21 The Biophysics of Sharks and Rays on the Great Barrier Reef

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21.1. INTRODUCTION

The Great Barrier Reef (GBR) is home to a wide array of chondrichthyan fishes—sharks, rays, skates, and chimaeras—which are henceforth referred to here as sharks and rays. Sharks and rays are typically mid- to high-level predators, occupying a wide range of GBR habitats and niches where they play a variety of ecological roles including transferring energy between habitats and trophic systems and affecting prey density and behaviour. Sharks and rays can even alter physical habitats and facilitate the survival of other species (Heithaus et al. 2022). Aside from their ecological roles, the sharks and rays of the GBR have important social, cultural, and economic values (Choat et al. 2019). Many of the First Nations Peoples of the GBR have special cultural connections with these species, including ongoing cultural uses and lore and cultural significance dating back more than 40,000 years (Gerhardt 2018). Meanwhile, sharks and rays are among the most sought-after tourist attractions by divers visiting the GBR, and they have also been important components of commercial fisheries.

Although sharks and rays can affect the ecosystems that they inhabit, shark and ray communities themselves are also affected by the physical environment in which they occur. In this chapter, we explore the biophysical relationships between sharks and rays and the habitats and ecological processes of the GBR. The chapter discusses how the physical structure of the GBR, a mosaic of interconnected habitats on a relatively shallow continental shelf, supports the rich diversity of sharks and rays present in the GBR and affects their movements and distributions. The impact of environmental variables in affecting species distribution and habitat is also explored, including that of extreme weather events such as cyclones. We also explore the energetic relationships between the GBR ecosystem and sharks and rays and discuss where sharks derive energy and how this energy flows through the GBR ecosystem. Lastly, we explore how the changing climate and the biophysical environment may affect sharks and rays. This overview of the biophysics of sharks and rays in the GBR not only provides both a synthesis of some of the key knowledge available on the subject to date but also highlights how much remains unknown about this morphologically and functionally diverse group of fishes that are instrumental to the GBR.

21.2. LINKAGES BETWEEN GBR PHYSICAL HABITATS AND SHARKS AND RAYS

21.2.1. Shark and Ray Diversity and Ecological Groupings

There are approximately 138 species of sharks and rays in the GBR including 10 skates, 82 sharks, 42 rays, and 4 chimaeras (Chin et al. 2010; Chin et al. 2023). These species range from small cryptic species, such as the cookie cutter shark (*Isistius brasiliensis* at 40 cm in length), to the whale shark (*Rhincodon typus*) that grows to 12 m in length. This diversity of species, sizes, and life history strategies is reflected in the diversity of their ecology and links to the physical environment.

The GBR is a mosaic of different habitats, each with their own biological communities and a characteristic set of ecological processes (Hutchings et al. 2019). Shark and ray communities are likewise associated with specific habitats and ecological processes. Compagno (1990) introduced the concept of shark and ray 'ecomorphotypes', where shark morphology and life history, and by extension the species present in a community, are shaped by the physical environment and a species' ecological adaptations to that environment. This concept has been applied to the sharks and rays of the GBR, where the recorded 140 species have been placed into six 'ecological groups' (Table 1) (Chin et al. 2010; Chin 2023). Each ecological group encompasses a discrete set of habitats and associated ecological processes, and the sharks and rays occurring in each group are the species that have adapted to these habitats and conditions. For example, the largetooth sawfish (*Pristis pristis*) is typically restricted to turbid freshwater and estuarine environments (Grant et al. 2019). This species has a large, toothed rostrum that, along with associated prey detection sensory modalities, evolved to ambush prey in low visibility water (Wueringer 2012), and juveniles spend their early years in the freshwater environment with fewer elasmobranch competitors and predators and greater prey availability (Whitty et al. 2009). As a result, the extensive freshwater and estuarine habitats of the GBR coast once supported a large sawfish community, and where impacts are low, these habitats continue to support globally significant sawfish populations (Grant et al. 2021). However, species such as the bull shark (*Carcharhinus leucas*) are ecologically flexible and

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TABLE 1

Ecological groups of GBR sharks and rays, their respective habitats, and example species.

