Chapter 1

General introduction

Guido Leurs

< The first bull shark (*Carcharhinus leucas*) we captured in the Bijagós. Holding the animal upside down in the water reduces stress and allows us to take measurements before safely releasing it again.

Globally, billions of people rely on the oceans to sustain their livelihood, for recreation, or to provide primary means of transportation (e.g., UNCTAD 2020, FAO 2022). All these human activities are in some way supported by healthy and functioning marine ecosystems: ocean currents are significant drivers of Earth's climate system (Lenton *et al.* 2008), healthy coral reefs sustain coastal livelihoods either through increased revenues from fisheries (White *et al.* 2000) or by ecotourism (Fezzi *et al.* 2023), and coastal ecosystems (e.g., mangrove forests or seagrass beds) are essential for coastal defense (Spalding *et al.* 2014). However, human activities continue to have a profound negative impact on the oceans. Rising sea temperatures as a result of climate change cause major ocean currents to change and even disappear (Ditlevsen and Ditlevsen 2023), coral reefs to bleach (Hughes *et al.* 2018), and threaten to displace millions from coastal communities due to sea level rise (Hauer *et al.* 2020). Over the past decades, the continuous discharge of hazardous chemicals and plastics have had devastating effects on marine life (Todd *et al.* 2010, Gall and Thompson 2015). Wide-scale loss and degradation of coastal habitats impact fish species using these habitats as nurseries, including those commercially exploited at later life stages (Nagelkerken *et al.* 2000, Lotze *et al.* 2006). Moreover, industrialization across the marine sectors has intensified the exploitation of marine resources (Swartz *et al.* 2010, Anderson *et al.* 2011), resulting in a collapse of many fish populations (Jackson *et al.* 2001, Lotze *et al.* 2006, Worm *et al.* 2006). Only strict, cross-boundary management interventions can potentially turn the tide for oceans (Worm *et al.* 2009).

As rivers, coastal systems, and pelagic waters are all connected, so are the influences of these anthropogenic stressors. However, these disturbances are concentrated in coastal regions, where pollutants enter the ocean through rivers and estuaries, habitats are degraded due to coastal development, and overexploitation correlates with the size and proximity of human populations (Lotze *et al.* 2006, Crain *et al.* 2009). From coastal regions, other oceanic regions are connected through currents and the movements of marine organisms, especially those that move over long distances and have important roles in marine ecosystems.

Marine predators as connectors and sentinels

Marine predators and megafauna (i.e., higher marine consumers and/or species of which adults are >45 kg in body mass) generally have large home ranges (Hays *et al.* 2016) and, like other predators, have a disproportionately large role: their abundance is lowest of all trophic levels, yet their role on the structure and diversity of lower trophic organisms can be profound (e.g., Estes *et al.* 2011, 2016, Heithaus *et al.* 2008).

Predators can influence prey populations directly through predation and indirectly by introducing risk effects (i.e., 'landscape of fear') (Estes *et al.* 2011, Garvey and Whiles 2016). Through their movements, marine predators can link different habitats and prey populations, for example, by migrating between different ecosystems in which they feed and reproduce, redistributing nutrients and resulting in meta-ecosystem connections (Loreau *et al.* 2003, Rosenblatt *et al.* 2013, Hays *et al.* 2016, Pimiento *et al.* 2020). For example, orcas link oceanic and coastal ecosystems by feeding on sea otters (Estes *et al.* 1998), devil rays link surface waters with bathypelagic waters by foraging at great depths (Thorrold *et al.* 2014), and mangrove-bird communities link their mangrove roosting habitat to terrestrial and pelagic feeding habitats (Buelow and Sheaves 2015). Through their important role in regulating and maintaining ecosystem functioning, marine predators also contribute to sustaining marine ecosystem services to benefit humans (Hammerschlag *et al.* 2019b). However, anthropogenic disturbances often impact predators due to their low natural abundance, relatively large body sizes, slow population growth, and relatively high exploitation rates (Estes *et al.* 2011, Garvey and Whiles 2016). Given their crucial role in structuring marine food webs and their long-distance movements across multiple ecosystems, marine predators embody a wide spectrum of environmental and ecosystem information. Therefore, they are considered prime indicators of ecosystem health or so-called ecosystem sentinels (Hazen *et al.* 2019). One of the most diverse, evolutionarily distinct, widely distributed, and threatened groups of marine predators are sharks and rays (i.e., elasmobranch fishes).

"*What escapes the eye, is a much more insidious kind of extinction: the extinction of ecological interactions.*"

Daniel H. Janzen (1974)

Sharks and rays: perfectly adapted predators

Evolution and Diversity

The earliest archeological records confirm that the earliest shark-like fishes swam the world's oceans approximately 440 million years ago, with the divergence of modern-day sharks and rays taking place in the Jurassic period (145-200 mya). Approximately 536 species of sharks and 670 species of rays are known to science, resulting in over 1,200 extant elasmobranch species (unless specified differently, 'shark' refers to both sharks and rays collectively; Ebert *et al.* 2021). However, every year, scientists worldwide describe an estimated 14 to 16 new species of elasmobranchs (White *et al.* 2022). Sharks and rays inhabit a wide range of aquatic habitats, including the Greenland shark (*Somniosus microcephalus*) in the cold waters of the Arctic, Caribbean reef sharks (*Carcharhinus perezi*) on tropical Caribbean reefs, bull sharks (*Carcharhinus leucas*) venturing thousands of miles upriver into freshwater, Amazonian freshwater stingrays (Potamotrygonidae), the common stingray (*Dasyatis pastinaca*) inhabiting coastal sandy flats, the bioluminescent velvet lantern shark (*Etmopterus spinax*) present at great depths, and the shortfin mako shark (*Isurus oxyrinchus*) roaming the open ocean. It is fair to say that the diversity of sharks and rays is much greater than the shark diversity portrayed in popular media, which is often limited to only three species: the white shark (*Carcharodon carcharias*), bull shark, and tiger shark (*Galeocerdo cuvier*).

