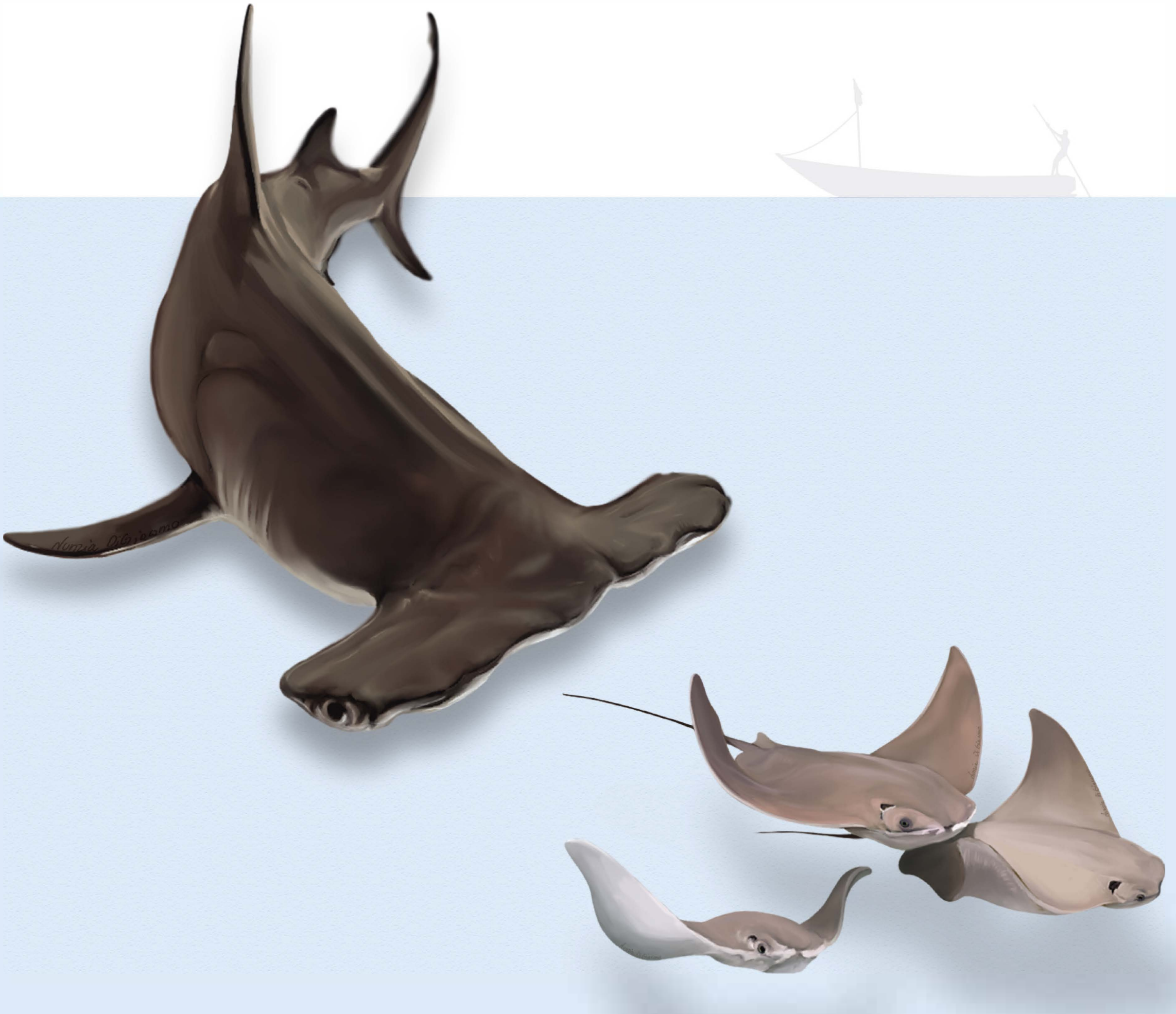
SHARKS AND RAYS
IN
TROUBLED WATERS

Threatened species in dynamic intertidal ecosystems



Guido Leurs

Sharks and Rays in Troubled Waters
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Sharks and Rays in Troubled Waters

Threatened species in dynamic intertidal ecosystems

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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).

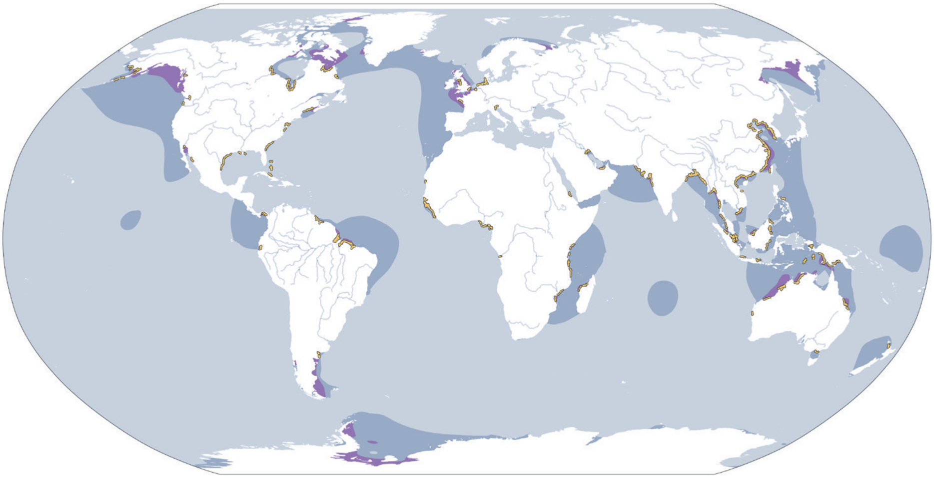

Figure 1.2 Global distribution of the largest 100 intertidal areas (yellow; adapted from Murray *et al.* 2019). Intertidal areas are mostly distributed in areas in river (blue lines) estuaries and where tidal ranges are high (light blue = microtidal <2.0m, dark blue = mesotidal 2.0-4.0m, purple = macrotidal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

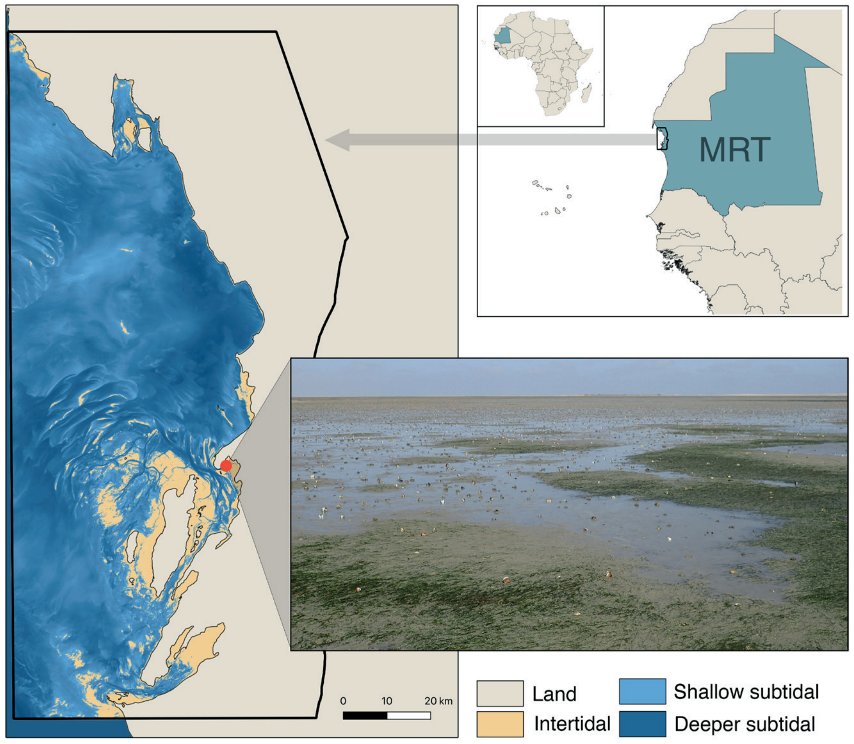

Figure B1 Overview of the Banc d’Arguin (Mauritania, MRT) with a representative example of its intertidal habitat. Colors indicate the upland (beige), intertidal (yellow), shallow subtidal (light blue) and subtidal (dark blue).

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.

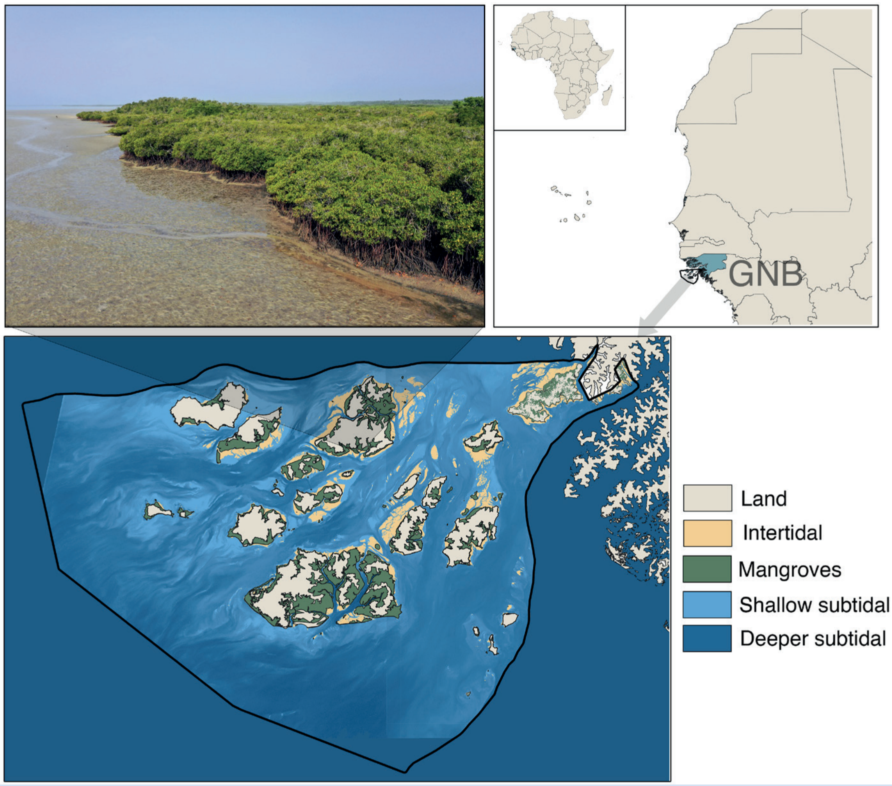

Figure B2 Overview of the Bijagós Archipelago (Guinea-Bissau, GNB) with a representative example of its intertidal habitat. Colors indicate the upland (beige), mangroves (green), intertidal (yellow), shallow subtidal (light blue) and subtidal (dark blue).

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.

SECTION I

Fisheries

Chapter 2

Industrial fishing near West African Marine Protected Areas and its potential effects on mobile marine predators

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Abstract

Marine Protected Areas (MPAs) are increasingly implemented to facilitate the conservation of marine biodiversity and key habitats. However, these areas are often less effective in conserving mobile marine species like elasmobranchs (i.e., sharks and rays). Industrial fishing near MPA borders possibly impacts vulnerable species utilizing these protected areas. Hence, we aimed to study spatiotemporal patterns of industrial fisheries near MPAs in relation to the bycatch of elasmobranchs. Specifically, we analyzed the spatiotemporal fishing effort within the West African region, mapped fishing effort in the direct vicinity of the Parc National du Banc d'Arguin (Mauritania) and the Bijagós Archipelago (Guinea-Bissau) and compared the seasonal overlap between elasmobranch bycatch and fishing effort near these MPAs. We combined Automatic Identification System data and local fisheries observer data, determined fishing effort for each gear type and compared this with bycatch of elasmobranchs. We found that industrial fishing effort was dominated by trawling, drifting longlines and fixed gear types. Although no industrial fishing was observed within both MPAs, 72% and 78% of the buffer zones surrounding the MPAs were fished for the Banc d'Arguin and Bijagós, respectively. Within the Banc d'Arguin buffer zone, trawling and drifting longlines dominated, with longlines mainly being deployed in the fall. In the Bijagós buffer zone, trawling and fixed gears were most prevalent. Fisheries observer data for Mauritania showed that elasmobranch catches increased during the most recent sampling years (2016 to 2018). Elasmobranch catches within the waters of Guinea-Bissau peaked in 2016 and decreased in the following two years. Seasonal patterns in elasmobranch bycatch within the waters of both countries are likely caused by increased catches of migratory species. Catches of rays peaked in May and June for Mauritania and in October for Guinea-Bissau. Shark catches were highest in February and July in Mauritanian waters and in May and October in the waters of Guinea-Bissau. Our study indicates that industrial fisheries near the border of ecologically important MPAs may have potentially major implications for ecosystem functioning through the removal of (migratory) predatory species.

Introduction

To halt the degradation of marine ecosystems and to counter the overexploitation of marine resources, an increasing number of Marine Protected Areas (MPAs) have been implemented over the last two decades (Watson *et al.* 2014, McDermott *et al.* 2018). The majority of these implemented MPAs cover coastal areas, like vegetated wetlands and coastal reefs, which can be important for marine megafauna species (Fox *et al.* 2012, Sievers *et al.* 2019). Megafaunal species (e.g., sharks, rays, sirenians, cetaceans and sea turtles) frequently utilize coastal areas as nursery grounds in early life stages (e.g., Bangley *et al.* 2018) or as breeding areas (e.g., Waerebeek and Read, 2014), foraging areas (e.g., Eckert *et al.* 2006, Sievers *et al.* 2019) and predator-free refuge areas later in life (e.g., Heithaus *et al.* 2009). However, megafauna species generally have large home ranges and are often migratory (Lewison *et al.* 2016). They, therefore, only spend a limited but essential proportion of their life cycle in such areas. Within these coastal areas, megafaunal species exhibit essential ecological roles, including as (top) predators (Ferreira *et al.* 2017). In addition, due to their migratory nature, these species form important functional links (e.g., transferring nutrients) between coastal areas and other systems, such as the pelagic zone (Williams *et al.* 2018, Sievers *et al.* 2019).

Coastal areas like seagrass meadows, rocky shores, tidal flats, and mangroves also provide an essential nursery habitat for pelagic and commercial fish species (Stål *et al.* 2008, Binet *et al.* 2013, Honda *et al.* 2013). Designating such vital areas as MPAs can result in increased species richness and biomass of commercial fish species in surrounding areas, the so-called spillover effects (Stobart *et al.* 2009, Polunin and Roberts, 1993). Consequently, fisheries might be attracted to the borders of MPAs (Lorenzo *et al.* 2016). However, this phenomenon may not be problematic for highly productive species with small home ranges (i.e., small teleosts). Concentrated fishing activities might pose threats to vulnerable species with large home ranges, migratory behavior or species that only utilize the protected areas during a certain life stage (Burgess *et al.* 2013, Dulvy *et al.* 2014, Lewison *et al.* 2014).

Elasmobranchs (i.e., sharks and rays) are a species group susceptible to bycatch, and with their low recruitment rates, high maturity ages and other K-selected life history characteristics, many species of this group are particularly vulnerable to any non-natural mortality rates (MacKeracher *et al.* 2018). In addition, the status of many elasmobranch species remains unknown, and many species have wide home ranges, which challenges the effective conservation of this species group (MacKeracher *et al.* 2018, Dulvy *et al.* 2014).

As a consequence of stricter fishing regulations in many developed countries, distant-water fleets of these nations moved to the territorial waters of developing countries, including many countries in West Africa (Balmford *et al.* 2004, Worm *et al.* 2009). The high productivity of these waters, caused by the upwelling of the Canary Current, attracts fishing fleets from nations all over the world (Belhabib *et al.* 2019). Consequently, fishing effort within this region is among the highest in the world (Pauly and Christensen, 1995, Grecian *et al.* 2016). The region also contains highly diverse marine ecosystems that are threatened by habitat degradation, overexploitation and pollution (Tittensor *et al.* 2010, Stuart-Smith *et al.* 2013). Furthermore, the West African region is known for its data deficiency and high prevalence of endangered marine species, in particular species like hammerhead sharks (*Sphyrna spp.*), Lusitanian cownose rays (*Rhinoptera marginata*) and blackchin guitarfishes (*Glaucostegus cemiculus*).

There are two large intertidal MPAs of high ecological importance within the region: Parc National du Banc d'Arguin (PNBA) in Mauritania and the Bijagós Archipelago (BA) in Guinea-Bissau (Figure 2.1). Both areas are considered to play an important role as spawning and nursery areas for commercial fish species and for migratory species, including elasmobranchs (Jager, 1993, Valadou *et al.* 2006). Declines in the annual catch per unit effort of rays and sharks within the boundaries of these MPAs have sparked concerns among park managers, conservationists, scientists and the local communities about the status of these species groups within the region (Lemrabott *et al. unpublished data*, Leurs *pers. obs.*). Although fishing pressure through artisanal practices and bycatch rates within the MPAs are also substantial (Campredon and Cuq, 2001, Valadou *et al.* 2006, Diop and Dossa, 2011), fishing effort of industrial fleets at the borders of these MPAs could potentially have negative effects on the population status of marine megafauna utilizing these coastal areas (Guénette *et al.* 2014, Di Lorenzo *et al.* 2016). Herein we describe the industrial fishing activity within the West African region between 2012 and 2018 with three main objectives: (1) to analyze the spatiotemporal extent of gear-specific fishing efforts within the region, (2) to map fishing activity in the direct vicinity of the two largest West African MPAs, Parc National du Banc d'Arguin and the Bijagós Archipelago and (3) to link the industrial fishing effort with seasonal bycatch of elasmobranchs (i.e., sharks and rays) to estimate its effect on nature conservation goals of coastal MPAs.

Methods

Study area

We focused on the Eastern Central Atlantic (major fishing area 34 as defined by the Food and Agriculture Organization of the United Nations, FAO) as our main study area. This study site ranges from the territorial waters of Morocco in the north to the territorial waters of the Democratic Republic of Congo in the south (Figure 2.1). Geographical data on the EEZs of all nations within this region were extracted from the "MarineRegions" dataset (Lonneville *et al.* 2019). Areas outside of any EEZ were classified as the high seas.

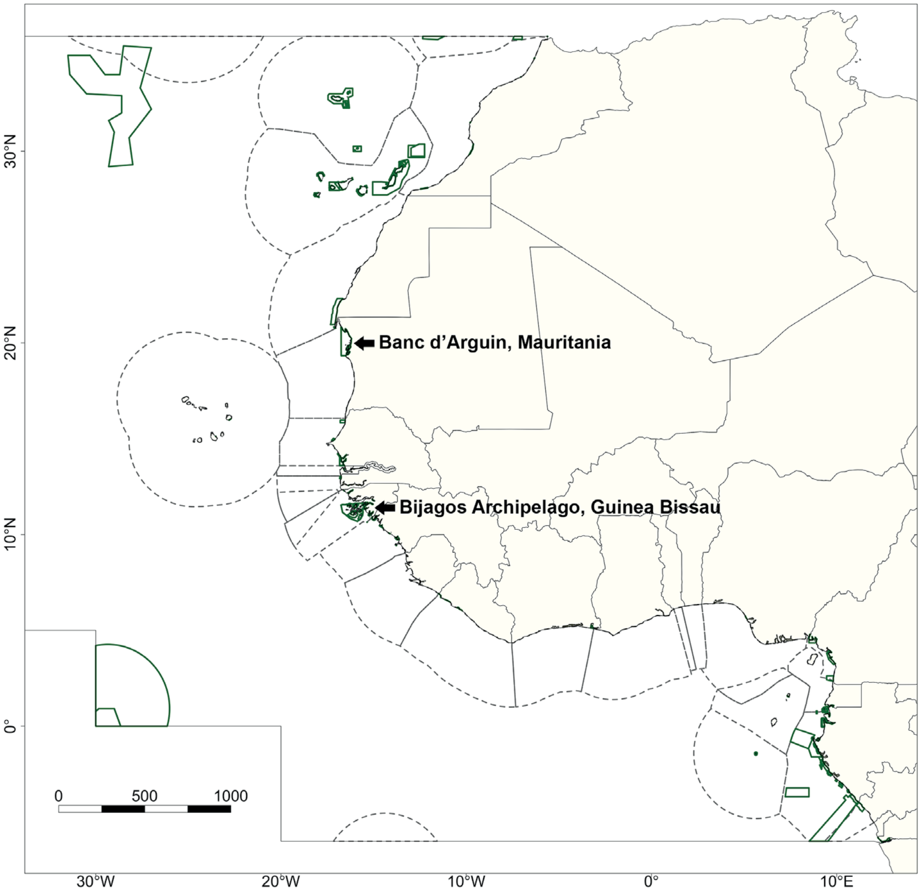

Figure 2.1 Defined study area indicating the Exclusive Economic Zones (EEZs; dashed lines) and Marine Protected Areas (MPAs; green lines) within the West African region. The inner gray border represents the northern and southern edges of the study area. The two focal MPAs, the Parc National du Banc d'Arguin (Mauritania) and the Bijagós Archipelago (Guinea-Bissau) are indicated.

Within our study area, we focused on two large MPAs: Parc National du Banc d'Arguin (PNBA; N20°14'5", W16°6'32") and the Bijagós Archipelago (BA; N11°15'0", W16°5'0") (Figure 1), for which spatial delineation was obtained from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2019). The PNBA is the largest marine park in West Africa. It was designated as a RAMSAR site in 1982 and as a UNESCO World Heritage site in 1989. The entire national park is 12,000 km^2, of which 5,600 km^2 is marine (Binet *et al.* 2013). The area comprises a large variety of habitats, from bare tidal flats and intertidal seagrass meadows to extensive subtidal areas. The BA covers a 12,958 km^2 archipelago consisting of 88 islands and islets. The archipelago was designated as a UNESCO Biosphere Reserve in 1996 and as a RAMSAR site in 2014. The Bijagós contains dense mangrove forests, tidal flats, complex gully systems and extensive subtidal areas. Within the Bijagós Biosphere Reserve, the islands of Formosa, Orango, and João Vieira are designated as MPAs. Both MPAs are considered to be important for a large variety of (commercial) fish species, elasmobranchs and migratory shorebirds.

Data collection

Fishing effort data (2012 - 2018) was obtained from the Global Fishing Watch (GFW; www.globalfishingwatch.net), based on processed Automatic Identification System (AIS) transmissions of large vessels (Kroodsma *et al.* 2018). The GFW applied artificial neural network algorithms to the AIS data, which determined fishing activity and gear type used based on the speed and movement pattern of the vessel. As AIS is mandatory for all vessels above 300 gross tonnage, the dataset only includes large industrial vessels.

In total, 15 different gear categories within West African waters were identified, which we reclassified into six more general categories (Table 2.1). In addition, the GFW linked Maritime Mobile Service Identity (MMSI) information to the AIS transmissions, providing the flag state of registration for each vessel. The fishing effort, as the total number of fishing hours (in kilo hours, kh), was then determined per vessel, flag state, gear type and year for every 0.1° longitude/latitude grid cell over 2012-2018.

Fishery-dependent data was collected as part of fisheries observer programs by the national fisheries institutes Institut Mauritanien de Recherches Océanographique et de Pêches (IMROP) and Centro de Investigação Pesqueira Aplicada (CIPA), for Mauritania and Guinea-Bissau respectively. The data from the Mauritanian EEZ is based on logbook data documented and curated by the National Fisheries Institute IMROP. Data for this area was reported in the total catch per functional group, and the fishing effort was documented from 2012 to 2018. The data from Guinea-Bissau was collected by observers, who recorded the catch (in kg) per functional group (e.g., “Rays”, “Sharks”, “Diverse pelagics”). Observers also recorded the effort (in hours) for each vessel. The total catch per functional group and the total fishing effort was collected from 2012 to 2016 (CIPA, 2012, 2013, 2014, 2015, 2016). Vessel-based observer data was combined with fleet-wide landing data to extrapolate bycatch observations to the fleet level. No data on the survey effort was recorded for this data. The data presented thus reflects non-standardized survey efforts per month.

Table 2.1 New categories based on categories assigned by the Global Fishing Watch (GFW).

Category	**GFW label**
Trawlers	“trawlers”
Drifting longlines	“drifting longlines”
Fixed gear	“set longlines” “pots and traps” “set gillnets” “other fixed gears”
Purse seines	“tuna seines” “purse seines” “other seines”
Other gear	“pole and line” “dredge” “squid jiggers” “trollers” “other gears”
Unknown gear	“fishing”

Data processing

A 0.1° grid (±11x11 km near the equator) was superimposed on the study area, and industrial fishing effort was calculated per grid cell. The fished extent was determined as the proportion of fished grid cells relative to the total number of grid cells (n = 224,926). To determine and visualize the annual, gear-specific fishing effort in the direct vicinity of both MPAs, we created two buffer zones around each MPA of 1.5 and 2.0 times the surface area of the MPA. We also calculated the cumulative fishing effort over increasing distance from each MPA of each gear type specifically. Fishing effort based on the AIS data was not compared between years, as the number of vessels detected by the GFW algorithms increased every study year due to technological enhancements. For this reason, 2018 is reported for the most recent fishing effort calculations. For annual trends in fishing effort, we used the fishery-dependent data.

The fishery-dependent observer data contained information on both catches (in tons) and fishing effort (in fishing days). Catches were classified into functional groups, as limited information on species identification was available. From 2012 to 2015, both focal countries reported elasmobranch catches as part of diverse groups like “Diverse pelagic” or “Diverse demersal”. Since 2016, catches of sharks and rays have been reported separately (i.e., catches were not grouped together as elasmobranchs or grouped into other functional groups). Our data analysis only includes those catches reported as elasmobranchs, resulting in a conservative estimate of catches. Rays included all species labeled as “Raia”, and sharks included all species of hammerhead sharks (*Sphyrna spp.*), or species labeled as “Elasmobranchii” or “Caudo”. Fishing effort was registered as the number of hours that a vessel was actively fishing during a fishing expedition, separated per gear type. Seasonality of elasmobranch catches was investigated using catch recordings, for both countries separately. In addition, the total fishing effort was determined from the registered fishing effort and was subsequently compared to the AIS-based fishing effort of the GFW. For this, seasons were determined as winter (December-February), spring (March-May), summer (June-August) and fall (September-November).

Results

Spatiotemporal fishing activity off West Africa

A total of 5,449 kh (0.39 h^{-1} km^{-2}) of fishing effort by AIS-operating vessels were observed within the entire West African region, including the high seas, between 2012 and 2018 (Figure 2.2A, Appendix 2.3), with an average annual effort of 778 ± 466 kh (mean ± s.d.). Over the 6-year study period, at least 42.2 % of the West African region (5.9 x 10^6 km^2) was fished at least once (at our 0.1° resolution), with a mean annual extent of 21.9 ± 6.7% (3.9 ± 0.9 x10^6 km^2) (Appendix 2.1). Fishing effort concentrated in coastal waters (70% in EEZs compared to 30% in high seas), with the EEZs of Mauritania (10%), Western Sahara (8%), Morocco (8%) and Guinea-Bissau (7%) together containing over 36% of the total fishing effort (Appendix 2.3). The spatial distribution of the fishing effort peaked between the longitudes -18.45 and -15.45 (70.3 ± 56.6 kh) and off Sierra Leone between the latitudes 3.15 to 5.65 (27.2 ± 19.6 kh) (Figure 2.2). From the six gear types observed within the study area, trawlers (2,625 kh; 48.2%) and drifting longlines (1,901 kh; 34.9%) were the most deployed gear. The fishing effort of other gear types was relatively low (~200 kh combined; Appendix 2.3). Drifting longlines mainly operated on the high seas (80.3% of total effort by longliners). Trawlers were concentrated within the coastal zones and only covered 1.2 ± 0.3% of the entire region.

Over the entire study period, vessels from 60 flag states were observed within the West African region, although only ten flag states were responsible for 88% of the total fishing effort. The five most active flag states within the region were Spain (24%), China (15%), Japan (12%), Morocco (11%) and Ghana (6%).

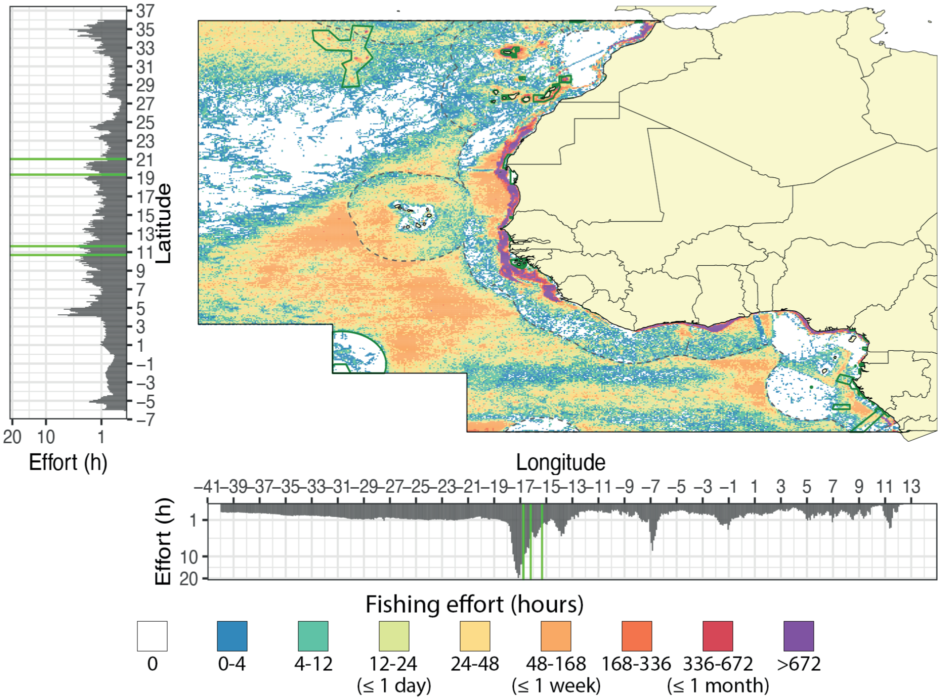

Figure 2.2 Total fishing effort off West Africa from 2012 to 2018. Color scale indicates the total hours of fishing within each grid cell (low = blue, moderate = yellow/orange, high = purple). Histograms on the axis show the total fishing effort in hours over the longitudinal and latitudinal range of the region. The longitudinal and latitudinal ranges of both MPAs are indicated with green lines.

Fishing activity near MPAs

Parc National du Banc d'Arguin (PNBA)

AIS-registered vessels showed a total of 560.7 kh fishing effort (3,2 h^{-1} km^{-2}) within the Mauritanian EEZ over the study period, covering 95.3% of the EEZ. Based on the fishery-dependent data, the fishing effort of the entire fleet operated within the Mauritanian EEZ ranged between $26.7 \cdot 10^3$ days in 2013 and $54.1 \cdot 10^3$ fishing days in 2018 (Figure 2.3A). No significant increase in fishing effort was found for the

Mauritanian EEZ. In total, 41 flag states operated within this EEZ during the study period, with Spain (36.4%), China (30.4%), and Mauritania (7.7%) being the dominant fleets (Appendix 2.3). Fishing vessels deployed all gear types, with trawlers as the most dominant gear type (353.3 kh; 63.0%). Because these trawlers mainly operated in coastal waters (Figure 2.4), the fished extent was relatively small (35.1% of the EEZ). Fishing effort increased over short distances from the PNBA, with trawlers showing the highest increase in efforts near the MPA and within the buffer zones (Appendix 2.2). Fishing effort within the 2.0x buffer zone around the PNBA was 117.5kh in 2018, with no industrial fishing observed within the boundaries of the PNBA. In 2018, 42.0% of the grid cells within the buffer zone were fished at least once, with trawlers dominating in both effort (89.3kh) and extent (33.2%).

The spatial distribution of trawlers was relatively constant throughout the year, while effort was highest in July (4.2 ± 3.8 kh) and December (4.4 ± 2.8 kh). There was a clear seasonal change in the spatial distribution of drifting longlines and fixed gears within the Mauritanian EEZ. Drifting longlines were constantly present but gradually increased from spring (3.3 kh) to fall (8.4 kh). Fixed gear types showed higher fishing effort in fall and winter (Figure 2.4). Overall fishing effort within the 2.0x-buffer zone peaked in the months of July, August and December (Figure 2.4C). Seasonal patterns in fishing effort between the AIS data (2.0x buffer zone) and the fishery-dependent data (Mauritanian EEZ) showed similar patterns (Figure 2.3C).

Traceable catches of sharks and rays were only documented in 2016, 2017 and 2018. Elasmobranch catches peaked at 85.8 tons in 2018, of which 55.5 tons were rays (64.7%) and 30.3 tons were sharks (35.3%) (Figure 2.3A). Ray catches were highest from April to July (8.4 ± 3.3 tons; mean ± se), whereas shark catches peaked in February (7.3 ± 3.4 tons) and July (6.0 ± 2.3 tons) (Figure 2.3B).

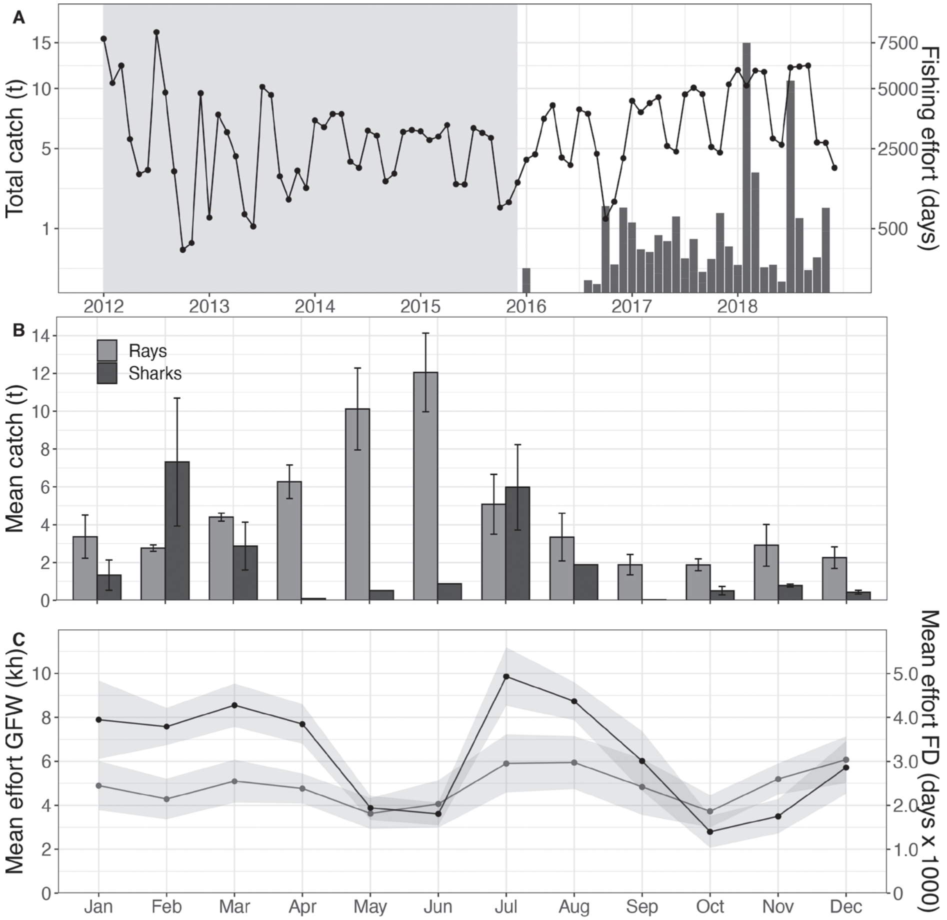

Figure 2.3 Total elasmobranch catches (bars) and fishing effort (line) within the Mauritanian EEZ, with no-data periods for elasmobranchs indicated in gray (A); with a close-up of the monthly mean catches, separated for sharks (black) and rays (grey), over the 2016-2018 period (B), in relation to fishing effort within the PNBA 2x buffer zone based on the AIS data (gray; in kh), and the total fishing effort in the Mauritanian EEZ as reported by the fisheries institute (black; in fishing days, FD) (C).

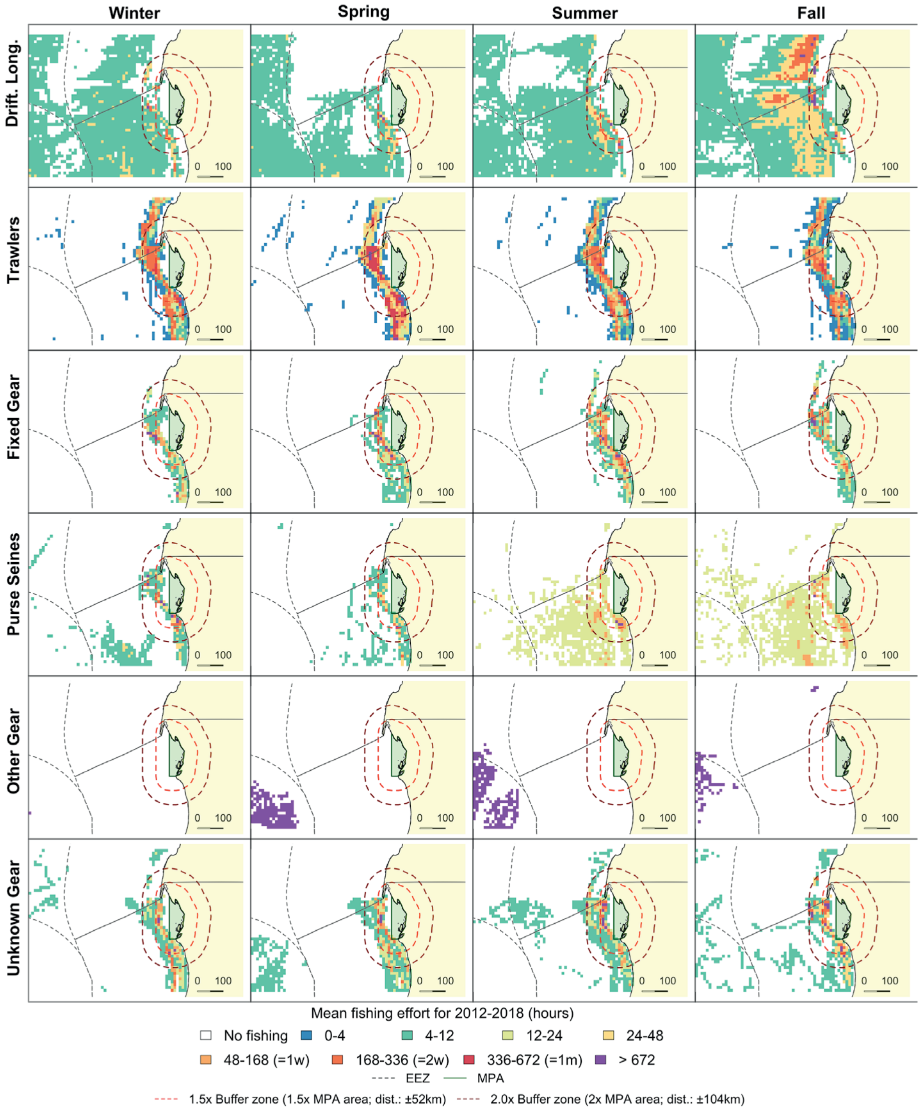

Figure 2.4 Fishing effort in the direct vicinity of PNBA (green) in Mauritania. Grid cell colors indicate seasonal mean fishing effort over the 2012 to 2018 period. Orange and red dashed lines represent 1.5x and 2.0x buffer zones of the PNBA. Exclusive Economic Zones (EEZ) are indicated as gray dashed lines.

Bijagós Archipelago (BA)

Fishing effort within the EEZ of Guinea-Bissau totaled to 386.0 kh (3.4 h^{-1} km^{-2}) in the study period, with a total fished extent of 73.5%. Based on fishery-dependent data, the fishing effort significantly increased ($ß = 12.39$, $t = 5.05$, $p < 0.01$) with 12.4 days per month from $10.4 \cdot 10^3$ days in 2013 to $27.8 \cdot 10^3$ fishing days in 2016 (Figure 2.5A). A total of 21 flag states were active within the EEZ, dominated by mainly Spain (34.3%), China (28.8%) and Senegal (9.8%) (Appendix 2.3). During the study period, all six gear types (Table 2.1) were observed. Trawlers showed the highest effort (374 kh; 96.9%), and were concentrated near the coast (48.4% of EEZ) (Figure 2.6). Unidentified gear types were the second most dominant, with a fishing activity of 8.7 kh (2.3%).

No industrial fishing effort was observed within the BA boundaries, but high effort was observed near the MPA borders (Appendix 2.2). Within the 2.0x buffer zone, fishing effort was 88.3 kh in 2018, with an extent of 42.9%. Trawlers were dominant in both effort (65.4%) and extent (41.2%) in 2018, based on AIS data. The fished extent within the buffer zone remained relatively constant throughout the year for all gear types, but fishing effort peaked in spring (Figure 2.5C, Figure 2.6). Seasonal patterns in fishing effort between the AIS data (2.0x buffer zone) and the fishery-dependent data (entire EEZ) showed similar patterns (Figure 2.5C).

Elasmobranch catches within the EEZ of Guinea-Bissau were reported separately in 2012 and from 2014 to 2018 (Figure 2.5A). In other years, catches were integrated into other functional groups and are therefore not included here. Reported catches were highest in 2016, with 262.92 tons, of which 18.97 tons (7.2%) were ray species and 243.95 tons (92.8%) were shark species. In the most recent year of the study (2018), total elasmobranch catches were 39.46 tons, with catches existing of 35.79 tons of rays (90.7%) and 3.68 tons of sharks (9.3%). Ray catches were highest in April and May, with 7.95 ± 3.04 (mean ± se) and 6.80 ± 1.13 tons, respectively (Figure 2.5B). Shark catches were also highest in October, with a mean weight of 23.74 ± 17.86 tons, and in May (23.49 ± 10.42 tons)

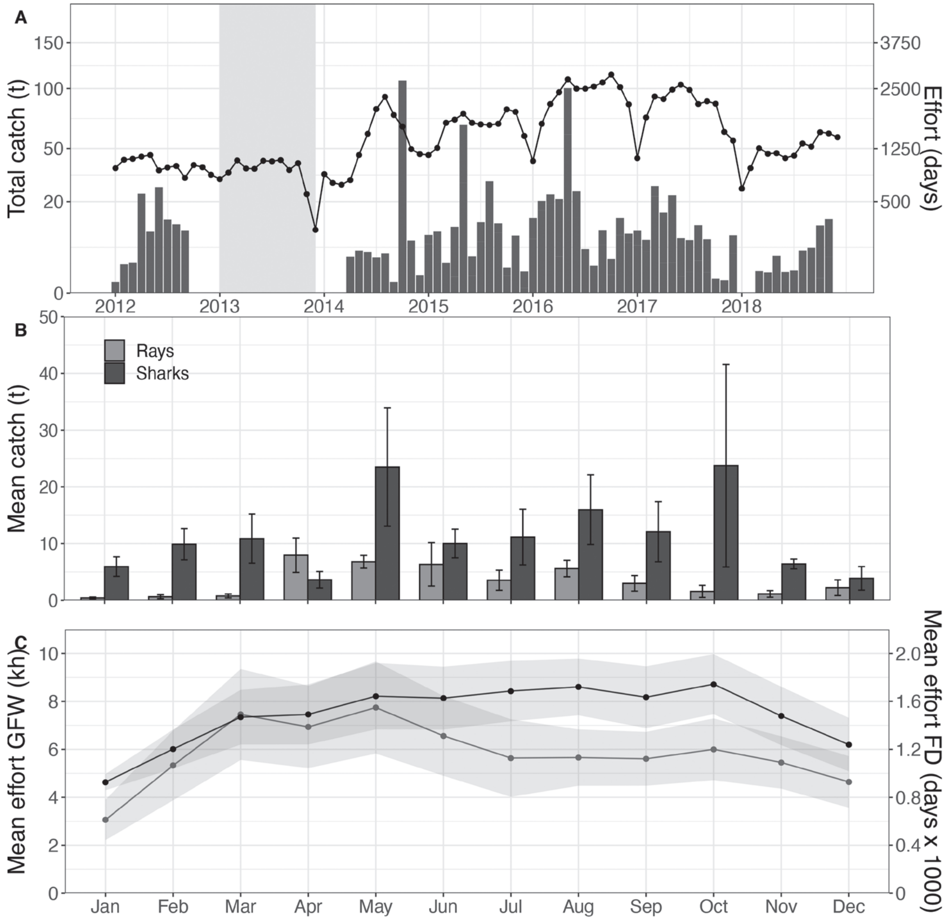

Figure 2.5 Total elasmobranch catches (bars) and fishing effort (line) within the Guinea-Bissau EEZ, with no-data periods for elasmobranchs indicated in gray (A), with a close-up of the monthly mean catches, separated for sharks (black) and rays (grey), over the 2014-2016 period (B), in relation to fishing effort within the BA 2x buffer zone based on the AIS data (gray; in kh), and the total fishing effort in the EEZ of Guinea-Bissau as reported by the fisheries institute (black; in fishing days, FD) (C).

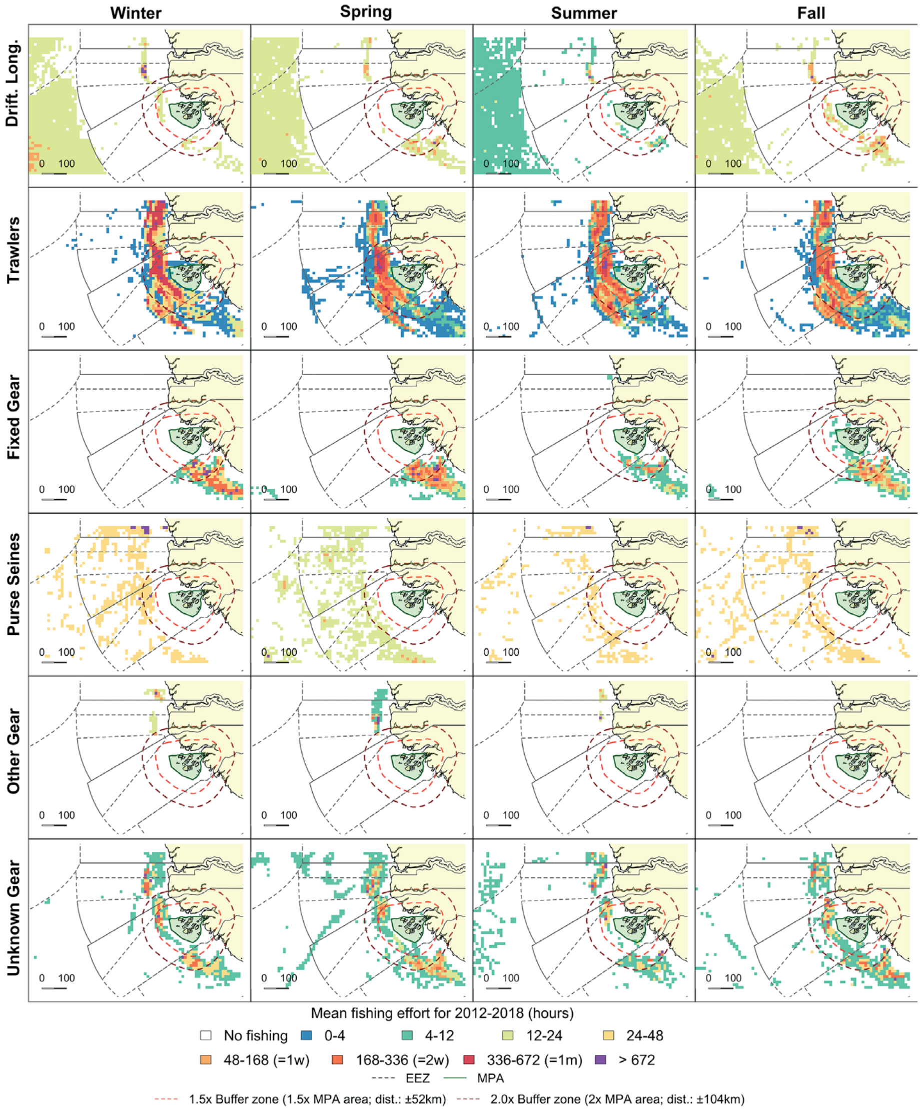

Figure 2.6 Fishing effort in the direct vicinity of the BA in Guinea-Bissau (in green). Grid cell colors represent seasonal mean fishing effort over the 2012 to 2018 period. Orange and red dashed lines indicate 1.5 and 2.0 buffer zones, respectively. Exclusive Economic Zones (EEZ) are indicated as gray dashed lines.

Discussion

In this study, we provide new insights into the recent (2012-2018) effort and spatiotemporal distribution of industrial fisheries in West Africa. In addition, we focused on fishing efforts in the vicinity of two large coastal MPAs. AIS records demonstrated that fishing activity is concentrated near the borders of MPA: Parc National du Banc d'Arguin (PNBA, Mauritania) and the Bijagós Biosphere Reserve (BA, Guinea-Bissau). Fishing effort within the Mauritanian EEZ was relatively stable, whereas effort within the EEZ of Guinea-Bissau increased significantly with 12 fishing days a month. Industrial fishing activity was mainly dominated by trawlers, drifting longlines and fixed gears. These gears mainly target mackerel (*Scomber* spp.), sardinella (*Sardinella* spp.), horse mackerels (*Trachurus* spp.) and cephalopods (Belhabib *et al.* 2013, Belhabib and Pauly 2015), but have bycatches of sharks and rays. In the waters from both Mauritania and Guinea-Bissau, the catches of elasmobranchs peaked in the most recent years of the study period. Seasonal peaks in industrial shark and ray catches were observed as well, but these did not coincide with seasonal maxima in industrial fishing efforts. We showed that industrial fisheries (especially trawlers) are concentrated within a thin belt surrounding both MPAs. This concentrated fishing effort could have potential effects on mobile marine predators such as elasmobranchs and other species that utilize coastal MPAs for a part of their life cycle only. Hence, fishing concentrations near MPA borders may impair the role of coastal MPAs for the protection of endangered, highly mobile marine megafauna. The inclusion of seasonal migration patterns and seasonal fishery bans near MPAs could aid in the conservation of mobile marine megafauna.

Although fishing efforts near the PNBA and BA showed a seasonal pattern, a similar pattern was not visible in reported elasmobranch catches from both EEZs. The observed peaks are probably explained by the higher temporal abundances of these species, indicating their migratory behavior. In Mauritania, sharks were caught most in February and July. These observations are congruent with those described by Zeeberg *et al.* (2006), who report the highest catches in August for hammerhead sharks and February for other shark species. The scalloped hammerhead shark (*Sphyrna lewini*), for instance, utilizes shallow coastal habitats during early life stages (e.g., mangrove areas) before it moves to more pelagic and deeper habitats (Hoyos-Padilla *et al.* 2014, Coiraton *et al.* 2020). The species migrates back to coastal, shallow habitats for parturition during the boreal summer (Capapé *et al.* 1998, Hazin *et al.* 2001). Recent findings suggest that scalloped hammerhead sharks are more dependent on coastal habitats than previously hypothesized (Coiraton *et al.* 2020). The PNBA is also hypothesized to be an important feeding and parturition site for the Lusitanian cownose ray (*Rhinoptera marginata*). Within the PNBA, ray catches by artisanal fishermen peak from November to the end of February (Lemrabott *in prep*.). A similar season (September to December) is reported for industrial fisheries and scientific surveys outside the PNBA (Hofstede 2001, Krakstad *et al.* 2004, Krakstad *et al.* 2005). Our study, on the other hand, shows that the catches of rays peak in April and July within the Mauritanian EEZ. Differences might be caused by the fact that the temporal scales of the studies do not overlap with the temporal scale of this study. Alternatively, annual differences in coastal upwelling events might cause changes in catches.

For Guinea-Bissau, we demonstrated increased catches of sharks and rays in May, October, and November. However, little information is available on elasmobranch abundance and habitat use. The scientific reports, based on observer data, additionally comprise limited species-specific information and have little consistency in registration. The actual numbers thus may be uncertain. However, the reported bycatch of elasmobranchs is supported by other studies (Belhabib and Pauly, 2015), sometimes showing much higher catch rates. We, therefore, argue that our estimates probably underestimate actual catches.

We demonstrated that trawlers were present during the whole year and dominated both fishing effort and spatial extent near the PNBA and BA. Drifting longlines were absent near BA but peaked near the PNBA in fall. Both gears generally have a high bycatch of sharks and rays (Zeeberg *et al.* 2006, Oliver *et al.* 2015). Drifting longlines were not present near BA, but the presence of this gear type near the PNBA peaked in fall. Trawlers have reported bycatch to mainly consist of pelagic teleosts (31%), hammerhead sharks (28%) and other shark species (19%) (Hofstede *et al.* 2001). Similarly, Zeeberg *et al.* (2006) reported that 42% of all bycatch for trawlers operating off Mauritania was hammerhead sharks, with other bycatch including large teleosts (i.e., sunfish *Mola mola* and billfishes; 26%), reef manta rays (*Manta birostris*; 9%), other sharks (9%), cetaceans (8%), benthic rays (5%) and sea turtles (1%). Bycatch of longline gear types within the region is characterized by species such as the Atlantic blue marlin (*Makaira nigricans*), blue sharks (*Prionace glauca*) and smooth hammerhead sharks (*Sphyrna zygaena*) (Coelho *et al.* 2015, Fernandez-Carvalho *et al.* 2015). Hence, trawlers and longliners surrounding the MPAs pose a conservation threat to elasmobranchs within the MPAs.

Our results show that the overall fishing effort was mainly concentrated near the borders of both MPAs. MPAs are known to increase local fish biomass, drawing fishing vessels to their borders to target the 'spillover' from these areas (Di Lorenzo *et al.* 2016). Another possible explanation for the concentrated fishing in this area is the local upwelling of the Canary Current, which makes the coast off the Western Sahara and Mauritania one of the richest fishing areas in the world (Goffinet, 1992). However, this does not explain why fishing effort is also concentrated near the Bijagós Archipelago, as it is located south of the upwelling's boundary (Goffinet, 1992). This upwelling is strongest during the short period from December to March (Cushing, 1971), which could result in elevated fishing activity due to higher local production. Indeed, it partly coincides with elevated fishing effort within the Mauritanian EEZ, but not with peaks in fishing effort in the waters of Guinea-Bissau, as migratory species utilize coastal areas for (parts) of their lifecycle and migrate between multiple habitats. For instance, American cownose rays (*Rhinoptera bonasus*) can migrate over distances of more than 1,500 km, and scalloped hammerhead shark movements could be traced at 684 km from coastal areas (Diemer *et al.* 2011, Ogburn *et al.* 2018). Our results from the 2.0x buffer zones around the PNBA and BA could indicate that this concentrated fishing activity might interfere with the migratory nature of these marine megafauna species.

In this study, we revealed spatiotemporal patterns of industrial fisheries in West Africa. We showed seasonal fluctuations but overall high concentrations of effort near the borders of the Banc d'Arguin National Park and the Bijagós Archipelago MPAs. Furthermore, we showed seasonal patterns in elasmobranch bycatch recordings within the EEZs of the corresponding countries, illustrating the migratory behavior of these species. We, therefore, conclude that the high concentration of fishing effort surrounding these important coastal areas conflicts with the migratory nature and vulnerability of elasmobranch species using these areas. This may lead to a further decrease of these vulnerable species in both pelagic and coastal habitats and their associated ecological role in linking these habitats. The increasing removal of predatory species from marine ecosystems can cascade through the ecosystem, with consequences for (both ecological and economic) ecosystem services (Martin *et al.* 2010, Barbier *et al.* 2011, Estes *et al.* 2011). For example, the removal of top predators like cod (*Gadus morhua*) is assumed to be the most likely explanation for the observed increase in mid-sized fishes, which in turn has caused increases in macro-algae recruitment (ecologic) or a weakening of the biological pump of nutrients from great depths, possibly negatively influencing productivity of fisheries (economic) (Sieben *et al.* 2011, Hammerschlag *et al.* 2019). The densely concentrated fishing activity near the border of such protected areas, therefore, not only undermines the conservation value of these areas for these megafauna species but might cascade into reduced functioning of coastal ecosystems and associated local livelihoods.

Acknowledgments

Many thanks to the Global Fishing Watch for the open-access data that provides valuable insight into these remote waters. Especially to Tyler Clavelle and David Kroodsma for the advice and help with the newest version of the dataset. We would like to thank all fisheries observers, statisticians and all other staff from IMROP (Mauritania) and CIPA (Guinea-Bissau) for collecting and providing the fishery-dependent data used in this study. Finally, we would like to thank Fábio Barroso and Tommaso Saccà. The MAVA Foundation funded the 'Waders of the Bijagós' project. LLG was funded by the Dutch Research Council (NWO016.VENI.181.087). KJR was funded through a grant from the Dutch Gieskes-Strijbis Fund.

Chapter 3

Overfishing of threatened bycatch species in a marine protected area: the elasmobranchs of the Banc d'Arguin, Mauritania

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Manuscript

Abstract

Elasmobranch (i.e., shark and rays) populations are vulnerable to overexploitation due to their generally slow growth, late maturity, and low fecundity. Now that these species are amongst the most threatened marine fish, their continued exploitation raises concerns at a global level. Although the impact of industrial fisheries on elasmobranchs has been documented on a global and regional scale, information on the effects of coastal (artisanal) fisheries remains scarce, especially for the data-deficient West African region. We describe the historical trends between 1998 and 2020 in catches of sharks and rays in the artisanal fisheries in the Parc National du Banc d'Arguin (PNBA), Mauritania (West Africa). We show that 16 shark and 17 ray species are captured in this area, of which 15 (94%) and 13 (76%) species are threatened with extinction, respectively. Initially caught as bycatch in the local small-scale fishery targeting migratory teleosts, elasmobranch fishing has been practiced in the PNBA for over four decades. Within the park, two main gear types are used to catch elasmobranchs- shark and meagre fixed gill nets- with catches comprising over 60% of elasmobranchs. This indicates that elasmobranchs are not only considered bycatch but targeted elasmobranch fisheries are also common. Fishing effort increased in 2006 and has remained high recently, whereas catch-per-unit-effort and occurrences of once common species have declined. Our results highlight significant declines in the catches of elasmobranch species, representing a decline in the population of these species. We propose that conservation and management approaches in the national park should focus on restricting fishing in areas with the highest occurrence of threatened species in the catches, introducing new regulations on fishing gear types, and restricting trade in elasmobranch products from the PNBA.

Introduction

Elasmobranch species (i.e., sharks and rays) are threatened globally and are now one of the most threatened vertebrate species groups. According to recent estimates, one-third of all shark and ray species are currently threatened with extinction, with overfishing and habitat degradation being the main anthropogenic threats (Dulvy *et al.* 2021). Generally, larger shark and ray species experience disproportionally more significant threats (Dulvy *et al.* 2014, Fernandes *et al.* 2017). Sharks and rays are susceptible to increased fishing pressure due to their relatively large body size and low intrinsic population growth due to K-selected life history traits (i.e., slow individual growth rates, late maturity, and low fecundity, Dulvy *et al.* 2014, Parton *et al.* 2019), but are also vulnerable to other threats, such as habitat degradation due to their use of coastal areas (e.g., mangroves, Knip *et al.* 2010).

Small-scale fisheries are often considered relatively more sustainable compared to industrial fisheries. In the context of ecosystem services, these traditional and subsistence fisheries are central to coastal communities (Campredon and Cuq 2001). However, artisanal fisheries worldwide have developed over the past decades, causing these fisheries to increase in size in most regions (Palomares & Pauly, 2019). These fisheries contribute to up to half the global yield in fisheries (The & Pauly 2018, Derrick *et al.* 2023) and can thus have a significant impact on coastal resources. The effect of these fisheries on vulnerable species such as sharks and rays within coastal marine protected areas in the West African region remains unknown. This is especially concerning due to the deteriorating conservation status of sharks and rays within the region (Dulvy *et al.* 2021), the high proportion of endemic species within the region (Stein *et al.* 2018), and their use of coastal areas during early life stages and as feeding refugia (Knip *et al.* 2010, Leurs *et al.* 2023).

The West African region contains large coastal ecosystems, such as the Banc d'Arguin in Mauritania and the Bijagós Archipelago in Guinea-Bissau, which are considered hotspots for many shorebird species (Catry *et al.* 2015, Oudman *et al.* 2020), commercial fish species (Binet *et al.* 2013, Correia *et al.* 2021), and in particular for threatened endemic species of sharks and rays (Stein *et al.* 2018, Leurs *et al.* 2023). It is therefore identified as a global priority area for the conservation of endemic shark and ray species (Stein *et al.* 2018). This importance is illustrated by the recent discovery of the False Shark Ray (*Rhynchorhina mauritaniensis*), a unique large-bodied species of wedgefish only known from the shallow waters of Banc d'Arguin (Séret and Naylor 2016). Oceanic upwelling combined with shallow nursery grounds qualify the Mauritanian coast as one of the most productive and richest fishing grounds in the world (Alder and Sumaila 2004, Merem *et al.* 2019), attracting both national and international fishing fleets (Leurs *et al.* 2021). Sharks and rays using coastal areas within the region are potentially threatened by industrial fisheries operating directly outside these coastal areas (Leurs *et al.* 2021) and also face a potential threat from fisheries occurring within these shallow-water areas (Lemrabott *et al.* 2023).

This study presents a historical and current perspective on shark and ray fisheries within the Banc d'Arguin National Park (PNBA). For this, we use fisheries-dependent data collected at the main landing sites within the national park for over two decades. To gain more insight into the status of fisheries within the PNBA, a landing site survey was initiated in 1997 and is still ongoing. As part of this program, fish landings are recorded in all nine fishing villages within the boundaries of PNBA (Figure 3.1). Traditionally, species targeted in the artisanal Imraguen fisheries were limited to teleosts, mainly mullet (*Mugil cephalus*), meagre (*Argyrosomus regius*), and several other species, such as tilapia and catfish. However, fisheries have increasingly also targeted elasmobranch species (Lemrabott *et al.* 2023, Lemrabott *et al. 2024*).

More than 30 elasmobranch species have been documented from the waters of the PNBA, with some of them using this area as nursery and feeding areas (Ducrocq 2004, Valadou *et al.* 2006). Although the elasmobranch populations within the PNBA have been fished for over four decades, their current conservation status remains uncertain. We report the statistics of these landing site surveys specifically to determine the historical and current status of large-bodied sharks (i.e., hammerhead and requiem sharks), large rays (i.e., eagle and cownose rays) and guitarfishes (i.e., blackchin guitarfish, *Glaucostegus cemiculus*) within the borders of the national park. Specifically, we aim to (1) determine the spatiotemporal trends in elasmobranch landings within the PNBA from 1998 until 2020, (2) describe the trend of total effort and gear-specific effort, and (3) identify potential management opportunities to conserve sharks and rays within the PNBA more effectively.

Methods

Study area

The Banc d'Arguin (PNBA) is a 12,000 km^2 shallow intertidal area (<20 m depth) off the coast of Mauritania (West Africa; Figure 3.1) and is both a Ramsar Wetland site (1983) and UNESCO World Heritage site (1989). The PNBA comprises a complex network of intertidal flats, seagrass beds and tidal channels. The PNBA, due to its ecological role and the high value for elasmobranch conservation, was once described as one of the largest sanctuaries for sharks and rays in Africa and the Atlantic Ocean (Ducrocq 2004). 114 fishing boats are operational in the nine fishing villages within the PNBA, making up currently the maximum number of vessels with exclusive access to the park's waters. Fishing is conducted during single-day or multiple-day trips and is increasingly year-round. Fishing rights are exclusive to the local Imraguen communities, subject to the use of artisanal fishing methods and non-motorized wooden sailing boats known as "lanches" (Lemrabott *et al.* 2023, Lemrabott *et al.* 2024).

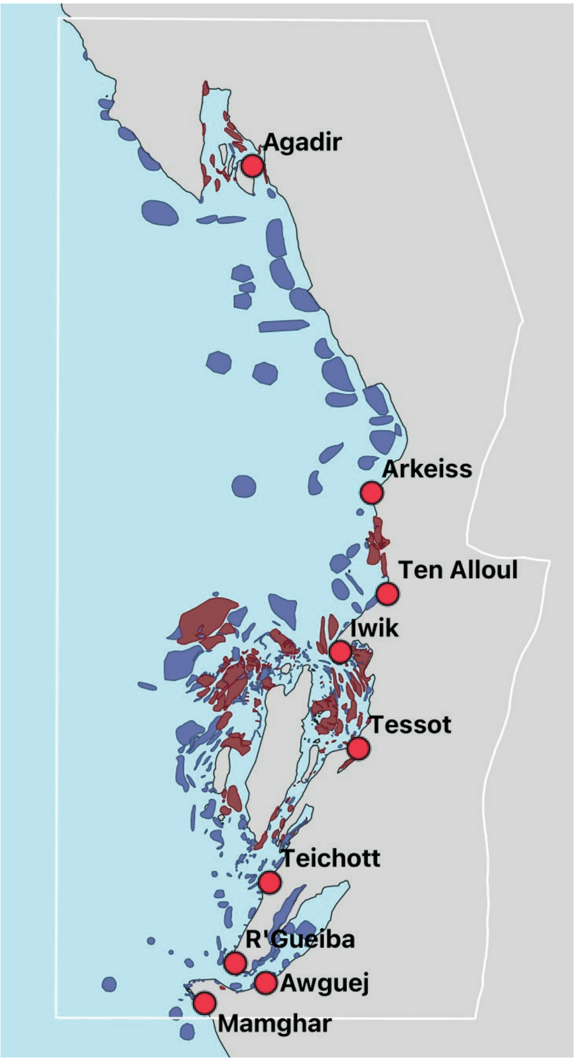


Figure 3.1 Map of the Parc National du Banc d'Arguin (PNBA) in Mauritania, showing the Imraguen villages (red circles) and boundaries of fishing areas as identified by fishers within PNBA (n > 500). Fishing areas considered intertidal (i.e., exposed during low tide) are indicated in red and subtidal fishing areas in blue.

Data processing and analyses

Banc d'Arguin artisanal fisheries have been monitored since 1997 in the framework of a joint monitoring program between IMROP and the PNBA. At six landing sites, local community members trained by the National Fisheries Institute of Mauritania IMROP assist a team of scientific researchers in collecting data. Boat captains and fishers volunteer to share details on catches and the fishing trip, which the fisheries researchers are permitted to record. A more detailed description of the landing site monitoring program and reporting on catch data is provided in Lemrabott *et al.* (2023).

Table 3.1 Characteristics of gear types and fishing methods in the Banc d'Arguin small-scale fisheries.

Local name	English name	Mesh sizes (mm)	Fishing method
Filet courbine	Meagre net	>200	Fixed floating gill net & seine fishing
Filet tollo	Shark net	140 – 180	Fixed floating gill net
Filet mulet	Mullet net	100 – 120	Fixed floating gill net & seine fishing
Ligne a main	Handline	100 – 120	Handlining

Table 3.2 Species categories used.

Category	Species	English name	Maximum size (cm)
Large sharks	*Carcharinus brevipinna*	Spinner shark	300
	Carcharinus limbatus	Blacktip shark	286
	Carcharinus obscurus	Dusky shark	420
	Carcharinus plumbeus *Carcharhinus spp.*	Sandbar shark	300
	Sphyrna lewini	Scalloped hammerhead shark	430
	Sphyrna zygaena	Smooth hammerhead shark	500
	Ginglymostoma cirratum	Atlantic nurse shark	430
	Negaprion brevirostris	Lemon shark	340
	Galeocerdo cuvier	Tiger shark	750
Guitarfish	*Glaucostegus cemiculus*	Blackchin guitarfish	242
Large rays	*Rhinoptera marginata*	Lusitanian cownose ray	200
	Aetomylaeus bovinus	Duckbill eagle ray	222

We analyzed the data on shark and ray catches from 1998 to 2020. First, we analyzed the temporal trends in the total fishing effort and catches of this fishery. The total effort summarizes the effort accounted for by four different gear types in these fisheries: handlines, mullet nets, meagre nets, and shark nets (Table 3.1). Handline fishing comprises a small fraction of the total effort, and in this fishery, less than 10% of catches in terms of weight are comprised of elasmobranchs (Figure 3.5A). Although mullet net fisheries represent a substantial proportion of total effort, elasmobranch catches are generally low (Figure 3.5A, 3.5B). Fisheries using shark nets and meagre nets constitute a significant part of the total fishing effort (> 50% in the first half of the reporting period), and catches with these gear types comprise a large portion of elasmobranchs (~70% and 60% of the catch in weight, respectively). Therefore, we limited data analysis to the effort and catch data of shark and meagre net fisheries.

We determined the catch-per-unit-effort (CPUE) as an indicator for changes in elasmobranch abundance. We used generalized additive models with a Gaussian distribution to assess changes in the three main focus species groups (i.e., large-bodied sharks, large benthopelagic rays and guitarfish). For this, we used the gam() function of the 'mgcv' package with restricted maximum likelihood (REML; Wood, 2017) in R v.4.3.1 (R Core Team). To produce a more detailed analysis of the species groups of interest, we focused on elasmobranchs with high conservation value, which are among the top ten most caught species. Species-group analyses were therefore limited to (1) large-bodied sharks (i.e., requiem sharks Carcharhinus spp., hammerhead sharks *Sphyrna spp.*, lemon sharks *Negaprion brevirostris*, and tiger sharks *Galeocerdo cuvier*), (2) large benthopelagic rays (i.e., duckbill eagle rays *Aetomylaeus bovinus*, Lusitanian cownose rays *Rhinoptera marginata*), and (3) guitarfishes (i.e., blackchin guitarfish *Glaucostegus cemiculus*) (Table 3.2). In addition, we report the occurrence of sharks and rays in catches between 1998 and 2020 at a species level.

Results

Long-term trend of total fishing effort, catch, and CPUE

The total fishing effort shows a significant increase, from a mean of ~1,000 days at sea from 1998 to 2005 to more than twice as high from 2007 and onwards (Figure 3.2A). This trend in fishing effort comprises four gear types: handlines, mullet nets, meagre nets, and shark nets (Table 3.1). In terms of fishing effort, handlines are used for <10% of the total fishing effort and the catch comprises less than 10% of elasmobranchs (i.e., in terms of weight; Figure 3.3). Mullet nets are used more as their proportion of the total fishing effort varies between 20 and 65%, though elasmobranch catches are generally low. Fisheries using shark- and meagre nets constitute a substantial part of the total fishing effort. However, this has decreased from approximately 50% of the total fishing effort between 1998 and 2010 to approximately 30% in the last four years (2016-2020). The catches of these nets comprise 60 to 75% of elasmobranchs (Figure 3.3).

The catch increase corresponds with the rise in total fishing effort, from 50 tons per month in 2005 to approximately 130 tons per month in 2010 (Figure 3.2B). After 2010, catches show a decreasing trend to approximately 50 tons per month in 2020. The decrease in CPUE indicates that daily catches have decreased from 150kg/day in 1998/1999 to about 20 kg/day in 2020 (R^2 = 0.47; Figure 3.2C). This is an overall difference of 86.7% in elasmobranch landings between the start and the end of the study period. Considering the monthly variation in catches, month and year explained 52% of the deviance in CPUE of elasmobranchs (Table 2).

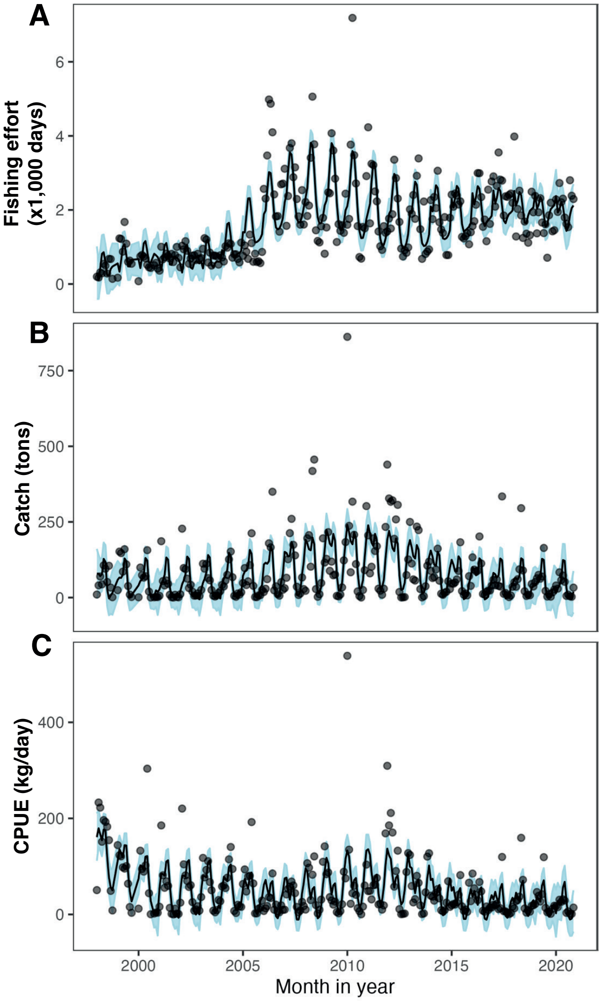


Figure 3.2 Overall trends during the entire study period in (A) fishing effort (in 1,000 sea days), (B) total catch (in tons), and (C) catch-per-unit-effort (CPUE in kg/days) per month for all elasmobranch species caught in shark, meagre, and mullet nets, and handlines. Plots indicate model fit (black lines) and 95% confidence interval (light blue).

Gear-specific analysis shows that the use of shark and meagre nets increased in 2005 and 2006, though fishing effort with either net was subsequently reduced towards the end of the study period (Figure 3.4). Catches of sharks constituted 54% of catches with shark nets, which was higher compared to ray catches in these nets (19%, Figure 3.3A). Similarly, ray catches were considerably higher in meagre nets (41%) than shark catches (21%, Figure 3.3A). Ray caches were low (<380 tons per year) in the period 1998-2006 and were relatively high between 2008 and 2012 (550 to 1200 tons per year; Figure 3.4B). After 2012, ray catches decreased to less than 50 tons/year in shark nets and to 250 tons/year in meagre nets from 2017 onward (Figure 3.4). Gear-specific CPUE for shark nets was higher for sharks between 2016 and 2019, with between 120 and 300 kg/day. The CPUE of rays in meagre nets was highest between 2011 and 2013, with 110 to 220 kg/day (Figure 3.4).

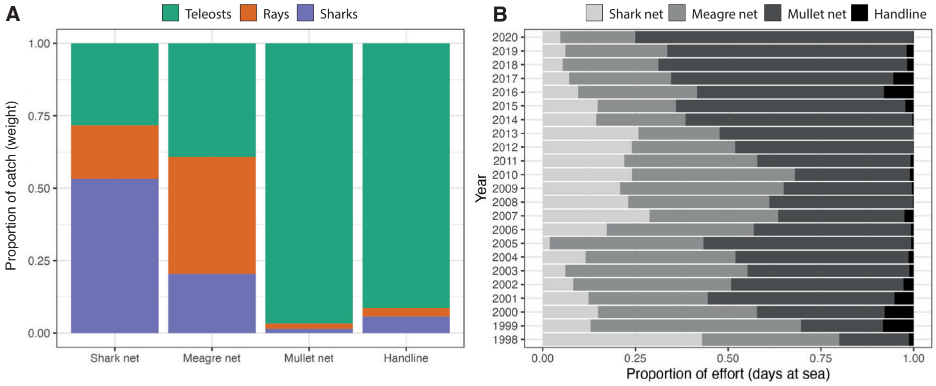


Figure 3.3 (A) The proportion of teleosts, rays and sharks in the annual catches in weight (tons). (B) The proportion of fishing effort that a gear type is used annually (in terms of sea days).

Table 3.3 Summary table of the generalized additive model (GAM) results for total effort (days at sea), total catch (weight in kg), and CPUE (kg/day at sea) overall gear types from 1998 to 2020 in Banc d'Arguin (edf: effective degrees of freedom; R-sq (adj): adjusted R-squared, and Dev. expl.: Deviance explained, p-value per smoother).

Response	edf	R-sq. (adj)	Dev. expl. (%)	p-value
Total effort		0.65	68	
s(Year)	7.8			<2e-16
s(Month)	6.7			<2e-16
s(Year, Month)	10.8			<2e-16
Total catch		0.44	49	
s(Year)	5.7			<2e-16
s(Month)	7.9			<2e-16
s(Year, Month)	10.0			0.00903
CPUE		0.47	52	
s(Year)	7.6			<2e-16
s(Month)	7.7			<2e-16
s(Year, Month)	8.7			<2e-16

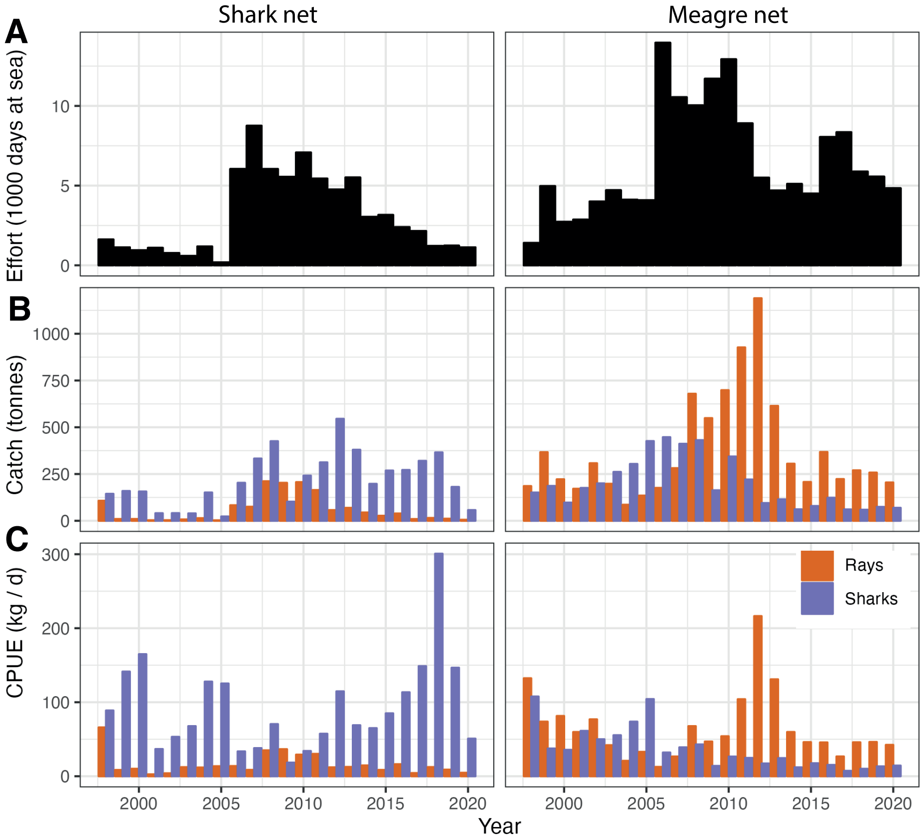


Figure 3.4 (A) Overall annual total fishing effort (in 1,000 sea days), (B) total catch (tons), and (C) catch per unit of effort (kg/sea day) (CPUE) for sharks (purple) and rays (orange) in shark nets (left) and in meagre nets (right).

Species group trends and species-specific occurrences

The CPUE of large sharks (Figure 3.5A) and blackchin guitarfish (Figure 3.5B) decreased prior to 2010 to remain below a CPUE of 2.5 and 12 kg/day for these two species groups, respectively. Contrastingly, the CPUE of the large benthopelagic rays increased during this period from a CPUE below 10 kg/day before 2005 to a CPUE between 30 and 40 kg/day between 2008 and 2011 (Figure 3.5C). After 2011, the CPUE of this species declined continuously, with the CPUE approaching 10 kg/day in 2020. To further explain these species group trends, we show the species-specific occurrence in catches over the 1998 to 2020 period within the PNBA (Figure 3.6). In total, 33 species of elasmobranchs (16 sharks and 17 rays) were identified at the species-level during the study period (Figure 3.6).

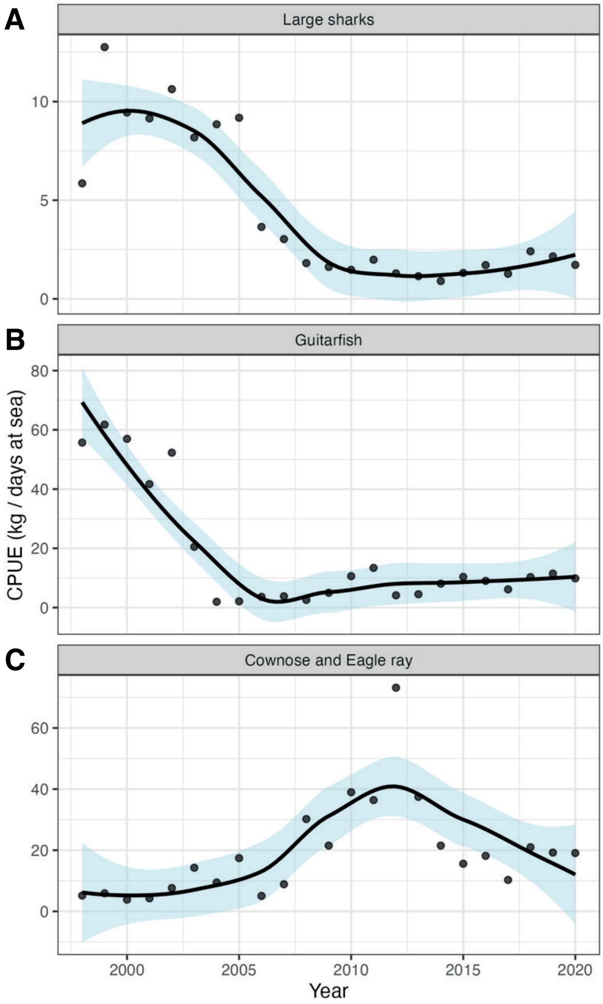


Figure 3.5 Trends in catch-per-unit-effort (CPUE) in focal species groups of elasmobranchs of (A) large sharks (i.e., hammerhead sharks, requiem sharks, nurse shark, lemon shark and tiger shark), (B) blackchin guitarfish and (C) rays (i.e., Lusitanian cownose ray and duckbill eagle ray), landed by shark nets and meagre nets over the study period 1998-2020. Plots indicate a fitted trend (black) through the summed annual data with a 95% confidence interval (blue; Table 4).

The majority of these species (85%, n = 28) are currently listed as threatened with extinction (i.e., IUCN category Critically Endangered, Endangered, and Vulnerable) and are generally species that attain large maximum sizes (> 150 cm). We show that the occurrence of large shark and ray species in catches in the PNBA is higher during the first half of the study period (i.e., before 2010) and that the occurrence of smaller-bodied species (e.g., milk shark *Rhizoprionodon acutus*, and stingray species *Dasyatis/Fontitrygon spp.*) remained throughout the study period (Figure 3.6). Of all elasmobranch species confirmed in the catches within the PNBA, nine species were not observed in the landings for more than a decade.

Table 3.4. Summary table of the generalized additive model (GAM) results for sharks, blackchin guitarfish and rays CPUE in shark nets and meagre nets derived from 1998 to 2020 in Banc d'Arguin (edf: effective degrees of freedom; R-sq (adj): R squared adjusted, and Dev. expl.: deviance explained).

Fishery	Response	edf	R-sq. (adj)	Dev. expl. (%)	p-value
Large sharks	CPUE	7.4	0.98	99	< 0.001
Blackchin guitarfish	CPUE	4.6	0.87	90	< 0.001
Large rays	CPUE	5.8	0.69	77	< 0.001

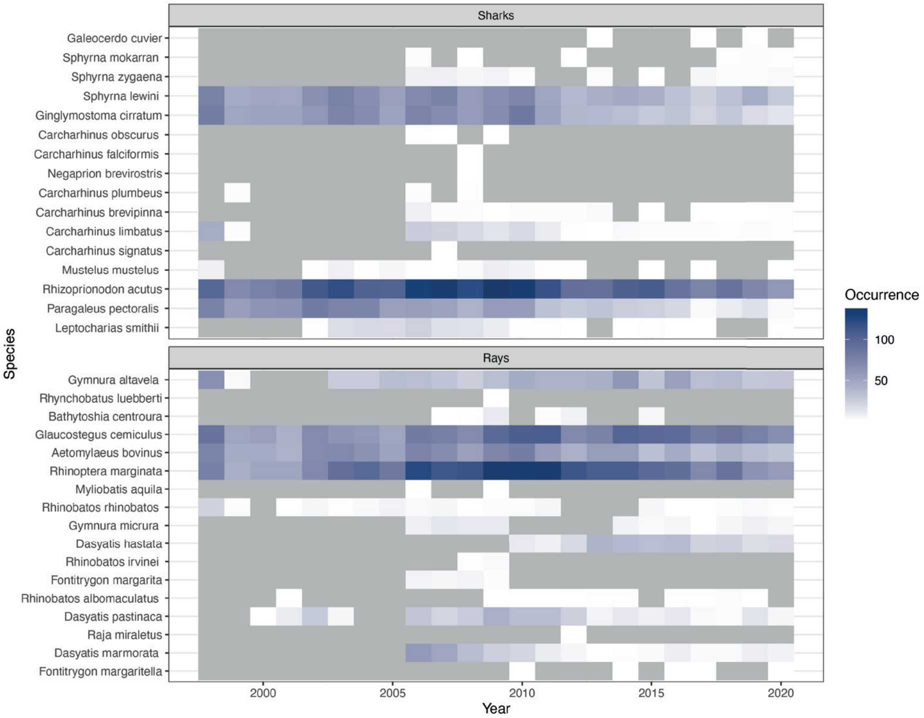


Figure 3.6 Species occurrence in the catches, organized by year and by decreasing the maximum size of the species for the two elasmobranch species groups (A) sharks, and (B) rays. Gray values indicate missing values.

Discussion

Based on over twenty years of fisheries-dependent data, we show how fisheries on shark and ray species in the Banc d'Arguin (PNBA) changed from small-scale to more commercialized fisheries targeting sharks and rays until catches severely declined (between 2010 and 2020). We interpret the decrease in CPUE to represent a decreasing abundance of these vulnerable species within the national park. Catches of large sharks, guitarfish, and large rays (i.e., eagle and cownose rays) decreased respectively by 90%, 80% and 50% between 1998 and 2020.

The elasmobranch fishery in PNBA is not driven by local demand as the local communities do not consume elasmobranch species. Therefore, commodities are exported to (international) markets. Substantial elasmobranch catches in the PNBA did not commence until the early 1980s (Lemrabott *et al. in press*). This practice was incentivized by the emerging international trade in shark fins and dried ray meat, and Imraguen fishers within the Banc d'Arguin gained access to international trade networks (Ducrocq 2004). Initially, elasmobranchs were considered bycatch in large-bodied teleost fisheries targeting species like meagre (*Argyrosomus regius*). However, we show that elasmobranchs represent 60% and 70% of the total catches in gear types used in meagre fisheries and by using shark nets, respectively. These catches often occur in shallow areas, especially in the intertidal which rays frequently use. Our results, therefore, indicate that elasmobranchs in PNBA are not bycatch but represent targeted catches, especially due to the existence of a gear type specifically used to catch sharks (i.e., shark nets) and the deployment of large-mesh meagre nets (pelagic species) in intertidal waters to target rays.

Within the boundaries of the PNBA, targeted catches of sharks and rays are illegal (Diop and Dossa 2011), but we show that the capture of these species has developed into an important economic driver of fisheries within the park over the past decades compared to the traditional teleost fisheries (Lemrabott *et al. in press*). To improve the situation for elasmobranchs in the PNBA, the priority is to implement regulations against targeted elasmobranch fisheries in locations with high occurrences of threatened species. Furthermore, deployment of large mesh-size nets should be discontinued in occurrence areas of elasmobranchs and shallow waters or tidal channels frequented by guitarfish, cownose rays and eagle rays during their tidal movements (Leurs *et al.* 2023).

Among elasmobranch species, the ones most threatened at a global level encompass the highest catches, further deteriorating the conservation status of these species (Stein *et al.* 2018, Dulvy *et al.* 2021) within the region and undermining the potentially important role that areas like the PNBA play in the lifecycle of these threatened elasmobranch species (Leurs *et al.* 2023). Globally, elasmobranchs are threatened by targeted catches or as bycatch in small-scale or industrial fishing (Stevens *et al.* 2000, Fernández *et al.* 2005, Dulvy *et al.* 2021, Leurs *et al.* 2021). Within the Banc d'Arguin, 85% of elasmobranch species captured in the fisheries are currently threatened with extinction, including ten species (36%) that are critically endangered. In general, fish species with large maximum sizes (> 149 cm) are especially vulnerable to exploitation (Fernandes *et al.* 2017). Many of the elasmobranchs we studied reach large maximum sizes (most > 200cm). However, in the PNBA ecosystem, the smaller, juvenile individuals are often the ones experiencing high mortality through fisheries due to their use of the intertidal and shallow-water habitats as a refuge during early life stages (Knip *et al.* 2010, Leurs *et al.* 2010). This implies that exploitation in this national park may impose a critical bottleneck for species with slow life histories that are often already categorized as threatened with extinction and which depend on these habitats.

