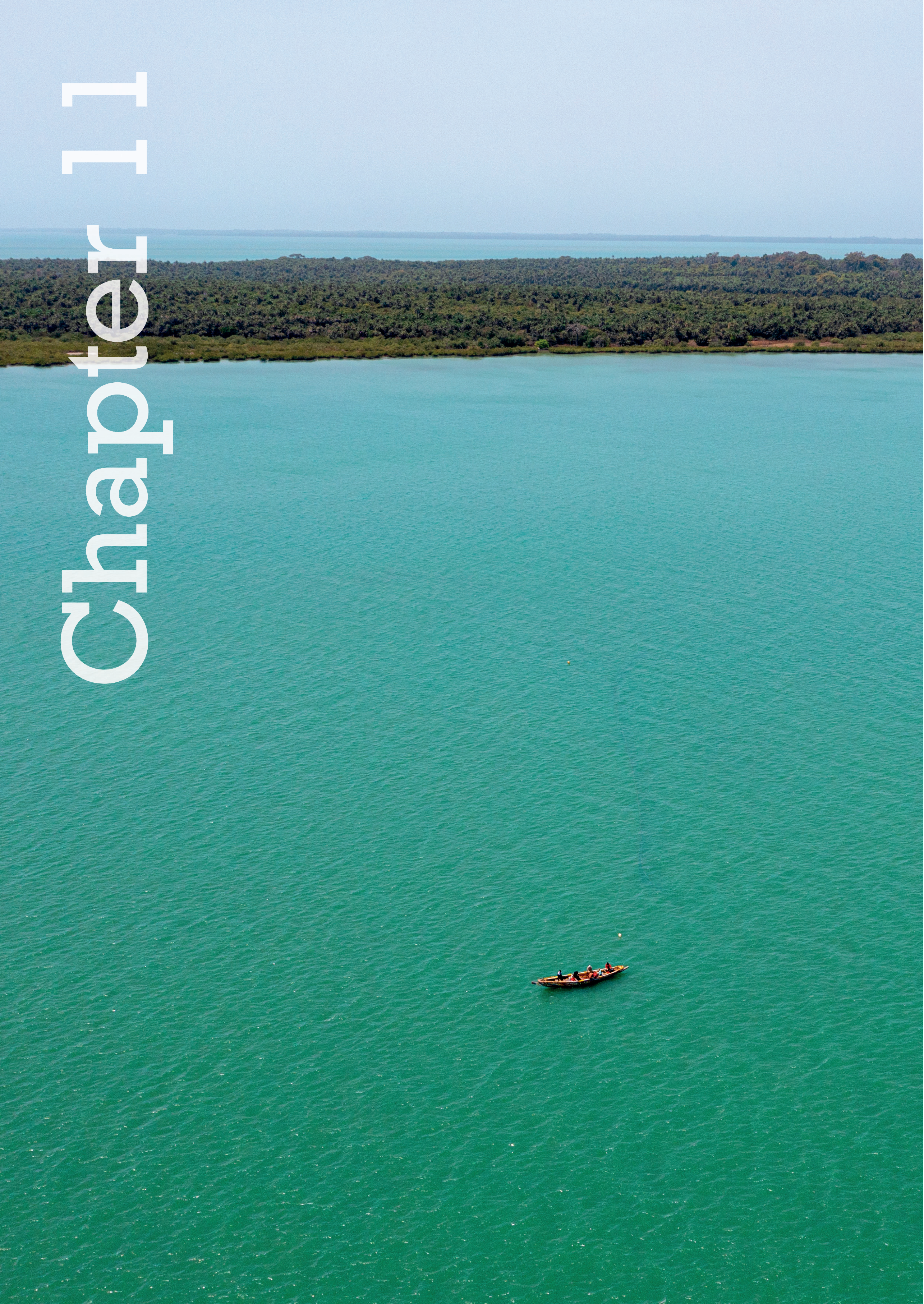
# Chapter 11



# 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.

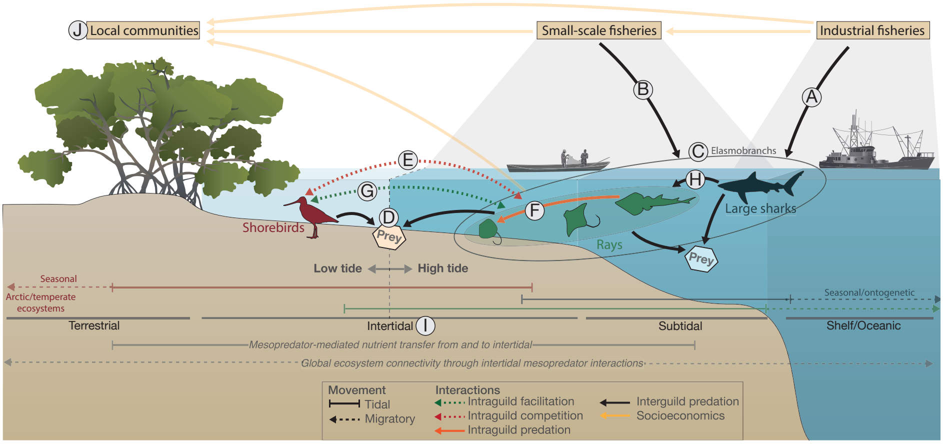


**Figure 11.1** Overview of interactions and processes discussed in this chapter in the context of intertidal area functioning and connectivity: The impact of industrial (A) and small-scale fisheries (B); The differences in elasmobranch diversity between my study areas (C); Trophic niche overlap between 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**).

