). Artificial provisioning could therefore be of major interest in habituating sharks to human presence, defined as a gradual decrease in the animals' negative response to divers (Bejder et al. 2009). Far from increasing the bite risk, it could also represent an opportunity to ensure a better satiation of species that may present “problem individuals” for humans, hunger being one of the triggering motivations for predatory bites (Klimley & Curtis 2006).

It is important to remember that most bites are not linked to a willingness to predate humans, but rather to a response to a specific context, for instance a competition in which a spearfisherman might wish to defend his catch from a shark (*Publication 7*). This motivational separation of bites differs profoundly from the one used by the ISAF (International Shark Attack File), which distinguishes "provoked" bites, where sharks have been significantly teased by swimmers, divers, or fishermen, from "unprovoked" bites on innocent victims practicing an activity which is not supposed to trigger any shark reaction (Schultz 1967). The example of the non-lethal bite by a sicklefin lemon shark (*Negaprion acutidens*) on a surfer on Makemo Island (French Polynesia) (Clua & Haguenauer 2019), could be categorized as "unprovoked" according to the ISAF, but was attributed to a "dominance" motivation. Thus, although the stimulus sent by the victim is often generated unconsciously, these incidents are nonetheless "provoked", as an identified trigger directly induced the reaction of the shark. In this case, the term "attack", which is often used in the media, does not appear to be objective, since the shark alone cannot be held responsible for the incident (Neff & Hueter 2013). Another frequently popular theory concerning shark bites on humans may be undermined if the contextual classification of bites is accurate. The "mistaken identity” hypothesis explains bites by sharks mistaking a human for their natural prey (Ryan et al. 2021). In this case, the risk of bites would be directly linked to the number of people in contact with sharks in the ocean. Nevertheless, the situation encountered in French Polynesia following the COVID-19 Anthropause could not be explained by the “mistaken identity” hypothesis, since the number of bites significantly increased despite a greatly reduced human presence in the marine environment (*Publication 7*). This study provides another line of rebuttal of this theory, potentially dangerous in terms of shark risk perception, and merges the demonstrations highlighting the superficial injuries concerning most bites, which could not fit with a predatory motivation (Ritter & Quester 2016, Clua & Meyer 2023).

1.3 On shark personality and cognitive skills: are sharks intelligent animals?

A further clue to the existence of personalities within shark populations was provided by the study of bull sharks (*Carcharhinus leucas*) frequenting the Yakawe reef in Fiji. Indeed, this work demonstrates the existence of significantly different intra-populational behaviors, particularly regarding the "boldness-shyness" continuum, which fulfils one of the three criterions defining the existence of personalities within an population (*Publication 8*). To fully validate the possibility of "individuality" in animals, it is also needed to confirm the repeatability of these behavioral traits over time and among different contexts, as well as their heritability (Réale et al. 2007, Gervais et al. 2020). However, this work represents an unprecedented first step, as it has enabled the study of a large adult free-ranging shark population, when most studies ran either in captive or semi-captive environments, or on young animals (Finger et al. 2017). The results are in line with previous research on the personality hypothesis, having notably highlighted the high repeatability of individual differences in boldness and stress reactivity for the Port Jackson shark (*Heterodontus portusjacksoni*), the repeatability of social traits for the small spotted catshark (*Scyliorhinus canicula*), but also their short- and long-term consistency for juvenile lemon sharks (*Negaprion brevirostris*). Thus, predatory bites on humans could be better explained by the existence of particularly bold and exploratory personalities in sharks (Clua & Linnell 2018), as has been demonstrated for other marine predators, such as polar bears (*Ursus maritimus*) (Towns et al. 2009) or grey seals (*Halichoerus grypus*) (Graham et al. 2011).

An important unexpected result has been found during this PhD, thanks to the COVID-19 pandemic, allowing unprecedent opportunities to study wildlife behavior during a worldwide Anthropause (Bates et al. 2020, Rutz et al. 2020). Indeed, as provisioning was completely stopped in the tourism sites over the world, it allowed the determination to the resilience of conditioning, directly linked to the memory retention capacity displayed by free-ranging sharks. Blacktip reef sharks (*Carcharhinus melanopterus*) and bull sharks (*Carcharhinus leucas*) were able to come back since the reopening of feeding activities after respectively 6 weeks and 1 year of closure (*Publication 4*, *Publication 5*). These results are in line with previous studies ran in captive or semi-captive environments, showing a memory retention capacity possibly exceeding 40 days for juvenile Port Jackson sharks (*Heterodontus portusjacksoni*) (Guttridge & Brown 2014), 10 weeks for adult, and 12 weeks for juvenile lemon sharks (*Negaprion brevirostris*) (Clark 1959, Heinrich et al. 2021), and more than 50 weeks for juvenile grey bamboo sharks (*Chiloscyllium griseum*) (Fuss & Schluessel 2015). These important capabilities are suggesting strong cognition in the two studied shark species. This is corroborated by the fact that bigger brains are generally found in sharks living in complex habitats, such as coral reefs, and displaying strong levels of sociability (Yopak et al. 2012, Yopak & Lisney 2012). The differences in term of return to "business as usual" levels might be attributed to the respective ecologies of bull shark and blacktip reef shark. Indeed, the first is an apex predator, and the second a mesopredator (Roff et al. 2016). As blacktip reef sharks might be predated, including by bigger sharks, they potentially need more energy to avoid predation, compared to bull sharks which would have more energy to allocate to foraging, explaining their faster return to the provisioning site, despite longer time of lockdown. Such trade-offs to ensure a better fitness were already observed in mesopredators such as tarpons (*Megalops atlanticus*) choosing between food assimilation, with risks to meet bull sharks (*Carcharhinus leucas*), and energy-consuming osmoregulation allowing them to reduce predation risk (Hammerschalg et al. 2012b). Despite nothing is currently known about the link between personality and cognition in sharks, both might strongly influence their fitness, as animals within a population will differently respond to situations potentially impacting their survival or reproduction capacity (Brown & Schluessel 2023). Furthermore, both attributes might be very important for a better human perception, and then for conservation. Indeed, a shark could have the opportunity to switch from an image of a mindless killer to an image depicting a unique individual among others, displaying an intelligence comparable to mammals or birds (Finger et al. 2017, Brown & Schluessel 2023). Such a new vision of these animals by the public may change their negative perception toward a more positive and objective one. May our work contribute to this critically important process for decades to come.

2. On the importance to propose guidelines to improve human-sharks relationship

2.1 To improve shark-risk management

The occurrence and frequency of biting events raises a risk to shark conservation, since each incident can be followed by an amplification of negative perceptions of the fear felt towards these animals (Lucrezi et al. 2019). Thus, a better understanding of motivations (*Publication 7*), causes (*Publication 8*) as well as the development of effective monitoring tools (*Publication 9*) may bring new beneficial solutions for the human-shark relationship. Given the existence of problem individuals, a major question persists on their effective and sustainable management. Indeed, it appears that these animals may present a propensity for recidivism, and thus may continue to represent a risk for humans (*Publication 9*). These results allow to envisage two possible ways to manage the risk: by trying to prevent the occurrence of biting events, or by acting on the "deviant" animal. Two technologies have been developed to try to prevent bites. The first involves the use of a specific fiber to reinforce the resistance of a neoprene fabric. Although effective in reducing blood loss after a bite, it could not entirely protect its wearer from a predatory bite, mainly from a large-sized shark (Whitmarsh et al. 2019). Another approach explored is the use of "shark deterrents", either personal or forming a barrier. The concept is to overwhelm the ampullae of Lorenzini - the shark's electroreceptors - with electrical pulses, to redirect them from the holder. Despite promising initial results regarding the exclusion of target species in a defined area (O'Connell et al. 2014, O'Connell et al. 2018), the repulsion effect seems to differ significantly depending on the systems employed, but also considering the motivational state of the shark (Huveneers et al. 2013, Huveneers et al. 2018).

Regarding the direct control of potentially "at-risk" animals, very few techniques today allow for the selective extraction of problem individuals. Indeed, alternatives to culling campaigns, such as the implementation of SMART (Shark Management Alert in Real Time) drumlines, enable the extraction of possibly dangerous species, without however targeting the "more than average dangerous" shark. Furthermore, and unfortunately, bycatch and mortality including non-targeted endangered species might happen (Guyomard et al. 2019). One possible solution lies in selective fishing campaigns on individuals that have already inflicted predatory bites on humans (Clua et al. 2020). The method involves DNA collection from the wounds of a victim and the performance of a "fingerprinting", i.e. the sequence of the individual nuclear DNA of the biter (*Publication 9*, Stock et al. 2017, Fotedar et al. 2019, Clua et al. 2020). The results obtained will be compared with the genetic data previously collected through the creation of an extensive database, listing the sharks roaming in a certain area. If a match is observed, this catalogue allows to find the culprit animal thanks to its morphological characteristics highlighted by photo-identification (Clua & Linnell 2018, Clua et al. 2020). Nevertheless, this ambitious project requires total collaboration between researchers, decision-makers, fishermen, and other sea users, in order to build the database as exhaustively as possible, as well as to involve different stakeholders in the search for the identified deviant. This cooperative dynamic is therefore as promising as it is challenging to achieve.

To establish an understanding of the singularity of this animal, as well as a strong respect for free-ranging shark populations by the public, the future of the identified problem individual must be determined in a spirit of ethics and mutual discussions. Indeed, another obstacle to the development of this project could lie in the increasingly present "human-human" conflicts concerning sharks (Simpfendorfer et al. 2021b). Although fear remains dominant in human populations, an increasing number of people seem to be opposed to any campaign involving the lethal removal of several or even a single animal (Pepin-Neff & Wynter 2017, Le Busque et al. 2021, Casola et al. 2022). Thus, further research aimed to confirm or refute the personality hypothesis needs to be carried out urgently, particularly concerning the potential heredity of deviant behaviors, which remains today largely unexplored in sharks (Finger et al. 2017). Indeed, the most effective approach to conservation could be different depending on the results obtained. In the case of a demonstrated personality with a high probability of vertical transmission, it could be more sustainable and effective to eliminate a single animal, rather than multiplying the risk involved, potentially strengthening the negative perception of the dangerousness of sharks. If the emergence of deviant traits occurs randomly, the use of telemetry protocols linked to warning system (McAuley et al. 2016) adapted to a specific individual could be a more ethical approach finding a greater social approval. Ultimately, the risk-management method to operate must strongly be in line with the real human-danger incurred, the state of threats faced by sharks locally and the current scientific knowledges and recommendations.

2.2 To ensure an optimized safety of ecotourism operations

Despite provisioning tourism can be a solid help to promote non-consumptive value of sharks (*Publication 2*, Clua et al. 2011, Vianna et al. 2011, Vianna et al. 2012, Cisneros-Montemayor et al. 2013, Anna & Saputra 2017), and present a potential of being sustainable (*Publication 4, Publication 5, Publication 6*, Hammerschlag et al. 2012a, Brunnschweiler & Barnett 2013, Becerill-Garcia et al. 2019, Becerill-Garcia et al. 2020), the close proximity of humans with these animals may induce impacts on their ecology or on the safety of participants if not well-managed. The demonstration of the high level of conditioning retention in sharks (*Publication 4*, *Publication 5*) also undermines the idea these animals can be "dishabituated" from artificial provisioning practices through the implementation of waiting periods, as usually proposed (Newsome et al. 2004, Buray 2015, Clua 2018). Thus, it would be more appropriate to focus efforts on creating concrete regulations, staying adaptive with the development of scientific knowledge. Indeed, no standardized code of conduct is currently available for ecotourism operators. However, growing evidence is showing the negative impact of certain practices. Despite banning shark provisioning is not the best solution, it is now crucial to ensure the sustainability and safety of this practice, for both humans and sharks, to make it perennial and better accepted.

Sharks, with their developed cognition capacities, can associate several stimuli, the first being olfactory in the context of artificial provisioning, linked to the reward offered by the bait (Brown & Schluessel 2023). The second stimulus potentially enabling a link between humans and food is mainly considered as auditive or visual, although other senses may also be responsible for this association. Indeed, previous studies revealed that animals conditioned to artificial feeding can react to sound signals as well, as demonstrated for Port-Jackson sharks (*Heterodontus portusjacksoni*) (Vila Pouca & Brown 2018). This phenomenon was also observed in the wild for blacktip reef sharks (*Carcharinus melanopterus*) or great white sharks (*Carcharodon carcharias*), arriving at the provisioning site as soon as the sounds of engines of boats were heard (*Publication 4*, Bruce & Bradford 2013). On the other hand, avoidance behaviors have been observed in non-artificially provisioned whale sharks (*Rhincodon typus*), although they were used to the regular presence of snorkelers. Indeed, they were seen deserting the area if excessive paddling or splashing noises were generated (Araujo et al. 2017). In other circumstances, these human-induced sound stimuli could as easily induce an attractive effect, particularly if a reward is delivered. Thus, as proposed in *Publication 4*, it seems important to raise awareness among customers and guides to approach animals respectfully, and to avoid splash entry in the water from boats, as well as loud fin kicking when swimming.

Among the visual elements that can impact tourist safety, holding and distributing food directly by hands appears particularly at-risk. Indeed, sharks are likely to associate the hands of the feeder - or even other divers - with a potential source of food, especially as a shaking motion is often performed to catch the attention of targeted animals (Clua & Torrente 2015). Thus, these hand-feeding practices are likely to facilitate "begging" behavior towards both the feeder and other divers, and possibly generating aggressive behavior, as already observed in other taxa (Zhao & Deng 1992, Orams 2002, Christiansen et al. 2016, Sen Majumder et al. 2016). Therefore, it seems wise to minimize this risk of negative association by preferring to place the bait in reef crevices while keeping a conservative distance for observation (Clua 2018). Furthermore, hand-feeders are often presenting their skin in contact with fish uncovered. This may reinforce the clumsiness of sharks, as some species exhibit only monochromatic vision (Van Eyk et al. 2011). Then, wearing protective gloves that contrast with the color of the bait flesh could protect against possible bites if hand feeding is necessary. Another element of visual origin, possibly also happening in non-provisioned situations, may increase the risk of negative interactions with sharks: the isolated people within a group. Indeed, a significant proportion of bites have already occurred in this scenario (Neff 2012, Lagabrielle et al. 2018, Clua et al. 2021), despite the presence of other people in the water. Thus, it is important to advocate small groups when observing sharks, in which cohesion is easier to maintain by the guide, particularly on snorkeling trips. Concerning scuba diving, reinforcing the notion of buddy teams is essential.

The surface provisioning is a particularly risky practice, since it combines these two stimuli and encourages sharks to trigger vertical movements. Furthermore, agonistic behavior may be directly linked to spatial context in fishes (Bolyard & Rowland 1996). Many sharks used to forage on or close to the bottom could then be more aggressive (Clua 2018). Moreover, surface feeding increases competition between the predators present, potentially developing negative reactions towards other animals - including humans - or even towards inert devices such as boats (Nelson & Johnson 1980, Clua et al. 2013). This adds another clue on the importance to develop a feeding system that is completely adapted to the ecology of the targeted species, and thus to favor near-bottom feeding for reef species, as already demonstrated for sicklefin lemon sharks (*Negaprion actutidens*) (Clua 2018).

Despite daily visits to places where sharks present a strong probability be observed, no specific training regarding the right conduct to adopt in the event of an encounter is generally legally required for diving or snorkeling guides (C. Séguigne, pers. obs.). As a result, and despite their skills, they are often unable to recognize the onset of an agonistic behavior, although particularly precise ethograms describing shark behavior are available (Klimley et al. 2023). In the context of higher-risk activities, it could be interesting to provide a specific training for guides to maximize safety by reducing the risk of bites, through the acquisition of a better expertise. The activities covered could include whale watching, where the species encountered are often large and pelagic, such as oceanic whitetip sharks (*Carcharhinus longimanus*), often associated with marine mammals (Clua et al. 2021), or artificial provisioning, where the human-shark distance is deliberately reduced (Topelko & Dearden 2005, Gallagher et al. 2015). Some countries already offer this type of measures, by creating a specific license for tourism operators, notably in the context of cage diving activities in contact with great white sharks (*Carcharodon carcharias*) in Australia, South Africa or New Zealand (Bruce & Tasmania 2015, Richards et al. 2015). In addition, the established code of conduct should be strictly respected, since operators are fully liable, and can be penalized in the event of non-compliance (Catlin et al. 2012, Smith et al. 2014).

The decisions to ban all artificial provisioning activities seems to be associated with a drastic reduction in the number of animals observed by divers, and potentially even with their total disappearance of the site (*Publication 4*, *Publication 5*). In order to continue to satisfy participants, tourism operators may be tempted to pursue their activities illegally, giving free rein to totally anarchic practices, generating high risks of incidents (*Publication 3*, Healy et al. 2020). This educational vision, linked to a better training of dive and snorkeling leaders, to the respect of a code of conduct, and/or to the obtention of a specific license, could be preferred to total bans, as tourism professionals are directly involved in the safety of both participants and sharks.

