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Analysis of shark aggregations and ecology in the Maldives. Assessing a protocol for the survey of the species by the use of non-invasive methods.

Parmegiani Andrea

Registration number 848162

Tutor: Prof. Galli Paolo

Supervisor: Prof. Montano Simone, Gherli Alberto

Coordinator: Prof. Malusà Marco Giovanni

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ABSTRACT

Sharks are essential for maintaining coral reef ecosystem health and balance, yet their populations face threats from overfishing and environmental changes in most of the Indian Ocean territories. The Republic of Maldives, a shark sanctuary declared in 2010, serves as a hotspot for conservation and shark-tourism in the central Indian Ocean. Despite protections, knowledge about shark population dynamics, aggregation ecology, and species interactions in the country remains limited.

This research combines non-invasive underwater visual surveys, laser photogrammetry, behavioral observations collected by researchers and citizen scientist. It examines the structure, composition, and ecological role of grey reef sharks (*C. amblyrhynchos*) in two separate channels, Villingili Kandu and Miyaru Kandu. Results show consistent, female-biased groups demonstrating the importance of channels as key habitats used by individuals as mating and nursery ground as well as feeding grounds and cleaning spots. We derived an equation by a linear regression between pre-caudal and total length ($R^2 = 0.97$) resulting in a reliable index enhancing non-invasive size estimates.

The study also reports previously undocumented interactions between grey reef sharks and whale sharks, suggesting smaller species may use larger ones to assist with parasite removal and predator deterrence.

Additionally, the study presents the first confirmed sightings of bull sharks in the Maldives, 23 cases from 2013 to 2023 expand the known range of this species into central and southern atolls, often near inhabited centers and dive sites where shark feeding is practiced.

A detailed review of color disorders, using images collected from researchers, published and unpublished studies focusing on piebaldism, is included. Twenty- five confirmed cases across 17 shark species and 11 families are analyzed to clarify terminology, anatomical distribution, and potential evolutionary relevance of these color anomalies. The work demonstrates the value

of ecotourism images and citizen science in identifying rare phenotypic variations in large marine animals.

Overall, this thesis demonstrates the effectiveness of low-cost and non-invasive methods, especially laser photogrammetry and long-term citizen-science observations, for studying shark ecology in remote, challenging areas. The results establish a reference for collecting data on aggregation hotspots in the Maldives and provide a framework for evidence-based conservation efforts throughout the Central Indian Ocean.

CHAPTER 1

General introduction: The Maldives Shark Sanctuary in the Central Indian Ocean: Management Context, Aggregation Ecology, and Methodological Advances in Population Assessment

1.1. THE MALDIVIAN ARCHIPELAGO ROLE IN THE CENTRAL INDIAN OCEAN AS ELASMOBRANCH BIODIVERSITY HOTSPOT AND ITS CONSERVATION STATUS.

The Maldivian Archipelago consists of 16 atolls, five oceanic faros (ring-shaped reefs exposed to the open ocean), and four oceanic platform reefs, encompassing 2041 reef structures and a total of 1192 coral reef islands (Hilmi et al., 2023). Its extensive coral reef system covers approximately 4500 km^2 and accounts for around 5% of the global reef area (Naseer and Hatcher, 2004; Spalding et al., 2001). These reefs provide vital ecosystem services, including food resources and tourism, and are crucial in maintaining the island geomorphology by serving as natural wave energy barriers. The significance of the reefs to the archipelago is underscored by the fact that over 80% of Maldivian land is situated less than one meter above mean sea level, rendering coastal defences essential (Hilmi et al., 2023).

Recent mass coral bleaching events, triggered in 1998, 2016, and more recently in 2024, have significantly contributed to reef degradation, with some areas experiencing less than 2% coral cover (McClanahan, 2000; Morri et al., 2015; Pisapia et al., 2016; Perry and Morgan, 2017). Additionally, land reclamation efforts aimed at expanding habitability and promoting tourism pose a long-term threat to reef coverage and recovery.

Despite these challenges, the country is recognized for its strong resilience and ecological diversity within the IUCN Global Ecosystem Typology, hosting 33 distinct biogeographic ecotypes, ranging from coral reefs to seagrass meadows and deep-sea environments, thereby creating one of the most significant regional biodiversity hotspots in the Indian Ocean (Toor et al., 2022).

In response to the threats posed by anthropogenic and environmental hazards, the Maldives has established an ambitious goal to protect 30% of its marine, coastal, and terrestrial ecosystems by 2030, as outlined in the National Framework for Protected and Conserved Areas (Ministry of Climate Change, Environment and Energy, 2024). Currently, the Maldives manages 91 Protected and Conserved Areas (PCAs), covering approximately 62894.55 hectares (628.9 km²). Of these, Marine Protected Areas (MPAs) encompass around 472 km², constituting approximately 0.1% of the country' s territorial oceanic space (Ministry of Climate Change, Environment and Energy, 2024). The significance of MPAs has been recognized as a vital instrument for conserving marine biodiversity, enhancing ecosystem resilience, supporting climate change mitigation, and providing economic benefits (MacNeil et al., 2020). MPAs with full or high protection status, in accordance with local legislation, have been demonstrated to substantially increase marine biodiversity and fish biomass, thereby strengthening habitat resilience and facilitating more rapid recovery following severe degradation (Mellin et al., 2016; Jacquemont et al., 2022). Furthermore, these environmental benefits translate into economic advantages for local populations through improved fisheries, ecotourism, and employment opportunities (Albers and Ashworth, 2022). The Maldivian economy is primarily driven by two key sectors: the fishing industry, which generated revenue of $156.2 million in 2023 (FAO, 2025), and the tourism sector, which contributed approximately $5.6 billion, representing 21% of the nation's Gross Domestic Product (World Bank, 2025). Notably, the fishing industry, predominantly focused on tuna fisheries, has evolved from small-scale operations to an internationally recognized exporter. It continues to employ traditional pole-and-line techniques to reduce bycatch and mitigate environmental impact, in contrast to other fishing methods such as longlining or bottom trawling (Sinan and Whitmarsh, 2010; Miller et al., 2017). Meanwhile, ecotourism, particularly diving activities attracted by the rich marine biodiversity, is valued at approximately $43 million annually (Schuhbauer et al., 2025), serving as a significant component of the scuba diving industry.

Furthermore, Zimmerhackel et al. (2019) reported that shark diving activities generate direct earnings of $14.4 million per year, establishing shark and manta ray diving as some of the Maldives' major attractions.

An illustrative example within the Maldives is the South Ari Marine Protected Area (SAMPA), renowned for its year- round whale shark aggregation and generating revenues estimated between $7.6 and $9.4 million from 72.000 to 78.000 visitors (Cagua et al., 2014), as well as Hanifaru Bay UNESCO Biosphere Reserve, where, during the Southwest Monsoon, manta rays gather to feed on plankton that accumulates within the bay (Armstrong et al., 2021; Harris et al., 2021). Therefore, no-take reserves like these have proven to be highly effective and beneficial to the local tourism sector. However, recent surveys have revealed that many Maldivian MPAs, instead, lack effective management and enforcement, with the absence of formal plans leading to issues related to stakeholder representation, government commitment, and regulatory effectiveness (Shabbir et al., 2016; Rasheed and Abdulla, 2020). The extensive marine areas within the archipelago, coupled with the challenges faced by local authorities and rangers in conducting effective surveys of these MPAs, often results in ineffectiveness or, in the case of SAMPA, overexploitation of sites, thereby increasing risks of harm to marine life and ecosystem degradation (Zimmerhackel et al., 2016; Harvey- Carrol et al., 2021).

The significance of shark and ray tourism in the Maldives can be traced back to 2010 when the Maldivian government instituted a comprehensive ban on shark fishing activities (Ali, 2015). This prohibition followed decades of overexploitation of deep-sea sharks for their liver oil products and reef sharks to meet demand in Asian markets (Anderson et al., 1992). Consequently, conflicts between fisheries and tourism operators emerged as a persistent issue, with the latter regarding declining shark stocks and a consequent substantial reduction in revenue derived from diving tourism. In this case, the government opted to prioritize long-term ecosystem health alongside tourism revenue considerations (Ali and Sinan, 2015), contributing to the Maldives being designated as a Shark Sanctuary, yielding notable economic benefits (Ali and Sinan, 2015). Regarding shark abundance, certain surveys indicate that shark populations are recovering in some atolls, whereas in others, sightings during dive surveys remain significantly below average (Sattar et al., 2013). Despite these benefits, local fishermen report increased shark depredation, with losses exceeding 21% of daily earnings (Ali and Sinan, 2014; Robinson et al., 2022), leading to socioeconomic challenges that threaten to undermine conservation objectives.

In contrast to the nationwide export ban on shark products, legislation currently lacks an import ban, enabling numerous souvenir shops to sell shark products purportedly imported from other countries. Furthermore, evidence of illegal shark fishing activities persists, with sightings reported by tourists and attempts by locals to illegally trade fins and meat (Ali and Sinan, 2014). The perceived increase in shark populations has prompted the government to consider a gradual loosening of the ban on three occasions: in 2021, in 2024 with the reopening of longline fisheries, and finally in 2025 concerning the lifting of restrictions on gulper sharks (Scientific name). The ban on deep-sea and gulper sharks is supposed to be lifted from November 2025, despite evidence indicating that these populations had been depleted by approximately 97% prior to the ban (Anderson et al. 1993). The absence of robust scientific evidence, coupled with limited stakeholder participation and a scarce scientific literature on shark populations in the Maldives, renders the country vulnerable, as recent policy decisions lack scientific backing regarding the conservation status of targeted species and appropriate catch quotas. This deficiency has eroded trust among local fishermen regarding conservation policies aimed at protecting shark populations (Ali and Sinan, 2014; Robinson et al., 2016), resulting in the support from some representatives of political parties to the reopening of shark-based fisheries.

1.2. REVIEW OF SHARK RESEARCH IN THE MALDIVES: EARLY DEVELOPMENT, CURRENT FOCUS, AND FUTURE DEVELOPMENT.

The benefits derived from scientific research have been demonstrated to effectively inform policy development and influence public perception (Suazo-Galdames et al., 2025). In particular, data regarding shark populations, such as population status, genetic diversity, habitat requirements, and anthropogenic impacts, are vital for addressing issues including trade, overfishing, depredation, and habitat conservation (Simpfendorfer et al., 2009; Domingues et al., 2017; Birkmanis et al., 2020; Mitchell et al., 2022).

Scientific initiatives aimed at enhancing the understanding of shark populations in the Maldives started in the late 1980s, beginning with Anderson et al. (1990), who conducted exploratory fisheries surveys documenting the presence of reef-associated species such as silky sharks (*Carcharhinus falciformis*), oceanic white-tip sharks (*Carcharhinus longimanus*), blue sharks (*Prionace glauca*), silvertip sharks (*Carcharhinus albimarginatus*), tiger sharks (*Galeocerdo cuvier*), and shortfin mako sharks (*Isurus oxyrinchus*). Early exploratory fishing studies also documented the intense exploitation of deepwater gulper sharks (*Centrophorus spp.*), which were the focus of targeted fisheries in the early 1980s and subsequently collapsed due to overfishing (Anderson and Ahmed, 1993). Indeed, Anderson and Ahmed (1993) conducted a significant study analyzing shark fisheries in the Maldives. Their research revealed a fivefold increase in shark landings compared to the early 1970s and served as an initial warning regarding the unsustainability of existing fisheries, particularly for grey reef and silvertip sharks.

During the 2000s, research expanded into the assessment of benefits derived from shark and ray tourism. The first quantitative economic evaluation of sharks and ray watching was conducted by Anderson (1998, 2001), demonstrating that encounters with elasmobranchs contributed significantly to millions of dollars in annual revenue. This study further influenced the implementation of a shark ban in 2010.

Later, growing attention was directed towards the whale shark population, particularly in South Ari Atoll within the SAMPA, where Riley et al. (2010) documented regular aggregation habitats primarily for juvenile males and noted persistent foraging of whale sharks. Riley et al. (2009) valued free-swimming sharks, emphasizing the non-consumptive value of live sharks in comparison to fisheries. Further research advanced the ecological understanding of whale sharks in the Maldives, revealing site fidelity, anthropogenic injuries, and the risks associated with over tourism (Donati et al., 2016; Perry et al., 2018; Allen et al., 2021). The initial tagging study on whale sharks was conducted by Reynolds et al. (2022), and the impacts of climate change and sea surface temperature on species distribution were examined by Gibson (2017) and Reynolds et al. (2024). A recent study by Gobbato et al. (2023) provided also additional evidence that whale sharks serve as ecological substrates for other shark species, such as grey reef sharks in the Maldives, which utilize whale sharks' skin as a scraping surface for parasite removal.

Parallel socio-economic studies, assessing the significance of shark diving and tourism, further supported the necessity for sustainable management. The demand for tourism increased notably in the second half of 2010, accompanied by growing interest in the sector's economics and its impact on local fisheries (Ali, 2015; Cagua et al., 2014; Zimmerhackel et al., 2016, 2018; Miller et al., 2018; Robinson et al., 2022).

As evidenced by the literature, most current studies focus on whale sharks or the effects of shark bans. Few investigations address other species of sharks. The Maldives currently hosts

39 shark species, distributed across various regions (De Maddalena, 2023). Recent research in Fuvahmulah has concentrated on the ecology of the largest tiger shark (*Galeocerdo cuvier*) aggregation worldwide, along with its gestational patterns and behaviors (Sulikowski et al., 2024; Vossgaetter et al., 2024; Reinero et al., 2025). Additional studies by Russo and De Maddalena (2021) and Parmegiani et al. (2023) have assessed the presence of spinner sharks (*Carcharhinus brevipinna*) and bull sharks (*Carcharhinus leucas*) as ecologically significant species in the Maldives.

Lea et al. (2012) focused on the abundance of reef sharks, complemented by surveys from the SHARKWATCH program, Ushan and Sattar (2012), and Sattar et al. (2013). Skin depigmentation has been examined particularly in blacktip reef sharks (*Carcharhinus melanopterus*; Bruckner and Coward, 2018) and other species, as reviewed by Whitehead et al. (2025).

Despite these studies recognizing the importance of the Maldives as a shark sanctuary, further research on the population inhabiting the archipelago remains necessary. Specifically, genetic data is essential to establish connectivity or isolation of the population within its borders, alongside evidence of large-scale movements for large predatory species such as hammerheads (*Sphyrna spp.*). New techniques for large-scale species surveys, such as environmental DNA and Next Generation Sequencing, have demonstrated their utility in the field (Liu et al. 2022). However, the government currently lacks policies for handling genetic data in compliance with the Nagoya Protocol.

Recently, the Important Shark and Rays Areas (ISRA) initiative was established by a team from the IUCN Shark Specialist Group (Kyne et al. 2023), identifying 27 ISRA and areas of potential interest within the Maldives. When aligned with governmental policies, this initiative could serve as a significant incentive for the continued expansion of Marine Protected Areas (MPAs) within the country.

The ongoing challenges and research gaps underscore the necessity for sustained, multidisciplinary efforts to ensure the conservation of sharks and the interests of stakeholders. Additionally, nationwide projects are imperative to comply with international laws concerning the protection, trade, and conservation of these species.

1.3. SHARK AGGREGATIONS: DEFINITION, FUNCTION AND DRIVING FACTORS

Initial examples of shark grouping appeared in existing scientific literature through field observations of Scalloped Hammerhead sharks (*Sphyrna lewini*) by Kimley and Nelson (1984) and McKibben and Nelson (1986). Further studies demonstrated that various shark species effectively form aggregations, and social-structuring analyses drew public attention to better understand the drivers and factors influencing the formation of these groups. Studies focusing on the aggregation drivers of species such as sevengill sharks (Ebert, 1991), grey reef sharks at Johnston Atolls (Economakis and Lobel, 1998), whale sharks with seasonal aggregations in Ningaloo Reef, Belize, Honduras, and South Africa (Wilson et al., 2001; Heyman et al., 2001; Gifford et al., 2007), aggregations of blacktip reef sharks (Heupel and Simpfendorfer, 2005), and the notable aggregation of great white sharks in Guadalupe (Doemeier and Lucas, 2006) have been documented.

Understanding the factors that lead to shark aggregation remains a significant challenge for scientists, primarily due to the difficulties in surveying highly mobile species such as basking sharks (Lieber et al., 2020; Sims et al., 2022) or species that are logistically challenging, such as deep-sea sharks (Finucci, 2015). Consequently, the term "aggregation" generally refers to groups that may have formed due to the co-occurrence of one or more environmental or social factors. Vague descriptions of aggregating behavior, such as those pertaining to nursery areas, have resulted in the classification of large portions of the coastal zone as nursery grounds (Heupel et al. 2007). This has led policymakers to designate extensive coastal areas, difficult and costly to manage, until more specific definitions, as provided by Heupel et al. (2007), were adopted. More recently, an aggregation has been defined as: the co-occurrence of two or more individuals in space and time, driven deliberately by a common factor (McInturf et al. 2023). A driver can refer to a resource or an abiotic condition that determines the function, nature, scale, and predictability of the aggregation (McInturf et al. 2023). Several potential drivers have been identified by Carrier et al. (2022).

Foraging is the most common driver. It is defined as instances where animals consume or prey upon other individuals. Several distinct types of foraging can be identified.

Local enhancement constitutes a form of indirect social learning in which an observing individual is attracted to a specific location or point of interest due to the presence or activity of another individual already engaged in foraging there. An example includes nurse sharks (*G. cirratum*) following a pod of bottlenose dolphins (*T. truncatus*) to attempt predation on benthic prey previously disturbed by the passage of the mammal pod (White et al., 2022).

Public information involves sharks making foraging decisions based on the success or failure rates observed in other sharks or species. Certain sharks have been documented escorting Hawaiian monk seals (*Monachus schauinslandi*) to kleptoparasitize prey located by the seals (Parrish et al., 2008). Based on observations of white sharks near a seal rookery off northern California, these sharks have been sighted patrolling in proximity to other sharks (Klimley et al., 2001); the hypothesis was that these sharks maintain proximity to sense predation events or to scavenge carcasses. Another example of social foraging involves grey reef sharks, where individuals acoustically tagged in the French Polynesian channel have been recorded maintaining multi-year dyadic associations, returning to a central larger social group during the day, particularly in core resting areas, and dispersing at night to forage individually or in smaller groups. Individual-based models suggest that simulations of individuals sharing a central location and utilizing social information during foraging (i.e., local enhancement) outperform non-central place social foragers (Papastamatiou et al., 2018, 2020).

Social information can also be shared among individuals of different species. For example, it has been demonstrated that the foraging success of grey reef sharks increased in the proximity of whitetip reef sharks (*Triaenodon obesus*), which act as kleptoparasites stealing attempted prey from the latter (Labourgade et al., 2020). Unlike local enhancement and public information, protocooperation occurs when predators hunt in groups without any coordination to enhance their foraging success by injuring or weakening their prey. A clear example of this is the hunting strategy of sailfish (Herbert-Read et al., 2016). Although there is currently no confirmed evidence of protocooperation among sharks, ongoing analyses of species feeding on baitballs are being conducted.

Cooperation in foraging is observed among marine mammals (Pitman and Durban, 2012), yet it has not been definitively confirmed in sharks. Nevertheless, certain instances of cooperative effort have been documented in sevengill sharks (Ebert, 1991), which have been observed forming loose circles around seals until the formation tightens, subsequently performing attacks only when the circle is sufficiently close to the prey. Additionally, coordination among blacktip sharks has been observed, whereby they work collectively to chase fish onto the beach, thereby enhancing the chances of consumption by other individuals. However, it remains unclear whether these behaviors can be distinguished from proto-cooperation (Wetherbee et al., 1990).

In conclusion, foraging is a significant driver of shark aggregation, typically occurring in areas where there is evidence of specific food sources. Such aggregation may be driven by environmental variables, which are sometimes predictable, such as the spawning of grey reef groupers or the aggregation of whale sharks near Qatari offshore platforms to consume fish spawn (Robinson et al., 2013; Robbins et al., 2015; Mourier et al., 2016; Rhodes et al., 2019).

Aggregation driven by mating events is well documented in sharks. Mating in sharks is preceded by pre-copulatory behavior that consists of a group or a single male chasing a female, attempting to bite her and induce a state of catatonia (Wyffels et al., 2025), followed by copulation and post-copulatory mechanisms. Polyandrous behavior leads to multiple paternity in sharks (Daly-Engle et al., 2006). The mating process is stressful for females and may result in death; the presence of several bites on females during specific periods of the year may serve as indicators of mating seasons. Consequently, females possess thicker skin compared to males (Hagood et al., 2023).

Some shark species have been shown to form sexually differentiated groups to avoid harassment from males or to facilitate better conditions for gestation and growth (Sims et al., 2006; Whitehead et al., 2022). Female-segregated groups have been observed in silky sharks (Whitehead et al., 2022), dusky sharks, and sandbar sharks (Bigal et al., 2024), with males approaching female groups during mating periods. There is also hypothesized evidence of leks-aggregations of males in specific areas for designated periods, visited by females (Emlen and Oring, 1977). Two proposed examples of leks include seasonal sex-migrations of male white sharks to pelagic habitats, with females moving in and out of these defined leks (Jorgensen et al., 2012). Another example involves observations by Papastamatiou et al. (2015) of smalltooth sawfish (*Pristis pectinata*), which demonstrate high residency in mangrove habitats seasonally, with females briefly moving and residing within these areas.