Ecological group	Habitat types and processes	Species
Freshwater and estuarine	Species occurring in rivers and streams, riparian habitats, mangroves and saltmarsh, and shallow intertidal and subtidal habitats such as seagrass beds and mudflats. Key biophysical processes include coastal runoff, wave- and wind-driven currents, and resuspension, erosion, and deposition of the coastal zone.	4 species including the largetooth sawfish *Pristis pristis*; freshwater whipray *Urogymnus dalyensis*; bull shark *Carcharhinus leucas*; and the spear-tooth shark *Glyphis glyphis*
Coastal and inshore	Species occurring in habitats extending from coastal subtidal habitats to the midshelf platform or ribbon reefs. Habitats include estuaries and bays, subtidal seagrass beds, inshore fringing reefs, rocky shoals, sponge gardens, and other benthic habitats of the GBR lagoon to 30 m depth. Key biophysical processes include coastal runoff, wave- and wind-driven currents and resuspension, GBR lagoonal currents, and circulation patterns that drive inshore productivity.	52 species including the narrow sawfish *Anoxypristis cuspidata*; Australian cownose ray *Rhinoptera neglecta*; pigeye shark *Carcharhinus amboinensis*; tiger shark *Galeocerdo cuvier*; bull shark *Carcharhinus leucas*; blacktip reef shark *Carcharhinus melanopterus*; great hammerhead shark *Sphyrna mokarran*; giant shovelnose ray *Glaucostegus typus*; zebra shark *Stegastoma tigrinum*
Reefal	Species occurring in habitats on and immediately adjacent to midshelf and outer shelf coral reefs, down to a maximum depth of 40 m in the GBR lagoon to 60 m adjacent to the outer shelf reefs. Key biophysical processes include coral reef processes, lagoonal currents, and circulation patterns, (especially in the outer reef zones).	28 species including the bluespotted fantail ray *Taeniura lymma*; ornate eagle ray *Aetomylaeus vespertilio*; blacktip reef shark *Carcharhinus melanopterus*; whitetip reef shark *Triaenodon obesus*; bull shark *Carcharhinus leucas*; grey reef shark *Carcharhinus amblyrhynchos*; epaulette shark *Hemiscyllium ocellatum*; ornate wobbegong *Orectolobus ornatus*; zebra shark *Stegastoma tigrinum*
Shelf	Species occurring in deeper water and seabed habitats between the midshelf and outer reefs, extending to the continental slope edge. Includes waters from the surface to 200 m (approximately the shelf edge) and benthic habitats such as deepwater seagrass beds and Halimeda mounds, rocky shoals, and sponge gardens (40–60 m depth). Key biophysical processes include deep water currents and circulation, upwellings and pelagic influences, deposition.	28 species such as the eastern angel shark S*quatina albipunctata*; short-tail torpedo ray *Torpedo macneilli*; piked spurdog *Squalus megalops*; white shark *Carcharodon carcharias*; pencil shark *Hypogaleus hyugaensis;* tiger shark *Galeocerdo cuvier* spot-tail shark *Carcharhinus sorrah;* great hammerhead shark *Sphyrna mokarran*; argus skate *Dipturus polyommata*
Bathyal	Species occurring in deep water, benthic habitats of the continental slope and beyond, and bathypelagic waters below 1,000 m depth. Key biophysical processes include deep water currents, upwellings, and deposition.	50 species including the argus skate *Dipturus polyommata*; longspine chimaera *Chimaera macrospina*; blackfin ghostshark *Hydrolagus lemures*; bartail spurdog *Squalus notocaudatus*
Pelagic	Species occurring in the epipelagic and mesopelagic zones of open ocean waters extending from the edge of the outer reefs and beyond into the Coral Sea, with vertical depth to 1,000 m. Key biophysical processes include upwellings, water currents, and thermoclines.	13 species including the Oceanic whitetip shark *Carcharhinus longimanus*; blue shark *Prionace glauca*; whale shark *Rhincodon typus*; oceanic manta ray *Manta birostris*

Source: Adapted from Chin et al. (2010) and Chin et al. (2023)

occupy a range of different habitats. As such, these species occur in more than one ecological group.

The six ecological groups and their respective shark and ray species illustrate the connections between the physical environment and GBR sharks and rays. Each ecological group comprises specific habitats with different biophysical characteristics, and the shark and ray community of each ecological group reflects these characteristics. More specific examples of these connections are provided in the following.

21.2.2. Biophysical Relationships Shape Shark and Ray Behaviour and Community Composition

The biophysical relationships between habitats and sharks and rays are illustrated in the ways that the structural and physical characteristics of habitats have shaped shark and ray morphology, physiology, diversity, and population structure. These examples range from the adaptations and behaviours of individual species to the ecological functions provided by habitats that shape entire shark and ray communities.

A species-focused example of this relationship is the epaulette shark (*Hemiscyllium ocellatum*). This small carpet shark resides in shallow reef and seagrass habitats (typically < 5 m deep), including shallow reef lagoons, and forages for invertebrates in very shallow water. The epaulette sharks' morphology and physiology reflect this habitat. The species has a long, slender body form that is very flexible, and the fins are small and rounded, which enable it to squeeze into small cervices between corals and within the reef matrix (Last and Stevens 2009). The fin morphology and musculature also enable the shark to 'walk' out of one tidal pool into another (Porter et al. 2022), giving rise to their name of 'walking sharks' (Dudgeon et al. 2020). However, these morphological adaptations make this small catshark a very poor swimmer that is highly susceptible to predators. To compensate for these limitations, the epaulette shark is mainly nocturnal (Wheeler et al. 2022) and also has adaptations that enable it to exploit coral reef habitats inaccessible to larger predators (Dudgeon et al. 2020). The species has physiological adaptations that enable it to remain in very shallow reef lagoons at low tide during low oxygen conditions when water temperatures rise during the day or at night when photosynthesis declines, dissolved oxygen levels decrease (Wise et al. 1998; Hickey et al. 2012), and PCO_2 levels increase, thereby decreasing water pH (Heinrich et al. 2014, 2015). Here, this species has developed morphological and physiological adaptations and behaviours that are shaped by the biophysical characteristics of its shallow, coral reef habitat.

Biophysical characteristics, such as depth, water currents, and physical habitat complexity, can also shape entire shark and ray population structures and community dynamics. Shallow coastal areas are key nursery habitats for many shark and ray species. These shallow environments include mud and sand flats, mangroves, and seagrass beds, which provide ample prey and shallow water refuge from predators for highly vulnerable neonate and juvenile sharks and rays (Figure 1) (Heupel et al. 2007; Martins et al. 2018; Martins et al. 2020b).

FIGURE 1 Shallow habitats provide neonate and juvenile sharks and rays, such as these blacktip reef sharks (*C. melanopterus*), with protection from predators.