3. On the necessity to actively communicate, collaborate and educate for a better shark conservation

3.1 To fight against cognitive bias in media

The portrayal of sharks in French Polynesian written media is predominantly positive, in sharp contrast to the particularly sensationalized, fear-based image depicted in the journals from USA or Australia (Philpott 2002, Muter et al. 2013). However, the decline in traditional ecological knowledge nowadays observed (*Publication 1*) indicates that the spiritual vision of sharks in ancestral cultures alone cannot explain this difference in media treatment. Instead, it could be more attributed to the facilitated direct contact with wild shark populations for the inhabitants of French Polynesia. Indeed, the creation of a human-shark bond provides a solid basis to acquire knowledge about them, and thus to offer a greater tolerance to their existence (McClellan et al. 2016, Acuña-Marrero et al. 2018, Afonso et al. 2020). A similar process has already been observed for other terrestrial predators, such as American alligators (*Alligator mississippiensis*) (Skupien et al. 2016), or brown bears (*Ursus arctos*) (Johansson et al. 2019). A possible way to offer the possibility to encounter sharks to an increased number of people could result in their promotion in public aquariums, which have already demonstrated their usefulness in raising public awareness for their conservation (Friedrich et al. 2014).

Despite the predominantly positive view in the media of French Polynesia, several important caveats should be noticed. Incidents of shark bites are still widely qualified as "attacks", with 100% of articles studied reporting these events by using this term (*Publication 10*). This observation is in line with most of the media worldwide, leading to the widespread use of this highly emotional and misleading expression (Neff & Hueter 2013, McCagh et al. 2015, Pepin-Neff 2019, Giovos et al. 2021). Thus, journalists should be aware of the implications of employing such kind of potentially strong words, even in the context of superficial bites (Pepin-Neff 2019). A first attempt to better define negative human-shark interactions, based on ISAF bite categorizations, has been proposed, dissociating "encounters", from "unprovoked" or "provoked attacks by sharks" (Le Busque et al. 2019). Nevertheless, this initial effort to better describe human-shark interactions may also present biases, and could evolve towards a motivational classification of incidents, such as that described in this doctoral work (*Publication 7*). Although the terms used in written media require particular attention, the impact of visual and audio elements, such as photographs or soundtracks, on viewers' attitudes towards sharks should not be ignored (Nosal et al. 2016, Bombieri et al. 2018).

On the other hand, the predominantly positive discourse relayed by the French Polynesian written media was unable to match the perception of local populations, with almost half of respondents to a survey indicating that sharks are dangerous for humans (*Publication 3*). Furthermore, *La Dépêche de Tahiti* also failed to provide information about the implications of Polynesian sanctuarization (*Publication 1*). This failure could be explained by a predominantly oral tradition of information transmission in Polynesian societies, which could have persisted over time, mainly in remote areas (Babadzan 1985, King et al. 2007, Mateata-Allain 2009, Pearce et al. 2010). Considering this fact, the non-governmental organizations (NGOs) could play a crucial role in the direct communication of science through raising awareness campaigns and can be a great complement to traditional media. As an example, the communication about an endangered species, the whale shark (*Rhincodon typus*), was ensured successfully in Philippines by a synergy between NGOs conferences and television programs (Aca 2016). However, NGOs speakers must take care to disseminate scientifically validated knowledge, as well as real mediators between science and society. Indeed, small groups of non-profits have already been seen misrepresenting the state of science while claiming to use science-based arguments (Schiffman et al. 2021). This could be confounding for people, and possibly led to a decline of the interest in shark conservation.

Another explanation of the non-consciousness about the sanctuary implications may lie in the limited local scope of the written media, which cannot be exported to all the islands of French Polynesia. Indeed, this territory covers 5.5 million km^2, with islands particularly remote from Tahiti, some of which are only serviced by boat for freight transport (C. Séguigne, pers. obs.). Thus, access to other types of audiovisual or digital media could be easier, despite most of them still reflect a particularly negative image of sharks. This has been proved among many films (Le Busque & Litchfield 2022) or through Facebook (Le Busque et al. 2019). However, social networks might present interesting perspectives, with a potentially positive influence on shark conservation by Youtube, presenting many positive messages (Beall et al. 2022, Casola et al. 2022), but also Twitter, where documentary films broadcasted during Shark Week generate a lot of enthusiasm (O'Donnell 2019). This category of films and this type of event also present an opportunity to disseminate knowledge about sharks in an entertaining way and can therefore be extremely useful, as long as false or non-factual documentaries are not promoted (O'Bryhim & Parsons 2015, O'Donnell 2019).

Thus, the promotion of shark conservation is linked to the dissemination of an unbiased, unsensationalized, and accurate media content, to enable the sustainable creation of pro-shark conservation behavior among the public. To achieve this objective, it is important to fight the extreme duality of messages that may exist between science and medias. This can create a veritable emotional paradox towards these animals (Neff 2015, McCagh et al. 2015), which can fuel a "human-human" conflict particularly deleterious to shark protection initiatives (Simpfendorfer et al. 2021b). Indeed, scientists seem to be less and less associated with media discourse, including when it comes to research topics (Hardiman et al. 2019). To ensure the truthfulness of the discourse, to combat cognitive bias and to serve the environmental protection policies in place, it seems crucial to re-establish a privileged connection between scientists, policymakers and journalists. In French Polynesia, this kind of harmony can be observed through the example of humpback whales (*Megaptera novaeangliae*). Many contents are spread on the ecology of these animals, as well as on the guidelines in front an encounter to avoid disturbance and ensure personal safety, via various media (radio, television, press, social networks) (C. Séguigne, pers. obs.). It may also be possible for sharks. Indeed, in past centuries, the general perception of marine mammals was strongly negative, and these animals were vilified and considered as very dangerous for sea users. However, they can be considered today as revered and loved by human populations (Neves et al. 2022).

3.2 To develop citizen science

Citizen science, as demonstrated by the example of the NGO of the Polynesian Shark Observatory (ORP), can be particularly important for scientific research, offering unprecedented spatial and temporal possibilities for data collection. Indeed, new information concerning the specific diversity, the distribution, the seasonality, and the abundance of numerous elasmobranch species were gathered thanks to the active participation of volunteer dive instructors to this program (*Publication 11*). This effective partnership between scientists, sea users and a local NGO could be extended to other issues, such as the creation of a database listing the individuals present in an area, as proposed for the implementation of a risk management based on individualities (Clua et al. 2020, *see section 2.1*). Dive instructors could easily provide pictures taken by divers, to enable scientists to enrich catalogs and collect information on the individuals present thanks to photo-identification. Indeed, such programs have already been occurred for grey nurse sharks (*Carcharias taurus*) in Australia (Barker & Williamson 2010). Meanwhile, scientists could inform dive leaders about potential problem individuals reported in the area, offering increased monitoring and safety possibilities, as well as greater willingness to follow scientifically approved codes of conduct. Involving volunteers in individual-scale sampling could provide opportunities to answer new scientific questions. Indeed, research on shark population size, social network analysis, growth rate or healing potential is also mainly based on photographic analysis (Graham & Roberts 2007, Holmberg et al. 2009, Chin et al. 2015, Jacoby et al. 2021).

The recent development of technical diving around the world is also creating new possibilities in terms of citizen science. Indeed, mesophotic coral ecosystems (MCEs), i.e., habitats located between 30 meters and reaching depths of over 150 meters, are now regularly visited by trimix divers, but remain largely unexplored by scientists, due to the logistical, financial and safety constraints that these committed dives entail (Turner et al. 2017, Pyle & Copus 2019). Consequently, MCEs remain one of the least studied ecosystems on Earth (Shipley et al. 2017). However, recent scientific advances show that they could serve as a refugia for many species, facing growing biotic and abiotic threats, such as climate change (Semmler et al. 2017, Turner et al. 2017, Goodbody-Gringley et al. 2021) or overfishing (Lindfield et al. 2016, Pinheiro et al. 2016). Collecting data on deep-diving sharks could enable us to study and understand the vertical movements of these animals in the water column highlighted for the Galapagos shark (*Carcharhinus galapagensis*) (Papastamatiou et al. 2015), or for the Caribbean reef shark (*Carcharhinus perezi*) (Shipley et al. 2017). These movements might boost the conservation motivation for these animals. Indeed, they could suggest a major role of sharks for coral ecosystems, since they could represent significant transporters of nutrients from shallow to mesophotic reefs (Papastamatiou et al. 2015), and thus be the guarantee of the resilience of our surface reefs.

Fishermen, who frequent both reef and pelagic ecosystems, display as well significant empirical knowledge of sharks. Thus, they can successfully be involved in citizen science initiatives, as proved in previous studies (Follett & Strezov 2015, Araujo et al. 2017, Filippo et al. 2018, Alvarado et al. 2020). Raising their awareness is particularly important, as they represent one of the social categories the most opposed to shark conservation (*Publication 1*, *Publication 3*). The privileged communication with scientists, enabled by citizen science, may offer the opportunity for fishermen to become more conscious of the indirect use value of sharks. Indeed, their abundance is a sign of healthy reefs, and thus of potential catches (Friedlander & DeMartini 2002, Sherman et al. 2020). Such results have already been demonstrated with the help of collaborative research programs, knowledge exchange between scientific community and fishermen, and more transparent communication between these two parties (Iwane et al. 2021). Thus, citizen science programs could indirectly help to limit Illegal, Unreported & Unregulated (IUU) fisheries that can occur even within protected areas (Ward-Paige & Worms 2017, Clua & Millot 2018). Nevertheless, this awareness alone could be insufficient in some cases, given the significant depredation that sharks can exert on catches. Other potential directions to improve the relationship between fishermen and sharks will be discussed in *section 4.1*.

3.3 To educate young generations

Although the education of younger children is not developed in this doctoral work, it could represent an interesting long-term perspective for the future of shark conservation. As with adults, children tend to vilify sharks, describing potential interactions with these animals as terrifying (Lane & Chazan 1989, McWhirter & Weston 1994). Fortunately, there is growing evidence that the perception of potentially dangerous animals tends to improve significantly as awareness of their importance increases. This principle has been verified for snakes with junior undergraduates in Georgia (Makashvili et al. 2014) and seems to be particularly promising with sharks (O'Bryhim & Parsons 2015, Tsoi et al. 2016, Ostrovski et al. 2021). Nevertheless, children tend to think in the simplest and most straightforward way possible (Groves & Pugh 2002, Grotzer & Basca 2003). Additionally, they are most of the time trained to reflect on extremely simplified environmental issues (Griffiths & Grant 1985, Munson 1994, Barman et al. 1995, Leach et al. 1996). Even though understanding the role of sharks in their ecosystem seems to be the key to a better perception (Røskaft et al. 2003, DiEnno & Hilton 2005, Prokop & Tunnicliffe 2008, Tsoi et al. 2016), the causal links causing their disappearance are complex to convey. Indeed, naive children tend to think that the removal of sharks could lead to an enrichment of biodiversity (Tsoi 2010), or that the "shark catchers" have a greater responsibility for the vulnerability of shark populations than the "fin eaters" (Tsoi et al. 2016). Thus, to ensure a better understanding of the functioning of food webs or anthropogenic impacts, schools should be helped to build a curriculum framework in primary ecological studies (Jordan et al. 2009, Tsoi et al. 2016). In addition to the many challenges involved in educating the younger people, marine environments are often under-represented in school curricula, and thus generally remain a minor topic of discussion, compared with terrestrial environments (Cava et al. 2005, Thornton & Scheer 2012).

Different tools can be considered to educate children to shark conservation. Firstly, it should be emphasized that the awareness of the younger people cannot be totally dissociated from the awareness of their parents, since the vertical transmission of a positive discourse is often correlated with a significantly more positive perception (Tsoi 2011). On the other hand, the use of educational materials is particularly effective on children, if they do not reflect cognitive biases (Tsoi et al. 2015). As for adults, television documentaries are particularly effective, as are readings (Tsoi et al. 2015). Nevertheless, a previous study showed that children aged between 6 and 8 showed an increased interest in marine science if reading materials were digital rather than paper (Syarah et al. 2019). Shark awareness should therefore be thought of via entertaining and modern resources, using the latest technologies available. One such example has been achieved to raise awareness of the conservation of the giant panda (*Ailuropoda melanoleuca*) (Chen et al. 2019). Indeed, the iPANDA initiative has created a particularly innovative digital product, which encourages children to explore their environment and accumulate knowledge to better protect the planet. This technology is based on the adoption of an artificial pet, stuffed with sensors, enabling children to discover, via the use of a connected tablet, how several physico-chemical parameters may influence the life of their panda (Chen et al. 2019). Although this technology is more difficult to consider on a marine animal like the shark, it is important to note that it has the potential to transmit positive behaviors towards nature, as well as creating powerful bonds with wildlife.

4. On the necessity of ownership of the conservation measures by the local population

4..1 By egalitarian conservation measures

It should be recognized that conservation measures can be profoundly inegalitarian, and thus represent a potential source of important social conflicts. Indeed, it is critical that shark protection present equally distributed costs, in order to avoid being deleterious to a part of the population (*Publication 2*, Balmford & Whitten 2003, Bennett et al. 2019, Griffiths et al. 2019, Booth et al. 2021, Giron-Nava et al. 2021). The main sea users who can suffer from limiting access to the consumptive value of sharks are fishermen. Indeed, it may not be enough to make this social category aware of the role played by sharks in coral ecosystems, as a ban on fishing may result in a significant loss of income for them (Booth et al. 2021, Malpica-Cruz et al. 2021). Indeed, economic damage can be direct, as traders of shark products (Booth et al. 2021, Malpica-Cruz et al. 2021) or indirect, linked to the increase in their abundance, generating more depredation (Iwane et al. 2021, Robinson et al. 2022). Fishermen, generally representing a less wealthy portion of the population, could then lose the willingness to support conservation initiatives, or even be tempted to practice illegal fishing (Booth et al. 2021, Robinson et al. 2022). Furthermore, the cessation of fishing activities is likely to generate even greater revenues thanks to the high non-consumptive value of sharks (Mustika et al. 2020). These incomes would mainly benefit to another profession: tourism operators. This situation could generate particularly virulent conflicts, even though conservation is ethically bound not to harm any social category (Balmford & Whitten 2003, Poudyal et al. 2018, Newing & Perram 2019).

One way to address the problems faced by fishermen, and thus their potential disengagement from conservation measures, could reside in their involvement in ecotourism. Indeed, a study in Palau showed that the number of visitors induced by tourism activities could, thanks to the consumption of caught fish, enable fishermen to surpass their earnings from the sale of caught sharks (Vianna et al. 2012). Nevertheless, the most promising solution lies in a strong collaboration between governments, fishermen and tourism operators, via payments for ecosystem services (PES), still underdeveloped. Indeed, the distribution of revenues linked to the promotion of alive rather than dead sharks must benefit all economic sectors ensuring the sustainability of these animals' populations (Vianna et al. 2012, Vianna et al. 2018). This can be achieved by collecting funds via taxes or donations requested from tourists, and by reinvesting them in conservation initiatives, including economic compensation for fishermen (Brunnschweiler 2010, Clua & Pascal 2014, Vianna et al. 2018). A particularly virtuous example takes place in Fiji, within the Shark Marine Reserve, where a share of the benefits generated by diving ecotourism is redistributed to two villages, having exchanged their right to perpetuate their fishing rights for this new source of income. In addition, an annual sponsorship program enables the villages to send a volunteer to be trained to divemaster level, which is a professional certification of dive leader (Brunnschweiler 2010).

4.2 By a cultural rebirth and a recognition of Traditional Ecological Knowledges

This doctoral work also showed that the lack of ownership in front of the shark conservation measures can be an obstacle to their effectiveness. This is particularly the case in French Polynesia, where the most remote islands consider the decision to create a sanctuary covering all the EEZ as "a decision taken in Tahiti", which is not in line with their more traditional way of life (*Publication 1*). The link between nature and culture, which is very important in societies of Oceania, seems to be impaired by the duality between management based on Western science and management based on Traditional Ecological Knowledges (TEKs) (Huffer & Qalo 2004). However, as shown in previous studies, a synergy between TEKs and Western science can be particularly effective in terms of environmental management, and to develop a sense of shared responsibility for the well-being of ecostystems (Tropics 2001, Becker & Ghimire 2003, Moller et al. 2004, Drew 2005, Maine 2020, Montgomery et al. 2020). Indeed, TEKs are particularly interesting because of the large body of knowledge accumulated on a local scale, concerning, for example, the species present in an area, and their migratory movements (Drew 2005, Friedlander et al. 2018). Thus, a re-established dialogue between scientists and the guardians of this knowledge could become a powerful tool for discovery, for the reinforcement of knowledge or for the development of management techniques applied to an improved shark conservation, while at the same time being a veritable incubator of social cohesion (Drew 2005, Mazzocchi 2006).

Furthermore, this re-established sense of mutual belonging could be particularly promising in vast territories such as French Polynesia, where ensuring compliance with fishing bans is not an easy task (*Publication 1*). Following the example of the Shark Marine Reserve in Fiji, a collaboration between fishermen, tourism operators and government bodies, through Fisheries Departments, could enable the monitoring and control of ecological zones that are particularly important for sharks (Brunnschweiler 2010). This cohesion around conservation could be strongly encouraged by the implementation of local citizen science programs (*Section 3.2*) or by the introduction of payments for ecosystem services (*Section 4.1*). Such initiatives could be favored by the direct implication of NGOs (*Publication 11*), as they already have proved being able to implement programs that align with the fulfilment of international and regional obligations for elasmobranch conservation (Koehler & Lowther 2022).