Sexual segregation has been shown to provide benefits related to reproductive strategies, habitat use, and resource allocation (Mucientes et al., 2009). However, conservation policies must consider these dynamics, in fac, sex aggregation can lead to sex-biased vulnerability to fisheries, particularly if one sex is more exposed to targeted areas (Mucientes et al., 2009). Recognizing sex- segregation behaviors within shark populations is crucial for conserving different habitats across seasons effectively (Werry and Clua, 2013).

Another driver of aggregating behavior is the hydrodynamic advantages conferred by bathymetric features. It has been demonstrated that updraft regions, primarily occurring near oceanic drop-offs or sloping sections of reefs, play a crucial role in the aggregation of sharks. This phenomenon has been observed in grey reef sharks (Papastamatiou et al., 2021; Laurioux et al., 2024), which congregate in areas with current-induced updrafts that enable them to surf along the slopes, thereby conserving approximately 10-15% of their energy expenditure. Bathymetric features such as shallow waters near steep slopes adjacent to deep water are strongly associated with upwelling zones, increasing primary productivity and attracting prey. These areas are thus particularly advantageous for foraging and thermoregulation (Copping et al., 2018; Valsecchi et al., 2021).

Forming groups is a significant advantage in predator defense, deterrence, and evasive group maneuvers (Heithaus and Vaudo, 2012). By forming groups, individuals benefit from the "dilution effect," where the likelihood of an individual being targeted by a predator decreases as group size increases. Blacktip sharks form large seasonal aggregations during migrations and are targeted by large, solitary Great Hammerheads (Doan and Kajiura, 2020). To avoid this, they often form aggregations in shallow, nearshore waters, using these areas as refuges where larger predators are less likely to follow (Doan and Kajiura, 2020). Studies have shown that these aggregations are most prominent during the day, dispersing at night when predation risk is lower (George et al., 2019). Additionally, research has demonstrated the seasonality of these aggregations, coinciding with periods of increased predator presence offshore (Kajiura and Tellman, 2016; Ayres et al., 2021). Although sharks are generally considered apex predators, group defense is not exclusive to juvenile species; adults also employ this strategy. For instance, grey reef sharks predated by great hammerhead sharks in French Polynesia (Mourier et al., 2012) or by bull sharks (*Carcharhinus leucas*) in the Maldives (Parmegiani et al., 2023) often form groups, which may facilitate rapid responses to approaching predators, similar to fish bait groups.

Shark aggregation can also be influenced by external factors, notably human activities. Anthropogenic actions can either promote or hinder the formation of associations among elasmobranchs. The primary factors include fishing, tourism, coastal development, and climate change (McInturf et al., 2025).

Fishing activities can directly contribute to population decline through mortality, while also exerting indirect effects that influence the social structure within groups. The removal of specific individuals can fragment social connections, thereby disrupting the network (Shizuka and Johnson, 2019), such as the removal of adult, mature females from a shark aggregation. A study on blacktip reef sharks demonstrated that the network of these specimens was resilient to fishing pressures, with adaptive learning abilities observed from negative interactions with fish (Mourier et al., 2017b). The research further indicated that the removal of individuals can induce cascading effects on network structure, prompting internal reorganization of social connections among individuals, which may result in positive, negative, or neutral impacts on population functioning. Satellite tracking of multiple shark species has revealed that sharks tend to select and aggregate in predictable oceanic hotspots characterized by high productivity and thermal fronts (Queiroz et al., 2016). These areas are also frequently targeted by longline fishing fleets, leading to significant spatial overlap between shark aggregations and fishing activities. This overlap exposes populations to risks of overexploitation and decline (Queiroz et al., 2016, 2019).

Although many consider shark fishing as a primary factor influencing aggregation patterns and ecology, climate change is a significant driver in the shifts observed in habitat suitability, migration, and aggregation locations (Santos et al., 2024). A clear example is the phenomenon known as vertical habitat compression, caused by ocean warming and the expansion of low-oxygen zones, which compels sharks to migrate into shallower, more productive surface waters, thereby reshaping their vertical movement patterns (Vedor et al., 2021). As sea temperatures rise, certain shark species such as whale sharks and hammerhead sharks (Sequeira et al., 2014; Pereira Santos et al., 2024) are shifting their aggregation sites poleward or towards deeper waters; additionally, tiger sharks distributions are likely to shift, with females dispersing southward during warmer periods and juvenile males preferring warmer temperatures (Niella et al., 2021). A study by Birkmanis et al. (2020) predicts a shift in the locations of suitable shark habitats in Australia, with a decrease anticipated for requiem sharks and an increase for mackerel sharks by 2050–2099. These movements and habitat shifts are potentially and currently causing sharks to move outside protected areas, thereby exposing them to increased threats (Rosa et al., 2017; Pereira Santos et al., 2024).

Anthropic development in coastal areas has been demonstrated to lead to notable changes in shark aggregation patterns, composition, and health. Coastal power plants, tourism infrastructure, and urban development create warmer, nutrient-rich waters that attract mixed-species groups (Barash et al., 2018; Zemah-Shamir et al., 2022; Bigal et al., 2024).

Species aggregating near coastal areas have been characterized by Hammerschlag et al. (2022) as' urban sharks, ' with analyses of their spatial usage revealing consistent residency in these regions. Although these sites may appear as aggregation hotspots, it has been demonstrated that they function more as ecological traps, thereby altering shark behavior and ecology (Bigal et al., 2024). Furthermore, sharks in coastal developed areas are exposed to pathogens and pollutants, as evidenced by the detection of pharmaceutical and illicit drugs in these animals (Gelsleichter et al., 2013; Hauser-Davis et al., 2024). Heavy metals and persistent organic pollutants (POPs) have been identified in various species; these contaminants have been shown to cause DNA damage and physiological dysfunctions that could potentially impact the biological well-being of individual sharks (Mohammed and Mohammed, 2017; Wosnick et al., 2021; Rangel et al., 2022).

Another factor contributing to shark aggregation is associated with provisioning sites. These activities facilitate the formation of short-term multispecies elasmobranch aggregations during feeding events (Brunnschweiler et al., 2014). Provisioning may exert minimal influence on the movements and diel spatial use of certain wide-ranging shark species, such as tiger sharks (Hammerschlag et al., 2017). Recent research has examined the development of social networks among individuals that are presumed to be highly mobile predators and predominantly solitary (Reinero et al., 2025). The long-term effects of provisioning sites remain to be thoroughly evaluated, particularly concerning highly migratory species that may be impacted in the short term. Nonetheless, species exhibiting high residency patterns and limited dispersal, such as blacktip reef sharks, have been shown to experience alterations in their spatial distribution, especially regarding the sexes and limited dispersal of individuals (Mourier et al., 2020).

1.4. SURVEYING SHARK AGGREGATION: AN OVERVIEW OF NON-INVASIVE TECHNIQUES TO GATHER DATA FOR CONSERVATION STRATEGIES.

The rise of non-invasive research techniques has advanced the study of shark ecology by allowing for behavioral, morphological, and population assessments while reducing or supplementing more invasive methods that may rely on fishery data or techniques such as longline capture or surgical tagging (Hammerschlag et al., 2011). These invasive methods can, for some species, cause significant stress, injury, or death (Hammerschlag et al., 2011). Besides conforming to modern standards of ethics and animal welfare, non-invasive techniques, when combined with machine learning, 3D modelling, and automated recognition algorithms, are broadening the scope and detail of data collection (Tuia et al., 2022).

Current non-invasive methodologies are employed in numerous studies include:

Drones or Unmanned Aerial Vehicle (UAV)

In marine ecosystems, aerial surveys have been employed to examine the populations of cetaceans (Gilles et al., 2009; Laran et al., 2017), sirenians (Pollock et al., 2006), sea turtles (Cardona et al., 2005), and elasmobranchs such as sharks (Rowat et al., 2009). These surveys have demonstrated significant value in elucidating the spatial distribution and population abundance of elasmobranchs within both coastal and pelagic habitats.

With the recent development of Unmanned Aerial Vehicles (UAVs), also known as Remotely Piloted Aerial Systems (RPAs) or drones, there has been a considerable increase in the application of aerial surveys to shark research (Butcher et al., 2021). Drones have been used to investigate the distribution (Rieucau et al., 2018), abundance (Kelaher et al., 2020), and behavioral patterns (Raoult et al., 2018) of marine wildlife. Beyond their scientific applications, UAVs are also recognized as socially acceptable methods for mitigating shark- related hazards through hazard reduction, providing an alternative to more invasive culling methods (Butcher et al., 2019), thereby enhancing public perceptions of beach safety (Mitchell et al., 2022). UAV technology offers extensive opportunities for conducting underwater animal surveys. For example, drones have documented the use of shallow waters by blacktip sharks as a predation evasion strategy from hammerhead sharks (Doan and Kajura, 2020). Studies involving drones on basking sharks (*Cethorinus maximus*) have provided insights into their subsurface behaviors and feeding habits (Hawkes et al., 2020). Moreover, drones are increasingly employed to obtain precise, non-invasive measurements of sharks, demonstrating that, when considering factors such as drone altitude and shark size, measurements can achieve an accuracy within 5% of the actual length. This presents a valuable alternative to traditional diver-based measurements using various photogrammetry systems (Piacenza et al., 2022; Rex et al., 2024).

Baited remote underwater video stations (BRUVS)

Baited remote underwater video stations (BRUVS) involve the deployment of cameras underwater, consisting of a frame supporting a video camera and a bait canister designed to attract fish fauna within the field of view (fov). The use of BRUVS is particularly suitable for sampling predatory species or rare species and has been employed across a wide range of habitats and depths (Cappo et al., 2001, 2004; Harvey et al., 2007). These techniques have gained international acceptance for sampling shark assemblages across various habitats and depths (Rhodes et al., 2020). Furthermore, BRUVS studies have been recognized as an alternative to longline surveys, providing comparable estimates of shark abundance (Brooks et al., 2011). Additionally, due to the reduced cost of action cameras, BRUVS have been demonstrated to be an effective and cost-efficient video-based sampling technique (Struthers et al., 2015).

There are two types of Baited Remote Underwater Video systems (BRUVs) commonly employed in shark research: Benthic (Cundy et al., 2017) and Pelagic (Bouchet and Meeuwig, 2015; Espinoza et al., 2020; Cambra et al., 2021), as well as Deepwater variants below 200 meters (Koslow, 2000; Kine and Simpfendorfer, 2007).

Additionally, some studies have implemented stereo-video systems to extrapolate three-dimensional measurements of individual animals (Watson et al., 2010; Santana-Garcon et al., 2014; Schramm et al., 2020).

It is widely acknowledged that BRUVS are effective tools for estimating species abundance, with the most commonly used metric in statistical analyses being MaxN, which represents the maximum number of individuals of each species observed at any point during the video recording. Several studies have indicated that this index tends to underestimate the true abundance of sharks; consequently, it has been proposed to equip BRUVS with a full spherical 360-degree view (Kilfoil et al., 2017).

Environmental DNA (eDNA)

Environmental DNA, or eDNA, refers to the collective DNA extracted from environmental samples such as water, soil, sediment, snow, or air (Taberlet et al., 2012a). It has been demonstrated as a reliable detection method, often matching or surpassing traditional survey techniques (Thomsen et al., 2012; Valentini et al., 2016), particularly in identifying rare and elusive species that are difficult to observe with operators either within or outside the water. An illustrative example is a study conducted by Boussaire et al. (2018), which compared shark species detection rates through 2758 underwater visual censuses and 358 Baited Remote Underwater Video System (BRUVS) deployments, alongside 22 eDNA samples. The analysis revealed that eDNA detected 13 shark species, representing a 44% increase compared to the 9 species identified using other methods, thereby challenging the necessity for larger eDNA campaigns to enhance shark monitoring efficacy.

The application of environmental DNA (eDNA) can be categorized into two primary approaches. The first involves barcoding, which aims to confirm the presence of a specific species through the use of PCR or quantitative PCR (qPCR) (Simpfendorfer et al., 2016; Davison et al., 2016; Weltz et al., 2017). In contrast, metabarcoding employs a multi-species methodology, simultaneously identifying multiple taxa from an environmental sample without prior knowledge of the targeted species (Taberlet et al., 2012b). Metabarcoding analysis uses high-throughput sequencing technologies to provide a comprehensive overview of an ecosystem, revealing hundreds of taxa from a single sample (Yamamoto et al., 2017; Miya et al., 2020).

However, several challenges are associated with eDNA studies. The most prevalent issues include contamination during sample collection, storage, and laboratory procedures, as well as the subsequent occurrence of false positives and false negatives (Darling and Mahon, 2011). Sharks are characterized by low shedding rates and the release of biological material, which negatively influences their detectability (Postaire et al., 2020). Another factor affecting the detection of shark eDNA in water is the small fraction of eDNA that can be obtained from water samples, in comparison to the eDNA of other organisms present within the same sample. The variability of environmental DNA is subject to degradation by various biotic and abiotic factors (Thomsen et al., 2012; Weltz et al., 2017). Additionally, capture rates may fluctuate depending on currents or atmospheric events (Weltz et al., 2017), thereby posing current challenges in standardizing a cost-effective method.

Despite these challenges, eDNA has proven to be a valuable tool for collecting crucial data on endangered shark and ray species, identifying critical habitats, and serving as a non-invasive method for assessing distribution and abundance.

Divers operated Surveys: UVC, DOV, photogrammetry, Photo-ID.

With the increase in SCUBA diving and snorkeling, scientific research using these techniques has grown significantly. Many survey methods can be employed by SCUBA divers, and they have proven effective in surveying shark aggregations. SCUBA diving also allows citizen scientists or local dive guides to participate in the project after a brief training (Hermoso et al., 2021), thereby increasing the amount of data collected. The simplest and one of the most common techniques to gather data on species composition and abundance is the underwater visual census (UVC). Counts from UVC have been used to describe and monitor spatial and temporal trends in populations and communities (DeMartini et al., 2008; Sandin et al., 2008). Although it is used for monitoring and is a valuable tool for direct observation, the accuracy of visual estimates depends heavily on the training and experience of the diver. Moreover, visual census has been shown to be prone to overestimation, especially during non-instantaneous counts where the diver records all the animals sighted within one transect (Ward-Paige et al., 2010).

The diver-Operated Video (DOV) enhances Underwater Visual Census (UVC) methods by providing a permanent visual record that can be replayed and analyzed subsequent to the dive. Divers are able to capture high-resolution footage, facilitating detailed assessment of species identification, behavior, and real-time counts within an aggregation (Barker et al., 2011). To mitigate the risk of overestimating the number of individuals within transects, a study conducted by Smith et al. (2020) suggested for the use of stereo-DOV systems equipped with GPS and high swimming speeds when surveying highly mobile sharks, thereby yielding more accurate estimates of species densities. Stereophotogrammetry in DOV employs paired cameras to capture three-dimensional measurements of freely swimming individuals. This method has been employed by Klimley and Brown (1983) on *Sphyrna lewini* aggregations and has been used in various studies across different species (Salinas de León et al., 2016; Sequeira et al., 2016; Meekan et al., 2020).

Another tool for retrieving biometric measures underwater is laser photogrammetry, which employs parallel and calibrated laser devices projected onto the animal's body, which should preferably be parallel to the camera (Rohner et al., 2011). This technique has proven useful in numerous studies across various species (Bansemer and Bennet, 2009; Rezzolla et al., 2014; Guttridge et al., 2017). Limitations of stereophotogrammetry methods include avoiding parallax errors caused by the movement of individuals and ensuring proper calibration and parallel alignment of lasers to prevent inaccuracies in size estimation (Jeffreys et al., 2013; Leurs et al., 2015).

Laser photogrammetry and stereophotogrammetry, when conducted during underwater surveys, represent accurate, accessible, and versatile methodologies that significantly contribute to the management and conservation of elasmobranchs (Ferreira et al., 2024).

Another instrument to enhance data collection quality during underwater surveys is the photo identification of sharks from videos or images obtained underwater. Photo identification is defined as the use of natural markings, recorded via photographs or videos, that have been used since the work of Myrberg and Gruber (1974). This method relies on pigmentation spots, body markings, scars, and fin morphology (Marshall and Pierce, 2012). The expanding photo-ID databases, such as Sharkbook (https://www.sharkbook.ai/), have enabled a series of citizen scientists to participate in these initiatives and contribute to the enrichment of these platforms, thereby enhancing the understanding of various species, particularly large migratory species such as bull sharks (Brunnschweiler and Baesch, 2011) and whale sharks (Arzoumanian et al., 2005; Brooks et al., 2010; Andrzejaczek et al., 2016). Photo-identification has proven to complement studies involving telemetry (Bonfil, 2005; Guttridge et al., 2017). Furthermore, data collected through these techniques can be valuable for population studies, tracking site fidelity, movement patterns, and residency of species (Towner et al., 2013; Lewis et al., 2020; Kohler et al., 2023; Jung et al., 2024). The quality of images obtained through the optimal resolution of modern cameras permits the extraction of substantial information, including health-related data such as parasite loads (Mucientes et al., 2008), infections, and skin diseases (Whitehead et al., 2025).

1.5. SHARK FISHERIES STATUS IN THE INDIAN OCEAN AND POTENTIAL CONSEQUENCES ON THE MALDIVES

Shark fisheries in the Indian Ocean are extensive and involve multiple countries, with overfishing posing a significant threat to the population numbers and recovery efforts (Cheung et al., 2016; Osuka et al. 2024). While certain countries such as the Maldives and the British Indian Ocean Territory, including the Chagos Archipelago, have implemented legal protections against shark fishing, shark fisheries in the Indian Ocean remain persistent (Harris, 2014). The depletion of shark populations is most acute in the Indian Ocean and the Western Pacific, as evidenced by recent studies (MacNeil et al., 2020).

Fisheries in the Southwest Indian Ocean (SWIO) are predominantly characterized by small-scale, artisanal, and semi-industrial activities, providing vital economic resources to coastal communities, which are highly dependent on fisheries as their primary source of food (Cheung et al., 2016). Despite their small scale, these fisheries exhibit high exploitation rates, with Kenya alone registering landings of 79% of threatened shark and ray species, of which 97% are neonate and immature individuals among sharks and 46% among rays (Osuka et al., 2024; Temple et al., 2024). In Mozambique, it is estimated that small-scale fisheries catch is three times higher than that of the industrial sector (Blythe et al., 2013). Furthermore, this region exhibits the highest levels of data deficiency concerning sharks and rays (Dulvy et al., 2021), resulting in a lack of species-specific trend data that could mask declines in particular species (Sherman et al., 2022).

The Eastern Indian Ocean and Arabian Sea, represents a major hub for shark fisheries. India and Indonesia are considered the major contributors, fisheries are charachterized by target shark fishing industries and high-bycatch rates in tuna fisheries (Fahmi and Dharmadi, 2015). IUCN Red List assessment of chondrichthyans in the Arabian Sea and adjacent waters highlights that with 78 of 153 species threatened with an elevated risk of extinction (50.9%), this region has one of the highest proportions of threatened chondrichthyan species in the world (Jabado et al. 2018). The region is currently experiencing declining catches as a result of reduced stock in response to increased fishing effort as demonstrated by the increased fishing vessel in the region (Valinassab et al., 2006; CMFRI 2010; Mohamed and Veena, 2016).

Global trade in shark products comprises high-value dried fins, substantial quantities of meat, and a smaller segment consisting of liver oil, skin, and cartilage (Clarke et al.2013). The trade remains predominantly concentrated in East and Southeast Asia, with Hong Kong serving as a principal processing hub, closely linked with China (Guangzhou) and transit nodes such as Singapore (Clarke et al., 2006; Cardenosa et al., 2020; Drescher et al., 2022). Analysis of traded products has identified these three markets as the primary recipients of pelagic shark products, particularly species such as the blue shark (*Prionace glauca*), silky shark (*Carcharhinus falciformis*), hammerhead sharks (*Sphyrna spp*.), and mako sharks (*Isurus spp*.) (Cardenosa et al., 2020; Drescher et al., 2022). Surveys have further documented the fin trade involving small and juvenile sharks. Despite the fact that most traded species are classified as threatened by the IUCN or listed under CITES, there are cases involving unregulated species (Cardenosa et al., 2024). Hong Kong remains the principal importer of fins, with Singapore and Taiwan functioning as important retail and transit ports. Conversely, shark meat is primarily traded through South American and European countries, where Brazil stands as the leading importer of shark meat, often labeled as "cação" (Almeròn-Souza et al., 2018; Zuccolo et al., 2023), followed by Italy and Spain as key importers in Europe, where species identification is frequently indicated with generic labels or substituted to obscure provenance and conservation status (Marchetti et al., 2020; Hasan et al., 2023).

Smaller streams come from liver oil-derived squalene, sourced from deep sea sharks and used in pharmaceutical and cosmetics applications (Hall et al., 2016;). Studies have already found alternatives to reduce the exploitation of these low reproductive and depleted species stocks, especially gulper sharks (*Centrophorus spp.*); however the supply chain persists especially in countries where traceability is weak (Kadfak et al., 2024). Some countries as the Maldives are returning to this market after 15 years of shark fishing ban (Ministry of Fisheries, 2025).