Biology and Life History

Sharks and rays differ from bony fishes (i.e., teleosts) in various characteristics, with three of the most important being: (1) their skeleton is made up entirely of cartilage, which is more lightweight and allows for more agility and maneuverability; (2) their skin is covered with placoid scales (or 'dermal denticles') in contrast to scales, these teeth-like structures form a tough armor and reduce drag underwater; (3) sharks and rays do not have swim bladders and instead maintain their buoyancy with a large oil-filled liver (i.e., up to two-thirds of the body weight) and by lift generated by their pelvic and pectoral fins (refer to Klimley 2013 and for a complete overview of differences). In addition, rays differ from sharks in that their gills are positioned on the ventral side (underside), their bodies are flattened, and their pectoral fins are fused to the head.

Figure 1.1 A wider head, as seen in the great hammerhead shark (*Sphyrna mokarran*) and blackchin guitarfish (*Glaucostegus cemiculus*), likely has several advantages. However, one hypothesis is that it provides more space for the Ampullae of Lorenzini to detect minute electromagnetic fields emitted by prey hiding under the sediment.

Next to the five senses that we have as humans (i.e., tactile perception, gustation, olfaction, audition and vision), sharks have two additional senses: the lateral line organ that all fishes have, which enables them to detect movements and vibrations, and electroreceptors called the Ampullae of Lorenzini distributed around their snout and mouth (Klimley 2013, Meredith *et al.* 2022). This seventh sense is used to detect minute electromagnetic fields emitted by hiding prey or to navigate along the Earth's magnetic fields. This is likely one explanation for the evolution of extra-wide heads in some species, like hammerhead sharks and guitarfishes (Figure 1.1), used for finding benthic prey (Klimley 2013, Meredith *et al.* 2022).

In contrast to (most) other fishes, sharks and rays use internal fertilization, with the males possessing two reproductive organs called claspers. Embryonic development differs among species, but generally, four main modes are now recognized: oviparity or egg-laying (e.g., skates and catsharks), yolk-sac viviparity in which embryos feed off yolk (e.g., dogfish and guitarfish), oophagy in which embryos feed on each other (e.g., sand tiger shark *Carcharias taurus*) or on unfertilized ova (e.g., mackerel sharks), and histotrophy in which the mother secretes nutrient-rich substances after the yolk is depleted (e.g., butterfly rays and hammerhead sharks) (Abel and Grubbs 2020). Reproduction for smaller species can occur annually, whereas most species reproduce once every two to three years (Klimley 2013). Fecundity ranges from only one pup in American cownose rays (Fisher *et al.* 2013) to an estimated 200-300 pups in whale sharks (*Rhincodon typus;* this represents the largest known litter size of any elasmobranch) (Joung *et al.* 1996). Sharks and rays generally grow slowly and only reach maturity relatively late in their lifecycle. For example, common stingrays mature around 6.3-6.5 years old (Yigin and Ismen 2012), Caribbean reef sharks at approximately 14.8 years (Talwar *et al.* 2022), and Greenland sharks only mature when they reach an age of >156 years (Nielsen *et al.* 2016). Longevity ranges from only a couple of years in small-bodied species to 40 years for white sharks (Hamady *et al.* 2014) and at least 272 years for the Greenland shark, making it the longest-living vertebrate species (Nielsen *et al.* 2016). The slow growth, late maturity and high longevity, combined with low fecundity and long reproductive cycles, cause the intrinsic population growth of sharks and rays generally to be low compared to other fishes (i.e., K-selected traits compared to r-selected traits; Frisk *et al.* 2001).

Ecological roles

Shark and ray species can connect habitats through their long-distance movements. For example, reef sharks feeding on pelagic food sources connect coral reefs with adjacent pelagic systems (McCauley *et al.* 2012, Williams *et al.* 2018), while bull sharks link temperate and tropical systems (Heupel *et al.* 2015). Sharks and rays also likely play important roles in redistributing prey, nutrients and energy across different spatial scales (Wirsing *et al.* 2007, McCauley *et al.* 2012, Williams *et al.* 2018, Heithaus *et al.* 2022). However, many shark and ray species are relatively small and have smaller home ranges (Mull *et al.* 2022), resulting in a more localized ecological role. The roles that sharks and rays play in marine food webs vary among species, populations and life stages. Most sharks and ray species are relatively small and likely have a meso-predatory role in their marine food webs, where these species exert diffuse predation on prey communities (Heupel *et al.* 2014, Navia *et al.* 2016). Large-bodied predatory species such as hammerhead sharks, bull sharks and white sharks occupy positions near the top of the food web and, therefore, fulfill a more top-predator or even apex-predator position (Heupel *et al.* 2014, Navia *et al.* 2016). However, these larger species often act as transient top-predators, meaning they are not permanently present but exert concentrated predation pressure on mesopredators (Heupel *et al.* 2014). Both meso-predatory and top-predatory elasmobranchs can exert top-down effects on lower trophic organisms, impacting their abundance and restructuring prey communities (Flowers *et al.* 2021, Heithaus *et al.* 2022). The removal of these predatory species is hypothesized to have cascading consequences on overall ecosystem functioning and marine ecosystem services (e.g., carbon sequestration) (Heithaus *et al.* 2008, Atwood *et al.* 2015). However, studies focusing on the cascading effects of shark removal provide mixed results (e.g., Bascompte *et al.* 2005, Myers *et al.* 2007, Ferretti *et al.* 2010, Navia *et al.* 2010, Grubbs *et al.* 2016, Roff *et al.* 2016), with cascading effects likely reduced in predator-rich ecosystems (e.g., coral reefs) due to the relatively high ecological redundancy within predator communities (Roff *et al.* 2016). In addition to the direct effects of predation, predatory sharks also influence prey behavior with their presence. These so-called "risk effects" of sharks can influence prey species' behavior, distribution and physiology (Wirsing *et al.* 2007, Hammerschlag *et al.* 2015, 2019a, 2022, Rasher *et al.* 2017).