On the other hand, a more intense partnership between science and culture could be highly beneficial to raise awareness among the whole population. Indeed, the co-integration of Western and traditional knowledge has led to a greater efficiency in science teaching in South Africa (Le Grange 2007). Similarly, in India, the co-involvement of spiritual leaders and scientific mediators during an educational street performance on the whale shark (*Rhincodon typus*) allowed to educate the population about the lack of danger posed by this large species (Joshi et al. 2007). Thus, the tourism operators, in direct contact with tourists, as well as the NGOs, might be precious to help the transmission of both ecological and cultural knowledges, and reinforce the attractiveness of their operations while promoting the non-consumptive value of sharks (*Publication 2*). For instance, they could promote both knowledge and cultural rebirth with the communication around traditional myths, or with the use of local language to qualify the vernacular name of the shark species observed.

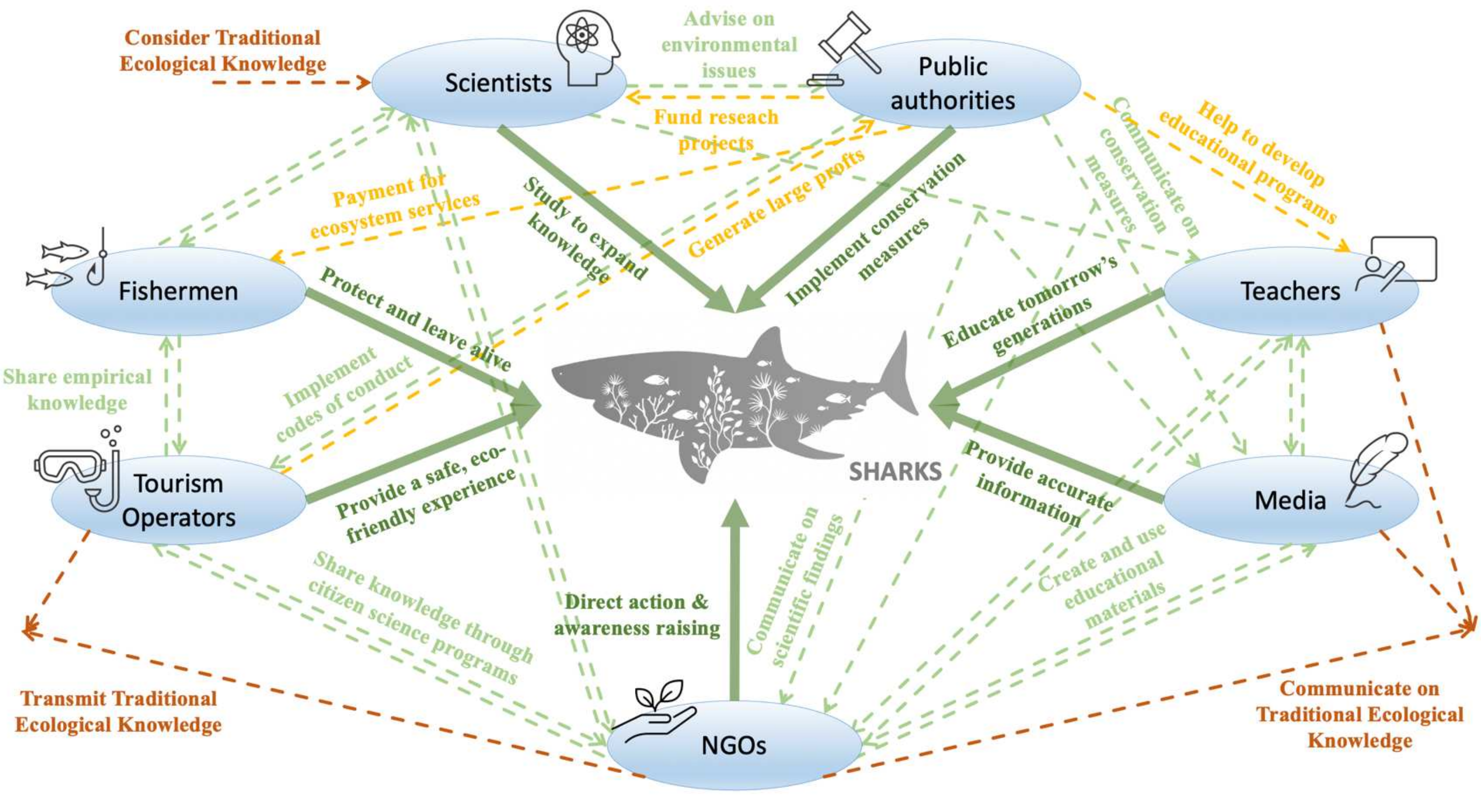

Figure 2: The virtuous circle of shark conservation. Actions in green are related to the discipline of ecology, those in yellow to economy and those in orange to socio-anthropology.

This PhD demonstrated the importance of the ecosystem services provided by sharks to human populations, through the plurality of their values, combining ecological balance, economic well-being, and cultural traditions. However, protection measures are still not sufficiently effective to really fight the threats faced by these animals. The use of all these disciplines is essential to their conservation, in order to optimize the management of shark populations, as well as to improve their perception by humans. In addition, this doctoral work has highlighted the importance of a restored social cohesion to ensure a sharing of knowledge, an equity and an ownership required for a genuine re-harmonization of Nature and Society (*Figure 2*).

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ANNEXE

Traduction en français de l'introduction, discussion & conclusion

INTRODUCTION

Les requins, des animaux menacés

La classe des Chondrichtyens regroupe les requins, les raies et les chimères. Elle constitue l'un des taxons de vertébrés les plus anciens sur Terre, survivant à plus de cinq grandes extinctions massives durant leurs 420 millions d'années d'existence (Cappetta 1987, Sibert & Rubin 2021). Une première évaluation des menaces auxquelles ce taxon fait face a été effectuée par l'UICN en 2014 pour la constitution de sa liste rouge. Au total, plus d'un quart des plus de 1000 espèces répertoriées présentait un risque d'extinction (Dulvy et al. 2014). Malgré cet avertissement, une accélération globale de la dégradation de l'état de santé des populations de Chondrichtyens a été observée, ces animaux faisant face à toujours plus de pressions anthropiques. En effet, plus d'un tiers des espèces est aujourd'hui considéré comme en danger (Dulvy et al. 2021). Bien que plusieurs causes puissent être incriminées, telles la perte et la dégradation de l'habitat, l'impact du changement climatique ou la pollution, la surpêche reste la menace majeure, principalement pour les squales (Dulvy et al. 2021, Parcoureau et al. 2021, Sherman et al. 2023). En effet, les populations de requins sont particulièrement peu résilientes face aux pêcheries, puisque ces animaux sont généralement caractérisés par des taux de croissance lents, des taux de reproduction faibles, un temps de gestation important et une maturité sexuelle tardive (Barker & Schluessel 2005). Les produits d'intérêt issus des requins incluent les nageoires, la chair, le foie, la peau, le cartilage ou les mâchoires et dents (Musick 2005). Ils peuvent présenter des usages variés, liée à leur consommation directe (Chen et al. 1996, Camhi et al. 1998), à l'industrie textile (Vannuccini 1999), cosmétique (Kuang 1999), ou pharmaceutique (Hallgreen & Larsson 1962, Broholt et al. 1986, Moore et al. 1993, Sills et al. 1998, Rao et al. 2000), ou à leur usage en tant qu'objets de souvenirs ou de curiosité (Rose 1996). Il est intéressant de constater que la chair et les nageoires sont respectivement une source de protéine particulièrement bon marché, et l'un des ingrédients culinaires les plus chers au monde. L'exploitation de ces deux produits à l'échelle mondiale contribue ainsi significativement à des taux importants de mortalité des requins par action de pêche (Vannuccini 1999).

En effet, la demande constante de nourriture humaine, particulièrement importante dans les pays en voie de développement, a généré la très forte activité de pêcheries de requins à petite échelle, souvent illicites, non déclarées et non réglementées dans de nombreux villages côtiers frappés par la pauvreté (Vannuccini 1999, McVean et al. 2006, Lestari et al. 2017, Glaus et al. 2018, Yulicanto et al. 2018, Booth et al. 2018, Prasetyo et al. 2021, Seidu et al. 2022). Dans de telles communautés, souvent vulnérable sur le plan socio-économique, les pêcheurs locaux commercialisent la chair des requins localement, tandis que leurs nageoires sont exportées vers le marché international (Seidu et al. 2022). L'intérêt des nageoires de requins repose sur leur usage en tant qu'ingrédient principal de la soupe à l'aileron, un repas de luxe traditionnel dans la culture chinoise (Musick 2005, Clarke et al. 2007). Certaines nageoires de premier choix peuvent être particulièrement onéreuses, comme pour celles du requin sombre (*Carcharhinus obscurus*) atteignant des prix entre 400 et 500 USD par kilogramme. Une telle importance économique a le potentiel d'influencer directement le risque d'extinction de nombreuses espèces de requins, et constitue potentiellement le déterminant majeur de la survie de leurs populations (Clarke et al. 2007, Davidson et al. 2016, McClenachan et al. 2016). En effet, les estimations issues du marché de Hong Kong suggèrent qu'entre 26 et 73 millions de requins pourraient avoir été abattus dans le monde entier pour la commercialisation de leurs nageoires au cours de l'année 2000 (Clarke et al. 2006).

Cependant, la consommation de produits issus du requin peut s'avérer dangereuse pour la santé humaine. En tant que prédateurs, ces animaux peuvent être fortement affectés par la bioaccumulation des métaux et métalloïdes, ainsi que par la biomagnification de certains d'entre eux. Par exemple, des taux élevés de mercure (Hg) ou d'arsenic (As), bien au-delà des recommandations médicales, ont déjà été rapportés dans leur chair et leurs nageoires (Gilbert et al. 2015, Amorim-Lopes et al. 2020, Shipley et al. 2021). D'autre part, malgré la forte importance socio-économique de la pêche, les requins offrent une grande variété d'autres services écosystémiques, contribuant directement ou indirectement au bien-être humain ainsi qu'à la génération de revenus potentiellement importants reposant sur leur non-prélèvement.

La valeur culturelle & spirituelle des requins

Bien que la consommation de requins soit liée à une meilleure tonicité, à des vertus aphrodisiaques ou à l'accès à la prospérité dans la culture chinoise (Clarke et al. 2007, Fabinyi 2012), ces animaux présentent également une forte valeur non-consommatrice d'ordre spirituel dans de nombreuses cultures océaniennes (Techera 2012). En effet, bien que certains produits issus du requin puissent également être utilisés à des fins alimentaires, cérémonielles ou pratiques, notamment les dents pour la création d'armes ou d'outils de coupe (Kirch 1985, Taylor 1993, McDavitt 2005, Drew et al. 2013), ces pratiques restent largement minoritaires dans le Pacifique. Les requins représentent le lien entre l'Océan et la Terre, entre les Dieux et les Hommes, entre les Vivants et les Morts et sont considérés comme des animaux puissants, gracieux, et respectables (McDavitt 2005, Gerhardt 2018, Torrente et al. 2018). À Anaa, un atoll isolé de Polynésie Française, la mythologie présente un requin nommé *Tumu-mago* (origine – requin) comme l'origine masculine de la vie, aux côtés de *Tumu-rito* (origine – croissance végétale), l'origine féminine. Les requins sont considérés comme les représentations des dieux sur Terre dans de nombreuses sociétés traditionnelles, comme aux Fidji (Techera 2012), à Hawaï (Puniwai 2020), en Polynésie (Torrente et al. 2018), ou aux Tonga (Techera 2012), ce qui les rend *tapu*, c'est-à-dire à ne pas tuer. De nombreuses cultures ancestrales d'Océanie considèrent que pêcher un requin sans respecter des règles strictes est puni par les dieux à travers des morsures, parfois mortelles

(McDavitt 2005, Clua & Guiart 2015, Torrente 2015). Par ailleurs, les sociétés aborigènes sont divisées en groupes familiaux appelés clans. Chacun d'entre eux représente ses ancêtres à travers un groupe unique et distinct d'animaux totémiques (McDavitt 2005, Gerhardt 2018, Puniwai 2020). Les requins représentent généralement des familles influentes, comme pour le clan australien Yolngu, où le puissant *Mäna* est un puissant requin-totem, représentant la vengeance justifiée et la force de surmonter les obstacles (McDavitt 2005).

Le savoir encyclopédique dont font preuve les clans traditionnels d'Océanie leur a généralement permis de développer une utilisation durable de leurs ressources marines (Friedlander 2018). Cependant, l'effondrement des sociétés ancestrales suite à la colonisation occidentale a conduit à un déclin significatif de ce précieux savoir culturel (Babadzan 1983, Alévêque 2009). De plus, les structures gouvernementales centralisées, le développement économique et la mondialisation sont aujourd'hui des freins à la réappropriation culturelle des peuples du Pacifique (Friedlander 2018). La perception occidentale moderne des requins s'est rapidement répandue, allant de pair avec le développement d'une peur injustifiée face à ces animaux, héritée de la colonisation. À titre d'exemple, le résultat d'entretiens menés à Hawaï dans un centre chrétien pour enfants montre que pour la plupart des sondés, leur animal totem a été oublié ou n'a jamais été connu (Pukui 1972, Taylor 1993). La vision occidentale des requins est particulièrement influencée par le best-seller de Peter Benchley, Les Dents de la mer, suivi de la superproduction qui lui est associée, sortie en salle en 1975. Les effets ont été immédiats, puisque les activités de "pêche au monstre" n'ont jamais été aussi populaires qu'après cette date (Hueter 1991, Neff & Hueter 2013). Ainsi, la perte des connaissances traditionnelles semble avoir directement conduit à une perte d'intérêt pour l'utilisation culturelle non-consommatrice des requins, en dépit de la forte importance spirituelle qu'ils revêtaient auparavant.

La valeur écologique des requins

Les requins ont également une valeur d'usage indirecte importante, en tant que piliers de l'équilibre des écosystèmes coralliens. En effet, ces animaux, considérés selon les espèces comme des prédateurs apicaux ou comme de larges mésoprédateurs, peuvent fortement influencer leur écosystème. En effet, leur simple présence génère des réponses anti-prédateurs de leur potentielles proies, influençant potentiellement la démographie, la croissance, la morphologie et le comportement des autres organismes vivants peuplant le récif (Heithaus et al. 2007, Wirsing et al. 2007, Asunsolo-Rivera et al. 2023). La réduction de l'abondance de certains prédateurs apicaux, au sommet de la chaîne trophique, comme le requin tigre (*Galeocerdo cuvier*) ou le grand requin marteau (*Sphyrna mokarran*), peuvent même entraîner d'importants effets cascade, potentiellement hautement délétères pour la productivité et la santé des écosystèmes coralliens (Friedlander & DeMartini 2002, Ferretti et al. 2010, Heithaus et al. 2012, Heupel et al. 2014, Frisch et al. 2016, Sherman et al. 2020). Plus récemment, des études in situ ont démontré que pour des récifs exposés à des stress importants, la présence des requins favorisait de hautes densités de poissons herbivores grâce à la prédation de mésoprédateurs. Ainsi, ils pourraient contribuer à la survie et à la croissance corallienne, en aidant à limiter la prolifération algale (Ruppert 2013, Ruppert 2016).

Cependant, la perception négative des requins fait craindre que la bonne santé de leurs populations n'entraîne une augmentation du nombre d'incidents de morsure. De plus, les cas de morsures, bien qu'extrêmement rares, sont rapportés avec sensationnalisme dans les médias écrits, audiovisuels ou numériques. Ce phénomène amplifie le besoin de consommation médiatique, principale source d'information pour la population humaine, et exagère considérablement le danger réel encouru (Muter et al. 2012, Neff & Hueter 2013, Bombieri et al. 2018, Sabatier & Huveneers 2018, Hardiman et al. 2020). Le discours anxiogène autour des interactions homme-requin et la personnification de ces animaux, dépeints comme des criminels, sont générés par l'emploi de métaphores et d'un vocabulaire caractéristique tel que « mangeur d'Hommes », « requin renégat », « attaque », ainsi que par l'utilisation de photographies angoissantes dans de nombreux articles (Thomson & Mintzes 2002, Neff & Hueter 2013, McCagh et al. 2015, Neff 2015, Pepin-Neff & Wynter 2018, Sabatier & Huveneers 2018). Cette stratégie éditoriale négative, également connue chez d'autres prédateurs (Bombieri et al. 2018), peut générer des biais cognitifs importants chez les lecteurs. Dans le cas des requins, cette peur persistante, appelée « *Jaws effect* », peut même entraîner le désir d'éradiquer ces animaux afin d'assurer la sécurité de l'humanité (Neff 2015). Il est intéressant de remarquer que les campagnes d'abattage envisagées pour la gestion du risque requin imitent exactement celles dépeintes dans la fiction Les Dents de la mer. Elles ont été réellement reproduites en réaction à des clusters de morsures en Égypte, en Russie, aux Seychelles, au Mexique, en Australie occidentale et dans les territoires français d'outre-mer de l'île de la Réunion (O'Connell et al. 2011, Ritter et al. 2013, Neff 2015, Chin et al. 2017) et, plus récemment, en Nouvelle-Calédonie. En conséquence, des centaines de requins sont tués inutilement chaque année, y compris appartenant à des espèces menacées d'extinction. D'autre part, une plus grande tolérance à l'exploitation des populations de ces animaux est actuellement observée, associée à une forte passivité face aux mesures de conservation en place (Neff 2015, Hardiman et al. 2020, Dulvy et al. 2021).