Overfishing constitutes the primary cause of global declines in shark populations, with significant implications for species survival and genetic diversity. Genetic depletion diminishes sharks' capacity to adapt to environmental changes, thereby increasing their risk of extinction and compromising ecosystem stability (Williamson et al., 2024).

This activity is particularly detrimental to sharks due to their slow growth rates, late maturity, and low reproductive output, factors that impede population recovery. Research has indicated that large-bodied, reef-associated sharks have experienced population declines ranging from 60 to 73%, with some species now locally extinct in heavily fished regions (Mac Neil et al., 2020; Simpfendorfer et al., 2023). Currently, over one-third of all shark and ray species face the threat of extinction, with overfishing identified as the primary cause in 99.6% of these threatened species (Dulvy et al., 2021; Sherman et al., 2023; Dulvy et al., 2024).

This intense and unsustainable fishing pressure, especially on reef-associated and pelagic migratory species, results in genetic depletion within populations (Dulvy et al., 2021).

A reduction in effective population size (Wright, 1931; Frankham et al., 2010) leads to an amplified loss of allelic diversity and an increased risk of inbreeding. Grey reef sharks are considered semi-migratory species with high site fidelity to specific reef systems and limited gene flow between reef systems separated by deep-water barriers (Momigliano et al., 2017; Espinoza et al., 2022). These characteristics render the species particularly susceptible to local depletion, especially when large mature females are removed, causing bottleneck effects that reduce reproductive variance and accelerate genetic drift (Momigliano et al., 2017).

Migratory sharks such as blue sharks, silky sharks, oceanic whitetip sharks, and scalloped hammerhead sharks exhibit significant genetic differentiation across ocean basins and regions, which aids in maintaining genetic diversity and mitigating the risk of severe depletion despite fishing pressures (Verissimo et al., 2017; Harned et al., 2022; Li et al., 2022). Nonetheless, some of these migratory species often display high genetic differentiation between ocean basins, frequently attributed to female philopatry (Bernard et al., 2016, 2021; Klein et al., 2023).

Satellite tagging studies indicate that the fishing mortality rates for migratory sharks, such as the shortfin mako, are up to ten times higher than previously suggested by traditional data (Queiroz et al., 2016; Lopez et al., 2020). Migratory shark species are continually exposed to threats due to their extensive movements across multiple national Exclusive Economic Zones (EEZs) and on the high seas, where fisheries regulation remains limited; moreover, up to 76% of their core habitats overlap with active fishing zones (Dulvy et al., 2017; Queiroz et al., 2019). This is evident in countries such as the Maldives, where elasmobranch fishing is prohibited within its 200-nautical-mile EEZ. Instances of illegal and unreported shark fishing have been documented within Maldivian borders (Parmegiani et al. unpublished). Nevertheless, the greatest threats reside in the vicinity of countries such as India and Sri Lanka, where shark and ray consumption is permitted and elasmobranch fisheries are well established, potentially exposing migratory species within the Maldives to significant risks.

An additional pressing issue is the absence of genetic data and information concerning the movements of species residing within Maldivian waters. The Maldives, situated at the center of the Indian Ocean and recognized as one of the most prominent shark sanctuaries globally, occupies a strategic position for coordinating conservation efforts with neighboring nations. However, the notable deficiency of genetic data and understanding of migratory routes for populations within the archipelago leaves these populations vulnerable to ecological overexploitation, genetic erosion, and inadequate institutional conservation policies.

1.6. AIMS OF THE STUDY

The aim of this project research is to provide insights on the ecological dynamics, behavioral patterns, and methodological approaches associated with shark aggregations in the Maldivian archipelago, an understudied area of interest within the central Indian Ocean. The study seeks with non-invasive methods to provide information on the ecology and behavior of different species in different parts of the Maldives.

The study focused on five different topics:

Firstly, the study aims to describe the spatial and temporal structure of grey reef shark (*Carcharhinus amblyrhynchos*) aggregations across reef channels. Special emphasis is placed on population composition, size- frequency distributions, and sex ratios, utilising a combination of standardized underwater visual surveys, laser photogrammetry, and long- term citizen science video recordings spanning from 2013 to 2024. This integrated approach enables a comprehensive assessment of the persistence of aggregations, their ecological functions, and the identification of potential reproductive and nursery habitats essential to the species' life cycle within the archipelago.

Secondly, the research investigates rare behaviors exhibited by *C. amblyrhynchos* by documenting and interpreting interspecific interactions with whale sharks (*Rhincodon typus*). These rare observations offer novel insights into the potential use of larger species as mobile cleaning stations or as a means of predator avoidance, thereby broadening the current understanding of interspecific ecological interactions among elasmobranchs in reef and pelagic environments.

Thirdly, this thesis presents novel data and the first verified records of bull sharks (*Carcharhinus leucas*) in the Maldives, establishing a scientific baseline for a species previously undocumented in the region. By analysing 23 confirmed sightings across central and southern atolls and examining their relationship with anthropogenic influences and environmental variables, this research provides critical preliminary data for future monitoring, population assessment, and management of this apex predator within Maldivian waters.

Fourthly, the study investigates the occurrence, taxonomy, and ecological implications of chromatic disorders, focusing on piebaldism in elasmobranchs. By synthesizing both published and unpublished observations, encompassing 25 cases across 17 species and 11 families, this work contributes to clarifying the terminology, distribution, and potential evolutionary significance of pigmentation anomalies in sharks. It further highlights the growing importance of ecotourism and citizen science as valuable tools for documenting rare phenotypic traits in marine megafauna.population assessment, and management of this apex predator in Maldivian waters.

Collectively, this project aims to: strengthen the empirical foundation for evidence-based conservation and management of Maldivian shark populations; contribute novel ecological, behavioral, and methodological insights into key reef-associated and pelagic species and establish a reproducible, non-invasive research framework applicable to elasmobranch monitoring across the Indo-Pacific region.

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CHAPTER 2

Insights into the structure of grey reef shark aggregation, *Carcharhinus amblyrhynchos* (Bleeker, 1856), in two distinct channels of the Maldivian Archipelago, Indian Ocean.

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2.1. ABSTRACT

The grey reef shark *Carcharhinus amblyrhynchos* is one of the most frequently encountered reef-associated shark species in the Maldives, yet very little is known about its local size structure or population dynamics. This study provides new insights into two aggregations of *C. amblyrhynchos* in the Maldives, based on biometric measurements obtained with laser photogrammetry, standardized visual surveys, opportunistic behavioural observations, and video analyses of citizen science data spanning 2013–2024. In particular, between 2022 and 2023, biometric data and visual observations from two distinct sites, Villingili Kandu in North Huvadhu Atoll and Miyaru Kandu in Vaavu Atoll, were collected in order to preliminarily characterise the composition of these aggregations and to provide information on the ecology of grey reef sharks. The results revealed a pronounced female-biased sex composition and occurrences of mating in both channels, as well as a potential nursery area in Miyaru Kandu. Combining these data with predation and cleaning events recorded, we suggest that these channels might constitute important key habitats for grey reef shark aggregations. Laser photogrammetry data from 353 individuals were analysed, and a robust relationship between pre-caudal length and total length ($R^2 = 0.97$) was established, enabling to derive a correction index through linear regression to predict and enhance accuracy of size estimates. Finally, long-term video records demonstrate that Villingili Kandu currently hosts the largest documented aggregation of *C. amblyrhynchos* in the Maldives. These initial findings provide a baseline for further studies on the drivers influencing the aggregations of this species and its life history within the archipelago.

2.2. INTRODUCTION

Shark related tourism has become a significant source of income for marine ecotourism in the Maldives, with revenues starting at about USD 2.3 million in 1991 (Anderson and Ahmed, 1993) and recently surpassing USD 51 million (Zimmerhackel et al., 2019). This economic growth demonstrates the significance of shark tourism compared to shark fishing activities which, before the total shark ban of 2010, generated an estimated revenue of around USD 0.5 million (Anderson and Ahmed, 1993; Zimmerhackel et al. 2019). This comparison clearly demonstrates the shift in national priorities, from extractive exploitation to conservation-driven economic strategies that benefit both biodiversity and local communities.

The rich biodiversity of elasmobranchs in the Maldives has played a pivotal role in the development of diving sector, with reoccurring or resident aggregations of charismatic elasmobranch species driving these activities, such as Reef manta ray (*Mobula alfredi*) (Harris et al. 2020; Armstrong et al. 2021; Harris & Stevens, 2021), whale sharks (*Rhincodon typus*) (Riley et al. 2010; Valsecchi et al. 2021) and other predatory species such as tiger sharks (*Galeocerdo cuvier*) (Vossgaetter et al. 2024) and bull sharks (*Carcharhinus leucas*) (Parmegiani et al.2023). With the term aggregation, we refer to the co-occurrence of two or more individuals in both space and time, generally facilitated by ecological or behavioural drivers (McInturf et al., 2023). The typical drivers that are fundamental for forming such aggregations may vary depending on the species and environmental context, with foraging being one of the most important (Sims et al. 1998; Ketchum et al. 2012; Towner et al. 2016). In particular, sharks generally locate favourable conditions to forage or hunt together, as documented for *R. typus* in several places around the world (La Parra et al. 2011; Robinson et al. 2013; Andrzejaczek et al. 2016; Norman et al. 2017; Copping et al. 2018; Perry et al. 2018; Whitehead et al. 2019; Rohner et al. 2020). Other aggregation drivers include mating and reproductive behaviour, where females form sex-segregated aggregations, such as

Carcharhinus falciformis in Mexico (Whitehead et al. 2022), or aggregation defense mechanisms, usually found for *Carcharhinus limbatus* (Quoy & Gaimard, 1824), which effectively form groups for protection against predators (Doan & Kajura, 2020). Furthermore, another driver for shark aggregations is the hydrodynamic efficiency, as sharks minimize energy expenditure through specific formations that reduce the energy outlay of both individual specimens and the group (Porter et al. 2020; Papastamatiou et al. 2021). More recently, *C. amblyrhynchos* has also been observed forming aggregations at isolated reef ledges where individuals show resting behaviour, remaining largely unresponsive (Bullock et al. 2024)

One of the most frequently observed reef-associated shark aggregations in the Maldives is composed of grey reef sharks, *C. amblyrhynchos*, along atoll channels or reefs (Clarke et al. 2012). However, at present, limited information is available regarding the local size structure or population dynamics of this species. The only published data consist of a report by Anderson et al. (1992). Despite the Maldives' importance as a shark sanctuary in the Indian Ocean (Robinson et al. 2022), substantial gaps still remain in the scientific literature concerning shark behaviour, general ecology, and aggregation dynamics within different habitats. In particular, many known aggregation sites remain poorly studied or lack sufficient data to be considered for conservation initiatives from governmental entities. Recently, the IUCN Shark Specialist group saw the delineation of portions of habitats critical to shark species nominated Important Shark and Ray Areas (ISRAs), and 27 of these areas have been identified in the Maldives (Jabado et al. 2023); however, of the two areas surveyed in the present study only one has been identified as Area an of Interest. Moreover, the increasing availability of underwater video footage and observations from recreational divers is enhancing possibilities of shark research, with citizen science providing broad spatiotemporal datasets that, once validated, represent a valuable tool for advancing ecological and behavioural studies (Araujo et al. 2020; Bargnesi et al. 2020; Gobbato et al. 2024).

In this context, our study aimed to evaluate and provide an overview of shark aggregations in these two key channels sites: Villingili Kandu, in Gaafu Alifu Atoll, and Miyaru Kandu in Vaavu Atoll, the latter of which is a designated Marine Protected Area (MPA) since 1995. Using in situ observational and photographic methods, the study focused on assessing the ecological importance of the two channels, obtain biometric data, and provide insights on the ecology of *C. amblyrhynchos*.

2.3. MATERIALS AND METHODS

Study site

The study was conducted in two sites called Villingili Kandu and Miyaru Kandu. Kandu means "channel" in the local Dhivehi language, indicating the strip of water between two islands at the edge of an atoll. In particular, Villingili Kandu is a channel situated in Huvadhu Atoll, in the southern region of the Maldives archipelago (Figure 1). The channel is flanked by two inhabited islands: Villingili Island, located on the north corner, serves as the capital of Northern Huvadhu Atoll (Gaafu Alifu), and Kooddoo Island, located on the south corner, houses a fish processing plant, a local airport, and a resort. Conversely, Miyaru Kandu is located in Vaavu Atoll, in the central area of the Maldives archipelago. On the southern reef stands the Alimatha resort, while the northern side is defined by a shallow reef area that begins at a depth of 3 meters.

Villingili Kandu is characterized by an oceanic drop-off that descends to a depth of 30-35 m, and the channel's orientation is toward the east, with an approximate span of 450 m between the northern and southern corners. Miyaru Kandu faces eastward too; its oceanic drop-off stands at a depth of 30-32 m with a distance between the two corners of approximately 230 m, and it is also characterised by a bathymetric feature within the channel resembling an internal drop-off, where sharks tend to aggregate with specific current conditions. Channels experience two types of currents depending on the season and tidal cycle: incoming currents occur when water flows from the ocean into the inner atoll; outgoing currents happen when water moves from the inner atoll to the open ocean.

Sampling method

Fieldwork was conducted during the seasonal operational routes of White Wave Maldives onboard of M.Y. Island Safari 1 and M.Y. Island Safari 2, which provided logistical access to Villingili Kandu from January to March and Miyaru Kandu from October to December, as well as from March to the end of April. Between 2022 and 2023, we conducted over 100 dives, totalling approximately 80 hours of underwater observations at Villingili Kandu and 20 hours at Miyaru Kandu. Dive duration in channel environments is highly variable, ranging from about 20 minutes to over one hour depending on current intensity; therefore, we reported total cumulative observation time rather than average dive length.

Laser photogrammetry was performed on five occasions at Villingili Kandu and four at Miyaru Kandu. We selected these dives based on optimal conditions, including high water clarity and low current intensity, while on other occasions, photogrammetry was not feasible due to the heavy presence of divers from multiple facilities, which altered shark behaviour and limited measurement opportunities to avoid interfering with other divers activities. The diving group responsible for collecting biometric measurements equipped with one device, followed a linear transect from one corner to the opposite corner of the channel, maintaining a consistent direction of navigation along the oceanic drop-off or the internal drop-off in Miyaru Kandu. Moreover, whenever diver activity altered shark movement pattern, data collection was suspended to avoid potential bias. This approach ensured a standardized protocol for each survey conducted and minimized the risk of recounting individuals observed in the aggregation during the data collection. Eight out of the nine instances of biometric data collection were conducted along the oceanic drop-off of both Villingili and Miyaru Kandu with incoming current, while in one instance, measurements were collected following the inner drop-off in Miyaru Kandu with outgoing current condition.

During the photogrammetry sessions, we obtained biometric measurement of total length (TL) and pre-caudal length (PCL) from individuals within aggregations, along with associated metadata (date, time, and dive site). Additionally, we also recorded shark behaviours by visual census and extrapolation from videos taken by citizen science, excluding the regular schooling behaviour of grey reef sharks. These behaviours included: mating attempts, which encompass active chasing behaviours, physical interactions and sometimes visible scarring on females (Carrier et al. 1994; Salinas-de-León et al. 2017); predation events; chafing behaviours, involving rubbing the body against surfaces or other species to remove parasites, which may also play a role in social or ecological interactions (Ritter, 2011; Williams et al. 2021; Pancaldi et al. 2022; Gobbato et al. 2024); and visits to cleaning stations, specific reef sections or seamounts where sharks and large marine organisms go for parasite and dead tissue removal by cleaner fish, involving altered swimming behaviour or posture to facilitate cleaning (Oliver et al. 2011; Wheeler et al. 2013).

Finally, we compiled opportunistic photographic and video materials taken from divers during recreational dives spanning from 2013 to 2024 at Villingili Kandu. These records, being from citizen-science operators, were carefully screened and validated by the authors to ensure data quality and consistency. In this context, video characteristics such as duration and field of view varied considerably, therefore, to minimize this bias, all videos were reviewed frame by frame, and the frame with the maximum number of *C. amblyrhynchos* observed (MaxN) was extracted. Indeed, this is a conservative and widely applied metric (Ellis and DeMartini, 1995; Priede et al. 1994; Schobernd et al. 2013) for estimating relative abundance in non-standardized footage, enabling comparisons while avoiding double-counting. The selected frame was uploaded to ImageJ and analysed using the ‘Multi-point’ function to count individual sharks. Each record was collected with associated metadata (Date – Month, Year, Dive Site, and MaxN value). This approach provides a conservative yet reliable estimate of aggregation size and support the evidence that Villingili Kandu hosts one of the largest aggregations of *C. amblyrhynchos* recorded in the Maldives.

Laser construction, calibration, and operation

During the two-year survey period, two measurement devices were custom-made from an inox steel tube, measuring a total length of 35 cm and 30 cm, used in 2022 and 2023 and 2024, respectively (Supporting information S1, Figure S1). Two green underwater laser pointers (Archon J1 - Archonlight Xiware Technologies Ltd.) were positioned on the sides of the tube and secured in place with the two clamps. A GoPro Hero 9 camera was mounted in the center of the tube using a mounting bracket attached to the top of the stainless-steel custom mounting plate welded to the tube. The action camera was used to capture videos at a resolution of 2.7K at 30 frames per second (fps) in linear mode.

As described by Deakos (2010; 2011), several factors can introduce inaccuracies in measurements, including image distortion due to light refraction, the use of a wide-angle lens, non-parallel alignment of the lasers, and parallax error. In the current study, we used a linear field of view ranging from 24 mm to 49 mm. Moreover, we executed a two-step calibration process to mitigate the non-parallel alignment issue of laser pointers, as described accurately in the Supporting information S1 and S2 (Figure S2).

Laser biometric analysis

To minimize potential measurement inaccuracies associated with non-perpendicular angles, only photographs in which the body of the shark was fully extended and the laser dots pointed at a 90° angle to the flank were used. Images taken at non-parallel angles, as per Rohner et al. (2011), were systematically excluded from our analyses. To achieve that, each video was examined using QuickTime Player and the most suitable frame for each measurement was selected and extracted.

Measurements were inferred by importing the images into ImageJ software (version 1.54g). The number of pixels between the two laser points was counted and then converted using the scaling factor derived from the known distance between the two dots. From each shark, we derived pre-caudal length (PCL) measurements from the tip of the snout to the insertion of the caudal fin, as well as total length (TL) measurements from the tip of the snout to the tip of the upper caudal fin. Given that the caudal fin curvature caused by swimming movements can affect TL estimates, we meticulously recorded PCL values for all individuals, following the recommendations of Rohner et al. (2011).

To analyse the relationship between PCL and TL, we used a linear regression model to initially test and quantify their correlation to be able to derive an equation to predict TL form PCL, allowing us to generate predicted total length (PTL) values for individuals in which only PCL could be reliably measured.

Furthermore, for each shark measured, we documented species and sex according to the criteria outlined in Hendon et al. (2013), using the presence of potential mating wounds as an indicator of sexual maturity. Larger female individuals exhibiting a noticeable bulge on the ventral and lateral sides of the body, potentially indicating a pregnancy status (Figure 2a; Acuña-Marrero et al. 2014; Lea et al. 2015; Robinson et al. 2016; Ramirez-Macias et al. 2017; Hedrick et al.

2019) were classified simply as Mature Females, as this condition cannot be confirmed without ultrasound examination or dissection (Sulikowski et al. 2024).

Estimating the size and maturity of *Carcharhinus amblyrhynchos*

The determination of sexual maturity in male individuals is typically based on the elongation and complete calcification of the claspers, coupled with their ability to fully rotate (Francis and Maolagain 2000). However, in our sampling methodology, assessing the calcification state of claspers is challenging and susceptible to potential biases. This challenge is amplified when determining the maturity stage of female individuals, which, in our case, can only be reliably assessed by visual observation of females exhibiting potential signs of pregnancy. Due to variability in the classification of mature and non-mature individuals reported in studies from different regions around the world (Wetherbee et al. 1997; Robbins et al. 2006; Robbins et al. 2015; Smart et al. 2016; Bradley et al. 2017), we extensively reviewed the literature and following the classification provided by Smart et al. (2016), Bradley et al. (2017), and Ebert et al. (2021) we divided measured specimens into three size-based categories: Young of the Year (YOY), Non-Mature (NM), and Mature (M).

The sexual maturity threshold for females was determined based on available literature (Wetherbee et al. 1997; Ebert et al. 2013; Simpfendorfer et al. 2020), with the smallest female showing potential maturity used as reference (Figure 2b). For males, we sat the maturity threshold by combining the smallest measured individual exhibiting fully elongated claspers and the criteria outlined by Bradley et al. (2017) (Figure 2c). YOY classification followed Smart et al. (2016) and was further supported by two observations recorded by Anderson and Ahmed (1993), who documented a pregnant female caught in Haa Alif Atoll, Maldives, carrying two embryos measuring 48 cm and 49 cm TL and a free-swimming new-born measuring 53 cm TL. Based on this evidence, individuals were classified as YOY if ranging from 45–72 cm TL, NM if ranging from 73–119 cm TL, and M if ≥ 120 cm TL. Sex was not reported for YOY individuals due to their small size (Figure 2d).

