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).

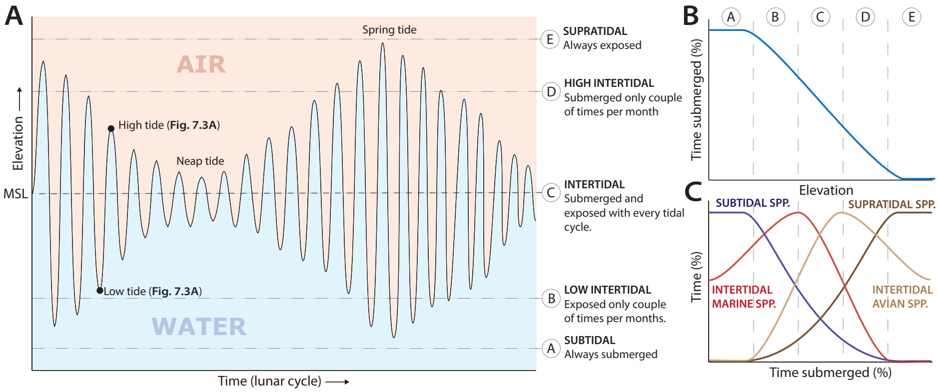

Figure 7.1 Intertidal habitats are strongly influenced by the tide, being submerged and exposed at least once per day (A). Compared to subtidal (i.e., always submerged habitat) or supratidal habitats (i.e., always exposed habitat), intertidal habitats are submerged for a certain amount of time each day (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).

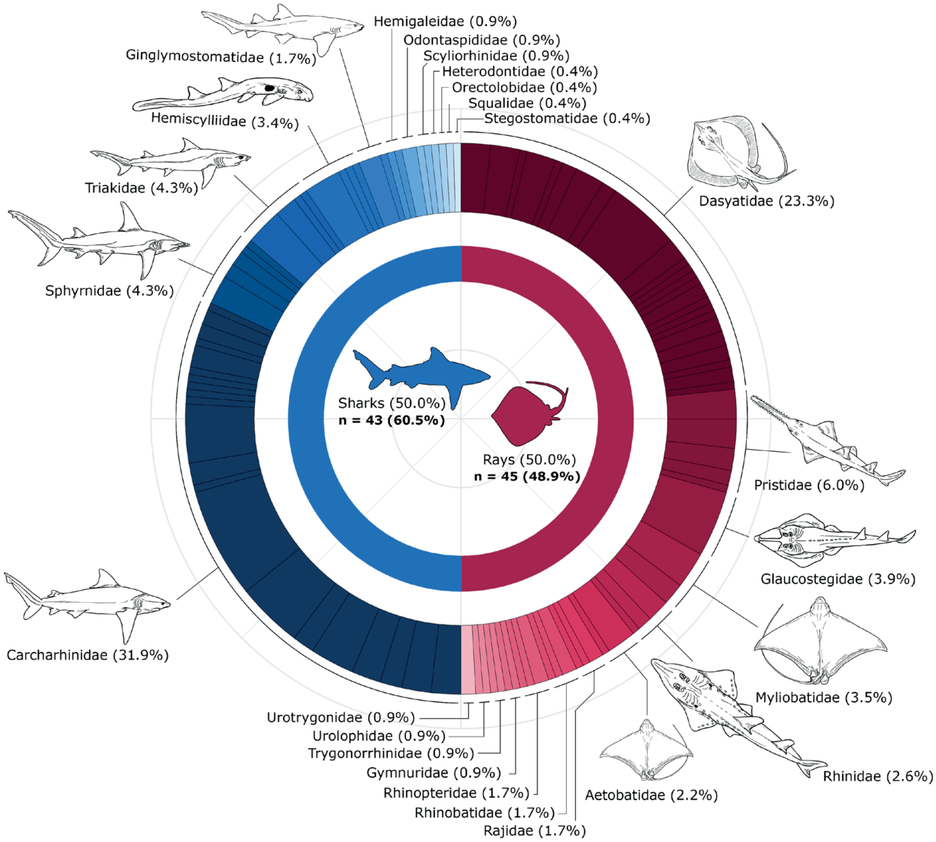

Figure 7.2 The shark (blue) and ray (red) families for which intertidal habitat use has been confirmed. Percentages indicate the relative number of observations of a family in the reviewed studies. The different species for which intertidal habitat use was confirmed are indicated by the different segments (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).

