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Rangiroa free-ranging bottlenose dolphins' (*Tursiops truncatus*) behavioral responses to scuba diving tourism: Risks, tolerance, and temperament

Réponses comportementales des grands dauphins (*Tursiops truncatus*) de Rangiroa au tourisme de plongée sous-marine : risques, tolérance et tempérament

Soutenue par

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Our relationship with other animals is a complex, ambiguous, challenging, and frustrating affair, and we must continually reassess how we should interact with our non-human kin.

Marc Bekoff, 2009

Ethics and marine mammals

In “Encyclopedia of Marine Mammals [Second Edition]”, p396

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CHAPTER 5. GENERAL DISCUSSION

Glossary

The terms defined are highlighted by an asterisk (*) when first used in the text.

Adaptation (*at the individual animal level*)**:** The use of regulatory systems, with their behavioral and physiological components, in order to allow an individual to cope with its environmental conditions (Broom & Johnson, 2019).

Anthropomorphism: The act of attributing human characteristics, intentions, motivations, and emotions to non-human animals or objects (Guthrie, 2013).

Behavioral repertoire: Here, all the bottlenose dolphins' behaviors recorded toward scuba divers.

Boldness: Individual's reaction to a risky but not new situation (Réale *et al.*, 2007; Toscano *et al.*, 2016). Here, we assessed bottlenose dolphins' boldness toward scuba divers via their willingness to express affiliative behaviors at <3m from divers.

(*Dolphin*) **Community:** Dolphins that share most of their vital range and interact with each other more frequently than with dolphins from adjacent areas. The term community emphasizes the geographical and social relationships of the individuals (Wells *et al.*, 1987).

(*Operant*) **Conditioning:** Learning process where voluntary behaviors are modified by association with the addition, or removal, of reward or aversive stimuli. The frequency or duration of the behavior may increase through reinforcement or decrease through punishment or extinction (Ramirez, 1999).

(*To*) **Cope:** To have control of mental and bodily stability (Fraser & Broom, 1990, p437).

Domestication: Long-term evolutionary process during which humans selectively breed animals for desirable traits (Bekoff, 2009).

Ethics: The study of moral issues (Broom & Johnson, 2019).

Ethogram: A detailed description of the behavioral features of a particular species (Broom & Johnson, 2019).

Habituation: The relatively permanent waning of a response as a result of repeated stimulation (Thorpe, 1963, p61). Here, we understand habituation as an adaptation to human presence in a way that humans are not seen as potential predators but are essentially ignored (Ellenberg *et al.*, 2009).

Mascaret: Name given to breaking waves created by currents that move from Rangiroa lagoon to the Pacific Ocean via Tiputa pass (Carzon, 2017).

Moral: Pertaining to right rather than wrong (Broom & Johnson, 2019).

(*Behavioral*) **Plasticity:** Variation in scores for a given behavior as a function of variation in internal or external stimuli (Stamps & Biro, 2016).

Sensitization: An increase in response to continuing or repeated stimulation (Broom & Johnson, 2019).

Sentient: Having the awareness and cognitive ability necessary to have feelings (Broom & Johnson, 2019).

Stimulus: An environmental change which excites one or more receptors or other parts of the nervous system of an animal (Broom & Johnson, 2019).

Stress: Environmental effect on an individual which overtaxes its control systems and reduces its fitness or appears likely to do so (Broom & Johnson, 2019).

Sustainable: A system or procedure is sustainable if it is acceptable now and if its expected future effects are acceptable, in particular in relation to resource availability, consequences of functioning and morality of action (Broom & Johnson, 2019).

Temperament (*considered here as a synonym of "personality"*)**:** Behavioral and physiological differences among individuals of the same species which are stable over time and across different contexts or situations (Carere & Maestripieri, 2013).

Tolerance: The intensity of disturbance that an individual tolerates without responding in a defined way (Nisbet, 2000). Here, the disturbance is the repeated close presence of humans.

Welfare: The state of an individual as regards its attempts to cope with its environment (Broom & Johnson, 2019). The definition encompasses the extent to which the individual fails to cope, or has difficulties in coping, or easily copes (Broom, 2017). It varies over a range from very good to very poor (Broom, 2016).

Western: Refers to the heritage of social norms, ethical values, and belief systems of the Western world (Shvili, 2021).

Wildlife tourism: Here, we restrict wildlife tourism to the non-consumptive use of wild animals in their natural habitats (i.e., viewing or interaction activities, Tapper, 2006).

Chapter 1

General introduction

1. Wildlife tourism*, scuba diving and whale watching

Wildlife tourism is based on encounters with non-domesticated animals in the animals' natural environments or in captivity (Higginbottom, 2004), and encompasses non-consumptive and consumptive (i.e., killing or capturing wildlife) activities (Duffus & Dearden, 1990; Tablado & D'Amico, 2017). Here, we restrict wildlife tourism to the non-consumptive use of wild animals in their natural habitats (i.e., viewing or interaction activities, Tapper, 2006).

Over the past 60 years, the cultural conditioning of wildlife perceptions and a quest for authenticity and uniqueness have encouraged a desire to encounter free-ranging animals in the world's last remaining wild areas (Duffus & Dearden, 1990; Reynolds & Braithwaite, 2001). With this has come a proliferation and diversification of opportunities to experience wildlife throughout the world, and wild animals became the major motivation for tourism in several locations and countries (e.g., the Galápagos Islands, de Groot, 1983; Kenya, Akama, 1996).

Wildlife tourism increased dramatically in recent years as wild animals stimulate tourists with new experiences and emotions in a world where about 60% of the population live in cities (Higginbottom & Scott, 2004; UNFPA, 2023). For example, the annual number of tourists visiting Ngorongoro Crater in Tanzania has increased from about 350 000 in 2006 to more than 700 000 in 2019 and, during the peak season, an estimated 250 vehicles enter the crater every day to observe its wide variety of wildlife (Cottam, 2023). In 2017, it was estimated that 7% of world tourism related to wildlife and that the number of participants to wildlife tourism was between 79 and 440 million (Trave *et al.*, 2017; UNWTO, 2023).

Nowadays, one of the fastest-growing segments of wildlife tourism focuses on marine species (Wiener, 2015; Pagel *et al.*, 2020). Prior to the 1950s, most of the marine environments were "protected" from tourist use by their inaccessibility, safety concerns, and the relatively high cost of recreating in the sea (Orams, 1998). However, an increase in opportunities to watch, photograph and otherwise interact with marine animals from land, on boats and in the water over the past four decades converted coastal and marine environments into highly popular and profitable destinations (Pagel *et al.*, 2020). For example, manta ray (*Manta* spp.) tourism is estimated to contribute USD 140 million annually to the global economy (Murray *et al.*, 2020).

Here, we focus on marine wildlife tourism, and will briefly introduce scuba diving and whale watching.

1.1. Scuba diving tourism

SCUBA is the acronym for "Self-Contained Underwater Breathing Apparatus". Scuba diving became an important component of marine wildlife tourism due to technological advances and the role of popular culture (Higham & Lück, 2007; Dimmock *et al.*, 2013). Broader interest for this activity was generated in Europe and elsewhere with the release of books, films and television documentaries by Hans and Lotte Haas, and Jacques-Yves Cousteau (Dimmock *et al.*, 2013). In the 1960s and 1970s, Cousteau's wide media coverage emphasized the dramatic nature of exploring beneath the surface of the oceans and had a tremendous impact on the public perception of what was seen as remote and dangerous settings (Forestell, 2009).

From the 1980s, scuba diving tourism has grown in popularity to become a multi-billion-dollar industry mostly featured in tropical to temperate locations (e.g., the Middle East, Southeast Asia, Australia, the South Pacific, the Caribbean, Cater, 2008; Ong & Musa, 2011; Lucrezi *et al.*, 2017). In 2015, scuba diving tourists were visiting coral reefs in 91 countries and the number of certifications issued worldwide by the largest diving organization PADI (i.e., Professional Association of Diving Instructors) has increased from under one million in 1980 to about ten million in the 1990s and 29 million in 2022 (Dimmock *et al.*, 2013; Johansen, 2013; PADI, 2023).

1.2. Whale watching tourism

Whale watching (i.e., recreational cetacean viewing in the wild) is a particularly well documented dimension of marine wildlife tourism (Hoyt, 2001; O'Connor *et al.*, 2009). Although the term "whale" is used, the activity refers to all cetacean species. Originated in the 1950s, whale watching boomed by the end of the 1970s along with the large-scale diffusion of underwater images of cetaceans, popular descriptions of whales as "gentle, clever, passive, and rationale beings", and the prodigious impact of the newly described humpback whale (*Megaptera novaeangliae*) song on the public (Hudnall, 1977, p904; Mazzoldi *et al.*, 2019).

In 2008, it was possible to watch almost any cetacean species in more than 119 countries (O'Connor *et al.*, 2009). Some destinations are particularly renowned as they have been offering whale watching activities for many decades and enjoy a great diversity of whale and dolphin species that can be observed at short distances from shore (e.g., Argentina, Australia, Canada, New Zealand, Williams *et al.*, 2002; Argüelles *et al.*, 2016; Senigaglia *et al.*, 2019; Fumagalli

et al., 2021). The number of whale watchers grew from four million in 1991 to nine million in 1998, and 13 million in 2008 with the growth rate being most rapid (13.6%) in the mid- to late 1990s (Hoyt, 2001; O'Connor *et al.*, 2009).

Whale watching incorporates shore-based, air-based, boat-based, and in-water activities that can be seasonal or take place throughout the year (Allen *et al.*, 2007). Whales and dolphins are attractive species and the recent appeal of "swimming with whales and dolphins" as well as a few diving with cetaceans options has created globally distributed hotbeds of highly lucrative tourism activities (Wiener, 2015; Hoarau *et al.*, 2020; Sprogis *et al.*, 2020).

2. A narrow tourist interest for certain wildlife

Before centering on wildlife responses to tourism, we will overview factors that influence tourists' perceptions of wildlife, and especially dolphins since they are the focus of this thesis. Indeed, some species considered as "charismatic" or "iconic" seem to be valued more highly in terms of conservation, research, and public interest, and widely used by marketers as flagships for promoting tourism (Higginbottom, 2004; Batt, 2009; Apps *et al.*, 2018; Bègue-Shankland, 2022; Shang & Luo, 2023). For example, first-time visitors to Australia are most interested in viewing koalas (*Phascolarctos cinereus*) and kangaroos (*Macropus* spp., Fredline & Faulkner, 2001), and tourists are willing to pay more to view grizzly bears (*Ursus arctos horribilis*) rather than any other Alaskan wildlife (Penteriani *et al.*, 2017).

Human perceptions of wildlife are mostly based on culture, age, gender, education, and experience that will in turn influence attitudes and behavior (Moscardo & Saltzer, 2004; Giovos *et al.*, 2019; Bègue-Shankland, 2022). These perceptions play an essential role in the area of conservation as they can lead to extreme and paradoxical relationships between humans and wildlife that may have positive or negative impacts on individuals, populations, and species (Bekoff, 2009; Knight, 2008; Batt, 2009; Gouabault, 2010; Wynne, 2010; Nekaris *et al.*, 2016). For example, Corkeron (2006) stressed that we "like, revere or honor" animals we view as "lovelies" (e.g., giant pandas, *Ailuropoda melanoleuca*), and we wish to conserve them. At the other end of the spectrum, we "fear or loathe" animals we consider as "nasties" (e.g., spiders), and we would like to thin them out (Corkeron, 2006, p162; Knight, 2008; Baker *et al.*, 2020; Basak *et al.*, 2023). Large predators often promote anger, fear, and disgust but some species

generate fascination besides (e.g., big cats, crocodiles, sharks, Dobson, 2006; Gouabault, 2010; Castillo-Huitrón *et al.*, 2020).

Human perceptions of wildlife evolve over time. In Western* societies, the utilitarian attitude is currently declining while the concept of animal welfare* and ethical animal treatment is on the rise (Broom & Johnson, 2019; Giovos *et al.*, 2019). There is a growing social movement in favor of protecting animals' interests and habitats (i.e., One Health, One Welfare, Lindenmayer & Kaufman, 2021) with for instance pet owners and vegetarians displaying high level of psychological attachment and closeness toward animals in general (Amiot & Bastian, 2017). In addition, current animal usages challenge the conscience of many consumers and animal rights advocates point out that animals' lives have inherent value (i.e., they are not valuable because of their utility to humans or because they look or behave like us, Bekoff, 2009; Broom & Johnson, 2019).

Still, most people remain attracted and more empathetic toward non-human entities that show perceived similarity to humans (Batt, 2009; Curtin, 2009) and anthropomorphism* was documented to encourage pro-animal attitudes regarding animal welfare likewise (Butterfield *et al.*, 2012; Amiot & Bastian, 2017). In addition, numerous studies published over the past 20 years showed that public attention and affective preferences tend to focus on species that are thought to be harmless, are aesthetically pleasing, show dramatic behaviors, or are symbolic, exotic, or rare and endangered (Reynolds & Braithwaite, 2001; Tapper, 2006; Stokes, 2006; Dimmock *et al.*, 2013; Albayrack *et al.*, 2021; Klebl *et al.*, 2021). Moreover, there is an influence of neoteny, or "cute effect", on greater predilection for particular types of wildlife (Knight, 2008; Borgi *et al.*, 2014), and larger animals are generally preferred over smaller ones (Ward *et al.*, 1998; Woods, 2000).

Dolphins are decked out with several of the aforementioned features and are therefore ideal candidates for wildlife tourism.

2.1. The friendly dolphin of Western societies

From the 1970s, considerable literature was published on human perceptions and attitudes toward dolphins that details how Western people are imbued with strong social stereotypes about these animals and their behavior (Fraser *et al.*, 2006). Our historically recent enthusiasm for dolphins is essentially driven by media exposure (Fraser *et al.*, 2006; Wearing

et al., 2011), popular cultures focusing on myths, legends, and symbiotic relationships between dolphins and humans (Busnel, 1973; Servais, 2005; Mazzoldi *et al.*, 2019), and theme parks (Gouabault, 2006). Dolphinariums throughout the world have developed the persona of dolphins as "entertainers", and this perception promoted by guides and boat captains strongly influences participants' expectations during wild encounters (Wiener, 2015).

Additionally, our anthropomorphism is exacerbated when it comes to dolphins (Amante-Helweg, 1996; Curtin, 2009). Humans assume that dolphins enjoy swimming with them as much as we are keen on swimming with dolphins (Servais, 2005; Wiener, 2015) and visible signs of stress* in the animals can be neglected or misinterpreted as playful behavior (Patroni, 2018). The ubiquitous bottlenose dolphins' "smile" makes these animals look like "happy friends" (Forestell, 2009; Wiener, 2015; Cholley-Gomez *et al.*, 2022), eye contact with dolphins gives participants a sense of acknowledgment (Patroni, 2018), and some individual dolphins' curiosity, opportunism, or habituation* to humans consolidate an impression of harmony, connectivity, and success in dolphin-human interactions (DeMares, 2000; Curtin, 2006; Chanvallon, 2013).

Different studies documented that these animals appear to validate human uniqueness (Amante-Helweg, 1996; Fraser *et al.*, 2006) and may help people improve or maintain positive self-esteem (Gouabault, 2010; Schulz *et al.*, 2020). Participants to dolphin-human interactions report that their life was changed by their encounter with a dolphin (Servais, 2005) and studies described the intense and powerful emotional responses humans can feel during and after their interactions with dolphins (Mayes, 2017; Yerbury & Boyd, 2018). In general, evidence suggests that animals can meet human needs of affiliation and interaction, reduce stress, and promote positive moods and attitudes (Yerbury & Boyd, 2019). However, "while many people swim and wade with dolphins, few if any truly dance or howl with wolves (*Canis* spp.)" (Bekoff, 2009, p397).

Most dolphin lovers are unacquainted with scientific knowledge related to these animals (Barney *et al.*, 2005) and tour operators rarely mention that dolphins may behave roughly in the presence of humans (Besio *et al.*, 2008; Carzon *et al.*, 2023). The stereotypical dolphin fashioned in modern Western cultures is a mixture of facts, suppositions and beliefs that may be fueled by romanticism, mysticism, or fantasy and give rise to paradoxes (Amante-Helweg, 1996; Servais, 2005; Delfour, 2007; Besio *et al.*, 2008). Hence, dolphins are constructed as simultaneously wild *and* domestic, friendly, peaceful, harmless, compassionate, helpful,

altruistic, anthropophilic, intelligent, spiritual, social, playful, moral*, and sentient* beings (Fraser *et al.*, 2006; Besio *et al.*, 2008; Wiener, 2015; Yerbury & Boyd, 2018; Trianasari *et al.*, 2021; Cholley-Gomez *et al.*, 2022). These marine mammals are the scene of highly charged subjective opinions and passions (Bekoff, 2009), and an extreme example of appropriation is carried by the New Age movement where dolphins would have alien origins, extrasensory abilities, and healing powers, and would have come to Earth as messengers and initiators among men to help them improve their physical and spiritual wellbeing (Amante-Helweg, 1996; Servais, 2005; Gouabault, 2006; Delfour, 2007).

From this review, we can conclude that Western humans' perceptions and emotions in the presence of dolphins are highly positive. This helps understand the tourists' increased desire to personally interact with dolphins at close range in their natural habitats.

3. A desire for proximity

Proximity to wildlife is associated with tourist satisfaction and close observations or physical interactions with wild animals are commonly emphasized by marketers to attract tourists (Schänzel & McIntosh, 2000; Moscardo *et al.*, 2001; Curtin & Kragh, 2014; Bach & Burton, 2017). For example, Cong *et al.* (2014) examined tourists' encounters with giant pandas in a Chinese national park and concluded that tourist contentment levels increased with closer encounters and interaction with the pandas. In Bali, Indonesia, most tourists participating in dolphin-watching tours expected to see the dolphins *close enough*, and a few expressed the desire to touch them (Trianasari *et al.*, 2021). A study carried out on nearly 5 000 visitors in Australia and New Zealand showed that overall, the tourists surveyed wanted to be able to get close to rare and unique wildlife behaving naturally in a natural environment (Moscardo & Saltzer, 2004). It is worth noting that a "natural" environment is not necessarily a pristine or untouched environment and that most tourists have a strongly biased idea of what are behaviors displayed by wild animals (e.g., Finlay *et al.*, 1988; Tapper, 2006; Higham & Lück, 2007).

The motivation of being close to animals stems from the hope to observe them in more details, to interact or connect with them on a more intimate level and being able to touch a dolphin is a considerable incentive for many people (Curtin, 2006).

Moreover, the "David Attenborough Effect" perpetuates the tourists' expectations of close encounters with wild animals and gives the impression that wildlife is spontaneously within reach (Wearing *et al.*, 2011). In the case of dolphins, swim-with, feeding, and petting

pool programs where participants can get close to, touch, feed and-or give hugs to captive dolphins may also teach people that it is permissible to behave similarly with free-ranging animals (Besio *et al.*, 2008; Bekoff, 2009).

Additionally, the tourists' expectations to observe or interact with wildlife in close proximity have been encouraged by the relatively recent emergence and contents of social media (Nekaris *et al.*, 2016; Lenzi *et al.*, 2020; Otsuka & Yamakoshi, 2020). Taking photographs or videos is a common way for tourists to capture the experience and share pleasant memories, and a high number of tourists use to post images online of themselves partaking in wildlife tourism experiences (Gretzel, 2017). The prevalence of "wildlife selfies" (i.e., photographs taken by a tourist in close enough proximity to a wild animal that they both appear in the frame) on social media has grown 292% globally since 2014 and facilitates the promotion of harmful tourism encounters with wild animals (Lenzi *et al.*, 2020; Kredens & Vogt, 2023). For example, videos of humans and mountain gorillas (*Gorilla beringei beringei*) together obtain more views and "likes" in cases where physical contact or close proximity with gorillas are clearly observed, compared with those that do not include close human-gorilla interactions (Otsuka & Yamakoshi, 2020).

Overall, dramatic, or "funny" images of wildlife are rapidly shared by users who do not take the time to consider what might have gone into capturing them (Roth, 2020). One example of serious consequences of social media publications for the individual welfare and species conservation of wild animals comes from Nekaris *et al.*'s (2016) study on videos of IUCN Red List Vulnerable, Endangered or Critically Endangered slow lorises (*Nycticebus* spp.). The authors documented that the most popular lorises' images violated basic welfare concerns, and that most individuals liking and commenting on the videos were from Europe and North America. They concluded that the potential for a sick, scared or stressed slow loris to appear as the norm exists even in cultures that are more likely to know about, and adhere to, welfare and conservation issues (Nekaris *et al.*, 2016).

This modern trend stimulates increased visitation at wildlife tourism destinations, puts pressure on operators and professional guides who seek to provide close encounters to entertain visitors, and encourages intrusive, abusive, and illegal behaviors toward wildlife and sensitive wildlife habitats (Higham & Lück, 2007; Otsuka & Yamakoshi, 2020; Cottam, 2023).

4. Wildlife responses to tourism

4.1. Wildlife tourism as a new source of human-induced rapid environmental change

It is argued that wildlife tourism, including scuba diving and whale watching, creates incentives for area protection and wildlife conservation and offers sustainable* alternatives to local human-animal conflicts and lethal resource exploitation (e.g., generating income for local communities, protecting wildlife from poaching, Dearden *et al.*, 2007; Curtin & Kragh, 2014; Lucrezi *et al.*, 2017). This is the case for tigers (*Panthera tigris*) in India (Buckley, 2012) and mountain gorillas in Rwanda (Shackley, 2009) where the survival of animals and their habitats is highly dependent on the continued presence of tourists.

However, there is also an antagonism between the need to protect the environment and the global market's needs for production of profit (Butler, 1989; Reynolds & Braithwaite, 2001), and wildlife tourism is increasingly considered as a new source of human-induced rapid environmental change (also termed "HIREC", Geffroy *et al.*, 2018).

Furthermore, not all tour-operators are environmentally and socially responsible, and visitor experiences often take exclusive priority over concerns for the impacts associated with those experiences (Higham & Lück, 2007). Though it is assumed that an increasing number of tourists have positive attitudes toward conservation and empathize with animal welfare issues (Curtin, 2009; Yerbury & Boyd, 2019), even animal-lovers can cause unwitting and unexpected damage (Berle, 1990; Karp & Root, 2009; Huang *et al.*, 2011).

For example, mountain gorilla tourism generates important revenue for conservation efforts but brings with it the threat of disease transmission into the gorilla population (Sandbrook & Semple, 2006). Heavily dived sites have a higher incidence of coral disease (Lamb *et al.*, 2014) and several studies suggest that ecological impacts at scuba diving sites is partly related to diver experience and technical skills (e.g., poor buoyancy control and finning techniques, Barker & Roberts, 2004; Roche *et al.*, 2016). Researchers studying disturbance responses of Adélie penguins (*Pygoscelis adeliae*) concluded that "tourism does adversely affect breeding penguins, almost irrespective of how well-behaved the tourists are" (Culik & Wilson, 1991). Since the 2000s, the International Whaling Commission formally addressed in-water engagement with free-ranging dolphins, stating that even the most well-intentioned human contact is accompanied by unpredictable and cumulative risks (Wiener, 2015).

Hence, as wildlife tourism has grown, so have concerns about threats to wildlife. These concerns are exacerbated by the tourists' willingness to see vulnerable or threatened species at close distance and to travel to remote and-or sensitive locations (e.g., resting, feeding, and breeding areas, Johnson *et al.*, 1998; Lusseau *et al.*, 2009; Schofield *et al.*, 2020). In addition, the recent COVID-19 outbreak likely emerged because of humans' careless disregard for wildlife and wild places, and some authors advocate that we should redefine our relationships with animals taking better care of them or, at least, adopting some behavioral distancing with them for their sake and the sake of the environment (Lindenmayer & Kaufman, 2021).

4.2. Tourists' approach distances and behaviors

The effects of wildlife tourism on wildlife depend on various factors such as the scale of tourism development (e.g., geographic and time extent, number of tourists, Johns, 1996; Grossberg *et al.*, 2003; Szott *et al.*, 2019), the species' features, the frequency and intensity with which an animal experiences adverse stimuli (e.g., frequencies and intensities of sounds not normally encountered in its environment, Karp & Root, 2009; Huang *et al.*, 2011), if the same animal endures the stimuli during sensitive times of its life cycle (Green & Giese, 2004), and individual temperaments* (Martin & Réale, 2008).

Also, it will highly depend on visitors' approach distances and behaviors (e.g., Lott & McCoy, 1995; Cassini, 2001; Karp & Root, 2009; Geffroy *et al.*, 2017). For example, cheetah (*Acinonyx jubatus*) tourism in Kenya involves vehicles moving between the cheetah and its prey so tourists can get a better view. This interferes with the cheetah's ability to catch its prey and can separate mothers from cubs (Marker, 2019).

In the Central African Republic, higher levels of fecal glucocorticoid metabolites (a proxy for physiological stress) in habituated western lowland gorillas (*Gorilla gorilla gorilla*) were significantly associated with increased frequency of violation of the 7m distance rule by observers (Shutt *et al.*, 2014).

Scuba divers using cameras approach marine species more closely than other divers and may cause significant behavioral disruptions and physical contact with coral reefs and cryptobenthic fauna (Barker & Roberts, 2004; de Brauwer *et al.*, 2018; Giglio *et al.*, 2018).

In cetaceans, changes in boat speed and route and short distance approaches were documented to cause behavioral disruptions (Barr & Slooten, 1999; Constantine, 2001; Williams *et al.*, 2002). Swim-with whale and dolphin tours engender more impact than standard, vessel-based whale watching, as boats must get closer to the animals and usually intend to place swimmers in the path of the animals to maximize the chances of observing them in the water (Constantine & Baker, 1997; Constantine, 2001; Corkeron, 2006; Stensland & Berggren, 2007). Moreover, it is not uncommon for swimmers to abruptly jump in the water, slap the surface in an attempt to attract the animals, create deliberate noise as a form of generating interactions with them, attempt to chase and touch cetaceans, with some people grabbing the fins and riding dolphins that are highly tolerant* to human presence (Samuels *et al.*, 2000; Wilke *et al.*, 2005; Cunningham-Smith *et al.*, 2006; Christiansen *et al.*, 2010; Martinez *et al.*, 2012).

Overall, wildlife tourism raises numerous ethical questions about human intrusions into the lives of other animals (Bekoff, 2009) and generates short- to long-term changes in the behavior and physiology of the animals targeted.

4.3. Obvious and subtle wildlife responses

Changes in behavior are usually the first visible reaction of animals to environmental challenges (Blumstein *et al.*, 2017) but one needs to have good knowledge of an animal and-or species biology and ethogram*, and of the context of the observations, to interpret them correctly (Broom & Johnson, 2019).

Changes in behavior underlie various physiological responses and researchers usually measure animal responses to tourism by investigating behavior, physiology, or both together (e.g., Ellenberg *et al.*, 2006; Maréchal *et al.*, 2011; Bateman & Fleming, 2017; Saltz *et al.*, 2018). Moreover, observation of behavior often helps interpreting physiological measures (Broom, 2017), and an aggregate of several measures is preferable to a single measure because of the diversity of coping* methods used by animals (Broom & Johnson, 2019).

The changes triggered by repeated human visitation may be immediate and obvious to a human observer (e.g., orientation reaction, startle response, strong avoidance, attraction), subtle (e.g., changes to an animals' hormone levels in blood and other body fluids, increasing heart rate, changes in social behavior, Green & Giese, 2004; Semeniuk *et al.*, 2009; Ellenberg *et al.*, 2013; Shutt-Phillips *et al.*, 2021), and they may evolve over time (e.g., habituation, sensitization*, impairment in immune system function, reduced life expectancy, Broom, 2017).

Whether an animal's responses to tourism appear positive or negative, its fitness is reduced if it is more likely to die and less likely to have offspring (Broom & Johnson, 2019).

Evident short-term behavioral changes were documented in many animal species. For example, harp seal (*Phoca groenlandica*) mothers tend to leave the ice when tourists arrive, and those which remain with their pups do not provide sufficient care (Kovacs & Innes, 1990). When approached by divers, hawksbill sea turtles (*Eretmochelys imbricata*) spend less time eating, investigating, and breathing (Hayes *et al.*, 2017), and active approaches on feeding manta rays result in feeding cessation (Murray *et al.*, 2020).

In cetaceans, the short-term behavioral responses most commonly recorded in a tourist context are modifications of breathing sequences, (e.g., Williams *et al.*, 2002; Lusseau, 2003), alterations of swimming speed and orientation (e.g., Barr & Slooten, 1999; Lusseau, 2004), changes in group composition, dispersion or cohesion (e.g., Bejder *et al.*, 1999; Carrera *et al.*, 2008), disruptions of current states and events (e.g., Constantine *et al.*, 2004; Stensland & Berggren, 2007; Peters *et al.*, 2012), modifications of areas frequented and habitat use (e.g., Carrera *et al.*, 2008; Pérez-Jorge *et al.*, 2016), and variations in the animals' acoustic signals (e.g., alterations in whistle frequency and duration, van Parijs & Corkeron, 2001; Guerra *et al.*, 2014).

Short-term behavioral and physiological changes in individual animals that are repeatedly targeted by tourist activities may translate into long-term deleterious effects (Bejder *et al.*, 2006; Shannon *et al.*, 2017; Geffroy *et al.*, 2018). These effects may be difficult to quantify, especially when they are cumulative rather than catastrophic (Bejder *et al.*, 2006; Pirotta *et al.*, 2015) and because of the multitude of interacting factors that affect wildlife population dynamics and community structure (Shannon *et al.*, 2017).

Recently, Geffroy *et al.* (2018) provided an integrated picture of tourism impacts on a short-lived Tetra fish (*Odontostilbe pequira*) by investigating the expression of genes involved in stress response and neurogenesis, as well as behavioral and hormonal responses of animals consistently exposed to tourists. The study showed that tourism appeared to shift selection pressures, favoring a sensitive phenotype that does not thrive under natural conditions. Moreover, Geffroy *et al.* (2020) suggested the existence of similarities between the selection pressures exerted by intensive exposure to humans and domestication* (i.e., intense human contact immediately releases animals from predation pressure and then impose strong anthropogenic selection on traits).

In animals with long-life expectancies, the detection of significant responses to repeated human presence usually requires substantial logistics and time (e.g., at least ten years for dolphins, Pirotta *et al.*, 2015).

However, chronic behavioral and physiological changes are likely to affect physical and social conditions (e.g., Christiansen *et al.*, 2010; Symons *et al.*, 2014), the distribution, density and interactions among individuals and species on a location (Bejder *et al.*, 2006; Ilarri *et al.*, 2008; Shannon *et al.*, 2017; Trave *et al.*, 2017), reproductive success (e.g., Burger *et al.*, 1995; Higham, 1998) and survival (Geffroy *et al.*, 2015; Shannon *et al.*, 2017), above all if the animals lack control over important aspects of their environment (Broom, 2017).

For example, a study of Indiana bats (*Myotis sodalis*) in winter hibernacula showed the greatest weight loss in caves with the most human visitation (Johnson *et al.*, 1998). An elevation of glucocorticoid hormones in western lowland gorillas exposed to tourists was shown to reduce the gorillas' ability to control the extent of parasitic infections (Shutt-Phillips *et al.*, 2021). The ichthyofauna of some visited sites differ from similar pristine areas in adjacent headwater streams with tourism reducing fish abundance, specialist species, and favoring generalists (Bessa *et al.*, 2017).

*4.4. Wildlife habituation, sensitization, and conditioning**

Regular close encounters between humans and wildlife require a predictable occurrence of the target species on specific locations (Duffus & Dearden, 1990), and even elusive animals must be susceptible to proximate and protracted human viewing (Knight, 2009). A report on wildlife tourism written in 1988 suggested that successful activities should involve animals that are approachable and tolerant of human intrusion (*in* Reynolds & Braithwaite, 2001) and *there appear to be three main ways in which wild animals can be made available for human viewing, i.e., capture and confinement, habituation, and attraction* (Knight, 2009, p173).

Many species and individuals show weaker antipredator responses when they are repeatedly exposed to harmless or neutral humans compared to conspecifics in areas with less human visitation, a behavioral modification known as "increased tolerance toward humans" that may be due to a reduction in vigilance or a "habituation-like process" (Uchida *et al.*, 2023). Increased tolerance to human disturbance is one of the most observable behavioral responses of animals living in human-modified environments (Uchida & Blumstein, 2021). This is a form

of behavioral adaptation*, or phenotypic accommodation, induced by a novel environmental factor that allows individual animals to cope with alterations in their environmental conditions with or without increasing their fitness (Broom & Johnson, 2019). This learning process may lead to long-term habituation, i.e., *the relatively permanent waning of a response as a result of repeated stimulations* (referred to here as "habituation", Thorpe, 1963, p61) which is often very specific (Broom & Johnson, 2019). Such changes may result in reduced imposition of the environment on the animals, but some individuals' attempts to adapt to their environment may also be inadequate because the stimuli are excessive in intensity or duration, or otherwise noxious (e.g., shy individuals, Sih *et al.*, 2004). If that is the case, repeated exposure to adverse stimuli can lead to sensitization and poor welfare (Broom & Johnson, 2019). Moreover, a stimulus* that is initially tolerable may eventually reach an intolerable level (Broom & Johnson, 2019). For example, a study undertaken on the long-term impacts of vessel activity on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, demonstrated that there was no difference in dolphin abundance between periods with no tourism and periods in which one operator offered tours. However, as the number of tour operators increased to two, there was a significant average decline in dolphin abundance, approximating a decline of one per seven individuals (Bejder *et al.*, 2006).

Habituation occurs across a wide variety of organisms (Rankin *et al.*, 2008; Stamps, 2015) and tour-operators and guides frequently induce habituation in the animals to produce the desired experience that wildlife tourists are eager to see. For example, Ugandan park rangers at Kibale National Park repeatedly interacted with the chimpanzees (*Pan troglodytes*) under their care to "improve the quality of chimpanzee-watching tourism." Over time, the chimpanzees became used to the presence of humans which made them more likely to come closer and respond positively to photographers (Lowenberg, 2015).

Moreover, operant conditioning using positive reinforcers (e.g., food, pleasurable tactile contact) is commonly used to attract wildlife on certain areas. The provision of food is an effective way to readily increase the probability that animals will appear, allow close approach, and behave as expected (Reynolds & Braithwaite, 2001; Green & Giese, 2004).

In the Philippines, whale shark (*Rhincodon typus*) tourism implies daily shark provisioning activities allowing the shark-human interaction in nearshore waters where provisioned sharks are less likely to exhibit avoidance to people (Legaspi *et al.*, 2020). Attracting brown bears by means of artificial feeding sites is a common practice in North

America and Europe which increases bear densities and opportunities for people to take photographs (Penteriani *et al.*, 2017).

Yet, increased wildlife tolerance toward humans can be a double-edged sword (Uchida *et al.*, 2023). Indeed, habituation and conditioning may enhance and promote positive interactions, but they also teach people to expect wildlife to perform on demand (Green & Higginbottom, 2001) and increase the potential for negative outcomes for both the animals and humans (Geffroy *et al.*, 2015; Worrell *et al.*, 2017; Uchida *et al.*, 2023). For example, there is evidence that primates habituated for tourist viewing are at greater risk from poaching than non-habituated individuals (Kasereka *et al.*, 2006), and that tourists can serve as vectors for several diseases that can be harmful to wildlife (Murray *et al.*, 2016; Shannon *et al.*, 2017). In Shark Bay, Australia, calves born to provisioned female bottlenose dolphins experienced reduced care and higher mortality relative to calves of non-provisioned mothers (Mann & Kemps, 2003).

Moreover, although habituation is often assumed to have occurred when wild animals tolerate people at close distance (Herrero *et al.*, 2005), numerous studies focusing on physiological stress responses in the absence of obvious behavioral responses showed that wildlife species may appear to be tolerant of humans while significant impacts still occur (e.g., Higham, 1998; Ellenberg *et al.*, 2006; 2009; Charuvi *et al.*, 2020). At the behavioral level, Allan *et al.* (2020) showed that human observers are not perceived as neutral but instead viewed as a high-ranking social threat by habituated Afromontane chacma baboons (*Papio ursinus griseipes*). Taken together, while humans may be perceived as low-risk stimuli to some extent, human activity is likely to impose some stresses and energetic costs on wildlife that may increase the vigilance level, which ultimately causes negative fitness consequences (Uchida & Blumstein, 2021).

In addition, food-conditioned wildlife can be offered inadequate diet, aggregate in restricted areas, and display high numbers of aggressive intraspecific behaviors (Hill, 1999; Semeniuk & Rothley, 2008; Clua *et al.*, 2010; Sorensen *et al.*, 2013; Newsome *et al.*, 2015). For example, carnivorous fish are unable to regulate high concentrations of blood glucose and show signs of hyperglycemia from eating bread offered by people (Bessa *et al.*, 2017). Near Sarasota Bay, Florida, food-conditioned dolphins were offered and consumed sandwiches, chips, pastries, fruits, and ice (Cunningham-Smith *et al.*, 2006).

The provision of food leads to reduced animal vigilance toward potential threats (Geffroy *et al.*, 2015) and to the appearance of specific behaviors that may make animals become nuisances or dangerous for humans and be killed for safety or comfort (Penteriani *et al.*, 2017; Behrendorff *et al.*, 2023). Dolphins tend to remain near boats and people, to beg head out of the water and mouth wide open and may initiate forceful contacts with humans to access artificial food resources (Orams *et al.*, 1996; Samuels & Bejder, 2004; Finn *et al.*, 2008). In Gibraltar, visitors have traditionally enticed Barbary macaques (*Macaca sylvanus*) with "junk" foods such as chocolates to stroke and touch them, and these contacts sometimes result in macaques biting tourists (Fa, 1992). In Singapore, the human's indiscriminate, year-round, feeding of long-tailed macaques (*Macaca fascicularis*) made them become more demanding, and aggressive when food was found, leading to the capture, and culling of 206 individuals in 2007 (Yeo & Neo, 2010).

Touching and handling wildlife raise concerns like those associated with habituation and food-provisioning, and an increasing number of reports detail how animals can be used, abused, and exploited this way (Belicia & Islam, 2018). For example, in Manaus, Brazil, anacondas (*Eunectes murinus*), caimans (*Caiman crocodilus*) and sloths (*Bradypus variegatus*) are made available for handling by tourists, particularly for use as photo props (D'Cruze *et al.*, 2017). Island species which lost appropriate antipredator responses and may become extremely tame (Blumstein & Daniel, 2005) are appealing targets for wildlife tourism, where some animals easily tolerate being touched (e.g., iguanas, *Cyclura cychlura*, Hines, 2011; quokkas, *Setonix brachyurus*, Worell *et al.*, 2017).

Humans were seen riding, holding the tail fluke, shoving fingers into the blowhole, eyes, and ears, putting objects in the blowhole, hanging on the flippers, and opening the jaws of free-ranging dolphins that tolerate or seek out physical contact with them (Carzon *et al.*, 2023). Conversely, human-tolerant free-ranging dolphins displayed intrusive, abrupt, aggressive, and sexual behaviors toward humans that are detailed in **Chapter 2**.

5. Understanding individual variation in wildlife behavioral responses to tourism

We overviewed that different individuals may respond differently to similar or identical stimuli, and that seemingly positive responses to tourism may lead to unpredictable risks involving poor welfare and reduced individual fitness. It is therefore perilous to infer that tourist activities do not generate deleterious impacts on a wildlife species or population without examining behavioral and-or physiological variation at the individual level. Moreover, it is not reasonable to conclude from coarse-grained observations of wildlife responses to tourism that such activities are sustainable and ethically acceptable.

The question of sustainability is important indeed when decisions are made about whether a system for exploiting resources (such as wildlife tourist activities) should be used, and *the fact that something is profitable and there is a demand for the product is not now sufficient reason for the continuation of production* (Broom, 2016, p47).

5.1. Behavioral plasticity and temperament*

Over the past two decades, the fields of ethology, comparative psychology, and behavioral ecology have experienced a renewed interest in animal plasticity and temperament (e.g., Stamps, 2015; McMahon *et al.*, 2022). These two topics are of interest to better understand individual animal responses to environmental changes, including repeated human presence.

In this thesis, we consider that behavioral plasticity is variation in scores for a given behavior as a function of variation in internal or external stimuli (Stamps & Biro, 2016). Stamps (2015) suggested a framework for categorizing the many different types of behavioral plasticities and we present a simplified version of this framework in **Table 1**.

Table 1. Simplified version of Stamps' (2015) categories of behavioral plasticities.

Exogenous plasticities Responses to external stimuli, experiences, environments
A.1. *Contextual plasticities* Immediate effects of external stimuli on behavior
A.2. *Developmental plasticities* Effects of past experience on current behavior
Endogenous plasticities Spontaneous changes in behavior resulting from temporal changes in internal stimuli

Habituation and sensitization, universal learning mechanisms which result from the effects of past experiences on current behavior, are relatively simple examples of developmental plasticities observed in wild animals in the context of chronic human presence (**Table 1** *Section* **A.2**).

To properly study habituation and sensitization, individuals must be followed over time and repeated exposure. For example, Uchida & Blumstein (2021) assessed 15 years' population and individual-level yellow-bellied marmots' (*Marmota flaviventris*) responses to sustained exposure to humans and their relation to fitness outcomes. They documented an average decrease in flight initiation distances (i.e., the distance at which an animal flees from approaching humans) over time that suggested that marmots habituated to humans. However, long-term human disturbance also had negative fitness consequences as marmots in highly disturbed colonies gained less body mass over time compared to conspecifics in less disturbed colonies. Additionally, the authors detected what they called "individuality" in flight initiation distances as marmots that fled at greater distances became sensitized with repeated approaches (Uchida & Blumstein, 2021). Their results confirm that we should not expect all individuals to have identical responses to humans, and that it is relevant to include temperament in studies of wildlife responses to tourist activities.

Temperament refers to behavioral and-or physiological differences among individuals of the same species which are consistent over time and across different contexts or situations (Carere & Maestripieri, 2013). "Consistent" does not mean that trait values cannot change with

age or environmental conditions, but that differences between individuals are largely maintained (Réale *et al.*, 2007). The main traits and methods used to study animal temperament vary according to the research field. For example, the five-factor model (i.e., agreeableness, conscientiousness, extraversion, openness, and neuroticism) is often used as a basis to analyze animal temperament in comparative psychology (Úbeda *et al.*, 2019; Morton *et al.*, 2021) whereas boldness*, exploration, activity, sociability, and aggressiveness are ubiquitous temperament categories in behavioral ecology (Réale *et al.*, 2007).

Besides, a specific trait can have different meanings depending on the authors and studies. For example, boldness was defined as *an individual's reaction to any risky situation, but not new situations* (Réale *et al.*, 2007), a *reaction to novelty* (Guenther *et al.*, 2018), a *novelty-seeking behavior* (Díaz López, 2020), and as *curiosity and investigation* (Hill *et al.*, 2019).

Lilley *et al.* (2018) stressed that there are differences between boldness, neophilia and curiosity, and we decided to keep the definition proposed by Réale *et al.* (2007) all along this thesis. Wild animals' *reaction to any risky but not new situation* was measured using various techniques. As illustrations, Réale *et al.* (2000) focused on the trappability of individual bighorn sheep ewes (*Ovis canadensis*) which was assumed to be an expression of their willingness to accept the risk of being handled in order to obtain access to a salt bait, and Bubac *et al.* (2018) determined female gray seals' (*Halichoerus grypus*) boldness according to the response of each female to human approach and handling of her pup.

Behavioral plasticity and temperament are linked and influence each other (Mitchell & Houslay, 2021). For example, several authors documented individual differences in habituation rates (Ellenberg *et al.*, 2009; Bell & Peeke, 2012; Dingemanse *et al.*, 2012), and wildlife tolerance toward humans was shown to be modulated by plasticity (Geffroy *et al.*, 2017), temperament (Carrete & Tella, 2013), and interactions between the two (Lowry *et al.*, 2013; Stamps, 2015; Arroyo *et al.*, 2017; Uchida & Blumstein, 2021).

Individual temperaments generate boundaries to plasticity (Rodríguez-Prieto *et al.*, 2010; Carere & Locurto, 2011; Massen *et al.*, 2013) and whether organisms avoid, ignore, or are attracted to a stimulus can depend on their general level of boldness (Sih *et al.*, 2023). Arroyo *et al.* (2017) showed that temperament effects can lead to directional selection of certain phenotypes in contexts involving repeated human presence. They studied Montagu's harriers' (*Circus pygargus*) responses to increasing exposure to humans through nest visits over 19 years

and documented a gradual disappearance of shy individuals leading to a greater proportion of bolder harriers and a more behaviorally homogeneous breeding population.

Additionally, a recent study linked temperament traits and levels of welfare in captive killer whales (*Orcinus orca*, Úbeda *et al.*, 2021) showing that individual variation in behavioral responsiveness to humans may have major implications for both welfare and conservation issues.

5.2. Influences of plasticity and temperament on wildlife responses to tourism

Several studies investigated the influence of plasticity on animals' responses to wildlife viewing activities (e.g., Shutt *et al.*, 2014; Maréchal *et al.*, 2016; Bertrand *et al.*, 2022), but few examined the influence of temperament. Martin & Réale (2008) recorded behavioral and physiological individual responses of eastern chipmunks (*Tamia striatus*) to visitor disturbance and documented that temperament traits related to exploration, the grooming-scanning continuum, emotionality, and docility caused the chipmunks to distribute themselves non-randomly in response to human disturbance. Pritchard *et al.* (2014) used intraspecific behavioral measures of 12 free-ranging provisioned adult Tibetan macaques (*Macaca thibetana*) to pinpoint behavioral proxies for established temperament traits in the macaques in a tourist context.

Martin & Réale (2008) stressed that in the absence of knowledge on animal temperament, wildlife tourism impact can be under- or overestimated. This is notably true in the case of dolphins, as they spend most of their time out of human sight and some individuals seem to tolerate or to be attracted to human presence (Carzon *et al.*, 2023). These animals' proximity or positive behaviors toward tourists generate millions of dollars annually (Hunter Jr. *et al.*, 2021; Uchida *et al.*, 2023). Yet, they are seen to have short- to long-term negative consequences for both the dolphins and humans, and close interspecific interactions are now viewed as ethically questionable (Bejder *et al.*, 2009; Broom & Johnson, 2019). Consequently, it is critical to learn more about tourism effects on individual dolphins, and the risks associated with dolphins' responses to tourism, for an optimal and proactive management of flourishing whale watching activities.

5.3. Our case study: Rangiroa bottlenose dolphins

As a case study, we explored free-ranging bottlenose dolphins' (*Tursiops truncatus*) behavioral responses to scuba diving tourism in Rangiroa, a remote oceanic atoll located in the Tuamotu Islands, French Polynesia. On the north coast of Rangiroa, an area centered on a natural channel that connects the Pacific Ocean to the lagoon [i.e., Tiputa pass, **Figure 1(a)**] hosts a small bottlenose dolphin community* of about 30 individuals (Carzon, 2017). Seven to 10 dolphins are seen there every day whereas the other individuals are captured on the area up to 12 times a month throughout the year (Carzon, 2017). In 2024, 52% of these dolphins had been captured on the Tiputa pass area for 15 years or more, and 41% were born on the area between 2011 and 2024 and regularly captured on site since then (*pers. obs.*). Indeed, the Tiputa pass area is an important socializing and resting ground for the dolphins and it is suspected to be a foraging ground too (*pers. obs.*). The dolphins can be viewed from shore when they come to surf and leap into breaking waves (locally termed mascaret*) generated by strong outgoing currents that run through Tiputa pass two times a day [**Figure 1(c)**].

Also, Tiputa pass and its close surroundings are hotspots for human activities (i.e., shipping, yachting, fishing, and tourism). Tourist activities include daily boat-based dolphin watching, snorkeling and scuba diving tours that take place throughout the year and rely on the presence of the easily accessible bottlenose dolphins [**Figure 1(b)**].

In 1985, the first dive shop was founded in Rangiroa Atoll, but scuba divers barely watched the dolphins underwater. Yet, local people were used to seeing bottlenose dolphins on the area well before the implementation of scuba diving activities.

From the 1990s, the dolphins began to be viewed underwater at distance from scuba divers, and some individuals appeared to be curious of divers using camera housings and lights, and approached them opportunistically [*pers. com.*, **Y. Lefèvre** and **U. Mazzavillani**, **Figure 1(d)**]. Reciprocally, scuba divers repeatedly attempted to attract, approach, and-or touch the dolphins, and the dolphins' tolerance to scuba divers' intrusive behaviors increased sharply from the mid-2000s. At this time, a juvenile female dolphin began to interact with scuba divers closely and repeatedly. In 2007, this same individual first tolerated physical contacts initiated by scuba divers (*pers. com.*, **U. Mazzavillani**).

This dolphin's particular behavior toward divers was transmitted both vertically (i.e., to its own calves) and horizontally (i.e., to some of its associates, and associates' associates) across the dolphin community (*pers. obs.*). Between 2007 and 2024, 3 to 33% of the dolphins that

belonged to the community tolerated and-or looked for physical contacts with scuba divers, regularly or opportunistically (*pers. obs.*). From the 2000s, they became the main attractions of scuba diving tourism in Rangiroa. In 2024, six dive shops running one to six inflatable boats each organize up to four dive tours daily on a <1km² area widely used by the dolphins.

In 2001, a four-week study overviewed demographic and social data collected on Tiputa bottlenose dolphins (Brasseur *et al.*, 2002). In 2009, a longitudinal study was initiated on these dolphins by the NGO *Groupe d'Étude des Mammifères Marins* and continued from 2019 by the NGO *Dauphins de Rangiroa*. Between 2014 and 2016, a MSc thesis was conducted on Tiputa bottlenose dolphins' demographic parameters and social organization (Carzon, 2017).

Figure 1. Our case study. (**a**) Tiputa pass viewed from the ocean side. (**b**) Dolphin watching tour boats into Tiputa pass. **(c)** Dolphin leaping into the pass photographed from shore. **(d)** Dolphin interacting with scuba diver equipped with camera housing and light (*photo*©**Bob François**).

Research objectives and thesis structure

We investigated the case of non-provisioned free-ranging bottlenose dolphins exposed to scuba diving tourism at Rangiroa Atoll, French Polynesia. We studied the dolphins' neutral, avoidance, and affiliative behaviors toward scuba divers. Our aims were to understand how individual dolphins tolerate repeated close interactions with wildlife tourism, how close interactions may impact both the dolphins and humans, and how they should be managed to limit deleterious outcomes. Accordingly, we built this work around the three following topics:

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1 Deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins

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Keywords

Animal encounter, close interaction, human-dolphin interaction, deleterious behavior, risk management, wildlife tourism

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In **Chapter 1**, we recalled that dolphins have a positive image of anthropophilic animals in modern Western societies, and that some individual dolphins tolerate or may be attracted to humans and human activities. Yet, these marine mammals can display aggressive and unpredictable behaviors to people as well (e.g., Shane *et al.*, 1993; Samuels *et al.*, 2000), and close dolphin-human interactions are often poorly or not supervised (Kessler & Harcourt, 2013; Sitar *et al.*, 2016) and may concurrently impact the dolphins through inappropriate or adverse human behavior.

To get a better understanding of the risks for both the dolphins and humans related to close interspecific interactions in the wild, we reviewed 240 sources published over seven decades that documented close encounters in the context of human recreational activities, and close interactions between humans and lone, sociable dolphins. We could identify a number of deleterious behaviors and risks recorded for both parties and summarized this information to

show that not only close interactions are widely and increasingly distributed worldwide, but that they may not be as harmless as it is usually believed. As such, clear and informed management and enforcement measures must be considered to minimize the negative impacts of these interactions.

This work was published as a review in the journal *Biological Conservation* in March 2023. The paper titled "Deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins: A review" was written in collaboration with Drs É. Clua, F. Delfour, and K. Dudzinski and makes the second chapter of this thesis.

Following this publication, a comment named "On the legality of swimming with wild dolphins" was submitted by E. Simon to *Biological Conservation*. We sent an argued answer to the journal titled "On the lack of explicit and enforced regulations to manage swim-with dolphin activities: A reply to Simon (2023)". Both comments were published in June 2023.

This review work allowed us to design an overall though not fully comprehensive picture of the current worldwide status of close recreational interactions between free-ranging dolphins and humans. In addition, it enabled us to pinpoint gaps in the dolphin-human interaction literature that may be filled thanks to the privileged observation conditions specific to Rangiroa Atoll. One of these gaps relates to the notions of tolerance and habituation which are the focus of the next chapter.

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2 Rangiroa bottlenose dolphins' tolerance to scuba diving tourism

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Keywords

Behavioral plasticity, dolphin behavior, habituation, human-dolphin interaction, tolerance, wildlife tourism

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In **chapter 1**, we stressed that wildlife tolerance and habituation to humans may lead to unpredictable risks for both parties involving poor welfare and reduced individual fitness. Additionally, Bejder *et al.* (2009) raised the importance of semantics when interpreting wildlife responses to humans as some terms such as "habituation" may be misleading and cause flawed conservation plans and detrimental consequences for wildlife. Consequently, quantification of the tolerance status of individual cetaceans targeted by tourism should be one priority for impact assessment studies (Bejder *et al.*, 2009).

We used the favorable context of Rangiroa Atoll to study the consequences of repeated interspecific interactions on known free-ranging bottlenose dolphins' tolerance to scuba divers. We took advantage of the opportunity to collect dolphin data from shore in a scuba diver-free area, and underwater in the presence of tourist divers. We focused on the dolphins' neutral and avoidance behaviors in the close (i.e., <10m) presence of active divers [e.g., divers holding their hand(s) out to the dolphins] to quantify their tolerance status.

We hypothesized that a majority of, and individual consistency in, neutral (i.e., no overt dolphin reaction) behaviors would indicate dolphin tolerance to the close presence of active divers. Also, we assumed that dolphin avoidance behavior would relate to specific divers' behaviors, and we tested the influence of sex, sexual maturity, tourist-site fidelity, the number of divers and the number of dolphins on the dolphins' tolerance to scuba divers.

The paper "Free-ranging bottlenose dolphins' tolerance to scuba divers is modulated by their age, social context, and by the divers' behaviors" written in co-authorship with Drs É. Clua and F. Delfour was submitted to the journal *Behaviour* in June 2024 and makes the third chapter of this thesis. This article illustrates the value of focusing on dolphin fine-scale responses to tourist activities to inform contextual management measures.

3 Rangiroa bottlenose dolphins' boldness toward scuba divers

Keywords

Boldness, dolphin behavior, human-dolphin interactions, temperament, wildlife tourism

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In **Chapter 1**, we saw that individual temperament influences wild animals' responses to repeated human presence (Carrete & Tella, 2013; Lowry *et al.*, 2013).

We chose the validated shyness-boldness axis to identify temperament traits in known non-provisioned bottlenose dolphins monitored over three years in the presence of active scuba divers. We measured the occurrence, duration, and frequency of affiliative behaviors used as proxies to illustrate dolphin boldness toward divers and referred to as "bold behaviors". We also tested if sex and sexual maturity were potential predictors of the dolphins' tendency to display bold behaviors toward scuba divers.