Source: Photo credit: Andrew Chin

In the GBR, sheltered coastal environments protect seagrass beds and mangroves from strong wave action and currents, which promotes growth and development thereby enhancing the capacity of coastal environments to provide shelter for sharks and rays in vulnerable life stages. Although the role of these habitats in providing energy to growing neonates and juveniles is widely reported, in the GBR, it seems likely that the most important function of these areas is as a refuge from predators. Trophodynamic research in the GBR has shown that two stingray species inhabiting shallow coastal environments derived little energy from mangrove systems (Martins et al. 2022). Moreover, different shark species in shallow foreshore environments exhibited a high level of niche partitioning, which suggests that resources were limited and resulted in different species adopting different foraging strategies (Kinney et al. 2011). Meanwhile, these tidal and subtidal habitats are too shallow for larger predators, so they are inhabited by neonates and juveniles who remain in these areas while growing. For example, the mangroves and shallow flats of Orpheus Island in the Central GBR provide critical habitats for cowtail rays (*Pastinachus ater*) and mangrove whiprays (*Urogymnus granulatus*), which have been recorded as hiding within mangrove roots during high tide when larger predators can access the system (Davy et al. 2015; Martins et al. 2020a; Martins et al. 2022). Similarly, these shallow coastal habitats provide sheltered nursery habitats for the early life stages of blacktip reef sharks (*Carcharhinus melanopterus*) (Chin et al. 2016; George et al. 2019; Bouyoucos et al. 2022) that remain in these areas until reaching a large enough size that enables them to disperse to other habitats, including offshore coral reefs (Chin et al. 2013).

These examples provide an overview as to how biophysical factors shape shark and ray communities. These concepts are explored in more detail in sections *Effects of Biophysical Factors on Shark and Ray Movement and Distribution* and *The Physiological Linkages between Sharks and Rays and Their Environment*. However, sharks and rays themselves can alter the biophysics of the systems that they inhabit, and these interactions are explored here in sections *Sharks and Rays as Habitat Engineers* and *Trophodynamics of GBR Sharks and Rays*.

21.2.3. SHARKS AND RAYS AS HABITAT ENGINEERS

Biophysical factors can shape shark and ray communities; however, in some instances, sharks and rays themselves can act as 'ecological engineers' that alter the biophysics of their environment. One of the most obvious examples of this effect is bioturbation during stingray feeding. Many stingrays are benthic predators that forage for invertebrates in the substrate. One of their feeding behaviours involves pumping water into the substrate and turning over the sediment, leaving large depressions known as ‘feeding pits’ behind. This activity can be significant, with one study estimating that 42% of the soft sediment in one study area (equivalent to an estimate of ~42,000 m^2) would be turned over by stingrays every year (O’Shea et al. 2012). Although bioturbation is an important mechanism that can oxygenate sediments, affect pH, and influence chemical and nutrient cycling (Krantzberg 1985; Sarker et al. 2021), the pits themselves create habitat rugosity in areas that may otherwise be uniform (Figure 2), thus creating habitats that are colonised by other organisms such as ostracods and amphipods (O’Shea et al. 2012). Ray-mediated bioturbation can also alter habitats by inhibiting the growth of other organisms. Cownose rays (*Rhinoptera bonasus*) reportedly can inhibit the growth of eelgrass (*Zostera marina*) by disrupting the rhizomes while foraging in the sediment, thus affecting the physical habitat and associated biodiversity (Orth 1975). However, different ray species may have different effects. For example, the Australian whipray (*Himantura australis*) creates larger feeding pits than the cowtail ray (*Pastinachus ater*); however, the cowtail ray forages over a wider area and may thus exert bioturbation influences over a larger area (Crook et al. 2022). Nevertheless, stingrays (and their feeding pits) are commonly found across many different GBR habitats and coastal areas (Crook 2020; Martins et al. 2022) and despite inter-specific differences in foraging behaviours and associated biophysical effects, are likely to have widespread influences on habitats and biodiversity across the GBR.

Sharks can also alter the physical environment through indirect effects. The presence of sharks can alter prey behaviour and feeding strategies (Frid et al. 2008; Rizzari et al. 2014b; Lester et al. 2020), which, in turn, create indirect effects on habitat structure. Some species, such as tiger sharks (*Galeocerdo cuvier*), are top-level predators that exert influence throughout a food web that results in changes to seagrass beds. The presence of tiger sharks has been shown to affect the foraging depth of dugongs (*Dugong dugon*) and whether dugongs forage by cropping or excavating seagrasses (Wirsing et al. 2007). When tiger sharks were present, dugongs foraged on deeper seagrass beds, and because they were warier, dugongs fed by grazing or cropping seagrasses instead of excavating seagrasses and their rhizomes. In turn, these changes altered the nature of disturbance to seagrass meadows and the turnover and succession of seagrass species (Wirsing et al. 2008). Although these studies have not been repeated in the GBR, both tiger sharks and dugongs are present in the GBR, and it seems likely that this dynamic would exist in the GBR where both species co-occur.

FIGURE 2 Stingrays such as the porcupine ray (*Urogymnus asperrimus*) can act as habitat engineers through bioturbation and excavating feeding pits.

Source: Photo credit: Henriette Grimmel | © Save Our Seas Foundation

21.3. TROPHODYNAMICS OF GBR SHARKS AND RAYS

Trophodynamics are ‘the dynamics of nutrition and metabolism’ (Lindeman 1942) and crucial in understanding how energy flows through ecosystems (Libralato et al. 2014; Bierwagen et al. 2018). Research on shark and ray trophodynamics has been ongoing for some time but only more prominently on the GBR since trophodynamic work on reef fishes was highlighted by Polunin (1996). The scope of diversity in sharks and rays on the GBR makes the description of their trophodynamics a complex task. Hence, this topic is as equally difficult to describe with any definitive assuredness without underpinning elements of inference, particularly when describing ecological interactions of sharks and rays. This is not unexpected in the context of coral reefs, which are widely known for their substantial complexity and diversity. The reason behind inferences of ecological patterns is often due to a lack of specific and time-intensive data needed for these semi-open, complex systems that require research at correct spatial scales (Sale 2002). For species that have a large distribution and/or home range, the geomorphology and scale of the GBR must also be considered, as entire assemblages can change both through latitudes and across the continental shelf. Thus, the range of species, each with different distributions and movement patterns, creates a diverse array of interactions with different levels of trophic connectivity that are difficult to quantify and generalise.