Status and Threats

After 400 million years of evolution, surviving six mass-extinction events, and occupying most aquatic habitats, sharks and rays now face a variety of threats due to a combination of factors, including their life history traits, overexploitation (both as targeted catch and bycatch) and habitat degradation. Species that specialized through natural selection, such as the great hammerhead shark (*Sphyrna mokarran*) and blackchin guitarfish (*Glaucostegus cemiculus*), which have enlarged heads, are now increasingly vulnerable to be captured in nets due to their unique evolutionary adaptations (Figure 1.1). By losing sharks and rays, we also risk losing their ecological roles and interactions, millions of years of evolutionary distinctiveness (Stein *et al.* 2018), and their important socio-cultural roles in many indigenous cultures (**Box A**).

Shark and ray catches increased over the past decades and started to decrease in 2003 due to declines in shark and ray populations (Dulvy *et al.* 2014). Although well-managed and sustainable shark fisheries do exist (Simpfendorfer and Dulvy 2017, Shiffman *et al.* 2023), in the majority of fisheries around the world, sharks and rays are still exploited at unsustainable levels, and many populations have been severely depleted (Worm *et al.* 2013, Simpfendorfer and Dulvy 2017). Sharks and rays are fished for a range of products: their liver is used to extract squalene (i.e., liver oil) for cosmetics and medicines, their skin as sandpaper or leather, and their cartilage for medicinal purposes. Gills and fins to make traditional medicine and shark-fin soup and shark meat are consumed in many countries around the world (e.g., Haque and Spaet 2021, Niedemüller *et al.* 2021, Prasetyo *et al.* 2021). The trade in shark fins and meat constitutes the largest share of the total trade in shark products, causing these two commodities to drive the majority of shark and ray fisheries (Clarke *et al.* 2007, Niedemüller *et al.* 2021).

Currently, more than one-third of all shark and ray species are threatened with extinction, making chondrichthyan fishes (i.e., sharks, rays and chimeras) the second most threatened species group of vertebrates (after amphibians; Dulvy *et al.* 2021). Although overexploitation is the major driver of this extinction risk in sharks and rays, habitat degradation also contributes to the decline in the conservation status of about 31% of the species (Dulvy *et al.* 2021). Nearshore habitats like mangroves, seagrass forests and coral reefs are important for many shark and ray species. Some species use nearshore habitats during early life stages as nursery areas, while other species use these habitats throughout their lifecycle or as seasonal feeding areas (Knip *et al.* 2010). Furthermore, some species of sharks and rays are specifically adapted to these shallow-water habitats, mostly taking advantage of the high abundance of benthic prey species and relative safety due to the absence of large predatory species (Knip *et al.* 2010). Therefore, the continued degradation and loss of these important habitats due to coastal development, climate change and pollution also impacts the species of sharks and rays that depend on them (Knip *et al.* 2010, Dulvy *et al.* 2021). One type of habitat often overlooked in shark and ray ecology is the intertidal, the habitats that this thesis focuses on.

Intertidal Areas

Value, Distribution and Threats

Intertidal areas represent the transition between terrestrial and marine ecosystems. These areas contain extensive intertidal flats comprising rocks, coral, sand or mud exposed during low tide and submerged during higher tidal phases. These flats are often connected by vast networks of tidal channels and gullies, lined with mangrove forests or tidal marshes, covered with seagrass or contain large (intertidal) lagoons and pools. They form under combinations of sufficient sediment supply from rivers or atmospheric dust and sufficient tidal amplitude/energy (Figure 1.2). Intertidal areas are essential for many ecosystem services, like food production (e.g., shellfish, fish and shrimp fisheries) and as a natural form of coastal protection (Bouma *et al.* 2014, Murray *et al.* 2019). Intertidal areas are closely linked to coastal communities and provide livelihoods and protection for millions globally. Their extent is comparable to that of the world's mangrove forests, and although often directly associated with mangrove forests, intertidal areas have a global distribution (Murray *et al.* 2019).