Statistical analyses

All graphs and statistical analyses were produced using RStudio (Version 2023.06.2+561). Prior to analysis, total length (TL) data were assessed for normality using the Shapiro–Wilk test. Differences in TL distributions between sites were evaluated using a Wilcoxon rank-sum test, selected as a non-parametric alternative when the assumption of normality could not be confirmed. As sampling effort varied among the 9 dates, we summarized sex ratio as the average of per-date female:male (F:M) ratios. Differences in life-stage composition (YOY, NM, and M individuals) between sites and across sampling dates were assessed using Fisher's Exact Test, a non-parametric test suitable with small-expected frequencies.

Ethical statement

All research was conducted in accordance with relevant ethical guidelines for animal research. Non-invasive methods, including laser photogrammetry and diver-operated video recordings, were used exclusively to ensure minimal disturbance to *C. amblyrhynchos* specimens. No animals were captured, handled, or harmed during this study.

2.4. RESULTS

A total of 505 grey reef sharks were measured during dive surveys, in particular 402 in Villingili Kandu and 103 in Miyaru Kandu, respectively. Out of the total number of grey reef sharks measured, 68.1% (n=274) in Villingili Kandu and 76.7% (n=79) in Miyaru Kandu, met the criteria established in this study to minimize parallax error; therefore, 353 individuals were included in the statistical analyses, while the remaining were not considered for the statistical analysis or the biometric data collection.

The linear regression analyses resulted in a strong linear relationship observed between PCL and TL, with a highly significant model ($P < 0.001$, $R^2 = 0.97$). These results strongly support using PCL as a robust predictor of TL for *C. amblyrhynchos* (Figure 3).

The aggregation composition revealed differences in both size and sex between the two sites examined. A Wilcoxon rank-sum test ($W = 4396$, $P < 0.001$) demonstrated a significant difference in total length (TL) distributions between the two sites, with Miyaru Kandu exhibiting a wider size range.

Mature individuals exhibited a mean TL of 137 ± 11.3 cm at Villingili Kandu (n=223) and 144 ± 14.9 cm at Miyaru Kandu (n=21). Non-mature individuals, instead, had an average TL of 109 ± 9 cm at Villingili Kandu (n=51) and 86.1 ± 15.2 cm at Miyaru Kandu (n=40) (Figure 4a). Notably, young-of-the-year individuals (n=18) were observed exclusively at Miyaru Kandu, showing a mean TL of 67.8 ± 4.51 cm (Figure 4a).

Analysis of the sex ratio revealed a significant female bias at both locations. At Villingili Kandu, the average F:M ratio across dates was 12.6 females for every male in the 5 sampling dates. Conversely, at Miyaru Kandu, the average F:M was not estimable because males were absent on every sampling date.

The temporal assessment of life-stage composition (Figure 4b) revealed significant variability at Miyaru Kandu across sampling dates (Fisher’s Exact Test, $P < 0.001$), indicating fluctuations in the proportions of YOY, NM, and M sharks throughout the sampling periods (Figure 4d). Conversely, the demographic composition at Villingili Kandu remained consistent over time (Fisher’s Exact Test, $P = 0.499$) (Figure 4c).

Behavioural observation

During our surveys, we documented mating attempts and mating scars on females within the aggregation during January 2022 and December 2024 in Miyaru Kandu, as well as in February 2024 in Villingili Kandu, as illustrated in Figure 5. The presence of mature males in the aggregation during mating periods strongly suggests that the two channels may serve as breeding ground for the species.

Moreover, in both channels, *C. amblyrhynchos* individuals have been observed visiting and taking advantage of the cleaning station located in the southern corner of the channels (Figure 6). At these spots, they typically approach the cleaning station in a vertical position, facilitating the access for cleaner fish, primarily Labridae, to remove parasites and dead tissue, highlighting the ecological importance of cleaning interactions in maintaining shark health. Additionally, in Villingili Kandu area, instances of chafing behaviour by *C. amblyrhynchos* on *R. typus* have been observed during year 2022, suggesting that this species may serve as a scraping surface (Williams et al. 2022; Gobbato et al. 2024).

Furthermore, two predation events were documented on separate occasions, specifically on 28 January 2020 and 2 February 2020. In the initial event (Supporting information, Video 1), individuals were observed aiming and focusing on prey located on the reef located on the channel drop-off, with the entire sequence lasting 27 seconds. During the second event lasting 15 seconds (Supporting information, Video 2), the predatory response of a grey reef shark appeared to be triggered by a predation attempt outside the camera’s focus; throughout this event, the aggregation trajectory changed following an attack by a dogtooth tuna (*Gymnosarda unicolor*) on a different target, leading to a rapid change of direction from the group pursuing a different prey.

Assessment of MaxN recorded between 2013 and 2024

MaxN was derived from 11 opportunistic videos recorded by divers between 2013 and 2024 in Villingili Kandu (Table 1). The counts ranged from 28 individuals in January 2015 to 78 in February 2021. Counts exceeding 60 individuals in a single frame were observed in February 2021, February 2024, and March 2024.

These values represent conservative abundance estimates, as they are based on the maximum shark number observed simultaneously in a video frame, avoiding repeated counts of the same individuals within a recording.

2.5. DISCUSSION

Understanding the ecological drivers behind shark aggregations is essential to develop evidence-based conservation strategies and management of key habitats for these animals. In this context, the preliminary findings presented in this study provide a baseline for further research on grey reef sharks aggregation dynamics in the Maldives.

Several factors must be taken into consideration to explain the aggregations of *C. amblyrhynchos* as this species is known for its strong residency and site fidelity (Vianna et al. 2013; Espinoza et al. 2015; Micarelli et al. 2024). Generally, adult males exhibit greater mobility than females, likely due to reproductive migration to potential mating grounds in different areas that could promote genetic dispersion, as previously documented in populations of the Great Barrier Reef (Momigliano et al. 2017; Bonnin et al. 2019, Lesturgie et al. 2023). The average sex-ratio recorded in both channels highlighted a strong female bias with 12.6 females recorded per male in Villingili Kandu and no males recorded in Miyaru Kandu, suggesting that these two aggregations are mainly formed by female individuals, however, additional data are required to investigate what are the environmental or hormonal factors that determine the beginning of the mating season inside the aggregation. Nevertheless, we recorded evidence of reproductive activities, including records of mating attempts and mating scars on females in both the aggregation, particularly in January 2022 and December 2024 in Miyaru Kandu, and February 2024 in Villingili Kandu (Figure 5), suggesting that these two channels may act as reproductive habitats, potentially serving as mating grounds for mature individuals.

Notably, we recorded the presence of YOY in Miyaru Kandu and the absence of YOY individuals in Villingili Kandu, which does not necessarily exclude the possible presence of a nursery area in proximity to the aggregation. Current literature indicates that, in addition to sex segregation, there also exists a segregation based on size, where juvenile individuals tend to aggregate in different size groups compared to adults, as observed in species as Dusky sharks (*Carcharhinus obscurus*) and Sandbar sharks (*C. plumbeus*) in the Mediterranean Sea (Bigal et al. 2024) and Western Australia (Pember et al. 2023), as well as Whale shark *(Rhincodon typus*) in Gulf of California and the Maldives (Riley et al. 2010, Ketchum et al. 2012), Blacktip reef sharks (*C. melanopterus)* in French Polynesia (Mourier et al. 2013) and Silky Shark (*C. falciformis*) in the Pacific Ocean (Kindong et al. 2022). Despite this evidence, in Miyaru Kandu, we recorded YOY and NM individuals swimming alongside adult individuals on several occasions, an uncommon behaviour for other reef species (Matich et al. 2017) (Figure 7). In the same channel, we documented and observed YOY individuals throughout the 2023 survey period, demonstrating ongoing use of the channel through time, as confirmed also by archival photographic and observational records on the presence of YOY in multiple previous years (Supporting information, Video 3). Together, these observations, according with Heupel

(2007), lead us to hypothesize that this specific site may function as a nursery area for *C. amblyrhynchos* in this region.

Beyond reproductive behaviours, another significant factor that may influence the abundance of grey reef sharks is the presence of low trophic order fish biomass aggregations, which have been demonstrated to attract predators, especially during their spawning events. (Tickler et al. 2017; Rhodes et al. 2019). In Villingili and Miyaru Kandu, we consistently recorded the presence of numerous potential prey species from the *Caesionidae*, *Carangidae,* and *Priacanthidae* families (Supporting information, Figure S6). These species are known to form groups and spawning events, providing a readily available food source. We recorded predation events on two different occasions (Supporting Information, Videos 1 and 2), suggesting, as Mourier et al. (2016) noted, that sharks may benefit from the presence of these schools as a food source that might reduce the need for long foraging trips outside the channel.

Additionally, hydrodynamic conditions further support aggregation behaviour, as the presence of strong currents can reduce the need for continuous swimming, as seen in French Polynesian atoll channels with grey reef sharks aggregating along oceanic drop-offs or in specific areas within the channel to take advantage of updraft areas created by these bathymetric features in conditions of incoming and outgoing currents to rest and move with minimal energy expenditure (Papastamatiou et al. 2021; Laurioux et al. 2025). Similarly, we recorded consistent patterns at both our study sites, wherein *C. amblyrhynchos* aggregated along channel drop-offs during incoming currents. Under outgoing current conditions, sharks were seen moving in two different areas between sites: in Miyaru Kandu, they were observed aggregating inside the channel, where the bathymetry of the inner drop-off creates an alternative updraft area; in Villingili Kandu, instead, the aggregation moved below the drop-off, potentially to avoid unfavourable current conditions and optimize energy expenditure (Supporting Information, Video 4). Although considered obligate ram ventilators (Dapp et al. 2015; Tickler et al. 2017), recent observations have documented *C. amblyrhynchos* individuals aggregating at isolated reef ledges in the Republic of Seychelles, where they were observed resting and unresponsive (Bullock et al. 2024). Similar behaviour has been recorded in specific locations in the Maldives (De Maddalena, 2023; Parmegiani, pers. obs., 2025; Supporting Information, Figure S7). While such behaviour was never recorded within channels, these observations further suggest that this species may use not just updraft regions but also sheltered reef areas to rest and potentially avoid predators.

In both channels, we observed grey reef sharks visiting cleaning stations near the oceanic drop-off (Figure 6). Although we do not have enough data to determine if this behaviour is favoured by determinate tidal or current conditions, our sightings align with patterns observed in other regions (Wheeler et al. 2013) and among other elasmobranch species, which use specific cleaning stations, coral formations, or particular areas of the reef (O'Shea et al. 2010; Oliver et al. 2011, 2019; Carpenter et al. 2024). We recognize these specific areas as aggregation hotspots within the channels, where mutualistic interactions between cleaners and hosts may promote site fidelity.

In comparison to previous studies from the Maldives, shark sightings at Villingili Kandu were notably higher. SharkWatch surveys, which provided baseline data on reef shark distribution and abundance across the Maldives, reported that favourable sites for shark sightings typically averaged n = 29 individuals (Sattar et al. 2013). Conversely, our surveys documented larger aggregations at Villingili Kandu, with photographic evidence collected from several videos showing MaxN of up to 78 *C. amblyrhynchos* in a single frame (Supporting Information, Figure

S4f). Considering that this count is a conservative estimate, as it does not include all individuals observed in the video footage (Supporting Information, Videos 5 and 6), these findings through different years indicate that Villingili Kandu currently hosts the largest recorded aggregation of *C. amblyrhynchos* in the Maldives.

Moreover, to ensure consistent biometric data retrieval in different field conditions, we derived all predicted total length (PTL) values from a linear regression model based on the measured values of precaudal length (PCL) and total length (TL). The model demonstrated a strong fit, indicating that PTL can be a reliable predictor of TL, especially in cases where measurements may be influenced by tail flexion or when entire body measurements are impractical. This is particularly significant in environments such as channels, where the strong current creates significant challenges for video capture, especially for less experienced divers. Moreover, it can be very useful for non-scientist contributors who are playing an expanding role in citizen science efforts related to conservation initiatives (Roff et al. 2016; Araujo et al. 2020; Siena et al. 2025; Whitehead et al. 2025), as this model may serve as a reliable tool for validating citizen science data and enhancing its scientific utility.

In conclusion, although our data provide an initial overview of two shark aggregation sites and further surveys are needed, these locations clearly represent important habitats similar to those super habitats recently demonstrated on grey reef shark aggregations in French Polynesia, where a single channel can serve multiple purposes, including foraging, refuge, mating, and parturition for over 500 resident individuals (Papastamatiou et al. 2025). These findings should be considered for further protection and included within recent ISRA initiatives to identify sensible areas for elasmobranchs in the region. Moreover, recent ID techniques used to identify individuals from different species of requiem sharks could be integrated to better evaluate the site fidelity and movement in the channels (Micarelli et al. 2024; Lionnet et al. 2025). Merging these data with diver observations and local community knowledge facilitates the identification of important shark aggregation habitats, enhancing targeted conservation strategies, supporting the development of locally adapted management measures, and contributing to regional efforts committed to ensuring the long-term viability of reef shark populations.

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2.7. TABLES

Table 1. Opportunistic shark aggregation observations at Villingili Kandu (2013–2024) based on guest-recorded videos. Sampling dates are listed by month and year. The MaxN frame indicates the maximum number of sharks visible in a single image from each video. Representative frames were analysed with the multi-point function in ImageJ (Supporting Information, Figures S3–S5).

	Date	**Dive Site**	**MaxN per frame**
Supp. Info. Figure S3(a)	February 2013	Villingili Kandu	**30**
Supp. Info. Figure S3(b)	January 2014	Villingili Kandu	**51**
Supp. Info. Figure S3(c)	January 2015	Villingili Kandu	**28**
Supp. Info. Figure S3(d)	March 2019	Villingili Kandu	**32**
Supp. Info. Figure S4(e)	January 2020	Villingili Kandu	**60**
Supp. Info. Figure S4(f)	March 2020	Villingili Kandu	**43**
Supp. Info. Figure S4(g)	February 2021	Villingili Kandu	**78**
Supp. Info. Figure S4(h)	March 2022	Villingili Kandu	**31**
Supp. Info. Figure S5(i)	February 2023	Villingili Kandu	**50**
Supp. Info. Figure S5(j)	February 2024	Villingili Kandu	**69**
Supp. Info. Figure S5(k)	March 2024	Villingili Kandu	**71**

2.8. FIGURES

Figure 1 Overview of the study area of Miyaru Kandu and Villingili Kandu, the channels in Vaavu Atoll and Gaafu Alifu Atoll, Maldives. Map created by MapTiler and Google Earth Pro.

Figure 2 Example of *C. amblyrhynchos* individuals measured: (a) Mature Female with suspected pregnancy; (b) Mature Female; (c) Mature male; and (d) Young of the year.

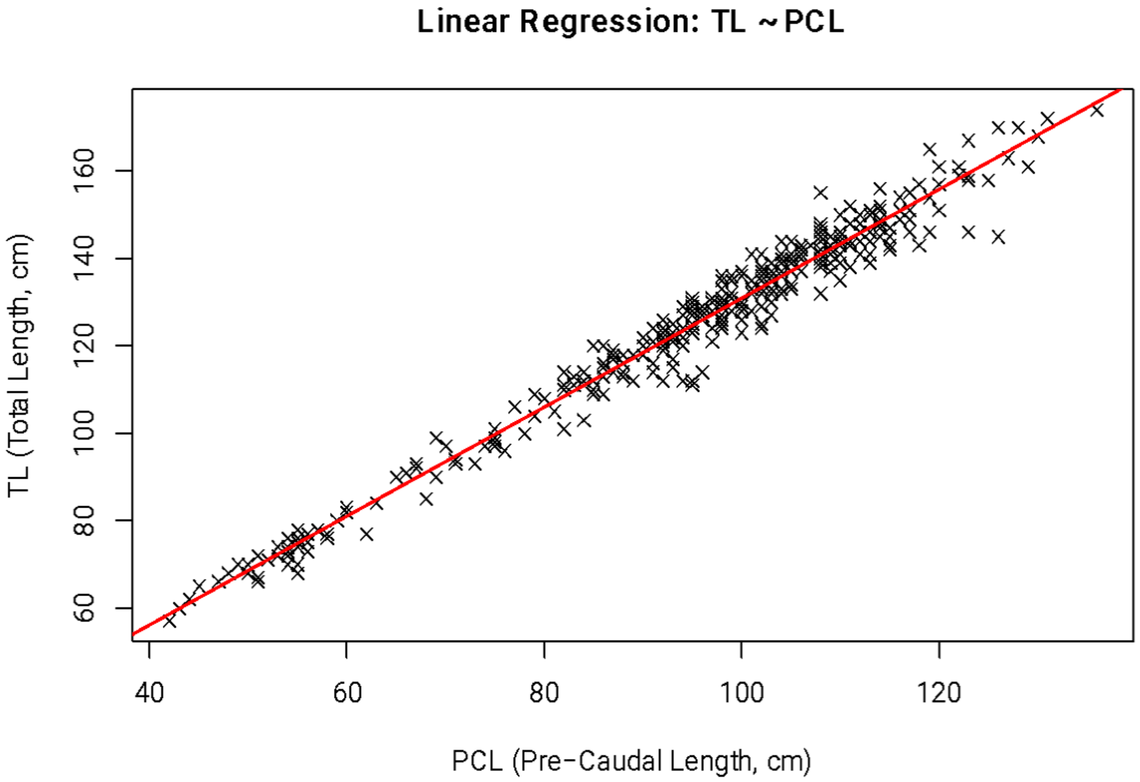

Figure 3 Linear regression of pre-caudal (PCL) and total lengths (TL) in cm. of *C. amblyrhynchos* (y = 6.47 + 1.244 * x). Symbol (X) indicates specimens recorded in both channels.

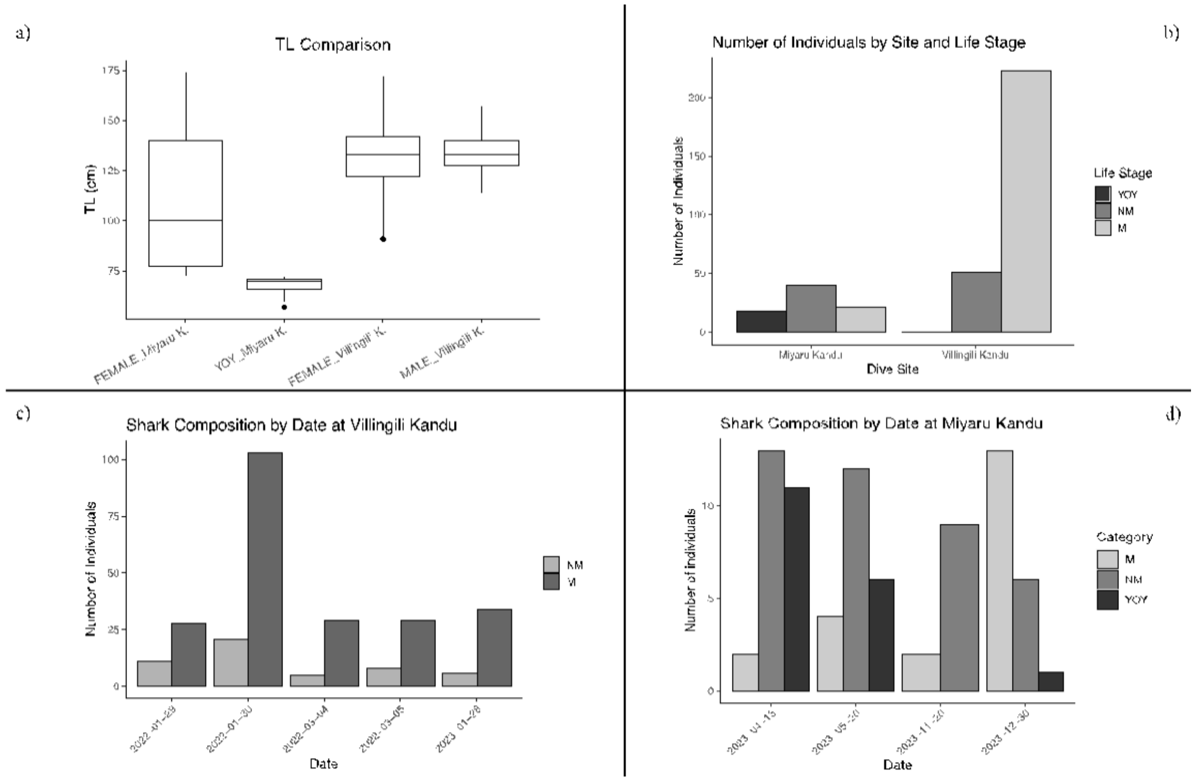

Figure 4 Overview of length and size class distributions of shark in the two sites: (a) Boxplot showing total length (TL) in centimeters of sharks grouped by sex and site; (b)bar plot displaying the number of individuals measured per life stage category (YOY, NM, M) at two dive sites; (c) bar plot showing the measured sharks by life stage category (M and NM) across five sampling dates at Villingili Kandu; and (d) bar plot showing the number of measured sharks by life stage category (M, NM, and YOY) across four sampling dates at Miyaru Kandu.