The paper "Individual variation of boldness in free-ranging bottlenose dolphins interacting with scuba divers in French Polynesia" was written in collaboration with Drs É. Clua and F. Delfour and submitted in June 2024 to the journal *Applied Animal Behaviour Science*. It makes the fourth chapter of this thesis and reveals interindividual variability and intraindividual consistency in Rangiroa bottlenose dolphins' boldness toward divers. Also, we detected differences across bold dolphins looking at finer scale behaviors displayed by the dolphins in the close presence of active divers.

In Rangiroa, scuba diving tourism promotes intrusive human behaviors toward the dolphins and some dolphins' boldness in the presence of humans undoubtedly prompts the destination's popularity. Still, dolphin-human interactions have the potential to negatively impact both the dolphins and divers and should be managed accordingly.

RESEARCH QUESTIONS + THESIS STRUCTURE

How do individual free-ranging dolphins tolerate repeated close interactions with wildlife tourism?
What are the risks related to close dolphin / human interactions?
How should close dolphin / human interactions be managed to limit deleterious outcomes?

1

How do close interactions negatively impact both the dolphins and humans?

How should close interactions be managed to limit deleterious outcomes?

Review on the deleterious behaviors and risks related to close dolphin / human interactions, including the impacts of increased dolphin tolerance to humans, and management indications

2

How did free-ranging dolphins' cumulative experience with scuba diving tourism influence their tolerance to scuba divers?

Quantification of the dolphins' habituation to the presence of scuba divers

Dolphins' presence / absence on diver / diver-free areas

Quantification of the dolphins' tolerance to divers who display intrusive behaviors toward them

Dolphins' neutral responses to divers

Influence of scuba divers' behaviors on the dolphins' tolerance to divers

Dolphins' avoidance responses to divers

Influence of the dolphins' sex, sexual maturity, tourist-site fidelity, the number of divers, and the number of dolphins on the dolphins' tolerance to intrusive scuba divers

3

How do individual dolphins' responses to intrusive scuba divers variate along the shyness-boldness axis?

Identification of the dolphins' behaviors indicating their boldness toward divers [termed 'bold behaviors']

Dolphins' affiliative behaviors toward scuba divers at close range, and dolphins' involvement in physical interactions with divers

Quantification of interindividual variability and intraindividual consistency in the dolphins' bold behaviors

Effects of sex and maturity on the dolphins' bold behaviors

Potential consequences of individual variation in the dolphins' responses to tourism
Benefits and risks of close dolphin / diver interactions
Management indications applicable to the context of Rangiroa

Chapter 2

Deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins: A review

Abstract

Nature-based tourism has surged in recent years with the desire for up-close interactions and "connections" with wild animals. The conservation value, animal welfare considerations, visitor satisfaction, and profitability of wildlife tourism are often in direct conflict with trade-offs commonly accepted. In this paper, we reviewed more than four decades of literature on the deleterious behaviors and risks documented during close tourist and other recreational interactions between humans and free-ranging dolphins, and encounters between humans and lone, sociable dolphins. Our compilation provides a geographical, chronological, and qualitative overview of these encounters, reviews both humans' and dolphins' deleterious behaviors during interspecific interactions and summarizes the main risks to both humans and dolphins during close encounters. Based on this review, we outline and discuss how both animal welfare and human safety should be managed such that these activities are sustainable; the demand for personal wildlife experiences continues to grow at an alarming rate and the economic pressures placed on wild animal populations run the risk of damaging the very environmental assets that support this industry if they cannot be managed effectively.

Keywords

Animal encounter, close interaction, human-dolphin interaction, deleterious behavior, risk management, wildlife tourism

1. Introduction

In an increasingly urbanized world where encounters with "wild" animals seem to satisfy a human need to reconnect with nature (Miller, 2005; Newsome *et al.*, 2005 *in* Garrod, 2007), many wildlife viewers want more than "just to observe"; they want to make contact with exotic, rare, and charismatic species through regular and thrilling interactions (Moeran, 1983 *in* Cater, 2008; Newsome & Rodger, 2008). In parallel, a rising number of commercial operators market their wildlife tours with the promise of close-up views (Knight, 2009), with opportunities ranging from walks and hikes to get close to apes and monkeys (Fa, 1992; Johns, 1996; Grossberg *et al.*, 2003; Sandbrook & Semple, 2006), penguins (Fowler, 1999; Ellenberg *et al.*, 2006; 2007), dingoes (*Canis lupus dingo*, Orams, 2002), bears (Smith *et al.*, 2005), iguanas (Hines, 2011), or sea lions (Corral *et al.*, 2017), to elephant rides that allow close encounters with rhinoceros (Lott & McCoy, 1995). Close in-water encounters as part of snorkeling and scuba diving activities focusing on different aquatic species are expanding as well (e.g., turtles, Tapper, 2006; rays, Semeniuk *et al.*, 2009; sharks, Brena *et al.*, 2015; manatees, Shackley, 1992; seals, Scarpaci *et al.*, 2005; Scheer, 2020; whales, Mangott *et al.*, 2011; and dolphins, Samuels *et al.*, 2000).

1.1. Focus on close interactions with dolphins

Since the 1950s, there has been renewed enthusiasm for dolphins, popularized by marine parks, television, and cinema (Fraser *et al.*, 2006; Forestell, 2009). The great sociability and pseudo smile of bottlenose dolphins, which embody the human view of the dolphin, indeed favor a perception of these animals closer to myth and romantism than reality (DeMares, 2000; Wearing *et al.*, 2011; Wiener, 2015).

The market for watching wild dolphins surfed on the growth of the animal rights movement, which concurred to the closure of some dolphinaria (Hughes, 2001). From the mid-1980s, these iconic animals have experienced a rapid increase in demand for interaction opportunities in their natural habitat (Orams *et al.*, 1996; Barnhill *et al.*, 2022) leading to considerable development of whale and dolphin watching activities (i.e., commercial, and recreational viewing in the wild, Hoyt, 2001; O'Connor *et al.*, 2009).

Dolphin watching encompasses operations that were first mostly conducted from boat and land. In-water encounters expanded significantly from the early 1990s and involve regular and close interactions between the public and these cetaceans worldwide (Senigaglia *et al.*,

2020). Intentional, accidental (e.g., around human fisheries, Díaz López, 2017; Kovacs *et al.*, 2017), and structured and unstructured food provisioning activities also occur in some places that promote close contact with dolphins in their natural settings (Newsome & Rodger, 2008). Finally, close encounters between humans and dolphins were popularized by the publicized presence of lone, sociable dolphins, which gave rise to particularly intimate relationships between these cetaceans and their admirers (Lockyer, 1990; Müller, 1998; Nunny & Simmonds, 2019).

1.2. Behavioral processes that facilitate close interactions between humans and wildlife

Bejder *et al.* (2009) consider responses of wildlife to non-lethal forms of human disturbance as "a continuum of individual tolerances (i.e., the intensity of disturbance that an individual tolerates without responding in a defined way, Nisbet, 2000)." Differences in levels of tolerance can eventually lead to sensitization or habituation of individuals involved in interactions, i.e., "adaptive behavioral modifications exhibited by individual animals in response to exposure to a stimulus that is repetitious or continuous" (Bejder *et al.*, 2009). According to Knight (2009), two strategies may be used to facilitate close interactions between humans and wildlife: *habituation* and *attraction*. Habituation is a non-associative learning process that occurs where an initial disposition to escape from humans will wane as a result of repeated stimulation and be replaced by tolerance of a human presence (Thorpe, 1963, p61). Habituation is usually achieved through a slow longitudinal process involving considerable effort on the part of humans (Bejder & Samuels, 2003). Attraction may be performed through some conditioning involving positive reinforcement (e.g., the provision of food; Orams, 2002; Smith *et al.*, 2005) and can drastically speed up a process of familiarization (i.e., the experience of being familiar with humans, Whittaker & Knight, 1998; Newsome & Rodger, 2008). Young individuals are usually more responsive to habituation and conditioning than adult animals (e.g., bears, Gilbert, 1989; dolphins, Samuels & Bejder, 2004; macaques, Ménard *et al.*, 2013). Both processes impact the "wild" quality of the behavior of the animals on view (i.e., their pattern of mobility is no longer informed by human avoidance, Knight, 2009), though they have a priori tourism benefits by ensuring predictable and reliable viewing of the wildlife on which operators base their business (Garrod, 2007).

1.3. Deleterious behaviors and risks related to close interactions between humans and wildlife

Numerous studies conducted over half a century on animals' behaviors displayed during close interactions between humans and wildlife and their consequences (e.g., Mattson *et al.*, 1992; Newsome & Rodger, 2008; Ménard *et al.*, 2013; Penteriani *et al.*, 2017; Nunny & Simmonds, 2019) have revealed that close encounters involve enough risks for humans and targeted species to call into question the usual considerations that such activities correlate primarily and directly with conservation (e.g., Isaacs, 2000; Neves, 2010; Dubois & Fraser, 2013; Barnhill *et al.*, 2022). Globally, Geffroy *et al.* (2015) argue that increased tolerance and habituation to humans often reduce animals' fearfulness and antipredator strategies, with cascading effects on populations and communities. In a review on issues and impacts related to wildlife provisioning for tourism purposes, Orams (2002) reports that deliberate, long-term conditioning of wildlife through food provision alters natural behavior patterns at population levels related to intra- and interspecific aggression with important health implications. For example, a long-term study on grizzly bears thoroughly conditioned to man through food-provisioning showed that such animals developed behavioral patterns that made them extremely dangerous, with bear-man interactions sometimes ending in human injury or death (Craighead & Craighead, 1971; Jope, 1985). In Africa, Brennan *et al.* (1985) described the human-animal conflict rising between artificially fed vervet monkeys (*Chlorocebus pygerythrus*) and tourists at a tourist lodge in Kenya, with *pest* primates attacking and injuring the tourists. Studies on Humboldt (*Spheniscus humboldti*) and yellow-eyed (*Megadyptes antipodes*) penguins exposed to unregulated tourism showed significantly lower breeding success in these animals compared to those living in undisturbed areas (Ellenberg *et al.*, 2006; 2007). Semeniuk *et al.* (2009) demonstrated that tourist-exposed southern stingrays (*Dasyatis americana*) exhibit hematological changes indicative of physiological costs of wildlife tourism.

Dolphins are no exception: Samuels & Bejder (2004) observed that the lives of conditioned free-ranging bottlenose dolphins were *strikingly* different from those of dolphins that did not interact with humans; conditioned dolphins were engaging in interactions with humans during most of the time they were studied and were remaining at a small location. Christiansen *et al.* (2016) found that the association with already conditioned animals strongly affected the probability of bottlenose dolphins becoming conditioned to human interactions and that conditioned dolphins were more likely to be injured by human interactions when compared with unconditioned animals. Nunny & Simmonds (2019) stressed that several lone, sociable dolphins were deliberately injured and killed by humans and that these animals are, to a great

extent, at the mercy of people's desire to interact with them. A high occurrence of serious injuries and mortality of lone, sociable dolphins was likewise referenced by Samuels *et al.* (2000).

Indeed, many studies illustrate how paradoxical close relationships between man and wildlife can be, with some *nuisance* animals ultimately being destroyed by humans (e.g., grizzly bears, Mattson *et al.*, 1992; dingoes, Dubois & Fraser, 2013; bottlenose dolphins, Vail, 2016) when their behaviors go beyond the limits of human tolerance.

Even so, close interactions between humans and dolphins are still actively promoted, sought out by humans, and being launched new in various locations where they often remain poorly or partially managed (Scarpaci *et al.*, 2003; Finn *et al.*, 2008; Sitar *et al.*, 2016).

Within an ecological context requiring urgent and effective management of human interactions with wildlife, an updated review of the deleterious behaviors and risks documented for both dolphins and humans in the context of close interspecific encounters seems relevant to help promote animal welfare, human safety, and the viability of these activities in the near future. This is the goal of this review.

1.4. Structure of the review

We constrained our review to the deleterious behaviors and risks documented from the 1950s in ongoing tourist and other recreational activities involving close interactions between humans and free-ranging dolphins and encounters between humans and lone, sociable dolphins [see Lockyer (1990) and Müller (1998) for a review of lone, sociable dolphins documented before the 1950s]. We chose to compile data on lone, sociable dolphins apart from ongoing activities as interactions between humans and lone, sociable dolphins often illustrate the most intimate and sustained encounters that take place between humans and individual dolphins in their natural habitat.

Throughout this paper, we **1)** provide a geographical, chronological, and qualitative overview of close encounters between humans and free-ranging dolphins, **2)** review dolphins' and humans' deleterious behaviors documented during these interspecific interactions, and **3)** identify the main risks recorded within these close interactions, for both dolphins and humans.

As previous work (Samuels *et al.*, 2000; Nunny & Simmonds, 2019) stated that lone, sociable dolphins are at high risk of being injured or killed in the context of their interactions

with humans and human activities, we also compared the number of locations where deleterious behaviors and risks were documented for ongoing activities and for lone, sociable dolphins.

Based on recommendations given in the reviewed literature, we then propose directions to promote animal welfare, human safety, and the establishment of sustainable activities (i.e., activities that ensure the balance between conservation values, animal welfare considerations, visitor satisfaction, and profitability).

2. Methods

It is difficult to succinctly provide comprehensive data on such a wide and ever-growing subject. To optimize our approach, we limited our research to a review of peer-reviewed papers and other references (details on references are available below) published from the 1950s for ongoing tourist and other recreational activities involving close interactions between humans and free-ranging dolphins (hereafter "ongoing activities") and interactions between humans and lone, sociable dolphins (*Cf.* **Table 1** for a detailed definition of terms used in this review).

Most managers and wildlife biologists do not publish their work in peer-reviewed journals and most peer-reviewed papers on this topic originate from four countries (i.e., Australia, the United States, and New Zealand for ongoing activities, and the United Kingdom for lone, sociable dolphins). We thus decided to include material that was not published in peer-reviewed journals in order to highlight the tremendous and relatively recent global increase in close interactions between humans and dolphins in their natural habitat. Yet, peer-reviewed papers were privileged over any other type of reference when multiple sources were available for a specific situation.

Table 1. Glossary

TERM	DEFINITION
Close interactions	We consider *close interactions* between humans and dolphins as occurring during wading, swimming, free diving, scuba diving, and/or food provisioning activities. They may be regular or occasional and may or may not involve physical contact between humans and dolphins.
Deleterious behaviors	*Deleterious behaviors* are gathered in behavioral categories adapted from Samuels & Spradlin (1995). Dolphin deleterious behaviors are **aggressive** (e.g., jaw clapping), **submissive** (e.g., avoidance), **sexual** (e.g., rubbing genitals against humans), **intrusive** (e.g., begging), or **abrupt** (e.g., pushy) dolphin behaviors directed to humans and/or human activities. Reciprocally, human deleterious behaviors are **aggressive** (e.g., shooting at dolphin), **sexual** (e.g., provoking sexual response), **intrusive** (e.g., touching), or **abrupt** (e.g., jumping on dolphin) human behaviors directed to dolphins. No human submissive behavior was documented in references.
Dolphins	Free-ranging Odontocetes (toothed whales) from the Delphinidae, Iniidae, and Monodontidae families are referred to here as *dolphins*.
Locations	Geographical areas where close interactions between humans and free-ranging dolphins have been documented. *Location* may refer to a country or part of a country (e.g., territory, state, region, province, archipelago, island, city). Locations where few or no research is available on close interactions, or information is redundant (e.g., same species involved, same risks identified) are considered on a wider geographical scale (e.g., India, Northeastern Canada, Gulf Coast in the USA).
Lone, sociable dolphin	Dolphins that are typically solitary, may seek out human company, and/or reorient part or all of their social behavior toward humans rather than conspecifics are labeled *lone, sociable dolphins* (from Samuels *et al.*, 2000 and Wilke *et al.*, 2005). Known individuals which belonged or are still belonging to known dolphin groups reviewed in the ongoing activities category (e.g., "Old Charlie" in Monkey Mia, Australia) are not considered as lone, sociable dolphins.
Ongoing tourist and other recreational activities	*Ongoing activities* refer to up-to-date opportunities for regular (i.e., specific dolphins approached daily or seasonally) or occasional (i.e., dolphins approached opportunistically) close interactions between humans and free-ranging dolphins, excluding encounters between humans and lone, sociable dolphins. These activities may be commercial or non-commercial, and structured or unstructured.
Risks	Short- to long-term negative impacts (e.g., injury, impairment of intraspecific social behavior) on dolphins, humans and/or human activities resulting from close interactions between humans and free-ranging dolphins are defined as *risks* (adapted from Frohoff, 2000).

Information was compiled and tallied to 240 sources (*Cf.* **Supplemental Data** for details on sources). We first used *Google Scholar*, open web searching and contacted authors to reference peer-reviewed papers (n=117, 48.8%) and graduate-level theses (n=14, 5.8%) using different combinations of the following keywords in English, Spanish and French: "swimming," "diving," "touching," "feeding," "wild," "lone," "sociable," "solitary," "dolphin(s)," "whale(s)." The same method was then used to reference books and book chapters (n=12, 5.0%), abstracts and presentations (n=14, 5.8%) and reports (n=40, 16.7%). We finally searched for official and tourism agencies', tour operators', NGOs', and local research

programs' websites (n=26, 10.8%) as well as personal communications with people on site (n=15, 6.3%) to gather details from locations where data are deficient. Media sources (n=2, 0.8%) were included for two recent (i.e., 2020) cases involving lone, sociable dolphins. The number of peer-reviewed papers compiled for each country is shown in **Figures 1a and 1b**.

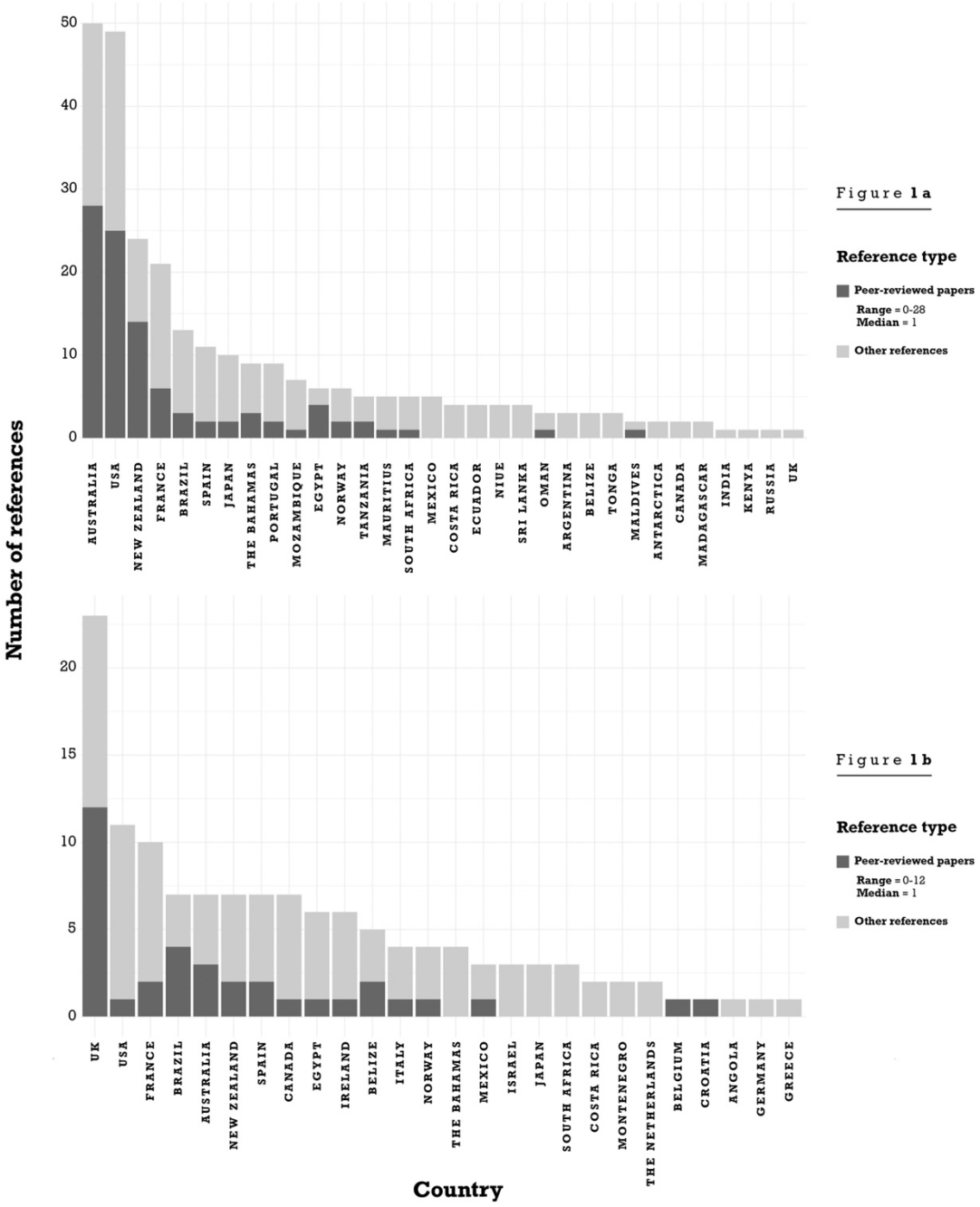

Figure 1. Stacked bar plots showing the number of peer-reviewed papers (dark gray) and other references (light gray) compiled for each country where close interactions between

humans and dolphins were documented for (**1a**) ongoing activities and (**1b**) lone, sociable dolphins. Range and median values are given in legend for peer-reviewed papers.

All information available on the type of activities (e.g., swimming, scuba diving) encouraging close interactions, dolphin species involved, dolphins' and humans' deleterious behaviors, and risks documented for dolphins and humans were chronologically tabled for each location identified according to the decade when first interactions occurred. Dolphin identities and years of sightings were specified when known for lone, sociable dolphins. Calves born to lone, sociable female dolphins were not considered in results.

Some terms frequent in the literature, such as "dominant," "boisterous," or "harassment" typically lacked precision or clarification, but we chose to report the information as it was presented. Moreover, it was often a challenge to disentangle the specific effects of in-water encounters, food provisioning, or other features related to close interactions (e.g., the presence of boats) in the source material; thus, we reported deleterious behaviors documented in each location without distinguishing between their specific causes.

We then designed distribution maps showing locations, chronology, main species, and activities encouraging close interactions for ongoing activities and lone, sociable dolphins. In addition, we synthesized the information available on deleterious behaviors and risks documented for both dolphins and humans for each location for ongoing activities and lone, sociable dolphins. We used a χ^2 analysis to compare the number of locations where deleterious behaviors and risks were documented for ongoing activities and for lone, sociable dolphins. We concurrently created heatmaps from the proportion of deleterious behaviors and risks observed for ongoing activities and for lone, sociable dolphins to better visualize potential differences between both situations. This approach was found to be a good compromise to allow a global but rather detailed overview of the situation.

3. Results

3.1. Distribution of locations and activities encouraging close interactions

In 2022, we reviewed 54 locations distributed in 32 countries where ongoing activities occur (**Figure 2**). Still, we consider a majority of these locations (n=28, 51.9%) as being data deficient primarily because they are reported but have not been studied so far.

In five locations (9.3%), interactions were first recorded in the 1960s and 1970s. Most locations (n=34, 63.0%) began engaging in these activities in the 1980s and 1990s and 15 locations (27.8%) initiated activities between 2000 and 2020.

Fifty-three (98.1%) locations offered wading, swim-with and/or free diving with dolphins, 16 (29.6%) had scuba diving activities and eight (14.8%) included food provisioning activities. Two (3.7%) of the locations reviewed prohibited swim-with dolphin activities recently [i.e., Northland Region in New Zealand (2019), and Mediterranean Coast in France (2021)].

For lone, sociable dolphins, 47 locations distributed in 26 countries, and 135 different dolphins were identified between 1950 and 2022 (**Figure 3**). In 39 (83.0%) of the locations considered, wading, swim-with, and/or free diving activities with these dolphins were recorded; scuba diving was documented in 17 (36.2%) locations, and food provisioning of lone, sociable dolphins was identified in 18 (38.3%) locations.

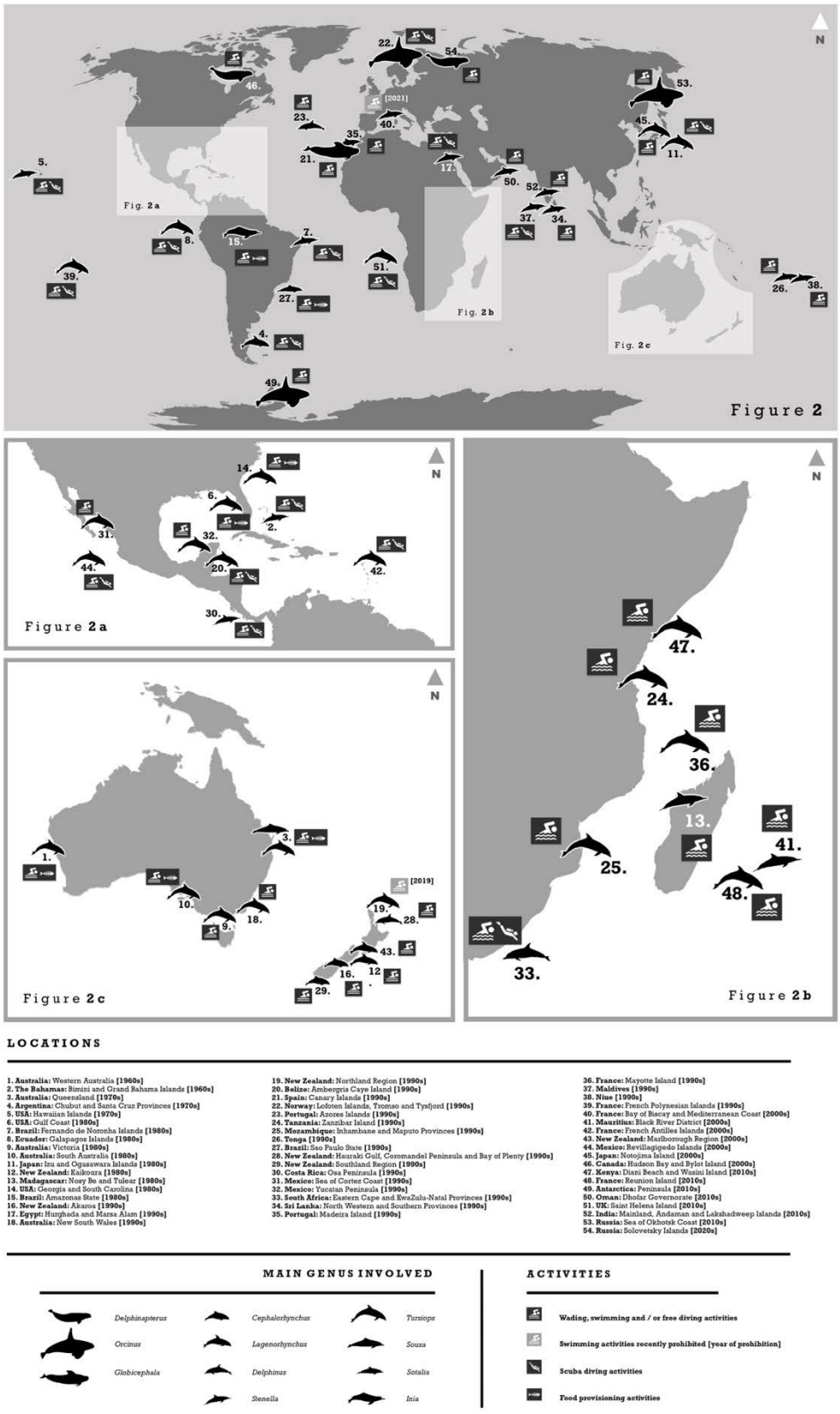

Figure 2. Distribution of locations, activities, and main dolphin genus involved in ongoing activities. The decade when activities began is given in brackets for each location. Locations are numbered chronologically based on accurate or approximate first year of activities.

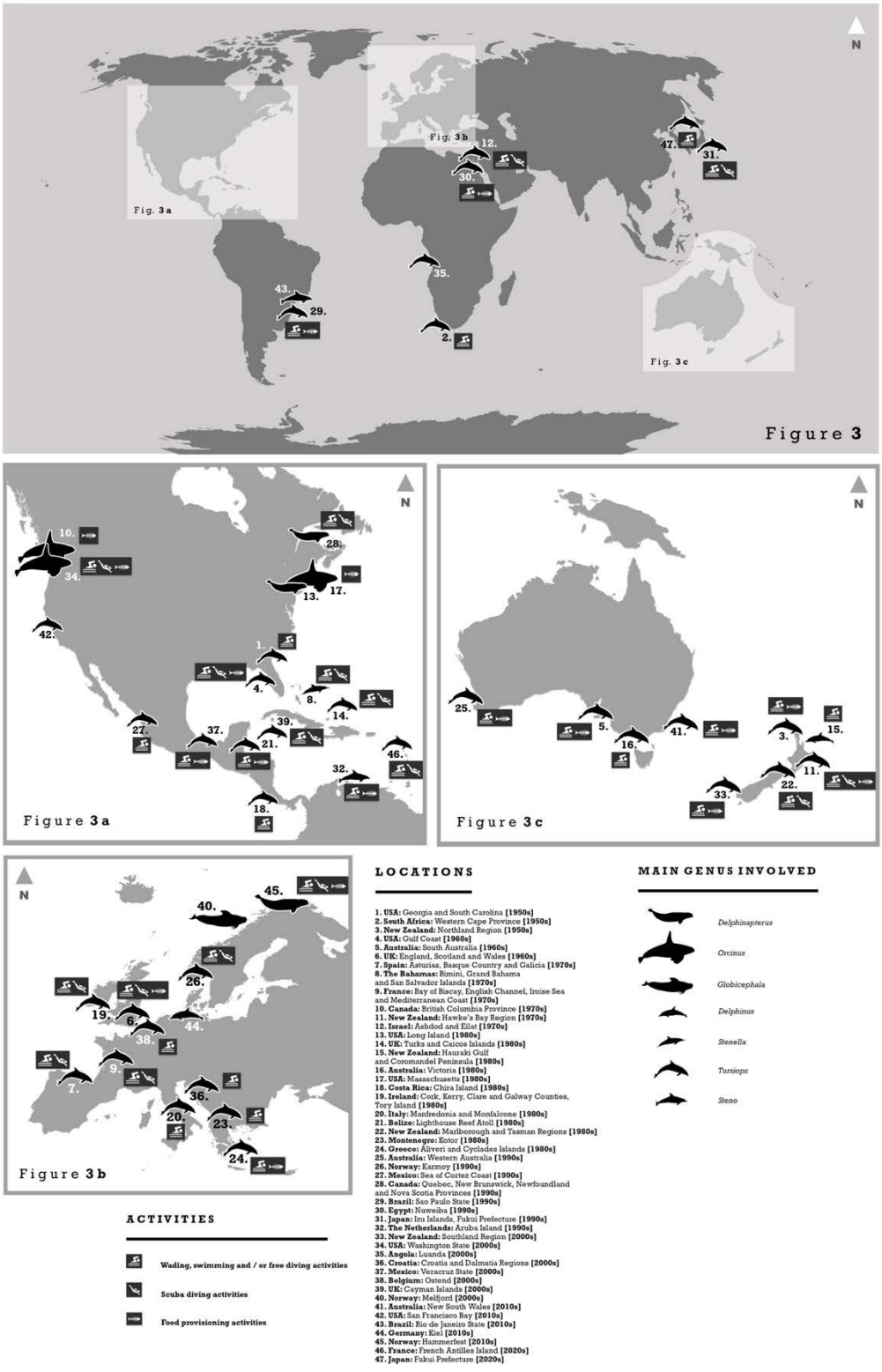

Figure 3. Distribution of locations, activities, and main dolphin genus involved for lone, sociable dolphins. The decade when lone, sociable dolphin(s) were first seen is given in brackets for each location. Locations are numbered chronologically based on accurate or approximate first year of close interactions.

3.2. Species involved in close interactions

Twenty-five species were identified in ongoing activities and 12 species for lone, sociable dolphins. The species most identified in all types of close interactions with humans were bottlenose dolphins [*Tursiops* spp., n=38, (70.4%) locations for ongoing activities; n=37 (78.7%) locations for lone, sociable dolphins].

In terms of individual lone, sociable dolphins, bottlenose dolphins outnumber other species as well (n=99, 73.3%) followed by 19 belugas (*Delphinapterus leucas*) representing 14.1% of all lone, sociable dolphins reviewed.

Spinner dolphins (*Stenella longirostris*) were absent from the lone, sociable dolphins' database but were the second species most identified in ongoing activities (n=19, 35.2% locations). The species is specifically targeted by swim-with and free diving activities.

Other locally abundant species represented major targets for close interactions in ongoing activities (e.g., common dolphins, *Delphinus* spp.; dusky dolphins, *Lagenorhynchus obscurus*; pilot whales, *Globicephala* spp.) while some of them were opportunistically involved in swim-with activities (e.g., rough-toothed dolphins, *Steno bredanensis*).

3.3. Dolphins' and humans' deleterious behaviors

Dolphins' deleterious behaviors documented in the presence of humans and humans' deleterious behaviors documented in the presence of dolphins are detailed for each behavioral category in **Table 2**.

Table 2. Details on dolphins' and humans' deleterious behaviors. Deleterious behaviors are listed per category for ongoing activities and lone, sociable dolphins. Terms lacking precision are shown in quotes.

	FROM DOLPHINS TO HUMANS / HUMAN ACTIVITIES		FROM HUMANS TO DOLPHINS	
	Ongoing activities	**Lone, sociable dolphins**	**Ongoing activities**	**Lone, sociable dolphins**
AGGRESSIVE	Head shaking, jaw clapping, buzzing, charging, grabbing, pulling, biting humans	"Intolerance to humans," "sudden aggression and extreme violence," "dominant," "possessive," "unpredictable," "threat displays," "repelling" and "attacking" humans, emitting high, squeaking sounds, head shaking, jaw clapping, tail slapping, pushing humans down against the seabed, tossing humans clear of the water, splitting couples, pushing roughly, displacing, nipping, hitting, gripping, biting, rushing, ramming, breaching on, ducking, swapping with tail, pulling, dragging humans around, "abducting" humans out to sea	"Injuring," shooting at dolphins	"Threatening," "injuring," hitting, spearing, throwing explosives and shooting at dolphins, dragging dolphin to the beach, trying to tie objects to flippers, killing dolphins
SUBMISSIVE	Avoidance	Avoidance	-	-
SEXUAL	-	Nudging with rostrum at humans' genital area, erection, rubbing genitals against humans, buoys, and boats, thrusting movements directed at humans, ejaculation	-	"Sexual behavior being actively encouraged by swimmers," stroking and provoking dolphins' sexual response
INTRUSIVE	Begging, scavenging, depredating, touching humans, rubbing against boats	Begging, "soliciting physical contact," rubbing against humans, boats, buoys, and ropes, "interest in boats, paddles and oars," putting head or pushing flanks right up against boat engines and spinning propellers, interacting with chains, ropes, buoys and fishing gear, lifting anchors, entangling small boats	"Harassment," chasing, squealing, touching, rubbing, grabbing, holding onto dorsal fin, holding tail, riding dolphins	"Harassment," chasing, circling, touching, rubbing, grabbing, riding dolphin, holding onto fins, hanging on flippers, holding tail, shoving fingers onto blowhole, eyes, and ears, putting objects in blowhole, turning and spinning dolphin, opening dolphin's jaws
ABRUPT	Approaching quickly, circling rapidly, pushy with humans	"Defensive," "boisterous," "snappy," pushy, swimming quickly, circling rapidly, dislodging fin tows, pulling at humans' flippers, nudging, holding humans by the snorkel or facemask, removing facemask, pulling hair, tapping head with rostrum, knocking off surfboards and water-skis, landing on and smashing up surfboards, leaping close to or over humans, preventing humans from returning to shore or vessels, pushing, lifting, bumping, and tossing boats, towing small and large boats	-	Jumping from a bridge on top of dolphin

The proportion of locations where dolphins' and humans' deleterious behaviors were documented is shown for each behavioral category in **Figure 4**.

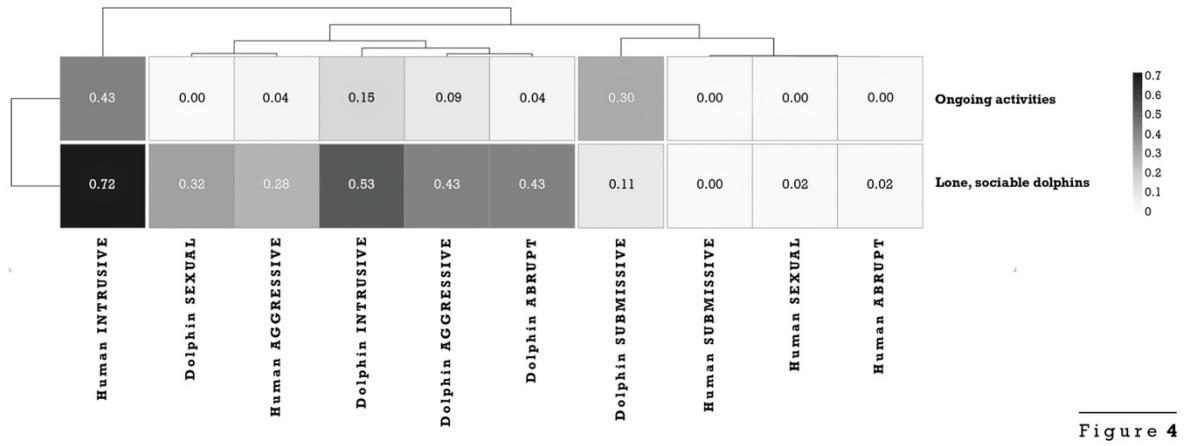

Figure 4. Grayscale cluster heatmap representing the proportion of locations where dolphins' and humans' deleterious behaviors (shown as behavioral categories) were documented. The higher values are being represented by the darkest gray. Rows and columns were ordered according to hierarchical clustering based on average linkage and Euclidean distance.

Overall, the number of locations where dolphin deleterious behaviors were documented is higher for lone, sociable dolphins than for ongoing activities ($n_{lone,\ sociable} = 33$, $n_{ongoing} = 22$; χ^2 test, df = 1, $p < 0.05$). The number of locations where human deleterious behaviors were documented is likewise higher for lone, sociable dolphins ($n_{lone,\ sociable} = 34$, $n_{ongoing} = 23$; χ^2 test, df = 1, $p < 0.05$).

For ongoing activities, human intrusive (n=23, 42.6% locations) and dolphin submissive behaviors (n=16, 29.6% locations) were the deleterious behavioral responses most frequently documented with harassment, touching, and chasing being the most common human intrusive behaviors recorded toward dolphins. Dolphin intrusive behavioral responses were mostly represented by begging behavior in locations where dolphins are food provisioned.

Dolphin aggressive responses to human presence were documented in Western Australia, Fernando de Noronha in Brazil, French Polynesian Islands, Canary Islands and Hawaiian Islands where they were displayed by bottlenose dolphins, short-finned pilot whales (*Globicephala macrorhynchus*) and spinner dolphins. Aggressive behavior from humans to dolphins was documented in two locations (i.e., Western Australia and Gulf Coast in the USA) where dolphins were shot.

For lone, sociable dolphins, human intrusive behaviors (n=34, 72.3% locations) appeared most, and aggressive (n=13, 27.7% locations) human behaviors directed to lone, sociable dolphins were more common than for ongoing activities (n=2, 3.7% locations). Intrusive (n=25, 53.2% locations), abrupt (n=20, 42.6% locations), aggressive (n=20, 42.6% locations) and sexual (n=15, 31.9% locations) dolphin behaviors were likewise more documented than for ongoing activities; they were displayed by both male and female lone, sociable dolphins. No human submissive behavior was recorded either for lone, sociable dolphins or ongoing activities.

3.4. Risks for dolphins and humans

Risks documented for dolphins and humans were tallied with a total of 20 risks documented for dolphins, and five risks documented for humans/human activities. Details on risks and proportion of locations where risks were documented are shown in **Figure 5**.

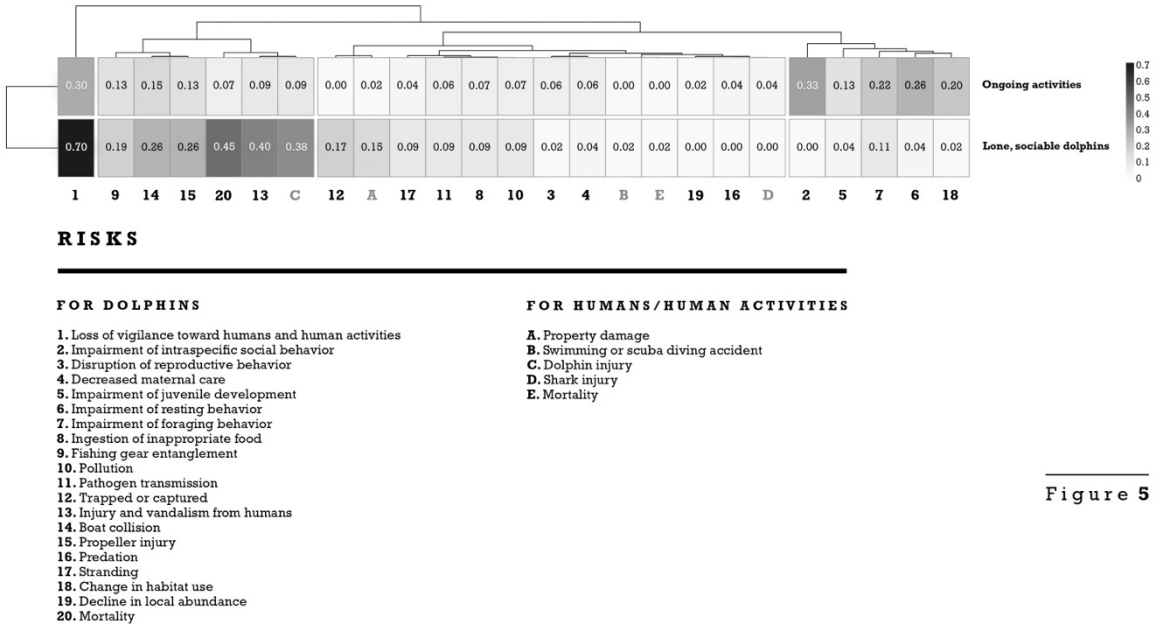

Figure 5. Grayscale cluster heatmap representing the proportion of locations where risks for dolphins and humans were documented. Details on risks associated with close interactions between humans and free-ranging dolphins are reported in legend. The higher values are being represented by the darkest gray. Rows and columns were ordered according to hierarchical clustering based on average linkage and Euclidean distance.

Overall, the number of locations where risks were documented for dolphins is higher for lone, sociable dolphins than for ongoing activities ($n_{lone,\ sociable} = 38$, $n_{ongoing} = 28$; χ^2 test, df = 1, $p < 0.05$). The number of locations where risks were documented for humans is likewise higher for lone, sociable dolphins than for ongoing activities ($n_{lone,\ sociable} = 21$, $n_{ongoing} = 6$; χ^2 test, df = 1, $p < 0.05$).

In addition, the risks most commonly reported for dolphins for ongoing activities are different in nature than those reported for lone, sociable dolphins. In both cases a loss of vigilance toward humans and human activities was reported in dolphins (n=33, 70.2% locations for lone, sociable dolphins; n=16, 29.6% locations for ongoing activities). However, the risks most frequently recorded in ongoing activities were an impairment of social (n=18, 33.3% locations), resting (n=14, 25.9% locations), and foraging (n=12, 22.2% locations) behaviors. A change in habitat use was also documented in 20.4% of the locations reviewed.

For lone, sociable dolphins, mortality (n=21, 44.7% locations), injury and vandalism from humans (n=19, 40.4% locations), and injuries related to interactions with boats (collisions: n=12, 25.5% locations; propeller wounds: n=12, 25.5% locations) were recorded most. In addition, interactions with lone, sociable dolphins involved humans being injured by dolphins in 38.3% of the locations reviewed. One case of swimming accident was recorded in England, UK, where a man entered the water to swim with a lone, sociable dolphin in heavy seas and was trapped under cliffs before being saved by a rescue helicopter and one case of human mortality was recorded in Sao Paulo State, Brazil, and involved a lone, sociable dolphin ramming a man in response to abuse.

4. Discussion

First documented in the 1960s, regular close interactions between humans and free-ranging dolphins during ongoing tourist and other recreational activities increased dramatically since the 1990s, often as part of a new kind of *nature-based mass* tourism (Berle, 1990; Orams, 2002). These programs encompass widely distributed commercial and recreational, structured, and unstructured activities, and involve 22 Delphinid, the two Monodontid (i.e., narwhal, *Monodon monoceros*, and beluga) and one Iniid (i.e., river dolphin) species in at least 54 locations worldwide. They take the form of wading, swim-with, free diving, and/or scuba diving encounters with dolphins, and food provisioning activities.

Lone, sociable dolphins were recorded from the 1950s and involved 10 Delphinid and the two Monodontid species in 47 locations mainly distributed in North and Central America, Europe, Australia, and New Zealand.

Bottlenose dolphins are the primary species documented in any type of close interaction and the most popular in nature-based tourism and other recreational activities involving close interactions between humans and free-ranging dolphins. This is probably due to their wide distribution in coastal waters, rich behavioral repertoire (Lusseau, 2006) and tendency of some individual dolphins to show novelty-seeking behavior in the presence of human activities (Díaz López, 2020).

The spinner dolphin is the second most common species targeted in ongoing activities, but it is absent from the lone, sociable dolphin records. The predominance of spinner dolphins as a focus species in ongoing activities is probably due to the species' intertropical distribution in often shallow-coastal habitats and to its predictable diel behavioral patterns [the dolphins congregate in sheltered bays to rest and socialize during daylight hours (Norris & Dohl, 1980; Tyne *et al.*, 2018; Shawky *et al.*, 2020)].

The number of locations where dolphins' and humans' deleterious behaviors and risks were recorded was higher for lone, sociable dolphins than for ongoing activities. Moreover, except for human intrusive behaviors and a loss of vigilance of dolphins toward humans and human activities that are profusely mentioned in both situations, the deleterious behaviors and risks most frequently documented are different in nature for ongoing activities and lone, sociable dolphins.

For ongoing activities, dolphin submissive behavior (i.e., avoidance of human presence), impairments of social, resting, and foraging activities which are vitally important for the animals' welfare (e.g., Constantine, 2001; Christiansen *et al.*, 2010; New *et al.*, 2013; Senigaglia *et al.*, 2016), and a change in habitat use were relatively frequent. Dolphin intrusive, aggressive, abrupt, and human aggressive behaviors were mostly reported in locations where dolphins are food-provisioned and/or regularly touched by people.

For lone, sociable dolphins, human aggressive and dolphin intrusive, abrupt, aggressive, and sexual behaviors were frequently documented as well as dolphin mortality, injury and vandalism from humans, injuries related to interactions with boats and humans being injured by dolphins. Despite the belief that it is riskless to interact with female dolphins (*pers. obs.*) both male and female lone, sociable dolphins displayed deleterious behaviors toward humans.

This echoes a study conducted on swimmer-dolphin interactions in captivity where Samuels & Spradlin (1995) documented both male and female dolphins engaging in activity that put swimmers at risk.

These results should be interpreted with caution as most references focused on dolphins' rather than humans' behaviors. For example, it is noteworthy that no human submissive behavior was mentioned in all of the literature reviewed as we can presume that dolphin aggressive, sexual and/or abrupt behaviors directed to humans should provoke submissive responses from the people involved, such as flight behavior (Dixon, 1998). In addition, the risks identified for dolphins were more numerous and detailed than those reviewed for humans, which may be due in part to a lack of data sharing from people involved in interactions that did not meet their expectations. Behaviors and risks related to close interactions with lone, sociable dolphins likewise appear to be better documented than those associated with ongoing activities. This might be explained by the relatively easy access to these dolphins by a large number of people, a particularly high degree of tolerance from such animals to human proximity that may evolve into familiarity between both species (Lockyer, 1990; Müller, 1998) and a more contagious spread of communication related to the behaviors (e.g., aggressive, sexual) that may be considered funny or outrageous by the public (e.g., Bloom, 1991; Santos, 1997; Nunny & Simonds, 2019).

Finally, deleterious behaviors and risks associated with close interactions have been well studied in a few countries (e.g., Australia, the United States, New Zealand) from which most information on this subject is available. In many locations (e.g., Caribbean and Pacific Islands, Central America), incidents were scarcely if never reported neither for dolphins nor for humans which could be due to the relatively recent development of these activities and/or the fact that these locations are non or understudied. Consequently, our results are likely to underestimate the actual global increase in anthropogenic pressure on dolphins due to close tourist and recreational interactions and behavioral responses and risks associated over time.

4.1. Risks associated with increased dolphin tolerance to humans and human activities

Most studies did not document dolphin habituation or conditioning (except for Christiansen *et al.*, 2016, and Senigaglia *et al.*, 2019) but a general loss of vigilance concomitant with an increased tolerance toward humans and human activities. Samuels & Bejder (2004) described behaviors such as remaining close to humans and begging as being "indicative of

chronic human interaction." Such behavioral shift was frequently mentioned in lone, sociable dolphins and dolphins that are food-provisioned and/or regularly touched by people where a higher proportion of deleterious human behaviors and risks for dolphins was also documented (Donaldson *et al.*, 2012; Christiansen *et al.*, 2016; Nunny & Simmonds, 2019). It illustrates how increased tolerance can make dolphins more vulnerable to deleterious encounters with humans and human activities.

In addition, the degree of tolerance of one or more dolphins to human presence will often determine the animals' popularity, with over-popularity sometimes leading to an escalation of the dolphins' behavior from punctual tolerance to increased confidence, assertiveness, pushiness, and eventual aggression toward humans (Dudzinski *et al.*, 1995; Orams *et al.*, 1996; de Sá Alves *et al.*, 2011). The risks generated by this process are difficult to control and can lead to serious injury for humans. As a result, a dolphin once considered *friendly* can easily become viewed as a nuisance or threat and deliberately destroyed (Bryant, 1994; Knight, 2009). Food provisioning activities and/or regular physical contact between people and dolphins (e.g., scuba diving tourism at Rangiroa Atoll, French Polynesia, and Socorro Island, Mexico) can speed up the evolution of a *friendly* dolphin into a *trespasser* (Donaldson *et al.*, 2012).

Finally, social learning can facilitate the acquisition of undesirable and maladaptive behaviors by conspecifics (Mazur & Seher, 2008) and impact the fitness and welfare of a biologically significant proportion of a dolphin population (Bejder & Samuels, 2003; Donaldson *et al.*, 2012; Christiansen *et al.*, 2016), with juvenile animals being particularly at risk (Samuels & Bejder, 2004; Cunningham-Smith *et al.*, 2006; Ménard *et al.*, 2013).

4.2. Management of close interactions

Forty years of research completed on the impacts of dolphin watching show that close interactions between dolphins and people, if not properly managed, appear to be another form of pollution that cannot be labelled *ecotourism* (Wall, 1997; Constantine & Bejder 2007; Higham *et al.*, 2009; Ménard *et al.*, 2013).

Human intrusive behaviors were much more documented than any other deleterious behavior in this review and show that management of close encounters with wildlife is chiefly about managing human behavior (Fumagalli *et al.*, 2021).

A general lack of knowledge about the species and behaviors observed, coupled with a natural tendency to anthropomorphism by operators and the general public, maintain the myth

of a friendly and harmless dolphin (Delfour, 2007). In addition, the public will often seek encounters with wild dolphins like those offered by dolphinaria (Samuels & Bejder, 2004; Senigaglia *et al.*, 2020), increasing the potential for inappropriate actions that could lead to a deleterious outcome (Amante-Helweg, 1996; Wilke *et al.*, 2005; Bearzi, 2017).

In the case of ongoing activities, such records have led to the implementation of locally adapted regulations like those developed in Monkey Mia, Bunbury and Tangalooma, Australia (Orams, 1996; Foroughirad & Mann, 2013; Senigaglia *et al.*, 2019). In New Zealand, the Bay of Islands' bottlenose dolphin population became sensitized to swim attempts from commercial swim-with-dolphin boats and increased their avoidance of swimmers (Constantine, 2001), which resulted in a recent ban on swim-with dolphin activities in this area (Fumagalli *et al.*, 2021). In mainland France, swim-with dolphin activities were legally prohibited in 2021 and three companies which had been offering swim-with dolphin tours on the Mediterranean coast for many years were recently sentenced for '*misleading business practices*' and '*intentional disturbance of a protected wild species*' (Le Figaro, 2022). In the USA, swim-with and feeding wild dolphins is illegal under the Marine Mammal Protection Act (Bryant, 1994; Samuels & Bejder, 2004) and tourism industries have long been under pressure to change their ways. In the main Hawaiian Islands, NOAA Fisheries recently published a final rule to prohibit swimming with and approaching spinner dolphins within 45 m to prevent their disturbance (NOAA, 2021).

Nevertheless, all these initiatives are not being successful (Scarpaci *et al.*, 2004; Foroughirad & Mann, 2013; Powell *et al.*, 2018; Senigaglia *et al.*, 2019) and various management indications (summarized in **Table 3**) were suggested in the literature reviewed that should help promoting animal welfare, human safety, and the establishment of sustainable activities.

Table 3. Management indications to promote animal welfare, human safety, and the establishment of sustainable activities are listed with examples given in the literature reviewed.

