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REVIEW

Mangrove use by sharks and rays: a review

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ABSTRACT: A wide variety of species depend on mangroves, making them essential habitats in tropical and subtropical regions. While the function of mangrove habitat is well studied for taxa such as teleost fishes, limited attention has been directed towards their value for elasmobranchs. Here, we review the available literature on how and why elasmobranchs use mangrove habitats based on 65 papers identified through literature searches. The use of mangrove habitat as nursery areas in combination with other coastal habitats has been well examined, although we found taxonomic and regional biases in research. Additionally, mangrove habitats are considered to offer elasmobranchs feeding opportunities and refuge from predators, yet such functions have rarely been tested. In particular, the ecological role of elasmobranchs within mangrove habitats is poorly known; as it is difficult to study their behaviour in complex mangroves, their feeding ecology is understudied as are trophic linkages between mangrove and adjacent ecosystems. For a greater understanding of the association between mangroves and elasmobranchs, direct observations of elasmobranch behaviour in mangrove habitats are needed. Given global concern regarding mangrove loss, understanding how this affects elasmobranch populations will require long-term studies, particularly in those regions where losses are greatest. We identify 8 key research questions that will help improve this understanding.

KEY WORDS: Elasmobranch · Coastal wetland · Habitat function · Nursery · Connectivity · Nearshore

1. INTRODUCTION

Mangroves are among the most productive components of intertidal zones, rivers and estuaries of the tropics and subtropics (Kathiresan & Bingham 2001). In the strictest sense, the term mangroves refers to both mangrove plants and the areas dominated by mangrove trees and shrubs (Spalding et al. 2010). Mangroves occur as narrow fringes along shorelines, estuaries and rivers, or as broad forests covering wide areas of deltas or estuaries (Spalding et al. 2010). Mangroves are characterised by unique combinations of structural complexity and biological productivity. Mangrove roots and trunks offer physical structure, which aids in trapping sediments (Furukawa & Wolanski 1996, Chen et al. 2018), dampening

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*Corresponding author: shiori.kanno@my.jcu.edu.au coastal erosion (Thampanya et al. 2006, Mazda et al. 2007) and offering inhabitants shelter from extreme hydrodynamic events (e.g. tsunamis, cyclones) (Dahdouh-Guebas et al. 2005, Alongi 2008). Mangroves are highly productive ecosystems, with their primary production equal to that of tropical forests. This productivity is mediated by above- and below-ground biomass, such as mangrove trees (e.g. leaves, seedlings) and algae colonising roots and covering the forest floor (Robertson et al. 1992, Alongi 2014). Mangrove-derived nutrients then flow through coastal food webs via water movement (i.e. tides, currents) or active animal movement and are used and recycled inside and outside mangrove systems (Adame & Lovelock 2011, Gillis et al. 2014).

As mangrove habitats occur at the interface between marine, estuarine and freshwater areas, both biotic and abiotic factors undergo large changes (Knip et al. 2010). In mangroves, environmental factors such as water depth, temperature, salinity, turbidity, wave intensity and dissolved oxygen levels are constantly changing at tidal, daily and seasonal time scales (Lam et al. 2005). Such fluctuations in environmental factors ultimately determine a pattern in the accessibility of mangrove habitat on a daily or seasonal basis and how useable it is for associated organisms (Bradley et al. 2020). Thus, there is no such thing as a 'general' or 'typical' mangrove habitat and so their functions must be considered carefully and local context taken into account (Chittaro et al. 2005, Bradley et al. 2020).

Mangroves provide important habitats to an array of terrestrial and aquatic organisms, including economically and ecologically important species (Nagelkerken et al. 2008, Luther & Greenberg 2009, Rog et al. 2017), offering inhabiting species shelter, breeding and feeding grounds, and nesting sites (Nagelkerken et al. 2008). A wide range of micro- and macro- organisms (e.g. barnacles, tunicates, sponges, molluscs and crustaceans) are found in mangrove trees, roots and sediments, and many of those are the base of mangrove food webs that support mangrove ecosystems (MacDonald & Weis 2013). Mangrove habitats are also used by teleosts and other megafauna, including sea turtles, dolphins, dugongs, crocodiles, and sharks and rays (elasmobranchs) (Sievers et al. 2019). Thus, mangroves host a high diversity of species of bacteria, fungi, plants and animals, and they form a complex ecosystem as a whole, supporting and sustaining populations of a variety of organisms (Nagelkerken et al. 2008, Spalding et al. 2010). Despite these important roles, mangroves have been lost at alarming rates over the past century (Polidoro et al. 2010, Spalding et al. 2010). Between 1980 and 2005, more than one-third of mangrove areas were lost globally (FAO 2007). Although the most recent rate of deforestation has dropped to 3.4% between 1996 and 2020, the loss of mangrove cover is ongoing globally at 0.16% area lost per year, and is more severe in some regions (Friess et al. 2019). For example, in Southeast Asia, Central America and the Caribbean, loss is up to 0.7% area lost per year (Hamilton & Casey 2016, Bunting et al. 2022). Major threats to mangroves include coastal development for human activities, such as aquaculture, agriculture, infrastructure and tourism (Richards & Friess 2016, Friess et al. 2019, Goldberg et al. 2020), and climate change, particularly ocean warming and sea level rise (Lovelock et al. 2015, Walden et al. 2019). The loss of mangroves affects those organisms that use and benefit from them (e.g. Shinnaka et al. 2007, Carugati et al. 2018), and the loss of biodiversity is negatively affecting ecological functions in coastal systems (Carugati et al. 2018).

The importance and function of mangrove habitats in coastal systems have received growing attention, with increasing concerns for global mangrove loss. For example, the value of mangrove habitats and associated coastal systems for teleost fish has been intensively studied for the last 50 yr, and the findings have been widely reviewed (e.g. Faunce & Serafy 2006, Nagelkerken et al. 2008, Lee et al. 2014, Whitfield 2017). For elasmobranchs, there are studies that have examined the importance and function of nearshore or intertidal habitats where mangroves are present (e.g. Knip et al. 2010, Leurs et al. 2023). Yet compared to teleosts, fewer studies have been conducted that focus on the importance of mangroves, mangrove habitat and associated coastal systems. At the very least, there is no review available on the value, function and role of mangroves and associated coastal systems to elasmobranchs.