Figure 5: Mating attempts in the two surveyed channels: (a) Sequence from a mating attempt in Miyaru Kandu in January 2022, (a1)-(a2) Male shark attempting to mate with a female displaying bites from previous attempts/mating; Sequence (b1)-(b4) a male smelling and directly chasing a female with bite marks in the pelvic area in Villingili Kandu, January 2024; (c1)-(c2) Male smelling and chasing a female in Miyaru Kandu, November 2024.

Figure 6: Sequences of grey reef sharks visiting a cleaning station in Miyaru Kandu, Southern Corner, May 2024

Figure 7 Grey reef sharks—juveniles and YOY individuals schooling with adults in Miyaru Kandu in: (a) April 2023, (b) May 2023; (c) May 2024, and (d) December 2023.

2.8. SUPPORTING INFORMATION

S1. Calibration of the laser photogrammetry system device

First, the calibration was performed outside the water by measuring a fixed reference object at distances of 5, 10, and 25 meters and adjusting the laser positioning until accurate measurements were achieved. Subsequently, we conducted three underwater calibrations in a lagoon with a sandy bottom. To establish reference distances, we used a rope marked at 3, 6, 9, and 12 meters, moving down to a depth of 10 meters. A calibration object, comprised of a plastic structure with a total length of 75 cm, featured two fixed reference points at a distance of 30 cm. Two operators worked underwater, one ensuring the object's stability during measurements while the other moved to the designated distances for the calibration process. The measurements were repeated 3 times at each distance to assess the precision and accuracy of the measurements. The image clarity was satisfactory at distances of 3 to 6 meters, but at 9 meters, the laser beams began to lose definition due to the reduced power of the device. In contrast, at 12 meters, the laser dots became almost invisible on the surface of the reference object.

Finally, to minimize parallax error, we followed the procedure outlined in Rohner et al. (2011), conducting measurements of the 75 cm reference object at varying angles of 0°, 20°, and 45° using a diving compass. Subsequently, we processed the captured images with ImageJ, from which we derived an estimated error for each angle.

Underwater data collection was conducted by a diver who used the laser device to point the two lasers directly at the region situated between the gills and the caudal peduncle of the sharks. This designated area serves to prevent potential errors associated with tail flexion and to avoid projecting the lasers directly into their eyes, which can deter and disturb their natural behaviors.

Figure S1. Laser photogrammetry device used by divers collecting biometric data

Figure S2. Calibration at 0°, 10°, 45°

S2. Calibration results

The device calibration indicated a distance between the two laser rays of 35.4 ± 0.3 cm for the first device and 30.4 ± 0.5 cm for the second device (Table 1).

Table S1. Laser photogrammetry calibration test result

Laser calibration at 35 cm				
Distance to the object	**Laser Distance 1**	**Laser Distance 2**	**Laser Distance 3**	**Mean ± SD**
3 mts	35.0	35.0	35.0	35.0 ± 0.0
6 mts	35.3	35.2	35.3	35.2 ± 0.1
9 mts	36.0	35.7	35.9	35.9 ± 0.2
Combined mean ± SD				35.4 ± 0.3

Laser calibration at 30 cm				
Distance to the object	**Laser Distance 1**	**Laser Distance 2**	**Laser Distance 3**	**Mean ± SD**
3 mts	30.0	30.0	30.0	30.0 ± 0.0
6 mts	30.2	30.4	30.5	30.4 ± 0.2
9 mts	30.7	31.0	30.9	30.9 ± 0.2
Combined mean ± SD				30.4 ± 0.3

Table S2. Parallax error assessment

Parallax Error at 35 cm			
Distance to the object	**Rotation angle**	**Laser distance**	**Error %**
3 mts	0°	35.0 cm	0%
3 mts	10°	35.7 cm	+2%
3 mts	45°	46.0 cm	+31.4%
Parallax Error at 30 cm			
Distance to the object	**Rotation angle**	**Laser distance**	**Error %**
3 mts	0°	30.0 cm	0%
3 mts	10°	32.7 cm	+9.1%
3 mts	45°	41.6 cm	+38.7%

Images captured from different angles showed a 2% increase in the known distance between laser dots at a 10° angle. Additionally, there was a 31.4 % increase relative to the known distance in photos taken at 45° (Table 2). The shorter laser device produced larger errors, with 9.1% at 10° and 38.4% at 45°.

In our study, we employed two distinct laser photogrammetry setups (Figure 1S): one at a distance of 35 cm and the other at 30 cm. Error increased with angular displacement (Table 2), especially in the 30 cm setup, reaching 38.7% error at a 45° rotation angle, compared to 31.4%

at the same angle for the 35 cm setup. This difference can be attributed to the narrower triangulation baseline, which amplifies angular distortion and measurement inaccuracy. However, considering the optimal field of view of grey reef sharks (Lisney et al., 2007), making them particularly sensitive to disturbances caused by laser photogrammetry as seen in the video collected during the surveys (see Supporting Information 2), we opted for the smaller photogrammetry device. This design choice helped in minimize visual disturbance and consequent disruptions of the aggregation and to avoid accidental pointing of the laser in the sharks' line of sight during data collection. Furthermore, the compact setup also proved more effective for close-range measurements, particularly of young-of-the-year (YOY) individuals, and better suited for strong currents encountered in Maldivian channel environments.

S3. Video analysis of Villingili Kandu aggregation

Figure S3. Visualization of MaxN 2013-2019: (a) MaxN = 30, Villingili Kandu, February 2013; (b) MaxN = 51, Villingili Kandu, January 2014; (c) MaxN = 28, Villingili Kandu, January 2015; and (d) MaxN = 32, Villingili Kandu, March 2019.

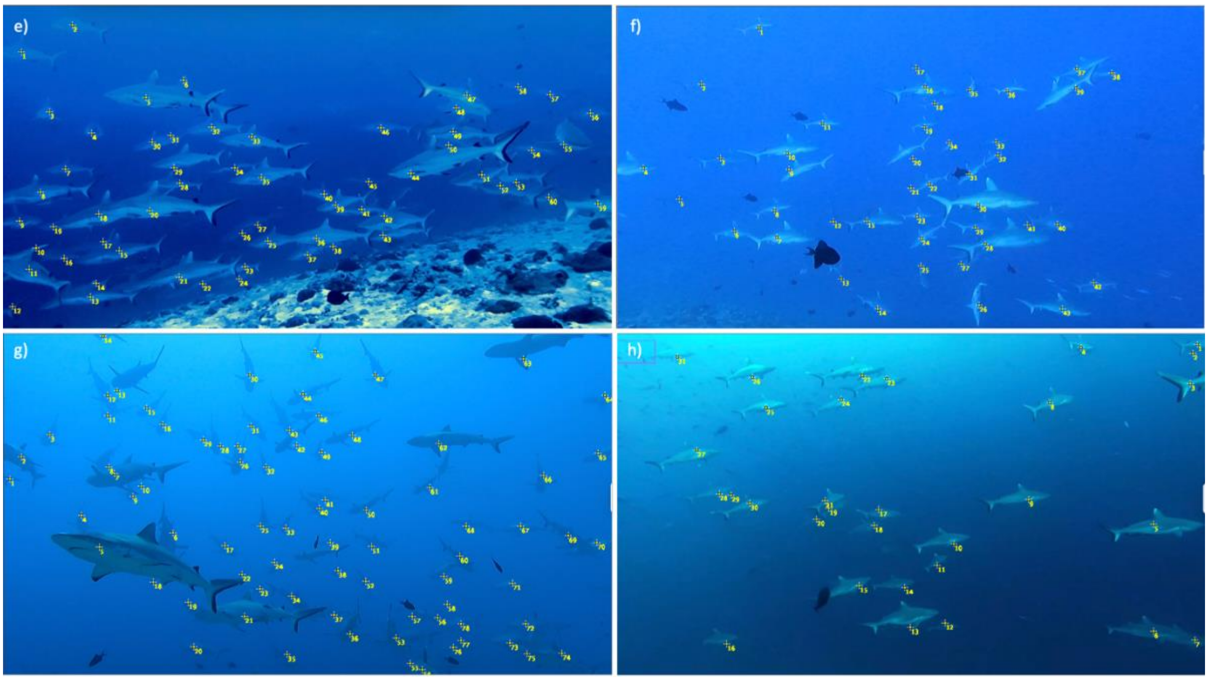

Figure S4. Visualization of MaxN 2020-2022: (e) MaxN = 60, Villingili Kandu, January 2020; (f) MaxN = 43, Villingili Kandu, March 2020; (g) MaxN = 78, Villingili Kandu, February 2021; and (h) MaxN = 31, Villingili Kandu, March 2022.

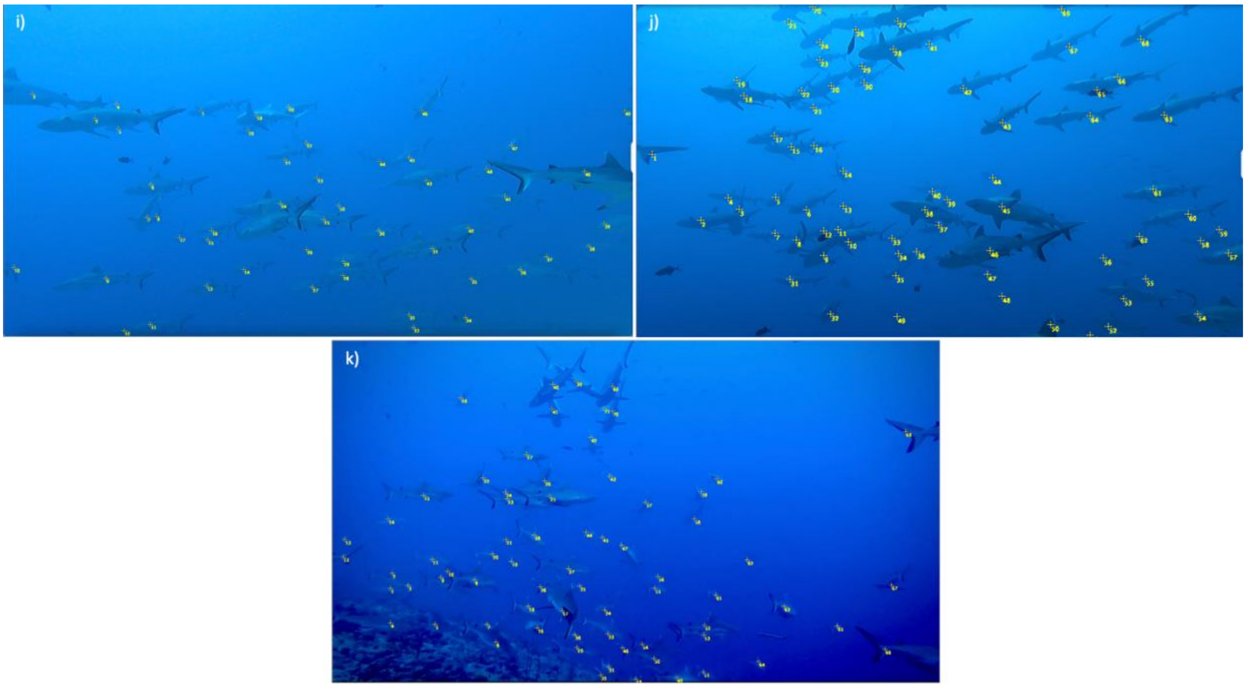

Figure S5. Visualization of MaxN 2023-2024: (i) MaxN = 50, Villingili Kandu, February 2023; (j) MaxN = 69, Villingili Kandu, February 2024; and (k) MaxN = 71, Villingili Kandu, March 2024.

Figure S6. Grey reef sharks in Miyaru Kandu and Villingili Kandu, swimming alongside groups of *Caesionidae, Carangidae, and Priacanthidae*. This species is known to prey on the latter and serves as a potential food source for the aggregation.

Figure S7. Grey reef shark resting under a reef edge in Raa Atoll, Republic of Maldives.

CHAPTER 3

New evidence of grey reef sharks (*Carcharhinus amblyrhynchos*) displaying chafing behaviors on whale shark (*Rhincodon typus*) individuals in the Maldives.

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***Joint first authorship**

3.1. ABSTRACT

Sharks rubbing against ocean floor or rocks are common events in marine environments, while instances of interspecific sharks chafing behavior have been observed much less frequently. This behavior has garnered scientific interest in recent years, and usually involves a smaller shark rubbing against a larger species, utilizing dermal denticles to rid itself of parasites or dead skin cells. Despite the costs and benefits of this behavior being not yet fully understood, we report new evidences of grey reef sharks (*Carcharhinus amblyrhynchos*; Bleeker 1856) engaging in chafing behavior against whale shark (*Rhincodon typus*, Smith 1828) in the Maldives. This behavior suggests that grey reef sharks may engage in chasing behavior for cleaning purposes or take advantage of larger sharks as an anti-predation tactic.

These records contribute to shed light on previously unexplored aspect of elasmobranch interspecies interactions and highlights the need for further research into this topic. The prevalence of such behavior across different regions suggests its potential significance in the ecological dynamics of shark population.

3.2. INTRODUCTION

For decades, Maldives has long been recognized as one of the most attractive countries for scuba divers and shark enthusiasts thanks to the biodiverse coral reef systems and the great abundance of megafauna (Robinson et al. 2022). After the 1995 fishing ban (Ali and Sinan 2015; Zimmerhackel et al. 2019), shark activities and the development of ecotourism activities emerged as a valuable and effective alternative to the fishing industry (Zimmerhackel et al. 2019; Harvey-Carroll et al. 2021). During the years, sharks have become an important socio-economic source of income on global scale, not only in Maldives, but also in many other countries (Gallagher and Hammerschlag 2011; Araujo et al. 2016; Rohner et al. 2018, 2020;

Petatàn-Ramìrez et al. 2020; Valsecchi et al. 2021). Simultaneously, citizen science has received significant attention and importance as a crucial development in the field of shark research (Rowat and Brooks 2012; Vianna et al. 2013; Gibson et al. 2019; Araujo et al. 2020; Bargnesi et al. 2020). This approach has provided scientists with a wealth of data, aiding in the exploration of shark biology and ecology (Araujo et al. 2020; Bargnesi et al. 2020; Séguigne et al. 2023). Despite the potential limitations arising from non-experts contributing to the field, this information, after control and validation by experts, is now widely utilized in research across various regions worldwide (Norman et al. 2017; Araujo et al. 2020, 2022; Magson et al. 2022).

In the Maldives, one of the most considered species is the whale shark (*Rhincodon typus*, Smith 1828), known to gather in the coastal waters, displaying a seasonal presence and semi-annual residency pattern related to productivity and change in ocean currents (Anderson and Ahmed 1993; Wilson et al. 2001; Riley et al. 2010; Anderson et al. 2011; Cagua et al. 2014; Donati et al. 2016). One of the most important locations in the Maldives is the aggregation site in the South Ari Marine Protected Area (SAMPA), located in Ari Atoll, specifically designed to protect the whale shark population (Cagua et al. 2014; Stevens et al. 2015; Valsecchi et al. 2021). Similarly to other aggregation sites around the world, this area is mainly inhabited by juvenile males (Riley et al. 2010; de La Parra et al. 2011; Rowat and Brooks 2012; Robinson et al. 2013; Andrzejaczek et al. 2016; Donati et al., 2016; Perry et al., 2018; Whitehead et al., 2019; Allen et al., 2021; Harvey-Carroll et al., 2021; Araujo et al. 2022), displaying a notable level of site fidelity over the years, as suggested by the significant rate of individuals re-sighting (Valsecchi et al. 2021). Furthermore, the rare encounters with adult males and females, along with the rare sighting of newborns, suggest that this area serves as a “secondary nursery area”, providing an ideal developmental habitat for juveniles (Perry et al. 2018; Allen et al. 2021; Harvey-Carroll et al. 2021).

While moving around the atolls, whale shark individuals cruise through the habitat and aggregation points of one of the most abundant shark species in Maldivian waters, the grey reef sharks (*Carcharhinus amblyrhynchos*; Bleeker 1856) (Sattar et al. 2013). Grey reef sharks are a reef-associated shark species, broadly distributed throughout the Indian, Western, and Central Pacific Oceans (Robbins 2009; Graham et al. 2010; Rizzari et al. 2014). This species is known to form social groups, mostly composed of females, displaying year-round residency and commonly observed in coastal areas in , such as reef edges and drop-offs depending on current intensity and direction (Economakis et al. 1998; Vianna et al. 2013; Espinoza et al. 2014; Robbins et al. 2015).

The coexistence of different species of shark in the same habitat creates the optimal condition for interspecific interaction. In this context, the interspecific chafing behaviors displayed by elasmobranch have gained scientific interest in the last years (Williams et al. 2021; Pancaldi et al. 2022; Moya-Serrano and Salinas-de-Leòn 2022; Green et al. 2023). Chafing typically involves a smaller and a larger species, and it has been defined as cleaning behavior (Papastamatiou et al. 2007; Ritter 2011; Berthe et al. 2017). During this interaction, the smaller individual rubs its body against the rough surface of the larger one, taking advantage of the dermal denticles covered skin to free itself from parasites, bacteria, and dead skin cells (Ritter 2011; Berthe et al. 2017; Williams et al. 2021; Moya-Serrano and Salinas-de-Leon 2022). This type of interspecific behavior in elasmobranchs has been reported in the past few years in the Galapagos islands (Pancaldi et al. 2022; Green et al. 2023). Both the galapagos shark (*Carcharhinus galapagensis*, Snodgrass and Heller 1905) and the silky shark (*Carcharhinus falciformis*, Müller and Henle 1839) have been reported to engage in chafing behavior with whale sharks (Williams et al. 2021; Pancaldi et al. 2022; Green et al. 2023). These interactions usually begin with a close pursuit or following of whale sharks by the requiem shark species, which suddenly perform a burst of speed with a readily obvious body contortion as they try to efficiently rub themselves against various parts of the whale sharks' bodies. These incidents have increased curiosity and the need for a better understanding of the purpose, ecological significance, and frequency of these behaviors in sharks, which prompts opportunities for further research on this topic.

3.3. RESULT AND DISCUSSION

In this short communication, we present the first documented instances of a chafing interaction between a whale shark and grey reef sharks reported in the Maldives. The first chafing event between *C. amblyrhynchos* and *R. typus* was documented by two dive guides from the White Waves Maldives diving team on the outer reef of Kooddoo Island, near the southern corner of Villingili Kandu in Gaafu Alifu atoll, Maldives (0°44'30.1"N; 73°26'21.5"E; Fig. 1).

The incident was witnessed at a depth of approximately 18-24 m involving a juvenile female whale shark swimming southward along the drop-off just outside of the channel, while being trailed by a heterogeneous group of 20 – 25 grey reef sharks (Fig. 2a; Supporting_Video 7).

The second instance was captured in a video a year earlier showing the same situation at the same dive site and was recorded by another Safari Boat crew. In this case, the whale shark was swimming followed by a heterogeneous group of 35 – 40 grey reef sharks (Fig. 2b; Supporting_Video 8).

The video used for this study were taken from non-professional scuba divers directly in the presence of authors or from social media platforms. These videos were invaluable contributions from citizen scientists for this report. As such, given their non-professional nature, divers recorded the footage to the best of their abilities, considering the constraints posed by varying camera qualities and the rapid cruising speed of the sharks.

The first video (Supporting_Video 7) has been recorded by a guest diver of White Waves Maldives PVT. LTD and despite the resolution, the direct experience underwater confirmed the episode of chafing by the two dive guides leading during the recorded event. Indeed, in both cases, it can be noticed that initially *C. amblyrhynchos* swim calmly behind or parallel to the *R. typus* individual, without displaying any signs of interspecific aggressive behavior. Then, in turn, some of the grey reef sharks adventured closer to the whale shark, performing in some cases chafing against the flank of the precaudal part of the whale shark, as can be seen in the second video record, as highlighted by the slow-motion applied (Supporting_Video 8,9; Fig. 2b).

Based on the available literature at the time of writing, similar events have been recorded just on two other occasions: in the Maldives in January 2023 in Maarehaa Kandu (Gaafu Alifu Atoll) (Supporting_Video 10), where a whale shark was followed by a group of six grey reef sharks; and in French Polynesia in 2015, where more than 20 individuals of grey reef sharks were observed approaching a whale shark individual from behind (Fig. 3a; Supporting_Video 11). Furthermore, there is a single instance of similar behavior documented in March 2020 in Fuvahmulah southern plateau in the southern region of Maldives, where grey reef sharks were observed following a giant oceanic manta ray (*Mobula birostris*; Walbaum 1792) (Supporting_Video 12; Fig. 3b).

Although interspecific chafing interaction between coral reef associated fishes' species and reef sharks has been demonstrated (Papastamatiou 2007; Thompson and Meeuwig 2022), there is little understanding about interspecific interaction and cleaning in elasmobranch. From these limited data, we may suggest that grey reef sharks observed in the Maldives appear to engage in chasing behavior on solitary *R. typus* individuals for cleaning porpoises, in what can be defined as a "mobile cleaning station" (Williams et al. 2021).

Thus, it is likely that Carcharhinidae such as silky shark, galapagos shark, or grey reef sharks may take advantage of this peculiar interaction with whale sharks or manta rays as these species do not pose a direct predatory risk to their survival, contrary to other shark species, such as great hammerheads (*Sphyrna mokarran*; Rüppell 1837) (Mourier et al. 2013).