MANAGEMENT INDICATIONS	EXAMPLES	REFERENCES
Minimization of human intervention	Strongly discourage habituation, conditioning, and any type of interaction with humans; keeping (lone, sociable) dolphin's identity and location a secret.	**Spradlin** *et al.* (1999, 2001); **Wilke** *et al.* (2005); **Corkeron** (2006); **Christiansen** *et al.* (2016); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019)
Precautionary, site-specific, and adaptive management	Consider threats of significant adverse impact on the behavioral patterns or physiological welfare of local dolphin populations, as well as safety concerns for humans; adjust and improve management actions regularly to accommodate new information.	**Higginbottom** *et al.* (2003); **Constantine** *et al.* (2004); **Scarpaci** *et al.* (2004); **Tapper** (2006); **Allen** *et al.* (2007); **Carlson** (2012); **Fumagalli** *et al.* (2019); **Barnhill** *et al.* (2022)
Collaboration between stakeholders	Tour operators, conservationists, academic institutions, government agencies and the local population should show mutual respect, communicate with each other, share information, and monitor current practices to ensure activities are managed sustainably.	**Scarpaci** *et al.* (2004); **Allen** *et al.* (2007); **Lewis & Walker** (2018); **Nunny & Simmonds** (2019)
Easily understood, adapted, and enforced regulations	Permits granted by the appropriate authority; no-go protected areas based on preferred habitats for socializing, resting, feeding; temporal zoning; prohibition of intrusive activities; safety distances; restricted number of operators, vessels, and swimmers; rangers on site; independent inspection of activities; penalties for breaches; publicized enforcement campaigns.	**Green & Higginbottom** (2001); **Birtles** *et al.* (2002); **Constantine** *et al.* (2004); **Scarpaci** *et al.* (2004); **Wilke** *et al.* (2005); **Corkeron** (2006); **Cunningham-Smith** *et al.* (2006); **Allen** *et al.* (2007); **Carlson** (2012); **Christiansen** *et al.* (2016); **Powell** *et al.* (2018)
Scientific monitoring	Evaluation of the environmental, social, and economic carrying capacity of the activity; continuous or regular ecological, biological, and behavioral monitoring of dolphins targeted by activities; evaluation of management effectiveness and limits of acceptable changes.	**Kinsman & Frohoff** (2005); **Corkeron** (2006); **Carlson** (2012); **Lewis & Walker** (2018); **Chazot** *et al.* (2020); **Barnhill** *et al.* (2022)
Education, training, and supervision	Training of tour operators and other stakeholders; comprehensive briefings and guidelines in multiple languages including behavioral information and details on regulation, risks, and the protocol to follow in the water; public campaigns that increase awareness that wild animals should not be assumed to behave as do those in zoos or aquariums; presence of an appropriately trained guide to supervise people, avoid intrusive and disrespectful behaviors to the animals, and act as a valuable conservation agent.	**Sommer** (1972) *in* **Finlay** *et al.*, 1988; **Forestell** (1993); **Orams** (1994); **Kinsman & Frohoff** (2005); **Tapper** (2006); **Curtin** (2010); **Carlson** (2012); **Christiansen** *et al.* (2016); **Bach & Burton** (2017); **Lewis & Walker** (2018); **Nunny & Simmonds** (2019)

Responsible communication	Encourage realistic expectations to avoid disappointment and pressure on animals; discourage inappropriate communication such as guaranteed swim-with experiences, the promotion of illegal activities and greenwashing operations; create a label; promote responsible tour operators.	**Corkeron** (2006); **Pirotta & Lusseau** (2015)
Genuine ecotourism	Promote multi-day tours that give more time to educate the public and relieve the pressure on animals; incorporate other activities to redirect the focus of the tour away from the dolphins; involve the public in data collection through citizen science; provide benefits to local communities.	**Tapper** (2006); **Scarpaci & Parsons** (2014)
Funding of conservation programs	Payment of an entrance and/or permit fee used to fund local conservation programs.	**Kessler & Harcourt** (2010)

4.3. Assessing animal welfare and considering interindividual differences

Caution is warranted when assessing close interactions and their impact on individuals, communities, and populations because of a lack of wild dolphin welfare studies and a lack of consistent management of human behavior toward the animals across interactions.

Physiological indicators (e.g., fecal glucocorticoid metabolites concentration, Millspaugh & Washburn, 2004; Shutt *et al.*, 2014; Mercera *et al.*, 2021) could help objectively assess stress levels experienced by individual animals in the context of repeated interactions with humans, especially in the case of animals that look undisturbed but may physiologically experience high level of stress due to human presence (Gill *et al.*, 2001; Tyne *et al.*, 2018). In addition, the study of certain behaviors (e.g., occurrence of affiliative social behaviors, Clegg *et al.*, 2017) within an animal's repertoire is increasingly believed to be a relevant approach to measure welfare at an individual scale (Clegg & Delfour, 2018) and to pinpoint interindividual differences on various time scales (Martin & Réale, 2008; Díaz López, 2020).

Indeed, interspecific interactions will have disproportionate influences on different individuals depending on a range of factors such as sex, age, kinship, temperament, hormonal state, social relationships, previous experience with humans, current fitness, and life history strategies (Mattson *et al.*, 1992; Lusseau, 2003; Lusseau & Bejder, 2007; Bejder *et al.*, 2009; Higham & Shelton, 2011; Symons *et al.*, 2014; Geffroy *et al.*, 2015). A similar situation may thus be experienced differently by different individuals and impact their welfare in different ways (Olson *et al.*, 1997; Ellenberg *et al.*, 2009).

At one extreme, a bold dolphin may be actively and repeatedly looking for an interaction with humans (Samuels & Bejder, 2004; Martinez *et al.*, 2012). At another extreme, shy individuals may respond to chronic human presence either by staying in suboptimal areas where they will tolerate the stress incurred (Smith & Blumstein, 2013; Tyne *et al.*, 2018), avoiding the source of disturbance (Lusseau, 2003; Shawky *et al.*, 2020) or leaving the location (Bejder *et al.*, 2006). Bold individuals may take more risks and might thus suffer higher mortality (e.g., from boat strikes, retaliatory behaviors from humans, ingestion of inappropriate or contaminated items, Cunningham-Smith *et al.*, 2006; Donaldson *et al.*, 2010; Christiansen *et al.*, 2016; Vail, 2016) than shy individuals (Bremner-Harrison *et al.*, 2004; McDougall *et al.*, 2006; Ménard *et al.*, 2013; Smith & Blumstein, 2013; Geffroy *et al.*, 2015). Integrating temperament into studies of the stress response of wildlife to humans (as suggested by Martin & Réale, 2008) could therefore help better understand the impact of close interactions on free-ranging dolphins.

5. Conclusions

From 1975, the potential impacts of whale and dolphin watching on cetaceans began to be discussed by the International Whaling Commission (IWC, 2018). Studies documenting the behaviors and risks associated with chronic and intrusive human-cetacean interactions have been published since, reiterating findings and suggestions. It would be interesting to conduct a thorough analysis of the extent to which these recommendations were efficiently implemented or not, and for what results. At last, to improve management of these interactions and the safety and welfare of both dolphins and humans, it is essential to consider the unique features of each operation and species observed as well as the contextual and multidimensional aspects of behavioral responses in order to reshape and adapt our modes of interactions while minimizing negative short- to long-term impacts on wildlife.

On the lack of explicit and enforced regulations to manage swim-with dolphin activities: A reply to Simon (2023)

Abstract

Simon (2023) pointed out an incorrect citation of Samuels & Bejder's (2004) article on chronic interactions between humans and free-ranging dolphins in Panama City, Florida, in our review on deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins. The author also provided details on the legality of swimming with wild dolphins under the U.S. Marine Mammal Protection Act (MMPA).

Although the MMPA does not explicitly prohibit swim-with dolphin activities (except in the case of Hawaiian spinner dolphins), we consider that most attempts to swim with wild dolphins correspond to "harassment" as defined in the MMPA. Overall, we state that the lack of adapted, explicit, consistent, and enforced regulations to oversee close encounters between humans and free-ranging dolphins, and numerous beliefs about "anthropophilic" dolphins' behaviors toward humans, clear the way for various (mis)interpretations of existing regulations and of dolphins' behaviors in the presence of swimmers.

Keywords

Cousteau, ecotourism, friendly dolphin, human-dolphin interactions

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We are grateful to Simon (2023) for his useful comments on our review about deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins. We thank the author for providing details on the U.S. Marine Mammal Protection Act (MMPA), and we apologize for our misinterpretation of Samuels & Bejder's (2004) comment on the legality of swimming with wild dolphins in U.S. waters.

It is a confusing topic. The MMPA clearly states that it is prohibited to feed or attempt to feed marine mammals in the wild, but the term "harassment" that can apply to swim-with

dolphin activities cannot be interpreted unequivocally. The NOAA Fisheries website specifies that Level B harassment refers to any act of "pursuit, torment, or annoyance which have the *potential to disturb* a marine mammal (…) in the wild by causing disruption of behavioral patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding, or sheltering." It also states that "interacting with wild marine mammals should not be attempted" (NOAA, 2022a). As noted by Simon (2023), "NOAA Fisheries Service does not support, condone, approve, or authorize activities that involve closely approaching, interacting, or attempting to interact with whales, dolphins, seals, or sea lions in the wild." This statement is supplemented by the following sentence: "This includes attempting to swim with, pet, touch, or elicit a reaction from the animals." Finally, the NOAA guidelines recommend to "avoid touching or swimming with wild marine mammals, even if they approach you."

Few commercial and non-commercial activities dedicated to close in-water encounters with dolphins in their natural habitat involve people behaving passively in the presence of dolphins. Swimmers usually approach or attempt to attract dolphins with postures, gestures, and sounds. According to the definitions provided on the NOAA website, such human behaviors can be referred to as "harassment" and are thus illegal.

Moreover, different studies carried out in the U.S. and elsewhere demonstrated that swim-with dolphin activities have the *potential* to disrupt behavioral patterns (e.g., Danil *et al.*, 2005), particularly when coastal and resident dolphins experience intense viewing pressure like in the Red Sea (Fumagalli *et al.*, 2018) or in Mozambique (Rocha *et al.*, 2023). In their study on the Bay of Plenty common dolphins, Meissner *et al.* (2015) noted that their research "raises concerns about the *potential* disruption to feeding, a biologically critical behavior."

However, except for the recent decision to prohibit swim-with spinner dolphin activities in Hawaiian waters, and disapproval mentioned on any attempt to interact and swim with wild dolphins, there is indeed no explicit U.S. regulations prohibiting such activities. This situation not only opens the door for various subjective interpretations of the MMPA but the lack of enforcement, some conditioned dolphins' behaviors, and the "flow of people" (as stated by Simon) who wish to closely interact with free-ranging dolphins do not encourage tour operators and the general public to exercise restraint in the presence of dolphins. On the NOAA website, we can read: "(…) Close interactions between humans and spinner dolphins continue to occur despite the prohibitions, guidelines, outreach, and stewardship efforts that were already in place.

(…) We have determined that additional regulations are required to protect Hawaiian spinner dolphins from activities that result in harassment and other forms of disturbance."

This situation is not unique to the U.S. For example, the French Polynesian "Code de l'Environnement" stipulates that it is strictly forbidden to "intentionally disrupt" the natural development of protected wild species and associated ecosystems. Intentional disruption refers to "any human action that might modify the natural behavior of a wild animal for entertainment purposes." At the same time, the French Polynesian "Arrêté n°466CM" specifies that we must respect a safety distance of 30 meters with wild dolphins "except if the dolphins voluntarily reduce the distance between them and humans" (Code de l'Environnement de la Polynésie française, 2017).

As Simon (2023) said, "this language undoubtedly is well intended." Still, these regulations are vague, not being enforced, and clear the way for various interpretations. For example, scuba diving tourism in Rangiroa, French Polynesia, has been encouraging daily physical contacts with protected common bottlenose dolphins for about 20 years. Tour operators and scuba divers justify these activities stating that "the dolphins are coming to divers on their own." Yet, long-term observations show that these dolphins' behaviors have been actively modified by scuba divers' behaviors over time "for entertainment purposes."

We agree with Simon (2023) on the dolphins being victims of their own popularity. Numerous beliefs about "anthropophilic" dolphins' behaviors toward humans motivate the public to look for up-close encounters and encourage operators to offer intrusive tours and-or to familiarize dolphins to repeated human presence (e.g., through conditioning) without concrete limitations or knowledge on the animals' behaviors (Fraser *et al.*, 2006; Wiener, 2015).

"Only the dose makes the poison" (Paracelsus, 1538 *in* *The third defense in writing new prescriptions*, p510). It may be the choice of some dolphins to approach humans, but to our knowledge there is no study that demonstrated precisely which (non-provisioned) individual dolphins are involved in affiliative interactions with humans, in what contexts, and what are these animals' behaviors and fate on the medium- to long-term. In addition, we raise doubts about the dolphins' ability to understand the concept of "mutual respect" considered by Taylor & Carter (2013). Dolphins will undoubtedly give meaning to their surroundings, but a situation "that fulfills human aesthetic standards does not guarantee that animals will act, perceive, or enact" a world like the ones of humans who want to interact with them (Delfour, 2010).

In their time, Cousteau and his team undertook amazing pioneering work, but their activities also faced criticism for environmental damage, mistreatment and killing of marine life including dolphins (*Cf.* Cousteau & Malle, 1956; Landsburg & Cousteau, 1972).

To conclude, many operators and agencies are now promoting "ecotours" or "ecotourism", making it difficult for the public to disentangle ethical activities from greenwashing. Education has long been put forward as a necessary tool to induce changes in the people's expectations and behaviors (Orams, 1994) but it must complement adapted, explicit, consistent, and enforced regulations.

Chapter 3

Free-ranging bottlenose dolphins' tolerance to scuba diving tourism is modulated by their age, social context, and by the divers' behaviors

Abstract

Marine wildlife tourism encouraging close human-dolphin encounters generates short- to long-term behavioral changes in the animals targeted and may promote some dolphins' increased tolerance and habituation to humans. Yet, little is known on the tolerance status of individual dolphins targeted by tourism.

We carried out sequential shore-based and underwater sightings of 18 non-provisioned bottlenose dolphins (*Tursiops truncatus*) exposed to scuba diving tourism for at least one year in Rangiroa Atoll, French Polynesia, to understand how individual dolphins' cumulative experience with tourism influenced their tolerance to humans.

We compared the dolphins' sighting rates in a diver-free area and in the presence of divers, and measured the occurrence of, and consistency in, the dolphins' neutral behaviors in the close (i.e., <10m) presence of scuba divers. We also tested the influence of sex, sexual maturity, tourist-site fidelity, the number of divers, and the number of dolphins on the dolphins' tolerance to divers and quantified the relationships between the dolphins' avoidance behaviors and three divers' behaviors [i.e., actively approaching dolphins, holding hand(s) out to dolphins, swimming after dolphins].

Our results indicated that the dolphins are habituated to the presence of scuba divers on the tourist site and that they tolerate the close presence of divers. Yet, their tolerance is modulated by their age, social context, and by the divers' behaviors. Immature dolphins responded more positively to scuba divers than mature individuals, the dolphins showed more neutral behaviors when the number of dolphins was high, and the more the divers displayed held-out-hand and swim-after-dolphin behaviors, the more the dolphins displayed avoidance behavior. In addition, we documented interindividual variation in the dolphins' tolerance to scuba divers.

These results suggest that young dolphins may be more prompt to take risks than mature individuals in the context of tourist activities and that temperament traits might influence these dolphins' responses to tourism. Moreover, they highlight the need to enforce optimal management strategies to curb intrusive practices from tour operators, guides, and tourists.

Keywords

Behavioral plasticity, dolphin behavior, habituation, human-dolphin interaction, tolerance, wildlife tourism

1. Introduction

Wild animals are regularly exposed to both familiar and unfamiliar stimuli in their environment, and their ability to adapt ultimately results in increased fitness and both individual and species survival (Lopes *et al.*, 2016). If perceived as beneficial, stimuli can lead to attraction (Goldberg, 2010). If perceived as aversive, they can elicit avoidance and-or agonistic responses (e.g., aggression, Knight, 2009) and potentially lead to sensitization (Broom & Johnson, 2019, p19). When a repetitious or continuous stimulus is perceived as neutral (i.e. neither beneficial nor aversive) behavioral responsiveness usually decreases over time in a non-associative learning process called habituation (Thorpe, 1963; Bejder *et al.*, 2009).

The human footprint is noticeable across the globe (Sanderson *et al.*, 2002) and virtually all wildlife is now facing human-induced stimuli in their environment (Abrahms *et al.*, 2023). When first approached by humans, almost all wild animals exhibit marked avoidance behaviors (Price, 1984; Beale, 2007) but such avoidance can be reduced over time and animals can become habituated to non-threatening humans (Price, 1984; MacSweeney & Murphy, 2009), human-made environments (Whittaker & Knight, 1998; Samia *et al.*, 2015), and human disturbance (i.e., any human activity that changes the contemporaneous behavior or physiology of one or more individuals, Nisbet, 2000; Bejder *et al.*, 2009).

Avoidance distance, also called flight initiation distance (i.e., the distance between an approaching human and a focal animal at which the latter flees, Tarlow & Blumstein, 2007) is frequently used to determine species- and individual-specific thresholds of tolerance to human presence and human disturbance (e.g., Fowler, 1999; Tarlow & Blumstein, 2007; Saltz *et al.*, 2018). For example, Martínez-Abraín *et al.* (2008) used flight initiation distance to demonstrate that yellow-legged gulls (*Larus michahellis*) showed marked tendency to habituate rapidly to human visitors if they move along well-established pathways.

However, wildlife responses to humans are influenced by a range of factors (e.g., extent and intensity of human activities, Szott *et al.*, 2019; humans' approach distances and behaviors, Geffroy *et al.*, 2017) and different species and individuals respond differently to human presence and disturbance (Carrete & Tella, 2013; Geffroy *et al.*, 2015). For example, black

(*Ursus americanus*) and grizzly (*Ursus arctos horribilis*) bears can occupy areas of intense human use while still avoiding people (Mattson *et al.*, 1992; Whittaker & Knight, 1998) while Rottnest Island quokkas (*Setonix brachyurus*) are described as 'tame', 'unperturbed by human activity', and regularly approached by tourists who touch the animals (Worrell *et al.*, 2017). Yellow-eyed penguins (*Megadyptes antipodes*) differ significantly in their habituation potential to wildlife tourism, and individual variation depends on previous experience with humans, sex, and temperament traits (Ellenberg *et al.*, 2009).

Generalists or more flexible organisms should adjust better to changes provoked by human presence than specialists or less flexible ones (Sih, 2013). The social bottlenose dolphins (*Tursiops* spp.) exhibit high level of behavioral plasticity (Weaver, 2021), imitative ability (Marino, 2004), and some of these dolphins' behaviors are known to be transmitted within matrilines (Krützen *et al.*, 2005). Different studies documented avoidance behaviors in bottlenose dolphins repeatedly engaged with tourist activities (e.g., Constantine, 2001; Lusseau, 2003), but individual dolphins can habituate to non-threatening human presence as well (Hunter Jr. *et al.*, 2021). Moreover, even though no study formally demonstrated habituation to human presence in free-ranging dolphins, some bottlenose, Atlantic spotted (*Stenella frontalis*) and Hector's (*Cephalorhynchus hectori*) dolphin groups are considered as habituated to recurrent human visitation (Connor & Smolker, 1985; Stone & Yoshinaga, 2000; Kogi *et al.*, 2004; Herzing *et al.*, 2012).

Increased wildlife tolerance and habituation to humans may promote positive interspecific interactions, but also increase the potential for negative outcomes for both the animals and humans (Geffroy *et al.*, 2015; Uchida *et al.*, 2023). For example, there is evidence that primates habituated for tourist viewing are at greater risk from poaching than non-habituated individuals (Kasereka *et al.*, 2006) and that tourists can serve as vectors for several diseases that can be harmful to wildlife (Murray *et al.*, 2016; Shannon *et al.*, 2017). In Australia, calves born to provisioned female bottlenose dolphins (*Tursiops aduncus*) experienced reduced care and higher mortality relative to calves of non-provisioned mothers (Mann & Kemps, 2003). Accordingly, measuring tolerance to human disturbance is an essential first step to properly regulate human-wildlife interactions (Uchida *et al.*, 2023).

Here, we aimed at understanding how free-ranging non-provisioned bottlenose dolphins' (*Tursiops truncatus*) cumulative experience with scuba diving tourism influenced their tolerance to scuba divers.

We carried out sequential shore-based and underwater focal observations (Altmann, 1974) of dolphins regularly exposed to scuba divers for at least one year to quantify **1)** their habituation to the presence of divers on the tourist site, and **2)** their tolerance to divers who displayed active, often intrusive, behaviors toward them [e.g., actively approaching dolphins, holding their hand(s) out to dolphins, swimming after dolphins]. Also, we investigated the influence of sex, sexual maturity, tourist-site fidelity, the number of divers and the number of dolphins on the dolphins' tolerance to divers.

2. Methods

Definitions of terms used in this paper are available in **Table 1**.

Table 1. Glossary.

TERM	DEFINITION
Avoidance behavior	Withdrawal response in the presence of an unpleasant, distressing, or threatening stimulus (Goldberg, 2010). We considered that a dolphin displayed avoidance behavior when it withdrew from scuba divers.
Habituation	We understand habituation here as an adaptation to human presence in a way that humans are not seen as potential predators but are essentially ignored (Ellenberg *et al.*, 2009).
Neutral behavior	No overt behavioral response in the presence of divers. Here, it indicated dolphin tolerance to scuba divers.
Tolerance	The intensity of disturbance that an individual tolerates without responding in a defined way (Nisbet, 2000). Here, the disturbance is the presence of scuba divers.

2.1. Study area and population

Rangiroa Atoll (S14°58 × W147°37) lies in an oligotrophic oceanic environment in the northwestern Tuamotu Islands, French Polynesia (Carzon *et al.*, 2016; Vollbrecht *et al.*, 2021). Its northern reef hosts about 30 bottlenose dolphins which inhabit the outer slope, the two channels connecting the open ocean to the lagoon (locally called 'passes'), and the lagoon of the atoll (Carzon, 2017). Tiputa pass is a local biological hotspot traversed by strong tidal currents where the dolphins can be observed from shore as they come daily to surf and leap into

breaking waves created by currents that move from the lagoon to the ocean (Carzon, 2017; Vollbrecht *et al.*, 2021).

Our small (i.e., about 1km²) study area is centered around Tiputa pass and its close surroundings which are hotspots for human activities as well (i.e., shipping, yachting, fishing, and tourism, **Figure 1**). Tourist activities include daily boat-based dolphin watching, snorkeling and scuba diving tours that take place throughout the year and rely on the presence of the easily accessible dolphins. Indeed, despite the implementation of local regulations to supervise cetacean viewing in French Polynesia in 2002, scuba divers have been encouraging close interactions with the dolphins for about two decades using postures, gestures, objects and sounds, and the dolphins' increasing tolerance to humans offers opportunities for underwater observations performed with good to excellent water clarity (i.e., often >30m, Carzon *et al.*, 2019).

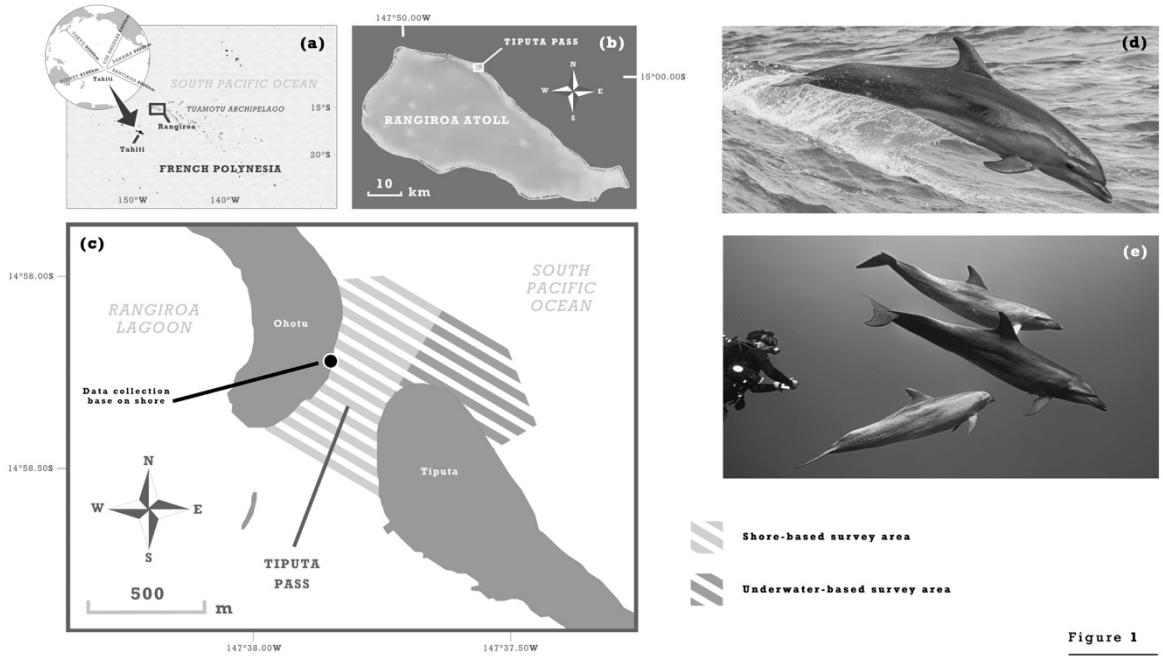

Figure 1(a) Location of Rangiroa Atoll in French Polynesia. **(b)** Close view of the atoll. **(c)** Detailed map of Tiputa pass and its surroundings showing the shore- and underwater-based survey areas. **(d)** Example of shore-based dolphin sighting. **(e)** Example of underwater dolphin sighting.

2.2. Sampling protocol

We used data collected from shore and underwater over three years in 2018, 2019 and 2020 (before and after the two-month COVID-19 lockdown). The shore and underwater datasets were compiled separately, and in both cases one day was considered an independent sampling period.

Shore-based data were collected into Tiputa pass' waves during 1:30 sighting sessions conducted over 196 sampling periods between April 2018 and December 2020 [**Supplemental data, Table 1(a)**]. The dolphins were photographed with full frame DSLR cameras equipped with 100-400mm lenses to check for the presence and absence of individuals. Tiputa pass' waves are dangerous for humans. As such, they are never purposefully frequented by scuba divers and were therefore considered a diver-free area.

Underwater video data were collected over 204 sampling periods between February 2018 and December 2020 [**Supplemental data, Table 1(b)**]. Our goals were to identify the dolphins on view, to tally the number of dolphins and scuba divers, to approximate distances between the dolphins and divers, and to record the dolphins' and scuba divers' behaviors in the presence of each other. The lead author and two dedicated scuba diver observers were trained to simultaneously take high-resolution video footage of the dolphins while diving together as part of commercial dives including diving instructors and tourists. The lead author used a full frame DSLR camera equipped with a 16-35mm lens, and the two observers filmed with action cameras. If dolphins were seen during a dive, the lead author and observers had to film them from the moment the first dolphin was spotted by the divers until the last dolphin could not be sighted anymore to obtain what is referred to as a 'dolphin sighting'.

2.2.1. Determination of the dolphins' sex and sexual maturity status

A longitudinal study of the dolphins was initiated in 2009 and we took advantage of previous data collected over ten years. Natural markings were used to identify the dolphins (Wells & Scott, 1990) and the sex of all individuals was determined by direct observation of their genital area. We considered the dolphins as being either sexually mature or sexually immature (hereafter 'mature' and 'immature'). Mature females were seen at least one time pregnant, showing prominent mammary glands, and-or regularly escorted by the same calf. We considered males over ten years old as being mature (Mead & Potter, 1990; Wells, 2014).

Immatures from both sexes were not showing any of the aforementioned characteristics across the three-year study period.

2.2.2. Determination of the dolphins' tourist-site fidelity

Individual shore-based sighting rates were calculated for each dolphin as the proportion of the total number of sampling periods a dolphin was captured from shore on the total number of shore-based sampling periods across the three years.

Hierarchical cluster analysis (Ward's method) was performed on the sighting rates using *hclust* function in R and the associated dendrogram was cut into two clusters to assign each dolphin to a fidelity category (i.e., 'resident' or 'non-resident' on the tourist site).

2.3. Dolphin habituation to scuba divers

We used the dolphins' sighting rates in the absence and presence of scuba divers as a proxy to document their habituation to the presence of divers. Annual individual shore-based (i.e., in the absence of divers) and underwater (i.e., in the presence of divers) sighting rates were calculated for each dolphin following the procedure detailed in the subsection *Determination of the dolphins' tourist-site fidelity*. Underwater sighting rates were calculated as the proportion of the number of sampling periods a dolphin was captured underwater on the total number of underwater sampling periods on a given year.

We compared the results of two different methods (i.e., Spearman's rank correlation using *cor.test* function and the R package *spearmanCI*, and permutation tests using the R package *lmPerm*) to check for a correlation between shore-based and underwater sighting rates in each of the three years and to identify dolphins that might be rarely if ever captured underwater. Such dolphins would not be considered as habituated to the presence of scuba divers.

2.4. Underwater data extraction and analysis

The next analyses were performed using the underwater dataset only. We selected the dolphins which were sighted at <10m from scuba divers on at least ten sampling periods over the three years, and on at least one sampling period each year, to assess consistency in their behaviors over time. One immature resident female (i.e., TP40) died prematurely at age 5 in

July 2019 and was the only individual included that was present on two years instead of three for a total of 50 sampling periods. We decided to keep it as it had been sighted on a regular basis before it died.

To approximate distances between dolphins and scuba divers, we estimated Rangiroa dolphins' lengths from Sergeant *et al.* (1973) considering that they are slightly bigger than Florida bottlenose dolphins: adult male (2.8m), adult female (2.6m), immature ≥5 years (2.4m), and immature <5 years (2.0m). We used these lengths to visually estimate distances between a dolphin and divers, and single observations filmed simultaneously by two or three cameras to estimate distances between a dolphin and the cameramen on the cameramen's videos.

The occurrence, frequency, and duration of each dolphin's neutral and avoidance behaviors displayed at <10m from scuba divers, and all divers' behaviors directed to each dolphin, were logged in a database, and used as proxies to document dolphin tolerance to scuba divers.

We categorized the divers' behaviors toward the dolphins as being either 'active' or 'passive' (Gómez-García *et al.*, 2021). Passive divers remained still and did not emit any sound in the presence of dolphins.

Seven diver behaviors were identified and grouped into the active category: **1)** actively approaching dolphins (76.6% of sightings), **2)** making sounds in regulator, using shaker and-or knocking on tank (74.3% of sightings), **3)** holding hand(s) out to dolphins (57.2% of sightings), **4)** swimming after dolphins which are moving away (46.5% of sightings), **5)** spinning around (22.3% of sightings), **6)** swimming like dolphins (22.0% of sightings), and **7)** presenting object (i.e., a glove) to dolphins (5.5% of sightings). We discarded the sightings with passive divers only and retained the sightings where at least one diver displayed any active behavior in the presence of dolphins.

To minimize sampling bias, we used the *sample* function in R to randomly choose ten sightings per dolphin taken from ten independent sampling periods over the three years (**Supplemental data, Table 2**).

2.5. Dolphin tolerance to scuba divers

We expected tolerant dolphins to consistently display neutral behavior at <10m from active divers, and on more than 50% of the individual sighting durations.

We used a stacked bar plot to visually check the proportion of time each dolphin displayed neutral responses over the ten randomly chosen individual sightings. The total individual sighting durations were used as the denominators.

To assess consistency in the dolphins' neutral responses, we then used the proportion of time each individual displayed neutral behavior at <10m from active divers on each of the ten sightings and calculated the intraclass correlation coefficient (ICC2, i.e., two-way random-effects model with both subjects and sightings considered as random effects, Koo & Li, 2016) using the R package *psych*.

2.6. Effects of five variables on the dolphins' tolerance to divers

We estimated the influence of sex, sexual maturity, tourist-site fidelity, the number of divers and the number of dolphins on the proportion of time each dolphin displayed neutral behavior at <10m from active scuba divers on each of the ten individual sightings. We fitted two Bayesian beta regression mixed-effects models (R package *brms*, Bürkner, 2017) to account for the data hierarchical structure and response variable bounded at 0 and 1 (Douma & Weedon, 2019). Sex, sexual maturity, and tourist-site fidelity modalities were included as predictors in the first model, and the number of divers and the number of dolphins in the second model.

The beta distribution excludes the extremes 0 and 1 therefore we chose to transform the data according to the following equation so that it can be used:

$$y^* = \frac{y(n-1) + 0.5}{n}$$

with y being the response variable for a given sighting and n the total number of observations in the dataset (Zuur *et al.*, 2013).

Sex, sexual maturity, site fidelity, the number of divers and the number of dolphins were considered as population-level effects, and individual dolphins as a group-level effect. Population-level and group-level effects were given uninformative priors. The distributions of

the parameters of the models were estimated using Markov chain Monte Carlo (MCMC) algorithms and the estimates of the coefficients were based on samples from the MCMC chains. We fitted the models using four chains. Models were run for 10 000 iterations with a thinning interval of one and a burn-in period of 5 000 iterations. Model convergence was examined by visualizing trace plots that should appear stationary and well-mixed (Douma & Weedon, 2019) and the $\hat{R}$ value that should not be larger than one (Bürkner, 2017). Every parameter was summarized using the mean and the standard deviation of the posterior distribution as well as two-sided 95% credible intervals based on quantiles (Bürkner, 2018). Population-level effects were considered significant if the associated credible intervals of the posterior distribution did not cross zero.

2.7. Dolphin avoidance behavior

We expected dolphin avoidance to be related to specific divers' behaviors. We therefore selected three divers' behaviors which were assumed to be particularly intrusive at close distance: **1)** divers actively approaching dolphins (DAP), **2)** divers holding their hand(s) out to dolphins (HOU), and **3)** divers swimming after dolphins which are moving away (SAD).

We used the number of DAP, HOU, and SAD behaviors displayed toward each dolphin on each of the ten individual sightings as predictors. The number of avoidance behaviors displayed by each dolphin was used as the response variable.

The response variable showed obvious zero-inflation thus we decided to fit a Bayesian zero-inflated Poisson model using four chains, 2 000 iterations, a thinning interval of one, and a burn-in period of 1 000 iterations (Bürkner, 2018). As sample size was small, we did not include any group-level effect for the model to converge properly. We thus assumed a constant zero-inflation probability across individuals.

All statistical analyses were performed on R 4.3.0 (R Core Team, 2023).

Ethical Note

We only carried out careful free-ranging dolphins' shore-based and underwater observations at distance that fully adhere to the French Polynesian regulations. No dolphin was touched or otherwise harassed by the lead author and our observers. Since the study did not require any manipulation or handling of the animals, the local authorities contacted for this purpose did not consider it appropriate to grant a specific permit.

3. Results

Thirty-three different dolphins were identified over the course of the study: 32 from shore and 31 underwater. Three dolphins captured one or two times and five calves born over the study period were discarded from the datasets. The remaining 25 individuals were captured from shore between seven and 126 sampling periods (median=48) and used to carry out the analyses detailed in the subsections *Determination of the dolphins' tourist-site fidelity* and *Dolphin habituation to scuba divers*.

Eighteen individuals were selected for the underwater analyses including eight males, ten females, 11 mature, and seven immature dolphins (**Supplemental data, Table 2**). These dolphins were captured underwater at <10m from active scuba divers between 11 and 109 sampling periods (median=24.5). The sex-ratio of the immatures was strongly biased in favor of females (SR=0.17).

The underwater dataset contained 381 sightings including 360 sightings where at least one diver displayed active behavior in the presence of dolphins (**Supplemental data, Tables 3a, 3b, and 4**).

3.1. Determination of the dolphins' tourist-site fidelity

A clear break was visible on the dendrogram with all shore-based sighting rates being either ≤0.25 or ≥0.41 (**Supplemental data, Table 5 and Figure 1**). The 12 dolphins with sighting rates ≤0.25 were considered as non-residents and the 11 individuals with sighting rates ≥0.41 were considered as residents. Two calves were then assigned to their mothers' categories (i.e., one resident and one non-resident).

3.2. Dolphin habituation to scuba divers

The correlations between individual shore-based and underwater annual sighting rates were positive, high, and significant (**Table 2**) indicating that each dolphin was captured similarly in the absence and presence of divers in 2018, 2019 and 2020. The 25 dolphins regularly observed from shore were thus considered as habituated to the presence of scuba divers on the area.

Table 2. Results of Spearman's rank correlations and permutation tests used to compare the dolphins' shore-based and underwater annual sighting rates.

	Spearman's ρ	Spearman's ρ 95%CI	*p*-values from Spearman's rank correlations*	Coefficient estimates from permutation tests	*p*-value from permutation tests*
2018 (n=25)	0.84	0.73 – 0.94	1.588^{e-07}	0.60	$< 2^{e-16}$
2019 (n=25)	0.88	0.79 – 0.97	5.124^{e-09}	0.78	
2020 (n=24)	0.91	-	4.527^{e-10}	0.84	

*Analyses based on the 0.05 significance level

3.3. Dolphin tolerance to scuba divers

The stacked bar plot revealed a majority of neutral behaviors in the 18 dolphins, except for two immatures (i.e., TP31 and TP48) which mostly displayed affiliative behaviors toward scuba divers (**Figure 2**).

The ICC results showed moderate to excellent consistency in each dolphin's proportion of neutral behaviors over the ten sightings (κ=0.79, 95%CI=0.60 – 0.91, *P* value<0.05). The 18 dolphins were thus considered to tolerate active scuba divers at <10m.

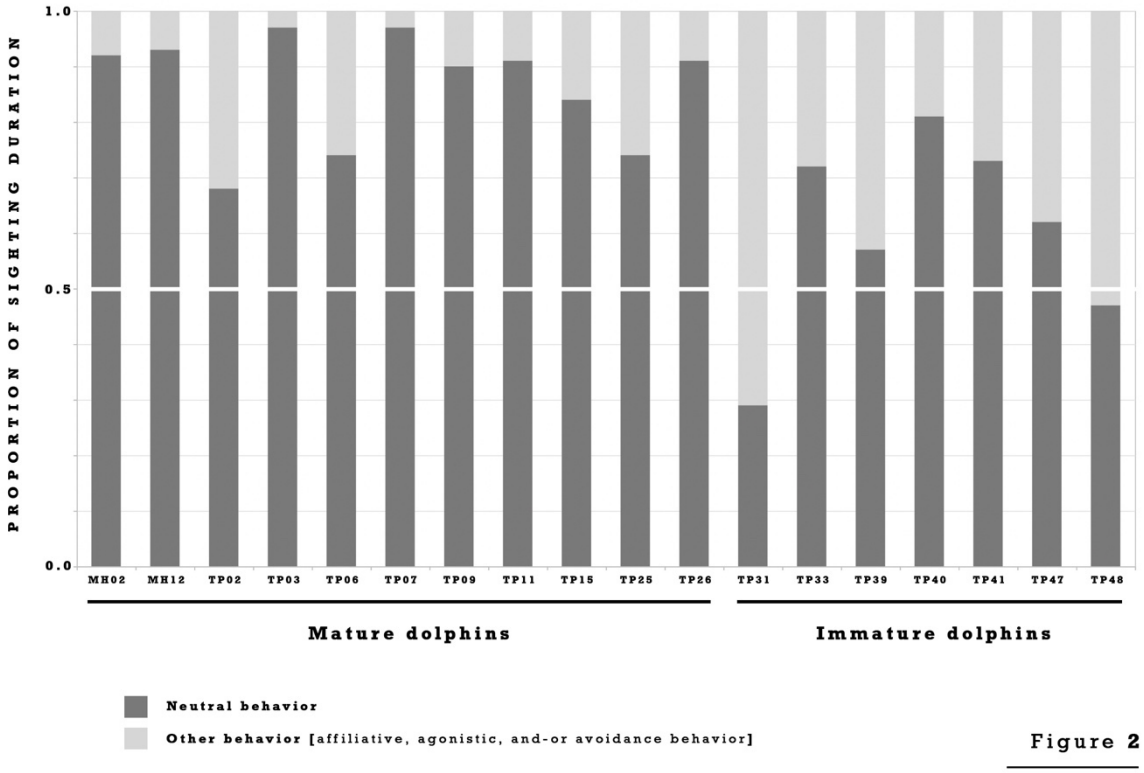

Figure 2. Proportion of sighting duration each dolphin displayed neutral behavior at <10m from active scuba divers in ten individual sightings randomly chosen over 2018, 2019 and 2020. The 50% threshold is shown as a white line.

3.4. Effects of five variables on the dolphins' tolerance to divers

The results of the mixed-effects models are presented in **Figures 3** and **4**. Mixing of chains was good ($\hat{R}$ values=1.00) in both models. According to the model parameter estimates, two predictors had a significant bearing on the dolphins' tendency to display neutral behavior: sexual maturity and the number of dolphins. Immature dolphins displayed fewer neutral behaviors than mature ones, and more neutral behaviors were documented when higher numbers of dolphins were observed. All other estimates lacked statistical significance therefore the study did not demonstrate any influence of sex, tourist-site fidelity, and of the number of divers on the occurrence of dolphin neutral behavior. Additionally, interindividual variation was documented in the dolphins' proportion of time spent displaying neutral behavior in the presence of scuba divers [**Figure 3(c)**].

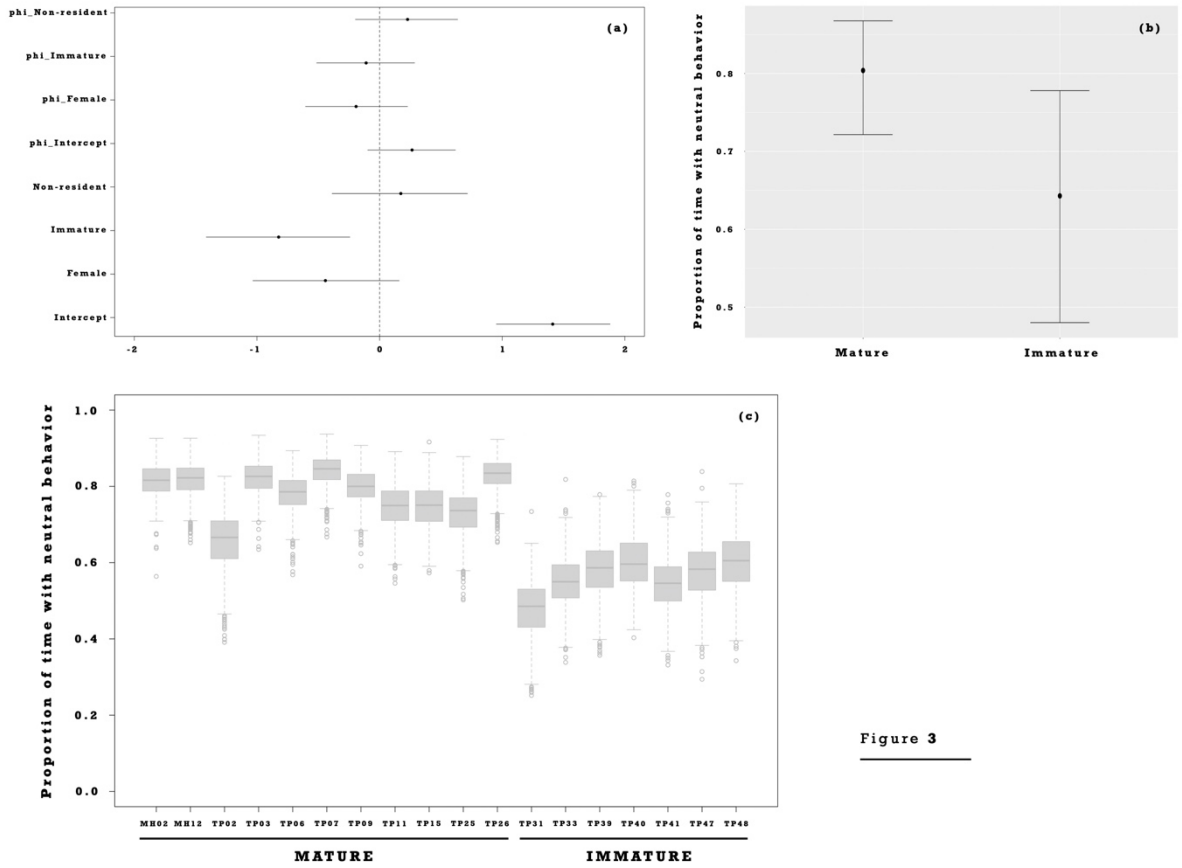

Figure 3

Figure 3(a) Parameters (population-level effects) of the model y ~ SEX + MATURITY + FIDELITY + (1 | ID) with μ=logit and ϕ=log using the proportion of time each dolphin (n=18) displayed neutral behavior in ten randomly chosen sightings as the response variable, and sex, sexual maturity and tourist-site fidelity as categorical predictors, and their credible intervals. **(b)** Conditional effect of categorical predictor 'maturity' on the dolphins' proportion of neutral behaviors. **(c)** Aggregation of the posterior fitted values predictions per individual.

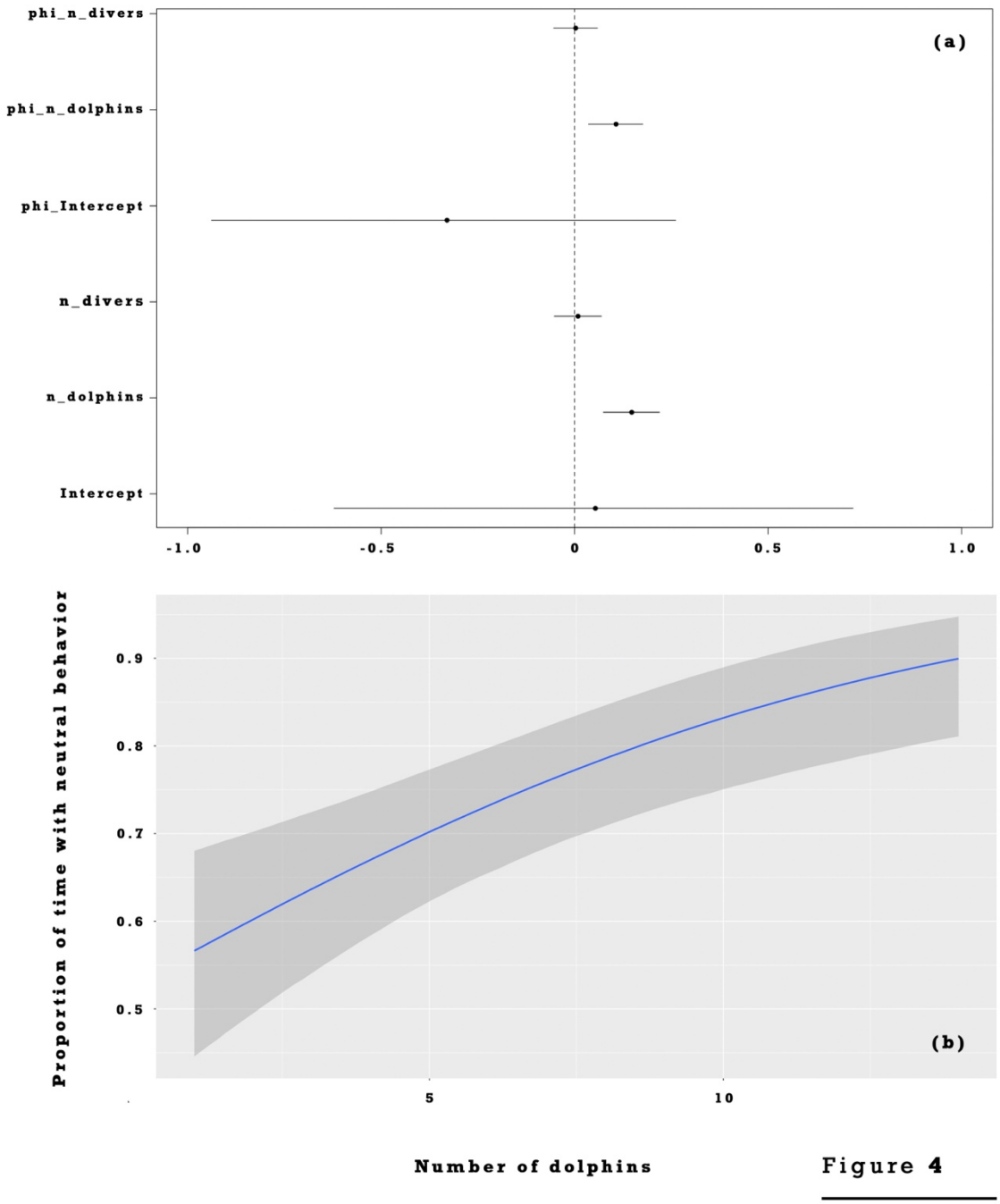

Figure 4. Parameters (population-level effects) of the model y ~ n_divers + n_dolphins + (1 | ID) with μ=logit and ϕ=log using the proportion of time each dolphin (n=18) displayed neutral behavior in ten randomly chosen sightings as the response variable, and the number of divers and the number of dolphins as predictors, and their credible intervals. **(b)** Conditional effect of predictor 'number of dolphins' on the dolphins' proportion of neutral behaviors.

3.5. Dolphin avoidance behavior

The zero-inflated Poisson model showed a significant positive relationship between the number of divers' 'held-out-hand' and 'swim-after-dolphin' behaviors and the number of dolphin avoidance behaviors. In other words, the more the divers held their hand(s) out to dolphins, or swam after dolphins, the more the dolphins displayed avoidance behaviors (**Figure 5**).

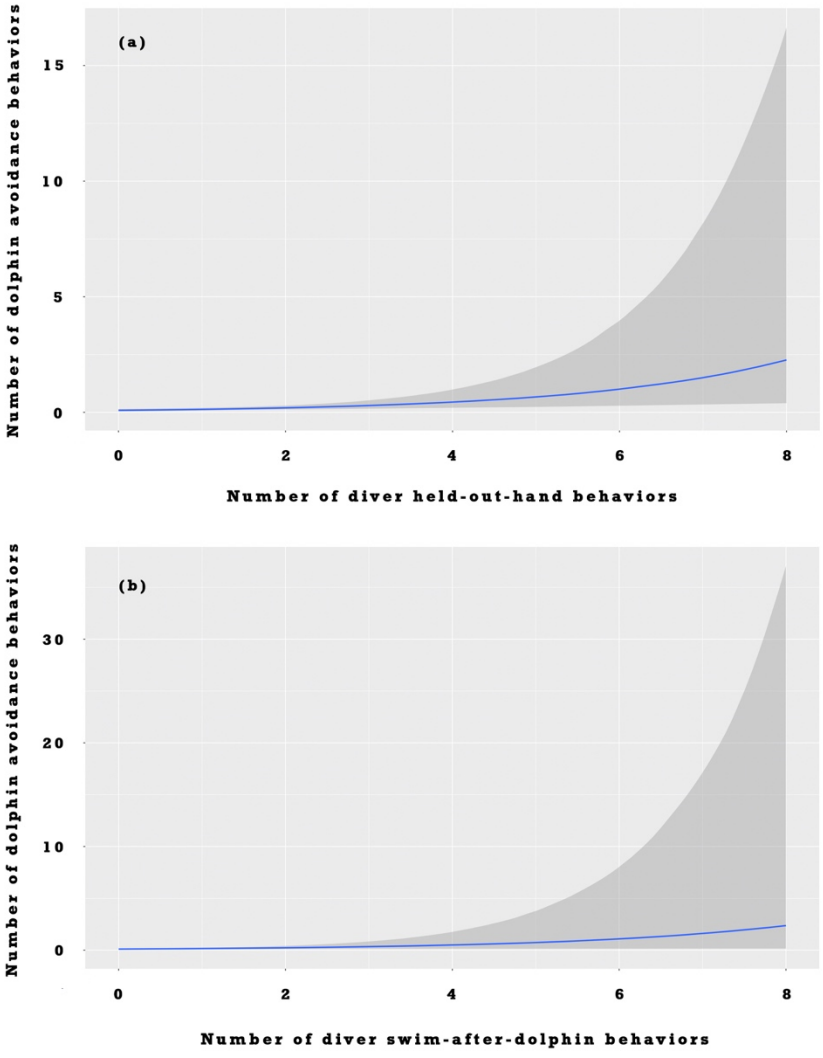

Figure 5

Figure 5(a) Conditional effect of predictor 'number of HOU behaviors' [i.e., divers holding their hand(s) out to dolphins] on the number of dolphin avoidance behaviors. **(b)** Conditional effect of predictor 'number of SAD behaviors' (i.e., divers swimming after dolphins which are moving away) on the number of dolphin avoidance behaviors.

4. Discussion

To our knowledge, this is the first study to focus on free-ranging non-provisioned dolphins' tolerance to scuba diving tourism. Our results showed that the dolphins are habituated to the presence of scuba divers on the tourist site and that they tolerate the close (<10m) presence of active divers.

Sexually immature dolphins were more responsive to active divers than mature individuals, and two immatures actually showed a majority of affiliative behaviors toward scuba divers. Moreover, more neutral behaviors were documented when higher numbers of dolphins were observed, and the dolphins' avoidance behaviors were significantly and positively correlated to the divers' tendency to hold their hand(s) out to the dolphins, and to swim after the dolphins.

From these results, we conclude that the dolphins' tolerance to scuba diving tourism is modulated by their age, social context, and by the divers' behaviors.

4.1. Dolphin habituation to scuba divers

The similar dolphin sighting rates in the absence and presence of scuba divers indicate their habituation to the presence of scuba divers on the area. Moreover, the number of scuba divers did not significantly influence the dolphins' tolerance to close diver presence although the effects of disturbance are likely to increase with number of visitors (Beale & Monaghan, 2004). This pattern might be associated with the displacement of less human-tolerant dolphins over time (i.e., phenotypic sorting, Møller, 2017) and-or the imperative of ecological factors (Beale, 2007; Blumstein, 2016; Bejder *et al.*, 2009) that maintain all dolphins on the tourist site despite chronic human disturbance.

Tiputa pass is a biological hotspot located in an oligotrophic marine environment (Nanninga & Spaet, 2017; Vollbrecht *et al.*, 2021) and a low number of dolphins are captured on the area annually (~ 30 individuals, Carzon, 2017). Small, island-associated populations of bottlenose dolphins were identified around numerous oceanic islands which is likely due to habitat discontinuities between nearshore and offshore waters (Gorgone *et al.*, 2003; Milmann *et al.*, 2016; Martien *et al.*, 2024) and may limit the dolphins' access to viable alternative habitats.

4.2. Dolphin context-dependent tolerance to scuba divers

The number of dolphins predicted the dolphins' propensity to display neutral behavior in the presence of divers: the more dolphins, the more neutral responses.

In bottlenose dolphins, social behavior is an important component of daily activities (Shane *et al.*, 1986) and involve various intraspecific interactions (Gowans *et al.*, 2007). Larger dolphin groups often contain young calves (Carzon, 2017) and provide more opportunities for resting, foraging, socialization, and social learning than smaller groups (Weir *et al.*, 2010). All these factors may make the dolphins less responsive to non-threatening environmental stimuli such as the presence of scuba divers. In addition, large groups offer increased protection against potential threats (Gowans *et al.*, 2007; Bouveroux *et al.*, 2018) and might provide a buffer against stress for individuals that are less tolerant to the close presence of active divers. In Tibetan macaques (*Macaca thibetana*), it was suggested that the increased proximity to conspecifics observed when tourists were present may help these animals cope with tourist pressures (Pritchard *et al.*, 2014).

Yet, the positive and significant relationship between the dolphins' avoidance behaviors and the divers' 'held-out-hand' and 'swim-after-dolphin' behaviors suggest that some humans' behaviors are perceived as unpredictable and-or aversive and not fully or consistently tolerated by the dolphins (Koolhaas *et al.*, 1999).

Studies undertaken on manta rays' (*Manta* spp.) behavioral responses to divers showed that active divers' behaviors (e.g., swimming after, diving under, obstructing the ray's movements) and interactions within 3m caused increased avoidance responses in the mantas compared to passive observers (Murray *et al.*, 2020; Gómez-García *et al.*, 2021) and a study conducted on whale shark (*Rhincodon typus*) behaviors in the presence of swimmers showed that swimmers touching, using flash photography, or diving toward the sharks provoked shark directional changes and violent shuddering (Quiros, 2007).

A lack of knowledge about how to behave correctly in the presence of wildlife is evident for many guides and tourists worldwide and scuba diving tourism is no exception (Barker & Roberts, 2004; Lagouy & Clua, 2016; Otsuka & Yamakoshi, 2020). However, in Australia, dive staff was seen to influence diver behavior toward grey nurse sharks (*Carcharias taurus*) and to have the potential to provide persuasive messages that communicate appropriate behaviors and understanding of sharks and their environments (Apps *et al.*, 2015).