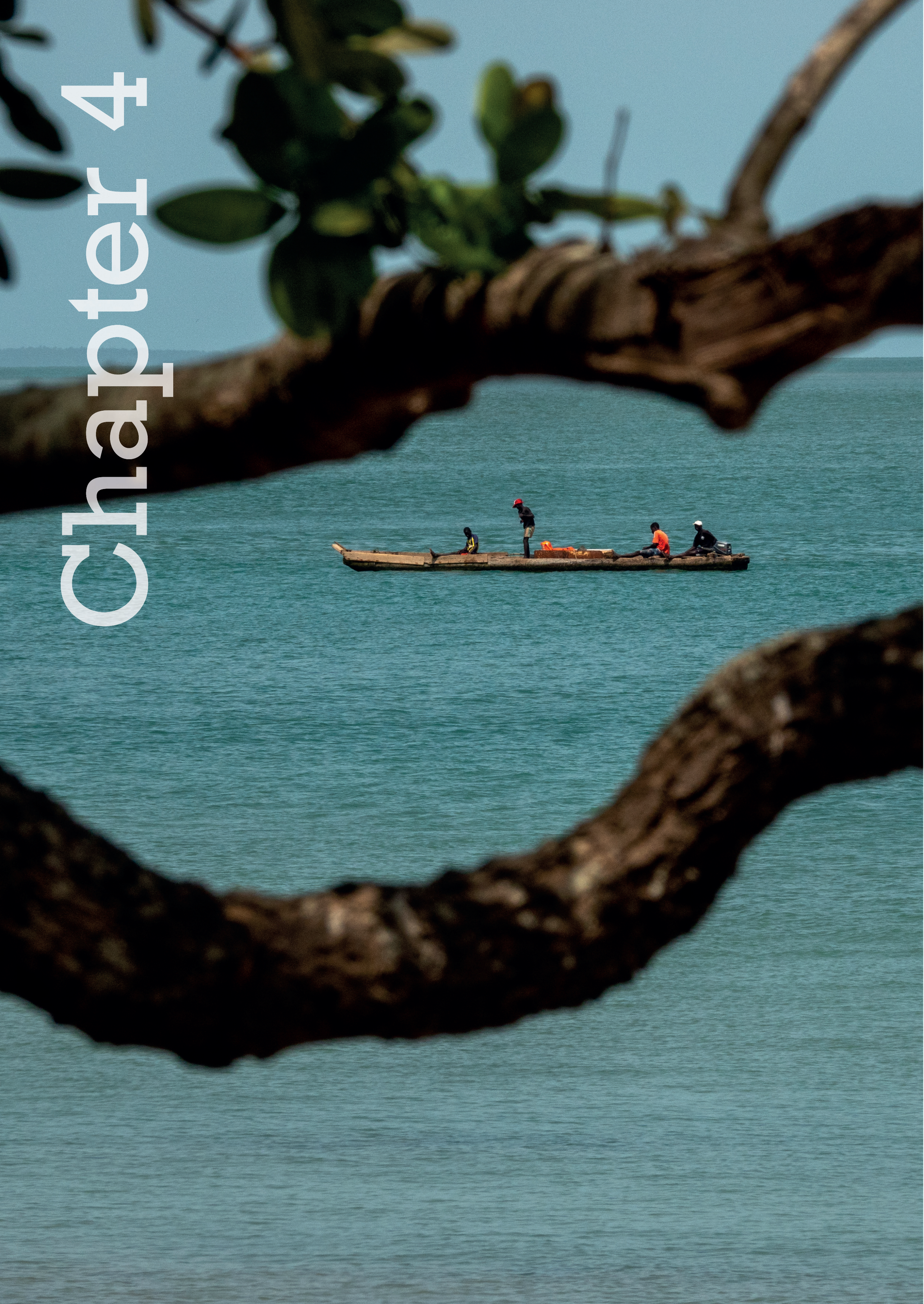
We show that elasmobranch species are declining severely in populations in the Banc d'Arguin, with the most common species likely disappearing from the area if these negative trends are not reversed. Some large *Carcharhinidae* and Sphyrnidae sharks fished earlier in the 1980s for their high-priced fins (Lemrabott *et al.* 2024) have not been recorded in the landings over the last decades. Hammerhead sharks have experienced similar decreasing trends. The rays *Rhinobatos irvinei*, *Rhynchobatus luebberti*, *Myliobatis aquila*, and *Fontitrygon margarita* were sighted only a few times during the study period and then disappeared from the catches from 2009 onwards, which may also be caused by misidentification of species due to these species being difficult to differentiate from similar species (e.g., within the Fontitrygon genus). The Banc d'Arguin is especially important for blackchin guitarfish (*Glaucostegus cemiculus*), with adults and juveniles using the PNBA as mating and nursery areas (Valadou *et al.* 2006). This species showed declines in its CPUE to critically low levels since targeted catches started in the 1990s (Lemrabott *et al.* 2024, Boulay 2013), likely motivated by the demand for its relatively large fins as an alternative after the depletion of large sharks (Kyne *et al.* 2020). These large-bodied rays have been subject to high fishing pressure, which is evident from their significant declines in CPUE before 2005, after which CPUE remained low for the remainder of the study period.

The increased catches of threatened species and the decrease of elasmobranch diversity over time raise concerns for elasmobranchs in the PNBA. Sharks and rays represent an important predatory group, occupying roles as both top- and meso-predators in marine systems (Heupel *et al.* 2014, Navia *et al.* 2016). In large intertidal areas such as the PNBA, their loss can potentially affect the ecological functioning of these large intertidal systems (Leurs *et al.* 2023). Our results show that in the Banc d'Arguin, some elasmobranch species may have already disappeared or are close to disappearance, or their abundance is now so low that their ecological roles are redundant. These results are alarming as other iconic elasmobranch species have already disappeared from the West African region, such as sawfishes (*Pristis spp.*), the false shark ray (*Rhynchorhina mauritaniensis)* and the African wedgefish (*Rhynchobatus luebberti*) have disappeared entirely or from parts of the region (Campredon and Cuq 2001, Jabado *et al.* 2006, Séret and Naylor 2016, Moore 2017). Overall, this may lead to a simplification of the food web of these large intertidal ecosystems. For instance, the increase in catches of sharks in the last years of the study period is caused by an increase in catches of milk sharks, a relatively fast-growing shark species. This simplification of elasmobranch communities and a shift towards fast-growing species (i.e., small-bodied sharks and small stingrays) can have consequences for the ecological functioning of coastal ecosystems.

Our findings lead to several suggestions for improved management of sharks and rays within the PNBA. Elasmobranchs were often caught in the meagre nets deployed in shallow waters and in the sharks nets specialized for capturing sharks. This is because meagre nets are used outside the target species' season and habitat and are deployed year-round in the shallow intertidal habitats of rays. In addition, meagre nets have larger mesh sizes than shark nets, originally intended to prevent the capture of smaller non-target species. As such, it is large mesh-sized nets intended for fishing of teleost that are effectively used to target rays in shallow water habitats and to interfere with their tidal movements from and to intertidal habitats (Leurs *et al.* 2023). Compared to fast-growing teleosts that can sustain levels of exploitation, applying the same fishing pressure and techniques to elasmobranchs can significantly impact their slow-growing populations. The label bycatch used to tolerate the landings of elasmobranchs by the authorities at Banc d'Arguin has been misleading, as they are targeted by specialized nets set in habitats frequented by elasmobranchs through their tidal movements. Only some elasmobranchs captured in mullet nets (comprising less than 10% of the catch) should be reasonably considered bycatch.

The managers of the Parc National du Banc d'Arguin face a challenging task to stop unsustainable fishing of threatened elasmobranchs. In 2006-2020, total catches of elasmobranchs increased with the expansion of the fishery to include species not targeted before (e.g., the large rays). We suggest the next step towards effective management of elasmobranch species within the PNBA include: (1) lowering fishing effort directed towards sharks and rays by closing fishing areas with high shark and ray catches for large mesh-sized nets or shark-specific gear types and (2) enforce the ban on trade in shark and ray products originating from within the PNBA with trade controls and onboard catch controls. These measures are unlikely to be successful without ensuring the promotion and availability of an alternative, sustainable fishery practice or alternative incomes for local Imraguen fishers.

Chapter 4



Reconstructing historical population trends of threatened sharks and rays based on fisher ecological knowledge

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Manuscript

Abstract

The lack of historical shark and ray catch information often hampers the management of small-scale fisheries. We reconstructed historical population trends and current fishing pressure by combining local ecological knowledge, satellite-based vessel counts, and a short-term landing site survey. To demonstrate the effectiveness of this methodology, we focused on the Bijagós Archipelago (Guinea-Bissau, West Africa), where historical fisheries data are lacking. We conclude that benthic rays (stingrays/butterfly rays), benthopelagic rays (eagle/cownose rays), guitarfish, requiem sharks, and hammerhead sharks have declined in abundance by 81.5 to 96.7% (species dependent) between 1960–2020. Fishing effort increased annually: fishing trip duration by 42.0 ± 3.4% (1960-2020) and number of vessels by 12.0 ± 1.1% (2007-2022). We estimated that in 2020, fishing vessels collectively captured approximately 340 sharks and up to 2,553 rays per day within the archipelago. However, this likely underestimates the actual catch since vessels from neighboring countries operating in these waters were unaccounted for. We recommend reducing shark and ray catches through the regulation and enforcement of fishing fleet size and reinforcing boundaries of protected areas to safeguard these vulnerable species within the archipelago. Our study demonstrates the value of this innovative three-pronged approach in determining historical trends and fishing pressures in regions lacking such baseline data, which is a common challenge in areas with small-scale fisheries and limited research capacity.

Introduction

The impact of global fisheries on marine ecosystems, marine biodiversity and fish populations is profound (Jackson *et al.* 2001, Lotze *et al.* 2007). These changes have been linked to shifts in ecosystem functioning and a loss of ecosystem services (Jackson *et al.* 2001, Lotze *et al.* 2006, Worm *et al.* 2006). One of the most affected species groups is sharks and rays (i.e., elasmobranchs), highlighted by their deteriorating global conservation status. Indeed, an estimated one-third of all shark and ray species are threatened with extinction (Dulvy *et al.* 2021). The impact of industrial fisheries on shark and ray populations has been documented extensively (e.g., Baum *et al.* 2003, Worm *et al.* 2013, Queiroz *et al.* 2019). Many of these fisheries are managed through regional fisheries bodies (e.g., tuna Regional Fisheries Management Organization) and fishing agreements (e.g., Sustainable Fisheries Partnership Agreements), which include requirements on catch data reporting, and whereby industrial vessel fishing locations can be traced (Kroodsma *et al.* 2018) and potential illegal activities can be predicted (Welch *et al.* 2022). The majority of these industrial fishing fleets are restricted to deep waters (> 200 m depth) or to a certain distance from the shore (e.g., five nautical miles) and operate on the edge of coastal areas and in pelagic realms (Kroodsma *et al.* 2018, Leurs *et al.* 2021). Therefore, these fisheries are mostly expected to impact pelagic shark and ray species (Pacoureau *et al.* 2021) that move over long distances (Queiroz *et al.* 2019) and species moving away from coastal reproductive and feeding areas (Leurs *et al.* 2021).

Within coastal areas, where most shark and ray species occur, the combined effects of fisheries and habitat degradation are disproportionately high (Dulvy *et al.* 2021). Here, sharks and rays are mostly affected by small-scale fisheries (i.e., fisheries using small (coastal) vessels and minimal use of technological gear, Chuenpagdee *et al.* 2006, Guillemot *et al.* 2014), and their interaction with industrial fisheries can be limited. Globally, catches associated with small-scale fisheries make up a large proportion of total fish catches (Teh and Pauly 2018, Palomares and Pauly 2019), especially in regions where these fisheries have a close link with local communities and are important for food security (Palomares and Pauly 2019). Small-scale fisheries have increased steadily over the past decades (Teh and Pauly 2018, Palomares and Pauly 2019) and can have high targeted and incidental catch of sharks and rays (e.g., Temple *et al.* 2019, Karnad *et al.* 2020, Haque *et al.* 2021). Due to the spatially concentrated nature of small-scale fisheries in nearshore areas, their overlap with coastal shark and ray species can be relatively high, likely exerting high localized pressure on their populations. In addition, these fisheries can impact the vulnerable early life stages of shark and ray species using nearshore areas as nursery and feeding areas (Knip *et al.* 2010). Despite the increase of these fisheries and their importance to local communities for income or subsistence (Teh and Pauly 2018, Haque *et al.* 2021), they are often unregulated, with little or no reporting of catches (Belhabib *et al.* 2014, Ekpo and Essien-Ibok 2019, Haque *et al.* 2021). Such limited data availability and low traceability of fishing efforts make the assessment of the impact of these fisheries on sharks and rays challenging.

Here, we attempt to determine the historical and current population trends of sharks and rays in areas where fisheries-dependent data collection is scarce or nonexistent. We focused on one of the largest coastal ecosystems in one of the most data-deficient regions of the world: the Bijagós Archipelago off the coast of Guinea-Bissau in West Africa. In West Africa, both industrial and small-scale fisheries have rapidly expanded over the past decades (Campredon and Cuq 2001, Lemrabott *et al.* 2023, Leurs *et al.* 2021). Sharks and rays are often targeted or retained when incidentally caught for their fins, destined for international markets, and their meat for local or regional markets (Diop and Dossa 2011). Coastal areas in the region are potentially important for the various life-history stages of sharks and rays (Campredon and Cuq 2001, Valadou *et al.* 2006, Knip *et al.* 2010, Leurs *et al.* 2023a, 2023b). However, it is unclear how small-scale fisheries have affected these species, what their current status is, and how high the current fishing pressure is. We used a novel three-pronged approach combining (i) fisher local ecological knowledge (LEK), (ii) satellite-based small-scale fishing vessel counts, and (iii) a short-term landing site survey to determine the historical and current population status of sharks and rays within the Bijagós Archipelago. Specifically, we (1) determined the historical population trends of shark and ray species based on fisher LEK, (2) evaluated changes in fishing effort when considering the number of fishing vessels, fishing trip duration and gear used, and (3) estimated the daily catches of sharks and rays under different levels of small-scale vessel activity scenarios. We show that this combination of methods enables the reconstruction of historical and current fishing pressure on vulnerable taxa, yielding insight into urgently needed management interventions.

Methods

Study area

The Bijagós Archipelago (11°15’N, 16°05’W) is located off the coast of Guinea-Bissau (West Africa) and consists of 88 islands and islets, of which approximately 20 are permanently inhabited (Figure 4.1). The archipelago is situated in the estuary of the Geba River and comprises a complex system of islands fringed by mangrove forests and extensive intertidal flats connected through a system of small tidal creeks and channels. The archipelago is internationally recognized as a wetland of international importance

(Ramsar site; 2014) and as a UNESCO Biosphere Reserve (1996). Within the Bijagós, sharks and rays play an important role in the socio-cultural traditions and beliefs of the archipelago's indigenous communities (Cross 2014) and in the functioning of this large intertidal ecosystem (Leurs *et al.* 2023). Sharks and rays are occasionally targeted for offerings in traditional ceremonies (Cross 2014). However, over the past decades, the international demand for shark and ray products has increased targeted fisheries and retention of incidental catch across the entire West African region (Campredon and Cuq 2001, Diop and Dossa 2011). Within the archipelago, since 1985, small-scale fisheries have developed from a seasonal to a year-round operation that often targets sharks and rays (Campredon and Cuq 2001). Fishers mostly use human-powered dug-out canoes or larger wooden pirogues (Appendix 4.1) powered with one or multiple outboard engines or use beach seine nets deployed on foot. Historical and current catch data on the (artisanal) small-scale fisheries operating within the archipelago waters are nonexistent.

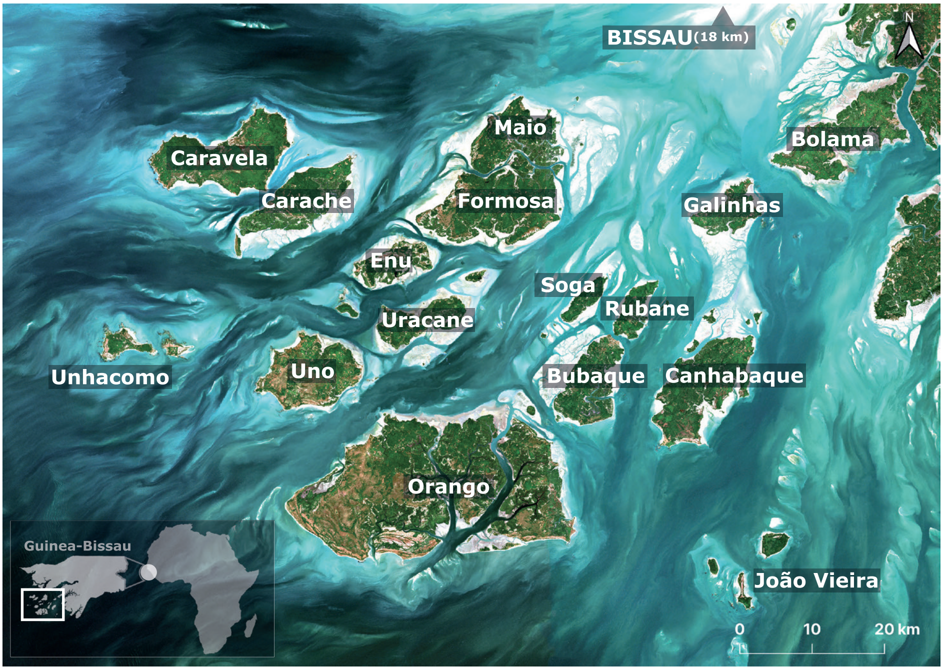

Figure 4.1 The Bijagós Archipelago (11°15'N, 16°05'W) in Guinea-Bissau consists of 88 islands and islets, of which approximately 20 are inhabited year-round.

Elicitation of fishers' ecological knowledge

Two local researchers were trained to conduct in-depth structured interviews with fishers that operate within the Archipelago. Interviews were conducted in Portuguese

Creole from February to June 2021 at the largest small-scale fish market in the country: the Alto Bandim fish market in Bissau (11°50’29” N, 15°35’19” W). To identify participants, snowball sampling was used whereby respondents were asked to recommend other fishers to be included in the study (Goodman 1961), but by considering spread sampling efforts across the entire age range of the fishing community. The central objective of these interviews was to capture perceptions of changes in species abundance, fishing effort, gear use and species utilization over the past decades. Fishers were primarily asked about (1) their demographics, (2) fishing gear use, (3) fishing areas, and (4) species-specific captures. Open-ended discussions focused on the current management of fisheries and any other information fishers wanted to share (Appendix 4.2). To increase the accuracy of data collected from fishers, we recorded change by asking about the moments a fisher could recall best: when the fisher started fishing and the most recent year of fishing (or if a fisher was not active anymore, about the last year of fishing which was subsequently recorded) (e.g., Tesfamichael *et al.* 2014). Although this approach leads to fewer data points per fisher, data points collected are likely the ones a fisher can recall the most accurately (Appendix 4.3). This approach was used in all questions intended to capture change (e.g., changes in catches and gear use). We combined this approach by interviewing fishers of all ages in the fishing communities, which enabled us to reconstruct historical trend lines (Appendix 4.2). Photographic species cards were used throughout the interview to establish a mutual understanding of species identity. As species in Creole are grouped, and fishers were unable to differentiate between species, species were grouped in the following functional species groups: benthic rays (i.e., stingrays *Hypanus* spp., *Dasyatis* spp., *Fontitrygon* spp. and butterfly rays *Gymnura* spp.), benthopelagic rays (i.e., duckbill eagle ray *Aetomylaeus bovinus* and Lusitanian cownose ray *Rhinoptera marginata*), guitarfishes (i.e., common guitarfish *Rhinobatos rhinobatos* and blackchin guitarfish *Glaucostegus cemiculus*), requiem sharks (i.e., *Carcharhinus* spp. and milk shark *Rhizoprionodon acutus*) and hammerhead sharks (i.e., *Sphyrna* spp.) (Appendix 4.4). For each group, specific information such as individuals caught per fishing expedition, average length of captured individuals, processing, and trade were recorded. Fishers were asked to indicate the total lengths of captured individuals on a metric scale for comparison. Interview duration ranged between 1 and 2.5 hours since fishers were encouraged to expand on their experience.

Ethics statement

Before each interview, informed consent was obtained from each participant by explaining the purpose of the interview and the study’s objectives. We communicated that the interviewee could terminate the interview at any given time or not answer specific questions. Once the interviewee had a clear understanding of the intentions of the study, the researcher asked permission to make an audio recording of the interview solely for translation and note-taking purposes. To guarantee the interviewee's anonymity, no names or contact information was written down or recorded, and no information was stored that could lead to identifying participants. All files and information collected during the interview were treated as confidential. All research was conducted in accordance with regulations of the national Instituto da Biodiversidade e das Áreas Protegidas and the national Instituto Nacional de Investigação das Pescas e Oceanografia of Guinea-Bissau (permit #06/10/IBAP/2021). All data was collected and stored securely, conforming to the regulations and guidelines of the University of Groningen.

Landing site surveys

From February to November 2021, a landing site survey was initiated in collaboration with INIPO. An enumerator with experience in fisheries research was trained to document shark and ray landings at the Alto Bandim fish market. By interviewing fishers at the point of landing at peak landing times in the morning (6-9 AM, three times a week) and documenting species, the enumerator was able to collect data on the fishing area (i.e., location name, distance from shore, depth), gear specifications (i.e., gear type, length, mesh/hook size, material), and details on the catch (i.e., species, number of individuals, lengths, sex).

Small-scale fishing vessels abundance

To determine the number of small-scale vessels operating within the boundaries of the archipelago and how this has changed over the past decades, we used satellite imagery of the Alto Bandim small-scale fishing port. We used the historical satellite imagery option in Google Earth Pro (v.7.3). The resolution of this imagery between January 2007 and December 2023 was appropriate (~0.5m/pixel; imagery sources: Airbus and Maxar Technology) to count individual small-scale fishing vessels (~8-20 meters in length, see Appendix 4.1). We exported each satellite image (n = 95) and used ImageJ (v. 1.53k) to crop each image to a standardized bounding box around the port. We then annotated each fishing vessel within this bounding box as a proxy for the number of fishing vessels actively fishing in the Bijagós. Images were available for multiple months for most years (Appendix 4.5). This approach only included an estimation of small-scale fishing vessels from Guinea-Bissau, not including any vessels from neighboring countries (e.g., Senegal and Guinea) also known to operate in the waters of the archipelago, but that land their catches in their respective countries and would therefore not have appeared in the imagery.

Data analyses

Data analyses were conducted using R (v.4.3.0). We analyzed changes through time based on interview data using mixing models to account for the variation in responses between fishers. We used generalized linear mixed models with a Poisson distribution to analyze changes in gear type use (e.g., number of sets, gear length, and soak time). Beach seine nets were included as small multifilament nets based on their material, but mostly as small multifilament nets. We used a negative binomial distribution when overdispersion was determined in the Poisson models. We used the same approach to analyze changes in the number of fishing vessels observed by fishers at their fishing sites and in the duration of their fishing trips. For all these models, we used 'year' as a fixed effect and the unique (anonymous) identifier for each fisher (i.e., 'fisher ID') as a random effect. The number of vessels in the primary small-scale fishing port was analyzed by modeling the 90% quantile. We applied a quantile regression model with year as a fixed effect to determine the maximum number of fishing vessels active each year. To determine changes in the abundance of species groups based on fisher experience, we used generalized additive mixed models with a negative binomial distribution to account for overdispersion. In these models, we used the number of individuals of a species group captured per fishing trip as a response variable, year as a fixed variable and fisher ID as a random effect. If fishers provided a range (e.g., two to four individuals captured) during the interviews, we used the midpoint for further data analysis. We used the prediction of fishing trip duration as offset to transform the number of individuals captured per fishing trip to the number of individuals captured per day per vessel. Species composition was determined for each decade between 1960 and 2020 and compared using a permutational analysis of variance (i.e., 'permanova'). Before applying species group models and species composition analysis, we removed the top 5% of the data to minimize the influence of outliers caused by overestimation by interviewees. As data points of a fisher are linked (i.e., one data point when the fisher started fishing and when one stopped or in 2020), both data points were removed when one (or both) were within the top 5% of the data. We used generalized linear mixed models with a gamma distribution to analyze changes in the total length of species groups, with year as a fixed variable and fisher ID as a random effect. We removed values below the reported smallest size-at-birth and above the maximum size for species in each species group to correct for under/overestimation. We extrapolated the number of individuals captured per day by one vessel to the number of individuals captured daily throughout the archipelago by the entire active small-scale fishing fleet. To account for the uncertainty in the species group models and predictions of vessel numbers in the Alto Bandim fish market, we simulated these models for 1,000 Monte Carlo iterations. To determine the influence of fleet activity (i.e., the percentage of vessels counted on satellite imagery that are actively fishing that day), we repeated these simulations for each 10% increment between 10% and 200% fleet activity. We then multiplied each species group's predicted catch-per-unit-effort (i.e., individuals per day) for each species group with the number of vessels for each iteration. We used 10,000 bootstrap iterations to estimate the activity of interviewed fishers by calculating the proportion of weekdays spent fishing in 2020. We then used this estimate to describe daily catches of sharks and rays within the archipelago of the maximum estimated number of fishing vessels at the landing site.

Results

A total of 75 interviews were conducted with fishers operating throughout the Bijagós Archipelago (Figure 4.2, Appendix 4.6). The fishing experience of fishers ranged from 6 to 56 years (29.3 ± 12.4 years; mean ± s.d.), corresponding to a retrospective period from 1964 to 2020 (Figure 4.2AB). As part of the landing site survey, 122 vessels active throughout the archipelago were sampled (Figure 4.2CD). Vessels operating within the archipelago were monitored from February to November 2021. However, the majority of vessels were sampled in March (n = 21, 17.2%), June (n = 17, 13.9%) and July (n = 18, 14.8%; Figure 4.2C). Spatially, the combination of interviews and monitoring of the landing site covered fishers and vessels of the archipelago's main islands (Figure 4.2D).

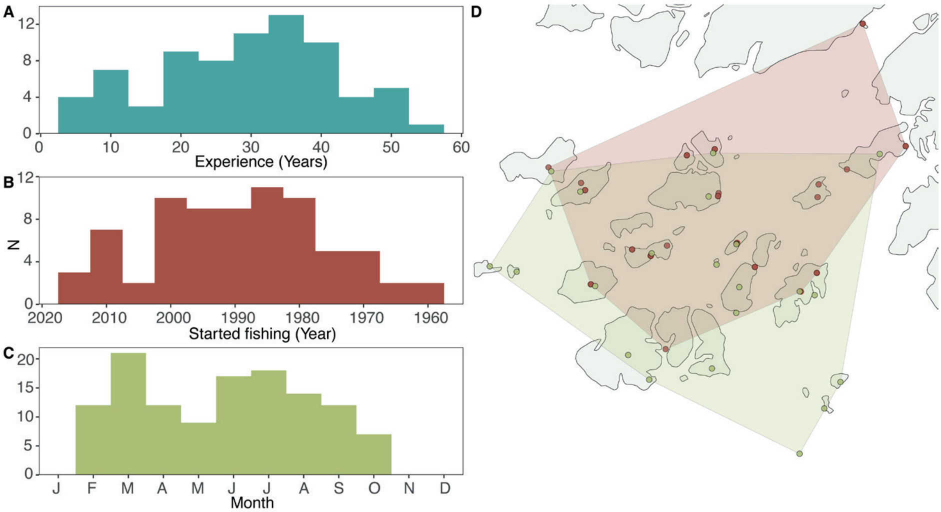

Figure 4.2 Overview of demographics of fishers captured by two different methods in this study: (A) respondent fishing experience in years, (B) the year a fisher started fishing, (C) the number of vessels sampled each month during landing site surveys, and (D) the spatial coverage of the interviews (i.e., the place of residence of fishers; red) and the landing site survey (i.e., base of every fishing vessel; green) indicated by the place of residence of each fisher or fishing vessel.

Species group trends and composition

Based on the interviews with fishers, we determined that the catch-per-unit-effort (in individuals per day) significantly decreased for all ray and shark species groups (Figure 4.3). Decreases over the entire study period ranged from 81.5 ($CI_{95\%}$: 77.8-82.6%) to 96.7% ($CI_{95\%}$: 91.4-97.6%), whereas decreases over the past two decades (2000-2020) ranged from 43.0 ($CI_{95\%}$: 42.4-44.4%) to 71.8% ($CI_{95\%}$: 69.6-72.8%). Although significant declines were noted in catch-per-unit-effort (CPUE; $p < 0.01$, Appendix 4.7), the most frequently captured elasmobranch group throughout the study period remains the benthic rays with an estimated 7.88 ± 1.31 individuals captured per day in 2020 ($p < 0.01$, Appendix 4.7). Overall, the steepest declines (96.7%, $CI_{95\%}$: 91.4-97.6%; $p < 0.001$) between 1960 and 2020 were noted for guitarfish, with on average 20.44 ± 7.45 individuals captured per vessel per day in 1960 and 0.66 ± 0.08 individuals captured per vessel per day in 2020. Other groups experiencing similar rates of declines over the same period were the requiem (93.0%, $CI_{95\%}$: 72.0-95.0%; $p < 0.001$) and hammerhead sharks (89.8%, $CI_{95\%}$: 71.8-92.3%; $p < 0.001$). In terms of individuals captured per day, in 2000, fishers caught an estimated 4.12 ± 0.74 and 1.35 ± 0.24 individuals of requiem and hammerhead sharks per day, whereas in 2020 this was 1.16 ± 0.18 and 0.43 ± 0.07, respectively. This represents a decline of 71.8% ($CI_{95\%}$: 69.6-72.8%) and 67.8% ($CI_{95\%}$: 66.8-68.3%) over the last two decades for requiem and hammerhead sharks, respectively. The average size of captured individuals of benthopelagic rays, guitarfishes, requiem sharks, and hammerhead sharks decreased significantly (Appendix 4.8). The average guitarfish captured in 1962 was 134.1 ± 10.1 cm in total length (TL) and 86.7 ± 3.9 cm TL in 2020 ($\beta = -0.01 \pm 0.03$, $z = -4.9$, $p < 0.001$). For requiem sharks, this was 148.8 ± 14.2 cm TL in 1960 and 72.1 ± 4.4 cm TL in 2020 ($\beta = -0.22 \pm 0.03$, $z = -6.7$, $p < 0.001$), and for hammerhead sharks 179.0 ± 18.5 cm TL and 90.6 ± 6.2 cm TL ($\beta = 0.21 \pm 0.04$, $z = -5.9$, $p < 0.001$). Species composition of catches did not differ significantly across decades (d.f. = 5, F = 1.0, $p = 0.3$), with rays making up 85.4 ± 1.7% of the catches over the study period and sharks 14.6 ± 1.7% (Appendix 4.9). Based on the landing site survey only encompassing boats that captured elasmobranchs, the highest proportion of elasmobranch catches were the blackchin guitarfish (22.6%, *Glaucostegus cemiculus*), milk shark (27.3%, *Rhizoprionodon acutus*), and scalloped hammerhead shark (7.7%, *Sphyrna lewini*).

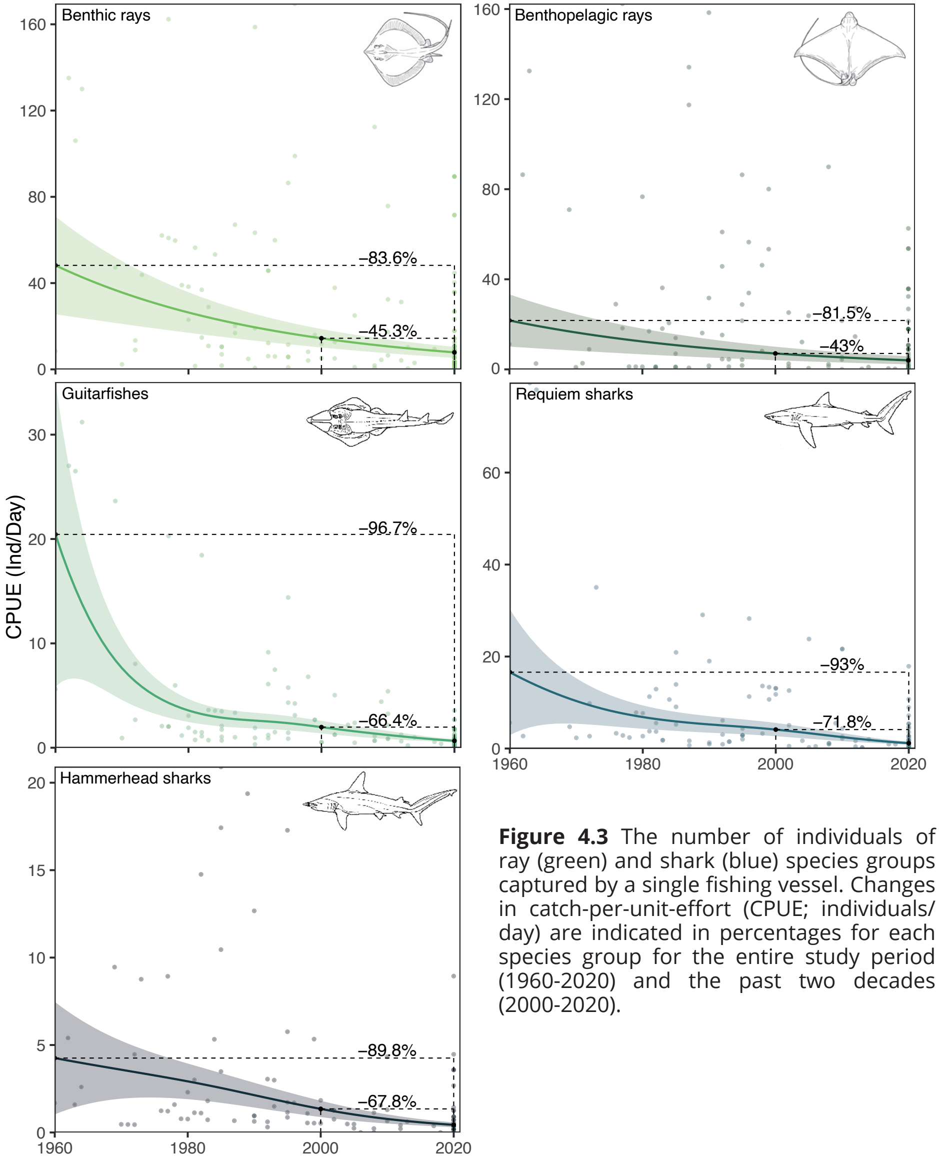

Figure 4.3 The number of individuals of ray (green) and shark (blue) species groups captured by a single fishing vessel. Changes in catch-per-unit-effort (CPUE; individuals/day) are indicated in percentages for each species group for the entire study period (1960-2020) and the past two decades (2000-2020).

Gear use and fishing effort

In terms of gear use, large multifilament (>40mm mesh), small multifilament (≤40mm mesh) and longlines were the most common gear types based on interviews. In contrast, small monofilament nets (≤40mm mesh) are the second-most common gear type based on landing site surveys (Figure 4.4A). Based on the landing site surveys, in terms of overall fishing effort, large multifilament, small monofilament, and longlines were the most prevalent gear types. Target catches predominantly consisted of teleost species groups. However, 29.7% and 26.3% of fishers used large multifilament and small monofilament nets to target elasmobranchs, respectively (Figure 4.4B). Fishers mostly used demersal small monofilament nets to target benthic rays. The realized catch (i.e., fishers stating catches of certain species groups with a gear type) shows that elasmobranchs are captured using all gear types, but mostly with longlines (66.7%), small monofilament (53.6%), large multifilament (57.1%) and small multifilament nets (45.1%; Figure 4.4C). The mean soak time of large multifilament nets significantly increased by 26.8%, from 5.6 ($CI_{95\%}$: 4.1-7.3) hours in 1960 to 7.1 ($CI_{95\%}$: 5.5-9.1) hours per deployment in 2020 ($\beta = 0.07 \pm 0.03$, $z = 2.43$, $p = 0.02$). However, no significant changes in the number of sets, gear length, and soak times were reported for most gear types (Appendix 4.10).

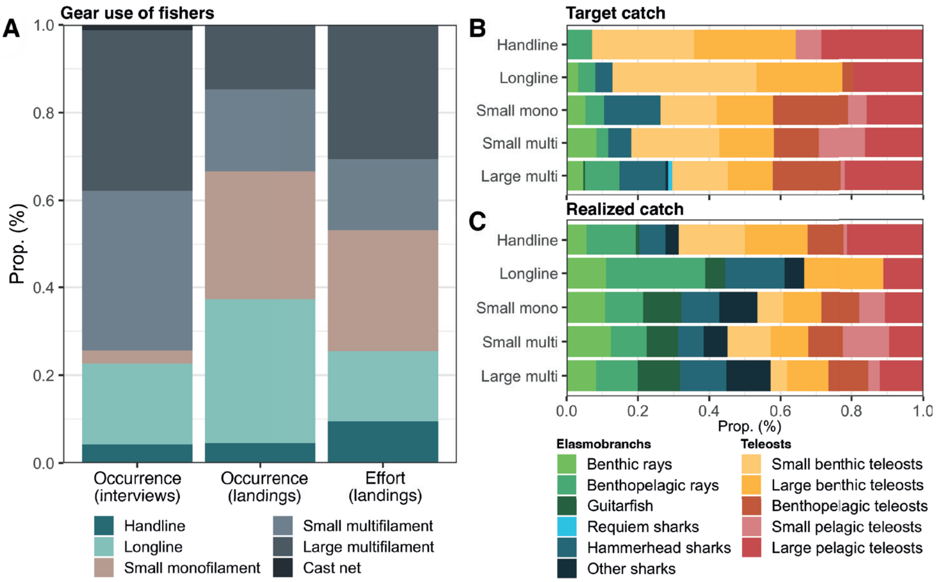

Figure 4.4 The use of different fishing gear in the Bijagós Archipelago small-scale fishery. (A) The prevalence of different gear types as a proportion of interviewed fishers that use this gear, the occurrence of gear on vessels sampled during the landing site survey, and the effort (hours soak time) gear was used during fishing trips. (B) Fishers were asked which species were targeted for each gear type ('target catch') and (C) which species were captured ('realized catch'). Gear type sizes are >40mm mesh for large multifilament nets and ≤40mm for small multifilament and monofilament nets.

Fishers indicated that the number of vessels observed at their fishing locations increased from 4.0 ± 0.4 vessels in 1960 to 11.5 ± 0.6 in 2020 ($\beta = 0.31 \pm 0.03$, $z = 11.07$, $p < 0.001$; Figure 4.5A), representing an increase by 187.5%. In addition, we determined that the total number of small-scale fishing vessels operating within the archipelago increased by 12.0 ± 1.1% (mean ± s.e.) on an annual basis and by a total of 443.7% between 2007 (46.4 ± 5.9) and 2022 (252.5 ± 14.8; $\beta = 0.11 \pm 0.01$, $t = 9.93$, $p < 0.001$)

(Figure 4.5B). Furthermore, fishers indicated that the duration of their fishing trips increased from 1.8 (1.5-2.1) days in 1960 to 5.6 (5.2-6.0) days in 2020 ($\beta = 0.35 \pm 0.03$, $z = 10.38$, $p < 0.001$; Figure 4.5C). Based on the landing site survey, fishing vessels catching sharks and rays were at sea for 7.4 ± 0.5 days in 2021 per fishing trip (Figure 4.5C).

Predicting daily fleet-wide catches

We used the models predicting historical catches of species groups based on fishers' local ecological knowledge and the reconstruction of the increase in small-scale fishing vessels to predict the current number of individuals of each species group captured on a single day in the last study year, 2020 (Figure 4.6). We determined the number of fishing vessels actively fishing on a single day within the archipelago under different activity levels (Figure 4.6A) and determined, based on interviews with fishers, that this activity level was approximately 80% (mean: 80.6%, $CI_{95\%}$: 76.5-84.8%) in 2020 (Figure 4.6B). Under this scenario, we estimate that approximately 191.5 ± 1.5 (mean ± s.e.; interquartile range, IQR: 159.4 - 214.5) fishing vessels were fishing on a single day in 2020 (Figure 4.6A). Together, these vessels captured an estimated 1,595.6 ± 32.6 (IQR: 867.3 - 2,1092) benthic rays, 815.5 ± 18.0 (IQR: 438.3 - 1,036.8**)** benthopelagic rays, 141.2 ± 4.3 (IQR: 50.4 - 194.1) guitarfishes, 241.9 ± 6.6 (IQR: 103.5 - 319.7) requiem sharks, and 97.5 ± 3.2 (IQR: 24.7-141.4) hammerhead sharks on a single day within the archipelago in 2020 (Figure 4.6B). We further show how lower and higher fleet activity levels influence the daily catches of these species groups.

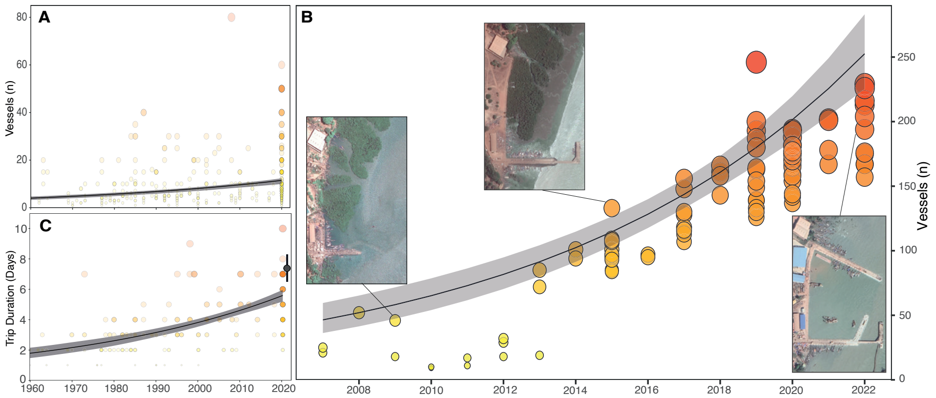

Figure 4.5 The fishing effort of small-scale fishing vessels within the archipelago has increased over the past decades. (A) Fishers were asked to estimate how many vessels they would observe in their fishing area. (B) Satellite imagery provided an overview of the increase of small-scale fishing vessels and the expansion of the primary port of Alto Bandim in Bissau from 2007 to 2022. The curve represents 90% quantile regression with a 95% confidence interval. (C) Based on interviews, the mean duration of a fishing trip significantly increased over time. The trip duration of fishing vessels sampled in the 2021 landing site survey is given with a 95% confidence interval (black point). The number of gear sets, length, and soak times did not significantly increase over time (Appendix 4.10). Satellite imagery taken from Google Earth Pro (downloaded on September 2nd, 2023).

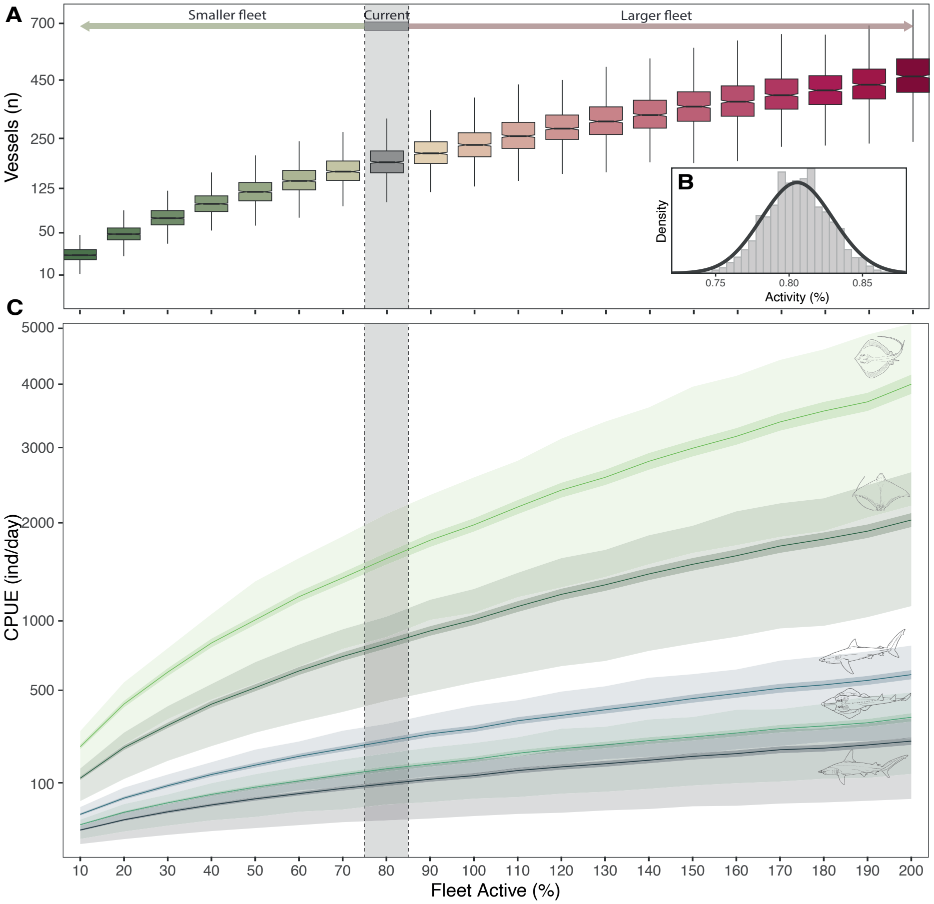

Figure 4.6 (A) The estimated number of small-scale fishing vessels in the Alto Bandim port on a day in 2020 under different fleet activity levels. (B) Based on fisher interviews, bootstrapped estimates of fleet activity in 2020 were between 75% and 85%. Green colors (in A) indicate a lower fleet activity (<80%), and red colors indicate a higher fleet activity (>80%). (C) We then simulated daily catches for the entire small-scale fishing fleet for a day in 2020 for each 10%-increment in fleet activity. Lines indicate the mean 1,000 Monte Carlo simulations, dark-shaded areas represent two times the standard error of the mean, and light-shaded areas indicate the 50% interquartile range. Shark species are indicated in blue, and ray species in green. The gray bar indicates the current situation (i.e., fleet activity 75-85%, B). Note that y-axes have a square-root transformation for visualization purposes.

Discussion

We show that a novel combination of readily available approaches can be successfully used to shed light on small-scale fisheries and historical catches of vulnerable marine species such as sharks and rays. Our findings indicate severe declines in catches and landings of all shark and ray species groups (83–97% depending on the species group) in the Bijagós Archipelago, Guinea-Bissau. At the same time, the size of the fishing fleet continues to increase exponentially. Although current catches and landings are still substantial from a population perspective (daily catches are approximately 340 sharks and up to 2,553 rays), they are now only a fraction of historical catches despite no noteworthy changes in gear use over time that may have influenced changes in shark and ray catches. This is concerning considering the threatened status of most shark and ray species found in Guinea-Bissau and the limited fisheries management measures in place.

Globally, sharks and rays face increasing threats, but overfishing has led to drastic declines in populations of more than a third of species over the past decade (e.g., Dulvy *et al.* 2021). The conservation status of sharks and rays in the West African region has been challenging to assess due to the limited data available. However, the available species level information indicates severe declines (e.g., fisheries independent data from Mauritania for common guitarfish *Rhinobatos rhinobatos* and common smoothhound *Mustelus mustelus*; Jabado *et al.* 2021a, 2021b). Our findings confirm that this is not limited to a few species, and populations of all elasmobranch species are likely to have severely deteriorated. The negative population trends of guitarfishes and hammerhead sharks are especially worrying, as these species groups include some of the most threatened vertebrates globally (Dulvy *et al.* 2021, Kyne *et al.* 2020). Other coastal areas where small-scale fisheries are predominant have also reported declines in historical shark and ray catches and size over the past decades (e.g., Kyalo and Stephen 2013, Humber *et al.* 2017, Vianna *et al.* 2020, Fernando and Stewart 2021, Wambiji *et al.* 2022). However, the declines we report here are amongst the most severe. Declines in catch-per-unit-effort and average size of elasmobranchs are clear signs of overfishing (Froese 2004, Hoggarth *et al.* 2006) and were already reported almost two decades ago in this region (Diop and Dossa 2011). Our estimates show that high catches of sharks and rays continue to date while the fishing effort continues to increase to feed a growing coastal population. Our estimates are likely still an underestimation, as fishers report that many vessels from neighboring countries (especially from Senegal and Guinea) target sharks and rays within the archipelago (Campredon and Cuq 2001, Diop and Dossa 2011). As these vessels land catches in their respective countries, these are unaccounted for in our satellite-based vessel count. Further, our work does not account for industrial vessels often operating legally and illegally in the waters of Guinea-Bissau that likely have large catches of sharks and rays (Leurs *et al.* 2021). Overall, this highlights that current fishing pressure on sharks and rays is likely much higher than we report here and significantly impacts these species.

Declines in shark and ray populations can potentially impact the ecological functioning of coastal areas (e.g., Ferreti *et al.* 2010). Depending on the species and life stage, sharks and rays can have a large variety of food web roles in large coastal ecosystems (Navia *et al.* 2016, Hammerschlag *et al.* 2019, Heithaus *et al.* 2022). We show that the average size of the majority of elasmobranch species groups has declined over time, which could be explained by a within-group shift in species composition (e.g., a shift from larger carcharhinid species (>1 m total length) to generally smaller milk sharks (<1 m total length), as larger individuals are threatened more by fisheries, e.g., Dulvy *et al.* 2021), or by the disappearance of adult individuals of these species groups. Changes in the composition of the elasmobranch community, or even a complete loss of species groups (e.g., guitarfish), could lead to a loss of ecological roles, impairing coastal ecosystem functioning. Fisher's ecological knowledge indicates that species once common, such as sawfishes, have disappeared from most of the coast of West Africa (e.g., Leeney and Poncelet 2015). Additional research in neighboring Mauritania and Senegal also suggests that wedgefishes and some species of guitarfishes are now locally extinct (R.W. Jabado *unpubl. data*). Community elders in the Bijagós also indicated they are worried that 'kasapai' (i.e., guitarfishes) face the same fate (G. Leurs, *unpubl. data*). Species-specific information was possible to collect from LEK surveys because of distinct morphological features that fishers could describe (i.e., rostrum of sawfishes, coloration and large fins of wedgefishes; Jabado *et al.* 2015). However, while declines at the group level were possible to estimate, the lack of species-specific information may have masked larger declines in certain species that fishers could not accurately identify. Further research is needed to accurately determine changes in the species composition of catches in this region.

The disappearance of sharks and rays from these coastal areas may also have socioeconomic repercussions for coastal communities. Our results suggest that fishers go to sea more often or for longer periods but consistently catch less. This aspect of overfishing can have significant implications for local incomes and subsistence (Golden *et al.* 2016). Shark fisheries are often linked to local consumption of shark and ray meat, and (shark) fisheries are a crucial part of local economic systems (Glaus *et al.* 2018, Booth *et al.* 2019, Karnad *et al.* 2020). This is often the case in regions where poverty levels are high and food security is low (Golden *et al.* 2016). Therefore, regulating and managing (shark) fisheries is crucial to contributing to the alleviation of poverty and to strengthening food security in coastal regions. Within the Bijagós archipelago, sharks and rays also have a central role in spiritual ceremonies and traditions (Diop and Dossa 2011, Cross 2014, Leeney and Poncelet

2015). The sawfish features on the regional currency (West African CFA Franc), villages have buildings and ornaments inspired by this species, and sawfish, guitarfish, and hammerhead sharks are often represented in traditional masks and costumes (Cross 2014, Leeney and Poncelet 2015). The loss of the sawfish may also represent a loss of the cultural value of these species. These socioeconomic and ecological considerations render small-scale (shark) fisheries management complex (Booth *et al.* 2019, Haque *et al.* 2021). Finally, while the loss of shark and ray species constitutes an ecological loss in West African coastal communities, it can also constitute a loss of tradition, values, and culture.

We modeled how a reduction (or increase) of small-scale fishing vessel fleet size can affect current catches of sharks and rays within the archipelago. The small-scale fishing fleet has been reduced in other coastal areas to reduce catches of species of concern. However, it can only succeed if alternative incomes and livelihoods are mobilized for fishing communities (Salas *et al.* 2007, Pomeroy 2012). Although marine protected areas are also an effective strategy to conserve some shark and ray species, for larger and mobile elasmobranch species, some protected areas may not be as beneficial (White *et al.* 2017, Mackeracher *et al.* 2019). Our results show that fishing pressure throughout the archipelago remains high, including within the protected areas of Orango and the community-managed national park of Urok. Improving enforcement of existing regulations and limiting fishing capacity by reducing fleet sizes and overall fishing pressure within these areas will likely benefit shark and ray populations. This is particularly important since these large coastal areas are mostly used by early life-stage elasmobranchs with relatively smaller home ranges (Knip *et al.* 2010, Leurs *et al.* 2023a). However, other strategies to minimize the continued exploitation of these vulnerable species should also be further studied and implemented. This may include enforcing and extending the monofilament net ban within and outside the protected areas, a retention ban of highly threatened species like hammerhead sharks, and seasonal closures of fishing areas in key areas (e.g., reproductive areas). The latter should be studied further, as the presence of some elasmobranch species is likely linked to the rainy season (Leurs *et al.* 2023b). In conjunction with improved actions to support the conservation of these species, a monitoring system, including the collection of fishery-dependent data, will be essential to measure impact and effectiveness.

Our reconstructed historical catch trends relied on the local ecological knowledge of the fisher communities in combination with other monitoring approaches (i.e., satellite-based vessel counts and landing site surveys). Local ecological knowledge is considered a key approach to studying the biology of species (e.g., Neis *et al.* 1999, Gilchrist *et al.* 2005, Anadón *et al.* 2009), their distribution (Lopes *et al.* 2019) and temporal changes in abundance (Gilchrist *et al.* 2005, Beaudreau *et al.* 2014). This approach also ensures the inclusion of resource users in decision-making and can lead to a broader understanding of the socio-ecological system at hand (Gilchrist *et al.* 2005, Beaudreau *et al.* 2014, Lopes *et al.* 2019). However, effective species management also requires quantitative information (Gilchrist *et al.* 2005, Tesfamichael *et al.* 2014). Studies capturing local ecological knowledge can be limited to the collection of qualitative (e.g., Gilchrist *et al.* 2005) or low-resolution quantitative information (e.g., high, low abundance; Neis *et al.* 1999, Silvano and Valbo-Jørgensen 2008, Anadón *et al.* 2009). In many cases, quantitative information is also collected at vague temporal scales difficult to recall by the interviewee (e.g., abundance in the year 2000, 2010; Azzurro *et al.* 2011, Beaudreau *et al.* 2014, Colloca *et al.* 2020). The resulting information can be highly variable or lack appropriate resolution, limiting adequate statistical analyses for inclusion in management strategies. For this study, we only focused on the moments a fisher can recall best: when one started fishing and the current situation (e.g., Tesfamichael *et al.* 2014). We show that this methodology can be used to reconstruct temporal change when combined with a sampling scheme that targets fishers across the age range (i.e., experience) of the fishing community. Using this method, we confirm severe declines of all elasmobranch species groups but also that younger fishers are likely used to catching fewer elasmobranchs compared to older generations. This baseline shift (Pauly 1995) is similar to the shift in generational sawfish baselines within the Bijagós Archipelago and other African coastal areas (Leeney and Poncelet 2015, Braulik *et al.* 2020). Two aspects that can increase the sampling error and variability in fisher ecological knowledge data are the willingness of fishers to share information (e.g., when information would indicate non-compliance to regulations or increase competition; Anadón *et al.* 2009) and the fishers' ability to identify the species of concern correctly (Anadón *et al.* 2009). The former was evident as we compared the use of monofilament (forbidden in the archipelago) by interviewed fishers, which was low, to monofilament use on boats sampled by the fisheries observer, which was higher. The latter was addressed by establishing a mutual understanding of the species through visual aids (i.e., species photographic cards). Fishers often have accurate knowledge of species identification, especially species that are easily recognizable or closely linked to communities, as is the case with sharks and rays in the Bijagós (Neis *et al.* 1999, Jabado *et al.* 2015). This suggests that fishers were comfortable with these discussions and that the data collected reflected the current state of shark and ray fisheries in the Bijagós Archipelago.

We showed that a combination of LEK and conventional methods (e.g., landing site surveys and satellite boat counts) can provide important baseline information needed to improve the management of threatened marine species, especially in regions with limited resources and capacity. This information is the basis for future (adaptive) management of these vulnerable species of ecological and socioeconomic importance to coastal communities, such as in the Bijagós Archipelago. Considering the current conservation status of sharks and rays in the region, immediate action needs to be taken to reduce mortality through improved fisheries management measures as well as monitoring and enforcement of established regulations.

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SECTION II

Diversity & Life History

Chapter 5

Addressing data-deficiency of threatened sharks and rays in a highly dynamic coastal ecosystem using environmental DNA

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Abstract

Marine biodiversity loss is accelerating, leading to the elevated extinction risks of many species, including sharks and rays. To mitigate these losses, information on their distribution and community composition is needed. Monitoring these (often) mobile species is challenging, especially in remote, highly dynamic and turbid coastal areas. Here, we use an environmental DNA (eDNA) approach to (1) establish the presence and distribution of elasmobranch species, (2) compare this to a conventional fisheries-dependent approach, and (3) determine the influence of season, area-based protection and habitat on elasmobranch community composition in the highly dynamic Bijagós Archipelago in Guinea-Bissau (West Africa). We collected 127 seawater samples and detected elasmobranch DNA in 58 (45.7%) of these samples, confirming the presence of 13 different elasmobranch species (2 sharks, 11 rays), including seven threatened species. Eight species detected by the eDNA approach were also recorded in a fisheries observer program, which recorded another eight species not detected by the eDNA approach. The most commonly occurring species, based on the number of eDNA sampling locations, were the pearl whipray (*Fontitrygon margaritella*), smalltooth stingray (*Hypanus rudis*), scalloped hammerhead shark (*Sphyrna lewini*), and the blackchin guitarfish (*Glaucostegus cemiculus*). Species composition and richness differed significantly before (January-March) and after the rainy season (November-December). Furthermore, we showed that community composition and species richness did not differ between protected (MPA) and non-protected areas of the archipelago. Thus, we confirm that eDNA approaches are a valuable and non-invasive tool to study threatened shark and ray species in data-deficient and dynamic coastal areas, especially when combined with conventional monitoring methods such as fisheries-dependent information.

Introduction

Globally, coastal ecosystems are threatened by anthropogenic stressors, such as pollution and coastal development, causing a collapse in the richness and diversity of associated species (Worm *et al.* 2006, Cardinale *et al.* 2012). The loss of species may hamper the functioning and health of ecosystems and can lead to a loss of ecosystem services (Worm *et al.* 2006, Palumbi *et al.* 2009). Therefore, monitoring the status of biodiversity and individual species within ecosystems is essential to ensure future ecosystem health and the preservation of ecosystem services (Millenium Ecosystem Assessment 2005, Cardinale *et al.* 2012).

In marine ecosystems, top and meso-predators such as sharks and rays (i.e., elasmobranchs), can have important roles in coastal ecosystems (e.g., Heithaus 2010, Heupel *et al.* 2014, Roff *et al.* 2016, Heithaus *et al.* 2022). However, recent findings suggest that approximately 33% of all shark and ray species are threatened with extinction due to overfishing and habitat degradation (Dulvy *et al.* 2021). Due to their ecological roles, the loss of these species may influence ecosystem services of marine ecosystems, such as productivity of fisheries, detoxification of marine waters, and carbon sequestration ('blue carbon', Heithaus *et al.* 2008, Atwood *et al.* 2015, Küpper and Kamenos 2018).

Assessing species' conservation status (e.g., IUCN Red List status) is an important step toward implementing management actions that enable protection. However, specific information for the appropriate assessment of conservation status is missing for many shark and ray species or local/regional populations (Dulvy *et al.* 2021). This includes information on local presence, distribution and abundance of elasmobranch species. Monitoring biodiversity is costly and requires appropriate (research) capacity, causing data deficiency to be more profound in developing regions. The resulting deficiency of essential information impairs species' status evaluation and hampers the implementation of (cost-)effective conservation strategies.

A relatively novel approach to monitoring the occurrence of marine species is the use of environmental DNA (eDNA), which involves the metabarcoding of DNA traces of marine species in the water column or associated sediments (e.g., Thomsen *et al.* 2012). This approach simplifies species monitoring, increases species coverage (i.e., including cryptic, rare and highly mobile species and limiting misidentification), and is non-invasive and cost-effective compared to other traditional monitoring approaches (Thomsen *et al.* 2012, Miya 2022). Over the past years, the application of environmental DNA has been increasingly used to confirm the presence of fish species in both freshwater and marine waters and, more recently, to study the composition of elasmobranch communities (Bakker *et al.* 2017, Boussarie *et al.* 2018, Dunn *et al.* 2022). In addition, eDNA approaches have been successfully applied to determine seasonal abundance (Postaire *et al.* 2020), population sizes (Sigsgaard *et* *al.* 2016), and the presence of highly cryptic species, for example, the presence of sawfishes (*Pristis spp.*) in estuaries (Lafferty *et al.* 2018, Schweiss *et al.* 2019, Lehman *et al.* 2020). Although these relatively novel approaches are promising to address elasmobranch communities in highly data-deficient regions, less is known about the success of this technique in studying elasmobranch communities in highly dynamic environments such as intertidal ecosystems experiencing strong (tidal) currents.

To determine if environmental DNA can be used to tackle data deficiency in highly dynamic, tropical coastal ecosystems, we aimed to study a highly data-deficient shark and ray community in the West African region. The coastal waters of the West African bioregion have a high occurrence of threatened endemic elasmobranch species (Derrick *et al.* 2020) and are a global hotspot for the most evolutionary distinct elasmobranch species (i.e., a measure of a species' evolutionary isolation) (Stein *et al.* 2015). However, the region currently also experiences one of the highest levels of fishing effort in the world (Kroodsma *et al.* 2018, Leurs *et al.* 2021). Industrial fisheries surrounding protected coastal areas in West Africa (Leurs *et al.* 2021) and small-scale fisheries within these areas both threaten elasmobranch populations due to their high targeted and non-targeted catches (Kyne *et al.* 2020, Lemrabott *et al.* in prep, Leurs *et al.* in prep., Moore *et al.* 2019). However, the presence and community composition of elasmobranch fishes in coastal areas within the region remains poorly understood, hampering adequate conservation of this threatened species group. In addition, the recent disappearance of species like largetooth sawfish (*Pristis pristis*) from the wider region and the occurrence of cryptic species, such as the African wedgefish (*Rhynchobatus luebberti*), asks for a more comprehensive approach to elasmobranch monitoring (Leeney and Poncelet 2015, Moore 2017).

Here, we determined if the environmental DNA approach can be used to successfully study elasmobranch communities in a tropical, data-deficient and highly dynamic intertidal environment. Specifically, we used an eDNA approach to (1) establish the presence and distribution of elasmobranch species within a highly dynamic tropical intertidal ecosystem, (2) compare the eDNA-based species richness and composition of the archipelago to preliminary small-scale fisheries data, and (3) determine if eDNA-based species richness and community composition differed across seasons (i.e., before and after the rainy season), across tidal phases, between protected and non-protected areas and with distance to mangrove forest. Although the Bijagós Archipelago is one of the largest intertidal areas in the region, supporting local (artisanal) fisheries and likely functioning as a nursery area for both coastal and pelagic fish species (including commercial species captured in the industrial fisheries in the wider region) (Correia *et al.* 2021), information on the distribution of elasmobranch species in lacking. The only information on elasmobranch species within this area originates from inferred species distributions (IBAP 2012), studies limited to a single species or island (Cross 2015, Leeney and Poncelet 2015), and recorded captures by industrial fishing fleets operating outside the archipelago (Diop and Dossa 2011, Leurs *et al.* 2021). We aimed to provide information that is essential for the successful implementation of more efficient conservation measures for these threatened species, for future ecological studies focusing on the ecosystem functioning of the Bijagós, and to learn if and how this relatively novel approach can be used in remote, highly dynamic, and data-deficient environments to study sharks and rays.

Methods

Study area

The Bijagós Archipelago (11° 15' 0" N, 16° 5' 0" W) is located in Guinea-Bissau (Figure 5.1), in the extended estuary of the Geba River. The archipelago comprises 88 islands and islets lined by dense mangrove forests and intertidal mudflats connected through a complex system of gullies and channels.

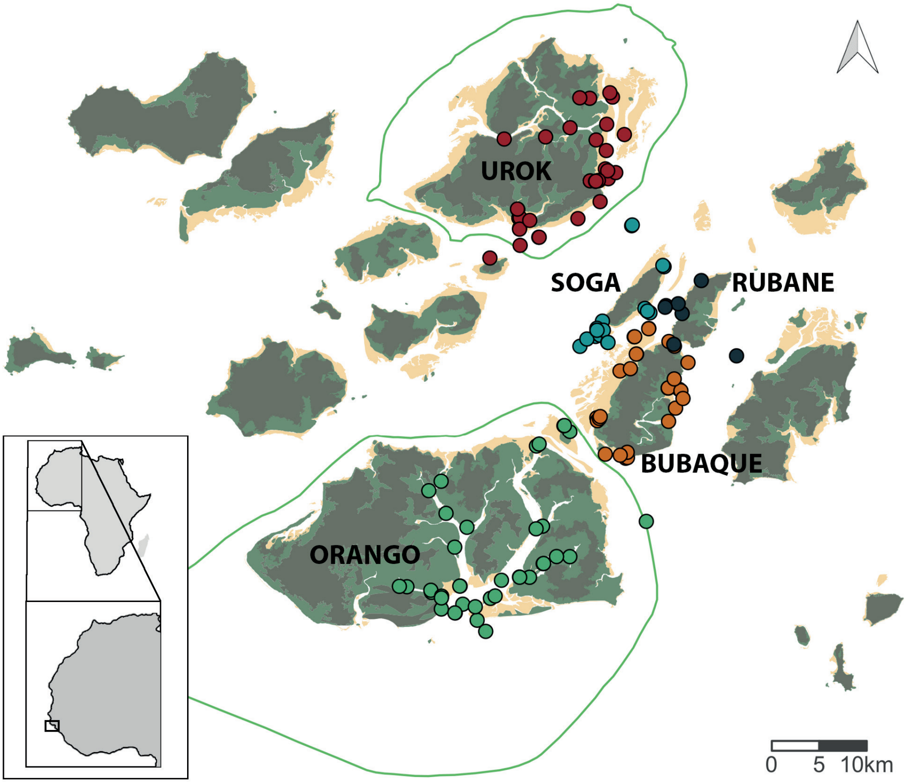

Figure 5.1 Overview of the sampling locations in the Bijagós Archipelago in Guinea-Bissau. Sampling was conducted in five different regions: Urok (n = 35; red), Soga (n = 19; light blue), Rubane (dark blue), Bubaque (n = 28; orange), and Orango (n = 38; green). The island's upland (dark green), mangroves (green) and intertidal areas (yellow) are shown. The marine protected areas (MPAs) are outlined in green.

With over 350 km^2 of mangrove forests and 760 km^2 of intertidal flats, the archipelago is recognized as an important area for (migratory) shorebirds (Salvig *et al.* 1994, Meijer *et al.* 2021), teleosts (Correia *et al.* 2021), and sea turtles (Catry *et al.* 2002), and was designated as a UNESCO Biosphere Reserve in 1966 (IBAP 2012, UNESCO 2020). In 2014, the archipelago was also recognized as an important wetland under the RAMSAR Convention (IBAP 2012, RAMSAR 2014).

Sample collection and preservation

We sampled surface water in five regions within the archipelago: Urok, Soga, Rubane, Bubaque, and Orango (Figure 5.1). Samples were collected before (January and February) and after (October to December) the rainy season in 2019. At each sampling location, we took a 2-liter water sample using a sterilized sampling bottle (i.e., using a 10% bleach solution) and by submerging the bottle completely underwater to prevent sampling the biofilm on the water surface. For each sample, we recorded the surrounding habitat (Table 5.1), geographic coordinates, and storage time (i.e., time between sample collection and filtration). Retrospectively, we determined the distance of the sampling location to the entrance of the Geba River, the distance to the nearest mangrove edge, and whether a sample was taken in or outside one of the two marine protected areas (Figure 5.1). Sampling time was used to determine the tidal phase and amplitude based on the tide table for Bubaque (11.33° N/15.87° W). We estimated that compared to the high tide in Bubaque, the high tide was one hour later in the Urok sampling region and one hour earlier in the Orango region. To account for potential variability in these high and low tide estimates, we considered samples taken within 30 minutes to or from high tide as ‘high-tide samples’ and similarly for low tide. Samples taken between low and high tides are referred to as ‘receding tides’ and ‘incoming tides’. Straight after sample collection, samples were wrapped in aluminum foil and stored in an insulated cooling box until filtration. Upon return to the base camp or whenever the situation in the field permitted, samples were filtered as soon as possible using a portable, battery-operated vacuum pump (Makita 16V vacuum pump). The pump was connected to a Nalgene Erlenmeyer flask with a sterilized filter holder and funnel on top. Samples were filtered using sterile mixed cellulose ester filters (MERCK and PALL filters, 47mm Ø, 0.45μm pore size). We used multiple filters to filter a single 2-liter sample depending on the suspended material. As access to electricity during expeditions was not always guaranteed due to the remoteness of the field sites, each filter was subsequently stored in a Longmire’s lysis buffer, which allows for sample storage without cooling (Williams *et al.* 2016, Spens *et al.* 2017, Taberlet *et al.* 2018). Sampling bottles, filter holders, and funnels were sterilized using a 10% bleach solution between sampling efforts. To determine any contamination during sampling and equipment sterilization, we took a negative control sample for each sterilized batch of equipment by filtering bottled mineral water (i.e., equipment blank). The filters of these controls were stored the same way as filters used for sample filtration.

Table 5.1 The definitions of habitats assigned to each sample (see Leurs *et al.* 2023).

Habitat	Definition
Intertidal	Habitat that is submerged during high tide and emerges at low tide (generally shallower than 5 meters in depth).
Gulley	Water stream embedded in intertidal flats and/or mangrove forests (width of less than 250 meters).
Minor channel	A water stream that is more than 250m and less than 1 km wide and has no direct connection to the ocean.
Main channels/subtidal waters	Main water bodies with a width of over 1 km and a direct connection to the ocean.

Metabarcoding of samples

DNA extraction

In the lab (genetics lab of the University of Groningen), prior to DNA extraction, all filters (and buffer solution) belonging to the same field sample were pooled together in a sterile 50 ml vial and were stored submerged by adding Longmire's lysis buffer. Filter pooling was conducted in an ultra-violet (UV) box with sterilized forceps. Materials were sterilized using 50% bleach and subsequent rinsing with DNA-free water. Samples were then stored in the fridge (at about 2 °C) until DNA extraction. We applied a standard phase-separation and precipitation DNA extraction method based on phenol-chloroform (Minamoto *et al.* 2016). DNA quantities of every sample were determined using a spectrophotometer (Nanodrop 2000). Subsequently, DNA extracts were cleaned by gel extraction using the Promega Wizard® SV Gel and PCR Clean-Up System. This clean-up step was necessary because of the carry-over of PCR inhibitor originating from ingredients of Longmire's lysis buffer. The obtained clean DNA was then used as the PCR template.

Primer details

For species identification in elasmobranchs, the fast-evolving, mitochondrial protein-coding gene NADH dehydrogenase subunit 2 (NADH2) has been successfully applied (Naylor *et al.* 2005, 2012). The universal elasmobranch primers of Naylor *et al.* (2005), binding to the ASN and ILE tRNA regions, target a 1,044 bp fragment of NADH2. To amplify a shorter fragment from eDNA samples with potentially degraded DNA, we used the ASN primer variant called ‘ChimeraF’ (‘5-AAGGACTACTTTGATAGAGT-‘3) (Naylor *et al.* 2005) in combination with two newly designed reverse primers yielding an amplicon of ca. 320 bp. The first reverse primer NADH2 ‘miniSharkR2’ (‘5-GGAATRATGGCTAATGTGTT-‘3) targets both sharks and rays, and the second reverse primer ‘miniSharkR5’ (‘5-CCTATTCAAACTAGGAGTC-‘3) was specifically designed to target shark species. For subsequent sequencing, the following tails were attached to the primer: 5’-GATGTGTATAAGAGACAG_Forward-primer-3’ and 5’-CGTGTGCTCTTCCGATCT_Reverse-primers-3’.

PCR and sequencing

Polymerase Chain Reaction (PCR) was set up in a DNA-free room. Each sample was amplified in triplicate to avoid PCR bias. AccuStart II PCR ToughMix© was used, as DNA in the collected samples may have been degraded due to biological processes or degradation caused by exposure to UV light. The reaction volume was 10 μl including 5 μl AccuStart, 1μl of each primer (10 μM), 1 μl ddH2O and 2μl DNA template. The PCR profile was 3 min at 94°C, followed by 35 cycles of 1 min at 94°C, 30 sec at 48°C, and 1 min at 72°C, and a final extension at 72°C for 10 min. The annealing temperature was set to 48°C to minimize taxonomic bias (Ishii and Fukui, 2001). PCR products were sequenced on a MiSeq© (Illumina) Sequencer at the Department of Human Genetics, Leiden University Medical Center, with the aim for a read-depth set at 50,000 reads per sample. Libraries were prepared with the MiSeq© V3 kit, generating 300-bp paired-end reads. Since the V3-kit does not normalize, i.e., leaves the relative presence of the initial PCR product intact, this library preparation method allows assessing the relative contribution of taxa to read abundance of each PCR product.

Lab controls

For each sampling period (before and after the rainy season) two negative extraction controls were included to test the Longmire’s lysis buffer stock solution as a source of contamination: one with the first and one with the last batch of extractions. Additionally, negative control samples were taken from each PCR master mix to track possible contamination of PCR reagents.

Creation of OTU table

We extracted unique, high-quality barcode reads (molecular operational taxonomic units, abbreviated as OTU) using the software USearch 9.2 (Edgar 2010). First, paired-end reads were merged into a consensus sequence, removing the sequencing adaptors.

Primer sequences were removed by truncating each end by 25bp, the length of the longest PCR primer. The full dataset quality filtering was set at the default E-value of 0.4 and read-truncation to 220bp. To simplify clustering, truncated reads were de-replicated by assigning a count to unique reads, merging identical reads in both orientations. Subsequently, the singletons were removed (e.g., Frøslev *et al.* 2017). Using the UPARSE-OTU algorithm (Edgar, 2010), reads that were minimally 97% identical were clustered. This was replicated using a threshold of 100% similarity for clustering and yielded no differences in species detection. The consensus sequence of each cluster was assigned an OTU ID, resulting in an OTU sequence table. This algorithm also filters chimeras. For each sample, the number of reads (paired and with truncated primers) that matched with each OTU was determined, resulting in an OTU frequency table. The default identity match of 97% was used. The final OTU frequency table was adjusted for the negative extraction and PCR controls by deducting the number of reads found for an OTU in the pooled negative extraction controls from each cell in the OTU table. The final OTU table was blasted against the mitochondrial genome database of Chondrichthyes constructed and curated by the Florida Program for Shark Research (FPSR) at the Florida Museum of Natural History of the University of Florida (see Naylor *et al.* 2012). At the time of this analysis, the database contained 94% of known genera and 72% of known chondrichthyan species, plus potential new species and population-level variants. The database has been curated by taxonomic experts to exclude any wrongly identified haplotypes. Only the match with the lowest E-value was retained during blasting for each OTU.

Of the 127 samples we collected and sequenced, 58 (45.7%) contained elasmobranch DNA. Of 886,097 reads, 88.1% (780,581) could be taxonomically assigned to 110 unique OTUs; 40 OTUs were assigned with high taxonomic certainty using a percentage identity of ≥ 95% and query coverage of ≥ 85%. Of these, 25 OTUs were assigned to 13 elasmobranch species, accounting for 218,047 (24.6%) reads. The remaining 15 OTUs were assigned to teleosts (7.16% of reads; primarily *Sarotherodon melanotheron*), humans (0.04% of reads) and plant/bacteria (< 0.01% of reads). Of these elasmobranch species, 11 ray species were identified, accounting for 180,227 reads (82.7%) of the total number of reads. Two shark species were detected, accounting for the rest of the reads (17.3%). Elasmobranch reads per sample ranged from 0 to 6,521 (399.4 ± 976.2, mean ± standard deviation) after corrections for contamination.

Fisheries Observer Program

Data from a pilot fisheries observer program was used to compare the number of species detected in the eDNA survey. From February to September 2021, 122 fishing boats operating within the Archipelago were sampled in the main fishing port of Bissau. Of each boat, the elasmobranch catches were identified to species level and information on the fishing trip (e.g., fishing location, duration) was documented. To compare the fisheries observer data to the eDNA results, only boats fishing within the Urok, Soga, Rubane, Bubaque, and Orango regions were included in the analyses (n = 44). Due to the limited sample size, species richness and composition between fisheries observer and eDNA data could only be compared on an archipelago level.

Statistical analyses

To minimize the influence of species presence due to cross-contamination, a species was considered present when the number of reads exceeded ten. To study the species composition across different variables (e.g., season, tidal phase, MPAs), we determined the frequency of occurrence for each species by dividing the total number of locations that a species was detected by the total number of sample locations. We used non-metric dimensional scaling to visualize the species composition of sampling locations at which at least one species was detected and determined significant differences in relative species composition across the different seasons, protected areas and tidal phases using a permutational analysis of variance (PERMANOVA). We determined the species richness for each sampling location as the number of detected species (S). We used a generalized linear model with a negative binomial error distribution to determine the relation between species richness and predictor variables. We conducted a Tukey's range test to test for differences among sampling season and tidal phases. Since the number of reads for a specific species can be influenced by PCR conditions (Taberlet *et al.* 2018) or ecological events (e.g., a deceased individual or reproduction/spawning, Barnes and Turner 2016**)**, we limited species-specific analyses to presence-absence. We used a general linear model with a binomial error distribution to determine the significance of independent variables in predicting the presence of a species. We included season, region, distance to the nearest mangrove, distance to the Geba River entrance, habitat, and tidal phase as independent variables. The presence of a species was only modeled for species detected at ten or more sampling locations, resulting in an exclusion of rare species from this analysis. Model selection was based on Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC).

Results

Species presence and distribution

A total of 13 species were detected as part of our eDNA survey, with 7 (53.8%) of these species currently listed as threatened on the IUCN Red List. The four most common species in the study area based on the total number of sample points that a species was detected are the pearl whipray (18.9%; N = 24 locations), smalltooth stingray (*Hypanus rudis*, 14.2%; N = 18 locations), scalloped hammerhead shark (12.6%; N = 16 locations), and blackchin guitarfish (11.8%; N = 15 locations) (Figure 5.2A). These four species were detected in the majority of study regions, except for the blackchin guitarfish and smalltooth stingray, which were not detected in the Rubane and Soga regions, respectively (Figure 5.3). Relatively rare species, such as the African cownose ray (*Rhinoptera peli*) and the marbled stingray (*Dasyatis marmorata*), were only detected in Urok and southern Orango (Appendix 5.1).

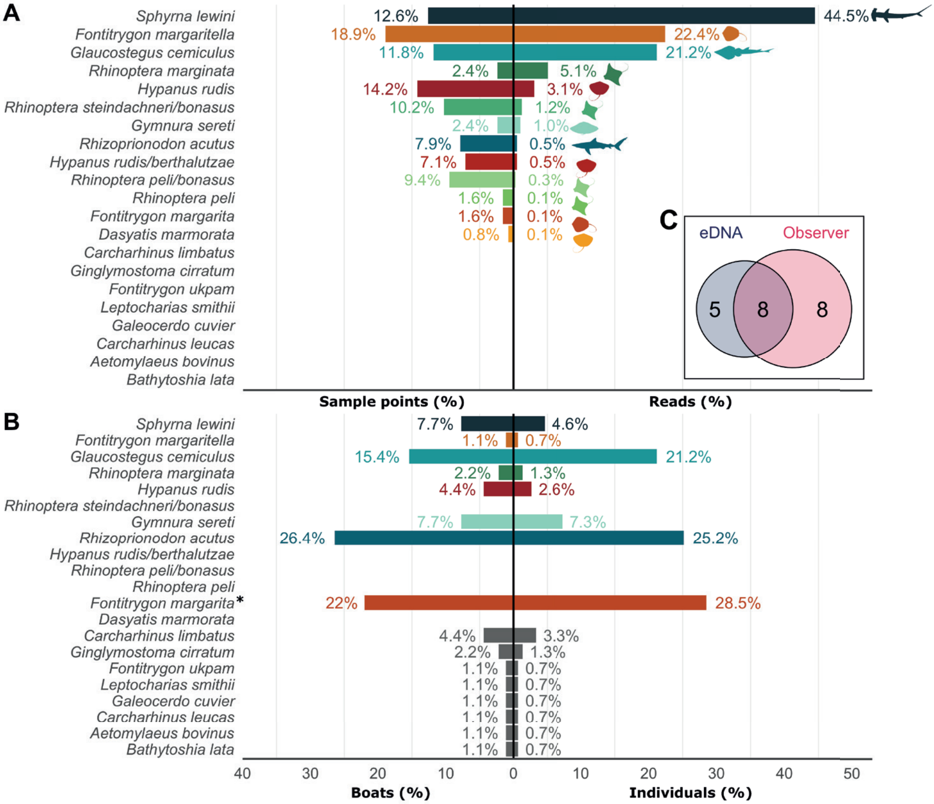

Figure 5.2 The species that were detected using environmental DNA in 2020 as a proportion of sampling points (n = 127) that a species was detected and as a proportion of the total number of reads (A). The species observed during the fisheries observer program in 2021 are shown as a proportion of the boats that captured the species and the proportion of the total number of individuals of elasmobranchs that were captured (B). Species were detected either by both methods or only by the eDNA survey or by the observer (C). Different colors indicate different species detected as part of the eDNA survey, with color tint indicating species group (sharks = blue, benthic rays = orange/red, benthopelagic rays = green, guitarfishes = light blue). Species only detected as part of the observer program are shown in gray.

**Possibly includes observations of F. margaritella due to misidentification.*

When considering the total number of reads per species, the most common species were the scalloped hammerhead shark (44.5%), pearl whipray (22.4%), blackchin guitarfish (21.2%), and the Lusitanian cownose ray (*Rhinoptera marginata*, 5.1%). This differed from fisheries-dependent information, as the most caught species were the milk shark (*Rhizoprionodon acutus*, 26.4%), daisy whipray (*Fontitrygon margarita* 22.0%, but likely includes *F. margaritella* due to frequent misidentification), blackchin guitarfish (15.4%), scalloped hammerhead shark (7.7%), and Seret's butterfly ray (*Gymnura sereti*, 7.7%) (Figure 5.2B). The eDNA approach and observer program overlapped in documenting the presence of eight species, whereas five additional species were only detected with the eDNA approach and eight other species were recorded only in the catches of local fishers (Figure 5.2C).

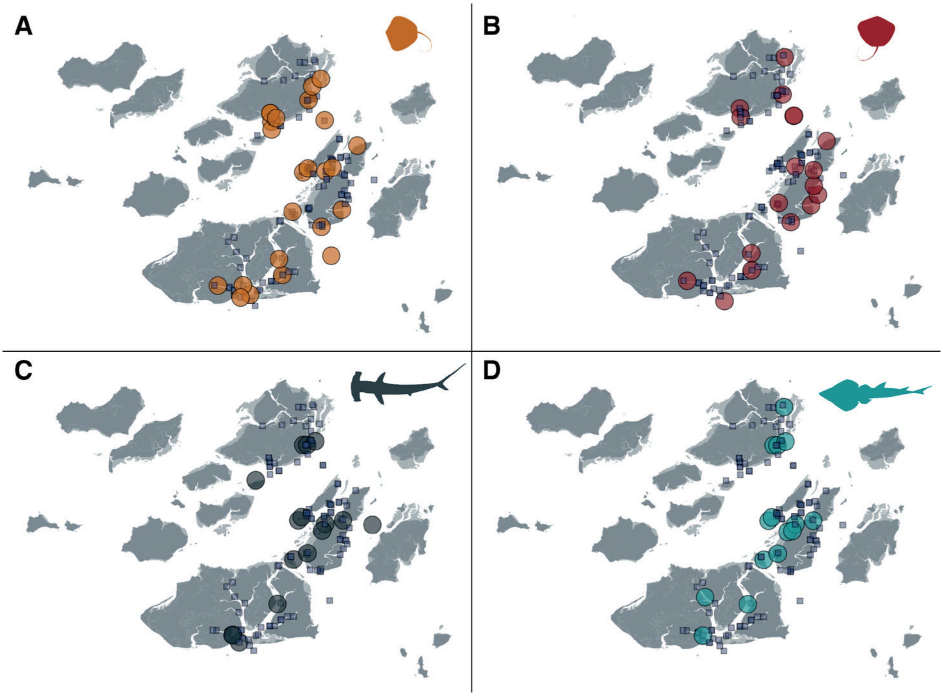

Figure 5.3 The sample points where the four most common species were detected using eDNA: (A) pearl whipray (*Fontitrygon margaritella*), (B) smalltooth stingray (*Hypanus rudis*), (C) scalloped hammerhead shark (*Sphyrna lewini*), and (D) blackchin guitarfish (*Glaucostegus cemiculus*). Grey squares indicate locations where the species was not detected. The distribution maps of the remaining species detected in this study are shown in Appendix 5.1.

We determined that eDNA-based species richness within the study area ranged from 0 to 7 species per location, with a mean of 1.0 spp. (95% CI: 0.75-1.27 spp.) (Figure 5.4). Seven of the species detected using the eDNA approach are classified as threatened based on the IUCN Red List: The milk shark (*Rhizoprionodon acutus*) and pearl whipray (*Fontitrygon margarita*) are listed as Vulnerable, the Seret's butterfly ray (*Gymnura sereti*) as Endangered, and the scalloped hammerhead shark, blackchin guitarfish, Lusitanian cownose ray (*Rhinoptera marginata*), and the smalltooth stingray are listed as Critically Endangered. The fisheries observer recorded seven additional threatened species not detected using the eDNA approach. Of these, the blacktip shark (*Carcharhinus limbatus*), nurse shark (*Ginglymostoma cirratum*), barbeled houndshark (*Leptocharias smithii*), bull shark (*Carcharhinus leucas*), and brown stingray (*Bathytoshia lata*) are listed as Vulnerable, and the thorny whipray (*Fontitrygon ukpam*) and duckbill eagle ray (*Aetomylaeus bovinus*) as Critically Endangered.

Effects of season, protective status and habitat

We determined that both species richness and species composition differed significantly before and after the rainy season (Figure 5.5A-C; Richness: d.f. 1, F = 4.46, p = 0.04, composition: d.f. = 1, F = 7.79, $p < 0.01$) and that species composition differed between non-protected and protected areas when seasonality is taken into account. These seasonal differences are caused by a higher occurrence of the pearl whipray and the cownose ray *Rhinoptera steindachneri cf. bonasus* after the rainy season and a higher occurrence of the scalloped hammerhead shark and the blackchin guitarfish before the rainy season (Figure 5.5B). This was supported by a higher detection probability of the scalloped hammerhead (d.f. = 1, $X^2 = 10.4$, $p < 0.01$) and blackchin guitarfish (d.f. = 1, $X^2 = 11.1$, $p < 0.01$) before the rainy season (Appendix 5.6).

Although we determined that both species richness and composition across protected and non-protected areas did not differ significantly (Figure 5.5D-F), species composition differed significantly between protected and non-protected waters if seasonality is taken into consideration (d.f. = 1, F = 2.29, p = 0.04) (Figure 5.5G). After the rainy season, species composition within the MPAs significantly differed from locations outside the MPAs (d.f. = 1, F = 3.67, p = 0.03), but also from locations both in- and outside MPAs before the rainy season (d.f. = 1, F = 6.40, p = 0.001; d.f. = 1, F = 6.51, p = 0.002). These differences are caused by a higher occurrence of the pearl whipray within the MPAs after the rainy season and the higher occurrence of the scalloped hammerhead shark and guitarfish before the rainy season in both protected and non-protected areas (Figure 5.5H).