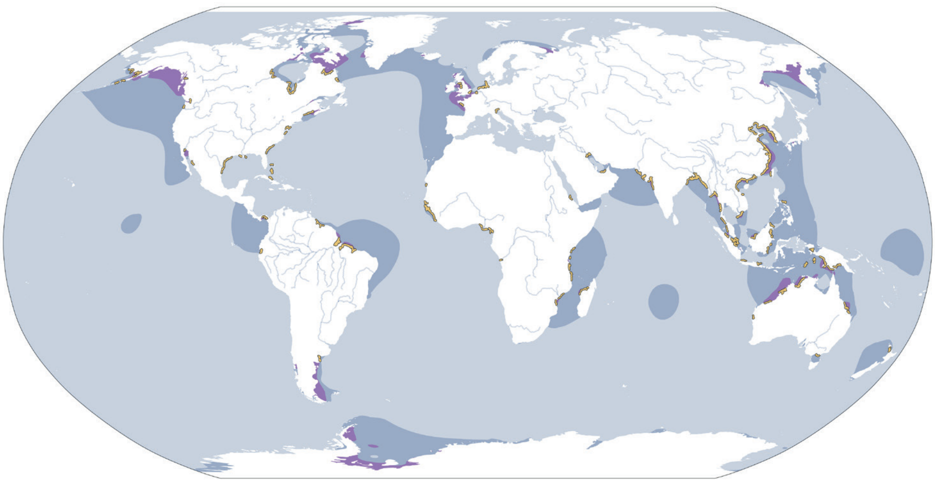

Figure 1.2 Global distribution of the largest 100 intertidal areas (yellow; adapted from Murray *et al.* 2019). Intertidal areas are mostly distributed in areas in river (blue lines) estuaries and where tidal ranges are high (light blue = microtidal <2.0m, dark blue = mesotidal 2.0-4.0m, purple = macrotidal >4.0m).

Asia contains, by far, the most intertidal flat habitat, containing 44% of the global extent of intertidal flats. Intertidal flats are most common in areas with high sedimentation rates (e.g., estuaries and deltas), large tidal ranges, and coastlines that are naturally low and gradually sloping (Murray *et al.* 2019). Like many coastal ecosystems, intertidal areas are threatened by several anthropogenic disturbances. Coastal development, coastal erosion or changes in sediment deposition, and continued rising sea levels cause many intertidal areas to degrade or disappear (Lotze *et al.* 2006, Murray *et al.* 2019, Hill *et al.* 2021). The first estimate on the status of intertidal flat habitats on a global scale concluded that 16% of the extent of intertidal flats was lost between 1984 and 2016 (Murray *et al.* 2019), and only 31% is currently located within protected areas (Hill *et al.* 2021).

The ecology of the Intertidal

Intertidal areas are highly dynamic areas, which are challenging areas for species to live due to the continuous cycle of incoming and receding tides. Large intertidal areas are often associated with mangrove forests, seagrass or macro-algae beds, and shellfish reefs, which form the basis of the intertidal food web, offer protections for species using the intertidal, and stabilize sediments against erosion (Nagelkerken *et al.* 2000, Minello *et al.* 2003, Deegan *et al.* 2012). Intertidal areas are known for their rich invertebrate life, supporting many species of bivalves, polychaetes, gastropods, echinoderms and crustaceans. In the rocky intertidal, where space is limited, the organization of invertebrate communities is largely determined by competition for space and the top-down effects of predation (Paine 1974). In soft-bottom intertidal flats, space is often a less limiting factor, making predation the most important structuring factor for invertebrate communities (Lewis *et al.* 2007). However, other physical factors (i.e., elevation and exposure to waves) will likely influence species distribution and community composition across these habitats (Peterson 1991). These lower trophic organisms represent an important prey community for higher trophic consumers.

Many fish species use the intertidal as nursery and feeding areas, including commercially important species (Binet *et al.* 2013, Correia *et al.* 2021), highlighting the importance of intertidal areas for commercial fisheries. Terrestrial mammals like Chacma baboons (*Papio ursinus*), gray wolves (*Canis lupus*), striped hyenas (*Hyaena hyaena*) and brown bears (*Ursus arctos*) feed in the intertidal on bivalves, crabs and barnacles (Carlton and Hodder 2003), and marine mammals like bottlenose dolphins (*Tursiops truncatus*) trap and prey on fish (Vermeulen 2018) on submerged tide flats, and the Antillean manatee (*Trichechus manatus manatus*) enters the intertidal zone to feed on vegetation (Spiegelberger and Ganslosser 2005). Waders (order Charadriiformes, in this thesis also referred to as wading birds) represent one of the most numerous predatory groups in the intertidal, with millions of waders migrating between intertidal areas annually. For example, close to 200,000 red knots (*Calidris canutus*) and 250,000 bar-tailed godwits (*Limosa lapponica*) visit the Banc d'Arguin (Mauritania) every year during the boreal winter months (Oudman *et al.* 2020). Shorebirds (i.e., waders, Charadriiformes) use tropical intertidal areas as wintering habitats, depending on the rich endobenthic communities, to fuel up for their long return migrations north. The predation of (migratory) shorebirds on invertebrates (i.e., endobenthos) in soft-bottom intertidal flats can impact the community structure of these prey species (Thrush *et al.* 1994, Zwart and Ens 1999, Zharikov and Skilleter 2003), but can also directly influence the biogeochemistry (van Gils *et al.* 2012) and biogeomorphology of intertidal areas through cascading effects of predation (Booty *et al.* 2020). The number of shorebirds along the migratory flyways has dwindled over the past decades, with the habitat quality of intertidal areas, climate change and other disturbances along these pathways as likely causes (Oudman *et al.* 2020, van Gils *et al.* 2016).