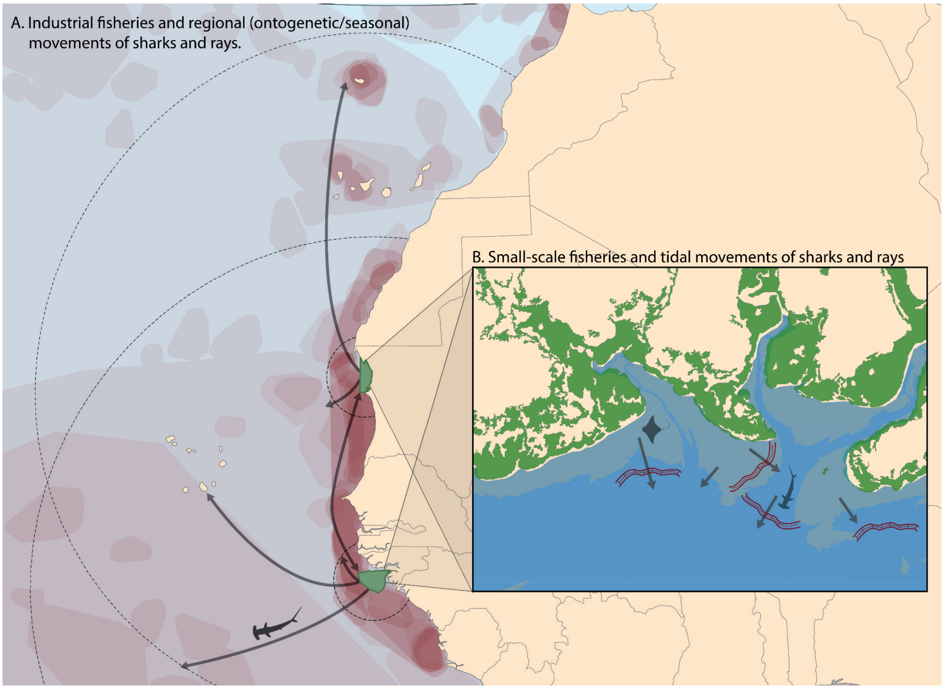


**Figure 11.2** A conceptual overview of the overlap between fisheries and shark and ray movements in the West African region. (A) Industrial fisheries concentrated on the continental shelf (red; data from Chapter 2) overlap with ontogenetic or seasonal movements of sharks using the Banc d'Arguin and 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**).