From a physical perspective, energy needs and, thus, energy flows between organisms are dictated by the biomass and availability of basal sources of nutrition derived from coral reefs, which comprise both benthic and pelagic inputs. In general, the GBR is driven by bottom-up processes where nutrients are assimilated between different levels of biomass to form, in the simplest of terms, a resource-limited pyramid structure. Larger-bodied organisms with substantial biomass per individual at the top of the pyramid require the most energy per individual and, therefore, in theory, will be limited in abundance compared to lower trophic levels. On coral reefs, this pyramid is more diffuse and unconsolidated where reef predators, such as sharks and rays, occupy a variety of dietary niche breadths at multiple trophic levels (Wilson et al. 2008) and may also transfer nutrients from the pelagic system to coral reefs.

To make sense of the complex nature of these systems, generalisations are often made to gain some perspective of the ecological groupings of sharks and rays. Research focus also tends to concentrate heavily on the more 'charismatic' and less cryptic species. For instance, reef sharks are often described in the literature as a conglomerate of three main species, namely, grey reef sharks (*C. amblyrhynchos*), white-tip reef sharks (*T. obesus*), and blacktip reef sharks (*C. melanopterus*). Other apex species that occupy higher trophic levels, such as bull sharks (*C. leucas)*, hammerheads (*Sphyrna spp.*), and tiger sharks (*G. cuvier*), are often the focus of coral reef research but are less resident and more roving than other reef-associated species. All other sharks and rays are usually classed as benthic or demersal-dwelling species occurring on coastal and shelf ecological groups (Table 1). Many of these species groups, however, occupy vastly different niche breaths and use reef resources differently, thus deriving energy from varying sources. Sharks and rays also occupy different habitats across ontogeny, where nutrients assimilated and rates of consumption as a juvenile may be entirely different than during adult life stages (Dale et al. 2013). Rays are also only just beginning to be studied in terms of ecological research on the GBR, and the description of ecological function in this group of organisms is limited (Crook 2020; Martins et al. 2022).

The discussion of ecological roles of sharks and rays often equates with their importance to the ecosystem and a need to understand what happens in the event of their removal or loss. There is a documented element of top-down control by high-order predators through both consumptive and fear-related behavioural effects (Cortes 1999; Rizzari et al. 2014b; Frisch et al. 2016; Lester et al. 2020). However, evidence of collapse of these controlling effects, effectively creating a cascading breakdown of a balanced system (e.g., trophic cascade), is mostly anecdotal and extremely limited in cases that have actually been able to report this observed effect from a single causal source such as species removal or loss (Ferretti et al. 2010; Ruppert et al. 2013; Grubbs et al. 2016). Irrespective of the lack of *in situ* observations, models attempting to reproduce cascades have shown that top-down control has weak effects on coral reefs (Casey et al. 2017), but these models may also not accurately represent trophic structure appropriately based on our most up-to-date understanding of ecological roles (e.g., use of reef sharks grouping as an apex predator when they are currently considered to be a mesopredator) (Ruppert et al. 2019). Alternatively, the lack of food web linearity in reef systems assumes a great degree of redundancy across trophic levels, which may inherently create more stability when considering the loss of a single species and may explain why ecosystem models are unable to detect significant impacts. These models also do not often account for loss of sharks and rays in lower trophic levels and the wider consequences of the loss of ecological services that they provide, such as bioturbation (Dulvy et al. 2017).

Although there is no question of very high levels of shark diversity on the GBR (MacNeil et al. 2020), there is mixed evidence in terms of abundance of these species (Robbins et al. 2006; Heupel et al. 2009; Rizzari et al. 2014b; Bierwagen 2019) and, therefore, of the influence that they may carry in their ecological roles. For instance, the influence of a species that is highly abundant in isolated remote environments compared to lower abundance in semi-open environments is likely ecologically distinct. Grey reef sharks, which were assumed to be limited in their diet by their mouth gape size, have been known to socially forage in groups for larger prey items (Mourier et al. 2016) and are subject to kleptoparasitism by foraging among other species such as whitetip reef sharks (Labourgade et al. 2020), increasing their ability to successfully capture organisms. These examples illustrate how their overall ecological influence may change between remote and isolated reef systems and the shallow and highly interconnected reefs of the GBR.

Ecological relevance is also difficult to interpret among species occupying similar trophic levels. Some sharks and rays are comparable in carbon and nitrogen enrichment to large-bodied teleosts (such as mesopredators), and other species derive nutrients from entirely different basal sources (Frisch et al. 2016; Roff et al. 2016; Bierwagen 2019; Espinoza et al. 2019). This means that assumed trophic redundancy across reef-dwelling species is not the case in some instances. There has also been little research until recently on scaling up the bioenergetic needs of these animals. Even for the most commonly occurring reef sharks on the GBR such as the grey reef shark (*C. amblyrhynchos)*, there is only a paucity of information available regarding the energy needs of the species (Mourier et al. 2016; Dunn et al. 2022). However, recent research has shown that reef sharks are responsible for transferring more nutrients and energy from pelagic sources to reefs than previously considered, which makes their and any mobile marine predator's role in nutrient cycling likely critical for reefs (Williams et al. 2018; Bierwagen 2019).

There are also a great many unknowns in what processes are occurring on reefs and the anomalies that affect our understanding of energy flow in terms of behavioural adaptations that require direct observation. These overall impacts may be significant in terms of effects on ecosystems and are usually unexpected. For example, white sharks (*Carcharodon carcarias*, which are one of the most commonly cited examples of an apex predator) in South Africa have been documented to change distribution as a response to predation events by orcas (*Orcinus orca*), creating a space for the bronze whaler (*Carcharhinus brachyurus)* to increase its presence in coastal areas (Towner et al. 2022). Bonnethead sharks (*Sphyrna tiburo*), known previously as entirely carnivorous, exhibit herbivorous feeding behaviours, with a significant portion of seagrass found in their diet (Leigh et al. 2018).