Intertidal Sharks and Rays (Thesis Outline)

Intertidal areas have so far mostly been studied from a "low-tide perspective", focusing on what happens in exposed mudflats during low tide, often with (migratory) shorebirds as the primary intertidal predators. This thesis focuses on sharks and rays using the intertidal, especially at high tide. Specifically, we studied which species use these challenging habitats, how these predatory elasmobranchs interact with migratory waders and how anthropogenic disturbances in intertidal areas threaten sharks and rays. For this, we focus on the two largest tropical, soft-bottom intertidal areas in West Africa, located along the East Atlantic Flyway for shorebirds: the Banc d'Arguin in Mauritania and the Bijagós Archipelago in Guinea-Bissau (see **Box B**). In both areas, we collaborated with local researchers, conservationists and community members (see **Box C**).

This thesis consists of four themes that focus on intertidal sharks and rays: (**I**) Fisheries, (**II**) Diversity & Life History, (**III**) Species Interactions, and (**IV**) Conservation. The first section focuses on how fisheries impact sharks and rays within the region (**I. Fisheries**). For this, we studied the distant-water industrial fishing vessels operating in the waters of Mauritania and Guinea-Bissau and determined their potential effects on mobile shark and ray species using intertidal areas (**Chapter 2**). In addition, we determined the historical population trends for sharks and rays in the Banc d'Arguin based on a long-term monitoring program of fish landing sites (**Chapter 3**), and we reconstructed historical population trends for the Bijagós Archipelago: a place where historical data on sharks and rays is lacking. For this, we turned to those who know the waters of the archipelago best: fishers (**Chapter 4**).

We then focus on the distribution, community structure, and life history traits (**II. Diversity & Life History**). These studies focused on describing the diversity and community composition of sharks and rays in the Bijagós Archipelago based on a combination of an environmental DNA (eDNA) approach and a pilot fisheries observer program (**Chapter 5**). In addition, we determined important life history parameters of the most common elasmobranch species of the Bijagós: the pearl whipray (*Fontitrygon margaritella*; **Chapter 6**).

In the next section (**III. Species Interactions**), we focused on the ecological role of sharks and rays in intertidal areas, how they interact with other intertidal predatory species groups, and how they can potentially change intertidal landscapes. Specifically, we first review what is known about the intertidal habitat use of sharks and rays, why these areas are important to these species and *vice versa*, why sharks and rays may have important ecological roles in intertidal areas (**Chapter 7**). We then determined if sharks and rays using intertidal habitats in the Banc d'Arguin and the Bijagós Archipelagos overlap in trophic niche (i.e., use the same intertidal resources) as migratory waders and what the implications of this interaction could be (**Chapter 8**). In addition, we focus on how benthic rays and their role as intertidal predators can potentially change the entire intertidal landscape and what this means for their conservation (**Chapter 9**).

In the last section, we focused on the conservation of elasmobranchs and their roles in ecosystems and coastal livelihoods (**IV. Conservation**). To ensure that newly designated marine protected areas (MPAs) can incorporate the most ecologically important areas for sharks and rays, we determined criteria and guidelines for delineating Important Shark and Ray Areas (ISRAs; **Box F**). This is especially timely given the 30x30 initiative (i.e., protecting 30% of the marine environment by 2030) agreed upon by the Conference of Parties of the Convention on Biological Diversity. For conservation strategies aimed at improving the status of sharks and rays to be successful, the socio-cultural and economic importance of sharks cannot be ignored. Millions of livelihoods depend on the trade in sharks and rays, and including these aspects in conservation strategies will improve the existing management of sharks and rays. We determined important lessons learned from researchers worldwide on how to conduct and map shark value chains (**Chapter 10**).

Lastly, I combined the findings of all these studies and put them into a wider ecological and conservation context (**Chapter 11, General Discussion**). I focused on which shark and ray species have important intertidal roles, how these roles are potentially impacted by their deteriorating conservation status, what this means for other predatory species groups using intertidal areas, and what this implies in a global context of intertidal ecology.

BOX A: SOCIO-CULTURAL AND ECONOMIC VALUE OF SHARKS

Sharks and rays can play an important role in marine ecosystems (Heupel *et al.* 2014, Flowers *et al.* 2021) but also play an important role in the culture and socio-economics of coastal communities (e.g., Puniwai 2020). Besides the lucrative shark fin trade, other shark commodities can also be important drivers of local, regional, national or even international trade or be an important pillar for food security (Hasan *et al.* 2017, Niedemüller *et al.* 2021). In areas where multiple shark commodities are processed and traded, products such as shark skin, liver oil or meat can be important sources of income for local communities (Haque and Spaet 2021). Globally, the shark meat trade has a total estimated value of 2.6 billion USD (shark fins: 1.5 billion USD), with likely millions of people in coastal communities directly depending on shark fisheries for income or as a main source of protein (Niedemüller *et al.* 2021). Archeological records from Peru show that shark fisheries have existed on the country's coastline since as early as 1500-1100 BC, indicating that sharks likely played an important role in the daily subsistence of local Peruvian communities throughout history (Prieto 2021). Nowadays, shark-based ecotourism, like dive tourism or recreational catch-and-release fishing, can be important pillars of the local economy of coastal communities or even national economies (Cisneros-Montemayor *et al.* 2013).

Besides the economic importance of sharks, these species can also play an important role in the culture and traditions of coastal communities. The curing of the meat of the Greenland shark (*Somniosus microcephalus*) for the Icelandic dish Kæstur hákari is considered an art and is regarded as one of the most important national delicacies (Weichselbaum *et al.* 2009). In other cultures, in addition to being an important food source, sharks have important roles in traditional ceremonies and indigenous beliefs. In these indigenous societies, sharks and rays have positive associations and values, often representing strength and bravery, similar to how bears, lions and eagles are used in Western symbolism (McDavitt 2005). For example, sharks represent ancestral creators (i.e., 'totems') for Aboriginal societies of Australia's Top End (northernmost region of the Northern Territory). Here, the shark represents justified vengeance, stingrays symbolize cultural survival, and sawfish are the creators of rivers (McDavitt 2005).