Understanding the relationship between elasmobranchs and mangroves is of growing importance because coastal elasmobranchs are increasingly threatened with extinction. More than one-third of elasmobranchs are now threatened with extinction, and more than 50% of those threatened species inhabit coastal habitats (Dulvy et al. 2021). Habitat loss and degradation is one of the major threats to species, and ongoing degradation of coastal vegetated habitat, including mangroves, can negatively affect coastal elasmobranch populations by lowering the survival rate of juvenile sharks (e.g. Jennings et al. 2008, Dulvy et al. 2021). Therefore, a better understanding of the value and importance of mangroves for this group is urgently required to predict how mangrove loss and alteration of mangrove ecosystem functions will affect elasmobranch populations and their recovery potential, as well as to help guide habitat-based conservation processes both for mangrove habitats and coastal elasmobranch populations.

The objectives of this work were to (1) describe the current understanding of the relationship between elasmobranchs and mangroves, (2) identify the important functions of mangrove habitats and associated coastal systems for elasmobranch species, and (3) identify a series of key research questions that will help improve knowledge on the importance of mangroves, mangrove habitats and associated coastal systems to elasmobranch populations. For the purpose of this review, we specifically used literature where research has been conducted to examine the importance and functional role of mangroves towards the studied species and included research conducted directly inside mangroves (mangrove habitats) and in associated coastal systems.

2. LITERATURE REVIEW METHODS

We reviewed research articles that studied the relationships between mangroves and elasmobranch species; for example, direct utilisation of mangrove habitat (e.g. rays resting among the root structures), occurrence in mangrove habitats or associated coastal systems (e.g. juveniles showing habitat preference and spending their first several years in coastal systems that include mangrove habitat) or evidence of direct or indirect trophic linkage (e.g. species consuming mangrove-derived carbon sources). Conversely, this review did not include studies that were merely conducted in coastal systems and did not discuss the value and/or use of associated mangrove habitat for the studied species.

Literature searches were conducted using Google Scholar and Web of Science, with the search string using a combination of the terms 'mangrove*', 'shark*', 'ray*', 'elasmobranch*' and 'batoid*'. After the search, articles were carefully read and excluded from the list when search terms were used in a different context, such as *mangroves* in *Shark* River or when the study merely described the presence of mangroves but did not discuss their importance or functional role to the studied elasmobranch species. The reference lists of searched articles were also examined and added to the review if relevant. After the literature search, each article was examined and checked as to whether the research discussed or mentioned the importance or the roles of mangroves for the studied elasmobranch species. This process was performed to differentiate studies that merely described the presence of mangroves in a study site from studies that actually focused on the benefits or roles of mangrove presence.

3. OCCURRENCE OF ELASMOBRANCHS IN MANGROVE SYSTEMS

We identified 65 papers that recorded shark or ray species occurring in mangrove habitats or associated coastal systems and ascertained the relationship between mangroves and species i.e. value, use and linkage (see the Supplement at www.int-res.com/articles/suppl/m724p167_supp.pdf). While research on mangroves has occurred globally within their distribution, research on the use of mangrove habitat and associated coastal systems by elasmobranchs is more geographically limited and biased. Of the 65 papers identified, research was most commonly conducted in The Bahamas (18), Florida, USA (16) and Queensland, Australia (14) (Fig. 1). As some studies conducted research on multiple species and one study was conducted in multiple locations, a sum of total species and locations studied was 100. Unfortunately, there is little overlap between well-studied areas and the regions that have suffered from large net loss of mangroves, including Asia, Africa and North (outside of Florida), Central and South America (FAO 2007, Richards & Friess 2016, Goldberg et al. 2020), and where elasmobranch populations are most threatened, including the Indo-West Pacific around Southeast Asia, South America, and East and West Africa (Dulvy et al. 2021). Research is urgently needed in those regions to better understand how mangrove loss is potentially affecting elasmobranch populations.

Research on the relationships between elasmobranchs and mangrove systems has been conducted for 28 species, representing 13 genera and 7 families (sharks: 18 species, 6 genera and 3 families; rays: 10 species, 7 genera and 4 families) (Fig. 2). Of the 100 species–locations studied, 67 were restricted to 2 groups: 39 studies of requiem sharks (Family Carcharhinidae) and 20 of sawfishes (Family Pristidae), followed by 8 of stingrays (Family Dasyatidae). Whether this taxonomic representation is the result of bias in research studies (e.g. size, commercial value, conservation status, ease of study) or a reflec-

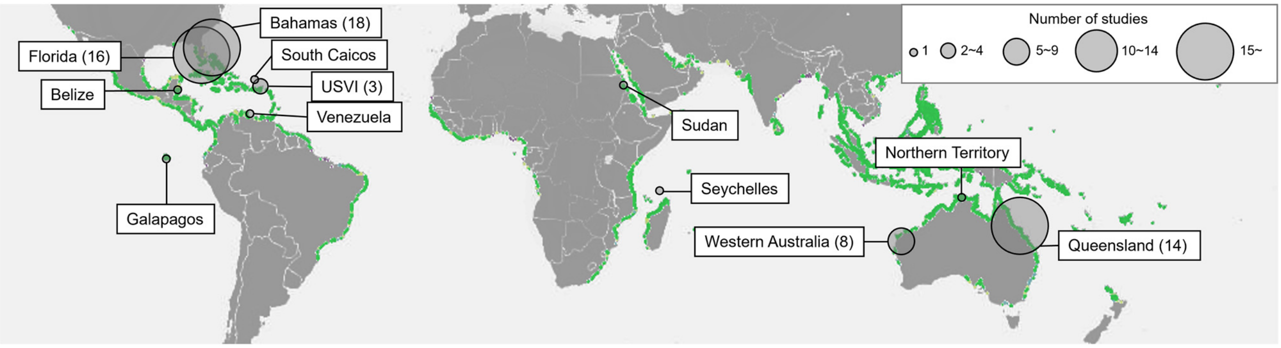

Fig. 1. Studied areas where research on the relationships between mangroves and elasmobranchs has been conducted. The data only include studies that discussed the relationship between mangroves and species; i.e. studies that merely mentioned the presence of mangroves in the study site but did not discuss the relationship were not counted. Green dots: distribution of mangroves. Mangrove distribution map was sourced from Mapping Ocean Wealth Explorer (https://maps.oceanwealth.org/mangrove-restoration/)