In Rangiroa, most dive shops and staff willingly foster illegal intrusive diver behaviors toward the dolphins in order to get the dolphins' attention (PC, *pers. obs.*). Locally, there is a strong need to concurrently educate people about dolphins and their behaviors, supervise the instructors' briefings and behaviors in the presence of dolphins, proscribe any unpredictable and intrusive behavior toward the dolphins, and enforce explicit regulations. Overall, passive diver behavior should prevent daily disturbances for the dolphins and other marine wildlife.

4.3. Dolphin age-dependent tolerance to scuba divers

There were no obvious differences between male and female, and resident and non-resident dolphins' responses to divers. Bottlenose dolphins are generalist species that can cope with a wide range of habitats (Wells & Scott, 2018) and exhibit K-selected life history traits that are a prerequisite to pronounced plastic responses to novel environments (Mery & Burns, 2010; Snell-Rood, 2013). Accordingly, all individuals may have the potential to quickly learn to tolerate scuba divers, especially since the dolphins studied had already been in the presence of divers on a regular basis for at least one year. Besides, social learning and maternal effects may have helped them to readily adjust their behaviors to the presence of divers (e.g., Fairbanks, 1996; Mery & Burns, 2010; Bossley *et al.*, 2018; Evans *et al.*, 2021).

Still, our results unveiled that sexual maturity had a significant influence on the dolphins' responses to divers: mature dolphins displayed more neutral behavior toward scuba divers than immature individuals. Also, two immatures displayed more affiliative than neutral behaviors toward scuba divers.

Curiosity, play (Constantine, 2001; Herzing *et al.*, 2012), and-or exploratory approach behavior (Higham & Shelton, 2011) might explain such behaviors in maturing dolphins. Behavior is more plastic in young individuals which may be due to temporal changes in internal stimuli (Stamps, 2015; Stamps & Krishnan, 2017) and be advantageous to immatures by allowing them immediate adjustment to rapid human-induced changing environments (Snell-Rood, 2013). However, it can be costly for these young individuals as they may take more risks and be more vulnerable than mature dolphins to detrimental effects (e.g., boat collision, pathogen transmission) associated with repeated close human presence (Samuels & Bejder, 2004; Berger-Tal *et al.*, 2011; Carzon *et al.*, 2023).

Seven immature dolphins were considered in our study, among which one resident female was seriously injured by a propeller in 2018 (at age 5) and another one died soon after

a ship collision in 2019 (at age 5). Although the causes of this individual's premature death were not investigated, a third immature female dolphin considered in our study was found dead on northern Rangiroa reef in 2022 (at age 10). For comparison, among the 11 mature dolphins surveyed underwater, all individuals were still alive and not showing any visible human-induced injury in 2024.

As experience at an early age affects the behaviors expressed at subsequent ages (MacDonald, 1985; Fairbanks, 1996; Stamps, 2015), it would be worth collecting longitudinal data on the dolphins that were exposed to scuba diving tourism since their birth to compare their life trajectories and individual fitness to the fitness of dolphins that were exposed later in life (Geffroy *et al.*, 2015).

4.4. Interindividual variability in the dolphins' tolerance to divers

Interindividual variation was documented in the dolphins' tolerance to active scuba divers. Tolerance is constrained indeed by an individually fixed susceptibility to disturbance (Sih *et al.*, 2004; Carrete & Tella, 2013; Arroyo *et al.*, 2017). Bolder animals have higher response thresholds for avoiding potential danger and should therefore be more likely to exploit opportunities or ignore humans and human activities than fearful, reactive individuals (Martin & Réale, 2008; Sih, 2013). The existence of a shyness-boldness temperament axis was demonstrated by Díaz-López (2020) in free-ranging bottlenose dolphins, and we strongly suspect an influence of boldness traits on Tiputa dolphins' responses to scuba divers.

4.5. Understanding the dolphins' responses to repeated close interactions

There exists a hazardous belief that wildlife tolerance and habituation to humans mean that tourist activities do not impact animals (Bejder *et al.*, 2009). Such belief often leads to misleading communication, intrusive practices from tour-operators, guides and tourists, and adverse wildlife management consequences (Geffroy *et al.*, 2017; Uchida *et al.*, 2023). To better understand the dolphins' responses to repeated close interactions, it would be of interest to focus on their behavioral time budgets (Geffroy *et al.*, 2017), intraspecific behaviors (Maréchal *et al.*, 2016), temperament traits (Martin & Réale, 2008) and physiological responses which may underpin an absence of perceptible behavioral responses (Ellenberg *et al.*, 2006).

5. Conclusions

Increased tolerance and habituation to humans may cause serious welfare and conservation issues (e.g., by increasing human-wildlife conflicts), mostly when potentially harmful stimuli are considered as harmless, or when it clears the way for wildlife conditioning to human presence. Consequently, tourist activities that promote wildlife habituation are far from being neutral and must be supervised with great care.

Chapter 4

Individual variation of boldness in free-ranging bottlenose dolphins interacting with scuba divers in French Polynesia

Abstract

Marine wildlife tourism is known to affect target species across multiple spatial and temporal scales, from short-term behavioral responses to changes in relative abundance and habitat use patterns. However, despite a growing number of population and community-level studies, little is known on individual responses to wildlife tourism, particularly on free-ranging cetaceans.
Between 2018 and 2020, we investigated the behavioral responses of 20 non-provisioned bottlenose dolphins (*Tursiops truncatus*) to recreational scuba divers in Rangiroa Atoll, French Polynesia, to understand whether these individuals that had been repeatedly exposed to scuba diving tourism on at least one year exhibited temperament traits along the 'shyness-boldness' axis. We also considered potential variation in boldness in relation to age and sex.
The study documented five bold dolphins. There was no variation in boldness according to sex, but age significantly influenced the dolphins' boldness with immature dolphins being bolder than mature individuals. The more extreme case of boldness involved four dolphins that tolerated repeated physical interactions with scuba divers.
In Rangiroa, scuba diving tourism promotes repeated intrusive interactions with dolphins that might make bold individuals particularly vulnerable to collateral threats associated with human activities. It is therefore crucial to consider individual variation in the dolphins' behavioral responses to tourism to implement optimal tourism management measures.

Keywords

Boldness, dolphin behavior, human-dolphin interactions, temperament, wildlife tourism

1. Introduction

Individual animals differ consistently in their responses toward the same environmental stimuli (Dingemanse & Réale, 2005). These differences occur along with plasticities (e.g., modulation of behavior through habituation, Martin & Réale, 2008; Hulthén *et al.*, 2013; Lowry *et al.*, 2013) and behavioral variations that may occur between categories such as age and sex (Wilson *et al.*, 1994). Behavioral and physiological differences among individuals within a species which are relatively stable over time and across different contexts or situations are termed behavioral syndromes (Sih *et al.*, 2004), coping styles (Koolhaas *et al.*, 1999), personality traits (Dingemanse & Réale, 2005; Carere & Maestripieri, 2013), or temperament traits (Réale *et al.*, 2007). They generate trade-offs and boundaries to unlimited plasticity and often become conspicuous and easily measurable when individuals must cope with challenges in their environments (Carere & Locurto, 2011). For example, several authors documented individual differences in habituation rates (Ellenberg *et al.*, 2009; Bell & Peeke, 2012; Dingemanse *et al.*, 2012) and Arroyo *et al.* (2017) showed that temperament effects can lead to directional selection of certain phenotypes in contexts involving repeated human presence.

Indeed, temperament traits may have consequences on individual fitness (Wilson, 1998; MacDougall *et al.*, 2006; Smith & Blumstein, 2008; Sih *et al.*, 2012) and also help to explain suboptimal (i.e., seemingly maladaptive) behaviors in wild animal populations (Geffroy *et al.*, 2015; Toscano *et al.*, 2016). For example, 'bold' individuals may be inappropriately bold in situations where they should be cautious, becoming human commensals or pests that increase human-wildlife conflicts and lead to their killing for human safety or comfort (Sih *et al.*, 2004; Merrick & Koprowski, 2017; Penteriani *et al.*, 2017).

Temperament traits are often regarded as bimodal (e.g., shy vs bold), although individuals may vary considerably along a continuum (MacDougall *et al.*, 2006; Réale *et al.*, 2007). The shyness-boldness continuum has been investigated extensively across species (Blaszczyk, 2020) and considers an individual's reaction to a risky but not new situation (Réale *et al.*, 2007; Toscano *et al.*, 2016). Risk-averse (often referred to as 'reactive' or 'shy') and risk-prone ('proactive' or 'bold') individuals react differently to the range of environmental conditions they encounter which can lead to various outcomes (Wilson *et al.*, 1994; Wilson, 1998). For example, a study showed that wild bold bighorn sheep ewes (*Ovis canadensis*) reproduced earlier and had higher weaning success compared to shy ewes (Réale *et al.*, 2000). Yet, excessive risk-taking behavior also predicted early death in male rhesus macaques

(*Macaca mulatta*; Higley *et al.*, 1996) and in captive-bred swift foxes (*Vulpes velox*) released in the wild (Bremner-Harrison *et al.*, 2004).

In bottlenose dolphins (*Tursiops* spp.), the existence of individual differences in infants' exploratory behavior has been documented for more than 20 years (Mann, 1997) and there has been rising interest in the research on these dolphins' temperament traits during the last two decades, both in comparative psychology and behavioral ecology (e.g., Hill *et al.*, 2007; Kuczaj II *et al.*, 2012; Birgersson *et al.*, 2014; Díaz López, 2020; Morton *et al.*, 2021). For example, Hill *et al.* (2007) described maternal styles in bottlenose dolphins that appear to be differentiated by level of maternal control over a restrictive-permissive continuum. Morton *et al.* (2021) showed that captive bottlenose dolphins possessed four personality domains (i.e., openness, sociability, disagreeableness, and directedness). Directedness described behavioral consistency, focus, boldness, and low emotional arousal, and was unique to bottlenose dolphins (Morton *et al.*, 2021). Díaz López (2020) documented that bold free-ranging bottlenose dolphins had more central positions and stronger associations in their social network than shy individuals.

The development of wildlife tourism contributes to the increased human encroachment on natural habitats (Green & Giese, 2004; Lowry *et al.*, 2013; Sih *et al.*, 2016) and a small number of studies showed that temperament traits mediate animal responses to tourist activities (Martin & Réale, 2008; Geffroy *et al.*, 2017). Numerous short-term impacts of dolphin watching activities were recorded for the dolphins (e.g., modification of breathing sequences, Lusseau, 2003; avoidance responses, Constantine, 2001; changes in group composition, dispersion or cohesion, Carrera *et al.*, 2008; alterations in whistle frequency and duration, Guerra *et al.*, 2014) and a few studies documented long-term deleterious effects (decline in local abundance, Bejder *et al.*, 2006; higher risk of injury and death, Christiansen *et al.*, 2016). Yet, no study focused on the effects of the dolphins' temperament traits on their responses to tourism.

Here, we examined the boldness of 20 free-ranging non-provisioned bottlenose dolphins (*Tursiops truncatus*) toward scuba divers at a highly frequented diving site in Rangiroa, French Polynesia. We aimed at understanding individual variations in their responses to the presence of divers along the shyness-boldness axis in relation to age and sex. We also investigated intraindividual consistency of responses over the course of our 3-year study period.

In accordance with a previous study (Carzon *et al.*, *submitted*) which documented interindividual variability in the dolphins' tolerance to the close presence of scuba divers, and immature dolphins' affiliative behaviors toward divers, we expected young dolphins to be bolder than mature individuals, and sex not to influence the dolphins' boldness.

2. Methods

2.1. Study area and population

Rangiroa Atoll (S14°58 × W147°37) is located in the northwestern Tuamotu Islands, French Polynesia. Its large lagoon (200 kilometer-perimeter) is encircled by a series of islets and connected to the open ocean by two channels locally called 'passes' (i.e., Avatoru pass and Tiputa pass) situated on the north coast of the atoll. About 30 bottlenose dolphins inhabit Tiputa pass and its surroundings year-round (Carzon, 2017).

Our small study area is about 0.5km² and encompasses approximately 700 meters of outer reef located on the east ocean side of Tiputa pass (**Figure 1**). It is frequented all year long by shipping, yachting, fishing, and tourist activities (i.e., scuba diving, snorkeling, and dolphin-watching tours aboard motorboats that can accommodate up to 20 passengers).

Scuba diving tourism first took place on the Tiputa pass area in 1985. From the mid-1990s, scuba divers have been repetitively encouraging close interactions with Tiputa dolphins using postures, gestures, objects and sounds to get the dolphins' attention (PC, *pers. obs.*). In the 2000s, physical interactions began to be reported between scuba divers and some dolphins. In 2002, regulations were implemented in French Polynesia to supervise whale and dolphin watching activities but have never been enforced.

In 2009, we initiated a longitudinal study which focuses on bottlenose dolphins in Tiputa and on their response to scuba divers. The local conditions, including water visibility (often >30m) and the dolphins' tolerance to scuba divers offered opportunities for underwater observations.

Individual dolphins were identified from the surface using standard photo-identification methods (Wells & Scott, 1990) and underwater from photos and videos that clearly showed the dolphins' dorsal fin shape and additional features (e.g., permanent scars, color patterns). Sex was identified by observation of their urogenital region. Ages were known for the individuals born after 2009. In this study, we considered the dolphins as being either sexually mature or immature (hereafter 'mature' or 'immature'). Mature females were seen at least one time

pregnant, showing prominent mammary glands and-or regularly escorted by the same calf. We considered males over ten years old as being mature (Mead & Potter, 1990; Wells, 2014). Immatures from both sexes were not showing any of the aforementioned characteristics across the three-year study period.

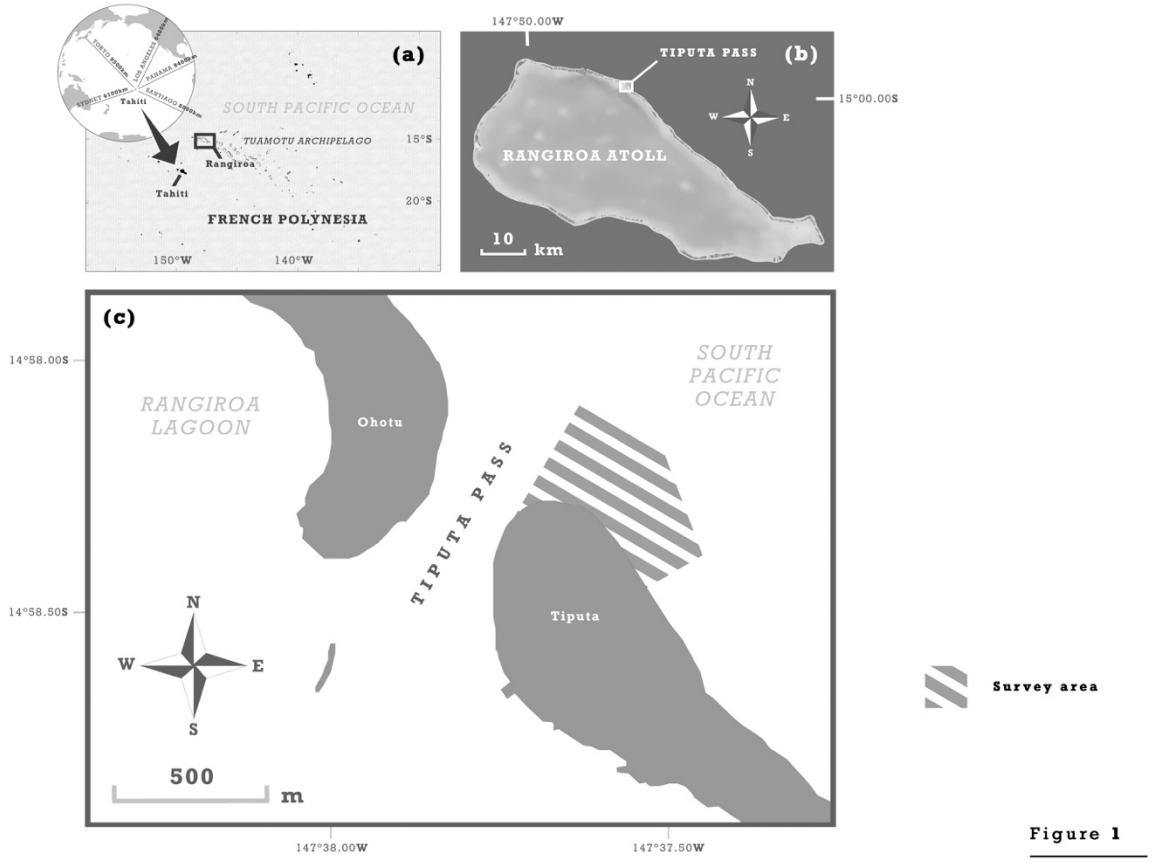

Figure 1(a) Location of Rangiroa Atoll in French Polynesia. **(b)** Location of Tiputa pass in Rangiroa. **(c)** Detailed map of Tiputa pass and its surroundings showing our survey area.

2.2. Sampling protocol

We used data collected underwater between February 2018 and December 2020. In 2020, data were collected before and after the two-month COVID-19 lockdown. One day was considered an independent sampling period.

The lead author and two dedicated scuba diver observers were trained to simultaneously take high-resolution video footage of the dolphins while diving together as part of commercial dives including diving instructors and tourists. The lead author used a full frame DSLR camera

(i.e., Canon EOS 5D Mark II + EF 16-35mm F2.8 lens) equipped with an Aquatica housing. The dedicated scuba diver observers used action cameras.

If dolphins were sighted during the dives, the lead author and observers filmed them from the moment the first dolphin was visible to the moment the last dolphin was out of sight to obtain what is referred to as a 'dolphin sighting'. We selected the sightings where all dolphins on view could be filmed and identified. We then selected the dolphins that were not born over the study period, that were seen on at least 10 sampling periods across the study, and on at least two sampling periods each year, considering that repeatability of a trait can be estimated if a minimum of two measurements are available for each individual (Réale *et al*., 2000).

An exception was made for one immature female (i.e, TP40) that died prematurely at age 5 in July 2019. We decided to keep this individual as it had been sighted on a regular basis (i.e., 33 sampling periods in 2018 and 26 sampling periods in 2019) before it died.

2.3. Data extraction and analysis

The video sequences were examined repetitively by the lead author-only using focal animal sampling (Altmann, 1974). The minimum distance between an individual dolphin and scuba divers was recorded as being either less than, or more than, 3m as we assumed that this distance which corresponds to a Rangiroa bottlenose dolphin's maximum length was relevant to illustrate boldness in these animals. We estimated Rangiroa dolphins' lengths for each of the following categories from Sergeant *et al.* (1973) considering that Rangiroa dolphins are slightly bigger than Florida dolphins: adult male (2.8m), adult female (2.6m), immature ≥ 5 years (2.4m), and immature < 5 years (2.0m). We then used these lengths to visually approximate the distances between a dolphin and divers, and single observations filmed simultaneously by two or three cameras to estimate the approximate distances between a dolphin and the cameramen on the cameramen's videos.

Subjects are usually assessed for boldness via their willingness to approach risky but not new situations. The occurrence, frequency, and duration of each dolphin's affiliative behaviors displayed within 3m from scuba divers, and all divers' behaviors directed to each dolphin, were logged in a database. A behavioral repertoire was built and supplemented during video analysis to get a comprehensive and well-defined review of the dolphins' and divers' behaviors identified on the sequences. The dolphins' behaviors were mutually exclusive. The dolphins' behaviors identified within the 3m limit (n=5) were considered as 'bold behaviors'.

To exemplify boldness, we additionally accounted for each dolphins' involvement in physical interactions with scuba divers (i.e., 186 physical contacts documented in our dataset, 99% of which were initiated by scuba divers, **Table 1** and **Supplemental data, Figure 1**).

Table 1. Dolphins' bold behaviors toward scuba divers and dolphins' involvement in physical interactions with scuba divers.

NAME OF BEHAVIOR	CODE	DEFINITION
Swim around diver(s)	**SWA**	Dolphin swimming around diver(s) or swimming from one diver to another at slow or moderate speed without stopping.
Swinging tail fluke	**SFL**	Dolphin swinging its tail fluke horizontally in front of diver(s).
Interest for camera	**CAM**	Dolphin facing and-or almost touching camera housing with any part of its body.
Stationary near diver(s)	**SND**	Dolphin remaining motionless near diver(s).
Vertical drop down	**VDD**	Dolphin sinks vertically head on top.
Physical interaction with diver(s)	**TOU**	Diver(s) touching, petting, rubbing, grabbing and-or hugging dolphin.

2.4. Interindividual variability, and effects of sex and maturity on the dolphins' boldness

To determine the existence of interindividual variability in the expression of the dolphins' five bold behaviors toward scuba divers and partition our 20 individuals according to their degree of boldness, we performed a Principal Component Analysis (PCA) using the R package *FactoMineR* on the proportion of time (min) each dolphin displayed each of the behaviors (SWA, SFL, CAM, SND, VDD). In addition, we accounted for the proportion of time each dolphin interacted at <3m from active scuba divers (INT) and the proportion of time each dolphin was documented physically interacting with scuba divers (TOU). We used the total duration of dolphin underwater footage as a common denominator.

We looked at the percentages of inertia associated with each dimension to select the most relevant plane. We also examined which variables were constructing the selected dimensions most calculating the correlation coefficients (R^2) between the individuals' coordinates and each of the variables. To check for each dolphin's quality of representation on

the factorial plane, we summed its square cosine (Cos^2) results on the selected dimensions and looked at those individuals with a $Cos^2 \geq 0.5$ on both dimensions.

Sex and sexual maturity were considered as illustrative qualitative variables (i.e., not used to build the factorial plane) and positioned at the centroid of the individuals that formed such categories to assess if any of them indicated a relevant area on the factorial plane. The Eta squared (η^2) was used to measure the proportion of variance for the coordinates of the individuals on the dimensions that is explained by each of these qualitative variables in an ANOVA.

We also used v-tests to profile the qualitative variables' modalities (i.e., male, female, mature, immature) on the selected components. The larger the v-test in absolute value, the more the group of individuals occupies a specific position and characterizes the region of the factorial plane where they are. Values larger than 2 were used to spot those categories that had an eccentric position.

2.5. Intraindividual consistency in the dolphins' boldness toward divers

We considered two variables to assess repeatability of behavior in the presence of active divers: **1)** the dolphins' tendency to interact with scuba divers at <3m from them (ACT<3m), and **2)** the dolphins' tendency to be involved in physical interactions with scuba divers (PHY).

We used the *sample* function in R to randomly choose a certain number of sampling periods per individual. For the variable ACT<3m, the sampling periods were chosen in the complete individual databases. For the variable PHY, the sampling periods were chosen in databases that only contained sampling periods where each dolphin was observed at <3m from scuba divers.

We carried out two analyses on the response variable ACT<3m. The first one included the 20 dolphins and ten sampling periods per dolphin. The second analysis was performed on 30 sampling periods randomly chosen in each of the 12 dolphins for which we had a minimum number of 35 sampling periods over the entire study period. The analysis undertaken on the response variable PHY included the 15 dolphins that were documented on at least 10 sampling periods at <3m from divers.

We transformed the response variables into binomial variables according to the presence (1) or absence (0) of the behaviors of interest. Repeatability estimations were performed with *rptR* package using GLMM method and logit link on binary data (Stoffel *et al.*, 2017). The

dolphins' identities were fitted as a random effect. Uncertainty was assessed through parametric bootstrapping, with each model set to 1 000 bootstrap samples. According to Bell *et al.* (2009), we categorized the repeatability results into low (<0.2), moderate (>0.2 to 0.4) and high (>0.4). High repeatability estimates imply that individuals behave differently from each other and at the same time behave consistently over observation periods (Bell *et al.*, 2009).

All statistical analyses were performed on R 4.3.0 (R Core Team, 2023) and based on the 0.05 significance level.

Ethical note

We only carried out careful free-ranging dolphins' observations that fully adhere to the French Polynesian regulations. No dolphin was touched or otherwise harassed by the lead author and our observers. Since the study did not require any manipulation or handling of the animals, the local authorities contacted for this purpose did not consider it appropriate to grant a specific permit.

3. Results

Our dataset totaled 381 dolphin sightings with all-filmed and identified dolphins taken over 204 sampling periods (**Table 2**) including 360 sightings and 195 sampling periods where divers displayed active behavior(s) in the presence of dolphins (**Supplemental data, Table 1**).

Table 2. Underwater sampling effort in 2018, 2019 and 2020.

	2018	2019	2020
Number of dolphin sightings	112	140	129 (31 before and 98 after the two-month COVID-19 lockdown)
Number of sampling periods	57	70	77 (19 before and 58 after the two-month COVID-19 lockdown)
Total duration of video sequences showing dolphins	5:01'50"	5:01'56"	4:23'31"
Total number of dolphins identified	28	29	26
Number of dolphins per sighting	Mean = 4 ± 3 SE Median = 3 Range = 1-13	Mean = 5 ± 3 SE Median = 4 Range = 1-13	Mean = 4 ± 3 SE Median = 4 Range = 1-14
Number of divers per sighting	Mean = 8 ± 3 SE	Mean = 7 ± 4 SE	Mean = 6 ± 3 SE

	Median = 8 Range = 2-16	Median = 6 Range = 2-21	Median = 6 Range = 2-20

A total of 31 different dolphins were identified over the three years including 20 dolphins which were selected for the analyses. Our subjects included 13 mature individuals that were regularly seen on the tourist area for at least eight years and seven immature dolphins (**Supplemental data, Table 2**). There were nine males and 11 females. In immatures, the sex-ratio was strongly biased in favor of females (SR=0.17). All these dolphins were captured underwater between 15 and 123 sampling periods (median=45) over the three-year study period. The total duration of individual dolphin sightings ranged from 9.75 minutes to 400 minutes (median=62.49 minutes).

3.1. Interindividual variability, and effects of sex and maturity on the dolphins' boldness

The first and second dimensions of the PCA showed a cumulative percentage of variance of 95.84% thus summarized well the information contained in our data. The analysis did not detect any outlier, but the variable SWA (i.e., swim around divers) appeared as a synonym of SND (i.e., stationary near divers) without having such a high quality of representation on dimensions 1 and 2 (Cos^2_{SWA}=0.952 and Cos^2_{SND}=0.991). We therefore decided to redo the analysis considering the SWA behavior as a supplementary quantitative variable that was not used as an active variable. In this new analysis, the first and second dimensions showed a cumulative percentage of variance of 96.09%. The first factor was dominant (81.07% of the data variability, **Figure 2**).

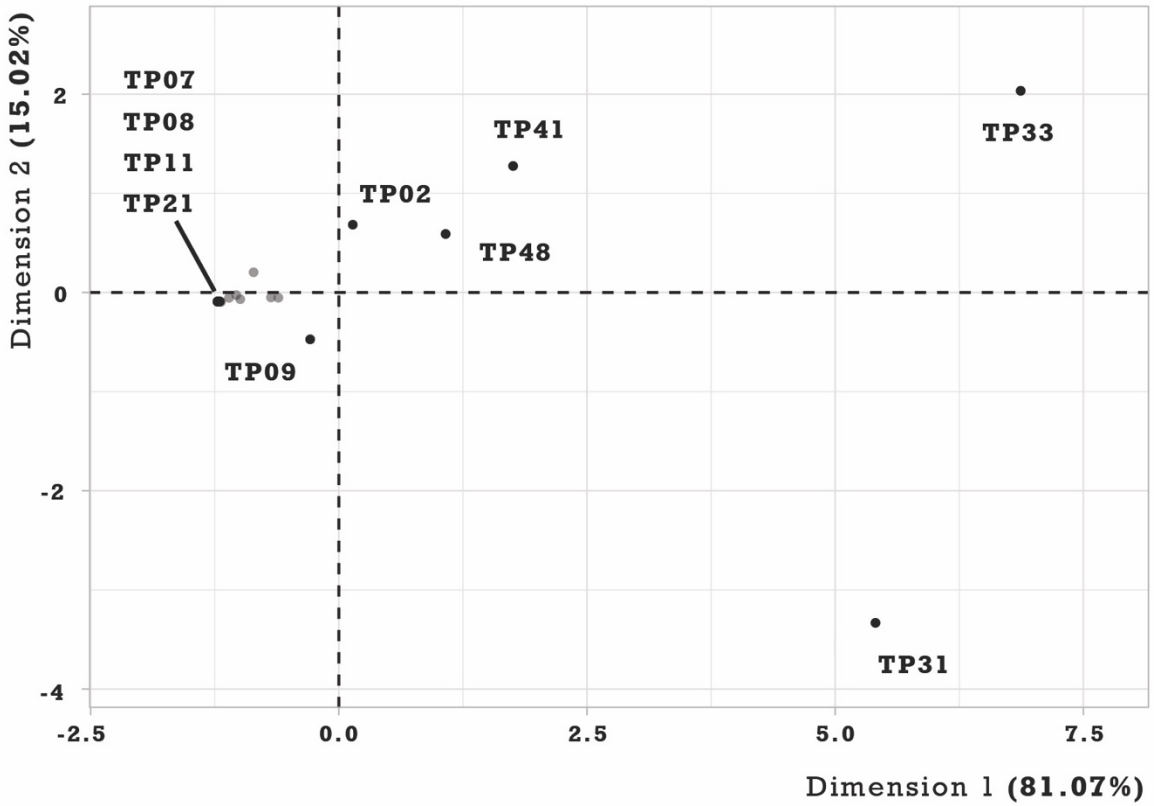

Figure 2. PCA plot of the 20 individuals showing the ten dolphins which contributed most to the construction of the factorial plane. INT, SFL, CAM, SND, VDD and TOU were used as active variables, and SWA as a supplementary variable.

The six active variables (INT, SFL, CAM, SND, VDD and TOU) were positively and significantly (p-value < 0.05) correlated with the first dimension. Unsurprisingly, the highest significant correlation was found for the variable INT (the proportion of time a dolphin interacted at <3m from active scuba divers) that could be used alone to summarize the first dimension (R^2=0.993). The variable SND (stationary near diver) showed a similar result (R^2=0.990), followed by VDD (vertical drop down, R^2=0.965), SFL (swinging tail fluke, R^2=0.884), CAM (interest for camera, R^2=0.792), and TOU (physical interaction with divers, R^2=0.758).

The only variables that had significant correlations with the second dimension were TOU (R^2=0.645) and CAM (R^2=-0.580).

Consequently, we considered the individuals that scored positively on the first dimension (n=5) as the boldest dolphins, the dolphins having positive values on the first and

second dimensions (n=4) as bold individuals particularly involved in physical interactions with scuba divers, and the dolphin having a positive value on the first dimension and a negative value on the second dimension as a bold individual mostly interested in cameras. Four mature dolphins (two males and two females) had a strongly negative coordinate on the first axis and contributed well to the construction of dimension 1 as the least interactive dolphins.

One individual (i.e., TP09) had a $Cos^2<0.5$ on both dimensions and was considered as poorly represented on this plane. The 19 other dolphins were well represented on the two first components ($Cos^2 \geq 0.64$).

The qualitative variable 'maturity' was the only one to be significantly and positively related to the first dimension (3.7% of the variability of the coordinates were explained by this variable). No qualitative variable was significantly associated with the second dimension (**Figure 3**).

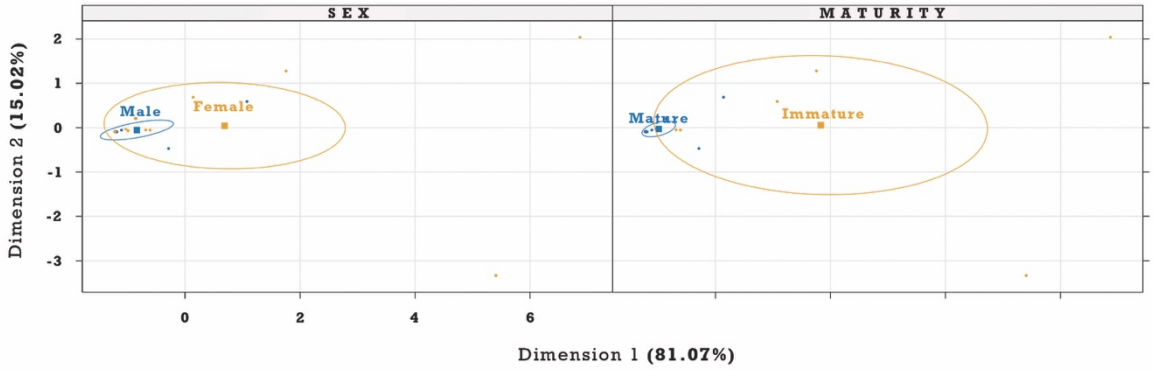

Figure 3. PCA plot of the additional qualitative variables 'sex' and 'maturity' with ellipses representing uncertainties.

Moreover, sexual maturity was the best qualitative variable to illustrate the distance between individuals on the selected plane. Immature dolphins tended to have more extreme positions on the positive (i.e., boldest) side of the first component while mature dolphins' centroids were mostly located on the negative side (**Table 3**).

Table 3. Distances to the barycenter, coordinates, and v-test values on dimension 1 of the two qualitative variables' modalities.

	Distance to the barycenter	Coordinate on dimension 1	v-test results
Male	0.853	0.839	-1.501
Female	0.698	0.687	1.501
Mature	0.995	-0.986	**-2.656***
Immature	1.848	1.831	**2.656***

***Significant values**

3.2. Intraindividual consistency in the dolphins' boldness toward divers

Between-sampling periods repeatability at the level of individuals for both ACT<3m (dolphin's interaction with scuba divers at <3m from them) and PHY (dolphin's involvement in physical interactions with scuba divers) variables were significant and ranged from moderate ($R_{ACT<3m}$=0.39) to high (R_{PHY}=0.59). The relatively high standard errors and large confidence intervals nevertheless suggest that our sample size was too small to get reliable estimates (**Table 4** and **Supplemental data, Figures 2, 3, and 4**).

Table 4. Repeatability estimates for the ACT<3m and PHY variables.

Variable	*R**	SE	95% CI	*P*	N
ACT<3m (20 dolphins x 10 sampling periods)	0.398	0.118	0.150 – 0.604	<0.05	200
ACT<3m (12 dolphins x 30 sampling periods)	0.393	0.122	0.129 – 0.588	<0.05	360
PHY (15 dolphins x 10 sampling periods)	0.588	0.264	0.022 – 0.949	<0.05	150

*Link-scale approximation; **SE:** Standard Error; **CI:** Confidence Interval; *P* values calculated using Likelihood Ratio Tests

4. Discussion

We examined free-ranging non-provisioned bottlenose dolphins' underwater behaviors toward scuba divers to document their boldness in the context of their interactions with tourist activities. We recorded five affiliative behaviors displayed by 20 dolphins at <3m from scuba

divers that were used as proxies to describe their boldness, and also used the dolphins' participation in physical interactions with scuba divers to further detail individual degrees of boldness.

Five bold dolphins were identified in our study including four which were typically involved in physical interactions with scuba divers and one which showed a strong interest for cameras.

Intraindividual consistency was recorded in the dolphins' tendency to closely interact with scuba divers, and in their tendency to physically interact with divers. However, repeatability estimates must be interpreted with caution as they showed large confidence intervals probably due to our small sample size. Biro & Stamps (2015) calculated that most studies providing estimates of behavioral repeatability typically have sample sizes too low for rigorous estimates and that one would need to sample about 100 individuals, five times each in order to estimate an *R* value of 0.4 with reasonable precision.

There was no variation in boldness according to sex, but the dolphins' age had a significant effect on their boldness. The four boldest dolphins were immature individuals, and the ten dolphins that were least involved in affiliative interactions with divers were sexually mature. More precisely, the three boldest individuals were immature dolphins independent from their mothers, individuals that are frequently referred to as 'juveniles' in the literature (e.g., MacHugh *et al.*, 2011; Krzyszczyk *et al.*, 2017; Galezo *et al.*, 2020).

Similar results were found in captive Antillean manatees (*Trichechus manatus manatus*, Charles *et al.*, 2022) and in captive chimpanzees (*Pan troglodytes*, King *et al.*, 2008; Massen *et al.*, 2013) where young individuals had a higher score in boldness than older ones. In Gibraltar, infants, and juvenile Barbary macaques (*Macaca sylvanus*) were the age classes most commonly observed to initiate contact with humans (O'Leary & Fa, 1993) and Campbell Island juvenile southern elephant seals (*Mirounga leonina*) were seen to approach and investigate tour parties at close range while adult seals were lacking similar interest (Higham & Shelton, 2011).

In a study on underwater interactions between humans and Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas, juvenile females were the main interactive individuals (Herzing *et al.*, 2012) and juvenile bottlenose dolphins were the most likely age group to maintain interactions with human swimmers in the Bay of Islands, New Zealand (Constantine, 2001).

Juvenility is a period of social exploration in bottlenose dolphins and juveniles often engage in interactions with a large number of conspecifics (Wells, 2014; Galezo *et al.*, 2020).

In addition, immature dolphins are more curious, active, and playful than mature individuals (Birgersson *et al.*, 2014). Juveniles seem more predisposed to approach and interact with environmental stimuli than older individuals, and it would be worth examining if Rangiroa immature dolphins' boldness toward scuba divers remains consistent after these individuals reach sexual maturity. Indeed, in a review on the development of animal temperament across ontogeny, Cabrera *et al.* (2021) found that temperament traits, including boldness, tend to be stable within life stages but typically are not consistent across critical developmental events (e.g., sexual maturation). The authors reviewed 14 studies that measured boldness across life stages and only two found juvenile boldness to predict adult boldness. Besides, Petelle *et al.* (2013) studied the development of boldness in a long-term study of yellow-bellied marmots (*Marmota flaviventris*) and found that this temperament trait was repeatable only in yearlings.

Surprisingly, not all bold individuals were involved in physical interactions with scuba divers, and a bold immature female was the only dolphin especially interested in cameras. Some of this immature female's behaviors were actually unique as it was the only bold dolphin that never tolerated any type of physical contact with scuba divers (i.e., it systematically withdrew from divers who attempted to touch it) and the only dolphin apparently captivated by camera housings' fisheye domes (i.e., it used to face such domes and stay very close to camera housings using them).

These observations indicate that each bold dolphin scores differently for each bold behavior, thus there are different degrees of boldness across bold individuals. In addition, we are conscious that we selected the dolphins' most obvious behaviors to illustrate their boldness toward scuba divers and that there certainly exist other behaviors associated with boldness in these animals. For example, Réale *et al.* (2007) mentioned the 'docility' or 'tameness' phenotype within the shyness-boldness category which was used in the specific context of reaction to humans and applied to domestic, captive, and wild animals (e.g., cattle, *Bos taurus*; black rhinoceros, *Diceros bicornis*; eastern chipmunks, *Tamia striatus*; bighorn sheep). Bottlenose dolphins, notably individuals involved in physical interactions with scuba divers, might display tameness traits in the presence of humans as well but this assumption remains to be tested.

Moreover, in Rangiroa, scuba divers commonly attempt to attract the dolphins on view using gestures (e.g., held out hand), postures (e.g., spinning around), and sounds (e.g., vocalizing in regulator; PC, *pers. obs.*) thus it would be relevant to study if bold dolphins' behaviors and regular involvement in physical interactions with scuba divers are partly

conditioned by the divers' attitudes. Dolphins have the potential to learn to associate scuba divers with positive reinforcers (i.e., pleasurable tactile contacts, Palmer & Weddell, 1964; Ramirez, 1999) and bold individuals, which are expected to experience more of their environment than other dolphins (Sih *et al.*, 2004), might be more prompt to learn and take advantage of such associations.

Although bold individuals establish local tourist activities' popularity, the dolphins' boldness toward scuba divers raises several welfare and conservation issues.

On the one hand, bold animals which behavior toward humans is intensely encouraged by tour-operators, guides, and tourists, which is the case in Rangiroa, can be potentially dangerous to tourists because dolphins may direct behaviors toward humans that they would be reluctant to display if they were more fearful of people (Price, 2002). Dolphins may become forceful and even aggressive with humans who choose to interact with them (Orams *et al.*, 1996; Carzon *et al.*, 2023) and such dolphin behavior toward scuba divers would be of particular concern as there also exist inherent risks associated with scuba diving activities that can seriously impair the divers' safety.

On the other hand, high level of boldness toward humans may lead the dolphins to behave inadequately in potentially harmful anthropogenic contexts and reduce individual fitness (Geffroy *et al.*, 2015). For example, in Rangiroa, we suspect that bold dolphins might suffer more from boat strikes and propeller injuries than other individuals (PC, *pers. obs.*).

Even though boldness is frequently related to higher reproductive success, it is also associated with lower survival (Smith & Blumstein, 2008; Sih, 2013) and there are in fact a number of instances where free-ranging dolphins had become so used to interacting with humans that their future became seriously compromised (e.g., Samuels & Bejder, 2004; Finn *et al.*, 2008; Vail, 2016; Christiansen *et al.*, 2016; NOAA, 2022).

5. Conclusions

Differences in temperament may lead to individual differences in behavior patterns relevant to animal welfare and conservation, and human safety. As wildlife tourism increasingly promotes close, often intrusive, interactions with dolphins in their natural settings, it is essential to consider the intricacy of dolphins' responses to tourism, and to record long-term dynamics associated with these responses, to get a comprehensive picture of the effects of tourism on these animals and execute appropriate and effective management measures. Finally, it is necessary to properly supervise tour-operators', guides', and tourists' behaviors toward the dolphins as ultimately it is not the dolphins being managed but people.

Core results

Our aims were to understand how individual dolphins tolerate repeated close interactions with wildlife tourism, how close interactions may impact both the dolphins and humans, and how they should be managed to limit deleterious outcomes. First, we examined several papers describing close encounters between humans and free-ranging dolphins to review the deleterious behaviors and risks associated with such activities [**Chapter 2**]. Then, we focused on individual bottlenose dolphins that have been exposed to scuba diving tourism for at least one year in Rangiroa Atoll, French Polynesia, to quantify their tolerance status to scuba divers [**Chapter 3**]. Finally, we observed the dolphins' boldness in the context of their interactions with scuba divers [**Chapter 4**].

Chapter 2 provides useful background information on the current status of close dolphin-human interactions in the wild. These activities are widely distributed worldwide and involve more than 20 delphinid, the two monodontid (i.e., beluga and narwhal), and one iniid (i.e., Amazon River dolphin, *Inia geoffrensis*) species. Bottlenose dolphins are the primary species documented in any type of close interaction with humans.

Most studies undertaken on the risks related to close human-dolphin interactions originate from a few countries (e.g., Australia, the United States, New Zealand) and are therefore not representative of the recent global development of these activities (O'Connor *et al.*, 2009). As such, we are likely to underestimate the actual increase in anthropogenic pressure on dolphins due to close tourist and other recreational interactions, and behavioral responses and risks associated over time. Moreover, there is a lack of information on humans' compared to dolphins' behaviors.

The number of locations where dolphins' and humans' deleterious behaviors and risks were recorded is higher in the case of lone, sociable dolphins than for other activities. In addition, the harmful behaviors and risks documented for lone, sociable dolphins are typically direct and violent (e.g., dolphin ramming people, human hitting dolphin, dolphin mortality, Samuels *et al.*, 2000) whereas those detailed in the case of other recreational activities are subtler and more insidious (e.g., dolphins avoiding people, humans chasing dolphins, impairment of dolphin resting behavior, Shawky *et al.*, 2020; Rocha *et al.*, 2023), except in

locations where dolphins are food-provisioned and-or regularly touched by people (e.g., Vail, 2016; Senigaglia *et al.*, 2019).

Overall, increased tolerance to humans and human activities makes dolphins more vulnerable to deleterious effects which can translate into poorer welfare and reduced individual fitness, and humans more exposed to dolphin agonistic and sexual responses, and zoonoses.

A strongly biased human perception of dolphins coupled with a lack of successful management measures are the main causes of inappropriate actions and adverse outcomes. The paper recommends various management indications gleaned from the literature to promote animal welfare, human safety, and the establishment of sustainable and ethical activities (e.g., education, training and supervision of tour-operators, guides, and tourists; implementation of easily understood, adapted, and enforced regulations). We also stress the need to consider interindividual differences when assessing the impacts of close interactions on delphinids.

Chapter 3 focuses on the behavioral consequences of individual bottlenose dolphins' cumulative experience with scuba diving tourism in Rangiroa Atoll, French Polynesia. We measured 18 known dolphins' tolerance to the repeated close presence of intrusive scuba divers over three years and show that the dolphins' responses to divers are multifaceted and need careful consideration before drawing conclusions on dolphin habituation to tourist activities.

Indeed, our results indicate that the dolphins are habituated to the presence of scuba divers on the tourist site and that they tolerate the close presence of active scuba divers. Yet, their tolerance to divers is modulated by their age, social context, and by the divers' behaviors. Immature dolphins were more responsive to divers than mature individuals, the dolphins displayed more neutral behaviors when the number of dolphins was high, and the number of divers' held-out-hand and swim-after-dolphin behaviors were positively and significantly related to the number of dolphin avoidance responses to divers. Moreover, there was interindividual variation in the dolphins' tolerance to active divers.

As suggested by different studies and reviews (e.g., Geffroy *et al.*, 2015; Saltz *et al.*, 2018; Carzon *et al.*, 2023), young dolphins' higher tolerance to intrusive human behaviors may make them especially vulnerable to detrimental effects (e.g., boat collision, pathogen transmission) associated with human activities.

We recommend collecting longitudinal data on the dolphins observed on the tourist area to assess their fitness regarding their responsiveness to divers. Additionally, we suggest to simultaneously monitor the dolphins' behavioral and physiological responses in the presence

of scuba divers to understand if the absence of obvious behavioral response echoes an absence of physiological response.

Finally, we highlight the need to promote passive diver behavior in the presence of dolphins, to educate tour-operators, guides, and tourists about dolphins, to better supervise the divers' underwater behaviors, and to implement and enforce explicit regulations that are adapted to the particular context of Rangiroa. Indeed, the widely held assumption that habituation has a positive or neutral outcome for animals and that it is a desirable outcome for tourism may lead to inappropriate decisions about the threats human interactions pose to both wildlife and tourists (Bejder *et al.*, 2009).

Chapter 4 reveals for the first-time bottlenose dolphins' temperament traits in the context of their interactions with tourism. Rangiroa dolphins' affiliative behaviors toward scuba divers, and the dolphins' involvement in physical interactions with scuba divers, were used as proxies to measure their boldness.

We found out interindividual variation and intraindividual consistency in the dolphins' boldness over time, two features typically used to highlight temperament traits in non-human species. In addition, it was possible to pinpoint finer scale differences across bold individuals. For example, bold dolphins were especially involved in physical interactions with scuba divers. The boldest dolphins were immature individuals and most of them were juveniles (i.e., independent from their mothers).

Although bold dolphins establish local tourist activities' popularity, their boldness toward scuba divers raises several welfare and conservation issues. High level of dolphin boldness may be risky for scuba divers and lead to immature dolphins' maladaptive behaviors if these responses are to be transferred to threatening sources. In addition, we suggest that some dolphins' bold behaviors might be conditioned by the divers' attitudes.

The multi-dimensional aspect of dolphin responses to scuba divers, and the risks associated, emphasize the need to develop locally adapted and effective management strategies to supervise tourist activities that can ensure animal welfare and conservation, and human safety, on the short- to long-terms.

Highlights

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1 Close encounters between free-ranging dolphins and humans boomed worldwide

2 We lack knowledge on the actual increase and impacts of close interspecific interactions

3 Dolphin habituation and conditioning make both the dolphins and humans more vulnerable to deleterious effects associated with close interspecific interactions

4 The dolphins' age, social context, and human behaviors influence habituated bottlenose dolphins' tolerance to scuba divers

5 Bottlenose dolphins display boldness traits when interacting with scuba divers

6 There exist different degrees of boldness across bold dolphins

7 The boldest dolphins are immature individuals, and especially juveniles

8 It is of prime importance to consider individual variation in the dolphins' responses to close interspecific encounters to implement optimal management strategies

Chapter 5

General discussion

1. Research strengths and limitations

The present study provides new information on free-ranging non-provisioned bottlenose dolphins' fine-scale behaviors in the context of repeated intrusive tourist activities (**Chapters 3** and **4**). It was carried out in a remote location that have been frequented by scuba diving tourism for more than three decades and enjoyed privileged environmental conditions (i.e., a combination of relative accessibility, warm waters, and good visibility all year long) allowing simultaneous longitudinal shore-based and underwater data collection.

Overall, Tiputa dolphins' tolerance to scuba divers offers opportunities to collect data on detailed underwater behaviors, including intraspecific social behaviors and parameters related to the dolphins' life history traits (e.g., gestations, nursing bouts) and to investigate dolphin-human interactions from both the dolphins' and humans' sides. It is therefore a relevant case study for interdisciplinary research.

There exist several locations worldwide where increasing wildlife tolerance to humans improved access to animals for research purposes. For example, from 1952, artificial provisioning of Japanese macaques (*Macaca fuscata*) at Koshima Island, Japan, facilitated short-distance observation and allowed for individual recognition and long-term studies whereby individual and social behaviors could be described in detail (Sugiyama, 2015). Since the 1960s, bottlenose dolphins of the east side of Peron Peninsula in Shark Bay, Australia, were provisioned and occasionally touched by local residents and regular visitors (Connor & Smolker, 1985). This situation improved access to the dolphins to researchers who established a long-term study of Shark Bay dolphins in 1984 (Mann *et al.*, 2000). Since the early 1970s, a free-ranging community of Atlantic spotted dolphins in the northern Bahamas has been habituated to humans, and data were collected on Bahamian spotted and bottlenose dolphins every summer since 1985 (Herzing, 1993; Dudzinski, 1996).

Here, we built a comprehensive underwater behavioral repertoire specific to the dolphin-diver interactions and highlighted neutral, avoidance, and affiliative behaviors which illustrate different degrees of dolphin tolerance toward scuba divers. By simultaneously considering several dolphin responses to divers, we developed a detailed understanding of the behavioral consequences of dolphin repeated exposure to humans. Moreover, we could benefit from a long-term monitoring of the dolphin community initiated in 2009 which gave us good previous knowledge on the dolphins at the individual level (e.g., sex, age, reproductive status,

matriline, main social partners). All mature individuals had regularly been identified on the tourist area for at least eight years before the research started, and all immature dolphins were born to identified females and regularly seen on the area since their birth.

Still, our study met a number of limiting factors that can prevent the findings from being extrapolated beyond certain boundaries, i.e., small sample size, relatively short timescale, lack of naïve individuals, uncontrolled diver behavior, and sampling bias. All these factors are briefly discussed below.

1.1. Small sample size

The bottlenose dolphin community which inhabits the Tiputa tourist area is small as it annually numbers about 30 dolphins with some individuals being regularly but scarcely captured on site (Carzon, 2017). To carry out the study, we had to select the dolphins for which we had enough data (i.e., individuals sighted underwater at close distance from active scuba divers on at least ten days over three years) and exclude all the calves born over the study period. Ultimately, we worked on 18 to 20 different individuals which were found to be a good compromise between an acceptable number of dolphins (i.e., more than 15 individuals) and a reasonable quantity of data per individual (i.e., the dolphin selected for which we had minimum information was captured underwater on 13 different days and 8'00" distributed over three years).

Wildlife studies by their nature are often characterized by small sample size, as are studies on large animals' behavioral traits. For example, Díaz López (2020) worked on 24 free-ranging bottlenose dolphins to examine the relationships between their boldness scores and network centrality measures, and Kudo *et al.* (2021) considered 22 green turtles (*Chelonia mydas*) in a study on their boldness and exploration traits. In captivity, Charles *et al.* (2022) studied 16 manatees to explore their boldness, sociality, and reactivity to humans. Morton *et al.* (2021) worked on an exceptionally high number of individuals as they examined personality structure in 134 captive bottlenose dolphins.

Bissonette (1999) suggests that one of the most profitable uses of small data sets is to generate interesting questions and hypotheses for future studies. Indeed, even though we had extra information available on Tiputa dolphins (e.g., immatures' matriline identities, mature individuals' reproductive status) we could not account for this data because of our small sample size. To overcome this limitation, it would be worth working on larger temporal scales to

include more individuals sharing similar genetic and demographic characteristics. This could allow us to identify additional variables that might have a significant effect on the dolphins' responses to tourist activities.

1.2. Relatively short timescale

Bottlenose dolphins are long-lived mammals that operate over large temporal scales. Most studies undertaken on these animals' responses to tourism focus on short-term behaviors which provide fragmented knowledge on the real impacts of tourist activities on cetaceans at various levels (Bejder *et al.*, 2006).

Our three-year data collection period allowed us to get a glimpse of the dolphins' responses to scuba divers, and it would clearly be relevant to work on data collected over larger time scales (i.e., at least ten years) to corroborate current results and capture long-term dynamics associated with the dolphins' responses to scuba diving tourism.

Some studies focusing on similar topics could benefit from such datasets. For example, Christiansen *et al.* (2016) used more than 45 years of dolphin data, and more than 1 100 individuals, to document the effects of food-provisioning on bottlenose dolphins' survival in Sarasota Bay, Florida. Similarly, Foroughirad & Mann (2013) worked on data collected from 1988 to 2011 to study the long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins in Shark Bay, Australia.

1.3. Lack of naïve individuals

Part of the usual process of establishing a monitoring program is the consideration and delineation of an appropriate control site (Bejder & Samuels, 2003). Here, we lacked behavioral data from dolphins which never experienced human presence, and therefore used an "impact only" design (Bejder, 2005) focusing on the consequences of the dolphins' cumulative exposure to tourist activities.

We nevertheless compared data collected from shore in a scuba diver-free area to data collected underwater over the same period to check if some Tiputa dolphins would be intolerant enough to the presence of scuba divers to be regularly seen from shore, but scarcely or never underwater. Still, we are conscious that the shiest and-or sensitized individuals may prematurely leave the disturbed area, which would make them intrinsically difficult to capture either from shore or underwater (Bejder *et al.*, 2009).

It would have been interesting to collect data prior to, and during, the onset of tourism on the Tiputa area to get a broader perspective on the range of dolphin behavioral responses to recurrent scuba diving activities and describe habituation and sensitization processes. Such configuration is rare in studies on whales and dolphins' responses to tourism, but Bejder *et al.* (2006) could compare dolphin abundance between tourism and control sites over three periods wherein tourism levels increased from zero, to one, to two dolphin-watching operators to evaluate the long-term impacts of vessel activity on bottlenose dolphins in Australia. We do not have similar material on Rangiroa dolphins as scuba diving tourism was initiated on the Tiputa area in 1985 whereas we began collecting regular dolphin data from 2009. We could gather older, but scant, video data that helped reconstructing a partial history of some dolphins' responses to scuba divers, nonetheless.

It would be of interest, at any rate, to compare the long-term dynamics of the Tiputa dolphin community to those of communities which barely or never interacted with human activities around Tuamotu Islands sharing similar ecological characteristics (e.g., Toau, Fakarava).