Species richness was influenced by the tidal phase (d.f. = 3, F = 3.75, p = 0.01), with the highest number of species detected in samples taken during incoming tide (1.59 ± 0.28 spp.) (Appendix 5.2). This coincides with the higher probability of detecting the most commonly detected species, the pearl whipray, during incoming tide (d.f. = 1, z = 2.18, p = 0.03) (Appendix 5.6).

Although the distance to the Geba River had no significant influence on the species richness and detection probability of a species, the distance to the nearest mangrove forest had a significant influence on the probability of detecting three ray species, the pearl whipray, blackchin guitarfish, and the cownose ray *Rhinoptera steindachneri cf. bonasus* (Figure 5.6). Samples taken further away from the mangrove edge had a higher probability of detecting the pearl whipray (d.f. = 1, $X^2 = 4.5$, p = 0.03) and *Rhinoptera steindachneri cf. bonasus* (d.f. = 1, $X^2 = 5.9$, p = 0.02). In contrast, the probability of detecting a blackchin guitarfish decreased when moving further from the mangrove edge (d.f. = 1, $X^2 = 4.0$, p = 0.05).

Sampling effort and storage

Lastly, increased sampling effort correlated with an increase in the number of species detected in our study. The maximum species richness (S = 13) was reached at 124 samples taken, which constitutes 96% of the total sampling effort of this study (Appendix 5.3). We also determined that extended storage times (0.03 - 7.2 hours) due to the remoteness of the study sites did not negatively impact the number of species detected (*Spearman* r = 0.09).

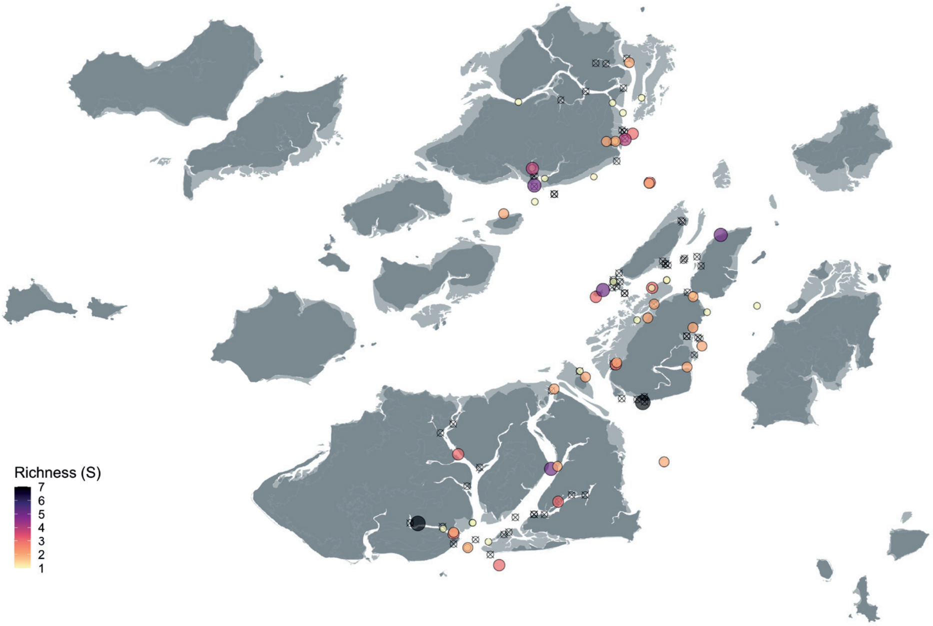

Figure 5.4 Species richness - the number of detected species - for every sampling point within the study area. Sampling points with a low species richness are indicated by a small yellow/ orange point, and sampling points with a high species richness are indicated by dark purple colors and a larger point. Sampling points with no elasmobranch species detected are indicated with crossed dots.

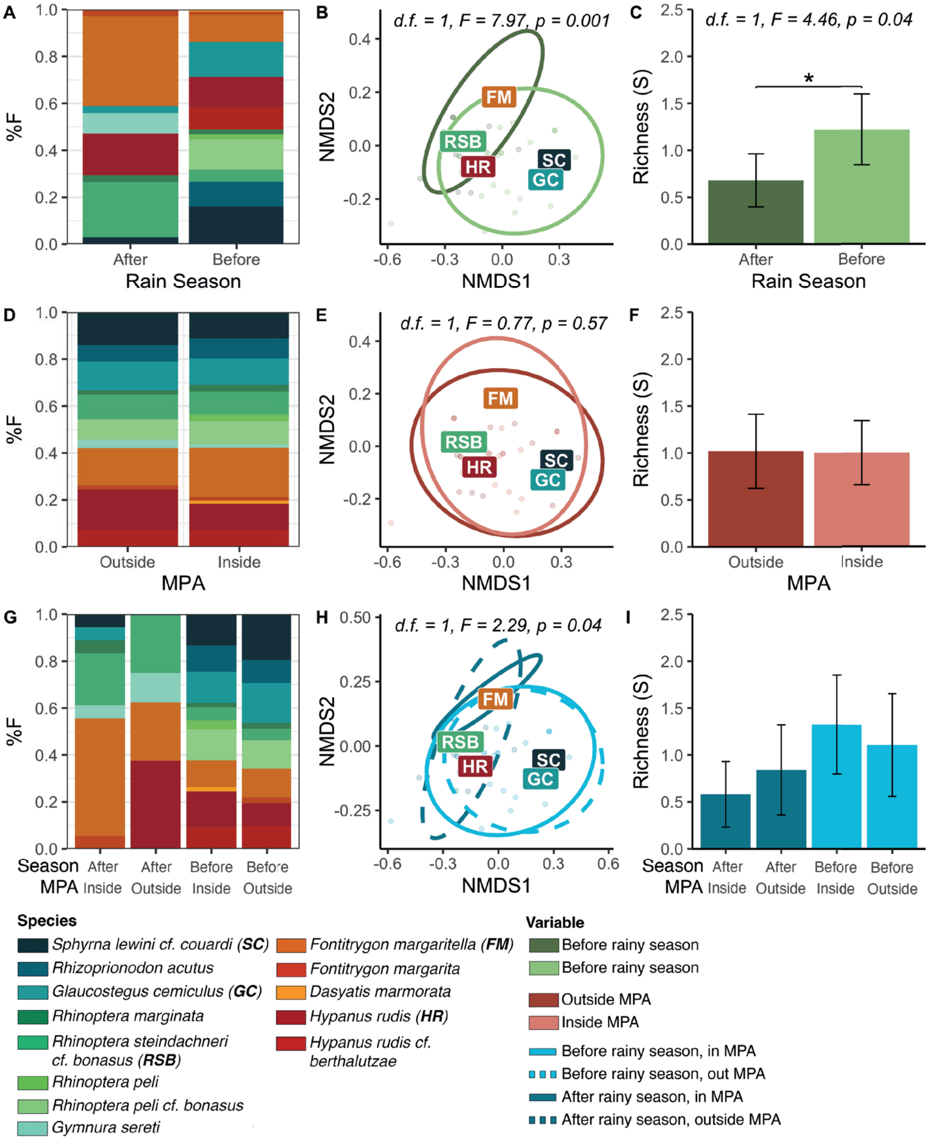

Figure 5.5 The influence of season (A-C), marine protected areas (D-F) and their interaction between (G-I) on the frequency of occurrence of a species (%F; left column), species composition (NMDS; center column), and the species richness (S; right column). Species are indicated by their different colors, with the five most common species indicated in the NMDS (FM = *Fontitrygon margaritella*, RSB = *Rhinoptera steindachneri cf. bonasus*, HR = *Hypanus rudis*, SC = *Sphyrna lewini cf. couardi*, GC = *Glaucostegus cemiculus*).

Discussion

For effective marine conservation, information on species presence, richness, and community composition is essential, especially in regions where resources for conservation are limited. In remote, highly dynamic and often highly turbid ecosystems like intertidal areas, resolving data deficiency of a species group can be challenging as many other observational methods are either unsuitable or require high research and financial capacity.

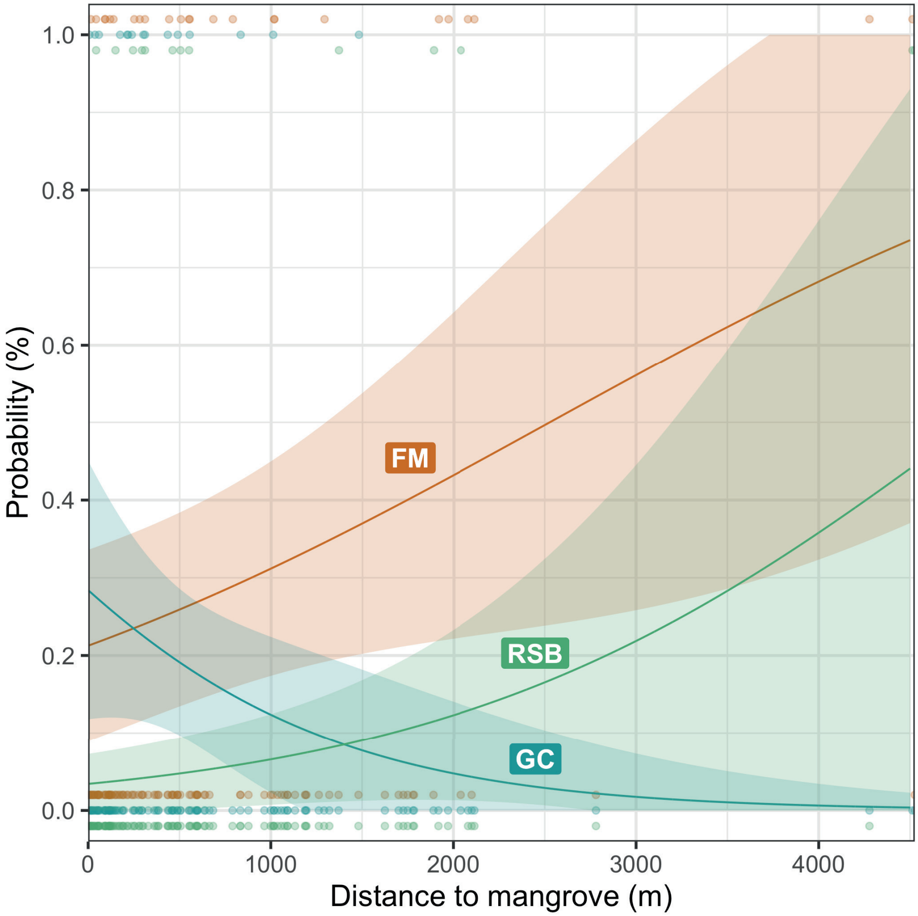

Figure 5.6 The probability of detecting the pearl whipray (Fontitrygon margaritella, FM), the cownose ray Rhinoptera steindachneri cf. bonasus (RSB), and the blackchin guitarfish (Glaucostegus cemiculus, GC) with increasing distance from the mangrove edge.

In this study, we aimed to solve data deficiency of elasmobranch species in the remote and dynamic Bijagós Archipelago in Guinea-Bissau, comparing an eDNA approach with fisheries observer data. We confirmed the presence of 13 elasmobranch species (2 sharks and 11 rays, including 7 threatened species) in the Bijagós Archipelago using an eDNA approach, including the spatial distribution of these threatened species throughout the archipelago. An additional 8 species, including 7 IUCN threatened species, were solely detected by the fisheries observer program. In addition, our study confirms that species composition and richness of the elasmobranch community are mostly influenced by seasonal changes related to changes before and after the rainy season and less by differences between habitats (e.g., proximity to mangroves and estuary) or protective status of the sampling area. Our results show that an eDNA approach can successfully be used to tackle data deficiency on the presence of threatened shark and ray species on a local scale in highly dynamic coastal areas, including the indication of priority areas for the conservation of critically endangered species.

Species presence and distribution

The four most commonly detected species, the pearl whipray, scalloped hammerhead shark, smalltooth stingray and the blackchin guitarfish, were detected in sampling locations throughout the archipelago. These results suggest that the Bijagós Archipelago is an important area for these elasmobranch species. Coastal areas are known to be important nurseries or feeding areas for many elasmobranch species (Knip *et al.* 2010). Intertidal areas such as the Bijagós Archipelago and the habitats it provides can play an important role as (seasonal) feeding refugia for (early life stages of) sharks and rays (Leurs *et al.* 2023). For example, the scalloped hammerhead shark is known to use shallow coastal areas during early life stages before moving to a more pelagic habitat in deeper waters (Simpfendorfer and Milward, 1993, Zanella *et al.* 2019). This is confirmed by our preliminary results of the observer program, which shows that the majority of scalloped hammerheads captured within the archipelago are immature (Leurs, unpublished data).

Like many (early life stages of) elasmobranch species (Nagelkerken *et al.* 2008, White and Potter 2004), the blackchin guitarfish likely relies on the extensive mangrove forests of the Bijagós Archipelago. Our results show a higher probability of detecting this species close to the mangroves, which coincides with the catches of newborns and young-of-the-year individuals close to the mangrove edge, suggesting this species uses the mangrove edge as a nursery habitat (Leurs, unpublished data). Alternatively, for the pearl whipray, all life stages are likely to use coastal areas, including intertidal habitats, for feeding (Clements *et al.* 2022, Nauta *et al.* submitted).

The relative abundance of the species is potentially site-specific, as the pearl whipray is one of the most captured species in other coastal areas in The Gambia and Senegal (Moore *et al.* 2019, Jabado *et al.* 2021), but catches in the Banc d'Arguin in Mauritania are low (Lemrabott 2023).

Rare species like the largetooth sawfish (*Pristis pristis*) and African wedgefish (*Rhynchobatos luebberti*) were not detected in this study. Sawfishes are considered to be extinct from the West African region, with the last documented sawfish record originating from 2004 from the Bijagós Archipelago (Robillard and Seret 2006, Diop and Dossa 2011, Leeney and Poncelet 2015). Observations of the African wedgefish are increasingly rare within the region (Moore 2017). However, recent in-depth interviews and photographic evidence with fishers confirmed the capture of one specimen in March 2021 in the Bijagós (Leurs *et al.* unpublished). Novel eDNA approaches have a higher sensitivity for species-specific detection of rare and cryptic species compared to the approaches used in our study (e.g., Droplet Digital PCR, see Lehman *et al.* 2020).

Effects of season and protective status

We showed that species composition and richness of elasmobranch communities in the Bijagós Archipelago are mainly influenced by seasonality, with a higher species richness before the rainy season resulting in different species composition across the two seasons. The region's rainy season causes freshwater influx between June and October, significantly lowering salinity levels (Lafrance 1994, Cross 2014). As salinity can be one of the most important drivers of elasmobranch species composition in estuarine areas (Plumlee *et al.* 2018), it is likely that the observer changes are caused by changes in the abundance of species. In the Bijagós Archipelago, the differences between the two seasons are likely caused by the blackchin guitarfish and scalloped hammerhead shark, the presence of which was significantly lower after the rainy season. The fact that the movements of hammerhead sharks and guitarfishes can be influenced by changes in precipitation has been confirmed for other coastal areas (Hensley *et al.* 1998, Corgos and Rosende-Pereiro 2022). However, increased precipitation has also been linked to increased availability of crustaceans, the main prey of many guitarfishes (Lara-Mendoza *et al.* 2015). A decrease can also cause elasmobranch species to move away from coastal areas due to higher metabolic rates associated with maintaining osmoregulation (Meloni *et al.* 2002). Our results suggest that the blackchin guitarfish and scalloped hammerhead shark possibly move to waters with a relatively higher salinity during or right after the rainy season.

Furthermore, our results show that the richness and composition of elasmobranch species were similar between samples taken from protected and non-protected areas. This can be explained by the influences of horizontal water mixing due to tidal currents (Miya 2022) or by the mobility of shark and ray species, which likely move between protected and non-protected areas within the archipelago. Another explanation for the fact that no differences were found between protected and non-protected waters is the continued (targeted) fishing of elasmobranchs within both areas (Moranghajogo 2012**)**. These results suggest that the eDNA approach can successfully determine changes in species composition of elasmobranch communities across seasons and habitats in dynamic coastal areas.

eDNA-based monitoring of elasmobranch communities

The eDNA approach and fishery observer program differed in the number of species that were recorded, suggesting that a combination of monitoring methods is recommended for a complete overview of the elasmobranch community in highly dynamic (coastal) environments (Polanco Fernandez *et al.* 2021). eDNA-approaches have been described to resolve the phantom diversity of sharks and rays (Ip *et al.* 2021). However, in our study, no shark species of the genus *Carcharhinus* was detected using the eDNA approach, despite species from the genus being recorded amongst catches of the small-scale fisheries. Moreover, the large majority of eDNA reads assigned to elasmobranchs were assigned to ray species (82.7%). Possible explanations for differences in relative read abundance in eDNA approaches are differences in mobility or site fidelity of species, physiological differences, or the use of the eDNA methodology itself. Sharks are generally thought to move over larger distances compared to benthic ray species (Braccini *et al.* 2016). This may cause DNA concentrations of more mobile species to be low compared to species with high fidelity to the sample site. However, the differences in DNA shedding rates between species can also cause a bias in relative read abundance within marine communities (Tréguier *et al.* 2014, Stewart 2019). Benthopelagic myliobatid rays (i.e., eagle rays) excrete considerably more mucus compared to other elasmobranch species (e.g., guitarfish, sharks) (Meyer and Seegers 2012), possibly causing an imbalance in the detection of rays and shark species when the whole elasmobranch community is studied. However, another likely explanation for the differences could be caused by a lower occurrence of sharks within the archipelago due to their continued exploitation in and outside the archipelago. Differences in relative read abundances may also have a methodological origin. For example, PCR conditions might favor the DNA amplification of specific species (Miya 2022). For this reason, we used two different primers to amplify ray and shark DNA in each sample separately and pooled the PCR products prior to sequencing. The storage time of samples (i.e., time between sample collection and fixation) can influence the read abundance (Eichmiller *et al.* 2016). However, storage time in our study was not correlated with a change in species richness. We emphasize that the translation of relative read abundance to relative species abundance should be done with caution and recommend that - if likely factors influencing relative read abundance are not addressed - eDNA-data should be translated into the presence/absence of species (Tréguier *et al.* 2014, Barnes and Turner 2016, Stewart 2019, Miya 2022).

Implications for elasmobranch monitoring and conservation

The eDNA approach used in our study successfully detected elasmobranch species throughout the study area but failed to detect some species that were detected in the fisheries observer program. Other studies have concluded that the combination of eDNA-approaches with conventional monitoring methods, such as the collection of fisheries data, underwater visual census and (baited) video monitoring, can improve the quality of collected data (Boussarie *et al.* 2018, Budd *et al.* 2021, Ip *et al.* 2021). Conventional methods often underestimate the presence of cryptic and rare elasmobranch species, are selective to specific species (e.g., due to elusiveness or selection bait used), or are less suitable to be used in specific areas (e.g., due to limited underwater visibility or a lack of fisheries to monitor). Hence, the locality of the study area and the elasmobranch community at hand determines which combination of monitoring methods is most appropriate, also considering the objectives of the monitoring program.

Our results suggest that the large majority (54%) of shark and ray species detected in this study are threatened with extinction on a global scale. In addition, in more than half of the samples collected, no shark or ray DNA was detected, and only two shark species were identified based on the eDNA approach: the milk shark and the scalloped hammerhead shark. Elasmobranchs within the wider West African region are at risk of being caught within coastal areas like the Bijagós Archipelago by artisanal small-scale fisheries (Lemrabott 2023, Moore *et al.* 2019) or by industrial fisheries on the outer edges of these areas once certain species leave their coastal habitats (e.g., ontogenetic habitat shifts/migrations) (Zeeberg *et al.* 2006, Leurs *et al.* 2021). The fishing effort of both types of fisheries has increased over the past decade and is a threat to the conservation status of sharks and rays within the wider West African region (Campredon and Cuq 2001, Dossa and Diop 2011, Kroodsma *et al.* 2018).

Our results show that an eDNA approach to elasmobranch monitoring can successfully be used in highly dynamic coastal areas with continued high exploitation of elasmobranchs to address the data deficiency on elasmobranch presence, distribution and community composition. Especially when this method is combined with conventional monitoring methods such as the collection of fisheries-dependent data. The information of this novel combination of techniques provides solid evidence on the distribution and status of threatened shark and ray species that benefits the more effective conservation of remote and highly dynamic coastal ecosystems.

Acknowledgments

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BOX D: SPECIAL OBSERVATIONS IN THE BIJAGÓS ARCHIPELAGO

Over the past five years, our team has studied the sharks and rays of the Bijagós Archipelago. During our expeditions, we worked with local fishers, conducted scientific fishing surveys (i.e., catch and release), interviewed fishers, and conducted landing site and market surveys. Below, we present important observations that have not (yet) been published.

Cryptic and elusive

The African wedgefish (*Rhynchobatus luebberti*) is the only species of wedgefish that occurs within the region (i.e., Mauritania to Democratic Republic of Congo). However, its range and abundance have significantly decreased over the past decades (Kyne and Jabado 2019). However, in March 2021, during our fisheries surveys (i.e., **Chapter 4**) with local researcher Assana Camará, we confirmed the first observation of this species within the waters of the Bijagós since 2006 (**Figure D1**; Moore 2017). This large male African wedgefish was captured near the island of Boloma and measured approximately 180 to 240 cm in total length. The species is likely captured more often in the Bijagós, as fishers referred to this species as 'casapai pintado' (spotted guitarfish) and indicated catching this species in recent years. This suggests that this species still occurs in the Bijagós and that the area may be an important refuge for this critically endangered species.

The relatively large thorny whipray (*Fontitrygon ukpam*) was initially only known from freshwater lakes and rivers from Nigeria to the Democratic Republic of Congo (Last *et al.* 2016). However, in February 2019, we sampled a fishing boat that had just captured four specimens in the (marine) waters around the island of Orango.

Figure D1 The African wedgefish (*Rhynchobatus luebberti*; left) and the thorny whipray (*Fontitrygon ukpam*; right) were captured in the Bijagós Archipelago.

We confirmed species identification by genetic sequencing in collaboration with the Florida Museum for Natural History (i.e., home to the curated database of the Chondrichthyan Tree of Life project). We determined this was a significant range and habitat extension for this species. Based on the known size-at-birth of this species (~30cm disc width), these four individuals represented early life stages (39-44 cm disc width). As a result, this range extension is now included in the latest IUCN Red List assessment of this species, which determined the species to be critically endangered (Jabado *et al.* 2021).

In addition, we confirm that large-bodied sharks are still present within the archipelago. Large (>2m total length) nurse sharks (*Ginglymostoma cirratum*) and tiger sharks (*Galeocerdo cuvier*) were observed during scientific research and landing site surveys. Large bull sharks (*Carcharhinus leucas*) were observed breaching out of the water completely, which has been described to be indicative of feeding behavior in juveniles of the species (Curtis and Macesic 2011).

Newborns and potential nursery areas

Coastal, shallow-water areas lined with mangrove forests such as the Bijagós Archipelago are often important refuge and nursery areas for the early life stages of elasmobranch species (Knip *et al.* 2010). However, the value of the Bijagós as a potential nursery area for sharks and rays remains unclear. Due to a large number of catches of newborn blackchin guitarfish (*Glaucostegus cemiculus*) in shallow-water mangrove habitats over the past years, we can conclude that these mangrove habitats are likely important nursery habitats for this critically endangered species. We regularly captured specimens between 30 to 35 cm in length with remnants of the umbilical cord, indicating birth within the last ~14 days (**Figure D2**; Debaere *et al.* 2023). Blackchin guitarfish can reach a maximum total length of 265 cm (Last *et al.* 2016). Similarly, we captured and documented newborn pearl whiprays (*Fontitrygon margaritella*), blacktip sharks (*Carcharhinus limbatus*), bull sharks (*Carcharhinus leucas*), and scalloped hammerhead sharks (*Sphyrna lewini*) of which umbilical scars were not fully closed (i.e., an indication of birth within the past <36 days, Debaere *et al.* 2023). In addition, we observed pregnant and near-term females of milk sharks (*Rhizoprionodon*) and *Fontitrygon*-species captured within the waters of the archipelago.

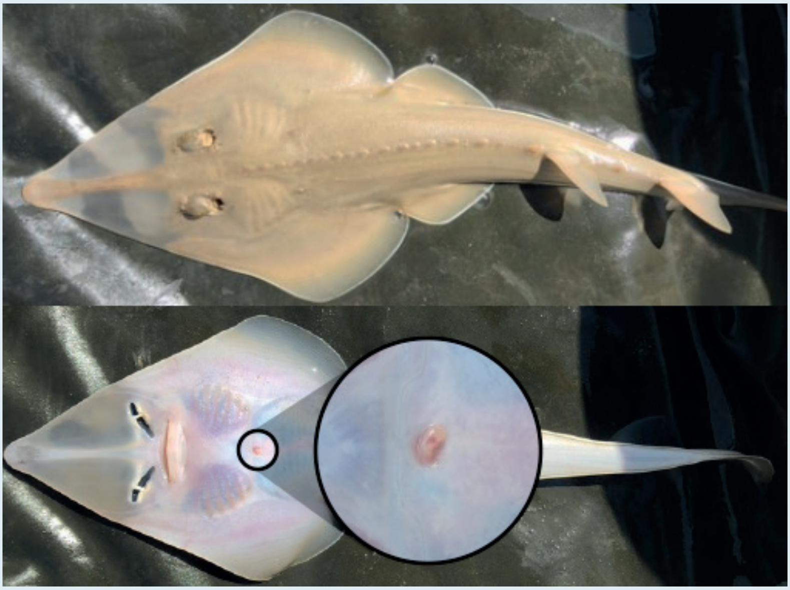

Figure D2 A newborn blackchin guitarfish (*Glaucostegus cemiculus*) with remnants of the umbilical scar visible (bottom).

Chapter 6

Growth, maturity, and diet of the pearl whipray (*Fontitrygon margaritella*) from the Bijagós Archipelago, Guinea-Bissau

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Abstract

The pearl whipray *Fontitrygon margaritella* (Compagno and Roberts 1984) is a common elasmobranch in coastal western African waters. However, knowledge of their life history and trophic ecology remains limited. Therefore, we aimed to determine the growth, maturity and diet of *F. margaritella* from the Bijagós Archipelago in Guinea-Bissau. Growth was modeled using von Bertalanffy, Gompertz and logistic functions. Model selection revealed that no model significantly outperformed another. The sampled age ranged from less than one year to seven years (1.8 ± 1.9 cm, mean ± standard deviation), and size (disc width) ranged from 12.2 cm to 30.6 cm (18.7 ± 5.2 cm). Size-at-maturity was estimated at 20.3 cm (95% CI: 18.8-21.8 cm) for males and 24.3 cm for females (95% CI: 21.9-26.5 cm), corresponding to ages of 2.2 and 3.9 years. The diet differed significantly among young-of-the-year (YOY), juveniles and adults ($p = 0.001$). Diet of all life stages consisted mainly of crustaceans (27.4%, 28.5%, 33.3%) and polychaetes (12.5%, 26.7%, 20.3%), for YOY, juveniles and adults, respectively. This study shows that *F. margaritella* is relatively fast-growing, matures early and experiences ontogenetic diet shifts. These results contribute to status assessments and conservation efforts of *F. margaritella* and closely related species.

Introduction

The abundance of sharks and rays (i.e., elasmobranchs) is often considered an indicator of healthy marine ecosystems, as these species have important ecological roles as top and mesopredators. Their population trends may indicate overexploitation of these species, which can potentially alter ecosystem functioning (Barría *et al.* 2015, Flowers *et al.* 2021, Navia *et al.* 2007, Vaudo and Heithaus, 2011). Determining such population trends requires information about the life history of a species, such as the age-at-maturity, maximum age and growth coefficients (Mejía-Falla *et al.* 2014). A lack of knowledge of life-history parameters can impair the status assessment of elasmobranch species, hampering effective management of these K-selected species (*i.e.*, late maturity, low fecundity and slow growth) (Ismen 2003, O'Shea *et al.* 2013). Furthermore, understanding the trophic ecology of a species is required to determine a species' ecological role within an ecosystem (Vaudo and Heithaus 2011). The trophic ecology of a species can help determine the structuring roles, energy flow, and bioaccumulation of ecological contaminants within an ecosystem (Bowes and Thorp 2015, MacNeil *et al.* 2005). Thus, understanding the life history and trophic ecology of individual species is an essential step in preserving ecosystem functions and services (Coll *et al.* 2013).

Elasmobranch species off the West African coast remain largely unstudied, with the necessary data for population trend analysis and conservation status often missing. This is especially the case for endemic species in the region, like *F. margaritella*. Although this species is one of the most common species in coastal fisheries throughout the region, its life-history characteristics and trophic ecology remain poorly understood (Moore *et al.* 2019). This species ranges from Mauritania to Angola, and it can be found in shallow marine and estuarine soft-bottom habitats (Marshall and Cronin 2016). The maximum attained size is thought to be around 34 cm, and females can have up to 3 pups per litter (Moore *et al.* 2019). Understanding the life history and trophic ecology of *F. margaritella* may also provide broader insights into the biology of other *Fontitrygon*-species, which mostly occur in data-deficient regions off West Africa and the northern coast of South America. Here, we aim to fill a critical knowledge gap surrounding this species by determining the growth, size- and age-at-maturity, and diet of *F. margaritella* from the Bijagós Archipelago in Guinea-Bissau.

Methods

The Bijagós Archipelago comprises 88 islands and islets and is located off the coast of Guinea-Bissau. The archipelago is listed as a UNESCO Biosphere Reserve and RAMSAR site. The coastal zone of the archipelago consists of mangrove forests, soft-bottom intertidal flats, gullies and deep channels. We collected ray specimens between October and December 2019 from artisanal fishers and were caught around Urok (11.4833° N, 15.9667° W), Bubaque (11.2448° N, 15.8701° W), Soga (11.3500° N, 15.8667° W) and Orango (11.2494° N, 162212° W) or from an unknown location within the Bijagós Archipelago (Figure 6.1). All rays were stored in a field freezer (-10°C) until processing. To rule out any misidentification of this species with the related daisy whipray (*Fontitrygon margarita*), we sequenced tissue samples of the pelvic fins for species identification. This was done using the ASNM and ChimeraF primer ("AAGGACTACTTTGATAGAGT" a variant of ILEM) adapted from Naylor *et al.* (2012).

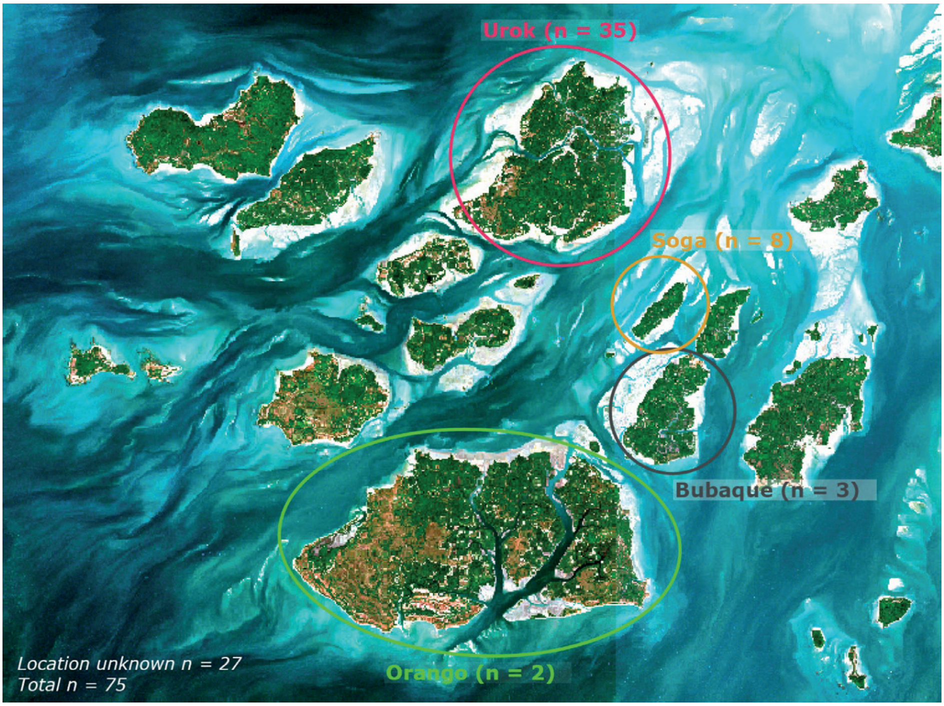

Figure 6.1 Overview of the study sites in the Bijagós Archipelago, Guinea-Bissau. The colors indicate the different sampling regions and their respective sample sizes (purple = Urok, orange = Soga, gray = Bubaque, and green = Orango). Specimens for which the origin within the archipelago could not be confirmed were labeled as 'location unknown'.

Ethical statement

For this study, we collaborated with the local fishing communities within the Bijagós Archipelago. All rays were obtained from catches by local fishers and were solely captured for consumption. After collecting the required samples, all rays were returned to the local communities for consumption. All rays were deceased at the time of sampling. All research and use of animals was conducted with permission and per the regulations of the Instituto da Biodiversidade e das Áreas Protegidas (IBAP), the responsible national institute in Guinea-Bissau (reference number: 396/IBAP/2019 and 393/IBAP/2019).

Age and Growth

For each individual that was sampled, we recorded sex, body size as disc width (DW) and total length (TL) and weight. In addition, five to ten anterior vertebrae were stored in 70% ethanol for each individual. In the laboratory, vertebrae were cleaned by removing excess tissue, after which one vertebra per individual was fixated in clear epoxy resin (Poly-Pox THX 500 resin and Poly-Pox 155 hardener) following the instructions of Campana (2014). A centered sagittal cross-section with a thickness of 500 μm was cut for each vertebra to create a typical 'bowtie' cross-section, which was fixed to a microscope slide and used for aging (see Campana, 2014). Each cross-section was photographed using a compound light trinocular microscope (Zeiss) at 5x10 magnification. As growth band deposition in other dasyatid rays like the blue stingray (*Dasyatis chrysonota*), the brown stingray (*Dasyatis lata*) and the diamond stingray (*Dasyatis dipterura*) is annual. We assumed deposition in *F. margaritella* also to be annual (Cowley 1997, Dale and Holland 2012, Smith and Merriner 2007). Age was determined independently by two researchers by counting growth bands. All age readings that differed were taken out of the analysis. Previously, using a multi-model approach for growth studies has been advocated to incorporate candidate models with alternative characteristics (Smart *et al.* 2016). Hence, the following three growth functions were fitted:

A logistic growth function, adapted from MacKendrick and Kesava (1911):

$$DW_{age} = \frac{DW_{inf}}{1+\left(\frac{DW_{inf}-DW_{birth}}{DW_{birth}}\right)e^{-k\times age}} \tag{1}$$

A Gompertz growth function, adapted from Ricker (1975):

$$DW_{age} = DW_{birth} \times exp\ (ln\ ln\ \left(\frac{DW_{inf}}{DW_{birth}}\right)\ (1 - exp\ exp\ (-k \times age)\ )) \tag{2}$$

A von Bertalanffy growth function, adapted from von Bertalanffy (1938):

$$DW_{age} = DW_{birth} + ((DW_{birth} - DW_{inf}) \times (1 - exp\ exp\ (-k \times age)\ ) \qquad (3)$$

These growth functions describe the relationship between age and body size (disc width; DW), with the asymptotic disc width DW_{inf}, the size at birth DW_{Birth}, the growth coefficient k, the estimated age based on vertebrae growth band counts (age), and the predicted size-at-age DW_{age}. Parameters were estimated using Bayesian MCMC models (Bürkner 2017, 2018).

The prior values for size at birth (10 cm) and maximum disc width (34 cm) are based on data recorded by Moore *et al.* (2019) and given a lognormal prior as these were positive parameters. Hence, for the size at birth (DW_{Birth}) prior, a lognormal distribution of 10 and a standard deviation of 1 was used. For the maximum disc width prior, a lognormal distribution of 34 and a standard deviation of 1 was used for the maximum disc width prior. Lastly, for the growth coefficient (k), a prior with a normal distribution of -1 and a standard deviation of 1 was used. For each model, four chains were run with 3500 iterations each, including 1000 discarded warm-up iterations, so a total of 10000 iterations were sampled for each model. Effective sample sizes for each model parameter exceeded 1000. Convergence and mixing of chains were monitored with trace plots and R-hat statistics. Model performance was compared using the leave-one-out cross-validation using the 'loo' R-package (Vehtari *et al.* 2017, Yao *et al.* 2018).

Table 6.1 Developmental stages of reproductive organs used to assess maturity stage (immature or mature). Adapted from Osaer *et al.* (2015).

Sex		***Immature***	***Mature***
Female	**Ovaries**	Not distinguishable	Distinguishable
	Follicles	Underdeveloped or in groups with different sizes	Well-developed or atretic and vitellogenic
	Uteri	Between tubular and wide in shape with developed walls	Tubular to wide in shape, developed walls, possibly with embryos
	Epigonal organ	Predominant	Present
Male	**Testis**	Lobulated, low blood supply	High volume, lobulated, increased blood supply
	Ductus deferens	Barely or not undulated	Strongly undulated
	Epigonal organ	Present	Limitedly present

Maturity

We determined the maturity stage as either 'immature' or 'mature'. Females are regarded as mature when epigonal organs are present, ovaries contain well-developed follicles of similar sizes or are atretic and vitellogenic in groups or singular, and uteri are tubular to wide in shape, with developed walls or with distinguishable embryos. Lastly, males are regarded as mature when a little epigonal organ is present, testis have a high volume, are fully lobulated with increased blood supply or pale and decreased in size, and ductus deferens is strongly undulated. Individuals were regarded as immature if their reproductive organs were less developed than described above. Table 6.1 provides short descriptions used to determine the maturity stage. To calculate the median disc width at maturity (DW_{50}) for both sexes combined and separated, we used the following logistic maturity formula (Mollet *et al.* 2000):

$$Y = (1 + e^{-(a+bX)})^{-1} \tag{4}$$

Median size at maturity is calculated using Equation (5) similarly, for this model, 3,500 iterations and 1000 warm-up iterations were used. The priors used were uninformative, namely 10 following a normal distribution with a standard deviation of 5 for both a and b, as this could not be based on previous values.

$$DW_{50} = -a/b \tag{5}$$

Diet

The stomachs of sampled specimens were removed and weighed before determining stomach contents. Excess moisture was removed from stomach contents using paper towels to remove weight bias by stomach fluids. Stomach contents were sorted into one of six categories: crustaceans, polychaetes, bivalves, other mollusks, teleosts or unidentified (unrecognizable prey items). Appendix 6.1 provides a representative photo of each taxa encountered in stomach contents. These taxa categories were not defined prior to data collection but based on prey items encountered due to the lack of description for benthic species from our study area. We recorded the number of prey items and mass for each group to the nearest centigram. To prevent bias of large prey items, we calculated the diet composition using the index of importance (IOI) as proposed by Gray *et al.* (1997). First, the percentage of each prey group relative to the body weight of the individual ($\%W_a$) was calculated as:

$$\%W_a = (100 \times W_a)/W_{body} \tag{6}$$

where W_a is the sum weight of prey group a (Gray *et al.* 1997).

Secondly, the frequency of occurrence for prey group a ($\%F_a$) was calculated as:

$$\%F_a = (100 \times S_a)/S \tag{7}$$

where S_a is the number of stomachs containing for a given prey group, and S denotes the total number of stomachs containing food (Hyslop, 1980).

Lastly, the index of importance for each prey group (IOI_a) was calculated as:

$$IOI_a = 100 \times \ HI_a / \sum_{a=1}^{n} HI \tag{8}$$

with:

$$HI_a = \%F_a + \%W_a \tag{9}$$

Diet composition was analyzed for three different life stages: YOY (individuals < 1 year of age), juveniles (individuals >= 1 year, but have not reached DW_{50}) and adults (mature individuals, > DW_{50}). Raw data is provided in Appendix 6.2. We performed a PERMANOVA (R-package ‘vegan’) (Oksanen *et al.* 2020) and a pairwise Adonis function (Martinez Arbizu, 2016) to determine which life stages differ in their diet composition.

Results

A total of 75 individual *F. margaritella* were sampled, consisting of 38 males and 37 females (0.5:0.5 m:f ratio) ranging from 12.2 to 30.6 cm DW and body mass ranging from 59 to 1,208 g.

Age and growth

71 Individuals (m = 38, f = 33) were used for size-at-age analysis. Measured disc widths ranged from 12.2 cm to 30.6 cm (18.7 ± 5.1 cm), and age ranged from less than one to seven years (1.8 ± 1.9 years). All three growth functions estimated similar values for disc width size-at-birth: 13.87, 14.01 and 14.01 cm (von Bertalanffy, Gompertz and Logistic growth functions, respectively). Maximum disc width estimates varied between the three growth functions. The logistic growth function estimated a maximum disc width of 34.46 cm, close to the observed maximum size of 34 cm, recorded by Moore *et al.* (2019), whereas the von Bertalanffy function estimated 44.70 cm and the Gompertz function 38.09 cm (Table 6.2). Model selection showed that no model outperformed any of the others based on LOO information criterion (LOOIC) (Table 2). However, there is likely little reliable difference in the predictive capability between these models, as the difference in LOOIC values was less than two between all models. When considering the maximum reported size by Moore *et al.* (2019) to be 34 cm as the maximum disc width, *F. margaritella* individuals seem to reach their maximum size between 10 and 12 years (Figure 6.2). Additionally, *F.*

margaritella seems to attain between 40.3% and 64.7% of their maximum disc width within their first year, based on the largest and smallest rays of one year old.

Table 6.2 Model and model selection estimates for the von Bertalanffy, Gompertz and the logistic growth function. (n) sample size for size at age analysis. (LOOIC) LOO information criterion. (SE) standard error of the LOOIC values. (DW_∞) asymptotic disc width. (DW_{Birth}) disc width at birth. (K) growth rate. (95% CI) credible interval.

Model	n	LOOIC	SE	DW_∞ (cm)	95% CI DW_∞	DW_{BIRTH} (cm)	95% CI DW_{BIRTH}	K $(year)^{-1}$	95% CI K
Von Bertalanffy function	71	278.7	14.2	44.7	33.1 - 75.2	13.9	13.3 - 14.4	0.1	0.04 - 0.2
Gompertz function	71	279.4	14.8	38.1	30.9 - 55.1	14.0	13.3- 14.6	0.2	0.1- 0.3
Logistic function	71	280.1	15.1	34.5	29.4 - 44.2	14.0	13.5 - 15.0	0.3	0.2 - 0.4

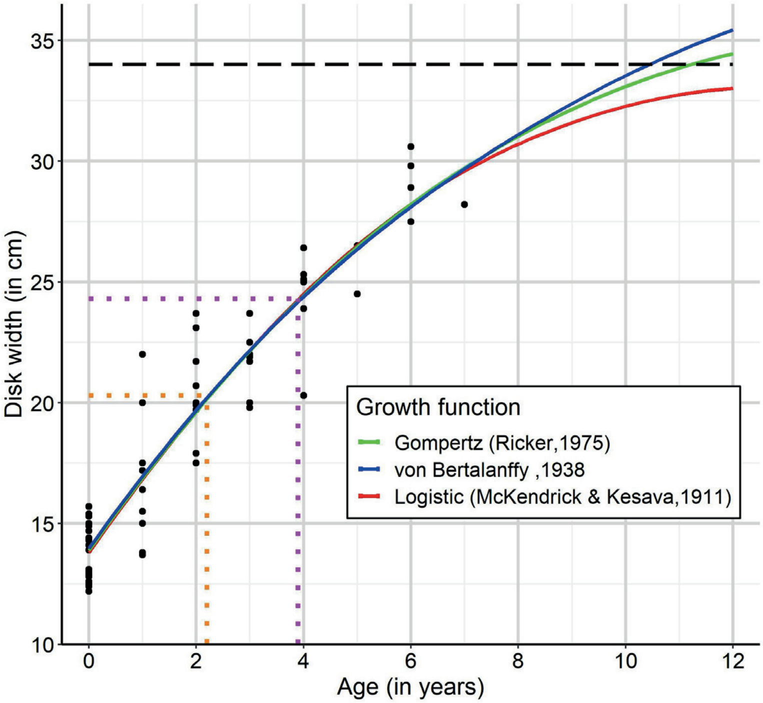

Figure 6.2 Growth functions fitted to size-at-age data of *F. margaritella* (Gompertz curve in green, von Bertalanffy curve in blue and the logistic growth curve in red). The horizontal dashed line represents the maximum reported disc width of 34 cm (Moore *et al.* 2019). The median disc width at which males reach maturity (DW_{50}) is shown in orange (DW = 20.3 cm, age = 2.2 years old) and magenta for females (DW = 24.3 cm, age = 3.9 years old).

Maturity

We determined the maturity stage of 69 individuals (m = 35, f = 34). Of six individuals, the reproductive state was unclear due to fishery-related damages or (partial) decomposition of organs. The disc width of the largest sampled immature male was 23.7 cm, and the largest immature female had a disc width of 30.6 cm. Based on the binomial logistic regression, median size-at-maturity is reached at 20.3 cm DW (CI 95% 18.8-21.8 cm) for males and 24.3 cm DW (CI 95% 21.9-26.5 cm) for females (Table 6.3). Based on the von Bertalanffy growth function, this size-at-maturity corresponds with an age-at-maturity of 2.2 and 3.9 years for males and females, respectively.

Table 6.3 Summary of size-at-maturity parameter estimates and 95% credible interval (CI) values for males, females, and both sexes combined.

Sex	a	95% CI	b	95% CI	DW_{50}	95% CI
Male	-9.05	-13.91 – -4.94	0.45	0.24 – 0.70	20.1	18.8 – 21.8
Female	-8.29	-13.07 – -4.82	0.36	0.21 – 0.57	23.0	21.9 – 26.5
Combined	-9.01	-12.99 – -5.95	0.43	0.28 – 0.61	21.0	19.7 – 22.3

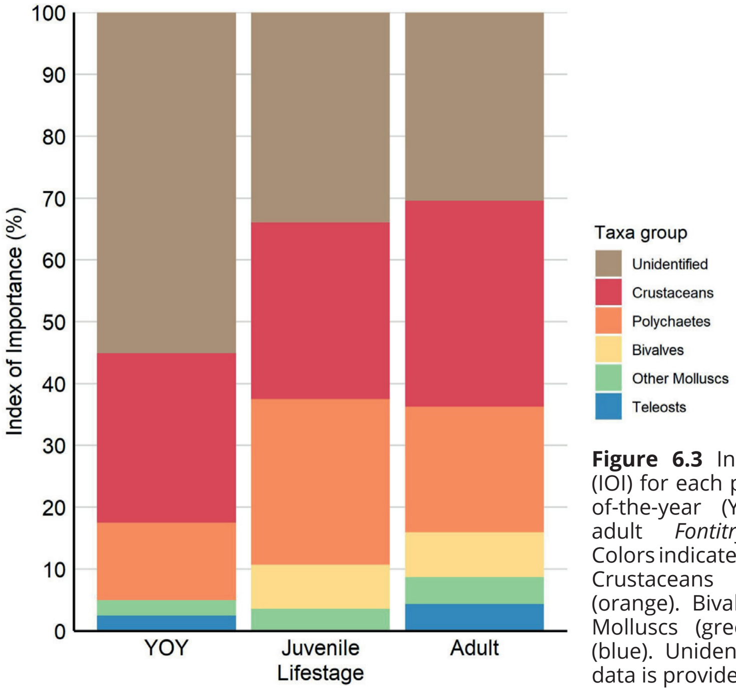

Figure 6.3 Index of Importance (IOI) for each prey taxa for young-of-the-year (YOY), juvenile and adult *Fontitrygon margaritella*. Colors indicate the prey group taxa. Crustaceans (red). Polychaetes (orange). Bivalves (yellow). Other Molluscs (green). Teleost fishes (blue). Unidentified (brown). Raw data is provided in Appendix 6.2.

Diet

For diet analysis, we used a total of 65 stomachs sampled (1.19 ± 1.25 g). We identified 22 individuals as young-of-the-year (YOY; <1 year of age), 19 as juvenile (>= 1 year of age and smaller than DW_{50}) and 24 as adults (>= DW_{50}). Based on the Index of Importance, the same prey species made up the majority of *F. margaritella's* diet across all life stages: crustaceans: 27.4%-33.3%, polychaetes: 12.5%-26.7%, Bivalves: 12.5-20.3, other mollusks: 0%-7.2%, Teleosts: 0%-4.3%, and unidentified prey: 30.4%-55.0% (Figure 6.3). Besides unidentified prey, crustaceans and Polychaetes were the most common prey items for all age classes in terms of mass and number of individual prey (Table 6.4).

Diet composition differed significantly between life stages (PERMANOVA DF = 2, sum of squares = 2.3, F = 22.6, R^2 = 0.27 p = 0.001), and a post-hoc test revealed that all life stages have a significantly different diet composition (YOY-Juveniles: F = 7.8, R^2 = 0.1, p = 0.002) (YOY-Adults: F = 17.2, R^2 = 0.28, p = 0.001) (Juveniles-Adults: F = 6.0, R-squared = 0.1, p = 0.001.

Table 6.4 Summary of the total mass (grams), total count (n) and percentage of stomachs that contained crustaceans and polychaetes for young-of-the-year (YOY), juveniles and adults.

	YOY	Juvenile	Adult
Crustaceans mass (g)	0.8	3.5	17.5
Crustaceans count (n)	224	270	331
Nr. stomachs (%)	50	84.2	95.8
Polychaetes mass (g)	1.0	1.4	5.5
Polychaetes count (n)	68	99	331
Nr. stomachs (%)	22.7	78.9	58.3

Discussion

Elasmobranchs are still subject to fisheries in the coastal waters of West Africa despite their vulnerability to fishing (Moore *et al.* 2019). Understanding the life history and trophic ecology of elasmobranch species is essential for the risk assessment of both these species and the ecosystems in which they often play a key role. This study is the first to present detailed data about the growth, median size-at-maturity and diet of the poorly studied *F. margaritella* in the Bijagós Archipelago, Guinea-Bissau.

Based on the growth curves of *F. margaritella,* it seems to achieve the maximum recorded disc width size of 34 cm between 10 and 12 years. Surprisingly, the maximum age of our sampled specimens was only 7 years (n=1). One-year-old *F. margaritella* are between 40.3% and 64.7% of their maximum disc width, comparable to the fast-growing Roger's stingray (*Urotrygon rogersi*) (Mejía-Falla *et al.* 2014). In addition, a slow-growing batoid species (*Dasyatis fluviorum*) has been observed to have a growth coefficient of around 0.03 year^{-1} (Pierce and Bennett 2010), which is around a third of the growth coefficient observed for *F. margaritella* of 0.10 year^{-1}. The growth rate that we found is comparable to other fast-growing species, such as Roger's stingray (*Urotrygon rogersi*), Kuhl's maskray (*Neotrygon kuhlii*) and the Diamond stingray, which is between 0.1 and 0.24 year^{-1} (Mejía-Falla *et al.* 2014, Temple *et al.* 2020).

Our study indicates that in the Bijagós Archipelago, male *F. margaritella* mature earlier than females. This has also been confirmed in other ray species, such as the brown stingray (*Dasyatis lata*) and the common stingray (*Dasyatis pastinaca*; Ismen 2003, Dale and Holland 2012). This sex difference in size at maturity can have several possible causes. For instance, this could be related to male biting behavior during reproduction, which is common in many elasmobranch species (Kajiura *et al.* 2000). Unlike males, large females of Haller's round ray (*Urolophus halleri*) have been observed to obtain a relatively thicker disc with increased disc width, which may help minimize damage from male reproductive biting behavior (Nordell 1994). Alternatively, larger females are thought to produce larger litters and, therefore, have a greater reproductive output (Lyons *et al.* 2017), which could be a reason female *F. margaritella* mature later and at a larger body size. Perhaps a more likely explanation may be that size-at-maturity may also vary based on the increased energetic expenditure during the gestation period (Goodwin *et al.* 2002). Females of *F. margaritella* reach maturity at around 32.5% of their lifespan, and males reach maturity at around 18.3% (considering a maximum age of 12 years). This is similar to other species, such as the Kuhl's maskray (*Neotrygon kuhlii)* and the blackspotted whipray (*Maculabatis gerradi)*, which mature between 19-41% of their lifespan (Temple *et al.* 2020). However, whether size-at-maturity differs in other areas remains unknown. Our estimates of male and female median size-at-maturity should be interpreted cautiously due to low sample sizes. However, a study on Baraka's whiprays (*Maculabatis ambigua*) by Temple *et al.* (2020) provided an accurate estimate for size-at-maturity for males based on a low sample size. Furthermore, the approximation of male maturity by Last *et al.* (2016) (~21 cm DW) differs only 7 mm (0.3%) from our estimation and is within the range of our 95% credible interval (18.8-21.8 cm), supporting our median size-at-maturity estimations for male *F. margaritella.*

Additionally, the gestation period and frequency need verification to assess the reproductive rate of *F. margaritella*, as this is thought to vary within the family of

Dasyatidae (Carlson *et al.* 2020, Notarbartolo di Sciara *et al.* 2015). Hence, a well-rounded comprehension of the life history of *F. margaritella* gestation period and frequency should also be studied.

We found that the diet of *F. margaritella* within the Bijagós Archipelago consisted mostly of crustaceans and polychaetes. This indicates that *F. margaritella* acts as a small, low trophic-level meso-predator that links benthic communities with top predators in the Bijagós Archipelago. The presence of teleost items in the stomach contents of *F. margaritella* suggests that the species occasionally consumes teleost prey, as observed in other batoid species (Lim *et al.* 2019, Farias *et al.* 2006). Whereas other studies show that batoids ontogenetically include more teleost prey (Gray *et al.* 1997, Lim *et al.* 2019, Farias *et al.* 2006), in our study one YOY was observed to have consumed small teleost prey. The high proportion of unidentified prey encountered likely results from soft-bodied prey (e.g., polychaetes and small crustaceans), which may digest faster (Farias *et al.* 2006). The unidentified prey items could also be inorganic matter, sediment and plant matter ingested during prey consumption (Ajemian and Powers., 2011). DNA metabarcoding on stomach contents could improve estimates of prey abundance and, combined with environmental DNA analysis of benthos, may highlight prey preference (Harms-Tuohy *et al.* 2016). We found that *F. margaritella* undergoes an ontogenetic diet shift, and adults seem to incorporate more diverse prey into their diet, such as teleosts and a higher abundance of crustaceans, possibly giving older individuals a slightly higher trophic level. Ontogenetic diet shifts could result from changes in teeth morphology, jaw teeth strength, body size and sensory sensitivity of the peripheral (Smith and Merriner 1985, Nordell 1994, Kempster *et al.* 2013, Lim *et al.* 2019). Ontogenetic diet shifts may also result from different energetic needs and local prey availability coinciding with ontogenetic differences in distribution (Lim *et al.* 2019). Regardless, ontogenetic diet shifts could suggest that different life stages fulfill different trophic roles and affect food webs differently.

Comprehensive knowledge of the life history and ecology of a species is necessary to establish adequate conservation efforts (Ismen 2003, O'Shea *et al.* 2013). With many elasmobranch populations declining globally, the need for insight into their life history and trophic ecology for conservation increases. This study presents one of the first known estimates for growth, median size-at-maturity, and diet composition of *F. margaritella*. Compared to other ray species, *F. margaritella* seems to be a fast-growing and early-maturing species. The diet description presented in this paper may provide preliminary insights into their trophic role in the coastal ecosystems of West Africa. Additionally, fishing intensity, natural mortality rate and recruitment rate of *F. margaritella* require study to assess fishing vulnerability (Le Quesne and Jennings 2012). This study contributes to the knowledge of *F. margaritella*, a commonly exploited elasmobranch species in the West African region, and may help conservation efforts of similar species.

Conclusions

F. margaritella is a small, fast-growing ray species, reaching maturity after 2.2 and 3.9 years for males and females, respectively. The diet of this species within the Bijagós Archipelago consists primarily of polychaetes, but the contribution of harder prey species (e.g., crustaceans) increases ontogenetically. This study presents the first description of the growth, median size-at-maturity and diet of *F. margaritella*, which is needed for science-based management of coastal fisheries and ecosystems. These results fill an important knowledge gap on the life history and trophic ecology of this species and this data-deficient genus of whiprays.

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SECTION III

Species Interactions

Chapter 7

Where land meets the sea: intertidal areas as key-habitats for sharks and rays

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Abstract

Intertidal habitats (i.e., marine habitats that are (partially) exposed during low tide) have traditionally been studied from a shorebird-centered perspective. We show that these habitats are accessible and important to marine predators such as elasmobranchs (i.e., sharks and rays). Our synthesis shows that at least 43 shark and 45 ray species, of which 54.5% are currently threatened, use intertidal habitats. Elasmobranchs use intertidal habitats mostly for feeding and as refugia but also for parturition and thermoregulation. However, the motivation for intertidal habitat use remains unclear due to limitations in observing elasmobranch behavior in these dynamic habitats. We argue that elasmobranch predators can play an important role in intertidal food webs by feeding on shared resources during high tide (i.e., "high-tide predators"), which are accessible and also consumed by terrestrial or avian predators during low tide (i.e., "low-tide predators"). In addition, elasmobranchs are able to change the bio-geomorphology of intertidal habitats by increasing habitat heterogeneity due to feeding activities, which may also alter resource availability for other consumers. We discuss how the ecological role of elasmobranchs in intertidal habitats is being affected by the continued overexploitation of these species and, conversely, how the global loss of intertidal areas poses an additional threat to an already vulnerable taxonomic group. We conclude that studies on intertidal ecology should include both low-tide (e.g., shorebirds) and high-tide (e.g., elasmobranchs) predatory guilds and their ecological interactions. The global loss of elasmobranch predatory species and intertidal habitat provides additional compelling arguments for the conservation of these areas.

Introduction

Coastal habitats are vital to both coastal and oceanic marine species, like marine mammals, teleost fishes and elasmobranchs (i.e., sharks and rays). Coastal reefs, estuaries, saltmarshes and soft-bottom flat habitats play an important role in the life cycle of many species, for example, as nursery habitats for early life stages, feeding areas, or sites for mating or spawning/parturition (Knip *et al.* 2007, Sievers *et al.* 2019). Among coastal habitats, the intertidal harbors some of the most dynamic habitats in the world. The intertidal is the transition zone between land and sea, between low and high tide levels, where the same habitat is exposed during low tide and submerged during high tide (Figure 7.1A). With global distribution, intertidal ecosystems deliver important ecosystem services, such as food production and coastal protection (Koch *et al.* 2009, Beninger 2019, Murray *et al.* 2019). However, intertidal ecosystems are threatened by coastal development, rising sea levels, and coastal erosion. Since 1984, approximately 16% of the global areal of intertidal flat areas has been lost (Murray *et al.* 2019). The ongoing degradation of these habitats threatens its associated species, some of which already face significant anthropogenic disturbances like overexploitation, pollution, and climate change (Lotze *et al.* 2006, Halpern *et al.* 2008, Pendleton *et al.* 2012, Lu *et al.* 2018).

Intertidal habitats are constantly influenced by the rhythm of the tide. Compared to (sub)tidal habitats, which are always submerged, species using the intertidal face additional challenges and constraints as a result of the never-ending cycle of the incoming and receding tide (Figure 7.1).

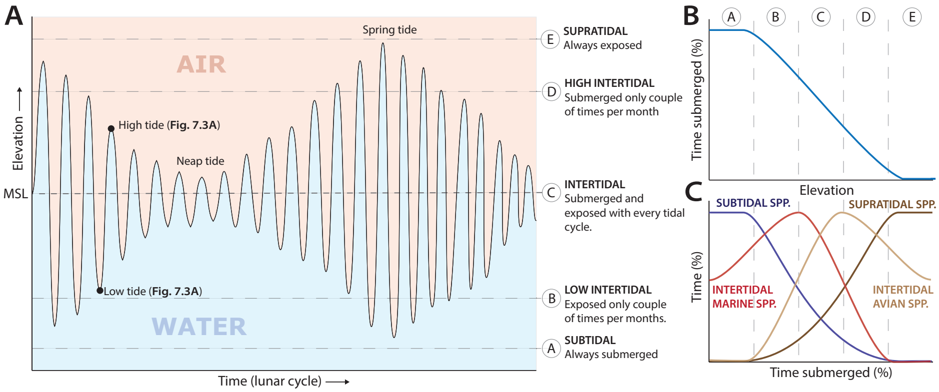


Figure 7.1 Intertidal habitats are strongly influenced by the tide, being submerged and exposed at least once per day (A). Compared to subtidal (i.e., always submerged habitat) or supratidal habitats (i.e., always exposed habitat), intertidal habitats are submerged for a certain amount of time each day (B). These habitats are used by species adapted to these challenges, such as mobile sharks, rays, and teleosts, which use intertidal habitats during high tide and wading shorebirds, which use the same habitat during low tide (C). Larger-bodied sharks, rays and teleosts are restricted to subtidal habitats.

Intertidal habitats are only exposed or submerged for a certain period of time, depending on the elevation of the habitat and the local tidal regime. For example, high intertidal habitats such as saltmarshes are only submerged occasionally, whereas habitats like intertidal flats and mangroves are often exposed for a certain number of hours each day (Figure 7.1). These changes in tidal phases are often influenced by strong hydrodynamic forces and severe changes in temperature and/or salinity (e.g., Smith 1956. Hernandez *et al.* 2002). The interplay of tides in areas bordering land and sea makes these habitats accessible to both marine and terrestrial/avian species (Figure 7.1C).

The value of intertidal habitats has been recognized for species groups such as migratory wading birds (Piersma *et al.* 1993, Deppe, 1999), marine mammals (Vermeulen 2018, Wilson and Jones, 2018), teleost fishes (Deppe 1999, Gibson and Yoshiyama 1999) and even for some terrestrial mammals (Carlton and Hodder, 2003). For instance, migratory wading birds use intertidal flats as stop-over sites between wintering and breeding grounds along their migratory flyways as feeding areas to profit from the high availability of benthic prey species (Zwarts *et al.* 1990, Piersma *et al.* 1993). Marine mammals such as small cetaceans and pinnipeds use intertidal habitats for feeding (Vermeulen, 2018) and for resting (Wilson and Jones, 2018), whereas terrestrial mammals benefit from the extra feeding opportunities that intertidal habitats provide (Carlton and Hodder, 2003). During high tide, marine species such as teleost fishes use intertidal habitats for feeding, refuge, and as a nursery habitat (Gibson 1986, Gibson and Yoshiyama 1999). This often includes the early life stages of many commercial and pelagic fish species (Rangeley and Kramer 1995, Jin *et al.* 2007).

Although the importance of coastal and nearshore habitats to elasmobranch species is generally well understood (Heithaus *et al.* 2010, Knip *et al.* 2010), less is known about the use of tidal habitats (i.e., habitats strongly influenced by tidal water movements). Furthermore, knowledge of intertidal habitat use (i.e., habitats that are only available during a certain phase in the tidal cycle due to exposure) is often completely absent or remains undocumented. This is surprising, as these species may play an essential role in the functioning of these marine ecosystems (Heupel *et al.* 2014, Atwood *et al.* 2015), and intertidal habitats potentially allow elasmobranchs to indirectly interact with other (terrestrial and/or avian) predator guilds.

Ecosystem functioning (i.e., defined as the fluxes of material and energy within an ecosystem (Brandl *et al.* 2019)) is sustained by species interacting within food webs and their abiotic environment (Boero and Bonsdorff, 2007, Brandl *et al.* 2019).

Keystone species often play an important role in the functioning of ecosystems by maintaining the diversity and structure of ecological communities (Mills *et al.* 1993, Power *et al.* 1996). Within marine food webs, large-bodied, mobile sharks have been recognized as top predators (Heupel *et al.* 2014, Navia *et al.* 2016), and smaller shark and ray species often occupy meso-predatory positions (Navia *et al.* 2016). Both top-predatory sharks and meso-predatory rays have been identified as having keystone roles in coral reef and intertidal habitats, respectively (Power *et al.* 1996, Heithaus *et al.* 2010, Ruiz and Wolff 2011). According to recent estimates, 31% of all shark species and 36% of all ray species are currently threatened with extinction (Dulvy *et al.* 2021), jeopardizing their key role in the functioning of marine ecosystems (Ferretti *et al.* 2010, Atwood *et al.* 2015, Hammerschlag *et al.* 2019).

We aimed to address the knowledge gaps surrounding the intertidal habitat use of elasmobranchs. We provide a global synthesis of available information on intertidal habitat use by sharks and rays in order to describe how these species use these habitats and to conceptualize how these habitats allow elasmobranchs to interact with other (low tide) predatory guilds. Specifically, we aimed to (1) describe which elasmobranch species and which life stages of their populations use intertidal habitats and for what purpose, (2) describe novel perspectives on how sharks and rays potentially interact with other species and predator guilds, with a focus on potential trophic interactions between different predatory guilds using intertidal habitats, and (3) discuss how the removal of sharks and rays from these areas could undermine the functioning of intertidal ecosystems and their communities, and conversely how the loss of intertidal habitats could affect sharks and rays.

Methods

To identify literature describing the intertidal habitat use by elasmobranchs, we performed a literature search on the Web of Science. This literature search was conducted using a combination of the search terms “elasmobranch*”, “shark*”, “ray*”, “skate”, “batoid*”, and “chondrichthyan*” with “tidal*” and “intertidal*”. After deleting irrelevant studies (i.e., studies outside the scope of this study), this search resulted in 150 studies. Secondly, we included additional literature based on the initial literature search by following the snowball principle (see Lecy and Beatty 2012), resulting in a total of 403 studies to be included in our review process. Each study was assessed by two different researchers and was only included if the study described elasmobranchs utilizing intertidal habitats, defined as shallow coastal habitats that are influenced by the tidal cycle, that emerge during low tide and are submerged during high tide (i.e., differing from tidal habitats that are not necessarily exposed during low tide; Table 7.1). These habitats included soft-bottom mudflats and sandflats, including beaches, and vegetated soft-bottom flats (e.g., intertidal seagrass beds, mangroves or saltmarshes), and hard-bottom reef flats that are exposed for a certain time of the day (i.e., depending on the tidal regime and lunar cycle). Additionally, we added studies that describe species utilizing tide pools, tidal creeks and channels that connect intertidal flat habitats, such as within large intertidal mangrove and saltmarsh areas (Table 7.1). We excluded studies for which it was uncertain if the focal species used the intertidal part of the study, resulting in a conservative selection of 119 publications describing the intertidal habitat use of elasmobranchs. For each study, we then extracted observations of species using one or more of the defined habitats. For each species, we then described all defined habitats for which habitat use of that species was documented, which life stages of the species use these habitats, and which behavior was observed or hypothesized to motivate their intertidal habitat use (Appendix 7.4). Habitats were classified according to their definitions (Table 7.1).

Table 7.1 Definitions of intertidal habitats, with differentiation of soft- and hard-substrate flats, tidal creeks and tidal pools. Definitions were based on Rafaelli and Hawkins (1999), Mitra and Zaman (2016), and Kaiser *et al.* (2020).

Intertidal habitat: shallow coastal habitat that is influenced by the tidal cycle, emerging during low tide and submerged during high tide.	
Soft-bottom flats	Sand or mud flats are regularly exposed during low tide while submerged during high tide. This includes vegetated soft-bottom flats (e.g., intertidal seagrass, mangroves or salt marshes).
Reef flats	Coral or rocky reef flats are regularly exposed during low tide while submerged during high tide.
Tide pools	A water body isolated during low tide and (partially) connected with surrounding waters during high tide. These include tide pools and tidal lagoons.
Tidal creeks and channels	Creeks and channels that are dependent on tidal flow and connect or flow through intertidal areas. Creeks and channels can partially or completely fall dry during low tide.

In instances where a study described a species using multiple intertidal habitats, all used habitats were recorded. Life stages (when specified) were classified as neonates, young-of-the-year (YOY), juveniles, or adults. If multiple life stages of a species were documented to use a habitat, all were documented. We classified behavior into four non-exclusive categories: feeding, refuge, reproduction and thermoregulation. If more than one motivation for intertidal habitat use was hypothesized in the study, all of these motivations were recorded. We classified feeding behavior if the authors could determine that the species used the habitat for foraging or predation. Reproduction indicates that the area was used for mating, parturition, or egg-laying, and thermoregulation was used if the authors indicated the elasmobranch species used the area to regulate their body temperature.

Intertidal habitat use by sharks and rays

We selected 119 studies from 20 different countries covering six continents that adequately described elasmobranchs utilizing intertidal habitats (Appendix 7.1, 7.4). The large majority of studies were conducted in Oceania (62.5%) and North America (23.3%), whereas the lowest number of studies were conducted in South America (1.7%), Africa (4.7%), and Europe (0.4%). This contrasts with the global distribution of both intertidal areas and elasmobranch species. The majority of intertidal habitats are located in East Asia (e.g., China, Malaysia) and Western Europe (Murray *et al.* 2019, 2022), whereas global hotspots for coastal shark and ray biodiversity are located off the northern and eastern coast of Australia, the Indo-West Pacific, Japan, China, Taiwan, the southwest Indian Ocean and western Africa (Stein *et al.* 2018, Derrick *et al.* 2020, Dulvy *et al.* 2021). These differences are likely due to the relatively higher number of elasmobranch-focused studies conducted in Australia and the United States (Momigliano and Harcourt, 2014) or due to limited (published) research in other regions due to economic (e.g., limited resources and capacity) and social barriers (e.g., limited integration and of non-English researchers) (Graham *et al.* 2022). This imbalance maintains existing knowledge gaps related to the ecology of elasmobranchs within large intertidal areas, such as the trophic ecology and spatiotemporal use of intertidal habitats, and generally how these habitats contribute to the overall fitness of a (specific life stage of) elasmobranch species. The lack of studies on intertidal habitat use of elasmobranchs in European waters can be caused by the great decline that these species experienced in the region due to overfishing and habitat degradation. For example, once common, elasmobranch species are now rare in the Wadden Sea, the largest intertidal area in the world (Wolff 2005).

Species using intertidal habitats

Selected studies describe a total of 232 observations of elasmobranch species using intertidal habitats, with the number of observations divided equally among sharks (n = 116) and rays (n = 116). Observations describe intertidal habitat use of 88 elasmobranch species belonging to 25 different families (Figure 7.2). The three most frequently described species are the blacktip reef shark (*Carcharhinus melanopterus*, Carcharhinidae; n = 15), sicklefin lemon shark (*Negaprion acutidens*, Carcharhinidae; n = 9), and the giant shovelnose ray (*Glaucostegus typus*, Glaucostegidae; n = 9). Most species described in the selected studies belonged to the families of requiem sharks (Carcharhinidae, 31.9%), stingrays (Dasyatidae, 23.3%), sawfishes (Pristidae, 6.0%), hammerhead sharks (Sphyrnidae, 4.3%), and houndsharks (Triakidae, 4.3%).

Early life stages use intertidal habitats more compared to adult elasmobranchs (Appendix 7.2A). The high percentage of neonates (7.4%), young-of-the-year (YOY, 5.3%), and juveniles (38.5%) compared to adults (25.7%) using the intertidal suggest that these habitats are important habitats for early life stages of elasmobranchs, providing both refuge and feeding opportunities. The discrepancy between juveniles and adults using intertidal habitats is more evident for large-bodied shark species (e.g., requiem sharks, hammerhead sharks and nurse sharks, Ginglymostomatidae) compared to small-bodied sharks (e.g., houndsharks and longtailed carpetsharks, Hemiscyliidae) and rays (e.g., stingrays). This suggests that intertidal habitats may be an important component of coastal nursery areas of these species to minimize the risks posed by adult conspecifics or other predators (Heupel *et al.* 2007, Speed *et al.* 2010, Martins *et al.* 2014). Previous studies underline the importance of nearshore habitats for the early life stages of sharks (Knip *et al.* 2010, Chin *et al.* 2016) and rays (Vaudo and Heithaus 2012, Martins *et al.* 2018). These results show that early life stages possibly rely more on intertidal habitats than adult elasmobranchs.

Elasmobranchs were mostly documented in soft-bottom intertidal habitats (56.9%), with most observations being stingrays (31.8%, Dasyatidae) and requiem sharks (22.9%, Carcharhinidae) (Appendix 7.2B). Tidal creeks and channels were mostly used by requiem sharks (61.9%), and sawfishes (11.9%), and reef flats were mostly used by requiem sharks (41.2%, Carcharhinidae), stingrays (23.5%, Dasyatidae), and longtailed carpetsharks (14.7%, Hemiscylliidae). Tidal pools and lagoons (4.0%) were documented to be used by species like the blacktip reef shark, nurse shark (*Ginglymostoma cirratum*, Ginglymostomatidae), and shortnose guitarfish (*Zapteryx brevirostris*, Trygonorrhinidae).

Sharks and rays use the productive intertidal mainly for feeding but also as refuge, reproduction and thermoregulation (Figure 7.3A). Elasmobranch species use these highly dynamic habitats as soon as these become available with the incoming tide, moving in from connected habitats. Utilization of intertidal habitats by elasmobranchs peaks during high tide (Ackerman *et al.* 2000, Matern *et al.* 2000, Campos *et al.* 2009, Carlisle and Starr 2010). During receding tide, elasmobranchs move to adjacent (edge) habitats such as the shallow subtidal, tidal creeks or channels to seek refuge or to feed during the low tide phase (Campos *et al.* 2009, Brinton and Curran 2017, Martins *et al.* 2020). Some elasmobranch species have been documented to remain in shallow (semi-)enclosed water bodies like tide pools or lagoons during low tide (Figure 7.3A).

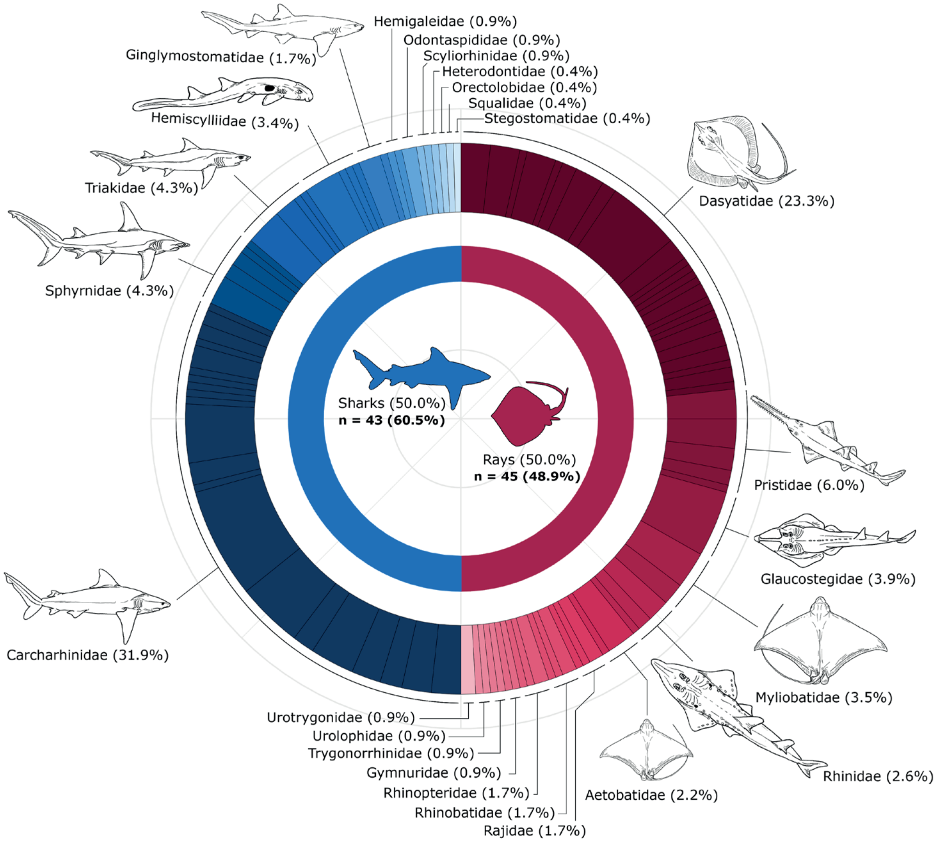


Figure 7.2 The shark (blue) and ray (red) families for which intertidal habitat use has been confirmed. Percentages indicate the relative number of observations of a family in the reviewed studies. The different species for which intertidal habitat use was confirmed are indicated by the different segments (black lines within each family), and colors indicate the taxonomic family. The total number of species confirmed to use intertidal habitats is given for both sharks and rays, with the proportion of threatened species given in parenthesis.

Feeding in intertidal habitats

Most studies described the feeding behavior of elasmobranchs in intertidal habitats (32.3%, Appendix 7.2C). Stingrays (57.4%, Dasyatidae) and eagle rays (10.3%, Myliobatidae) accounted for most feeding observations by rays, as these species often leave distinctive feeding pits on intertidal soft-bottom flats (e.g., Hines *et al.* 1997, O'Shea *et al.* 2012, Takeuchi and Tamaki 2014) (Figure 7.3A). Of all sharks, intertidal feeding behavior was mainly described for requiem sharks (62.1%, Carcharhinidae), houndsharks (24.1% Triakidae), and hammerhead sharks (10.3% Sphyrnidae). Feeding activities of elasmobranchs may have direct (i.e., removal of prey species) and indirect effects (i.e., changing biogeomorphology, biogeochemistry) on intertidal habitats.

Direct trophic effects

In nearshore ecosystems, large-bodied sharks like the great hammerhead shark (*Sphyrna mokarran*, Sphyrnidae), tiger shark (*Galeocerdo cuvier*, Carcharhinidae), and bull shark (*Carcharhinus leucas*, Carcharhinidae), occupy top-predatory niches and can control the abundance of lower trophic species (Heithaus 2001, Atwood *et al.* 2015, Navia *et al.* 2016, Hammerschlag *et al.* 2019). In coastal areas, large sharks are often defined as generalist predators (e.g., Nowicki *et al.* 2019, Hussey *et al.* 2015), with a diet consisting of large teleost fishes, rays, smaller shark species, and sea turtles (Figure 7.3B). Depending on the habitat, ontogenetic changes, and individual specialization, large sharks can also be specialist predators (Matich *et al.* 2017). For example, great hammerhead sharks were found to be specialized shark and ray predators in eastern Australia (Raoult *et al.* 2019). The niches of some shark species are wider and more resilient to (environmental) changes (Munroe *et al.* 2014). Our results show that adults of large-bodied shark species rarely use intertidal habitats. This could be explained by the physical constraints of shallow habitats for large-bodied sharks, and a lack of larger prey. However, Roemer *et al.* (2016) show that adult great hammerhead sharks venture into shallow waters to feed on small sharks or eagle rays. This suggests that large sharks - as vagrant predators occupying a top-predatory position (Heupel *et al.* 2014, Navia *et al.* 2016) – may use shallow habitats like the intertidal opportunistically but spend the large majority of time in (adjacent) subtidal waters (Figure 7.1C). As large sharks can control prey abundance through top-down processes (e.g., Bascompte *et al.* 2005), the removal of large sharks is hypothesized to release prey species from predation, causing an increase in their abundance (Ward and Myers 2005, Myers *et al.* 2007, Ferretti *et al.* 2010, Atwood *et al.* 2015), but these predator-prey dynamics need further investigation (e.g., Grubbs *et al.* 2016).

We found that intertidal habitats are mostly used by early life stages and small-bodied elasmobranchs (e.g., Knip *et al.* 2011, George *et al.* 2019), which typically occupy a meso-predatory position in coastal food webs (Navia *et al.* 2016, Flowers *et al.* 2021). Ray species feeding in intertidal habitats can have a generalist or specialist feeding strategy.

For example, generalist species like the New Zealand eagle ray (*Myliobatis tenuicaudatus*, Myliobatidae), bat ray (*Myliobatis californicus*, Myliobatidae), the American cownose ray (*Rhinoptera bonasus*, Rhinopteridae), and Indonesian sharpnose ray (*Telatrygon biasa*, Dasyatidae) consume a wide variety of prey species as part of their opportunistic feeding strategy (Gray *et al.* 1997, Hines *et al.* 1997, Collins *et al.* 2007, Lim *et al.* 2018,). Specialist mesopredators like the leopard shark (*Triakis semifasciata*, Triakidae) feed primarily on a narrow range of prey species, limited to a diet consisting of a small number of polychaete or bivalve species (Ackerman *et al.* 2000). Ajemian and Powers (2011) show that the feeding strategy of American cownose rays possibly switches between specialist and opportunistic generalist feeding strategies depending on location and prey availability. Adult bat rays consume larger and harder prey (e.g., large bivalves and crustaceans), compared to juvenile conspecifics, which have a more generalist feeding strategy and feed on a wider variety of prey (e.g., small bivalves and shrimp) (Gray *et al.* 1997).

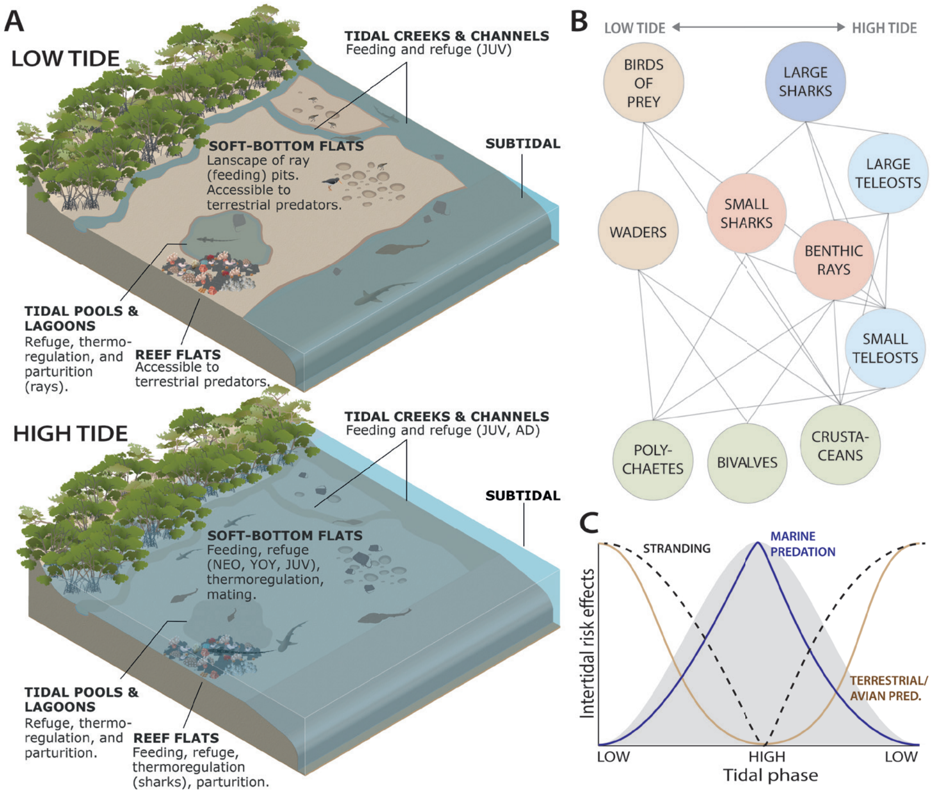


Figure 7.3 A: Conceptual visualization of intertidal habitat use by elasmobranchs for both tidal phases, low tide (top) and high tide (bottom). (NEO = neonates, YOY = young-of-the-year, JUV = juveniles, AD = adults). B: Simplified intertidal food web consisting of intertidal prey species (green), low-tide predators (brown), and marine predators (elasmobranch meso-predators in red, elasmobranch top-predators in dark blue, and teleosts in light blue). C: The risk-effects induced by intertidal predators and the stranding risk for marine predators.

A similar ontogenetic shift was shown for other ray and benthic shark species (Bethea *et al.* 2007, Lim *et al.* 2018, Clements *et al.* 2022). Hollensead *et al.* (2016) describe that juvenile smalltooth sawfishes (*Pristis pectinata*, Pristidae) most likely use the edge of intertidal flats to ambush schools of mullet (Mugilidae), leaving the intertidal habitat during the receding tide. Collectively, meso-predatory elasmobranchs primarily feed on crustaceans, bivalves, polychaetes and small teleosts in intertidal habitats during high tide (Talent 1982, Haeseker and Cech 1994, Ackerman *et al.* 2000) (Figure 7.3B). These meso-predators can affect (benthic) prey abundance through direct predation (Reidenauer and Thistle 1981, Pridmore *et al.* 1990, O'Shea *et al.* 2012). For instance, a local increase of red stingrays (*Hemitrygon akajei*, Dasyatidae) in Japan was directly linked to declines in ghost shrimp (*Neotrypaea harmandi*, Callianassidae) populations (Flach and Tamaki 2001, Takeuchi *et al.* 2013, Takeuchi and Tamaki 2014).

Indirect effects of elasmobranch predation

Depending on sediment characteristics and water turbidity, the feeding activity of elasmobranchs can be monitored both during high and low tide. On more coarse sediment and hard-bottom substrates, feeding traces are not preserved, limiting observations of elasmobranch feeding to high tide observations (Kanno *et al.* 2019, Lim *et al.* 2018). If water visibility allows, these methods can be used to document feeding activity and the duration of intertidal habitat use (Kanno *et al.* 2019).

The feeding activity of elasmobranchs during high tide on soft-bottom intertidal flats might still be visible during low tide (Figure 7.3A). In these areas, the feeding behavior of stingrays and eagle rays can leave distinct sediment depressions or excavations, so-called 'ray pits' (e.g., Grant 1983, Lynn-Myrick and Flessa 1996, O'Shea *et al.* 2012, Takeuchi and Tamaki 2014). With their feeding behavior, rays can change the biogeomorphology of soft-bottom intertidal habitats through bioturbation and thereby act as ecosystem engineers (Kristensen *et al.* 2012). O'Shea *et al.* (2012) determined that up to 42% of the soft-sediment habitat in Mangrove Bay (Australia) is reworked by stingrays every year. On Debidue Flat (United States), researchers estimate excavation activity by rays to turn over the top layer of the entire flat every 100 to 1,000 days (D'Andrea *et al.* 2004), and in Bahía La Choya (Mexico), rays only need about 72 days to overturn the entire top layer (Lynn-Myrick and Flessa 1996). Differences in these turnover rates between studies are dependent on ray densities, species, perceived risk (discussed in 3.3. 'Risk effects and avoidance in intertidal habitats'), and methodological differences across studies (Flowers *et al.* 2021). The increased bioturbation by rays can potentially lead to changes in biogeochemistry as a result of bioturbation effects on grain size and sediment stability (Lohrer *et al.* 2004, Meysman *et al.* 2006, Laverock *et al.* 2011). Increased bioturbation can also lead to increased primary production in intertidal systems (Giorgini *et al.* 2019) and cause changes in the composition of benthic species (Thrush *et al.* 2006). In addition, newly formed excavations by benthic rays can provide new habitats for other organisms that are using the intertidal. As the water in ray pits often remains during low tide, these can act as a habitat for smaller, secondary users like small teleost fish, gastropods and (burrowing) crabs (Zajac *et al.* 2003, O'Shea *et al* 2012).

Predation risk effects and avoidance among elasmobranchs

Shallow, nearshore areas are known to provide refugia for many (early life stages of) fish species, including elasmobranchs (Knip *et al.* 2010), which are prone to predation from large-bodied (conspecific) predators in adjacent subtidal waters. Our results show that the early life stages of large-bodied elasmobranchs and small-bodied elasmobranchs use the intertidal as a refuge when tides are high (Pierce *et al.* 2011, Vaudo and Heithaus 2011, Cerutti-Pereyra *et al.* 2014). Especially vegetated intertidal habitats such as mangroves and seagrass beds are thought to offer increased protection and lower predation risks, especially in ray species. After feeding activity, refuge behavior and risk aversion was the most common motivation provided for intertidal habitat use by elasmobranch species (15.5%, Appendix 7.2C). Among ray species, refuge was mostly reported for stingrays (50.0%, Dasyatidae) and sawfishes (25.0%, Pristidae). Shark species using intertidal refugia were mostly young individuals of requiem shark (79.1%, Carcharhinidae) and hammerhead shark species (12.5%, Sphyrnidae). However, authors often provide limited evidence of active prey avoidance, and the motivation of habitat selection remains an important knowledge gap for shallow (intertidal) habitats (Knip *et al.* 2010, Flowers *et al.* 2021). In addition, the presence of predators can induce predation risk effects in other, lower trophic species, causing changes in their behavior, habitat selection, and limiting foraging time (Morrissey and Gruber 1993, Heithaus and Dill 2002, Wirsing *et al.* 2007, Peacor *et al.* 2020, Flowers *et al.* 2021, Hammerschlag *et al.* 2022). The presence of large-bodied predators in subtidal waters can potentially increase the usage of adjacent intertidal areas as feeding refugium by meso-predatory species as soon as these are accessible in the tidal cycle.