For indigenous societies in Pacific Island Nations like the Solomon Islands and Hawaii, sharks are regarded as embodiments of gods or are offered to significant community members and family during traditional ceremonies and special occasions (Thaman *et al.* 2010, Hylton *et al.* 2017, Puniwai 2020). However, this cultural importance is losing significance due to the increasing pressure on shark populations and fishing communities due to the development of international markets in valuable shark commodities over the past decades (Hylton *et al.* 2017).

Figure A1 Examples of sharks and rays in the Bijagó culture: the regional currency (Central African Franc) displays a sawfish-inspired symbol (top-left), the construction of a saw-fish inspired community building on the island of Formosa (center), and a shark-inspired mask with teeth of a bull shark (*Carcharhinus leucas*) used in traditional ceremonies (right).

Many of these countries or communities symbolize the importance of sharks to their culture on their currency (e.g., the Central African CFA Franc, used in Guinea-Bissau; **Figure A1**), code of arms (e.g., Solomon Islands, Hylton *et al.* 2017), shark and ray-based masks and ceremonial attire, or even buildings. In the Bijagós Archipelago (Guinea-Bissau), traditional Bijagó ceremonies such as the coming-of-age ceremony for men (i.e., 'fanado') typically involve ceremonial dances with masks representing cows, sharks or rays (Figure A1). Some masks in the shape of sawfish symbolize companionship and strength, whereas masks based on hammerhead and other sharks symbolize strength and power. Sawfish are considered to be important species to both Aboriginal and Bijagó communities, which is highlighted by the construction of sawfish-shaped community buildings along the Angurugu River (Australia, McDavitt 2005) and on the island of Formosa in the Bijagós Archipelago (**Figure A1**). In addition, many indigenous societies have many different names for different shark and ray species, further indicating the significance of these species to their culture. For example, in the Bijagós Archipelago, the local Bijagó communities have more than 20 names for sawfish (Leeney and Poncelet 2015).

The value of sharks and rays to local or even national socioeconomic systems, traditions and food security should be considered when designing and implementing management strategies (Barker and Schluessel 2005, Booth *et al.* 2019). Failing to do so may negatively impact conservation efforts and compliance (Jaiteh *et al.* 2016).

BOX B: STUDY AREAS

Banc d'Arguin, Mauritania

The Banc d'Arguin (or Parc National du Banc d'Arguin, PNBA; 20º 14'N, 16º 06'W) is located on the west coast of Mauritania (**Figure B1**). The national park covers 12,000 km^2 and about 30% of the Mauritanian Atlantic coast. The Banc d'Arguin National Park was established in 1976 and designated as a RAMSAR Wetland site in 1982 and a UNESCO World Heritage Site in 1989. Formed as a delta of the ancient Tamanrassett River, the Banc d'Arguin now contains many habitats, forming a complex and diverse landscape. The park is characterized by sand dunes, intertidal flats, intertidal and subtidal seagrass beds, networks of channels and shallow gullies, and deeper subtidal waters. The permanent upwelling of the Canary Current off the coast of Mauritania drives high productivity in these coastal ecosystems. This results in highly productive fishing grounds for offshore fisheries (Arístegui *et al.* 2009). This upwelling and the variety of habitats enable the Banc d'Arguin to support many terrestrial and marine species.

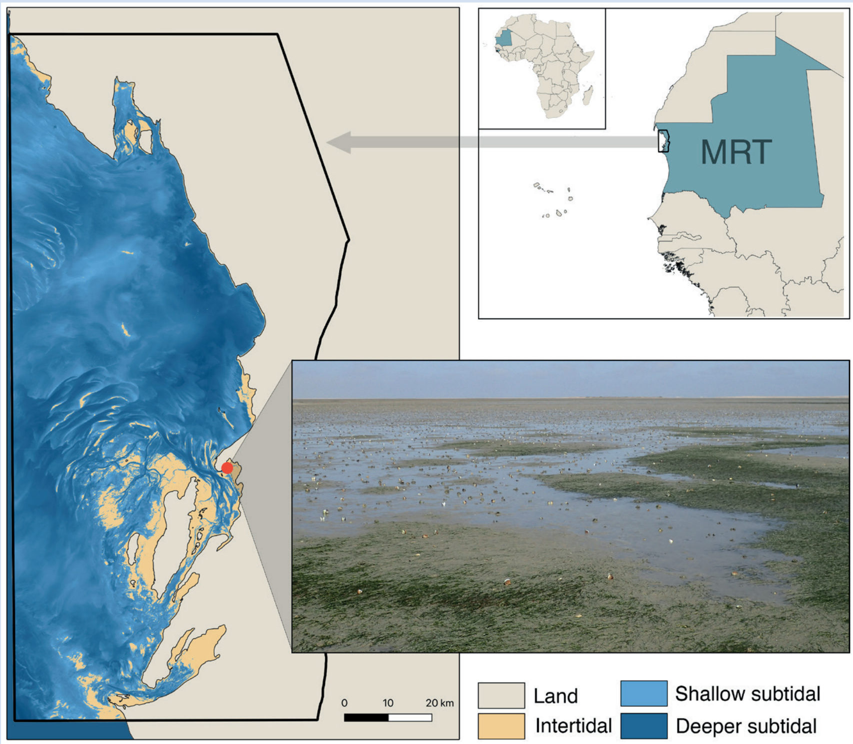

Figure B1 Overview of the Banc d'Arguin (Mauritania, MRT) with a representative example of its intertidal habitat. Colors indicate the upland (beige), intertidal (yellow), shallow subtidal (light blue) and subtidal (dark blue).