1.4. Uncontrolled diver behavior

Field experiments often suffer from an inability to control environmental conditions during the test and this may affect our way of estimating an individual's behavioral consistency (Martin & Réale, 2008). Indeed, external stimuli (e.g., human-induced background noise) will vary from test to test in evident or subtle ways that may act on the behavior of at least a portion of the individuals in the sample.

In our study, we considered the day-to-day surroundings experienced by the dolphins where all environmental variables could obviously not be controlled for during the data collection process. For example, it was impossible to control the divers' behaviors in the presence of dolphins. The small Tiputa dive site is frequented daily, between 8:00am and 5:30pm, by one to six dive shops, their instructors and tourist divers. Before a dive, most divers are briefed by their instructors to behave actively in the presence of dolphins to initiate an interaction with them. Underwater, many instructors who are usually imitated by tourist divers attempt to attract the dolphins on sight (e.g., producing sounds, swimming to the dolphins, holding their hands out to the dolphins, *pers. obs.*).

It would be necessary to dive before the arrival of the first instructors and tourist divers, and to control trained divers' postures, gestures, and sounds, to test for an influence of particular divers' behaviors on the dolphins' behaviors.

1.5. Sampling bias

Undeniably, even though our data was collected relatively consistently over the three years, we obtained an uneven number of sightings per dolphin and unequal individual sighting durations. Some individuals had higher probabilities of being captured than others due to factors such as higher site fidelity (i.e., they spend more time on the tourist area), a higher tolerance threshold to human presence (i.e., they display neutral behavior at closer distances from scuba divers), and higher boldness (i.e., they interact positively with scuba divers more often).

We first tried to get over these difficulties by checking if the dolphins were equally sighted from shore, in a diver-free area, and underwater. Then, we randomly chose an equal number of sightings per dolphin, taken over different survey days distributed over the three years to perform our analyses on balanced individual datasets.

2. Variation in the dolphins' behaviors in the presence of scuba divers

Our results indicate that the dolphins are habituated to human presence and that their behaviors in the presence of scuba divers vary according to the divers' behaviors, the dolphins' social context, their sexual maturity status (i.e., age), and consistent behavioral traits associated with boldness (**Chapters 3** and **4**). Hence, their responses to tourism are modulated by both their plasticities and temperaments.

To our knowledge, behavioral responses to human disturbance due to a combination of plasticity and temperament were never studied in free-ranging dolphins, but recorded in other animal species (e.g., reptiles, Rodríguez-Prieto *et al.*, 2011; birds, Arroyo *et al.*, 2017).

We based on Stamps' (2015) framework presented in **Chapter 1** to propose that exogenous (i.e., contextual, and developmental) and endogenous plasticities intervene in the dolphins' responses to divers. Indeed, **1)** dolphin habituation to scuba divers on the tourist area is a form of developmental plasticity based on learning, **2)** varying dolphin responsiveness according to the number of dolphins, and to the divers' behaviors, relates to contextual

plasticity, and **3)** mature dolphins displayed more neutral behaviors toward scuba divers than immature individuals, suggesting the existence of age-dependent changes in behavior (i.e., endogenous plasticity).

Behavioral plasticity and adaptive adjustments are important in facilitating resource use in human-dominated environments (Bateman & Fleming, 2014), and bottlenose dolphins appear to be relatively plastic in the context of anthropogenic disturbance compared to other marine mammals.

For example, plastic behavioral responses to immediate exposure to coastal construction were studied in identified bottlenose dolphins in Florida and showed that the dolphins learned to cope with human-induced disturbance by adjusting their behaviors in two ways, i.e., **1)** establishing feeding locations outside of the construction zone, and **2)** shifting the temporal rhythm of behaviors that they continued to exhibit in the construction zone to later in the day when construction activities were minimized (Weaver, 2021).

By contrast, spinner dolphins are considered particularly vulnerable to human pressures due to the typical constrained behavioral patterns of the species that feed at night and rest during the day (Tyne *et al.*, 2017; Fumagalli *et al.*, 2018). For example, Tyne *et al.* (2017) documented that regular, extensive, long-term use of spinner dolphins' Hawaiian resting bays as tourism sites has not resulted in abandonment of the bays, but rather in the decline of the dolphin population.

Additionally, a three-year study on minke whales' (*Balaenoptera acutorostrata*), bottlenose dolphins', and gray seals' responses to increases in vessel traffic in Ireland showed that bottlenose dolphin presence was positively correlated with overall vessel numbers whereas the presence of both minke whales and gray seals was negatively correlated with the overall number of vessels (Anderwald *et al.*, 2013).

In Sardinia, Italy, Díaz López (2019) documented a significant upward trend over nine consecutive years in density of bottlenose dolphins in a coastal area subject to significant use and pressure by humans (i.e., marine finfish aquaculture and gill-net fisheries). Also, the dolphins preferred a coastal area with higher human pressure and showed a reduction of their social interactions associated to a temporal switch to the food sources provided by human activities, demonstrating the remarkable adaptability of these animals.

Besides, Rangiroa dolphins are not unique in their behaviors toward scuba divers as remote Revillagigedo Islands' (Mexico) bottlenose dolphins, which live in similar ecological

conditions, also display tolerance, and bold behaviors, in the presence of divers (Carzon *et al.*, 2023).

According to these results, we propose that bottlenose dolphins as species have the potential to accommodate to various types of environments and may have greater success in novel environments created by anthropogenic activities than other marine mammals.

In addition, our study revealed that, individually, some dolphins possess behavioral traits that are inherently well suited to help them adjust to chronic human presence. Being bold in temperament might correlate with higher tolerance to various anthropogenic stimuli and allow an animal to live close to humans without experiencing chronic stress (Lowry *et al.*, 2013). Overall, Lowry *et al.* (2013) suggest that habituation is often only partial and that other types of plasticities, and temperaments, are important features for succeeding in human contexts.

Tiputa bottlenose dolphins' individual responses to divers illustrate indeed that the use of unitary terms like "habituation" may be too simplistic and that we must consider behaviors at the individual scale before drawing conclusions on the effects of tourism on wildlife.

3. Potential consequences of individual variation in the dolphins' responses to tourism

It is hazardous to predict the long-term consequences for the dolphins that could arise from their individual responses to tourist activities. A "snapshot" and contextual view of the dolphins' plasticity and boldness provides indeed very partial foundations for an understanding of their outcomes across ecological and evolutionary scales of time and space (Sih *et al.*, 2004; Stamps & Groothuis, 2010; Stamps & Biro, 2016).

Yet, it is commonly accepted that plasticity and temperament likely affect several components of an animal's life including habitat use, predation avoidance, dispersal, or social behavior (Dingemanse *et al.*, 2003; Dall *et al.*, 2004; Sih *et al.*, 2004; Dingemanse & Réale, 2005). For example, individuals do not seem to be distributed randomly with respect to human frequentation and bolder individuals usually occupy ranges in the most frequented areas (Martin & Réale, 2008; Lowry *et al.*, 2013).

In our study, we assume that the boldest dolphins might better adjust to ubiquitous human activities and remain on the tourist area despite intrusive human presence both at the surface and underwater, and sustained human-induced background noise. Their higher tolerance may minimize costs associated with responding to benign humans and permit coexistence with

human activities (Blumstein, 2016).

Concurrently, we hypothesize that the boldest dolphins, and especially young individuals, may not always be able to discriminate between different levels of threat related to human presence (Bateman & Fleming, 2014). As a result, they may be particularly vulnerable to collateral risks associated with anthropogenic activities as they might under-avoid real dangers (Sih *et al.*, 2023).

For example, dolphins involved in illegal feeding practices in Cockburn Sound, Australia, were also more predisposed to boat strikes and entanglement in fishing gear than other individuals in the population (Donaldson *et al.*, 2010). In Rangiroa, we suspect that bold dolphins may be more vulnerable to boat strikes, propeller injuries, pathogen transmission, and vandalism from humans than other individuals (Carzon *et al.*, 2023).

Moreover, we suggest that bold dolphins' high tolerance to tourist activities promotes an increase in site popularity and tourism frequency over time, increasing human-induced disturbances in their environment (*Cf.* notion of "niche-construction" formulated by Stamps & Groothuis, 2010) thus the potential for deleterious outcomes.

Finally, early experience may have a strong effect on preferences and could result in a less than optimal resource or activity being preferred by bold individuals after they reach sexual maturity which might negatively impact their reproductive success and life expectancy (Broom & Johnson, 2019).

The individuals that display lower tolerance to human presence may leave disturbed zones, favoring artificial selection of specific phenotypes (Carrete & Tella, 2010; Møller, 2017), or have no other option but to stay when disturbance is concentrated on critical habitats (Bejder, 2005; Beale, 2007; Bejder *et al.*, 2009; Blumstein, 2016).

The Tiputa pass area is both a tourist and biological hotspot located in an oligotrophic marine environment (Nanninga & Spaet, 2017; Vollbrecht *et al.*, 2021) and the only one across the 80 Tuamotu Islands to permanently host a dolphin community (*pers. obs.*). Additionally, Tiputa pass is a playground for the bottlenose dolphins which daily come to surf and leap into its mascaret (Carzon, 2017). The tourist area might therefore be a major ecological and social landscape for the dolphins, and it would be opportune to test how less human-tolerant individuals adapt to repeated human presence.

4. Benefits and risks of close interactions between dolphins and scuba divers

The predictability of dolphin sightings, the dolphins' habituation to the presence of scuba divers, and some dolphins' tendency to closely interact with scuba divers provide a wide range of benefits for humans and local tourism (Hunter Jr. *et al.*, 2021; Uchida *et al.*, 2023). Indeed, dolphins are highly popular animals (*Cf.* **Chapter 1**) and Rangiroa is an ideal, albeit expensive, destination for those tourists who wish to watch and closely interact with bottlenose dolphins in their natural habitat. Truly, Tiputa dolphins have become a major local attraction and an essential economic asset for local dive companies (Lagouy & Clua, 2016).

In addition, direct interactions with nature are increasingly recognized as providing a wide range of health and welfare benefits for people (Bègue-Shankland, 2022, p50; Uchida *et al.*, 2023), and some authors argue that marine mammal encounters in the animals' natural habitat contribute to an ecocentric view and allow Western people to consider their effects on nature (Yerbury & Weiler, 2020).

We did not notice such a contribution locally, but close dolphin-diver interactions typically enhance tourist scuba diver satisfaction and dive instructors encourage daily intimate interactions with bold dolphins for personal purposes as well (*pers. obs.*).

From the bold dolphins' perspective, close affiliative interactions with scuba divers may provide immediate benefits through opportunities to enjoy pleasant physical contact and-or play. Dolphins have an exceptionally well-developed tactile sense (Palmer & Weddell, 1964) and rubbing on or otherwise physically touching objects and substrates may have hygiene (e.g., parasite removal, sloughing) and sensual (i.e., pleasure) functions (Sakai *et al.*, 2006; Dudzinski *et al.*, 2012). In zoos, stroking of the body can be an effective reward in the training of some individual bottlenose dolphins (Defran & Pryor, 1980) and Samuels *et al.* (1989) noted that one observed dolphin which received infrequent rubbing from conspecifics rubbed its body against objects (*in* Dudzinski *et al.*, 2012). Dolphin self-rubbing is observed on the Tiputa area where individuals use to rub their rostrum on sponges (*Dactylospongia metachromia*) exposed on the outer reef, or certain parts of their body (e.g., head, flanks, genitals) on dead coral stones that accumulate into the pass (*pers. obs.*). Hence, scuba divers might act as a "rubbing station" for bold dolphins, and notably help them remove parasites and-or slough off old skin.

Besides, play is an important component of dolphin life (Janik, 2015) and dolphins seem to be motivated to play because it is pleasurable (Bekoff, 2007; Kuczaj & Eskelinen, 2014).

Juvenile dolphins engage in solitary play more than other age groups and juvenile play partners may vary by play state (Cappiello *et al.*, 2018).

In Rangiroa, young dolphins are routinely seen playing with plastic waste and scuba divers' bubbles, alone or with conspecifics, and more rarely with seaweed, jellyfish, and porcupinefish (*Diodon hystrix*, *pers. obs.*). Moreover, dolphins sometimes play in ways that suggest they are testing the boundaries of safety (Kuczaj & Eskelinen, 2014), which might be the case when Rangiroa dolphins display bold behaviors toward scuba divers.

Close interspecific interactions therefore provide benefits to both humans and bold dolphins, but we reviewed in **Chapter 2** that they also have the potential to generate deleterious short- to long-term impacts for both parties (e.g., pathogen transmission, aggression) and that negative outcomes may be considerable when the dolphins are food-conditioned and-or regularly touched by people.

In Rangiroa, dive leaders use to grab the boldest dolphins' tail fluke to rub it (**Figure 1**), and some divers embrace these dolphins or hold on their dorsal fin when they swim or remain motionless at close distance. It is not unusual to watch three scuba divers or more concurrently encircling and touching a dolphin (**Figure 2**), and such situations sometimes trigger passionate human reactions where the desire for a privileged interaction with a dolphin override reasonable limits with the animal (e.g., divers touching the dolphins' eyes, blowhole, mouth, or genitals) and basic respect for other divers (e.g., divers pushing other divers to reach a dolphin).

Five bold dolphins were documented in our study including four regularly involved in physical interactions with scuba divers. Among these four individuals, one was seriously injured by a propeller in 2018 (at age 5, **Figure 3**), and another one was found dead on the reef in 2022 (at age 10). The third one is an adult female of about 25 years old in 2024 who began to display bold behaviors toward scuba divers as a juvenile. This female gave birth to three known calves that displayed themselves bold behaviors toward divers. Two of the calves disappeared prematurely and the third one is now eight years old and keeps looking for regular physical contact with scuba divers on the Tiputa area. Accordingly, it would be interesting to collect longer-term demographic data on Tiputa dolphins to compare the boldest *vs* other dolphins' reproductive success and life expectancy.

Figure 1. Dive leader grabbing dolphin's tail fluke to rub it.

Figure 2. Scuba divers encircling and touching a dolphin.

Figure 3. 5-year-old bold dolphin injured by a boat propeller.

The health and welfare of humans cannot be maximized independently of the health and welfare of the dolphins, and there exists a true challenge to meet the needs of tourists without compromising the needs of dolphins (García Pinillos *et al.*, 2016; Lindenmayer & Kaufman, 2021). Indeed, contact with free-ranging dolphins is exciting and positively reinforcing to humans and many people are reluctant to voluntarily sacrificing opportunities for intimate interactions with these animals (Frohoff *et al.*, 2005).

In a report on high-risk situations for various species of lone, sociable whales and dolphins, Frohoff *et al.* (2005) considered human encouragement of sociable contact with solitaries as one of the most problematic yet common human response to the presence of these individuals, as the long-term implications are that they increase the likelihood that the animals will become injured or killed, intentionally or accidentally, by humans and human activities (Samuels *et al.*, 2000; Carzon *et al.*, 2023).

Winter (2020) argues that many tourists are aware, at least to some degree, that their activities may cause harm to animals, which causes them to experience cognitive dissonance (Bègue-Shankland, 2022). At the same time, they are adept in offering innumerable defenses to justify their behavior (e.g., the animals' freedom of choice) with the result that few appear to be dissuaded from using animals for their own entertainment (Winter, 2020).

Ziegler *et al.* (2018) studied the tourist perspectives on the ethics* of feeding whale sharks in the Philippines and documented that tourists weighed the pros and cons of these activities but let their desire to see the guaranteed, close sightings of whale sharks guide their decision-making. Tourists reported feeling guilty for participating in an activity that they personally identified as ecologically questionable, but *TripAdvisor* reviewers defended their participation by claiming that this activity could not be that bad since the sharks seemed happy and were not being held captive (Ziegler *et al.*, 2018; 2019). In Rangiroa, dive leaders and tourists use similar sophisms to defend their behaviors toward the dolphins (*pers. obs.*).

Several authors suggest that wild animals are still viewed as "commodities" as market environmentalism fuels an anthropocentric worldview where animals are resources to be used by humans for entertainment or economic gain (Forestell, 2009; Duffy, 2015; Belicia & Islam, 2018). Anthropocentrism and utilitarianism currently dominate the forms of animal use in tourism and place the convenience of humans above any concern for the impacts on the animals (Winter, 2020). Some scholars caution that animals do not only have value insofar they are useful to people, and that animal welfare, ethics, and conservation should receive more attention from the tourism field (Schweiggart, 2024; Edelbutte *et al.*, 2023).

Furthermore, humans may also suffer from negative consequences associated with close interactions with dolphins. For example, in Rangiroa, scuba divers were seen to touch dolphins with apparent granulomatous skin disorder that looks like lobomycosis-like disease (Félix *et al.*, 2019). Humans may acquire lobomycosis through contact with infected dolphins, and skin lesions in people develop slowly over time and the disease never disappears (Lupi *et al.*, 2005; Bermudez *et al.*, 2009).

Rangiroa dolphins were also recorded displaying intrusive, abrupt, and-or aggressive behaviors toward scuba divers (e.g., pushing divers, pulling divers' fins and regulator hoses, buzzing, or jaw clapping at divers, *pers. obs.*). Such dolphin behavior occurs alongside with inherent risks specific to scuba diving activities, and the mere presence of dolphins was seen to impair the divers' safety through divers' uncontrolled ascent and descent, and hyperventilation (*pers. obs.*).

Close encounters between humans and free-ranging dolphins therefore raise several safety, ethical, and conservation issues that rarely translate into appropriate management tools and may simultaneously lead to the long-term unprofitability of the industry. We based on the data collected in **Chapter 2** to summarize risks associated with repeated close interactions between dolphins and scuba divers on the Tiputa area (**Table 1**).

Table 1. Summary of risks associated with repeated close interactions between dolphins and scuba divers in Rangiroa.

	Direct		**Indirect**	
	Short-term	*Long-term*	*Short-term*	*Long-term*
For the dolphins	Impairment of resting and intraspecific social behavior Injury and vandalism from humans Pathogen transmission	Loss of vigilance toward humans and human activities Impairment of juvenile development	Boat collision Propeller injury Predation	Decreased maternal care Reduced life expectancy Decline in local abundance
For the divers	Dolphin abrupt, aggressive, and-or intrusive behavior leading to direct and-or indirect injury or accident Pathogen transmission	-	Scuba diving accident Property damage	Unprofitability and disappearance of tourist activity

5. Management implications

Many whale and dolphin watching guidelines throughout the world prohibit swimming, scuba diving, touching, and feeding activities as part of "basic principles" related to whale watching supervision (Carlson, 2008). The risks associated with repeated close dolphin-human interactions indicate indeed that it is neither reasonable nor ethical to encourage such interactions.

In Rangiroa, promoting passive scuba diver behavior in the presence of dolphins would be a useful strategy to limit the incidence of deleterious outcomes, as individual dolphins which seek out physical contact with divers are likely to lose interest for this type of interaction over time if all scuba divers stop encouraging them (Kuczaj II & Xitco Jr., 2002).

However, the value of wildlife tourism, including scuba diving and whale watching, is not often reflected in management decisions that allow consumptive use of fragile ecosystems which already face numerous threats caused by human activities (e.g., Lamb *et al.*, 2014; Halpern *et al.*, 2015; Cornwall *et al.*, 2021). Policy and planning responses are hindered by the political priority ascribed to the social and economic development dimensions of tourism, at the expense of sustainable management (Higham *et al.*, 2009).

Yet, when not or improperly managed, ecosystems under pressure from tourist activities are likely to become depleted from overuse (Pirotta & Lusseau, 2015), and destination areas carry with them the potential seeds of their own destruction as they allow themselves to become more commercialized and lose the qualities which originally attracted tourists (Plog, 1974).

As French Polynesia strives for sustainable tourism (Tahiti Tourisme, 2023), it should recognize that sustainability cannot be defined as exclusively human-centered and develop proactive management strategies that consider humans, wildlife, and the environment together (Fennell & Sheppard, 2021).

According to Moorhouse *et al.* (2015), tourism activities in which none of the revenue is invested in conservation, animal welfare, or local communities, should be considered an exploitation of the focal species for profit, and Carlson (2008) states that *cetacean watch operators should have a duty to care for the animals that they exploit*.

The escalating growth in wildlife tourism warrants the need for the industry's operation to be managed with sustainable principles (Dimmock *et al.*, 2013), especially since wildlife is the main resource on which business success is dependent (Cater & Cater, 2007).

Still, with few notable exceptions, there appears to be a tendency for most stakeholders to wait for dangerous situations to develop, rather than addressing them preventatively (Frohoff *et al.*, 2005).

5.1. Wildlife tourism and its management in French Polynesia

In French Polynesia, tourism is the main source of income and the local tourism industry is heavily dependent upon nature as a key resource (Andréfouët & Adjeroud, 2019). Wildlife tourism developed from the 1980s and became a well-established element of the local tourism sector. For example, French Polynesia has experienced a strong annual average growth rate (i.e., 30%) of whale watching activities targeting humpback whales and spinner dolphins between 1998 and 2005, and a study conducted in 2016 reviewed 258 companies that were involved in wildlife viewing activities throughout the territory including 56 dive centers (O'Connor, 2008; Lagouy & Clua, 2016).

The Tuamotu Islands are notorious among French Polynesian diving destinations as they provide scuba divers with opportunities to watch iconic coral reef wildlife such as marine turtles, rays, and a variety of sharks. Rangiroa Atoll was initially made famous among divers for its abundance of grey reef sharks (*Carcharhinus amblyrhynchos*) and the seasonal presence of great hammerhead sharks (*Sphyrna mokarran*).

In the 2000s, when bottlenose dolphins began to display increasing tolerance to scuba divers, Rangiroa became renowned as well as a privileged location to interact with these popular marine mammals. It is the only place in French Polynesia, and one of the few places worldwide, where it is possible to scuba dive with free-ranging dolphins on a daily basis. In 2016, local dive shops sold about 36 900 dives for an estimated direct expenditure of USD 2.4 million (Lagouy & Clua, 2016). In 2024, six dive shops were basing their business on the small (i.e., <2km²) Tiputa pass area representing substantial tourist pressure on the only location in French Polynesia where bottlenose dolphins are known to reside all year round (*pers. obs.*).

Some marine wildlife-related tourist activities (e.g., whale watching) are regulated in French Polynesia, but few are the tour-operators and guides who respect the law. Clearly, the management of wildlife tourism activities is far from being successful and do not meet the

ecological, economic, and safety challenges of marine wildlife tourism (*Cf.* Lagouy & Clua, 2016; Chazot *et al.*, 2020).

In Rangiroa Atoll, tourism management is obviously deficient in the case of dolphin watching. In practice, it has been plagued with problems that are notably attributed to remoteness, fast unmanaged expansion of activities, impactful and misleading communication from tour-operators, travel agencies and tourists, vague regulations that were never enforced, a lack of funding for scientific research, and a failure of coordination and communication between stakeholders (*pers. obs.*).

Still, knowledge can be gathered from destinations which have a long-lasting experience of cetacean tourism management (e.g., Australia, New Zealand) that could help turn French Polynesian whale watching activities into safer, more educative, ethical, and sustainable practices. Below, we discuss four components related to the recommendations suggested in **Chapter 2** that appear to stand out in the case of Rangiroa.

5.2. A need to adopt the precautionary principle

If a wildlife tourism action has a suspected risk of causing harm to human health, animals, or their habitat, in the absence of scientific consensus that the action is harmful, then the burden of proof that it is *not* harmful falls on those proposing the actions (Kriebel *et al.*, 2001; Burns *et al.*, 2011).

The precautionary principle is relevant in many situations as attaining baseline data is time consuming and may be inconclusive in variable-noisy environments (Ziegler *et al.*, 2019). For example, in a study on the ethics of feeding whale sharks in the Philippines, Ziegler *et al.* (2019) stated that *there is no evidence that provisioning is not detrimental to the sharks, and consequently the precautionary principle should be invoked whereby the onus to prove no detrimental impact should be on the proponents of provisioning whale sharks*.

In a review of whale watch guidelines and regulations around the world Carlson (2008) likewise stated: "*Before allowing cetacean-watching activities to commence, the Parties should make a formal assessment of their potential impact on the favorable conservation status of cetaceans. […] No new cetacean-watching activities should be authorized if there are threats of significant adverse impact on the behavioral patterns or physiological well-being of cetaceans*" (p2).

In Rangiroa, although dolphins have been interacting with scuba divers for more than two decades, we still advocate a similar approach based on the literature reviewed about close dolphin-human interactions (**Chapter 2**) and this thesis' results (**Chapters 3** and **4**).

We previously explained why regular physical contacts between divers and dolphins can be harmful for both parties and should be avoided. In addition, we recommend discouraging any attempt to closely interact with immature individuals, and all efforts made to attract dolphins to prevent conditioning and daily disturbances for the dolphins and other marine wildlife.

5.3. A need to adapt management strategies to local and evolutive contexts

Parameters such as tourists' behaviors and approach distances are commonly acknowledged to influence animals' behavioral responses to humans (*Cf.* **Chapter 1**) and considered in most management measures that regulate whale watching tourism (Carlson, 2008). Yet, each species, community, individual, location, and tourist operation have their own characteristics that need to be considered for an effective management of tourist activities at local scales. For example, Lusseau & Higham (2004) suggested that determining critical dolphin habitat (e.g., socializing, or resting locations) where boats are prohibited would be effective to protect bottlenose dolphins in Doubtful Sound, New Zealand. In Monkey Mia, Australia, Mann & Kemps (2003) recommended shorter and fewer tourist visitations to the provisioning beach to allow dolphin calves to regain contact with their provisioned mothers more quickly and allow for the dolphins to spend more time engaging in natural behavior away from the beach. Recently, local authorities prohibited swimming after, encircling, and touching whales and dolphins, and going whale watching before 9am and after 6pm in La Réunion Island, France (Quiétude, 2021).

Rangiroa Atoll is characterized by its insularity and remoteness. All bottlenose dolphin viewing activities focus on a restricted area intensively used by a small number of dolphins (Carzon, 2017). Tourism pressure is ubiquitous and consistent on this area as tourist activities take place from both the surface and underwater, all day and all year long.

Accordingly, it would be appropriate to circumscribe no-go protected areas based on the dolphins' preferred habitats for critical behaviors, and to limit the number of boats, swimmers, and scuba divers on the tourist site.

Additionally, tourist divers are supervised by dive leaders *in situ* who willingly ignore the law showing their customers how to attract and handle the dolphins. It would therefore be relevant to perform regular independent anonymous inspections of the leaders' briefings and underwater behaviors toward the dolphins to discourage illegal intrusive diver behavior.

Moreover, it would be necessary to carry out routine funded scientific monitoring of the dolphins' interactions with tourist activities to provide updated practical information that will inform the adaptation of management guidelines to the circumstances. Quantifiable limits of acceptable change should be clearly stated (e.g., animal injuries and fatalities, reproductive rates, changes in the behavioral budget of the focal community, Higham *et al.*, 2009), and communication between management agencies, industry operators, NGOs, researchers, and local communities should be improved (Guerra & Dawson, 2016).

5.4. A need to educate visitors and locals

The management of dolphin-human interactions is currently dominated by regulatory strategies and considerable potential exists to increase the role of education-based management schemes (Orams, 1996). Millions of travelers participate indeed in wildlife tourism activities that are detrimental to the animals involved and place themselves at risk, but few realize it. In Rangiroa, most divers focus on their short-term once-in-a-lifetime experience with dolphins and they are rarely able to look beyond to the cumulative impacts of all visitors on these animals over an extended period of time (Higham & Lück, 2007; Moorhouse *et al.*, 2015).

In addition, there exist huge gaps in the tour-operators', guides', and customers' knowledge about dolphins (**Chapter 1**). For example, we frequently witness inappropriate readings of the dolphins' behaviors on the part of dive leaders and tourists (e.g., agonistic dolphin behaviors that are interpreted as affiliative behaviors, *pers. obs.*), and most instructors are not able to identify the dolphins they interact with, except the individual which was injured by a boat propeller.

Sustained education programs, training courses, and communication tools based on actual and accurate scientific knowledge about dolphins, tourism impacts, and existing regulations should be developed and adapted to different audiences (i.e., tourists, guides, tour-operators, travel agencies, authorities, schoolchildren, local communities) to manage humans' expectations and behaviors toward these animals (Curtin, 2008; Egresi & Prakash, 2019;

Dybsand, 2020; Cottam, 2023). They should propose concrete positive solutions to enjoy the dolphins and their environment ethically and sustainably, and give people opportunities to act, through for example citizen science and volunteering programs.

Still, we are conscious that education does not mean that all people will change their behaviors and attitudes toward dolphins. For example, the investigation of Scarpaci *et al*. (2003) into tour operator compliance with regulations on swim-with-dolphins tours in Port Phillip Bay, Australia, after the government introduced new regulations showed that operators willingly ignore several rules to maintain the status quo.

In Rangiroa, most dive shops and instructors behave likewise with little or no response by the relevant authorities (*pers. obs.*). It is therefore necessary to simultaneously educate people and enforce clear regulations to stop illegal intrusive behaviors toward marine wildlife.

5.5. A need to enforce clear regulations

This topic was discussed in our "reply to Simon" (**Chapter 2**). Since 2002, French Polynesia is a marine mammal sanctuary and regulations were locally developed to manage whale watching activities. Yet, compliance is negligible in dolphin-human encounters and there is chronic lack of enforcement or punishment.

Tour-operators appear to comply better with conditions that are easily quantified (e.g., maximum number of people in the water) and operational guidelines written in a clear and concise manner (Scarpaci *et al.*, 2004; Parsons, 2012).

In French Polynesia, current regulations state that it is strictly forbidden to *intentionally disrupt the natural development of protected wild species and associated ecosystems*, with intentional disruption referring to *any human action that might modify the natural behavior of a wild animal for entertainment purposes*.

At the same time, the French Polynesian "Arrêté n°466CM" specifies that we must respect a safety distance of 30 meters with wild dolphins *except if the dolphins voluntarily reduce the distance between them and humans* (Code de l'Environnement de la Polynésie française, 2017). As Simon (2023) said, *this language undoubtedly is well intended*, but it is not adapted to the context of Rangiroa and clears the way for various interpretations. Clearly, it would be appropriate to prohibit any attempt to touch protected species, may the animals be tolerant or not to human contact.

Finally, there is an obvious need to sanction illegal behaviors and deceitful communication practices. In a workshop report on viewing marine mammals in the wild, the NOAA's National Marine Fisheries Service recognized the important role of enforcement in protecting wild marine mammals, particularly in the case of repeat offenders (Spradlin *et al.*, 2001). Indeed, even though it is not straightforward to prosecute cases, financial and personal resources are always limited, and sanctions may promptly deter illegal behaviors.

We summarize in **Table 2** the management indications suggested here, in the specific context of dolphin-human interactions in Rangiroa.

Table 2. Summary of management indications adapted to the context of Rangiroa.

	Management measures and approaches
General	Develop proactive management that considers humans, wildlife, and the environment together Improve communication between stakeholders
Management of tourist activities on the Tiputa area	Circumscribe no-go protected areas based on the dolphins' preferred habitats Limit the number of boats, swimmers, and scuba divers Quantify limits of acceptable change (e.g., animal injuries and fatalities, reproductive rates)
Management of humans' underwater behaviors	Discourage efforts made to attract dolphins Discourage attempts to closely interact with young dolphins Prohibit physical contacts with dolphins Promote passive human behavior
Education and involvement	Develop sustained education programs, training courses, and communication tools based on actual and accurate scientific knowledge about dolphins, tourism impacts, and regulations Adapt education programs to different audiences (i.e., tourists, guides, tour-operators, travel agencies, authorities, schoolchildren, local communities) Propose concrete positive solutions to enjoy the dolphins ethically and sustainably Give people opportunities to act (e.g., citizen science, volunteering programs)
Regulations	Enforce clear regulations adapted to the local context Sanction illegal behaviors and deceitful communication practices
Monitoring	Carry out routine funded scientific monitoring of the dolphins' interactions with tourism Perform regular independent anonymous inspections of guides' briefings and underwater behaviors toward the dolphins and other marine wildlife

6. Recommendations for future research

Up-close tourist encounters with bottlenose dolphins in Rangiroa are a relatively recent phenomenon and their impacts on the dolphins have not been investigated previously. As interest grows in developing the tourism potential of Rangiroa Atoll, this PhD thesis is a first step to acquire baseline knowledge on the dolphins' responses to scuba diving tourism. Further studies are needed to monitor the effects of tourism on dolphins, and dolphins' behaviors on tourism, and we share below some recommendations to guide future research.

First, it is possible to improve the collection of underwater dolphin data. Depending on the research questions, it may be convenient to invite tourist divers to share their videos, to use remote underwater video stations (e.g., Titus *et al.*, 2015), to dive into tourists' groups, or to set up groups of dedicated trained observers who can dive at specific times. Also, it is of interest to use 360 cameras that shoot in all directions at once to comprehensively film the dolphins and their behaviors.

Next, it is essential to focus on both behavioral and physiological dolphin responses to tourist activities to get a more integrated picture of tourism impacts over time. Recent studies measured glucocorticoid concentrations in marine mammal fecal samples to assess physiological responses to anthropogenic stressors (e.g., Mercera *et al.*, 2021; Pirotta *et al.*, 2023) and such methods should be applicable to Rangiroa bottlenose dolphins.

Additionally, it is crucial to understand how dolphin behaviors on the short-term will impact individuals and the community on the long-term. It takes years or decades to comprehensively measure bottlenose dolphins' reproductive success and mortality rates and we recommend that longitudinal research supported by appropriate logistical and financial resources monitors individual developmental trajectories and community dynamics to inform an optimal management of dolphin-human encounters in Rangiroa and elsewhere.

Besides, it is worth studying how dolphin behaviors in the presence of scuba divers propagate across individuals and whether certain behaviors displayed toward divers are cultural. Indeed, there is strong evidence for the existence of cultures in bottlenose dolphins (Whitehead *et al.*, 2004; Krützen *et al.*, 2005), and some Tiputa dolphins' behaviors appear to be consistent over time while others are arbitrary (i.e., "fads", Bossley *et al.*, 2018).

Lastly, we mentioned in the subsection *Research strengths and limitations* that our case study is relevant for interdisciplinary research which would draw knowledge from academic disciplines such as behavioral ecology, sociology, psychology, veterinary sciences, economics, and ethics. Also, the case of Tiputa dolphins would benefit from transdisciplinarity (which includes non-academic stakeholders), as sustainability challenges require new ways of knowledge production and decision-making (Lang *et al.*, 2012).

Conclusions

Dolphins are extensively used in the wildlife tourism industry to provide pleasurable tourist experiences which did not prove their sustainability.

Much of the popularity of dolphin-based tourism relies on highly tolerant animals, but not all dolphins display identical responses to anthropogenic disturbance and individuals' degrees of tolerance and boldness may impact both the dolphins and humans in various ways. Accordingly, the impacts of wildlife tourist activities must be studied and interpreted carefully to develop efficient management strategies and genuine ecotourism that consider safety, welfare, ethical, and conservation issues together.

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Supp. data

Chapter 2

Deleterious behaviors and risks related to close interactions between humans and free-ranging dolphins: A review

Tables 1(a) and 1(b). Summary of deleterious behaviors and risks documented for dolphins and humans as part of close interactions between free-ranging dolphins and humans/human activities.
1(a) ongoing tourist and other recreational activities
1(b) lone, sociable dolphins

Tables legend

* See distribution maps in Figures 2 and 3, for more details on each location.
** **SWA:** *Wading, swim-with and-or free diving activities*; **SDA:** *Scuba diving activities*; **FPA:** *Food provisioning activities*

RISKS FOR DOLPHINS

1. Loss of vigilance toward humans and human activities
2. Impairment of intraspecific social behavior
3. Disruption of reproductive behavior
4. Decreased maternal care
5. Impairment of juvenile development
6. Impairment of resting behavior
7. Impairment of foraging behavior
8. Ingestion of inappropriate food
9. Fishing gear entanglement
10. Pollution
11. Pathogen transmission
12. Trapped or captured
13. Injury and vandalism from humans
14. Boat collision
15. Propeller injury
16. Predation
17. Stranding
18. Change in habitat use
19. Decline in local abundance
20. Mortality

RISKS FOR HUMANS/HUMAN ACTIVITIES

A. Property damage
B. Swimming accident
C. Dolphin injury
D. Shark injury
E. Mortality

Table 1(a) Ongoing tourist and other recreational activities [p. 1 / 4]

Estimated beginning of activities	Countries (locations)*	Species involved	Type of activities**	Dolphins' deleterious behaviors in the presence of humans/human activities	Humans' deleterious behaviors in the presence of dolphins	Risks for dolphins	Risks for humans/human activities	References
1960s	**AUSTRALIA** (New South Wales; Queensland; South Australia; Victoria; Western Australia)	*D. delphis* *S. sahulensis* *T. aduncus* *T. australis*	**SWA** **FPA**	**Aggressive** (biting) **Submissive** (avoidance) **Intrusive** (begging, scavenging, depredating) **Abrupt** (pushy)	**Aggressive** (shooting at dolphins) **Intrusive** ("harassment," touching, grabbing, holding onto dorsal fin, riding)	**1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 15, 17, 18, 20**	**C**	**Connor & Smolker** (1985); **Wilson** (1994); **Hoyt** (1995, 2001); **Orams** (1995, 1997, 2002); **Orams** *et al.* (1996); **Weir** *et al.* (1996); **Garbett & Garbett** (1997); **Müller** (1998); **Orams & Hill** (1998); **Neil & Brieze** (1998); **Webster** *et al.* (1998); **Constantine** (1999); **Mann & Barnett** (1999); **Mann** *et al.* (2000); **Samuels** *et al.* (2000, 2003); **Scarpaci** *et al.* (2000, 2003, 2004, 2005); **Jarvis & Ingleton** (2001); **Spradlin** *et al.* (2001); **Mann & Kemps** (2003); **Bejder** (2005); **Finn** (2005); **Wilke** *et al.* (2005); **Allen** *et al.* (2007); **Zeppel** (2007); **Blewitt** (2008); **Finn** *et al.* (2008); **Neil & Holmes** (2008); **Newsome & Rodger** (2008); **Smith** *et al.* (2008); **O'Connor** *et al.* (2009); **Donaldson** *et al.* (2010, 2012); **IWC** (2010); **Holmes & Neil** (2012); **Peters** *et al.* (2012); **Steckenreuter** *et al.* (2012); **Foroughirad & Mann** (2013); **Filby** *et al.* (2014, 2017); **Bach & Burton** (2016); **Marchernis** *et al*. (2018); **Patroni** *et al.* (2019); **Senigaglia** *et al*. (2019)
1960s	**THE BAHAMAS** (Bimini and Grand Bahama Islands)	*S. frontalis* *T. truncatus*	**SWA** **SDA**	-	-	**1, 14, 15**	-	**Marx** (1982); **Tippon & Humphreys** (1989); **Herzing** (1993, 1997); **Dudzinski** (1996, 1998a); **Frohoff** (1996); **Soury** (1996); **Melillo** *et al.* (2009)
1970s	**ARGENTINA** (Chubut and Santa Cruz Provinces)	*C. commersonii* *L. obscurus*	**SWA** **SDA**	-	-	-	-	**Carlson** (2012); **Iñiguez & Tossenberger** (2015); **CMS** (2017)
1970s	**THE UNITED STATES** (Georgia and South Carolina; Gulf Coast; Hawaiian Islands)	*T. truncatus* *S. longirostris* *S. bredanensis* *G. macrorhynchus* *P. crassidens*	**SWA** **SDA** **FPA**	**Aggressive** (grabbing and pulling swimmer) **Submissive** (avoidance) **Intrusive** (begging, scavenging, depredating)	**Aggressive** ("injuring," shooting at dolphins) **Intrusive** ("harassment," chasing, squealing, touching, grabbing, riding)	**1, 2, 4, 5, 6, 7, 8, 9, 11, 13, 14, 15, 16, 17, 18, 20**	**A, C, D**	**Shane** *et al.* (1993); **Bryant** (1994); **Frohoff & Packard** (1995); **Hoyt** (1995); **Shane** (1995); **Constantine** (1999); **Spradlin** *et al.* (1999, 2001); **Frohoff** (2000); **Samuels** *et al.* (2000, 2003); **Forest** (2001); **Hoyt & Hvenegaard** (2002); **Östman-Lind** *et al.* (2004); **Samuels & Bejder** (2004); **Cunningham-Smith** *et al.* (2005); **Danil** *et al.* (2005); **Lewandowski** (2005); **Cunningham-Smith** *et al.* (2006); **Courbis** (2007); **Delfour** (2007); **Van Atta & LeFors** (2007); **Courbis & Timmel** (2008); **Wells** *et al.* (2008); **O'Connor** *et al.* (2009); **Powell** (2009); **Scheer** (2010); **Powell & Wells** (2011); **Carlson** (2012); **Duda** *et al.* (2013); **Kovacs & Cox** (2014); **Perrtree** *et al.* (2014); **Engleby** (2015); **Wiener** (2015); **Baird** (2016); **Christiansen** *et al.* (2016); **Hazelkorn** *et al.* (2016); **Vail** (2016); **CMS** (2017); **Heenehan** *et al.* (2017); **Tyne** *et al.* (2017, 2018); **Machernis** *et al.* (2018); **Powell** *et al.* (2018); **Patroni** *et al.* (2019); **Wiener** *et al.* (2020); **Shinn & Rowley** (2021); **NOAA Fisheries** (2021) https://www.sharkattackfile.net/spreadsheets/pdf_directory/1999.07.26-Knowles.pdf [*accessed 30 October 2022*]
1980s	**BRAZIL** (Amazonas State; Fernando de Noronha Islands; Sao Paulo State)	*S. longirostris* *S. guianensis* *I. geoffrensis*	**SWA** **SDA** **FPA**	**Aggressive** (biting, buzzing) **Intrusive** (begging, rubbing against boats) Intraspecific "aggressive" and "dominant" behaviors	**Intrusive** ("harassment," touching, grabbing, riding)	**1, 2, 5, 7, 8, 10, 13, 18**	**C**	**Hoyt** (1995); **Soury** (1996); **Samuels** *et al.* (2000, 2003); **Santos** *et al.* (2000); **O'Connor** *et al.* (2009); **IWC** (2010); **de Sá Alves** *et al.* (2011, 2013); **Scheer** *et al.* (2014); **Iñiguez & Tossenberger** (2015); **CMS** (2017); **Machernis** *et al.* (2018)
1980s	**ECUADOR** (Galapagos Islands)	*T. truncatus* *S. longirostris* *D. delphis* *O. orca*	**SWA** **SDA**	-	-	-	-	**IWC** (2010); **Iñiguez & Tossenberger** (2015); pers. com. **Étienne Rastoin**, **Godfrey Merlen**

Table 1(a) Ongoing tourist and other recreational activities [p. 2 / 4]

1980s	**JAPAN** (Izu and Ogasawara Islands; Notojima Island)	*T. aduncus* *S. longirostris*	**SWA** **SDA**	**Submissive** (avoidance)	**Intrusive** ("harassment," chasing, touching)	**1**	-	**Hoyt** (1995); **Dudzinski** (1998b); **Müller** (1998); **Ichiki** (2003); **Samuels** *et al.* (2000, 2003); **Kogi** *et al.* (2004); **O'Connor** *et al.* (2009); **IWC** (2010); **CMS** (2017)
1980s	**MADAGASCAR** (Nosy Be and Tulear)	*S. longirostris* *T. aduncus* *S. attenuata*	**SWA**	-	-	-	-	**Hoyt** (1995); pers. com. **Arthur Guillemain d'Echon** (*Mada Megafauna*)
1980s	**NEW ZEALAND** (Akaroa; Hauraki Gulf, Coromandel Peninsula and Bay of Plenty; Kaikoura; Marlborough Region; Northland Region; Southland Region)	*L. obscurus* *C. hectori* *D. delphis* *T. truncatus* *G. melas* *O. orca* *P. crassidens*	**SWA**	**Submissive** (avoidance)	**Intrusive** ("harassment")	**1, 2, 3, 5, 6, 7, 9, 14, 18, 19**	-	**Barr** (1997); **Constantine & Baker** (1997); **Orams** (1997); **Barr & Slooten** (1999); **Bejder** *et al.* (1999); **Constantine** (1999, 2001); **Samuels** *et al.* (2000, 2003); **Stone & Yoshinaga** (2000); **Nichols** *et al.* (2001); **Constantine** *et al.* (2004); **Orams** (2004); **Neumann & Orams** (2006); **IWC** (2010); **Lundquist** *et al.* (2012); **Martinez** *et al.* (2011); **Martinez** *et al.* (2012); **Tezanos-Pinto** *et al.* (2013); **Meissner** *et al.* (2014, 2015); **Tezanos-Pinto** *et al.* (2014); **CMS** (2017); **Fumagalli** *et al.* (2021)
1990s	**EGYPT** (Hurghada and Marsa Alam)	*S. longirostris* *T. aduncus* *S. plumbea*	**SWA** **SDA**	-	**Intrusive** ("harassment")	**2, 6**	-	**Hoyt** (2001); **Notarbartolo di Sciara** *et al.* (2008); **O'Connor** *et al.* (2009); **Fumagalli** *et al.* (2018, 2019); **Shawky** *et al.* (2020)
1990s	**MEXICO** (Revillagigedo Islands; Sea of Cortez Coast; Yucatan Peninsula)	*T. truncatus* *S. attenuata* *O. orca*	**SWA** **SDA**	-	**Intrusive** (touching)	**1**	-	**Iñiguez & Tossenberger** (2015); pers. com. **Mauricio Hoyos** https://whale-expeditions.com; https://sdmdiving.com; https://www.bluewaterdivetravel.com/ [*accessed 17 May 2022*]
1990s	**SOUTH AFRICA** (Eastern Cape and KwaZulu Natal Provinces)	*T. aduncus* *D. capensis* *S. plumbea*	**SWA** **SDA**	**Submissive** (avoidance)	-	**2**	-	**Hoyt** (1995); **Samuels** *et al.* (2003); **Koper** *et al.* (2015) https://biganimals.com/; https://bigfishexpeditions.com/ [*accessed 17 May 2022*]
1990s	**SRI LANKA** (North Western and Southern Provinces)	*S. longirostris* *S. coeruleoalba* *T. truncatus* *T. aduncus* *S. plumbea* *G. macrorhynchus* *O. orca*	**SWA**	-	-	-	-	**CMS** (2017) https://adrenalinelk.com/; https://mirissadivecenter.com; https://www.slam.lk [*accessed 17 May 2022*]
1990s	**BELIZE** (Ambergris Caye Island)	*T. truncatus* *S. longirostris*	**SWA** **SDA**	-	-	-	-	**Hoyt** (1995); **O'Connor et al.** (2009) https://belizedivehaven.com [*accessed 17 May 2022*]
1990s	**SPAIN** (Canary Islands)	*G. macrorhynchus* *T. truncatus* *S. bredanensis* *S. frontalis*	**SWA** **FPA**	**Aggressive** (head shaking, jaw clapping) **Submissive** (avoidance)	-	**1, 2, 7**	-	**Hoyt** (1995); **Ritter** (1996); **Soury** (1996); **Samuels** *et al.* (2000, 2003); **Ritter** (2002); **Scheer** *et al.* (2004); **Elejabeitia & Urquiola** (2009); **O'Connor** *et al.* (2009); **Carlson** (2012); **Scheer** *et al.* (2014)

Table 1(a) Ongoing tourist and other recreational activities [p. 3 / 4]

1990s	**NORWAY** (Lofoten Islands, Tromso and Tysford)	*O. orca*	**SWA SDA**	-	-	-	-	**Pagel** *et al.* (2016); **Chanvallon** *et al.* (2017); pers. com. **Pierre Robert de Latour** https://bigfishexpeditions.com/; https://www.whaleswim.com/; https://waterproof-expeditions.com/ [*accessed 17 May 2022*]
1990s	**PORTUGAL** (Azores Islands; Madeira Island)	*S. frontalis* *D. delphis* *S. coeruleoalba* *T. truncatus* *G. griseus*	**SWA**	**Submissive** (avoidance)	**Intrusive** ("harassment")	**6**	-	**Soury** (1996); **Samuels** *et al.* (2000, 2003); **Barradell & Ritter** (2007); **O'Connor** *et al.* (2009); **Silva** (2015); **Cecchetti** *et al.* (2019); pers. com. **Serge Viallelle** (*Espaço Talassa*) https://madeiraislandactivities.com/ [*accessed 17 May 2022*]
1990s	**TANZANIA** (Zanzibar Island)	*T. aduncus* *S. plumbea* *S. longirostris*	**SWA**	**Submissive** (avoidance)	**Intrusive** ("harassment")	**2, 6, 7**	-	**Spradlin** *et al.* (2001); **Stensland & Berggren** (2007); **O'Connor** *et al.* (2009); **Christiansen** *et al.* (2010) zanzibardolphintours.com [*accessed 17 May 2022*]
1990s	**MOZAMBIQUE** (Inhambane and Maputo Provinces)	*T. aduncus* *S. plumbea*	**SWA**	-	-	**1, 18**	-	**Hoyt** (2001); **Samuels** *et al.* (2003); **O'Connor** *et al.* (2009); **Carlson** (2012); **MacCaffery & Walker** (2012); **Rocha** *et al.* (2020) http://extremenaturetours.co.za; thedolphincentre.com; dolphinencountours.org [*accessed 17 May 2022*]
1990s	**TONGA**	*S. longirostris*	**SWA**	-	-	-	-	**Hoyt** (1995); **Carlson** (2012); **CMS** (2017)
1990s	**COSTA RICA** (Osa Peninsula)	*S. attenuata* *S. longirostris* *T. truncatus* *P. crassidens*	**SWA SDA**	-	-	-	-	**IWC** (2010); **Iñiguez & Tossenberger** (2015); **CMS** (2017) https://divinedolphin.com [*accessed 17 May 2022*]
1990s	**FRANCE** (Mainland: Mediterranean Coast; French Antilles Islands; French Polynesian Islands; Mayotte Island; Reunion Island)	*T. truncatus* *T. aduncus* *S. longirostris* *S. attenuata* *S. coeruleoalba* *S. bredanensis* *S. plumbea* *P. electra* *G. macrorhynchus* *G. melas* *G. griseus*	**SWA SDA**	**Aggressive** (buzzing, jaw clapping and charging scuba divers) **Submissive** (avoidance) **Intrusive** (touching) **Abrupt** (quick approach, rapid circling, pushy)	**Intrusive** ("harassment," chasing, touching, rubbing, grabbing, holding tail)	**1, 2, 5, 6, 9, 10, 15, 20**	**D**	**Soury** (1996); **Gannier** (2002); **Hoyt & Hvenegaard** (2002); **Samuels** *et al.* (2003); **Gannier & Petiau** (2006); **Mayol** *et al.* (2007); **IWC** (2010); **Pusineri** (2011); **Carlson** (2012); **Lagouy & Clua** (2016); **Mayol** *et al.* (2016); **Carzon** (2017); **Carzon** *et al.* (2019); **Chazot** *et al.* (2020); **Hoarau** *et al.* (2020); **Quintana Martín-Montalvo** *et al.* (2021); pers. com. **Jeremy Kiszka**, **Xavier Curvat** (*Marquises Dives*), **Caroline Rinaldi** (*Association Évasion Tropicale*), **Emmanuel Antongiorgi** (*Duocéan*), **Anne Littaye** (*Objectif Sciences International*)
1990s	**MALDIVES**	*S. longirostris* *S. bredanensis*	**SWA SDA**	-	-	-	-	**Anderson** *et al.* (2012) https://lovethemaldives.com [*accessed 17 May 2022*]
1990s	**NIUE**	*S. longirostris*	**SWA**	-	-	-	-	**Samuels** *et al.* (2003); **O'Connor** *et al.* (2009); **Carlson** (2012) https://www.niueisland.com/ [*accessed 17 May 2022*]
2000s	**MAURITIUS** (Black River District)	*S. longirostris* *T. aduncus*	**SWA**	-	**Intrusive** ("harassment," chasing)	**6, 18**	-	**Gowreesunkar & Rycha** (2015); **Webster** (2016); **Lewis & Walker** (2018); pers. com. **Adèle de Toma** (*Mauritius Marine Conservation Society*), **Thomas Vignaud**
2000s	**THE UNITED KINGDOM** (Saint Helena Island)	*T. truncatus* *S. attenuata* *S. bredanensis*	**SWA SDA**	-	-	-	-	http://divesainthelena.com/ [*accessed 17 May 2022*]

Table 1(a) Ongoing tourist and other recreational activities [p. 4 / 4]

2000s	**CANADA** (Bylot Island and Hudson Bay)	*D. leucas* *M. monoceros*	**SWA**	-	-	-	-	**CMS** (2017) https://churchillwild.com; https://sdmdiving.com; https://bigfishexpeditions.com/ [*accessed 17 May 2022*]
2010s	**INDIA** (Mainland; Andaman and Lakshadweep Islands)	*S. longirostris* *S. plumbea* *T. aduncus* *D. delphis* *G. griseus*	**SWA**	-	-	-	-	**CMS** (2017)
2010s	**KENYA** (Diani Beach and Wasini Island)	*T. aduncus*	**SWA**	-	-	-	-	**CMS** (2017)
2010s	**ANTARCTICA** (Peninsula)	*O. orca*	**SWA**	-	-	-	-	**CMS** (2017) https://whale-expeditions.com [*accessed 17 May 2022*]
2010s	**OMAN** (Dhofar Governate)	*T. aduncus* *S. longirostris* *D. capensis*	**SWA**	-	-	-	-	**Ponnampalam** (2011); **CMS** (2017) http://www.sidabseatours.com [*accessed 17 May 2022*]
2010s	**RUSSIA** (Sea of Okhotsk Coast; Solovetsky Islands)	*O. orca* *D. leucas*	**SWA**	-	-	-	-	https://whale-expeditions.com [*accessed 17 May 2022*]

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Table 1(b) Lone, sociable dolphins [p. 1 / 4]