La valeur économique des requins

Plutôt que de considérer les requins comme de simples prises ou nuisances, il conviendrait de les envisager comme formidables partenaires commerciaux. En effet, de nombreux plongeurs ou randonneurs subaquatiques en quête d'aventure choisissent une destination de voyage en fonction de l'opportunité d'observer certaines espèces charismatiques, souvent rares ou massives (Orams et al. 2002, Topelko & Dearden 2005). Les observations d'animaux emblématiques, tels que les requins baleines (*Rhincodon typus*), en danger à l'échelle mondiale (Pierce & Norman 2016), ont généré des profits de 3.7 millions USD au Belize (Graham 2004), de 4.99 millions USD aux Seychelles (Rowat & Engelhardt 2007), ou de 10.4 millions USD en Indonésie (Anna & Saputra 2017). Le requin tigre (*Galeocerdo cuvier*), quasi menacé (Ferreira & Simpfendorfer 2019), et le grand requin blanc (*Carcharodon carcharias*), vulnérable (Rigby et al. 2022) génèrent respectivement 1.62 et

4.99 millions USD pour l'économie sud-africaine (Dicken & Hosking 2009, Hara et al. 2003). Dans le Pacifique, le requin citron faucille (*Negaprion acutidens*), en danger (Simpfendorfer et al. 2021a), pèse 5.4 millions USD à lui seul en Polynésie Française (Clua et al. 2011), quand l'ensemble du tourisme d'observation des requins représente 25.5 millions USD en Australie (Huveneers et al. 2017), 42.2 millions USD aux Fidji (Vianna et al. 2011), et même 18 millions USD à Palau, ce qui constitue 8% du produit intérieur brut de cet archipel (Vianna et al. 2012). Au total, plus de 590 000 touristes et plus de 314 millions USD ont été générés dans le monde, soutenant plus de 10 000 emplois, selon une étude de 2013. Ces mêmes recherches ont également permis de prévoir un essor drastique de l'écotourisme requin, avec des gains estimés à plus de 780 millions USD pour 2033, c'est-à-dire 150 millions USD de plus que les profits générés par l'industrie de la pêche (Cisneros-Montemayor et al. 2013). Ce n'est pas le seul exemple où la valeur économique générée par le tourisme d'observation tend à être plus élevée que celle des pêcheries (Clua et al. 2011, Vianna et al. 2011, Vianna et al. 2012). En effet, bien que la pêche au requin soit particulièrement active en Indonésie, il apparaît que l'écotourisme requin dépasse localement la valeur de leurs exportations annuelles de 1,45 fois (Mustika et al. 2020). Cependant, la génération de tels revenus dépend largement de la satisfaction des touristes, qui s'attendent à rencontrer leurs espèces cibles dans des conditions optimales de proximité ou d'abondance (Orams et al. 2002, Topelko & Deaden 2005). Pour assurer la meilleure prestation possible, une grande majorité d'opérateurs touristiques a recours à l'appâtage pour attirer les requins (Orams et al. 2002, Gallagher & Hammerschlag 2011, Clua 2018), par le biais de diverses pratiques allant de la simple attraction olfactive avec du sang et/ou des parties de poissons liquéfiés (« *smelling* » ou « *chumming* ») au nourrissage avec de gros morceaux de poissons (*« feeding »*) (Laroche et al. 2007, Clua et al. 2010, Gallagher et al. 2015).

Ces pratiques d'appâtage font face à d'importantes polémiques les accusant de présenter de potentiels effets délétères sur la biologie des espèces cibles, ainsi que de créer des situations dangereuses pour les participants (Orams et al. 2002). En effet, certains effets négatifs ont déjà été relevés sur l'écologie des requins, tels que la modification de la composition des communautés d'élasmobranches (Meyer et al. 2009, Brunnschweiler et al. 2014), des changements dans la mobilité et dans l'utilisation de l'habitat (Clua et al. 2010, Bruce & Bradford 2013, Mourier et al. 2021), ou des patterns d'activité altérés (Bruce & Bradford 2013, Barnett et al. 2016). D'autres impacts ont également été observés sur le comportement des requins, avec notamment une compétition intra- et interspécifique plus élevée (Clua et al. 2010, Brunnschweiler et al. 2014). Cependant, de récentes études ont révélé de nombreux cas où le nourrissage artificiel n'a pas présenté d'impact significatif – si impact il y a – sur l'écologie et le comportement des requins, comme chez le grand requin blanc (*Carcharodon carcharias*) en Afrique du Sud (Laroche et al. 2007) ou au Mexique (Becerrill-Garcia et al. 2019, Becerrill-Garcia et al. 2020), le requin de récif (*Carcharhinus perezii*) aux Bahamas (Maljković & Côté 2011), le requin tigre (*Galeocerdo cuvier*) dans la Caraïbe (Hammerschlag et al. 2012a), et le requin bouledogue (*Carcharhinus leucas*) aux Fidji (Brunnschweiler & Barnett 2013). D'autre part, le nombre d'incidents impliquant des requins n'a pas significativement augmenté à proximité des sites d'appâtage, si une règlementation stricte est respectée par les opérateurs (Gibbs & Warren 2014, Clua 2018). Ainsi, il semblerait que le nourrissage artificiel des requins présente des effets différentiels en fonction des espèces et des pratiques, et qu'il pourrait potentiellement être considéré comme durable si un code de conduite approprié est établi (Clua 2018, Mourier et al. 2021). Cependant, la perception actuelle de cette activité touristique a mené à son interdiction en 2017 en Polynésie Française, et ainsi à un risque de réduction de la valeur non-consommatrice des requins dans le cas où la satisfaction des touristes décroisse à l'issue de cette décision.

Objectifs

Ces constatations montrent qu'il est urgent de revaloriser l'importance des services écosystémiques rendus par les requins, en dehors de leur simple valeur consommatrice. En effet, leur utilité et leur intérêt ont été profondément dévalués par de forts biais cognitifs entretenant une peur viscérale de ces animaux, basés sur des croyances populaires plutôt que sur des faits scientifiques avérés. Cependant, la mise en avant de leurs valeurs culturelles et spirituelles ainsi que de leur contribution à l'équilibre écosystémique et au bien-être écotouristique pourrait permettre aux sociétés humaines de mieux connaître les bénéfices apportés par la conservation des requins. En effet, malgré l'existence de nombreux programmes de protection dans le monde, allant de simples restrictions de pêche à des interdictions totales sur de vastes zones (MacNeil et al. 2020), les initiatives menées pour la conservation des requins ne montrent pas la même efficacité que pour d'autres taxa, comme les mammifères marins ou les tortues marines (Moore et al. 2009, Roman et al. 2013). Ainsi, une prise de conscience de l'Homme face à l'importance de populations de requins en bonne santé est nécessaire à une augmentation de l'efficacité des mesures de protection mises en œuvre.

L'objectif de cette thèse de doctorat est de rechercher des axes permettant la réconciliation de l'écologie, de l'économie et de la socio-anthropologie, afin d'optimiser les mesures de préservation existantes. En effet, repenser la gestion des populations de requins à la croisée de ces trois champs disciplinaires pourrait permettre le développement d'une approche « développement durable » de la conservation des requins, basée sur les trois piliers que sont la nature, les populations humaines et l'économie (Purvis et al. 2019). Ainsi, un triple objectif a été déterminé : (i) Investiguer les liens existants entre ces disciplines dans le contexte de la conservation des requins, (ii) Réduire les perceptions négatives actuellement ressenties par la majorité du grand public, (iii) Fournir des informations scientifiques fiables à destination des décideurs et des opérateurs touristiques, afin d'optimiser les prises de décisions concernant la relation Homme-requin.

STRUCTURE DE LA THÈSE

Ce travail regroupe 11 publications scientifiques soumises, en cours de révision ou publiées dans des revues de rang A, dans lesquelles j'ai contribué au travail effectué en tant que première auteure (n =7) ou comme co-auteure (n = 4) (*Tableau 1*). Ces articles ont été divisés en 4 chapitres structurant la thèse : (**Chapitre 1**) Les relations Homme-requin dans le plus grand sanctuaire requin au monde, (**Chapitre 2**) Les effets potentiels du nourrissage artificiel sur le comportement et l'écologie des requins, (**Chapitre 3**) La compréhension des morsures en soutien à la conservation, (**Chapitre 4**) Les perspectives d'amélioration des mesures de protection en place.

Le Chapitre 1 est centré sur le cas de la Polynésie Française, une région du Pacifique caractérisée par la sanctuarisation de ses eaux depuis 2006, pour toutes les espèces de requins, à l'exception du mako (*Isurus oxyrinchus*), également protégé depuis 2012. L'ensemble de la zone économique exclusive de la Polynésie française, couvrant 5.5 millions de km^2, interdit toute pêche et tout commerce de produits dérivés du requin. De plus, ce territoire est l'une des destinations les plus emblématiques au monde pour l'observation des élasmobranches. L'objectif de ce chapitre consiste en la description de la vision sociale des mesures de protection des requins sur plusieurs îles de Polynésie Française, toutes différentes de par leur degré d'occidentalisation ainsi que par leur distance à la capitale, Papeete (*Publication 1*) ; en la quantification de l'importance économique locale de l'écotourisme d'observation des requins (*Publication 2*) ; mais également en la détermination de la perception humaine des pratiques récréatives associées à l'écotourisme (*Publication 3*). Ce travail vise également à identifier les biais cognitifs potentiels persistant dans la population polynésienne, l'état des connaissances écologiques traditionnelles locales, et le public le plus réticent face aux initiatives de conservation des requins.

Afin d'apporter des réponses face à la controverse autour de l'appâtage écotouristique, le **Chapitre 2** a pour objectif de répondre à deux questions : Les requins conditionnés peuvent-ils devenir dépendant du nourrissage artificiel ? Existe-t-il des impacts négatifs sur l'écologie et le comportement des espèces ciblées ? Deux études ont été menées à la suite des confinements liés à la pandémie de la COVID-19, et ainsi à l'arrêt de l'appâtage, pour deux espèces sur deux sites et écosystèmes distincts. La première concerne les requins à pointes noires (*Carcharhinus melanopterus*) observés dans le lagon de Moorea (Polynésie Française), ciblés par des pratiques de nourrissage qui ont été stoppées pendant 6 semaines, lors de l'Anthropause (*Publication 4*). La seconde s'intéresse à une espèce potentiellement dangereuse pour l'Homme, le requin bouledogue (*Carcharhinus leucas*), privé de stimulus alimentaire artificiel sur le récif de Yakawe (Fidji) pendant plus d'une année (*Publication 5*). De plus, un jeu de données précédemment collecté à Tahiti (Polynésie Française) a été utilisé pour explorer l'impact de l'appâtage, effectué en pente externe, sur la fidélité au site et l'abondance de requins tigres (*Galeocerdo cuvier*) avant son arrêt définitif en 2017 (*Publication 6*).

Le **Chapitre 3** investigue les raisons des morsures de requins sur l'Homme, et apporte une réflexion sur les meilleures stratégies de gestion du risque à appliquer. À l'aide d'une importante base de données des morsures en Polynésie Française, plusieurs hypothèses liées aux motivations de ces incidents ont été confrontées. L'objectif est d'expliquer l'augmentation du nombre d'accidents enregistrés suivant le déconfinement de la COVID-19, bien que le nombre d'humains fréquentant l'environnement marin soit largement réduit (*Publication 7*). Des investigations sur l'existence de traits de personnalité chez le requin bouledogue ont également été effectuées. Celles-ci ont permis le test de l'hypothèse selon laquelle la probabilité d'être en situation d'une morsure dite « de prédation » serait différente entre les individus d'une même population, et ainsi dépendante des niveaux individuels d'audace et d'agressivité (*Publication 8*). Nous avons également proposé une nouvelle possibilité d'identification d'un potentiel « requin à problèmes », qui a mordu l'Homme de manière répétée, par le biais de différentes méthodes. Ceci offre de nouvelles perspectives pour une gestion plus responsable et efficace du risque requin (*Publication 9*).

Le **Chapitre 4** recherche des moyens permettant l'amélioration de la connaissance et de la perception des requins, à travers le discours médiatique et l'implication directe du grand public. L'impact de la sanctuarisation de 2006 sur la couverture médiatique en Polynésie Française a été étudié afin d'analyser l'évolution de l'image des requins dépeinte dans les journaux en amont d'un évènement positif de conservation (*Publication 10*). D'autre part, les potentiels effets des initiatives de sciences participatives pour la conservation mais également pour l'éducation ont été investigués grâce à un vaste projet mené par l'Observatoire des Requins de Polynésie (ORP), regroupant de nombreux instructeurs de plongée du territoire polynésien (*Publication 11*).

Une synthèse des résultats proposes par ces publications scientifiques, incluses dans les pages suivantes, est présenté en amont de la discussion.

Chapitre	Publication	Titre	Auteurs	Contribution personnelle	Journal	Journal IF	Statut (Déc. 2023)
Chapitre 1: Les relations Hommes-requin dans le plus grand sanctuaire requins au monde	*Publication 1*	Knowledge, perception and ownership by local stakeholders among the world's largest shark sanctuary a decade after its inception	**C. Séguigne**, M. Bond, A. Goyaud, M. Heithaus, G. Siu, Z. Rowe, F. Torrente, E. Clua	Analyse de données, Visualisation de données, Préparation du manuscrit original, Relectures et corrections	Humanities and Social Sciences Communications	2.731	Seconde review
	Publication 2	Economic importance of elasmobranch ecotourism in French Polynesia prior to the cessation of provisioning activities and the COVID-19 pandemic	**C. Séguigne**, M. Ombrouck, N. Pascal, A. Brathwaite, E.Clua	Collecte de données, Analyse de données, Visualisation de données, Préparation du manuscrit original, Relectures et corrections	Regional Studies in Marine Science	2.166	Première review
	Publication 3	Human perception of sharks' dangerousness and vulnerability among the world's largest shark sanctuary: perspectives for improved coexistence and conservation	**C. Séguigne**, M. Bond, A. Goyaud, M. Heithaus, G. Siu, F. Torrente, E. Clua	Analyse de données, Visualisation de données, Préparation du manuscrit original, Relecture et corrections	Marine Policy	4.315	Première review
Chapitre 2: Effets potentiels du nourissage artificiel des requins sur leur comportement et leur écologie	*Publication 4*	Effects of a COVID-19 lockdown-induced pause and resumption of artificial provisioning on blacktip reef sharks (*Carcharhinus melanopterus*) and pink whiprays (*Pateobatis fai*) in French Polynesia	**C. Séguigne**, J. Mourier, T. Vignaud, N. Buray, E. Clua	Analyse de données, Visualisation de données, Préparation du manuscrit original, Relectures et corrections	Ethology 128(2)	1.897	Publié en 2022 (5 citations)
	Publication 5	Long-lasting memory of a free-ranging top marine predator, the Bull shark *Carcharhinus leucas*	**C. Séguigne**, T. Vignaud, C. Meyer, J. Bierwirth, E. Clua	Collecte de données, Analyse de données, Visualisation de données, Préparation du manuscrit original, Relectures et corrections	Behaviour 1(aop)	1.991	Publié in 2023
	Publication 6	Provisioning ecotourism does not increase tiger shark site fidelity	**C. Séguigne**, M. Bègue, C. Meyer, J. Mourier, E. Clua	Analyse de données, Visualisation de données, Préparation du manuscrit original, Relectures et corrections	Scientific Reports 13(1)	4.997	Publié in 2023 (2 citation)
Chapitre 3: Comprendre les morsures de requins pour renforcer les mesures de conservation	*Publication 7*	Humans experience an increase in coastal shark bite frequency linked to the COVID-19 lockdown	E. Clua, C. Meyer, **C. Séguigne**, A. Wirsing	Analyse de données, Visualisation de données, Relectures et corrections	Global Ecology and Conservation	3.97	Seconde review
	Publication 8	Exploring personalities in wild adult Bull sharks, *Carcharhinus leucas*	T. Vignaud, C. Meyer, **C. Séguigne**, E. Clua	Analyse de données, Visualisation de données, Relectures et corrections	Behaviour 1(aop)	1.991	Publié in 2023
	Publication 9	Evidence of individual sharks repeatedly targeting humans.	E. Clua, C. Meyer, S. Baksay, M. Freeman, A. Haguenauer, J.D.C. Linnell, **C. Séguigne**, S. Surina, M. Vély, T. Vignaud, S. Planes	Analyse de données (fréquences alléliques), Relectures et corrections	Scientific Reports	4.997	Seconde review
Chapitre 4: Perspectives d'amélioration de la conservation des requins	*Publication 10*	The perception of sharks in French Polynesia in the written media from 1996 to 2006	Z. Rowe, E. Clua, A. Goyaud, **C. Séguigne**	Supervision de Z. Rowe, Prépatation du manuscrit original, Relectures et corrections	Oceans	0.6	Première review
	Publication 11	Citizen science provides valuable data to evaluate elasmobranch diversity and trends throughout the French Polynesia's shark sanctuary	**C. Séguigne**, J. Mourier, E. Clua, N. Buray, S. Planes	Analyse de données, Visualisation de données, Préparation du manuscrit original, Relectures et corrections	PLOS ONE	3.752	Publié in 2023 (3 citations)

Tableau 1 : Présentation des articles sur lesquels sont basés cette thèse de Doctorat. Le statut de la publication et ma contribution en tant qu'auteure sont précisés.