Predation risk effects induced by elasmobranchs as predators

Besides facing predation risk effects from larger (conspecific) predators, meso-predatory elasmobranchs may simultaneously induce predation risk effects among prey communities (Rasher *et al.* 2017, Flowers *et al.* 2021). Meso-predatory rays induce behavioral and physiological responses among prey species and communities (Flowers *et al.* 2021). Ex-situ experiments show that the presence of rays influences the movement (Barrios-O'Neill 2017) and feeding times of mussels (Castorani and Hovel 2016). Sharks and rays utilizing intertidal habitats are forced to move in coherence with the tide, causing the risk effects induced by these predators on intertidal prey to be linked with the tidal cycle (Figure 7.3C). For example, Rasher *et al.* (2017) found that the presence of reef-associated sharks significantly lowered the browsing and grazing of herbivorous fish during times when sharks had access to the habitat (i.e., high tide). The risk effects for intertidal prey species do not cease when predatory fish and elasmobranchs lose access to these habitats, as the predation risk effects induced by terrestrial and avian predators increase with the lowering tide (Figure 7.3C).

Stranding risk effects and avoidance

Marine predators such as sharks and rays using intertidal habitats are faced with an additional risk: the risk of stranding upon tidal flat emergence with the receding tide (Campos *et al.* 2009, Brinton and Curran 2017). When the receding tide sets in, the stranding risk for sharks and rays seeking refuge or feeding in intertidal habitats increases (Figure 7.3C) (Wosnick *et al.* 2022). Sharks feeding in intertidal habitats are thought to limit the use of the intertidal until the incoming tide reaches its highest levels, leaving the intertidal as soon as the tide starts to recede, possibly by sensing barometric changes (Campos *et al.* 2009, Rasher *et al.* 2017). For example, brown smoothhound sharks (*Mustelus henlei*, Triakidae), a species that is vulnerable to strandings (Wosnick *et al.* 2022), show more directed movements to leave the intertidal upon the turn of the tide (Campos *et al.* 2009). To reduce the risk of stranding and/or predation, rays exert directed tidal movements during receding and incoming tidal phases (Davy *et al.* 2015, Brinton and Curran 2017, Martins *et al.* 2020). However, these directed movements could also be motivated due to increased feeding opportunities (Kanno *et al.* 2019). Hence, intertidal habitat utilization by (early life stages of) sharks and rays is a trade-off between lower predation risk effects, increased feeding opportunities, and the risk effects of stranding (Figure 7.1, 7.3).

Reproduction and parturition in intertidal habitats

Sharks and rays are known to use nearshore habitats for mating (e.g., Smith 2005), gestation (e.g., Jirik and Lowe 2012), parturition (e.g., Mourier and Planes 2013, Feldheim *et al.* 2013), and oviparity (e.g., Day *et al.* 2019). Our results show that some sharks and rays use intertidal habitats for reproduction-related behavior. Among rays, this has mostly been described for pelagic eagle ray (25.0%, Aetobatidae) and stingray (16.7%, Dasyatidae) species. Reproductive behavior as motivation for intertidal habitat use of sharks has mostly been described for requiem sharks (46.2%, Carcharhinidae), hammerhead sharks (23.1%, Sphyrnidae) and houndsharks (15.4%, Triakidae). Smith (2005) described that leopard sharks mate on intertidal soft-bottom flats in California. Shortnose guitarfish potentially use tide pools for parturition (Wosnick *et al.* 2019). This limited evidence suggests that some shark and ray species use the intertidal for reproductive purposes, to maximize mating success, maximize gestational development, and increase the survival of egg cases.

Thermoregulation in intertidal habitats

Abiotic factors play an important role as drivers of distribution, movement and habitat selection of sharks and rays (Schlaff *et al.* 2014). As most shark and ray species are ectotherms, ambient temperatures directly influence metabolic and physiological processes and are therefore considered one of the main drivers of their distribution, movement, and habitat selection (Morissey and Gruber 1993, Bernal *et al.* 2012, Schlaff *et al.* 2014). Elasmobranchs select shallow coastal waters due to their higher temperature to increase digestion rates (Papastamatiou *et al.* 2015), (embryonic) growth rates, and to shorten gestation times (Jirik and Lowe 2012, Wosnick *et al.* 2019). Our review shows that sharks and rays might select intertidal habitats for thermoregulatory purposes, as intertidal water temperatures are often higher compared to adjacent subtidal waters (Bridges 1993, Hernández *et al.* 2002). However, only a limited number of studies describe the behavioral thermoregulation of sharks and rays in intertidal habitats. For stingrays, requiem sharks, and houndsharks, two studies describe thermoregulation in intertidal habitats for each of the species' groups. Thermoregulation of sawfishes, giant guitarfishes (Glaucostegidae), eagle rays, wedgefish (Rhinidae), and round stingrays (Urotrygonidae) was only described in one study of each of these families. For example, Jirik and Lowe (2012) describe how pregnant round stingrays (*Urobatis helleri*, Urotrygonidae) use intertidal habitats in months of high water temperatures to increase embryonic development. Di Santo and Bennett (2011) describe that the Atlantic stingray (*Hypanus sabinus*, Dasyatidae) may use the thermal variability across habitats to maximize energy uptake by balancing evacuation and absorption rates. This may cause some ray species to use warmer habitats like the intertidal to regulate digestion rates.

Differentiating between different drivers of intertidal habitat use in sharks and rays is challenging due to existing knowledge gaps caused by the challenges of studying these species in such highly dynamic habitats. It is likely that intertidal habitat selection is an interplay of different biotic and abiotic drivers, in which abiotic drives such as salinity, water temperature, and emergence time of the habitat likely play a key role.

Physiological adaptations to the challenges of intertidal habitat use

The reason sharks and rays select intertidal habitats is equivocal, with the most likely motivation for intertidal habitat selection being a combination of lower predation risk effects and increased feeding opportunities. However, elasmobranchs using these shallow and highly dynamic habitats are also faced with extremes in environmental factors like fluctuations in temperature, salinity, pH, and oxygen levels (Lam *et al.* 2006). These challenges require specific physiological adaptations to enable an organism to use intertidal habitats. Intertidal habitats are often located in estuaries with associated fluctuations in salinity due to freshwater outlets (Murray *et al.* 2019) and high evaporation rates (Wheatly 1988, Lam *et al.* 2006). Our overview shows that species using intertidal habitats are often euryhaline species, tolerating wide salinity ranges (Martin 2005). For example, we show that euryhaline species such as the bull shark, the speartooth shark (*Glyphis glyphis*, Carcharhinidae), stingray species including the Atlantic stingray (*Hypanus sabinus*, Dasyatidae), and sawfish species like the largetooth sawfish (*Pristis pristis*, Pristidae) often use intertidal areas (De Vlaming and Sage 1973, Martin 2005). These species are able to tolerate wide ranges of salinities due to their ability to secrete solutes and, therefore, maintain osmolarity in habitats with lower salinities or even with large freshwater influxes (Chew *et al.* 2006, Ballantyne and Robinson 2010). Some species of elasmobranchs have higher temperature tolerances compared to other species or even compared to conspecifics in other life stages. This allows these species to adapt to the high temperature fluctuations of intertidal habitats. For example, juvenile ribbontail stingrays (*Taeniura lymma*, Dasyatidae) have a small thermal niche with high temperature preferences to sustain high temperature fluctuations in their (intertidal) nursery areas. Sustaining these high temperatures can separate juveniles from older conspecifics in deeper and cooler waters (Dabruzzi *et al.* 2013). Another example of how some elasmobranch species are adapted to use intertidal habitats is the use of tide pools and intertidal reef flats by the epaulette shark (*Hemiscyllium ocellatum*, Hemiscylliidae). Oxygen levels in these tide pools can drop to as low as 30% of air saturation during low tide phases (Kinsey and Kinsey 1966). Epaulette sharks have a high hypoxic tolerance, sustaining oxygen levels as low as 5% of air saturation without serious functional impairments (Wise *et al.* 1998) or even anoxic conditions for up to one hour (Renshaw *et al.* 2002, Nilsson and Östlund-Nilsson 2006). Moreover, as intertidal habitats force organisms continuously to move in coherence with the tide, this may select more mobile species (e.g., small shark species, juvenile sharks) or species morphologically adapted to use shallow (benthic) habitats to be able to move in proximity to the flood line (e.g., benthic rays). Our review shows that the majority of species using intertidal habitats are either benthic rays or small-bodied/juvenile mobile shark species.

Ecological interactions in intertidal habitats: a shark and ray perspective

Traditionally, ecological interactions in the intertidal have been considered from a terrestrial and shorebird perspective, the low-tide predators of intertidal areas (Beninger 2019). Shorebirds occupy a central niche in intertidal food webs and are considered one of the most important predator guilds in the intertidal (Kuwae *et al.* 2012, Mathot *et al.* 2019). Through this global synthesis, we have shown that it is very likely that (meso-)predators such as sharks and rays (i.e., high-tide predators) occupy a similar central niche in intertidal food webs and should, therefore, be considered in intertidal ecology.

Benthic primary consumers

Within the intertidal, the most abundant and common prey species groups are crustaceans, bivalves, polychaetes, and benthic teleosts (Pridmore *et al.* 1990, Jing *et al.* 2007, Philippe *et al.* 2016) (Figure 7.3B). These prey species occur in high-density patches or are dispersed across intertidal habitats, creating distinct feeding landscapes for predators. These prey species are accessible to avian and terrestrial predators during low tide phases and are accessible to meso-predators like benthic rays, small-bodied sharks and teleosts during high tide (Figure 7.3B) (Smith and Merriner, 1985). The duration that these prey species are accessible to each of these predatory guilds depends on how long the habitat is exposed or submerged, which is determined by the relative elevation of the habitat and the tidal amplitude. Hence, low intertidal habitats (i.e., low elevation) are accessible to marine predators for longer periods of time as the habitat is submerged during most of the tidal cycle. In contrast, habitats with a relatively high elevation are exposed for most of the tidal cycle, so prey in these habitats are more accessible to avian and terrestrial predators (Figure 7.1C).

Avian and mammalian predators

Shorebirds select intertidal habitats for feeding opportunities along their migratory flyways and depend on the resources provided by these intertidal areas to fuel their long migrations (Wanink and Zwarts, 1993, Ens *et al.* 1994, Iwamatsu *et al.* 2007, Jing *et al.* 2007). These shorebirds can have a generalist feeding strategy, such as sanderlings (*Calidris alba*) and American golden plovers (*Pluvialis dominica*, Charadriidae) (Lourenco *et al.* 2015, Faria *et al.* 2018), or a more specialist strategy, such as bar-tailed godwits (*Limosa lapponica*, Scolopacidae) and red knots (*Calidris canutus*, Scolopacidae) (Zharikov and Skilleter 2003, van Gils *et al.* 2012). Similar to benthic ray species using the intertidal, these shorebirds occupy a meso-predatory niche in the intertidal food web (Buchanan 2012, Kuwae *et al.* 2012, Beninger 2019), and are in turn preyed upon by bird-of-prey species (Page and Whitacre, 1975, van den Hout *et al.* 2008) (Figure 7.3B).

The impact of meso-predatory rays on prey populations and community composition is not well understood (Flowers *et al.* 2021). Some studies indicate no effect of ray foraging on prey abundance (Ajemian and Powers 2013), while other studies show that prey densities were negatively impacted by combined predation effects of shorebirds and rays (Thrush *et al.* 1994) or by predation effects of rays alone (Peterson *et al.* 2001). However, differentiating between predation effects in a multiple-predator system remains challenging and can cause predation effects to be wrongly attributed to a specific species (Grubbs *et al.* 2016, Flowers *et al.* 2021). The effects of shorebird predation have been studied extensively and are better understood (Figure 7.3B). Shorebirds can locally deplete prey species (Zharikov and Skilleter, 2003) and change benthic community composition (Thrush 1994, Mendonca *et al.* 2007). A potential overlap in resource use might cause indirect competition by means of common resource depletion with elasmobranch predators (Figure 7.4A). However, it is likely that some prey species compensate for depletion with increased reproduction and survival, potentially masking the effects of resource depletion (Kalejta, 1993). The effects of shorebirds on intertidal prey species can be considered to differ seasonally as many shorebird species are migratory and use intertidal areas as (wintering) stopover sites (Wanink and Zwarts, 1993, Ens *et al.* 1994).

Benthic rays may also change the foraging landscape for other intertidal predators. For example, sediment depressions, created by rays while feeding, provide a habitat for prey species (e.g., O'Shea *et al.* 2012) and change the bio-geomorphology of the intertidal habitat (e.g., D'Andrea *et al.* 2004). Similarly, depressions created by greater flamingos and fiddler crabs, in combination with hydrodynamic forces on an intertidal flat, resulted in higher concentrations of organic matter and biofilms, promoting resource availability for other taxa on intertidal habitats (El-Hacen *et al.* 2018). The mosaic of microhabitats created by benthic rays can, therefore, be expected to promote resource availability in intertidal habitats, indirectly facilitating other (intertidal) predatory guilds like shorebirds. Bioturbation and the creation of new habitats by rays on a relatively large scale can thus be expected to have an important ecological role in (intertidal) soft-bottom ecosystems.

Although documented observations are scarce, some terrestrial mammals use the intertidal during low tide (Carlton and Hodder, 2003). For example, coyotes (*Canis latrans*, Canidae) have been observed feeding on brachyuran crabs and polychaetes (Rose and Polis 1998, Carlton and Hodder, 2003), and opossums and rodents have been documented to consume brachyuran crabs, bivalves and gastropods (Carlton and Hodder, 2003). Hence, it is plausible that terrestrial mammals consume similar prey species during low tide compared to elasmobranch predators during high tide, resulting in potential trophic niche overlap between these predatory guilds.

Avian and mammalian predators are also known to feed on sharks and rays within coastal systems. For example, coyotes scavenge stranded or hunt live stingrays along the coast of the Gulf of California (Rose and Polis 1998). Seabirds such as the Caspian tern (*Hydroprogne caspia*, Laridae) and great blue heron (*Ardea Herodias*, Ardeidae) are known to hunt newborn leopard sharks, brown smoothhound sharks and Atlantic stingrays (Ajemian *et al.* 2011, Russo 2015). Gastropods and seagulls were found to be the main predators of (stranded) egg cases of skates and sharks (Cox and Koob 1993, Seguel *et al.* 2022). Given that intertidal areas provide an important shallow-water habitat for elasmobranchs with an elevated risk of stranding and the importance of these habitats to avian and mammalian species, it is likely that these species groups predate or scavenge on elasmobranchs in the intertidal. How important elasmobranchs are as a food source to these predators or elasmobranchs are only scavenged opportunistically needs more investigation.

Humans as intertidal predators

The consumptive effects of (local) human populations should also be considered when determining the impact of predators on benthic prey species (Hockey and Bosman 1986, Castilla 1998). Traditionally, humans have targeted shellfish and polychaetes on soft-bottom intertidal flats for consumption and as fishing bait, respectively

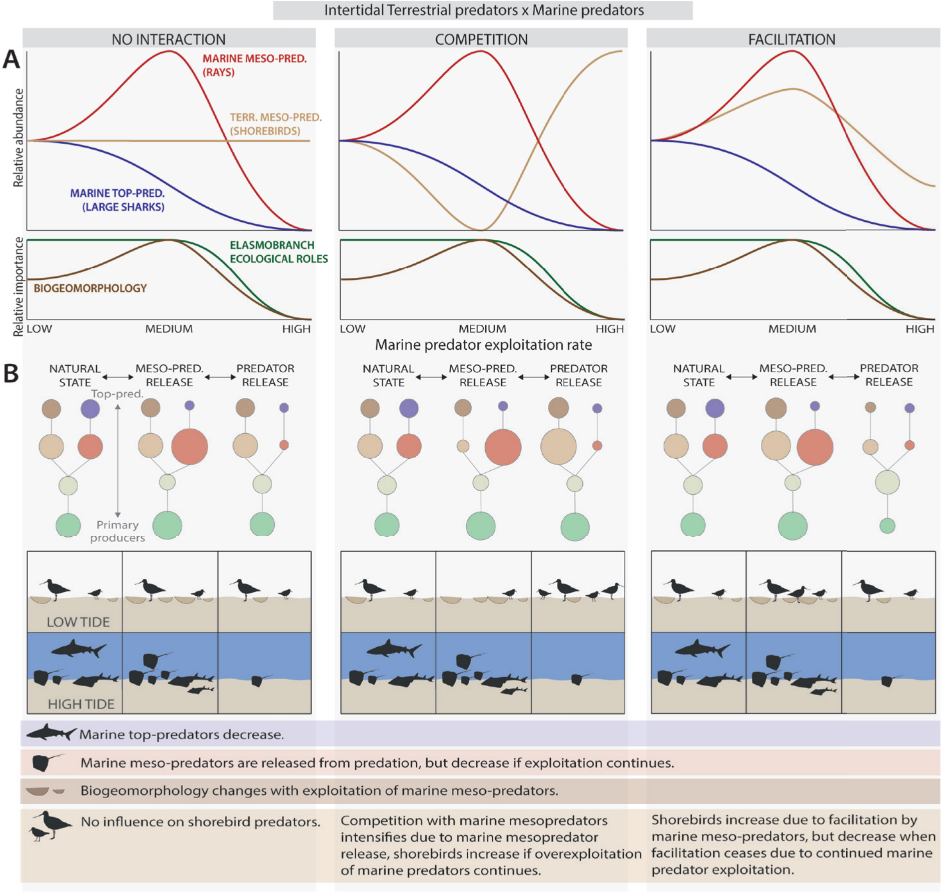
(Watson *et al.* 2017, Benninger 2019). De Boer and Longamane (1996) determined that consumption of intertidal prey in Mozambique by both shorebirds and humans was responsible for 18% of the annual biomass removal. However, the authors of this study neglected the consumption of intertidal prey by high-tide predatory guilds like elasmobranchs and teleosts. The intertidal is thus used by human communities around the world for the extraction of food sources (Benninger 2019, Murray *et al.* 2019), which has both a direct impact (i.e., resource extraction) and indirect (i.e., disturbances of other predators or bioturbation resulting from extraction activities) impact on these systems. Hence, both trophic and non-trophic effects of these activities should be considered in the field of intertidal ecology (Benninger 2019).

Elasmobranch intertidal habitat use in the Anthropocene

The role of elasmobranch contribution to intertidal ecosystem functionality potentially faces rapid changes due to a combination of anthropogenic disturbances.

Elasmobranch removal from intertidal areas

Coastal areas harbor a high diversity of elasmobranch species, including many endemic species with unique ecological roles, many of which are now severely threatened (Stein *et al.* 2018). These elasmobranch species face ongoing population declines due to overfishing and habitat degradation (Knip *et al.* 2010, Dulvy *et al.* 2021). Sharks and rays in intertidal areas are targeted by (local) fisheries in the intertidal and adjacent shallow subtidal waters (e.g., White *et al.* 2013, Tobin *et al.* 2014, Adkins *et al.* 2016). In addition, these mobile species are also at risk of being captured by industrial fisheries while migrating away from these coastal areas (Leurs *et al.* 2021). These activities impact intertidal predator abundance and their potential ecological function in intertidal areas (Lemrabott *et al.* in prep., Leurs *et al.* in prep.). Of all 88 species that were found to use intertidal habitats, 54.5% are currently threatened with extinction (Appendix 7.3). In total, 21 species are listed as Vulnerable, 16 as Endangered and 11 as Critically Endangered on the IUCN Red List. Two species have been classified as Data Deficient, and thus, their population status and trends are unknown. The high proportion of threatened species using intertidal habitats suggests that if the causes of population declines are not reversed, some species might disappear from coastal ecosystems. For example, in the Dutch part of the Wadden Sea, rays were like the common stingray (*Dasyatis pastinaca*, Dasyatidae) and thornback ray (*Raja clavata*, Rajidae) were once common, but have almost disappeared completely due to combined effects of habitat destruction, overexploitation, and pollution (Wolff 2005). The removal of elasmobranchs from intertidal areas can have different effects depending on the type of interaction (i.e., competition or facilitation) between low-tide and high-tide meso-predators (Figure 7.4).



Marine top-predators decrease.

Marine meso-predators are released from predation, but decrease if exploitation continues.

Biogeomorphology changes with exploitation of marine meso-predators.

No influence on shorebird predators.

Competition with marine mesopredators intensifies due to marine mesopredator release, shorebirds increase if overexploitation of marine predators continues.

Shorebirds increase due to facilitation by marine meso-predators, but decrease when facilitation ceases due to continued marine predator exploitation.

Figure 7.4 Conceptual overview of the influences that elasmobranch overexploitation in intertidal areas can have on low-tide predators like shorebirds, depending on the type of interaction (competition or facilitation) and assuming that decreases in top-predator abundance will lead to increases in mesopredators. A: the relative abundance of marine top-predators (e.g., large sharks; blue), marine meso-predators (e.g., rays; red), and terrestrial meso-predators (e.g., shorebirds; brown) when there is no interaction between predatory guilds (left), competition (middle) or facilitation (right). In addition, the relative changes in ecological importance of elasmobranchs (green) and the bio-geomorphology of intertidal habitats (dark brown) are given. B: changes in a simplified intertidal food web between different predator exploitation states (with marine top-predators in blue, terrestrial top-predators in dark brown, marine meso-predators in red, terrestrial meso-predators in brown, primary consumers in light green and primary producers in green).

The effects of large-bodied shark removal from marine ecosystems are under continuous debate and are likely highly context-dependent. Studies on coastal marine systems conclude that the removal of large-bodied sharks has been linked to population increases of meso-predatory species (i.e., meso-predator release), causing an increase of meso-predation on lower trophic prey species (Heithaus *et al.* 2008, Ruppert *et al.* 2013, Ferretti *et al.* 2010) or changes in the diet of prey species (Barley *et al.* 2017). Other studies indicate that shark removal does not impact meso-predatory species like cownose rays or coral reef fish (e.g., Grubbs *et al.* 2016, Casey *et al.* 2017). For example, on predator-rich coral reefs, large shark removal did not influence prey species possibly due to the presence of large teleost predators that consumed similar prey, making large sharks ecologically redundant (Barley *et al.* 2020). Ecological redundancy may be common in predator-rich ecosystems in which predators are more likely to share the limited number of available trophic niches (Finke and Denno 2004, Frisch *et al.* 2016). In these rich systems, safeguarding ecosystem functioning does not only hinge on the conservation of sharks, since the cascading effects of shark removal can be reduced if other predator species with a similar niche are present (Barley *et al.* 2020). However, predator richness in intertidal areas is expected to be low due to challenges and constraints associated with intertidal habitat use (e.g., risk of stranding, need for physiological adaptations), making it less likely that large-bodied sharks are ecologically redundant predators in these systems. In addition, current exploitation rates in coastal areas cause whole functional groups (i.e., large-bodied sharks and teleosts, high trophic level species) to be removed, possibly enabling a release of meso-predators due to the removal of multiple non-redundant species groups. Therefore, the removal of large-bodied sharks from intertidal areas could lead to an increase in predation pressure on lower trophic organisms caused by meso-predatory elasmobranchs (Figure 7.4).

These meso-predatory elasmobranchs may use the same intertidal prey species as terrestrial/avian meso-predatory species. An increase in predation by marine meso-predators can, therefore, intensify common resource depletion and possibly lead to interspecific competition between species of both guilds (Figure 7.4). If overexploitation of elasmobranchs continues and increasingly also targets mesopredatory rays (e.g., Moore *et al.* 2019), the abundance of these species is also expected to decline (i.e., ‘fishing down the food chain’, Pauly 1998). This may result in lower resource depletion by these meso-predatory rays, possibly increasing resource availability for other predatory guilds.

If benthic rays do not overlap or compete for resources with other meso-predatory guilds on intertidal habitats, or if these benthic ray species can be considered trophically redundant, their role as ecosystem engineers (i.e., changing biogeomorphology of intertidal habitats) can still be important in intertidal areas (Figure 7.4). An increase in benthic rays and associated bioturbation due to feeding and excavation activity may cause changes to the biogeomorphology and biogeochemistry of soft-bottom intertidal flats (Lohrer *et al.* 2004, Meysman *et al.* 2006, Laverock *et al.* 2011). In addition, increased bioturbation can increase primary and secondary production in intertidal habitats (Giorgini *et al.* 2019), affect the displacement of prey species (vanBlaricum, 1982), and provide newly created microhabitats to other (prey) species like brachyuran crabs (O'Shea *et al.* 2012). Increasing bioturbation has caused shifts in dominant species in benthic communities on soft-bottom intertidal habitats, can impact species richness of these microbenthic communities (Berkenbusch *et al.* 2000, Thrush *et al.* 2006), and can negatively impact habitat-building species like seagrass light may be limited in systems with higher turbidity (Govers *et al.* 2014, Suykerbuyk *et al.* 2016). By changing the landscape heterogeneity of intertidal habitats and changing benthic communities, benthic rays may indirectly facilitate other predatory guilds using intertidal habitats, such as migratory shorebirds, who rely on prey species like polychaetes and crustaceans during their stay on wintering grounds (Piersma 2012). However, if continued overexploitation of elasmobranchs also impacts benthic ray species, the effects of benthic rays on sediment dynamics will likely change (O'Shea *et al.* 2012). This may lead to changes in the habitat heterogeneity and sediment dynamics of intertidal habitats due to decreased bioturbation. This will, in turn, also affect biogeochemistry, and likely cause changes in benthic community composition (Thrush *et al.* 2006, Giorgini *et al.* 2019). Hence, exploitation may negatively impact the role of benthic rays as facilitators for other predatory guilds using intertidal habitats (Giorgini *et al.* 2019).

The loss of intertidal habitats

Sharks and rays can have an important ecological role within marine food webs, and our review shows that this includes a pivotal role in intertidal food webs. Conversely, intertidal habitat also plays an important role in the lifecycle of coastal shark and ray species. Recent estimates show that the areal extent of soft-bottom intertidal areas has declined by 16% between 1984 and 2016, indicating that intertidal habitats are threatened by human-induced stressors such as coastal development, coastal erosion, and sea level rise (Murray *et al.* 2019). Galbraith *et al.* (2002) estimated that under a global warming scenario of 2° C, between 20 to 70% of intertidal habitat would be lost to sea level rise. Our review shows that, in addition to shorebirds and other terrestrial predators, the intertidal is especially important to the early life stages of many coastal elasmobranch species. These elasmobranchs most likely select intertidal habitats as a trade-off between feeding opportunities and lower predation risk effects. Even if elasmobranchs do not directly use intertidal habitats such as saltmarshes, these habitats can still provide trophic benefits to elasmobranchs using habitats in the near vicinity of the intertidal (Niella *et al.* 2022). Sea level rise will make current intertidal habitats more accessible to marine predators, including larger-bodied predators, which could threaten the role of intertidal habitats as a feeding refugium for early life stages and small-bodied elasmobranchs. In addition to changing intertidal habitats to (shallow) subtidal habitats, sea level rise possibly also influences the duration for which intertidal habitats are accessible to either low-tide or high-tide predators.

Globally, sea temperatures are increasing, and the ocean is becoming more acidic (i.e., Ocean Acidification) due to global climate change (IPCC, 2022). As a result, temperatures in intertidal habitats are also expected to increase, likely making intertidal habitats less suitable for many marine species with limited temperature tolerance ranges (IPCC, 2007). This might include elasmobranchs (Gervais *et al.* 2018, Lear *et al.* 2019) but also intertidal prey species that are sensitive to heat stress due to elevated seawater temperatures (Raymond *et al.* 2022). In addition, many intertidal prey species like polychaetes, crustaceans and bivalves are negatively impacted by ocean acidification (Ries *et al.* 2009). Continued temperature increases and acidification can therefore be expected to negatively impact intertidal prey availability and associated interaction between low-tide and high-tide predatory guilds. The loss of intertidal habitat or the deterioration of habitat quality will, therefore, not only be a risk to marine species but also to other terrestrial/avian species (Galbraith *et al.* 2002) and their mutual ecological interactions. This emphasizes that the conservation of intertidal areas should be considered from both a high-tide and low-tide perspective and that the importance of this habitat is recognized for both marine and terrestrial/avian species in the future.

The decline of intertidal areas around the world, given their ecological value, is alarming. Furthermore, the first global assessment of the status of these ecosystems was only conducted in 2019 (Murray *et al.* 2019, 2022). The presented ecological importance of intertidal areas for both (migratory) shorebirds and vulnerable elasmobranchs should be considered when assessing the risk of collapse of intertidal ecosystems under the IUCN Red List of Ecosystems (Keith *et al.* 2015). For example, intertidal areas have been considered as a critical habitat in the United States for the critically smalltooth sawfish, and have been included in management plans of these species (Strickland 2009). Although intertidal habitats are recognized to be vital habitats for wading shorebirds, and their decline in the Yellow Sea initiated a situation analysis by IUCN (MacKinnon *et al.* 2012), intertidal habitats should also be considered important habitats in risk assessments for coastal sharks and rays.

Conclusions and future perspectives

Although the available information on intertidal habitat use by elasmobranchs is limited, our synthesis shows that these habitats are important to a variety of species in this highly threatened species group. We show that elasmobranchs play an important trophic role in intertidal ecosystems and that these areas provide important habitats for many coastal elasmobranch species at the same time. In addition, we provide novel insights into possible ecological interactions in intertidal systems that include the functional role of elasmobranchs. This emphasizes the importance of an integrative perspective on intertidal food webs that includes both high-tide (e.g., elasmobranchs) and low-tide (e.g., terrestrial and avian species) predators. Furthermore, we identified the ongoing decline of these habitats as a serious threat to elasmobranchs and their ecological interactions with low-tide predator guilds. We propose that future research and conservation efforts focus on:

1. Determining the motivation for sharks and rays to use these productive but dynamic and challenging habitats. This contributes to the understanding of how important intertidal habitats are for the lifecycle of specific elasmobranch species and further elucidates their ecological role in these habitats.

2. Studying how different predator guilds (indirectly) interact in intertidal habitats. Understanding these ecological interactions can improve targeted conservation efforts of these habitats by understanding how population trends of different predatory guilds affect ecosystem functioning. It will be important to consider the (a) possible ecological redundancy of elasmobranch species, (b) influences of elasmobranchs on (intertidal) prey populations, and (c) potential niche overlap between high-tide and low-tide predators.

3. Determining how anthropogenic stressors such as overexploitation, habitat degradation, and climate change impact predatory guilds in intertidal areas.

4. Considering the ecological importance of these habitats from a low- and high-tide predator perspective, use an approach that integrates the ecology of the diverse species groups that use these habitats.

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Chapter 8

Separated by the tide but united by resources: shared intertidal resource use by avian and marine mesopredators

This chapter has been removed from this version and will be published online at a later stage!

Guido Leurs, *et al.*

Manuscript

BOX E: WHO EATS THE RAYS?

Within the Bijagós Archipelago, communities generally believe that the decline of hammerhead sharks in their waters has caused an increase in smaller benthic stingrays. This apparent mesopredator release has also been hypothesized, discussed and disputed in scientific studies (e.g., Myers *et al.* 2007, Grubbs *et al.* 2016). I further discuss the potential of mesopredator release of rays and cascading effects in **Chapter 11**. However, for a mesopredator release to occur, the mesopredator needs to make up a considerable proportion of the diet of the removed predator (Grubbs *et al.* 2016). Based on our studies in the Banc d'Arguin and the Bijagós Archipelago and previous research (e.g., based on Flowers *et al.* 2021), I show that various marine predators may consume rays. Cownose rays, eagle rays, stingrays and round rays have mostly been documented in the diet of hammerhead sharks and other shark species. However, marine mammals and birds also predate on these species (**Figure E1**). Our research shows that in intertidal areas, large guitarfish (Glaucostegidae) and butterfly rays may predate on stingrays (**Chapter 8**, Last *et al.* 2016, Dean *et al.* 2017). We show that large teleost species, like cobias (*Rachycentron canadum*), predate on stingrays in the Bijagós Archipelago. Although these ray species have primarily been documented in the diet of large sharks, their contribution is often less than 20% of the overall diet (**Figure E1**).

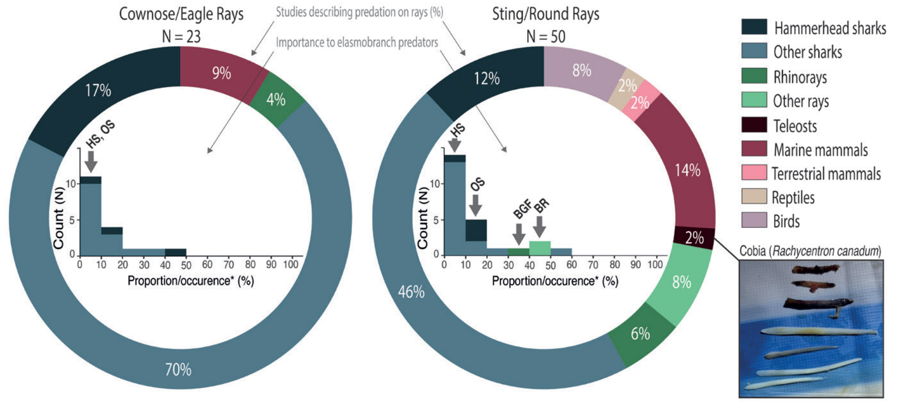

Figure E1 The proportion of documented cases of predation on cownose/eagle rays (left circle) and sting/round rays (right circle) by different predator groups. The inner bar graphs show the number of studies describing the occurrence or proportion of rays in the diet of different elasmobranch groups. Arrows indicate the estimated contribution of the two ray species groups to the diet of hammerhead sharks (HS), other sharks (OS), blackchin guitarfish (BGF; *Glaucostegus cemiculus*) and spiny butterfly ray (BR; *Gymnura altavela*; **Chapter 8**). The photo (right) shows our finding of stingray barbs embedded in the jaw and stomach wall of Cobias (*Rachycentron canadum*) in the Bijagós Archipelago. **Combined study outcomes for stable isotope analysis, frequencies of occurrence in stomach contents or relative important indices.*

Chapter 9

Bioturbation by benthic stingrays alters the biogeomorphology of intertidal flats

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Abstract

Fishing-down-marine-food-webs has resulted in alarming declines of various species worldwide. Benthic rays are one example of such overexploited species. On tidal flats, these rays are highly abundant and play an ecologically important role. They use tidal flats as refuge, feeding, and resting grounds, during which they bury into the sediment, which results in sediment bioturbation. Changes in bioturbation intensity following ray removal may affect the biogeomorphology of tidal flats with possible cascading effects on the macrozoobenthic community. However, it is poorly understood how these indirect effects could influence ecosystem function. We therefore studied the geomorphic impact of benthic rays (specifically the pearl whipray/stingray *Fontitrygon margaritella*) on the tropical tidal flats of the Bijagós Archipelago, Guinea-Bissau on a landscape-scale. We investigated 1) bioturbation rates by rays using drone- and ground-surveys, 2) the spatial distribution of ray pits on multiple tidal flats, 3) the impact of rays on sediment properties and macrozoobenthos by experimental exclusion (15 months). Benthic rays bioturbated 3.7±0.35% of the tidal flat's sediment surface per day over one single 24-hour period, which equals a complete top-sediment-surface turnover every 27 days. The spatial distribution of ray pits was affected by tidal flat geomorphology since pits decayed faster in areas exposed to strong hydrodynamic forces. Predator exclusion altered sediment properties, leading to changes in sedimentation (-17%) and erosion (-43%) rates. In addition, macrozoobenthic species composition changed, marked by an increase of Capitellidae worms and a greater biomass of Malacostraca over time. These changes indicated substantial effects of ray bioturbation on the biotic and geomorphic landscape of tidal flats. Overall, we conclude that changing abundances of benthic rays can have clear landscape-wide geomorphological effects on intertidal ecosystems. These indirect consequences of fisheries should be incorporated into integrative management plans to preserve tidal flats and connected ecosystems.

Introduction

Intertidal flats are prominent and productive geomorphic systems that provide valuable ecosystem services such as carbon storage, nutrient fluxes, coastal defense, primary and secondary productivity, fisheries enhancement and connection between marine and terrestrial ecosystems (Temmerman *et al.* 2013, Alongi 2014, 2018, van de Koppel *et al.* 2015, van der Zee *et al.* 2016). However, 16% of the world's intertidal flats have been lost due to anthropogenic pressures between 1984 and 2016 (Murray *et al.* 2019). Anthropogenic stressors, such as fishing, may disrupt natural equilibria with potential consequences for associated fauna and the ecological interaction networks they are part of (Pinnegar *et al.* 2000). Knowledge gaps on the interaction between threats (e.g., coastal fisheries), ecological functioning (e.g., food web structure, community composition) and the geomorphological development of intertidal flats (e.g., sedimentation, elevation) need to be addressed to improve effective management of these ecologically important areas, especially given the ongoing global loss of intertidal areas (Hill *et al.* 2021, Murray *et al.* 2022).

Fishing activities have caused dramatic declines in Chondrichthyes – shark, ray, and chimera populations on a global scale (Stevens *et al.* 2000, Baum *et al.* 2003, Baum and Myers 2004, Sherman *et al.* 2023), leading to an estimated 32% of 1,199 species currently being threatened with extinction (Dulvy *et al.* 2021). Although shark and ray species that use intertidal habitats are mostly affected by coastal mixed-species fisheries, they are also affected by industrial fisheries that operate on the edges of intertidal waters to catch animals that migrate into subtidal offshore areas (Dulvy *et al.* 2014, Leurs *et al.* 2021).

Most elasmobranchs are characterized by slow growth rates, late maturity, and low fecundity, and consequently highly vulnerable to direct human exploitation and bycatch mortality (Winemiller and Rose 1992, Jennings *et al.* 2001). Larger individuals are predicted to feed at higher trophic levels as size determines the dimensions of prey sizes that a predator can consume (Cohen *et al.* 1993). Larger predator overexploitation can control prey abundance through top-down processes (Bascompte *et al.* 2005), causing an increase in prey abundance (Myers *et al.* 2007, Ferretti *et al.* 2010, Sherman *et al.* 2020). However, these predator–prey dynamics need further investigation (Grubbs *et al.* 2016). On the other hand, when species of larger body size decline, fishing pressure may shift to smaller elasmobranchs such as benthic rays, known as 'fishing down the food web' (Pauly 1998). However, knowledge of the consequences of reduced ray numbers on ecosystem functioning is limited (Flowers *et al.* 2021).

Bioturbating benthic rays actively alter their habitats (i.e., habitat-modifiers) in search of food or resting grounds. To do so, these rays excavate and rework the sediment (hereafter referred to as 'ray pits') through a combination of protrusion of the jaws, water-jetting through the spiracles and movement of their pectoral fins (Freitas *et al.* 2019). These bioturbating activities can alter sediment erosion and composition (Takeuchi and Tamaki 2014) and create physical microhabitats that can benefit other species (Figure 9.1). For instance, ray pits can collect high amounts of organic matter, which benefits benthic detritus feeders (O'Shea *et al.* 2012). Bioturbation by rays thus alters geomorphological and ecological processes, which may ultimately affect the ecosystem functioning of intertidal flats (Lynn-Myrick and Flessa 1996, Needham *et al.* 2011, O'Shea *et al.* 2012). Moreover, these rays can be highly abundant in intertidal ecosystems and can play an important ecological role (Leurs *et al.* 2023a).

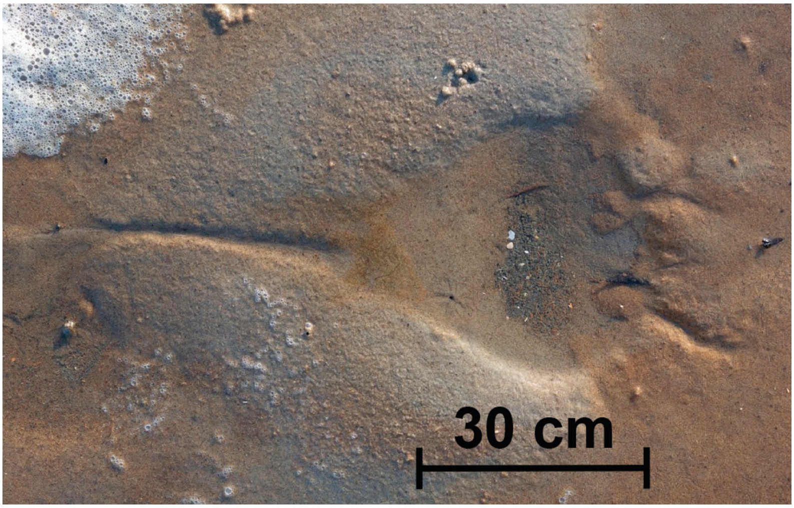


Figure 9.1 Excavation of the sediment created by benthic rays, called a 'ray pit'.

While the local-scale bioturbating effects of benthic rays are well studied (Grant 1983, O'Shea *et al.* 2012, Myrick and Flessa 2017), approaches to upscale these processes to a landscape scale are limited. In addition, experimental approaches to support ray bioturbation effects are inadequate (O'Shea 2012, Flowers *et al.* 2021). We studied the geomorphological impact of benthic rays using the tropical intertidal flats of the Bijagós Archipelago, Guinea-Bissau. Specifically, we quantified (1) the extent and intensity of benthic ray bioturbation at the intertidal flat landscape scale by conducting ground and drone surveys, (2) the spatial distribution and longevity of ray pits by looking at ray pit densities throughout the archipelago to test if the abundance of ray pits could be influenced by intertidal flat morphology (e.g., ray pits erode faster under highly hydrodynamic conditions O'Shea *et al.* 2012), and (3) the effect of ray bioturbation on sediment properties and macrozoobenthos by means of a ray exclusion experiment. The study area was chosen to investigate the effects of benthic ray feeding behavior since intertidal flats are key habitats for benthic rays (Leurs *et al.* 2023a). In the Bijagós Archipelago, 896 to 2,685 rays were captured daily in 2020 if, respectively, 30% and 100% of the fishing fleet was active in 2020 (Leurs *et al. in prep.*). This is likely an underestimation of the actual catch as vessels from neighboring countries were unaccounted for (Leurs *et al. in prep.*). As global (including West African) coastal fisheries are currently increasing at an alarming rate (Dulvy *et al.* 2021, Leurs *et al.* 2021), studying the geomorphic effects of bioturbating rays now is relevant as changes in population densities of these fishery-targeted species may affect their ecosystem and the conservation status of benthic rays continues to deteriorate (Sherman *et al.* 2023).

Methods

Study site

The Bijagós Archipelagos (Guinea-Bissau) supports extensive protected intertidal flat areas where fisheries are restricted (Diop and Dossa 2011, Hill *et al.* 2021). These areas provide refuge for globally threatened elasmobranchs, including benthic rays (Diop and Dossa 2011, Campredon and Catry 2016). Therefore, this area is highly suitable for studying the landscape scale effects of these habitat-modifying species. As observed on intertidal flats, *Fontitrygon margaritella* is the most common species that could make these ray pits (Leurs *et al.* 2023). However, ruling out *Fontitrygon margarita* completely is impossible only from pit formations. We also know that the large majority (i.e., 140 out of 143, 97.9%) of *Fontitrygon* spp. sampled in the archipelago were *F. margaritella* from fish market sampling for stomach contents (Clements *et al.* 2022). Combined, these results indicate that the large majority of pits are created by *F. margaritella*. The archipelago islands consist of 88 islands and islets, which are the remaining peaks of the eroded and flooded sedimentary basin of the ancient delta of the Rio Grande and Rio Geba, off the coast of West Africa (Bird 2011), surrounded by mangroves and 760 km^2 of intertidal flats (Meijer *et al.* 2021). These islands are located at the southern end of the Senegalo-Mauritanien sedimentary basin, and sediments originate mostly from the Corubal and Geba rivers (Campredon and Catry 2016). These sediments are deposited and transported by complex hydrodynamic forces in a network of river channels. On the other hand, high annual rainfall (2200 mm) leads to high surface erosion rates (Bird 2011). The temperate southern Africa realm has a relatively stable tidal wetland (intertidal flats, tidal marsh and mangrove ecosystems) coastline (Murray *et al.* 2022). The Bijagós Archipelago has the highest tidal range of the West African coast, with spring tides reaching up to 4.5 m amplitude and strong currents up to 78 cm/s (Campredon and Catry 2016). These intertidal flats support up to 600,000 waders along the East-Atlantic Flyway (Salvig *et al.* 1994, Van Roomen *et al.* 2011, Campredon and Catry 2016), and because of the archipelago's extraordinary biodiversity, it was classified as a UNESCO Biosphere Reserve in 1996 and as a Ramsar site in 2014 (Ramsar Convention Secretariat 2014). Our research in the Bijagós Archipelagos occurred between October-December 2019 and February 2021 (Figure 9.2A).

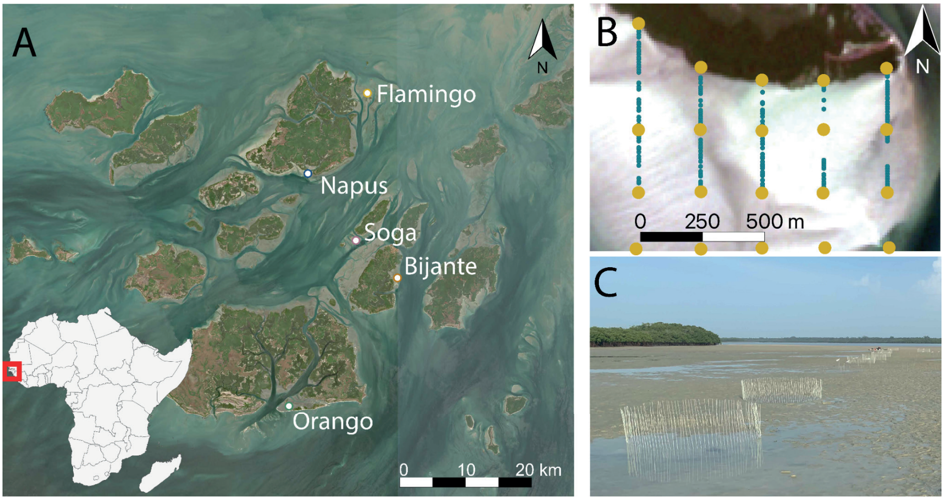


Figure 9.2 (A) Overview of the Bijagós Archipelago in Guinea-Bissau, West Africa (Sentinel-2 L2A, resolution: 10m, True color, 0% cloud cover, date: 2019/03/16). Napus, Orango, Bijante, Flamingo, and Soga are the intertidal flats. (B) An example of the transect survey at Napus (250 m between each transect) perpendicular to the mangrove fringe towards the subtidal area, where dots indicate ray pit abundances (blue) and sample locations of macrozoobenthos cores (yellow). (C) picture of the predator exclosure experimental setup.

Quantifying the extent of benthic ray bioturbation - drone survey

We mapped benthic-ray bioturbation pits of the Napus mudflat with a DJI Mavic 2 Pro drone (RGB) on the 15th and 16th of February 2021. For this, the high-resolution images (ground resolution = 0.5 cm/pixel) taken by the drone were stitched together using PIX4D. The mapped area covered an L-shape section of ~ 4.6 hectares, where the L-shape area was chosen to cover as much intertidal flats heterogeneity (e.g., sediment type and bathymetric elevation) as possible within the drone battery supply for one day. This image was overlaid with 64 squares of 16 m^2 each and positioned to capture as much spatial variation in ray pit abundance as possible. In every square, ray pits were manually annotated by visual observations in QGIS v.3.6.3 (QGIS Development Team 2018). To identify ray pits from other excavations (formed by other organisms or footprints), we color-marked all observed excavations in the field and consequently detected the differences in the size and shape of the excavations on drone images. Other organisms (i.e., other than stingrays) that may bioturbate the sediments of the Bijagós Archipelago are cownose rays, fiddler crabs and calianassid shrimps (Suchanek and Colin 1986, El-Hacen *et al.* 2019, Flowers *et al.* 2021). We identified the ray pits in this study from other excavations based on the size and shape of the pits that relate to the maximum disc width of the ray (~34 cm; Figure 9.1; Leurs *et al. in prep.*). Cownose ray pits (disc width up to 1 m; (Smith and Merriner 1985) are bigger than stingrays (Leurs *et al.* 2023a), and fiddler crabs and calianassid shrimps create smaller excavations (Suchanek and Colin 1986). For each of these squares, we compared the image of February 15th to that of February 16th and counted all newly formed ray pits. We analyzed the distribution of the newly formed ray pits according to normal (linear models; LM) and concentrated distribution (generalized linear models with Poisson or negative binomial distribution) and compared the Akaike Information Criteria for small sample sizes (AICs). To translate ray pit surface coverage into bioturbation rates, we used the amount of newly formed pits and the average pit volume measured in November 2019.

We performed all statistical analyses in R v.4.0.3 (R Core Team 2017). We validated all model assumptions by plotting (1) residuals versus fitted values to verify homogeneity, (2) QQ-plots of the residuals to test for normality and (3) residuals versus each explanatory variable to check for independence. In addition, Shapiro-Wilks's test ($p > 0.05$) and Bartlett's test ($p > 0.05$) were used to test for normality and homogeneity of variance, respectively. Surface bioturbation per day was log-transformed to meet model assumptions and analyzed by LM. Post-hoc comparisons were used to test for significant differences between the five intertidal flats (r-package 'emmeans'; (Lenth 2019). The relationship between pit counts on the 15th and 16th of February was fitted using a linear regression model.

Landscape-scale spatial ray pit distribution – observation surveys across the region

We quantified ray pit occurrence through transect counts for five sites across the archipelago (Figure 9.2B; Bijante = Bijante, Bubaque, N11° 15′ 24.3″ W15° 50′ 09.6″; Flamingo = Banco de Flamingo, Maio, Urok, N11° 33′ 18.1″ W15° 53′ 14.3″; Orango = Adonge, Orangozinho, N11° 02′ 10.2″ W16° 00′ 58.0″; Napus = Napus, Formosa, Urok, N11° 25′ 33.1″ W15° 58′ 59.3″; and Soga = Encromas, N11° 18′ 47.1″ W15° 54′ 01.1″). At each location, we sampled transects (n = 5 per location, but Soga n = 4, with 250 m distance between the transects) that covered the entire morphologic landscape of the intertidal flat and that was accessible by foot (from the edge of the subtidal to the mangrove edge). All ray pits within 1 meter of the transect line were measured along each transect. The length diameter, width diameter, depth radius, and water depth of each ray pit were measured. Additionally, the location of each ray pit was measured at 1cm precision with an RTK dGPS (Trimble R8, GNSS-receiver) connected to a local base station as a reference point. Small benthic rays in the Bijagós Archipelago are mostly represented by the most occurring stingray species, the pearl stingray (*Fontitrygon margaritella*; Leurs *et al.* 2023b). Hence, pit volume was calculated by treating the pits as a semi-ellipsoidal shape based on the body shape of the pearl stingray using equation 1 (O'Shea 2012, O'Shea *et al.* 2012, Myrick and Flessa 2017):

$$pit\ volume = (4/3\,\pi(Lr * Wr * Dr))/2$$

in which Lr is length radius (diameter/2), Wr is width radius (diameter/2) and Dr is depth radius.

The surface area covered with ray pits of the transects was log-transformed and consequently analyzed by LM and Tukey's posthoc comparisons to test for significant differences between the five intertidal flats (r-package 'emmeans'; Lenth, 2019).

Because of the spatial heterogeneity of the intertidal flats, we related the ray pit abundances to environmental parameters. To do so, we measured and/or obtained the parameters of the mudflat characteristics, macrozoobenthos, sediment properties and emergence time. First, we defined mudflat characteristics (i.e., distance to mangrove forests, gullies and subtidal waters) through QGIS based on the habitat classification of (Meijer *et al.* 2021); i.e., mangrove, mudflat and water depth). Habitat characteristics were manually verified by comparing the habitat classification of Meijer *et al.* (2021) to the satellite images (Sentinel-2 L2A, resolution: 10m, True color, 0% cloud cover, date: 2019/03/16) and adjusted if needed. For instance, based on field observations, gullies that were known to remain inundated during low tide were added to the gully map. Second, to look at possible food sources of the rays, macrozoobenthos were sampled in a grid of 250 m spread across each intertidal flat (Figure 9.2B, n = 20 per intertidal flat) with a PVC core of Ø 15 cm to a depth of ~25 cm. Each sample was sieved over a 1 mm round mesh (Compton *et al.* 2013). After sample collection, all macrozoobenthos samples were stored in 10% formaldehyde and identified to species level in the laboratory. After identification, species were dried for 24 h at 60°C and incinerated for 4 hours at 550°C to determine Ash Free Dry Weight (AFDW). Third, sediment samples were taken in the same 250 m grid as the macrozoobenthos samples. To analyze sediment composition, we sampled the top-1 and top-5 cm of the sediment surface with a small core of Ø 2.5 cm and determined the organic matter content of the soil, median grain size D50 (μm) and silt% (grain size <63 μm). For the calculation of organic matter content, the AFDW of sediment samples was determined, and the percentage weight loss on ignition (LOI_{wt}%) was calculated. To measure median grain size and silt%, sediment samples were freeze-dried (-550 C, 48 h), sieved over 1-mm mesh and analyzed with the Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, United Kingdom, serial number 34403/139, model APA 2000 with Hydro G 2000 introduction unit and Autosampler 2000). Last, emergence time was derived from the results of (Granadeiro *et al.* 2021) that estimated exposure with Sentinel-2 satellite imagery.

To correlate the environmental parameters to the ray pit abundances, we performed ordinary kriging to interpolate any missing data points for median grain size D50, silt% and macrozoobenthos AFDW based on the 250 m grid samples (n = 20 samples per intertidal flat with a sampling and interpolation coverage of 0.5-0.75 km^2; r-package: ‘automap’; Hiemstra, 2022) in R (R Core Team 2020). The function ‘autoKrige’ fits a variogram model to the given data set and returns the results of the interpolation: prediction, variance and standard deviation. The environmental parameters of ray pit abundance were modeled with a generalized additive model (GAM) with smooth splines to allow fitting any non-linear pattern (r-package ‘mgcv’; Wood 2017), where intertidal flats were modeled as a random factor. Ray pit abundance was zero-inflated and tested with r-package ‘DHARMa’ (Hartig 2023). We tested if the smooth terms were necessary by running the model with and without smooth terms for each predictor separately. The lowest AIC was reached by including smooth terms on all the predictors, except sediment median grain size D50, and the significance of smoothers was tested via an adapted Wald test (Wood 2017). The GAM’s smoothers were estimated through restricted maximum likelihood to prevent overfitting.

Residual spatial autocorrelation was inspected by fitting a GAM with a tensor product of the coordinates to the residuals of the original GAM (Wood 2017). GAM model selection was performed by ranking all possible subsets of the full GAM based on AICc (r-package 'MuMin'; (Bartón 2022)). The optimal subset approach was used because it performs best when comparing models that contain correlating measurements. Adjusted R-squared values were used to assess overall model performance.

To test for the sensitivity of the ray pits longevity to exposure, we measured the longevity of artificial pits (*n*=20, starting pit size was 25x24x4 [LxWxD]) in two locations with expected high and low exposure to hydrodynamic forces. High exposure locations were situated exposed to the incoming tide at 100-300 m to the subtidal waters, whereas low exposure locations were situated at the mangrove edge, sheltered by the intertidal flat at 300-500 m to the subtidal waters. Measurements were taken for 84 h with a 12-36 h interval depending on accessibility.

Although we expected differences in exposure to hydrodynamic forces, the locations were chosen based on a comparable elevation, with, on average, a relative difference of +8.9 cm at the mangrove edge compared to the exposed location, measured at 1-cm precision with an RTK dGPS (Trimble R8, GNSS-receiver) connected to the local base station as a reference point. Ray pit longevity was analyzed with linear regression models.

Ray bioturbation effects on sediment and macrozoobenthos – exclusion experiment

To test the consequences of benthic ray absence on sediment properties and macrozoobenthos, we experimentally excluded predators (e.g., rays and birds) with a 15-month exclosure experiment. We installed 30 circular experimental plots (diameter of 2 m) in October 2019 (Figure 9.2C). We deployed the following experiment treatments: *i)* predator exclosure (exclosure, *n* = 12), *ii)* effect of exclosure (one-sided, open exclosure; *n* = 6), and *iii)* no exclusion (control; *n* = 12). Predators were excluded with barriers made of glass-fiber sticks (1 x 0.003 m, length x diameter) inserted halfway (50 cm) into the sediment at a 5 cm interval. For the open exclosure, we constructed plots with only half of the circle (Ø 2 m) covered by glass-fiber sticks to test for the geomorphic effects of the exclosure method on sediment properties. These open exclosures were installed with the opening to each of the cardinal directions (*n* = 3 per cardinal direction, north, east, south and west; total *n* = 12). The plots were spaced 3.5m apart in a randomized block design. The contours of the control plots were marked by four sticks, which had no further exclosure function. After counting ray pits in the experimental plots, we could confirm that the exclosures were effective for benthic rays since 0 ± 0% (mean ± s.e.) of the exclosures contained ray pits, compared to 48 ± 6% and 33±6% in the open exclosures and control, respectively (Appendix 9.1). However, the exclosures also seemed to be effective in excluding wading birds since we observed bird tracks in 5 ± 0 % of the exclosures, compared to 42±6% and 45±6% in the open exclosure and control. For the entire duration of the experiment, plots were inspected and maintained for fouling, scouring, and missing sticks once every two months on average. After 15 months of deployment of the exclosures, we sampled macrozoobenthos and sediment properties. The macrozoobenthos were sampled with a PVC corer of ⌀ 15 cm to a depth of ~25 cm, sieved over a 1 mm round mesh (Compton *et al.* 2013), fixated in 10% formaldehyde and identified to species level in the laboratory. After identification, we measured species abundance and biomass. Species were dried for 24 h at 60°C and incinerated for 4 hours at 550°C to determine Ash Free Dry Weight (AFDW). Sediment properties were sampled with a small core of ⌀ 2.5 cm (the top-1 and top-5 cm of the sediment surface) and analyzed for organic matter content of the soil, median grain size D50 (μm) and silt% (grain size <63 μm). To calculate organic matter content (percentage weight loss on ignition (LOI $_{wt}$%)), sediment samples were dried for 24 h at 60°C and incinerated for 4 hours at 550°C. To measure median grain size and silt%, sediment samples were freeze-dried (-550 C, 48 hours), sieved over 1-mm mesh and analyzed with the Malvern Mastersizer 2000 (Malvern Instruments, Worcestershire, United Kingdom, serial number 34403/139, model APA 2000 with Hydro G 2000 introduction unit and Autosampler 2000). In addition, the effect of ray exclusion on sediment dynamics was investigated with sediment erosion pins (Nolte *et al.* 2013). Upon installation in 2019, each plot was equipped with two sediment pins that consisted of a thin one-meter-long metal rod anchored ~85 cm into the sediment, with a loosely fitting metal ring surrounding it at the sediment surface. This allowed us to track maximum erosion, sediment accretion and net change of the sediment's surface elevation over the experimental period of 15 months.

The impact of predatory exclusion on macrozoobenthos was visualized using Non-Metric Multidimensional Scaling (NMDS) (Kruskal and Wish 1978) on Bray-Curtis dissimilarity indices (Clarke and Green 1988) using r-package 'vegan' (Oksanen 2019). For this analysis, rare species, defined as species with less than two total occurrences, were excluded to prevent them from appearing too influential in the graphical representation of the ordination (Poos and Jackson 2011). Differences between the treatments were tested with permutational multivariate analysis of variance (PERMANOVA, 999 permutations), incorporating experimental blocks as a random intercept. To test for the effect of predator exclusion on abiotic parameters, we used linear mixed-effect models (LMM) with ‘block’ as a random factor. Post-hoc comparisons were used to test for significant differences between the effect of predator exclosure, open exclosure and control (r-package ‘emmeans’; Lenth 2019).

Results

Benthic ray sediment bioturbation

To examine benthic bioturbation rates, we surveyed newly formed ray pits and volumes on two consecutive days at the intertidal flat Napus. The distribution of ray pits varied between 0 and 2 newly formed ray pits m^{-2}. The distribution of these pits related to the environmental predictors (distance to creek, distance to mangroves and elevation) was best described according to concentrated foraging patterns (negative binomial distribution) versus random distribution (normal distribution; Appendix 9.2). To estimate the surface that was bioturbated by the excavation of these pits, we used the average pit volume of 1475.87 cm3 (n = 440 at Napus 2019) to calculate the bioturbation rates based on the number of newly formed ray pits on one single 24-hour period in February 2021. To estimate the surface that was bioturbated by the excavation of these pits, we used the average pit volume of 1475.87 cm^3 (*n* = 440 at Napus 2019) to calculate the bioturbation rates based on the number of newly formed ray pits over one single 24-hour period in February 2021. We found that ray pit excavation bioturbated the sediment surface with 3.7±0.4% per day (mean±SE) and up to 14.3% per day. This equals a volume of, on average, 765.3 ± 73.0 cm^{3}m^{-2}day^{-1} measured over one single 24-hour period and is equivalent to a turnover rate of 27 days. The total surface covered with ray pits on the intertidal flats of Napus on the 15th of February was 4.97 ± 0.68% (mean ± s.e.; Figure 9.3).

Consequently, we used the relationship between the total amount of pits and newly formed pits measured in 2021 to estimate the bioturbation rates on all five intertidal flats measured in 2019. The relation between the total amount of ray pits on February 15th and the newly formed pits on February 16th could be described according to linear regression*:* $y = 5.58 + 0.274x$ (Figure 4b, *R2* = 0.52). Implementation of this linear regression on the measurements of November 2019 (start of the experiment, described in section 3.2 below) implied that bioturbation rates at that particular moment ranged between 0.14±0.04 and 0.44±0.10% (mean±SE, Figure 4c, 1-way

ANOVA, $F_{4,19} = 7.1314$, $p < 0.001$). These bioturbation rates in February 2021 were 8.4 times higher at Napus compared to November 2019, and therefore, it is likely that bioturbation rates vary daily, seasonally and/or yearly.

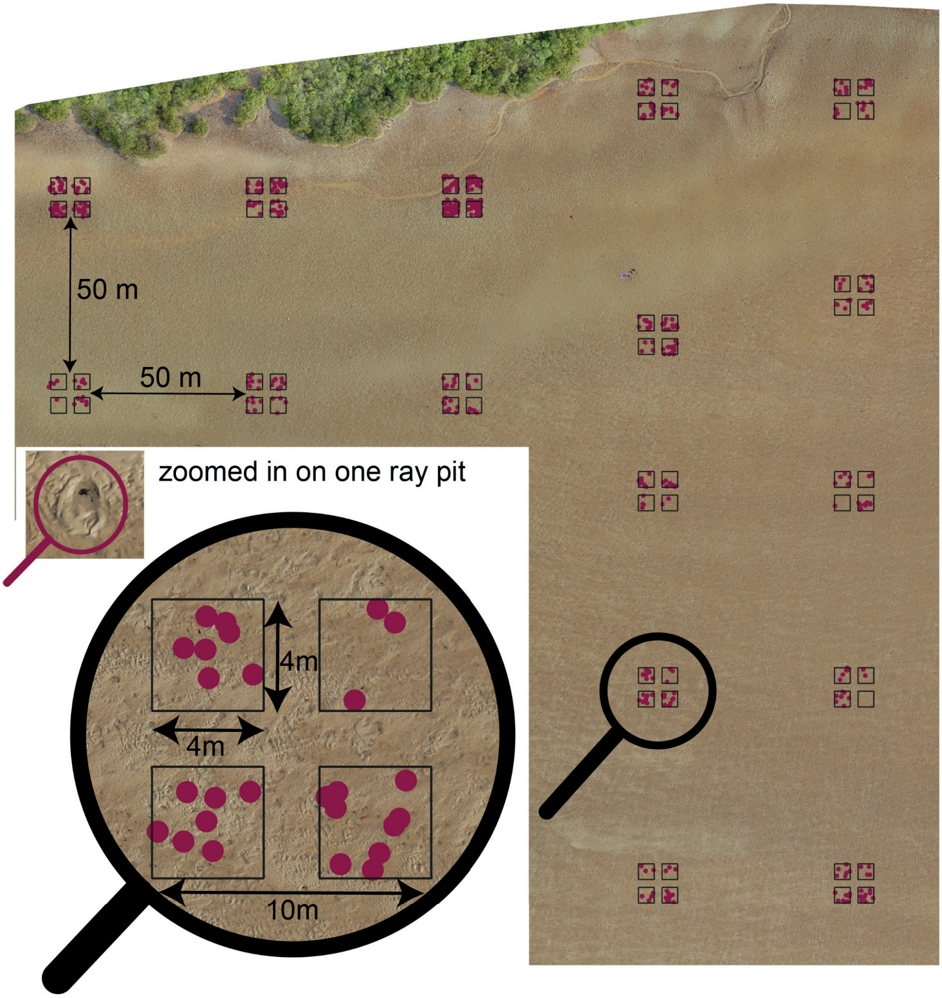


Figure 9.3 Annotations of new ray pits on the tidal flat Napus on February 16th, 2021. An example of one zoomed-in ray pit is shown (insert, top-left). High bioturbation of 3.70 ± 0.35% of the surface area per day was observed and measured over one 24-hour period (mean ± SE). This bioturbation had a volume of 765.31 ± 72.97 cm3 m-2 day-1 (mean ± SE).

Benthic ray pit abundance, spatial distribution and longevity

We determined if the abundance of ray pits could be influenced by the intertidal flat morphology. For example, ray pits erode faster under highly hydrodynamic conditions (O'Shea *et al.* 2012). We counted the number of ray pits at five intertidal flats through a field survey in November 2019. We found that the total excavated surface area significantly differed among intertidal flats and ranged between 0.39 ± 0.50 and 1.30 ± 1.64% of the total intertidal flat surface area (mean ± s.e.) (Figure 4a, one-way ANOVA, $F_{2,19} = 5.566$, $p = <0.001$). In addition, there was a great level of ray pit spatial heterogeneity within the intertidal flats. To explain the spatial distribution of ray pits within the intertidal flat landscape, we investigated the relation of pit abundance to environmental parameters (Table 9.1). The distribution of these ray pits could be predicted (deviance explained 35.3%) based on sediment characteristics: median grain size D50, silt%, organic matter content, distance to the subtidal and emergence time (Table 9.1).

To test for a relationship between ray pit abundance and morphology, we measured the longevity of hand-made ray pits at two locations with differing exposure but comparable elevation (on average +8.9 cm at the mangrove edge compared to the exposed location). We found a 3.5 times faster pit volume decay rate at the exposed location with a coefficient of -2.87 ($R^2 = 0.88$), compared to -0.81 ($R^2 = 0.46$) at a location sheltered by the intertidal flat itself (mangrove edge; Appendix 9.3). This means that, after 24 hours, only 17.2% of ray pit volume remained in exposed areas, in contrast to 74.0% of the original pit volume remaining in sheltered areas.

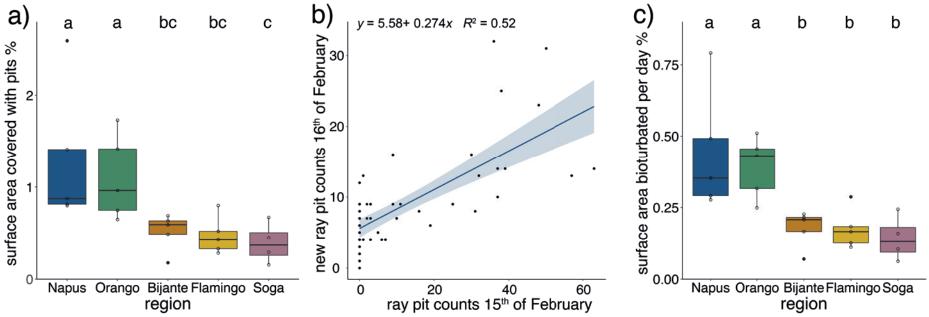
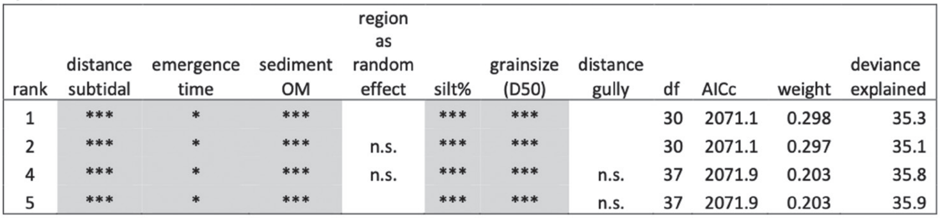


Figure 9.4 (A) High tidal flat surface area covered with ray pits in percentage, based on the observational survey with transects (n = 5 per tidal flat, Soga n = 4) in November 2019. Letters indicate significant differences tested with Tukey's posthoc; **(B)** relation between ray pit counts on the 15th of February and newly formed pit counts on the 16th of February 2021. The surface of the tidal flats bioturbated per day was calculated using linear regression and the ray pit abundances of Figure 9.3, resulting in **(C)** total surface area percentage bioturbated per day per tidal flat in November 2019 (n = 5 per tidal flat, Soga n = 4).

Predator exclusion effects on sediments and macrozoobenthos

The exclusion of predators such as rays and shorebirds created muddier and more stabilized sediments, a higher abundance of Capitellidae worms, and a greater biomass of Malacostraca over time (15 months). Silt and organic matter content were 20% (Tukey, $p<0.01$) and 10% (Tukey, $p<0.001$) higher, respectively, in the top-5 sediment layer of the exclosures than in the control plots in February 2021 (Table 9.2), while there were no differences in sediment properties at the start of the experiment (November 2019, Appendix 9.1). In addition, the exclosures showed -17% sedimentation (Tukey, $p<0.01$) and -43% erosion (Tukey, $p<0.0001$) after 15 months (Table 9.2), indicating higher sediment stability. Furthermore, we found no effects of the open exclosures on sediment properties (e.g., median grain size, silt%, organic matter content, erosion, accretion) as the open exclosures yielded results similar to the controls (Table 9.2). We can therefore safely assume that the effects of the exclosures on sediment properties are the result of predator exclusion and not an effect of the exclosure structures themselves. Moreover, predator exclusion altered the macrozoobenthic community composition (after 15 months) based on species biomass (Figure 5; PERMANOVA, n = 999, $F = 6.38$, $p < 0.001$) and species abundance (Appendix 9.4; PERMANOVA, n = 999, $F = 3.52$, $p < 0.01$). In February 2021, this difference could partly be explained by a 1.8 times higher abundance of polychaete worms of the Capitellidae family and a 4.0 times higher biomass of Malacostraca in the exclosure compared to control, while a 0.6 times lower abundance of both Pilargidae and Nereididae was observed (Appendix 9.5, 9.6). The biomass of the bivalves *Tagellus adonsonii* and *Senilia senilis* in the exclosure are responsible for outliers at both the start (three times higher compared to control in November 2019) and end (25 times higher compared to control in February 2021) (Appendix 9.5, 9.6). .

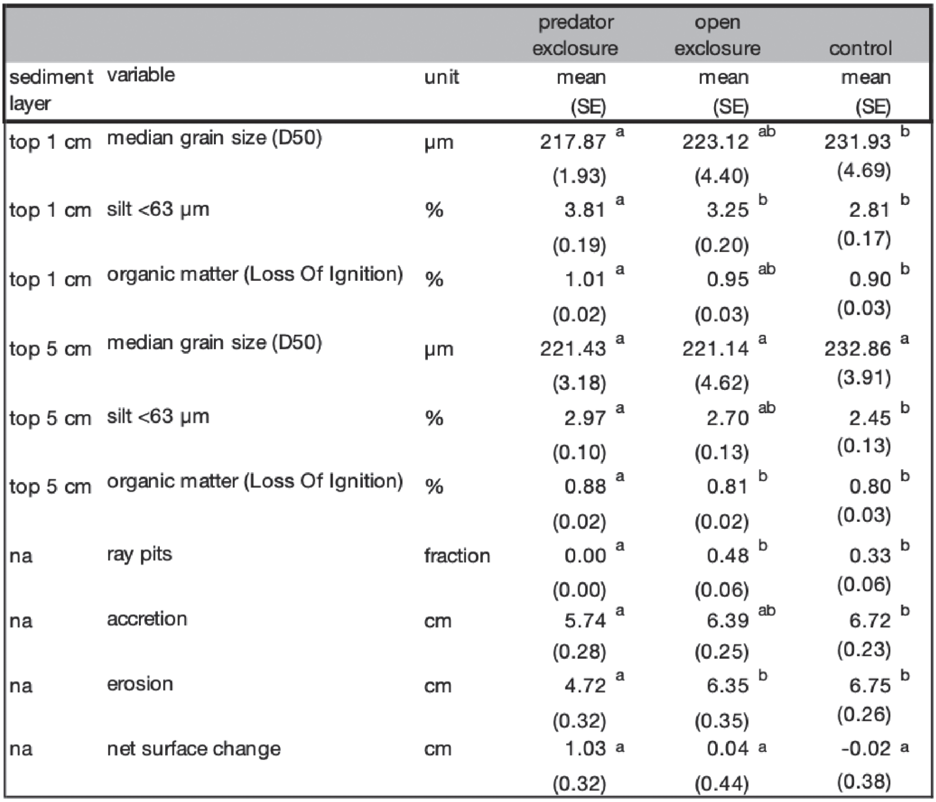
Table 9.1 Significance of smoothers and model summary statistics of four best model subsets ranked by lowest AICs of the GAM predicting ray pit abundance. The predictors are distance to subtidal water, emergence time, sediment median grain size D50 in µm, sediment silt%, sediment organic matter content (OM), and region of the tidal flats as a random effect. If the environmental parameter is included in the model, it shows a significance level. Therefore, empty cells indicate that the specific parameter is not included in that model. The ray pit abundance data includes all five flats, with the flat as a random factor. ***<0.001, **<0.01, ns means not significant.



rank	distance subtidal	emergence time	sediment OM	region as random effect	silt%	grainsize (D50)	distance gully	df	AICc	weight	deviance explained
1	***	*	***		***	***		30	2071.1	0.298	35.3
2	***	*	***	n.s.	***	***		30	2071.1	0.297	35.1
4	***	*	***	n.s.	***	***	n.s.	37	2071.9	0.203	35.8
5	***	*	***		***	***	n.s.	37	2071.9	0.203	35.9

At the start of the experiment, the macrozoobenthic communities did not differ between the exclosure and control for both species' biomass and abundance (Appendix 9.7, 9.8; PERMANOVA, n = 999, abundance: *F* = 0.53, *p* = 0.809, biomass: *F* = 0.76, *p* = 0.674)

Table 9.2 The effects of predator exclosure on sediment properties, accretion and erosion levels compared to the open exclosure and control treatments. Letters indicate significant differences tested with Tukey's post-hoc.



			predator exclosure	open exclosure	control
sediment layer	variable	unit	mean (SE)	mean (SE)	mean (SE)
top 1 cm	median grain size (D50)	μm	217.87^{a} (1.93)	223.12^{ab} (4.40)	231.93^{b} (4.69)
top 1 cm	silt <63 μm	%	3.81^{a} (0.19)	3.25^{b} (0.20)	2.81^{b} (0.17)
top 1 cm	organic matter (Loss Of Ignition)	%	1.01^{a} (0.02)	0.95^{ab} (0.03)	0.90^{b} (0.03)
top 5 cm	median grain size (D50)	μm	221.43^{a} (3.18)	221.14^{a} (4.62)	232.86^{a} (3.91)
top 5 cm	silt <63 μm	%	2.97^{a} (0.10)	2.70^{ab} (0.13)	2.45^{b} (0.13)
top 5 cm	organic matter (Loss Of Ignition)	%	0.88^{a} (0.02)	0.81^{b} (0.02)	0.80^{b} (0.03)
na	ray pits	fraction	0.00^{a} (0.00)	0.48^{b} (0.06)	0.33^{b} (0.06)
na	accretion	cm	5.74^{a} (0.28)	6.39^{ab} (0.25)	6.72^{b} (0.23)
na	erosion	cm	4.72^{a} (0.32)	6.35^{b} (0.35)	6.75^{b} (0.26)
na	net surface change	cm	1.03^{a} (0.32)	0.04^{a} (0.44)	-0.02^{a} (0.38)

Discussion

Rays are sensitive to overfishing and rapidly disappearing from intertidal flat ecosystems (Dulvy *et al.* 2021). Rays can be important in determining the community structure and morphology of intertidal flats through natural physical disturbance by bioturbating the sediment. Bioturbation is a key factor in sediment transport, porosity and permeability (Thistle 1981, Thrush *et al.* 1991, Meysman *et al.* 2006). However, the ecological role of these foundation species in intertidal ecosystems is still poorly understood. We therefore linked ray bioturbation – and the absence of this behavior – to landscape-scale intertidal flat geomorphology in a relatively less-exploited (i.e., high abundance of benthic rays) tropical intertidal system (Leurs *et al.* 2023b).

These ray abundances are estimated based on small-scale fisheries ray catches by Leurs *et al.* (*in prep.)* using satellite-based vessel counts and a short-term observer program that estimated that 896 to 2,685 rays were captured daily in 2020 in the Bijagós Archipelago (Leurs *et al. in prep.*). We found that benthic rays affect intertidal flat sediment dynamics by digging excavations and bioturbating 3.7% of the total sediment surface per day over one single 24-hour period. This implies that the entire sediment surface area is reworked by rays every 27 days. These bioturbation rates varied substantially on a landscape level, among years, intertidal flats and within one intertidal flat landscape. Furthermore, the absence of natural physical disturbance by rays, simulated by a long-term exclosure experiment, increased sediment stability (reduced erosion and accretion) and increased silt% and organic matter content in the top sediment layer.

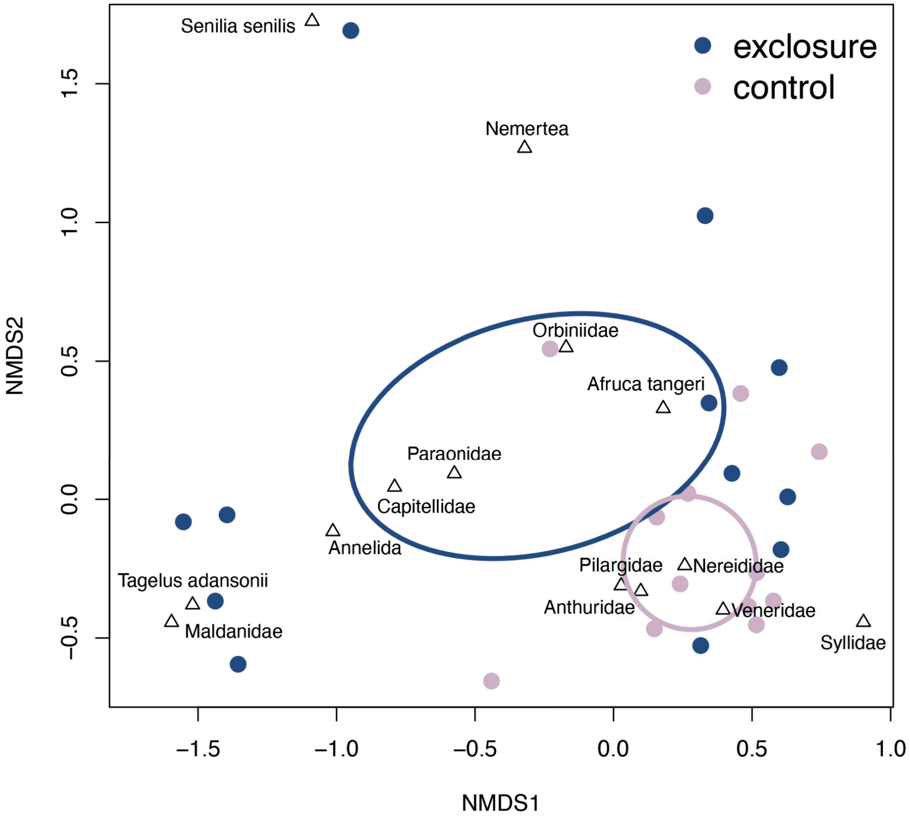


Figure 9.5 Ordination of taxa composition based on species biomass (ash-free dry weight m^{-2}) in the predator exclosures compared to the control plots without any exclusion visualized with Non-Metric Multidimensional Scaling (nMDS) on Bray-Curtis dissimilarity indices and reliable ordination (stress value < 0.2). Ellipses indicate the precision of the estimated centroid (SE) with a 95% confidence interval.

This indicates the importance of natural physical disturbance by benthic rays on intertidal flat biogeomorphology. In addition, the long-term (15 months) exclosure experiment changed the macrozoobenthos community composition by a higher abundance of Capitellidae worms and a greater biomass of Malacostraca over time. Although we were unable to separately exclude rays or wading birds in the predator exclosure experiment, we can safely assume that the bioturbation effects are due to ray excavation, given that birds feed without bioturbating the sediment surface (Lourenço *et al.* 2017, 2018). Furthermore, previous research found that bioturbation by benthic rays can change the sediment biogeochemistry of sandflats by rapid remineralization of organic matter, slowed flushing near the ray pits and increased reactive carbon supply (D'Andrea *et al.* 2002). Hence, overexploitation of benthic rays may alter the ecosystem functioning of threatened intertidal flat seascapes.

Benthic rays can substantially alter intertidal flat sediment turnover by sediment bioturbation, and the magnitude of sediment displacement rates (mean of 765.31 $cm^3m^{-2}day^{-1}$) found in this study further underlines the importance of these ray-induced processes for intertidal flat morphology. The sediment bioturbation rates that we found (on average 3.7% and a maximum of 14.3% day^{-1} over one single 24-hour period) were higher than the previously reported stingray bioturbation rates e.g., 2.42% in seven days in Ningaloo reef in Australia (Grant 1983, Sherman *et al.* 1983, O'Shea *et al.* 2012) or 1.4% day^{-1} on intertidal sand flats of the North Island of New Zealand (Thrush *et al.* 1991). Our sediment displacement rates fall within the range of previously reported studies (Lynn-Myrick and Flessa 1996, O'Shea *et al.* 2012). However, previous research elaborates that benthic ray bioturbation has the most relevance at the micro- and mesoscale (O'Shea *et al.* 2012) or studied at smaller tidal areas (0.11 km^2 and only one intertidal flat; (Takeuchi and Tamaki 2014), we demonstrated that ray bioturbation plays a significant role on a landscape-scale throughout the region (study area of 0.5-0.75 km^2 per intertidal flat * five intertidal flats). This is comparable to the landscape scale at which flamingos and fiddler crabs create essential microhabitats in Mauritanian intertidal flats (El-Hacen *et al.* 2019). Bioturbation rates may vary across studies because of differences in local ray densities, species-specific bioturbating behavior and body size, or the visibility of the pit on the intertidal flat surface (Flowers *et al.* 2021).

Benthic ray bioturbation rates are influenced by the ray densities (biotic) and pit longevity (abiotic). First, ray densities are affected by the season or year (Leurs *et al.* 2023b). Leurs *et al.* (2023b) found that seasonal differences in species richness and species composition of elasmobranch are caused by changes in stingray (the pearl whipray *Fontitrygon margaritella)* abundances, and that species composition differed between non-protected and protected areas when seasonality is taken into account. In addition, we found 8.4 times higher bioturbation rates in February 2021 compared to November 2019, and (Thrush *et al.* 1991) observed a prevalence of rays during summer (November to March in New Zealand). Likewise, industrial fishing activities show the highest mean catches of benthic rays in April-June along the coast of Guinea-Bissau (Leurs *et al.* 2021). Second, ray densities can vary among intertidal flats within the region. For example, our study shows a bioturbation rate ranging from 0.2% to 14.3% per day. Third, ray spatial distribution can differ within the intertidal flat landscape because of spatial heterogeneity such as food availability (Hines *et al.* 1997, Ajemian and Powers 2012), predator risk (Strong *et al.* 1990, Stephens *et al.* 2007) and the risk of entrapment in areas that will fall dry with the receding tides (Brinton and Curran 2017, Leurs *et al.* 2023a). On the other hand, we found that exposure to hydrodynamic forces of the intertidal flat played an important role in the longevity of the ray pits (abiotic) as a result of more exposure to hydrodynamic forces and less cohesive soil (Wang *et al.* 2019). Our study showed that only 17.2% of pit volume was left after 24 h in exposed areas compared to 74.0% in an area sheltered by the intertidal flat. Thus, shorter longevity (<1 day) of ray pits in highly exposed areas might give an underestimation of benthic ray bioturbation. In summary, the interplay of biotic and abiotic factors determines the measured intertidal flats' bioturbation rates by benthic rays and, in addition to bioturbation, benthic rays further impact the environment by foraging on macrozoobenthos (Lynn-Myrick and Flessa 1996, O'Shea *et al.* 2013, Lim *et al.* 2019).

We found that predator exclusion significantly changed the macrozoobenthic community, specifically higher Capitellidae abundances and malacostraca biomass. However, these results should be interpreted with caution since we were not able to exclude rays only, but also excluded shorebirds. Previous research observed no impact and suggested ineffective ray exclusion (O'Shea 2012) or used a limited number (*n*=2) of replicates and reported scouring (VanBlaricom 1982). In addition, (Thrush *et al.* 1994) found fewer bivalve recruits in predator (ray + bird) exclosure but could not distinguish ray and bird effects due to seasonality. In the Bijagós, the most abundant meso-predatory ray, *F. margaritella*, shows a generalist's diet with relative contributions of 30%–35% by crustaceans and 17%–25% by polychaetes (Clements *et al.* 2022). These dietary preferences match the observed community changes in the exclosure experiment. Overall, a ray's turbulent foraging strategy may especially affect long-lived, sedentary species (O'Shea 2012, Jacobsen and Bennett 2013, Freitas *et al.* 2019). As the standing macrozoobenthic biomass in the Bijagós Archipelago is, on average, low compared to other intertidal flat ecosystems (Lourenço *et al.* 2018, Meijer *et al.* 2021), it is likely that the observed high ray pit abundances (up to a mean of 1.30% per total surface area), combined with low macrozoobenthic biomass, indicate a high foraging pressure by benthic rays and other (meso-) predators such as shorebirds. Shorebirds are predators with small trophic niches that feed without bioturbating the mudflat (Catry *et al.* 2016, Lourenço *et al.* 2017, 2018). Shorebirds in the Bijagós Archipelago forage on fiddler crabs, polychaetes (*Nereis*, *Glycera* and *Marphysa*) and the bivalve *Dosinia isocardia* (Lourenço *et al.* 2017) but consume, in general, a high diversity of prey (Correia *et al.* 2023). Shorebirds are major players in intertidal food webs because they occupy a central niche (Mathot *et al.* 2018). Recent findings suggest that (meso)predators such as sharks and rays (i.e., high-tide predators in the intertidal) occupy a similar central niche as shorebirds in intertidal food webs and should therefore be considered in intertidal ecology (Leurs *et al.* 2023a). High foraging pressure of rays may even cause a food conflict with shorebirds foraging on the same intertidal flats and competing for the same scarce prey species (Lourenço *et al.* 2017, 2018), and affect intertidal, subtidal and terrestrial food webs through shorebird migration along the East Atlantic Flyway.

The importance of ray bioturbation to the ecosystem depends on the magnitude of other environmental and biotic factors that can disturb the sediment, such as tidal waves and currents, extreme weather events, and the impact of other bioturbating organisms. High forces of water movement can displace large volumes of sediments that may overrule the impact of ray bioturbation. For example, (D'Andrea *et al.* 2002) described that ray pits are short-term depositional centers for reactive organic matter that alter the sediment structure for 1 – 4 days. This study is limited by the information we collected regarding sediment displacement rates of intertidal flats controlled by water movement. However, it is known that the Bijagós Archipelago is a relatively stable intertidal ecosystem with low changes in the intertidal flat area compared to other intertidal areas of the world (Murray *et al.* 2019, 2022). In addition, West Africa has relatively low chances of extreme weather events such as cyclones because most Atlantic tropical cyclones are developed in the West African region, moving from east to west (Goldenberg and Shapiro 1996, Hopsch *et al.* 2007). Moreover, we observed a low presence of burrows from other bioturbation species, such as calianassid shrimps (Calianassidae), that can overturn sediments at an estimated peak rate of 0.47 - 0.56 m^{-3} m^{-2} $year^{-1}$ (Suchanek and Colin 1986, Myrick and Flessa 2017). Although this study has limitations, our results show that short-term ray bioturbation effects on the sediment are maintained at a landscape scale and may co-shape intertidal flat morphology and abiotic settings.

Our study showed that complex biogeomorphic interactions, in which organisms influence sedimentary processes, underpin intertidal flats ecosystem functioning. The protection of bioturbating species should be better integrated into coastal management plans for intertidal flat conservation, given that the natural physical disturbance by rays plays an important role in sediment turn-over rates and structuring of the macrozoobenthic community on landscape scales. Since intertidal flats are highly connected ecosystems globally, the need for protection, both locally and internationally, on a highly interconnected habitat level is further emphasized. For example, fishing activities in adjacent marine habitats affect the ray population in intertidal ecosystems (Dulvy *et al.* 2021, Leurs *et al.* 2021). Hence, disruption of intertidal flats' high ecological value can affect other connected ecosystems and vice versa.