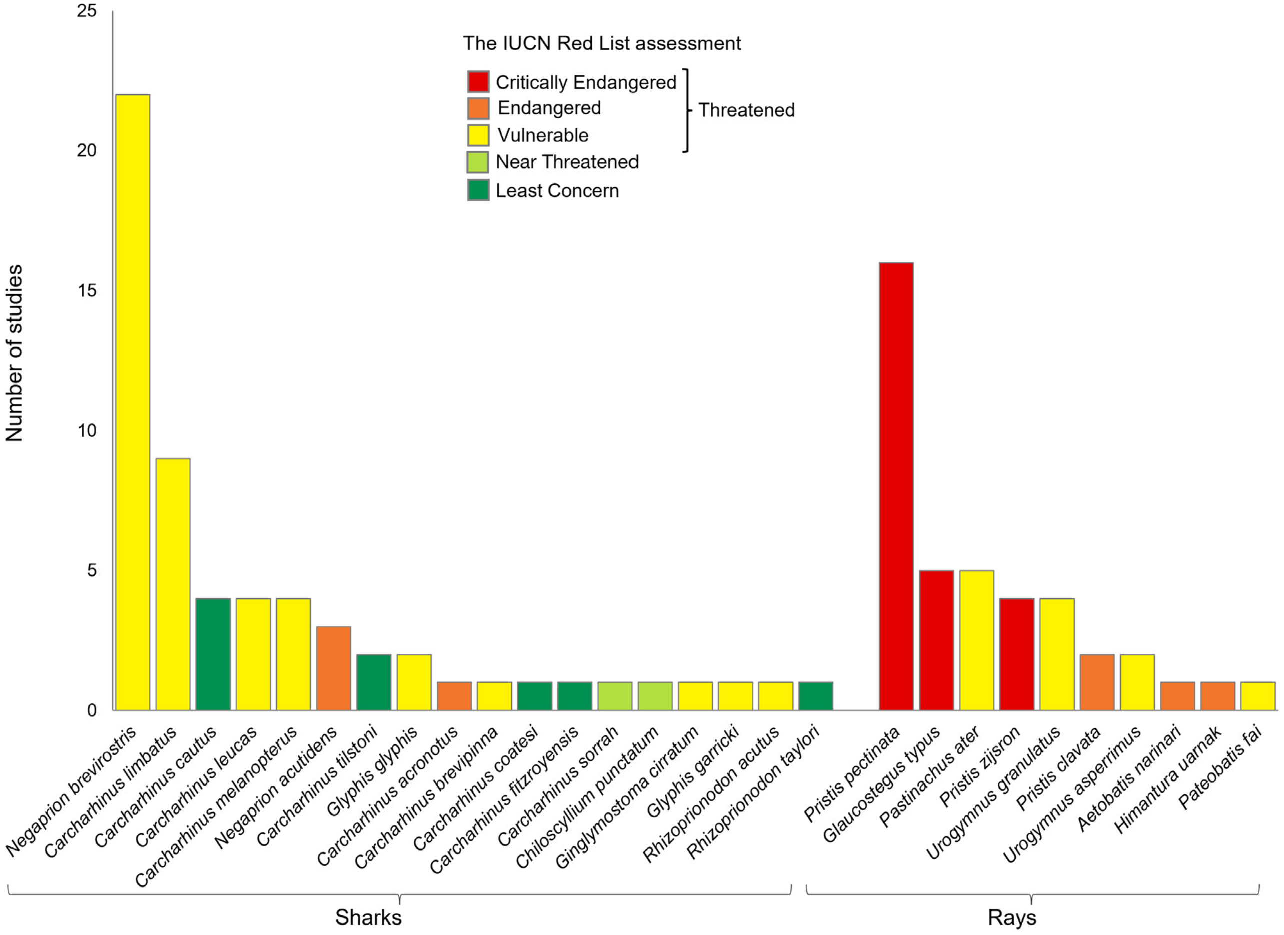

Fig. 2. Number of research articles on the relationships between mangroves and elasmobranchs for each species

tion of the groups that occur commonly in coastal tropical areas, and as such are most likely to have the opportunity to use mangrove systems, is currently unclear. A small number of species within the 3 most commonly reported families account for much of the research available (Fig. 2). Amongst sharks, the lemon shark *Negaprion brevirostris* is the most studied species (Fig. 3a), with multiple studies also on

Fig. 3. Shark and ray species swimming and resting among the mangrove roots: (a) lemon shark *Negaprion brevirostris*; (b) cowtail ray *Pastinachus ater*; (c) juvenile mangrove whipray *Urogymnus granulatus* and (d) sub-adult mangrove whipray. Photo credits: Baylie Fadool and Bimini Biological Field Station Foundation (a); C. A. Simpfendorfer (b–d)

common blacktip *Carcharhinus limbatus*, bull *C. leucas*, blacktip reef *C. melanopterus* and nervous *C. cautus* sharks. Lemon sharks have been studied for more than 40 yr in Bimini, The Bahamas, and nearly two-thirds of all the studies found in this review are from this region. The smalltooth sawfish *Pristis pectinata* is the most commonly studied ray species, and 2 other sawfish species have also been studied (*P. clavata* and *P. zijsron*). An increasing number of studies have revealed a close relationship between sawfishes (*Pristis* spp.) and mangroves, with conservation concern for this family increasing research needs and interests (Dulvy et al. 2016). Other commonly studied rays include the giant guitarfish *Glaucostegus typus*, mangrove whipray *Urogymnus granulatus* and cowtail ray *Pastinachus ater* (Fig. 3b–d).

One of the challenges in interpreting studies on elasmobranchs and mangrove habitats is that many previous studies have not clearly demonstrated how closely species were associated with mangrove habitats or associated coastal systems. For example, Simpfendorfer & Milward (1993) identified 6 species of shark from Cleveland Bay, Australia, from fishing surveys and noted that they occurred close to mangrove habitats (i.e. in a mangrove-fringed bay) but the study did not demonstrate direct use of mangrove habitat by those species. As other examples, White et al. (2014) and Pikitch et al. (2005) reported on the habitat preference of juvenile sharks and rays to coastal systems, but how those species interact with mangrove habitats within these systems or if they benefit from the presence of mangroves is unknown. By contrast, Davy et al. (2015) and George et al. (2019), using acoustic telemetry at Orpheus Island, Australia, reported specific use of mangrove habitat (i.e. inside the mangrove root habitat) and associated coastal habitats by mangrove whipray and blacktip reef sharks that were repeatedly resting under or swimming within the root structure (Fig. 3). Newman et al. (2010) is another example of a study that investigated a detailed role of mangrove habitat and associated coastal system, finding overlap between lemon shark diet and mangrove communities (e.g. the community composed of mangroves and mangrove-associated organisms, including micro-organisms, plants and animals; Kathiresan & Bingham 2001), suggesting that sharks relied on the mangrove community for their diet. This level of detail is what is needed from more studies to closely assess the functional role of mangroves to elasmobranchs. Our understanding of how important mangroves are for this group is limited due to a lack of research on how closely shark and ray species are associated with mangrove habitats.