SYNTHÈSE DES RÉSULTATS

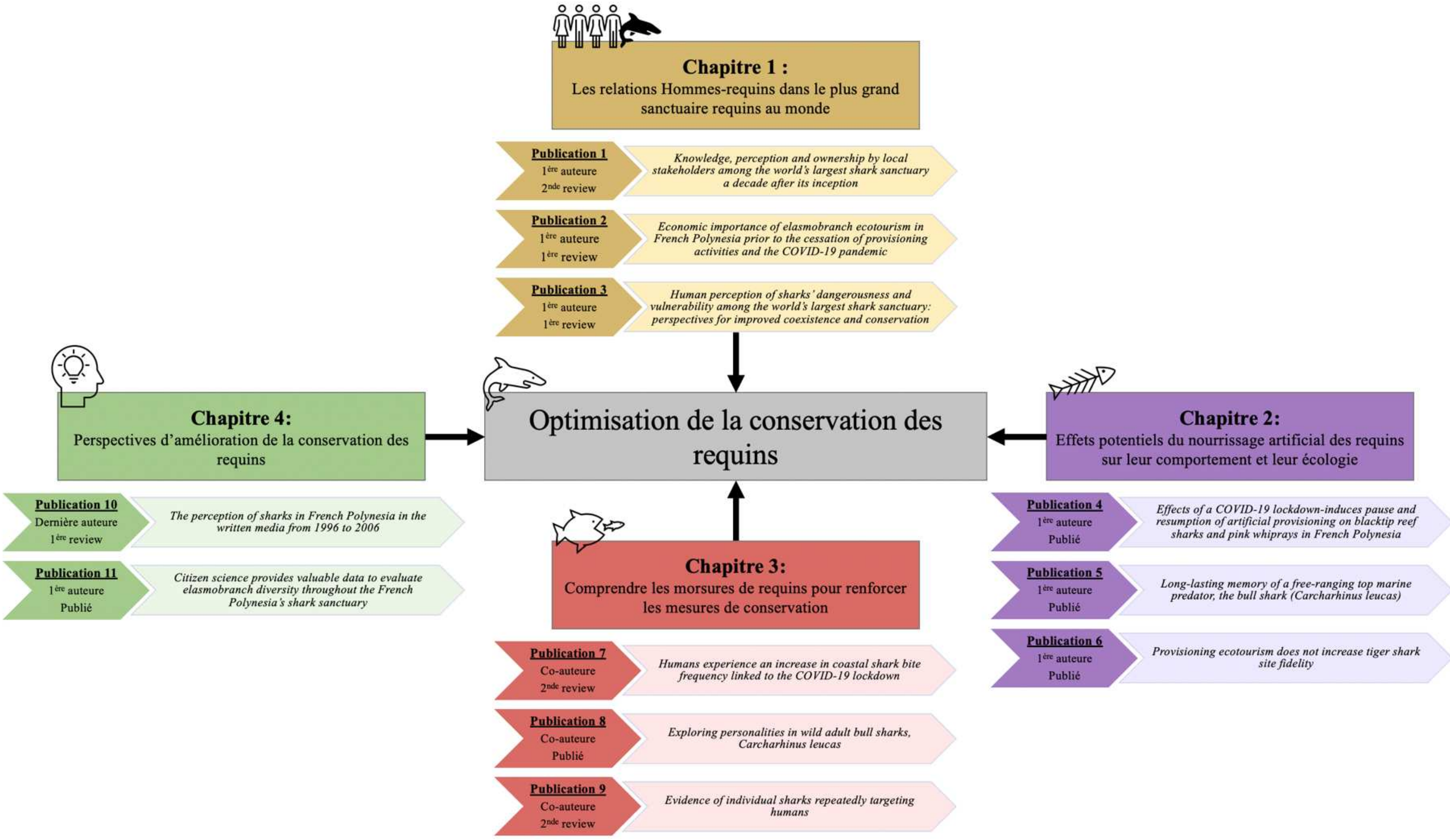

Figure 1 : Résumé de la structure de la thèse visant à optimiser la conservation des requins à travers une approche globale entre écologie, économie et socio-anthropologie

Toutes les publications issues de cette thèse de Doctorat, à la croisée de plusieurs champs disciplinaires, ont mis en lumière de nombreux obstacles rencontrés par les mesures de protection des requins, mais également des perspectives pour améliorer leur efficacité (*Figure 1*).

Le **Chapitre 1** montre que même au sein du plus grand sanctuaire requin au monde, de nombreuses personnes font preuve d'une volonté de tuer cet animal. Ce résultat peut être attribué à un manque de connaissance des mesures de protection en place, à la vision des requins comme des compétiteurs potentiellement dangereux, et au déclin des connaissances écologiques traditionnelles. De plus, leur importance économique majeure via l'écotourisme semble être ignorée, et les pratiques associées de nourrissage artificiel sont majoritairement critiquées.

Pourtant, les résultats présentés dans le **Chapitre 2** renforcent la possibilité de mettre en place un nourrissage artificiel durable, voire un « éco-appâtage ». En effet, malgré la forte résilience du conditionnement, expliquée par la forte capacité de rétention mémorielle des requins, aucune dépendance de ces animaux aux pratiques de nourrissage, ou aucune évolution temporelle significative de leur abondance ou de leur indice fidélité au site n'ont été observées.

Le **Chapitre 3** a fourni des explications concrètes aux incidents de morsures, qui pour la plupart ne sont marqués par aucune intention de consommation alimentaire, mais par une réponse à une situation particulière à laquelle l'animal fait face. Les morsures de prédation pourraient être majoritairement expliquées par l'existence de fortes différences dans les personnalités inter-individuelles, y compris au sein d'une même espèce. Certains requins, particulièrement audacieux, pourraient ainsi être considérés comme des « individus à problèmes » pour l'Homme. L'utilisation des techniques de photo-identification et de génétique via la collecte d'ADN nucléaire sur les blessures par morsure offrent d'importantes nouvelles opportunités pour la gestion éco-responsable de ces individus.

Les perspectives d'amélioration de la relation Homme-requin proposées dans le **Chapitre 4** permettent de repenser l'utilisation des médias en tant qu'outil de dissémination d'une information positive pour la conservation. Les sciences participatives sont également particulièrement prometteuses, puisqu'elles offrent une possibilité de transmission directe de connaissance entre science et société, et une réappropriation des mesures de protection en place par les populations humaines elles-mêmes.

DISCUSSION

1. Développer des connaissances écologiques et comportementales pour une meilleure relation Homme-requin

1.1 Sur l'impact des pratiques de nourrissage artificiel : Un "éco-appâtage" existe-t-il ?

Ce travail a souligné l'importance de la collecte d'informations écologiques et comportementales sur les requins. En effet, il est crucial de comprendre quelles menaces impactent majoritairement leur écologie. Les résultats obtenus dans cette thèse rejoignent un corpus grandissant de résultats montrant que la polémique autour du nourrissage artificiel ne devrait pas être une priorité de la conservation des requins, du fait des dommages considérables générés par les pêcheries (Healy et al. 2020). Cependant, il est impératif de considérer les caractéristiques écologiques des espèces cibles, puisque les impacts potentiels des pratiques touristiques pourraient dépendre fortement de la mobilité naturelle des requins. Des espèces hautement migratrices pourraient être plus difficile à fidéliser sur les sites d'appâtage que les espèces résidentes. Par exemple, les requins tigres (*Galeocerdo cuvier*) (*Publication 6*, Hammerschlag et al. 2012a), les grands requins blancs (*Carcharodon carcharias*) (Laroche et al. 2007, Becerill-Garcia et al. 2019, Becerill-Garcia et al. 2020) ou les requins bouledogues (*Carcharhinus leucas*) (Brunnschweiler & Barnett 2013), associés à de hauts niveaux de mobilité et de variation dans leurs patterns de déplacement, n'ont présenté aucune variabilité temporelle significative concernant leur résidence aux sites de nourrissage. À l'inverse, d'autres espèces, comme le requin citron faucille (*Negaprion acutidens*) (Clua et al. 2010, Clua 2018) ou le requin à pointes noires (*Carcharhinus melanopterus*) (Mourier et al. 2021) ont montré une augmentation de leur indice de fidélité au site dans le temps. Cependant, il est important de remarquer que cette même population de requins à pointes noires n'a fait preuve d'aucune dépendance à l'appâtage, puisque les animaux ont complètement déserté le site de Tiahura dès le premier jour de l'arrêt des activités de nourrissage à la suite du confinement COVID-19, comme prouvé par des survols de drones (*Publication 4*). Ce résultat renforce celui déjà obtenu pour une autre espèce hautement résidente, le requin corail (*Triaenodon obesus*), pour lequel les appâts consommés sur les sites touristiques ne représentent pas leur source de nourriture principale (Abrantes et al. 2018). D'autres recherches sont requises pour comprendre plus profondément quelles techniques d'appâtage minimisent les impacts sur une espèce cible donnée, afin de réellement promouvoir un « éco-nourrissage » pour les requins.

Les effets négatifs ou neutres du nourrissage artificiel des requins sont souvent mis en avant. Néanmoins, à l'exception d'un intérêt économique significatif, d'autres effets positifs potentiels restent à étudier afin d'assurer une meilleure reconnaissance de la valeur non-consommatrice de ces animaux. En effet, des effets positifs ont déjà été observés chez d'autres espèces, et la supplémentation alimentaire a même joué un rôle direct dans certains programmes de conservation, comme pour la crécerelle de Maurice (*Falco punctatus*), en danger (Jones et al. 1995), ou pour l'autour des palombes (*Accipiter gentilis*) (Ward & Kennedy 1996). Le travail mené pendant cette thèse aux Fidji sur les requins bouledogues (*Carcharhinus leucas*) a permis de proposer l'hypothèse que l'appâtage pourrait détourner les requins des pêcheries. En effet, lors de la reprise des activités touristiques, après plus d'un an de confinement lié à la COVID-19, une augmentation significative du nombre d'hameçons a été observée sur les requins préalablement photo-identifiés (*Publication 5*, T. Vignaud & C. Séguigne pers. obs.). Cela pourrait suggérer que leurs interactions avec les pêcheurs se sont intensifiées pendant l'arrêt des pratiques touristiques. Les requins sont des animaux particulièrement opportunistes, et les déplacements de nombreuses espèces semblent s'expliquer par la disponibilité alimentaire ou les agrégations de proies, comme pour le requin bouledogue (*Carcharhinus leucas*) (Motta & Wilga 2001, Brunnschweiler & Barnett 2013, Espinoza et al. 2016), ou le requin tigre (*Galeocerdo cuvier*) (Meyer et al. 2009). De plus, ces animaux ont souvent été observés en action de déprédation sur des bateaux de pêche, et sont ainsi à risque d'être capturés volontairement ou accidentellement (Mitchell et al. 2018, Malara et al. 2021). Ainsi, le développement de sites de nourrissage artificiel fixes et suivis pourrait permettre de maintenir les requins à distance de leur principale menace, particulièrement dans les zones où aucune mesure de protection n'est implémentée.

La Polynésie Française est considérée comme le plus grand sanctuaire requin au monde (Clua et al. 2018) et a ouvert la voie au développement de mesures de protections similaires dans le Pacifique. Cependant, la mesure d'interdiction de l'appâtage de 2017 contribue à la stigmatisation du tourisme d'observation des requins (*Publication 3*). Cela entraîne également le risque d'une perte économique majeure pour le pays, particulièrement concernant les pratiques lagonaires (*Publication 2*). Cette interdiction est en phase avec un mouvement éthique moderne, généralement davantage attribué aux Occidentaux, qui considère la protection de la nature comme plus efficiente si tout lien avec l'Homme est brisé (Bruckner 2013). Cet écologisme rejette à la fois les doctrines capitalistes et socialistes, et souligne le profond dégoût de l'humanité envers elle-même, tenue pour responsable de l'ensemble des menaces à laquelle une vision idéalisée de la Nature fait face (Bruckner 2013). Ce pathos n'est pas une solution, puisque les mesures de conservation ne peuvent être efficaces que si l'Humanité se reconnecte réellement avec la Nature et restaure une réelle harmonie entre la Société et l'Environnement, comme le promeut le développement durable (Dogaru 2013, Dogaru 2021, Mikhno et al. 2021). De plus, dans le cas de la Polynésie Française, une telle interdiction est finalement liée à une profonde déliquescence des croyances traditionnelles culturelles, alors que les cultures ancestrales Océaniennes et la Nature sont généralement considérées comme symbiotiques (*Publication 1*, Kana'iaupuni & Malone 2006, Fisher 2015, Clua and Guiart 2020).

1.2 Sur les évènements de morsures : Comment mieux comprendre les motivations des requins ?

Il est intéressant de constater le manque de compréhension des incidents de morsures à l'échelle mondiale, notamment en Polynésie Française. Toutes les morsures rapportées depuis l'interdiction du nourrissage artificiel de 2017 ont été systématiquement reconnues comme une conséquence directe de cette pratique par les populations locales (C. Séguigne, pers. obs.). Cependant, les deux seules morsures de prédation – qui auraient pu être fatales – de Polynésie Française, attribuées à un requin longimane (*Carcharhinus longimanus*) lors d'une sortie d'observation des baleines (Clua et al. 2021), ainsi qu'à un requin tigre (*Galeocerdo cuvier*) lors du contrôle quotidien d'une ferme aquacole (Clua et al. 2023) se sont toutes deux produites après l'interdiction, dans des contextes n'incluant aucun stimulus olfactif artificiel et à distance des anciennes zones de nourrissage. De plus, l'augmentation des morsures de dominance à la suite de la réouverture des activités nautiques à la suite du déconfinement de la COVID-19 a mis en avant l'importance de partager l'environnement marin dans le respect des requins afin d'assurer notre propre sécurité (*Publication 7*). L'appâtage artificiel peut ainsi présenter un intérêt majeur pour l'habituation des requins à la présence humaine, définie comme une décroissance graduelle des réponses négatives de ces animaux face aux plongeurs (Bejder et al. 2009). Loin d'augmenter le risque de morsure, cela peut également représenter une opportunité d'entraîner la satiété d'espèces pouvant présenter des « individus à problèmes » au sein de leurs populations, la faim étant l'une des motivations principales des morsures de prédation (Klimley & Curtis 2006).

Il est important de rappeler que la plupart des morsures ne sont pas liées à une volonté de prédater l'Homme, mais plutôt à une réponse à un contexte bien précis, comme la compétition avec un chasseur sous-marin souhaitant défendre sa prise face à un requin (*Publication 7*). Cette séparation par motivation des morsures diffère profondément de celle utilisée par l'ISAF (International Shark Attack File), qui distingue les morsures « provoquées », où les requins sont significativement stimulés par des nageurs, des plongeurs ou des pêcheurs, des morsures « non provoquées » sur des victimes innocentes pratiquant une activité qui n'est pas destinée à entrainer la moindre réaction de la part des requins (Schultz 1967). L'exemple de la morsure non létale d'un requin citron faucille (*Negaprion acutidens*) sur un surfeur sur l'île de Makemo (Polynésie Française) (Clua & Haguenauer 2019), aurait pu être caractérisée de « non provoquée » selon l'ISAF, mais a été reliée à une motivation de « dominance ». Ainsi, bien que le stimulus envoyé par la victime soit souvent généré inconsciemment, ces évènements n'en restent pas moins « provoqués », puisqu'un déclencheur humain est la cause de la réaction du requin. Dans ce cas, le terme « attaque », souvent utilisé par les médias, ne semble pas objectif, puisque le requin à lui seul ne pourrait être tenu responsable de l'incident (Neff & Hueter 2013). Une autre théorie populaire à propos des morsures de requins sur l'homme peut être mise à mal si la classification motivationnelle des morsures est considérée comme judicieuse. L'« hypothèse de l'erreur » explique que les requins pourraient confondre les humains avec leurs proies naturelles (Ryan et al. 2021). Dans ce cas, le risque de morsure serait directement lié au nombre de personnes en contact avec les requins dans l'océan. Cependant, la situation mise en avant en Polynésie Française à la suite de l'Anthropause de la COVID-19 ne peut être expliquée par l'« erreur », puisque le nombre de morsures a significativement augmenté malgré une présence humaine hautement réduite en mer (*Publication 7*). Cette étude apporte une autre pierre à la réfutation de cette théorie, potentiellement dangereuse en termes de perception du risque requin, et renforce les observations marquant le caractère superficiel de la plupart des morsures, qui ne peuvent correspondre à une motivation de prédation (Ritter & Quester 2016, Clua & Meyer 2023).