Regarding following behavioral patterns, the observed behavior of grey reef sharks trailing behind whale sharks or larger sharks may be indicative of a retaliation of the strategic anti-predation tactic, wherein these sharks utilize trailing behavior to position themselves within the blind spot of the potential predator; they are potentially reducing the likelihood of becoming a target for predation. This phenomenon finds support in studies of fish species that have been shown to adopt similar trailing behaviors to enhance their survival prospects when co-existing with potential predators in their ecological niche (Papastamatiou 2007; Williams et al. 2021).

To conclude, this is the first documented report of chafing behavior between grey reef sharks and whale shark in the Maldives. Despite chafing behavior among elasmobranch species has been rarely observed and documented, the presence of multiple records from several locations of *C. amblyrinchos* displaying this behavioral pattern could indicate that this behavior is more common than previously thought for this species. Further studies are necessary to verify this hypothesis and investigate the possibility of extending it to other elasmobranch species. With this communication, our objective is to shed light on interspecific behavior between *R. typus* and *C. amblyrinchos* contributing to unravelling new aspects of elasmobranch ecology and interspecies interactions.

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3.5. FIGURES

Fig. 1 Locations of sightings of chafing behavior, displayed by white icons, around Koddoo Island in Huvadhoo Atoll. Each location accounts for a single sighting. Map created by MapTiler loaded in QGIS.

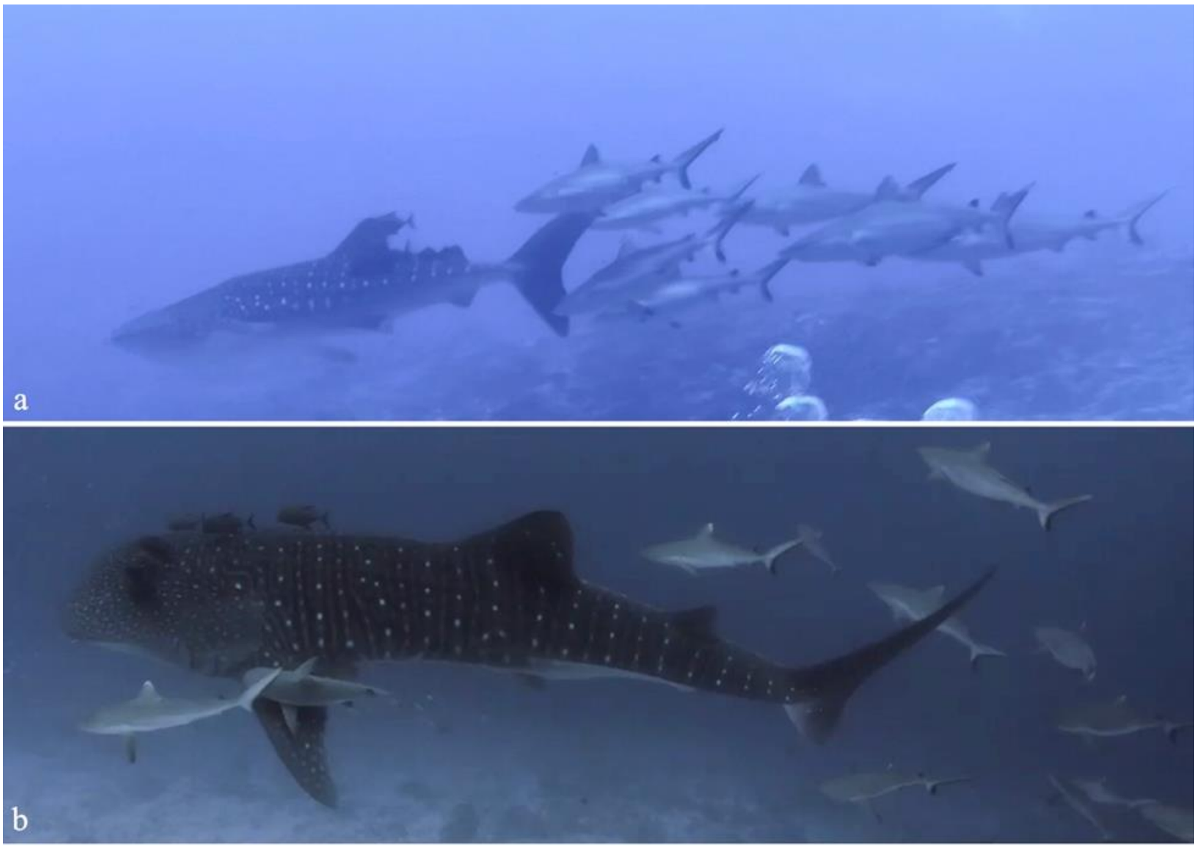

Fig. 2 Two distinct examples of following and chafing behavior between grey reef sharks (*Carcharhinus amblyrhynchos*) and whale sharks (*Rhincodon typus*) in Kooddoo Island, Maldives, recorded in **a** 2022 from White Wave Maldives team and **b** 2021 from social media mining, Carlos Martinez, Blue Force Fleet.

Fig. 3 Additional examples of interaction between Elasmobranch: **a** grey reef sharks (*Carcharhinus amblyrhynchos*) following a whale shark (*Rhincodon typus*) individual and attempting chafing behavior, in French Polynesia, 2015 from social media mining, Dani Brinton; **b** grey reef sharks following a giant oceanic manta ray (*Mobula birostris*) in Fuvahmulah, Maldives, 2020.

CHAPTER 4

First record of the Bull Shark *Carcharhinus leucas* (Valenciennes, 1839) from the Maldivian Archipelago, Central Indian Ocean.

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4.1 ABSTRACT

Verified records of the bull shark *Carcharhinus leucas* are lacking in the Maldives. This study provides the first confirmed evidence of 23 sightings observed from 2013 to 2023 in the central and southern atolls of this archipelago. Most of the sightings occurred in close proximity of inhabited areas, where food waste is often discarded into the water, or in several dive sites, suggesting the presence of this species in different location around Central and Southern Atolls. Although further research is required to fully investigate the *C. leucas* population in the Maldives, this report documents and confirms its presence in this region.

4.2 INTRODUCTION

The Republic of Maldives is renowned for the abundance of pelagic species and megafauna found in its waters. The significant diversity and abundance of shark species have increasingly attracted divers and shark enthusiasts and, since the 2010 shark fishing ban, shark tourism in the Maldives has become a significant source of income for the tourism sector, one of the primary resources of the country (Ali and Sinan, 2015; Zimmerhackel et al., 2018, 2019).It has been estimated that a single shark can be worth more than $800,000 during its lifetime, which is significantly more than its meat or fins (De Maddalena and Galli, 2017).

In the Maldives, a total of 37 species of sharks have been recorded in the Maldives, 14 of which belong to the requiem shark family (De Maddalena and Galli, 2017), including the recently added *Carcharhinus brevipinna* (Spinner shark; Müller and Henle, 1839) after its sighting in the dive site outside of Kooddoo harbour (Russo and De Maddalena, 2021). In the past two years, another dive spot emerged in front of Hulhumale harbour, gaining attention thanks to the high probability of sighting dozens of *C. brevipinna* during a single dive. Interestingly, *C. leucas* (Bull shark; Valenciennes, 1839), another important apex predator, has been repeatedly sighted in both locations along with *C. brevipinna*. However, it is interesting to notice that previous works, such as those by Randall and Anderson (1993) and De Maddalena and Galli (2017), did not mention *C. leucas* in the shark species of the Maldives, contrary to other cosmopolitan or Indo-Pacific distributed *Carcharhinus*, such as *C. albimarginatus* (Silvertip shark, Rüppell, 1837), *C. amblyrhynchos* (Grey reef shark, Bleeker, 1856), *C. altimus* (Bignose shark, Springer, 1950), *C. brevipinna*, *C. falciformis* (Silky shark, Bibron, 1839), *C. limbatus* (Blacktip shark, Valenciennes, 1839) *C. longimanus* (Oceanic whitetip shark, Poey, 1861) *C. melanopterus* (Blacktip reef shark, Quoy and Gaymard, 1824), and *C. sorrah* (Spottail shark, Müller and Henle, 1839).

The bull shark, being a euryhaline species, has a circumglobally distribution inhabiting the tropical, subtropical, and warm temperate regions of all ocean basins (Ebert et al., 2013). This species usually spends most of its life in shallow environment, typically in the first 30 m of the water column (Ebert et al., 2013), where they forage on a variety of animals, including teleost fish, invertebrates, elasmobranchs, turtles, dolphins and birds (Compagno 1984, Snelson et al., 1984). Nevertheless, different studies have demonstrated that this species exhibits a remarkable migratory behavior, particularly when faced with specific requirements (Smoothey et al., 2019; Soria et al., 2021). Additionally, their ability to traverse vast stretches of open ocean provides further evidence for their potential presence in geographically isolated regions such as the Maldives archipelago (Lea et al. 2015). The bull shark is a large, slow-growing species with a total length that usually ranges between 257 cm and 314 cm, with a maximum length reported of 400 cm (McCord and Lamberth, 2009) and a sexual dimorphism where females grow slightly larger than males (Wintner et al., 2002; Cruz-Martinez et al., 2005).

Diving centres and safari boats in the Maldives have claimed the presence of bull sharks for many years, especially in coastal areas where fish waste discharge happens and shark feeding is carried out. Despite the significant presence and ecological importance of *C. leucas*, only few unsustainable reports and no verified records of this species in the Maldives are available in literature (Voigt and Weber, 2011; Ali and Sinan, 2015).

During a 10-year period between 2013 and 2023, a total of 23 sightings of *C. leucas* were reported in various dive sites throughout the central and southern atolls of the Maldives. The study area included the central atolls of Kaafu Atoll, Alifu Dhaalu Atoll, Meemu Atoll and Southern Atolls of Gaafu Alifu and Gnaviyani Atoll (Figure 1).

the Maldives: A) Alifu Dhaalu Atoll; B) Kaafu Atoll; C) Gaafu Alifu Atoll; D) Meemu Atoll; and E) Gnaviyani Atoll. Each location account for single or multiple sightings. Map created by MapTiler loaded in QGIS.

4.3 MATERIAL AND METHODS

The sightings were obtained through different techniques and provided by different group of people: the older records were collected by opportunistic sightings made by the safari boat crew of "Island Safari 1" between 2013 and 2020, confirmed by video evidence; the other records were obtained from visual census and video recording during diving activities of the White Wave Maldives diving team in 2022 and 2023. In addition, one of the sightings was captured using drifting Baited Remote Underwater Video Station (BRUVS; Supporting video 13) systematically deployed by the authors over the last two years to survey the shark population in the Maldivian central and southern atolls. In the latter, BRUVS were placed at 25 m in front of Koddoo fish factory harbour in Gaafu Alifu atoll, for a total time of 73 minutes. Each image and video collected was analysed to confirm the accuracy of the species identification based on the morphological description provided by Smith et al. (1997) stating that *C. leucas* is a stout shark with a short, broad blunt snout, and small eyes, and lack of an interdorsal ridge. However, these characteristics may not be sufficient to distinguish this species, as sharks belonging to the genus *Carcharhinus* pose a challenge in identification due to the presence of numerous similar-looking species within the genus. Specifically, in the case of *C. leucas*, the species is often prone to misidentification and confusion with its close relative, the sibling species *C. amboinensis* (Pigeye shark, Müller & Henle, 1839). Since the available data only consist of images and videos obtained from our observations or citizen science, genetic or further analyses cannot be conducted. Instead, to provide support in distinguishing and differentiating these closely related species, a thorough examination of the morphometric features has been employed. In fact, the ratio of the first to the second dorsal fin has been used as the sole investigative method based on the multimedia materials. Specifically, if the aforementioned ratio exceeds 3.1:1, the species would be classified as *C. amboinensis* (Brunnschweiler & Compagno, 2008). However, in the present study, all the specimens exhibited a ratio equal or below 3.1:1, confirming their positive identification as *C. leucas* (Figure 2). Furthermore, the sex of the individuals has been defined by presence or absence of claspers according to Hendon et al. (2013).

After the collection of data and analyses, the sightings of *C. leucas* were associated with all the relevant metadata: dive site, conformation of the site, depth, number of individuals, sex of the specimens and the presence of chum in the water during the observation (Table 1).

Regarding the sites considered in the study area, three different categories of site conformation were considered: House Reef, Kandu, and Thila. The term "*House Reefs"*, instead, refers to coral reefs placed in front of local island and resorts, easily accessible from the land. The Dhivehi (Maldivian local language) term "*Kandu"* refers in to the channel entrance found on the outer island that limit the atolls. These sites are usually recognized as important aggregation spots for pelagic fauna, including predatory fishes like sharks, thus attracting a significant number of recreational divers. The term "*Thila", instead,* refers to the submerged pinnacles found inside atolls or channels, usually characterized by a top reef at around 10-15m.

Moreover, the presence of feeding activities was evaluated in each site to differentiate the sightings that occurred in baited/feeding situation from those occurred in natural situations.

4.4 RESULTS AND DISCUSSION

The 23 sightings of *C. leucas* were spread in seven different locations in the central and southern atolls, 18 of which were observed in House Reefs where feed was often present. The most recurrent site, with 13 sightings, was the dive site located in front of Hulhumale House Reef (Figure 1B; Figure 3). This higher occurrence can be explained by the presence of significant amount of fish waste repeatedly discharged by fish factories, diving centres, and safari boats especially in the morning and afternoon. Further evidence of the attraction related to feeding is given by the other 5 sightings recorded in front of Koddoo House Reef (Supporting information 1), where similar feeding conditions are present, as well as one individual sighted close to the Fuvahmulah harbour entrance in Gnaviyani Atoll (Supporting information 2), where diving centres exploit feeding to attract tiger sharks, *Galeocerdo cuvier* (Péron and Lesueur, 1822).

Among the remaining sightings, 4 occurred in *Kandu*, in particularly Nilandhoo Kandu (Supporting Video 14, 15) and Maamendhoo Kandu (Supporting video, 16), where *C. leucas* were sighted on the drop-off of the channels. In Muli Kandu (Supporting information 3), a female *C. leucas* was sighted on the corner and another large female was spotted cruising at 26 m in Bodufinholu Thila (Supporting information 4).

The videos recorded in Nilandhoo and Maamendhoo Kandu (Supporting video 14, 15, 16) showed how the presence of *C. leucas* creates a high level of disturbance among *C. amblyrhynchos* aggregations, causing them to flee from its predatory behaviour. While the behaviour exhibited in channels may suggest a prevalence or even a predatory behaviour of *C.*

leucas over *C. amblyrhynchos*, in other locations, such as Hulhumale and Koddoo House Reefs, bull sharks were sighted alongside *C. brevipinna* and *C. amblyrhynchos* (Bleeker, 1856), appearing to coexist even with the presence of feed in the water. This may be related to the different personalities that different specimens of one shark species can exhibit, as it was reported by Dhellemmes et al. (2021). Through the examination of the images captured on both identical and distinct days, we have successfully distinguished two distinct individuals: a female displaying an absent lower caudal lobe (Figure 3C, Supporting information 5,6) and another female characterized by the absence of the tip of the first dorsal fin (Figure 3A, 3B).

Although there are not enough observations to hypothesize a possible social interaction or aggregation among different individuals, it is known that the presence of feed in the water can attract different shark species at once (Brunnschweiler et al. 2014). In this context, a recent study has demonstrated that shark feeding facilitates the development of social association between *C. leucas* (Bouveroux et al., 2021).

The individual recorded by one of the two drifting BRUVS systems deployed at Koddoo House Reef, instead, was sighted after 49 min swimming under the video station and returned at 57 min without showing any interest in the bait in both the occasions. This suggest that this species is present in the area beside the presence of bait, possibly confirming its typical distribution in shallow coastal waters (Erbert et al., 2013) with most of the observations in House Reefs.

In the 23 bull shark sightings, a total of 30 individuals were counted, with 25 identified as females, 2 as males, and 3 of undetermined sexes due to poor visibility conditions and video quality. Hence, the majority of the *C. leucas* observed were adult females, especially at Hulhumale House Reef where no males were recorded among the individuals observed. While this database certainly requires further development, these observations suggest a trend towards female dominance, consistent with the sex-based aggregation patterns observed both in this species (Werry and Clua, 2013) and other species, such as *C. amblyrhynchos* (Economakis et al., 1998), *C. melanopterus* (Speed et al., 2011), and *Sphyrna lewini* (Scalloped hammerhead shark, E. Griffith & C. H. Smith, 1834; Klimley et al., 1987). Moreover, the observations of bull sharks in the channel drop-off and their active predatory behaviour (Supporting video 14, 15 and 16) may indicate that this area function as a potential hunting ground for these sharks, with *C. amblyrhynchos* being a potential prey, as observed with *Sphyrna mokarran* (Great hammerhead shark, Rüppell, 1837; Mourier et al, 2013).

We recognize the importance of gathering additional data to enhance our understanding of the biology and ecology of *C. leucas*. However, it is crucial to highlight that our ten-year study strongly verifies the presence of this species in the region. The extent of spatial connectivity between the Maldivian population of bull sharks and other populations in the Indian Ocean remains largely unknown, necessitating further investigation that only tagging studies, along with the use of acoustic or satellite telemetry, could reveal. Currently, there is a lack of knowledge regarding the migration behavior of bull sharks in the North and Central Indian Ocean, despite its potential for interesting population connections. Sightings of bull sharks have been recorded in various locations, including the Seychelles, the continental coast of the Indian Subcontinent, Sri Lanka and Reunion Island (Nevill et al., 2013; Fernando, 2014; Hoarau et al., 2021; Blaison et al., 2015). This remarkable distribution raises intriguing questions about their reproductive behavior, as they rely on low-salinity environments like estuaries, river mouths, and freshwater rivers (Heupel et al., 2007; Snelson et al., 1984; Tillet et al., 2012; Gausmann et al., 2021). Therefore, it is more plausible that the Maldives serves as a foraging ground for adult bull sharks rather than a primary region for reproduction or nursery areas, as supported by our observations predominantly consisting of large female individuals. Understanding the location of nursery areas for the Maldivian population becomes therefore crucial to provide insights into the complex ecological dynamics and spatial distribution of bull sharks in the vast expanse of the Indian Ocean.

Furthermore, advancing our understanding of the ecological dynamics related to bull sharks can assist authorities in formulating effective conservation strategies to protect this species and enhance our overall comprehension of its role within the Maldivian ecosystem, as well as contribute to shark diving tourism in the Maldives thanks to this iconic species.

4.5. REFERENCES

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4.6. TABLES

Table 1. Overview of *Carcharhinus leucas* records in the Maldives analyzed by the authors. (H.R. = House Reef; n.d. = non detected).