The majority (44 out of 65) of studies on sharks and rays associated with mangrove habitats focused on juveniles, often identifying mangrove habitat or associated coastal systems as nursery areas (see Section 4.3 for more on this topic). The preponderance of studies on juveniles may be because, for many coastal species, the youngest animals are found in the shallowest waters, and so would be more likely to be associated with coastal systems where mangrove trees can survive. However, adult individuals of some species are known to occur adjacent to mangrove habitats and may gain benefits from mangrove ecosystems (e.g. blacktip reef sharks *C. melanopterus*, Chin et al. 2016; nervous sharks *C. cautus*, Escalle et al. 2015; spottail sharks *C. sorrah*, Knip et al. 2012; freshwater sawfish *Pristis pristis*, Morgan et al. 2015). Further research focused on adults associated with mangrove habitats or associated coastal systems will help resolve the reasons for this bias in studies and better elucidate the importance of mangrove habitats for adult elasmobranchs.

The conservation status of most species of elasmobranch associated with mangrove habitats and associated coastal systems is of concern. Of 28 species studied that were found in our literature search, 21 are in a threatened category based on recent International Union for Conservation of Nature (IUCN) Red List assessments: 13 Vulnerable, 5 Endangered and 3 Critically Endangered (Fig. 2). The only species not in a threatened category were 4 carcharhinids that occur only in northern Australia and southern Papua New Guinea. All ray species found in this review are categorised as threatened. This result is not surprising, given that coastal elasmobranch species are the most threatened elasmobranch group (Dulvy et al. 2021). Further research to understand the level of association with and benefits derived from mangroves will benefit conservation efforts for these species. One successful example of where research is informing conservation of a threatened elasmobranch species is found in the work on sawfish in US waters (e.g. Norton et al. 2012, Dulvy et al. 2016, Brame et al. 2019). This work is underpinning increased conservation efforts.

4. FUNCTIONS OF MANGROVES FOR ELASMOBRANCH SPECIES

Mangroves have been documented to provide a broad range of ecosystem goods and services, in part because they occur at the junction of the marine and terrestrial realms, have high primary productivity and complex trunk and root structures. These functions include providing habitat for both terrestrial and aquatic organisms, refuge from adverse conditions, a source of primary productivity and areas for feeding, mating and birthing, improving water quality, reducing coastal erosion and mitigating storm impacts on coastal systems (Alongi 2008, Nagelkerken et al. 2008, Lee et al. 2014). Here, we consider only those functions that have been identified, or hypothesised, to be relevant for elasmobranchs.

4.1. Physical shelter and refuge from predation

Densely growing mangrove trees offer effective shelter from potential predators where organisms can hide and rest between or under the complex structures formed by the trunks and roots (e.g. Cocheret de la Morinière et al. 2004, Mumby 2006). This function has been demonstrated for a number of shark and ray species using at least 2 different approaches. Firstly, experimental studies have been conducted to understand predation risk and habitat use in a controlled setting. For example, Stump et al. (2017) demonstrated that juvenile lemon sharks (~60 cm precaudal length [PCL]) tended to swim close to artificial mangrove units when a large potential predator (a 116 cm PCL lemon shark) was present, suggesting the importance of root-like structures for their anti-predator behaviour. The second line of evidence is direct observation using either video or photos (e.g. Davy et al. 2015, Kanno et al. 2019), or telemetry (e.g. George et al. 2019, Martins et al. 2020a,b). For example, Kanno et al. (2019) used video cameras mounted in mangrove trees to demonstrate that small mangrove whiprays used mangrove root habitats during high tides, while large sharks were excluded. Martins et al. (2020a,b) confirmed this behaviour using satellite-linked data loggers and acoustic telemetry. Based on field observations, a range of species are hypothesised to display refuging behaviour in structurally complex mangroves, such as smalltooth sawfish (Simpfendorfer et al. 2010, Poulakis et al. 2011, Hollensead et al. 2018, Lear et al. 2019), dwarf sawfish (Stevens et al. 2008), mangrove whiprays, cowtail rays (Kanno et al. 2019, Martins et al. 2020b) and blacktip reef sharks (George et al. 2019). Additionally, turbid water in mangrove habitats is thought to reduce the ability of predators to locate prey, decreasing predation risk for inhabitants (Cerutti-Pereyra et al. 2014), but this is yet to be specifically tested.

The ability of elasmobranchs to use mangrove habitat as a refuge from predation is likely to be a function of a number of physical features of the habitat. The level of tidal inundation is one important factor since habitats can only be accessed when there is sufficient water present (Davy et al. 2015). Given the nature of tides, greater access to the habitat would be available during spring tides compared to neap tides. Indeed, depending on the amount of tidal variation, there may be some periods during neap tides when no access to mangroves is available. In some microtidal systems, such as in parts of the Caribbean, there is near-continuous access to mangrove habitat, albeit very shallow (Sheaves 2005, Krumme 2009). A second physical characteristic that affects the level of refuge is the complexity of the mangrove habitat. This is a function of at least 2 things: the density of trees and the form of their root structure. Across the full range of mangrove species (73 species and hybrids; Spalding et al. 2010), there are many root structures, from simple straight trunks and pneumatophores and knee roots (e.g. *Avecinnia*, *Bruggeria*) to moderately complex buttress roots (e.g. *Heritiera*) to highly complex prop roots (e.g. *Rhizophora*) (Ewel et al. 1998). Hollensead et al. (2018) demonstrated, using acoustic tracking, that juvenile smalltooth sawfish were more commonly found in areas with higher prop root density, supporting the hypothesis that more complex habitats are likely to provide greater refuge.