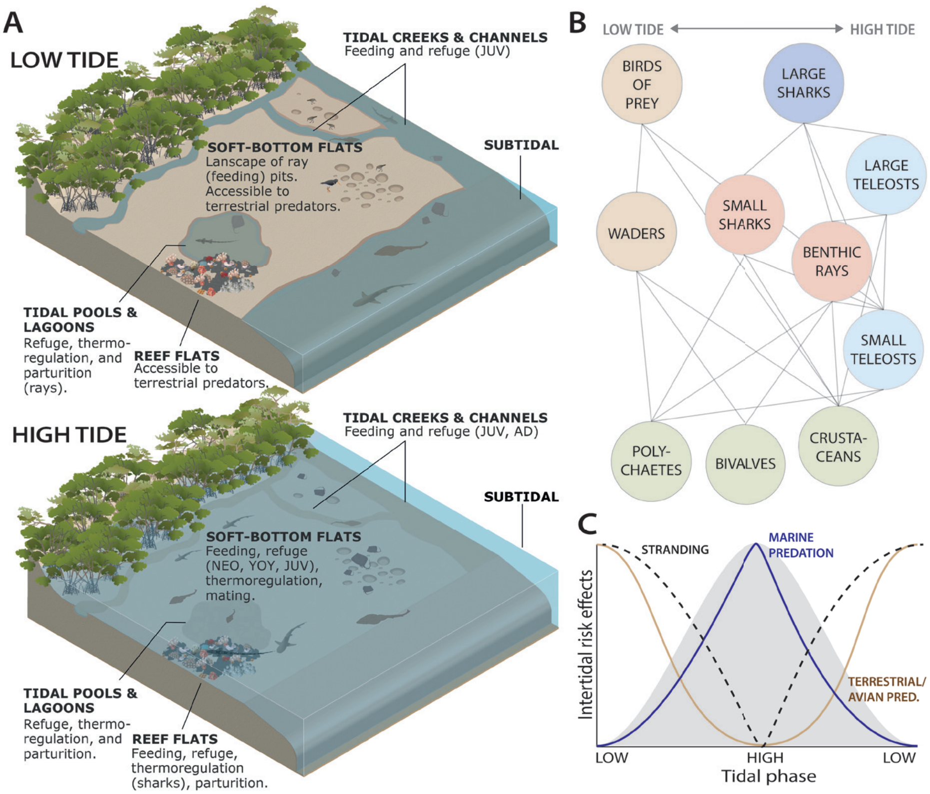

Figure 7.3 A: Conceptual visualization of intertidal habitat use by elasmobranchs for both tidal phases, low tide (top) and high tide (bottom). (NEO = neonates, YOY = young-of-the-year, JUV = juveniles, AD = adults). B: Simplified intertidal food web consisting of intertidal prey species (green), low-tide 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).

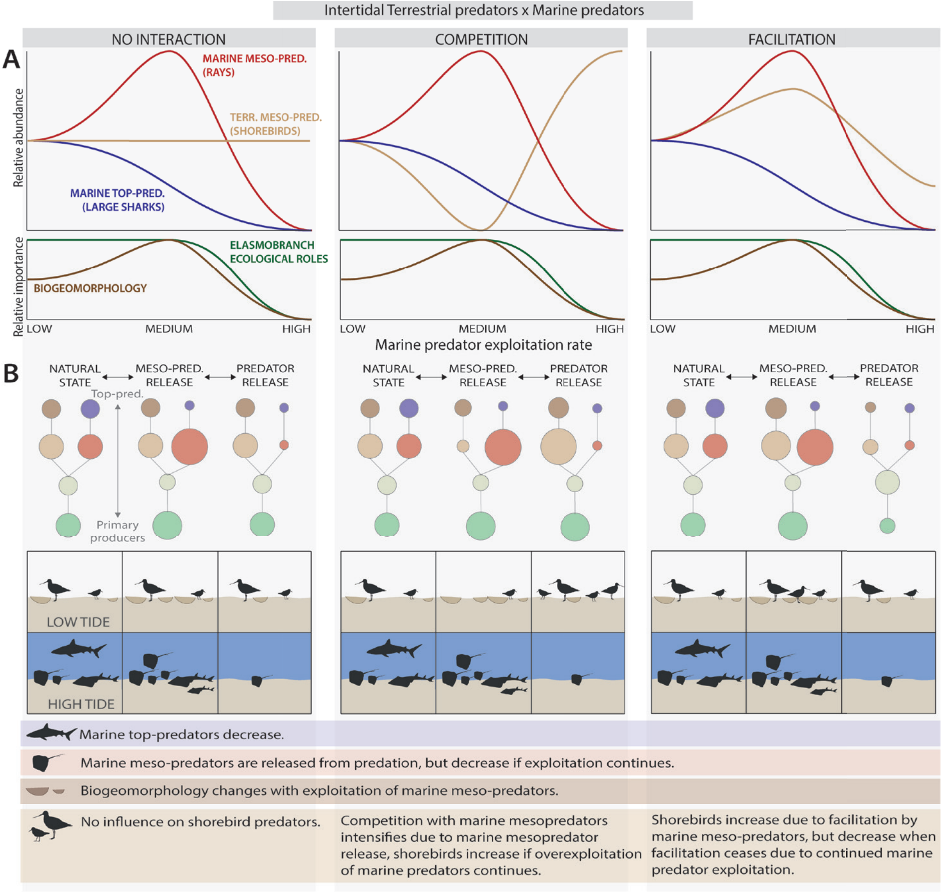

Figure 7.4 Conceptual overview of the influences that elasmobranch overexploitation in intertidal areas can have on low-tide predators like shorebirds, depending on the type of interaction (competition or facilitation) and assuming that decreases in top-predator abundance will lead to increases in mesopredators. 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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