These examples highlight that although literature has documented some clear examples of shark and ray contributions and performance in terms of trophodynamics, the interpretation of their ecological role and importance to the environment still involves substantial inferences, where the use of such language, particularly in terms of management, should be restrictive. This is especially important considering the risk of overexploitation and significant loss to these groups of species (MacNeil et al. 2020; Sherman et al. 2022). In addition to exploitation, climate change is also expected to significantly change the range distributions of migratory species (Heupel et al. 2019) or pose increased risk to the species whose ranges are extremely limited (e.g., walking sharks) (Gervais et al. 2018), which also has flow-on effects for our current understanding of ecological roles.

21.4. EFFECTS OF BIOPHYSICAL FACTORS ON SHARK AND RAY MOVEMENT AND DISTRIBUTION

Biophysical relationships between the GBR and sharks and rays are bidirectional. Despite having the ability to engineer their physical environment to varying degrees, the distributions and movements of sharks and rays are also largely influenced by a range of biophysical conditions (Espinoza et al. 2014; Rizzari et al. 2014a). The broad ecological and functional diversity of elasmobranchs on the GBR means that these species occupy a range of habitats including freshwater and estuarine systems, shallow coastal habitats, coral reefs, and pelagic environments (Table 1). The sheer diversity of form and function in this group makes the task of identifying key influential factors difficult, but fundamentally, the distribution of sharks and rays on the GBR is influenced by a complex interplay of environmental, ecological, and anthropogenic factors (Ceccarelli et al. 2013; Schlaff et al. 2014).

Broad-scale surveys of sharks along the GBR have revealed that the complexity of hard coral cover, proximity to reef systems, and associated biomass and diversity of prey influence shark and ray diversity and species richness (Espinoza et al. 2014). More specifically within reef systems, the reef slope habitats are areas that have an overall higher abundance and diversity of reef sharks (e.g., grey reef sharks *C. amblyrhynchos*, blacktip reef sharks *C. melanopterus*) across the length of the GBR (Rizzari et al. 2014a). Other biophysical variables, such as salinity and temperature, are strong drivers of seasonal distributions and movements of euryhaline and freshwater species (e.g., freshwater sharks *Glyphis* spp., sawfishes *Pristis* spp.), and they dynamically impact coastal and offshore shark and ray distributions (Yates et al. 2015; Lyon et al. 2017). For example, pregnant sawfishes (*Pristis* spp.) may move upstream into lower salinity environments for parturition, but the pups remain in low salinity habitats for their early years to avoid predators. Meanwhile, prey availability, together with oceanic currents and tidal patterns, drive distributions and migratory behaviours of large pelagic migratory species of sharks and rays on the east coast of Australia (Werry et al. 2014; Armstrong et al. 2016).

21.4.1. Biophysical Drivers of Movement

Although the long-term distribution patterns of marine species reflect broader scale habitat requirements, mobile species such as sharks and rays have the ability to leave an area should the local environmental conditions exceed thresholds for maintaining key physiological processes (Schlaff et al. 2017). A number of biophysical factors influence the movement behaviours of sharks and rays, which act across multiple spatial and temporal scales, and affect different species and different life stages in different ways. These factors include extrinsic parameters (i.e., temperature, salinity, and dissolved oxygen) or ecological dynamics (i.e., predator-prey dynamics, ontogenetic shifts, and reproductive activity) that change or limit how individuals move and select habitats, with extrinsic factors and ecological dynamics often working synergistically (Mull et al. 2022). Here, we discuss a few variables that have been identified as key drivers in the context of shark and ray movements, which may also influence seasonal changes on the movement and distribution of GBR sharks and rays.

21.4.1.1. Water Temperature

Temperature is a key variable that effects the physiology of ectotherms, and, in turn, has a strong influence on the movement patterns of sharks and rays. Individual species may actively seek out and occupy specific temperatures or traverse thermal gradients, which is termed behavioural thermoregulation. In general, seasonal fluctuations in water temperatures are known to be cues for specific movement behaviours in some sharks and rays, which can trigger migratory behaviours (Heupel 2007) or influence residency patterns within specific habitats (Kessel et al. 2014).

21.4.1.2. Salinity

Sharks and rays have different tolerances to water salinity, from euryhaline species that can exploit a wide range of salinities to the more common stenohaline species of sharks and rays that occupy a narrow salinity range (Grant et al. 2021). Fluctuating salinities in coastal and estuarine habitats during the onset of monsoonal runoffs are often a key driver of movements for shark and ray species that inhabit euryhaline environments across northern Australia (e.g., immature bull sharks *Carcharhinus leucas*, speartooth sharks *Glyphis glyphis*; Dwyer et al. 2020). Notwithstanding their osmoregulatory adaptations (see *The physiological Linkages between Sharks and Rays and their Environment*), species-specific behavioural responses to changing salinities help individuals balance the energetic demands of ion regulation with optimal habitat requirements.

21.4.1.3. Dissolved Oxygen

The availability of oxygen in the environment and the species-specific tolerance to varying levels of oxygen depletion in certain habitats drive movements in many shark and ray species. As previously described, species that have a high tolerance to hypoxic conditions, such as the epaulette shark (*H. ocellatum*), have the ability to access and remain in habitats such as shallow reef platforms during large tidal fluctuations (Wise et al. 1998). Meanwhile, the limiting influence of dissolved oxygen also plays a role in restricting access to depth in pelagic systems, with some shark species with lower hypoxic tolerances restricted from accessing deep waters (Abascal et al. 2011).