Every year, between 1 to 1.5 Million migratory shorebirds visit the Banc d'Arguin, located along the East Atlantic Flyway, to spend the boreal winter months and to feed on the rich benthic resources that the intertidal flats have to offer (Oudman *et al.* 2020). Dense groups of fiddler crabs (*Afruca tangeri*) roam the intertidal flats during low tide, and high densities of bivalves (including the large West African bloody cockle *Senilia senilis*) form an important intertidal food source for many species. The area is also important to several shark and ray species and is known to be the only site where the endemic false shark ray (*Rhynchorhina mauritaniensis*) was ever recorded based on a small number of observations from 1998 to 2012 (Séret and Naylor 2016). The Banc d'Arguin serves as a nursery area for both (commercially important) bony fishes, sharks and rays. The Banc d'Arguin is further an important site for sea turtles, such as the green sea turtle (*Chelonia mydas*), and for marine mammals like the bottlenose dolphin (*Tursiops truncatus*), Atlantic humpback dolphin (*Sousa teuszii*), the Mediterranean monk seal (*Monachus monachus*) and terrestrial mammals like the Dorcas gazelle (*Gazella dorcas*) and African golden wolf (*Canis lupaster*).

Within the park's boundaries, seven villages of the local Imraguen (meaning 'fishermen' in Berber) tribe are located. Their economy is based on fishing, whichonce was subsistence using traditional methods but has developed into more commercial fisheries (e.g., targeting sharks and rays) over the past decades (Lemrabott 2023). Historically, Imraguen fishers have a symbiotic fishing method in collaboration with bottlenose dolphins that, in the past, would drive dense schools of mullet into shallow waters for fishers to catch (Campredon and Cuq 2001). Within the Banc d'Arguin, the Imraguen have exclusive fishing rights and can only use artisanal methods (e.g., no engine or other mechanical aid). Traditional fishing methods are also under increasing threat from other fishers illegally entering the park and from distant-water industrial fisheries.

Bijagós Archipelago, Guinea-Bissau

The Bijagós Archipelago (BA; 11º 15'N, 16º 05'W) consists of 88 islands and islets and is located off the coast of Guinea-Bissau (**Figure B2**). The entire archipelago spans an area of 12,958 km^2 and was recognized for its importance to biodiversity and local communities. It was designated as a UNESCO Biosphere Reserve in 1996 and a RAMSAR Wetland site in 2014. The archipelago was formed from an ancient delta of the Geba and Grande de Buba rivers and now consists of various marine and terrestrial habitats. The islands of the archipelago are lined with sandy beaches, dense mangrove forests and large intertidal flats. The islands are connected through a network of tidal channels and gullies, which connect shallow habitats to deep subtidal waters. During the rainy season (May to October), the archipelago experiences influxes of large amounts of freshwater.

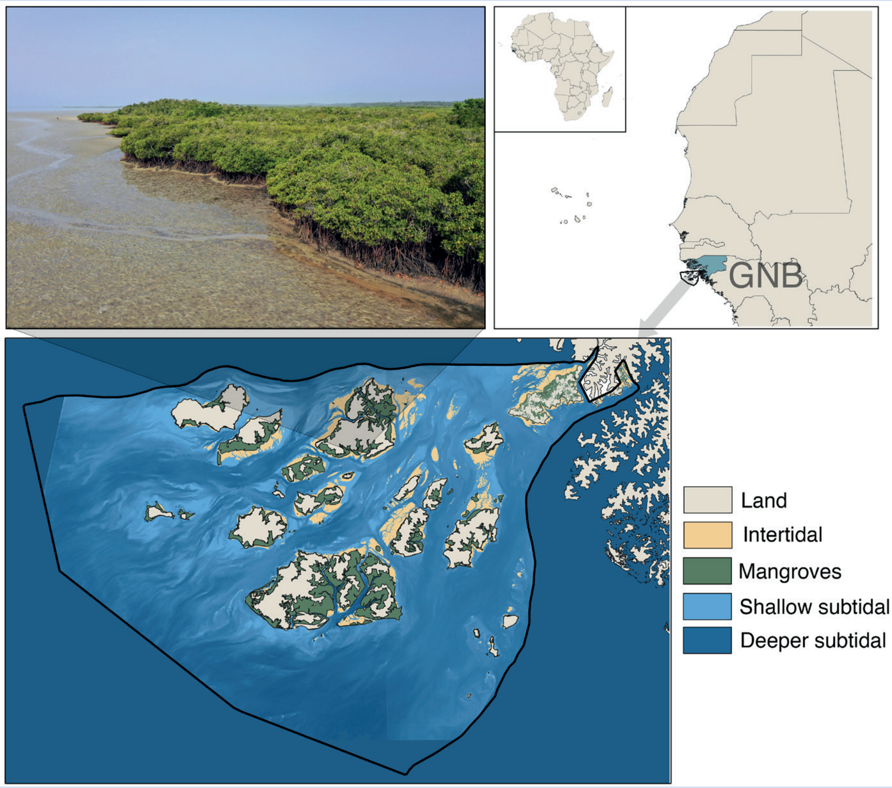

Figure B2 Overview of the Bijagós Archipelago (Guinea-Bissau, GNB) with a representative example of its intertidal habitat. Colors indicate the upland (beige), mangroves (green), intertidal (yellow), shallow subtidal (light blue) and subtidal (dark blue).