From	Countries (locations)*	Species	Individuals (calves born to lone, sociable females not considered in results)	Type of activities**	Dolphins' deleterious behaviors in the presence of humans/human activities	Humans' deleterious behaviors in the presence of dolphins	Risks for dolphins	Risks for humans/human activities	References
1950s	**THE UNITED STATES** (Georgia and South Carolina; Gulf Coast; Massachusetts; Long Island; San Francisco Bay; Washington State)	*T. truncatus* *D. leucas* *O. orca*	**Carolina Snowball** (1950s-1965); **Georgy Girl** (1960s); **Nudgy** (1965-1966); **Dolly** (1971); **Dolphin 56** (1979-2011); **Bella** (1980); **Nudgy** (1981); **Elsa** (1982); **BW** (1985); **Beggar** (1990-2012); **Springer** (2002); **Kaimi** (2016-2017); **Izzy** (2020-2022)	**SWA** **SDA** **FPA**	**Aggressive** (tail slapping, couple splitting) **Sexual** (rubbing genitals against objects and swimmers) **Intrusive** (begging, putting head close to boat engines and propellers) **Abrupt** (quick swim and rapid circling, leaping close to swimmers, preventing swimmers from returning to shore or vessels, pushing boats)	**Aggressive** (hitting, spearing and shooting at dolphin) **Intrusive** (touching, riding, holding onto fins for being towed)	**1, 7, 8, 10, 12, 13, 14, 20**	**A, C**	**Diolé & Cousteau** (1975); **Lockyer** (1990); **Frohoff** (2000); **Guyomard** (2003); **Cunningham-Smith** *et al.* (2005); **Frohoff** *et al.* (2005); **Hartley** *et al.* (2005); **Joyce** (2005); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019) https://www.fisheries.noaa.gov/feature-story/izzy-dolphin-making-her-story-matter [*accessed 30 December 2022*]
1950s	**SOUTH AFRICA** (Western Cape Province)	*T. truncatus*	**Fish** (1953); **Hoek** (1953)	**SWA**	-	**Intrusive** (touching, riding, holding onto fins for being towed)	-	-	**Müller** (1998); **Guyomard** (2003); **Goodwin & Dodds** (2019)
1950s	**NEW ZEALAND** (Hauraki Gulf and Coromandel Peninsula; Hawke's Bay Region; Marlborough and Tasman Regions; Northland Region; Southland Region)	*T. truncatus* *D. delphis* *L. obscurus*	**Opo** (1955); **Horace** (1978-1979); **Whitianga** (1981-1989) and her calves; **Rampal** (1984-1989); **Tammy** (1984); **Aihe** (1987-1993); **Jack** (1989-1990); **Maui** and her calf (1992-1997); **Siany** (1992-1994); **Harry (**1995-1997); **Scar** (2000s?); **Moko** (2007-2010)	**SWA** **SDA** **FPA**	**Aggressive** ("intolerance to humans," tail slapping, pushing swimmers roughly, "repelling" swimmers, "abduction" of swimmers out to sea) **Submissive** (avoidance) **Sexual** (erection, rubbing genitals against swimmers) **Intrusive** (seeking close body contact, interacting with moorings and fishing gear, lifting anchors, rubbing against boats, putting head close to spinning propellers) **Abrupt** ("boisterous," pushy, quick swim and rapid circling, dislodging fin tows, pulling at divers' flippers, knocking people off surfboards, preventing swimmers from returning to shore or vessels, bumping dinghies)	**Aggressive** (throwing explosives to dolphins) **Intrusive** ("harassment," touching, holding onto dorsal fin, riding)	**1, 5, 9, 13, 14, 17, 20**	**C**	**Lockyer** (1990); **Orams** (1997); **Müller** (1998); **Müller** *et al.* (1998); **Constantine** (1999); **Frohoff** *et al.* (2005); **Goodwin & Dodds** (2019)
1960s	**AUSTRALIA** (New South Wales; South Australia; Victoria; Western Australia)	*Tursiops* sp. *T. aduncus*	**Wallis** (1961-1962); **Big Momma** (1975-1989); **Indah** (1982-1983); **Billie** (1987-2009) and her calves; **Jock** (1988-1993); **Touch** (1990-1997); **Kattappi** (1992); **Twinkle** (2002); **Yera** (2012)	**SWA** **FPA**	**Sexual** (rubbing genitals against swimmers) **Intrusive** (begging, playing with oars, putting head close to spinning propellers) **Abrupt** ("boisterous")	**Intrusive** (touching)	**1, 7, 8, 9, 10, 12, 13, 14, 15, 17, 20**	-	**Müller** (1998); **Guyomard** (2003); **Bossley** (2005); **Wilke** *et al.* (2005); **Bossley** et al. (2018); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019)

Table 1(b) Lone, sociable dolphins [p. 2 / 4]

1960s	**THE UNITED KINGDOM** (Mainland: England, Scotland and Wales; Cayman Islands; Turks and Caicos Islands)	*T. truncatus* *D. delphis* *D. leucas*	**Charlie** (1962-1967); **Donald** (1972-1978); **Jojo** (1980-); **Percy** (1981-1984); **Simo** (1984-1986); **Freddie** (1987-1992); **#8** (1993-1994); **#10** (1993-1994); **Tonic** (2003); **Maurice** (2004-2005); **Jet** (2005); **Marra** (2006); **Dave** (2006-2007); **Chas** (2006-2007); **Cookie** (2007); **Sleekie** (2007); **Dolly** (2007); **Stinky** (2009-2012); **Stormy** (2014-2015); **Kylie** (2006-); **Benny** (2018); **Splashy** (2017-2018); **Danny** (2018-2020)	**SWA** **SDA** **FPA**	**Aggressive** ("sudden aggression and extreme violence," "dominant," "possessive," "unpredictable," emitting high, squeaking sounds, jaw clapping, tail slapping, couple splitting, "abduction" of swimmers and surfers out to sea, pushing divers or snorkelers down against the seabed, gripping, nipping people and hitting them on the head with rostrum, swimmers and snorkelers being rushed, butted, breached on, ducked, tail swapped, dragged around, pulled, bitten, tossed clear of the water) **Submissive** (avoidance) **Sexual** (nudging with rostrum at female swimmers' genital area, erection, thrusting movements directed at swimmers, rubbing genitals against swimmers and boats, ejaculation) **Intrusive** (seeking close body contact, playing with ropes, fishlines and pots, entangling small boats, lifting anchors) **Abrupt** ("boisterous," "defensive," quick swim and rapid circling, pulling at divers' flippers, preventing swimmers from returning to shore or vessels, landing on and smashing up surfboards, knocking people off water-skis, pushing, lifting, and tossing boats, towing small and large boats)	**Aggressive** (dolphin being shot and wounded, purposely hit by boat) **Sexual** ("sexual behavior being actively encouraged by swimmers," stroking and provoking sexual response) **Intrusive** ("harassment," circling, chasing, touching, rubbing, grabbing, riding, holding onto dorsal fin, hanging on pectoral fins, shoving fingers into blowhole, eyes and ears)	**1, 6, 7, 9, 10, 11, 12, 13, 14, 15, 17, 20**	**A, B, C**	**Lockyer** (1978); **Webb** (1978); **Lockyer & Morris** (1985); **Lockyer & Morris** (1986); **Morris & Lockyer** (1988); **Lockyer** (1990); **Bloom** (1991); **St John** (1991); **Bloom & Jager** (1994); **Bloom** *et al.* (1995); **Hoyt** (1995, 2001); **Soury** (1996); **Müller** (1998); **Wood** (1999); **Samuels** *et al.* (2000); **Guyomard** (2003); **Frohoff** *et al.* (2005); **Goodwin & Dodds** (2008, 2019); **O'Connor** *et al.* (2009); **Eisfeld** *et al.* (2010); **Nunny & Simmonds** (2019)
1970s	**SPAIN** (Mainland: Asturias, Basque Country and Galicia)	*T. truncatus*	**Nina** (1972); **Ercina** and her calf (1994-1997); **Enol** (1994); **Pakito** (1998-2005); **Unnamed** (2003-2005); **Elcano** (2013); **Manoliño** (2020-)	**SWA** **SDA**	**Aggressive** ("an increasing number of visitors made the dolphin 'Enol' becoming aggressive", biting) **Sexual** (rubbing genitals against swimmers or divers)	**Intrusive** (touching, holding tail, riding)	**1, 10, 13, 20**	**C**	**Diolé & Cousteau** (1975); **Guyomard** (2003); **Frohoff** *et al.* (2005); **Díaz López** *et al.* (2008); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019) https://www.lavanguardia.com/natural/20221227/8659509/avistan-al-delfin-manolino-jugando-con-un-nadador-pmv.html [*accessed 30 December 2022*]
1970s	**FRANCE** (Mainland: Bay of Biscay, English Channel, Iroise Sea and Mediterranean Coast; French Antilles Islands)	*T. truncatus*	**Jean-Louis** (1976-1987); **Fanny** (1987-1994); **Marine** (1988-1989); **Dolphy** (1989-1995); **Françoise** (1989-2001); **Dony** (2001-); **Jean Floc'h** (2002-2010); **Wifi** (2007-2011); **Clet** (2008-2018); **Fiete** (2016-2017); **Zafar** (2017-2020); **Blue** (2020-2021) ; **Parbatt** (2022-)	**SWA** **SDA**	**Aggressive** ("dominant," tail slapping, tossing swimmers out of the water, swimmers being seized, mouthed, bitten, pushed, butted, rammed, hit) **Submissive** (avoidance) **Sexual** (nudging with rostrum at female swimmers' genital area, erection, rubbing genitals against swimmers, moorings and boats) **Intrusive** ("interest in boats, paddles and oars," pushing beak or flanks right up against boat propellers, rubbing against ropes, playing with buoys) **Abrupt** (quick swim and rapid circling, preventing swimmers from returning to shore or vessels, pushing boats)	**Aggressive** (dolphin being hit, wounded, shot) **Intrusive** ("harassment," touching, holding onto fins, riding)	**1, 3, 9, 13, 14, 15, 20**	**A, C** *A man was hospitalized after he was tossed out of the water by* **'Dony'** *and suffered a heart attack*	**Pelletier** (1985); **Soury** (1996); **Müller** (1998); **Guyomard** (2003); **Simmonds** (2005); **Wilke** *et al.* (2005); **Nunny & Simmonds** (2019); **Goodwin & Dodds** (2019); **IJsseldijk** *et al.* (2020); pers. com. **Isabelle Brasseur**
1970s	**THE BAHAMAS** (Bimini, Grand Bahama and San Salvador Islands)	*S. frontalis* *T. truncatus*	**Sandy** (1976-1978); **Herbie** (1988)	**SWA** **SDA**	**Sexual** (erection, rubbing genitals against swimmers) **Intrusive** (rubbing against objects) **Abrupt** (nudging and holding people by the snorkel or facemask, removing facemasks, pulling hair, tapping people's head with rostrum, preventing swimmers from returning to shore or vessels, pushing boats)	**Intrusive** (touching)	**15**	-	**Lockyer** (1990); **Guyomard** (2003); **Frohoff** *et al.* (2005); **Goodwin & Dodds** (2019)

Table 1(b) Lone, sociable dolphins [p. 3 / 4]

1970s	**CANADA** (British Columbia Province; Quebec, New Brunswick, Newfoundland, and Nova Scotia Provinces)	*O. orca* *D. leucas* *M. monoceros*	**Miracle** (1977-1982); **Wilma** (1993-1998); **Unnamed** (1998); **Kuus** (1999); **Lenni** (2000-2002); **Charlie** (2001-2002); **Casper** (2001-2002); **Luna** (2001-2006); **Ce'Sea** (2003); **Unnamed** (2003); **Nar Billy** (2003); **Poco** (2003-2004); **Chance** (2004-2005); **Unnamed** (2004-2005); **Q** (2008-2010); **Luke** (2015); **Nepisiguit Beluga** (2017-2018); **Bluey** (2019-2021)	**SWA** **SDA** **FPA**	**Intrusive** (soliciting physical contact, "interacting with" boats, propellers, fishing gear, chains and ropes, playing with boat fenders, rubbing against swimmers and boats)	**Intrusive** ("harassment," touching)	**1, 9, 12, 13, 14, 15, 20**	**A**	**Spradlin** *et al.* (2001); **Chisholm** (2005); **Frohoff** *et al.* (2005); **Joyce** (2005); **Kinsman & Frohoff** (2005); **Goodwin & Dodds** (2008); **Nunny & Simmonds** (2019)
1970s	**ISRAEL** (Ashdod and Eilat)	*T. truncatus* *Tursiops* sp.	**Dobbie** (1979); **Crispy** (1992); **Kodo** (1995-1996); **Marco** (2006-2008)	**SWA** **SDA**	**Intrusive** ("soliciting physical contact")	**Aggressive** (shooting at dolphin) **Intrusive** (touching)	**1, 20**	-	**Guyomard** (2003); **Frohoff** *et al.* (2005); **Goodwin & Dodds** (2008, 2019)
1980s	**COSTA RICA** (Chira Island)	*T. truncatus*	**The Costa Rican** (1983)	**SWA**	**Abrupt** (pushing a canoe)	**Aggressive** (killing dolphin) **Intrusive** (touching)	**9, 20**	-	**Lockyer** (1990); **Frohoff** *et al.* (2005)
1980s	**IRELAND** (Cork, Kerry, Clare and Galway Counties, Tory Island)	*T. truncatus*	**Fungie** (1983-2020); **Dusty** (1999-); **Sandy** (2001-2003); **Maurice** (2004-2005); **Coulagh Bay dolphin** (2005); **Venus** (2005); **Duggie** (2006-2008); **Nimmo** (2015-)	**SWA** **SDA**	**Aggressive** ("attacking" swimmers, tail slapping, ramming swimmers) **Abrupt** (quick swim and rapid circling, leaping close to swimmers, preventing swimmers from returning to shore or vessels, pushing boats)	**Intrusive** ("harassment," touching, holding onto fins for being towed)	**1**	**C** **'Dusty'** *rammed a swimmer breaking two ribs, and attacked a swimmer resulting in internal injuries and hospital treatment*	**Hoyt** (1995); **Müller** (1998); **Guyomard** (2003); **Frohoff** *et al.* (2005); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019)
1980s	**ITALY** (Manfredonia and Monfalcone)	*T. truncatus*	**Romeo** (1985-1987); **Filippo** (1996-2004)	**SWA**	**Aggressive** (tail slapping, biting, pulling swimmers) **Sexual** (erection, rubbing genitals against swimmers) **Intrusive** (rubbing against objects) **Abrupt** (preventing swimmers from returning to shore)	**Intrusive** ("harassment," touching, riding)	**1, 10, 13, 14, 15, 20**	**C**	**Bearzi & Barbieri** (2001); **Guyomard** (2003); **Frohoff** *et al.* (2005); **Nunny & Simmonds** (2019)
1980s	**BELIZE** (Lighthouse Reef Atoll)	*T. truncatus*	**Pita** (1987-1994)	**SWA** **FPA**	**Aggressive** ("threat displays," tail slapping, displacing, hitting, ramming and bumping swimmers) **Sexual** (rubbing genitals against swimmers and boats) **Intrusive** (rubbing against objects and swimmers) **Abrupt** (pushy, leaping over swimmers, preventing swimmers from returning to shore)	**Aggressive** ("injuring" dolphin) **Intrusive** (chasing, touching, grabbing fins, riding)	**1, 13, 14, 15**	**C**	**Dudzinski** *et al.* (1995); **Frohoff** (1996); **Müller** (1998); **Goodwin & Dodds** (2008); **Nunny & Simmonds** (2019)
1980s	**MONTENEGRO** (Kotor)	*T. truncatus*	**Jotsa** and her calf (1988-2001)	**SWA**	**Aggressive** (tail slapping, pushing and bumping swimmers) **Sexual** (rubbing genitals against swimmers) **Abrupt** (quick swim and rapid circling, leaping close to swimmers, preventing swimmers from returning to shore)	**Aggressive** (throwing explosives to dolphins) **Intrusive** ("harassment," touching, holding onto dorsal fin, riding)	**1, 4, 13, 20**	**C**	**Müller** (1998); **Guyomard** (2003)

Table 1(b) Lone, sociable dolphins [p. 4 / 4]

1980s	**GREECE** (Aliveri and Cyclades Islands)	*T. truncatus*	**Kitsos** (1989-1990); **Evia** (1993-1994)	**SWA FPA**	**Intrusive** (begging)	**Aggressive** ("threatening" and shooting at dolphins) **Intrusive** (touching)	**1, 13, 20**	**A**	**Müller** (1998)
1990s	**NORWAY** (Hammerfest; Melfjord; Karmoy)	*T. truncatus* *G. melas* *D. leucas*	**Flipper** (1990-2002); **Ronald** (2000-) **Hvaldimir** (2019)	**SWA SDA FPA**	**Aggressive** (shaking head, biting, "abducting" swimmers out to sea) **Sexual** (erection, rubbing genitals against objects and swimmers) **Intrusive** (playing with ropes, buoys and boat fenders, rubbing against boats, putting head close to propellers) **Abrupt** (quick swim, rapid circling, pushing boats, knocking people off surfboards, preventing swimmers from returning to shore)	**Aggressive** (shooting at dolphin) **Intrusive** ("harassment," touching)	**1, 9, 11, 13, 14, 15**	**C**	**van der Toorn** *et al.* (1992); **Müller** (1998) https://www.norwegianorcasurvey.no [*accessed 10 July 2021*] https://orcachannel.com/title/hvaldimir/ [*accessed 28 May 2022*]
1990s	**MEXICO** (Sea of Cortez Coast; Veracruz State)	*T. truncatus*	**El Pechocho** (1992-); **Lucero** (2005-)	**SWA FPA**	-	**Intrusive** (touching, rubbing)	**1, 15**	-	**Frohoff** *et al.* (2005); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019)
1990s	**BRAZIL** (Rio de Janeiro State; Sao Paulo State)	*T. truncatus* *S. guianensis* *S. bredanensis*	**Tião** (1994-1995); **Viola** (1996-1999); **Unnamed** (2018-2019)	**SWA FPA**	**Aggressive** (tail slapping, ramming swimmers) **Intrusive** (begging) **Abrupt** ("defensive")	**Aggressive** (hitting, dragging dolphin to the beach, trying to tie things to flippers) **Intrusive** ("harassment," touching, grabbing, riding, holding onto fins for being towed, putting objects in blowhole)	**1, 7, 8, 13, 20**	**C, E** **'Tião'** *inflicted cuts and bruises to up to 29 bathers, and rammed a man in response of abuse*	**Santos** (1997); **Müller** (1998); **Santos** *et al*. (2000); **Frohoff** *et al.* (2005); **Goodwin & Dodds** (2019); **Nunny & Simmonds** (2019); **Maciel** *et al.* (2020)
1990s	**EGYPT** (Nuweiba)	*T. aduncus*	**Oleen** (1994-2004) and her calves	**SWA FPA**	**Aggressive** ("dominant," "intolerant," tail slapping, biting, butting with head, pushing swimmers roughly) **Submissive** (avoidance) **Intrusive** ("soliciting physical contact") **Sexual** (rubbing genitals against swimmers) **Abrupt** (quick swim and rapid circling)	**Intrusive** ("harassment," touching, turning, spinning, opening dolphin's jaws)	**1, 4, 5, 6, 13, 18, 20**	**C**	**Müller** (1998); **Müller** *et al.* (1998); **Spradlin** *et al.* (2001); **Frohoff** *et al.* (2005); **Goffman** *et al.* (2005); **O'Connor** *et al.* (2009)
1990s	**JAPAN** (Izu Islands; Fukui Prefecture)	*T. aduncus*	**Koko** (1995-1998) and her calf; **Suzu-chan** (2020-)	**SWA SDA**	**Aggressive** (biting, pulling, ramming, pushing swimmers roughly)	**Intrusive** (touching)	**1**	**C**	**Müller** (1998); **Goodwin & Dodds** (2019) https://mainichi.jp/english/articles/20220815/p2a/00m/0na/012000c [*accessed 30 December 2022*]
1990s	**THE NETHERLANDS** (Aruba Island)	*S. bredanensis*	**Unnamed** female dolphin (1998)	**SWA FPA**	**Aggressive** (hitting volunteers) **Intrusive** (begging)	**Intrusive** ("harassment," touching) **Abrupt** (jumping from a bridge on top of dolphin)	**1, 7, 8, 11, 12, 13, 20**	-	**Rodriguez-Lopez & Mignucci-Giannoni** (1999); pers. com. **Antonio Mignucci-Giannoni**
2000s	**ANGOLA** (Luanda)	*T. truncatus*	**Unnamed** (2003-2004)	-	-	-	**20**	-	**Goodwin & Dodds** (2019)
2000s	**CROATIA** (Croatia and Dalmatia Regions)	*S. coeruleoalba* *T. truncatus*	**SC1** (2004-2009); **Bobi** (2014-2016)	**SWA**	**Intrusive** (playing with buoys and moored vessels)	**Intrusive** (touching)	**1, 15**	**A**	**Nunny & Simmonds** (2019)
2000s	**BELGIUM** (Ostend)	*T. truncatus*	**Rudolf** (2007-2008)	**SWA**	-	-	-	-	**Nunny & Simmonds** (2019)
2010s	**GERMANY** (Kiel)	*D. delphis*	**Schwenteeny** (2019)	-	-	-	-	-	**Goodwin & Dodds** (2019)

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Table 2. Details on species involved in close interactions

*Number of locations where each species was documented in close interactions.
**Number of individual lone, sociable dolphins from each species.
[opp] Species opportunistically involved in close interactions.

	Ongoing activities	**Lone, sociable dolphins**	
	Number of locations, **N=54***	Number of locations, **N=47***	Number of individuals, **N=135****
Cephalorhynchus commersonii	**1**	-	-
Cephalorhynchus hectori	**3**	-	-
Delphinapterus leucas	**2**	**4**	**19**
Delphinus capensis	**2**	-	-
Delphinus delphis	**9**	**4**	**5**
Globicephala macrorhynchus	**5**	-	-
Globicephala melas	**2**	**1**	**1**
Grampus griseus **[opp]**	**3**	-	-
Inia geoffrensis	**1**	-	-
Lagenorhynchus obscurus	**3**	**1**	**1**
Monodon monoceros	**1**	**1**	**1**
Orcinus orca	**7**	**3**	**4**
Peponocephala electra **[opp]**	**2**	-	-
Pseudorca crassidens **[opp]**	**3**	-	-
Sotalia guianensis	**1**	**1**	**1**
Sousa plumbea	**7**	-	-
Sousa sahulensis	**1**	-	-
Stenella attenuata	**6**	-	-
Stenella coeruleoalba	**3**	**1**	**1**
Stenella frontalis	**4**	**1**	**1**
Stenella longirostris	**19**	-	-
Steno bredanensis **[opp]**	**7**	**2**	**2**
Tursiops sp.	-	**3**	**9**
Tursiops aduncus	**17**	**4**	**6**
Tursiops australis	**2**	-	-
Tursiops truncatus	**22**	**30**	**84**

Chapter 3

Free-ranging bottlenose dolphins' tolerance to scuba diving tourism is modulated by their age, social context, and by the divers' behaviors

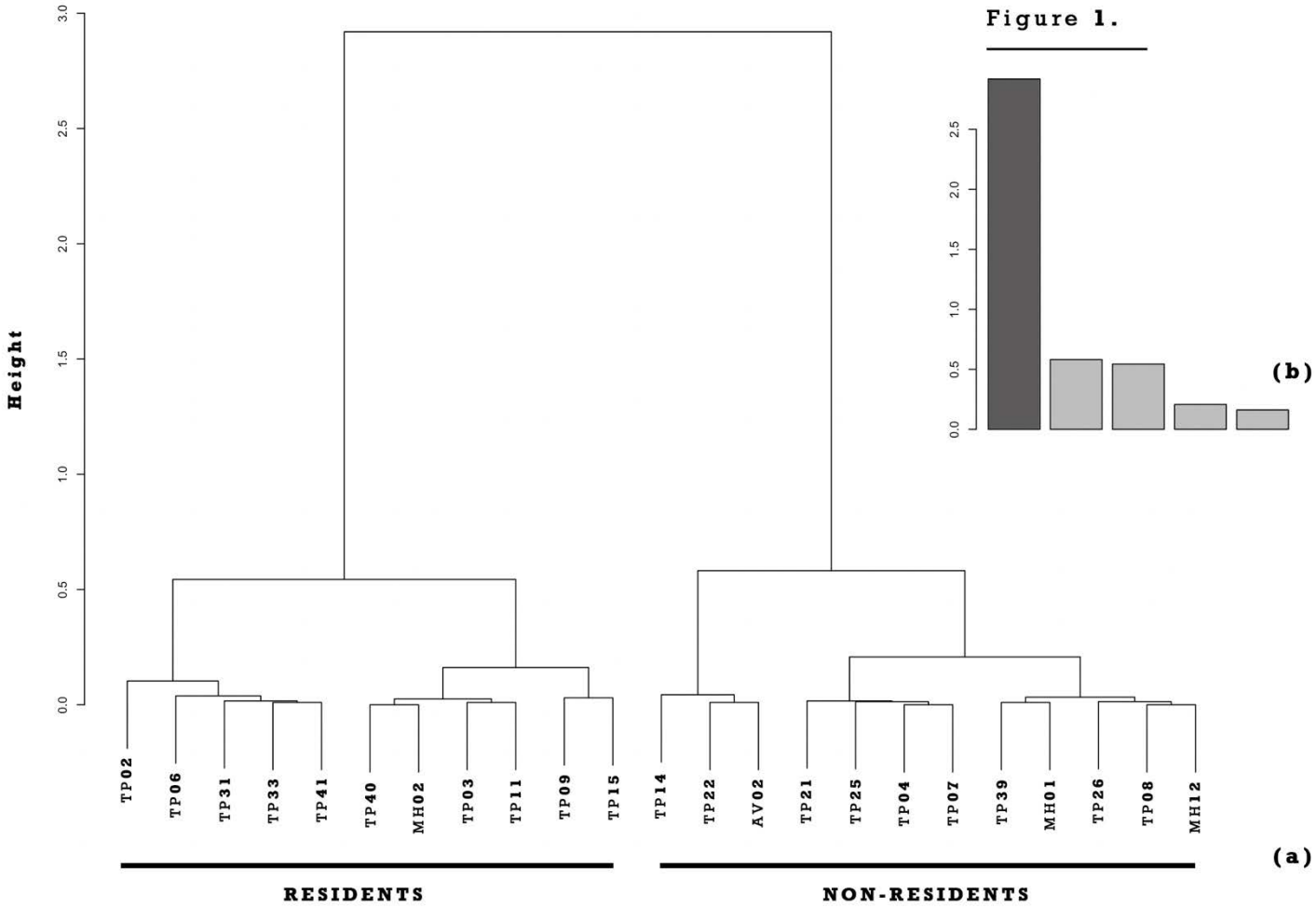

Figure 1(a) Cluster dendrogram and **(b)** inter-cluster inertia gains based on 23 bottlenose dolphins' sighting rates in a scuba diver-free area. Two calves (TP02's and TP21's) were then assigned to their mothers' categories (i.e., resident or non-resident on the area).

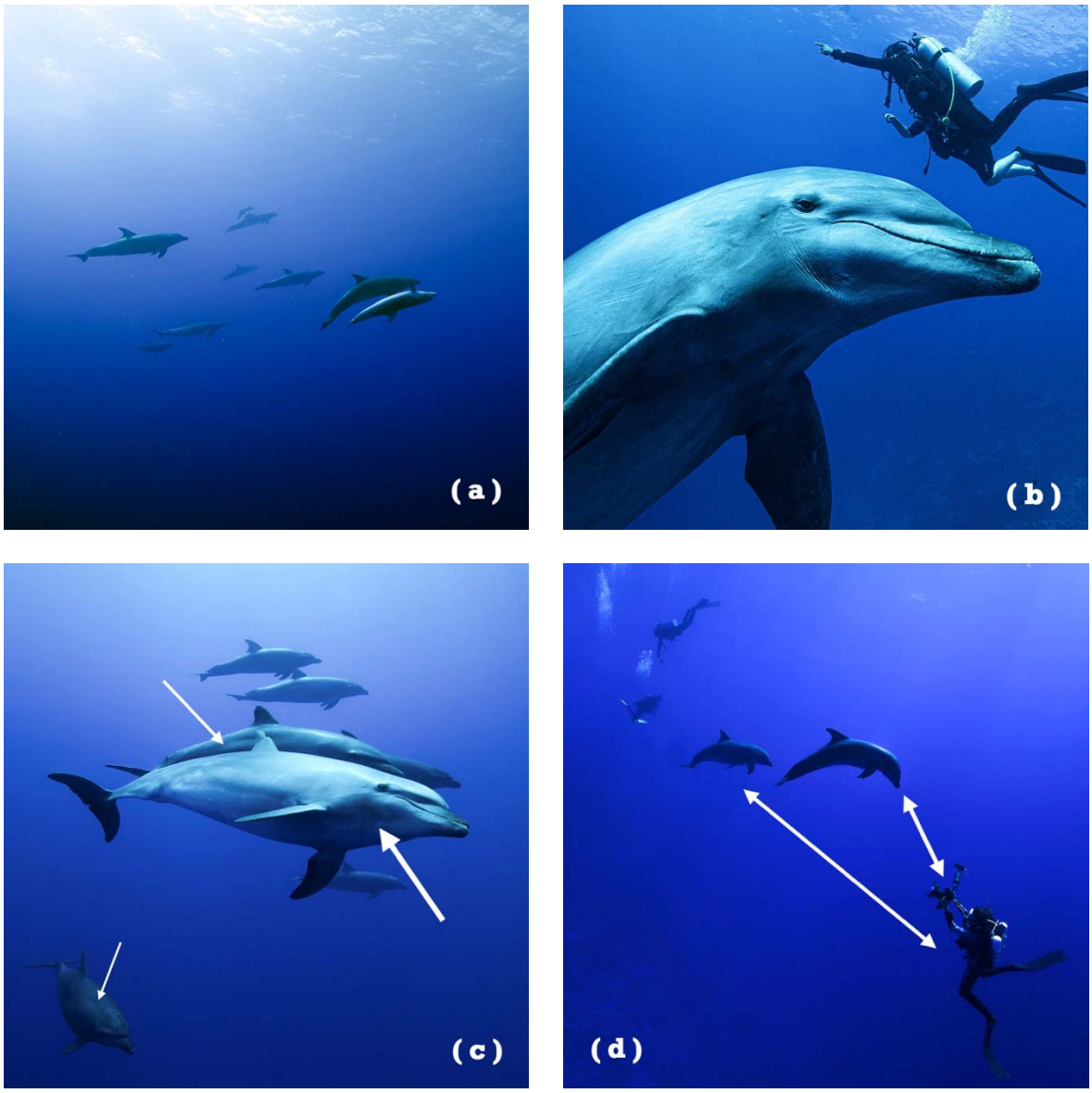

Figure 2. Examples of approximate distances (< or > 10m) between dolphins and scuba divers, and dolphins and the **cameraman** (i.e., the diver who took the picture).

(a) Dolphins located at >10m from the **cameraman** and other scuba divers.

(b) Dolphin located at <10m from the **cameraman** and other scuba divers.

(c) Dolphins located at < (*pointed by arrows*) and > 10m from the **cameraman**.

(d) Dolphins located at >10m from the **cameraman** and at <10m from another scuba diver using a camera (*pointed by double ended arrows*).

(e) Dolphins located at <10m from the **cameraman** and >10m from other scuba divers.

Table 1(a) Shore-based sampling effort in 2018, 2019 and 2020.

	2018	2019	2020
Number of dolphin sightings	32	93	71 20 before, 14 during, and 37 after the two-month French COVID-19 lockdown
Number of sampling periods	32	93	71 20 before, 14 during, and 37 after the two-month French COVID-19 lockdown
Total duration of sampling effort	48:00’	139:30’	106:30’
Total number of dolphins identified	28	31	30
Number of dolphins per sighting	Mean = 9 ± 5 SE Median = 9 Range = 1-20	Mean = 10 ± 5 SE Median = 9 Range = 1-21	Mean = 8 ± 4 SE Median = 7 Range = 1-19

Table 1(b) Underwater sampling effort in 2018, 2019 and 2020.

	2018	2019	2020
Number of dolphin sightings	112	140	129 31 before and 98 after the two-month French COVID-19 lockdown
Number of sampling periods	57	70	77 19 before and 58 after the two-month French COVID-19 lockdown
Total duration of video sequences showing dolphins	5:01’50”	5:01’56”	4:23’31”
Total number of dolphins identified	28	29	26
Number of dolphins per sighting	Mean = 4 ± 3 SE Median = 3 Range = 1-13	Mean = 5 ± 3 SE Median = 4 Range = 1-13	Mean = 4 ± 3 SE Median = 4 Range = 1-14
Number of divers per sighting	Mean = 8 ± 3 SE Median = 8 Range = 2-16	Mean = 7 ± 4 SE Median = 6 Range = 2-21	Mean = 6 ± 3 SE Median = 6 Range = 2-20

Table 2. Characteristics of the 18 dolphins selected for the underwater analyses.

							After random sampling of 10 sightings from 10 independent sampling periods			
ID code	**Sex**	**Sexual maturity**	**Est. size** (m)	**Mother's ID**	**Regularly captured on tourist site from**	**Tourist-site fidelity**	**Number of sightings 2018**	**Number of sightings 2019**	**Number of sightings 2020**	**Total sighting duration** (min)
MH02	♂	Mat	2.8	-	2010	R	2	5	3	16.9
MH12	♂	Mat	2.8	-	2009	NR	1	2	7	21.5
TP02	♀	Mat	2.6	-		R	1	6	3	20.3
TP03	♂	Mat	2.8	-		R	4	4	2	12.3
TP06	♂	Mat	2.8	-		R	3	4	3	20.6
TP07	♂	Mat	2.8	-		NR	3	4	3	10.3
TP09	♂	Mat	2.8	-		R	1	5	4	17.2
TP11	♀	Mat	2.6	-		R	3	4	3	11.7
TP15	♀	Mat	2.6	-		R	4	5	1	15.3
TP25	♀	Mat	2.6	-		NR	4	3	3	20.3
TP26	♂	Mat	2.8	-		NR	1	2	7	15.4
TP31	♀	Imm	2.4	**TP11**	2012*	R	3	4	3	17.2
TP33	♀	Imm	2.4	**TP02**	2013*	R	4	2	4	17.9
TP39	♀	Imm	2.4	**TP04**	2014*	NR	2	5	3	19.8
TP40	♀	Imm	2.4	**TP15**		R	5	5	-	23.1
TP41	♀	Imm	2.4	**MH01**		R	3	3	4	20.6
TP47	♀	Imm	2.0	*Dep* **TP21**	2016*	NR	5	2	3	21.8
TP48	♂	Imm	2.0	*Dep* **TP02**	2017*	R	3	3	4	20.0

Mat: Mature individual; **Imm:** Immature individual

R: Resident individual; **NR:** Non-resident individual

Dep: Calf; *Year of birth

Tables 3(a) and 3(b) legend

DAP = Actively approaching dolphin(s)
SOU = Making sounds in regulator, using shaker and-or knocking on tank
HOU = Holding hand(s) out to dolphin(s)
SAD = Swimming after dolphin(s)
SPA = Spinning around
SLD = Swimming like dolphin(s)
OBJ = Presenting object to dolphin(s)

Table 3(a) Number of dolphin sightings where scuba divers displayed each of the active behaviors.

Active behavior	2018 N = 112	2019 N = 140	2020 N = 129	All years N = 381
DAP	83	115	94	**292**
SOU	88	112	83	**283**
HOU	52	79	87	**218**
SAD	69	72	36	**177**
SPA	31	39	15	**85**
SLD	27	39	18	**84**
OBJ	12	8	1	**21**
Total sightings with active behaviors	107	133	120	**360**

Table 3(b) Number of underwater sampling periods where scuba divers displayed each of the active behaviors.

Active behavior	2018 N = 57	2019 N = 70	2020 N = 77	All years N=204
DAP	50	61	61	**172**
SOU	47	58	50	**155**
HOU	35	48	59	**142**
SAD	43	44	29	**116**
SLD	20	32	16	**68**
SPA	23	30	11	**64**
OBJ	11	7	1	**19**
Total sampling periods with active behaviors	56	68	71	**195**

Table 4. Proportion of individual sampling periods scuba divers displayed each of the active behaviors.

ID code	All behaviors cumulated	DAP	SOU	HOU	SAD	SLD	SPA	OBJ
MH02	0.80	0.55	0.70	0.27	0.32	0.07	0.02	0.00
MH12	0.70	0.48	0.61	0.43	0.09	0.04	0.09	0.00
TP02	0.87	0.66	0.72	0.38	0.32	0.16	0.10	0.00
TP03	0.83	0.53	0.77	0.17	0.17	0.13	0.04	0.00
TP06	0.76	0.56	0.66	0.15	0.24	0.14	0.03	0.00
TP07	0.75	0.42	0.63	0.29	0.13	0.13	0.00	0.00
TP09	0.74	0.43	0.60	0.21	0.19	0.11	0.04	0.00
TP11	0.86	0.49	0.77	0.20	0.23	0.11	0.00	0.00
TP15	0.87	0.49	0.76	0.18	0.31	0.11	0.00	0.02
TP25	0.83	0.50	0.67	0.44	0.33	0.11	0.06	0.00
TP26	0.79	0.42	0.63	0.32	0.00	0.05	0.00	0.00
TP31	0.93	0.80	0.85	0.52	0.45	0.25	0.31	0.07
TP33	0.94	0.81	0.72	0.66	0.55	0.18	0.17	0.08
TP39	0.95	0.76	0.67	0.62	0.29	0.19	0.19	0.05
TP40	0.95	0.81	0.85	0.36	0.54	0.19	0.22	0.12
TP41	0.92	0.76	0.76	0.59	0.43	0.10	0.15	0.09
TP47	0.94	0.78	0.72	0.33	0.33	0.22	0.06	0.11
TP48	0.94	0.73	0.79	0.46	0.33	0.16	0.15	0.03

Table 5. Shore-based sighting rates of 23 bottlenose dolphins over the three-year study. Sighting rates were sorted in ascending order. Individual tourist-site fidelity is shown.

ID code	Shore-based sighting rate	Tourist-site fidelity
AV02	0.04	NR
TP22	0.05	NR
TP14	0.08	NR
TP25	0.17	NR
TP04	0.18	NR
TP07	0.18	NR
TP21	0.19	NR
TP39	0.22	NR
MH01	0.23	NR
MH12	0.24	NR
TP08	0.24	NR
TP26	0.25	NR
TP11	0.41	R
TP03	0.42	R
MH02	0.43	R
TP40	0.43	R
TP15	0.48	R
TP09	0.51	R
TP31	0.55	R
TP41	0.56	R
TP33	0.57	R
TP06	0.59	R
TP02	0.64	R

R = Resident

NR = Non-resident

Chapter 4

Individual variation of boldness in free-ranging bottlenose dolphins interacting with scuba divers in French Polynesia

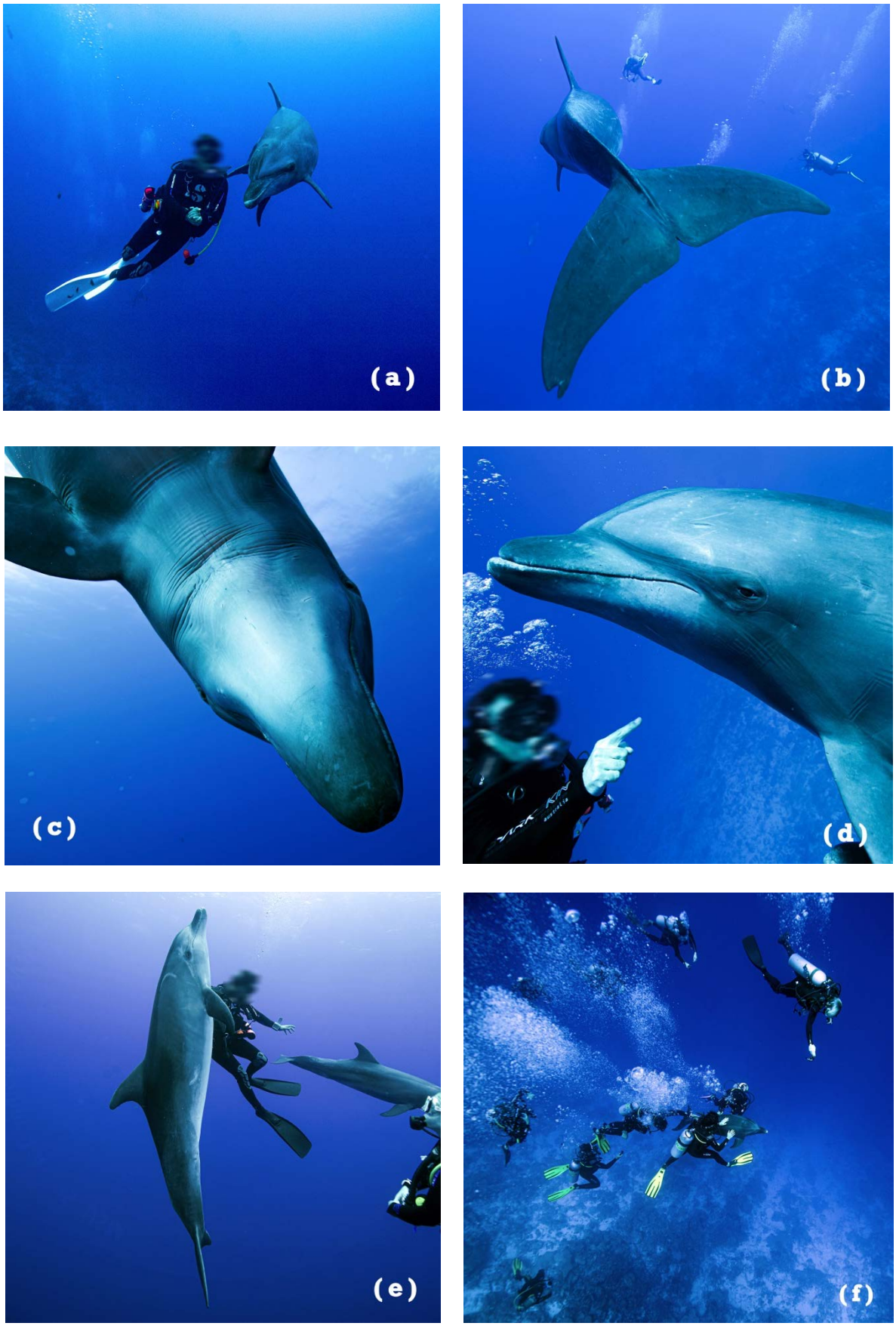

Figure 1. Illustrations of the dolphins' bold behaviors toward scuba divers, and involvement in physical interactions with scuba divers. **(a)** Swim around diver(s), **(b)** Swinging tail fluke, **(c)** Interest for camera, **(d)** Stationary near diver(s), **(e)** Vertical drop down, and **(f)** Physical interaction with diver(s).

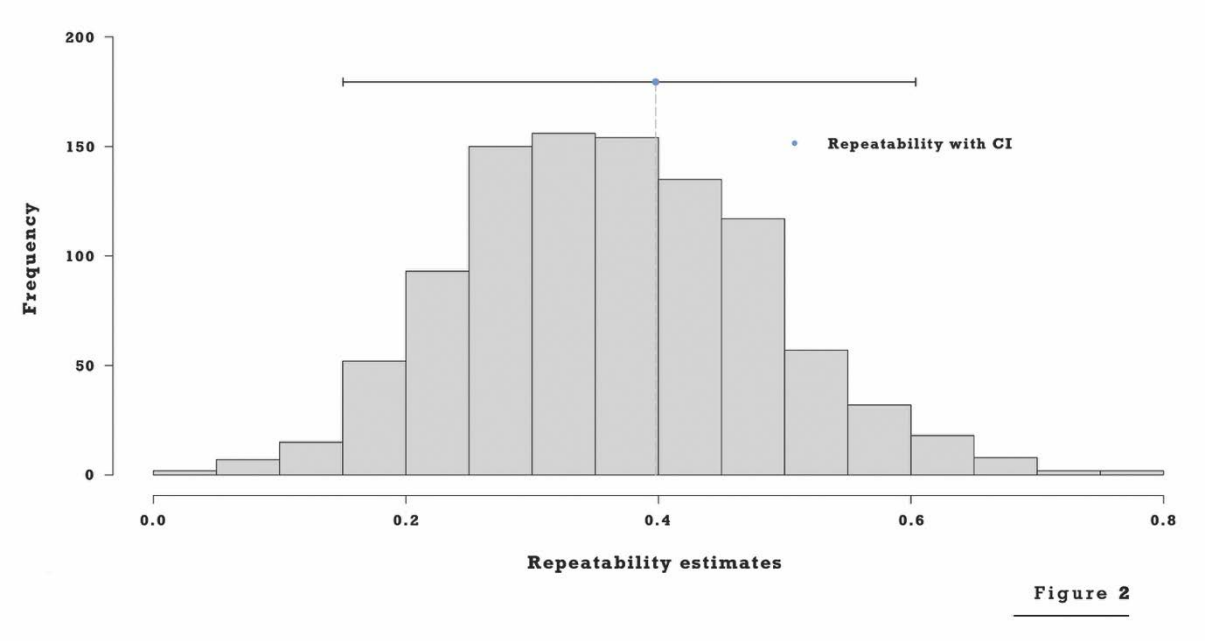

Figure 2. Link-scale approximation bootstrap repeatabilities for variable ACT<3m (dolphin's interaction with scuba divers at <3m from them) on 20 dolphins and ten sampling periods per dolphin.

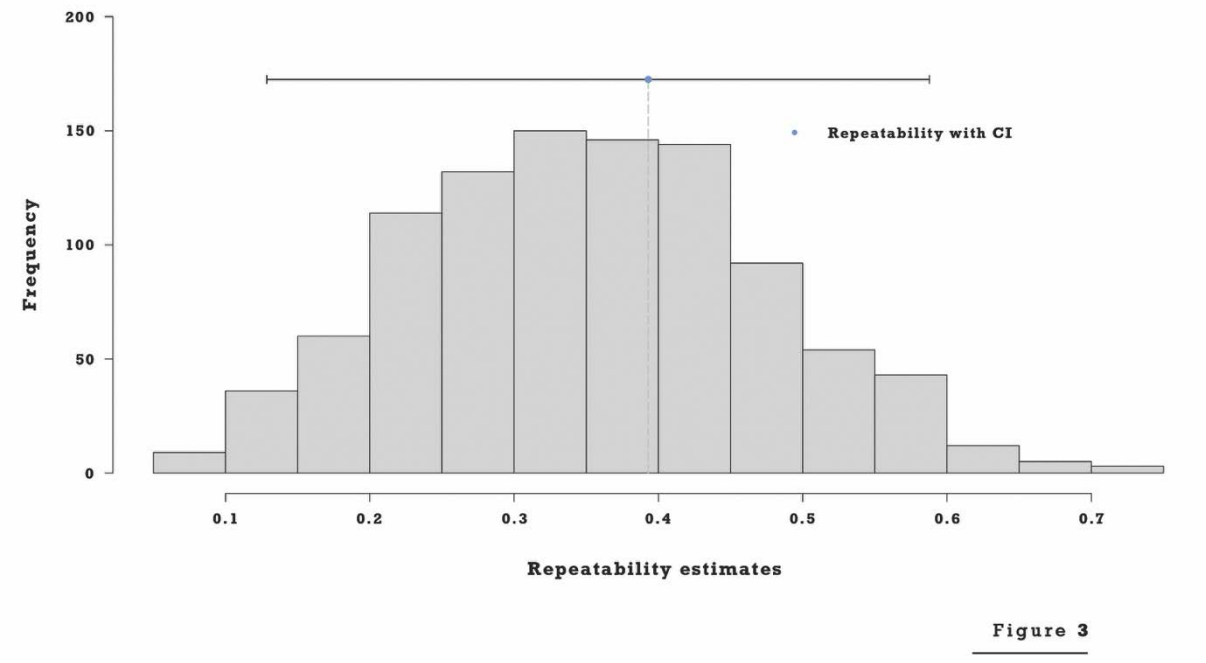

Figure 3. Link-scale approximation bootstrap repeatabilities for variable ACT<3m (dolphin's interaction with scuba divers at <3m from them) on 12 dolphins and 30 sampling periods per dolphin.

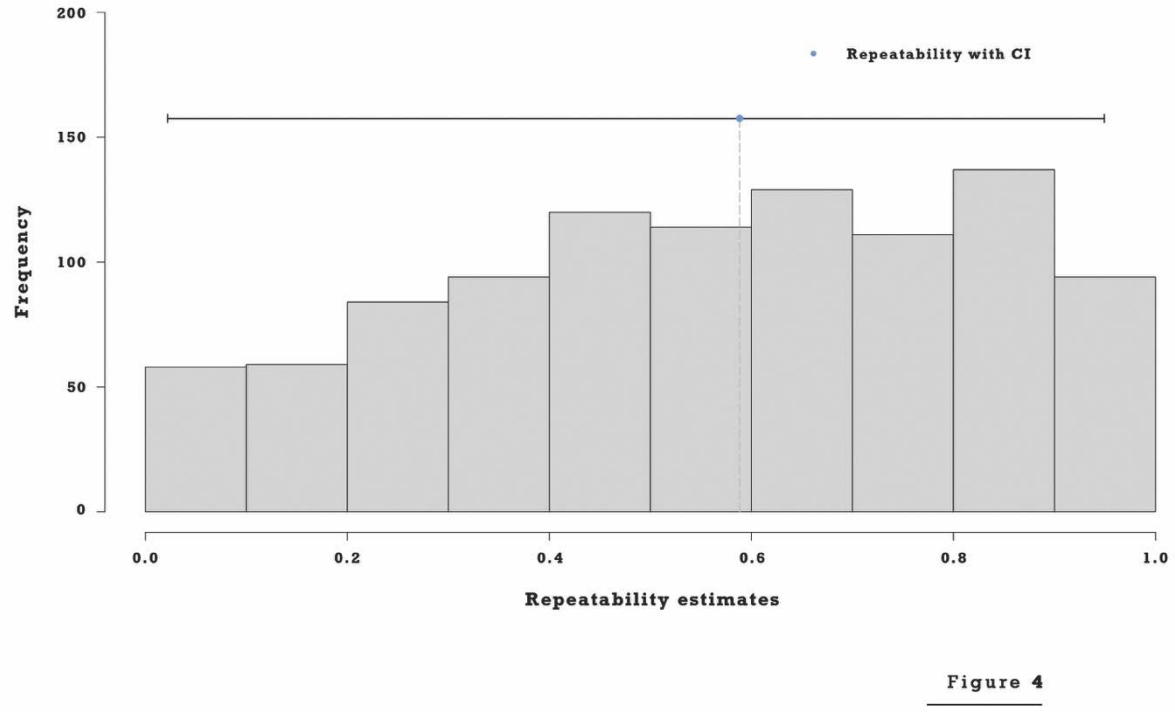

Figure 4. Link-scale approximation bootstrap repeatabilities for variable PHY (dolphin's involvement in physical interactions with scuba divers) on 15 dolphins and ten sampling periods per dolphin.

Table 1. Number of sampling periods each dolphin was captured underwater and total duration of individual underwater sightings, interaction with active scuba divers, and interaction at <3m from active scuba divers over 2018, 2019, and 2020.

ID code	**Number of sampling periods dolphin was captured underwater** (2018, 2019, 2020)	**Total duration of underwater sightings** (min)	**Total duration of interaction with active scuba divers** (min)	**Total duration of interaction at <3m from active scuba divers** (min)
MH02	**35** (10, 15, 10)	55.37	2.55	2.38
MH12	**16** (3, 3, 10)	31.02	1.77	1.48
TP02	**71** (15, 31, 25)	173.77	37.90	37.65
TP03	**39** (14, 16, 9)	47.18	2.65	2.23
TP06	**46** (7, 20, 19)	117.15	7.27	7.02
TP07	**18** (4, 6, 8)	21.82	0.40	0.30
TP08	**13** (3, 7, 3)	8.53	0.33	0.32
TP09	**39** (7, 14, 18)	60.52	11.50	11.35
TP11	**35** (12, 14, 9)	46.80	3.13	0.05
TP15	**39** (13, 22, 4)	62.40	6.73	6.20
TP21	**14** (10, 2, 2)	27.47	0.57	0.27
TP25	**15** (6, 5, 4)	32.48	9.50	6.72
TP26	**15** (2, 4, 9)	22.50	2.15	2.08
TP31	**70** (21, 34, 15)	260.12	155.18	154.97
TP33	**116** (35, 34, 47)	392.50	181.48	181.15
TP39	**20** (4, 8, 8)	49.35	24.90	24.90
TP40	**56** (33, 23, NA)	185.53	32.18	31.08
TP41	**93** (29, 29, 35)	295.37	83.50	81.23
TP47	**17** (8, 4, 5)	39.48	10.87	10.62
TP48	**75** (17, 31, 27)	187.67	64.10	63.77

Table 2. Characteristics of the 20 dolphins selected for the study.

ID code	Sex	Mother's ID	Regularly captured on tourist site from	Sexual maturity
MH02	♂	-	2010	Mat
MH12	♂	-	2009	Mat
TP02	♀	-		Mat
TP03	♂	-		Mat
TP06	♂	-		Mat
TP07	♂	-		Mat
TP08	♂	-		Mat
TP09	♂	-		Mat
TP11	♀	-		Mat
TP15	♀	-		Mat
TP21	♀	-		Mat
TP25	♀	-		Mat
TP26	♂	-		Mat
TP31	♀	**TP11**	2012*	Imm
TP33	♀	**TP02**	2013*	Imm
TP39	♀	**TP04**	2014*	Imm
TP40	♀	**TP15**		Imm
TP41	♀	**MH01**		Imm
TP47	♀	*Dep* **TP21**	2016*	Imm
TP48	♂	*Dep* **TP02**	2017*	Imm

Mat: Mature individual; **Imm:** Immature individual
Dep: Dependent calf; * Year of birth

Table 3. Decomposition of the total inertia.

	Eigenvalues					
	Dim. 1	**Dim. 2**	**Dim. 3**	**Dim. 4**	**Dim. 5**	**Dim. 6**
Variance	4.864	0.901	0.199	0.026	0.007	0.002
% of variance	81.070	15.025	3.321	0.439	0.116	0.029
Cumulative % of variance	81.070	96.095	99.416	99.855	99.971	100.000

Table 4. Distances to the barycenter, and coordinates, contributions and Cos^2 of the 20 dolphins on dimensions 1 and 2.

Individuals							
ID	**Distance**	**Dim. 1**	**Contribution**	**Cos^2**	**Dim. 2**	**Contribution**	**Cos^2**
MH02	1.207	-1.199	1.479	0.988	-0.091	0.046	0.006
MH12	1.215	-1.207	1.498	0.987	-0.091	0.046	0.006
TP02	0.786	0.140	0.020	0.032	0.685	**2.605**	0.761
TP03	1.207	-1.199	1.479	0.988	0.091	0.046	0.006
TP06	1.112	-1.107	1.259	0.990	-0.054	0.016	0.002
TP07	1.231	-1.222	**1.536**	0.985	-0.092	0.047	0.006
TP08	1.231	-1.222	**1.536**	0.985	-0.092	0.047	0.006
TP09	1.475	-0.287	0.085	0.038	-0.470	**1.225**	0.102
TP11	1.223	-1.215	**1.517**	0.987	-0.092	0.046	0.006
TP15	1.034	-1.033	1.096	0.998	-0.027	0.004	0.001
TP21	1.231	-1.222	**1.536**	0.985	-0.092	0.047	0.006
TP25	0.902	-0.859	0.758	0.906	0.204	0.230	0.051
TP26	1.194	-1.186	1.447	0.988	0.095	0.050	-0.006
TP31	6.357	5.405	**30.035**	0.723	-3.332	**61.582**	0.275
TP33	7.198	6.868	**48.488**	0.910	2.034	**22.949**	0.080
TP39	0.778	-0.684	0.481	0.773	-0.050	0.014	0.004
TP40	0.762	-0.609	0.382	0.639	0.053	-0.015	0.005
TP41	2.352	1.756	**3.168**	0.557	1.276	**9.027**	0.294
TP47	0.999	-0.993	1.013	0.988	-0.068	0.025	0.005
TP48	1.514	1.076	1.189	0.505	0.590	**1.932**	0.152

Table 5. Coordinates, contributions and Cos^2 of the six active variables and one supplementary variable on dimensions 1 and 2.