1.3 Sur la personnalité des requins et leurs capacités cognitives : les requins sont-ils des animaux intelligents ?

Une preuve supplémentaire à l'existence de personnalités au sein de populations de requins a été apportée par l'étude des requins bouledogues (*Carcharhinus leucas*) fréquentant le récif de Yakawe aux Fidji. En effet, ce travail démontre l'existence de comportements significativement différents entre les individus étudiés, particulièrement en ce qui concerne le continuum « témérité-timidité ». Cela satisfait le premier des trois critères définissant l'existence de personnalités au sein d'une population (*Publication 8*). Pour totalement valider de possibles « individualités » chez les animaux, il convient également de confirmer la répétabilité de ces traits comportementaux dans le temps et selon différents contextes, ainsi que leur héritabilité (Réale et al. 2007, Gervais et al. 2020). Cependant, ce travail représente une première étape sans précédent, puisqu'il a permis l'étude d'une population adulte sauvage, alors que la plupart des études ont été effectuées en captivité ou semi-captivité, ou sur des juvéniles (Finger et al. 2017). Les résultats concordent avec ceux de précédentes études concernant l'hypothèse de la personnalité, qui ont notamment souligné la forte répétabilité des différences individuelles en termes d'audace et de réaction au stress chez le requin de Port Jackson (*Heterodontus portusjacksoni*), la répétabilité des traits sociaux chez la petite roussette (*Scyliorhinus canicula*), mais également leur stabilité à court et long terme pour des requins citron juvéniles (*Negaprion brevirostris*). Ainsi, les morsures de prédation sur l'Homme pourraient être expliquées par l'existence d'individus présentant des personnalités particulièrement audacieuses et exploratrices chez les requins (Clua & Linnell 2018), comme cela a été démontré pour d'autres prédateurs marins tels les ours polaires (*Ursus maritimus*) (Towns et al. 2009) ou les phoques gris (*Halichoerus grypus*) (Graham et al. 2011).

Un résultat important et inattendu a été obtenu lors de cette thèse grâce à la pandémie COVID-19, ayant offert des opportunités sans précédent pour l'étude du comportement de la vie sauvage lors d'une Anthropause mondiale (Bates et al. 2020, Rutz et al. 2020). En effet, l'appâtage a complètement cessé sur l'ensemble des sites touristiques de la planète. Il a donc été possible de déterminer la résilience du conditionnement, directement liée à la capacité de rétention mémorielle des requins. Les requins à pointes noires (*Carcharhinus melanopterus*) et les requins bouledogue (*Carcharhinus leucas*) ont été capables de revenir dès la reprise des activités de nourrissage, respectivement après 6 semaines et plus d'un an de fermeture (*Publication 4*, *Publication 5*). Ces résultats concordent avec de précédentes études menées en environnement captif ou semi-captif, montrant une capacité de rétention mémorielle excédent potentiellement 40 jours pour des requins de Port Jackson juvéniles (*Heterodontus portusjacksoni*) (Guttridge & Brown 2014), 10 à 12 semaines pour des requins citron adultes ou juvéniles (*Negaprion brevirostris*) (Clark 1959, Heinrich et al. 2021), et plus de 50 semaines pour des requins-chabot gris juvéniles (*Chiloscyllium griseum*) (Fuss & Schluessel 2015). Ces importantes capacités suggèrent une cognition forte chez les deux espèces de requins étudiées. Ce résultat est corroboré par le fait que de plus gros cerveaux sont généralement observés chez les requins évoluant dans des habitats complexes, tels les récifs coralliens, et montrant des hauts degrés de sociabilité (Yopak et al. 2012, Yopak & Lisney 2012). Les différences en termes de retour aux abondances de « *business as usual* » peuvent être attribués aux écologies respectives du requin bouledogue et du requin pointes noires. En effet, le premier est un prédateur apical, et le second un mésoprédateur (Roff et al. 2016). Puisque le requin pointes noires peut être prédaté, y compris par des requins plus gros, ils ont potentiellement besoin de davantage d'énergie pour éviter la prédation. En comparaison, les requins bouledogue pourraient avoir plus d'énergie à allouer à la recherche alimentaire, expliquant leur retour plus rapide sur le site de nourrissage, malgré un temps plus long de confinement. De tels *trade-offs* pour assurer une meilleure fitness sont également observés chez d'autres mésoprédateurs comme les tarpons (*Megalops atlanticus*), faisant un compromis entre l'assimilation de nourriture, au risque de rencontrer des requins bouledogue (*Carcharhinus leucas*), et l'osmorégulation, très énergivore, leur permettant de réduire le risque de prédation (Hammerschalg et al. 2012b). Bien qu'aucune information ne soit aujourd'hui disponible concernant le lien entre personnalité et cognition chez les requins, ces deux caractéristiques pourraient fortement influencer leur fitness. En effet, les animaux d'une même population répondront différemment à des situations pouvant affecter leur survie ou leur capacité reproductive (Brown & Schluessel 2023). De plus, ces deux attributs peuvent être importants à mettre en avant pour une meilleure perception humaine, et ainsi pour la conservation. En effet, le requin pourrait passer d'une image de tueur instinctif à une image dépeignant un individu unique parmi d'autres, doté d'une intelligence comparable à celle des mammifères ou des oiseaux (Finger et al. 2017, Brown & Schluessel 2023). Une nouvelle image de ces animaux par le grand public pourrait permettre de changer les perception négatives en perceptions plus positives et objectives. Puisse notre travail contribuer à ce processus d'importance capitale pour les années à venir.

2. Importance de proposer des lignes directrices pour améliorer la relation Homme-requin

2.1 Pour améliorer la gestion du risqué requin

L'occurrence et la fréquence d'évènements de morsure menace la conservation des requins, puisque chaque incident peut être suivi par l'amplification des perceptions négatives et de la peur ressentie envers ces animaux (Lucrezi et al. 2019). Ainsi, une meilleure compréhension des motivations (*Publication 7*), des causes (*Publication 8*), ainsi que le développement d'outils de suivi efficaces (*Publication 9*), peuvent apporter de nouvelles solutions bénéfiques pour la relation Homme-requin. Étant donné l'existence d'individus à problèmes, une question majeure persiste quant à leur gestion durable et efficace. En effet, il semble que ces animaux puissent présenter une propension au récidivisme, et pourraient ainsi continuer à présenter un risque pour les humains (*Publication 9*). Ces résultats permettent d'envisager deux moyens possibles de gérer le risque : par la prévention de l'occurrence d'évènements de morsure, ou par action sur l'animal « à problèmes ». Deux technologies ont été développées pour tenter de prévenir les morsures. La première repose sur l'utilisation d'une fibre spécifique pour renforcer la résistance des tissus néoprènes. Bien qu'elle soit efficace pour réduire les pertes de sang après une morsure, elles ne sauraient complètement protéger le porteur d'une morsure de prédation, particulièrement si le requin est de grande taille (Whitmarsh et al. 2019). Une autre approche repose sur l'utilisation de « répulsifs de requins », qu'ils soient personnels ou utilisés comme une barrière. Le concept repose sur l'hyperactivation des ampoules de Lorenzini – les électro-récepteurs des requins – avec des pulsations électriques, afin de les détourner du porteur. Malgré des résultats initiaux prometteurs ayant permis l'exclusion d'une espèce ciblée d'une zone définie (O'Connell et al. 2014, O'Connell et al. 2018), l'effet répulsif semble différer significativement en fonction des systèmes utilisés, mais aussi en fonction de l'état motivationnel du requin (Huveneers et al. 2013, Huveneers et al. 2018).

Concernant le contrôle direct d'animaux potentiellement à risque, il n'existe aujourd'hui que très peu de méthodes permettant l'extraction sélective des individus à problèmes. En effet, des alternatives aux pêches punitives, comme l'implémentation de drumlines SMART (*Shark Management Alert in Real Time*), permettent l'extraction d'espèces potentiellement dangereuses, sans pour autant cibler des requins « plus dangereux que la moyenne ». De plus, et malheureusement, des captures accidentelles et de la mortalité impliquant des espèces en danger non visées peuvent se produire (Guyomard et al. 2019). Une solution possible réside en des campagnes de pêche sélective sur des individus ayant déjà perpétré des morsures de prédation sur l'Homme (Clua et al. 2020). La méthode implique la collecte d'ADN issu de la morsure sur la victime, et l'exécution d'un *« fingerprinting »*, c'est-à-dire le séquençage de l'ADN nucléaire individuel du mordeur (*Publication 9*, Stock et al. 2017, Fotedar et al. 2019, Clua et al. 2020). Les résultats obtenus seront comparés avec les données génétiques précédemment collectées grâce à la création d'une large base de données listant l'ensemble des requins présents dans une zone spécifique. Si une correspondance est observée, ce catalogue permet de trouver l'animal coupable grâce à ses caractéristiques morphologiques mises en évidence par la photo-identification (Clua & Linnell 2018, Clua et al. 2020). Néanmoins, ce projet ambitieux requière une collaboration totale entre les chercheurs, les décideurs, les pêcheurs et les autres usagers de la mer, afin de construire la base de données la plus exhaustive possible. Elle permet également l'implication de différentes parties prenantes dans la recherche de l'individu à problèmes identifié. Cette dynamique de coopération est cependant aussi prometteuse que complexe à instaurer.

Afin d'établir une compréhension de la singularité de cet animal, ainsi qu'un respect pour les populations de requins sauvages par le grand public, le futur des individus à problèmes identifiés doit être déterminé dans un esprit d'éthique et de discussions mutuelles. En effet, un autre obstacle au développement de ce projet pourrait résider dans le conflit « humain-humain », toujours plus présent sur le sujet des requins (Simpfendorfer et al. 2021b). Bien que la peur reste dominante dans les populations humaines, un nombre accru de personnes semble être opposé à toute campagne impliquant l'élimination d'un ou plusieurs animaux (Pepin-Neff &

Wynter 2017, Le Busque et al. 2021, Casola et al. 2022). Ainsi, de plus amples recherches visant à confirmer ou réfuter l'hypothèse de la personnalité ont besoin d'être urgemment conduites, particulièrement en ce qui concerne l'hérédité potentielle des comportements « déviants », qui reste aujourd'hui largement inexplorée chez les requins (Finger et al. 2017). En effet, l'approche la plus efficace pour la conservation pourrait être différente en fonction des résultats obtenus. Dans le cas avéré de l'existence d'une personnalité avec une forte probabilité de transmission verticale, il pourrait être plus efficace et durable d'éliminer un seul animal, plutôt que de multiplier le risque, augmentant potentiellement la perception négative de la dangerosité des requins. Si l'émergence de traits déviants se produit aléatoirement, l'utilisation de protocoles de télémétrie liés à des systèmes d'alerte (McAuley et al. 2016) pour des individus bien définis pourrait être une approche plus éthique rencontrant davantage d'approbation sociale. Finalement, la méthode de gestion du risque à employer doit impérativement être en ligne avec le danger réel encouru, avec les menaces locales auxquelles les requins font face, ainsi qu'avec les connaissances et recommandations scientifiques les plus récentes.

2.2 Pour assurer une sécurité optimisée lors des opérations écotouristiques

Bien que le tourisme utilisant l'appâtage puisse être une aide solide pour promouvoir la valeur non-consommatrice des requins (*Publication 2*, Clua et al. 2011, Vianna et al. 2011, Vianna et al. 2012, Cisneros-Montemayor et al. 2013, Anna & Saputra 2017) et présente le potentiel d'être durable (*Publication 4, Publication 5, Publication 6*, Hammerschlag et al. 2012a, Brunnschweiler & Barnett 2013, Becerill-Garcia et al. 2019, Becerill-Garcia et al. 2020), la forte proximité des humains avec ces animaux peut induire des impacts sur leur écologie ou sur la sécurité des participants en cas de gestion non optimale. La démonstration du haut degré de rétention d'un conditionnement chez les requins (*Publication 4*, *Publication 5*) affaiblit également l'idée que ces animaux puissent être « déshabitués » au nourrissage artificiel via l'implémentation de périodes d'arrêt de la pratique, comme souvent proposé (Newsome et al. 2004, Buray 2015, Clua 2018). Ainsi, il serait plus judicieux de concentrer les efforts sur la création de règles concrètes, qui pourront également s'adapter avec l'évolution des connaissances scientifiques. En effet, aucun code de conduite standardisé n'est aujourd'hui disponible pour les opérateurs écotouristiques. Cependant, des évidences grandissantes montrent les impacts négatifs de certaines pratiques. Bien que l'interdiction de l'appâtage ne soit pas la meilleure solution, il est maintenant impératif d'assurer la durabilité et la sécurité de cette pratique, tant pour les humains que pour les requins, afin de la rendre pérenne et mieux acceptée.

Les requins, avec leurs capacités cognitives développées, peuvent associer plusieurs stimuli, le premier étant olfactif dans le contexte du nourrissage artificiel, lié à la récompense potentielle issue de l'appât (Brown & Schluessel 2023). Le second stimulus pouvant potentiellement créer un lien entre humains et nourriture est principalement considéré comme auditif ou visuel, bien que d'autres sens puissent être également responsables de cette association. En effet, des études précédentes ont révélé que les animaux conditionnés à l'appâtage pouvaient également réagir à des signaux sonores, comme démontré pour les requins de Port-Jackson

(*Heterodontus portusjacksoni*) (Vila Pouca & Brown 2018). Ce phénomène a également été observé chez les requins à pointes noires sauvages (*Carcharinus melanopterus*) ou chez les grands requins blancs (*Carcharodon carcharias*), arrivant sur le site de nourrissage à l'instant où les bruits des moteurs de bateau pouvaient être entendus (*Publication 4*, Bruce & Bradford 2013). D'autre part, des comportements d'évitement ont été observés chez des requins baleines (*Rhincodon typus*) présents de manière naturelle pour se nourrir, sans appâtage, bien qu'habitués à une présence régulière de snorkeleurs. En effet, ils ont été observés fuyant la zone si des bruits excessifs de nage ou de sauts étaient générés par les nageurs (Araujo et al. 2017). Dans d'autres circonstances, ces sons induits par l'Homme pourraient également induire un comportement attractif, particulièrement si une récompense est délivrée. Ainsi, comme proposé dans la *Publication 4*, il semble important de sensibiliser les clients et les guides à une approche respectueuse des animaux, en évitant des mises à l'eau avec de nombreuses éclaboussures, ainsi qu'un palmage bruyant lors des nages.

Parmi les éléments visuels susceptibles d'affecter la sécurité des touristes, tenir et distribuer la nourriture directement à la main apparaît être une pratique particulièrement à risque. En effet, les requins peuvent associer les mains du donneur – ou même des autres plongeurs – à une source de nourriture potentielle, spécialement quand un mouvement d'agitation du bras est effectué pour attirer l'attention des animaux ciblés (Clua & Torrente 2015). Ainsi, ces pratiques de nourrissage à la main peuvent faciliter le comportement de « mendicité », à la fois envers le donneur et les autres plongeurs, et peut générer des comportements agressifs comme déjà observé chez d'autres taxa (Zhao & Deng 1992, Orams 2002, Christiansen et al. 2016, Sen Majumder et al. 2016). Par conséquent, il semble sage de minimiser ces risques d'association négative en préférant placer l'appât directement dans les crevasses du récif tout en maintenant une distance conservative pour l'observation (Clua 2018). De plus, les guides distribuant la nourriture à la main présentent souvent leur peau en contact direct avec le poisson. Cela peut renforcer la maladresse des requins, puisque certaines espèces ne montrent qu'une vision monochromatique (Van Eyk et al. 2011). Ainsi, des gants de protection qui contrastent avec la couleur de la chair du poisson pourrait protéger leur porteur contre des morsures potentielles dans le cas où le nourrissage à la main soit nécessaire. Un autre élément d'origine visuelle, se produisant également dans des situations non appâtées, peut augmenter le risque d'interactions négatives avec les requins : les gens isolés en marge d'un groupe. En effet, une importante proportion de morsures se sont déjà produites dans ce scénario (Neff 2012, Lagabrielle et al. 2018, Clua et al. 2021), malgré la présence d'autres personnes dans l'eau. Ainsi, il est capital de favoriser des petits groupes d'observation de requins, dans lesquels la cohésion est plus facile à maintenir par le guide, particulièrement concernant les activités de snorkeling. Pour les activités de plongée sous-marine, renforcer la notion de binôme est essentiel.