Characteristics of the elasmobranch species also are important for how mangrove habitat is used as a refuge. For example, body size is one of the characteristics that can affect mangrove refuge use. The complexity of mangrove habitats, especially those composed of mangrove species that have dense prop roots, means that smaller sized individuals will likely have greater access and manoeuvrability within mangrove habitat and so be more likely to take advantage of it as a refuge. This hypothesis is supported by research showing that most species confirmed to occur within mangrove habitats are often newborn or small juveniles, including lemon sharks (e.g. Morrissey & Gruber 1993), blacktip reef sharks (e.g. George et al. 2019) and mangrove whiprays (e.g. Davy et al. 2015). However, there are some reports of larger juveniles and even adults refuging within mangrove habitats, including adult dwarf sawfish (Stevens et al. 2008) and mangrove whiprays (C. A. Simpfendorfer unpubl. data) (Fig. 3d). In the case of dwarf sawfish, large potential predators (e.g. great hammerheads *Sphyrna mokarran*, tiger sharks *Galeocerdo cuvier* and estuarine crocodiles *Crocodylus porosus*) were observed in the area (Stevens et al. 2008), suggesting that the refuge function can still be important even for larger individuals. Additionally, body shape is also likely to play a role in the successful use of mangrove habitat as a refuge from predation. Dorso-ventrally flattened rays, for example, would be able to gain access to mangrove habitat on lower tidal heights than deeper bodied species such as sharks, allowing them to remain in shallow water longer, as their water depth requirements are lower. Respiratory mode may be another characteristic of species that allows for the use of mangrove habitat as a refuge. Species that can rest on the bottom and use buccal pumping and spiracles to enable water flow over their gills should be able to use the most complex of mangrove habitats, including resting under and among roots and trunks (Fig. 3). This type of behaviour is regularly observed with mangrove whiprays that spend long periods resting in complex structure (Davy et al. 2015). Such concealment would have significantly greater benefit for these species than for ram-ventilating species that must continue to swim and manoeuvre within complex habitats.

To date, few studies have considered the importance of the biological and physical features of elasmobranchs to the level of refuge from predation that elasmobranchs generate from mangrove habitats (e.g. Stump et al. 2017, Kanno et al. 2019). Future research that investigates those characteristics will enhance our understanding of the protective role that mangrove habitats play for elasmobranchs.

4.2. Feeding grounds and food hotspots

Due to their high primary productivity, mangrove communities are thought to be a good food source for a wide range of organisms, including crustaceans (Wassenberg & Hill 1993) and teleosts (Nagelkerken & van der Velde 2004b). The importance of mangrove communities for teleost feeding is well studied, and accordingly, both mangrove residents and migrants from adjacent habitats feed in mangrove habitats (e.g. Nagelkerken et al. 2000a, Nagelkerken & van der Velde 2004a,b, Verweij et al. 2006, Nanjo et al. 2008). Mangrove habitats attract a variety of invertebrates and vertebrates partly because of such substantial feeding opportunities, and thus are considered to host many potential prey items for some elasmobranchs. Newman et al. (2010) is one of the only studies that directly examined the stomach contents of a shark species and the faunal communities in a mangrove habitat where the sharks occur. They found a high overlap between the diet of juvenile lemon sharks *Negaprion brevirostris* and the faunal communities in the mangrove habitats in Bimini, The Bahamas. Recently, Kanno et al. (2019) conducted stationary video monitoring using above-water cameras, and observed stingray feeding behaviour among mangrove roots multiple times, which may be the first direct observation of an elasmobranch species feeding directly in mangrove habitats.

Although direct observation of feeding activity by elasmobranchs is scarce, an indirect approach is to compare mangrove-derived carbon stable isotope signatures and elasmobranch diets. For example, Hussey et al. (2017) conducted active acoustic telemetry tracking and stable isotope analysis (carbon and nitrogen isotopes) on juvenile lemon sharks in Bimini to assess the foraging locations of individuals within the mangrove and adjacent seagrass habitats. Their results highlighted that individuals with slow growth rates and small body sizes predominantly fed on prey from the sheltered mangrove habitats rather than more open seagrass beds. Shipley et al. (2019) conducted a multi-tissue stable isotope study in Florida Bay, USA, to investigate whether prey resources of coastal shark species were derived from mangrove or coastal neritic (seagrass and/or coral reef) ecosystems. Accordingly, at least for the short term (2–3 mo), all shark species tested obtained prey with carbon signatures originating from mangrove primary production, but over the long term (6–12 mo), the degree of contribution of mangrove- and neritic-ecosystem-derived food resources differed depending on species, possibly due to different lifestyle and residency patterns. These studies demonstrate that species do not have to physically occur within mangrove habitats to derive benefits from mangrove productivity. However, a recent study has found that this trophic linkage is not simple and differs between species or the local nutrition availability. Martins et al. (2022) showed that 2 species of stingray that commonly occur in mangrove habitats (mangrove whipray and cowtail ray) had carbon isotope signatures indicating that they fed from food webs based on algal productivity in adjacent habitats. This indicates that just because a species occurs in a mangrove habitat, it does not necessarily derive significant nutrition from food webs based on mangrove primary productivity.

From the reviewed literature, mangrove communities can play an important role in providing food resources to some elasmobranch species (at least indirectly). Overall, previous findings are limited and strongly biased towards a small number of well-studied locations (e.g. Bimini, The Bahamas, and Orpheus Island, Australia) and study species (e.g. lemon shark, mangrove whipray). Some mangrove habitats, particularly those with dense prop roots, may be too structurally complex to successfully hunt in, especially for those species that consume highly mobile prey (e.g. Newman et al. 2010, Lear et al. 2019). Thus, the common assumption that mangroves provide feeding opportunities to elasmobranch species remains to be fully tested. Further research is required for various species to confirm that mangrove habitats provide (or do not provide) food resources to elasmobranchs directly or indirectly.

4.3. Nurseries

One of the most commonly assigned functions of mangrove habitats and associated coastal systems is as nursery areas, not only for elasmobranchs (Heupel et al. 2018) but also teleosts (Nagelkerken et al. 2000b, Nagelkerken 2009) and crustaceans (Primavera 1998). For elasmobranchs, this review identified 28 research articles that met all 3 nursery criteria proposed by Heupel et al. (2007), demonstrating that mangrove habitats are important nursery areas for at least 22 species (Table 1). The use of coastal systems, and especially mangrove habitat within these systems, as nursery areas likely occurs for reasons often associated with nursery areas — an abundance of food and protection from predators (Heupel et al. 2007). As identified in Sections 4.1 & 4.2, both of these are features of mangrove habitat that are used by juvenile elasmobranchs.