Active variables						
	Dim. 1	**Contribution**	**Cos^2**	**Dim. 2**	**Contribution**	**Cos^2**
INT	0.993	**20.254**	0.985	0.010	0.010	0.000
SFL	0.884	16.048	0.781	-0.259	7.463	0.067
CAM	0.792	12.889	0.627	-0.580	**37.280**	0.336
SND	0.990	**20.151**	0.980	-0.075	0.624	0.006
VDD	0.958	18.850	0.917	0.275	8.411	0.076
TOU	0.758	11.807	0.574	0.645	**46.212**	0.417
Supplementary quantitative variable						
SWA	0.965	-	0.931	-0.024	**-**	0.001

INT = Proportion of time each dolphin interacted at <3m from active scuba divers

SFL = Proportion of time each dolphin swung its tail fluke horizontally in front of active scuba divers

CAM = Proportion of time each dolphin faced and-or almost touched camera housing with any part of its body

SND = Proportion of time each dolphin remained motionless near active scuba divers

VDD = Proportion of time each dolphin positioned itself vertically head on top and dropped down near active scuba divers

TOU = Proportion of time diver(s) touched, petted, rubbed, grabbed and-or hugged dolphin

SWA = Proportion of time each dolphin swam around diver(s) or swam from one diver to another at slow or moderate speed without stopping

Table 6. Distances to the barycenter, coordinates, Cos^2, and v-test results of two dolphins' attributes (*sex* and *maturity*) on dimensions 1 and 2.

Supplementary qualitative variables							
	Distance	**Dim. 1**	**Cos^2**	**v-test**	**Dim. 2**	**Cos^2**	**v-test**
Male	0.853	0.839	-0.968	-1.501	-0.054	0.004	-0.224
Female	0.698	0.687	0.968	1.501	0.044	0.004	0.224
Mature	0.995	**-0.986**	0.982	**-2.656**	-0.031	0.001	-0.191
Immature	1.848	**1.831**	0.982	**2.656**	0.057	0.001	0.191

Synthèse en Français

Réponses comportementales des grands dauphins (*Tursiops truncatus*) de Rangiroa au tourisme de plongée sous-marine : risques, tolérance et tempérament

Notre relation avec les autres animaux est une affaire complexe, ambigüe, frustrante et pleine de défis et nous devons sans cesse réévaluer notre manière d'interagir avec nos parents non-humains.

Marc Bekoff, 2009

Ethics and marine mammals

In "Encyclopedia of Marine Mammals [Seconde Édition]", p396

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Glossaire

Les termes définis sont suivis d'un astérisque (*) lorsqu'ils apparaissent pour la première fois dans le texte.

Adaptation (*à échelle individuelle*) **:** utilisation de systèmes de régulation physiologiques et comportementaux permettant à un animal de faire face aux conditions environnementales dans lesquelles il évolue (Broom & Johnson, 2019).

Anthropomorphisme : attribution de caractéristiques, d'intentions, de motivations et d'émotions humaines à des animaux non-humains ou à des objets (Guthrie, 2013).

Audace : réaction d'un individu à une situation connue et risquée (Réale *et al.*, 2007 ; Toscano *et al.*, 2016). Nous avons ici évalué l'audace des grands dauphins en observant les comportements affiliatifs qu'ils expriment à moins de trois mètres de plongeurs sous-marins.

Bien-être : état d'un individu qui fait face à son environnement (Broom & Johnson, 2019). Le bien-être varie le long d'un continuum allant de très bon à très mauvais (Broom, 2016).

Communauté (*de dauphins*) **:** dauphins partageant la plus grande partie de leurs domaines vitaux et interagissant entre eux plus fréquemment qu'avec des dauphins de zones adjacentes. Le terme se réfère aux relations géographiques et sociales des individus (Wells *et al.*, 1987).

Conditionnement (*opérant*) **:** processus d'apprentissage lors duquel des comportements volontaires sont modifiés par association avec, ou retrait de, stimuli positifs ou aversifs. La fréquence ou la durée d'un comportement peuvent augmenter par renforcement positif ou diminuer par renforcement négatif ou extinction (Ramirez, 1999).

Durable : système acceptable aujourd'hui et dans le futur. L'acceptabilité renvoie à la disponibilité des ressources, aux conséquences du système en termes de fonctionnement et à sa moralité d'action (Broom & Johnson, 2019).

Éthique : étude des questions morales (Broom & Johnson, 2019).

Faire face (*à des conditions environnementales*) **:** contrôler son équilibre mental et physique (Fraser & Broom, 1990).

Habituation : disparition relativement permanente d'une réponse à la suite d'une stimulation répétée (Thorpe, 1963, p61). Ici, nous l'entendons comme une adaptation à une présence humaine récurrente, les humains étant globalement ignorés (Ellenberg *et al.*, 2009).

Occidental : se réfère à l'héritage de normes sociales, de valeurs éthiques, de systèmes de pensées et de croyances du monde occidental (Shvili, 2021).

Plasticité (*comportementale*) **:** variation de score pour un comportement donné en fonction de la variation de stimuli internes ou externes (Stamps & Biro, 2016).

Répertoire comportemental : ici, toutes les réponses comportementales des grands dauphins vis-à-vis des plongeurs sous-marins.

Sensibilisation : augmentation d'une réponse suite à une stimulation continue ou répétée (Broom & Johnson, 2019).

Stimulus : modification de l'environnement d'un animal excitant un ou plusieurs récepteurs ou d'autres parties de son système nerveux (Broom & Johnson, 2019).

Stress : effet de l'environnement sur un animal qui surcharge ses systèmes de contrôle et réduit, ou semble réduire, son aptitude de survie (Broom & Johnson, 2019).

Tempérament : différences comportementales et physiologiques, stables dans le temps et dans des contextes variables, entre individus d'une même espèce (Carere & Maestripieri, 2013).

Tolérance : intensité de dérangement qu'un individu tolère sans réagir de manière définie (Nisbet, 2000). Ici, le dérangement est la présence répétée de plongeurs sous-marins.

Tourisme animalier : le terme se limite ici aux activités humaines d'observation et / ou d'interaction avec des animaux sauvages en milieu naturel (Tapper, 2006).

Introduction générale

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1. Le tourisme animalier*, la plongée sous-marine et le *whale watching* en bref

Dans le cadre de cette thèse, le terme 'tourisme animalier' se limite aux activités humaines d'observation et / ou d'interaction avec des animaux sauvages en milieu naturel (Tapper, 2006). Cette forme de tourisme a connu un formidable essor ces dernières décennies, car l'observation et les interactions avec la faune sauvage suscitent de fortes émotions chez les êtres humains dans un monde où près de 60% de la population mondiale vit en milieu urbain (Higginbottom & Scott, 2004 ; UNFPA, 2023).

L'une des dimensions contemporaines les plus populaires du tourisme animalier se focalise sur les espèces marines (Wiener, 2015 ; Pagel *et al.*, 2020) et nous nous intéressons ici à deux aspects majeurs du tourisme d'observation de la faune marine, à savoir la plongée sous-marine et le *whale watching*.

Le développement des activités de plongée sous-marine, à partir des années 1980, repose sur la diffusion de livres, de films et de documentaires télévisés produits par Hans et Lotte Haas et par Jacques-Yves Cousteau dans les années 1940-1970 (Dimmock & Cummins, 2013 ; Forestell, 2009). Aujourd'hui, la plongée sous-marine est une industrie touristique florissante qui rapporte chaque année plusieurs millions de dollars (Ong & Musa, 2011 ; Lucrezi *et al.*, 2017). En 2015, des plongeurs sous-marins ont visité des récifs coralliens dans 91 pays et le nombre de certifications délivrées par la plus grande école mondiale de plongée sous-marine, PADI (*Professional Association of Diving Instructors*), est passé d'un million en 1980 à 29 millions en 2022 (Dimmock & Cummins, 2013 ; Johansen, 2013 ; PADI, 2023).

Le *whale watching* ou 'observation des cétacés en milieu naturel' a, pour sa part, connu un fort développement à partir des années 1970 avec la diffusion des premières images sous-marines de baleines et de dauphins et du chant, nouvellement décrit, de la baleine à bosse (*Megaptera novaeangliae*, Forestell, 2009 ; Mazzoldi *et al.*, 2019).

En 2008, il était possible d'observer quasiment toutes les espèces de cétacés dans plus de 119 pays (O'Connor *et al.*, 2009) et le nombre de *whale watchers* est passé de quatre millions en 1991 à 13 millions en 2008, avec une augmentation particulièrement spectaculaire

(13,6%) observée dans la deuxième moitié des années 1990 (Hoyt, 2001 ; O'Connor *et al.*, 2009). Baleines et dauphins sont des animaux populaires auprès du grand public et le développement relativement récent du tourisme de nage avec ces mammifères marins a entraîné une prolifération d'activités extrêmement lucratives (Wiener, 2015 ; Hoarau *et al.*, 2020 ; Sprogis *et al.*, 2020).

2. Un intérêt limité des touristes pour certaines espèces animales

Avant de nous concentrer sur les réponses des animaux sauvages au tourisme, il semble approprié de recenser les principaux facteurs qui influencent notre perception de la faune et principalement des dauphins, puisqu'ils sont au cœur de cette thèse. Les espèces dites 'emblématiques' sont en effet largement plébiscitées par les tour-opérateurs et les destinations pour promouvoir le tourisme (Higginbottom, 2004 ; Batt, 2009 ; Apps *et al.*, 2018 ; Bègue-Shankland, 2022 ; Shang & Luo, 2022).

La perception qu'ont les humains de la faune sauvage est principalement basée sur leur culture, leur âge, leur genre, leur éducation et leur expérience, qui influencent à leur tour leurs attitudes et leurs comportements vis-à-vis des animaux (Moscardo & Saltzer, 2004 ; Giovos *et al.*, 2019 ; Bègue-Shankland, 2022). Ces perceptions évoluent avec le temps et, dans les sociétés occidentales*, les notions de bien-être* et d'éthique* animale prennent lentement le pas sur l'anthropocentrisme et l'utilitarisme (Broom & Johnson, 2019 ; Giovos *et al.*, 2019).

Malgré cela, la plupart des gens sont attirés et empathiques vis-à-vis des espèces perçues comme étant proches des humains (Batt, 2009 ; Curtin, 2009) et il a été démontré que l'anthropomorphisme* encourage les comportements humains positifs envers les animaux (Butterfield *et al.*, 2012 ; Amiot & Bastian, 2017).

En outre, de nombreuses études publiées depuis 20 ans révèlent que le grand public a des préférences affectives pour les animaux perçus comme inoffensifs, beaux, prompts à afficher des comportements spectaculaires, symboliques, exotiques, ou rares et menacés (Reynolds & Braithwaite, 2001 ; Tapper, 2006 ; Stokes, 2006 ; Dimmock & Musa, 2013 ; Albayrack *et al.*, 2019 ; Klebl *et al.*, 2021). La néoténie, ou 'effet mignon', influence également notre prédilection pour certaines espèces (Knight, 2008 ; Borgi *et al.*, 2014) et les grands animaux sont davantage appréciés que les petits (Ward *et al.*, 1998 ; Woods, 2000).

Les dauphins sont pourvus de plusieurs des caractéristiques susmentionnées et sont donc des candidats parfaits pour le tourisme animalier. Les Occidentaux sont en effet

imprégnés de puissants stéréotypes anthropomorphiques et positifs au sujet des dauphins (Fraser *et al.*, 2006) et la plupart des amoureux de ces animaux sont rarement au fait des connaissances scientifiques existantes à leur sujet (Barney *et al.*, 2005). Notre enthousiasme récent pour ces mammifères marins est principalement dû aux médias (Fraser *et al.*, 2006 ; Wearing *et al.*, 2011), aux cultures populaires (Busnel, 1973 ; Servais, 2005 ; Mazzoldi *et al.*, 2019) et aux parcs aquatiques (Gouabault, 2006) qui véhiculent l'image d'un animal créé pour nous divertir et influencent de manière substantielle les attentes des *whale watchers* lors d'une sortie en mer (Wiener, 2015).

Les humains pensent généralement que les dauphins adorent nager avec eux (Servais, 2005 ; Wiener, 2015) et des signes visibles de stress* chez ces animaux sont souvent négligés ou interprétés comme étant des comportements positifs (Patroni, 2018). L'éternel 'sourire' des grands dauphins (Forestell, 2009 ; Wiener, 2015) et la curiosité, l'opportunisme ou l'habituation* de certains individus à la présence humaine renforcent une impression d'harmonie, de connexion et de succès dans les interactions (DeMares, 2000 ; Curtin, 2006 ; Chanvallon, 2013). Par ailleurs, les tour-opérateurs omettent la plupart du temps de mentionner les comportements brutaux ou agressifs que les dauphins peuvent exprimer en présence d'êtres humains (Besio, 2008 ; Carzon *et al.*, 2023), ce qui nous aide à mieux comprendre pourquoi un nombre croissant de touristes désire interagir de manière intime avec ces animaux en mer.

3. Un désir de proximité

La proximité avec la faune sauvage est une caractéristique-clé de l'expérience touristique animalière. Elle est associée à la satisfaction des touristes et mise en avant par les tour-opérateurs pour attirer leur clientèle (Schanzel & McIntosh, 2000 ; Moscardo *et al.*, 2001 ; Curtin & Kragh, 2014 ; Bach & Burton, 2017). Le désir de proximité avec les animaux sauvages naît de l'espoir de les observer en détail, d'interagir ou de se connecter plus intimement avec eux, et la possibilité d'un contact physique avec un dauphin est une motivation considérable pour de nombreux touristes (Curtin, 2006 ; 2008).

En outre, l'émergence récente et les contenus des réseaux sociaux encouragent des comportements humains intrusifs envers la faune sauvage (Nekaris *et al.*, 2016 ; Lenzi *et al.*, 2020 ; Otsuka *et al.*, 2020). La prévalence des 'selfies avec animaux sauvages' (i.e., photographies où le photographe apparaît sur la photo avec l'animal) sur les réseaux sociaux

facilite la promotion de comportements déviants vis-à-vis des animaux (Lenzi *et al.*, 2020 ; Kredens & Vogt, 2023) et même des personnes appartenant à des cultures sensibilisées aux notions de bien-être et de conservation des animaux trouvent normales et amusantes des images violant des préoccupations fondamentales en matière de bien-être animal (Nekaris *et al.*, 2016).

Cette tendance moderne motive les opérateurs et guides professionnels à offrir des rencontres rapprochées dans le but de divertir les touristes et encourage des comportements intrusifs, abusifs et illégaux envers la faune sauvage (Higham & Lück, 2007 ; Otsuka *et al.*, 2020 ; Cottam, 2023).

4. Réponses de la faune sauvage au tourisme

Le tourisme animalier peut inciter à protéger des zones sensibles et à la conservation d'espèces menacées car il offre des alternatives durables* aux conflits entre les humains et les autres animaux et à une exploitation illimitée des ressources (e.g., Dearden *et al.*, 2007 ; Curtin & Kragh, 2014 ; Lucrezi *et al.*, 2017). Cependant, il existe un paradoxe fondamental entre la nécessité de protéger l'environnement et les besoins du marché en termes de production de profit (Butler, 1989 ; Reynolds & Braithwaite, 2001). Par conséquent, le tourisme animalier est de plus en plus considéré comme une nouvelle source de 'changement environnemental rapide induit par l'homme', aussi appelé HIREC (Geffroy *et al.*, 2018).

Les amoureux des animaux eux-mêmes peuvent être à l'origine de dommages involontaires et inattendus (Berle, 1990 ; Green & Giese, 2004 ; Karp & Root, 2009 ; Huang *et al.*, 2011). Par exemple, le tourisme d'observation des gorilles de montagne (*Gorilla beringei beringei*) génère des revenus importants qui soutiennent les efforts de conservation et véhicule le risque de transmettre des pathogènes aux gorilles (Sandbrook & Semple, 2006). Les sites de plongée les plus fréquentés ont une forte incidence de maladies coralliennes (Lamb *et al.*, 2014) et les plongeurs sous-marins peu expérimentés, tout comme les photographes, ont un impact considérable sur les récifs coralliens (Barker & Roberts, 2004 ; Roche *et al.*, 2016).

Ainsi, les inquiétudes augmentent au sujet des menaces que le tourisme représente pour la vie sauvage. Par ailleurs, l'épidémie récente de COVID-19 est probablement apparue en raison du mépris global des êtres humains pour les milieux naturels et les espèces qui y habitent, et certains auteurs préconisent l'adoption d'une distance comportementale avec les animaux pour leur bien-être, le nôtre, et celui de l'environnement (Lindenmayer & Kaufman, 2021).

Les effets du tourisme animalier sur la faune dépendent de nombreux facteurs tels que l'échelle de développement touristique (e.g., Johns, 1996 ; Grossberg *et al.*, 2003 ; Szott *et al.*, 2019), les caractéristiques des espèces ciblées, la fréquence et l'intensité avec lesquelles un animal endure des stimuli aversifs (e.g., Karp & Root, 2009 ; Huang *et al.*, 2011), si ces mêmes stimuli surviennent lors de phases sensibles du cycle de vie de l'animal (Green & Giese, 2004) et les tempéraments* individuels (Martin & Réale, 2008).

Ces effets dépendent également des distances d'approche et des comportements des touristes (e.g., Lott & McCoy, 1995 ; Cassini, 2001 ; Karp & Root, 2009 ; Geffroy *et al.*, 2017). Chez les cétacés, des changements de vitesse, de cap et une trop grande proximité des bateaux peuvent causer des perturbations comportementales (Barr & Slooten, 1999 ; Constantine, 2001 ; Williams *et al.*, 2002). Les activités de nage avec les cétacés engendrent un impact supplémentaire puisque les embarcations s'approchent davantage des animaux et placent généralement les nageurs sur leur route pour optimiser leurs chances de les voir sous l'eau (Constantine & Baker, 1997 ; Constantine, 2001 ; Corkeron, 2006 ; Stensland & Berggren, 2007). Par ailleurs, il arrive fréquemment aux nageurs de sauter brusquement dans l'eau, de frapper la surface de l'eau ou de crier pour tenter d'attirer et d'interagir avec les cétacés, d'essayer de toucher les animaux ou d'attraper les nageoires de dauphins particulièrement tolérants à la présence humaine (Samuels *et al.*, 2000 ; Wilke *et al.*, 2005 ; Cunningham-Smith *et al.*, 2006 ; Christiansen *et al.*, 2010).

Des changements comportementaux sont souvent les premières réactions visibles des animaux face aux défis de leur environnement (Blumstein *et al.*, 2017) et il est primordial de bien connaître la biologie et le comportement d'un animal et de l'espèce à laquelle il appartient pour les interpréter de manière correcte (Broom & Johnson, 2019). Toute modification comportementale s'accompagne de réponses physiologiques et les chercheurs mesurent généralement les réactions des animaux au tourisme en étudiant leurs comportements, leur physiologie, ou les deux à la fois (e.g., Ellenberg *et al.*, 2006 ; Maréchal *et al.*, 2011 ; Bateman & Fleming, 2017 ; Saltz *et al.*, 2018).

Les réponses déclenchées par des visites touristiques intrusives peuvent être immédiates et évidentes pour un observateur humain (e.g., sursaut, évitement, attraction) ; elles peuvent aussi être subtiles (e.g., modification des niveaux de certaines hormones, augmentation du

rythme cardiaque, modification de comportements sociaux, Green & Giese, 2004 ; Semeniuk *et al.*, 2009 ; Ellenberg *et al.*, 2013 ; Shutt-Phillips *et al.*, 2021) et évoluer au cours du temps (e.g., habituation, sensibilisation*, déficience du système immunitaire, réduction de l'espérance de vie, Broom, 2017).

Que les réponses d'un animal au tourisme nous semblent positives ou négatives, son aptitude de survie est réduite si ses réponses augmentent ses probabilités de mourir et diminuent ses probabilités d'avoir une descendance viable (Broom & Johnson, 2019).

Chez les cétacés, les réponses comportementales à court-terme les plus classiques observées dans un cadre touristique sont des modifications des séquences respiratoires (e.g., Williams *et al.*, 2002 ; Lusseau, 2003), des altérations de l'orientation et de la vitesse de nage (e.g., Barr & Slooten, 1999 ; Lusseau, 2004), des changements de composition, de dispersion et de cohésion des groupes (e.g., Bejder *et al.*, 1999 ; Carrera *et al.*, 2008), des interruptions des activités en cours (e.g., Constantine *et al.*, 2004 ; Stensland & Berggren, 2007 ; Peters *et al.*, 2012), des modifications des zones fréquentées et de l'utilisation de l'habitat (e.g., Lusseau, 2004 ; Carrera *et al.*, 2008 ; Pérez-Jorge *et al.*, 2016) et des variations dans les signaux acoustiques utilisés (e.g., altération des fréquences et des durées des sifflements, van Parijs & Corkeron, 2001 ; Guerra *et al.*, 2014).

Les réponses comportementales et physiologiques d'animaux ciblés de manière répétée par des activités touristiques peuvent générer des effets délétères à long-terme (Bejder *et al.*, 2006 ; Shannon *et al.*, 2017 ; Geffroy *et al.*, 2018). Ces derniers peuvent être difficiles à quantifier, surtout lorsqu'ils sont cumulatifs et non catastrophiques (Bejder *et al.*, 2006 ; Pirotta *et al.*, 2015), et en raison de la multitude de facteurs qui interagissent et affectent les dynamiques des populations et les structures des communautés animales (Shannon *et al.*, 2017).

Chez les espèces à longue espérance de vie, la détection de réponses significatives à la présence chronique d'êtres humains nécessite une logistique et un temps considérables (e.g., au moins dix ans pour les dauphins, Pirotta *et al.*, 2015). Cependant, des modifications répétées du comportement et de la physiologie des animaux sont susceptibles d'affecter les conditions physiques et sociales (e.g., Christiansen *et al.*, 2010 ; Symons *et al.*, 2014), la distribution, la densité et les interactions entre individus et espèces sur une zone touristique (Bejder *et al.*, 2006 ; Ilarri *et al.*, 2008 ; Shannon *et al.*, 2017 ; Trave *et al.*, 2017), le succès reproductif (e.g., Burger *et al.*, 1995 ; Higham, 1998) et la survie (Geffroy *et al.*, 2015 ; Shannon *et al.*, 2017).

Par ailleurs, les rencontres rapprochées régulières avec la faune sauvage requièrent une présence prévisible des espèces ciblées sur des zones spécifiques (Duffus & Dearden, 1990). D'après Knight, 2009, *il existe trois manières de faire en sorte que des animaux soient disponibles pour le tourisme : la capture et le confinement, l'habituation et l'attraction*.

De nombreuses espèces et individus manifestent en effet une diminution de leurs réponses anti-prédateurs lorsqu'ils sont exposés de manière répétée à des humains inoffensifs et / ou neutres, par rapport à leurs congénères vivant dans des zones moins fréquentées par l'homme. Une telle modification comportementale est connue sous le nom de 'tolérance* accrue envers les humains' et peut être due à une réduction de vigilance ou à un processus de type 'habituation' (Uchida *et al*., 2023).

Une tolérance accrue à la présence humaine est facilement observable chez des animaux vivant dans des milieux modifiés par l'homme (Uchida & Blumstein, 2021). Il s'agit d'une forme d'adaptation* comportementale, ou accommodation phénotypique, qui permet aux animaux de faire face* à des altérations de leurs conditions environnementales en augmentant, ou non, leur aptitude de survie (Broom & Johnson, 2019). Ce processus d'apprentissage peut mener à une habituation à long-terme, c'est-à-dire à la diminution relativement permanente d'une réponse de l'animal suite à une stimulation répétée (Thorpe, 1963, p61).

Cependant, les tentatives d'adaptation de certains individus (e.g., individus dits 'timides', Sih *et al.*, 2004) peuvent être inadéquates lorsque les stimuli sont excessifs en intensité ou en durée, ou autrement aversifs. Si tel est le cas, une exposition répétée à ces stimuli peut entraîner une sensibilisation et un mal-être chez ces individus (Broom & Johnson, 2019). De plus, un stimulus* initialement toléré peut devenir intolérable (Broom & Johnson, 2019). Par exemple, une étude menée sur les impacts à long-terme de la présence de bateaux sur des grands dauphins (*Tursiops* sp.) à Shark Bay, en Australie, a démontré qu'il n'y avait aucune différence d'abondance de dauphins entre les périodes sans tourisme et les périodes où un seul bateau opérait. En revanche, lorsque le nombre de bateaux est passé à deux, les auteurs ont observé une baisse moyenne significative du nombre de dauphins d'approximativement un individu sur sept (Bejder *et al.*, 2006).

Par ailleurs, un conditionnement* opérant utilisant des renforçateurs positifs (e.g., nourriture, contact physique agréable) peut être utilisé pour attirer des animaux sur certaines zones. L'approvisionnement en nourriture est un moyen rapide et efficace d'augmenter la probabilité que des animaux apparaissent, permettent une observation rapprochée et se

comportent de manière prévisible (Reynolds et Braithwaite, 2001 ; Green et Giese, 2004). Par exemple, attirer les ours bruns (*Ursus arctos*) au moyen de sites d'alimentation artificiels est une pratique courante en Amérique du Nord et en Europe, qui augmente les densités d'ours sur des zones données et les possibilités pour les touristes de les photographier (Penteriani *et al.*, 2017).

Pourtant, une tolérance accrue de la faune sauvage vis-à-vis des hommes est une arme à double tranchant (Uchida *et al.*, 2023). En effet, l'habituation et le conditionnement peuvent promouvoir des interactions positives mais elles peuvent également conditionner les touristes à exiger certains comportements de la part des animaux (Green & Higginbottom, 2001) et augmentent le potentiel d'issues négatives, tant pour la faune sauvage que pour les êtres humains (Geffroy *et al.*, 2015 ; Worrell *et al.*, 2017 ; Uchida *et al.*, 2023).

Il existe par exemple des preuves que les primates habitués au tourisme sont des cibles faciles pour les braconniers (Kasereka *et al.*, 2006). À Shark Bay, les jeunes de femelles grands dauphins nourries par les touristes reçoivent moins de soins maternels que les autres et pâtissent d'un taux de mortalité plus élevé que ces derniers (Mann & Kemps, 2003). Près de Sarasota Bay, en Floride, des dauphins conditionnés à recevoir de la nourriture se sont vu offrir et ont consommé des sandwiches, des chips, des pâtisseries, des fruits et de la glace (Cunningham-Smith *et al.*, 2006).

L'approvisionnement en nourriture entraîne une diminution de la vigilance des animaux face à des menaces potentielles (Geffroy *et al.*, 2015) et l'apparition de comportements spécifiques qui peuvent rendre les animaux nourris *nuisibles* ou dangereux pour les humains. Ces animaux peuvent alors être tués pour des raisons de confort ou de sécurité, ce qui soulève des préoccupations éthiques évidentes (Penteriani *et al.*, 2017 ; Behrendorf *et al.*, 2023).

Toucher et manipuler des animaux sauvages génèrent des problèmes similaires à ceux mentionnés ci-dessus et un nombre croissant de rapports détaillent comment des animaux sont utilisés, exploités et maltraités de la sorte (Belicia & Islam, 2018). Des humains ont été vus chevauchant, maintenant la nageoire caudale, enfonçant leurs doigts dans l'évent, les yeux ou les oreilles, mettant des objets dans l'évent, s'accrochant aux nageoires et ouvrant les mâchoires de dauphins qui tolèrent ou recherchent un contact physique avec eux. Réciproquement, des dauphins tolérants ont manifesté des comportements intrusifs, brusques, agressifs et sexuels envers des êtres humains (Carzon *et al.*, 2023).

5. Comprendre les variations individuelles dans les réponses comportementales des animaux au tourisme

Nous avons vu précédemment que différents individus peuvent répondre de manière différente à des stimuli similaires ou identiques. Nous avons également souligné le fait que des réponses apparemment positives au tourisme peuvent générer des risques imprévisibles impliquant un mal-être des animaux et une réduction de leur aptitude de survie. Il est donc risqué de conclure que des activités touristiques n'ont aucun impact délétère sur des espèces ou populations d'animaux sauvages sans examiner les variations comportementales ou physiologiques à l'échelle des individus.

En outre, il n'est pas raisonnable de conclure que ces activités sont éthiques et durables. La question de la durabilité est importante lorsque des décisions sont prises au sujet de l'utilisation d'un système qui exploite des ressources tel que le tourisme animalier et *le fait qu'un système engendre des bénéfices et qu'il y ait une demande pour un produit ne sont pas des raisons suffisantes pour en poursuivre la production* (Broom, 2016, p47).

5.1. Plasticité comportementale et tempérament individuel*

Depuis vingt ans, les mondes de l'éthologie, de la psychologie comparée et de l'écologie comportementale ont connu un intérêt renouvelé pour la plasticité et le tempérament des animaux non-humains (e.g., Stamps, 2015 ; MacMahon *et al.*, 2022). Ces deux notions sont intéressantes à explorer si l'on souhaite comprendre les réponses individuelles des animaux aux changements de leur environnement, dont ceux induits par la présence humaine.

Nous considérons que la plasticité comportementale est une variation de score pour un comportement donné en fonction de la variation des stimuli internes ou externes (Stamps & Biro, 2016). L'habituation et la sensibilisation, qui sont des mécanismes d'apprentissage universels résultant de l'effet d'expériences passées sur des comportements présents, sont des exemples relativement simples de plasticité observés chez des animaux sauvages dans le contexte d'une présence humaine récurrente. Pour étudier l'habituation et la sensibilisation, les individus doivent être suivis de manière répétée dans le temps. Par exemple, Uchida & Blumstein (2021) ont évalué les réponses individuelles sur 15 ans de marmottes à ventre jaune (*Marmota flaviventris*) à une exposition répétée à des êtres humains et la relation entre ces réponses et l'aptitude de survie des marmottes. Ils ont observé une décroissance moyenne des

distances de fuite (i.e., distance à laquelle un animal fuit un humain qui s'approche) au cours du temps, suggérant une habituation des marmottes aux humains. Cependant, ils ont aussi documenté que les marmottes les plus sollicitées par la présence humaine gagnaient moins de masse corporelle que leurs conspécifiques appartenant à des colonies moins dérangées. Par ailleurs, les auteurs ont détecté une 'individualité' dans les distances de fuite : les marmottes ayant la plus grande distance de fuite se sont en effet sensibilisées, plutôt qu'habituées, aux approches humaines répétées (Uchida & Blumstein, 2021).

Ces résultats illustrent le fait que tous les individus n'expriment pas des réponses identiques en présence d'êtres humains et qu'il est pertinent d'examiner les tempéraments individuels dans les études s'intéressant aux réponses de la faune sauvage au tourisme.

Les tempéraments individuels sont des différences comportementales et physiologiques, stables dans le temps et dans des contextes variables, entre individus d'une même espèce (Carere & Maestripieri, 2013). 'Stable' ne signifie pas que la valeur d'un trait tempéramental reste inchangée mais que les différences inter-individuelles sont relativement constantes (Réale *et al.*, 2007). Les principaux traits et méthodes utilisés dans le cadre des études sur le tempérament animal varient en fonction du champ d'étude. Par exemple, le modèle à cinq facteurs (i.e., agréabilité, conscienciosité, extraversion, ouverture et neuroticisme) est souvent utilisé comme base pour étudier le tempérament animal en psychologie comparative (Úbeda *et al.*, 2019 ; Morton *et al.*, 2021) tandis que l'audace*, l'exploration, l'activité, la sociabilité et l'agressivité sont des catégories omniprésentes en écologie comportementale (Réale *et al.*, 2007).

En outre, un trait spécifique peut être interprété de manière différente en fonction des auteurs et des études. Par exemple, l'audace a été définie comme *la réaction d'un individu à une situation connue et risquée* (Réale *et al.*, 2007), une *réaction à la nouveauté* (Guenther *et al.*, 2018), une *recherche de nouveauté* (Díaz López, 2020) et comme une tendance à *la curiosité et à l'investigation* (Hill *et al.*, 2019). Lilley *et al.* (2018) ont discuté le fait qu'il y ait des différences entre l'audace, la néophilie et la curiosité et nous avons décidé de garder la définition proposée par Réale *et al.* (2007) dans le cadre de cette thèse.

Les réactions d'animaux sauvages à une situation connue et risquée ont été mesurées en utilisant des techniques variées. Par exemple, Réale *et al.* (2000) se sont focalisés sur la 'capturabilité' de mouflons canadiens (*Ovis canadensis*) femelles, considérée comme une expression de la volonté des brebis d'accepter le risque d'être manipulées dans le but d'avoir

accès à un appât salé. Bubac *et al.* (2018) ont déterminé l'audace de femelles phoques gris (*Halichoerus grypus*) en notant leurs réponses à l'approche d'êtres humains et à la manipulation de leurs chiots.

La plasticité comportementale et le tempérament sont liés et s'influencent réciproquement (Mitchell & Houslay, 2021). Plusieurs auteurs ont par exemple documenté des différences individuelles dans les taux d'habituation (Ellenberg *et al.*, 2009 ; Bell & Peeke, 2012 ; Dingemanse *et al.*, 2012) et la tolérance d'animaux sauvages aux humains est modulée par leur plasticité (Geffroy *et al.*, 2017), leur tempérament (Carrete & Tella, 2013) et des interactions entre les deux (Lowry *et al.*, 2013 ; Stamps, 2015 ; Arroyo *et al.*, 2017 ; Uchida & Blumstein, 2021). Arroyo *et al.* (2017) ont par ailleurs montré que les effets du tempérament individuel peuvent mener à la sélection directionnelle de certains phénotypes dans un contexte de présence humaine répétée. Ils ont étudié les réponses de busards cendrés (*Circus pygargus*) à une augmentation de la présence d'êtres humains venant visiter leurs nids sur 19 ans et ont documenté une disparition graduelle des busards 'timides' et une proportion plus importante de busards 'audacieux', entraînant une homogénéisation tempéramentale de la population reproductive.

5.2. Influences de la plasticité et du tempérament sur les réponses de la faune au tourisme

Plusieurs études ont examiné l'influence d'une plasticité des réponses d'animaux sauvages au tourisme animalier (e.g., Shutt *et al.*, 2014 ; Maréchal *et al.*, 2016 ; Bertrand *et al.*, 2022) mais peu ont considéré l'influence des tempéraments individuels (e.g., Martin & Réale, 2008 ; Pritchard *et al.*, 2014). Martin & Réale (2008) ont souligné le fait qu'en l'absence de connaissances sur le tempérament des animaux, les impacts du tourisme animalier peuvent être sur- ou sous-estimés.

Cela est particulièrement vrai dans le cas des dauphins, car ces animaux passent le plus clair de leur temps hors de notre portée et certains individus semblent tolérer ou être attirés par la présence humaine (Carzon *et al.*, 2023). Les comportements positifs de ces dauphins vis-à-vis des touristes génèrent certes des millions de dollars annuellement (Hunter Jr. *et al.*, 2021 ; Uchida *et al.*, 2023) mais ils augmentent également les risques de conséquences négatives à court- et à long-terme, à la fois pour les dauphins et pour les humains. À ce titre, ces interactions interspécifiques proches sont aujourd'hui considérées comme éthiquement discutables (Bejder *et al.*, 2009 ; Broom & Johnson, 2019) et il est critique d'acquérir des connaissances plus

approfondies sur l'impact du tourisme sur les dauphins, et sur les risques associés aux réponses des dauphins au tourisme, dans le but de favoriser une gestion proactive et optimale d'activités touristiques en plein essor.

Pour cela, nous avons choisi d'explorer les réponses comportementales individuelles de grands dauphins (*Tursiops truncatus*) au tourisme de plongée sous-marine à Rangiroa, un atoll océanique de l'archipel des Tuamotu, en Polynésie française. Sur la côte nord de Rangiroa, la zone de Tiputa accueille une petite communauté* accessible de dauphins devenue l'attraction principale du tourisme-plongée. En effet, la tolérance voire l'attirance de certains dauphins pour les plongeurs sous-marins exprimant des comportements intrusifs (e.g., tentatives répétées d'attirer et de toucher les dauphins) ont augmenté depuis les années 1990 et un petit nombre d'individus recherche aujourd'hui un contact physique régulier avec les moniteurs de plongée et les touristes. Ces dauphins peuvent être observés au quotidien depuis la terre, lorsqu'ils viennent surfer et sauter dans les vagues déferlantes de la passe de Tiputa (i.e., chenal naturel qui connecte l'océan Pacifique au lagon de Rangiroa) et sous l'eau, sur une petite zone de tombant récifal externe où se déroule une grande partie des activités de plongée sous-marine.

Cœur de la thèse

Dans le cadre de cette thèse, nous avons étudié les comportements neutre, d'évitement et affiliatifs des dauphins vis-à-vis des plongeurs sous-marins. Nos objectifs étaient de mettre en évidence des variations individuelles dans les réponses comportementales de dauphins sauvages au tourisme et les risques, pour les dauphins et pour les plongeurs, associés aux interactions interspécifiques proches. Nous avons également considéré de quelle manière ces interactions peuvent être gérées afin d'en limiter les conséquences négatives.

Nous avons commencé par examiner de nombreuses publications traitant des interactions proches entre dauphins et humains en milieu naturel afin de recenser les comportements délétères et les risques associés à ces activités [**1**]. Ensuite, nous nous sommes penchés sur le cas des grands dauphins de Rangiroa afin de quantifier leur habituation à la présence de plongeurs sous-marins et leur tolérance aux plongeurs souvent intrusifs envers eux [**2**]. Enfin, nous avons observé les comportements affiliatifs des dauphins à proximité des plongeurs dans le but d'identifier des traits de tempérament individuels liés à l'axe timidité-audace chez ces animaux dans le contexte de leurs interactions avec le tourisme [**3**].

1 Comportements délétères et risques associés aux interactions proches entre humains et dauphins en milieu naturel

Mots-clés

Rencontres avec les animaux, interactions proches, interactions humains / dauphins, comportements délétères, gestion des risques, tourisme animalier

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Dans l'introduction, nous avons rappelé que les dauphins ont une image globalement positive dans les sociétés occidentales modernes où ils sont considérés comme des animaux anthropophiles et amicaux. Nous avons également souligné le fait que certains dauphins tolèrent ou peuvent être attirés par les activités humaines et qu'ils peuvent exprimer des comportements agressifs et imprévisibles envers les hommes (e.g., Shane *et al.*, 1993 ; Samuels *et al.*, 2000). Réciproquement, les interactions proches sont souvent mal ou non encadrées (Kessler & Harcourt, 2013 ; Sitar *et al.*, 2016) et peuvent impacter les dauphins via des comportements humains inappropriés.

Afin de mieux comprendre les risques, pour les dauphins et pour les humains, liés aux interactions interspécifiques proches en milieu naturel, nous avons examiné 240 références publiées au cours des sept dernières décennies. Ces références documentent des interactions proches entre dauphins et humains dans le cadre d'activités de type touristique et dans le cas particulier des dauphins solitaires, qui peuvent se fixer sur certaines zones côtières et interagir avec les humains.

Nous avons pu recenser plusieurs comportements délétères et risques, pour les dauphins et pour les humains, liés à ces situations et nous avons synthétisé ces informations. Nos résultats montrent que les interactions proches sont non seulement en pleine expansion au niveau mondial mais qu'elles sont loin d'être bénignes. Par conséquent, des mesures de gestion éclairées devraient être mises en application afin de minimiser les impacts négatifs liés à ces rencontres.

Le papier intitulé *Revue des comportements délétères et risques liés aux interactions proches entre humains et dauphins en milieu naturel* a été écrit en collaboration avec les **Drs É. Clua**, **F. Delfour** et **K. Dudzinski** et publié dans le journal *Biological Conservation* en mars 2023. Il fournit un panorama utile du statut des interactions proches entre dauphins et humains en milieu naturel.

Ces dernières sont largement distribuées au niveau mondial et impliquent plus de 20 delphinidés, les deux espèces de monodontidés (i.e., le béluga, *Delphinapterus leucas*, et le narval, *Monodon monoceros*) et une espèce d'iniidés (i.e., le dauphin de l'Amazone, *Inia geoffrensis*). Les grands dauphins (*Tursiops* spp.) sont les espèces les plus documentées dans tout type d'interaction proche avec les humains.

La plupart des études entreprises sur les risques liés aux interactions dauphins / humains proviennent d'un petit nombre de pays (e.g., l'Australie, les États-Unis, la Nouvelle-Zélande) et ne sont pas représentatives du développement global récent de ces activités (O'Connor *et al.*, 2009). Ainsi, nous sous-estimons probablement l'augmentation réelle des pressions anthropiques sur les dauphins dues aux interactions proches et la variété des réponses comportementales et risques associés. En outre, il existe un manque d'informations au sujet des comportements humains, en comparaison avec les comportements des dauphins.

Le nombre d'endroits dans le monde où des comportements délétères et risques ont été enregistrés tant pour les dauphins que pour les humains est plus élevé dans le cas des dauphins solitaires que dans celui des activités touristiques. De plus, les comportements délétères et risques documentés dans le cas des dauphins solitaires sont typiquement directs et violents (e.g., dauphin chargeant des humains, humains frappant un dauphin, mortalité du dauphin, Samuels *et al.*, 2000) tandis que ceux détaillés dans le cadre des activités touristiques sont plus subtiles (e.g., dauphins évitant des humains, humains poursuivant des dauphins, perturbation des activités de repos des dauphins, Shawky *et al.*, 2020 ; Rocha *et al.*, 2023), excepté dans les endroits où les dauphins sont nourris et / ou régulièrement caressés par des humains où les risques sont semblables à ceux documentés dans le cas des dauphins solitaires (e.g., Vail, 2016 ; Senigaglia *et al.*, 2019).

De manière générale, une tolérance accrue des dauphins aux humains les rend particulièrement vulnérables aux effets délétères liés aux activités humaines. Ces effets peuvent

entraîner une réduction du bien-être des animaux et de leur aptitude de survie individuelle. Par ailleurs, cela augmente le risque pour les humains d'être exposés à des comportements agonistiques et sexuels de la part des dauphins, et de contracter des zoonoses.

Une vision humaine fortement biaisée des dauphins, couplée à un échec global des mesures de gestion des interactions dauphins / humains, sont les principales causes identifiées d'actions humaines inappropriées et de conséquences négatives.

Notre revue propose des indications en termes de gestion inspirées de la littérature internationale à ce sujet dont l'objectif est de promouvoir le bien-être des dauphins, la sécurité des humains et la mise en place d'activités d'observation éthiques et durables (e.g., éducation, formation et encadrement des tour-opérateurs, guides et touristes ; mise en place et application de réglementations faciles à comprendre et adaptées à chaque situation). Nous insistons également sur le besoin de considérer les différences inter-individuelles dans les réponses des dauphins aux interactions proches lors de l'évaluation de l'impact de ces interactions.

En réponse à notre publication, un commentaire intitulé *À propos de la légalité de la nage avec les dauphins* a été soumis par E. Simon à *Biological Conservation*. Nous avons, à notre tour, envoyé une réponse argumentée au journal intitulée *À propos du manque de réglementations explicites et appliquées dans le contexte de la gestion des activités de nage avec les dauphins : réponse à Simon (2023)*. Les deux commentaires ont été publiés en juin 2023.

Cette revue nous a permis de brosser une image globale, bien que non exhaustive, du statut actuel des interactions proches entre humains et dauphins en milieu naturel. De plus, nous avons pu mettre le doigt sur des lacunes existantes dans la littérature traitant de ces interactions. Certaines de ces lacunes, telles que la mise en évidence de degrés de tolérance et d'une habituation chez les dauphins ciblés par le tourisme, peuvent être comblées grâce aux conditions d'observation privilégiées offertes par l'atoll de Rangiroa. La tolérance et l'habituation sont donc au cœur du chapitre suivant.

2 Tolérance des dauphins aux interactions répétées avec le tourisme de plongée sous-marine

Mots-clés

Habituation, tolérance, comportement des dauphins, plasticité comportementale, interactions humains / dauphins, tourisme animalier

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Dans l'introduction et la revue, nous avons souligné le fait qu'une tolérance accrue et l'habituation des animaux sauvages aux humains peuvent augmenter le potentiel d'issue délétère tant pour les animaux que pour les humains. Par ailleurs, Bejder *et al.* (2009) ont insisté sur l'importance de la sémantique lorsqu'il s'agit d'interpréter les réponses de la faune sauvage à la présence humaine. En effet, certains termes utilisés tels qu'habituation peuvent porter à confusion, initier la mise en place de plans de conservation inappropriés et provoquer des conséquences négatives. Au regard de cela, une quantification détaillée du statut de tolérance des cétacés ciblés par le tourisme doit être une priorité dans le cadre des études d'impact (Bejder *et al.*, 2009).

Nous avons tiré parti de la possibilité de collecter des données depuis la terre, dans une zone où les plongeurs sous-marins sont absents, et sous l'eau en présence d'activités touristiques de plongée, pour mieux comprendre comment les dauphins qui fréquentent la zone touristique de Tiputa tolèrent la présence de plongeurs sous-marins actifs (e.g., plongeurs s'approchant, tendant leurs mains vers les dauphins). Nous avons sélectionné les comportements neutres de 18 dauphins à proximité (i.e., < 10 m) de plongeurs sous-marins actifs et avons émis l'hypothèse qu'une majorité de, et une stabilité dans, l'expression des comportements neutres indiquent une tolérance des dauphins à la présence des plongeurs. Par ailleurs, nous avons émis l'hypothèse que les réponses d'évitement des dauphins aux plongeurs sont liées à des comportements spécifiques de la part des plongeurs sous-marins. Enfin, nous

avons testé l'influence du sexe, de la maturité sexuelle, de la fidélité des dauphins au site touristique, du nombre de plongeurs et du nombre de dauphins sur la tolérance aux plongeurs sous-marins.

Nos résultats indiquent que les réponses des dauphins aux plongeurs sont multiformes et qu'il est important de les considérer avec précaution avant de tirer des conclusions au sujet de leur habituation au tourisme. En effet, les dauphins sont habitués à la présence de plongeurs sous-marins sur la zone touristique et tolèrent la présence de plongeurs actifs à moins de 10 mètres d'eux. Cependant, leur tolérance est modulée par leur âge, leur contexte social et par le comportement des plongeurs.

Les dauphins immatures répondent davantage aux plongeurs que les individus matures et deux immatures ont exprimé plus de comportements affiliatifs que de réponses neutres envers les plongeurs sous-marins. Les dauphins réagissent moins aux plongeurs lorsque le nombre de dauphins présents est élevé et deux comportements des plongeurs sous-marins sont positivement et significativement corrélés aux réponses d'évitement des dauphins : la main tendue et la tendance à suivre des dauphins qui s'éloignent. Par ailleurs, des variations inter-individuelles de tolérance des dauphins aux plongeurs sous-marins ont été observées.

Une tolérance plus élevée des jeunes dauphins aux comportements humains intrusifs peut les rendre particulièrement vulnérables aux effets délétères (e.g., collisions avec des embarcations, transmission de pathogènes) associés aux activités humaines (e.g., Geffroy *et al.*, 2015 ; Saltz *et al.*, 2018 ; Carzon *et al.*, 2023).

Nous recommandons de collecter des données longitudinales sur ces dauphins afin d'évaluer leur aptitude de survie au regard de leur réactivité aux plongeurs. De plus, nous suggérons de surveiller simultanément les réponses comportementales et physiologiques des dauphins en présence de plongeurs sous-marins afin de comprendre si l'absence de réponses comportementales évidentes correspond à l'absence de réponses physiologiques.

Enfin, nous soulignons le besoin de promouvoir un comportement passif des plongeurs sous-marins en présence des dauphins, d'éduquer les tour-opérateurs, guides et touristes au sujet des dauphins, de mieux encadrer le comportement sous-marin des plongeurs et de faire appliquer des réglementations explicites adaptées au contexte de Rangiroa. En effet, la croyance selon laquelle l'habituation a un effet neutre ou positif pour les animaux, et qu'elle est désirable pour le tourisme, peut motiver la prise de décisions inappropriées quant à la gestion des risques liés aux interactions interspécifiques proches (Bejder *et al.*, 2009).

Le papier intitulé *La tolérance de grands dauphins sauvages aux plongeurs est modulée par leur âge, leur contexte social et par le comportement des plongeurs* a été écrit en partenariat avec les **Drs É. Clua** et **F. Delfour** et soumis au journal *Behaviour* en juin 2024. Cet article illustre l'importance de se focaliser sur les réponses fines des animaux aux activités touristiques dans le but d'informer des mesures de gestion contextuelles.

3 Audace des dauphins de Rangiroa envers les plongeurs sous-marins

Mots-clés

Tempérament, audace, comportement des dauphins, interactions humains / dauphins, tourisme animalier

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Dans l'introduction, nous avons vu que les tempéraments individuels influencent les réponses des animaux sauvages à la présence répétée d'êtres humains et activités humaines (Carrete & Tella, 2013 ; Lowry *et al.*, 2013).

Nous avons choisi l'axe timidité-audace, validé par la communauté scientifique, pour identifier des traits de tempérament individuels chez des grands dauphins de Rangiroa suivis pendant trois ans en présence de plongeurs sous-marins souvent intrusifs. Nous nous sommes basés sur un répertoire comportemental* spécifique aux interactions dauphins / plongeurs à Rangiroa et avons mesuré l'occurrence, la durée et la fréquence des comportements affiliatifs des dauphins exprimés à moins de trois mètres des plongeurs sous-marins (e.g., dauphin se positionnant verticalement tête en haut et se laissant couler). Ces comportements, que nous avons nommés 'comportements audacieux', ont été utilisés comme proxies pour illustrer l'audace des dauphins envers les plongeurs. Afin de mieux comprendre leur audace, nous avons également mesuré l'implication des dauphins dans des interactions physiques avec les plongeurs sous-marins. Enfin, nous avons testé si le sexe et la maturité sexuelle des dauphins prédisent leur tendance à exprimer des comportements audacieux vis-à-vis des plongeurs sous-marins.

Notre étude a révélé des traits de tempérament individuels chez les grands dauphins dans le contexte de leurs interactions avec le tourisme. En effet, nous avons observé une variation inter-individuelle et une stabilité intra-individuelle des comportements audacieux au cours du temps, deux caractéristiques typiquement utilisées pour mettre en évidence des traits de

tempérament chez des espèces non-humaines. De plus, il a été possible de mettre en évidence différentes expressions de l'audace chez les dauphins audacieux. Par exemple, certains dauphins audacieux sont particulièrement impliqués dans les interactions physiques avec les plongeurs sous-marins. Les dauphins les plus audacieux sont des individus immatures et la plupart sont des juvéniles (i.e., indépendants de leur mère).

Bien que les individus audacieux génèrent et entretiennent la popularité des activités touristiques locales, leur audace vis-à-vis des plongeurs sous-marins soulève des inquiétudes quant à leur bien-être à moyen- et long-terme et à leur conservation. Un fort degré d'audace chez les dauphins peut en effet être risqué pour les plongeurs sous-marins. Il peut aussi mener à des comportements inadaptés chez les dauphins si ces réponses sont transférées à des activités humaines à risque. Par ailleurs, nous suggérons que certains comportements audacieux des dauphins vis-à-vis des plongeurs sont conditionnés par l'attitude (e.g., émission de sons et utilisation de gestes pour attirer les dauphins) des plongeurs sous-marins.

L'aspect multidimensionnel des réponses des dauphins aux plongeurs sous-marins et les risques associés soulignent le besoin de développer des stratégies de gestion efficaces adaptées au contexte local dans le but d'encadrer des activités touristiques respectant à la fois le bien-être et la conservation des animaux et la sécurité des plongeurs, à court- et à long-terme.

Le papier intitulé *Variation individuelle de l'audace de grands dauphins sauvages interagissant avec des plongeurs sous-marins en Polynésie française* a été écrit en collaboration avec les **Drs É. Clua** et **F. Delfour** et soumis en juin 2024 au journal *Applied Animal Behaviour Science*.

À Rangiroa, le tourisme de plongée sous-marine promeut des comportements humains intrusifs vis-à-vis des dauphins et l'audace de certains dauphins en présence d'êtres humains participe sans nul doute de la popularité de la destination auprès des touristes. Cependant, ces interactions interspécifiques peuvent impacter négativement tant les dauphins que les plongeurs et doivent être encadrées en connaissance de cause.

La recherche en 8 points

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1 Les rencontres rapprochées entre dauphins et humains en milieu naturel ont connu un essor considérable à travers le monde

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2 Il existe un manque de connaissances au sujet de l'augmentation du nombre et des impacts réels de ces interactions interspécifiques

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3 L'habituation et le conditionnement des animaux rend les dauphins et les humains plus vulnérables aux effets délétères associés aux interactions proches

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4 L'âge et le contexte social des dauphins, ainsi que les comportements des humains, influencent la tolérance des dauphins aux plongeurs sous-marins

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5 Les grands dauphins expriment des traits d'audace dans le cadre de leurs interactions avec les plongeurs sous-marins

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6 Il existe différents types d'audaces chez les dauphins audacieux

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7 Les dauphins les plus audacieux sont des individus immatures et principalement des juvéniles

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8 Il est essentiel de considérer les variations inter-individuelles dans les réponses des dauphins au tourisme afin de mettre en place des stratégies de gestion optimales

Discussion générale

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1. Points forts et limites de la recherche

Notre étude fournit de nouvelles informations au sujet des réponses comportementales détaillées de grands dauphins aux activités touristiques intrusives et répétées. Elle a été menée sur une zone océanique isolée, fréquentée par le tourisme de plongée sous-marine depuis plus de trois décennies, et a bénéficié de conditions environnementales privilégiées (i.e., bonne accessibilité aux animaux, eaux chaudes, bonnes conditions de visibilité toute l'année) permettant la collecte simultanée de données depuis la terre et en plongée sous-marine.

De manière générale, la tolérance des dauphins aux plongeurs sous-marins sur la zone de Tiputa offre de nombreuses opportunités pour collecter des données comportementales sur ces animaux. Elle permet également d'enquêter sur les interactions hommes / dauphins, aussi bien du point de vue des dauphins que de celui des humains. Il s'agit donc d'un cas d'étude pertinent pour la recherche interdisciplinaire.

Dans le cadre de cette thèse, nous avons construit un répertoire comportemental sous-marin spécifique aux interactions dauphins / plongeurs et avons examiné les comportements neutre, d'évitement et affiliatifs des dauphins envers les plongeurs sous-marins pour quantifier leur tolérance aux activités touristiques et des traits de tempérament individuels chez ces animaux.

En considérant simultanément plusieurs réponses comportementales des dauphins aux plongeurs, nous avons développé une compréhension détaillée des conséquences d'une exposition répétée des dauphins aux humains. Nous avons en outre bénéficié d'un suivi à long-terme de la communauté de grands dauphins, initié en 2009, qui nous a fourni une bonne connaissance de base des dauphins à l'échelle individuelle (e.g., sexe, âge, statut reproductif, liens matrilinéaires, partenaires sociaux). Tous les dauphins matures ont été régulièrement identifiés sur la zone touristique pendant au moins huit ans avant que ne débute cette étude ; tous les dauphins immatures sont les petits de femelles identifiées et ont régulièrement été vus sur la zone depuis leur naissance.