21.4.1.4. Tidal Phase

Movements and access to shallower habitats are tidally restricted in nearshore environments. In coastal species, tidally driven movements are often associated with foraging tactics (Davy et al. 2015; Martins et al. 2020a); however, for juvenile individuals, access to more complex and shallow habitats (e.g., mangroves) may be more likely driven by predator avoidance tactics (see 21.2.2; George et al. 2019).

21.4.2. Influence of Extreme Weather Events

So far, we have discussed how long-term seasonal changes in biophysical variables may dictate movements and distributions of sharks and rays. However, acute and extreme changes of these variables over much smaller temporal scales also frequently occur across northern Australia in the form of tropical cyclones, floods, and heatwaves. Extreme weather events can have a significant impact on shark movements and distributions and can disrupt the physical and biological conditions of marine ecosystems, which, in turn, can affect the behaviour and distribution of sharks.

As mobile marine predators, most sharks and rays can leave an area should local environmental conditions change sufficiently in the face of extreme weather (Heupel et al. 2003). Individuals that leave, however, will encounter risks associated with finding a new, suitable habitat and may experience increased chances of predation, while those that stay must endure challenging conditions (Schlaff et al. 2014). Whether or not individuals that leave return to their original habitat or relocate permanently often depends on the length and severity of environmental fluctuations (Udyawer et al. 2013). Tropical cyclones on the GBR are common, and in a changing climate cyclones are likely to increase in intensity (Wu et al. 2022) and perhaps frequency. Past tracking work on coastal shark species has identified that elasmobranchs most likely use the abrupt change in barometric pressure as a cue to evacuate shallow habitats during the onset of tropical cyclones (Heupel et al. 2003; Gutowsky et al. 2021). Multi-species studies have shown that sharks have species-specific responses to tropical cyclones, with some species moving into deeper waters, and others staying within shallow habitats (Udyawer et al. 2013; Strickland et al. 2020). In the GBR, tropical cyclone Anthony (Category 2) and Tropical Cyclone Yasi (Category 5) caused three coastal shark species (Australian blacktip *Carcharhinus tilstoni*; spot tail *C. sorrah*; and pigeye sharks *C. ambionensis*) to seek refuge in deeper water before the storms' arrival (Udyawer et al. 2013), thus illustrating how biophysical factors, such as pressure, can trigger shark behaviours during the onset of extreme weather.

Similarly, marine heatwaves can have a significant impact on the distribution of sharks and rays (Espinoza et al. 2011; Matich and Heithaus 2012). Heatwave events can disrupt the physical and biological conditions of marine ecosystems, which, in turn, can affect the behaviour and distribution of species. During heatwave events, prolonged high temperature conditions are likely to cause water temperatures to exceed thermal tolerances (Matich and Heithaus 2012). In addition to exceeding species' thermal tolerance, prolonged heatwave conditions degrade other key biophysical variables within habitats, such as dissolved oxygen and habitat structure, and simultaneously disrupt prey availability, which has a detrimental impact on species that cannot move (Osgood et al. 2021). The effects of temperature and other biophysical variables on shark and ray physiology are explored in more detail in *The Physiological Linkages between Sharks and Their Environment.*

21.5. THE PHYSIOLOGICAL LINKAGES BETWEEN SHARKS AND RAYS AND THEIR ENVIRONMENT

Understanding the physiology of sharks and rays—and their 450-million-year evolutionary history (Miller et al. 2003)—has revealed numerous physiological traits related to life history, metabolism, osmoregulation and ion balance, and stress responses that are unique to this taxon and key to how they function in their environment.

Firstly, unlike most teleosts, sharks and rays are K-strategists, meaning that these species are long-lived and slow-growing, have a late age of sexual maturity and long reproductive cycles, and produce a low number of large, high-quality offspring (Conrath and Musick 2012). This alone has implications toward growth and energy utilisation, considering, for example, maternal size at parturition and maternal nutritional input or matrotrophy (Hussey et al. 2010; Weideli et al. 2019). Indeed, increased reproductive output can be seen with larger mothers (e.g., dusky shark *Carcharhinus obscurus* and spinner shark *C. brevipinna*), and provisioned energy reserves in the form of an enlarged liver can constitute approximately 20% of the total body mass of the neonate (Hussey et al. 2010).

Secondly, sharks and rays exhibit a unique energy metabolism compared to teleost fishes, where they preferentially oxidize ketone bodies and amino acids (i.e., as opposed to fatty acids in teleosts) for ATP production (reviewed in Speers-Roesch and Treberg 2010). Such stark differences in energy metabolism also have implications when considering environmental influences, such as elevated temperatures, hypoxia, and high CO_2. Although an increase in overall metabolic rates (e.g., as estimated via oxygen uptake rates) is the common response amongst ectotherms with elevated temperatures (reviewed in Bouyoucos et al. 2019), sharks and rays may also be metabolically compensating in other ways via unchanged metabolic enzyme activities (Tullis and Baillie 2005), via increasing plasma glucose concentrations (e.g., neonates of *C. melanopterus*; Bouyoucos et al. 2018), or haematologically via changes in haemoglobin concentrations (e.g., increased [Hb], neonates of *Negaprion acutidens*; Bouyoucos et al. 2018; decreased [Hb], neonates of *C. melanopterus* Bouyoucos et al. 2021) or increased temperature sensitivity of haemoglobin-oxygen binding affinity (e.g., neonates of *C. melanopterus*; Bouyoucos et al. 2020a). When epaulette sharks (*H. ocellatum*) are exposed to extreme hypoxia and transition to anaerobic glycolysis, they accumulate lactate but do not increase plasma glucose concentrations, as seen in hypoxia-tolerant teleosts (Routley et al. 2002), and their metabolic enzyme activities (e.g., citrate synthase) are not altered in the red muscle, heart, or brain upon extended exposure to elevated CO_2 (Heinrich et al. 2014). There may also be neuroprotective attributes of ketone bodies during challenging environmental conditions.