An estimated 200,000 to 600,000 migratory shorebirds visit the archipelago annually when migrating along the East Atlantic Flyway (Henriques *et al.* 2022). Similar to the Banc d'Arguin, the shorebirds spend the boreal winter months in the archipelago before migrating back north. The archipelago is home to various species of bony fish, sharks and rays. For many of these (commercial) species, the archipelago's shallow waters likely serve as a nursery area. The beaches of the archipelago are an important nesting site for the green sea turtle.

Furthermore, the archipelago provides important habitats for the Nile crocodile (*Crocodylus niloticus*), West African manatee (*Trichechus senegalensis*), bottlenose dolphins, and the most western, and only saltwater population of hippopotamus (*Hippopotamus amphibious*).

The Bijagós is home to an estimated population of 30,000, most of whom belong to the Bijagó ethnic group. Animals like cows, sharks and rays play an important role in the Bijagó culture (see **Box I**), especially in traditional ceremonies and celebrations. Traditionally, fishing was only done for subsistence, but it has developed over the past decades and is now one of the most important sources of income. Fishing boats now have outboard engines and different gear types (e.g., monofilament nets, longlines, and hand-lines), targeting bony fish, sharks and rays. Fishing boats entering the archipelago from neighboring countries or industrial vessels operating close to the archipelago are thought to threaten fish stocks and other marine fauna (Diop and Dossa, 2011).

BOX C: LOCAL PERSPECTIVES ON SHARK AND RAY RESEARCH

In both study areas, a lot of fisheries research and conservation studies are done by local researchers, conservationists, and community members. During our research over the past years, we have successfully collaborated with these stakeholders and experienced how important the local context is in the interface of ecological and socioeconomic systems, especially when focusing on shark and ray fisheries. These are the perspectives of local researchers on the status and research on sharks in their country.

Emanuel Dias, MSc. *Bijagós Archipelago, Guinea-Bissau*

Biologist and Director of the Orango National Park (Bijagós Archipelago)

Instituto da Biodiversidade e das Áreas Protegidas (IBAP), Guinea-Bissau

What are the main threats to sharks and rays in your study area and country?

We have a legal framework for fisheries, including the General Fisheries Law and the National Plan of Action for Sharks, which prohibits the targeted catch of cartilaginous species. However, in recent years, the pressure on this species group has significantly increased, especially from artisanal/small-scale fishers who target these species specifically.

Can you explain why sharks and rays are important in your study area?

Sharks and rays are species that play important roles as predators in the marine ecosystem and associated food webs. Their function is to control their prey.

What should the research and conservation priorities be for sharks and rays?

The research priorities for my country are to estimate the abundance, biomass, and diet of these species within the Bolama Bijagós Biosphere Reserve.

How can the status of sharks and rays be improved while considering the needs of local communities?

The pressure on this vulnerable species group can be reduced if national authorities and policymakers enforce the existing legal framework for these species. At the same time, this would also safeguard local communities' sustainable use of marine resources.

Dr. Sidi Yahya Cheikhna Lemrabott *Banc d'Arguin, Mauritania*

Fisheries Researcher

Institut Mauritanien De Recherches Océanographiques Et De Pêches, Mauritania

What are the main threats to sharks and rays in your study area and country?

The main threat for these species continues to be illegal fishing by both industrial and artisanal fisheries. This is worsened because these species are captured not only as incidental bycatch but also as target species. The high demand from (international) markets for these species increases targeted fishing pressure.

Can you explain why sharks and rays are important in your study area?
These species play an essential role in the diversity of the Banc d'Arguin by exerting top-down control as (top-)predators on lower trophic levels. Hence, they are critical to maintaining the ecological balance of marine food webs.

What should the research and conservation priorities be for sharks and rays?
We should address their conservation by considering their biological traits (e.g., slow growth and late maturity). Furthermore, we should end (targeted) fisheries for these species and monitor their catches and commercial trade.

How can the status of sharks and rays be improved while considering the needs of local communities?
To reduce the overexploitation of sharks and rays, fishers must be encouraged to switch to sustainable fisheries targeting other species. However, this should be combined with support measures to improve the livelihoods of the fishing communities.

Assana Camará, MSc. *Bijagós Archipelago, Guinea-Bissau*
Research technician
Instituto Nacional de Investigação das Pescas e Oceanografia, Guinea-Bissau

What are the main threats to sharks and rays in your study area and country?
The Bijagós Archipelago faces threats like overfishing and shark finning, harming marine biodiversity and disrupting ecosystems. Immediate actions are needed to safeguard these crucial areas.

Can you explain why sharks and rays are important in your study area?
In Guinea-Bissau, rays and sharks seem to have larger populations than other regions. The species are essential for the ecological balance of our marine environment, influencing the health of ecosystems and promoting biodiversity.

What should the research and conservation priorities be for sharks and rays?
We must improve the knowledge of the status of ray and shark populations, given that Guinea-Bissau is probably one of the last places with high diversity. In addition, very rare and overexploited species still exist in our waters, unlike in other parts of the world.

How can the status of sharks and rays be improved while considering the needs of local communities?
To mitigate the overexploitation of rays and sharks in Guinea-Bissau, reducing fishing pressure (mainly industrial) and expanding protected marine areas in the Exclusive Economic Zone is crucial. Compensatory measures for local communities, such as encouraging eco-tourism, are essential to balance conservation with local needs.