Conclusion

We conclude that benthic rays affect landscape-scale sediment processes and community structure through bioturbation and, thus, intertidal flat biogeomorphology. This study highlights that local ecological processes (ray bioturbation) play a significant role at the landscape scale. Neither marine nor terrestrial protected areas are developed to prioritize intertidal flat conservation, and intertidal flat conservation generally focuses on total coverage instead of targeting valuable ecosystem services or species (Dhanjal-Adams *et al.* 2016, Hill *et al.* 2021). Therefore, coastal management strategies to protect intertidal ecosystems may benefit from an integral and connective approach linking the subtidal offshore (industrial) fishing activities to intertidal ecosystem functioning. Changes in species abundance as a result of offshore fishing activities that target highly mobile species, such as benthic rays that migrate in both subtidal and intertidal waters, can affect sedimentary processes in the intertidal area. This has associated consequences for species composition, for example, the dominance of species due to reduced physical disturbance.

SECTION IV

Conservation

BOX F: PUTTING SHARKS ON THE MAP: A GLOBAL STANDARD FOR IMPROVING SHARK AREA-BASED CONSERVATION

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Area-based conservation is essential to safeguard declining biodiversity. Several approaches have been developed for identifying networks of globally important areas based on the delineation of sites or seascapes of importance for various elements of biodiversity (e.g., birds, marine mammals). Sharks, rays, and chimeras are facing a biodiversity crisis, with an estimated 37% of species threatened with extinction driven by overfishing. Yet spatial planning tools often fail to consider the habitat needs critical for their survival. The Important Shark and Ray Area (ISRA) approach is proposed as a response to the dire global status of sharks, rays, and chimaeras. A set of four globally standardized scientific criteria, with seven sub-criteria, was developed based on input collated during four shark, biodiversity, and policy expert workshops conducted in 2022 (**Figure F1**). The ISRA Criteria provide a framework to identify discrete, three-dimensional portions of habitat important for one or more shark, ray, or chimaera species, that have the potential to be delineated and managed for conservation. The ISRA Criteria can be applied to all environments where sharks occur (marine, estuarine, and freshwater) and consider the diversity of species, their complex behaviors and ecology, and biological needs. The identification of ISRAs will guide the development, design, and application of area-based conservation initiatives for sharks, rays, and chimaeras, and contribute to their recovery.

CRITERIA	DESCRIPTION
Criterion A Vulnerability	Areas important to the persistence and recovery of threatened sharks. **This criterion must be associated with an additional criterion.*
Criterion B Range Restricted	Areas holding the regular and/or predictable presence of range-restricted sharks, that are occupied year round or seasonally.
Criterion C Life-History	Areas that are important to sharks for carrying out vital functions across their life-cycle (i.e., reproduction, feeding, resting, movement, or undefined aggregations).
Sub-criterion C1 Reproductive Areas	Areas that are important for sharks mating, birth, egg laying, or providing refuge and other advantages to the young.
Sub-criterion C2 Feeding Areas	Areas that are important for shark nutrition at one or more life-cycle stages.
Sub-criterion C3 Resting Areas	Areas that are important for sharks to conserve energy, and are often related to environmental conditions or temporal factors.
Sub-criterion C4 Movement	Areas used by sharks regularly or predictably during their movements, such as migrations, which contribute to connectivity of important areas.
Sub-criterion C5 Undefined Aggregations	Areas where an aggregation or assemblage of sharks regularly and/or predictably occurs, year round or seasonally, but the function of the aggregation is currently unknown.
Criterion D Special Attributes	Areas important for sharks considered for distinct biological, behavioural, or ecological attributes (unique or associated with a unique habitat type), or which support an important diversity of species.
Sub-criterion D1 Distinctiveness	Areas where sharks display distinct biological, behavioural, or ecological characteristics.
Sub-criterion D2 Diversity	Areas that sustain an important diversity of sharks.

Figure F1 The Important Shark and Ray Areas (ISRAs) criteria.

Chapter 10

Opportunities and challenges in value chain analysis for sustainable management of sharks and rays

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Abstract

Studies on elasmobranch trade have often focused on a single commodity: shark fins. Such a narrow focus can result in an incomplete understanding of the socio-cultural importance of sharks, limiting discussion on the range and efficacy of potential management interventions. Assessments must be performed across the value chain from fisher to retail vendor to better conserve vulnerable elasmobranch species, offering a broader view of capture, use, and trade. Here, we collate insights from shark value chain assessments conducted in eight countries (Mexico, Peru, Guinea-Bissau, India, Bangladesh, Sri Lanka, Indonesia and Fiji) spanning five continents. Approaches and processes implemented in a shark value chain analysis (VCA) were reviewed to understand: (1) better approaches and tools and (2) to collate shared experiences. Our results demonstrate that VCAs broaden the outlook of fishery and trade assessments when capturing a more comprehensive range of economic and socio-cultural aspects (e.g., livelihoods, cultural use of commodities) of trade in all shark commodities. Time invested in various components of assessments produced different outcomes, with considerable returns from stakeholder selection, survey design, and assessor/stakeholder relationship building. Contrastingly, results demonstrated that efforts in communication with stakeholder groups and policymakers could be further streamlined to focus on key results using a variety of communication formats. Outcomes from this study offer guidance to those embarking on shark VCAs, facilitating improving the assessment process and outcomes.

Introduction

Many sharks and rays (hereafter referred to as ‘sharks’) targeted or inadvertently captured in fisheries have slow life history traits, such as late maturity and low fecundity, that make them vulnerable to overexploitation and their populations slow to recover (Castillo-Géniz *et al.* 1998; Dulvy *et al.* 2021). Due to stressors such as overfishing and habitat degradation, approximately one-third of all Chondrichthyan species (i.e., sharks, rays and chimeras) are currently threatened with extinction (Dulvy *et al.* 2021). With many sharks caught as bycatch, their outlook is uncertain due to challenges preventing their effective conservation (Juan-Jordá *et al.* 2022; Sherman *et al.* 2023). Recognition of the important ecological (e.g., Heupel *et al.* 2014, Bird *et al.* 2018) and socio-cultural system roles (e.g., Leeney and Poncelet, 2015) of sharks has led to a strengthening in their management and conservation. Management measures are either implemented at an international, national or regional level (Techera and Klein, 2011; FAO, 1999). However, the cross-border movements of sharks (Veríssimo *et al.* 2017; Nosal *et al.* 2021), and their fisheries and trade, can complicate management approaches, emphasizing the need for fishery and trade controls over various spatial scales and across jurisdictional boundaries (Friedman *et al.* 2018). Issues concerning the (mis)identification and mislabeling of shark species further complicate the management of trade and fisheries of these species (Hasan *et al.* 2023).

Multi-lateral environmental agreements like the Convention on International Trade in Endangered Species of Wild Fauna and Flora, also known as CITES, can contribute to shark conservation (https://cites.org/eng). Species listed on Appendix II of the convention come under provisions by a country to ensure both legality and sustainability of trade in that species and its commodities. Global efforts to strengthen governance have focused on shark fin due to its importance in driving exploitation and trade, stemming from its high value (Shiffman and Hueter, 2017). Focusing exclusively on this perspective of shark use fails to incorporate and manage other drivers of use and trade, such as the importance of other commodities like shark meat. Some information on other commodities such as meat (Bornatowski *et al.* 2018, Karnad *et al.* 2020, WWF, 2021), liver/squalene (Hasan *et al.* 2017), and skin (Dent and Clarke, 2015) exist, but background and time-series information remains limited. Additionally, the challenging task of identifying shark commodities other than fins in trade complicates efforts to improve sustainability (Hasan *et al.* 2023). For example, shark fins are an easily recognizable commodity, although identifying fins at the species level remains an ongoing challenge. Other shark commodities like meat are often destined for local or regional markets (Dent and Clarke, 2015) and are less easily discernable across shark species and from other fish. To address these issues, sharks of the Carcharhinidae family were all listed under CITES to ease implementation (CITES, 2022).

Once a species is CITES listed, parties are bound to deliver on the convention's provisions, yet many face challenges in implementing conservation strategies due to the limited availability of resources and capacity (Parker *et al.* 2012, Adenle *et al.* 2015). In response, some authorities have instituted retention or trade bans despite such bans being associated with potential increases in non-compliance across existing markets (Friedman *et al.* 2018).

Traditionally, investment in fisheries management predominantly focuses on understanding the population status of a species to guide levels of exploitation (e.g., with monitoring of catches and stock assessments to determine a measure of maximum sustainable yield, see Methot and Wetzel, 2013; Hilborn, 2020). Although stock assessments provide indicators and measures of the status of resource populations (Kleiber *et al.* 2009, Punt *et al.* 1998), translating this information into practical and effective management solutions consistent with the importance of sharks for people and the environment remains an ongoing challenge (Castellanos-Galindo *et al.* 2021). In addition, shark declines are often related to trade in shark-derived commodities (Pacoureau *et al.* 2021), highlighting the need to address knowledge gaps surrounding the entire value chain (VC) of use and trade in sharks. Recently, studies have suggested more holistic approaches to understanding the entire value chain of shark fisheries, aiming to disincentivize the unsustainable use of sharks (e.g., Booth *et al.* 2019; Haque *et al.* 2021). These approaches have been proposed to design and deliver a combination of locally appropriate management actions rooted in sustainability and inclusiveness (e.g., the inclusion of local community members and their needs in the process),

Gaining insights into the primary considerations underlying how sharks are fished, used, and sold offers broader opportunities for leverage points involved in adaptive management (Garcia *et al.* 2003, Staples and Funge-Smith, 2009). These types of insights are sought through value chain analysis (VCA) approaches (e.g., see Hellin and Meijer, 2006). In a VCA, researchers aim to map the socio-economic and ecological aspects of the full range of activities in a fishery, from the moment of commodity acquisition to disposal after use by the final consumer. This information identifies opportunities for improved or new policies for the adaptive management of sharks.

The social importance of sharks needs to be considered when designing policy changes, as a large variety of stakeholders depend on sharks due to the breadth of shark-derived commodities traded and the tourism sector relying on sharks.

In this study, we aim to identify crucial steps in conducting shark VCAs and provide important lessons learned by researchers experienced in conducting shark VCAs. To assist those designing and conducting shark VCAs, assessment programs currently active across five continents were reviewed to:

(1) document better approaches and tools, and

(2) collate shared experiences and current understanding.

The results of this study highlight how socio-cultural and economic aspects of shark fishery and trade management are included in shark VCAs. Importantly, recommendations are provided for researchers considering the added value, including which approach to take in running assessments to support the adaptive management of shark value chains.

Methods

Development of Guidance for Shark VCAs

To assist in VCAs focused specifically on sharks, the Food and Agriculture Organization of the United Nations (FAO) is developing generic shark and ray VCA guidance in close cooperation with managers and researchers. The guidance is aimed at fishery managers to support their efforts to assess the current state, management and sustainability of shark value chains. To date, the development of the guidance has been informed by ongoing work of the FAO under the Shark International Plan of Action (IPOA) umbrella (FAO, 1999) and expert meetings (ICAR, 2019) to assist country planning and implementation of shark VCAs. FAO's draft guidance describes five essential 'steps' of the VCA process, each describing respective 'tasks' to undertake in delivering a shark VCA (Table 10.1).

Data collection

Researcher teams from eight countries involved in shark VCAs were requested to participate in this study to share experiences and recommendations. Researchers were selected based on the workshop by the FAO and the Central Marine Fisheries Research Institute of India (CMFRI; Kochi, India 2019) or based on authorship of academic publications on shark value chains.

Lead researchers of participating teams were asked to collaborate in the study by:

(1) completing a semi-structured interview to describe their shark VCA process and experiences;

(2) sharing their shark VCA surveys and outputs (e.g., survey questionnaires, reports, draft manuscripts) for review; and

(3) taking part in a structured questionnaire to quantify the effort invested in relation to outputs and outcomes achieved in different VCA activities and tools.

Table 10.1 Overview of the steps and tasks for shark value chain assessments as described in the (draft) guidance by the Food and Agriculture Organization of the United Nations (FAO). Discussed during an expert workshop in Kochi (India) in 2019 (ICAR, 2019).

Step	Task
1. Establishment of a Monitoring, Evaluation and Reporting Process.	1.1. Identifying and documenting value(s) and objective(s) of the assessment.
	1.2. Searching out available information.
	1.3. Considering key stakeholders and key stakeholder groups.
	1.4. Preliminary value chain mapping and selection.
2. Designing a Survey.	2.1. Determine what will be measured.
	2.2. Decide on the form of the survey.
3. Deploying a Survey	3.1. Logistical planning of survey deployment.
	3.2. Survey deployment.
4. Management and Use of Data	4.1. Formatting and consolidating data.
	4.2. Data processing and analysis.
5. Communication and Adaptive Management	5.1. Identifying an adaptive management framework.
	5.2. Monitoring implementation and response of adaptive management.

The work of all participating teams covered a total of 94 ports and trade sites across Mexico, Peru, Guinea-Bissau, India, Sri Lanka, Bangladesh, Indonesia, and Fiji (Figure

10.1). Together, these countries are responsible for 33.1% (2010-2021) of production and 9.8% in exports (2019-2021) of elasmobranch commodities. However, production varies significantly amongst countries. For example, Guinea-Bissau is only responsible for 0.001%, and Indonesia has a 15.6% share in global reported production (FAO, 2023).

Semi-structured interviews

Semi-structured interviews, comprising 14 open-ended questions (Appendix 10.1), were conducted to understand approaches and tools used in shark VCAs and to identify lessons learned during their analysis. Participants were asked to describe their VCA process from planning and delivery to outputs, outcomes and communication (i.e., following the guidance steps and tasks described in Table 10.1). Participating researchers were also asked about their main objectives in conducting a VCA to determine if the primary objective of the VCA was: i) improving the population status of sharks (referred to as 'Resource'), ii) improving the livelihoods of fishery participants (referred to as 'Fisher'), or iii) measuring the impact(s) and effectiveness of management interventions by the relevant fisheries authority (referred to as 'Management'). In addition, for each step of their shark VCA, researchers were asked to report on the 'better' and 'poor' practices they had identified during the implementation of the shark VCA. These recommendations are defined as what was effective in terms of effort allocation and generated outcomes for adaptive management ('better practices') and examples of what was less effective or required adaptation during the process ('poor practices'). All recommendations were included in this study but were condensed and merged when multiple researchers referred to similar experiences.

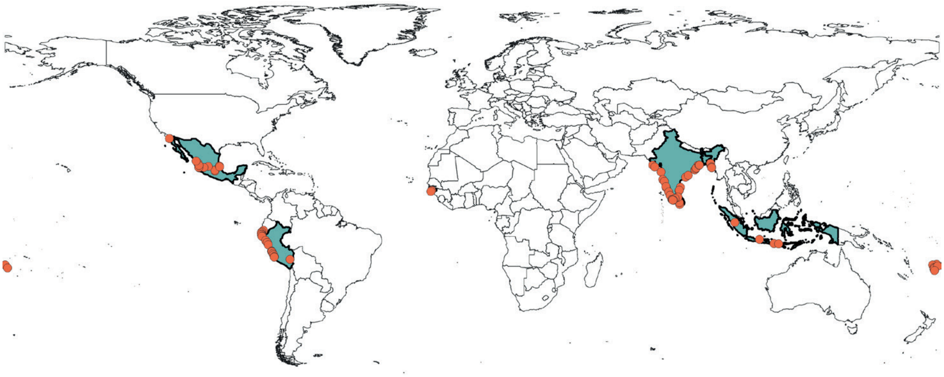


Figure 10.1 The global distribution of landing sites and ports where shark value chain assessments included in this study were conducted. Red points indicate single ports or landing sites where sampling was conducted, and countries of sampling studies are colored in blue (Fiji, Mexico, Peru, Guinea-Bissau, India, Sri Lanka, Bangladesh and Indonesia).

Questionnaire and output reviews

Researchers were asked to share questionnaires used in their respective shark VCA, and any (draft) outputs and outcomes resulting from their assessment (e.g., reports, manuscripts) were also shared. For each study, the VCA questionnaires were reviewed to determine and quantify the lines of inquiry with regard to further understanding the research focus along the three objectives stated earlier (resource, fisher or management focus) and the scale and breadth of the assessment (fisher, mid-chain, end-seller, exporter, consumer). Any reports (including manuscripts and final draft reports) describing the outcomes of VCAs were also reviewed to supplement the formerly described inquiry.

Table 10.2 The description of topics included in the value chain assessments.

	Topic	**Description**
←Social-Ecological System Continuum→	Diversity of species impacted	Species specific information before processing.
	Quantity of extraction	The number of kilograms or liters of a certain commodity.
	Fishing locations/habitats impacted	Description of fishing areas and marine habitats impacted by fisheries.
	Compliance and Environmental law	Knowledge, compliance, and description of environmental laws and regulations.
	Fisher demographics	Personal and demographic information (e.g., age, residence, family in the business).
	Fisher experience (temporal)	Questions describing the experience of the interviewee (e.g., years in fisheries/trading, job specification).
	Fishing effort	Information describing (a change in) fishing effort (e.g., soak times, fishing days) exerted on marine species within the respective study area.
	Traditional/Cultural links	Traditional and cultural use of shark commodities or fisheries.
	Livelihoods	Income, costs, and importance of fisheries to the livelihood.
	Gear and boats	The description of used gear and boats (e.g., specifics on boats, mesh size, crew size).
	Preservation and waste	
	Processing	Processing of sharks and rays.
	Commodity pricing	Prices of sharks and rays or related commodities.
	Trade logistics	The route along which commodities and traded or transported.

Shark VCA questionnaires were analyzed by classifying each question into topics along the social-ecological continuum (e.g., livelihoods, traditions, demographics, habitats impacted, commodity processing and prices) (Table 10.2). The proportion of each of these topics was calculated (i.e., the number of questions on a specific topic as the proportion of the total number of questions of the survey used), which was used as a proxy for the line of questioning used for each shark VCA concerning the main objective of the assessment (e.g., 'resource', 'fisher' or 'management' focus) or target-link of the value chain (e.g., fisher, mid-chain, seller). The differences in survey design were tested for significance using a Chi-squared test.

Structured survey

Based on the semi-structured interviews and review of VCA outputs, participants were asked to contribute through a structured survey comprising six closed and five open-ended questions. Researchers were asked to rank the steps and tasks of their shark VCA in terms of effort allocation (i.e., time and resources) and delivery in terms of insights gained or outcomes generated (protocol provided in supplementary material). In addition, the survey also included questions on how shark VCAs compared to or complemented traditional fishery assessments that were more focused on the status of shark stocks.

To allow participants to consider the inputs of others in the study before settling on their final responses, participant researchers were able to anonymously review all other responses after completion of the survey and adapt their responses before final submission (as per the Delphi method, see Hemming *et al.* 2018).

Researchers were asked to rank the steps and tasks of the shark VCA process (see Table 10.1) on an ordinal scale. For the steps, this was on a scale from 1 (most effort and/or most valuable outcomes) to 5 (least effort and/or least valuable outputs), and for the ranking of tasks within each step, this was on a scale from 1 (most effort and/or most valuable outputs) to 12 (least effort and/or least valuable outputs). Scoring of invested effort and generated outcomes of the structured survey were used to calculate rank indices for each step and task. A ranking index (RI) was calculated by taking the effort ranking (R_{effort}) minus the output ranking ($R_{outcome}$), divided by the number of available ranking positions (R_{max}; R_{max} = 5 for steps and 12 for tasks). For the draft FAO guidance 'steps' (n = 5), the RI ranges from -0.80 to 0.80, with -0.8 indicating the minimum efficiency (i.e., high effort and low generated outcome), 0.0 indicating a relatively balanced efficiency (i.e., no difference between invested effort and generated outcomes), and 0.8 indicated the maximum efficiency (i.e., a low invested effort led to high generated outcomes). For in-step tasks (draft FAO guidance 'tasks', n = 12), the RI ranges from -0.9 (low efficiency) to 0.9 (high efficiency). A one-sample Wilcoxon signed-rank test was used to determine if ranking indices differed significantly from zero. To determine if ranking indices differed among the three assessment focus groups, a non-parametric Kruskal-Wallis analysis of variance was used in combination with Dunn's post-hoc test.

Ethics statement

All participants were informed about the outline and intention of the study prior to data collection. Informed consent was given by all teams participating, and all were allowed to change their contribution to this study at any time. All participants approved the publication of their contribution as described in this manuscript.

Results

Shark VCA focus and objectives

The eight participating studies ranged from local, national and regional assessments of shark VCAs (Table 10.3). The common objective of all assessments was to elucidate information on the nature and extent of the shark fishery and trade, how this historically evolved, and the level of compliance with regulations. Two of the eight studies included assessments focused predominantly on the 'resource' (population trends and status), three on 'fishers' (the role and livelihood of the fishing community), and three on 'management' (assessments focused primarily on evaluating regulations while mapping trade). Five out of eight assessments included the primary links in the value chain (fisher, mid-chain and end-seller), and three assessments included additional links like exporters and consumers (Table 10.3).

Table 10.3 Overview of the shark value chain assessments analyzed as part of this study, including the scale (local, regional, national or international), the primary focus of the assessment (resource, fisher or management authority), links assessed in the VCA, and the main objective of each assessment.

			Links assessed					
Country	**Scale**	**Primary focus**	**Fisher**	**Mid-Chain**	**End-Seller**	**Exporter**	**Consumer**	**Main objective**
Peru	National	Fisher	•	•	•	•		Describe current and retrospective trade of non-fin shark and ray commodities within Peru.
Guinea Bissau	Local	Resource	•					Reconstruction of shark and ray fisheries and landings over the past decades, including reconstruction of population trends.
Sri Lanka	Regional	Fisher	•	•	•	•		Determine socio-economic drivers for shark fishing according to shark commodity and ascertain social reliance.
Bangladesh	National	Resource	•	•				Determine the baseline in landing data of sharks and rays in coastal fisheries and map national and international trade routes.
India	National	Management authority	•	•	•		•	Supplement stock assessments with information on the trade in shark and ray species.
Indonesia	National	Management authority	•	•	•		•	Map the trade of non-fin shark commodities and determine how these commodities are used within Indonesia.
Fiji	National	Fisher	•	•				Describe the characteristics of the fishery, determine if sharks are targeted or a bycatch species, describe how sharks are utilized and how they contribute to food security.
Mexico	National	Management authority	•	•	•			Determine how the market for shark commodities work with a focus on domestic shark meat market and the international market for other shark commodities.

Measuring effectiveness and efficiency across effort investment and outcomes of VCAs

Considering the multi-step process of establishing and implementing a VCA, the cross-study overview presented here showed that effort allocation and outcome returns were highest for investment in the survey questionnaire design step. This indicates that investing more effort in survey design leads to the most valuable outcome of the five-step assessment process (Figure 10.2A). Examining what could be learned across the various steps individually highlights specific learnings that can inform new assessments (Figure 10.2).

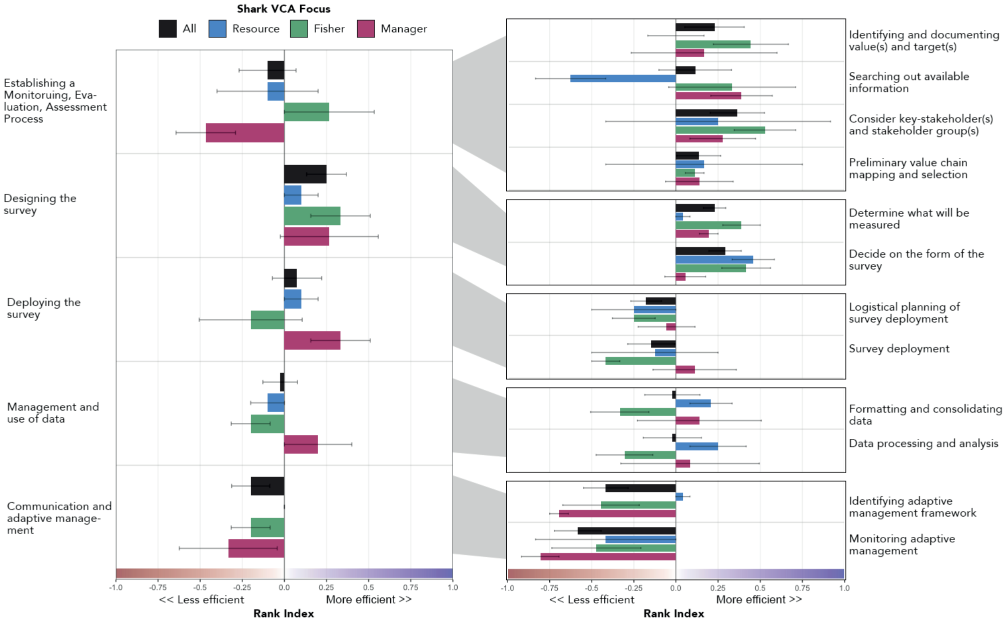


Figure 10.2 The mean ranking indices for each step (left) and associated tasks (right) as described in the FAO guidance for shark VCAs. Participants were asked to rank the steps and tasks of a VCA based on (1) effort and resources spent and (2) how these steps and tasks contributed to the valuable outcomes of their assessment. A negative ranking index indicates that the effort invested did not lead to more generated outputs (less efficient), an index of zero indicates that effort investment and generated outcomes are balanced, and a positive ranking index indicates that the effort invested led to more valuable outputs (more efficient). Error bars indicate the standard error of the mean, colors indicate the focus of the assessment (black = all assessments, blue = resource focused, green = fisher focused, red = management authority focused), and asterisks indicate significance.

Establishing a Monitoring, Evaluation and Reporting Process

The first step of a shark VCA is identifying and documenting the value(s) and objective(s) of the assessment, as well as searching for information and considering key stakeholders and stakeholder groups (i.e., establishing a monitoring, evaluation and reporting process). This initial step showed a lower ranking index when compared to other steps (RI = -0.10 ± 0.17; mean ± std. error), indicating that most researchers felt they invested more resources and time in this than necessary for the generated outputs (Figure 10.2A). However, when researchers were asked to rank the different tasks belonging to this step, these tasks were thought to contribute towards valuable outcomes of the overall assessment. Identifying key stakeholders was thought to be the most important of the tasks during this preparation step (RI = 0.36 ± 0.16, see Figure 10.2B). Searching for available information was also thought to be important but had the lowest ranking index (RI = 0.11 ± 0.22) of all four tasks in this step.

Designing a survey

The mean ranking index was highest for the second step of a shark VCA, the survey design step, but did not significantly differ from other steps (RI = 0.25 ± 0.12; $X^2 = 33.1$, d.f. = 11, $p = 0.09$, see Figure 10.2A). The ranking indices for the tasks within this step show the benefit of investing more effort in determining what will be measured (RI = 0.23 ± 0.07; V = 28, $p = 0.02$) and the correct format of the survey (RI = 0.29 ± 0.01; V = 33.5, $p = 0.04$, see Figure 10.2B).

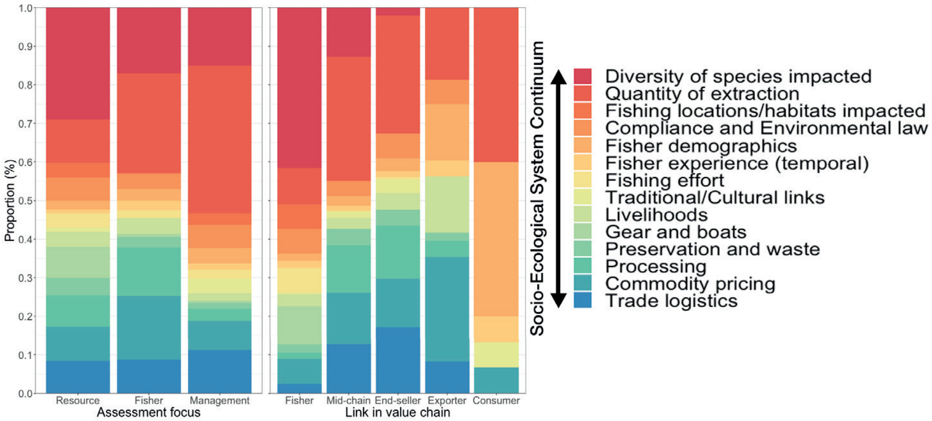


Figure 10.3 Reported relative importance of different topics along the continuum of social-ecological systems within value chain assessment questionnaires, considering the focus of the assessment (left) or the target links that comprise elements of the value chain (right).

The survey design did not markedly differ between assessments focused on resource use, fisher or management authority, or between surveys conducted within different links in the value chain (Figure 10.3). Generally, more information on species and commodity quantities was collected in fisher and mid-chain surveys. In contrast, the focus turned to processing and preservation of commodities in surveys with sellers and exporters. Also, researchers suggested that they spent less effort collecting biological data (e.g., species composition, length) when moving down the value chain (i.e., from fisher to consumer). In mid-chain surveys, the effort spent collecting commodity data (e.g., processing, commodity quantities, pricing and trade routes) increased to determine the flow of commodities and related economic measures. The collection of socio-cultural information (e.g., livelihoods, traditions, and demographics) also increased when moving up the value chain to allow researchers to determine the cultural and traditional motivation behind use and trade.

Deploying a survey

The investment versus return on survey deployment step was relatively balanced (RI = 0.01 ± 0.15; Figure 10.2), meaning that researchers indicated that the effort spent on this step aligned with the generated outcomes for the assessment. Contrastingly, both associated tasks show a negative ranking index, indicating that relatively more time and resources were invested in the logistical planning of survey deployment (RI = -0.18 ± 0.09) and the deployment itself (RI = -0.15 ± 0.14) concerning the contribution of these steps to the most valuable outcomes of the assessment.

Management and use of data

Participants highlighted that resource and time use should be better balanced, with the need for investment in the management and use of data (RI = -0.03 ± 0.10; Figure 10.2), as consolidating data (RI = -0.02 ± 0.16) and the processing data (RI = -0.02 ± 0.17) showed a balanced ranking index.

Communication and adaptive management

The last step of the shark VCA, the communication of findings and use of knowledge for adaptive management had the lowest ranking index of all steps (RI = -0.20 ± 0.11; Figure 10.2), indicating that efforts spent on this step contributed the least to generating valuable outcomes of their assessment relatively to other steps. Researchers indicated that the effort invested into identifying the management framework (RI = -0.42 ± 0.13) and monitoring adaptive management (RI = -0.58 ± 0.14) did not result in more desired outputs from the assessment compared to other tasks. These two tasks also significantly differed from the tasks with a positive ranking index (task 1-6; $H = 33.06$, $p > 0.001$).

Recommendations for shark VCA steps based on real-world experiences

Establishing a monitoring, evaluation and reporting process

All research teams indicated that investment in stakeholder selection and trust-building between surveyors and those surveyed (stakeholder groups and local communities) is crucial to the success of VCAs. Stakeholders should be selected based on preliminary research, during workshops, meetings, capacity-building activities and by involving local community members in the assessment design and deployment step of any planned survey (Table 10.4). During this process, researchers indicated that the objectives of the survey should be clearly communicated and that complex descriptions, jargon and long meetings should be discouraged. Appropriate community or region-specific messaging tools could be identified during preliminary research. In addition, shark VCA resources should be allocated based on the anticipated sample sizes and extent of study areas/regions to match investment across the preparation and delivery of a survey. Finally, researchers considered it important to identify sociocultural events that could potentially influence the success of fishery and/or trade surveys during preliminary research (e.g., active fishing times, fishery ban periods, and national holidays).

Designing a survey

Researchers recommended consulting and involving statistical experts in the design stages of the survey to ensure results will be suitable for anticipated statistical assessment (Table 10.4). This ensures that the outcomes generated are suitable for analyses against researchers' VCA objectives.

Prior to survey design, during preliminary research, researchers should identify possible 'units' used by fishery value chain participants, which are also well recognized across the focal fishery, trade, and use communities. Adopting such units allows better catch, length and volume measurement standardization across surveys. Although open and non-structured questions allow fishers, traders and community members to share more information and could be used to infer more understanding of issues like non-compliance, this type of question can negatively impact survey length. Researchers undertaking shark VCAs in large regions or different study areas should design flexible surveys that allow variations in fishery, trade and cultures to be collated and compared.

Deploying a survey

Most researchers indicated the importance of involving potential enumerators in the shark VCA process well before the deployment of surveys (Table 10.4). This allows researchers to train enumerators and standardize survey delivery, with enumerators having a clear understanding of the evolution of a survey. Involving enumerators with local insights enables researchers to more effectively reach and communicate with stakeholders, taking into account appropriate socio-cultural context and possibly gaining greater access to communities and information that may have been restricted to 'outsiders' or that are found to be isolated from mainstream knowledge. However, when involving local enumerators, researchers should ensure that they are free from conflicts of interest and can take a neutral position during the delivery of VCA information collection processes.

Spatially, sampling efforts should not be limited to landing sites and ports during survey deployment. Sampling design should also consider inland parts of the value chain and isolated markets and trade components.

Management and use of data

Researchers in this study involved local enumerators in processing collected data and asked them to collect additional field notes (Table 10.4). These field notes describe additional survey information, like the presence of specific traders or fishers at auctions, price changes, and events impacting prices, demand or supply of commodities. These field notes were valuable in confirming and explaining the results from the VCA.

Communication and adaptive management

Researchers highlighted the importance of visualizing outcomes for management authorities, policymakers, and local communities through methods such as flowcharts and graphical abstracts (Table 10.4), thus making results more accessible. This could include visual representations of trade routes, source and on-sale locations of commodity processing as well as aggregation areas, and commodity flow diagrams.

To strengthen long-term relations with stakeholders, scheduling reoccurring meetings with managers, policymakers, and local communities was thought to increase the delivery of key VCA outcomes, ensuring that outcomes were fed back to fishing communities and traders.

Table 10.4 Examples of better (left) and poor (right) practices reported by shark value chain assessment proponents. Responses are context-driven and based on the experience of the shark VCAs conducted in their own socio-cultural setting.

Establishing a Monitoring, Evaluation and Reporting Process	
Better practice	**Poor practice**
• Formulate goals and objectives into understandable jargon. • Use preliminary research to identify stakeholders and governance regimes. • Organize capacity-strengthening activities within local communities to improve inter-stakeholder relations. • Collaborate with experts to consolidate preliminary research. • Plan assessments considering cultural events and traditions.	• Allocate resources evenly over study areas without statistical analyses and sample size calculation. • Do not use long meetings and descriptions to convey study objectives. Determine the appropriate method for communicating with stakeholders.
Designing a Survey	
Better practice	**Poor practice**
• Ensure the outputs of questions are suitable for statistical analyses. • Include open or non-structured questions to ask about non-compliance and other problems stakeholders face. • Make surveys flexible and adaptable to changes in fisheries, trade, and culture between regions. • Use time references that are easy to recall (e.g., 'now' and 'when fishing started' rather than set dates).	• Prevent using different units between surveys. Standardize given answers such as catch quantities and prices. • Do not use complex survey tools (e.g., tablets) that limit the collection of unstructured data. It can also negatively impact data collection if stakeholders or enumerators are unfamiliar with tools. • Including many questions with potential overlapping responses increases the survey length. However, overlapping questions can also be used to confirm given responses, warranting their use in specific cases.
Deploying a Survey	
Better practice	**Poor practice**
• Potential (local) enumerators from local communities should be involved early in the process to facilitate training and delivery of the survey. • Respect the time of the interviewee and be flexible about pausing or discontinuing interviews. • Actively build networks within local communities to gain access to critical information (e.g., silent auctions, new stakeholders). • Follow the appropriate hierarchy to access information or interviewees. • Monitor additional activities (e.g., product transport) to confirm results and contextualize the VC.	• Familiarize with local socio-cultural aspects influencing data collection (e.g., illiteracy). This negatively impacts the quality and amount of collected information, and impacts stakeholder relations. • Do not limit study resources and effort to landing sites; doing so will cause the rest of the value chain to be overlooked (e.g., inland markets). • Going to landing sites or markets without local community members can limit data collection or interpretation of essential details.

Management and Use of Data	
Better practice	**Poor practice**
• Collect additional field notes to cover any additional information not covered in the structured survey, including observations to confirm survey outcomes.	• *None specified.*
Communication and Adaptive Management	
Better practice	**Poor practice**
• Visualize spatial and temporal information for managers, such as trade routes and hubs. • Include the perspectives and needs of local communities in the communication of outcomes. • Have reoccurring meetings with local communities and decision-makers to maintain communication and delivery of outcomes. • Published results should be accessible to local communities while also providing utility to local and national managers. • Communicate outcomes of non-compliance with (international) regulations with the national authority.	• Prevent sending a report to decision-makers without a visual summary. • Do not communicate outcomes to decision-makers before consulting with local stakeholders. • Formulate outcomes and recommendations for adaptive management in a constructive manner, e.g., prevent accusing or sensitive language. • Always ensure interviewee anonymity when communicating outcomes.

Discussion

This study sought to identify the most common approaches of research teams to VCAs for adaptive management of shark fisheries. The goal was to gain advice on refining VCAs when considering trade-offs between limited capacity and resources to optimize returns for management use. Our results showed that shark VCAs offer a holistic view of complex shark fisheries and trade in shark commodities, the importance of which is also highlighted by previous studies (e.g., Booth *et al.* 2019). Researchers contributing to this study indicated that those conducting shark VCAs in the future should invest the most effort and resources into (1) the selection process of key stakeholders, (2) building and maintaining trustworthy relations among stakeholders and researchers, and (3) adequate design of surveys prior to deployment (Figure 10.4). These three components were found to be the most beneficial in generating valuable insights for the adaptive management of sharks (e.g., improved communication and relations with stakeholders and collection of accurate information on trade and fisheries).

Our results indicate that organizing capacity-building and training activities during the early stages of the shark VCA process is essential, as it increases the volume and accuracy of data collected while also providing contextual information (Figure 10.4). Capacity-building activities include involving key stakeholders early in the process by organizing reoccurring stakeholder meetings, which has been identified as an important success factor in other VC studies (Dubay *et al.* 2010, Pradhan *et al.* 2022). Reoccurring events promote mutual understanding and trust but also aid in developing short- and long-term objectives. During these interactions, it was important to consider cultural norms, traditions, and hierarchical structure (Lückmann and Färber 2016). Diversity within the fisheries sector should also be considered (Ngwenya *et al.* 2012) and was also recommended by researchers participating in this study. For example, women constitute half of the workforce in global fisheries (World Bank, 2012). Neglecting their perceptions and perspectives could negatively impact the representation of shark VCA outcomes and hamper future decision-making.

After a broad range of stakeholders have been identified, our results show the importance of including these stakeholders early in the process of shark VCA survey design and deployment (Figure 10.4). Early involvement ensures that all aspects of the complex social-ecological system being examined are considered, with the capture of additional information, identification of differences in nomenclature, appropriate survey timing and accuracy of local ecological knowledge.

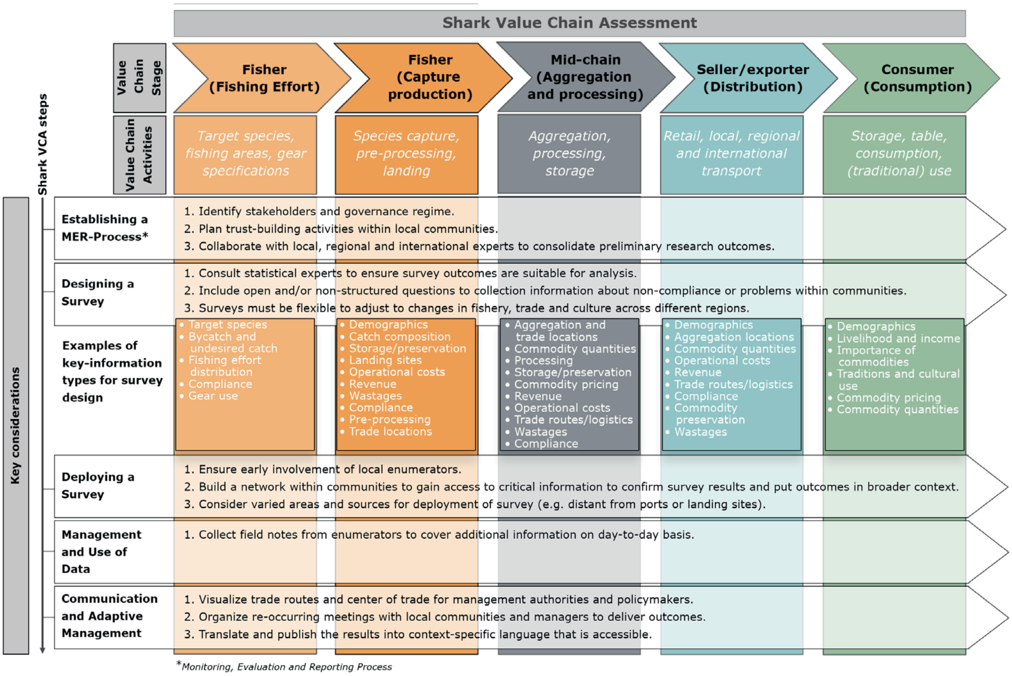
Including open-ended questions in surveys can be beneficial as they allow stakeholders to have direct conversations while also providing information not covered by a structured survey design. The information gained from these open-ended questions may offer insights into pain points linked to adaptive management and non-compliance to current governance regimes (Neuert *et al.* 2021). Also, including open questions in shark VCA surveys generated new lines of inquiry not known during the design phase (e.g., trade routes, new commodities, trading areas).

Another important aspect of survey design is addressing differences in common species nomenclature and units (e.g., commodity traded per kilogram, bucket) (Figure 10.4). For example, Leeney and Poncelet (2015) concluded that within the Bijagós Archipelago (Guinea-Bissau), approximately 66 different names for sawfish (Pristidae) are used. Within the same archipelago, sharks and fish are traded using either buckets or estimated kilograms (Leurs, personal observation). Using locally accepted paradigms that are cross-referenced to scientific measures improves the interpretation and accuracy of locally collected information and ensures that the assessment is flexible towards sociocultural differences, enabling better comparison within and between study areas (McCarter and Gavin 2014, Bernos *et al.* 2021).

Although globally, shark populations have declined over the past decades (Stevens *et al.* 2000; Dulvy *et al.* 2021), historical information on local populations is often lacking (Begossi 2010, Beaudreau and Levin 2014). Measuring temporal changes in species catch or catch compositions based on fishers' local ecological knowledge may be one of the only avenues to understand historical changes. However, it can be complicated due to shifting baselines (Pauly 1995, Sáenz-Arroyo *et al.* 2005). Not only this, but accurately recalling retrospective catch information from specific periods can be challenging for stakeholders (Beaudreau and Levin 2014, Early-Capistrán *et al.* 2020). Experienced fishers can provide valuable insights into historical changes in shark populations (Almojil, 2021). One method is asking stakeholders about catches and trades with decade-long increments. Another method to increase the accuracy of this temporal local ecological knowledge is to ask stakeholders about specific moments in time (e.g., when one started fishing and the current situation; Figure 10.4).

To ensure the accuracy of local knowledge collected, the timing and spatial extent of survey deployment need to be considered (Figure 10.4). Events such as traditional festivities can cause a rise in demand for shark commodities while seasons have differing fishing efforts. For example, the dish 'bacalao' in Mexico is traditionally consumed during Christmas and Easter, and the traditional cod is often substituted with shark meat (Lambarri *et al.* 2015). Shark curry is also consumed during local festivities on the western coast of Sumatra in Indonesia (Muttaqin *et al.* 2019). Considering these events and their influence on commodity demand is crucial in understanding VCs. Similarly, the spatial extent of trade should be considered and often requires a flexible survey deployment strategy, especially when new locations of interest are identified during the preliminary research phase or survey deployment. For example, shark products processed in coastal areas of India are transported inland near the northeastern Himalayan plateau to be traded within regional markets (Kizhakudan, personal communication). A VCA primarily focused on coastal areas would fail to cover this important facet of trade. Participatory mapping can also be incorporated into the survey design, allowing important trading and fishing sites to be mapped (Thiault *et al.* 2017). Exercises such as these can reduce uncertainty caused by inconsistency in area names across communities while also preventing difficulties experienced by stakeholders in describing areas of interest on a map.

Feeding back VCA outcomes to local stakeholders is essential for the design and implementation of successful management. Before communicating any outcomes for adaptive management purposes, researchers should identify if the adaptive management framework is passive (i.e., the management strategy is solely taking the influence of intervention on resources into account) or active (i.e., the management strategy anticipates the impact of intervention on learning as well as the resource being managed; Williams, 2011). Given the complexity of shark VCAs, researchers should distill their messaging to critical themes and identify appropriate communication tools to transmit assessment outcomes. Our study highlights the importance of local stakeholder involvement to facilitate effective communication. In addition, outcomes from shark VCAs should be communicated in a way that is accessible to local stakeholders (e.g., limited use of scientific jargon, using the correct local language or dialect, and using data visualization tools). Multiple researchers indicated that reoccurring meetings enabled stakeholders to be closely involved in the process, stimulating information uptake and positively impacting the mutual relationship between researchers and stakeholders.



Establishing a MER-Process*
1. Identify stakeholders and governance regime.
2. Plan trust-building activities within local communities.
3. Collaborate with local, regional and international experts to consolidate preliminary research outcomes.

Designing a Survey
1. Consult statistical experts to ensure survey outcomes are suitable for analysis.
2. Include open and/or non-structured questions to collection information about non-compliance or problems within communities.
3. Surveys must be flexible to adjust to changes in fishery, trade and culture across different regions.

Deploying a Survey
1. Ensure early involvement of local enumerators.
2. Build a network within communities to gain access to critical information to confirm survey results and put outcomes in broader context.
3. Consider varied areas and sources for deployment of survey (e.g. distant from ports or landing sites).

Management and Use of Data
1. Collect field notes from enumerators to cover additional information on day-to-day basis.

Communication and Adaptive Management
1. Visualize trade routes and center of trade for management authorities and policymakers.
2. Organize re-occurring meetings with local communities and managers to deliver outcomes.
3. Translate and publish the results into context-specific language that is accessible.

*Monitoring, Evaluation and Reporting Process

Figure 10.4 Summary of the most important study outcomes. The collection of key information differs among value chain links (i.e., fishers, mid-chains, end-sellers, consumers). The holistic value chain approach covers all three pillars of sustainability in comparison to traditional fishery assessments, which focus on environmental aspects. Key considerations are given for each step in a shark VCA, including key information to include in the survey design. Adapted from Kruijssen *et al.* (2020).

Fisheries are complex social-ecological systems in which the ecology of species is intertwined with the socio-cultural and economic aspects of the fishery, including trade in fishery commodities (Booth *et al.* 2019). Retrieving a management-relevant assessment of fishery VCs requires a paradigm shift in how stakeholders and social-environmental systems are included in surveys. The move to include a clearer view of the social-ecological system expands the assessment to be more akin to the ecosystem approach to fisheries (FAO, 2003) rather than a traditional stock-centered assessment (Figure 10.4). Compared to these conventional stock assessments, perspectives informed by VCA cover a broader array of socio-economic elements that are often drivers of the fishery (Rosales *et al.* 2017). This broadening of perspectives provides vital information on the reasons for fishing and trade, how commodities are processed, bought and sold, where wastages and commodity preservation occur, and information on traditions and cultural aspects that influence commodity acquisition, all of which are opportunities for management interventions (Figure 10.4) (Rosales *et al.* 2017, Booth *et al.* 2019, Kruijssen *et al.* 2020).

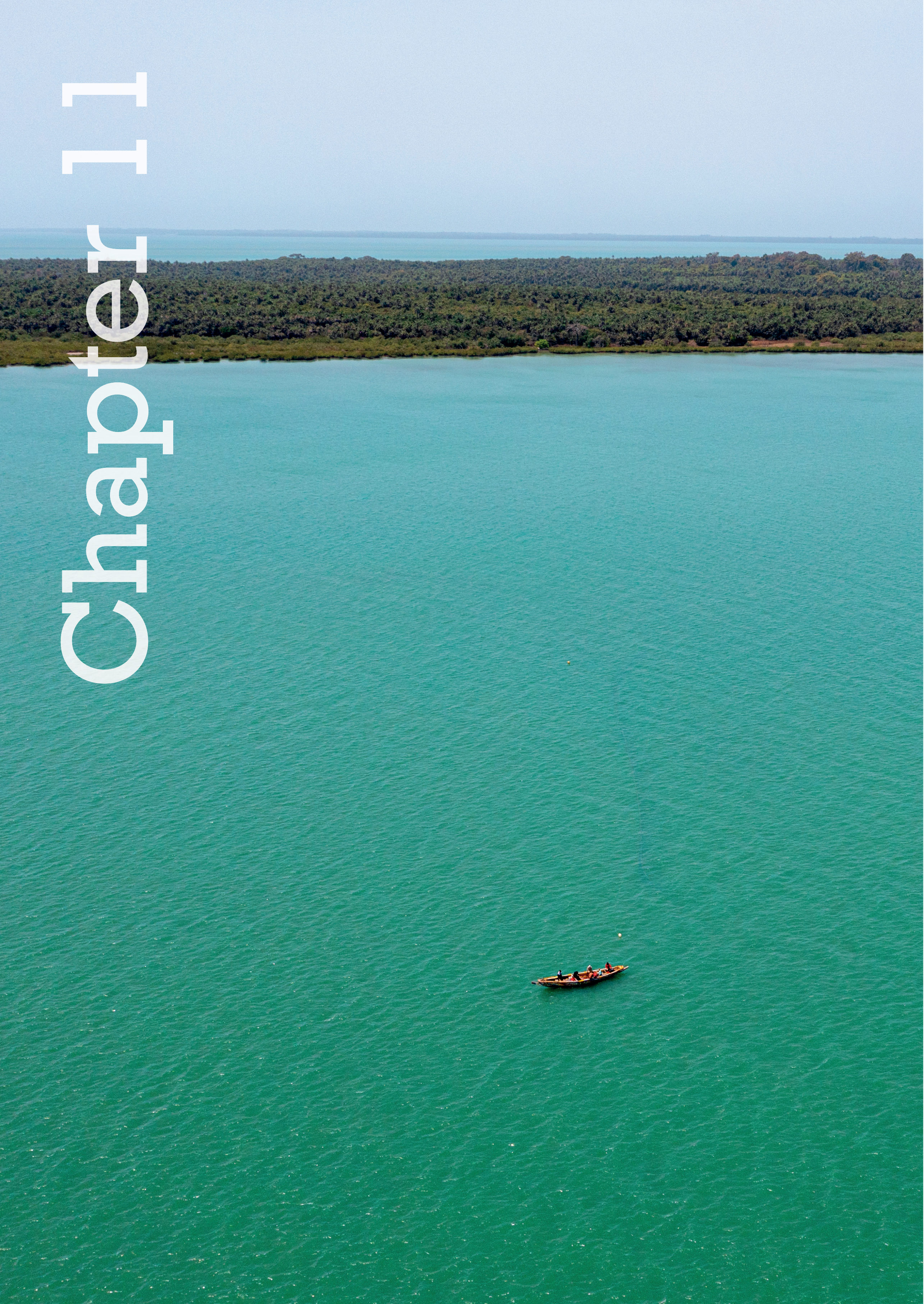
Conclusion

Shark fisheries and associated value chains are complex, involving interactions between socio-cultural, economic and ecological systems. These aspects need to be recognized for policy and management development to have the best chance of being effective. This study outlines lessons learned by shark VCA researchers, and we describe the ‘better’ (what to do) and ‘poor’ (what not to do) practices in shark VCAs conducted by research groups from five continents. Shark VCAs could provide a holistic approach to the adaptive management of shark populations. Most importantly, shark VCA assessments offered insights into the other causes of (over)exploited stocks (e.g., the underlying socio-economic system of shark fisheries), in addition to assessing the relative status and resilience of the fishery. Recommendations presented here can assist managers, researchers, and stakeholders in streamlining the collection of essential information for adaptive management of shark fishery and trade across fishery VCs, ultimately conserving shark populations more effectively.

Acknowledgments

This work was supported by the FAO regular program, the Japanese Government (“Biodiversity mainstreaming for sustainable fisheries”, part of GCP/GLO/173/JPN), collaboration and investment by the CITES Secretariat as well as a UN to UN project funded by the European Union (EP/INT/334/UEP, “CITES-FAO Collaboration to Strengthen the Capacity of Developing Countries to Ensure the Sustainability, Legality and Traceability of International Trade in CITES-listed Species, with a Focus on Commercially-Exploited Aquatic Species”).

Chapter 11



General discussion

Guido Leurs

In this thesis, I examine the diversity and ecological roles of sharks and rays (i.e., elasmobranchs) in intertidal areas and the impact of fisheries on these vulnerable species. For this, I focused on the two largest intertidal areas in the West African region, the Banc d'Arguin and the Bijagós Archipelago (**Box B**). Furthermore, we determined guidelines on how to incorporate shark and ray ecology into area-based management and how best to map the socioeconomics of shark fisheries to improve the management of these complex systems.

In this chapter, I aim to discuss our findings in the broader context of intertidal and conservation ecology. **Figure 11.1** provides an overview of the interactions and processes that I discuss in this chapter (i.e., *the letters in Figure 11.1 correspond to section titles of this chapter*). I begin by exploring the impact of industrial and small-scale fisheries on elasmobranchs in the West African region and provide recommendations for enhanced conservation and management of shark populations. I then discuss how intertidal mesopredators interact in the intertidal, the plausibility of trophic cascades, and briefly discuss the consequences of a combined loss of shorebirds and elasmobranchs from intertidal areas. Finally, I discuss the area-based conservation of elasmobranchs in the intertidal and how this should be inclusive of the 'human dimensions' of shark and ray conservation.

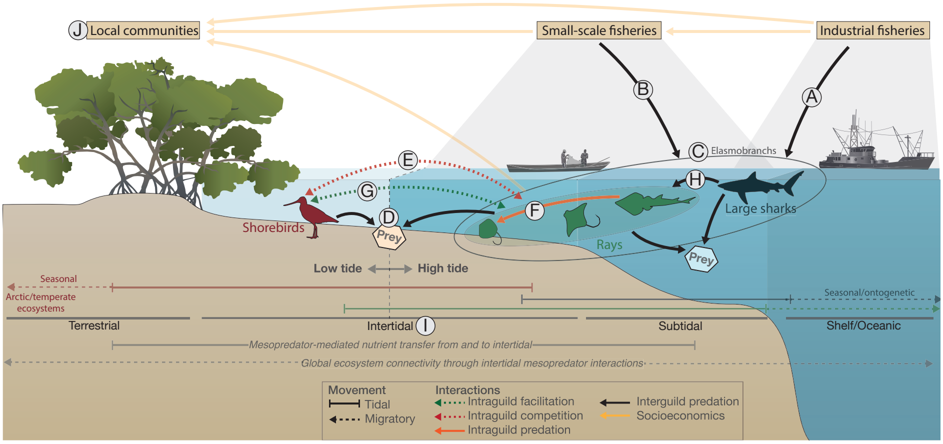


Figure 11.1 Overview of interactions and processes discussed in this chapter in the context of intertidal area functioning and connectivity: The impact of industrial (A) and small-scale fisheries (B); The differences in elasmobranch diversity between my study areas (C); Trophic niche overlap between intertidal mesopredators (D); intraguild interactions including niche partitioning and competition (E); intraguild predation (F); and facilitation between intertidal predator guilds (G); the plausibility of trophic cascades due to marine mesopredator removal (H); the conservation of intertidal areas for both avian and marine species (I); and the importance of including local communities in these efforts (J). *Letters link to section titles in this chapter.*

Fisheries

The West African region is considered to be one of the most productive fishing grounds in the world (Braham *et al.* 2014), where seasonal upwelling causes a high abundance of (small) pelagic fish (e.g., sardines, sardinella, shads, mackerels). This high productivity supports a diversity of marine and avian predators but also attracts fisheries from all over the world (Braham *et al.* 2014, Grecian *et al.* 2016). Here, I discuss the interactions between industrial and small-scale fisheries and the movement ecology of sharks and rays. As sharks and rays use coastal areas at least for part of their lifecycle, some species may only interact with small-scale fisheries operating within these coastal areas. In contrast, other species may interact with both small-scale and industrial fisheries during their lifecycle (**Figure 11.2**).

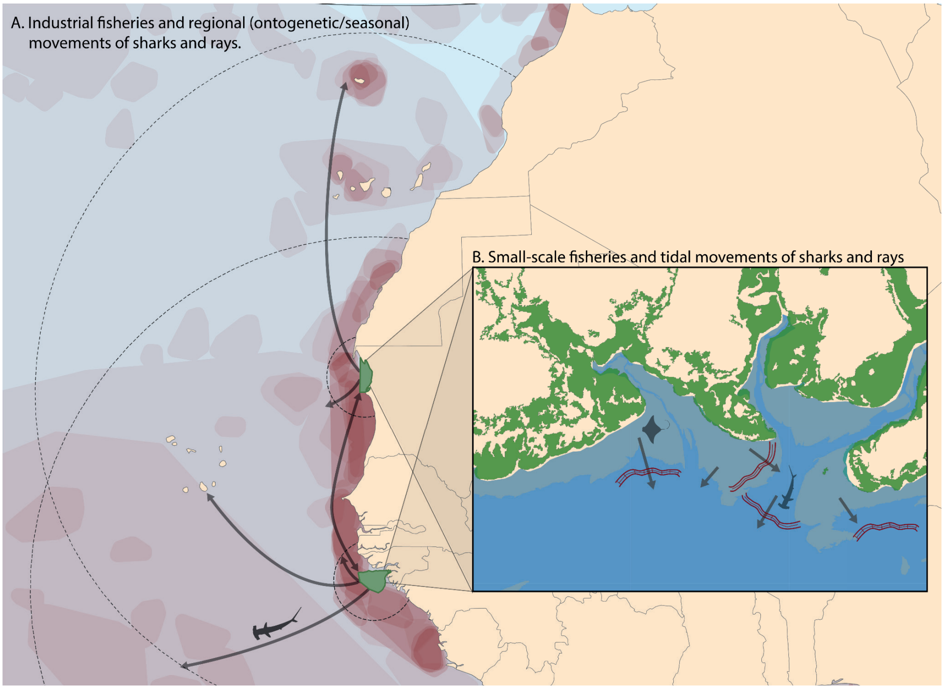


Figure 11.2 A conceptual overview of the overlap between fisheries and shark and ray movements in the West African region. (A) Industrial fisheries concentrated on the continental shelf (red; data from Chapter 2) overlap with ontogenetic or seasonal movements of sharks using the Banc d'Arguin and Bijagós Archipelago (green) during their life cycle. For example, the average long-distance movement (small dashed circle; >140km, Diemer *et al.* 2011) and maximum long-distance movement (large dashed circle; >1600km, Kohler and Turner 2001) of the scalloped hammerhead shark (*Sphyrna lewini*) are shown (grey arrows, conceptual). (B) Daily shark and ray movements (grey arrows, conceptual) overlap within these coastal areas with small-scale fisheries. Gear types such as gill nets are placed on or alongside intertidal flats (light brown) or to close off gulley networks (red), interfering with the tidal movement of sharks and rays using intertidal habitats (grey arrows, conceptual).

Industrial fisheries and regional movements of sharks and rays (A)

Currently, more than half of the ocean's surface area is fished by industrial fisheries (Kroodsma *et al.* 2018). In **Chapter 2**, we show that industrial fisheries have increased in both extent and fishing time (effort) over the past decades and are concentrated on the border of coastal areas within the West Africa region. The increase in industrial fisheries throughout the West African region is caused by an increased demand for seafood, developing international markets, and technological advances (e.g., freezer trawlers). Stricter management in the waters of developed nations and Fishing Partnership Agreements with less developed countries caused distant-water fleets to operate far from their countries of origin. These distant-water fleets often operate in the waters of countries with lower capacities for fisheries management and enforcement (Worm *et al.* 2009, Gagern and van der Bergh 2013). We show that these industrial fisheries operating in the waters of Mauritania and Guinea-Bissau catch a large number of sharks and rays (**Chapter 2**). This is also supported by earlier studies that determined that hammerhead sharks make up 42% of all megafauna bycatch (Zeeberg *et al.* 2006).

Mobile species like the scalloped hammerhead shark (*Sphyrna lewini*) can move over long distances. Sharks of up to 9.6 years old already undertake long-distance movements of up to 140 km (Diemer *et al.* 2011), with maximum recorded distances of over 1,600 km (Kohler and Turner 2001). This species probably overlaps with industrial fisheries operating on the border of these coastal areas once it undertakes seasonal or ontogenetic migratory movements away from coastal areas (Daly-Engel *et al.* 2012; **Figure 11.2A**). The scalloped hammerhead shark is now globally critically endangered (Rigby *et al.* 2019). These species use coastal areas during part of their life cycle and, in addition, may also face intensified small-scale fisheries.

Small-scale fisheries and local movements of sharks and rays (B)

During their early life stages, mobile species like hammerhead sharks mostly stay within coastal areas (Zanella *et al.* 2019, Corgos and Rosende-Pereiro 2022). Smaller and less mobile species may spend their entire life cycle in coastal waters (Knip *et al.* 2010). Sharks and rays interact more with small-scale coastal fisheries than industrial fisheries in these coastal areas. We show that these fisheries have increased rapidly over the past decades in the Banc d'Arguin (**Chapter 3**) and the Bijagós Archipelago

(**Chapter 4**). In terms of fishing effort, the number of fishing days per year in the Banc d'Arguin has more than doubled between 1998 and 2020 (**Chapter 3**). Meanwhile, the number of fishing vessels in the Bijagós Archipelago increased by more than 440% between 2007 and 2022 (**Chapter 4**). In both areas, catches of sharks and rays have increased over the past decades in response to a higher demand for shark fins (international trade) and shark and ray meat (regional and local markets). Our studies show concerning declines of shark and ray populations in both the Banc d'Arguin (**Chapter 3**) and the Bijagós Archipelago (**Chapter 4**), with declines ranging between 50-90% and 82-97%, respectively.

Small-bodied or young sharks and rays use coastal (intertidal) areas as feeding and refuge areas (**Chapter 7**, Knip *et al.* 2010), and their movements are mainly associated with the tide (e.g., Ackerman *et al.* 2000, Conrath and Musick *et al.* 2010, Kanno *et al.* 2019). Small-scale fisheries use these tidal movements to increase catches by placing fishing gear on or along intertidal flats or closing off tidal channels (**Figure 11.2B**). The habitat availability for these marine predators reduces rapidly with the receding tide, driving these species into fishing gear placed alongside or in intertidal habitats. Although an effective fishing method, closing entire tidal channels or gulleys with fixed gillnets leaves little to no escape for non-targeted shark and ray species, making their bycatch inevitable. Similarly, the survivability of bycatch is compromised when these gear types are placed in intertidal habitats that are exposed during low tidal phases. While this may not be a primary concern for targeted species, it diminishes the chances of live release and survival of vulnerable bycatch species.

Management recommendations

Mobile sharks and rays interact with small-scale and industrial fisheries throughout their life cycle in the West African region (**Figure 11.2**). Although elasmobranchs are mostly considered bycatch, these interactions with fisheries caused severe declines in their abundance. However, whether industrial or small-scale fisheries are the biggest threat to sharks and rays using intertidal areas depends mostly on the interplay between the spatiotemporal distribution of fisheries and the movement ecology of these species. The degree of movement is species- and life-stage dependent in elasmobranchs (Speed *et al.* 2010). Based on our research conducted over the past years, I describe recommendations to improve the management of sharks and rays (**Table 11.1**).

Regulations for sharks and rays that prohibit targeted elasmobranch catches and prohibit the use of monofilament nets exist in both Mauritania and Guinea-Bissau. These are included in management plans for fisheries, marine protected areas (MPAs) or National Action Plans for Sharks. However, these regulations are poorly enforced and widely disregarded. These regulations should be expanded with retention bans on the most critically endangered species (e.g., hammerhead sharks and guitarfishes; Yan *et al.* 2021), and their live release should be encouraged (**Table 11.1**). Live release of guitarfish is feasible due to their relatively high survival rate (Pytka *et al.* 2023). The ecology of threatened elasmobranchs must be considered in area-based management strategies. This includes accounting for the different conservation needs of small-bodied and large-bodied species in MPA design (**Box F, Table 11.1**). Although small-scale MPAs may effectively conserve small-bodied elasmobranch species or species with a high site fidelity (Barnett *et al.* 2012, Yates *et al.* 2016), mobile large-bodied species require larger MPAs with connective corridors covering their movements between different habitats (Hooker *et al.* 2011, White *et al.* 2017, Daly *et al.* 2018, Gallagher *et al.* 2020). Area-based management strategies should also include seasonal closures or the reduction of fishing effort in areas with high elasmobranch abundance (e.g., the high catches of newborn blackchin guitarfish *Glaucostegus cemiculus* in beach seines near mangroves in the Bijagós, **Box D**) (**Table 11.1**). Currently, enhanced management strategies for elasmobranchs are hampered by the lack of species-specific information from industrial fisheries and overall landing data of small-scale fisheries. As such, strengthening local research capacity may ensure long-term fisheries monitoring to contribute to the adaptive management of sharks and rays.

Diversity and Life History (C)

Despite their different intertidal habitats (i.e., seagrass meadows versus mangroves), the Banc d'Arguin and the Bijagós Archipelago host relatively similar elasmobranch richness. We show that the same species are amongst the most captured species in both areas: the milk shark (*Rhizoprionodon acutus*), scalloped hammerhead shark, blackchin guitarfish (*Glaucostegus cemiculus*), and the Lusitanian cownose ray (*Rhinoptera marginata*) (**Chapters 3-5**). However, although species richness is relatively similar, the areas differ in their elasmobranch community composition. For example, the most abundant species in the Bijagós is the pearl whipray (*Fontitrygon margaritella*), a small ray species (**Chapter 5**) that constitutes approximately 0.1% of monthly elasmobranch catches in the Banc d'Arguin (**Chapter 3**). We determined that this species is a fast-growing and early-maturing stingray species (**Chapter 6**) and is likely capable of relatively fast population growth and recovery after exploitation.

Table 11.1 Overview of focus points for improved monitoring and management of industrial and small-scale fisheries within the West African region. Colors indicate the theme of each focus point (green = improved data collection, orange = catch selectivity, blue = area-based management, yellow = regulating fishing effort, gray = other).

Fisheries	Recommendation	PNBA	BA
Industrial/ offshore	🟩 Species-specific data collection of shark and ray bycatch.	X	X
	🟧 Mandatory use of bycatch deterrents or gear adjustments to increase selectivity.	X	X
	🟧 Enforce prohibition of targeted shark catches.	X	X
	🟧 General retention bans of species on a prohibited species list.	X	X
	🟦 Seasonal closures of areas with high shark and ray catches or ecologically important areas.	X	X
	🟦 A conservation corridor linking coastal areas with pelagic/deep-water habitats (e.g., along migratory swimways).	X	X
	🟦 Incorporate/improve the financial contribution of Fisheries Partnership Agreements to strengthen local monitoring and enforcement capacity and the conservation of protected areas.	X	X
	🟨 Implementation and enforcement of shark and ray catch quota.	X	X
	🟨 Ban transshipment of catches to reduce overall catch capacity and improve transparency.		X
Small-scale/ coastal	🟩 Improve data collection on small-scale fisheries on a species-specific level and with spatial information of catches.		X
	⬜ Determine and ensure equality across the value chain of fisheries commodities.	X	X
	🟧 Restrict or adjust fishing gears with high shark and ray catches to improve selectivity.	X	X
	🟧 Instate retention bans and make the live release of sharks and rays mandatory. This should be based on a national list of prohibited species.	X	X
	🟦 Enforce protected area boundaries and extend with connective corridors.	X	X
	🟦 Restrict or limit the use of specific fishing gear in intertidal habitats (i.e., no survivability due to exposure) or the closing of tidal channels (i.e., allow escape).	X	X
	🟨 Reduce overall fishing effort by limiting the number of active fishing vessels (i.e., preventing intrusion by illegal/foreign vessels) and/or gear-specific restrictions (e.g., limiting trip durations and/or net lengths).		X
General	🟩 Improved fishery-dependent data collection and documentation by strengthening research capacity.		X
	🟩 Determine the importance of sharks and rays to local and regional food security and ensure equality in trade (e.g., both offshore and coastal resources benefit the local economy and food security).		X
	🟨 Minimize Illegal, Unreported, and Unregulated (IUU) fisheries by strengthening monitoring and enforcement capacity.	X	X
	⬜ Implementation of international (trade) conventions (e.g., CITES).	X	X
🟩 Data collection	🟧 Selectivity	🟦 Area-based	🟨 Fishing effort

In the Bijagós, this species feeds on intertidal flats in large numbers as a mesopredator and probably also plays a vital role in shaping these flats due to their high abundance

(**Chapter 9**). Dense intertidal seagrass beds and patches of the large bloody cockle (*Senilia senilis*) in the Banc d'Arguin may be less favorable for this small, soft-sediment mesopredator, which may explain these differences. In other soft-bottom areas throughout its range, the pearl whipray is one of the most common ray species (e.g., Moore *et al.* 2019). However, the lower abundance of the pearl whipray may also be explained by a difference in fisheries: this species is often caught in beach seine fisheries, which is uncommon in the Banc d'Arguin (Lemrabott *et al.* 2023a, 2023b). This underlines the risk of reconstructing ecological community composition only based on fishery-dependent data (**Chapter 5**; Starr *et al.* 2010, Tessier *et al.* 2016).

In addition to the difference in benthic stingrays, the Banc d'Arguin has a higher occurrence of shark species. Species such as the barbeled houndshark (*Leptocharias smithii*) and Atlantic weasel shark (*Paragaleus pectoralis*) are relatively common among catches, which respectively have only been recorded once and not at all in the waters of the Bijagós (**Chapter 5**). In addition, two ray species seem to be much more common in the Banc d'Arguin: the large spiny butterfly ray (*Gymnura altavela*) and the marbled stingray (*Dasyatis marmorata*). The latter was only detected at one location in the Bijagós using an eDNA approach (**Chapter 5**). It is important to note that these differences are possibly (partly) caused by the difference in the monitoring effort of landing sites. The fisheries observer program in the Banc d'Arguin was started in 1998 (**Chapter 3**). In contrast, there is no ongoing catch monitoring of small-scale fisheries operating in the Bijagós (we started a 10-month pilot survey in 2021, **Chapter 4**). Therefore, there is almost no basic information on species and life stage occurrence of elasmobranchs in the Bijagós. I describe important new observations made over the past four years while studying sharks and rays in the Bijagós Archipelago that have not been published elsewhere (**Box D**). These observations highlight the data deficiency of elasmobranch species within the region, especially cryptic and rare species such as the false shark ray (*Rhynchorhina mauritaniensis*) and African wedgefish (*Rhynchobatus luebberti*).

We show that the presence of some species in the Bijagós differs across the rainy and dry seasons (**Chapter 5**). In addition, the seasonal difference in regional upwelling of the Canary Current off the Banc d'Arguin influences the presence of marine species in the region (Lathuilière *et al.* 2008, Braham *et al.* 2014, Grecian *et al.* 2016). For example, catches of the Lusitanian cownose ray within the Banc d'Arguin differ across seasons (**Chapter 3**). Seasonal differences in species presence and abundance lead to seasonal elasmobranch composition shifts (**Chapter 5**). As a result, the top-down effects of these predator species on lower trophic levels and the strength of interactions with other (intertidal) mesopredators may temporarily change.

Species Interactions

Intertidal habitat use and niche overlap (D)

We describe how various shark and ray species use intertidal areas worldwide and highlight that it is primarily small-bodied and early life stage elasmobranchs using these shallow-water habitats as feeding refugia (**Chapter 7**). For sharks and rays, the intertidal is a challenging environment. It continuously requires balancing the potential risks of stranding (i.e., prolonged intertidal use) and predation (i.e., less exposure to large predators in the intertidal) with maximizing intake rates of intertidal prey while accessible (**Chapter 7**). Although sharks and rays both use intertidal habitats and the associated resources, the use of these shallow-water habitats by rays is more common (**Chapter 8**). Rays, including guitarfishes, are better adapted to shallow-water habitats due to their flattened body types, which reduces the risk of stranding and allows them to use these shallow habitats to seek refuge from larger-bodied predators (e.g., sharks; Elston *et al.* 2022). Amongst stingrays, juveniles predominantly use shallow-water flats as the predation risk for larger individuals in subtidal waters is lower (Elston *et al.* 2021). Ontogenetic changes in the fitness landscape of juveniles using intertidal habitats possibly explain the (seasonal) migration of elasmobranch species away from intertidal areas during later life stages (Fokkema *et al.* 2020). For example, the predation risk reduces as juvenile elasmobranchs grow larger (Kindsvater *et al.* 2016, Mull *et al.* 2022), but the larger body size likely increases the stranding risk of intertidal habitat use. In addition, dietary requirements often increase ontogenetically with larger individuals feeding at higher trophic levels (Daly *et al.* 2013, TinHan and Wells 2021, Mull *et al.* 2022), which may require adult elasmobranchs to move to deeper or more pelagic habitats. Therefore, intertidal habitat use mostly benefits early life stages and small-bodied elasmobranch species (**Chapter 7**).

We show that the intertidal habitat use of elasmobranchs, particularly by rays, causes overlap in trophic niches with migratory shorebirds. This niche overlap between shorebirds as 'low-tide predators' and rays as 'high-tide predators' can be as high as 42% of the total niche space these mesopredator groups occupy. On average, species-specific overlap is 33% of occupied niche space (**Chapter 8**). As migratory shorebirds rely exclusively on intertidal prey during their wintering months in these tropical intertidal areas (Piersma 2012), we can conclude that the overlap between rays and shorebirds also indicates the proportion of the diet of a ray species that consists of intertidal prey (**Figure 11.3**, **Chapter 8**).

Studies on the niche overlap between benthic rays report niche overlap proportions of 44 to 70% (Yick *et al.* 2011, O'Shea *et al.* 2013). Niche overlap between shorebirds is generally low but can be as high as 44 to 88% of the occupied niche space (Lourenço *et al.* 2015, 2017). Generally, trophic niche overlap is considered high when the overlap is >60% of occupied niche space, with increased risks of competitive interactions and exclusion amongst predators (Zaret and Rand 1971). However, we report a niche overlap in resources that are only accessible to each mesopredator group for a limited amount of time and are thus inherently partitioned by the tide.

Intraguild niche partitioning and competition (E)

High trophic niche overlap amongst mesopredators can indicate either that prey biomass is not limiting, that top-predators strongly regulate mesopredator abundance, or that resources are partitioned along other ecological axes (e.g., space or time, Tinker *et al.* 2008, Vaudo and Heithaus 2011). Resource partitioning is especially important in systems with high predator richness and limited prey biomass as it prevents competitive exclusion through the extinction of prey (Vandermeer and Pascual 2006, Garvey and Whiles 2016).

Similar to temporal habitat partitioning between diurnal and nocturnal birds, mammals or insects (e.g., between butterflies and moths or between insectivorous birds and bats; Kronfield-Schor and Dayan 2003, Bennie *et al.* 2014, Curras *et al.* 2022), intertidal habitat and resource use by intertidal mesopredators are partitioned temporally across the tidal cycle. During low tide, when intertidal habitats are exposed, intertidal resources are accessible to avian and terrestrial predators. Hours later, when submerged during high tide phases, these same habitats and associated resources are accessible to marine predators (**Chapter 7**). The temporal period that intertidal prey is accessible to each mesopredator guild is determined by the length of the tidal phases and the tidal amplitude.

During the limited time that intertidal prey communities are accessible, predators must maximize energy intake and limit prey handling times by exploiting the proportion of prey biomass that is harvestable by the predator (MacArthur and Pianka 1966). Mesopredator species may favor mobile benthic prey if prey handling times can be limited and prey is abundant (e.g., sanderlings *Calidris alba* predating on shrimp in the Wadden Sea, Penning *et al.* 2022). The burrowing depth of endobenthic prey can cause prey to be inaccessible to benthic predators, whose burrowing (i.e., rays) or probing (i.e., shorebirds) depths are restricted (**Box G**; Zwarts and Wanink 1993). Similarly, durophagous mesopredators are especially limited in their range of harvestable prey sizes by their body size and gape (i.e., rays) or gizzard (i.e., shorebirds) sizes (Lifjeld 1984, Zwarts and Blomert 1992, van Gils *et al.* 2003, Fisher *et al.* 2011). In addition, burrowing depths and prey size can increase prey handling times and limit the intake rates of intertidal predators (Zwarts and Blomert 1992, Piersma *et al.* 1993, Fisher *et al.* 2011). Therefore, maximizing prey biomass intake by these intertidal mesopredators under the optimal foraging theory (MacArthur and Pianka 1966) means balancing the exploitation of prey at greater burrowing depths (i.e., longer searching and excavation times) with the prey size (i.e., prey near the maximum harvestable prey sizes represent a higher intake of biomass). This would mean that these intertidal mesopredator groups are most likely to exploit resources in top sediment layers (**Box G**) and of intermediate-size classes, causing elevated levels of predation pressure of these prey and possibly competition between intertidal mesopredators (**Figure 11.3**).

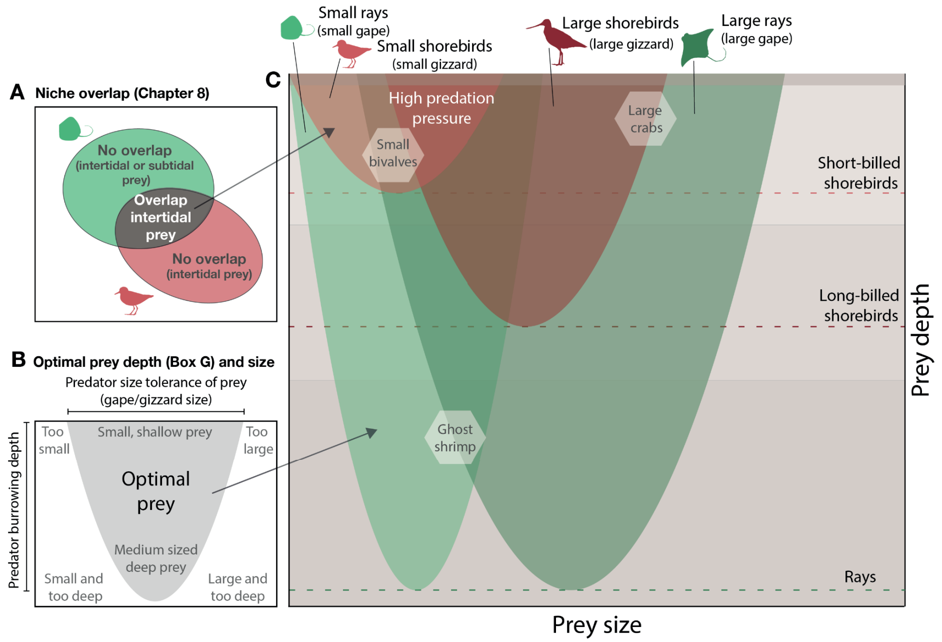


Figure 11.3 (A) Trophic niche overlap between shorebirds (red) and rays (green) indicates the proportion of intertidal resources both mesopredators exploit (**Chapter 8**). To maximize prey intake rate while these intertidal prey are accessible, predators minimize handling times and maximize prey intake. However, predators are constrained by their maximum burrowing or probing depths (**Box G**), and the maximum prey sizes a predator can handle is limited by their gizzard size (shorebirds, e.g., Lifjeld 1984, van Gils *et al.* 2003) or gape size (rays, Fisher *et al.* 2011). (B) This means that the optimal prey is either small prey at shallow depths (i.e., which maximizes intake rates by minimizing burrowing depths), medium-sized prey at greater burrowing depths (i.e., which maximizes intake rates by balancing per prey biomass and burrowing times), or larger prey at shallower depths (i.e., which maximizes intake rates with high per prey biomass at short burrowing times). (C) Overlapping the optimal prey for groups of rays and shorebirds can help predict the predation pressure on intertidal prey and competition amongst intertidal mesopredators.

Characterized by relatively wide niche breadths and flexibility in prey selection, we show that shorebirds and elasmobranchs are generalist mesopredators in intertidal areas (**Chapter 8**; Garvey and Whiles 2016, Correia *et al.* 2023). These predatory species may further partition resources by exploiting other harvestable prey at higher costs (e.g., involving longer excavation and handling times or foraging under increased predation risk). This includes, for example, the predation on deep-burrowing ghost shrimp by red stingrays (Takeuchi and Tamaki 2014), red knots feeding on medium-sized but abundant bivalve species high in sulfides (van Gils *et al.* 2013, Oudman *et al.* 2014), or the exploitation of thick-shelled bloody cockles (*Senilia senilis*) by large ray species (**Chapter 8**, Summers 2000, Collins *et al.* 2007, Fisher *et al.* 2011). Although shorebirds rely entirely on intertidal prey during their use of intertidal areas, sharks and rays also exploit subtidal resources that are always accessible (**Chapters 7 and 8**). Therefore, if intraspecific competition for intertidal resources is high, elasmobranchs may increase their intake of subtidal prey at the cost of higher predation risks. Partitioning intertidal resources by these generalist mesopredators enables their co-existence in intertidal areas (Hanski *et al.* 1991, Vandermeer and Pascual 2006). This is especially important during the wintering months when these shorebirds visit these intertidal areas in large numbers and rely entirely on intertidal prey (Piersma 2012, Oudman *et al.* 2020).

Intraguild predation (F)

Traditionally, large-bodied sharks such as hammerhead sharks have been considered the predominant predators of rays (e.g., Myers *et al.* 2007). Although some shark species in specific areas are specialized ray predators (e.g., Raoult *et al.* 2019), in other systems, rays may experience diffuse predation from multiple predator species, including teleosts and marine mammals (**Box E**). Based on stable isotope ratios, we show that the diet of the blackchin guitarfish and spiny butterfly ray (*Gymnura altavela*) consists partly of stingrays (**Chapter 8**, **Box F**). Although these results are based on stable isotope (which can be inaccurate due to the similarity of prey isotope ratios, Newsome *et al.* 2012), these trophic interactions have been described before for these species. Stingray spines embedded in the jaws of giant guitarfish, wedgefish and sawfish suggest predation on these species (Dean *et al.* 2017). The diet of spiny butterfly rays consists partly of exceptionally large prey and sometimes includes stingrays (Last *et al.* 2016). Opportunistic predation by these species is supported by the high abundance of the pearl whipray in the Bijagós Archipelago (**Chapter 5**) and the marbled stingray (*Dasyatis marmorata*; **Chapter 3**) in the Banc d'Arguin.

This suggests that large guitarfish may opportunistically feed on stingrays while competing for shared (endobenthic) prey with these rays (**Figure 11.4**). Intraguild predation is important in food web organization, maintaining predator diversity and the resilience of food webs against external stressors (Holt and Huxel 2007, Wang *et al.* 2019). Intraguild predation reduces predation pressure on shared prey species through (1) satisfying the energetic needs of the intraguild predator by the inclusion of the intraguild prey into its diet, (2) controlling intraguild prey abundance, and (3) changing the behavior of both intraguild predators (i.e., more time spent on intraguild predation) and intraguild prey (i.e., more time spent on risk avoidance from an intraguild predator) (Griffen and Byers 2006, Holt and Huxel 2007, Wang *et al.* 2019). As the predator effects of an intraguild predator and prey are nonadditive and reduce predation pressure on shared resources (i.e., may differ amongst species and life stages), intraguild predation reduces the redundancy of predator species in food webs and promotes predator coexistence (e.g., with shorebirds; Griffen and Byers 2006, Wang *et al.* 2019).

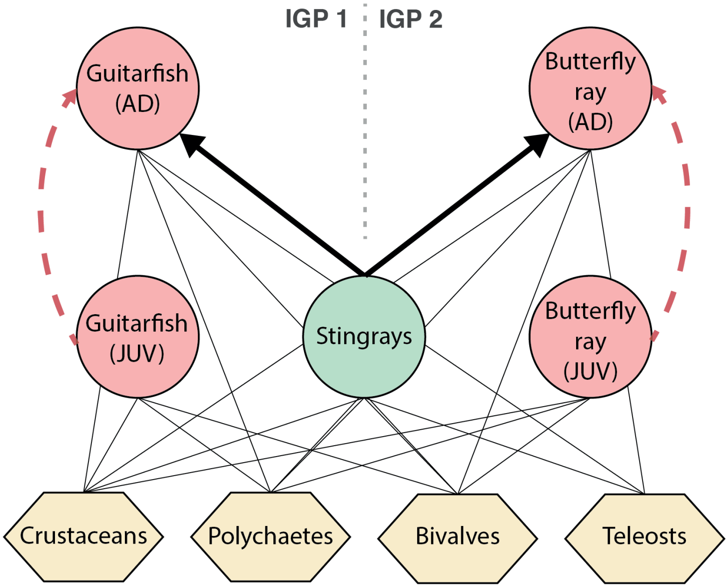


Figure 11.4 Two conceptual modules of intraguild predation (IGP) in large intertidal systems: the predation on stingrays by adult blackchin guitarfish (IGP1) and adult spiny butterfly rays (*Gymnura altavela*, IGP2). The intraguild predation (highlighted by black arrows) occurs when intraguild predators (red) predate on an intraguild prey species (green; **Box E**), with which it also competes for resources (yellow) during early and adult life stages (red dashed line).

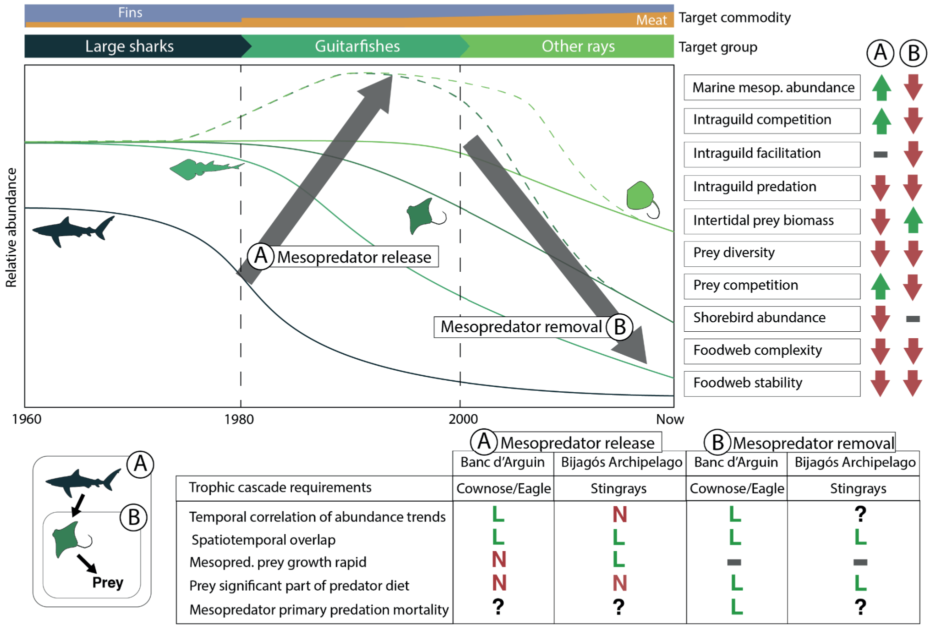
Intraguild facilitation (G)

Besides competing for shared resources, intertidal mesopredators can facilitate other species in the same guild and promote food web stability by increasing resource availability (Bruno *et al.* 2003, Assaneo *et al.* 2013). We show that the abundant pearl whipray (*Fontitrygon margaritella*) has an important role in changing the intertidal landscape of the Bijagós Archipelago and changes the community composition of the endobenthic community (**Chapter 9**). Feeding activities of benthic predators may facilitate other species within the same guild in three ways: (1) their feeding activity creates new habitats for prey species (O'Shea *et al.* 2012), (2) their predation pressure alleviates competition amongst benthic communities and promotes the abundance of other prey species (van Gils *et al.* 2013, El-Hacen *et al.* 2020), and (3) by their benthic feeding activity, predators resuspend nutrients that indirectly benefit (shared) prey species (Cadée 2001). The feeding activity by the pearl whipray creates a heterogenous landscape of feeding pits (i.e., 'ray pits'; **Chapters 7 and 9**). These microhabitats are used by intertidal prey (e.g., crabs, shrimp, juvenile fish; O'Shea *et al.* 2012), which may contribute to their population growth (Schaffmeister *et al.* 2006).