Neonates and small juveniles (the age classes that occupy nursery areas) of some elasmobranch species are regularly observed within fringing, riverine and dwarf mangroves at many locations, and there is a consensus that habitats in mangrove systems are often used as pupping grounds or nursery areas (e.g. Heupel et al. 2018). Although parturition has rarely been directly observed, anecdotal evidence suggests that some species give birth in mangroves habitats or associated coastal systems, including lemon sharks (Gruber et al. 2001, Feldheim et al. 2002, DeAngelis et al. 2008, Henderson et al. 2010), sicklefin lemon sharks *Negaprion acutidens* (Oh et al. 2017), blacktip

Table 1. Species known to use mangrove systems as a nursery area. Literature cited as a reference in this table is a comprehensive list of research articles that meet all 3 nursery criteria proposed by Heupel et al. (2007). LC: Least Concern; VU: Vulnerable; EN: Endangered; CR: Critically Endangered

Species	IUCN Red List status	Location	Mangrove systems	Reference
Sharks				
Carcharhinus coatesi	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer & Milward (1993)
Carcharhinus fitzroyensis	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer & Milward (1993)
Carcharhinus leucas	VU	Florida, USA	Estuarine and riverine mangroves	Simpfendorfer et al. (2005) Wiley & Simpfendorfer (2007) Heupel & Simpfendorfer (2008) Heupel et al. (2010) Curtis et al. (2011)
Carcharhinus limbatus	VU	United States Virgin Islands, USA	Coastal fringing mangroves	DeAngelis et al. (2008) Legare et al. (2015)
		Santa Cruz Island, Galapagos	Coastal fringing mangroves	Llerena et al. (2013)
		Queensland, Australia	Coastal fringing mangroves	Simpfendorfer & Milward (1993)
Carcharhinus melanopterus	VU	Queensland, Australia	Coastal fringing mangroves	Chin et al. (2013)
Carcharhinus tilstoni	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer & Milward (1993)
Ginglymostoma cirratum	VU	Glover's Rees, Belize	Coastal fringing mangroves	Pikitch et al. (2005)
Glyphis garricki	VU	Western Australia	Estuarine and riverine mangroves	Morgan et al. (2011)
Glyphis glyphis	VU	Western Australia and Northern Territory, Australia	Estuarine and riverine mangroves	Pillans et al. (2009)
		Queensland, Australia	Riverine mangroves	Lyon et al. (2017)
Negaprion acutidens	EN	Western Australia	Coastal fringing mangroves	Oh et al. (2017)
Negaprion brevirostis	VU	Bimini, Bahamas	Coastal mangroves	Morrissey & Gruber (1993) Feldheim et al. (2002) Chapman et al. (2009) Guttridge et al. (2012)
		United States Virgin Islands, USA	Coastal fringing mangroves	DeAngelis et al. (2008) Legare et al. (2015)
Rhizoprionodon acutus	VU	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer & Milward (1993)
Rhizoprionodon taylori	LC	Queensland, Australia	Coastal fringing mangroves	Simpfendorfer & Milward (1993)
Rays				
Glaucostegus typus	CR	Western Australia	Fringing mangroves	Cerutti-Pereyra et al. (2014)
Himantura uarnak	EN	Western Australia	Fringing mangroves	Cerutti-Pereyra et al. (2014)
Pastinachus ater	VU	Western Australia	Fringing mangroves	Cerutti-Pereyra et al. (2014)
		Queensland, Australia	Fringing mangroves	Davy et al. (2015)
Pristis clavata	EN	Western Australia	Estuarine and riverine mangroves	Morgan et al. (2011)
Pristis pectinata	CR	Florida, USA	Coastal, estuarine and riverine mangroves	Wiley & Simpfendorfer (2007) Simpfendorfer et al. (2010) Poulakis et al. (2011) Norton et al. (2012) Poulakis et al. (2013) Carlson et al. (2014)
Pristis pristis	CR	Western Australia	Estuarine and riverine mangroves	Whitty et al. (2008)
Pristis zijsron	CR	Western Australia	Estuarine and riverine mangroves	Morgan et al. (2011) Morgan et al. (2015)
		Red Sea, Sudan	Fringing mangroves	Elhassan (2018)
Urogymnus asperrimus	VU	Western Australia	Fringing mangroves	Cerutti-Pereyra et al. (2014)
Urogymnus granulatus	VU	Queensland, Australia	Fringing mangroves	Davy et al. (2015)

reef sharks *Carcharhinus melanopterus* (Chin et al. 2013, Oh et al. 2017), nurse sharks *Ginglymostoma cirratum* (Pikitch et al. 2005), smalltooth sawfish (Poulakis et al. 2016), giant shovelnose rays *Glaucostegus typus* (White et al. 2014) and southern stingrays *Hypanus americana* (Pikitch et al. 2005). Lemon sharks in Bimini, The Bahamas, have been well studied using long-term tagging and genetic methods and revealed that mature females return to their natal nursery area associated with mangrove habitats to give birth (known as natal philopatry) (Feldheim et al. 2014). Similarly, pregnant female smalltooth sawfish show philopatric movement to mangrove-lined nearshore nurseries in mangrove-fringed estuarine systems for parturition (Poulakis et al. 2016). After pupping, neonates tend to remain in their natal areas for an extended period, suggesting the importance of those habitats for juvenile survival as potential nursery grounds (Gruber et al. 2001, Chapman et al. 2009).

Mangrove-associated nursery sites have often been considered to be used by juvenile individuals for their first 2–3 yr (Gruber et al. 1988, Morrissey & Gruber 1993); however, the duration of nursery dependence varies by species and is not well tested. Chapman et al. (2009) is the exception, testing the question of how long individuals stay within nurseries. They found that more than half of up to 6 yr old lemon sharks still remained in the same nursery area. Similarly, Morgan et al. (2011) and Morgan et al. (2015) revealed that largetooth sawfish *Pristis pristis* stayed in nursery sites in tidal mangrove creeks for 3–4 yr, and thus the nursery areas are critical for largetooth sawfish early life-history stages from neonates to sub-adults. These findings suggest that mangrove habitats and associated coastal systems can act as a nursery longer than previously expected, and not only small-sized individuals (e.g. neonates) are using these systems as nursery sites, but also relatively large-sized individuals (e.g. 5–6 yr old, possible sub-adults).

The use of mangrove habitats and associated coastal systems as nursery areas by elasmobranchs is relatively well documented in research publications and has demonstrated that they can play an important role in supporting species at their most vulnerable life stage. It must be noted, however, that most of these previous studies were conducted in estuarine or coastal areas fringed by mangroves rather than directly in mangrove habitats, and thus have not investigated the direct association between mangrove habitats and elasmobranchs. Therefore, whether the presence of mangrove habitats actually benefits elasmobranchs or whether it is a coincidence based on preference for similar physical environments (e.g. shallow, low-salinity areas) is unknown for many species but should be tested with further research. Furthermore, fish–mangrove research has now come to the consensus that nursery function is context-dependent and not equivalent between mangrove habitats and associated coastal systems in different locations (e.g. Igulu et al. 2014), and the function for elasmobranchs may also be variable depending on context and environmental factors specific to a location.