L'appâtage en surface est une pratique particulièrement risquée, puisqu'elle combine ces deux stimuli tout en encourageant les requins à engager des mouvements verticaux. De plus, le comportement agonistique peut

être directement lié au contexte spatial chez les poissons (Bolyard & Rowland 1996). De nombreux requins, habitués à se nourrir sur ou proche du fond, pourraient ainsi être plus agressifs (Clua 2018). De plus, le nourrissage en surface augmente la compétition entre les prédateurs présents, en développant de potentielles réactions négatives envers d'autres animaux – incluant les humains – ou même envers des engins inertes comme les bateaux (Nelson & Johnson 1980, Clua et al. 2013). Cela renforce l'importance de développer un système de nourrissage qui soit complètement adapté à l'écologie des espèces ciblées, et ainsi de favoriser un nourrissage proche du fond pour les espèces récifales, comme déjà démontré chez le requin citron faucille (*Negaprion actutidens*) (Clua 2018).
Malgré des visites quotidiennes sur des sites où les requins présentent une forte probabilité d'être observés, aucune formation concernant la bonne conduite à adopter dans le cadre d'une rencontre n'est généralement légalement requise pour les guides de plongée ou de snorkeling (C. Séguigne, pers. obs.). Par conséquent, et malgré leurs compétences, ils sont souvent incapables de reconnaître l'apparition d'un comportement agonistique, bien que des éthogrammes particulièrement précis décrivant les comportements des requins soient disponibles (Klimley et al. 2023). Dans le contexte d'activités plus à risque, il pourrait être intéressant d'offrir une formation spécifique aux guides pour maximiser la sécurité en réduisant le risque de morsures via l'acquisition d'une meilleure expertise. Les activités concernées pourraient inclure l'observation des baleines, où les espèces rencontrées sont souvent pélagiques et de grande taille, comme le requin longimane (*Carcharhinus longimanus*), souvent associé aux mammifères marins (Clua et al. 2021). Elles peuvent également intégrer les activités d'appâtage, où la distance Homme-requin est volontairement réduite (Topelko & Dearden 2005, Gallagher et al. 2015). Certains pays offrent déjà ce type de mesures, via la création de permis spéciaux pour les opérateurs touristiques, notamment dans le cadre des activités de plongée en cage au contact des grands requins blancs (*Carcharodon carcharias*) en Australie, Afrique du Sud ou Nouvelle Zélande (Bruce & Tasmania 2015, Richards et al. 2015). De plus, le code de conduite établi doit être strictement respecté, puisque les opérateurs sont complètement responsables de tout évènement se produisant lors de l'activité, et peuvent être punis dans le cas de non-conformité (Catlin et al. 2012, Smith et al. 2014).

Les décisions de bannir toute activité de nourrissage artificiel semblent être associées avec une réduction drastique du nombre d'animaux observés par les plongeurs, et même potentiellement à leur totale disparition du site (*Publication 4*, *Publication 5*). Afin de continuer à satisfaire les participants, les opérateurs touristiques pourraient être tentés de poursuivre leurs activités illégalement, laissant libre court à des pratiques totalement anarchiques, générant de forts risques d'incidents (*Publication 3*, Healy et al. 2020). Cette vision éducative, liée à une meilleure formation des responsables de la plongée et du snorkeling, au respect d'un code de conduite et/ou à l'obtention d'un permis spécifique pourrait être préférée à des arrêts totaux de la pratique, puisque les professionnels du tourisme sont ici directement impliqués dans la sécurité des participants et des requins.

3. Nécessité d'activement communiquer, collaborer et éduquer pour une meilleure conservation des requins

3.1 Pour combattre les biais cognitifs dans les médias

La représentation des requins dans les médias écrits de Polynésie Française est majoritairement positive, ce qui contraste fortement avec l'image anxiogène décrite dans les journaux américains ou australiens (Philpott 2002, Muter et al. 2013). Cependant, le récent déclin des connaissances écologiques traditionnelles (*Publication 1*) montre que la vision spirituelle des requins, caractéristique des cultures ancestrales, ne peut expliquer à elle seule cette différence de traitement médiatique. Cela pourrait plutôt être attribué au contact direct que les habitants de Polynésie Française ont avec les populations de requins sauvages. En effet, la création d'un lien homme-requin apporte une base solide pour acquérir des connaissances sur ces animaux, ce qui offre une tolérance plus importante à leur existence (McClellan et al. 2016, Acuña-Marrero et al. 2018, Afonso et al. 2020). Un processus similaire a déjà été observé pour d'autres prédateurs terrestres, comme les alligators d'Amérique (*Alligator mississippiensis*) (Skupien et al. 2016) ou les ours bruns (*Ursus arctos*) (Johansson et al. 2019). Pour permettre à un plus grand nombre de personnes de rencontrer des requins, il pourrait être envisagé de promouvoir leur observation dans des aquariums publics, qui ont déjà démontré leur utilité pour sensibiliser à leur conservation (Friedrich et al. 2014).

Malgré la vision majoritairement positive des requins dans les médias de Polynésie Française, quelques réserves importantes doivent être émises. En effet, les incidents de morsure sont toujours largement qualifiés d' « attaques », avec 100% des articles étudiés rapportant ces évènements en employant ce terme (*Publication 10*). Cette observation est similaire avec celles faites dans la plupart des médias mondiaux, menant à l'usage très répandu de cette expression trompeuse et émotionnellement chargée (Neff & Hueter 2013, McCagh et al. 2015, Pepin-Neff 2019, Giovos et al. 2021). Ainsi, les journalistes devraient être sensibilisés aux implications qu'entraîne l'emploi de ces mots particulièrement forts, même dans le contexte de morsures superficielles (Pepin-Neff 2019). Une première tentative de mieux définir les interactions négatives entre l'Homme et le requin a été proposée, basée sur la catégorisation des morsures de l'ISAF, dissociant les « rencontres » des « attaques provoquées » ou « non provoquées » (Le Busque et al. 2019). Pourtant, cet effort initial de mieux décrire les interactions Homme-requin peut également présenter des biais et pourrait évoluer vers une classification motivationnelle des incidents, comme décrit dans ce travail doctoral (*Publication 7*). Bien que les termes utilisés dans les médias écrits requièrent une attention particulière, l'impact sur les spectateurs des éléments visuels et audios, comme les photographies ou les bandes sonores, ne doit pas être ignoré (Nosal et al. 2016, Bombieri et al. 2018).

D'autre part, le discours majoritairement positif relayé par les médias écrits de Polynésie Française ne correspond pas à la perception des populations locales, avec près la moitié des sondés indiquant que les requins sont des animaux dangereux pour les humains (*Publication 3*). De plus, *La Dépêche de Tahiti* a également échoué à apporter des informations quant aux implications de la sanctuarisation des eaux polynésiennes (*Publication 1*). Cet échec peut s'expliquer par une transmission de l'information principalement orale dans les sociétés polynésiennes, qui pourrait avoir persisté au cours du temps, principalement dans les zones reculées (Babadzan 1985, King et al. 2007, Mateata-Allain 2009, Pearce et al. 2010). Ainsi, les organisation à but non lucratif (ONGs) locales pourraient jouer un rôle majeur dans la communication direct de la science à travers des campagnes de sensibilisation, et pourraient être un bon complément aux approches médiatiques classiques. Par exemple, la communication sur une espèce en danger, le requin baleine (*Rhincodon typus*), a été assurée avec succès aux Philippines grâce à une véritable synergie entre des conférences données par une association et des programmes télévisuels (Aca 2016). Cependant, les représentants des associations doivent être vigilants à disséminer des connaissances scientifiquement validées, en tant que médiateurs entre recherche et société. En effet, de petits groupes d'organisations à but non lucratifs ont déjà été pris à déformer le discours des chercheurs, tout en prétendant utiliser des arguments basés sur la science (Schiffman et al. 2021). Cela peut être particulièrement déroutant pour le grand public, et peut potentiellement conduire à un désintérêt pour la conservation des requins.

Une autre explication de la non-connaissance des implications du sanctuaire peut résider dans la portée limitée des médias écrits, qui ne peuvent s'exporter dans toutes les îles de Polynésie Française. En effet, ce territoire couvre 5.5 millions de km^2, avec des îles particulièrement éloignées de Tahiti, certaines n'étant desservies que par bateau pour le transport de fret (C. Séguigne, pers. obs.). Ainsi, l'accès à d'autres types de médias audiovisuels ou digitaux pourrait être plus aisé, bien que beaucoup d'entre eux reflètent encore une image des requins particulièrement négative. Cela a été mis en avant pour de nombreux films (Le Busque & Litchfield 2022) ou sur Facebook (Le Busque et al. 2019). Pourtant, les réseaux sociaux peuvent présenter des perspectives intéressantes, avec une influence potentiellement positive pour la conservation des requins via Youtube, présentant une grande quantité de messages positifs (Beall et al. 2022, Casola et al. 2022), mais également Twitter, où les documentaires diffusés pendant la *Shark Week* génèrent beaucoup d'enthousiasme (O'Donnell 2019). Cette catégorie de films et ce type d'évènement peut également offrir l'opportunité de disséminer de la connaissance sur les requins d'une manière divertissante et peut ainsi être extrêmement utile, tant que des documentaires non-factuels ou déformant la réalité ne sont pas mis en avant (O'Bryhim & Parsons 2015, O'Donnell 2019).

Ainsi, la promotion de la conservation des requins est liée à la dissémination d'un contenu médiatique non-biasé, non-sensationnalisé et exact, afin de permettre la création durable d'un comportement en faveur de la conservation du requin chez le grand public. Afin de réaliser cet objectif, il est important de combattre l'extrême dualité des messages qui peut exister entre science et médias. En effet, celle-ci peut créer un véritable paradoxe émotionnel vis-à-vis de ces animaux (Neff 2015, McCagh et al. 2015), et être l'initiateur d'un conflit « Homme-Homme » particulièrement délétère aux initiatives de protection des requins

(Simpfendorfer et al. 2021b). En effet, les scientifiques semblent être de moins en moins associés au discours médiatique, y compris quand il concerne des sujets de recherche (Hardiman et al. 2019). Afin d'assurer la fiabilité des propos mis en avant, de combattre les biais cognitifs, et de servir les politiques de protection environnementales en place, il semble crucial de ré-établir une connexion privilégiée entre scientifiques, décideurs et journalistes. En Polynésie Française, ce type de synergie peut être observé chez un autre taxon, les baleines à bosses (*Megaptera novaeangliae*). De nombreux contenus concernant l'écologie de ces animaux ainsi que les conduites à tenir lors d'une rencontre afin d'éviter le dérangement et d'assurer sa propre sécurité sont accessibles dans de nombreux médias (radio, télévision, presse, réseaux sociaux) (C. Séguigne, pers. obs.). Cela peut également être envisagé pour les requins. En effet, au cours des siècles passés, la perception générale des mammifères marins était fortement négative. Ces animaux étaient diabolisés et considérés comme très dangereux pour les usagers de la mer. Pourtant, ils sont aujourd'hui adorés et défendus par les populations humaines (Neves et al. 2022).

3.2 Pour développer la science participative

La science participative, comme démontré par l'exemple porté par l'ONG de l'Observatoire des Requins de Polynésie (ORP), peut être particulièrement utile à la recherche scientifique puisqu'elle offre des possibilités de collecte de données sur des échelles spatiales et temporelles extrêmement importantes. En effet, de nouvelles informations concernant la diversité spécifique, la distribution géographique, la saisonnalité et l'abondance de nombreuses espèces d'élasmobranches ont été récoltées via la participation active d'instructeurs de plongée volontaires (*Publication 11*). Ce partenariat efficace entre scientifiques, usagers de la mer et association locale pourrait être étendu à d'autres objectifs, comme la création d'une base de données listant les individus présents dans une zone, comme proposé pour l'implémentation d'une gestion du risque basée sur les individualités (Clua et al. 2020, *see section 2.1*). Les moniteurs de plongée peuvent facilement récupérer les photos prises par leurs plongeurs, afin de permettre aux scientifiques d'enrichir les catalogues et de collecter des informations sur les individus présents grâce à la photo-identification. En effet, de tels programmes ont déjà vu le jour pour le requin taureau (*Carcharias taurus*) en Australie (Barker & Williamson 2010). En parallèle, les chercheurs peuvent renseigner les professionnels de plongée sur les individus à problèmes potentiels rapportés dans la zone, offrant des possibilités accrues pour la surveillance et la sécurité, ainsi qu'une plus grande volonté de suivre des codes de conduites scientifiquement validés. Impliquer des volontaires dans l'échantillonnage à l'échelle des individus peut offrir des opportunités de répondre à de nouvelles questions scientifiques. En effet, des recherches sur la taille des populations, sur l'analyse des réseaux sociaux, sur le taux de croissance ou sur la capacité de cicatrisation sont également basées sur des approches photographiques (Graham & Roberts 2007, Holmberg et al. 2009, Chin et al. 2015, Jacoby et al. 2021).

Le récent développement mondial de la plongée technique a également créé de nouvelles possibilités pour les sciences participatives. En effet, les écosystèmes coralliens crépusculaires (ECCs), c'est-à-dire les habitats généralement situés entre 30 et 150 mètres, sont maintenant visités de manière régulière par des plongeurs au trimix, mais restent largement inexplorés par les scientifiques du fait des contraintes logistiques, financières et de sécurité induites par l'engagement de ces plongées (Turner et al. 2017, Pyle & Copus 2019). Par conséquent, les ECCs restent l'un des écosystèmes les moins étudiés de notre planète (Shipley et al. 2017). Pourtant, de récentes avancées scientifiques montrent qu'ils pourraient servir de refuge pour de nombreuses espèces, affrontant des menaces biotiques et abiotiques grandissantes, comme le changement climatique (Semmler et al. 2017, Turner et al. 2017, Goodbody-Gringley et al. 2021) ou la surpêche (Lindfield et al. 2016, Pinheiro et al. 2016). Collecter des données sur les requins en profondeur pourrait nous permettre d'étudier et de mieux comprendre les mouvements verticaux dans la colonne d'eau démontrés chez le requin des Galapagos (*Carcharhinus galapagensis*) (Papastamatiou et al. 2015), ou chez le requin de récif (*Carcharhinus perezi*) (Shipley et al. 2017). Ces mouvements pourraient booster la motivation de conservation de ces animaux. En effet, ils pourraient suggérer un rôle majeur des requins pour les écosystèmes coralliens, puisqu'ils pourraient jouer le rôle de transporteurs de grandes quantités de nutriments depuis les faibles profondeurs jusqu'aux récifs mésophotiques (Papastamatiou et al. 2015), et ainsi être garants de la résilience de nos récifs de surface.

Les pêcheurs, qui fréquentent à la fois les écosystèmes récifaux et pélagiques, montrent également une connaissance empirique importante concernant les requins. Ainsi, ils peuvent être impliqués avec succès dans des initiatives de sciences participatives, comme le démontrent de précédentes études (Follett & Strezov 2015, Araujo et al. 2017, Filippo et al. 2018, Alvarado et al. 2020). Leur sensibilisation est particulièrement importante, puisqu'ils représentent l'une des catégories sociales les plus opposées à la conservation des requins (*Publication 1*, *Publication 3*). La communication privilégiée avec les scientifiques, permise par les sciences participatives, pourrait offrir une opportunité aux pêcheurs d'être davantage conscients de la valeur d'usage indirecte des requins. En effet, leur abondance est le signe d'un récif en bonne santé, et donc de prises potentielles (Friedlander & DeMartini 2002, Sherman et al. 2020). De tels résultats ont déjà été obtenus grâce à l'aide de programmes de recherches collaboratifs, d'échanges de connaissances entre la communauté scientifique et les pêcheurs, et d'une communication plus transparente entre ces deux parties (Iwane et al. 2021). Ainsi, les programmes de sciences participatives pourraient aider indirectement à limiter les pêcheries illicites, non-déclarées et non-réglementées (INNs) qui peuvent se produite même au sein de zones protégées (Ward-Paige & Worms 2017, Clua & Millot 2018). Néanmoins, cette sensibilisation ne peut se suffire à elle-même dans certains cas, du fait de la déprédation significative que les requins peuvent exercer sur les prises. D'autres pistes de réflexions pour améliorer la relation entre pêcheurs et requins seront discutés dans la *section 4.1*.

3.3 Pour éduquer les jeunes générations

Bien que l'éducation des jeunes enfants ne soit pas développée dans ce travail doctoral, elle pourrait représenter une perspective à long terme intéressante pour le futur de la conservation des requins. Comme pour les adultes, les enfants tendent à diaboliser les requins, terrifiés par des interactions potentielles avec ces animaux (Lane & Chazan 1989, McWhirter & Weston 1994). Heureusement, de plus en plus de preuves montrent que la perception d'animaux potentiellement dangereux peut s'améliorer si la conscience de leur importance augmente. Ce principe a été vérifié pour les serpents sur des étudiants de premier cycle en Géorgie (Makashvili et al. 2014) et semble particulièrement prometteuse pour les requins (O'Bryhim & Parsons 2015, Tsoi et al. 2016, Ostrovski et al. 2021). Néanmoins, les enfants développent généralement leurs raisonnements de la façon la plus simple et directe possible (Groves & Pugh 2002, Grotzer & Basca 2003). De plus, ils sont le plus souvent éduqués à représenter des problématiques environnementales d'une manière extrêmement simplifiée (Griffiths & Grant 1985, Munson 1994, Barman et al. 1995, Leach et al. 1996). Même si la compréhension du rôle des requins dans leur écosystème semble être la clé d'une meilleure perception (Røskaft et al. 2003, DiEnno & Hilton 2005, Prokop & Tunnicliffe 2008, Tsoi et al. 2016), les liens de causalité menant à leur disparition sont complexes à transmettre. En effet, des enfants non entraînés pensent spontanément que le retrait des requins pourrait mener à un enrichissement de la biodiversité (Tsoi 2010), ou que les « pêcheurs de requins » ont une plus grande responsabilité dans la vulnérabilité des populations de ces animaux que les « mangeurs d'ailerons » (Tsoi et al. 2016). Ainsi, pour assurer une meilleure compréhension du fonctionnement des réseaux trophiques ou des impacts anthropiques, les écoles devraient être assistées pour la création d'un nouveau programme en écologie dès le primaire (Jordan et al. 2009, Tsoi et al. 2016). En plus des nombreux challenges à laquelle l'éducation des plus jeunes fait face, l'environnement marin est souvent sous-représenté dans les programmes scolaires, et reste ainsi un sujet de discussion mineur, en comparaison avec l'environnement terrestre (Cava et al. 2005, Thornton & Scheer 2012).