The feeding activity of shorebirds is hypothesized to alleviate competition in endobenthic communities and to cause an increased abundance of bivalves, which are in turn important to the diet of other intertidal predators (van Gils *et al.* 2013, El-Hacen *et al.* 2020). Similarly, predation by large ray species (i.e., cownose and eagle rays) on the dominant hard-shelled bloody cockle has been hypothesized to release other bivalves (i.e., *Dosinia sp.*) from competition (El-Hacen *et al.* 2020, 2023, Lemrabott *et al.* 2023b). These small bivalves are the main prey for shorebirds and are crucial in preparation for their long-distance return migrations (Piersma *et al.* 1993, Lourenço *et al.* 2015, 2017, van Gils *et al.* 2016).

Potential cascading effects of shark and ray removal (H)

The impact of fisheries on sharks and rays can be profound (Stevens *et al.* 2000, Dulvy *et al.* 2021, **Chapters 3 and 4**) and has been described to have potential cascading effects on other trophic levels and overall ecosystem functioning (Myers *et al.* 2007). However, these have since been disputed as the requirements for a trophic cascade to take place were not met (Grubbs *et al.* 2016). Similarly, trophic cascades due to shark removal on coral reefs have been challenged due to the high ecological redundancy of sharks (Roff *et al.* 2016). Here, I discuss the likelihood of (A) cascading effects caused by mesopredator release after shark removal and (B) the removal of mesopredators through continued overexploitation of elasmobranch species (**Figure 11.5**). I do so for both of these scenarios based on the requirements of trophic cascades described by Grubbs *et al.* (2016) and use the example of the Lusitanian cownose ray in the Banc d'Arguin and the abundant pearl whipray in the Bijagós Archipelago (**Figure 11.5**). We have described the food web consequences of these scenarios in depth in **Chapter 7**, so I will focus here on the likelihood of a trophic cascade in intertidal ecosystems following elasmobranch removal.



	A	B
Marine mesop. abundance	⬆	⬇
Intraguild competition	⬆	⬇
Intraguild facilitation	−	⬇
Intraguild predation	⬇	⬇
Intertidal prey biomass	⬇	⬆
Prey diversity	⬇	⬇
Prey competition	⬆	⬇
Shorebird abundance	⬇	−
Foodweb complexity	⬇	⬇
Foodweb stability	⬇	⬇

	A Mesopredator release		B Mesopredator removal	
	Banc d'Arguin	Bijagós Archipelago	Banc d'Arguin	Bijagós Archipelago
Trophic cascade requirements	Cownose/Eagle	Stingrays	Cownose/Eagle	Stingrays
Temporal correlation of abundance trends	L	N	L	?
Spatiotemporal overlap	L	L	L	L
Mesopred. prey growth rapid	N	L	−	−
Prey significant part of predator diet	N	N	L	L
Mesopredator primary predation mortality	?	?	L	?

Figure 11.5 Summarized overview and likelihood of changes in the Banc d'Arguin and Bijagós Archipelago caused by the sequential removal of large sharks (blue), guitarfish (green), and other rays (light green) due to international demand for shark and ray fins and meat (top). I describe two scenarios: (A) the mesopredator release due to shark removal and (B) the effects of mesopredator removal. For each scenario, I show the likelihood of a trophic cascade based on the requirements described by Grubbs *et al.* (2016) (bottom table, L = likely, N = not likely, L/N = likely for some species, ? = unknown). I do so by using the Lusitanian cownose ray (*Rhinoptera marginata*) as a model species for the Banc d'Arguin and the pearl whipray (*Fontitrygon margaritella*) for the Bijagós Archipelago. I also show the potential consequences of elasmobranch fisheries for intertidal food webs and shorebirds for both scenarios (left, red arrow = decrease, green arrow = increase; explained in depth in **Chapter 7**).

Marine mesopredator release following shark removal (Figure 11.5A)

Benthopelagic rays (e.g., cownose rays) in the Banc d'Arguin are hypothesized to have increased in abundance as a direct consequence of hammerhead shark declines (Oudman *et al.* 2020, Lemrabott 2023). Similarly, Bijagó village elders describe an increase in the abundance of small stingrays (e.g., pearl whiprays) due to the disappearance of hammerhead sharks. Here, I determine the likelihood of these described mesopredator releases based on the best available data for the Banc d'Arguin and the Bijagós Archipelago (**Figure 11.5A**).

We describe how a decrease in large-bodied sharks coincides with increased catches of large benthopelagic rays in the Banc d'Arguin (**Chapter 3**). In addition, the subsequent decline in guitarfish, as potential intraguild predators (**Figure 11.4**; Dean *et al.* 2017), may have further reduced predation on benthic stingrays. However, our analysis in the Bijagós Archipelago shows consistent declines in catches of small benthic rays and sharks over the past decades (**Chapter 4**). We show that fisheries-dependent data (**Chapters 3 and 4**) and environmental DNA (**Chapter 5**) indicate an overlap between sharks and rays in terms of spatiotemporal distribution in both study areas and enable these species to interact. However, the mesopredator release of cownose and eagle rays in the Banc d'Arguin is less likely due to their late maturity and low fecundity, resulting in low intrinsic population growth (Fisher *et al.* 2013, Grubbs *et al.* 2016). Grubbs *et al.* (2016) describe that the population growth of cownose rays is lower compared to large-bodied shark species. In contrast, we show that the most abundant ray species in the Bijagós Archipelago, the pearl whipray, is relatively fast-growing, especially compared to large-bodied sharks (**Chapter 6**). However, this potential mesopredator release is disputable as no increase in abundance of this species group was observed following significant declines in shark abundance. We show that shark species in both areas are generalist predators. Although their diet may opportunistically include rays, other marine predators, including marine mammals and large teleosts, may also feed on rays. Therefore, predation on rays in intertidal areas may be diffuse, leading to increased redundancy amongst ray predators. For instance, our field observations and conversations with local fishers indicate that cobias (*Rachycentron canadum*) in the Bijagós may frequently predate on stingrays (**Box E**), which is supported by Arendt *et al.* (2001), who concluded that cobias in the Gulf of Mexico feed on (young) cownose rays. The high redundancy amongst ray predators and the low contribution of rays to the diet of most shark species (**Box E**) decrease the likelihood that shark removal has led to an increase in mesopredatory rays. However, as large teleosts and sharks are simultaneously removed from intertidal areas through increased fisheries, the disappearance of a whole suite of ray predators may still cause these species to be relatively free from predation. In **Chapter 7**, we described how increased predation by rays in the intertidal may contribute to the declining abundance of shorebirds along the East

Atlantic Flyway (e.g., Oudman *et al.* 2020). However, the subsequent and continued exploitation of mesopredatory rays in both areas may also have mitigated these species' release from predation risk.

Cascading effects of marine mesopredator removal (Figure 11.5B)

Despite a decline in large sharks and large-finned rays (e.g., guitarfishes), high fishing pressure on rays remains high throughout the West African region (**Chapters 3 and 4**, Diop and Dossa 2011, Moore 2019). The potential consequences of this have been discussed in detail in **Chapter 7**. Here, I will focus on the likelihood that these changes have cascading effects based on the same requirements proposed by Grubbs *et al.* (2016) and the example in Figure 11.5B. We show that most elasmobranchs using intertidal habitats are threatened with extinction (**Chapter 7**), illustrating the gradual loss of rays and their role as mesopredators from intertidal areas. In **Chapters 3 and 4,** we discuss the significant declines of these species in both areas. However, the correlation between the abundance of rays and their benthic prey is lacking and is difficult to quantify (e.g., Flowers *et al.* 2021). However, the decline of the cownose and eagle rays from intertidal areas and increased rainfall within the region may explain the recent increases in the West African bloody cockle (El-Hacen *et al.* 2020, Lemrabott 2023). For both the Banc d'Arguin and the Bijagós Archipelago, we show that cownose rays and stingrays use intertidal habitats and overlap in spatiotemporal habitats with intertidal prey (**Chapters 8 and 9**). In the Banc d'Arguin, catches of these rays in the intertidal by fisheries (**Chapter 8**) and traces of intertidal feeding (El-Hacen *et al.* 2023) confirm the intertidal feeding behavior of large cownose and eagle rays. On the bare intertidal flats of the Bijagós Archipelago, intertidal 'ray pits' created during high tide allow for quantification of intertidal feeding behavior (**Chapter 9**). Although we show that, on average, intertidal resources make up >30% of the diet of rays in the Banc d'Arguin and the Bijagós Archipelago, we also show that these species are generalist mesopredators (**Chapter 8**). Therefore, it is debatable whether these species, which also have access to subtidal prey, are the primary cause of predation mortality in intertidal prey. Following the same reasoning, shorebirds are more likely to cause higher mortality rates among intertidal prey due to their reliance on these prey as primary food sources (Piersma 2012, Correia *et al.* 2023). Large rays are more likely to contribute to the mortality rates of bloody cockles, as they may be one of the only (marine) mesopredator species able to crack their hard shells (El-Hacen *et al.* 2023, Lemrabott 2023). These rays may indirectly increase food availability for molluscivore shorebirds by reducing this competitive bivalve (El-Hacen *et al.* 2020, Lemrabott 2023). However, large cownose rays have been described as generalists that may be unable to affect prey abundance (Ajemian and Powers, 2012, Collins *et al.* 2012). Overall, rays are characterized as generalist mesopredators, and their role in structuring benthic communities is unclear and needs further investigation (**Chapter 8**, Flowers *et al.* 2021). The decline in both shorebirds and rays is concerning, as this represents a scenario where two large groups of intertidal mesopredators are disappearing.

The decline of the intertidal mesopredator

The steep declines of sharks and rays in our two focal areas and the significant declines of many shorebirds along the East Atlantic Flyway (Oudman *et al.* 2020, Henriques *et al.* 2022) results in a simplification of the intertidal food web and a loss of ecological interactions. Although discussed at length in **Chapters 7 and 9**, I reiterate here the importance of the coexistence of these species.

Although these mesopredator groups overlap considerably in intertidal habitat and resource use (**Chapter 8**), their potential competition for resources and intraguild facilitation may be important in structuring intertidal communities (Garvey and Whiles, 2016), and these processes are likely to occur simultaneously. For example, cownose rays may indirectly facilitate shorebirds by reducing competition in prey communities, and stingrays are more likely to compete with a wider range of shorebirds due to their exploitation of similar prey (**Figure 11.3**). Therefore, a simplification of the elasmobranch community (i.e., a shift to fast-growing species such as milk sharks and small stingrays, Walker and Hislop 1998, Dulvy *et al.* 2000, Jabado *et al.* 2015) and general loss of mesopredator richness may cause a shift to dominant prey that in turn may outcompete other prey species that are important to food web functioning (e.g., dominance of the bloody cockle and lucinid bivalves in the Banc d'Arguin, van Gils *et al.* 2013, El-Hacen *et al.* 2020). The disappearance of probing and burrowing mesopredators may also have non-trophic cascading effects by lowering bioturbation rates, aeration of sediments, and decreasing habitat heterogeneity through a loss of microhabitat creation (**Chapter 9**, van Gils *et al.* 2013, O'Shea *et al.* 2012). Finally, a loss in these mesopredators also means a loss in global ecosystem connectivity, as migratory shorebirds link boreal ecosystems with tropical marine ecosystems through their interactions in the intertidal with elasmobranchs (**Figure 11.1; Chapter 8**). In **Box G** I show that intertidal areas that are important for shorebirds are likely also important for rays and that the species composition of both mesopredators may be correlated. This further highlights the importance of their coexistence for intertidal ecosystem functioning and that higher predators, such as large-bodied sharks, potentially maintain stable states of intertidal mesopredator coexistence.

Overall, the intertidal is an important and dynamic environment for shorebirds and elasmobranchs, which underlines the importance of these areas for conserving these vulnerable species and their ecological interactions.

Conservation

The importance of intertidal areas to the ecology of sharks and rays should be considered in area-based conservation measures while incorporating the needs of local communities reliant on marine resources. Recommendations for improved fisheries management were discussed above (**Table 11.1**). Here, I discuss the importance of including elasmobranch ecology and local communities in area-based conservation measures, which is especially important in the race to protect 30% of the ocean by 2030.

Conserving intertidal areas (I)

There is a general mismatch between the location of protected areas and biodiversity hotspots and important habitats (Lindegren *et al.* 2018, Moradi *et al.* 2019). This mismatch may undermine the objectives of marine protected areas (MPAs) to protect threatened species, areas of high biological diversity and essential habitats, and to maintain ecosystem services (Watson *et al.* 2014). As countries are bound to protect 30% of their territories by 2030 under the 30x30 Initiative of the Convention on Biological Diversity (Dinerstein *et al.* 2019), there is momentum to incorporate the ecology of vulnerable species groups into new area-based management strategies. As such, this may prevent protected areas from being designated based on economic and political decisions, which are less effective in achieving conservation objectives (Barr *et al.* 2013, Venter *et al.* 2018). Multiple initiatives now exist to delineate ecologically important areas for different vulnerable taxa to indicate where protected areas should be designated if conservation of that taxa is the objective (**Table 11.2**).

Table 11.2 Important area initiatives to delineate important ecological sites for avian and marine taxa. This now includes our efforts on the Important Shark and Ray Area (ISRA) initiative (**Box F**).

Initiative	Focal species	Year	Description
Important Bird and Biodiversity Areas (IBAs)	Birds	1970s	Donald *et al.* (2019)
Important Marine Mammal Areas (IMMAs)	Marine mammals	2016	Tetley *et al.* (2022)
Important Marine Turtle Areas (IMTAs)	Marine turtles	2019	Bandimere *et al.* (2021)
Important Shark and Ray Areas (ISRAs)	Sharks, rays and chimeras	2022	Hyde *et al.* (2022)

Sharks and rays are now considered the second-most threatened species group of all vertebrate taxa (after amphibians; IPBES 2019, Dulvy *et al.* 2021). Despite this, no initiative to delineate the important ecological areas for these species existed. In 2022, we worked with an international team of researchers from the IUCN Species Survival Commission Shark Specialist Group to determine that Important Shark and Ray Areas (ISRAs) should delineate areas that are (A) important to threatened species, (B) frequently used by range-restricted species, (C) important to their lifecycle (e.g., reproductive and feeding areas), and (D) have distinct biological, behavioral or ecological attributes or support important diversity of shark and ray species (**Box F**). ISRAs are primarily intended to provide information to decision-makers regarding priority areas to include in the development of area-based protective measures for sharks and rays. Similarly, Important Bird and Biodiversity Areas (IBAs) are now a main component of the Key Biodiversity Areas framework of the Convention of Biological Diversity (Donald *et al.* 2019). When considered collectively, these important areas highlight which are ecologically crucial for a variety of threatened taxa and, therefore, may be instrumental in maximizing the conservation of multiple taxa of interest. This is also true for intertidal areas, as we show that these are important to threatened shark and ray species (ISRA criterion A), many of which are endemic (ISRA criterion B) and use these areas as feeding refugia mostly during early life stages (ISRA criterion C; **Chapters 7 and 8**). Most large intertidal areas are already designated as IBAs, recognizing their importance to the ecology of shorebirds. The overlap between IBAs and ISRAs in intertidal areas further highlights the key ecological role of these areas to multiple threatened taxa. As such, it is clear that intertidal areas warrant enhanced conservation for these diverse mesopredator assemblages (**Box G**). Currently, 31% of intertidal areas are located in protected areas, which is considerably higher compared to the protected surface area of marine (6%) and terrestrial (13%) systems (Hill *et al.* 2021). As countries that are signatories to the 30x30 initiative are required to protect 30% of their territorial waters, the overlap in important areas presents an opportunity to maximize protection for vulnerable marine and avian taxa in intertidal areas. However, I want to stress that designating protected areas for shark conservation is just the start, as both the Banc d'Arguin and the Bijagós Archipelago are (or contain) marine protected areas. Yet, their elasmobranch populations are overexploited, and illegal fisheries persist.

Fisheries and local livelihoods (J)

The declines in shark and ray populations are concerning not only from an ecological perspective but also from a socioeconomic one. The declines observed in fish stocks worldwide, especially in coastal regions, pose a disproportionately high threat to the local communities that depend on marine resources as the primary source of subsistence or income (Golden *et al.* 2016). Shark and ray meat is an essential source of protein for many coastal communities worldwide (Glaus *et al.* 2019, Niedemüller *et al.* 2021). The total value of the trade in shark and ray meat is estimated to be 2.6 billion USD, whereas the total market value of the fin trade is estimated to be 1.5 billion USD (Niedemüller *et al.* 2021). Therefore, the decline of these species as a resource further impacts the resilience of communities that depend on them through the loss of income and food security.

In the Banc d'Arguin, shark and ray meat is destined for export, though fisheries are also crucial for the local economy and subsistence needs of Imraguen communities (Lemrabott *et al.* 2023). In the Bijagós Archipelago, shark and ray meat is consumed locally and is an important protein source (**Chapter 4**, Cross 2014). In both areas, shark fins are exported to international markets (Diop and Dossa 2011). In addition, sharks and rays have a high cultural value in Bijagó communities, and their disappearance would impact the long-standing traditions and beliefs of these communities (**Box A**). The impact of overfishing by small-scale fisheries is apparent, whereas the impact (or contribution) of industrial fisheries on coastal livelihoods is unknown. Although these large industrial vessels are mostly restricted to deeper waters, their intrusion into areas destined for small-scale fisheries does occur and is known to increase competition between these two fisheries elsewhere (Ponte *et al.* 2007, Ameyaw *et al.* 2021). I propose essential changes in fisheries management (**Table 11.1**) and want to underline that socioeconomic aspects need to be included in the management of (shark) fisheries and MPAs (e.g., Booth *et al.* 2019, Karnad *et al.* 2020). Based on the experience of field researchers working with local communities, we show that early involvement of local communities in study design, implementation, and communication of outcomes greatly improves the generation and uptake of information on shark and ray fisheries and trade (**Chapter 10**). This information, in turn, contributes to the adaptive management of these species while considering the needs of coastal communities (Booth *et al.* 2019, Glaus *et al.* 2019). This includes prioritizing the needs of local fishing communities by increasing the profitability of sustainable small-scale fisheries and local trade, and by providing alternative livelihoods when new conservation measures interfere with fisheries.

Main conclusions and future directions

Based on our findings, I conclude that intertidal areas are important ecological areas for sharks and rays. These dynamic coastal areas provide feeding refugia to the early life stages of vulnerable sharks and rays, and in doing so, these species interact with the abundant ‘low-tide mesopredators’ of the intertidal- shorebirds. Although the specifics of these interactions are species-dependent and require additional research, I emphasize that shorebirds and elasmobranchs together play an important role as intertidal mesopredators and likely shape intertidal communities through their interactions. However, in the West African region, sharks and rays are navigating ‘Troubled Waters’ under the continued risk of stranding by intertidal habitat use and subject to pressures from fisheries present within the intertidal areas and along its borders. In this region, the continued removal of sharks and rays by industrial and small-scale fisheries has caused their conservation status to deteriorate significantly, causing many to be threatened with extinction. The sequential decline of sharks, guitarfishes and now (smaller) rays may have altered these ecosystems considerably, including their quality as important wintering areas for migratory shorebirds. In turn, this also threatens the role of intertidal mesopredators in global ecosystem connectivity, as their interactions in the tropical intertidal connect Arctic/temperate terrestrial ecosystems (i.e., shorebird movements) to marine ecosystems (i.e., shark and ray movements). This global ecosystem connectivity highlights the importance of improved conservation of intertidal areas and their high- and low-tide predators throughout the entire range of their movements.

Future research efforts should prioritize tackling data deficiency of sharks and rays in the region by improving species-specific knowledge, including shedding light on how these species connect different ecosystems and populations, and how their movements overlap with both small-scale and industrial fisheries. This knowledge is crucial for their cost-effective conservation in West Africa. Strengthening existing local research capacity should be prioritized to stimulate long-term management strategies. Existing regulations for managing sharks and rays in both study areas should be implemented and enforced. However, new strategies are highly needed to enhance the protection of elasmobranchs, and this thesis has presented such recommendations, including the closure of important ecological sites and restricting targeted catches of threatened species. As intertidal areas, fisheries and elasmobranchs are closely linked to coastal communities, the involvement and livelihoods of those who rely on the sea the most should always be safeguarded.

BOX G: DIGGING DEEPER: INTERTIDAL ASSOCIATIONS OF SHOREBIRDS AND RAYS

The intertidal can be a challenging environment for both prey and predators, so species rely on their adaptations to use these highly dynamic habitats. To determine how shorebirds and rays interact in intertidal areas, I compare their burrowing capabilities and determine the correlation of species richness between these mesopredator groups for large intertidal areas (see methods in Appendix G.1).

Comparative burrowing depths of intertidal mesopredators

Intertidal prey species can adapt by moving with the tide to deeper waters or tide pools or by retreating into the sediment. Some species retreat into complex burrow networks (e.g., ghost shrimp and fiddler crabs). Yet, other species (e.g., bivalves) rely on their morphological adaptations to exchange oxygen and nutrients while buried in the sediment. These adaptations of intertidal prey species complicate their exploitation by intertidal (meso)predators whose foraging is already limited due to the continuous tidal cycle and associated accessibility to intertidal habitats and prey (Leurs *et al.* 2023). The ability of a predator to access potential endobenthic prey species is therefore not only determined by the time that the intertidal habitat is accessible but also by the interplay between prey burrowing depth and the probing or burrowing capabilities of the predator (e.g., Zwarts and Wanink 1984).

To support the hypothesis that shorebirds and rays use the same intertidal resources, I show that both mesopredator groups can access prey at similar sediment depths but mainly within the top sediment layers (<50mm depth; **Figure G1**). In these layers, all mesopredator taxa can access prey species. Generally, the richness and biomass of endobenthic prey are also highest in these layers (<60mm, e.g., Zwarts and Wanink 1993, Byers and Grabowski 2014). The generally deeper burrowing depth of stingrays, eagle rays, and cownose rays in intertidal habitats suggests their ability to exploit endobenthic prey that may be inaccessible to long-billed shorebird species (i.e., red stingrays *Hymitrygon akajei* accessing ghost shrimp at >200mm deep, Takeuchi and Tamaki 2014). Some prey species may increase their burrowing depths ontogenetically to lower predation risk (e.g., Zwarts and Wanink 1984, 1993). However, in doing so, prey may escape most, but not all, intertidal predators. Some prey species (e.g., bivalves) may increase shell-thickness or body size, making them inaccessible or unfavored prey even when within reach of the predators. As the optimal foraging theory describes, increased handling time due to increased burrowing depth, prey body size, or hardness may limit or even restrict predators in exploiting certain prey species (MacArthur and Pianka 1966, Zwarts and Wanink 1984). Therefore, accessing prey at different depths may be one axis along which trophic niches are partitioned amongst shorebirds and rays.

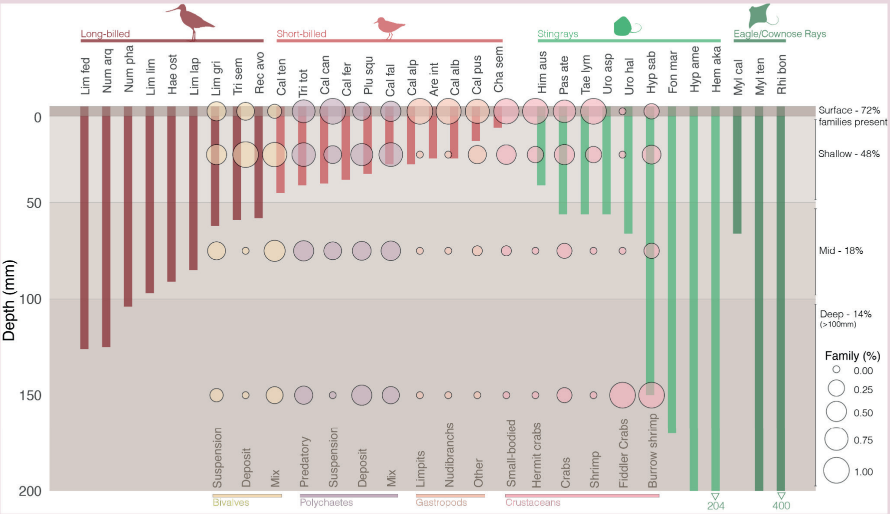


Figure G1 The comparative probing (red bars) and burrowing (green bars) depths of different species of shorebirds using intertidal areas. We show the probing depth for long-billed shorebirds (i.e., bill length >50 mm; dark red) and short-billed shorebirds (i.e., bill length <50mm; light red), and the burrowing depth for stingrays and round stingrays (families Dasyatidae and Urolophidae; light green) and eagle rays and cownose rays (families Myliobatidae and Rhinopteridae; dark green). We compare their probing and burrowing depths to the presence of (burrowing) endobenthic families (circles). Circle sizes represent the proportion of families of bivalves (yellow), polychaetes (purple), gastropods (orange), and crustaceans (pink) present in each sediment layer (surface, shallow 0-50mm, mid 50-100mm, and deep >100mm).

Intertidal mesopredator richness and associated taxa

Intertidal areas with a high species richness of shorebirds also support a high species richness of elasmobranchs (i.e., rays and sharks; **Figure G2A**). Whereas most shorebird species in intertidal areas are non-threatened, most elasmobranch species are threatened. The proportion of threatened elasmobranch species is highest in regions with a generally high species richness (e.g., Indian Ocean, Southern Pacific). Intertidal prey species influence the (global) distribution of intertidal mesopredators (Bom *et al.* 2018). Under the assumption that shorebirds, rays and sharks depend on similar intertidal prey, different taxa of shorebirds and rays may be associated. Although the occurrence of ray families in tidal areas is mainly correlated with other ray families, some shorebirds and ray taxa are associated in intertidal areas (**Figure G2B**). For example, stingrays are associated with curlews, shanks, and godwits. Plovers are mostly correlated with the occurrence of (pelagic) eagle rays. These results suggest that intertidal areas important for shorebirds are also important to (threatened) elasmobranchs. This further highlights the importance of the conservation of intertidal areas for shorebirds and elasmobranchs.

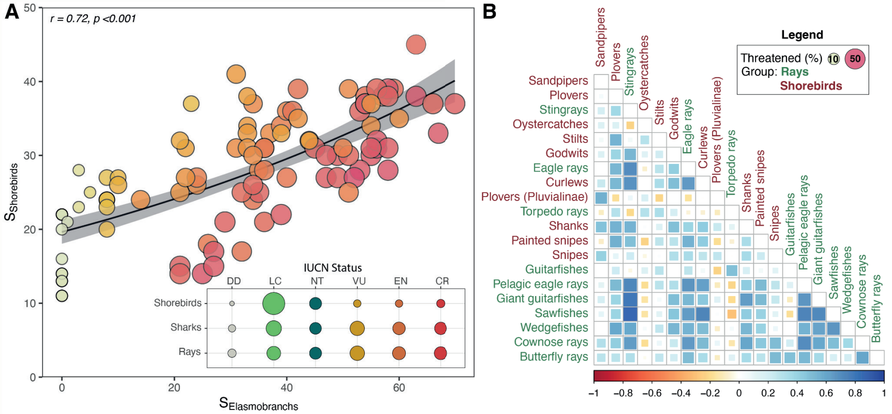
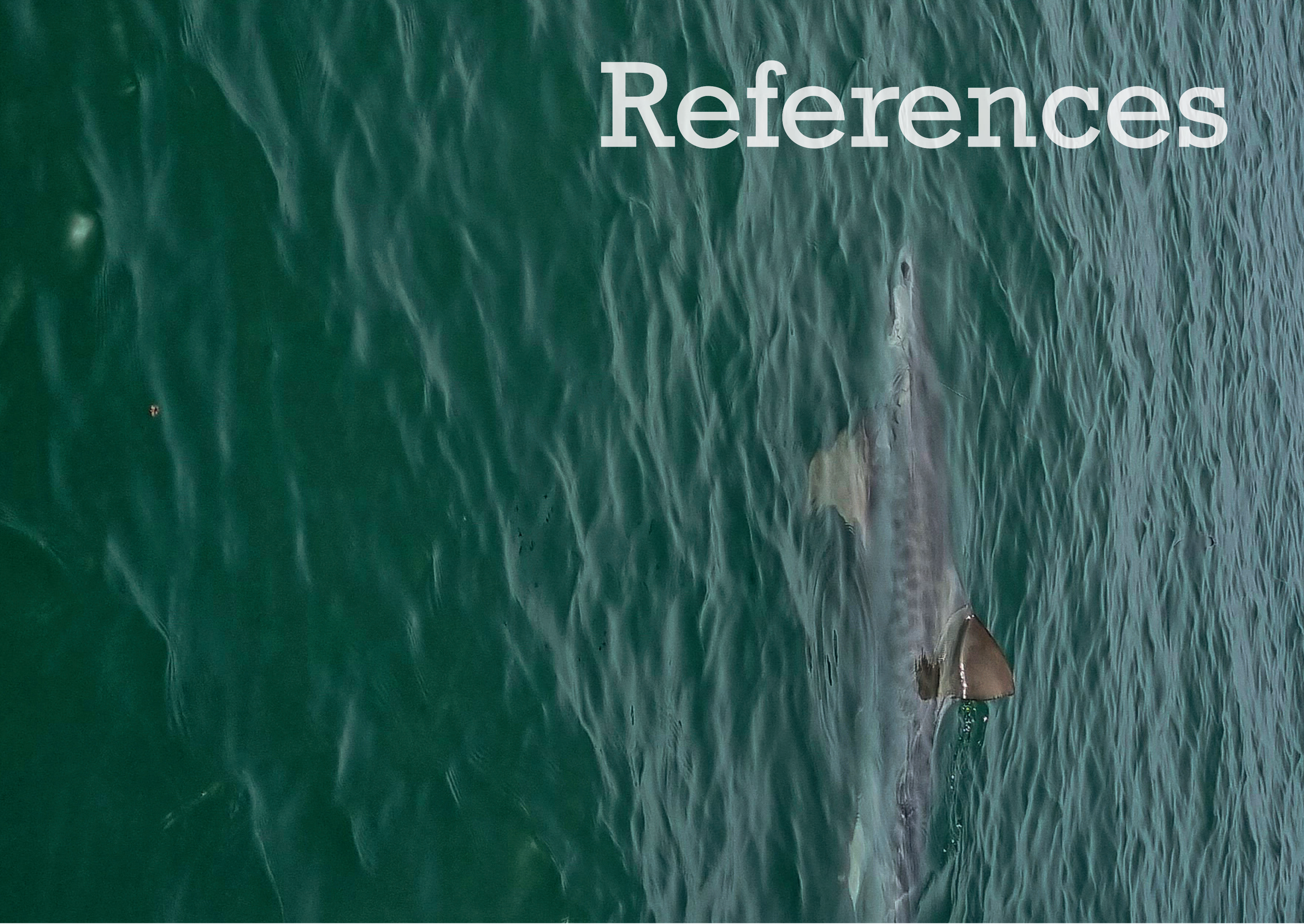


Figure G2 (A) The correlation between species richness (S) of elasmobranchs and shorebirds of the 100 largest intertidal areas. Circle size indicates the proportion of threatened species in an area. The insert plot shows the total proportion of shorebird, shark and ray species in each IUCN Red List category for all intertidal areas together (DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered; A species is considered threatened when VU, EN and CR). **(B)** Correlation matrix of occurrence of shorebird (red) and ray (green) species groups in intertidal areas (1 = positive correlation, -1 = negative correlation).

References



A

Abel, D. C., & Grubbs, D. R. (2020). Shark biology and conservation: Essentials for educators, students and enthusiasts. John Hopkins University Press.

Abrantes, K. G., & Barnett, A. (2011). Intrapopulation variations in diet and habitat use in a marine apex predator, the broadnose sevengill shark Notorynchus cepedianus. Marine Ecology Progress Series, 442, 133–148. https://doi.org/10.3354/meps09395

Ackerman, J. T., Kondratieff, M. C., Matern, S. A., & Cech, J. J. (2000). Tidal influence on spatial dynamics of leopard sharks, Triakis semifasciata, in Tomales Bay, California. Environmental Biology of Fishes, 58(1), 33–43. https://doi.org/10.1023/A:1007657019696

Adenle, A. A., Stevens, C., & Bridgewater, P. (2015). Global conservation and management of biodiversity in developing countries: An opportunity for a new approach. Environmental Science and Policy, 45(2015), 104–108. https://doi.org/10.1016/j.envsci.2014.10.002

Adkins, M. E., Simpfendorfer, C. A., & Tobin, A. J. (2016). Large tropical fishes and their use of the nearshore littoral, intertidal and subtidal habitat mosaic. Marine and Freshwater Research, 67(10), 1534–1545. https://doi.org/10.1071/MF14339

Ajemian, M. J., Dolan, D., Graham, W. M., & Powers, S. P. (2011). First evidence of elasmobranch predation by a waterbird: Stingray attack and consumption by the Great Blue Heron (Ardea herodias). Waterbirds, 34(1), 117–120. https://doi.org/10.1675/063.034.0116

Ajemian, M. J., & Powers, S. P. (2012). Habitat-specific feeding by cownose rays (Rhinoptera bonasus) of the northern Gulf of Mexico. Environmental Biology of Fishes, 95, 79–97.

Ajemian, M. J., Powers, S. P., & Murdoch, T. J. T. (2012). Estimating the potential impacts of large mesopredators on benthic resources: Integrative assessment of spotted eagle ray foraging ecology in Bermuda. PLoS ONE, 7(7). https://doi.org/10.1371/journal.pone.0040227

Alder, J., & Sumaila, U. R. (2004). Western Africa: A fish basket of Europe past and present. J. Environ. Dev, 13, 156–178. https://doi.org/10.1177/1070496504266092.

Almojil, D. (2021). Local ecological knowledge of fisheries charts decline of sharks in data-poor regions. Marine Policy, 132(June), 104638. https://doi.org/10.1016/j.marpol.2021.104638

Alongi, D. M. (2014). Carbon cycling and storage in mangrove forests. Annual Review of Marine Science, 6, 195–219.

Alongi, D. M. (2018). Blue carbon (1st ed.). Springer International Publishing.

Alves, J. A., Coelho, A. P., Carneiro, C., Nightingale, J., Barros, A. R., & Rocha, A. D. (2021). Ligações migratórias estabelecidas pelas aves limícolas do Arquipélago Dos Bijagós. Lucanus – Revista de Ambiente e Sociedade, V, 166–185.

Amandè, M. J., Ariz, J., Chassot, E., Molina, A. D., Gaertner, D., Murua, H., & Chavance, P. (2010). Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003-2007 period. Aquatic Living Resources, 23(4), 353–362. https://doi.org/10.1051/alr/2011003

Ameyaw, G. A., Tsamenyi, M., McIlgorm, A., & Aheto, D. W. (2021). Challenges in the management of small-scale marine fisheries conflicts in Ghana. Ocean and Coastal Management, 211(July 2020), 105791. https://doi.org/10.1016/j.ocecoaman.2021.105791

Anadón, J. D., Giménez, A., Ballestar, R., & Pérez, I. (2009). Evaluation of local ecological knowledge as a method for collecting extensive data on animal abundance. Conservation Biology, 23(3), 617–625. https://doi.org/10.1111/j.1523-1739.2008.01145.x

Anderson, J. L., Anderson, C. M., Chu, J., Meredith, J., Asche, F., Sylvia, G., & Valderrama, D. (2015). The fishery performance indicators: A management tool for triple bottom line outcomes. PLoS ONE, 10(5), 1–20. https://doi.org/10.1371/journal.pone.0122809

Anderson, S. C., Flemming, J. M., Watson, R., & Lotze, H. K. (2011). Rapid global expansion of invertebrate fisheries: Trends, drivers, and ecosystem effects. PLoS ONE, 6(3), 1–9. https://doi.org/10.1371/journal.pone.0014735

Arendt, M. D., Olney, J. E., & Lucy, J. A. (2001). Stomach content analysis of cobia, Rachycentron canadum, from lower Chesapeake Bay. Fishery Bulletin, 99(4), 665–670.

Arístegui, J., Barton, E. D., Álvarez-Salgado, X. A., Santos, A. M. P., Figueiras, F. G., Kifani, S., & Demarcq, H. (2009). Sub-regional ecosystem variability in the Canary Current upwelling. Progress in Oceanography, 83(1–4), 33–48. https://doi.org/10.1016/j.pocean.2009.07.031

Assaneo, F., Coutinho, R. M., Lin, Y., Mantilla, C., & Lutscher, F. (2013). Dynamics and coexistence in a system with intraguild mutualism. Ecological Complexity, 14, 64–74. https://doi.org/10.1016/j.ecocom.2012.10.004

Assessment, M. E. (2005). Ecosystems and human well-being: Synthesis. Island Press.

Atwood, T. B., Connolly, R. M., Ritchie, E. G., Lovelock, C. E., Heithaus, M. R., Hays, G. C., & Macreadie, P. I. (2015). Predators help protect carbon stocks in blue carbon ecosystems. Nature Climate Change, 5(12), 1038–1045. https://doi.org/10.1038/nclimate2763

Azzurro, E., Moschella, P., & Maynou, F. (2011). Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. PLoS ONE, 6(9), 1–8. https://doi.org/10.1371/journal.pone.0024885

B

Bakker, J., Wangensteen, O. S., Chapman, D. D., Boussarie, G., Buddo, D., Guttridge, T. L., & Mariani, S. (2017). Environmental DNA reveals tropical shark diversity in contrasting levels of anthropogenic impact. Scientific Reports, 1–11. https://doi.org/10.1038/s41598-017-17150-2

Ballantyne, J. S., & Robinson, J. W. (2010). Freshwater elasmobranchs: A review of their physiology and biochemistry. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology, 180(4), 475–493. https://doi.org/10.1007/s00360-010-0447-0

Balmford, A., Gravestock, P., Hockley, N., McClean, C. J., & Roberts, C. M. (2004). The worldwide costs of marine protected areas. Proceedings of the National Academy of Sciences, 101(26), 9694–9697. https://doi.org/10.1073/pnas.0403239101

Bandimere, A., Brenner, H., Casale, P., Dimatteo, A., Hurley, B., Hutchinson, B., & Wallace, B. (2021). Important marine turtle areas: Guidelines 1.0 (pp. 1–12). IUCN-SSC Marine Turtle Specialist Group.

Bangley, C. W., Paramore, L., Shiffman, D. S., & Rulifson, R. A. (2018). Increased abundance and nursery habitat use of the bull shark (Carcharhinus leucas) in response to a changing environment in a warm-temperate estuary. Scientific Reports, 8(1), 6018. https://doi.org/10.1038/s41598-018-24510-z

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. Ecological Monographs, 81(2), 169–193.

Barker, M. J., & Schluessel, V. (2005). Managing global shark fisheries: Suggestions for prioritizing management strategies. Aquatic Conservation: Marine and Freshwater Ecosystems, 15(4), 325–347. https://doi.org/10.1002/aqc.660

Barley, S. C., Clark, T. D., & Meeuwig, J. J. (2020). Ecological redundancy between coral reef sharks and predatory teleosts. Reviews in Fish Biology and Fisheries, 30(1), 153–172. https://doi.org/10.1007/s11160-019-09588-6

Barley, S. C., Meekan, M. G., & Meeuwig, J. J. (2017). Species diversity, abundance, biomass, size and trophic structure of fish assemblages on coral reefs in relation to shark abundance. Mar. https://doi.org/10.6084/m9.figshare.4009686

Barnes, M. A., & Turner, C. R. (2016). The ecology of environmental DNA and implications for conservation genetics. Conservation Genetics, 17(1), 1–17. https://doi.org/10.1007/s10592-015-0775-4

Barnett, A., Abrantes, K., Stevens, J. D., Yick, J. L., Frusher, S. D., & Semmens, J. M. (2010). Predator-prey relationships and foraging ecology of a marine apex predator with a wide temperate distribution. Marine Ecology Progress Series, 416, 189–200. https://doi.org/10.3354/meps08778

Barnett, A., Abrantes Ká, K. G., Seymour, J., & Fitzpatrick, R. (2012). Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLoS ONE, 7(5), 1–12. https://doi.org/10.1371/journal.pone.0036574

Barnett, A., Braccini, M., Dudgeon, C. L., Payne, N. L., Abrantes, K. G., Sheaves, M., & Snelling, E. P. (2017). The utility of bioenergetics modelling in quantifying predation rates of marine apex predators: Ecological and fisheries implications. Scientific Reports, 7(1), 1–10. https://doi.org/10.1038/s41598-017-13388-y

Barr, L. M., & Possingham, H. P. (2013). Are outcomes matching policy commitments in Australian marine conservation planning? Marine Policy, 42(2013), 39–48. https://doi.org/10.1016/j.marpol.2013.01.012

Barría, C., Coll, M., & Navarro, J. (2015). Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. Marine Ecology Progress Series, 539, 225–240. https://doi.org/10.3354/meps11494.

Barrios-O'Neill, D., Bertolini, C., & Collins, P. C. (2017). Trophic cascades and the transient keystone concept. Biological Conservation, 212(May), 191–195. https://doi.org/10.1016/j.biocon.2017.06.011

Barros, N. B., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (Tursiops truncatus) in Sarasota Bay, Florida. Journal of Mammalogy, 79(3), 1045–1059. https://doi.org/10.2307/1383114

Bartón, K. (2022). Package "MuMIn" multi-model inference [Computer software].

Bascompte, J., Melián, C. J., & Sala, E. (2005). Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America, 102(15), 5443–5447. https://doi.org/10.1073/pnas.0501562102

Battley, P. F., Warnock, N., Tibbitts, T. L., Gill, R. E., Piersma, T., Hassell, C. J., & Riegen, A. C. (2012). Contrasting extreme long-distance migration patterns in bar-tailed godwits Limosa lapponica. Journal of Avian Biology, 43(1), 21–32. https://doi.org/10.1111/j.1600-048X.2011.05473.x

Baum, J. K., & Myers, R. A. (2004). Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters, 7, 135–145.

Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., & Doherty, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. In Science (Vol. 299, pp. 389–392). https://doi.org/10.1126/science.1079777

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78, 699–714. https://doi.org/10.1111/j.1365-2656.2009.01531.x.

Beaudreau, A. H., & Levin, P. S. (2014). Advancing the use of local ecological knowledge for assessing data-poor species in coastal ecosystems. Ecological Applications, 24(2), 244–256. https://doi.org/10.1890/13-0817.1

Begossi, A. (2010). Small-scale fisheries in Latin America: Management models and challenges. Mast, 9(2), 7–31.

Belhabib, D., Cheung, W. W. L., Kroodsma, D., Lam, V. W. Y., Underwood, P. J., & Virdin, J. (2019). Catching industrial fishing incursions into inshore waters of Africa from space. Fish and Fisheries, 379–392. https://doi.org/10.1111/faf.12436

Belhabib, D., Gascuel, D., Abou Kane, E., Harper, S., Zeller, D., & Pauly, D. (2013). Preliminary estimation of realistic fisheries removals from Mauritania, 1950-2010. Fisheries Centre Research Reports, 20(3), 61–78.

Belhabib, D., Koutob, V., Sall, A., Lam, V. W. Y., & Pauly, D. (2014). Fisheries catch misreporting and its implications: The case of Senegal. Fisheries Research, 151, 1–11. https://doi.org/10.1016/j.fishres.2013.12.006

Belhabib, D., & Pauly, D. (2015). Fisheries in troubled waters: A catch reconstruction for Guinea-Bissau, 1950-2010. Fisheries Centre Research Reports, 23(3), 1–16.

Bender, M. G., Machado, G. R., Azevedo Silva, P. J., Floeter, S. R., Monteiro-Netto, C., Luiz, O. J., & Ferreira, C. E. L. (2014). Local ecological knowledge and scientific data reveal overexploitation by multigear artisanal fisheries in the Southwestern Atlantic. PLoS ONE, 9(10). https://doi.org/10.1371/journal.pone.0110332

Beninger, P. G. (2019). Mudflat Ecology. Aquatic Ecology Series, 7.

Bennie, J. J., Duffy, J. P., Inger, R., & Gaston, K. J. (2014). Biogeography of time partitioning in mammals. Proceedings of the National Academy of Sciences of the United States of America, 111(38), 13727–13732. https://doi.org/10.1073/pnas.1216063110

Bernal, D., Carlson, J. K., Goldman, K. J., & Lowe, C. G. (2012). Energetics, metabolism, and endothermy in sharks and rays. Biology of Sharks and Their Relatives, 227–254. https://doi.org/10.1201/b11867-15

Bernos, T. A., Travouck, C., Ramasinoro, N., Fraser, D. J., & Mathevon, B. (2021). What can be learned from fishers' perceptions for fishery management planning? Case study insights from Sainte-Marie, Madagascar. PLoS ONE, 16(11 November), 1–23. https://doi.org/10.1371/journal.pone.0259792

Bertalanffy, L. (1938). A quantitative theory of organic growth', Human Biology (Vol. 10, Issue 2, pp. 181–213). Wayne State University Press. http://www.jstor.org/stable/41447359.

Bethea, D. M., Hale, L., Carlson, J. K., Cortés, E., Manire, C. A., & Gelsleichter, J. (2007). Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, Sphyrna tiburo, from the eastern Gulf of Mexico. Marine Biology, 152(5), 1009–1020. https://doi.org/10.1007/s00227-007-0728-7

Binet, T., Failler, P., Chavance, P. N., & Abidine, M. (2013). First international payment for marine ecosystem services: The case of the Banc d'Arguin National Park, Mauritania. Global Environmental Change, 23(6), 1434–1443. https://doi.org/10.1016/j.gloenvcha.2013.09.015

Bird, C. S., Veríssimo, A., Magozzi, S., Abrantes, K. G., Aguilar, A., Al-Reasi, H., & Trueman, C. N. (2018). A global perspective on the trophic geography of sharks. Nature Ecology & Evolution, 13–15. https://doi.org/10.1038/s41559-017-0432-z

Bird, E. C. F. (2011). Coastal geomorphology: An introduction. John Wiley & Sons.

Boer, W. F., & Longamane, F. A. (1996). The exploitation of intertidal food resources in inhaca bay, mozambique, by shorebirds and humans. Biological Conservation, 78(96), 295–303.

Boere, G. C., & Stroud, D. A. (2006). The Flyway Concept: What it is and what it isn't. In C. A. Boere, C. A. Galbraith, & D. A. Stroud (Eds.), Waterbirds around the world (pp. 40–47). The Stationary Office.

Boero, F., & Bonsdorff, E. (2007). A conceptual framework for marine biodiversity and ecosystem functioning. Marine Ecology, 28, 134–145. https://doi.org/10.1111/j.1439-0485.2007.00171.x

Bom, R. A., Fouw, J., Klaassen, R. H. G., Piersma, T., Lavaleye, M. S. S., Ens, B. J., & Gils, J. A. (2018). Food web consequences of an evolutionary arms race: Molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds. Journal of Biogeography, 45(2), 342–354. https://doi.org/10.1111/jbi.13123

Booth, H., Squires, D., & Milner-Gulland, E. J. (2019). The neglected complexities of shark fisheries, and priorities for holistic risk-based management. Ocean and Coastal Management, 182(July), 104994. https://doi.org/10.1016/j.ocecoaman.2019.104994

Booty, J. M., Underwood, G. J. C., Parris, A., Davies, R. G., & Tolhurst, T. J. (2020). Shorebirds affect ecosystem functioning on an intertidal mudflat. Frontiers in Marine Science, 7(August). https://doi.org/10.3389/fmars.2020.00685

Bornatowski, H., Braga, R. R., & Barreto, R. P. (2018). Elasmobranchs consumption in Brazil: Impacts and consequences. In Advances in marine vertebrate research in latin america (pp. 251–262). https://doi.org/10.1007/978-3-319-56985-7

Bornatowski, H., Navia, A. F., Braga, R. R., Abilhoa, V., & Corrêa, M. F. M. (2014). Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. ICES J. Mar. Sci, 71, 1586–1592. https://doi.org/10.1093/icesjms/fsu025.

Bostic, D. L., & Banks, R. C. (1966). A record of stingray predation by the brown pelican. The Condor, 68(5), 515–516.

Botts, R. T., Eppert, A. A., Wiegman, T. J., Rodriguez, A., Blankenship, S. R., Asselin, E. M., & Allen, G. R. (2020). Circadian activity patterns of mammalian predators and prey in Costa Rica. Journal of Mammalogy, 101(5), 1313–1331. https://doi.org/10.1093/jmammal/gyaa103

Boulay, S. (2013). Mutations techniques, changements sociaux survenus chez les pêcheurs imrâgen, des années 1970 à nos jours.

Bouma, T. J., Belzen, J., Balke, T., Zhu, Z., Airoldi, L., Blight, A. J., & Herman, P. M. J. (2014). Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities & steps to take. Coastal Engineering, 87, 147–157. https://doi.org/10.1016/j.coastaleng.2013.11.014

Boussarie, G., Bakker, J., Wangensteen, O. S., Mariani, S., Bonnin, L., Juhel, J.-B., & Mouillot, D. (2018). Environmental DNA illuminates the dark diversity of sharks. Science Advances, 4(5), 9661. https://doi.org/10.1126/sciadv.aap9661

Bowes, R. E., & Thorp, J. H. (2015). Consequences of employing amino acid vs. Bulk-tissue, stable isotope analysis: A laboratory trophic position experiment. Ecosphere (Washington, D.C), 6(1). https://doi.org/10.1890/ES14-00423.1.

Braccini, M., Aires-da-Silva, A., & Taylor, I. (2016). Incorporating movement in the modelling of shark and ray population dynamics: Approaches and management implications. Reviews in Fish Biology and Fisheries, 26(1), 13–24. https://doi.org/10.1007/s11160-015-9406-x

Braham, C. B., Fréon, P., Laurec, A., Demarcq, H., & Bez, N. (2014). New insights in the spatial dynamics of sardinella stocks off Mauritania (North-West Africa) based on logbook data analysis. Fisheries Research, 154, 195–204. https://doi.org/10.1016/j.fishres.2014.02.020

Branco-Nunes, I. S. L., Albuquerque, F. V., Nunes, D. M., Oliveira, P. G. V., & Hazin, F. H. V. (2016). First record of predation between Dasyatis species. Journal of Fish Biology, 89(4), 2178–2181. https://doi.org/10.1111/jfb.13091

Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: Eight core processes and the role of biodiversity. Frontiers in Ecology and the Environment, 17(8), 445–454. https://doi.org/10.1002/fee.2088

Braulik, G., Kasuga, M., & Majubwa, G. (2020). Local ecological knowledge demonstrates shifting baselines and the large-scale decline of sawfishes (Pristidae) in Tanzania. African Journal of Marine Science, 42(1), 67–79. https://doi.org/10.2989/1814232X.2020.1728379

Bridges, C. R. (1993). Ecophysiology of intertidal fish. In J. C. Rankin & F. B. Jensen (Eds.), Fish ecophysiology (pp. 375–400). https://doi.org/10.1007/978-94-011-2304-415

Brinton, C. P., & Curran, M. C. (2017). Tidal and diel movement patterns of the Atlantic stingray (Dasyatis sabina) along a stream-order gradient. Marine and Freshwater Research.

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution, 18(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Buchanan, J. B. (2012). Change in merlin hunting behavior following recovery of peregrine falcon populations suggests mesopredator suppression. Journal of Raptor Research, 46(4), 349–356. https://doi.org/10.3356/JRR-11-75.1

Budd, A. M., Cooper, M. K., Port, A. L., Schils, T., Mills, M. S., Deinhart, M. E., & Strugnell, J. M. (2021). First detection of critically endangered scalloped hammerhead sharks (Sphyrna lewini). In Guam, micronesia, in five decades using environmental DNA. Ecological indicators (Vol. 127). https://doi.org/10.1016/j.ecolind.2021.107649

Buelow, C., & Sheaves, M. (2015). A birds-eye view of biological connectivity in mangrove systems. Estuarine, Coastal and Shelf Science, 152, 33–43. https://doi.org/10.1016/j.ecss.2014.10.014

Burgess, M. G., Polasky, S., & Tilman, D. (2013). Predicting overfishing and extinction threats in multispecies fisheries. Proceedings of the National Academy of Sciences, 110(40), 15943–15948. https://doi.org/10.1073/pnas.1314472110

Bürkner, P. C. (2018). Advanced bayesian multilevel modeling with the R package brms'. The R Journal, 10(July), 395–411.

Bürkner, P.-C. (2017). brms: An R package for bayesian multilevel models using stan'. Journal of Statistical Software, 1(ue 1). https://www.jstatsoft.org/v080/i01.

Buskirk, J., & Yurewicz, K. L. (1998). Effects of predators on prey growth rate: Relative contributions of thinning and reduced activity. Oikos (Copenhagen, Denmark), 82(1), 20. https://doi.org/10.2307/3546913

Byers J. E., & Grabowski J. H. (2014). Soft sediment communities. In Bertness M. D., Bruno J. F., Silliman B. R., & Stachowicz J. J. (Eds.), Marine Community Ecology (pp. 227–249). https://doi.org/10.1007/978-94-017-8801-4151

C

Cadée, G. C. (2001). Sediment Dynamics by Bioturbating Organisms. In Ecological Comparisons of Sedimentary Shores (Vol. 151, pp. 127–148). https://doi.org/10.1007/978-3-642-56557-17

Campana, S. E. (2014). Age determination of elasmobranchs with special reference to mediterranean species., GFCM. Studies and Reviews. http://www.fao.org/documents/card/en/c/48294ee7-cd21-4388-a51e-6f381035f407/.

Campos, B. R., Fish, M. A., Jones, G., Riley, R. W., Allen, P. J., Klimley, P. A., & Kelly, J. T. (2009). Movements of brown smoothhounds, Mustelus henlei, in Tomales Bay, California. Environmental Biology of Fishes, 85(1), 3–13. https://doi.org/10.1007/s10641-009-9462-y

Campredon, P., & Catry, P. (2016). Bijagós Archipelago (Guinea-Bissau). In The Wetland Book (pp. 1–8). Springer Netherlands.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. Nature, 489(7415), 326–326. https://doi.org/10.1038/nature11373

Cardinale, M., Chacate, O., Casini, M., Chaúca, I., & Helge Vølstad, J. (2014). CPUE trends of Hilsa kelee and Thryssa vitrirostris exploited by the artisanal finfish fisheries in Mozambique derived from an on-shore sampling of catches by trip. Sci. Mar, 78, 55–64. https://doi.org/10.3989/scimar.03826.06c.

Carlier, A., Chauvaud, L., Geest, M., Le Loc'h, F., Le Duff, M., Vernet, M., & Clavier, J. (2015). Trophic connectivity between offshore upwelling and the inshore food web of Banc d'Arguin (Mauritania): New insights from isotopic analysis. Estuarine, Coastal and Shelf Science, 165(August), 149–158. https://doi.org/10.1016/j.ecss.2015.05.001

Carlisle, A. B., & Starr, R. M. (2009). Habitat use, residency, and seasonal distribution of female leopard sharks Triakis semifasciata in Elkhorn Slough, California. Marine Ecology Progress Series, 380(June 2014), 213–228. https://doi.org/10.3354/meps07907

Carlisle, A. B., & Starr, R. M. (2010). Tidal movements of female leopard sharks (Triakis semifasciata) in Elkhorn Slough, California. Environmental Biology of Fishes, 89(1), 31–45. https://doi.org/10.1007/s10641-010-9667-0

Carlson, J., Charvet, P., Blanco-Parra, M. P., Briones Bell-lloch, A., Cardenosa, D., Derrick, D., Espinoza, E., Morales-Saldaña, J. M., Naranjo-Elizondo, B., Pacoureau, N., Schneider, E. V. C., Simpson, N. J., Pollom, R., & Dulvy, N. K. (2020). Hypanus americanus. In The IUCN Red List of Threatened Species 2020 (p. 181244884 104123787). https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T181244884A104123787.en

Carlton, J. T., & Hodder, J. (2003). Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities. Marine Ecology Progress Series, 256, 271–286.

Casey, J. M., Baird, A. H., Brandl, S. J., Hoogenboom, M. O., Rizzari, J. R., Frisch, A. J., & Connolly, S. R. (2017). A test of trophic cascade theory: Fish and benthic assemblages across a predator density gradient on coral reefs. Oecologia, 183(1), 161–175. https://doi.org/10.1007/s00442-016-3753-8

Castellanos-Galindo, G. A., Herrón, P., Navia, A. F., & Booth, H. (2021). Shark conservation and blanket bans in the eastern Pacific Ocean. Conservation Science and Practice, 3(7), 2–5. https://doi.org/10.1111/csp2.428

Castilla, J. C. (1998). Coastal marine communities: Trends and perspectives from human-exclusion experiments. Trends in Ecology and Evolution, 14(7), 280–283. https://doi.org/10.1016/S0169-5347(99)01602-X

Castillo-Géniz, J. L., Márquez-Farias, J. F., Cruz, M. C., Cortés, E., & Cid Del Prado, A. (1998). The Mexican artisanal shark fishery in the Gulf of Mexico: Towards a regulated fishery. Marine and Freshwater Research, 49(7), 611–620. https://doi.org/10.1071/MF97120

Castorani, M. C. N., & Hovel, K. A. (2016). Native predator chemical cues induce anti-predation behaviors in an invasive marine bivalve. Biological Invasions, 18(1), 169–181. https://doi.org/10.1007/s10530-015-1000-6

Castro, J. I. (1996). Biology of the blacktip shark, Carcharhinus limbatus. Bulletin of Marine Science, 59(3), 508–522.

Catry, P., Barbosa, C., Indjai, B., Almeida, A., Godley, B. J., & Vié, J. C. (2002). First census of the green turtle at Poilão, Bijagós Archipelago, Guinea-Bissau: The most important nesting colony on the Atlantic coast of Africa. Oryx : The Journal of the Fauna Preservation Society, 36(4), 400–403. https://doi.org/10.1017/S0030605302000765

Catry, T., Lourenço, P. M., Lopes, R. J., Carneiro, C., Alves, J. A., Costa, J., & Granadeiro, J. P. (2016). Structure and functioning of intertidal food webs along an avian flyway: A comparative approach using stable isotopes. Functional Ecology, 30(3), 468–478. https://doi.org/10.1111/1365-2435.12506

Caut, S., Angulo, E., & Courchamp, F. (2009). Variation in discrimination factors (Δ15N and Δ13C): The effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology, 46(2), 443–453. https://doi.org/10.1111/j.1365-2664.2009.01620.x

Cerutti-Pereyra, F., Thums, M., Austin, C. M., Bradshaw, C. J. A., Stevens, J. D., Babcock, R. C., & Meekan, M. G. (2014). Restricted movements of juvenile rays in the lagoon of Ningaloo Reef, Western Australia—Evidence for the existence of a nursery. Environmental Biology of Fishes, 97(4), 371–383. https://doi.org/10.1007/s10641-013-0158-y

Chapman, D. D., & Gruber, S. H. (2002). A further observation of the prey-handling behavior of the great hammerhead shark, Sphyrna mokarran: Predation upon the spotted eagle ray. Aetobatus Narinari. Bulletin of Marine Science, 70(3), 947–952.

Chew, S. F., Wilson, J. M., Ip, Y. K., & Randall, D. J. (2006). Nitrogen excretion and defense against ammonia toxicity. In A. L. Val, V. M. F. Almeida-Val, & D. J. Randall (Eds.), The physiology of tropical fishes (pp. 307–396). Acaemic Press.

Chin, A., Heupel, M. R., Simpfendorfer, C. A., & Tobin, A. J. (2016). Population organisation in reef sharks: New variations in coastal habitat use by mobile marine predators. Marine Ecology Progress Series, 544, 197–211. https://doi.org/10.3354/meps11545

Chuenpagdee, R., Liguori, L., Palomares, M. L. D., & Pauly, D. (2006). Bottom-up, global estimates of small-scale marine fisheries catches. Fisheries Centre Research Reports, 14(8), 105.

Cisneros-Montemayor, A. M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., & Sumaila, U. R. (2013). Global economic value of shark ecotourism: Implications for conservation. Oryx : The Journal of the Fauna Preservation Society, 47(3), 381–388. https://doi.org/10.1017/S0030605312001718

Clarke, K. R., & Green, R. H. (1988). Statistical design and analysis for a “biological effects” study. Marine Ecology - Progress Series, 46, 213–226.

Clarke, S., Milner-Gulland, E. J., & Trond, B. (2007). Social, economic, and regulatory drivers of the shark fin trade. Marine Resource Economics, 22(3), 305–327. https://doi.org/10.1086/mre.22.3.42629561

Clements, O. N., Leurs, G., Witbaard, R., Pen, I., Verkuil, Y. I., & Govers, L. L. (2022). Growth, maturity, and diet of the pearl whipray (Fontitrygon margaritella) from the Bijagós Archipelago, Guinea-Bissau. PeerJ, 10, 12894. https://doi.org/10.7717/peerj.12894

Cliff, G. (1995). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The Great hammerhead shark Sphyrna mokarran. South African Journal of Marine Science, 15(1), 105–114. https://doi.org/10.2989/025776195784156331

Cliff, G., & Dudley, S. F. (1991). Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark Carcharhinus leucas. South African Journal of Marine Science, 10(1), 253–270. https://doi.org/10.2989/02577619109504636

Cliff, G., Dudley, S. F. J., & Davis, B. (1989). Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark Carcharodon carcharias. South African Journal of Marine Science, 8(1), 131–144. https://doi.org/10.2989/02577618909504556

Coelho, A. P., Henriques, M., Rocha, A. D., Paulino, J., Schaars, L. K., Ramos, C., & Alves, J. A. (2022). Spatial and seasonal variation in macrozoobenthic density, biomass and community composition in a major tropical intertidal area, the Bijagós Archipelago, West Africa. PLoS ONE, 17(11 November), 1–27. https://doi.org/10.1371/journal.pone.0277861

Cohen, J. E., Pimm, S. L., Yodzis, P., & Saldaña, J. (1993). Body sizes of animal predators and animal prey in food webs. The Journal of Animal Ecology, 62, 67–78.

Coiraton, C., Amezcua, F., & Ketchum, J. T. (2020). New insights into the migration patterns of the scalloped hammerhead shark Sphyrna lewini based on vertebral microchemistry. Marine Biology, 167(5), 1–18. https://doi.org/10.1007/s00227-020-3668-0

Coll, M., Navarro, J., & Palomera, I. (2013). Ecological role, fishing impact, and management options for the recovery of a Mediterranean endemic skate by means of food web models'. Biological Conservation. Elsevier Ltd, 157, 108–120. https://doi.org/10.1016/j.biocon.2012.06.029.

Collins, A. B., Heupel, M. R., Hueter, R. E., & Motta, P. J. (2007). Hard prey specialists or opportunistic generalists? An examination of the diet of the cownose ray, Rhinoptera bonasus. Marine and Freshwater Research, 58(1), 135–144. https://doi.org/10.1071/MF05227

Colloca, F., Carrozzi, V., Simonetti, A., & Lorenzo, M. (2020). Using local ecological knowledge of fishers to reconstruct abundance trends of elasmobranch populations in the Strait of Sicily. Frontiers in Marine Science, 7(June), 1–8. https://doi.org/10.3389/fmars.2020.00508

Compagno, L. J. V., & Roberts, T. R. (1984). Marine and freshwater stingrays (Dasyatidae) of West Africa, with description of a new species. Proceedings of the California Academy of Sciences, 43(18), 283–300.

Compton, T. J., Holthuijsen, S., Koolhaas, A., Dekinga, A., Horn, J., Smith, J., Galama, Y., Brugge, M., Wal, D., Meer, J., Veer, H. W., & Piersma, T. (2013). Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. Journal of Sea Research, 82, 103–116.

Condit, R., & Le Boeuf, B. J. (1984). Feeding Habits and Feeding Grounds of the Northern Elephant Seal. Journal of Mammalogy, 65(2), 281–290. https://doi.org/10.2307/1381167

Conrath, C. L., & Musick, J. A. (2010). Residency, space use and movement patterns of juvenile sandbar sharks (Carcharhinus plumbeus) within a Virginia summer nursery area. Marine and Freshwater Research, 61(2), 223–235. https://doi.org/10.1071/MF09078

Convertino, M., Donoghue, J. F., Chu-Agor, M. L., Kiker, G. A., Muñoz-Carpena, R., Fischer, R. A., & Linkov, I. (2011). Anthropogenic renourishment feedback on shorebirds: A multispecies Bayesian perspective. Ecological Engineering, 37(8), 1184–1194. https://doi.org/10.1016/j.ecoleng.2011.02.019

Conway, J. N., & Mcfee, W. E. (2017). Ingestion of stingrays (Dasyatis spp.) by a common bottlenose dolphin (Tursiops truncatus). Aquatic Mammals, 1–10.

Corgos, A., & Rosende-Pereiro, A. (2022). Nursery habitat use patterns of the scalloped hammerhead shark, Sphyrna lewini, in coastal areas of the central Mexican Pacific. Journal of Fish Biology, 100(1), 117–133. https://doi.org/10.1111/jfb.14925

Correia, E., Granadeiro, J. P., Regalla, A., & Catry, P. (2021). Coastal waters of a marine protected area of the Bijagós Archipelago, West Africa, shelter juvenile fishes of economic and ecological importance. Regional Studies in Marine Science, 46, 101892. https://doi.org/10.1016/j.rsma.2021.101892

Correia, E., Granadeiro, J. P., Santos, B., Regalla, A., Mata, V. A., & Catry, T. (2023). Trophic ecology of a migratory shorebird community at a globally important non-breeding site: Combining DNA metabarcoding and conventional techniques. Marine Ecology Progress Series, 705, 127–144.

Cortés, E., & Gruber, S. H. (1990). Diet, feeding habits and estimates of daily ration of young lemon sharks, Negaprion brevirostris. Copeia, 1990(1), 204. https://doi.org/10.2307/1445836

Cowley, P. D. (1997). Age and growth of the blue stingray Dasyatis chrysonota chrysonota from the South-Eastern Cape coast of South Africa'. South African Journal of Marine Science, 7615(18), 31–38. https://doi.org/10.2989/025776197784161054.

Cox, D. L., & Koob, T. J. (1993). Predation on elasmobranch eggs. Environmental Biology of Fishes, 38, 117–125. https://doi.org/10.1007/978-94-017-3450-910

Crain, C. M., Halpern, B. S., Beck, M. W., & Kappel, C. V. (2009). Understanding and managing human threats to the coastal marine environment. In Annals of the new york academy of sciences (pp. 39–62). https://doi.org/10.1111/j.1749-6632.2009.04496.x

Cross, H. (2015). Elasmobranch capture by commercial small-scale fisheries in the Bijagós Archipelago, Guinea-Bissau. Fisheries Research, 168, 105–108. https://doi.org/10.1016/j.fishres.2015.03.018

Cross, H. C. (2014). The importance of small-scale fishing to rural coastal livelihoods: A comparative case-study in the Bijagós Archipelago Guinea-Bissau [University College London]. https://doi.org/10.1007/s13398-014-0173-7.2

Curras, M. R., Donadio, E., Middleton, A. D., & Pauli, J. N. (2022). Carnivore niche partitioning in a human landscape. American Naturalist, 199(4). https://doi.org/10.1086/718472

Curtis, T. H., & Macesic, L. J. (2011). Observations of breaching behavior in juvenile bull sharks, Carcharhinus leucas. Florida Scientist, 74(4), 253–257.

Cushing, D. H. (1971). Upwelling and the production of fish. Advances in Marine Biology, 9, 255–334.

D

Dabruzzi, T. F., Bennett, W. A., Rummer, J. L., & Fangue, N. A. (2013). Juvenile Ribbontail Stingray, Taeniura lymma (Forsskål, 1775) (Chondrichthyes, Dasyatidae), demonstrate a unique suite of physiological adaptations to survive hyperthermic nursery conditions. Hydrobiologia, 701(1), 37–49. https://doi.org/10.1007/s10750-012-1249-z

Dale, J. J., & Holland, K. N. (2012). Age, growth and maturity of the brown stingray (Dasyatis lata) around Oahu, Hawai'i'. Marine and Freshwater Research, 63(6), 475–484. https://doi.org/10.1071/MF11231.

Daly, R., Froneman, P. W., & Smale, M. J. (2013). Comparative feeding ecology of bull sharks (Carcharhinus leucas) in the coastal waters of the Southwest Indian Ocean inferred from stable isotope analysis. PLoS ONE, 8(10), 1–11. https://doi.org/10.1371/journal.pone.0078229

Daly, R., Smale, M. J., Singh, S., Anders, D., Shivji, M., Clare, C. A., & Barnett, A. (2018). Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators. Diversity and Distributions, 24(9), 1217–1230. https://doi.org/10.1111/ddi.12758

Daly-Engel, T. S., Seraphin, K. D., Holland, K. N., Coffey, J. P., Nance, H. a, Toonen, R. J., & Bowen, B. W. (2012). Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the endangered scalloped hammerhead shark (Sphyrna lewini). PLoS ONE, 7(1). https://doi.org/10.1371/journal.pone.0029986

D'Andrea, A. F., Aller, R. C., & Lopez, G. R. (2002). Organic matter flux and reactivity on a South Carolina sandflat: The impacts of porewater advection and macrobiological structures. Limnology and Oceanography, 47, 1056–1070.

D'Andrea, A. F., Lopez, G. R., & Aller, R. C. (2004). Rapid physical and biological particle mixing on an intertidal sandflat. Journal of Marine Research, 62(1), 67–92. https://doi.org/10.1357/00222400460744627

Darimont, C. T., Cooke, R., Bourbonnais, M. L., Bryan, H. M., Carlson, S. M., Estes, J. A., & Maclean, J. L. (2023). Humanity's diverse predatory niche and its ecological consequences. Communications Biology. https://doi.org/10.1038/s42003-023-04940-w

Darimont, C. T., Fox, C. H., Bryan, H. M., & Reimchen, T. E. (2015). The unique ecology of human predators. Science (New York, N.Y.), 349(6250), 858–860. https://doi.org/10.1126/science.aac4249

Davy, L. E., Simpfendorfer, C. A., & Heupel, M. R. (2015). Movement patterns and habitat use of juvenile mangrove whiprays (Himantura granulata) (pp. 481–492). Marine and Freshwater Research.

Day, J., Clark, J. A., Williamson, J. E., Brown, C., & Gillings, M. (2019). Population genetic analyses reveal female reproductive philopatry in the oviparous Port Jackson shark. Marine and Freshwater Research, 70(7), 986–994. https://doi.org/10.1071/MF18255

Deagle, B. E., Kirkwood, R., & Jarman, S. N. (2009). Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. Molecular Ecology, 18(9), 2022–2038. https://doi.org/10.1111/j.1365-294X.2009.04158.x

Dean, M. N., Bizzarro, J. J., Clark, B., Underwood, C. J., & Johanson, Z. (2017). Large batoid fishes frequently consume stingrays despite skeletal damage. Royal Society Open Science, 4(9). https://doi.org/10.1098/rsos.170674

Debaere, S. F., Weideli, O. C., Bouyoucos, I. A., Eustache, K. B., Trujillo, J. E., Boeck, G., & Stacy, N. (2023). Quantifying changes in umbilicus size to estimate the relative age of neonatal blacktip reef sharks (Carcharhinus melanopterus). Conservation Physiology, 11(1), 1–11. https://doi.org/10.1093/conphys/coad028

Deegan, L. A., Johnson, D. S., Warren, R. S., Peterson, B. J., Fleeger, J. W., Fagherazzi, S., & Wollheim, W. M. (2012). Coastal eutrophication as a driver of salt marsh loss. Nature, 490(7420), 388–392. https://doi.org/10.1038/nature11533

Den Hout, P. J., Spaans, B., & Piersma, T. (2008). Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons. Ibis, 150(SUPPL.1), 219–230. https://doi.org/10.1111/j.1474-919X.2008.00785.x

Dent, F., & Clarke, S. (2015). State of the global market for shark products. FAO Technical Paper, 196. http://www.fao.org/docrep/field/003/ab825f/AB825F00.htm#TOC

Deppe, F. (1999). Intertidal Mudflats Worldwide. Common Wadden Sea Secretariat.

Derrick, B., Burns, K., Zhu, A., Andreoli, V., Zeller, D., & Pauly, D. (2023). Small-scale fisheries catch and fishing effort in the Socotra Archipelago (Yemen) between 1950 and 2019. Frontiers in Marine Science, 10(June), 1–15. https://doi.org/10.3389/fmars.2023.1201661

Derrick, D. H., Cheok, J., & Dulvy, N. K. (2020). Spatially congruent sites of importance for global shark and ray biodiversity. PLoS ONE, 15(7 July), 1–19. https://doi.org/10.1371/journal.pone.0235559

Dhanjal-Adams, K. L., Hanson, J. O., Murray, N. J., Phinn, S. R., Wingate, V. R., Mustin, K., Lee, J. R., Allan, J. R., Cappadonna, J. L., Studds, C. E., Clemens, R., Roelfsema, C. M., & Fuller, R. A. (2016). The distribution and protection of intertidal habitats in Australia. Emu - Austral Ornithology, 116(2), 208–214. https://doi.org/10.1071/MU15046

Dicken, M. L., Hussey, N. E., Christiansen, H. M., Smale, M. J., Nkabi, N., Cliff, G., & Wintner, S. P. (2017). Diet and trophic ecology of the tiger shark (Galeocerdo cuvier) from South African waters. PLoS ONE, 12(6), 1–25. https://doi.org/10.1371/journal.pone.0177897

Diemer, K. M., Mann, B. Q., & Hussey, N. E. (2011). Distribution and movement of scalloped hammerhead Sphryna lewini and smooth hammerhead Sphyrna zygaena sharks along the east coast of Southern Africa. African Journal of Marine Science, 33(2), 229–238. https://doi.org/10.2989/1814232X.2011.600291

Dinerstein, E., Vynne, C., Sala, E., Joshi, A. R., Fernando, S., Lovejoy, T. E., & Wikramanayake, E. (2019). A global deal for nature: Guiding principles, milestones, and targets. Science Advances, 5(4), 1–18. https://doi.org/10.1126/sciadv.aaw2869

Diop, M., & Dossa, J. (2011). 30 Years of shark fishing. IUCN Shark Spec. Gr, 51. http://www.iucnssg.org/uploads/5/4/1/2/54120303/30yearseng.pdf.

Diouf, P. S., Deme-Gningue, I., & Albaret, J. J. (1994). L'Archipel des Bijagós environnment aquatique et peuplement de poissons. Ministere Des Peches de Guinee Bissau.

Ditlevsen, P. D., & Ditlevsen, S. (2023). Warning of a forthcoming collapse of the Atlantic meridional overturning circulation. Nature Communications, 14(4254), 1–12. https://doi.org/10.1038/s41467-023-39810-w

Donald, P. F., Fishpool, L. D. C., Ajagbe, A., Bennun, L. A., Bunting, G., Burfield, I. J., & Wege, D. C. (2019). Important Bird and Biodiversity Areas (IBAs): The development and characteristics of a global inventory of key sites for biodiversity. Bird Conservation International, 29(2), 177–198. https://doi.org/10.1017/S0959270918000102

Dubay, K., Tokuoka, S., & Gereffi, G. (2010). A Value Chain Analysis of the Sinaloa. Mexico Shrimp Fishery, 919.

Ducrocq, M., Lemine Ould Sidi, M., & Ould Yarba, L. (2004). Comment le Par national du Banc d'Arguin est devenu le plus grand sanctuaire d'Afrique pour ls requins. FIBA.

Dudley, S. F., & Cliff, G. (1993). Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark Carcharhinus limbatus. South African Journal of Marine Science, 13(1), 237–254. https://doi.org/10.2989/025776193784287356

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., Carlson, J. K., Davidson, L. N., Fordham, S. V., Francis, M. P., Pollock, C. M., Simpfendorfer, C. A., Burgess, G. H., Carpenter, K. E., Compagno, L. J., Ebert, D. A., Gibson, C., Heupel, M. R., Livingstone, S., SR, … W.T. (2014). Extinction risk and conservation of the world's sharks and rays. Elife, 3:e00590.

Dulvy, N. K., Metcalfe, J. D., Glanville, J., Pawson, M. G., & Reynolds, J. D. (2000). Fishery stability, local extinctions, and shifts in community structure in skates. Conservation Biology, 14(1), 283–293. https://doi.org/10.1046/j.1523-1739.2000.98540.x

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., … Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Current Biology : CB, 31, 4773–4787.

Dulvy, N. K., Sadovy, Y., & Reynolds, J. D. (2003). Extinction vulnerability in marine populations. Fish and Fisheries, 4(1), 25–64. https://doi.org/10.1046/j.1467-2979.2003.00105.x

Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N. K., Fordham, S. V., Bräutigam, A., Sant, G., & Welch, D. J. (2017). Challenges and priorities in shark and ray conservation. Current Biology, 27(11), 565–572. https://doi.org/10.1016/j.cub.2017.04.038

Dunn, N., Savolainen, V., Weber, S., Andrzejaczek, S., Carbone, C., & Curnick, D. (2022). Elasmobranch diversity across a remote coral reef atoll revealed through environmental DNA metabarcoding. Zoological Journal of the Linnean Society, 1–15. https://doi.org/10.1093/zoolinnean/zlac014

E

Early-Capistrán, M. M., Solana-Arellano, E., Alberto Abreu-Grobois, F., Narchi, N. E., Garibay-Melo, G., Seminoff, J. A., & Saenz-Arroyo, A. (2020). Quantifying local ecological knowledge to model historical abundance of long-lived, heavily-exploited fauna. PeerJ, 8, 1–34. https://doi.org/10.7717/peerj.9494

Ebert, D. A., Dando, M., & Fowler, S. (2021). Sharks of the world: A complete guide. Princeton University Press.

Eckert, S. A., Bagley, D., Kubis, S., Ehrhart, L., Johnson, C., Stewart, K., & DeFreese, D. (2006). Internesting and postnesting movements and foraging habitats of leatherback sea turtles (Dermochelys coriacea) nesting in Florida. Chelonian Conservation and Biology, 5(2), 239–248. https://doi.org/10.2744/1071-8443(2006)5

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. Bioinformatics (Oxford, England), 26(19), 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Eichmiller, J. J., Best, S. E., & Sorensen, P. W. (2016). Effects of temperature and trophic state on degradation of environmental DNA in lake water. Environmental Science and Technology, 50(4), 1859–1867. https://doi.org/10.1021/acs.est.5b05672

Ekpo, I., & Essien-Ibok, M. (2019). Development, prospects and challenges of artisanal fisheries in Akwa Ibom State, Nigeria. International Journal of Environmental Science, Management and Engineering Research, 2(3), 69–86.

El-Hacen, E. H. M., Bouma, T. J., Govers, L. L., Piersma, T., & Olff, H. (2019). Seagrass sensitivity to collapse along a hydrodynamic gradient: Evidence from a pristine subtropical intertidal ecosystem. Ecosystems (New York, N.Y.), 22(5), 1007–1023. https://doi.org/10.1007/s10021-018-0319-0

El-Hacen, E. H. M., Bouma, T. J., Oomen, P., Piersma, T., & Olff, H. (2019). Large-scale ecosystem engineering by flamingos and fiddler crabs on West African intertidal flats promote joint food availability. Oikos (Copenhagen, Denmark), 128, 753–764.

El-Hacen, E. H. M., Sidi Cheikh, M. A., Bouma, T. J., Olff, H., & Piersma, T. (2020). Long-term changes in seagrass and benthos at Banc d'Arguin, Mauritania, the premier intertidal system along the East Atlantic Flyway. Global Ecology and Conservation, 24, 01364. https://doi.org/10.1016/j.gecco.2020.e01364

El-Hacen, E., Lemrabott, S., Meijer, K., Piersma, T., Govers, L., Gils, J., & Olff, H. (2023). Growth and population structure of bloody cockles Senilia senilis at Banc d'Arguin and Bijagós with different environmental conditions and harvesting regimes. Marine Ecology Progress Series, 710, 71–83. https://doi.org/10.3354/meps14291

Ellis, W. L., & Bell, S. S. (2008). Tidal influence on a fringing mangrove intertidal fish community as observed by in situ video recording: Implications for studies of tidally migrating nekton. Marine Ecology Progress Series, 370(November 2015), 207–219. https://doi.org/10.3354/meps07567

Elston, C., Cowley, P. D., Brandis, R. G., & Lea, J. (2021). Residency and habitat use patterns by sympatric stingrays at a remote atoll in the Western Indian Ocean. Marine Ecology Progress Series, 662, 97–114. https://doi.org/10.3354/meps13632

Elston, C., Cowley, P. D., Brandis, R. G., & Lea, J. (2022). Stingray habitat use is dynamically influenced by temperature and tides. Frontiers in Marine Science, 8(January), 1–13. https://doi.org/10.3389/fmars.2021.754404

Ens, B. J., Piersma, T., & Drent, R. H. (1994). The dependence of waders and waterfowl migrating along the East Atlantic Flyway on their coastal food supplies. Ophelia, 6, 127–151.

Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B., & Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. Annual Review of Environment and Resources, 41. https://doi.org/10.1146/annurev-environ-110615-085622

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., & Wardle, D. A. (2011). Trophic downgrading of planet earth. Science (New York, N.Y.), 333(6040), 301–306. https://doi.org/10.1126/science.1205106

Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science (New York, N.Y.), 282(5388), 473–476. https://doi.org/10.1126/science.282.5388.473

Estupiñán-Montaño, C., Estupiñán-Ortiz, J. F., Cedeño-Figueroa, L. G., Galván-Magaña, F., & Polo-Silva, C. J. (2017). Diet of the bull shark, Carcharhinus leucas, and the tiger shark, Galeocerdo cuvier, in the eastern Pacific Ocean. Turkish Journal of Zoology, 41(6), 1111–1117. https://doi.org/10.3906/zoo-1610-31

Estupiñán-Montaño, C., Pacheco-Triviño, F., Cedeño-Figueroa, L. G., Galván-Magaña, F., & Estupiñán-Ortiz, J. F. (2018). Diet of three shark species in the Ecuadorian Pacific, Carcharhinus falciformis, Carcharhinus limbatus and Nasolamia velox. Journal of the Marine Biological Association of the United Kingdom, 98(4), 927–935. https://doi.org/10.1017/S002531541600179X

F

FAO. (n.d.). Database of measures on conservation and management of sharks. FAO. https://www.fao.org/ipoa-sharks/database-of-measures/en/

FAO. (1999). International Plan of Action for reducing incidental catch of seabirds in longline fisheries. International Plan of Action for the conservation and management of sharks. International Plan of Action for the Management of Fishing Capacity. Rome. https://doi.org/10.1163/9789004502789033

FAO. (2019). Report of the FAO working group on the assessment of small pelagic fish off Northwest Africa.

F.A.O. (2022). The state of the world fisheries and aquaculture 2022. Towards Blue Transformation. https://doi.org/10.4060/cc0463en

Faria, F. A., Albertoni, E. F., & Bugoni, L. (2018). Trophic niches and feeding relationships of shorebirds in southern Brazil. Aquatic Ecology, 52(4), 281–296. https://doi.org/10.1007/s10452-018-9663-6

Farias, I. (2006). Diet comparison of four ray species (Raja clavata, Raja brachyura, Raja montagui and Leucoraja naevus) caught along the Portuguese continental shelf. Aquatic Living Resources, 19(2), 105–114. https://doi.org/10.1051/alr:2006010.

Feldheim, K. A., Gruber, S. H., Dibattista, J. D., Babcock, E. A., Kessel, S. T., Hendry, A. P., & Chapman, D. D. (2014). Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. Molecular Ecology, 23(1), 110–117. https://doi.org/10.1111/mec.12583

Fernandes, P. G., Ralph, G. M., Nieto, A., Criado, M. G., Vasilakopoulos, P., & Maravelias, C. D. (2017). Coherent assessments of Europe's marine fishes show regional divergence and megafauna loss. Nature Ecology & Evolution, 1, 1–16. https://doi.org/10.1038/s41559-017-0200.

Fernández, L., Salmerón, F., & Ramos, A. (2005). Change in elasmobranchs and other incidental species in the Spanish deepwater black hake trawl fishery off Mauritania (1992-2001). J. Northwest Atl. Fish. Sci, 35, 325–331. https://doi.org/10.2960/J.v35.m534.

Fernandez-Carvalho, J., Coelho, R., Santos, M. N., & Amorim, S. (2015). Effects of hook and bait in a tropical northeast Atlantic pelagic longline fishery: Part II-Target, bycatch and discard fishes. Fisheries Research, 164(3), 312–321. https://doi.org/10.1016/j.fishres.2014.11.009

Fernández-Ordóñez, J. C., Lasso-alcalá, O. M., & Ron, E. J. (2016). First evidence of an Osprey (Pandion haliaetus) preying on elasmobranches. Revista Venezolana de Ornitología, 6, 65–67.

Fernando, D., & Stewart, J. D. (2021). High bycatch rates of manta and devil rays in the "small-scale" artisanal fisheries of Sri Lanka. PeerJ, 9, 1–35. https://doi.org/10.7717/peerj.11994

Ferreira, L. C., Thums, M., Heithaus, M. R., Barnett, A., Abrantes, K. G., Holmes, B. J., & Meekan, M. G. (2017). The trophic role of a large marine predator, the tiger shark Galeocerdo cuvier. Scientific Reports, 7(1), 7641. https://doi.org/10.1038/s41598-017-07751-2

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. Ecology Letters, 13(8), 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x

Fezzi, C., Ford, D. J., & Oleson, K. L. L. (2023). The economic value of coral reefs: Climate change impacts and spatial targeting of restoration measures. Ecological Economics, 203(March 2022), 107628. https://doi.org/10.1016/j.ecolecon.2022.107628

Finke, D. L., & Denno, R. F. (2004). Predator diversity dampens trophic cascades. Nature, 429(6990), 407–410. https://doi.org/10.1038/nature02554

Fisher, R. A., Call, G. C., & Grubbs, R. D. (2011). Cownose ray (Rhinoptera bonasus) predation relative to bivalve ontogeny. Journal of Shellfish Research, 30(1), 187–196. https://doi.org/10.2983/035.030.0126

Fisher, R. A., Call, G. C., & Grubbs, R. D. (2013). Age, growth, and reproductive biology of cownose rays in chesapeake bay. Marine and Coastal Fisheries, 5(1), 224–235. https://doi.org/10.1080/19425120.2013.812587

Flach, E., & Tamaki, A. (2001). Competitive bioturbators on intertidal sand flats in the European Wadden Sea and Ariake Sound in Japan. In Ecological Comparisons of Sedimentary Shores (Vol. 151, pp. 149–171). https://doi.org/10.1007/978-3-642-56557-18

Flowers, K. I., Heithaus, M. R., & Papastamatiou, Y. P. (2021). Buried in the sand: Uncovering the ecological roles and importance of rays. Fish and Fisheries, 22(1), 105–127. https://doi.org/10.1111/faf.12508

Fokkema, W., Jeugd, H. P., Lameris, T. K., Dokter, A. M., Ebbinge, B. S., Roos, A. M., & Olff, H. (2020). Ontogenetic niche shifts as a driver of seasonal migration. Oecologia, 193(2), 285–297. https://doi.org/10.1007/s00442-020-04682-0

Fox, H. E., Soltanoff, C. S., Mascia, M. B., Haisfield, K. M., Lombana, A. V., Pyke, C. R., & Wood, L. (2012). Explaining global patterns and trends in marine protected area (MPA) development. Marine Policy, 36(5), 1131–1138. https://doi.org/10.1016/j.marpol.2012.02.007

Freitas, R. H. A., Aguiar, A. A., AKCHA, F., Lima, S. M. Q., & Valentin, J. L. (2019). Unravelling the foraging behavior of the southern stingray, Hypanus americanus (Myliobatiformes: Dasyatidae). In In a southwestern atlantic MPA. Neotrop ichthyol 17. http://www.scielo.br/j/ni/a/fZ57Gygh6b5nLVxrBsQy3bS/abstract/?lang=en

Friedman, K., Gabriel, S., Abe, O., Adnan Nuruddin, A., Ali, A., Bidin Raja Hassan, R., & Ye, Y. (2018). Examining the impact of CITES listing of sharks and rays in Southeast Asian fisheries. Fish and Fisheries, 19(4), 662–676. https://doi.org/10.1111/faf.12281

Frisch, A. J., Ireland, M., Rizzari, J. R., Lönnstedt, O. M., Magnenat, K. A., Mirbach, C. E., & Hobbs, J. P. A. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. Coral Reefs (Online), 35(2), 459–472. https://doi.org/10.1007/s00338-016-1415-2

Frisk, M. G., Miller, T. J., & Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: A comparative life history study. Canadian Journal of Fisheries and Aquatic Sciences, 58(5), 969–981. https://doi.org/10.1139/f01-051

Froese, R. (2004). Keep it simple: Three indicators to deal with overfishing. Fish and Fisheries, 5(1), 86–91. https://doi.org/10.1111/j.1467-2979.2004.00144.x

Frøslev, T. G., Kjøller, R., Bruun, H. H., Ejrnæs, R., Brunbjerg, A. K., Pietroni, C., & Hansen, A. J. (2017). Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. Nature Communications, 8(1). https://doi.org/10.1038/s41467-017-01312-x

G

Gagern, A., & Bergh, J. (2013). A critical review of fishing agreements with tropical developing countries. Marine Policy, 38, 375–386. https://doi.org/10.4324/9781351216227

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., & Page, G. (2002). Global climate change and sea level rise: Potential losses of intertidal habitat for shorebirds. Waterbirds, 25(2), 173–183. https://doi.org/10.1675/1524-4695(2002)025

Gall, S. C., & Thompson, R. C. (2015). The impact of debris on marine life. Marine Pollution Bulletin, 92(1–2), 170–179. https://doi.org/10.1016/j.marpolbul.2014.12.041

Gallagher, A. J., Amon, D. J., Bervoets, T., Shipley, O. N., Hammerschlag, N., & Sims, D. W. (2020). The Caribbean needs big marine protected areas. Science (New York, N.Y.), 367(6479), 749. https://doi.org/10.1126/science.abb0650

Garcia, S. M., Zerbi, A., Aliaume, C., Do Chi, T., & Lasserre, G. (2003). The ecosystem approach to fisheries. FAO Fisheries Technical Paper, 443.