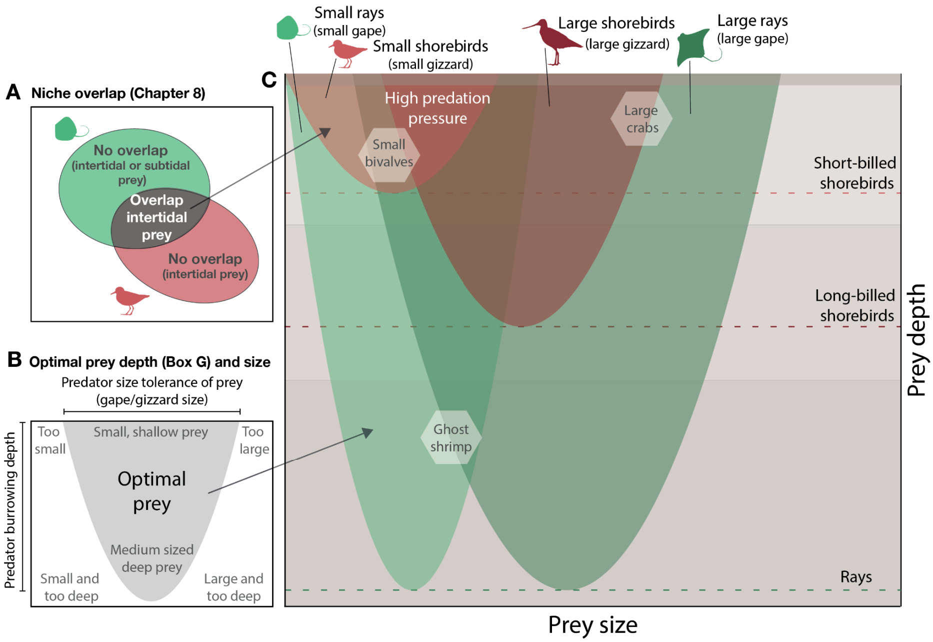


**Figure 11.3** (A) Trophic niche overlap between shorebirds (red) and rays (green) indicates the proportion of intertidal resources both mesopredators exploit (**Chapter 8**). To maximize prey intake rate while these intertidal prey are accessible, predators minimize handling times and maximize prey 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).

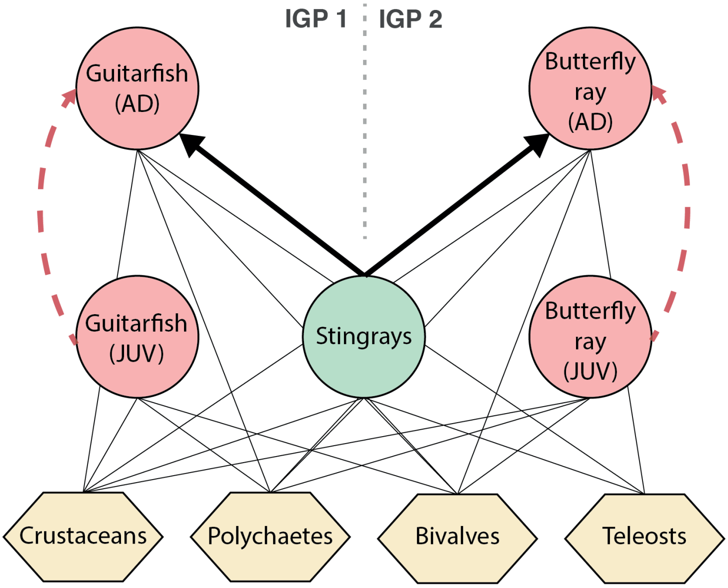


**Figure 11.4** Two conceptual modules of intraguild predation (IGP) in large intertidal systems: the predation on stingrays by adult blackchin guitarfish (IGP1) and adult spiny butterfly rays (*Gymnura altavela*, IGP2). The intraguild predation (highlighted by black arrows) occurs when intraguild predators (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).