Date	Dive Site	Atoll	Site charactreristics	Depth (m)	No. Individuals	Sex	Food Provisioning	Methods	Estimated size (m)
2013-05-13	Furana Kandu	Kaafu	Kandu	28	1	n.d.	no	Video Record	2- 2.5
2016-03-16	Bodufinholu Thila	Alifu Dhaalu	Thila	26	1	Female	no	Video Record	2.5 - 3
2017-04-09	Muli Kandu	Meemu Atoll	Kandu	25	1	Female	no	Video Record	2.5 - 3
2018-02-05	Nilandhoo Kandu	Gaafu Alifu	Kandu	35	1	Female	no	Video Record	2.5 - 3
2021-02-20	Maamendho Kandu	Gaafu Alifu	Kandu	30	1	Female	no	Video Record	2.5 - 3
2022-02-19	Koddoo H.R.	Gaafu Alifu	House Reef	38	1	Female	yes	Visual Census	2- 2.5
2022-02-23	Koddoo H.R.	Gaafu Alifu	House Reef	35	1	Female	yes	Visual Census	2- 2.5
2022-04-10	Hulhumale H.R.	Kaafu	House Reef	30	2	Female Female	yes	Video Record Video Record	2.5 - 3 2.5 - 3
2022-04-30	Hulhumale H.R.	Kaafu	House Reef	40	3	Female Female Female	yes	Visual Census	2- 2.5 2.5 - 3 2.5 - 3
2022-05-01	Hulhumale H.R.	Kaafu	House Reef	25	1	Female	yes	Visual Census	2.5 - 3
2022-05-08	Hulhumale H.R.	Kaafu	House Reef	40	1	Female	yes	Visual census	2- 2.5
2022-05-13	Hulhumale H.R.	Kaafu	House Reef	20	1	Female	yes	Video record	2.5 - 3
2022-06-22	Fuvahmulah	Gnaviyani	House Reef	10	1	Male	yes	Video Record	1.5 - 2
2022-11-24	Hulhumale H.R.	Kaafu	House Reef	40	1	n.d.	yes	Visual Census	2- 2.5
2023-03-02	Koddoo H.R.	Gaafu Alifu	House Reef	25	1	n.d.	yes	BRUV	2
2023-03-09	Koddoo H.R.	Gaafu Alifu	House Reef	35	1	Male	no	Video Record	2.5
2023-04-02	Hulhumale H.R.	Kaafu	House Reef	30	1	Female	no	Video Record	2.5 - 3
2023-04-09	Hulhumale H.R.	Kaafu	House Reef	30	1	Female	yes	Video Record	3
2023-05-06	Hulhumale H.R.	Kaafu	House Reef	30	2	Female Female	yes	Video Record Video Record	2.5 - 3 2.5 - 3

2023-05-06	Hulhumale H.R.	Kaafu	House Reef	30	2	Female	yes	Video Record	2.5 - 3
						Female		Video Record	2.5 - 3
2023-05-07	Hulhumale H.R.	Kaafu	House Reef	30	1	Female	no	Video Record	2- 2.5
2023-05-08	Hulhumale H.R.	Kaafu	House Reef	30	1	Female	yes	Visual census	2- 2.5
2023-05-13	Hulhumale H.R.	Kaafu	House Reef	30	3	Female	yes	Video Record	2.5 - 3
						Female		Video Record	2.5 - 3
						Female		Visual Census	2.5 - 3

4.7. FIGURES

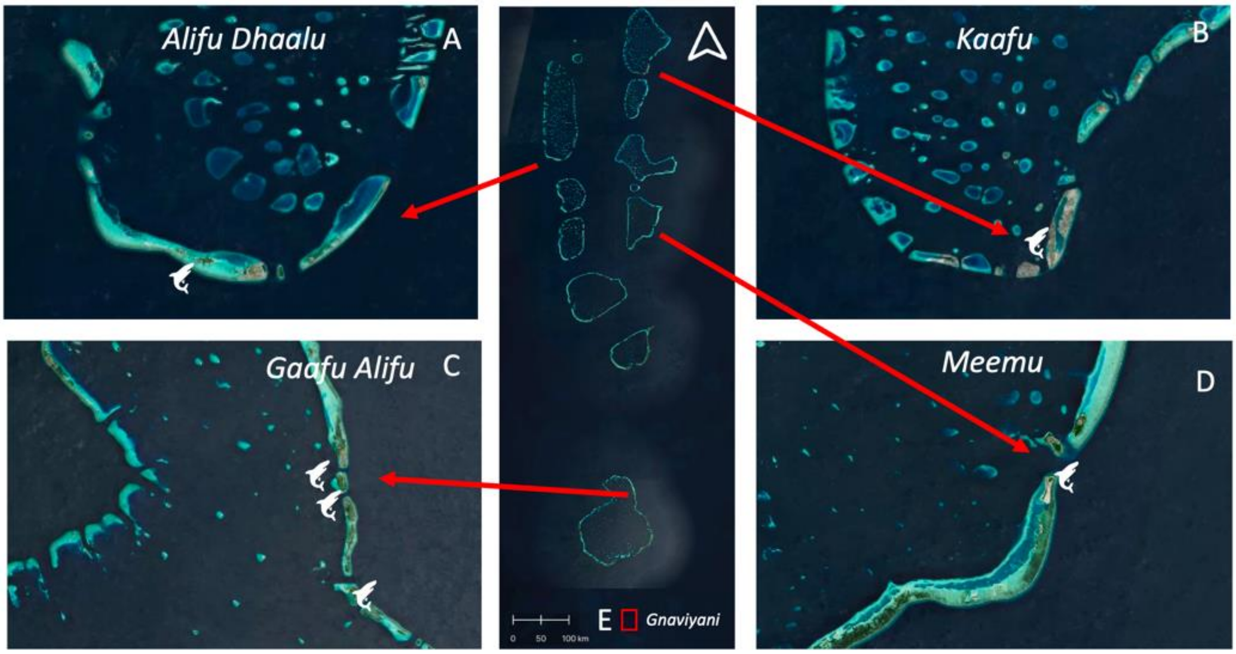


Figure 1. Overview of *Carcharhinus leucas* sightings locations displayed by shark icons in white colour around

Figure 2. Visual example of the first-second dorsal fin ratio. The specimen exhibited a ratio slightly below < 3.1:1 confirming the species identification as *Carcharhinus leucas*.

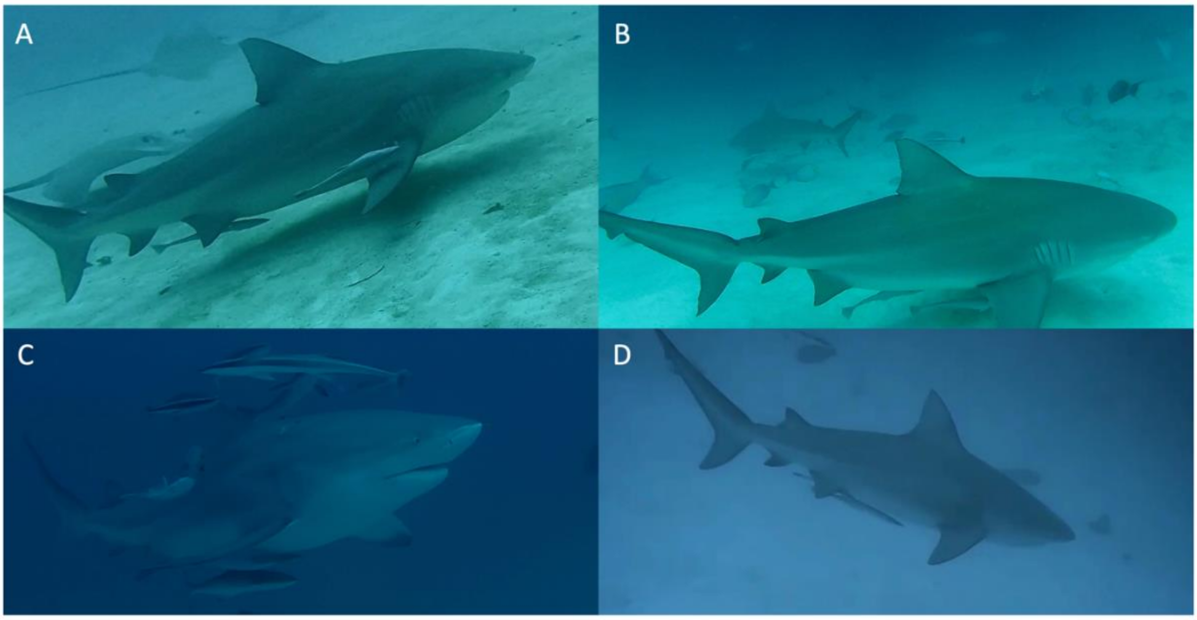


Figure 3. Examples of *Carcharhinus leucas* individuals sighted and recorded in Hulhumale House Reef on: A) 02nd April 2023 B) 06th May 2023 C) 10th April 2022 D) 13th May 2022

4.8. SUPPORTING INFORMATION

Supporting information 1 - 09 March 2023 Koddoo

Supporting information 2 - 22 June 2023 Fuvahmulah

Supporting information 3 - 09 April 2017 Muli Kandu

Supporting information 4 - 16 March 2016 Bodufinholu Thila

Supporting information 5 - 09 April 2023 Hulhumale

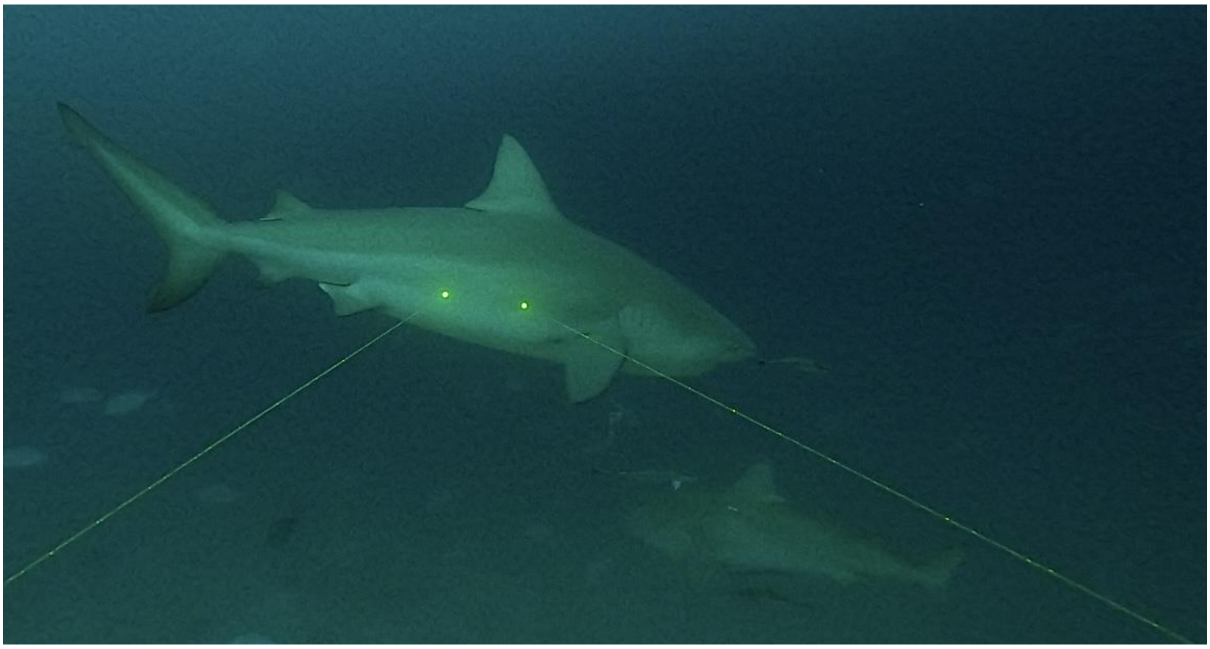
Supporting information 6 - 10 April 2022 Hulhumale

Supporting information 7 - 13 May 2013 Furana Kandu

Supporting information 8 - 08 May 2022 Hulhumale

Supporting information 9 - 10 April 2022 Hulhumale

Supporting information 10 – 6 May 2023 Hulhumale



Supporting information 11 - 13 May 2023 Hulhumale

Supporting information 12 - 07 May 2023 Hulhumale

CHAPTER 5

The Phenomenon of Piebaldism in Sharks: A Review of Global Sightings and Patterns.

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5.1 ABSTRACT

Chromatic disorders in elasmobranchs (sharks and rays) have been reported in several species, but little is known about their true abundance or consequences for survival and fitness. Piebaldism, a form of leucism characterized by partial loss of pigmentation, is among the rarest and least understood chromatic disorders reported in elasmobranchs. We conducted an extensive assessment of published and unpublished cases of piebaldism observed in sharks in the wild. Here, we report the observation of 25 incidences of this condition witnessed in 17 species of sharks from 11 families (Carcharhinidae, Dalatiidae, Galeocerdonidae, Ginglymostomatidae, Hexanchidae, Heterodontidae, Lamnidae, Odontaspidae, Scyliorhinidae, Squatinidae, and Sphyrnidae). The anatomical distribution and severity varied across shark families, with Ginglymostomatidae showing widespread aberrations on the flanks and pectoral fins, while piebaldism in Galeocerdonidae is more restricted. A single Sphyrnidae individual exhibited piebaldism across its body, while in the speciose Carcharhinidae family, piebaldism varied widely in intensity and distribution. We further discuss the taxonomic and geographical distribution of piebaldism reports, the potential fitness consequences, and uncertainty regarding the terminology used to discuss chromatic disorders in elasmobranchs. Finally, we comment on the importance of ecotourism and citizen science for improving our understanding of rare phenotypic conditions in marine megafauna such as elasmobranchs.

5.2 INTRODUCTION

Coloration is an important component of phenotype in most animals, facilitating the transfer of information between conspecifics, competitors, and potential predators (Johnstone, 1997). Research into the genetic basis of coloration, its ecological consequences, and evolution across generations has progressed rapidly since the 19th century (Baker and Parker, 1979; Cuthill et al. 2017). The spectrum of colors observed in the animal kingdom is now known to be produced by combinations of pigments and nanostructures (Shawkey and D'Alba, 2017). Genetically entrained intraspecific variation in coloration is relatively common across the animal kingdom and is frequently adaptive (McKinnon and Pierotti, 2010; Roulin, 2004). However, an array of chromatic disorders has also been described in animals, where individuals display abnormal pigmentation that appears to serve no adaptive benefit (e.g., Lucati and López-Baucells, 2017). Documenting chromatic disorders across animal diversity is key if we are to understand the true genetic basis of coloration and the consequences of disruption to 'wild' coloration for ecology and evolution.

Elasmobranchs, comprising sharks, rays, and skates, are a diverse and ancient group of cartilaginous fishes within the class Chondrichthyes. Originating around 383 million years ago (Frey et al. 2019), they have evolved a wide range of adaptations that enable them to thrive in various marine and freshwater environments (Compagno, 1999). Elasmobranchs play crucial ecological roles in aquatic ecosystems, namely as apex and mesopredators (Braasch et al. 2009; Stevens et al. 2000; Ebert et al. 2021; Dedman et al. 2024). Their evolutionary success and ecological significance make them a key focus of marine biological research and key indicators of a healthy marine ecosystem. Various pigmentation anomalies have been documented in sharks, apparently resulting from genetically inherited chromatic disorders (Quigley et al. 2018; Ratão et al. 2023; Shipley et al. 2023). In vertebrates, these disorders are typically classified as hypermelanosis or hypomelanosis, an excess or deficiency of pigmentation, respectively (Arronte et al. 2022). The term 'melanosis' refers to levels of the pigment melanin, which is among the primary determinants of animal colour (Bian et al. 2021).

Hypomelanosis in vertebrates can be categorized broadly as albinism, leucism, and a variation of leucism is defined as piebaldism. Albinism is a genetically inherited hypomelanistic condition characterized by the complete absence of pigmentation in the integumentary system and retina, resulting in an individual lacking dark pigments throughout the entire body, including the eyes (Clark, 2002; Ratão et al. 2023). In contrast, leucism is a hypomelanistic disorder where pigmentation is reduced or absent, but the extremities and eyes retain some color representative of the species (Bechtel, 1995; Clark, 2002; Ramos-Luna et al. 2022). Piebaldism is a rare autosomal dominant variation of leucism that leads to a partial loss of pigmentation across the body or fins while leaving the eyes normally pigmented. It typically manifests as white or pale patches on the otherwise normally pigmented body of the shark, caused by a genetic mutation affecting the anatomical distribution of melanin (Kelsh et al. 1996; Fertl and Rosel, 2009; Leroux et al. 2022; Shipley et al. 2023).

In the wild, piebaldism in sharks is rarely documented and largely unstudied relative to more commonly observed animals, such as terrestrial birds and mammals (Baker, 1981; Baker and Lott, 1983; Bennett and Cuthill, 1994; Crawford, 1990; Jensen and Møller, 2015). The absence of pigmentation in other animals is frequently linked to various health issues, including deficiencies, malformations, behavioral changes, and reduced survival rates (Corn 1986; Kehas et al. 2005; Perrault and Coppenrath 2019; Krecsák, 2008; Ratão et al. 2023; Slavik et al. 2015, 2016). However, shark skin depigmentation is poorly studied compared to other aspects of their biology, leading to an incomplete understanding of the causes and consequences of abnormal pigmentation in chondrichthyans. This study aims to consolidate and review all observed instances of piebaldism in sharks, providing a foundational knowledge base for future research and offering insights into this pigmentation anomaly and its potential fitness consequences in these iconic predators.

5.3 MATERIAL AND METHODS

Data Search and Filtering

This study compiled both published and unpublished records of piebaldism observed in sharks from public and scientific observations. Piebaldism is defined as a localized absence of pigmentation, resulting in a variable patchy distribution of dark and white areas (Abreu et al. 2013). Piebaldism is sometimes referred to as partial albinism (consequently some of the reports included here were originally categorized as albinism rather than piebaldism), however, it differs from this condition in that coloration of the eyes is not typically disrupted (Abreu et al. 2013).

A comprehensive evaluation of published studies in peer-reviewed journals was carried out by exploring scientific literature in web databases such as SCOPUS, Google Scholar, and Web of Science. During our search for relevant papers, we utilized various combinations of keywords, including: ‘piebaldism’, ‘sharks’, ‘cartilaginous fish’, ‘elasmobranch’,’ ‘albinism’ ‘leucism’ ‘chromatic disorders,’ ‘pigmentation anomalies’ along with phrases like “rare sightings” and “first reports”. Following this, data regarding the species, sex, location, year of record, and the type of record (e.g., dive observation, public observation, fishing interaction) were extracted.

Upon finding a scientific paper, we explored its references and citation records to uncover additional relevant sources. Unpublished records were gathered from a variety of platforms, including websites, Citizen Science platforms, social media, and personal communications. We extracted the same sighting metadata (species, sex, location, etc) from these unpublished sources as we did from the published records. Unverifiable records, or those where chromatic disorders other than true piebaldism (e.g., leucism, or partial/complete albinism) could not be ruled out, were excluded.

5.4 RESULTS

Piebaldism Sightings in Sharks

A total of 25 reports of piebaldism in sharks were identified spanning 17 species across 7 different orders – Carcharhiniformes, Heterodontiformes, Hexanchiformes, Lamniformes, Orectolobiformes, Squatiniform, and Squaliformes – and covering 11 families: Carcharhinidae, Dalatiidae, Galeocerdidae, Ginglymostomatidae, Heterodontidae, Hexanchidae, Lamnidae, Odontaspididae, Scyliorhinidae, Squatinidae, and Sphyrnidae (Table 1). Comparing the prevalence of piebaldism across these clades, the order Carcharhiniformes showed the highest number of recorded cases, with 10 species affected. Within this order, the family Carcharhinidae (requiem sharks) was the most impacted, accounting for 7 species. In contrast, each of the other nine families had only a single species affected (Table 1). It is important to note that this pattern may reflect sampling bias rather than a true biological prevalence, as Carcharhinidae includes many coastal and commercially important species that are more frequently encountered in fisheries bycatch and scientific surveys. Collectively records date back to 1952, with the most recent observations occurring in September 2024. The geographic distribution of these sightings was broad but biased, with the majority of observations concentrated in the Indian Ocean. This was followed by a significant number in the Atlantic Ocean and the Mediterranean Sea, while the Eastern Pacific Ocean and other regions had fewer sightings overall. This uneven spatial pattern likely mirrors global disparities in sampling effort, with higher observation frequencies in regions with more active fisheries, tourism, or scientific monitoring programs. Additionally, there were isolated observations recorded in the Gulf of Mexico, the Caribbean Sea, the Irish Sea, and the Arabian Sea.

Distribution and Severity of Piebaldism

The anatomical distribution and severity of piebaldism varied among species and families (Figure 1). In the Ginglymostomatidae family, individuals consistently exhibited color aberrations that extended across their entire flanks and both pectoral fins (Figure 1 G-K). In contrast, members of the Galeocerdonidae family consistently displayed abnormalities only on the leading edges of their pectoral and first dorsal fins, with no noticeable markings elsewhere (Figure 1 T-V). The single individual from the Sphyrnidae family showed clear piebaldism across its entire body and fins, particularly on the sides of its head and caudal fin (Figure 1L), where pigmentation was absent compared to the rest of its flanks similar to individuals observed with Scyliorhinidae (Figure 1S), Dalatidae (Figure 1E), Hexanchidae (Figure 1C) and Odontaspidae (Figure 1O). Among the Carcharhinidae family (Figure1 A, B, M, N, R, X), which has the most diverse range of species, individuals exhibited a wide variety of piebaldism intensities. Some individuals showed similar patterns or tendencies across their pectoral fins and bodies, while others displayed abnormalities only in specific areas, such as the lower part of the caudal fin or around the gills.

5.5 DISCUSSION

Our goal was to collect information on this rare chromatic disorder in sharks and establish a comprehensive global baseline regarding the prevalence of these pigmentation anomalies among this group of marine predators. Cumulatively, existing reports of piebaldism in sharks cover six of the nine extant orders (Weigmann et al 2011), with only Echinorhiniformes and Pristiophoriformes lacking confirmed reports, which may be due to the fact that they are seldomly caught in fisheries and for the most part inhabit deep sea environments or remote benthic zones (Table 1). Indeed, this absence is likely due to limited sampling opportunities:

Echinorhiniformes are deep-water species that are rarely observed or captured, while Pristiophoriformes (sawsharks) are relatively rare and have restricted distributions, making encounters uncommon in most survey and fishery contexts. The majority of existing reports are from Carcharhiniformes, which is not overly surprising given that this is the most speciose order of sharks (Ebert et al. 2021). Moreover, considering their spatial distribution and habitat usage, Carcharhiniformes species are frequently observed in coastal and reef environments by recreational fishers and ecotourists, further increasing the likelihood of encountering individuals with rare chromatic disorders, and consequently reported. Chance observations by recreational fishers or ecotourists would be far less likely in the case of taxa that occur exclusively in pelagic or deep-water environments. Consequently, on the basis of the limited existing data, there is no reason to suggest that piebaldism is more prevalent in some shark lineages than others, and we consider the taxonomic bias observed to be merely symptomatic of biased sampling.