Garvey, J. E., & Whiles, M. (2016). Trophic Ecology. Trophic Ecology. CRC Press. https://doi.org/10.1201/9781315367804

Gelsleichter, J., Musick, J. A., & Nichols, S. (1999). Food habits of the smooth dogfish, Mustelus canis, dusky shark, Carcharhinus obscurus, Atlantic sharpnose shark, Rhizoprionodon terraenovae, and the sand tiger, Carcharias taurus, from the northwest Atlantic Ocean. Environmental Biology of Fishes, 54, 205–217. https://doi.org/10.1023/A

George, L. W., Martins, A. P. B., Heupel, M. R., & Simpfendorfer, C. A. (2019). Fine-scale movements of juvenile blacktip reef sharks Carcharhinus melanopterus in a shallow nearshore nursery. Marine Ecology Progress Series, 623, 85–97. https://doi.org/10.3354/meps13010

Gervais, C. R., Nay, T. J., Renshaw, G., Johansen, J. L., Steffensen, J. F., & Rummer, J. L. (2018). Too hot to handle? Using movement to alleviate effects of elevated temperatures in a benthic elasmobranch. Hemiscyllium Ocellatum. Marine Biology, 165(11), 1–12. https://doi.org/10.1007/s00227-018-3427-7

Gibson, R. N. (1986). Intertidal teleosts: Life in a fluctuating environment (pp. 388–408). The Behaviour of Teleost Fishes. https://doi.org/10.1007/978-1-4684-8261-415

Gibson, R. N., & Yoshiyama, R. M. (1999). Intertidal fish communities. In M. H. Horn, K. L. M. Martin, & M. A. Chotkowski (Eds.), Intertidal fishes: Life in two worlds (pp. 264–297). Academic Press.

Gilchrist, G., Mallory, M., & Merkel, F. (2005). Can local ecological knowledge contribute to wildlife management? Case studies of migratory birds. Ecology and Society, 10(1). https://doi.org/10.5751/ES-01275-100120

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew, L., Lester, S. E., Barnes, M., & Fox, H. E. (2017). Capacity shortfalls hinder the performance of marine protected areas globally. Nature, 543(7647), 665–669. https://doi.org/10.1038/nature21708

Gils, J. A., Geest, M., Jansen, E. J., Govers, L. L., Fouw, J., & Piersma, T. (2012). Trophic cascade induced by molluscivore predator alters pore-water biogeochemistry via competitive release of prey. Ecology, 93(5), 1143–1152. https://doi.org/10.1890/11-1282.1

Gils, J. A., Geest, M., Leyrer, J., Oudman, T., Lok, T., Onrust, J., & Piersma, T. (2013). Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. Proceedings of the Royal Society B: Biological Sciences, 280(1763). https://doi.org/10.1098/rspb.2013.0861

Gils, J. A., Lisovski, S., Lok, T., Meissner, W., Ozarowska, A., Fouw, J., & Klaassen, M. (2016). Climate change: Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. Science (New York, N.Y.), 352(6287), 819–821. https://doi.org/10.1126/science.aad6351

Gils, J. A., Piersma, T., Dekinga, A., & Dietz, M. W. (2003). Cost-benefit analysis of mollusc-eating in a shorebird: II. Optimizing gizzard size in the face of seasonal demands. Journal of Experimental Biology, 206(19), 3369–3380. https://doi.org/10.1242/jeb.00546

Giorgini, M., Miguez, A., Esquius, K. S., Astarloa, C. D., Iribarne, O., Fanjul, E., & Escapa, M. (2019). Regenerative bioturbation by intertidal burrowing crabs modifies microphytobenthic composition and enhances primary production in SW Atlantic mudflats. Marine Ecology Progress Series, 632, 43–57. https://doi.org/10.3354/meps13134

Glaspie, C. N., & Seitz, R. D. (2017). Role of habitat and predators in maintaining functional diversity of estuarine bivalves. Marine Ecology Progress Series, 570(April), 113–125. https://doi.org/10.3354/meps12103

Glaus, K. B. J., Adrian-Kalchhauser, I., Piovano, S., Appleyard, S. A., Brunnschweiler, J. M., & Rico, C. (2019). Fishing for profit or food? Socio-economic drivers and fishers' attitudes towards sharks in Fiji. Marine Policy, 100(November 2018), 249–257. https://doi.org/10.1016/j.marpol.2018.11.037

Golden, C. D., Allison, E. H., Dey, M. M., Halpern, B. S., J., M. D., Matthew, S., & Vaitla, B. (2016). Fall in fish catch threatens human health. Nature, 534(7607), 317–320.

Goldenberg, S. B., & Shapiro, L. J. (1996). Physical mechanisms for the association of el niño and west african rainfall with atlantic major hurricane activity. Journal of Climate, 9, 1169–1187.

Goodman, L. A. (1961). Snowball Sampling. The Annals of Mathematical Statistics, 32(1), 148–170. https://doi.org/10.1214/aoms/1177705148

Goodwin, N. B., Dulvy, N. K., & Reynolds, J. D. (2002). Life-history correlates of the evolution of live bearing in fishes. Philosophical Transactions of the Royal Society B: Biological Sciences, 357(1419), 259–267. https://doi.org/10.1098/rstb.2001.0958.

Govers, L. L., Pieck, T., Bouma, T. J., Suykerbuyk, W., Smolders, A. J. P., & Katwijk, M. M. (2014). Seagrasses are negatively affected by organic matter loading and Arenicola marina activity in a laboratory experiment. Oecologia, 175(2), 677–685. https://doi.org/10.1007/s00442-014-2916-8

Granadeiro, J. P., Belo, J., Henriques, M., Catalão, J., & Catry, T. (2021). Using sentinel-2 images to estimate topography, tidal-stage lags and exposure periods over large intertidal areas. Remote Sensing, 13, 1–17.

Grant, J. (1983). The relative magnitude of biological and physical sediment reworking in an intertidal community. Journal of Marine Research, 41(4), 673–689. https://doi.org/10.1357/002224083788520469

Gray, A. E., Mulligan, T. J., & Hannah, R. W. (1997). Food habits, occurrence, and population structure of the bat ray, Myliobatis californica, in Humboldt Bay, California. Environmental Biology of Fishes, 49(2), 227–238. https://doi.org/10.1023/A:1007379606233

Grecian, W. J., Witt, M. J., Attrill, M. J., Bearhop, S., Becker, P. H., Egevang, C., & Votier, S. C. (2016). Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. Biology Letters, 12(8), 20160024. https://doi.org/10.1098/rsbl.2016.0024

Griffen, B. D., & Byers, J. E. (2006). Intraguild predation reduces redundancy of predator species in multiple predator assemblage. Journal of Animal Ecology, 75(4), 959–966. https://doi.org/10.1111/j.1365-2656.2006.01115.x

Grubbs, R. D., Carlson, J. K., Romine, J. G., Curtis, T. H., McElroy, W. D., McCandless, C. T., & Musick, J. A. (2016). Critical assessment and ramifications of a purported marine trophic cascade. Scientific Reports, 6(February), 20970. https://doi.org/10.1038/srep20970

Guénette, S., Meissa, B., & Gascuel, D. (2014). Assessing the contribution of marine protected areas to the trophic functioning of ecosystems: A model for the Banc d'Arguin and the Mauritanian shelf. PLoS ONE, 9(4), 94742. https://doi.org/10.1371/journal.pone.0094742

Guillemot, N., Rocklin, D., Chen, C., & Le, M. (2014). A frameworkfor mapping small-scale coastal fisheries using fishers' knowledge. ICES Journal of Marine Science, 71, 1781–1792.

H

Haeseker, S. L., & Cech, J. J. (1994). Food habits of the brown smoothhound shark (Mustelus henlei) from two sites in Tomales Bay. California Fish and Game, 79, 96–114.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., & Watson, R. (2008). A global map of human impact on marine ecosystems. Science (New York, N.Y.), 319(5865), 948–952. https://doi.org/10.1126/science.1149345

Halpin, P. M. (2000). Habitat use by an intertidal salt-marsh fish: Trade-offs between predation and growth. Marine Ecology Progress Series, 198, 203–214. https://doi.org/10.3354/meps198203

Hamady, L. L., Natanson, L. J., Skomal, G. B., & Thorrold, S. R. (2014). Vertebral bomb radiocarbon suggests extreme longevity in white sharks. PLoS ONE, 9(1), 84006. https://doi.org/10.1371/journal.pone.0084006

Hammerschlag, N., Broderick, A. C., Coker, J. W., Coyne, M. S., Dodd, M., Frick, M. G., & Hawkes, L. A. (2015). Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. Ecology, 96(8), 2117–2126. https://doi.org/10.1890/14-2113.1

Hammerschlag, N., Fallows, C., Meÿer, M., Seakamela, S. M., Orndorff, S., Kirkman, S., & Creel, S. (2022). Loss of an apex predator in the wild induces physiological and behavioural changes in prey. Biology Letters, 18(1). https://doi.org/10.1098/rsbl.2021.0476

Hammerschlag, N., Meÿer, M., Seakamela, S. M., Kirkman, S., Fallows, C., & Creel, S. (2017). Physiological stress responses to natural variation in predation risk: Evidence from white sharks and seals. Ecology, 98(12), 3199–3210. https://doi.org/10.1002/ecy.2049

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., & Cooke, S. J. (2019). Ecosystem function and services of aquatic predators in the anthropocene. Trends in Ecology and Evolution, 34(4), 369–383. https://doi.org/10.1016/j.tree.2019.01.005

Hammerschlag, N., Williams, L., Fallows, M., & Fallows, C. (2019). Disappearance of white sharks leads to the novel emergence of an allopatric apex predator, the sevengill shark. Scientific Reports, 9(1), 6–11. https://doi.org/10.1038/s41598-018-37576-6

Hanski, I. (1991). Specialist predators, Generalist predators and the Microtine Rodent cycle. Journal of Applied Ecology, 60(1), 353–367.

Haque, A. B., Cavanagh, R. D., & Seddon, N. (2021). Evaluating artisanal fishing of globally threatened sharks and rays in the Bay of Bengal. Bangladesh. PLoS ONE, 16. https://doi.org/10.1371/journal.pone.0256146

Haque, A. B., & Spaet, J. L. Y. (2021). Trade in threatened elasmobranchs in the Bay of Bengal, Bangladesh. Fisheries Research, 243(June), 106059. https://doi.org/10.1016/j.fishres.2021.106059

Haque, A. B., Washim, M., D'Costa, N. G., Baroi, A. R., Hossain, N., Nanjiba, R., & Khan, N. A. (2021). Socio-ecological approach on the fishing and trade of rhino rays (Elasmobranchii: Rhinopristiformes) for their biological conservation in the Bay of Bengal, Bangladesh. Ocean and Coastal Management, 210(August 2020), 105690. https://doi.org/10.1016/j.ocecoaman.2021.105690

Hardin, G. (1960). The competitive exclusion principle. Science, 131(3409), 1292–1297.

Harms-Tuohy, C. A., Schizas, N. V., & Appeldoorn, R. S. (2016). Use of DNA metabarcoding for stomach content analysis in the invasive lionfish pterois volitans in Puerto Rico. Marine Ecology Progress Series, 558, 181–191. https://doi.org/10.3354/meps11738.

Hartig, F. (2023). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. http://florianhartig.github.io/DHARMa/

Hasan, M. M., Nazru, K. M. S., Rashed Parvej, M., Alam Patwary, M. S., & Uddin, A. M. M. B. (2017). Shark and shark products trade channel and its conservation aspects in Bangladesh. Journal of Fisheries & Livestock Production, 05(01), 1–8. https://doi.org/10.4172/2332-2608.1000221

Hauer, M. E., Fussell, E., Mueller, V., Burkett, M., Call, M., Abel, K., & Wrathall, D. (2020). Sea-level rise and human migration. Nature Reviews Earth and Environment, 1(1), 28–39. https://doi.org/10.1038/s43017-019-0002-9

Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., Bailey, H., & Thums, M. (2016). Key questions in marine megafauna movement ecology. Trends in Ecology and Evolution, 31(6), 463–475. https://doi.org/10.1016/j.tree.2016.02.015

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., & Bograd, S. J. (2019). Marine top predators as climate and ecosystem sentinels. Frontiers in Ecology and the Environment, 17(10), 565–574. https://doi.org/10.1002/fee.2125

Hazin, F., Fischer, A., & Broadhurst, M. (2001). Aspects of reproductive biology of the scalloped hammerhead shark, Sphyrna lewini, off northeastern Brazil. Environmental Biology of Fishes, 61, 151–159.

Heithaus, M. (2001). The biology of tiger sharks, Galeocerdo cuvier, in Shark Bay, Western Australia: Sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes, 2, 25–36.

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence. Ecology, 83(2), 1–12.

Heithaus, M. R., Dunn, R. E., Farabaugh, N. F., Lester, E., Madin, E., Meekan, M., & Wirsing, A. J. (2022). Advances in our understanding of the ecological importance of sharks and their relatives. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), Biology of sharks and their relatives (3rd editio, pp. 486–522). CRC Press.

Heithaus, M. R., Frid, A., Vaudo, J. J., Worm, B., & Wirsing, A. J. (2010). Unraveling the ecological importance of elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation (pp. 1–748). https://doi.org/10.1201/9781420080483

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution, 23(4), 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., & Dill, L. M. (2009). Towards a predictive framework for predator risk effects: The interaction of landscape features and prey escape tactics. Journal of Animal Ecology, 78(3), 556–562. https://doi.org/10.1111/j.1365-2656.2008.01512.x

Helfield, J. M., & Naiman, R. J. (2006). Keystone interactions: Salmon and bear in riparian forests of Alaska. Ecosystems (New York, N.Y.), 9(2), 167–180. https://doi.org/10.1007/s10021-004-0063-5

Hellin, J., & Meijer, M. (2006). Guidelines for Value Chain Analysis. FAO.

Hemming, V., Burgman, M. A., Hanea, A. M., McBride, M. F., & Wintle, B. C. (2018). A practical guide to structured expert elicitation using the IDEA protocol. Methods in Ecology and Evolution, 9(1), 169–180. https://doi.org/10.1111/2041-210X.12857

Henriques, M., Belo, S., JR, J, M., H, A., JA, P., T, D. T., & Roomen, M. (2022). The Bijagós Archipelago: A key area for waterbirds of the East Atlantic Flyway. In R. M, C. G, & C. O (Eds.), East atlantic flyway assessment 2020: The status of coastal waterbird populations and their sites. Wadden sea flyway initiative (pp. 81–93). Wetlands International, BirdLife International.

Hensley, R. A., McCoid, M. J., & Luer, C. A. (1998). Litter Variation in the Atlantic Guitarfish (Rhinobatidae: Rhinobatos lentiginosus) with Comments on Distribution in the Gulf of Mexico. The Southwestern Naturalist, 43(4), 501–504.

Hernández, C. E., Neill, P. E., Pulgar, J. M., Ojeda, F. P., & Bozinovic, F. (2002). Water temperature fluctuations and territoriality in the intertidal zone: Two possible explanations for the elevational distribution of body size in Graus nigra. Journal of Fish Biology, 61(2), 472–488. https://doi.org/10.1006/jfbi.2002.2054

Heupel, M. R., Knip, D. M., Simpfendorfer, C. A., & Dulvy, N. K. (2014). Sizing up the ecological role of sharks as predators. Marine Ecology Progress Series, 495, 291–298. https://doi.org/10.3354/meps10597

Heupel, M. R., Simpfendorfer, C. a, Espinoza, M., Smoothey, A. F., Tobin, A., & Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. Frontiers in Marine Science, 2(February), 1–7. https://doi.org/10.3389/fmars.2015.00012

Higuera-Rivas, J. E., Hoyos-Padilla, E. M., Elorriaga-Verplancken, F. R., Rosales-Nanduca, H., Rosenthal, R., & Urbán, R. J. (2023). Orcas (orcinus orca) use different strategies to prey on rays in the Gulf of California. Aquatic Mammals, 49(1), 7–18. https://doi.org/10.1578/AM.49.1.2023.7

Hilborn, R., Amoroso, R. O., Anderson, C. M., Baum, J. K., Branch, T. A., Costello, C., & Ye, Y. (2020). Effective fisheries management instrumental in improving fish stock status. Proceedings of the National Academy of Sciences of the United States of America, 117(4), 2218–2224. https://doi.org/10.1073/pnas.1909726116

Hill, N. K., Woodworth, B. K., Phinn, S. R., Murray, N. J., & Fuller, R. A. (2021). Global protected-area coverage and human pressure on tidal flats. Conservation Biology, 35(3), 933–943. https://doi.org/10.1111/cobi.13638

Hind, E. J. (2015). A review of the past, the present, and the future of fishers' knowledge research: A challenge to established fisheries science. ICES Journal of Marine Science, 2(72), 341–358.

Hines, A. H., Whitlatch, R. B., Thrush, S. F., Hewitt, J. E., Cummings, V. J., Dayton, P. K., & Legendre, P. (1997). Nonlinear foraging response of a large marine predator to benthic prey: Eagle ray pits and bivalves in a New Zealand sandflat. Journal of Experimental Marine Biology and Ecology, 216(1–2), 191–210. https://doi.org/10.1016/S0022-0981(97)00096-8

Hockey, P. A. R., & Bosman, A. L. (1986). Man as an intertidal predator in transkei: Disturbance, community convergence and management of a natural food resource. Oikos (Copenhagen, Denmark), 46(1), 3. https://doi.org/10.2307/3565373

Hoffmayer, E. R., & Parsons, G. R. (2003). Food habits of three shark species from the Mississippi Sound in the northern Gulf of Mexico. Southeastern Naturalist, 2(2), 271–280. https://doi.org/10.1656/1528-7092(2003)002

Hofstede, R. ter. (2001). Incidental catches of pelagic megafauna by the EU pelagic fleet in the Mauritanian Exclusive Economic Zone during the year. RIVO-Netherlands Institute for Fisheries Research.

Hoggarth, D. D., Abeyasekera, S., Arthur, R. I., Beddingtion, J. R., Burn, R. W., Halls, A. S., & Welcomme, R. L. (2006). Stock assessment for fishery management, A frame guide to the stock assessment tools of the Fisheries Management Science Programme. FAO. Fisheries Technical Paper. https://doi.org/10.1007/s13398-014-0173-7.2

Hollensead, L. D., Grubbs, R. D., Carlson, J. K., & Bethea, D. M. (2016). Analysis of fine-scale daily movement patterns of juvenile Pristis pectinata within a nursery habitat. Aquatic Conservation: Marine and Freshwater Ecosystems, 26(3), 492–505. https://doi.org/10.1002/aqc.2556

Holt, R. D., & Huxel, G. R. (2007). Alternative prey and the dynamics of intraguild predation: Theoretical perspectives. Ecology, 88(11), 2706–2712. https://doi.org/10.1890/06-1525.1

Honda, K., Nakamura, Y., Nakaoka, M., Uy, W. H., & Fortes, M. D. (2013). Habitat use by fishes in coral reefs, seagrass beds and mangrove habitats in the Philippines. PLoS ONE, 8(8), 1–10. https://doi.org/10.1371/journal.pone.0065735

Honkoop, P. J. C., Berghuis, E. M., Holthuijsen, S. J., Lavaleye, M. S. S., & Piersma, T. (2008). Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter. Journal of Sea Research, 60(4), 255–263. https://doi.org/10.1016/j.seares.2008.07.005

Hooker, S. K., Cañadas, A., Hyrenbach, K. D., Corrigan, C., Polovina, J. J., & Reeves, R. R. (2011). Making protected area networks effective for marine top predators. Endangered Species Research, 13(3), 203–218. https://doi.org/10.3354/esr00322

Hopsch, S. B., Thorncroft, C. D., Hodges, K., & Aiyyer, A. (2007). West African storm tracks and their relationship to atlantic tropical cyclones. Journal of Climate, 20, 2468–2483.

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., & Torda, G. (2018). Global warming transforms coral reef assemblages. Nature, 556(7702), 492–496.

Humber, F., Andriamahaino, E. T., Beriziny, T., Botosoamananto, R., Godley, B. J., Gough, C., & Broderick, A. C. (2017). Assessing the small-scale shark fishery of Madagascar through community-based monitoring and knowledge. Fisheries Research, 186, 131–143. https://doi.org/10.1016/j.fishres.2016.08.012

Hussey, N. E., Brush, J., McCarthy, I. D., & Fisk, A. T. (2010). δ15N and δ13C diet-tissue discrimination factors for large sharks under semi-controlled conditions. Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology, 155(4), 445–453. https://doi.org/10.1016/j.cbpa.2009.09.023

Hussey, N. E., MacNeil, M. A., Siple, M. C., Popp, B. N., Dudley, S. F. J., & Fisk, A. T. (2015). Expanded trophic complexity among large sharks. Food Webs, 4, 1–7. https://doi.org/10.1016/j.fooweb.2015.04.002

Hylton, S., White, W. T., & Chin, A. (2017). The sharks and rays of the Solomon Islands: A synthesis of their biological diversity, values and conservation status. Pacific Conservation Biology, 23(4), 324–334. https://doi.org/10.1071/PC17012

Hyslop, E. J. (1980). Stomach contents analysis—A review of methods and their application. Journal of Fish Biology, 17(4), 411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x.

I

IBAP. (2012). Archipel Des Bijagós – Motom Moranghajogo. IBAP.

ICAR. (2019). ICAR-CMFRI hosts FAO global expert meeting on shark trade. ICAR. https://www.icar.org.in/content/icar-cmfri-hosts-fao-global-expert-meeting-shark-trade

Ip, Y. C. A., Chang, J. J. M., Lim, K. K. P., Jaafar, Z., Wainwright, B. J., & Huang, D. (2021). Seeing through sedimented waters: Environmental DNA reduces the phantom diversity of sharks and rays in turbid marine habitats. BMC Ecology and Evolution, 21(1), 1–14. https://doi.org/10.1186/s12862-021-01895-6

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services. In Intergovernmental science-policy platform on biodiversity and ecosystem services (Vol. 45). https://zenodo.org/record/3553579#.YfmYTerMI2w

IPCC. (2007). Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. https://doi.org/10.1016/B978-008044910-4.00250-9

Ishii, K., & Fukui, M. (2001). Optimization of annealing temperature to reduce bias caused by a primer mismatch in multitemplate PCR. Applied and Environmental Microbiology, 67(8), 3753–3755. https://doi.org/10.1128/AEM.67.8.3753-3755.2001

Ismen, A. (2003). Age, growth, reproduction and food of common stingray (Dasyatis pastinaca L., 1758) in İskenderun Bay, the eastern Mediterranean'. Fisheries Research, 60(1), 169–176. https://doi.org/10.1016/S0165-7836(02)00058-9.

Iwamatsu, S., Suzuki, A., & Sato, M. (2007). Nereidid polychaetes as the major diet of migratory shorebirds on the estuarine tidal flats at Fujimae-Higata in Japan. Zoological Science, 24(7), 676–685. https://doi.org/10.2108/zsj.24.676

J

Jabado, R. W., Al Ghais, S. M., Hamza, W., & Henderson, A. C. (2015). The shark fishery in the United Arab Emirates: An interview based approach to assess the status of sharks. Aquatic Conservation: Marine and Freshwater Ecosystems, 25(6), 800–816. https://doi.org/10.1002/aqc.2477

Jabado, R. W., Al Ghais, S. M., Hamza, W., Shivji, M. S., & Henderson, A. C. (2015). Shark diversity in the Arabian/Persian Gulf higher than previously thought: Insights based on species composition of shark landings in the United Arab Emirates. Marine Biodiversity, 45(4), 719–731. https://doi.org/10.1007/s12526-014-0275-7

Jabado R. W., Badji L., Chartrain E., Bruyne G., Derrick D., Dia M., & Williams A. B. (2021). Fontitrygon margaritella. In The IUCN Red List of Threatened Species (p. 161520). https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T161520A124498844.en

Jabado, R. W., Chartrain, E., Bruyne, G., Derrick, D., Diop, M., Doherty, P., Keith Diagne, L., Leurs, G. H. L., Metcalfe, K., Sayer, C., Seidu, I., Tamo, A., VanderWright, W. J., & Williams, A. B. (2021). Fontitrygon ukpam. The IUCN Red List of Threatened Species.

Jabado, R. W., Chartrain, E., Cliff, G., Silva, C., Bruyne, G., Derrick, D., & Winker, H. (2021). Mustelus mustelus, common smoothhound. The IUCN Red List of Threatened Species, 39358 124405881. https://doi.org/10.1007/978-3-030-50032-0141

Jabado R.W, Pacoureau N., Diop M., Dia M., Ba A., Williams A.B., & Metcalfe K. (2021). Rhinobatos rhinobatos, Common Guitarfish. In The IUCN Red List of Threatened Species 2021: E.T63131A124461877. https://www.iucnredlist.org/species/63131/124461877

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., & Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. Science (New York, N.Y.), 293(5530), 629–637. https://doi.org/10.1126/science.1059199

Jacobsen, I. P., & Bennett, M. B. (2013). A Comparative Analysis of Feeding and Trophic Level Ecology in Stingrays (Rajiformes; Myliobatoidei) and Electric Rays (Rajiformes: Torpedinoidei). PLoS ONE, 8(8), e71348. https://doi.org/10.1371/journal.pone.0071348

Jager, Z. (1993). The distribution and abundance of young fish in the Banc d'Arguin, Mauritania. Hydrobiologia, 258, 185–196. https://doi.org/10.1007/BF00006196

Jaiteh, V. F., Lindfield, S. J., Mangubhai, S., Warren, C., Fitzpatrick, B., & Loneragan, N. (2016). Higher abundance of marine predators and changes in fishers' behavior following spatial protection within the world's biggest shark fishery. Frontiers in Marine Science, 3(April), 1–15. https://doi.org/10.3389/fmars.2016.00043

Jennings, S., Pinnegar, J. K., Polunin, N. V. C., & Boon, T. W. (2001). Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. The Journal of Animal Ecology, 70, 934–944.

Jeunen, G. J., Knapp, M., Spencer, H. G., Lamare, M. D., Taylor, H. R., Stat, M., & Gemmell, N. J. (2019). Environmental DNA (eDNA) metabarcoding reveals strong discrimination among diverse marine habitats connected by water movement. Molecular Ecology Resources, 19(2), 426–438. https://doi.org/10.1111/1755-0998.12982

Jin, B., Fu, C., Zhong, J., Li, B., Chen, J., & Wu, J. (2007). Fish utilization of a salt marsh intertidal creek in the Yangtze River Estuary, China. Estuarine, Coastal and Shelf Science, 73(3–4), 844–852. https://doi.org/10.1016/j.ecss.2007.03.025

Jing, K., Ma, Z., Li, B., Li, J., & Chen, J. (2007). Foraging strategies involved in habitat use of shorebirds at the intertidal area of Chongming Dongtan, China. Ecological Research, 22(4), 559–570. https://doi.org/10.1007/s11284-006-0302-7

Jing, Z., Kai, J., Xiaojing, G., & Zhijun, M. (2007). Food supply in intertidal area for shorebirds during stopover at Chongming Dongtan.

Jirik, K. E., & Lowe, C. G. (2012). An elasmobranch maternity ward: Female round stingrays Urobatis halleri use warm, restored estuarine habitat during gestation. Journal of Fish Biology, 80(5), 1227–1245. https://doi.org/10.1111/j.1095-8649.2011.03208.x

Joung, S. J., Chen, C. T., Clark, E., Uchida, S., & Huang, W. Y. P. (1996). The whale shark, Rhincodon typus, is a livebearer: 300 embryos found in one "megamamma" supreme. Environmental Biology of Fishes, 46(3), 219–223. https://doi.org/10.1007/BF00004997

Juan-Jordá, M. J., Murua, H., Arrizabalaga, H., Merino, G., Pacoureau, N., & Dulvy, N. (2022). Seventy years of tunas, billfishes. And Sharks as Sentinels of Global Ocean Health, 378(6620). https://doi.org/10.1126/science.abj0211

K

Kaiser, M. J., Attrill, M. J., Jennings, S., Thomas, D. N., Barnes, D. K. A., Brierley, A. S., & Kaartokallio, H. (2020). Marine ecology: Processes, systems, and impacts (3rd ed.). Oxford University Press.

Kajiura, S. M., Sebastian, A. P., & Tricas, T. C. (2000). Dermal Bite Wounds as Indicators of Reproductive Seasonality and Behaviour in the Atlantic Stingray, Dasyatis sabina. Environmental Biology of Fishes, 58(1), 23–31. https://doi.org/10.1023/A:1007667108362.

Kalejta, B. (1993). Intense predation cannot always be detected experimentally. Netherlands Journal of Sea Research, 31(4), 385–393.

Kanno, S., Heupel, M., & Simpfendorfer, C. (2019). Stationary video monitoring reveals habitat use of stingrays in mangroves. Marine Ecology Progress Series, 621, 155–168. https://doi.org/10.3354/meps12977

Karnad, D., Sutaria, D., & Jabado, R. W. (2020). Local drivers of declining shark fisheries in India. Ambio, 49(2), 616–627. https://doi.org/10.1007/s13280-019-01203-z

Keith, D. A., Rodríguez, J. P., Brooks, T. M., Burgman, M. A., Barrow, E. G., Bland, L., & Spalding, M. D. (2015). The IUCN red list of ecosystems: Motivations, challenges, and applications. Conservation Letters, 8(3), 214–226. https://doi.org/10.1111/conl.12167

Kelly, R. P., Gallego, R., & Jacobs-Palme, E. (2018). The effect of tides on nearshore environmental DNA. PeerJ, 2018(3). https://doi.org/10.7717/peerj.4521

Kempster, R. M. (2013). Sexual dimorphism of the electrosensory system: A quantitative analysis of nerve axons in the dorsal anterior lateral line nerve of the blue-spotted fantail stingray (Taeniura lymma). Brain, Behavior and Evolution, 81(4), 226–235. https://doi.org/10.1159/000351700.

Kernaléguen, L., Dorville, N., Ierodiaconou, D., Hoskins, A. J., Baylis, A. M. M., Hindell, M. A., & Arnould, J. P. Y. (2016). From video recordings to whisker stable isotopes: A critical evaluation of timescale in assessing individual foraging specialisation in Australian fur seals. Oecologia, 180(3), 657–670. https://doi.org/10.1007/s00442-015-3407-2

Kessel, S. T., & Hussey, N. E. (2015). Tonic immobility as an anaesthetic for elasmobranchs during surgical implantation procedures. Canadian Journal of Fisheries and Aquatic Sciences, 72(March), 1287–1291. https://doi.org/10.1139/cjfas-2015-0136

Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H., & Jones, R. I. (2006). A revised model for lipid-normalizing δ13C values from aquatic organisms, with implications for isotope mixing models. Journal of Applied Ecology, 43(6), 1213–1222. https://doi.org/10.1111/j.1365-2664.2006.01224.x

Kim, S. L., Casper, D. R., Galván-Magaña, F., Ochoa-Díaz, R., Hernández-Aguilar, S. B., & Koch, P. L. (2012). Carbon and nitrogen discrimination factors for elasmobranch soft tissues based on a long-term controlled feeding study. Environmental Biology of Fishes, 95(1), 37–52. https://doi.org/10.1007/s10641-011-9919-7

Kindsvater, H. K., Mangel, M., Reynolds, J. D., & Dulvy, N. K. (2016). Ten principles from evolutionary ecology essential for effective marine conservation. Ecology and Evolution, 6(7), 2125–2138. https://doi.org/10.1002/ece3.2012

Kinsey, D. W., & Kinsey, B. E. (1967). Diurnal changes in oxygen content of the water over the coral reef platform at heron island. Australian Journal of Marine and Freshwater Research, 18, 23–34.

Kleiber, P., Clarke, S., Bigelow, K., Nakano, H., Mcallister, M., Takeuchi, Y., Leeney, R. H., & Poncelet, P. (2009). North pacific blue shark stock assessment. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-PIFSC-17, February), 9(3), 411–430. https://doi.org/10.1002/aqc.2419

Klimley, A. P. (2013). The biology of sharks and rays. Univ. of Chicago Press.

Klokov, K., Gerasimov, Y., & Syroechkovskiy, E. (2023). Assessment of hunting pressure on Arctic-nesting shorebirds: First results from the Northeast of Russia. E3S Web of Conferences, 378. https://doi.org/10.1051/e3sconf/202337805003

Knip, D. M., Heupel, M. R., & Simpfendorfer, C. A. (2010). Sharks in nearshore environments: Models, importance, and consequences. Marine Ecology Progress Series, 402, 1–11. https://doi.org/10.3354/meps08498

Knip, D. M., Heupel, M. R., Simpfendorfer, C. A., Tobin, A. J., & Moloney, J. (2011). Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks Carcharhinus amboinensis in a tropical nearshore region. Marine Ecology Progress Series, 425, 233–246. https://doi.org/10.3354/meps09006

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M. E., Hacker, S. D., & Wolanski, E. (2009). Non-linearity in ecosystem services: Temporal and spatial variability in coastal protection. Frontiers in Ecology and the Environment, 7(1), 29–37. https://doi.org/10.1890/080126

Koch, R. (1999). The 80/20 principle: The secret of achieving more with less. Crown Currency. https://doi.org/10.1016/s0024-6301(97)80978-8

Kohler, N. E., & Turner, P. A. (2001). Shark tagging: A review of conventional methods and studies. Environmental Biology of Fishes, 60(191–223), 191–223.

Koppel J, Heide T, Altieri AH, Eriksson BK, Bouma TJ, Olff H, & Silliman BR. (2015). Long-distance interactions regulate the structure and resilience of coastal ecosystems. Annual Review of Marine Science, 7, 139–158.

Krakstad, J., Olsen, M., & Wagúe, A. (2004). Survey of the pelagic fish resources off north west africa. FAO.

Kristensen, E., & Kostka, J. E. (2013). Macrofaunal burrows and irrigation in marine sediment: Microbiological and biogeochemical interactions. In Interactions between macro- and microorganisms in marine sediments (pp. 125–157). https://doi.org/10.1029/CE060p0125

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., & Banta, G. T. (2012). What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Marine Ecology Progress Series, 446, 285–302. https://doi.org/10.3354/meps09506

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics, 34, 153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., & Worm, B. (2018). Tracking the global footprint of fisheries. Science (New York, N.Y.), 359(6378), 904–908. https://doi.org/10.1126/science.aao5646

Kruijssen, F., Tedesco, I., Ward, A., Pincus, L., Love, D., & Thorne-Lyman, A. L. (2020). Loss and waste in fish value chains: A review of the evidence from low and middle-income countries. Global Food Security, 26, 100434. https://doi.org/10.1016/j.gfs.2020.100434

Kruskal, J., & Wish, M. (1978). Multidimensional scaling. SAGE Publications, Inc.

Küpper, F. C., & Kamenos, N. A. (2018). The future of marine biodiversity and marine ecosystem functioning in UK coastal and territorial waters (including UK Overseas Territories. With an Emphasis on Marine Macrophyte Communities. Botanica Marina, 61(6), 521–535. https://doi.org/10.1515/bot-2018-0076

Kuwae, T., Miyoshi, E., Hosokawa, S., Ichimi, K., Hosoya, J., Amano, T., & Elner, R. W. (2012). Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. Ecology Letters, 15(4), 347–356. https://doi.org/10.1111/j.1461-0248.2012.01744.x

Kyalo, K. B., & Stephen, N. (2013). Shark bycatch—Small scale tuna fishery interactions along the Kenyan coast. Indian Ocean Tuna Commission. https://aquadocs.org/bitstream/handle/1834/7747/ktf0455.pdf

Kyne, P. M., & Jabado, R. W. (2019). Rhynchobatus luebberti, African wedgefish. In The IUCN Red List of Threatened Species:2019, 8235.

Kyne, P. M., Jabado, R. W., Rigby, C. L., Dharmadi, G., A., M., Pollock, C. M., & Dulvy, N. K. (2020). The thin edge of the wedge: Extremely high extinction risk in wedgefishes and giant guitarfishes. Aquatic Conservation: Marine and Freshwater Ecosystems, 30(7), 1337–1361. https://doi.org/10.1002/aqc.3331

L

Lafferty, K. D., Benesh, K. C., Mahon, A. R., Jerde, C. L., & Lowe, C. G. (2018). Detecting southern California's white sharks with environmental DNA. Frontiers in Marine Science, 5(OCT), 1–6. https://doi.org/10.3389/fmars.2018.00355

Lafferty, K. D., Garcia-Vedrenne, A. E., McLaughlin, J. P., Childress, J. N., Morse, M. F., & Jerde, C. L. (2020). At Palmyra Atoll, the fish-community environmental DNA signal changes across habitats but not with tides. Journal of Fish Biology. https://doi.org/10.1111/jfb.14403

Lambarri, C., Espinosa, H., Martínez, A., & Hernández, A. (2015). Cods for sale Do we know what we are buying? DNA Barcodes, 3(1). https://doi.org/10.1515/dna-2015-0004

Lara-Mendoza, R. E., Márquez-Farías, J. F., & Román-Reyes, J. C. (2015). Feeding habits of the speckled guitarfish Rhinobatos glaucostigma (Elasmobranchii: Rhinobatidae). Journal of Fish Biology, 87(2), 311–322. https://doi.org/10.1111/jfb.12720

Larson, W. A., Barry, P., Dokai, W., Maselko, J., Olson, J., & Baetscher, D. (2022). Leveraging eDNA metabarcoding to characterize nearshore fish communities in Southeast Alaska: Do habitat and tide matter? Environmental DNA, 1–13. https://doi.org/10.1002/edn3.297

Last, P., White, W., Carvalho, M., Séret, B., Stehmann, M., & Naylor, G. (2016). Rays of the World. CSIRO Publishing.

Lathuilière, C., Echevin, V., & Lévy, M. (2008). Seasonal and intraseasonal surface chlorophyll-a variability along the northwest African coast. Journal of Geophysical Research: Oceans, 113(5), 2000–2004. https://doi.org/10.1029/2007JC004433

Laverock, B., Gilbert, J. A., Tait, K., Osborn, A. M., & Widdicombe, S. (2011). Bioturbation: Impact on the marine nitrogen cycle. Biochemical Society Transactions, 39(1), 315–320. https://doi.org/10.1042/BST0390315

Layman, C. A., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology, 88(1), 42–48. https://doi.org/10.1890/08-0167.1

Le Quesne, W. J. F., & Jennings, S. (2012). Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. Journal of Applied Ecology, 49(1), 20–28. https://doi.org/10.1111/j.1365-2664.2011.02087.x.

Lear, K. O., Whitney, N. M., Morgan, D. L., Brewster, L. R., Whitty, J. M., Poulakis, G. R., & Gleiss, A. C. (2019). Thermal performance responses in free-ranging elasmobranchs depend on habitat use and body size. Oecologia, 191(4), 829–842. https://doi.org/10.1007/s00442-019-04547-1

Lear, K. O., Whitney, N. M., Morris, J. J., & Gleiss, A. C. (2021). Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. Proceedings of the Royal Society B: Biological Sciences, 288(1954). https://doi.org/10.1098/rspb.2021.0816

Leeney, R. H., & Poncelet, P. (2015). Using fishers' ecological knowledge to assess the status and cultural importance of sawfish in Guinea-Bissau. Aquatic Conservation: Marine and Freshwater Ecosystems, 25(3), 411–430. https://doi.org/10.1002/aqc.2419

Lehman, R. N., Poulakis, G. R., Scharer, R. M., Schweiss, K. E., Hendon, J. M., & Phillips, N. M. (2020). An environmental DNA tool for monitoring the status of the Critically Endangered Smalltooth Sawfish, Pristis pectinata, in the western Atlantic. Conservation Genetics Resources, 12(4), 621–629. https://doi.org/10.1007/s12686-020-01149-5

Lemrabott, S. Y. (2023). Fish and fisheries dynamics at Banc d'Arguin, Mauritania [PhD. thesis, University of Groningen]. https://doi.org/10.33612/diss.574910952

Lemrabott, S. Y. C., El-Hacen, E. M., Piersma, T., Sall, A. A., Sidina, E., Mahmoud, L. Y. A., & Leeuwen, A. (2023). Twenty years of monitoring reveal overfishing of bony fish stocks in the coastal national park Banc d'Arguin. In Mauritania. Aquatic conservation: Marine and freshwater ecosystems (pp. 833–844). https://doi.org/10.1002/aqc.3948

Lemrabott, S. Y., Van Leeuwen, A., Piersma, T., Braham, C.-B., Ball, A. C., Araujo, A., Olff, H., & El-Hacen, E.-H. (2024). The chronology of overfishing in a remote West African coastal ecosystem. *Ecology and Society*, *29*(1), art9. https://doi.org/10.5751/ES-13902-290109

Lenth, R. (2019). emmeans: Estimated marginal means, aka least-squares means. https:// CRANR-proje

Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., & Schellnhuber, H. J. (2008). Tipping elements in the Earth's climate system. Proceedings of the National Academy of Sciences of the United States of America, 105(6), 1786–1793. https://doi.org/10.1073/pnas.0705414105

Leurs, G., Nieuwenhuis, B. O., Zuidewind, T. J., Hijner, N., Olff, H., & Govers, L. L. (2023). Where land meets sea: Intertidal areas as key habitats for sharks and rays. Fish and Fisheries, 1–20. https://doi.org/10.1111/faf.12735

Leurs, G., Reijden, K. J., Cheikhna Lemrabott, S. Y., Barry, I., Nonque, D. M., Olff, H., Ledo Pontes, S., Regalla, A., & Govers, L. L. (2021). Industrial fishing near west african marine protected areas and its potential effects on mobile marine predators. Frontiers in Marine Science, 8. https://doi.org/10.3389/fmars.2021.602917

Leurs, G., Verkuil, Y. I., Hijner, N., Saalmann, F., Dos Santos, L., Regalla, A., Ledo Pontes, S., Yang, L., Naylor, G. J. P., Olff, H., & Govers, L. L. (2023). Addressing data-deficiency of threatened sharks and rays in a highly dynamic coastal ecosystem using environmental DNA. Ecological Indicators, 154(110795).

Lewis, T. L., Esler, D., & Boyd, W. S. (2007). Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. Marine Ecology Progress Series, 329, 131–144. https://doi.org/10.3354/meps329131

Lewison, R. L., Crowder, L. B., Read, A. J., & Freeman, S. A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology and Evolution, 19(11), 598–604. https://doi.org/10.1016/j.tree.2004.09.004

Lewison, R. L., Crowder, L. B., Wallace, B. P., Moore, J. E., Cox, T., Zydelis, R., & Safina, C. (2014). Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. Proceedings of the National Academy of Sciences, 111(14), 5271–5276.

Li, Y., Zhang, Y., Hussey, N. E., & Dai, X. (2016). Urea and lipid extraction treatment effects on δ15N and δ13C values in pelagic sharks. Rapid Communications in Mass Spectrometry, 30(1), 1–8. https://doi.org/10.1002/rcm.7396

Lifjeld, J. T. (1984). Prey selection in relation to body size and bill length of five species of waders feeding in the same habitat. Ornis Scandinavica, 15(4), 217–226. https://doi.org/10.2307/3675930

Lim, K. C., Chong, V. C., Lim, P.-E., Yurimoto, T., & Loh, K. H. (2019). Feeding ecology of three sympatric species of stingrays on a tropical mudflat. Journal of the Marine Biological Association of the United Kingdom, 99(4), 999–1007. https://doi.org/10.1017/S0025315418000759

Lindegren, M., Holt, B. G., MacKenzie, B. R., & Rahbek, C. (2018). A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. Scientific Reports, 8(1), 1–8. https://doi.org/10.1038/s41598-018-22419-1

Logan, J. M., & Lutcavage, M. E. (2010). Stable isotope dynamics in elasmobranch fishes. Hydrobiologia, 644(1), 231–244. https://doi.org/10.1007/s10750-010-0120-3

Lohrer, A. M., Thrush, S. F., & Gibbs, M. M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature, 431(7012), 1092–1095. https://doi.org/10.1038/nature03042

Lonneville, B., Oset García, P., Schepers, L., Vanhoorne, B., Hernandez, F., & Mees, J. (2019). MarineRegions.org. http://www.marineregions.org

Lopes, P. F. M., Verba, J. T., Begossi, A., & Pennino, M. G. (2019). Predicting species distribution from fishers' local ecological knowledge: A new alternative for data-poor management. Canadian Journal of Fisheries and Aquatic Sciences, 76(8), 1423–1431. https://doi.org/10.1139/cjfas-2018-0148

Loreau, M., Mouquet, N., & Holt, R. D. (2003). Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. Ecology Letters, 6(8), 673–679. https://doi.org/10.1046/j.1461-0248.2003.00483.x

Lorenzo, M., Claudet, J., & Guidetti, P. (2016). Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. Journal for Nature Conservation, 32, 62–66. https://doi.org/10.1016/j.jnc.2016.04.004

Lotze, H. K. (2007). Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. Fisheries Research, 87(2–3), 208–218. https://doi.org/10.1016/j.fishres.2006.12.009

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., & Jackson, J. B. C. (2011). Depletion, degradation, and recovery potential of estuaries and coastal seas. Journal of Physics A: Mathematical and Theoretical, 44(8), 1689–1699. https://doi.org/10.1088/1751-8113/44/8/085201

Lourenço, P. M., Catry, T., & Granadeiro, J. P. (2017). Diet and feeding ecology of the wintering shorebird assemblage in the Bijagós archipelago, Guinea-Bissau. Journal of Sea Research, 128(December 2016), 52–60. https://doi.org/10.1016/j.seares.2017.08.004

Lourenço, P. M., Catry, T., Piersma, T., & Granadeiro, J. P. (2015). Comparative feeding ecology of shorebirds wintering at Banc d'Arguin, Mauritania. Estuaries and Coasts, 39(3), 855–865. https://doi.org/10.1007/s12237-015-0029-1

Lourenço, P. M., Granadeiro, J. P., & Catry, T. (2018). Low macroinvertebrate biomass suggests limited food availability for shorebird communities in intertidal areas of the Bijagós archipelago (Guinea-Bissau). Hydrobiologia, 816, 197–212.

Lu, Y., Yuan, J., Lu, X., Su, C., Zhang, Y., Wang, C., & Sweijd, N. (2018). Major threats of pollution and climate change to global coastal ecosystems and enhanced management for sustainability. Environmental Pollution, 239, 670–680. https://doi.org/10.1016/j.envpol.2018.04.016

Lucifora, L. O., García, V. B., & Escalante, A. H. (2009). How can the feeding habits of the sand tiger shark influence the success of conservation programs? Animal Conservation, 12(4), 291–301. https://doi.org/10.1111/j.1469-1795.2009.00247.x

Lucifora, L. O., García, V. B., Menni, R. C., & Escalante, A. H. (2006). Food habits, selectivity, and foraging modes of the school shark Galeorhinus galeus. Marine Ecology Progress Series, 315, 259–270. https://doi.org/10.3354/meps315259

Lucifora, L. O., García, V. B., Menni, R. C., Escalante, A. H., & Hozbor, N. M. (2008). Effects of body size, age and maturity stage on diet in a large shark: Ecological and applied implications. Ecological Research, 24(1), 109–118. https://doi.org/10.1007/s11284-008-0487-z

Lucifora, L. O., Menni, R. C., & Escalante, A. H. (2005). Reproduction, abundance and feeding habits of the broadnose sevengill shark Notorynchus cepedianus in north Patagonia, Argentina. Marine Ecology Progress Series, 289, 237–244.

Lynn-Myrick, J., & Flessa, K. W. (1996). Bioturbation rates in Bahía la Choya, Sonora, Mexico. Ciencias marinas, 22, 23–46.

Lyons, K. (2017). Who's My Daddy? Considerations for the influence of sexual selection on multiple paternity in elasmobranch mating systems. Ecology and Evolution, 7(15), 5603–5612. https://doi.org/10.1002/ece3.3086.

M

Roomen M, Schekkerman H, Delany S, Winden E, Flink S, Langendoen T, & Nagy S. (2011). Overview of monitoring work on numbers, reproduction and survival of waterbird populations important in the Wadden Sea and the East Atlantic Flyway. SOVON. (2011).

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. The American Naturalist, 100(916), 603–609.

MacKendrick, A. G., & Kesava, P. M. (1911). The rate of multiplication of micro-organisms: A mathmatical study. Proceedings of the Royal Society of Edinburgh, 31, 649–653.

MacKeracher, T., Diedrich, A., & Simpfendorfer, C. A. (2019). Sharks, rays and marine protected areas: A critical evaluation of current perspectives. Fish and Fisheries, 20(2), 255–267. https://doi.org/10.1111/faf.12337

MacKinnon, J., Verkuil, Y. I., & Murray, N. (2012). IUCN situation analysis on East and Southeast Asian intertidal habitats, with particular reference to the Yellow Sea (including the Bohai Sea). Occasional Paper of the IUCN Species Survival Commission, 47.

MacNeil, M. A., Drouillard, K. G., & Fisk, A. T. (2006). Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Canadian Journal of Fisheries and Aquatic Sciences, 63(2), 345–353. https://doi.org/10.1139/f05-219

MacNeil, M. A., Skomal, G. B., & Fisk, A. T. (2005). Stable isotopes from multiple tissues reveal diet switching in sharks. Marine Ecology Progress Series, 302, 199–206. https://doi.org/10.3354/meps302199.

Malpica-Cruz, L., Herzka, S. Z., Sosa-Nishizaki, O., Lazo, J. P., & Trudel, M. (2012). Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: Empirical and modeling results. Canadian Journal of Fisheries and Aquatic Sciences, 69, 551–564. https://doi.org/10.1139/f2011-172

Manjarrez Acosta, C., Juárez Rentería, F., Rodríguez Espinoza, J. P., Díaz Duran, R., Lizárraga Humaran, X., & Vega Cerecer, A. E. (1983). Estudio sobre algunos aspectos biológicopesqueros del tiburón en la zona sur de Sinaloa. Universidad Autónoma de Sinaloa.

Marshall L. J., & Cronin E. S. (2016). Fontitrygon margaritella. In The IUCN Red List of Threatened Species 2016 (p. 161495 104172339, 8235).

Marshall, L. J., White, W. T., & Potter, I. C. (2007). Reproductive biology and diet of the southern fiddler ray, Trygonorrhina fasciata (Batoidea: Rhinobatidae), an important trawl bycatch species. Marine and Freshwater Research, 58(1), 104–115. https://doi.org/10.1071/MF05165

Martin, R. A. (2005). Conservation of freshwater and euryhaline elasmobranchs: A review. Journal of the Marine Biological Association of the UK, 85, 1049. https://doi.org/10.1017/S0025315405012105

Martinell, J., Gibert, J. M., Domènech, R., Ekdale, A. A., & Steen, P. P. (2001). Cretaceous ray traces?: An alternative interpretation for the alleged dinosaur tracks of La Posa, Isona, NE Spain. Palaios, 16(4), 409–416.

Martins, A. P. B., Heupel, M. R., Bierwagen, S. L., Chin, A., & Simpfendorfer, C. A. (2020). Tidal-diel patterns of movement, activity and habitat use by juvenile mangrove whiprays using towed-float GPS telemetry. Marine and Freshwater Research. https://doi.org/10.1071/MF20078

Martins, A. P. B., Heupel, M. R., Chin, A., & Simpfendorfer, C. A. (2018). Batoid nurseries: Definition, use and importance. Marine Ecology Progress Series, 595, 253–267. https://doi.org/10.3354/meps12545

Martins, A. P. B., Matley, J. K., Heupel, M. R., Fisk, A. T., Chin, A., & Simpfendorfer, C. A. (2022). Trophic ecology of sympatric juvenile stingrays within a nursery area. Marine and Freshwater Research, 1–11. https://doi.org/10.1071/mf21292

Matern, S. A., Cech, J. J., & Hopkins, T. E. (2000). Diel movements of bat rays, Myliobatis californica, in Tomales Bay, California: Evidence for behavioral thermoregulation? Environmental Biology of Fishes, 58(2), 173–182. https://doi.org/10.1023/A:1007625212099

Mathot, K., Piersma, T., & Elner, R. W. (2019). Shorebirds as Integrators and Indicators of Mudflat Ecology. In Mudflat Ecology (7th ed., pp. 309–338). Springer.

Matich, P., Heithaus, M. R., & Layman, C. A. (2011). Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. Journal of Animal Ecology, 80(1), 294–305. https://doi.org/10.1111/j.1365-2656.2010.01753.x

Maunder, M. N., & Punt, A. E. (2004). Standardizing catch and effort data: A review of recent approaches. Fish. Res, 70, 141–159. https://doi.org/10.1016/j.fishres.2004.08.002.

Maxwell, D., & Jennings, S. (2005). Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. Journal of Applied Ecology, 42(1), 25–37. https://doi.org/10.1111/j.1365-2664.2005.01000.x

McCarter, J., & Gavin, M. C. (2014). Local perceptions of changes in traditional ecological knowledge: A case study from Malekula Island, Vanuatu. Ambio, 43(3), 288–296. https://doi.org/10.1007/s13280-013-0431-5

McCauley, D. J., Young, H. S., Dunbar, R. B., Estes, J. A., Semmens, B. X., & Micheli, F. (2012). Assessing the effects of large mobile predators on ecosystem connectivity. Ecological Applications, 22(6), 1711–1717. https://doi.org/10.1890/11-1653.1

McDavitt, M. T. (2005). The cultural significance of sharks and rays in Aboriginal societies across Australia’s top end. Seaweek, 1–5.

McDermott, G. R., Meng, K. C., McDonald, G. G., & Costello, C. J. (2018). The blue paradox: Preemptive overfishing in marine reserves. Proceedings of the National Academy of Sciences, 116(12), 5319–5325. https://doi.org/10.1073/pnas.1802862115

Meijer, K. J., El-Hacen, E. H. M., Govers, L. L., Lavaleye, M., Piersma, T., & Olff, H. (2021). Mangrove-mudflat connectivity shapes benthic communities in a tropical intertidal system. Ecological Indicators, 130(December 2020), 108030. https://doi.org/10.1016/j.ecolind.2021.108030

Mejía-Falla, P. A. (2014). Age and growth of the round stingray Urotrygon rogersi, a particularly fast-growing and short-lived elasmobranch'. PLoS ONE, 9(4), 12–15. https://doi.org/10.1371/journal.pone.0096077.

Mendonça, V. M., Raffaelli, D. G., & Boyle, P. R. (2007). Interactions between shorebirds and benthic invertebrates at Culbin Sands lagoon, NE Scotland: Effects of avian predation on their prey community density and structure. Scientia Marina, 71(3), 579–591. https://doi.org/10.3989/scimar.2007.71n3579

Meredith, T. L., Kajiura, S. M., Newton, K. C., Tricas, T. C., & Bedore, C. N. (2022). Advances in the sensory biology of elasmobranchs. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), Biology of sharks and their relatives (third (pp. 143–168). CRC Press.

Merem, E. C., Twumasi, Y., Wesley, J., Alsarari, M., Fageir, S., & Crisler, M. (2019). Analyzing the tragedy of illegal fishing on the west african coastal region. Food Public Heal, 9, 1–15. https://doi.org/10.5923/j.food.20190901.01.

Merten, V., Christiansen, B., Javidpour, J., Piatkowski, U., Puebla, O., Gasca, R., & Hoving, H. J. T. (2017). Diet and stable isotope analyses reveal the feeding ecology of the orangeback squid Sthenoteuthis pteropus (Steenstrup 1855). In the Eastern Tropical Atlantic. PLoS ONE, 12(12). https://doi.org/10.1371/journal.pone.0189691

Methot, R. D., & Wetzel, C. R. (2013). Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fisheries Research, 142, 86–99. https://doi.org/10.1016/j.fishres.2012.10.012

Meyer, W., & Seegers, U. (2012). Basics of skin structure and function in elasmobranchs: A review. Journal of Fish Biology, 80(5), 1940–1967. https://doi.org/10.1111/j.1095-8649.2011.03207.x

Meysman, F. J. R., Middelburg, J. J., & Heip, C. H. R. (2006). Bioturbation: A fresh look at Darwin's last idea. Trends in Ecology and Evolution, 21(12), 688–695. https://doi.org/10.1016/j.tree.2006.08.002

Mills, L. S., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. BioScience, 43(4), 219–224. https://doi.org/10.2307/1312122

Minamoto, T., Naka, T., Moji, K., & Maruyama, A. (2016). Techniques for the practical collection of environmental DNA: filter selection, preservation, and extraction. Limnology, 17(1), 23–32. https://doi.org/10.1007/s10201-015-0457-4

Mitra, A., & Zaman, S. (2016). Threats to Marine and Estuarine Ecosystems. Basics of Marine and Estuarine Ecology. https://doi.org/10.1007/978-81-322-2707-610

Miya, M. (2022). Environmental DNA metabarcoding: A novel method for biodiversity monitoring of marine fish communities. Annual Review of Marine Science, 14, 161–185. https://doi.org/10.1146/annurev-marine-041421-082251

Mollet, H. F. (2000). Reproductive biology of the female shortfin mako, Isurus oxyrinchus Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fishery Bulletin, 98(2), 299–318.

Momigliano, P., & Harcourt, R. (2014). Sharks: Conservation, governance and management. In Sharks: Conservation, governance and management (pp. 89–106). https://doi.org/10.4324/9780203750292

Moore, A. (2017). Guitarfishes: The next sawfishes? Extincion vulnerabilites and an urgent call for conservation action. Endangered Species Research, 34, 75–88. https://doi.org/10.3354/esr00830

Moore, A. B. M., Séret, B., & Armstrong, R. (2019). Risks to biodiversity and coastal livelihoods from artisanal elasmobranch fisheries in a least developed country: The Gambia (West Africa) biodiversity and conservation. Springer Netherlands. https://doi.org/10.1007/s10531-019-01732-9.

Moradi, S., Sheykhi Ilanloo, S., Kafash, A., & Yousefi, M. (2019). Identifying high-priority conservation areas for avian biodiversity using species distribution modeling. Ecological Indicators, 97(October 2018), 159–164. https://doi.org/10.1016/j.ecolind.2018.10.003

Morrissey, J. F., & Gruber, S. H. (1993). Habitat selection by juvenile lemon sharks, Negaprion brevirostris. Environmental Biology of Fishes, 38(4), 311–319. https://doi.org/10.1007/BF00007524

Moss, B. (2017). Marine reptiles, birds and mammals and nutrient transfers among the seas and the land: An appraisal of current knowledge. Journal of Experimental Marine Biology and Ecology, 492, 63–80. https://doi.org/10.1016/j.jembe.2017.01.018

Moura, T., Figueiredo, I., Farias, I., Serra-Pereira, B., Neves, A., Borges, M. D. F., & Serrano Gordo, L. (2008). Ontogenetic dietary shift and feeding strategy of Raja undulata Lacepède, 1802 (Chondrichthyes: Rajidae) on the Portuguese continental shelf. Scientia Marina, 72(2), 311–318. https://doi.org/10.3989/scimar.2008.72n2311

Mourier, J., & Planes, S. (2013). Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (Carcharhinus melanopterus) in French Polynesia. Molecular Ecology, 22(1), 201–214. https://doi.org/10.1111/mec.12103

Mull, C. G., Andrzejaczek, S., Udyawer, V., & Dwyer, R. G. (2022). Advances in methods, understanding, and applications of elasmobranch movement ecology. In Biology of sharks and their relatives (pp. 357–399). CRC Press.

Munroe, S. E. M., Simpfendorfer, C. A., & Heupel, M. R. (2014). Habitat and space use of an abundant nearshore shark, Rhizoprionodon taylori. Marine and Freshwater Research, 65(11), 959–968. https://doi.org/10.1071/MF13272

Murray, N. J., Phinn, S. R., DeWitt, M., Ferrari, R., Johnston, R., Lyons, M. B., & Fuller, R. A. (2019). The global distribution and trajectory of tidal flats. Nature, 565(7738), 222–225. https://doi.org/10.1038/s41586-018-0805-8

Murray, N. J., Worthington, T. A., Bunting, P., Duce, S., Hagger, V., Lovelock, C. E., & Lyons, M. B. (2022). High-resolution mapping of losses and gains of Earth's tidal wetlands. Science, 376(6594), 744–749. https://doi.org/10.1126/science.abm9583

Musa, S. M., Ripley, D. M., Moritz, T., & Shiels, H. A. (2020). Ocean warming and hypoxia affect embryonic growth, fitness and survival of small-spotted catsharks, Scyliorhinus canicula. Journal of Fish Biology, 97(1), 257–264. https://doi.org/10.1111/jfb.14370

Muttaqin, E., Abdullah, A., Nurilmala, M., Ichsan, M., Simeone, B. M., Yulianto, I., & Booth, H. (2019). DNA-barcoding as molecular marker for seafood forensics: Species identification of locally consumed shark fish products in the world's largest shark fishery. IOP Conference Series: Earth and Environmental Science, 278(1). https://doi.org/10.1088/1755-1315/278/1/012049

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science (New York, N.Y.), 315(5820), 1846–1850. https://doi.org/10.1126/science.1138657

N

Nagelkerken, I., Blaber, S. J. M., Bouillon, S., Green, P., Haywood, M., Kirton, L. G., & Somerfield, P. J. (2008). The habitat function of mangroves for terrestrial and marine fauna: A review. Aquatic Botany, 89(2), 155–185. https://doi.org/10.1016/j.aquabot.2007.12.007

Nagelkerken, I., Velde, G., Gorissen, M. W., Meijer, G. J., Van't Hof, T., & Hartog, C. (2000). Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science, 51(1), 31–44. https://doi.org/10.1006/ecss.2000.0617

Navia, A. F., Cortés, E., & Mejía-Falla, P. A. (2010). Topological analysis of the ecological importance of elasmobranch fishes: A food web study on the Gulf of Tortugas, Colombia. Ecological Modelling, 221(24), 2918–2926. https://doi.org/10.1016/j.ecolmodel.2010.09.006

Navia, A. F., Mejía-Falla, P. A., & Giraldo, A. (2007). Feeding ecology of elasmobranch fishes in coastal waters of the Colombian Eastern Tropical Pacific. BMC Ecology, 7, 2–11. https://doi.org/10.1186/1472-6785-7-8.

Navia, A. F., Mejía-Falla, P. A., López-García, J., Giraldo, A., & Cruz-Escalona, V. H. (2016). How many trophic roles can elasmobranchs play in a marine tropical network? Marine and Freshwater Research, 68(7), 1342–1353. https://doi.org/10.1071/MF16161

Naylor, G. J. P. (2012). A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology'. Bulletin of the American Museum of Natural History, 367. https://doi.org/10.1206/754.1.

Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., Straube, N., & Lakner, C. (2012). Elasmobranch phylogeny: A mitochondrial estimate based on 595 species. Biology of Sharks and Their Relatives, 47–72. https://doi.org/10.1201/b11867-9

Naylor, G. J. P., Ryburn, J. A., Fedrigo, O., & Lopez, A. (2005). Phylogenetic relationships among the major lineages of modern elasmobranchs. In W. C. Hamlett (Ed.), Reproductive biology and phylogeny of chondrichthyes (pp. 1–26). CRC Press.

Needham, H. R., Pilditch, C. A., Lohrer, A. M., & Thrush, S. F. (2011). Context-specific bioturbation mediates changes to ecosystem functioning. Ecosystems (New York, N.Y.), 14, 1096–1109.

Neis, B., Schneider, D. C., Felt, L., Haedrich, R. L., Fischer, J., & Hutchings, J. A. (1999). Fisheries assessment: What can be learned from interviewing resource users? Canadian Journal of Fisheries and Aquatic Sciences, 56(10), 1949–1963. https://doi.org/10.1139/f99-115

Neuert, C., Meitinger, K., Behr, D., & Schonlau, M. (2021). The use of open-ended questions in surveys. A Journal for Quantitative Methods and Survey Methodology, 15(1), 3–6.

Newman, S. P., Handy, R. D., & Gruber, S. H. (2010). Diet and prey preference of juvenile lemon sharks Negaprion brevirostris. Marine Ecology Progress Series, 398, 221–234. https://doi.org/10.3354/meps08334

Newsome, S. D., Rio, C., Bearhop, S., & Philips, D. L. (2007). A niche for isotopic ecology. Frontiers in Ecology and the Environment, 5(8), 429–436. https://doi.org/10.1890/060150.01

Ngwenya, B. N., Mosepele, K. K., & Magole, L. (2012). A case for gender equity in governance of the Okavango Delta fisheries in Botswana. Natural Resources Forum, 36(2), 109–122. https://doi.org/10.1111/j.1477-8947.2012.001450.x

Niedemüller, S., Ainsworth, G., Juan, S., Garcia, R., Ospina-Alvarez, A., Pita, P., & Villasante, S. (2021). The shark and ray meat network. WWF. https://sharks.panda.org/images/downloads/392/WWFMMIGlobalsharkraymeattradereport2021lowres.pdf

Niella, Y., Raoult, V., Gaston, T., Goodman, K., Harcourt, R., Peddemors, V., & Smoothey, A. F. (2022). Reliance of young sharks on threatened estuarine habitats for nutrition implies susceptibility to climate change. Estuarine, Coastal and Shelf Science, 268(February), 107790. https://doi.org/10.1016/j.ecss.2022.107790

Nielsen, J., Hedeholm, R. B., Heinemeier, J., Bushnell, P. G., Christiansen, J. S., Olsen, J., & Stuiver, M. (2016). Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (Somniosus microcephalus). Science, 353(6300), 702–704. https://doi.org/10.1126/science.aaf1703

Nifong, J. C., & Lowers, R. H. (2017). Reciprocal intraguild predation between Alligator mississippiensis (american alligator) and elasmobranchii in the southeastern United States. Southeastern Naturalist, 16(3), 383–397. https://doi.org/10.1656/058.016.0306

Nilsson, G. E., & Östlund-Nilsson, S. (2006). Hypoxia tolerance in coral reef fishes. In A. L. Val, V. M. F. Almeida-Val, & D. J. Randall (Eds.), The physiology of tropical fishes (pp. 583–596). Academic Press.

Nordell, S. E. (1994). Observations of the mating behavior and dentition of the round stingray, Urolophus halleri. Environmental Biology of Fishes, 39(3), 219–229. https://doi.org/10.1007/BF00005124.

Nosal, A. P., Cartamil, D. P., Ammann, A. J., Bellquist, L. F., Ben-Aderet, N. J., Blincow, K. M., & Hastings, P. A. (2021). Triennial migration and philopatry in the critically endangered soupfin shark Galeorhinus galeus. Journal of Applied Ecology, 58(8), 1570–1582. https://doi.org/10.1111/1365-2664.13848

Nowicki, R., Heithaus, M., Thomson, J., Burkholder, D., Gastrich, K., & Wirsing, A. (2019). Indirect legacy effects of an extreme climatic event on a marine megafaunal community. Ecological Monographs, 89(3), 1–20. https://doi.org/10.1002/ecm.1365

O

OBIS. (2023). Ocean Biodiversity Information System. Intergovernmental Oceanographic Commission of UNESCO. OBIS. www.obis.org.

Ogburn, M. B., Bangley, C. W., Aguilar, R., Fisher, R. A., Curran, M. C., Webb, S. F., & Hines, A. H. (2018). Migratory connectivity and philopatry of cownose rays Rhinoptera bonasus along the Atlantic coast, USA. Marine Ecology Progress Series, 602(Mayr 1963), 197–211. https://doi.org/10.3354/meps12686

Oksanen, J. (2020). VEGAN: Community ecology package. https://cran.r-project.org/package=vegan.

Oliver, S., Braccini, M., Newman, S. J., & Harvey, E. S. (2015). Global patterns in the bycatch of sharks and rays. Marine Policy, 54, 86–97. https://doi.org/10.1016/j.marpol.2014.12.017

Ortega-ortiz, C. D., Lazcano-pacheco, C., Llamas-, M., Meza-yáñez, R., Ruano-cobian, S., & López-luna, D. G. (2023). Expanding information on the prey items and hunting tactics of the eastern tropical Pacific killer whale (Orcinus orca) ecotype. Examines Mar Biol Oceanogr., 6(2), 1–8. https://doi.org/10.31031/EIMBO.2023.06.000635

Osaer, F. (2015). Sexual development and maturity scale for the angel shark Squatina squatina (Elasmobranchii: Squatinidae), with comments on the adequacy of general maturity scales. Sexuality and Early Development in Aquatic Organisms, 1(2), 117–132. https://doi.org/10.3354/sedao00012.

O'Shea, O. R. (2012). The Ecology and Biology of Stingrays (Dasyatidae) at Ningaloo Reef [Murdoch University]. https://researchportal.murdoch.edu.au/esploro/outputs/doctoral/The-ecology-and-biology-of-stingays/991005543838807891#file-1

O'Shea, O. R. (2013). Growth of tropical dasyatid rays estimated using a multi-analytical approach. PLoS ONE, 8(10), 1–8. https://doi.org/10.1371/journal.pone.0077194.

O’Shea, O. R., Thums, M., Keulen, M., Kempster, R. M., & Meekan, M. G. (2013). Dietary partitioning by five sympatric species of stingray (Dasyatidae) on coral reefs. Journal of Fish Biology, 82, 1805–1820.

O’Shea, O. R., Thums, M., Keulen, M., & Meekan, M. (2012). Bioturbation by stingrays at Ningaloo Reef, Western Australia. Marine and Freshwater Research, 63(3), 189–197. https://doi.org/10.1071/MF11180

Oudman, T., Onrust, J., Fouw, J., Spaans, B., Piersma, T., & Gils, J. A. (2014). Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate. American Naturalist, 183(5), 650–659. https://doi.org/10.1086/675759

Oudman, T., Schekkerman, H., Kidee, A., Roomen, M., Camara, M., Smit, C., & El-Hacen, E. H. M. (2020). Changes in the waterbird community of the Parc National du Banc d’Arguin. Bird Conservation International, 30(4), 618–633. https://doi.org/10.1017/S0959270919000431

P

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., T., S., H., K., A., V. R., M., C., M., S., C., E.-H., & M, E. H. (2021). Half a century of global decline in oceanic sharks and rays. Nature, 589(4), 567–571. https://doi.org/10.1038/s41586-020-03173-9.Oudman

Page, G., & Whitacre, D. F. (1975). Raptor predation on wintering shorebirds. The Condor, 77, 73–83.

Paine, R. T. (1974). Intertidal community structure—Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia, 15(2), 93–120. https://doi.org/10.1007/BF00345739

Palomares, M. L. D., & Pauly, D. (2019). Coastal fisheries: The past, present, and possible futures. Coasts and estuaries: The future. Elsevier Inc. https://doi.org/10.1016/B978-0-12-814003-1.00032-0

Palumbi, S. R., Sandifer, P. A., Allan, J. D., Beck, M. W., Fautin, D. G., Fogarty, M. J., & Wall, D. H. (2009). Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and the Environment, 7(4), 204–211. https://doi.org/10.1890/070135

Papastamatiou, Y. P., Watanabe, Y. Y., Bradley, D., Dee, L. E., Weng, K., Lowe, C. G., & Caselle, J. E. (2015). Drivers of daily routines in an ectothermic marine predator: Hunt warm, rest warmer? PLoS ONE, 10(6), 1–16. https://doi.org/10.1371/journal.pone.0127807

Parker, C., Cranford, M., Oakes, N., & Leggett, M. (2012). The little biodiversity finance book: A guide to proactive investment in natural capital. CBD. https://www.cbd.int/financial/hlp/doc/literature/LittleBiodiversityFinanceBook_3rd%20edition.pdf

Parton, K. J., Galloway, T. S., & Godley, B. J. (2019). Global review of shark and ray entanglement in anthropogenic marine debris. Endanger. Species Res, 39, 173–190. https://doi.org/10.3354/esr00964.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology & Evolution, 10(10), 430. https://doi.org/10.1016/S0169-5347(00)89171-5

Pauly, D., & Christensen, V. (1995). Primary production required to sustain global fisheries. Nature, 374.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Pauly, D., Christensen, V., Jr, & T, F. (1998). Fishing Down Marine Food Webs. Science (New York, N.Y.), 279(5352), 860–863.

Peacor, S. D., Barton, B. T., Kimbro, D. L., Sih, A., & Sheriff, M. J. (2020). A framework and standardized terminology to facilitate the study of predation-risk effects. Ecology, 101(12), 1–10. https://doi.org/10.1002/ecy.3152

Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marbà, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., & Baldera, A. (2012). Estimating Global "Blue Carbon" Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. PLoS ONE, 7(9), e43542. https://doi.org/10.1371/journal.pone.0043542

Penning, E., Verkuil, Y. I., Klunder, L., & Reneerkens, J. (2022). Sanderlings feed on a diverse spectrum of prey worldwide but primarily rely on brown shrimp in the Wadden Sea. Ardea, 110(2), 187–199. https://doi.org/10.5253/arde.2022.a11

Peterson, C. H. (1991). Intertidal zonation of marine invertebrates in sand and mud. American Scientist, 79(3), 236–249.

Peterson, C. H., Fodrie, J. F., Summerson, H. C., & Powers, S. P. (2001). Site-specific and density-dependent extinction of prey by schooling rays: Generation of a population sink in top-quality habitat for bay scallops. Oecologia, 129(3), 349–356. https://doi.org/10.1007/s004420100742

Philippe, A. S., Pinaud, D., Cayatte, M. L., Goulevant, C., Lachaussée, N., Pineau, P., & Bocher, P. (2016). Influence of environmental gradients on the distribution of benthic resources available for shorebirds on intertidal mudflats of Yves Bay, France. Estuarine, Coastal and Shelf Science, 174, 71–81. https://doi.org/10.1016/j.ecss.2016.03.013

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology, 92(10), 823–835. https://doi.org/10.1139/cjz-2014-0127

Pierce, S. J., & Bennett, M. B. (2010). Destined to decline? Intrinsic susceptibility of the threatened estuary stingray to anthropogenic impacts. Marine and Freshwater Research, 61(12), 1468–1481. https://doi.org/10.1071/MF10073.

Pierce, S. J., Scott-Holland, T. B., & Bennett, M. B. (2011). Community composition of elasmobranch fishes utilizing intertidal sand flats in Moreton Bay, Queensland, Australia. Pacific Science, 65(2), 235–247. https://doi.org/10.2984/65.2.235

Piersma, T. (1987). Production by intertidal benthic animals and limits to their predation by shorebirds: A heuristic model. Marine Ecology Progress Series, 38(Smit 1981), 187–196. https://doi.org/10.3354/meps038187

Piersma, T. (2012). What is habitat quality? Dissecting a research portfolio on shorebirds. In Birds and habitat (pp. 383–407). https://doi.org/10.1017/cbo9781139021654.019

Piersma, T., Goeij, P., & Tulp, I. (1993). An evaluation of intertidal feeding habitats from a shorebird perspective: Towards relevant comparisons between temperate and tropical mudflats. Netherlands Journal of Sea Research, 31(4), 503–512. https://doi.org/10.1016/0077-7579(93)90062-W

Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J. S., Albouy, C., Rasher, D. B., & Griffin, J. N. (2020). Functional diversity of marine megafauna in the Anthropocene. Science Advances, 6(16). https://doi.org/10.1126/sciadv.aay7650

Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.-L., Hereu, B., Milazzo, M., Zabala, M., D'anna, G., & Pipitone, C. (2000). Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. Environmental Conservation, 27, 179–200.

Platell, M. E., Potter, I. C., & Clarke, K. R. (1998). Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. Marine Biology, 131(4), 719–734. https://doi.org/10.1007/s002270050363

Polanco Fernández, A., Marques, V., Fopp, F., Juhel, J. B., Borrero-Pérez, G. H., Cheutin, M. C., & Pellissier, L. (2021). Comparing environmental DNA metabarcoding and underwater visual census to monitor tropical reef fishes. Environmental DNA, 3(1), 142–156. https://doi.org/10.1002/edn3.140

Polunin, N. V. C., & Roberts, C. M. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series, 100(1–2), 167–176. https://doi.org/10.3354/meps100167

Pomeroy, R. S. (2012). Managing overcapacity in small-scale fisheries in Southeast Asia. Marine Policy, 36(2), 520–527. https://doi.org/10.1016/j.marpol.2011.10.002

Ponte, S., Raakjær, J., & Campling, L. (2007). Swimming upstream: Market access for African fish exports in the context of WTO and EU negotiations and regulation. Development Policy Review, 25(1), 113–138. https://doi.org/10.1111/j.1467-7679.2007.00362.x

Poos, M. S., & Jackson, D. A. (2011). Addressing the removal of rare species in multivariate bioassessments: The impact of methodological choices. Ecological Indicators, 18, 82–90.

Postaire, B. D., Bakker, J., Gardiner, J., Wiley, T. R., & Chapman, D. D. (2020). Environmental DNA detection tracks established seasonal occurrence of blacktip sharks (Carcharhinus limbatus) in a semi-enclosed subtropical bay. Scientific Reports, 10(1), 1–8. https://doi.org/10.1038/s41598-020-68843-0

Poulakis, G. R., Urakawa, H., Stevens, P. W., DeAngelo, J. A., Timmers, A. A., Grubbs, R. D., & Olin, J. A. (2017). Sympatric elasmobranchs and fecal samples provide insight into the trophic ecology of the smalltooth sawfish. Endangered Species Research, 32, 491–506. https://doi.org/10.3354/ESR00824

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., & Paine, R. T. (1996). Challenges in the quest for keystones defining keystones. BioScience, 46(8), 609–620.

Pradhan, S. K., Nayak, P. K., & Armitage, D. (2022). A social-ecological systems perspective on dried fish value chains. Current Research in Environmental Sustainability, 4(September 2021), 100128. https://doi.org/10.1016/j.crsust.2022.100128

Prasetyo, A. P., McDevitt, A. D., Murray, J. M., Barry, J., Agung, F., Muttaqin, E., & Mariani, S. (2021). Shark and ray trade in and out of Indonesia: Addressing knowledge gaps on the path to sustainability. Marine Policy, 133(July), 104714. https://doi.org/10.1016/j.marpol.2021.104714

Pridmore, R. D., Thrush, S. F., Hewitt, J. E., & Roper, D. S. (1990). Macrobenthic community composition of six intertidal sandflats in Manukau Harbour, New Zealand. New Zealand Journal of Marine and Freshwater Research, 24(1), 81–96. https://doi.org/10.1080/00288330.1990.9516404

Prieto, G. (2023). Shark fisheries during the second millennium BC in Gramalote, north coast of Peru. Journal of Island and Coastal Archaeology, 18(2), 165–195. https://doi.org/10.1080/15564894.2021.1910386

Puniwai, N. (2020). Pua ka wiliwili, nanahu ka manō: Understanding sharks in Hawaiian culture. Human Biology, 92(1), 11–17. https://doi.org/10.13110/humanbiology.92.1.03

Punt, A. E., Pribac, F., Walker, T. I., Taylor, B. L., & Prince, J. D. (2000). Stock assessment of school shark, Galeorhinus galeus, based on a spatially explicit population dynamics model. Marine and Freshwater Research, 51(3), 205–220. https://doi.org/10.1071/MF99124

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. Proceedings of the Royal Society B: Biological Sciences, 267(1456), 1947–1952. https://doi.org/10.1098/rspb.2000.1234

Pytka, J. M., Kyne, P. M., Carlson, J. K., Wosnick, N., & Jabado, R. W. (2023). A tangled web: Global review of fishing interactions with rhino rays. Reviews in Fish Biology and Fisheries, 0123456789. https://doi.org/10.1007/s11160-023-09821-3

Q

QGIS Development Team & Others. (2018). QGIS. Open Source Geospatial Foundation Project.

Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., Costa, I., Sequeira, A. M. M., & Sims, D. W. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. Nature, 572(7770), 461–466. https://doi.org/10.1038/s41586-019-1444-4

Quezada-Romegialli, C., Jackson, A. L., Hayden, B., Kahilainen, K. K., Lopes, C., & Harrod, C. (2018). tRophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. Methods in Ecology and Evolution, 9(6), 1592–1599. https://doi.org/10.1111/2041-210X.13009

R

R Core Team. (2017). R: A language and environment for statistical computing. https://www.R-project.org/

Rafaelli, D., & Hawkins, S. J. (1999). Intertidal Ecology (1st ed.). Kluwer Academic Publishers. https://doi.org/10.2307/1352485

RAMSAR. (2014). Archipel Bolama-Bijagós. RAMSAR. https://rsis.ramsar.org/ris/2198

Ramsar Convention Secretariat. (2014). Ramsar Sites Information Service. RAMSAR. https://rsis.ramsar.org/ris/2198.

Rangeley, R. W., & Kramer, D. L. (1995). Use of rocky intertidal habitats by juvenile pollock Pollachius virens. Marine Ecology Progress Series, 126(1–3), 9–17. https://doi.org/10.3354/meps126009

Raoult, V., Broadhurst, M. K., Peddemors, V. M., Williamson, J. E., & Gaston, T. F. (2019). Resource use of great hammerhead sharks (Sphyrna mokarran) off eastern Australia. Journal of Fish Biology. https://doi.org/10.1111/jfb.14160

Rasher, D. B., Hoey, A. S., & Hay, M. E. (2017). Cascading predator effects in a Fijian coral reef ecosystem. Scientific Reports, 7(1), 1–10. https://doi.org/10.1038/s41598-017-15679-w

Raymond, W. W., Barber, J. S., Dethier, M. N., Hayford, H. A., Harley, C. D. G., King, T. L., & McDonald, P. S. (2022). Assessment of the impacts of an unprecedented heatwave on intertidal shellfish of the Salish Sea. Ecology, 1–7. https://doi.org/10.1002/ecy.3798

Reid, W. D. K., Sweeting, C. J., Wigham, B. D., McGill, R. A. R., & Polunin, N. V. C. (2016). Isotopic niche variability in macroconsumers of the East Scotia Ridge (Southern Ocean) hydrothermal vents: What more can we learn from an ellipse? Marine Ecology Progress Series, 542, 13–24. https://doi.org/10.3354/meps11571

Reidenauer, J. A., & Thistle, D. (1981). Response of a soft-bottom harpacticoid community to stingray (Dasyatis sabina) disturbance. Marine Biology, 65(3), 261–267. https://doi.org/10.1007/BF00397120

Renz, J. R., Powilleit, M., Gogina, M., Zettler, M. L., Morys, C., & Forster, S. (2018). Community bioirrigation potential (BIPc), an index to quantify the potential for solute exchange at the sediment-water interface. Marine Environmental Research, 141(September), 214–224. https://doi.org/10.1016/j.marenvres.2018.09.013

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, 191, 1–382.

Ries, J. B., Cohen, A. L., & McCorkle, D. C. (2009). Marine calcifiers exhibit mixed responses to CO2-induced ocean acidification. Geology, 37(12), 1131–1134. https://doi.org/10.1130/G30210A.1

Rigby, C. L., Dulvy, N. K., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K., Jabado, R. W., Liu, K. M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R. B., & Winker, H. (2019). Sphyrna lewini. In The IUCN red list of threatened species 2019: E.T39385A2918526.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. Science (New York, N.Y.), 343(6167). https://doi.org/10.1126/science.1241484

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters, 12(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Robillard, M., & Seret, B. (2006). Cultural importance and decline of sawfish (Pristidae) populations in West Africa. Cybium, 30(4), 23–30.

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y. M., Krueck, N. C., Aurellado, E., & Mumby, P. J. (2016). The ecological role of sharks on coral reefs. Trends in Ecology and Evolution, 31(5), 395–407. https://doi.org/10.1016/j.tree.2016.02.014

Rose, M. D., Polis, G. A., Rose, M. D., & A, G. (2018). The distribution and abundance of coyotes: The effects of allochthonous food subsidies from the sea author. Wiley on Behalf of the Ecological Society of America Stable URL, 79(3), 998–1007.

Rosenblatt, A. E., Heithaus, M. R., Mather, M. E., Matich, P., Nifong, J. C., Ripple, W. J., & Silliman, B. R. (2013). The roles of large top predators in coastal ecosystems new insights from long term ecological research. Oceanography, 26(3), 157–167. https://doi.org/10.5670/oceanog.2013.59

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. Oikos (Copenhagen, Denmark), 98(1), 156–162.

Routley, M. H., Nilsson, G. E., & Renshaw, G. M. C. (2002). Exposure to hypoxia primes the respiratory and metabolic responses of the epaulette shark to progressive hypoxia. Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology, 131(2), 313–321. https://doi.org/10.1016/S1095-6433(01)00484-6

Ruiz, D. J., & Wolff, M. (2011). The Bolivar Channel Ecosystem of the Galapagos Marine Reserve: Energy flow structure and role of keystone groups. Journal of Sea Research, 66(2), 123–134. https://doi.org/10.1016/j.seares.2011.05.006

Ruppert, J. L. W., Travers, M. J., Smith, L. L., Fortin, M.-J., & Meekan, M. G. (2013). Caught in the Middle: Combined Impacts of Shark Removal and Coral Loss on the Fish Communities of Coral Reefs. PloS One, 8(9), 74648. https://doi.org/10.1371/journal.pone.0074648

Russo, R. A. (2015). Observations of predation and loss among leopard sharks and brown smoothhounds in San Fransisco Bay, California. California Fish and Game, 101(2), 149–157.

S

Sáenz-Arroyo, A., Roberts, C. M., Torre, J., Cariño-Olvera, M., & Enríquez-Andrade, R. R. (2005). Rapidly shifting of among. Proceedings: Biological Sciences, 272(1575), 1957–1962.

Salas, S., Chuenpagdee, R., Seijo, J. C., & Charles, A. (2007). Challenges in the assessment and management of small-scale fisheries in Latin America and the Caribbean. Fisheries Research, 87(1), 5–16. https://doi.org/10.1016/j.fishres.2007.06.015

Salvig, J. C., Asbirk, S., Kjeldsen, J. P., & Rasmussen, P. A. F. (1994). Wintering waders in the Bijagós Archipelago, Guinea-Bissau 1992-1993. Ardea, 82(1), 137–142.

Santo, V., & Bennett, W. A. (2011). Is post-feeding thermotaxis advantageous in elasmobranch fishes? Journal of Fish Biology, 78(1), 195–207. https://doi.org/10.1111/j.1095-8649.2010.02853.x

Saucedo Barrón, C. J., Colado Uribe, G., Martínez Adrián, J. G., Burgos Zazueta, S., Chacón Cortez, J. G., & Espinoza Fierro, J. (1982). Contribució n al estudio de la pesquerí a del tiburó n en la zona sur de Sinaloa. Memoria de Servicio Social Universitario, Escuela de Ciencias del Mar, thesis Universidad Autó noma de Sinaloa.

Schaffmeister, B. E., Hiddink, J. G., & Wolff, W. J. (2006). Habitat use of shrimps in the intertidal and shallow subtidal seagrass beds of the tropical Banc d'Arguin. Mauritania. Journal of Sea Research, 55(3), 230–243. https://doi.org/10.1016/j.seares.2005.10.003

Scheiffarth, G., & Nehls, G. (1997). Consumption of benthic fauna by carnivorous birds in the Wadden Sea. Helgolander Meeresuntersuchungen, 51(3), 373–387. https://doi.org/10.1007/BF02908721

Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: A review. Reviews in Fish Biology and Fisheries, 24(4), 1089–1103. https://doi.org/10.1007/s11160-014-9364-8

Schmitz, O. J., Hawlena, D., & Trussell, G. C. (2010). Predator control of ecosystem nutrient dynamics. Ecology Letters, 13(10), 1199–1209. https://doi.org/10.1111/j.1461-0248.2010.01511.x

Schweiss, K. E., Lehman, R. N., Drymon, J. M., & Phillips, N. M. (2020). Development of highly sensitive environmental DNA methods for the detection of Bull Sharks, Carcharhinus leucas (Müller and Henle, 1839). using Droplet DigitalTM PCR. Environmental DNA, 2(1), 3–12. https://doi.org/10.1002/edn3.39

Sciara, G. M. B., N., S., F., & Mancusi, C. M. (2015). Dasyatis marmorata, marbled stingray. In The IUCN red list of threatened species 2009 (p. 161748 5494614, 8235).