4.4. Thermal refuge

The shallow waters in which mangrove habitats occur can be rapidly heated during sunny days and reach temperatures that approach or even exceed those which the inhabitants can tolerate. Such temperatures can have physiological costs to sharks and rays even if they do not reach critical levels (Bouyoucos et al. 2018). Mangrove branches and leaves create shade that lowers water temperatures relative to surrounding open areas and in doing so may provide a thermal refuge to inhabitants (Cocheret de la Morinière et al. 2004, Davy et al. 2015). In the reviewed literature, few studies have tested whether elasmobranchs use mangroves as a thermal refuge. A recent physiological study found that juvenile mangrove whiprays selected cooler water during the hottest periods of the day to avoid the extreme temperature range, including by inhabiting mangrove habitat (Higgins 2018). While warm water appears to assist effective digestion and food intake in juvenile mangrove whiprays (Tenzing 2014), a cooler water refuge, such as mangrove shade, may also be beneficial to inhabitants, particularly when water temperatures in sunny areas approach or exceed critical thermal maxima (e.g. Cocheret de la Morinière et al. 2004, Davy et al. 2015, Higgins 2018). Further research into this potential benefit of mangrove habitat is needed before it can be conclusively shown to benefit any species of elasmobranchs.

5. FUNCTION OF ELASMOBRANCHS FOR MANGROVES AND ASSOCIATED COASTAL SYSTEMS

Elasmobranch species play various important ecological roles, such as prey population control, energy vectors and bioturbation (physical and ecological engineering) in habitats, including seagrass beds, sandflats and coral reefs (e.g. O'Shea et al. 2012, Heupel et al. 2014, Roff et al. 2016, Leurs et al. 2023). The ecological roles of elasmobranchs in mangrove habitats are also likely important, although there is limited research that has specifically investigated their functional roles. As highly mobile predators, elasmobranchs have possible ecological functions specifically in linking mangrove habitats with the adjacent habitats, including translocating nutrients by their movement. Here, we gathered information on activities of elasmobranch species that may contribute to the ecological function of mangrove ecosystems.

Active migration of animals between mangrove habitats and adjacent habitats is known to translocate biomass, nutrients and minerals to the other systems, resulting in resource links between habitats (e.g. Kneib 2000). Many elasmobranch species exhibit migration between mangrove and adjacent habitats due to tidal fluctuations (e.g. Stevens et al. 2008, Guttridge et al. 2012, Davy et al. 2015, George et al. 2019) and ontogenetic change in biological and ecological needs (e.g. Simpfendorfer et al. 2005, Whitty et al. 2009, Knip et al. 2011, Werry et al. 2011, Poulakis et al. 2013, Carlson et al. 2014, White et al. 2014, Davy et al. 2015). Given the large individual biomass and high mobility of elasmobranch species, their contribution to trophic linkages between different coastal systems is potentially significant (e.g. Shipley et al. 2023), although it has not been quantitatively tested.

In addition to the movement of nutrients between coastal habitats, feeding activities of sharks result in consumptive and non-consumptive effects on prey species (Ritchie & Johnson 2009 in Vaudo & Heithaus 2011). Fear effects, for example, cause the behavioural change of prey species, such as small teleosts and rays refuging in mangrove habitats. Bottom feeding by ray species, alternatively, causes bioturbation that creates, shapes and modifies the physical and biological properties of the habitat, altering microbial loops in the system and ultimately contributing to restructuring food webs and energy and nutrient transfer (O'Shea et al. 2012). Thus, the feeding and predation activities of elasmobranchs influence community structure and function. Furthermore, elasmobranchs using mangrove habitats may also supply nutrients through excretion and egestion (Allgeier et al. 2013, 2017). Such consumer-mediated nutrient supply can enhance primary production in nutrient-limited ecosystems and consequently influence ecosystem function (Allgeier et al. 2013); this has not been tested for elasmobranchs in mangrove habitats but has been demonstrated in coral reef habitats (Williams et al. 2018).

6. KNOWLEDGE GAPS AND FUTURE DIRECTION RELATED TO USE OF MANGROVE HABITAT BY ELASMOBRANCHS

This review of the available literature indicates that many gaps remain in our knowledge of the relationship between mangrove systems and elasmobranchs. Below, we identify 8 key questions that we believe need to be addressed and investigated to improve our understanding of this relationship. Data resulting from the suggested research can ultimately inform management and conservation decisions regarding elasmobranchs as well as mangrove habitats and associated systems.

6.1. What is the full range of elasmobranch biodiversity that benefits from mangrove habitat?

Research on elasmobranchs that benefit from mangrove habitats currently shows bias toward a small number of species within a limited number of families and in a limited number of geographic locations. Research across more species that potentially utilise and benefit from mangroves and associated coastal habitats is required to understand the extent of benefits that the systems provide. Particularly, given the common occurrence of ray species in shallow nearshore areas and their ecological and economic importance (e.g. Pierce et al. 2009, O'Shea et al. 2012, Cerutti-Pereyra et al. 2014, Barría et al. 2015, Haas et al. 2017), a greater focus on rays in future research would be beneficial. Data resulting from this type of research can be important to elasmobranch conservation efforts, as it will assist in understanding the importance of mangrove habitats across a greater number of species in more geographic locations. Further information on threatened or rare species can be gained that will help us understand the role that mangrove loss may play as a threat to various elasmobranch species. Research focused in areas where mangroves and elasmobranchs are most threatened, such as Southeast Asia, West and East Africa, and South America, will be valuable.

6.2. How does the mangrove–elasmobranch relationship change with mangrove habitat context?

To date, published research has focused on a small number of systems in a limited range of mangrove contexts (e.g. red mangroves *Rhizophora* and clear water adjacent to coral reefs in marine nearshore systems) and, thus, our current understanding of other mangrove contexts remains poor. For example, it is largely unknown how estuarine and riverine mangroves are used by euryhaline species. Given the unique life history and habitat use of euryhaline species, it would be beneficial for their conservation, as mangrove loss may be critical for this group due to their limited and often fragmented distribution (Grant et al. 2019). The ecology and interactions of euryhaline species with mangroves are understudied. Future research should focus on a broader range of contexts (e.g. tidal regimes, time of day, turbidity level, mangrove species, geomorphologies, seasons) to better document how these factors affect the relationship between mangrove habitat and elasmobranchs.