Thirdly, this unique energy metabolism in sharks and rays is thought to be related to their capacity to synthesise and accumulate high levels of urea that allows marine sharks and rays to be osmoconforming ionoregulators (i.e., as opposed to osmo- or iono-regulating teleosts). This allows them to maintain their osmolality very close to that of seawater while excreting ions (i.e., such as sodium and chloride, similarly to teleosts) to maintain a different internal ion concentration from that of seawater (Yancey 2001). However, at high levels, urea destabilises proteins, and to thus counteract these normally toxic effects, sharks and rays also co-accumulate methylated amines, such as trimethylamine oxide (TMAO) (Yancey 2001), which protect these protein conformations by binding tightly to water (Liao et al. 2017). Sharks synthesise urea by using their gills to absorb ammonia—the major nitrogenous waste product that other organisms release upon breaking down dietary protein—that has been excreted into the seawater (Wood and Giacomin 2016). This physiological trait that is unique to sharks and rays has implications in terms of coastal areas with high ammonia levels, which are areas that are expected to increase with future development, agricultural run-off, and aquaculture operations, as increased ammonia concentrations could alter habitat use or shift home ranges of species to optimize urea production (Wood and Giacomin 2016).

Finally, a fourth physiological trait that is unique to sharks and rays is related to the primary and secondary stress responses (reviewed by Skomal and Mandelman 2012). Teleosts use cortisol as the key glucocorticoid involved in the stress axis and liberate glucose as the fuel to restore post-stress homeostasis (Wendelaar Bonga 1997), whereas sharks and rays are thought to use 1α-hydroxycorticosterone (1α-OHB) and potentially glucose and ketone bodies (Anderson 2012). Moreover, although teleosts adrenergically swell their red blood cells as part of the secondary stress response to protect intracellular pH and, therefore, oxygen transport, sharks and rays do not (Schwieterman et al. 2021). Indeed, these differences make identifying stress biomarkers and their utility challenging, but advances are underway. Schoen et al. (2021) related changes in 1α-OHB, glucose, and ketone bodies to simulated heatwave conditions in neonates of *C. melanopterus* and determined the ontogenetic differences in 1α-OHB mobilisation between neonates and adults of the same species. However, more work is needed to utilize 1α-OHB as a classic stress biomarker in sharks and rays.

It is evident that studies are needed to identify useful biomarkers that will be meaningful given the new environmental challenges that sharks and rays are facing into the Anthropocene.

The physiology of sharks and rays, like any other taxonomic group, is inextricably linked to their morphology and behaviour, and no species or population can be truly understood without first comprehending its interactions within its environment. Highly mobile species can actively seek out and use environmental situations that best allow their morphological and physiological abilities to function adequately for survival and reproduction, thus enhancing fitness (e.g., *C. leucas*; Bangley et al. 2018; Birkmanis et al. 2020). For example, tiger sharks (*G. cuvier*) swim optimally in 22 °C waters and are therefore most abundant in these temperatures (Payne et al. 2018). In this light, changes in environmental conditions or fishing pressure can alter distribution patterns and range retractions that may impact a species' role ecologically and from a socioeconomic perspective (Gallagher and Hammerschlag 2011; Hammerschlag et al. 2019; Kendrick et al. 2019). Even species that are less-mobile can utilise various behaviours (e.g., avoidance, Bouyoucos et al. 2020a) to actively select conditions suited to their physiological capacities, but this may eventually lead to a reduction of performance in warming oceans (Lear et al. 2019). Tolerating a range of environmental temperatures by adjusting metabolic rates to correspond with optimal temperatures, diel patterns, and seasons to, for example, move, forage, or reproduce may be the strategy for other species (e.g., *H. ocellatum*; Gervais et al. 2018; Nay et al. 2021; Wheeler et al. 2022). Moreover, some strategies may be important for certain life history stages but not for others, as reproductive modes (e.g., at least 10 unique strategies, representing one of the most diverse arrays amongst vertebrates; Conrath and Musick 2012) and ontogenetic shifts frequently correspond with changes in habitat requirements and, therefore, often abiotic conditions as well (Wheeler et al. 2020). Consequently, the physiological linkages between these organisms and their environments are inseparable and must be investigated in concert. As such, with 140 species of sharks, skates, rays, and chimeras on the GBR, we could at the very least assume no fewer than

140 unique organism-environment relationships, and these are likely to change across space and time.

The physiological linkages between GBR species and their environments have been investigated with ecological and evolutionary objectives, management prioritisation, conservation outcomes, and since 2010, to understand the effects of climate change (Chin et al. 2010; Pereira Santos et al. 2021; Rummer et al. 2022). Overfishing remains the top threat to sharks and rays worldwide, and many studies have investigated physiological implications of catch-and-release and discard mortality in sharks (e.g., *C. plumbeus*, *C. limbatus*, *G. cuvier*, *C. brevipinna*, and *C. leucas*) using various haematological and stress biomarkers (Whitney et al. 2012), which helps refine management strategies. Although understanding the effects of climate change on sharks and rays remains critical, climate change was only explicitly identified as a threat to sharks and rays in 2010 (Chin et al. 2010); since then, there have still only been fewer than 50 studies on climate change effects on only 10–12 species of sharks and rays, only three of which are found on the GBR (Pereira Santos et al. 2021; Rummer et al. 2022). The available data suggest that of the climate change threats (e.g., ocean warming, acidification, and deoxygenation), ocean warming is likely to have the most pervasive effects on sharks and rays and is also the most well-studied to date (Rummer et al. 2022). Ocean warming and acidification together will affect swimming performance and locomotion (Vilmar and Di Santo 2022), development, and metabolism, but no study to date has addressed all three climate change stressors in combination (Pereira Santos et al. 2021).