Seguel, M. E., Sebastián Ramírez-Rivera, S., Concha, F., Espinoza, M., & Hernández, S. (2022). Predation and epibiosis on egg capsules of the Shorttail fanskate, Sympterygia brevicaudata. Revista de Biología Marina y Oceanografía, 57(Especial). https://doi.org/10.22370/rbmo.2022.57.especial.3314

Seidu, I., Brobbey, L. K., Danquah, E., Oppong, S. K., Seidu, M., & Dulvy, N. K. (2021). Fishing for survival: Importance of shark fisheries for the livelihoods of coastal communities in Western Ghana. Fisheries Research, 246(October 2021), 1–42. https://doi.org/10.1016/j.fishres.2021.106157

Séret, B., & Naylor, G. J. P. (2016). Rhynchorhina mauritaniensis, a new genus and species of wedgefish from the eastern central Atlantic (Elasmobranchii: Batoidea: Rhinidae. Zootaxa, 4138(2), 291–308. https://doi.org/10.11646/zootaxa.4138.2.4

Sergio, F., Newton, I., Marchesi, L., & Pedrini, P. (2006). Ecologically justified charisma: Preservation of top predators delivers biodiversity conservation. Journal of Applied Ecology, 43(6), 1049–1055. https://doi.org/10.1111/j.1365-2664.2006.01218.x

Sherman, C. S., Heupel, M. R., Moore, S. K., Chin, A., & Simpfendorfer, C. A. (2020). When sharks are away, rays will play: Effects of top predator removal in coral reef ecosystems. Marine Ecology Progress Series, 641, 145–157.

Sherman, C. S., Simpfendorfer, C. A., Pacoureau, N., Matsushiba, J. H., Yan, H. F., Walls, R. H. L., Rigby, C. L., VanderWright, W. J., Jabado, R. W., Pollom, R. A., Carlson, J. K., Charvet, P., Bin Ali, A., Fahmi, C., J, D., DH, H., KB, F., B, E., TD, P., … N.K. (2023). Half a century of rising extinction risk of coral reef sharks and rays. Nature Communications, 14(15).

Sherman, K. M., Reidenauer, J. A., Thistle, D., & Meeter, D. (1983). Role of a natural disturbance in an assemblage of marine free-living nematodes. Marine Ecology Progress Series, 11, 23–30.

Shibuya, A., Souza Rosa, R., & Gadig, O. B. F. (2005). Stomach contents of Galeocerdo cuvieri and Carcharhinus plumbeus (Elasmobranchii: Carcharhinidae) caught off Paraíba state, Brazil. Arquivos de Ciências do Mar, 38(1–2), 105–107.

Shiffman, D., Bangley, C., & Macdonald, C. (2023). A prized Pacific shark": The rise and fall (and rise again…?) of the world's first ecolabel certified sustainable shark fishery. Journal of Fish Biology. https://doi.org/10.1111/jfb.15467

Shiffman, D. S., & Hueter, R. E. (2017). A United States shark fin ban would undermine sustainable shark fisheries. Marine Policy, 85(July), 138–140. https://doi.org/10.1016/j.marpol.2017.08.026

Shipley, O. N., Gallagher, A. J., Shiffman, D. S., Kaufman, L., & Hammerschlag, N. (2019). Diverse resource-use strategies in a large-bodied marine predator guild: Evidence from differential use of resource subsidies and intraspecific isotopic variation. Marine Ecology Progress Series, 623, 71–83. https://doi.org/10.3354/meps12982

Sieben, K., Ljunggren, L., Bergström, U., & Eriksson, B. K. (2011). A meso-predator release of stickleback promotes recruitment of macroalgae in the Baltic Sea. Journal of Experimental Marine Biology and Ecology, 397(2), 79–84. https://doi.org/10.1016/j.jembe.2010.11.020

Sievers, M., Brown, C. J., Tulloch, V. J. D., Pearson, R. M., Haig, J. A., Turschwell, M. P., & Connolly, R. M. (2019). The role of vegetated coastal wetlands for marine megafauna conservation. Trends in Ecology and Evolution, 34(9), 807–817. https://doi.org/10.1016/j.tree.2019.04.004

Simpfendorfer, C. A., & Dulvy, N. K. (2017). Bright spots of sustainable shark fishing. Current Biology. https://doi.org/10.1016/j.cub.2016.12.017

Simpfendorfer, C. A., Goodreid, A. B., & Mcauley, R. B. (2001). Size, sex and geographic variation in the diet of the tiger shark, Galeocerdo cuvier, from Western Australian waters. Environmental Biology of Fishes, 61(1), 37–46. https://doi.org/10.1023/A:1011021710183

Simpfendorfer, C. A., & Milward, N. E. (1993). Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environmental Biology of Fishes, 37(4), 337–345. https://doi.org/10.1007/BF00005200

Smale, M. J. (2005). The diet of the ragged-tooth shark Carcharias taurus Rafinesque 1810 in the Eastern Cape, South Africa. African Journal of Marine Science, 27(1), 331–335. https://doi.org/10.2989/18142320509504091

Smart, J. J. (2016). Multimodel approaches in shark and ray growth studies: Strengths, weaknesses and the future. Fish and Fisheries, 17(4), 955–971. https://doi.org/10.1111/faf.12154.

Smith, J. W., & Merriner, J. V. (1985). Food habits and feeding behavior of the cownose ray, Rhinoptera bonasus, in lower Chesapeake Bay. Estuaries, 8(3), 305–310. https://doi.org/10.2307/1351491.

Smith, R. I. (1956). The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of Nereis diversicolor. Journal of the Marine Biological Association of the United Kingdom, 35(1), 81–104. https://doi.org/10.1017/S0025315400008985

Smith, S. E. (2005). Leopard shark mating observed off La Jolla, California. California Fish and Game, 91(2), 128–135.

Smith, W. D., Cailliet, G. M., & Melendez, E. M. (2007). Maturity and growth characteristics of a commercially exploited stingray, Dasyatis dipterura. Marine and Freshwater Research, 58(1), 54–66. https://doi.org/10.1071/MF06083.

Snelson, F. F., Mulligan, T. J., & Williams, S. E. (1984). Food habits, occurrence, and population structure of the bull shark, Carcharhinus leucas, in florida coastal lagoons. Bulletin of Marine Science, 34(1), 71–80.

Snelson, F. F., & Williams, S. E. (1981). Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River lagoon system, Florida. Estuaries, 4(2), 110–120. https://doi.org/10.2307/1351673

Soto, C. G. (2006). Socio-cultural barriers to applying fishers. In Knowledge in fisheries management: An evaluation of literature cases thesis submitted in partial fulfilment of the requirements for the degree of doctor of philosophy in the school of resource and environmental. Simon Fraser University.

Spalding, M. D., Ruffo, S., Lacambra, C., Meliane, I., Hale, L. Z., Shepard, C. C., & Beck, M. W. (2014). The role of ecosystems in coastal protection: Adapting to climate change and coastal hazards. Ocean and Coastal Management, 90, 50–57. https://doi.org/10.1016/j.ocecoaman.2013.09.007

Speed, C. W., Field, I. C., Meekan, M. G., & Bradshaw, C. J. A. (2010). Complexities of coastal shark movements and their implications for management. Marine Ecology Progress Series, 408, 275–293. https://doi.org/10.3354/meps08581

Spiegelberger, T., & Ganslosser, U. (2005). Habitat analysis and exclusive bank feeding of the Antillean manatee (Trichechus manatus manatus) in the coswine swamps of French Guiana, South America. Tropical Zoology, 18(1), 1–12. https://doi.org/10.1080/03946975.2005.10531210

Stål, J., Paulsen, S., Pihl, L., Rönnbäck, P., Söderqvist, T., & Wennhage, H. (2008). Coastal habitat support to fish and fisheries in Sweden: Integrating ecosystem functions into fisheries management. Ocean and Coastal Management, 51(8–9), 594–600. https://doi.org/10.1016/j.ocecoaman.2008.06.006

Staples, D., & Funge-Smith, S. (2009). Ecosystem approach to fisheries and aquaculture: Implementing the FAO Code of Conduct for Responsible Fisheries. FAO Regional Office for Asia and the Pacific.

Starr, R. M., Carr, M., Malone, D., Greenley, A., & McMillan, S. (2010). Complementary sampling methods to inform ecosystem-based management of nearshore fisheries. Marine and Coastal Fisheries, 2(1), 159–179. https://doi.org/10.1577/c08-056.1

Stein, R. W., Mull, C. G., Kuhn, T. S., Aschliman, N. C., Davidson, L. N. K., Joy, J. B., & Mooers, A. O. (2018). Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. Nature Ecology & Evolution, 2(2), 288–298. https://doi.org/10.1038/s41559-017-0448-4

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (Eds.). (2007). Foraging. University of Chicago Press.

Stevens, J. D. (1984). Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. Proceedings of the Royal Society of London B: Biological Sciences, 222(1226), 79–106.

Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57(3), 476–494. https://doi.org/10.1006/jmsc.2000.0724

Stevens, J. D., & Lyle, J. M. (1989). Biology of three hammerhead sharks (Eusphyra blochii, Sphyrna mokarran and S. lewini) from Northern Australia. Marine and Freshwater Research, 40(2), 46–129. https://doi.org/10.1071/MF9890129

Stewart, K. A. (2019). Understanding the effects of biotic and abiotic factors on sources of aquatic environmental DNA. Biodiversity and Conservation, 28(5), 983–1001. https://doi.org/10.1007/s10531-019-01709-8

Stillwell, C. E., & Kohler, N. E. (1982). Food, feeding habits, and estimates of daily ration of the shortfin mako (Isurus oxyrinchus) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 39(3), 407–414. https://doi.org/10.1139/f82-058

Stobart, B., Warwick, R., González, C., Mallol, S., Díaz, D., Reñones, O., & Goñi, R. (2009). Long-term and spillover effects of a marine protected area on an exploited fish community. Marine Ecology Progress Series, 384, 47–60. https://doi.org/10.3354/meps08007

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ, 2018(6), 1–27. https://doi.org/10.7717/peerj.5096

Strickland, T. L. (2009). Critical habitat for the endangered distinct population segment of the smalltooth sawfish. Federal Register, 74(169), 45353–45378.

Strong, W. R., Snelson, F. F., & Gruber, S. H. (1990). Hammerhead shark predation on stingrays: An observation of prey handling by Sphyrna mokarran. Copeia, 1990(3), 836–840.

Stroud, D. A., Baker, A., Blanco, D. E., Davidson, N. C., Delany, S., Ganter, B., & Zöckler, C. (2006). The conservation and population status of the world's waders at the turn of the millennium. Waterbirds around the World, 643–648.

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., & Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature, 501(7468), 539–542. https://doi.org/10.1038/nature12529

Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., & Fuller, R. A. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. Nature Communications, 8, 1–7. https://doi.org/10.1038/ncomms14895

Suchanek, T. H., & Colin, P. L. (1986). Rates and effects of bioturbation by invertebrates and fishes at Enewetak and Bikini Atolls. Bulletin of Marine Science, 38, 25–34.

Summers, A. P. (2000). Stiffening the stingray skeleton—An investigation of durophagy in myliobatid stingrays (Chondrichthyes, Batoidea, Myliobatidae). Journal of Morphology, 243(2), 113–126. https://doi.org/10.1002/(SICI)1097-4687(200002)243:2

Sutherland, W. J. (1982). Do oystercatchers select the most profitable cockles? Animal Behaviour, 30(3), 857–861. https://doi.org/10.1016/S0003-3472(82)80159-0

Suykerbuyk, W., Bouma, T. J., Govers, L. L., Giesen, K., Jong, D. J., Herman, P., & Katwijk, M. M. (2016). Surviving in changing seascapes: Sediment dynamics as bottleneck for long-term seagrass presence. Ecosystems (New York, N.Y.), 19(2), 296–310. https://doi.org/10.1007/s10021-015-9932-3

Swanson, H. K., Lysy, M., Power, M., Stasko, A. D., Johnson, J. D., & Reist, J. (2015). A new probalistic method for quantifying n-dimensional ecological niches and niche overlap. Ecology, 96(2), 318–324.

Swartz, W., Sala, E., Tracey, S., Watson, R., & Pauly, D. (2010). The spatial expansion and ecological footprint of fisheries (1950 to present). PLoS ONE, 5(12), 3–8. https://doi.org/10.1371/journal.pone.0015143

T

Taberlet, P., Bonin, A., Zinger, L., & Coissac, E. (2018). Environmental DNA: For biodiversity research and monitoring. Oxford University Press. https://doi.org/10.1093/oso/9780198767220.001.0001

Takeuchi, S., Takahara, Y., Agata, Y., Nasuda, J., Yamada, F., & Tamaki, A. (2013). Response of suspension-feeding clams to natural removal of bioturbating shrimp on a large estuarine intertidal sandflat in western Kyushu, Japan. Journal of Experimental Marine Biology and Ecology, 448, 308–320. https://doi.org/10.1016/j.jembe.2013.07.018

Takeuchi, S., & Tamaki, A. (2014). Assessment of benthic disturbance associated with stingray foraging for ghost shrimp by aerial survey over an intertidal sandflat. Continental Shelf Research, 84, 139–157. https://doi.org/10.1016/j.csr.2014.05.007

Talent, L. G. (1982). Food habits of the gray smoothhound, Mustelus californicus, the brown smoothhound, Mustelus henlei, the shovelnose guitarfish, Rhinobatos productus, and the bat ray, Miliobatis californica, in Elkhorn Slough, California. California Fish & Game, 68(4), 224–234.

Talwar, B. S., Bradley, D., Berry, C., Bond, M. E., Bouyoucos, I. A., Brooks, A. M. L., & Brooks, E. J. (2022). Estimated life-history traits and movements of the Caribbean reef shark (Carcharhinus perezi) in The Bahamas based on tag-recapture data. Marine Biology, 169(5), 1–19. https://doi.org/10.1007/s00227-022-04044-9

Techera, E. J., & Klein, N. (2011). Fragmented governance: Reconciling legal strategies for shark conservation. Marine Policy, 35(1), 73–78. https://doi.org/10.1016/j.marpol.2010.08.003

Teh, L. C. L., & Pauly, D. (2018). Who brings in the fish? The relative contribution of small-scale and industrial fisheries to food security in Southeast Asia. Frontiers in Marine Science, 4(FEB), 1–9. https://doi.org/10.3389/fmars.2018.00044

Temmerman, S., Meire, P., Bouma, T. J., Herman, P. M. J., Ysebaert, T., & Vriend, H. J. (2013). Ecosystem-based coastal defence in the face of global change. Nature, 504, 79–83.

Temple, A. J. (2020). Life-history, exploitation and extinction risk of the data-poor Baraka's whipray (Maculabatis ambigua) in small-scale tropical fisheries. Journal of Fish Biology, 97(3), 708–719. https://doi.org/10.1111/jfb.14425.

Temple, A. J., Wambiji, N., Poonian, C. N. S., Jiddawi, N., Stead, S. M., Kiszka, J. J., & Berggren, P. (2019). Marine megafauna catch in southwestern Indian Ocean small-scale fisheries from landings data. Biological Conservation, 230(August 2018), 113–121. https://doi.org/10.1016/j.biocon.2018.12.024

Ten key biological traits of marine benthic invertebrates surveyed in Northwest Europe (Version 2). (2022). [dataset]. Cefas. https://doi.org/10.14466/CEFASDATAHUB.123

Terborgh, J., & Estes, J. A. (Eds.). (2010). Trophic cascades: Predators, prey, and the changing dynamics of nature (Vol. 23). Island Press. https://doi.org/10.1007/s12045-018-0730-z

Tesfamichael, D., Pitcher, T. J., & Pauly, D. (2014). Assessing changes in fisheries using fishers' knowledge to generate long time series of catch rates: A case study from the red sea. Ecology and Society, 19(1). https://doi.org/10.5751/ES-06151-190118

Tessier, A., Descloux, S., Lae, R., Cottet, M., Guedant, P., & Guillard, J. (2016). Fish assemblages in large tropical reservoirs: Overview of fish population monitoring methods. Reviews in Fisheries Science and Aquaculture, 24(2), 160–177. https://doi.org/10.1080/23308249.2015.1112766

Tetley, M. J., Braulik, G. T., Lanfredi, C., Minton, G., Panigada, S., Politi, E., & Hoyt, E. (2022). The important marine mammal area network: A tool for systematic spatial planning in response to the marine mammal habitat conservation crisis. Frontiers in Marine Science, 9(March), 1–13. https://doi.org/10.3389/fmars.2022.841789

Thaman, R. R., Puia, T., Tongabaea, W., Namona, A., & Fong, T. (2010). Marine biodiversity and ethnobiodiversity of Bellona (Mungiki) Island, Solomon Islands. Singapore Journal of Tropical Geography, 31(1), 70–84. https://doi.org/10.1111/j.1467-9493.2010.00391.x

Thiault, L., Collin, A., Chlous, F., Gelcich, S., & Claudet, J. (2017). Combining participatory and socioeconomic approaches to map fishing effort in smallscale fisheries. PLoS ONE, 12(5), 1–18. https://doi.org/10.1371/journal.pone.0176862

Thistle, D. (1981). Natural physical disturbances and communities of marine soft bottoms. Marine Ecology Progress Series, 6, 223–228.

Thomsen, P. F., Kielgast, J., Iversen, L. L., Møller, P. R., Rasmussen, M., & Willerslev, E. (2012). Detection of a diverse marine fish fauna using environmental DNA from seawater samples. PLoS ONE, 7(8), 1–9. https://doi.org/10.1371/journal.pone.0041732

Thorrold, S. R., Afonso, P., Fontes, J., Braun, C. D., Santos, R. S., Skomal, G. B., & Berumen, M. L. (2014). Extreme diving behaviour in devil rays links surface waters and the deep ocean. Nature Communications, 5, 1–7. https://doi.org/10.1038/ncomms5274

Thrush, S. F., Hewitt, J. E., Gibbs, M., Lundquist, C., & Norkko, A. (2006). Functional role of large organisms in intertidal communities: Community effects and ecosystem function. Ecosystems (New York, N.Y.), 9(6), 1029–1040. https://doi.org/10.1007/s10021-005-0068-8

Thrush, S. F., Pridmore, R. D., Hewitt, J. E., & Cummings, V. J. (1994). The importance of predators on a sandflat—Interplay between seasonal changes in prey densities and predator effects. Marine Ecology Progress Series, 107(3), 211–222. https://doi.org/10.3354/meps107211

Tillett, B. J., Meekan, M. G., & Field, I. C. (2014). Dietary overlap and partitioning among three sympatric carcharhinid sharks. Endangered Species Research, 25(3), 283–293. https://doi.org/10.3354/esr00615

TinHan, T. C., & Wells, R. J. D. (2021). Spatial and ontogenetic patterns in the trophic ecology of juvenile bull sharks (Carcharhinus leucas) from the northwest Gulf of Mexico. Frontiers in Marine Science, 8(July), 1–12. https://doi.org/10.3389/fmars.2021.664316

Tinker, M. T., Bentall, G., & Estes, J. A. (2008). Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences of the United States of America, 105(2), 560–565. https://doi.org/10.1073/pnas.0709263105

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. Nature, 466(7310), 1098–1101. https://doi.org/10.1038/nature09329

Tobin, A. J., Mapleston, A., Harry, A. V., & Espinoza, M. (2014). Big fish in shallow water; use of an intertidal surf-zone habitat by large-bodied teleosts and elasmobranchs in tropical northern Australia. Environmental Biology of Fishes, 97(7), 821–838. https://doi.org/10.1007/s10641-013-0182-y

Todd, P. A., Ong, X., & Chou, L. M. (2010). Impacts of pollution on marine life in Southeast Asia. Biodiversity and Conservation, 19(4), 1063–1082. https://doi.org/10.1007/s10531-010-9778-0

Tojo, H. (1996). Habitat selection, foraging behaviour and prey of five heron species in Japan. Japanese Journal of Ornithology, 45(3), 141–158. https://doi.org/10.3838/jjo.45.141

Tréguier, A., Paillisson, J. M., Dejean, T., Valentini, A., Schlaepfer, M. A., & Roussel, J. M. (2014). Environmental DNA surveillance for invertebrate species: Advantages and technical limitations to detect invasive crayfish Procambarus clarkii in freshwater ponds. Journal of Applied Ecology, 51(4), 871–879. https://doi.org/10.1111/1365-2664.12262

Turner, T. F., Collyer, M. L., & Krabbenhoft, T. J. (2010). A general hypothesis-testing framework for stable isotope ratios in ecological studies. Ecology, 91(8), 2227–2233. https://doi.org/10.1890/09-1454.1

U

UNCTAD. (2020). The COVID-19 Pandemic and the Blue Economy: New challenges and prospects for recovery and resilience.

UNEP-WCMC. (2019). Protected planet: Marine protected areas.

UNESCO. (2020). Boloma-Bijagós Biosphere Reserve. UNESCO.

V

Valadou, B., Brethes, J., & Inejih, C. (2006). Observations biologiques sur cinq espéces d'Élasmobranches du Parc National du Banc d'Arguin (Mauritanie). Cybium, 30(4), 313–322.

Van Waerebeek, K., & Read, A. J. (1994). Reproduction of Dusky Dolphins, Lagenorhynchus obscurus, from Coastal Peru. Journal of Mammalogy, 75(4), 1054–1062. https://doi.org/10.2307/1382489

VanBlaricom, G. R. (1982). Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecological Monographs, 52(3), 283–305. https://doi.org/10.2307/2937332

Vandermeer, J., & Pascual, M. (2006). Competitive coexistence through intermediate polyphagy. Ecological Complexity, 3(1), 37–43. https://doi.org/10.1016/j.ecocom.2005.05.005

Vaudo, J. J., & Heithaus, M. R. (2011). Dietary niche overlap in a nearshore elasmobranch mesopredator community. Marine Ecology Progress Series, 425, 247–260. https://doi.org/10.3354/meps08988.

Vaudo, J. J., & Heithaus, M. R. (2012). Diel and seasonal variation in the use of a nearshore sandflat by a ray community in a near pristine system. Marine and Freshwater Research, 63(11), 1077–1084. https://doi.org/10.1071/MF11226

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing, 27(5), 1413–1432. https://doi.org/10.1007/s11222-016-9696-4.

Venter, O., Magrach, A., Outram, N., Klein, C. J., Possingham, H. P., Marco, M., & Watson, J. E. M. (2018). Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. Conservation Biology, 32(1), 127–134. https://doi.org/10.1111/cobi.12970

Veríssimo, A., Sampaio, Í., McDowell, J. R., Alexandrino, P., Mucientes, G., Queiroz, N., & Noble, L. R. (2017). World without borders—Genetic population structure of a highly migratory marine predator, the blue shark (Prionace glauca). Ecology and Evolution, 7(13), 4768–4781. https://doi.org/10.1002/ece3.2987

Vermeulen, E. (2018). Intertidal habitat use of bottlenose dolphins (Tursiops truncatus) in Bahía Aan Antonio, Argentina. Journal of the Marine Biological Association of the United Kingdom, 98(5), 1109–1118. https://doi.org/10.1017/S0025315417000856

Vianna, G. M. S., Hehre, E. J., White, R., Hood, L., Derrick, B., & Zeller, D. (2020). Long-term fishing catch and effort trends in the republic of the marshall islands, with emphasis on the small-scale sectors. Frontiers in Marine Science, 6(January), 1–13. https://doi.org/10.3389/fmars.2019.00828

Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology, 58(6), 1199–1217. https://doi.org/10.2307/1935076

Visser, I. (1999). Benthic foraging on stingrays by killer whales (Orcinus orca) in New Zealand waters. Marine Mammal Science, 15(1), 220–227.

Vlaming, V. L., & Sage, M. (1973). Osmoregulation in the euryhaline elasmobranch, Dasyatis sabina. Comparative Biochemistry and Physiology – Part A: Physiology, 45(1), 31–44. https://doi.org/10.1016/0300-9629(73)90006-6

Volpov, B. L., Hoskins, A. J., Battaile, B. C., Viviant, M., Wheatley, K. E., Marshall, G., & Arnould, J. P. Y. (2015). Identification of prey captures in Australian fur seals (Arctocephalus pusillus doriferus) using head-mounted accelerometers: Field validation with animal-borne video cameras. PLoS ONE, 10(6), 1–19. https://doi.org/10.1371/journal.pone.0128789

W

Walker, P., & Hislop, J. (1998). Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. ICES Journal of Marine Science, 55, 392–402. https://doi.org/10.1006/jmsc.1997.0325

Wambiji, N., Kadagi, N. I., Everett, B. I., Temple, A. J., Kiszka, J. J., Kimani, E., & Berggren, P. (2022). Integrating long-term citizen science data and contemporary artisanal fishery survey data to investigate recreational and small-scale shark fisheries in Kenya. Aquatic Conservation: Marine and Freshwater Ecosystems, 32(8), 1306–1322. https://doi.org/10.1002/aqc.3829

Wang, S., Brose, U., & Gravel, D. (2019). Intraguild predation enhances biodiversity and functioning in complex food webs. Ecology, 100(3), 1–10. https://doi.org/10.1002/ecy.2616

Wang, Y., Wang, Y. P., Yu, Q., Du, Z., Wang, Z. B., & Gao, S. (2019). Sand□mud tidal flat morphodynamics influenced by alongshore tidal currents. Journal of geophysical research. Oceans, 124, 3818–3836.

Wanink, J. H., & Zwarts, L. (1993). Environmental effects of the growth rate of intertidal invertebrates and some implications for foraging waders. Netherlands Journal of Sea Research, 31(4), 407–418. https://doi.org/10.1016/0077-7579(93)90057-Y

Ward, P., & Myers, R. A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology, 86(4), 835–847. https://doi.org/10.1890/03-0746

Watson, G. J., Murray, J. M., Schaefer, M., & Bonner, A. (2017). Bait worms: A valuable and important fishery with implications for fisheries and conservation management. Fish and Fisheries, 18(2), 374–388. https://doi.org/10.1111/faf.12178

Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. Nature, 515(7525), 67–73. https://doi.org/10.1038/nature13947

Weichselbaum, E., Costa, H., & Benelam, B. (2009). Synthesis report No 6: Traditional Foods in Europe. EUROFIR.

Welch, H., Clavelle, T., White, T. D., Cimino, M. A., Osdel, J., Hochberg, T., & Hazen, E. L. (2022). Hot spots of unseen fishing vessels. Science Advances, 8(44), 1–11. https://doi.org/10.1126/sciadv.abq2109

Wheatly, M. G. (1988). Integrated responses to salinity fluctuation. American Zoologist, 28(1), 65–77.

White, A. T., Vogt, H. P., & Arin, T. (2000). Philippine coral reefs under threat: The economic losses caused by reef destruction. Marine Pollution Bulletin, 40(7), 598–605. https://doi.org/10.1016/S0025-326X(00)00022-9

White, J., Heupel, M. R., Simpfendorfer, C. A., & Tobin, A. J. (2013). Shark-like batoids in pacific fisheries: Prevalence and conservation concerns. Endangered Species Research, 19(3), 277–284. https://doi.org/10.3354/esr00473

White, T. D., Carlisle, A. B., Kroodsma, D. A., Block, B. A., Casagrandi, R., Leo, G. A., & McCauley, D. J. (2017). Assessing the effectiveness of a large marine protected area for reef shark conservation. Biological Conservation, 207, 64–71. https://doi.org/10.1016/j.biocon.2017.01.009

White, W. T., O'Neill, H., & Naylor, G. P. (2022). Taxonomy and diversity of extant elasmobranchs. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), Biology of sharks and their relatives (third (pp. 31–58). CRC Press.

White, W. T., & Potter, I. C. (2004). Habitat partitioning among four elasmobranch species in nearshore, shallow waters of a subtropical embayment in Western Australia. Marine Biology, 145(5), 1023–1032. https://doi.org/10.1007/s00227-004-1386-7

Williams, J. J., Papastamatiou, Y. P., Caselle, J. E., Bradley, D., & Jacoby, D. M. P. (2018). Mobile marine predators: An understudied source of nutrients to coral reefs in an unfished atoll. Proceedings of the Royal Society B: Biological Sciences, 285(1875). https://doi.org/10.1098/rspb.2017.2456

Williamson, M. J., Tebbs, E. J., Dawson, T. P., & Jacoby, D. M. P. (2019). Satellite Remote Sensing in Shark and Ray Ecology, Conservation and Management. Frontiers in Marine Science, 6, 135. https://doi.org/10.3389/fmars.2019.00135

Wilson, S. C., & Jones, K. A. (2018). Behaviour of harbour seal (Phoca vitulina vitulina) mother-pup pairs in irish sea intertidal habitats. Biology and Environment, 118B(1, 13–27. https://doi.org/10.3318/BIOE.2018.02

Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: Implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences, 49, 2196–2218.

Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007). Fear factor: Do dugongs (Dugong dugon) trade food for safety from tiger sharks (Galeocerdo cuvier)? Oecologia, 153(4), 1031–1040. https://doi.org/10.1007/s00442-007-0802-3

Wise, G., Mulvey, J. M., & Renshaw, G. M. C. (1998). Hypoxia tolerance in the epaulette shark (Hemiscyllium ocellatum). Journal of Experimental Zoology, 281(1), 1–5. https://doi.org/10.1002/(SICI)1097-010X(19980501)281:13.0.CO;2-S

Wolff, W. J. (2005). The exploitation of living resources in the Dutch Wadden Sea: A historical overview. Helgoland Marine Research, 59(1), 31–38. https://doi.org/10.1007/s10152-004-0204-4

Wood, S. N. (2004). Stable and Efficient Multiple Smoothing Parameter Estimation for Generalized Additive Models. Journal of the American Statistical Association, 99(467), 673–686. https://doi.org/10.1198/016214504000000980

Wood, S. N. (2017). Generalized additive models: An introduction with R (second edition. 2nd Editio. Chapman an). https://reseau-mexico.fr/sites/reseau-mexico.fr/files/igam.pdf

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., & Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. Science (New York, N.Y.), 314(5800), 787–790. https://doi.org/10.1126/science.1132294

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., & Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. Marine Policy, 40(1), 194–204. https://doi.org/10.1016/j.marpol.2012.12.034

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., & Zeller, D. (2009). Rebuilding Global Fisheries. Science (New York, N.Y.), 325(5940), 578–585. https://doi.org/10.1126/science.1173146

Wosnick, N., Leite, R. D., Giareta, E. P., Morick, D., & Musyl, M. (2022). Global assessment of shark strandings. Fish and Fisheries, 23(4), 786–799. https://doi.org/10.1111/faf.12648

Wosnick, N., Rios, R. M., Rincon, G., & Nunes, J. L. S. (2019). Evidence of tide pool use by a viviparous elasmobranch as a parturition site. Acta Ichthyologica et Piscatoria, 49(2), 189–193. https://doi.org/10.3750/AIEP/02546

Y

Yadav, V. K., Jahageerdar, S., & Adinarayana, J. (2020). Use of different modeling approach for sensitivity analysis in predicting the Catch per Unit Effort (CPUE) of fish. Indian J. Geo-Marine Sci, 49, 129–1741.

Yan, H. F., Kyne, P. M., Jabado, R. W., Leeney, R. H., Davidson, L. N. K., Derrick, D. H., & Dulvy, N. K. (2021). Overfishing and habitat loss drives range contraction of iconic marine fishes to near extinction. Science Advances, 7(7), 1–11. https://doi.org/10.1126/sciadv.abb6026

Yao, Y. (2018). Using stacking to average bayesian predictive distributions. Bayesian Analysis, 13(3), 917–1007. https://doi.org/10.1214/17-BA1091.

Yates, P. M., Tobin, A. J., Heupel, M. R., & Simpfendorfer, C. A. (2016). Benefits of marine protected areas for tropical coastal sharks. Aquatic Conservation: Marine and Freshwater Ecosystems, 26(6), 1063–1080. https://doi.org/10.1002/aqc.2616

Yick, J. L., Tracey, S. R., & White, R. W. G. (2011). Niche overlap and trophic resource partitioning of two sympatric batoids co-inhabiting an estuarine system in southeast Australia. Journal of Applied Ichthyology, 27(5), 1272–1277. https://doi.org/10.1111/j.1439-0426.2011.01819.x

Yigin, C. C., & Ismen, A. (2012). Age, growth and reproduction of the common stingray, Dasyatis pastinaca from the North Aegean Sea. Marine Biology Research, 8(7), 644–653. https://doi.org/10.1080/17451000.2012.659667

Z

Zajac, R. N., Lewis, R. S., Poppe, L. J., Twichell, D. C., Vozarik, J., & DiGiacomo-Cohen, M. L. (2003). Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. Limnology and Oceanography, 48(2), 829–842. https://doi.org/10.4319/lo.2003.48.2.0829

Zanella, I., López-Garro, A., & Cure, K. (2019). Golfo Dulce: Critical habitat and nursery area for juvenile scalloped hammerhead sharks Sphyrna lewini in the Eastern Tropical Pacific Seascape. Environmental Biology of Fishes, 102(10), 1291–1300. https://doi.org/10.1007/s10641-019-00907-1

Zaret, T. M., & Rand, A. S. (1971). Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology, 52(2), 336–342. https://doi.org/10.2307/1934593

Zee, M., Angelini C, Govers LL, Christianen MJA, Altieri AH, Reijden KJ, Silliman BR, Koppel J, Geest M, Gils JA, Veer HW, Piersma T, Ruiter PC, Olff H, & Heide T. (2016). How habitat-modifying organisms structure the food web of two coastal ecosystems. Proceedings of the Royal Society B: Biological Sciences 283. https://doi.org/10.1098/rspb.2015.2326

Zeeberg, J. J., Corten, A., & Graaf, E. (2006). Bycatch and release of pelagic megafauna in industrial trawler fisheries off Northwest Africa. Fisheries Research, 78(2–3), 186–195. https://doi.org/10.1016/j.fishres.2006.01.012

Zharikov, Y., & Skilleter, G. A. (2003). Depletion of benthic invertebrates by bar-tailed godwits Limosa lapponica in a subtropical estuary. Marine Ecology Progress Series, 254, 151–162. https://doi.org/10.3354/meps254151

Zwarts, L., & Blomert, A. M. (1992). Why knot Calidris canutus take medium-sized Macoma balthica when six prey species are available. Marine Ecology Progress Series, 83(2–3), 113–128. https://doi.org/10.3354/meps083113

Zwarts, L., & Ens, B. J. (1999). Predation by birds on marine tidal flats. International Ornithological Congress, Durban, South Africa.

Zwarts, L., & Piersma, T. (1990). How important is the Banc d'Arguin, Mauritania, as a temporary staging area for waders in spring? Ardea, 78(1–2), 113–121.

Zwarts, L., & Wanink, J. (1984). How oystercatchers and curlews successively deplete clams. In Coastal waders and wildfowl in winter (pp. 69–83).

Zwarts, L., & Wanink, J. (1989). Siphon size and burying depth in deposit- and suspension-feeding benthic bivalves. Marine Biology, 100(2), 227–240. https://doi.org/10.1007/BF00391963

Zwarts, L., & Wanink, J. H. (1993). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Netherlands Journal of Sea Research, 31(4), 441–476. https://doi.org/10.1016/0077-7579(93)90059-2

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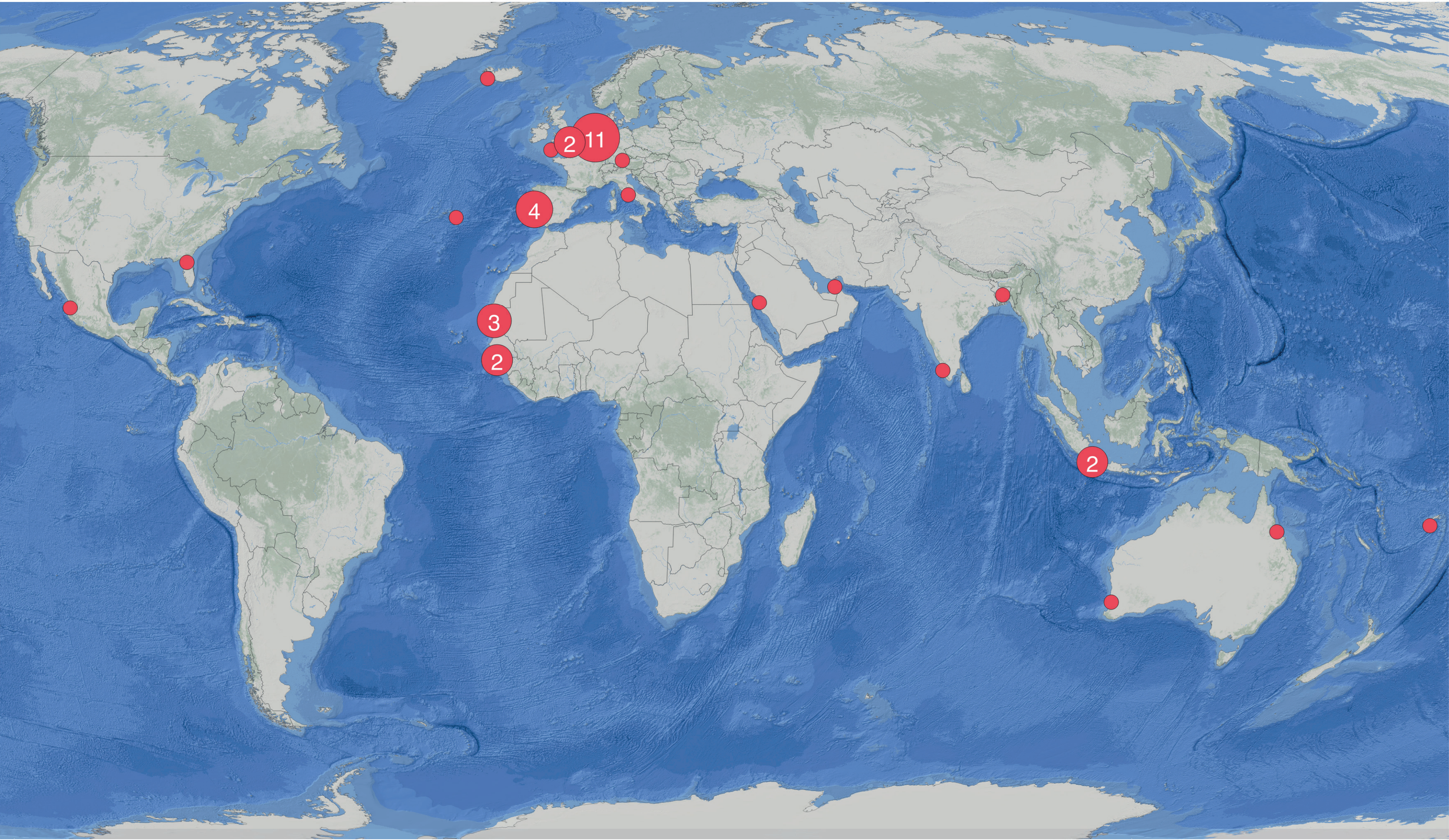

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Summaries

Summary

Populations of sharks and rays (*i.e.*, elasmobranchs) are under pressure from human activities. Combined with their slow population growth, this has resulted in declining shark and ray populations. The decline of sharks and rays threatens the functioning of marine ecosystems and local communities that depend on fisheries. The impact of human disturbances on the ecological role of sharks and rays in intertidal ecosystems - i.e., habitats (often soft-bottom flats) exposed during low tide - is poorly understood, especially in the West African region. In this thesis, I address this important knowledge gap by focusing on the two largest intertidal ecosystems in the West African region: the Banc d'Arguin in Mauritania and the Bijagós Archipelago in Guinea-Bissau, placing results into a regional and global (intertidal) context. This thesis addresses the central question: "How do fisheries impact the role of sharks and rays as intertidal predators, and how does this potentially impact other predators (e.g., migratory shorebirds) and ecosystem functioning?". I focus on four themes to address this question, which I summarized consecutively.

Fisheries

We studied the extent of industrial and small-scale fisheries to determine their impact on shark and ray populations in the Banc d'Arguin and the Bijagós Archipelago (**Section I**). For this, we used data from industrial fishing vessels' onboard 'Automatic Identification System' (AIS) to determine the distribution of their fishing activity near both study areas (**Chapter 2**). We then combined this with information on shark and ray catches by fishers in the waters of Mauritania and Guinea-Bissau. We found that industrial fishing effort is concentrated around the borders of the marine protected areas, with 72% and 78% of the area around the borders of the Banc d'Arguin and Bijagós Archipelago impacted by fishing activity, respectively. We further show that the bycatch of sharks and rays can be high in these waters.

We reconstructed the population changes over the past decades in both study areas to determine a historical baseline for sharks and rays. In the Banc d'Arguin, we based population trends on landing site surveys (**Chapter 3**) and fishers' ecological knowledge in the Bijagós Archipelago (**Chapter 4**). We concluded that shark and ray populations declined severely, with some species (groups), such as blackchin guitarfish (*Glaucostegus cemiculus*) and hammerhead sharks (*Sphyrna spp.*), declining by over 90% between 1960 and 2020.

These results show that sharks and rays are at risk from small-scale fisheries locally, whereas individuals moving outside these areas are at risk from industrial fisheries. In addition, the available marine habitat in intertidal areas shrinks dramatically with the receding tide, making these species even more susceptible to capture and decreasing survivability in intertidal fishing gear. Therefore, future research should quantify the relative risk of both fisheries to shark and ray populations in intertidal areas and examine how fisheries intervene with these species' movements across ecosystem boundaries.

Diversity & Life History

The lack of information on the occurrence of sharks and rays or their life cycle hampers the effective management of these species. This is especially relevant in the poorly studied West African waters. We used environmental DNA (eDNA) to determine the species richness of the elasmobranch community in the Bijagós Archipelago (**Chapter 5**). We show that this technique can successfully be used in remote and data-deficient intertidal areas to detect the presence of threatened sharks and rays. We concluded that the presence of some species differs across the dry and rainy seasons and that critically endangered scalloped hammerhead (*Sphyrna lewini*) and blackchin guitarfish are still widely distributed throughout the archipelago. In total, we detected 13 species (2 shark and 11 ray species), of which 54% are threatened with extinction. The pearl whipray (*Fontitrygon margaritella*) was found to be the most commonly occurring elasmobranch species. In **Chapter 6,** we specifically studied this species (pearl whipray) and showed that it is a fast-growing species that matures between 2.2 and 3.9 years of age and completes its entire lifecycle in the Bijagós Archipelago.

Species Interactions

Intertidal habitats are traditionally studied from a low-tide and shorebird perspective. However, we show that intertidal habitats are also used by various shark and ray species (**Chapter 7**). Globally, we identified 43 shark and 45 ray species that use intertidal habitats. These habitats are mainly used as feeding refugia by early life stages or small-bodied species. We conceptualize the shared intertidal habitat and resource use by sharks, rays, and shorebirds, and how the decline of elasmobranch populations can affect intertidal ecosystem functioning. In **Chapter 8**, we studied this potential overlap between sharks and shorebirds further and determined that elasmobranchs and migratory waders are likely to use similar intertidal habitats and food sources. The trophic niche overlap between shorebirds and rays is especially profound, as these species groups share 28 to 42% of their trophic niche and feed on similar foodweb positions (trophic positions 2.3 to 4.3). As such, although separated by the tide, rays and shorebirds exploit similar intertidal prey during high and low tide, respectively.

Next to playing a significant role in the ecosystem's food web, we also show that benthic rays in the Bijagós Archipelago can change the biogeomorphology and macrozoobenthic communities of intertidal habitats (**Chapter 9**). Benthic rays such as the common pearl whipray can turn over the entire top-sediment layer every 27 days. This is evidence of a landscape-wide impact of small benthic rays and suggests that removing their predators or fisheries directly targeting this species may impact the broader functioning of intertidal ecosystems.

Conservation

To enable the inclusion of ecologically important areas for sharks and rays into area-based conservation measures, we have described criteria for Important Shark and Ray Areas (ISRAs; **Box F**). These Important Shark and Ray Areas represent areas of importance to sharks and rays, such as migratory corridors, areas with many threatened species, or known nursery areas. ISRAs inform decision-makers about which areas to include in area-based strategies if the objective is to conserve shark and ray populations. However, sharks and rays are not only ecologically important but are also part of the complex socio-economic systems of many coastal communities, including in both study areas. We highlight important lessons learned from field researchers who conducted shark value chain assessments and emphasize the necessity to include local researchers and fishers in the process is essential for accurate data collection, communicating outcomes, and for adaptive management strategies to be effective (**Chapter 10**).

Management Implications

This thesis concludes that sharks and rays have an important role as predators and in socio-economic systems in (intertidal) coastal communities. However, as shown throughout the thesis, intertidal sharks and rays are threatened by fisheries in and outside these coastal areas. Therefore, **Chapter 11** outlines numerous recommendations to turn the tide for these species in West Africa. These include:

1. Improve data collection regarding industrial and small-scale fisheries catches by strengthening local research capacity.

2. Identify ecological areas for sharks and rays within large intertidal areas to prevent interactions between elasmobranchs and fisheries or other human activities.
3. Restrict the use of specific intertidal fishing methods to reduce fishing mortality of sharks and rays.
4. Enforce protected area boundaries and limit fisheries to registered vessels.
5. Involve local communities in enforcing fishing regulations and ensure equality across fisheries value chains.

Without appropriate interventions, the loss of sharks and rays from the Banc d'Arguin and the Bijagós Archipelago is imminent. Although future research is necessary to determine the consequences of this loss, it is clear that these species provide links across ecosystem boundaries. The role of sharks and rays in the functioning of intertidal ecosystems and their importance to coastal livelihoods should be integrated into future conservation strategies.

Samenvatting

Haaien en roggen *(*elasmobranchen) worden bedreigd door menselijke activiteiten. In combinatie met hun langzame populatiegroei heeft dit wereldwijd geleid tot afnemende haaien- en roggenpopulaties. Deze afname bedreigt het functioneren van mariene ecosystemen en lokale kustgemeenschappen die afhankelijk zijn van visserij. De invloed van menselijke verstoringen op de ecologische rol van haaien en roggen in waddengebieden (gebieden die tijdens laagtij droogvallen; waddengebieden) is onduidelijk. Er is vooral heel weinig bekend over deze soorten in West-Afrikaanse waddengebieden. In dit proefschrift richt ik me daarom op de twee grootste wadden ecosystemen van West-Afrika: de Banc d'Arguin in Mauritanië en de Bijagós Archipel in Guinee-Bissau, waarbij ik de resultaten ook in een internationaal perspectief plaats. De hoofdvraag die ik in dit proefschrift beantwoord is: "Hoe beïnvloedt visserij de rol van haaien en roggen in waddengebieden, en hoe beïnvloedt dit hun interactie met andere dieren aan de top van de voedselketen (bijvoorbeeld migrerende wadvogels) en het functioneren van deze ecosystemen?". Dit proefschrift is opgedeeld in vier thema's, die ik hier achtereenvolgens samenvat.

Visserij

We hebben de omvang van industriële- en kustvisserij bestudeerd voor de kust van West-Afrika, om vervolgens hun impact op de haaien- en roggenpopulaties in de Banc d'Arguin en de Bijagós Archipel te bepalen (**Hoofdstuk 1**). Hiervoor gebruikten we gegevens van het 'Automatic Identification System' (AIS) aan boord van industriële vissersschepen om zo de verspreiding van visserijactiviteiten in de buurt van beide studiegebieden te bepalen (**Hoofdstuk 2**). Dit hebben we gecombineerd met data van haaien- en roggenvangsten door industriële vissersschepen in de wateren van Mauritanië en Guinee-Bissau. Daarbij ontdekten we dat de industriële visserij zich concentreert rond de grenzen van beschermde gebieden, waarbij respectievelijk 72% en 78% van het gebied rond de grenzen van de Banc d'Arguin en de Bijagós Archipel wordt bevist. Ook laten we zien dat de bijvangst van haaien en roggen in deze wateren hoog kan zijn.

Verder hebben we de veranderingen in de haaien- en roggenpopulaties over de afgelopen decennia in kaart gebracht, om zo een idee te krijgen van de oorspronkelijke aanwezigheid van deze soorten. Dit konden we vervolgens gebruiken als referentie om de mate van populatieafname in te kunnen schatten. In de Banc d'Arguin baseerden we de populatietrends op visinventarisaties afkomstig van visserijhavens (**Hoofdstuk 3**) en in de Bijagós Archipel baseerden we deze op kennis van vissers die we voor dit doel hebben geïnterviewd (**Hoofdstuk 4**). We concludeerden dat de haaien- en roggenpopulaties zeer sterk zijn afgenomen in de afgelopen 60 jaar. Sommige soorten, zoals de zwartkin-gitaarrog (*Glaucostegus cemiculus*) en hamerhaaiensoorten (*Sphyrna spp.*), zijn zelfs met meer dan 90% afgenomen tussen 1960 en 2020.

Deze resultaten laten zien dat haaien en roggen op lokale schaal worden bedreigd door kustvisserij, terwijl soorten die zich ook buiten deze kustgebieden begeven daar ook in aanraking komen met industriële visserij. Bovendien krimpt de beschikbare mariene habitat in waddengebieden dramatisch tijdens afgaand tij, waardoor deze soorten tijdens eb nog vatbaarder worden voor vangst en hun overlevingskansen verder afnemen. Toekomstig onderzoek zou zich daarom moeten richten op het in kaart brengen van de risico's van beide visserijvormen voor haaien- en roggenpopulaties in waddengebieden.

Diversiteit & Levenscyclus

De bescherming van West-Afrikaanse haaien en roggen wordt momenteel sterk belemmerd door het gebrek aan informatie over hun aanwezigheid en populatiestatus. Daarom hebben we een relatief nieuwe methode, 'environmental DNA' (eDNA), gebruikt om de soortenrijkdom van de haaien- en roggengemeenschap in de Bijagós Archipel te bepalen (**Hoofdstuk 5**). Met deze techniek wordt dierlijk DNA uit een watermonster gefilterd om zo de aanwezigheid van een soort vast te stellen. We laten zien dat deze techniek succesvol kan worden gebruikt in afgelegen waddengebieden om de aanwezigheid van bedreigde haaien en roggen vast te stellen. Door middel van deze techniek konden we concluderen dat de met uitsterven bedreigde geschulpte hamerhaai (*Sphyrna lewini*) en de zwartkin-gitaarrog nog steeds wijdverspreid zijn in de archipel. In totaal hebben we de aanwezigheid van 13 soorten (2 haaiensoorten en 11 roggensoorten) vastgesteld, waarvan 54% met uitsterven wordt bedreigd. De rog *Fontitrygon margaritella* is de meest voorkomende soort. In **Hoofdstuk 6** bestudeerden we deze roggensoort (*Fontitrygon margaritella*) verder, en toonden we aan dat het een snelgroeiende soort is die tussen de 2,2 en 3,9 jaar geslachtsrijp wordt en dat alle levensstadia van deze soort (jonge en volwassen beesten) in de Bijagós voorkomen.

Soorteninteracties

Waddengebieden zijn tot nu voornamelijk onderzocht vanuit een laagwater- (eb) en wadvogelperspectief. In **Hoofdstuk 7** laten we echter zien dat haaien en roggen ook wadplaten gebruiken tijdens hoogwater (vloed). Wereldwijd hebben we 43 haaiensoorten en 45 roggensoorten geïdentificeerd die habitats in waddengebieden gebruiken. Deze habitats worden voornamelijk gebruikt als schuilplaats en als veilig foerageergebied omdat grote roofdieren er niet kunnen komen. Daarnaast beschrijven we de theorie dat zowel haaien en roggen, als wadvogels dezelfde habitat en voedselbronnen gebruiken, en hoe visserij deze interactie tussen deze soortgroepen zou kunnen beïnvloeden. In **Hoofdstuk 8** hebben we deze mogelijke overlap tussen haaien en wadvogels verder onderzocht en vastgesteld dat elasmobranchen en migrerende wadvogels gedeeltelijk vergelijkbare habitats en voedselbronnen gebruiken. De overlap tussen wadvogels en roggen is aanzienlijk, aangezien deze soortgroepen 28 tot 42% overlappen in hun gebruik van voedselbronnen in deze gebieden, en vergelijkbare posities (trofisch niveau 2.3 tot 4.3) innemen. Hoewel ze een gescheiden leven leiden als gevolg van het veranderende getij gebruiken roggen (tijdens hoogtij) en wadvogels (tijdens laagtij) toch vergelijkbare prooien in het waddengebieden.

Naast de belangrijke rol als roofdieren in mariene ecosystemen, laten we ook zien dat roggen in de Bijagós Archipel de biogeomorfologie en bodemfauna van waddengebieden kunnen veranderen (**Hoofdstuk 9**). Pijlstaartroggen zoals *Fontitrygon margaritella* kunnen elke 27 dagen de gehele toplaag van de bodem omwoelen. Dit is bewijs van een landschapsbrede impact van deze veelvoorkomende roggen en suggereert dat het verwijderen van hun predatoren, of directe visserij op deze soorten, het functioneren van wadden ecosystemen kan beïnvloeden.

Behoud van Soorten

Om ervoor te zorgen dat gebieden die ecologisch belangrijk zijn voor haaien en roggen in kaart worden gebracht en worden opgenomen in bestaande maatregelen voor natuurbehoud, hebben we criteria beschreven voor zogeheten ‘Important Shark and Ray Areas’ (ISRAs; **Box F**). Deze Important Shark and Ray Areas vertegenwoordigen gebieden die belangrijk zijn voor een of meerdere haaien- en roggensoorten, zoals migratieroutes, gebieden met veel bedreigde soorten of gebieden met een kraamkamerfunctie. Deze ISRA’s voorzien natuurbeheerders en beleidsmakers over welke gebieden beschermd zouden moeten worden als zij haaien- en roggenpopulaties beter willen beschermen. Haaien en roggen zijn echter niet alleen ecologisch belangrijk, maar maken ook deel uit van de complexe sociaaleconomische systemen van veel menselijke kustgemeenschappen. Dit is ook het geval in beide studiegebieden, waar visserij een belangrijke traditie is en een van de belangrijkste inkomstenbronnen is. In **Hoofdstuk 10** omschrijven we belangrijke lessen die veldonderzoekers wereldwijd hebben geleerd tijdens het bestuderen van de visserij en handel in haaien en roggen. Deze onderzoekers benadrukken de noodzaak om lokale onderzoekers en vissers bij visserijonderzoek te betrekken. Dit is essentieel voor het verzamelen van gevoelige informatie over visserij, het communiceren van resultaten en voor het stimuleren van effectiever (lokaal) beheer van haaien en roggen.

Beheeradvies

In dit proefschrift concludeer ik dat haaien en roggen een belangrijke rol spelen als roofdieren in waddengebieden en dat deze soorten bijdragen aan de tradities en economie van lokale kustgemeenschappen. We hebben echter in dit proefschrift aangetoond dat haaien en roggen bedreigd worden door de visserij binnen en buiten grote waddengebieden. In **Hoofdstuk 11** presenteer ik daarom een aantal aanbevelingen om het tij te keren voor de bescherming van haaien en roggen in West-Afrika. Dit zijn de belangrijkste:

1. Verbeter het verzamelen van vangstgegevens in de industriële en kustvisserij door lokale onderzoekscapaciteit te versterken.

2. Identificeer belangrijke ecologische gebieden voor haaien en roggen binnen deze gebieden om zo interacties tussen elasmobranchen en visserij te verminderen.

3. Beperk het gebruik van specifieke vismethoden in het waddengebied om overleving van haaien en roggen als bijvangst te vergroten.

4. Zorg ervoor dat grenzen van beschermde gebieden strenger worden gehandhaafd en beperk visserij tot geregistreerde vissers.

5. Betrek lokale gemeenschappen bij de handhaving van regelgeving en zorg voor gelijkheid in de lokale vishandel.

Zonder maatregelen dreigen haaien en roggen uit de Banc d’Arguin en de Bijagós Archipel te verdwijnen. Hoewel verder onderzoek nodig is om de gevolgen van dit verlies verder in kaart te brengen, is het duidelijk dat deze soorten een belangrijke schakel zijn tussen verschillende ecosystemen. De rol van haaien en roggen voor het functioneren van wadden ecosystemen én hun belang voor kustgemeenschappen moet vooropgesteld worden in het beheer van deze belangrijke gebieden.

Résumé

Les populations de requins et de raies (les élasmobranches) subissent la pression des activités humaines. Cette situation, en conjonction avec une croissance démographique lente, a entraîné un déclin des populations de requins et de raies. Ce déclin menace actuellement le fonctionnement des écosystèmes marins ainsi que les communautés locales qui dépendent de la pêche. L'impact des perturbations humaines sur le rôle écologique des requins et des raies dans les écosystèmes intertidaux - c'est-à-dire les habitats (souvent des fonds) exposés à marée basse - est mal connu, en particulier dans la région de l'Afrique de l'Ouest. Dans cette thèse, j'aborde cette importante lacune en me concentrant sur les deux plus grands écosystèmes intertidaux de la région ouest-africaine : le Banc d'Arguin en Mauritanie et l'Archipel des Bijagós en Guinée-Bissau, en plaçant les résultats dans un contexte (intertidaux) régional et mondial. Cette thèse aborde la question centrale: «Comment les pêcheries influencent-elles le rôle des requins et des raies en tant que prédateurs intertidaux, et comment cela affecte-t-il potentiellement d'autres prédateurs (par exemple, les oiseaux marins) et le fonctionnement de l'écosystème ? Pour répondre à cette question, je me concentre sur quatre thèmes, que je résume ici de façon consécutive.

Pêche

Nous avons étudié l'étendue de la pêche industrielle et artisanale afin de déterminer leur impact sur les populations de requins et de raies du Banc d'Arguin et de l'archipel de Bijagós (**Section I**). Pour cela, nous avons utilisé les données du système d'identification automatique (AIS) embarqué à bord des navires de pêche industrielle afin de déterminer la distribution de leurs activités de pêche à proximité des deux zones d'étude (**Chapitre 2**). Nous avons ensuite combiné ces données avec les informations sur les captures de requins et de raies par les pêcheurs dans les eaux de Mauritanie et de Guinée-Bissau. Nous avons constaté que l'effort de pêche industrielle est concentré autour des limites des aires marines protégées, avec 72% et 78% de la zone autour des limites du Banc d'Arguin et de l'Archipel des Bijagós touchée respectivement par l'activité de pêche. Nous montrons également que les prises accessoires de requins et de raies peuvent être élevées dans ces eaux.

Nous avons reconstruit les changements de population au cours des dernières décennies dans les deux zones d'étude afin de déterminer une base historique pour les requins et les raies. Au Banc d'Arguin, nous avons basé les tendances démographiques sur les études des sites de débarquement des produits de la pêche (**Chapitre 3)** et sur les connaissances écologiques des pêcheurs de l'archipel de Bijagós (**Chapitre 4)**. Nous avons conclu que les populations de requins et de raies ont fortement décliné, certaines espèces (groupes), telles que le raie-guitare (*Glaucostegus cemiculus*) et le requin-marteau (*Sphyrna spp.*), diminuant de plus de 90 % entre 1960 et 2020.

Ces résultats montrent que les requins et les raies sont menacés localement par la pêche à petite échelle, tandis que les individus se déplaçant en dehors de ces zones sont menacés par la pêche industrielle. En outre, l'habitat marin disponible dans les zones intertidales se réduit considérablement avec le recul de la marée, ce qui rend ces espèces encore plus susceptibles d'être capturées et diminue leur capacité de survie dans les engins de pêche intertidaux. Par conséquent, les recherches futures devraient quantifier le risque relatif des deux pêcheries pour les populations de requins et de raies dans les zones intertidales et devraient aussi examiner comment les pêcheries interviennent dans les mouvements de ces espèces à travers les frontières de l'écosystème.

Diversité et histoire de la vie

Le manque d'informations sur la présence des requins et des raies, ou sur leur cycle de vie, entrave la gestion efficace de ces espèces. Ceci est particulièrement vrai dans les eaux peu étudiées de l'Afrique de l'Ouest. Nous avons utilisé l'ADN environnemental ('environmental DNA', eADN) pour déterminer la richesse en espèces de la communauté d'élasmobranches dans l'archipel de Bijagós (**Chapitre 5**). Nous avons montré que cette technique peut être utilisée avec succès dans des zones intertidales éloignées et dépourvues de données pour détecter la présence de requins et de raies menacés. Nous avons conclu que la présence de certaines espèces diffère entre la saison sèche et la saison des pluies et que le requin-marteau halicorne (*Sphyrna lewini*) et la raie-guitare, qui sont gravement menacés d'extinction, sont encore largement répandus dans l'archipel. Au total, nous avons détecté 13 espèces (2 espèces de requins et 11 espèces de raies), dont 54% sont menacées d'extinction. La pastenague à perle (*Fontitrygon margaritella*) est l'espèce d'élasmobranche la plus répandue. Dans le **Chapitre 6,** nous avons étudié spécifiquement cette espèce *Fontitrygon margaritella* et nous avons montré qu'il s'agit d'une espèce à croissance rapide qui arrive à maturité entre 2,2 et 3,9 ans et qui accomplit tout son cycle de vie dans l'archipel des Bijagós.

Interactions entre espèces

Les habitats intertidaux sont traditionnellement étudiés du point de vue des marées basses et des oiseaux de rivage. Cependant, nous montrons que les habitats intertidaux sont également utilisés par diverses espèces de requins et de raies (**Chapitre 7)**. Globalement, nous avons identifié 43 espèces de requins et 45 espèces de raies qui utilisent les habitats intertidaux. Ces habitats sont principalement utilisés comme refuges alimentaires par les espèces en premiers stades de vie ou les espèces à petit corps. Nous conceptualisons l'habitat intertidaux partagé et l'utilisation des ressources par les requins, les raies et les oiseaux de rivage, ainsi que la manière dont le déclin des populations d'élasmobranches peut affecter le fonctionnement de l'écosystème intertidal. Au **Chapitre 8**, nous avons étudié davantage ce chevauchement potentiel entre les requins et les oiseaux de marins et nous avons déterminé que les élasmobranches et les oiseaux migrateurs sont susceptibles d'utiliser des habitats intertidaux et des sources de nourriture similaires. Le chevauchement des niches alimentaires entre les oiseaux de rivage et les raies est particulièrement important, car ces groupes d'espèces partagent 28 à 42% de leur niche alimentaire et se nourrissent sur des positions similaires du réseau alimentaire (positions trophiques 2.3 à 4.3). Ainsi, bien que séparés par la marée, les raies et les oiseaux de rivage exploitent des proies intertidales similaires, respectivement à marée haute et à marée basse.

En plus de jouer un rôle important dans le réseau alimentaire de l'écosystème, nous montrons également que les raies benthiques de l'archipel de Bijagós peuvent modifier à la fois la biogéomorphologie des habitats intertidaux ainsi que les communautés macrozoobenthiques qui y sont présents (**Chapitre 9)**. Les raies benthiques telles que la pastenague à perle peuvent retourner l'ensemble de la couche supérieure du sédiment tous les 27 jours. Cela prouve que les petites raies benthiques ont un impact sur l'ensemble du paysage et suggère que l'élimination de leurs prédateurs ou les pêcheries ciblant directement cette espèce peuvent avoir un impact sur le fonctionnement plus large des écosystèmes intertidaux.

Conservation

Pour permettre l'inclusion de zones écologiquement importantes pour les requins et les raies dans les mesures de conservation par zone, nous avons décrit des critères pour les zones importantes pour les requins et les raies (ISRA ; **Box F**). Les ISRA informent les décideurs sur les zones à inclure dans les stratégies par les zones humides côtières si l'objectif est de conserver les populations de requins et de raies. Cependant, les requins et les raies ne sont pas seulement importants d'un point de vue écologique. Ils font également partie des systèmes socio-économiques complexes de nombreuses communautés côtières, y compris dans les deux zones d'étude. Nous soulignons les leçons importantes apprises par les chercheurs de terrain qui ont mené des évaluations de la chaîne de valeur des requins et insistons sur la nécessité d'inclure les chercheurs et les pêcheurs locaux dans le processus, ce qui est essentiel pour la collecte de données précises, la communication des résultats et l'efficacité des stratégies de gestion adaptative (**Chapitre 10)**.

Implications en matière de gestion

Cette thèse conclut que les requins et les raies jouent un rôle important en tant que prédateurs et en vue de leur rôle dans les systèmes socio-économiques des communautés côtières (intertidales). Cependant, comme cela a été démontré tout au long de la thèse, les requins et les raies intertidales sont menacés par les pêcheries à l'intérieur et à l'extérieur de ces zones côtières. Par conséquent, le **Chapitre 11** présente de nombreuses recommandations visant à inverser la tendance négative pour ces espèces en Afrique de l'Ouest. Celles-ci comprennent :

1. Améliorer la collecte de données concernant les captures de la pêche industrielle et artisanale en renforçant les capacités de recherche locales.
2. Identifier les zones écologiques pour les requins et les raies parmi les grandes zones intertidales afin de prévenir les interactions entre les élasmobranches et les pêcheries ou d'autres activités humaines.
3. Restreindre l'utilisation de certaines méthodes de pêche dans la zone intertidale afin de réduire la mortalité par pêche des requins et des raies.
4. Faire respecter les limites des zones protégées et limiter la pêche aux navires enregistrés.
5. Impliquer les communautés locales dans l'application des règlements de pêche et garantir l'égalité entre les chaînes de valeur de la pêche.

Sans interventions appropriées, la disparition des requins et des raies du Banc d'Arguin et de l'archipel de Bijagós est imminente. Bien que des recherches futures soient nécessaires pour déterminer les conséquences de cette perte, il est clair que ces espèces assurent des liens entre les écosystèmes. Le rôle des requins et des raies dans le fonctionnement des écosystèmes intertidaux et leur importance pour les moyens de subsistance côtiers devraient être intégrés dans les futures stratégies de conservation.

Resumo

As populações de tubarões e raias (*ou seja*, elasmobrânquios) estão sob pressão das atividades humanas. Este facto, combinado com o seu lento crescimento populacional, resultou no declínio das populações de tubarões e raias. O declínio dos tubarões e raias ameaça o funcionamento dos ecossistemas marinhos e as comunidades locais que dependem da pesca. O impacto das perturbações humanas no papel ecológico dos tubarões e das raias nos ecossistemas intertidais - ou seja, nos habitats (muitas vezes bancos de sedimento mole) expostos durante a maré baixa - é pouco conhecido, especialmente na região da África Ocidental. Nesta tese, abordo esta importante lacuna de conhecimento centrando-me nos dois maiores ecossistemas intertidais da região da África Ocidental: o Banc d'Arguin, na Mauritânia, e o Arquipélago dos Bijagós, na Guiné-Bissau, colocando os resultados obtidos num contexto regional e global (intertidais). Esta tese aborda a questão central: "Como é que a pesca afeta o papel dos tubarões e das raias como predadores intertidais, e como é que isso afeta potencialmente outros predadores (por exemplo, aves costeiras migratórias) e o funcionamento do ecossistema?". Para responder a esta questão, concentro-me em quatro temas, que resumi consecutivamente.

Pescas

Estudámos a extensão da pesca industrial e da pesca artesanal para determinar o seu impacto nas populações de tubarões e raias no Banc d'Arguin e no Arquipélago dos Bijagós (**Secção I**). Para tal, utilizámos dados do 'Sistema de Identificação Automática' (AIS) a bordo dos navios de pesca industrial para determinar a distribuição da sua atividade de pesca perto das duas áreas de estudo (**Capítulo 2**). Em seguida, combinámos estes dados com as informações sobre as capturas de tubarões e raias efetuadas pelos pescadores nas águas da Mauritânia e da Guiné-Bissau. Verificámos que a pesca industrial se concentra em torno das fronteiras das áreas marinhas protegidas, com 72% e 78% da área em torno das fronteiras do Banc d'Arguin e do Arquipélago dos Bijagós afetada pela atividade de pesca, respetivamente. Mostramos ainda que o *bycatch* de tubarões e raias pode ser elevado nestas águas.

Reconstruímos as alterações populacionais ao longo das últimas décadas em ambas as áreas de estudo para determinar valores de referência históricos para tubarões e raias. No Banc d'Arguin, baseámos as tendências populacionais em inquéritos nos locais de desembarque (**Capítulo 3**) e no Arquipélago dos Bijagós, no conhecimento ecológico dos pescadores (**Capítulo 4**). Concluímos que as populações de tubarões

e raias registaram um declínio acentuado, com algumas espécies (grupos), como o peixe-viola-preto (*Glaucostegus cemiculus*) e os tubarões-martelo (*Sphyrna spp.*), a sofrerem um declínio superior a 90% entre 1960 e 2020.

Estes resultados mostram que os tubarões e as raias estão em risco devido à pesca de pequena escala a nível local, enquanto os indivíduos que se deslocam para fora destas áreas estão em risco devido à pesca industrial. Além disso, o habitat marinho disponível nas zonas intertidais diminui drasticamente com o recuo da maré, tornando estas espécies ainda mais suscetíveis de serem capturadas e diminuindo a sua capacidade de sobrevivência nas artes de pesca intertidais. Por conseguinte, investigações futuras devem quantificar o risco relativo de ambas as pescarias para as populações de tubarões e raias nas zonas intertidais e examinar a forma como as pescarias intervêm nos movimentos destas espécies através das fronteiras dos ecossistemas.

Diversidade e história de vida

A falta de informação sobre a ocorrência de tubarões e raias, ou sobre o seu ciclo de vida, dificulta a gestão efetiva destas espécies. Isto é especialmente relevante nas águas pouco estudadas da África Ocidental. Utilizámos o ADN ambiental (eDNA) para determinar a riqueza de espécies da comunidade de elasmobrânquios no Arquipélago dos Bijagós (**Capítulo 5**). Mostrámos que esta técnica pode ser utilizada com sucesso em áreas intertidais remotas e com poucos dados para detetar a presença de tubarões e raias ameaçados. Concluímos que a presença de algumas espécies difere entre as estações seca e chuvosa e que o tubarão-martelo (*Sphyrna lewini*) e a raia-viola (*Sphyrna lewini*), criticamente ameaçados, ainda estão amplamente distribuídos pelo arquipélago. No total, detetámos 13 espécies (2 espécies de tubarões e 11 espécies de raias), das quais 54% estão ameaçadas de extinção. A raia-pérola (*Fontitrygon margaritella*) foi a espécie de elasmobrânquio com maior ocorrência. No **Capítulo 6,** estudámos especificamente esta espécie (raia-pérola) e mostrámos que é uma espécie de crescimento rápido que amadurece entre os 2,2 e os 3,9 anos de idade e completa todo o seu ciclo de vida no Arquipélago dos Bijagós.

Interações entre espécies

Os habitats intertidais são tradicionalmente estudados na perspetiva da maré baixa e das aves costeiras. No entanto, mostramos que os habitats intertidais também são utilizados por várias espécies de tubarões e raias (**Capítulo 7**). Globalmente, identificámos 43 espécies de tubarões e 45 espécies de raias que utilizam habitats intertidais. Estes habitats são principalmente utilizados como refúgios alimentares por espécies em fase inicial de vida ou por espécies de pequeno porte. Conceptualizámos o habitat intertidal partilhado e a utilização de recursos por tubarões, raias e aves costeiras; e a forma como o declínio das populações de elasmobrânquios pode afetar o funcionamento do ecossistema intertidal. No **Capítulo 8**, estudámos mais aprofundadamente esta potencial sobreposição entre tubarões e aves limícolas (aves costeiras pernaltas) e determinámos que é provável que os elasmobrânquios e as aves limícolas migratórias utilizem habitats intertidais e fontes de alimento semelhantes. A sobreposição do nicho trófico entre as aves marinhas e as raias é especialmente profunda, uma vez que estes grupos de espécies partilham 28 a 42% do seu nicho trófico e alimentam-se em posições semelhantes da rede trófica (posições tróficas 2.3 a 4.3). Assim, embora separadas pela maré, as raias e as aves limícolas exploram presas intertidais semelhantes durante a maré alta e a maré baixa, respetivamente.

Além de desempenharem um papel importante na rede trófica do ecossistema, mostramos também que as raias bentónicas do Arquipélago dos Bijagós podem alterar a biogeomorfologia e as comunidades macrozoobentónicas dos habitats intertidais (**Capítulo 9**). As raias bentónicas, como a raia-pérola, podem revolver toda a camada superior do sedimento a cada 27 dias. Isto prova o impacto das pequenas raias bentónicas em toda a paisagem e sugere que a remoção dos seus predadores ou as pescarias diretamente dirigidas a esta espécie podem ter um impacto mais amplo no funcionamento dos ecossistemas intertidais.

Conservação

Para permitir a inclusão de áreas ecologicamente importantes para tubarões e raias em medidas de conservação baseadas na área, descrevemos critérios para Áreas Importantes para Tubarões e Raias (ISRAs; **Caixa F**). Estas Áreas Importantes para Tubarões e Raias representam áreas importantes para tubarões e raias, como corredores migratórios, áreas com muitas espécies ameaçadas ou áreas de berçário conhecidas. As ISRA informam os tomadores de decisões sobre as áreas a incluir nas estratégias baseadas na área, se o objetivo for conservar as populações de tubarões e raias. No entanto, os tubarões e as raias não são apenas ecologicamente importantes, mas também fazem parte dos complexos sistemas socioeconómicos de muitas comunidades costeiras, incluindo em ambas as áreas de estudo. Destacamos lições importantes aprendidas com investigadores no terreno que realizaram avaliações da cadeia de valor do tubarão e salientamos que incluir investigadores e pescadores locais no processo é essencial para a coleta de dados precisos, para a comunicação dos resultados e para a eficácia das estratégias de gestão adaptativa (**Capítulo 10**).

Implicações para a gestão

Esta tese conclui que os tubarões e as raias desempenham um papel importante como predadores e nos sistemas socioeconómicos das comunidades humanas costeiras (intertidais). No entanto, como demonstrado ao longo da tese, os tubarões e as raias intertidais estão ameaçados pela pesca dentro e fora destas zonas costeiras. Por conseguinte, **o Capítulo 11** apresenta numerosas recomendações para inverter a situação para estas espécies na África Ocidental. Estas incluem:

1. Melhorar a recolha de dados sobre as capturas da pesca industrial e da pequena pesca através do reforço da capacidade de investigação local.
2. Identificar zonas ecológicas para tubarões e raias em grandes áreas intertidais para evitar interações entre elasmobrânquios e a pesca ou outras atividades humanas.
3. Restringir a utilização de métodos de pesca intertidais específicos para reduzir a mortalidade por pesca de tubarões e raias.
4. Fazer respeitar os limites das zonas protegidas e limitar a pesca aos navios registados.
5. Envolver as comunidades locais na aplicação dos regulamentos relativos à pesca e garantir a igualdade nas cadeias de valor da pesca.

Sem intervenções adequadas, a perda de tubarões e raias do Banc d’Arguin e do Arquipélago dos Bijagós é iminente. Embora seja necessária investigação futura para determinar as consequências desta perda, é evidente que estas espécies estabelecem ligações entre as fronteiras de diferentes ecossistemas. O papel dos tubarões e das raias no funcionamento dos ecossistemas intertidais e a sua importância para os meios de subsistência costeiros devem ser integrados em futuras estratégias de conservação.

Curriculum Vitae

Guido Leurs was born on the 12th of November 1991 in Venlo, The Netherlands. He is a marine biologist and a specialist in the ecology of sharks and rays. Fascinated by sharks through documentaries and books at a young age, Guido set out to pursue a career in marine biology. He first did a bachelor's in Applied Biology at the HAS University of Applied Sciences in 's-Hertogenbosch, during which he conducted research projects on Caribbean reef sharks and white sharks and published his first peer-reviewed paper. Guido obtained his MSc. in Biology with a specialization in Marine Biology from Wageningen University in 2017. During his masters, Guido studied the movement of Caribbean reef sharks and nurse sharks, the growth of the great hammerhead shark, and shark fisheries in West Africa.

After a break to study silky sharks in the Dutch Caribbean waters, Guido continued his scientific career with a PhD. at the University of Groningen and The Royal Netherlands Institute for Sea Research, of which the result is in front of you. He is currently a PostDoc researcher at Wageningen University & Research, focusing on the ecology and fisheries of sharks and rays.

Guido is a member of the IUCN Shark Specialist Group and also serves as an advisor to local researchers focusing on shark fisheries and ecology. Always eager to talk about sharks and rays, Guido also co-organizes the annual Azores Shark & Ray Safari for recreational divers and has appeared in various media outlets as a shark and ray expert.

More Info!

List of Publications

Leurs, G., Jabado, R.W., Camará, A., Dos Santos, L., Manuel Nonque, D., Zuidewind, T.J., Barry, I., Campredon, P., Blaschke, B., de Boer, K., Hijner, N., Olff, H., Ledo Pontes, S., Regalla, R., Walsh Bjerregaard, M. & Govers, L.L. (in review). Reconstructing historical population trends of threatened sharks and rays based on fisher ecological knowledge.

Leurs, G., Walsh, M.B, Haque, A.B., Collins, C., Glaus, K., Kizhakudan, S.J., Menon, M., Muttaqin, E., Simeon, B., Tovar-Avila, J., Govers, L.L., Walker, P.A. & Friedman, K.J. (2024). Opportunities and challenges in value chain reporting for sharks and rays. *Marine Policy*

Nauta, J., **Leurs, G.**, Nieuwenhuis, B. O., Mathijssen, D. R. A. H., Olff, H., Bouma, T. J., Van Der Wal, D., Hijner, N., Regalla, A., Pontes, S. L., & Govers, L. L. (2024). Bioturbation by Benthic Stingrays Alters the Biogeomorphology of Tidal Flats. *Ecosystems*. https://doi.org/10.1007/s10021-024-00901-4

Leurs, G., Verkuil, Y. I., Hijner, N., Saalmann, F., Dos Santos, L., Regalla, A., Ledo Pontes, S., Yang, L., Naylor, G. J. P., Olff, H., & Govers, L. L. (2023). Addressing data-deficiency of threatened sharks and rays in a highly dynamic coastal ecosystem using environmental DNA. *Ecological Indicators*, *154*(March), 110795–110795. https://doi.org/10.1016/j.ecolind.2023.110795

Ebert, D. A., Garcias, A. C., Fahmi, Pestana, A. G., Muñoz, S. H., **Leurs, G.**, & Simeon, B. M. (2023). Searching for lost sharks: Extinct or alive? *Oryx*, *57*(4), 419–420. https://doi.org/10.1017/S0030605323000509

Leurs, G., Nieuwenhuis, B. O., Zuidewind, T. J., Hijner, N., Olff, H., & Govers, L. L. (2023). Where land meets sea: Intertidal areas as key-habitats for sharks and rays. *Fish and Fisheries*, *24*(3), 407–426. https://doi.org/10.1111/faf.12735

Hyde, C. A., Notarbartolo di Sciara, G., Sorrentino, L., Boyd, C., Finucci, B., Fowler, S. L., Kyne, P. M., **Leurs, G.**, Simpfendorfer, C. A., Tetley, M. J., Womersley, F., & Jabado, R. W. (2022). Putting sharks on the map: A global standard for improving shark area-based conservation. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.968853

Clements, O. N., **Leurs, G.**, Witbaard, R., Pen, I., Verkuil, Y. I., & Govers, L. L. (2022). Growth, maturity, and diet of the pearl whipray (Fontitrygon margaritella) from the Bijagós Archipelago, Guinea-Bissau. *PeerJ*, *10*, e12894–e12894. https://doi.org/10.7717/peerj.12894

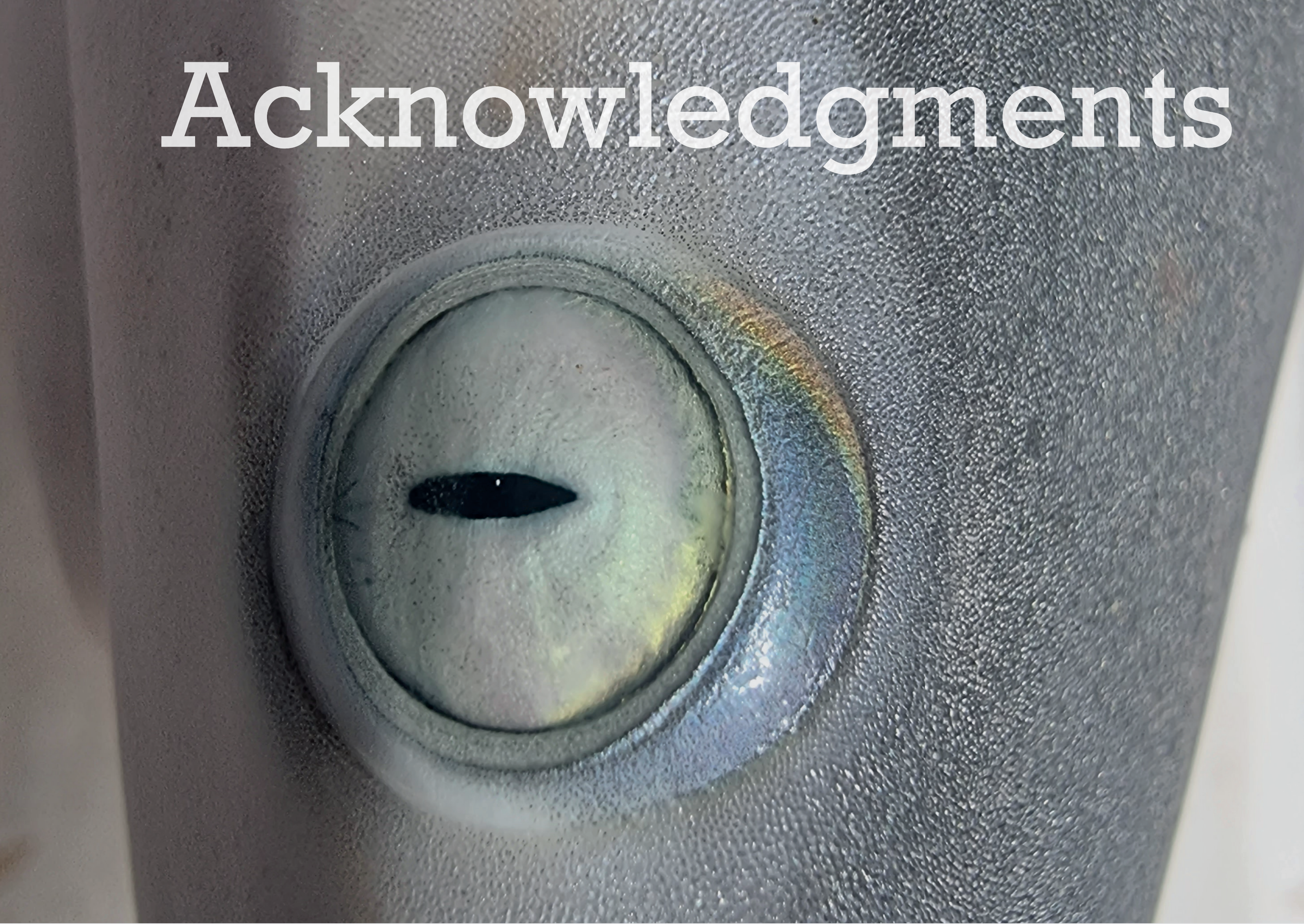
Leurs, G., van der Reijden, K. J., Cheikhna Lemrabott, S. Y., Barry, I., Nonque, D. M., Olff, H., Ledo Pontes, S., Regalla, A., & Govers, L. L. (2021). Industrial Fishing Near West African Marine Protected Areas and Its Potential Effects on Mobile Marine Predators. *Frontiers in Marine Science*, *8*(March), 1–13. https://doi.org/10.3389/fmars.2021.602917

Leurs, G., Boman, E., & Walker, P. (2018). Range extension of the lemon shark (Negaprion brevirostris) within the Dutch Caribbean: First records of young individuals in the waters of Sint Eustatius. *Matters*, 1–6. https://doi.org/10.19185/matters.201803000002

Leurs, G., O'Connell, C. P., Andreotti, S., Rutzen, M., & Vonk Noordegraaf, H. (2015). Risks and advantages of using surface laser photogrammetry on free-ranging marine organisms: A case study on white sharks Carcharodon carcharias. *Journal of Fish Biology*, *86*(6), 1713–1728. https://doi.org/10.1111/jfb.12678

O'Connell, C. P., & **Leurs, G.** (2016). A minimally invasive technique to assess several life-history characteristics of the endangered great hammerhead shark Sphyrna mokarran. *Journal of Fish Biology*, *88*(3), 1257–1264. https://doi.org/10.1111/jfb.12900

Acknowledgments



In this thesis, I argued that shark fisheries are complex systems with an important human dimension. The same goes for doing a Ph.D. It is the most incredible adventure I have faced, but I never felt alone in facing it. I will here address some, but probably not all, who - knowingly and unknowingly - contributed to the journey of which this book is the result.

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the only thing missing in the world is our own (karaoke) album. Nadia, thanks for all the great moments on and off expeditions, but please do not take another biopsy of your hand. Lisa and Drew, thank you for all the fantastic trips centered around stuffing ourselves with food. We miss you in Groningen, but Rachel and I can't wait to do that again in Costa Rica and China. Sidi Yahya and Hacen, thank you for the life-changing experiences in your beautiful Mauritania.
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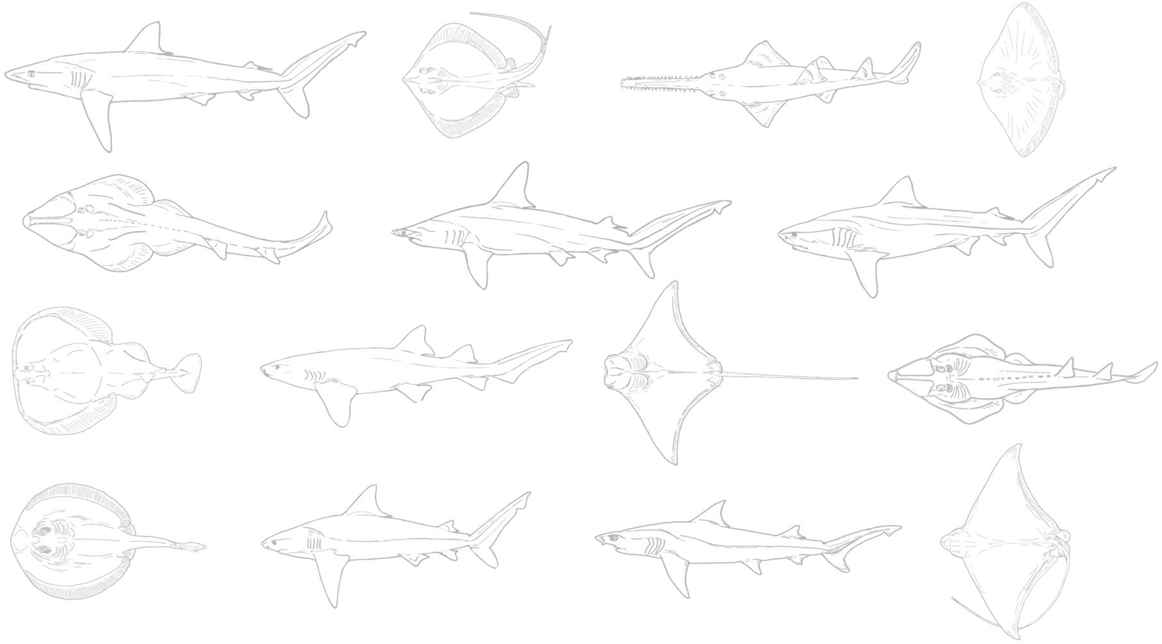
Rach, where to start? To this day, I am still amazed by how strong and caring you are, and how supportive you have been throughout my PhD. We both travel extensively for work or to see family and, whenever we have time left, also to explore the planet together. It is not always easy being apart, but home always feels like home with you. Thank you for our serious discussions, for the crazy moments, for letting home feel like a real home, and for being your beautiful self. Life is a *Roller Coaster*, but with you in the seat next to me, it is *Guaranteed* to be a beautiful ride. I can't wait to continue writing *our* story further.

Appendices

The thesis **appendices** and **photo/video** of our work in the Bijagós can be found online.



Shark and ray populations are in decline globally due to overfishing and habitat degradation, causing these species to disappear from marine ecosystems.

With a focus on the two largest intertidal areas in West Africa, the Banc d'Arguin (Mauritania) and the Bijagós Archipelago (Guinea-Bissau), we determined the ecological role of sharks and rays in large intertidal areas, examined how these species interact with other intertidal predators such as migratory shorebirds, and explored the impact of small-scale and industrial fisheries on these species. We conclude that many species using the intertidal are currently threatened with extinction. Furthermore, we show how these species interact with other intertidal predators, and how sharks and rays are often part of the complex socio-economic system of coastal communities.

Since intertidal habitats change rapidly with every tidal cycle and threats of fisheries are never far away, sharks and rays using intertidal areas must continuously navigate 'troubled waters'.