6.3. What is the behaviour of elasmobranchs within mangrove habitats?

There is limited information available on the behaviour (i.e. feeding, interacting with other species, resting, refuging, etc.) of elasmobranchs inside mangrove habitats. This is mainly because mangrove habitats can be difficult systems in which to conduct research due to the complexity of habitats, soft sediments, intermittent inundation and presence of dangerous animals (e.g. crocodiles); and high water turbidity in many coastal mangrove systems makes direct observation and photography and/or video difficult to impossible. As a result, limited data is available on what species are doing in mangrove habitats, and where it is available the data comes mostly from mangroves in clearer water (e.g. Bimini, The Bahamas, and Orpheus Island, Australia). Added to this, the habitat complexity makes traditional methods such as fishing and telemetry challenging. Developing techniques to study elasmobranch behaviour in turbid-water mangrove habitats will be important in understanding whether there are differences with clear-water habitats and, if so, what those differences are. Recent advancements in imaging sonar may help reveal the distribution, size and behaviour of species inside mangroves even in low-visibility conditions or at night (e.g. Frias-Torres & Luo 2009). This would provide knowledge on how elasmobranch species are using mangrove habitats during the day and at night in clear or turbid water.

6.4. How important is mangrove primary production that flows through coastal food webs to elasmobranchs?

There is limited information available on how important mangrove-derived carbon is for elasmobranchs, and the evidence that exists is somewhat contradictory (e.g. Shipley et al. 2019, Martins et al. 2022). The presence of mangroves may be important to elasmobranch species that are physically absent from mangrove habitats because mangroves potentially provide food resources indirectly to species living away from mangrove habitats. Conversely, the loss of mangroves may affect populations that have no direct or clear association with the mangrove habitat. Studies that track the flow of carbon derived from mangrove primary production (e.g. using carbon stable isotope studies) over a range of spatial and temporal scales will help answer this question.

6.5. How important are elasmobranchs to habitat connectivity in coastal systems?

Given the mobility of elasmobranchs and their high individual mass compared to other taxa that occur in mangrove habitats, it is hypothesised that they may contribute significantly to the translocation of mangrove-derived production. Work to quantify this by examining the role of elasmobranchs in mangrove food webs in conjunction with movement studies will address this question. A better understanding of the role of elasmobranchs in habitat connectivity will be helpful to consider the spatial scale of conservation measures based on essential ecological processes (e.g. migration, energy transfer and nutrient translocation) that, for example, have been well studied in coral reef systems (McCauley et al. 2012, Espinoza et al. 2015, Martín et al. 2020). Additionally, such knowledge is important to predict possible effects on habitat connectivity by loss of elasmobranch species from coastal systems.

6.6. What are the physiological benefits of occurring in mangrove habitats?

Preliminary research (e.g. Davy et al. 2015, Higgins 2018) suggests that elasmobranchs may derive some physiological benefit from occupying mangrove habitats and taking advantage of temperature differences as part of a behavioural thermoregulation strategy. Mangrove-occurring individuals may use mangrove habitats to adopt 'hunt warm, rest cool' or 'hunt cool, rest warm' strategies by shuttling inside and outside mangrove habitats where water temperatures are different (e.g. Di Santo & Bennett 2011). Alternatively, species may use the inside of mangrove habitats to avoid heat stress by resting under the shade when water temperature is excessively high (e.g. Bouyoucos et al. 2018). This hypothesis requires further investigation using a range of experimental and field studies. If there are physiological benefits from using mangrove habitats, then this work would provide information on the costs that the loss of mangroves would have on elasmobranch populations, especially those species with elevated risk of extinction.

6.7. What are the consequences of mangrove loss to elasmobranch populations?

Given the substantial loss of mangroves and the demonstrated roles that they play for elasmobranchs, it is likely that there are significant consequences of mangrove loss to elasmobranch populations. Loss and degradation of habitats is one of the major threats to coastal elasmobranchs (Dulvy et al. 2021), and to our knowledge, Jennings et al. (2008) is the only study that has investigated the impact of loss of mangrove habitats on the survival rate of local populations of an elasmobranch. The impacts of habitat loss and degradation can be broad, such as reducing the quantity and quality of food, losing the key habitat for the early life stages of species (i.e. breeding or nursery habitats), reducing habitat connectivity (Sievers et al. 2019) and affecting life history parameters (e.g. survival, growth, reproduction). There is a positive correlation between mangrove cover and teleost species diversity, and population decline of teleosts was attributed to the loss of mangrove habitats and connectivity due to loss of refuging or spawning habitats and reduction in survival and recruitment rates (e.g. Grol et al. 2011, Tran & Fischer 2017). A recent study found that the degradation of mangrove habitats significantly affected the biodiversity of meiofauna, resulting in the collapse of ecosystem functions due to the loss of the basis of food webs (e.g. production and storage of organic matter, primary production) (Carugati et al. 2018). This can cause bottom-up impact on animals at higher trophic levels.

6.8. How do elasmobranchs respond to mangrove restoration?

With the recognition that mangrove loss is detrimental to coastal systems, there has been significant action to restore mangroves (e.g. Ellison 2000, Bosire et al. 2008). As these restoration activities occur, it will be important to monitor how elasmobranchs use these habitats compared to natural habitats. One study from Florida showed that nurse sharks *Ginglymostoma cirratum* started using restored mangrove areas 15 yr after initial replanting (Enchelmaier et al. 2020). This suggests that time lags may be long between restoration and the recovery of functions for elasmobranchs, but further investigation is required.

7. CONCLUSIONS

We demonstrate, based on a review of the literature, that there are important relationships between elasmobranchs and mangroves. However, this understanding is fragmented and available for few species in limited geographic regions. Future research should aim to address key questions that will improve our understanding of both the functions that mangrove habitats provide to elasmobranchs as well as what benefits elasmobranchs can provide to mangrove habitats. Global mangrove deforestation is causing a degradation of habitat availability and quality, which is negatively affecting global coastal communities, and elasmobranch species that are closely associated with mangrove habitats most likely suffer from a loss of essential ecological services and functions of mangroves and the associated coastal systems. Due to the nature of ecological connectivity, the impacts of mangrove loss could be broad and complex. Conversely, the conservation of mangroves can provide substantial benefits, such as bottom-up trophic well-being and biodiversity support. Elasmobranchs play an important role in coastal systems, including mangrove habitats, and their roles can be integral for ecological function not only in these systems but also in wider coastal systems. Knowledge of the value of mangrove habitats and elasmobranch–mangrove relationships will be integral to ultimately understand such complex coastal connectivity and ecological functions.

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