Malgré cela, notre étude comporte un certain nombre de facteurs limitants tels qu'un échantillon de petite taille, une durée d'observation relativement courte, un manque d'individus naïfs, l'imprévisibilité du comportement des plongeurs et un biais d'échantillonnage. Tous ces facteurs sont brièvement discutés ci-dessous.

1.1. Échantillon de petite taille

La communauté de dauphins vivant sur la zone touristique de Tiputa est petite, puisqu'elle ne comporte qu'une trentaine d'individus dont certains sont régulièrement mais rarement capturés sur site (Carzon, 2017). Pour mener à bien notre étude, nous avons dû sélectionner les dauphins pour lesquels nous avions suffisamment de données (i.e., les individus observés sous l'eau à proximité de plongeurs sur au moins dix jours répartis sur trois ans) et exclure tous les petits nés sur la période d'étude. Nous avons travaillé sur 18 à 20 individus différents, qui se sont révélés être un bon compromis entre un nombre acceptable de dauphins (i.e., plus de 15 individus) et une quantité de données raisonnable par individu (i.e., le dauphin sélectionné pour lequel nous avions le moins d'informations a été capturé sous l'eau 13 jours différents et totalise 8 minutes d'observations distribuées sur trois ans).

Les études sur la faune sauvage sont classiquement caractérisées par des échantillons de petite taille, tout comme les études sur les traits comportementaux individuels d'animaux appartenant à des espèces de grande taille. Par exemple, Díaz López (2020) a travaillé sur 24 grands dauphins sauvages pour examiner les relations entre leurs scores d'audace et leurs mesures de centralité sociale tandis que Kudo *et al.* (2021) ont considéré 22 tortues vertes (*Chelonia mydas*) dans le cadre d'une étude sur leurs traits d'audace et d'exploration.

Bissonette (1999) suggère que les échantillons de petite taille sont intéressants à étudier pour générer des questions et hypothèses pertinentes pour de futures études. En effet, bien que nous ayons en notre possession des informations supplémentaires sur les dauphins de Tiputa (e.g., identité des mères des dauphins immatures, statut reproductif des dauphins matures), nous n'avons pu intégrer ces données car le nombre d'individus considéré ne le permettait pas.

Afin de dépasser cette limite, il serait intéressant de travailler sur des périodes plus longues nous permettant d'inclure davantage de dauphins partageant des caractéristiques génétiques et démographiques similaires. Cela permettrait en outre d'identifier des variables supplémentaires pouvant avoir un effet significatif sur les réponses des dauphins au tourisme.

1.2. Durée d'observation relativement courte

Les grands dauphins sont des animaux à longue espérance de vie et opèrent donc sur de longues échelles temporelles. La plupart des études menées sur les réponses de ces cétacés au tourisme se focalisent sur des comportements à court-terme qui fournissent des connaissances fragmentaires sur les impacts réels des activités touristiques sur les dauphins à différentes échelles (Bejder *et al.*, 2006).

Notre période de collecte de trois ans nous a permis d'obtenir un aperçu des réponses des dauphins aux plongeurs, et il serait pertinent de travailler sur des données collectées sur dix ans minimum afin de confirmer nos résultats et de capturer des dynamiques à long-terme associées aux réponses des dauphins au tourisme de plongée sous-marine.

Quelques travaux traitant de thématiques similaires ont pu bénéficier de jeux de données collectés sur de longues périodes. Par exemple, Christiansen *et al.* (2016) ont utilisé plus de 45 ans de données et plus de 1 100 grands dauphins pour documenter les effets du nourrissage artificiel sur leur survie dans la baie de Sarasota, en Floride. À Shark Bay, en Australie, Foroughirad & Mann (2013) ont travaillé sur des données collectées entre 1988 et 2011 pour étudier les impacts à long-terme du nourrissage sur le comportement et la survie de grands dauphins.

1.3. Manque d'individus naïfs

Le processus usuel de mise en place d'un programme de suivi est de considérer et de délimiter une zone de contrôle appropriée (Bejder & Samuels, 2003). Ici, nous n'avons aucune donnée sur des dauphins n'ayant jamais expérimentés de présence humaine. Nous utilisons donc un contexte d'étude que Bejder (2005) a qualifié *d'impact seul*, qui se focalise sur les conséquences d'une exposition cumulée des dauphins au tourisme.

Cependant, nous avons comparé des données collectées depuis la terre, dans une zone exempte de plongeurs, à des données collectées sous l'eau sur la même période (i.e., en présence de plongeurs) afin de vérifier si certains dauphins de Tiputa sont suffisamment intolérants à la présence de plongeurs sous-marins pour être régulièrement observés depuis la terre mais rarement, voire jamais, en plongée sous-marine.

Nous sommes cependant conscients que les individus les plus timides ou des dauphins sensibilisés à la présence humaine peuvent quitter prématurément une zone de dérangement, ce qui les rend intrinsèquement difficiles à capturer (Bejder *et al.*, 2009).

Il aurait été intéressant de collecter des données avant et pendant la mise en place des activités touristiques de plongée sur la zone de Tiputa afin d'obtenir une perspective plus exhaustive de l'étendue des réponses comportementales des dauphins aux plongeurs et de pouvoir décrire des processus d'habituation et de sensibilisation.

Une telle configuration est rare dans les études sur les réponses des baleines et des dauphins au tourisme mais Bejder *et al.* (2006) ont pu comparer l'abondance de dauphins entre une zone contrôle et une zone touristique sur trois périodes pendant lesquelles les niveaux de dérangement touristique sont passés de zéro à un, puis deux opérateurs de *whale watching*, afin d'évaluer les impacts à long-terme de la présence et de l'activité des embarcations sur des grands dauphins à Shark Bay.

Nous ne possédons pas de données similaires sur les grands dauphins de Rangiroa. En effet, les activités de plongée sous-marine ont débuté sur le site de Tiputa en 1985 tandis que nous avons commencé à y collecter des données régulières à partir de 2009. Toutefois, nous avons pu rassembler quelques données plus anciennes, qui nous ont aidé à reconstruire une histoire partielle des réponses de certains dauphins aux plongeurs.

Quoi qu'il en soit, il serait intéressant de comparer les dynamiques à long-terme de la communauté de dauphins de Tiputa à celles de communautés interagissant peu avec les activités humaines autour d'atolls des Tuamotu partageant des caractéristiques écologiques similaires (e.g., Toau, Fakarava).

1.4. Imprévisibilité du comportement des plongeurs

Les expériences de terrain pâtissent souvent d'une impossibilité à contrôler les conditions environnementales lors des périodes de test, ce qui peut affecter la manière dont la stabilité comportementale d'un individu est évaluée (Martin & Réale, 2008). En effet, des stimuli externes comme des bruits de fond induits par les activités humaines peuvent varier d'un test à l'autre de manière évidente ou subtile et influencer le comportement d'une partie au moins des individus échantillonnés.

Dans notre étude, nous avons considéré l'environnement quotidien vécu par les dauphins où toutes les variables environnementales n'ont évidemment pu être contrôlées lors du processus de collecte de données. Il était par exemple impossible de contrôler les comportements des plongeurs en présence de dauphins. La petite zone de Tiputa est fréquentée quotidiennement, entre 8h00 et 17h30, par un à six centres de plongée, leurs moniteurs et des

touristes-plongeurs. Avant et pendant une plongée, la plupart des moniteurs encouragent leurs plongeurs à initier une interaction avec les dauphins en se comportant de manière active et intrusive en présence des animaux (*obs. pers.*).

Il serait nécessaire de plonger sur le site touristique avant l'arrivée des premières palanquées de moniteurs et de touristes, et de contrôler les postures, gestuelles et sons émis par des plongeurs formés à cet effet, afin de tester l'influence de certains comportements humains sur le comportement des dauphins.

1.5. Biais d'échantillonnage

Bien que les données aient été collectées de façon relativement constante sur trois ans, nous avons obtenu un nombre et des durées d'observations inégales pour chacun des dauphins. Quelques individus avaient des probabilités plus importantes d'être capturés sous l'eau car ils passent plus de temps sur le site touristique, ont un seuil de tolérance plus élevé à la présence humaine (i.e., ils expriment des comportements neutres à plus faible distance des plongeurs) et sont plus audacieux (i.e., ils interagissent de façon positive avec les plongeurs plus fréquemment) que les autres dauphins.

Nous avons d'une part essayé de dépasser ces difficultés en vérifiant que les dauphins soient observés de manière identique depuis la terre, dans une zone sans plongeurs, et sous l'eau, en présence de plongeurs sous-marins. D'autre part, nous avons sélectionné aléatoirement un nombre similaire d'observations par dauphin provenant de journées d'échantillonnage exclusives distribuées sur trois ans. Cela nous a permis d'effectuer les analyses sur des jeux de données inter-individuels relativement équilibrés.

2. Variations dans les comportements des dauphins en présence de plongeurs sous-marins

Nos résultats indiquent que les dauphins sont habitués à la présence humaine et que leurs comportements en présence de plongeurs sous-marins varient en fonction du comportement des plongeurs, du contexte social des dauphins, de leur stade de maturité sexuelle (i.e., âge) et de traits comportementaux stables liés à l'audace. Par conséquent, les réponses des dauphins au tourisme sont modulées par leur plasticité et leur tempérament.

À notre connaissance, les réponses à la fois plastiques et tempéramentales de dauphins au dérangement humain n'ont jamais été étudiées jusqu'alors.

La plasticité comportementale et les ajustements adaptatifs sont importants pour faciliter l'utilisation des ressources dans des environnements dominés par les activités humaines (Bateman & Fleming, 2014) et les grands dauphins semblent être relativement plastiques dans un contexte de dérangement anthropique comparé à d'autres mammifères marins.

Par exemple, des réponses comportementales plastiques à l'exposition immédiate de grands dauphins à des travaux de construction côtière ont été étudiées en Floride, montrant que les dauphins apprennent à faire face au dérangement humain en ajustant leurs comportements de deux façons : **1)** en établissant de nouvelles zones de chasse à l'extérieur de la zone de construction et **2)** en changeant le rythme temporel des comportements qu'ils expriment sur la zone de construction plus tard dans la journée, lorsque les activités humaines y sont réduites (Weaver, 2021).

En comparaison, les dauphins à long bec (*Stenella longirostris*) sont particulièrement vulnérables aux pressions d'origines humaines car ils possèdent des schémas comportementaux rigides (i.e., ils se nourrissent la nuit et se reposent en journée, Tyne *et al.*, 2017 ; Fumagalli *et al.*, 2018). Par exemple, Tyne *et al.* (2017) ont observé que l'utilisation extensive, régulière et à long-terme des baies de repos des dauphins à long bec hawaiiens comme sites touristiques n'a pas entraîné l'abandon des baies par les dauphins mais un déclin de leurs populations.

En outre, une étude sur trois ans menée en Irlande sur les réponses de petits rorquals (*Balaenoptera acutorostrata*), grands dauphins et phoques gris à une augmentation du trafic maritime a montré que la présence des grands dauphins était positivement corrélée au nombre total d'embarcations tandis que la présence des rorquals et des phoques était négativement corrélée au nombre de bateaux (Anderwald *et al.*, 2013).

En Sardaigne, Díaz López (2019) a documenté une tendance significative à l'augmentation sur neuf ans de la densité de grands dauphins dans une zone côtière sujette à

une pression humaine significative (i.e., zone d'aquaculture marine et de pêche au filet maillant). En outre, les dauphins préféraient une zone côtière présentant une pression humaine plus importante et ont montré une réduction de leurs interactions sociales associée à un changement temporel de leur alimentation, plus axée sur des sources de nourriture générées par les activités humaines. Cette étude démontre l'adaptabilité remarquable de ces animaux.

Enfin, les dauphins de Rangiroa ne sont pas les seuls à être tolérants et audacieux en présence de plongeurs sous-marins puisque des grands dauphins de l'archipel océanique des Revillagigedo, au Mexique, se comportent de façon similaire dans le contexte du tourisme de plongée sous-marine (Carzon *et al.*, 2023).

Au vu de ces résultats, nous suggérons que les grands dauphins en tant qu'espèces disposent d'un potentiel d'accommodation à différents types d'environnements plus important que d'autres mammifères marins et peuvent, à ce titre, avoir plus de succès dans des environnements nouveaux créés par l'homme.

Par ailleurs, notre étude a révélé que certains dauphins, à échelle individuelle, possèdent des traits comportementaux qui les aident à s'ajuster à une présence humaine chronique. Être audacieux pourrait être corrélé à une plus grande tolérance à des stimuli anthropiques variés et permettre à un animal de vivre à proximité des activités humaines sans endurer de stress chronique (Lowry *et al.*, 2013).

3. Conséquences potentielles des variations individuelles dans les réponses des dauphins au tourisme

Il est hasardeux de prédire les conséquences à long-terme pour les dauphins de leurs réponses individuelles au tourisme. Une vision contextuelle et instantanée de la plasticité et de l'audace de ces animaux fournit en effet des fondations très partielles pour la compréhension de l'influence des variations individuelles sur des échelles de temps et d'espace propres à l'écologie et à l'évolution (Sih *et al.*, 2004 ; Stamps & Groothuis, 2010 ; Stamps & Biro, 2016). En revanche, il est communément admis que la plasticité et le tempérament peuvent affecter plusieurs composantes de la vie d'un animal, y compris son utilisation de l'habitat, sa manière d'éviter les prédateurs, ses déplacements et son comportement social (Dingemanse *et al.*, 2003 ; Dall *et al.*, 2004 ; Sih *et al.*, 2004 ; Dingemanse & Réale, 2005). Par exemple, les individus ne semblent pas être distribués de manière aléatoire au regard de la fréquentation humaine de

l'espace et les plus audacieux occupent généralement les zones les plus fréquentées par les activités humaines (Martin & Réale, 2008 ; Lowry *et al.*, 2013).

Dans notre étude, nous émettons l'hypothèse que les individus les plus audacieux puissent ajuster leurs réponses à des activités humaines omniprésentes et demeurer sur la zone touristique malgré une présence humaine soutenue et intrusive, à la fois en surface et sous l'eau. Leur tolérance élevée peut les aider à minimiser les coûts associés aux réponses chroniques à mettre en place en présence d'êtres humains non-menaçants et leur permettre de coexister avec les hommes (Blumstein, 2016).

Parallèlement, nous suggérons que les dauphins les plus audacieux, et particulièrement les jeunes individus, ne soient pas toujours capables de faire la distinction entre différents niveaux de menaces liés à la présence humaine (Bateman & Fleming, 2014). À ce titre, ils pourraient être particulièrement vulnérables aux risques collatéraux associés aux activités humaines en sous-estimant des dangers réels (Sih *et al.*, 2023). Par exemple, les dauphins impliqués dans les activités illégales de nourrissage à Cockburn Sound, en Australie, sont également prédisposés aux collisions avec des bateaux et à l'emmêlement dans du matériel de pêche (Donaldson *et al.*, 2010). À Rangiroa, nous suspectons que les dauphins audacieux puissent être particulièrement vulnérables aux collisions avec des bateaux, aux blessures par hélice, à la transmission de pathogènes et aux conséquences délétères d'actes inappropriés de la part d'êtres humains (Carzon *et al.*, 2023).

Par ailleurs, nous suggérons que la tolérance élevée des dauphins audacieux aux activités touristiques promeuve une augmentation de la popularité et de la fréquentation du site, augmentant du même coup le potentiel d'issues délétères (Cf. concept de *construction de niche* formulé par Stamps & Groothuis, 2010).

Enfin, l'expérience vécue par les jeunes dauphins peut avoir un effet substantiel sur leurs préférences futures et motiver le choix de ressources ou d'activité non-optimales une fois qu'ils atteignent la maturité sexuelle, choix pouvant impacter de manière négative leur succès reproductif et leur espérance de vie (Broom & Johnson, 2019).

Les individus moins tolérants à la présence humaine peuvent quitter les zones d'activités anthropiques, favorisant la sélection de phénotypes particuliers (Carrete & Tella, 2010 ; Møller, 2017), ou peuvent n'avoir d'autre option que de rester sur un site lorsque le dérangement se concentre sur des habitats critiques (Bejder, 2005 ; Beale, 2007 ; Bejder *et al.*, 2009 ; Blumstein, 2016).

La passe de Tiputa est à la fois un hotspot biologique et touristique situé dans un environnement marin oligotrophe (Nanninga & Spaet, 2017 ; Vollbrecht *et al.*, 2021). Il s'agit du seul endroit parmi les 80 îles des Tuamotu qui accueille de façon permanente une communauté de grands dauphins (*obs. pers.*). En outre, la passe de Tiputa est un terrain de jeu pour les dauphins qui viennent quotidiennement surfer et sauter dans ses vagues (Carzon, 2017). La zone touristique pourrait donc être un paysage écologique et social majeur pour les dauphins et il serait opportun d'évaluer la manière dont les individus moins tolérants s'adaptent à l'omniprésence humaine.

4. Bénéfices et risques des interactions proches entre dauphins et plongeurs

La prévisibilité des observations de dauphins, l'habituation des dauphins à la présence de plongeurs sous-marins et la tendance de certains dauphins à interagir avec les plongeurs fournissent un grand nombre de bénéfices pour les humains et le tourisme local (Hunter Jr. *et al.*, 2021 ; Uchida *et al.*, 2023).

En outre, un contact direct avec la nature fournit de nombreux bénéfices en termes de santé et de bien-être pour les êtres humains (Bègue-Shankland, 2022, p50 ; Uchida *et al.*, 2023) et certains auteurs soutiennent que les rencontres avec des mammifères marins dans leur milieu naturel contribuent au développement d'une vision écocentrique et permettent aux Occidentaux de reconsidérer leurs impacts sur l'environnement (Yerbury & Weiler, 2020). Nous n'avons pas noté de telles contributions à Rangiroa mais les interactions proches entre dauphins et plongeurs améliorent typiquement le niveau de satisfaction des plongeurs sous-marins et les moniteurs de plongée encouragent également des interactions intimes régulières avec les dauphins pour des raisons personnelles (*obs. pers.*).

Du point de vue des dauphins audacieux, les interactions affiliatives avec les plongeurs sous-marins peuvent apporter des bénéfices immédiats à travers l'opportunité d'un contact physique agréable ou de jouer. Les dauphins ont un sens du toucher très développé (Palmer & Weddell, 1964) et le fait de se frotter ou de toucher des objets ou le substrat peut avoir des fonctions hygiéniques (e.g., suppression de parasites, desquamation) et sensuelles (e.g., plaisir, Sakai *et al.*, 2006 ; Dudzinski *et al.*, 2012). En milieu captif, les caresses sont une récompense efficace pour l'entraînement de certains dauphins (Defran & Pryor, 1980) et Samuels *et al.* (1989) ont noté qu'un grand dauphin recevant peu de caresses de la part de conspécifiques avait pris l'habitude de frotter son corps sur des objets (*in* Dudzinski *et al.*, 2012). L'auto-frottement

est observé chez les dauphins de Tiputa où les individus frottent régulièrement leur rostre sur des éponges (*Dactylospongia metachromia*) exposées sur le récif externe et certaines parties de leur corps (e.g., tête, flancs, zone génitale) sur la soupe de corail qui s'accumule dans la passe (*obs. pers.*). Ainsi, les plongeurs sous-marins pourraient servir de 'stations de grattage' pour dauphins audacieux et les aider à se débarrasser de parasites et / ou de peaux mortes.

Par ailleurs, le jeu est une composante importante de la vie des dauphins (Janik, 2015). Les dauphins juvéniles s'engagent dans des jeux solitaires plus souvent que les autres classes d'âge et leurs partenaires de jeu peuvent varier selon le type de jeu en cours (Cappiello *et al.*, 2018). À Rangiroa, les jeunes dauphins sont observés de façon routinière jouant avec des déchets plastiques et les bulles des plongeurs, seuls ou avec des conspécifiques, et plus rarement avec des algues, des méduses et des poissons porc-épic (*Diodon hystrix*, *obs. pers.*). En outre, les dauphins jouent parfois pour tester les limites du danger (Kuczaj & Eskelinen, 2014), ce qui pourrait être le cas lorsque les dauphins de Rangiroa expriment des comportements audacieux vis-à-vis des plongeurs.

Les interactions proches fournissent donc bien des bénéfices aux humains et aux dauphins. Toutefois, nous avons vu précédemment qu'elles génèrent des impacts délétères à court- et à long-terme pour les deux parties (e.g., transmission de pathogènes, agression) et que les conséquences négatives peuvent être considérables lorsque les dauphins sont conditionnés par de la nourriture et / ou régulièrement touchés par les hommes.

À Rangiroa, les moniteurs de plongée ont l'habitude de saisir la nageoire caudale des dauphins les plus audacieux pour la frotter (**Figure 1**) et certains plongeurs enlacent ces dauphins ou s'accrochent à leur nageoire dorsale lorsqu'ils nagent ou restent immobiles à faible distance. Il n'est pas rare de voir trois plongeurs ou plus encercler et toucher un dauphin de manière simultanée (**Figure 2**) et de telles situations peuvent déclencher des réactions humaines passionnées où le désir d'une interaction privilégiée avec un dauphin dépasse toute limite raisonnable avec l'animal (e.g., les plongeurs touchent les yeux, l'évent, la bouche ou la zone génitale du dauphin) et tout respect pour les autres plongeurs (e.g., les plongeurs se bousculent pour accéder au dauphin).

Cinq dauphins audacieux ont été documentés dans le cadre de notre étude parmi lesquels quatre étaient régulièrement impliqués dans des interactions physiques avec les plongeurs sous-marins. Sur ces quatre individus, une femelle a été sérieusement blessée par une hélice de bateau

en 2018 (à l'âge de 5 ans, **Figure 3**) et une autre a été retrouvée morte sur le récif en 2022 (à l'âge de 10 ans). Une troisième, d'environ 25 ans en 2024, a commencé à exprimer des comportements audacieux envers les plongeurs lorsqu'elle était juvénile. Elle a donné naissance à trois petits connus qui sont ou ont eux-mêmes été audacieux envers les plongeurs. Deux des petits ont disparu prématurément et le troisième a maintenant huit ans et recherche toujours des contacts physiques réguliers avec les plongeurs sur la zone de Tiputa.

Il serait pertinent de collecter des données démographiques à long-terme sur les dauphins de Tiputa dans le but de comparer le succès reproductif et l'espérance de vie des dauphins audacieux à celui des autres dauphins.

Figure 1. Moniteur de plongée saisissant la nageoire caudale d'un dauphin pour la frotter.

Figure 2. Plongeurs sous-marins encerclant et touchant un dauphin.

Figure 3. Dauphin audacieux âgé de 5 ans blessé par une hélice de bateau.

La santé et le bien-être des humains ne peuvent être maximisés indépendamment de la santé et du bien-être des dauphins. À ce titre, satisfaire les besoins des touristes sans compromettre les besoins des dauphins est un véritable défi (García Pinillos *et al.*, 2016 ; Lindenmayer & Kaufman, 2021). En effet, l'idée d'un contact avec des dauphins en milieu naturel est motivante et considérée comme une récompense par les humains, et peu de gens sont disposés à sacrifier volontairement des opportunités d'interactions intimes avec ces animaux (Frohoff *et al.*, 2005).

Dans un rapport sur les situations à risque pour diverses espèces de baleines et de dauphins solitaires, Frohoff *et al.* (2005) ont considéré que l'encouragement de la part d'êtres humains de contacts sociaux avec les dauphins solitaires est l'une des réponses les plus communes, et les plus problématiques, observées en leur présence. En effet, ces contacts augmentent la probabilité que les dauphins soient blessés ou tués, intentionnellement ou accidentellement, par des humains ou des activités humaines (Samuels *et al.*, 2000 ; Carzon *et al.*, 2023).

Winter (2020) soutient que beaucoup de touristes sont conscients, au moins partiellement, que leurs activités peuvent nuire aux animaux, ce qui provoque chez eux une dissonance cognitive (Bègue-Shankland, 2022). Parallèlement, ils utilisent d'innombrables arguments pour défendre leurs comportements (e.g., la liberté de choix des animaux) et peu d'entre eux semblent réellement être dissuadés d'utiliser les animaux à des fins de divertissement personnel (Winter, 2020).

Ziegler *et al.* (2018) ont étudié les points de vue des touristes sur l'éthique du nourrissage artificiel de requins-baleines (*Rhincodon typus*) aux Philippines. Les auteurs ont documenté que les touristes pèsent généralement 'le pour et le contre' de ces activités mais laissent leur désir de voir des requins-baleines de près guider leur prise de décision. Des touristes témoignent se sentir coupables de participer à une activité qu'ils ont personnellement identifiée comme étant écologiquement douteuse, mais les évaluateurs de *TripAdvisor* défendent leur participation en prétendant que l'activité n'est pas si mauvaise puisque les requins ont l'air heureux et qu'ils ne sont pas maintenus captifs (Ziegler *et al.*, 2018 ; 2019).

À Rangiroa, les moniteurs de plongée et les touristes utilisent les mêmes sophismes pour justifier leurs comportements vis-à-vis des dauphins (*obs. pers.*).

De nombreux auteurs suggèrent que les animaux sauvages sont encore considérés comme des *marchandises*, car l'environnementalisme de marché alimente une vision du monde anthropocentrique où ils sont des ressources que les humains peuvent utiliser à leur guise à des fins de divertissement ou à des fins économiques (Forestell, 2009 ; Duffy, 2015 ; Belicia & Islam, 2018). L'anthropocentrisme et l'utilitarisme dominent nos modes d'utilisation actuels des animaux dans un contexte touristique et placent le confort des humains au-dessus de toute préoccupation quant aux impacts de ces activités sur les espèces et individus ciblés (Winter, 2020). Pourtant, certains chercheurs soutiennent que les animaux n'ont pas seulement de la valeur dans la mesure où ils sont utiles aux êtres humains et que le bien-être, l'éthique et la conservation des espèces non-humaines devraient recevoir davantage d'attention de la part du secteur touristique (Schweiggart, 2024 ; Edelbutte *et al.*, 2023).

En outre, les humains peuvent souffrir des conséquences négatives liées aux interactions étroites avec des dauphins. Par exemple, à Rangiroa, des plongeurs sous-marins ont été vus touchant des dauphins présentant une maladie cutanée granulomateuse semblable à la lobomycose (Félix *et al.*, 2019). Les humains peuvent contracter la lobomycose par contact avec des dauphins infectés, les lésions cutanées humaines se développant lentement au cours du temps et la maladie est incurable (Lupi *et al.*, 2005 ; Bermudez *et al.*, 2009).

Les dauphins de Rangiroa ont également été vus exprimant des comportements intrusifs, brusques et / ou agressifs vis-à-vis de plongeurs sous-marins (e.g., dauphins poussant des plongeurs, tirant sur les palmes et les flexibles, émettant des *buzzes* ou claquant des mâchoires, *obs. pers.*). De tels comportements des dauphins s'accompagnent de risques inhérents spécifiques à l'activité de plongée sous-marine et la simple présence de dauphins peut compromettre la sécurité des plongeurs via des remontées / descentes incontrôlées et des essoufflements (*obs. pers.*).

Les rencontres rapprochées entre humains et dauphins en milieu naturel soulèvent donc des questions relatives à la sécurité, à l'éthique, au bien-être et à la conservation, questions qui se traduisent rarement en mesures de gestion appropriées. Nous nous sommes basés sur les données collectées dans le cadre de notre revue [**1**] pour synthétiser dans le **tableau 1** les risques associés aux interactions proches répétées entre dauphins et plongeurs sur la zone de Tiputa.

Tableau 1. Risques associés aux interactions proches répétées entre dauphins et plongeurs à Rangiroa.

	Directs		**Indirects**	
	Court-terme	*Long-terme*	*Court-terme*	*Long-terme*
Pour les dauphins	Incapacité à exprimer des comportements sociaux intra-spécifiques Incapacité à se reposer Blessure et vandalisme d'origine humaine Transmission de pathogènes	Perte de vigilance vis-à-vis des humains et des activités humaines Incapacité pour les juvéniles à se développer correctement	Collisions avec des embarcations Blessures par hélice Prédation	Soins maternels insuffisants Réduction de l'espérance de vie Déclin de l'abondance locale
Pour les plongeurs	Comportements brusques, agressifs et / ou intrusifs des dauphins causant des blessures et accidents directs / indirects Transmission de pathogènes	-	Accidents de plongée Destruction de matériel	Non-rentabilité et disparition de l'activité touristique

5. Implications pour la gestion des interactions proches

De nombreuses directives d'observation des baleines et des dauphins à travers le monde interdisent la nage, la plongée sous-marine, le contact physique et le nourrissage des animaux dans le cadre de principes de base liés à la supervision des activités de *whale watching* (Carlson, 2008). Les risques associés aux interactions proches entre dauphins et humains montrent en effet qu'il n'est ni raisonnable, ni éthique d'encourager de telles interactions.

À Rangiroa, la promotion d'un comportement passif des plongeurs sous-marins envers les dauphins serait une stratégie efficace pour limiter la survenue de résultats négatifs. En effet, les dauphins qui recherchent un contact physique avec les plongeurs perdront probablement tout intérêt pour ce type d'interaction si les plongeurs ne les y encouragent plus (Kuczaj II & Xitco Jr., 2002).

Cependant, la valeur du tourisme animalier est rarement reflétée dans les décisions de gestion qui autorisent habituellement l'utilisation consommatrice d'écosystèmes fragiles faisant déjà face à de nombreuses menaces causées par les activités humaines (e.g., Lamb *et al.*, 2014 ; Halpern *et al.*, 2015 ; Cornwall *et al.*, 2021). Les réponses politiques sont entravées par la priorité accordée aux développements social et économique du tourisme, au détriment de toute gestion durable de ces activités (Higham *et al.*, 2009).

Pourtant, s'ils ne sont pas ou mal gérés, les écosystèmes soumis à la pression du tourisme risquent de s'épuiser par surexploitation (Pirotta & Lusseau, 2015), et les destinations portent en elles le germe de leur propre destruction lorsqu'elles se développent outre-mesure en perdant les qualités originelles qui attiraient les touristes (Plog, 1974).

Alors que la Polynésie française s'efforce de mettre en place un tourisme durable (Tahiti Tourisme, 2023), la destination devrait développer des stratégies de gestion proactives prenant en compte à la fois l'humain, la faune sauvage et l'environnement (Fennell & Sheppard, 2021).

D'après Moorhouse *et al.* (2015), les activités touristiques où aucun bénéfice n'est réinvesti dans la conservation, le bien-être animal et les communautés humaines locales doivent être considérées comme une simple exploitation des espèces sauvages pour le profit. De son côté, Carlson (2008) a déclaré que *les opérateurs de* whale watching *ont le devoir de prendre soin des animaux qu'ils exploitent*.

La croissance du tourisme animalier justifie la nécessité de gérer ces activités selon des principes durables (Dimmock *et al.*, 2013), d'autant plus que la faune sauvage est la principale ressource dont dépend le succès des entreprises touristiques (Cater & Cater, 2007).

Pourtant, à quelques exceptions notables près, la tendance des acteurs touristiques est d'attendre que des situations extrêmes se produisent plutôt que d'y remédier de manière préventive (Frohoff *et al.*, 2005).

5.1. Le tourisme animalier et sa gestion en Polynésie française

En Polynésie française, le tourisme est la principale source de revenus et l'industrie touristique locale est largement dépendante des ressources naturelles de la destination (Andréfouët & Adjeroud, 2019). Le tourisme animalier s'est développé à partir des années 1980 et est devenu un élément bien établi du secteur touristique polynésien. Par exemple, la Polynésie a connu un fort taux moyen de croissance annuelle (i.e., 30%) des activités de *whale watching* ciblant les baleines à bosse et les dauphins à long bec entre 1998 et 2005 et une étude menée en 2016 a recensé 258 entreprises impliquées dans le tourisme d'observation de la faune sauvage à travers le territoire, dont 56 centres de plongées (O'Connor, 2008 ; Lagouy & Clua, 2016).

L'archipel des Tuamotu est renommé en Polynésie française puisque certaines de ses îles offrent l'opportunité aux plongeurs sous-marins d'observer une vie récifale emblématique

(e.g., tortues marines, raies, nombreuses espèces de requins). L'atoll de Rangiroa a construit sa réputation autour de son abondance en requins gris de récif (*Carcharhinus amblyrhynchos*) et de la présence saisonnière de grands requins-marteaux (*Sphyrna mokarran*).

Dans les années 2000, lorsque la tolérance de certains grands dauphins envers les plongeurs sous-marins s'est accrue, Rangiroa est devenue célèbre en tant que destination privilégiée pour interagir avec ces mammifères marins emblématiques. Il s'agit du seul endroit en Polynésie française, et de l'un des seuls au monde, où il est possible de plonger avec des grands dauphins sauvages au quotidien. En 2016, les centres de plongée locaux ont vendu environ 36 900 plongées pour une dépense directe estimée à 2,4 millions de dollars (Lagouy & Clua, 2016). En 2024, six centres de plongée basent leur économie sur la petite zone de la passe de Tiputa (i.e., < 2 km²), représentant une pression touristique non négligeable sur la seule zone de Polynésie française où des grands dauphins résident à l'année (*obs. pers.*).

Certaines activités touristiques liées à la faune marine (e.g., *whale watching*) sont régulées en Polynésie française mais rares sont les tour-opérateurs et guides qui respectent la loi. À Rangiroa, la gestion du tourisme est clairement déficiente dans le cas des dauphins. En pratique, elle a été entravée par des problèmes attribués à l'éloignement et à l'isolement de l'atoll, au développement rapide et non maîtrisée des activités, à la communication percutante et trompeuse des tour-opérateurs, agences de voyage et touristes, à des réglementations vagues qui n'ont jamais été mises en application, à un manque de moyens financiers pour la recherche scientifique et à un échec de coordination et de communication entre les parties prenantes (*obs. pers.*).

Pourtant, des connaissances pourraient être recueillies auprès de destinations ayant une longue expérience en termes de gestion du tourisme d'observation des cétacés (e.g., Australie, Nouvelle-Zélande) et pourraient contribuer à convertir les activités d'observation des cétacés en Polynésie française en pratiques sûres, éducatives, éthiques et durables.

Ci-dessous, nous discutons quatre composantes de gestion suggérées dans notre revue [**1**] qui semblent être pertinentes dans le cas de Rangiroa.

5.2. Adopter le principe de précaution

Si une activité touristique animalière présente un risque suspecté de nuire à la santé humaine, aux animaux ou à leurs habitats, en l'absence de consensus scientifique au sujet du caractère nocif de l'activité, la charge de la preuve qu'elle *n'est pas* nocive incombe à ceux qui proposent les activités (Kriebel *et al.*, 2001 ; Burns *et al.*, 2011).

Le principe de précaution est pertinent dans de nombreuses situations car l'obtention de données de référence est chronophage et peut ne pas être concluante dans des environnements à bruit variable (Ziegler *et al.*, 2019). Par exemple, dans une étude sur l'éthique du nourrissage des requins-baleines aux Philippines, Ziegler *et al.* (2019) ont constaté *qu'il n'y a aucune preuve attestant que le nourrissage ne soit pas préjudiciable aux requins et, par conséquent, le principe de précaution devrait être invoqué selon lequel il incombe de prouver l'absence d'impact délétère par les partisans du nourrissage*.

Dans une étude des directives et réglementations relatives à l'observation des cétacés dans le monde, Carlson (2008) a également déclaré : *Avant d'autoriser la mise en place d'activités d'observation des cétacés, les Parties doivent procéder à une évaluation de leurs impacts potentiels sur l'état de conservation des cétacés. […] Aucune nouvelle activité d'observation des cétacés ne doit être autorisée s'il existe des menaces d'impacts négatifs significatifs sur le comportement ou le bien-être physiologique des cétacés*.

À Rangiroa, bien que des dauphins interagissent avec les plongeurs sous-marins depuis plus de deux décennies, nous préconisons une approche similaire basée sur la littérature examinée au sujet des interactions étroites entre dauphins et humains et les résultats de cette thèse de doctorat. Nous avons expliqué précédemment pour quelles raisons des contacts physiques réguliers entre plongeurs et dauphins peuvent être nuisibles pour les deux parties et doivent être évités. Additionnellement, nous recommandons de décourager toute tentative d'interaction étroite avec des individus immatures et tout effort déployé pour attirer les dauphins afin d'éviter de les conditionner et de minimiser le dérangement quotidien de ces animaux, et de la faune marine en règle générale.

5.3. Adapter les stratégies de gestion à des contextes locaux et évolutifs

Des paramètres tels que les comportements des touristes et les distances d'approche influencent les réponses comportementales des animaux aux humains et sont considérés dans la plupart des mesures de gestion s'intéressant au tourisme d'observation des cétacés (Carlson, 2008). Cependant chaque espèce, communauté, individu, lieu et opération touristique a ses propres caractéristiques qui doivent être prises en compte pour une gestion efficace de ces activités à des échelles locales. Par exemple, Lusseau & Higham (2004) ont suggéré que la détermination d'habitats critiques pour les dauphins (e.g., lieux de socialisation, de repos) où les bateaux sont interdits serait efficace pour protéger les grands dauphins de Doubtful Sound, en Nouvelle-Zélande. À Shark Bay, en Australie, Mann & Kemps (2003) ont recommandé une réduction du nombre et de la durée des visites touristiques à la plage où les dauphins sont nourris afin de permettre aux jeunes individus de réinitier plus rapidement un contact avec leur mère et de passer plus de temps à exprimer des comportements naturels à distance de la plage. Récemment, les autorités locales de l'île de La Réunion, en France, ont interdit la poursuite, l'encerclement et le contact physique avec les baleines et les dauphins ainsi que les sorties d'observation avant 9h00 et après 18h00 (Quiétude, 2021).

L'atoll de Rangiroa est caractérisé par son insularité et par son isolement. Toutes les activités d'observation des dauphins se focalisent sur une zone restreinte utilisée de manière intensive par un petit nombre de dauphins (Carzon, 2017). La pression touristique y est omniprésente et quasi-constante, ces activités ayant lieu depuis la surface et sous l'eau, tous les jours et toute l'année. Il serait par conséquent approprié de circonscrire des zones protégées interdites d'accès aux activités touristiques basées sur les habitats préférés par les dauphins et de limiter le nombre de bateaux, de nageurs et de plongeurs sous-marins sur site.

Par ailleurs, les touristes-plongeurs sont supervisés *in situ* par des moniteurs qui ignorent volontairement les réglementations existantes et montrent à leurs clients comment attirer et manipuler les dauphins. Il serait donc pertinent d'organiser des inspections régulières anonymes et indépendantes des briefings et des comportements sous-marins des guides envers les dauphins afin de décourager les attitudes intrusives et illégales.

Enfin, il serait nécessaire de mettre en place un suivi scientifique soutenu des dauphins et de leurs interactions avec les activités touristiques afin de fournir des informations pratiques à jour pour l'aménagement de lignes directrices adaptées aux circonstances. Des limites

quantifiables de changements acceptables devraient être énoncées de manière claire (e.g., nombre d'animaux blessés / morts, taux de reproduction, changements dans les budgets comportementaux des communautés focales, Higham *et al.*, 2009) et la communication entre les agences de gestion, les opérateurs touristiques, les ONGs, les chercheurs et les communautés locales devrait être améliorée (Guerra & Dawson, 2016).

5.4. Éduquer les touristes et les locaux

La gestion des interactions entre dauphins et humains est actuellement dominée par des stratégies de régulation et il existe un potentiel considérable pour augmenter le rôle des stratégies de gestion basées sur l'éducation (Orams, 1996). Des millions de voyageurs participent en effet à des activités touristiques néfastes pour les animaux, et risquées pour eux-mêmes, mais peu d'entre eux en ont véritablement conscience. À Rangiroa, la plupart des plongeurs se focalisent sur leur expérience à court-terme avec les dauphins et sont rarement capables d'appréhender les impacts cumulés de tous les visiteurs sur les animaux sur une longue période (Higham & Lück, 2007 ; Moorhouse *et al.*, 2015).

En outre, il existe de grosses lacunes en termes de connaissances sur les dauphins chez les tour-opérateurs, les guides et les clients. Nous assistons par exemple régulièrement à des interprétations erronées du comportement des dauphins par les moniteurs et les touristes (e.g., comportements agonistiques interprétés comme étant des comportements affiliatifs, *obs. pers.*) et la plupart des moniteurs ne savent pas identifier les dauphins avec lesquels ils interagissent régulièrement, excepté le dauphin blessé par une hélice de bateau.

Des programmes éducatifs réguliers, des formations et des outils de communication basés sur une connaissance scientifique réelle et précise des dauphins, des impacts du tourisme et des réglementations existantes devraient être développés et adaptés à différents publics (i.e., touristes, guides, tour-opérateurs, agences de voyage, autorités, scolaires, communautés locales) afin de mieux gérer les attentes et les comportements humains envers ces animaux (Curtin, 2008 ; Egresi & Prakash, 2019 ; Dybsand, 2020 ; Cottam, 2023). Ces programmes devraient proposer des solutions concrètes et positives pour observer les dauphins et leur environnement de manière éthique et durable et donner aux gens l'opportunité d'agir à travers, par exemple, les sciences participatives.

Nous avons néanmoins conscience que l'éducation n'est pas une solution toute-puissante. Par exemple, l'enquête de Scarpaci *et al*. (2003) sur le respect des réglementations encadrant les activités de nage avec les dauphins à Port Phillip Bay, en Australie, après que le gouvernement eut mis à jour lesdites réglementations, a montré que les opérateurs ignorent volontairement un certain nombre de règles afin de maintenir le *statu quo*.

À Rangiroa, la plupart des centres de plongée et moniteurs se comportent de la même manière, avec peu ou pas de réponse de la part des autorités compétentes (*obs. pers.*). Il est donc nécessaire d'éduquer les gens et de faire simultanément appliquer des réglementations claires pour mettre un frein aux comportements intrusifs illégaux envers la faune marine.

5.5. Faire appliquer des réglementations claires

Depuis 2002, la Polynésie française est un sanctuaire pour les mammifères marins et des réglementations ont été développées localement pour encadrer les activités de *whale watching*. Pourtant, le respect de ces réglementations est négligeable dans les rencontres entre dauphins et humains, avec peu ou pas de sanctions de la part des autorités.

Les tour-opérateurs semblent se conformer davantage à des conditions réglementaires faciles à quantifier (e.g., nombre maximum de personnes à l'eau) et aux règles de conduite écrites de manière claire et concise (Scarpaci *et al.*, 2004 ; Parsons, 2012).

En Polynésie française, les réglementations actuelles spécifient qu'il est strictement interdit de *déranger de manière intentionnelle le développement naturel des espèces sauvages protégées et des écosystèmes associés*, 'dérangement intentionnel' faisant référence à *toute action humaine qui pourrait modifier le comportement naturel d'un animal sauvage pour des fins de divertissement*.

Parallèlement, l'arrêté polynésien n°466CM spécifie que nous devons respecter une distance de sécurité de 30 mètres avec des dauphins sauvages, *excepté si les dauphins réduisent volontairement la distance entre eux et des humains* (Code de l'Environnement de la Polynésie française, 2017). Comme le disait Simon (2023), *ce langage est sans doute bien intentionné* mais il n'est pas adapté au contexte de Rangiroa et ouvre la porte à des interprétations multiples.

En clair, il conviendrait d'interdire toute tentative d'attirer et de toucher aux espèces protégées, que les animaux soient ou non tolérants, ou conditionnés, au contact humain.

Pour finir, il existe un besoin évident de sanctionner les comportements illégaux et les pratiques de communication fallacieuses. Dans le rapport d'un atelier sur l'observation des

mammifères marins en milieu naturel, le *National Marine Fisheries Service* de la NOAA a reconnu le rôle important de la mise en application des lois pour la protection des mammifères marins, particulièrement dans le cas des récidives (Spradlin *et al.*, 2001). En effet, bien qu'il ne soit pas simple d'engager des poursuites, les ressources financières et personnelles sont toujours limitées et des sanctions peuvent rapidement dissuader les comportements illégaux.

Nous avons synthétisé dans le **tableau 2** les indications de gestion suggérées dans le contexte spécifique des interactions dauphins / humains à Rangiroa.

Tableau 2. Indications de gestion adaptées au contexte de Rangiroa.

	Mesures et approches de gestion
Générales	Développer une gestion proactive tenant compte de l'humain, de la faune sauvage et de l'environnement Améliorer la communication entre les parties prenantes
Gestion des activités touristiques sur la zone de Tiputa	Délimiter des zones protégées interdites d'accès basées sur les habitats préférés par les dauphins Limiter le nombre de bateaux, de nageurs et de plongeurs sous-marins Quantifier des limites de changement acceptable (e.g., animaux blessés / tués, taux de reproduction)
Gestion des comportements humains sous-marins	Décourager tout effort déployé pour attirer les dauphins Décourager les tentatives d'interactions proches avec de jeunes dauphins Interdire les contacts physiques avec les dauphins Promouvoir un comportement humain passif
Éducation et implication	Développer des programmes d'éducation réguliers, des formations et des outils de communication basés sur un savoir scientifique réel et précis au sujet des dauphins, des impacts du tourisme et des réglementations Adapter les programmes éducatifs à différents publics (i.e., touristes, guides, tour-opérateurs, agences de voyage, autorités, scolaires, communautés locales) Proposer des solutions concrètes et positives pour observer les dauphins de manière éthique et durable Donner l'opportunité d'agir (e.g., sciences participatives, volontariat)
Réglementations	Appliquer des réglementations claires adaptées au contexte local Sanctionner les comportements illégaux et la communication fallacieuse
Suivi	Mener un suivi scientifique de routine des dauphins et de leurs interactions avec le tourisme Inspecter régulièrement et anonymement les briefings et comportements sous-marins des guides vis-à-vis des dauphins et de la faune marine en règle générale

6. Recommandations pour de futures recherches

Les rencontres rapprochées avec les grands dauphins de Rangiroa sont un phénomène relativement récent et leurs impacts sur les dauphins n'ont jamais été étudiés auparavant. Alors que l'intérêt pour le développement du potentiel touristique de l'atoll de Rangiroa grandit, cette thèse de doctorat constitue une première étape d'acquisition de connaissances sur les réponses des dauphins au tourisme de plongée sous-marine. Des études supplémentaires sont nécessaires pour surveiller les effets du tourisme sur les dauphins, et les effets du comportement des dauphins sur le tourisme, et nous partageons ci-dessous quelques recommandations destinées à orienter de futures études.

Premièrement, il est possible d'améliorer la collecte de données sous-marine sur les dauphins. En fonction des questions de recherche, il peut être préférable d'inviter les touristes à partager leurs vidéos, d'utiliser des stations d'enregistrement vidéo à distance (e.g., Titus *et al.*, 2015), de plonger au sein de palanquées de touristes, ou de former des groupes d'observateurs dédiés pouvant plonger à des horaires spécifiques. Par ailleurs, il est intéressant d'utiliser des caméras 360, qui filment dans toutes les directions, afin de filmer les dauphins et leurs comportements de manière exhaustive.

Ensuite, il est essentiel de se focaliser tant sur les réponses comportementales que physiologiques des dauphins aux activités touristiques afin d'obtenir une image plus complète des impacts du tourisme à différentes échelles. De récentes études ont mesuré les concentrations en glucocorticoïdes d'échantillons de fèces de mammifères marins pour évaluer leurs réponses physiologiques aux facteurs de stress d'origine anthropique (e.g., Mercera *et al.*, 2021 ; Pirotta *et al.*, 2023). De telles méthodes seraient applicables dans le cas des dauphins de Rangiroa.

Par ailleurs, il est crucial de comprendre comment les comportements des dauphins à court-terme impactent les individus et la communauté à long-terme. Une mesure exhaustive du succès reproductif et des taux de mortalité des grands dauphins nécessite des années voire des décennies d'investigations ; nous recommandons donc la poursuite d'un suivi longitudinal de ces animaux, soutenu par des ressources logistiques et financières appropriées, permettant de surveiller les trajectoires individuelles et la dynamique de la communauté. Cela permettra d'informer une gestion optimale des rencontres entre dauphins et humains, à Rangiroa et ailleurs dans le monde.

En outre, il est intéressant d'étudier de quelle manière les comportements des dauphins envers les plongeurs se propagent entre individus, et si certains de ces comportements sont culturels. Il existe en effet des preuves de l'existence de cultures chez les grands dauphins (Whitehead *et al.*, 2004 ; Krützen *et al.*, 2005) et certains comportements des dauphins de Rangiroa semblent être stables dans le temps tandis que d'autres sont temporaires (i.e., *modes*, Bossley *et al.*, 2018).

Enfin, nous avons déjà mentionné que notre cas d'étude est pertinent pour une recherche interdisciplinaire qui croiserait les savoirs de disciplines académiques telles que l'éthologie, l'écologie comportementale, la sociologie, la psychologie, les sciences vétérinaires, l'économie et l'éthique. Le cas des dauphins de Tiputa bénéficierait également d'une transdisciplinarité, qui implique des acteurs non-académiques, car les défis de durabilité nécessitent assurément de nouvelles méthodes de production de connaissances et de prise de décisions (Lang *et al.*, 2012).

Conclusions

Le dauphin est largement utilisé par l'industrie touristique pour offrir aux touristes des expériences agréables qui n'ont jamais prouvé leur durabilité. Bien que la popularité du tourisme animalier ciblant des dauphins en milieu naturel repose sur des animaux tolérants à la présence humaine, tous les individus n'expriment pas des réponses identiques au dérangement humain. Les variations inter-individuelles des réponses comportementales des grands dauphins de Rangiroa aux plongeurs sous-marins démontrent que l'impact des activités touristiques doit être étudié et interprété avec soin afin de développer des stratégies de gestion efficaces et un véritable écotourisme, qui considèrent à la fois la sécurité, le bien-être, l'éthique et la conservation des dauphins, des humains, et de leur environnement.

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RÉSUMÉ

Depuis une trentaine d'années, le tourisme animalier visant des espèces emblématiques telles que les dauphins est devenu une industrie extrêmement populaire et lucrative. Malgré cela, la gestion des activités touristiques et de leurs impacts sur les cétacés en milieu naturel est loin d'être un succès et représente un défi majeur et complexe, particulièrement dans le cas des interactions proches entre humains et dauphins. Les réponses comportementales des dauphins au tourisme peuvent en effet être difficiles à identifier et certains dauphins sont suffisamment tolérants à la présence humaine pour brouiller notre compréhension de l'influence du tourisme sur leur bien-être et leur aptitude de survie. Il est donc essentiel de se focaliser sur les réponses individuelles de ces animaux au tourisme afin d'éclairer la gestion d'activités en plein essor.

Nous nous intéressons ici au cas de grands dauphins (*Tursiops truncatus*) vivant en milieu naturel à Rangiroa, un atoll de Polynésie française. Ces animaux, non-nourris, sont exposés toute l'année au tourisme de plongée sous-marine et nous souhaitions comprendre comment ils réagissent à la présence répétée d'activité touristiques intrusives. Pour cela, nous avons étudié les comportements sur trois ans de 20 dauphins en présence de plongeurs sous-marins. Nous avons en outre examiné comment ces comportements peuvent impacter dauphins et humains. Nos résultats montrent que les dauphins sont habitués à la présence des plongeurs et que leurs comportements sont influencés par leurs plasticités et tempéraments individuels. Leur tolérance vis-à-vis des plongeurs dépend du contexte social des individus, de leur âge et de traits comportementaux stables liés à l'audace. Elle dépend également du comportement des plongeurs sous-marins. Les dauphins immatures réagissent davantage à la présence humaine que les individus matures, de manière significative et globalement positive. Nous avons également identifié différents degrés d'audace chez les dauphins audacieux vis-à-vis des plongeurs sous-marins.
Ces résultats suggèrent que les jeunes dauphins sont plus vulnérables que les adultes dans un contexte d'activités humaines intrusives. Un examen approfondi de la littérature traitant des risques liés aux interactions proches entre humains et dauphins en milieu naturel indique en effet qu'une tolérance accrue et l'habituation des animaux à la présence humaine augmente le potentiel d'issue délétère, à la fois pour les dauphins et pour les humains.

Une perception fortement biaisée du dauphin dans les cultures occidentales et un échec global des mesures de gestion du tourisme d'observation des cétacés expliquent en grande partie la multiplication de comportements inappropriés vis-à-vis de ces animaux. L'aspect multidimensionnel des réponses des dauphins aux plongeurs et les risques associés aux interactions proches soulignent le besoin d'appliquer des stratégies de gestion adaptées et efficaces qui permettront de garantir le bien-être des animaux et la sécurité des observateurs à court- et à long-terme.

MOTS CLÉS

Tourisme animalier, interactions humains-dauphins, comportement des dauphins, plasticité comportementale, tempérament animal, gestion du *whale watching*

ABSTRACT

Over the past few decades, wildlife tourism focusing on charismatic species such as dolphins has become a highly popular and lucrative industry. Yet, the management of tourism impacts on wild cetaceans is far from being successful and presents a complex and critical challenge, especially in the case of close dolphin-human encounters. Indeed, dolphins do not always display obvious responses to repeated up-close interactions with humans, and some individuals are sufficiently tolerant to chronic human presence to obscure our understanding of tourism effects on these marine mammals. It is thus fundamental to study fine scale responses of individual dolphins to tourism to properly inform management strategies.

We looked into the case of 20 non-provisioned free-ranging bottlenose dolphins (*Tursiops truncatus*) exposed to scuba diving tourism at Rangiroa Atoll, French Polynesia, to better understand how these animals individually cope with repeated intrusive tourist activities. We studied the dolphins' underwater behaviors in the presence of scuba divers over three years and examined how these behaviors may impact both the dolphins and humans. Our results indicate that the dolphins are habituated to the presence of divers on the tourist area and that their responses to intrusive diver behavior are notably shaped by individual plasticities and temperaments. The dolphins' responses to divers are modulated by their age, social context, and consistent behavioral traits associated with boldness. They are also influenced by the divers' behaviors toward the dolphins. Immature dolphins are significantly more responsive to human presence than mature ones. Also, we were able to pinpoint different degrees of boldness across bold individuals.
In the context of these findings, we argue that young dolphins may be more vulnerable to adverse consequences facilitated by human-induced behavioral shifts than adults. Definitely, a review of the literature pertaining to close interactions between humans and free-ranging dolphins worldwide emphasizes that dolphin enhanced tolerance and habituation to humans and human activities increase these animals' exposure to various deleterious outcomes, and humans' exposure to harmful dolphin behavior.

A strongly biased human perception of dolphins coupled with failure of management measures largely explain the expansion of inappropriate actions toward dolphins. The multi-dimensional aspect of dolphin responses to scuba divers and risks associated stress the need to implement and enforce locally adapted management strategies to supervise tourist activities that can ensure animal welfare and human safety on the short- to long-terms.

KEYWORDS

Wildlife tourism, dolphin encounter, dolphin behavior, behavioral plasticity, animal temperament, whale watching management