The three most well-studied GBR species within a climate change physiology context include *C. melanopterus*, *H. ocellatum*, and the brown banded bamboo shark *Chiloscyllium punctatum*. Neonates of *C. melanopterus* populations have been the most extensively investigated within the context of early life habitat use, where home ranges can be constrained to areas as small as 0.02 km^2 (Bouyoucos et al. 2020a), but it is thought that such small nursery areas are important for food quality and foraging success (Heupel et al. 2007; Chin et al. 2016; Weideli et al. 2019). However, the shallow, warm, periodically hypoxic, and otherwise anthropogenically influenced nursery areas that they inhabit during the first years of life (Mourier and Planes 2013) necessitate physiological tolerance (i.e., metabolism, growth, and escape behaviours) for survival (Bouyoucos et al. 2018; Rummer et al. 2020; Bouyoucos et al. 2020a, 2020b, 2021, 2022; Trujillo et al. 2022). Indeed, although less is known about adult life stages, neonates tolerate a wide range of environmental temperatures and are predicted to be generally unaffected by mid- or end-of-century ocean acidification conditions (Rummer et al. 2020; Bouyoucos and Rummer 2021). Neonates of *C. melanopterus* exhibited elevated haematocrit, which could indicate stress or metabolic compensation, and blood lactate concentrations, which could indicate prolonged recovery, but all other metrics, including foraging behaviour, activity, and lateralisation, were unaffected under simulated ocean acidification conditions (Rummer et al. 2020; Bouyoucos et al. 2020a; Bouyoucos and Rummer 2021).

Meanwhile, the shallow reef flat specialist, *H. ocellatum* (Figure 3), has been investigated across all life stages—developing embryos *in ovo*, neonates, juveniles, and both non- and reproducing adults—across all climate change stressors. With this species still noted as the most hypoxia-tolerant shark that has been investigated to date (Chapman et al. 2011) and robust to ocean acidification conditions across life stages (Heinrich et al. 2014, 2015; Johnson et al. 2016), recent research has focused on the effects of temperature. Early life stages are significantly affected upon acclimation to end-of-century warming scenarios, with shorter incubation periods and faster yolk consumption *in ovo*, higher metabolic costs, smaller sizes and reduced energy reserves at hatching (Wheeler et al. 2021), altered colouration (Gervais et al. 2016), and decreased survival (Gervais et al. 2018). However, juveniles through non-encapsulating females, regardless of sex or body size, exhibit no differences in their upper thermal tolerance limits (Wheeler et al. 2022), which could have implications for distribution patterns of this site-attached mesopredator; however, more work is needed in this realm. Finally, although syntheses suggest that sharks and rays should be robust to future elevated CO$_2$ conditions, given their evolutionary history (Rosa et al. 2017), as has been found in *H. ocellatum*, studies on *Chiloscyllium punctatum* indicate otherwise. This well-studied species exhibits decreased aerobic metabolism in the brain and increased activity of antioxidant enzymes but still exhibits neuro-oxidative damage as a result (Rosa et al. 2016a). Although the effects on digestion are equivocal (Rosa et al. 2016b), this species does exhibit reductions in body condition and survival, especially when exposed

FIGURE 3 Epaulette shark (*Hemiscyllium ocellatum*) in the shallow reef flats of the southern GBR. This species can tolerate the low oxygen and elevated CO$_2$ (low pH) conditions that occur during the night-time hours, which is when this species is most active, and can also tolerate the dramatic diel fluctuations in temperature that are experienced in these shallow reef flats.

Source: Photo credit: Kristian Laine for @physioshark to the combined stressors of elevated CO_2 and temperature (Rosa et al. 2014). These studies on only three GBR species, although thorough, emphasise that there remains a substantial knowledge gap with respect to the 140 species of sharks and rays on the GBR and how they physiologically respond to their environment, especially considering anthropogenic stressors that are increasing in frequency and intensity as we progress through the 21st century. However, these studies are a starting point to identify thresholds, limits, and trigger points for various stressors and potentially reveal adaptations necessary for future climate change conditions and/or determine which species will move to and thrive in more favourable habitats.

21.6. CONCLUSIONS AND FUTURE DIRECTIONS

Accordingly, the sharks and rays of the GBR are diverse and have a wide range of connections to their habitats and the biophysical characteristics of these habitats. Such characteristics shape shark and ray diversity and population structures, and, in turn, these species shape the environment around them. For example, different species select different habitats, and this can vary by life stage, such as juveniles spending their early years in nurseries. Connections to habitat and trophic relationships illustrate how sharks and rays affect and facilitate energy flow between different ecosystems in the GBR. Such characteristics drive species-specific morphological and physiological adaptations and explain how sharks and rays respond to and/or move in response to environmental parameters and major weather events. These characteristics also affect shark and ray physiology, which, in turn, will determine how these species respond to a changing climate. Meanwhile, our understanding of these connections remains limited. Even basic dietary information, which is essential to understanding the trophodynamic relationships between sharks and rays and their foodwebs, is sparse and only known for a handful of species. Similarly, physiological tolerances and performance characteristics are only known for a fraction of shark and ray species and in a rapidly warming world, represent an area that needs urgent attention. There is great scope for further exploration of these research areas, but this comes with a great challenge. Although many shark species in the GBR are relatively secure (Simpfendorfer et al. 2017), some species are at high risk and have already experienced declines (Tobin et al. 2010). As pressures mount on the GBR, it is urgent to better understand these species to help inform their ongoing management and safeguard such important social, cultural, economic, and ecological roles that they play in the World Heritage Area.

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