Différents outils peuvent être utilisés pour éduquer les enfants à la conservation des requins. Premièrement, il est important de souligner que la sensibilisation des plus jeunes ne peut être totalement dissociée de la sensibilisation de leurs parents, puisque la transmission verticale d'un discours positif est souvent corrélée à une meilleure perception (Tsoi 2011). D'autre part, l'utilisation de matériel pédagogique est particulièrement efficace chez les enfants, s'ils ne démontrent pas de biais cognitifs (Tsoi et al. 2015). Comme pour les adultes, les documentaires télévisuels sont particulièrement efficaces, ainsi que les lectures (Tsoi et al. 2015). Néanmoins, une étude précédente a montré que les enfants âgés entre 6 et 8 ans montraient davantage d'intérêt pour les sciences marines si les outils de lecture présentaient un support digital plutôt qu'un support papier (Syarah et al. 2019). La sensibilisation sur les requins devrait ainsi être envisagée via des ressources modernes et divertissantes, en utilisant les dernières technologies disponibles. Un exemple d'une telle démarche concerne la sensibilisation à la conservation du panda géant (*Ailuropoda melanoleuca*) (Chen et al. 2019). En effet, l'initiative iPANDA a créé un produit digital particulièrement innovant, qui encourage les enfants à explorer leur environnement et à accumuler des connaissances pour mieux protéger la planète. Cette technologie est basée sur l'adoption d'un animal robotique, bourré de capteurs, permettant à l'enfant de découvrir, grâce à l'utilisation d'une tablette connectée, comme plusieurs paramètres physico-chimiques peuvent influencer la vie de leur panda (Chen et al. 2019). Bien que ce type d'outil soit plus difficile à envisager sur un animal marin comme le requin, il est important de remarquer qu'iPANDA a présenté le potentiel de transmettre de bons comportements vis-à-vis de la nature, tout en créant un lien affectif puissant avec la vie sauvage.

4. Nécessité d'un sentiment d'appartenance des populations locales face aux mesures de conservation

4..1 Par des mesures de conservation égalitaires

Il est important de reconnaître que les mesures de conservation peuvent être profondément inégalitaires, et ainsi représenter une source potentielle d'importants conflits sociaux. En effet, il est crucial que la protection des requins présente des coûts équitablement distribués, afin d'éviter d'être délétère pour une partie de la population (*Publication 2*, Balmford & Whitten 2003, Bennett et al. 2019, Griffiths et al. 2019, Booth et al. 2021, Giron-Nava et al. 2021). Les principaux usagers de la mer qui peuvent souffrir d'un accès limité à la valeur consommatrice des requins sont les pêcheurs. En effet, il n'est probablement pas suffisamment efficace de sensibiliser cette catégorie sociale au rôle joué par les requins dans les écosystèmes coralliens, puisqu'une interdiction de la pêche peut leur causer des pertes de revenus significatives (Booth et al. 2021, Malpica-Cruz et al. 2021). En effet, les dommages économiques peuvent être directs, si ils commercent les produits issus des requins (Booth et al. 2021, Malpica-Cruz et al. 2021), ou indirects, liés à l'augmentation de leur abondance, générant davantage de déprédation (Iwane et al. 2021, Robinson et al. 2022). Les pêcheurs, qui représentent généralement une portion peu aisée de la population, pourraient ainsi perdre leur volonté de soutenir les initiatives de conservation, ou même être tentés de pratiquer la pêche illégale (Booth et al. 2021, Robinson et al. 2022). D'autre part, l'arrêt des activités de pêche est susceptible de générer des revenus plus importants du fait de la forte valeur non-consommatrice des requins (Mustika et al. 2020). Ces revenus bénéficieraient principalement à une autre profession : les opérateurs touristiques. Cette situation pourrait générer des conflits particulièrement virulents, alors même que la conservation est éthiquement tenue de ne nuire à aucune catégorie sociale (Balmford & Whitten 2003, Poudyal et al. 2018, Newing & Perram 2019).

Un moyen de résoudre les problèmes auxquels les pêcheurs font face, et ainsi d'éviter leur potentiel désengagement des mesures de conservation, pourrait résider dans leur implication dans l'écotourisme. En effet, une étude menée à Palau a montré que les visiteurs consommant du poisson localement, en augmentation du fait des activités touristiques, pouvaient à eux seuls permettre de surpasser les gains issus de la vente des requins capturés (Vianna et al. 2012). Néanmoins, la solution la plus prometteuse réside en une forte collaboration entre les gouvernements, les pêcheurs et les opérateurs touristiques via des paiements pour services écosystémiques (PES), encore peu développés. En effet, la distribution des revenus liés à la promotion de requins vivants plutôt que de requins morts peut bénéficier à l'ensemble des secteurs économiques tout en assurant la durabilité de ces populations animales (Vianna et al. 2012, Vianna et al. 2018). Ces PES peuvent être envisagés en collectant des fonds via des taxes bleues ou des dons des touristes, et par leur réinvestissement dans des initiatives de conservation, incluant des compensations économiques pour les pêcheurs (Brunnschweiler 2010, Clua & Pascal 2014, Vianna et al. 2018). Un exemple particulièrement vertueux est celui de la *Shark Marine Reserve* aux Fidji, où une partie des bénéfices générés par l'écotourisme plongée est redistribué à deux villages, ayant renoncé à leur droit de pêche pour cette nouvelle source de revenus. De plus, un programme annuel de formation permet à chaque village d'envoyer un volontaire pour qu'il devienne divemaster, ce qui correspond à une certification de guide de plongée professionnel (Brunnschweiler 2010).

4.2 Par une renaissance culturelle et la reconnaissance des savoirs écologiques traditionnels

Ce travail doctoral a également montré que le manque de sentiment d'appartenance aux mesures de conservation des requins pouvait être un obstacle à leur efficacité. Un exemple réside en le cas de la Polynésie Française, où les îles les plus reculées considèrent la décision de créer un sanctuaire couvrant l'ensemble de la ZEE comme « une décision prise à Tahiti », qui n'est pas alignée avec leur mode de vie encore traditionnel (*Publication 1*). Le lien entre nature et culture, très important dans les sociétés d'Océanie, semble être altéré par la dualité persistant entre une gestion basée sur la science occidentale et une gestion basée sur les savoirs écologiques traditionnels (Huffer & Qalo 2004). Cependant, de précédentes études montrent qu'une synergie est possible et que l'utilisation conjointe de la science occidentale et des savoirs écologiques traditionnels peut être particulièrement efficace en termes de gestion environnementale, ainsi que pour développer un sens partagé des responsabilités pour le bien-être des écosystèmes (Tropics 2001, Becker & Ghimire 2003, Moller et al. 2004, Drew 2005, Maine 2020, Montgomery et al. 2020). En effet, les savoirs écologiques traditionnels sont particulièrement intéressants du fait de l'importante quantité de connaissances accumulées à l'échelle locale, concernant par exemple les espèces présentes dans la zone et leurs mouvements migratoires (Drew 2005, Friedlander et al. 2018). Ainsi, la restructuration d'un dialogue entre les chercheurs et les gardiens de ces savoirs pourrait devenir un outil puissant pour la découverte, pour le renforcement des connaissances ou pour le développement de techniques de gestion optimisant la conservation des requins, tout en représentant un véritable incubateur de cohésion sociale (Drew 2005, Mazzocchi 2006).

D'autre part, ce sentiment ré-établi d'appartenance mutuelle peut être particulièrement intéressant dans des territoires vastes tels la Polynésie Française, où veiller au respect des interdictions de pêche n'est pas une tâche aisée (*Publication 1*). En suivant l'exemple de la *Shark Marine Reserve* aux Fidji, une collaboration entre les pêcheurs, les opérateurs touristiques et le gouvernement, via le département des pêches, a pu permettre la surveillance et le contrôle de zones écologiques particulièrement importantes pour les requins

(Brunnschweiler 2010). Cette cohésion autour de la conservation peut être fortement encouragée par l'implémentation de programmes de sciences participatives locaux (*Section 3.2*) ou par l'introduction de paiements pour services écosystémiques (*Section 4.1*). De telles initiatives peuvent être favorisées par l'implication directe d'ONGs (*Publication 11*), puisqu'elle ont déjà su prouver leur capacité à développer des programmes alignés sur le respect des obligations régionales comme internationales en matière de conservation des élasmobranches (Koehler & Lowther 2022).

D'autre part, un partenariat renforcé entre la science et la culture pourrait être hautement bénéfique concernant la sensibilisation de l'ensemble de la population. En effet, la co-intégration de connaissances occidentales et traditionnelles a induit une meilleure efficacité dans l'enseignement des sciences en Afrique du Sud (Le Grange 2007). De manière similaire, en Inde, la co-implication de chefs spirituels et de médiateurs scientifiques durant un spectacle de rue éducatif sur le requin baleine (*Rhincodon typus*) a permis d'éduquer la population sur l'absence de danger que représente cette espèce pourtant massive (Joshi et al. 2007). Ainsi, les opérateurs touristiques, en contact direct avec les touristes, ainsi que les ONGs, peuvent être précieux pour aider à transmettre tant les connaissances écologiques que culturelles, et renforcer l'attractivité de leurs opérations tout en promouvant la valeur non-consommatrice des requins (*Publication 2*). Par exemple, ils pourraient promouvoir à la fois le savoir et une renaissance culturelle grâce à la communication autour des mythes traditionnels, ou utiliser la langue locale pour qualifier le nom vernaculaire de l'espèce de requin observée.

CONCLUSION

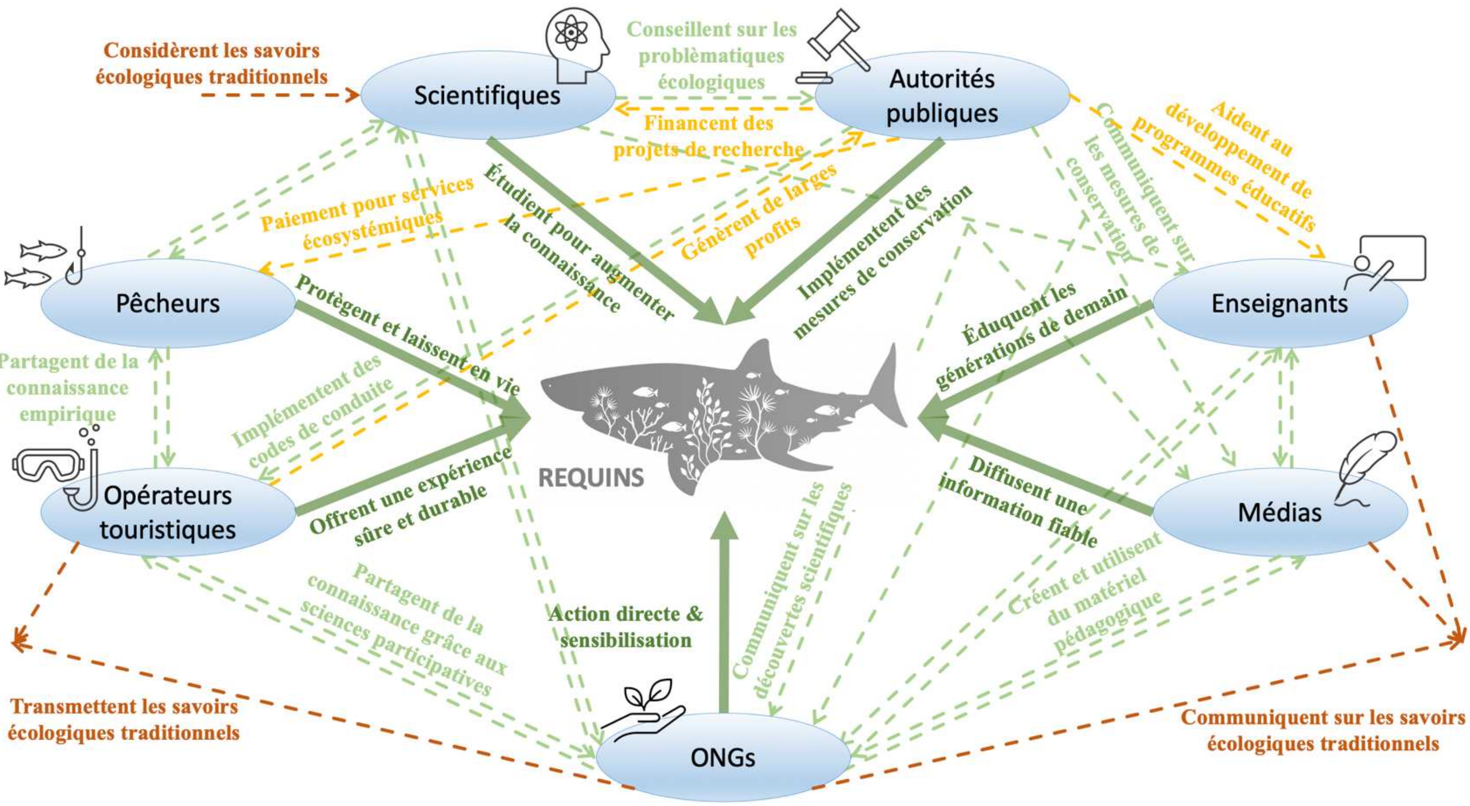

Figure 2 : Le cercle vertueux de la conservation des requins. Les actions en verts sont liées à la discipline de l'écologie, celles en jaune à l'économie et celles en orange à la socio-anthropologie.

Cette thèse de Doctorat a démontré l'importance des services écosystémiques apportés par les requins aux populations humaines, à travers la pluralité de leurs valeurs, combinant équilibre écologique, bien-être économique, et traditions culturelles. Cependant, les mesures de protection ne sont pas encore suffisamment efficaces pour combattre les menaces auxquelles ces animaux font face. L'utilisation de l'ensemble de ces disciplines est essentielle à leur conservation, afin d'optimiser la gestion des populations de requin, ainsi que d'améliorer leur perception aux yeux des humains. De plus, ce travail doctoral a souligné l'importance d'une cohésion sociale restaurée pour assurer un partage de connaissances, une équité, et un sentiment d'appartenance nécessaire à une véritable ré-harmonisation entre Nature et Société (*Figure 2*).

RÉSUMÉ

Les requins contribuent à l'équilibre et à la productivité des récifs coralliens. Ces animaux rendent à l'Homme des services écosystémiques variés et, outre leur fonction écologique majeure, servent de support tant à un écotourisme rentable qu'à des croyances culturelles riches. Malheureusement, ces rôles précieux sont actuellement remis en cause par une dégradation des populations de requins à l'échelle mondiale, principalement du fait de leur surpêche. Les efforts de conservation sont par ailleurs défavorisés par une perception moderne particulièrement négative de ces animaux, emplie de biais cognitifs, en comparaison avec des perceptions ancestrales plus positives, notamment en Océanie. L'objectif de cette thèse est d'optimiser l'efficacité des mesures de protection des requins en réconciliant Nature, Humain et Économie, qui représentent les trois piliers du développement durable. L'importance d'une approche globale, à la croisée des champs disciplinaires, a été particulièrement mise en avant. En effet, elle offre des perspectives d'optimisation des mesures de conservation, et un espoir pour les récifs coralliens de demain d'observer une meilleure santé des populations de requins ainsi qu'une dédiabolisation de leur image auprès de la société humaine.

MOTS-CLÉS

Conservation des requins, Services écosystémiques, Écotourisme, Savoir Écologique Traditionnel, Nourrissage artificiel, Valeur non-consommatrice

ABSTRACT

Sharks contribute to the balance and productivity of coral reefs. These animals provide a variety of ecosystem services to humans and, in addition to their major ecological function, support both profitable ecotourism and rich cultural beliefs. Unfortunately, these valuable roles are currently being undermined by a worldwide decline in shark populations, mainly due to overfishing. Conservation efforts are further hampered by a particularly negative modern perception of these animals, full of cognitive biases, compared with more positive ancestral perceptions, particularly in Oceania. The aim of this PhD is to optimize the effectiveness of shark protection measures by reconciling Nature, Humanity and Economy, the three pillars of sustainable development. The importance of a global approach, at the crossroads of disciplinary fields, has been highlighted. Indeed, this work offers prospects to optimize conservation measures, and a hope for future coral reefs to see healthier shark populations and a de-demonized image in human society.

KEYWORDS

Shark conservation, Ecosystem services, Ecotourism, Traditional Ecological Knowledge, Shark provisioning, Non-consumptive value