Piebaldism remains a rare and understudied condition in sharks across various orders and species. Genetic studies in zebrafish (*Danio rerio*) have established that one of the genes implicated in this disorder is the *kit* (kit receptor tyrosine kinase) gene, mutations of which led to dysfunctions in melanophores, disrupting their development, migration, and survival (Parichy et al. 1999). Infectious diseases caused by parasites or bacteria can also change skin appearance by targeting pigment cells or causing lesions. Nutritional deficiencies, particularly a lack of essential vitamins and minerals, can adversely affect skin health and pigmentation. Furthermore, environmental stressors, such as fluctuations in temperature and salinity, as well as exposure to chemicals and pollution, particularly in urban areas, may be drivers of changes in skin coloration. Understanding the multifactorial nature of skin coloration in sharks is essential for comprehensively addressing the causes of piebaldism and other pigmentation anomalies. Moreover, recent studies have linked skin pigmentation disorders in fishes to exposure to toxic elements such as copper and mercury (Nur et al. 2019; Qu et al. 2023). Considering both the genetic basis and the potential ecotoxicological factors that may trigger this effect, it would be valuable for future research to investigate the genetic basis of piebaldism in elasmobranchs, and the extent to which observed cases may be explained by environmental pollution. At least four of the reported cases (individuals of *G. cuvier* and *C. brevipinna* sighted in Hulhumale, see Figure 1) were observed in close proximity to residential/industrial areas, which may be consistent with elevated levels of environmental pollutants.

Although depigmentation in sharks can occur on the flanks, head, fins, and dorsal surface, no current studies have systematically examined which regions of the body are most susceptible to this condition. Given the limited sample size in this study and the absence of genetic analyses, it is not yet possible to determine whether specific areas of the body are more prone to piebaldism, or what factors may be influencing the pattern and extent of this condition. Further research, including genetic analyses on larger sample sizes, is needed to provide clearer insight into the factors underlying variation in the anatomical location and intensity of observed piebaldism.

Besides the frequency and taxonomic distribution of piebaldism in sharks, perhaps the most substantial unanswered question regards the consequences (or lack thereof) of piebaldism for individual fitness. As many shark species rely on camouflage to successfully hunt and avoid predation, it has been speculated that abnormal pigmentation could impact survivability by making individuals more conspicuous to both predators and prey (Bottaro et al. 2008). Beyond survival, it is also plausible that abnormal pigmentation could influence growth rates, fecundity, or other components of individual fitness (Denson and Smith, 1999; Dubovskiy et al. 2013). For example, reduced foraging efficiency due to impaired camouflage could limit energy intake and consequently slow growth. In terms of reproduction, conspicuous coloration might alter intraspecific interactions, such as mate recognition or selection, particularly in species that rely on visual cues during courtship (Pratt et al. 2005). Though speculative in the context of sharks, pigmentation-driven sexual selection has been documented in other taxa, and may warrant consideration as a potential, but currently untested, factor influencing fitness in elasmobranchs (Warner et al. 1975, Ball 2024, Dijkstra et al. 2024, Tripathy et al. 2025). However, none of the reported cases of piebaldism in sharks reviewed in this study appear to be associated with any abnormal morphology (Figure 1). In cases where video footage was available, no unusual behavior was observed, and the sharks appeared to swim and interact normally with their environment. While the lack of age data limits precise size assessments, there was no evidence of obvious growth anomalies relative to conspecifics observed in similar contexts. The observation of multiple adult piebald sharks also indicates that piebaldism likely does not drastically reduce survivorship, at least in the few species in which it has been identified. It has previously been suggested that larger-bodied generalist sharks may not suffer fitness consequences from piebaldism due to a relative lack of predators (Shipley et al. 2022), however, this does not explain observations of piebaldism in smaller species with many natural predators, such as *S. canicula* or *H. francisci*. Ultimately, we are fundamentally limited in our ability to determine the fitness costs of piebaldism in sharks as any individuals that do succumb to predation as a direct result of abnormal pigmentation are consumed and hence impossible to observe. Although estimating an expected baseline prevalence of piebaldism across shark species using comparative data from other taxa could, in principle, provide a framework to assess whether observed cases are under- or overrepresented, this would require genetic data and robust assumptions about developmental mutation rates across taxa, both of which are currently unavailable for sharks. Sharks held in laboratories and aquaria provide one potential solution to this issue, but to date, no cases of piebaldism have been published from such facilities.

Moreover, while the precise causes and consequences of piebaldism in sharks remain unclear, it is worth considering whether certain pigmentation anomalies may persist in populations due to neutral or even mildly beneficial effects. For example, in species like the oceanic whitetip shark (*Carcharhinus longimanus*), natural markings include irregular light patches on the tips of fins and body, which bear a superficial resemblance to some piebald patterns documented in this study. Although speculative, it is possible that ancestral piebald-like traits conferred some ecological or social advantage, such as camouflage against the dappled light of the open ocean. In this context, low-level depigmentation may not always be deleterious and could, under certain environmental or behavioral conditions, be selectively neutral or even advantageous (Myrberg, 1990, Wilson and Martin, 2001). This idea aligns with the broader concept that pigmentation anomalies are not always negative, and their persistence may reflect a complex interplay between genetic drift, selection, and context-dependent fitness outcomes. Further comparative and genomic studies could help clarify whether piebaldism in sharks occasionally crosses the threshold from neutral anomaly to adaptive trait.

One notable and recurring issue in the shark pigmentation literature is uncertainty around terminology. Until recently, the term albinism was frequently used to refer to any loss of pigmentation, regardless of its intensity or genetic underpinnings (e.g., Clark, 2002). This has resulted in many cases of leucism (and piebaldism) being mistakenly referred to as cases of complete or partial albinism (see reclassification of misidentified chromatic disorders in Skelton et al. 2024). Misuse of terminology and misclassification of chromatic disorders is a pervasive issue that has hampered research into pigmentation across different vertebrate lineages (Borteiro et al. 2021). Given that albinism and leucism can have distinct genetic underpinnings in other vertebrates, it is crucial to avoid misnomers when classifying chromatic disorders in sharks. All future studies should study ocular pigmentation to distinguish between true albinism and leucism and study the entire external surface of individuals to distinguish between full and partial albinism, and between leucism and piebaldism. Whilst the terms piebaldism and partial leucism are interchangeable, neither is interchangeable with albinism or partial albinism, as these represent genetically and phenotypically distinct conditions.

We encourage scientific societies and the expanding community of divers and ocean users to share their knowledge and data by reporting any sightings of these anomalies they encounter. There is undoubtedly a substantial geographical and taxonomic bias in existing reports of piebaldism and chromatic disorders in general. This bias will only be overcome through collaboration between researchers, commercial, artisanal, and recreational fishers, as well as with the collaboration of ecotourists, divers, and citizen scientists. Indeed, citizen science projects have been key to the study of chromatic disorders and pigmentation in other taxa (Aguillon and Shultz, 2023; Drury et al. 2019; Paiva et al. 2023). Whilst few of the reports in this study originated from citizen science projects, collaborations between researchers and the public have previously provided key insight into shark behavior and ecology (Séguigne et al. 2023; Whitehead and Gayford, 2023; Parmegiani et al. 2023; Gobbato et al. 2024). This is reflected also by our findings showing an increase in sightings in recent years, with 2024 recording the highest number of sightings. This surge is likely linked to the rise of citizen science and the growing popularity of recreational diving, engaging more people in marine ecotourism and documenting their experiences through social media and other platforms, which in turn contributes to a higher volume of recorded sightings (Gibson et al. 2019; Bargagnesi et al. 2020). Indeed, among the recorded species, *G. cirratum* stands out as the most frequently sighted, as one of the most likely interacting species in marine ecotourism. In contrast, earlier sightings, such as those from the 1950s, reflect a more limited scope of shark documentation, often tied to scientific publications or isolated fishing interactions. Today, however, the increased engagement of the public in marine conservation and documentation efforts has broadened the scope of our understanding of shark populations globally, reflecting the growing awareness of marine conservation and the role that both professionals and citizen scientists play in enhancing our understanding of shark ecology and biology. There is thus hope that future increases in the user bases of shark-focused citizen science projects may help improve our understanding of chromatic disorders. To support this, we encourage divers, underwater photographers, and ocean users to report sightings through established platforms such as iNaturalist, SharkPulse, GBIF.org, or local biodiversity monitoring apps, and to include details on pigmentation anomalies when possible. Clear documentation, including photographs, videos, date, location, and depth, can greatly enhance the value of these records for scientific analysis. Expanding this participatory approach may further close taxonomic and geographic gaps in the detection of piebaldism and other rare phenotypes.

Our comprehensive assessment of piebaldism in sharks reveals a notable prevalence of this rare chromatic disorder across various species and families, highlighting its potential underrepresentation in the existing literature. While our findings indicate that piebaldism is widespread, particularly within the Carcharhinidae family, the implications of this condition for individual fitness and survival remain largely unexplored. Given the potential ecological consequences, further research is essential to understand how abnormal pigmentation may influence predator-prey interactions and overall fitness. Collaboration with the broader community, including citizen scientists and divers, will be crucial in expanding our knowledge and addressing the geographical and taxonomic biases evident in current reports. By fostering such partnerships, we can enhance our understanding of piebaldism and its role within the dynamic ecosystems inhabited by these remarkable elasmobranchs.

Although many questions remain unanswered, our study highlights the potential of this research area and lays the groundwork for future discoveries. While recent advances in understanding the genetics of coloration have provided a foundation for studying chromatic disorders, much remains to be uncovered about the environmental and genetic factors driving piebaldism in sharks. Therefore, we believe that future analysis should also investigate the environmental and ecotoxicological aspects of this phenomenon, especially for piebald individuals frequently observed at provisioning sites and in close proximity to urban areas. In a globally changing climate, sharks face multiple stressors including increasing polluted environments and temperature shifts affecting their habitats. Further analysis of these rarely sighted individuals may offer valuable insights into their ecology and adaptation to the environments in which they live.

The rise of citizen science and recreational diving has significantly increased the visibility of shark sightings, offering an invaluable opportunity to gather more data on these anomalies. As seen with *Galeocerdo cuvier* and *Ginglymostoma cirratum*, commonly sighted species in ecotourism, engaging the general public in research will be essential to uncover the frequency and potential consequences of piebaldism in these and other species. Moving forward, a multidisciplinary approach combining genetics, ecotoxicology, and citizen science could provide critical insights into the causes and ecological implications of pigmentation disorders in sharks, ultimately enhancing our broader understanding of elasmobranch anomalies.

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5.7. TABLES

Sighting	Common Name	Species	Sighting type	Location	Year	Source
A	Oceanic black tip shark	*Carcharhinus limbatus* (Müller & Henle, 1839)	Fishing Interaction	Texas, USA	2015	Media Report
B	Blacktip Reef shark	*Carcharhinus melanopterus* (Quoy & Gaimard, 1824)	Observation	Maldives	2023	Social media mining
C	Broudnose Sevengill shark	*Notorynchus cepedianus* (Péron, 1807)	Fishing Interaction	Monterey Bay, California, USA	1952	Published Ebert, 1985
D	California Horn shark	*Heterodontus francisci* (Girard, 1855)	Dive Sighting	La Jolla, California, USA	2019	Published Skelton et al., 2024
E	Kitefin shark	*Dalatias licha* (Bonnaterre, 1788)	Fishing Interaction	Genoa, Italy	2003	Published Bottaro et al., 2008
F	Lemon shark	*Negaprion brevirostris* (Poey, 1868)	Fishing Interaction	Florida, USA	2023	Social media/ Media Report
G	Nurse shark	*Ginglymostoma cirratum* (Bonnaterre, 1788)	Dive Sighting	Black Point, Bahamas	2013	Social media
H	Nurse shark	*Ginglymostoma cirratum* (Bonnaterre, 1788)	Dive Sighting	Maio Island, Cabo Verde	2015	Published, Ratão et al., 2023
I	Nurse shark	*Ginglymostoma cirratum* (Bonnaterre, 1788)	Dive Sighting	Turks & Caicos islands,	2016	Media Report
J	Nurse shark	*Ginglymostoma cirratum* (Bonnaterre, 1788)	Dive Sighting	Utila, Honduras	2022	Published Shipley et al.,2022
K	Nurse shark	*Ginglymostoma cirratum* (Bonnaterre, 1788)	Dive Sighting	East Bahia Honda, Florida Keys, USA	2023	Published Becker etal.,2023
L	Scalloped Hammerhead shark	*Sphyrna lewini* (Griffith & Smith, 1834)	Dive Sighting	Fotteyo, Maldives	2014	Unpublished
M	Silky shark	*Carcharhinus falciformis*	Observation	San Jose Del Cabo, Mexico	2024	Unpublished

		(Müller & Henle, 1839)				
N	Silky shark	*Carcharhinus falciformis* (Müller & Henle, 1839)	Observation	Cabo San Lucas, Mexico	2024	Unpublished
O	Smalltooth Sandtiger shark	*Odontaspis ferox* (Risso, 1810)	Fishing Interaction	Keeling Islands, Greece	2004	Published Fergusson et al., 2007
P	Small Spotted Catfish shark	*Scyliorhinus canicula* (Linnaeus, 1758)	Fishing Interaction	Tunisia	2009	Published Mnasri et al., 2010
Q	Spadenose shark	*Scoliodon laticaudus* (Müller & Henle, 1839)	Fishing Interaction	Mangalore, India	2006	Published Veena et al., 2011
R	Spinner shark	*Carcharhinus brevipinna* (Müller & Henle, 1839)	Dive Sighting	Hulhumale, Maldives	2024	Unpublished
S	Spotted Dogfish shark	*Scyliorhinus canicula* (Linnaeus, 1758)	Fishing Interaction	Irish Sea	2017	Published Quigley et al., 2018
T	Tiger shark	*Galeocerdo cuvier* (Péron & Lesueur, 1822)	Dive Sighting	Hulhumale, Maldives	2023	Unpublished
U	Tiger shark	*Galeocerdo cuvier* (Péron & Lesueur, 1822)	Dive Sighting	Hulhumale, Maldives	2024	Unpublished
V	Tiger shark	*Galeocerdo cuvier* (Péron & Lesueur, 1822)	Dive Sighting	Hulhumale, Maldives	2024	Unpublished
W	Whitetip Reef shark	*Triaenodon obesus* (Rüppel, 1837)	Dive Sighting	Miyaru Kandu, Maldives	2019	Unpublished
X	Great White shark	*Carcharodon carcharias* (Linnaeus, 1758)	Observation	Saros Bay Turkey	2020	Published Kabaskal et al., 2020
/	Angel Shark	*Squatina Squatina* (Linnaes, 1758)	Report	Gran Canaria	2021	Published Jimenez-Alavarado et al., 2023

Table.1 complete overview of all sightings

5.8. FIGURES

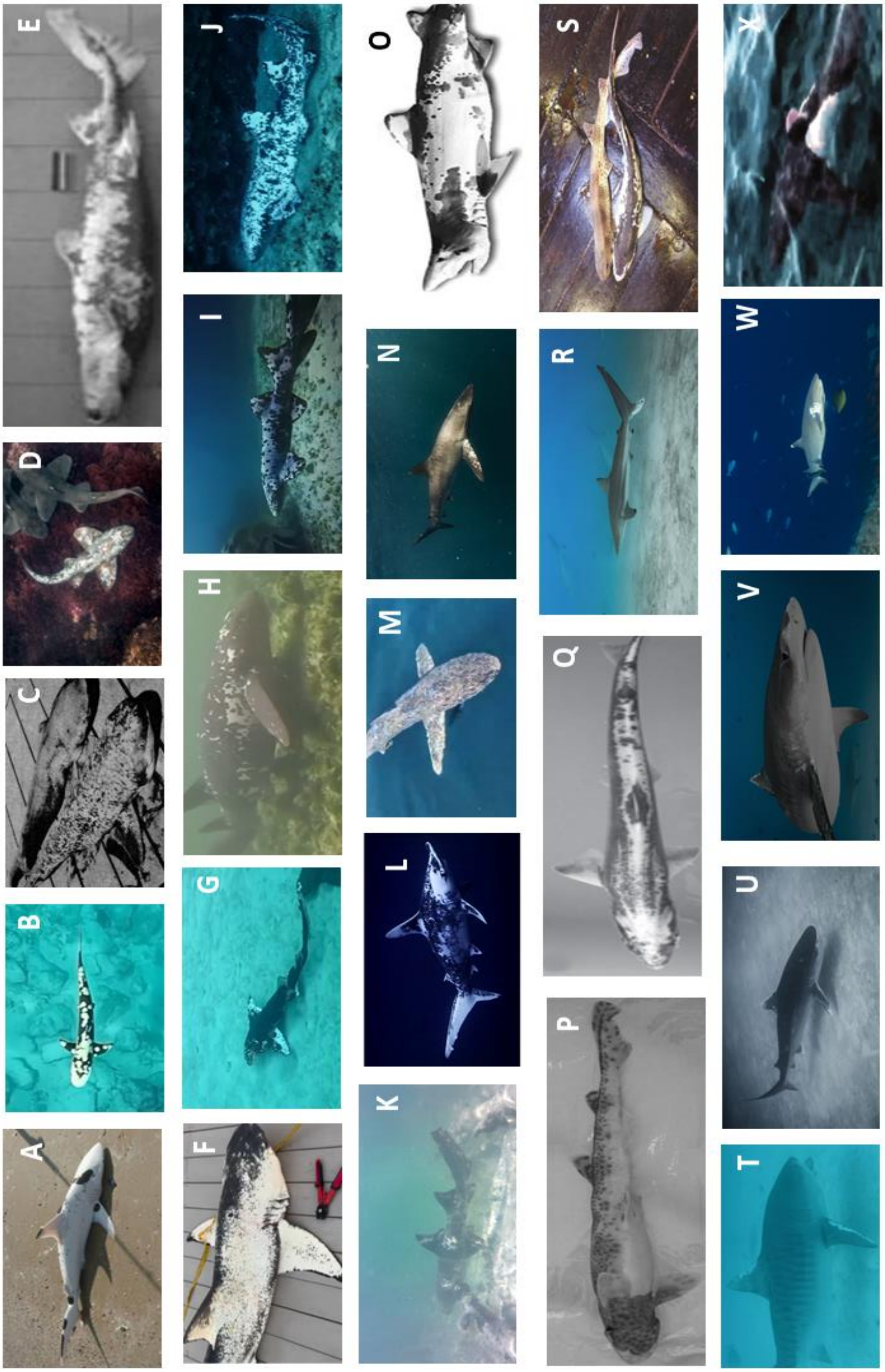

Figure 1. Patterns of piebaldism across records of shark species.

CHAPTER 6

Conclusions

6.1. GENERAL CONCLUSIONS

By using a method that integrates non-invasive field techniques, long-term observational data, and citizen science contributions, the study provides novel insights of elasmobranch population ecology in the Maldives; furthermore, it provides a robust replicable and low cost method to collect datas for the conservation and management of shark populations and important key habitats in the archipelago.

The investigation of *Carcharhinus amblyrhynchos* aggregations across two reef channels underscore the ecological significance of these habitats: notably Villingili Kandu and Miyaru Kandu, which represent multifunctional habitats supporting different life stages of grey reef sharks and important behaviors as feeding, cleaning, mating. The employment of laser photogrammetry complemented by visual census data demonstrated the efficacy and precision of non-invasive approaches in collecting reliable morphometric and information on the aggregation structure. The biometric data collected on 275 individuals facilitated the development of a correction index linking pre-caudal and total length measurements, thereby enhancing data comparability and standardization for future research.

The first published observation of interspecific chafing behavior between *C. amblyrhynchos* and *Rhincodon typus (*whale sharks) provided behavioral evidence of interspecific ecological interactions, involving chafing for cleaning behaviors instead of the use of common cleaning stations represented in Chapter 2. These findings contribute to the understanding of rarely observed behavior in reef and pelagic environments in different location.

Additionally, the confirmation of *Carcharhinus leucas* (bull shark) occurrence in Maldivian waters, based on 23 verified records from central and southern atolls, establishes the region's first scientific baseline for this species. The spatial distribution of sightings in relation to human activities, including waste disposal and dive tourism, indicates emerging human–shark interactions and underscores the necessity for ongoing monitoring to assess potential environmental and management implications.

A comprehensive assessment of piebaldism across seventeen shark species spanning eleven families provided new insights into the taxonomic, geographic, and phenotypic dimensions of pigmentation anomalies in elasmobranchs. This review clarified ambiguous terminology pertaining to pigmentation irregularities and emphasized the valuable role of ecotourism and citizen science in uncovering rare phenotypic traits in elusive marine species. Beyond its descriptive value, this work informs broader discussions regarding the evolutionary and ecological significance of pigmentation variations in shark species.

Collectively, these investigations demonstrate the effectiveness and scientific utility of non-invasive research methods, particularly laser photogrammetry and citizen-science data collection, in studying shark aggregations. The results affirm that low-cost, low-impact techniques can yield ecological insights while minimizing disturbances to target species and their habitats.

In conclusion, this manuscript not only provides ecological data for the comprehension of shark aggregation ecology in the Maldives but also offers a reproducible framework for the study of elasmobranch populations across different regions. By integrating behavioral ecology, population structure analysis, and methodological advancements, this work aims to contribute to long-term monitoring activities, enhancing the data collection to produce effective conservation strategies from competing authorities.

All the supporting videos are available at the following resource:

Parmegiani, Andrea (2025), “Parmegiani Andrea, Phd Thesis, Supporting video”, Bicocca Open Archive Research Data, V2, doi: 10.17632/772pdrfpzp.2

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Alle prossime avventure!!