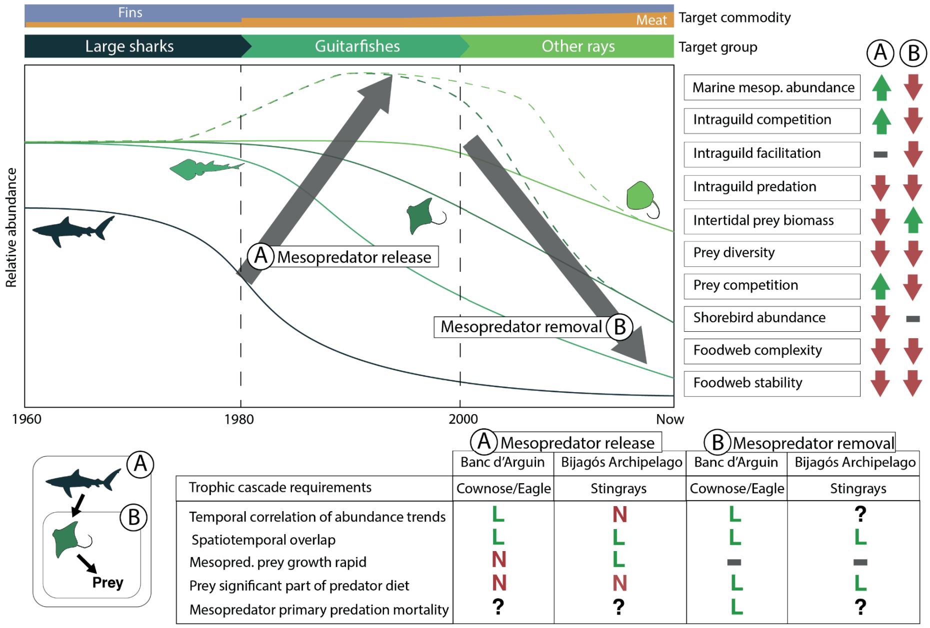
## *Intraguild facilitation (G)*

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.

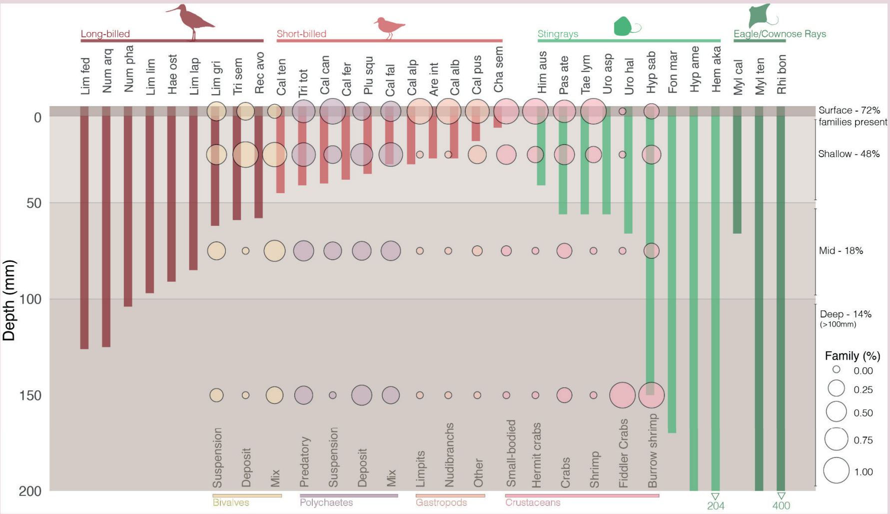


**Figure G1** The comparative probing (red bars) and burrowing (green bars) depths of different species of shorebirds using intertidal areas. We show the probing depth for long-billed shorebirds (i.e., bill length >50 mm; dark red) and short-billed shorebirds (i.e., bill length <50mm; light red), and 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.

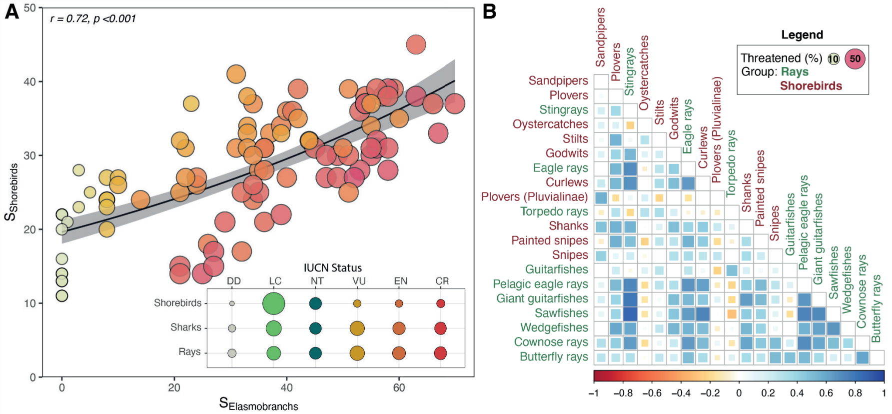


**Figure G2 (A)** The correlation between species richness (S) of elasmobranchs and shorebirds of the 100 largest intertidal areas. Circle size indicates the proportion of threatened species in an area. The insert plot shows the total proportion of shorebird, shark and ray species in each IUCN Red List 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).