WALKING (EPAULETTE) SHARKS

Mark V. Erdmann

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Mark V. ERDMANN
Conservation International, University of Auckland, Auckland, New Zealand

Christine DUDGEON
University of the Sunshine Coast, Sunshine Coast, QLD, Australia; The University of Queensland, Brisbane, Australia

SPECIES DIVERSITY, ECOLOGY, AND DISTRIBUTION

The epaulette[1] sharks in the genus *Hemiscyllium* (Müller & Henle, 1838) comprise a group of nine species restricted to northern Australia and New Guinea and a few of its satellite islands (including Halmahera, Aru, and the Raja Ampat Archipelago; Allen et al., 2016). Together with the seven Indo-Pacific species of bamboo shark in the genus *Chiloscyllium* Müller and Henle 1838, they comprise the family Hemiscyllidae in the carpetshark order Orectolobiformes. Members of the genus *Hemiscyllium* are small (usually less than 85 cm total length, TL, and frequently less than 70 cm TL) and are characterised by nasoral and perioral grooves, short nasal barbels, a small transverse mouth below the eyes, two similar-sized dorsal fins, and a long slender tail.

Previous reviews of the genus by Dingerkus and DeFino (1983) and Compagno (2001) recognised only five species (The Raja Ampat Epaulette Shark [*H. freycineti*], Papuan Epaulette Carpetshark [*H. hallstromi*], Epaulette Shark [*H. ocellatum*], Hooded Carpet Shark [*H. strahani*], and Speckled Carpetshark, [*H. trispeculare*]) with overlapping ranges across northern Australia and the reefs surrounding the island of New Guinea. However, research efforts have led to the description of four additional species (Gale's Epaulette Shark [*H. galei*] Allen & Erdmann, 2008, Halmahera Epaulette Shark [*H. halmahera*] Allen, Erdmann & Dudgeon, 2013, Henry's Epaulette Shark [*H. henryi*] Allen & Erdmann, 2008, and Michael's Epaulette Shark [*H. michaeli*] Allen & Dudgeon, 2010) and a more nuanced understanding of the highly restricted and non-overlapping distributions of the nine species. The distinctive colour patterns of each species, combined with their non-overlapping geographic ranges, provide the best means of differentiating the nine species, which are otherwise morphologically very similar (Allen et al., 2016). The review published by Allen et al. (2016) is liberally illustrated with colour photographs of all nine species and comparisons of the distinctive head and body markings of each species (Figure 1), and in particular, the post-cephalic markings (from where the common name of epaulette shark is derived; Figure 2). Interestingly, with those species of *Hemiscyllium* for which we have data on the colour pattern of newly hatched pups, epaulette sharks generally show a broad black and white or brown and white banding pattern (Figure 3) similar to that seen in related species of *Chiloscyllium* (though by contrast, adult *Hemiscyllium* are generally much more ornately patterned than the comparatively dull adults of *Chiloscyllium*).

Epaulette sharks are also known as 'walking sharks' due to their peculiar habit of using their paired pectoral and pelvic fins to 'walk' across the seafloor in search of their largely benthic prey (Goto et al., 1999; Allen et al., 2016). Walking sharks are nocturnal, bottom-dwelling sharks that shelter under coral heads or retreat into crevices in the reef during the day. They are typically found in shallow coral reefs and associated seagrass bed and mangrove habitats in depths of 1–10 m, occasionally to 20–30 m depth (Allen et al., 2016). In reef settings with extensive intertidal reef flats, they are frequently found in wading depths in isolated tide pools, often only partially submerged. Epaulette Shark on the Great Barrier Reef can tolerate hypoxic conditions during low tide periods and this species is even able to 'crawl' between isolated pools for short distances (Wise et al., 1998).

Epaulette sharks were thought to feed primarily on small bottom fishes, cephalopods, shelled molluscs, and crustaceans (Compagno, 2001), however, stomach content analyses of Epaulette Shark from the Great Barrier Reef reported worms and crabs to be the dominant prey items (Heupel & Bennett, 1998). Stomach contents analysed from Halmahera Epaulette Shark around Halmahera Island were found to contain mostly the remains of small fish, as well as various annelids and small crustaceans (Jutan et al., 2019).

At least three of the species of *Hemiscyllium* (The Raja Ampat Epaulette Shark, Halmahera Epaulette Shark, and Epaulette Shark) have been shown to be oviparous, depositing eggs on the seafloor in small (80–90 mm long), oval-shaped cases (Heupel et al., 1999; Allen et al., 2016; Jutan et al., 2018). The entire family Hemiscyllidae was surmised to be oviparous (Compagno, 2001). A review of the growth and reproduction data presented by Heupel (1999), Jutan et al. (2018), and West and Carter (1990) concluded that the various species of *Hemiscyllium* likely mature at 2–4 years of age, reach a maximum age of six to ten years, have an average generation length of 5.5 years, and produce on average 20 potential offspring per year (VanderWright et al., 2022). Using this information, a maximum population growth rate (rmax) of 0.736 (95% CI: 0.565–1089) was calculated and a population doubling time (Td) of only 1.22 years (CI: 1.55–0.89) (VanderWright et al., 2022), highlighting some key differences with larger-bodied sharks with slow life histories.

As oviparous bottom-dwelling sharks that are as likely to 'walk' as swim, the nine species of epaulette sharks are believed to have extremely limited dispersal capabilities. In reviewing the known ranges of each species and the overall restriction of the genus to the Sahul Shelf of Australia and New Guinea, it was concluded that epaulette sharks are unlikely to cross waters deeper than about 50–100 m and that the distribution of each species is generally bounded by either deepwater or habitat disjunctions caused by large river outlets with extensive soft-bottom turbid habitats (Allen et al., 2016). Figure 4 shows clearly the non-overlapping distributions of the nine species spread around northern Australia and encircling the island of New Guinea. Importantly, there are several 'blank spots' in our understanding of epaulette shark distributions. Additional research is urgently

'Epaulette Shark' refers to *H. ocellatum* and 'epaulette shark' refers to the *Hemiscyllium* genus.

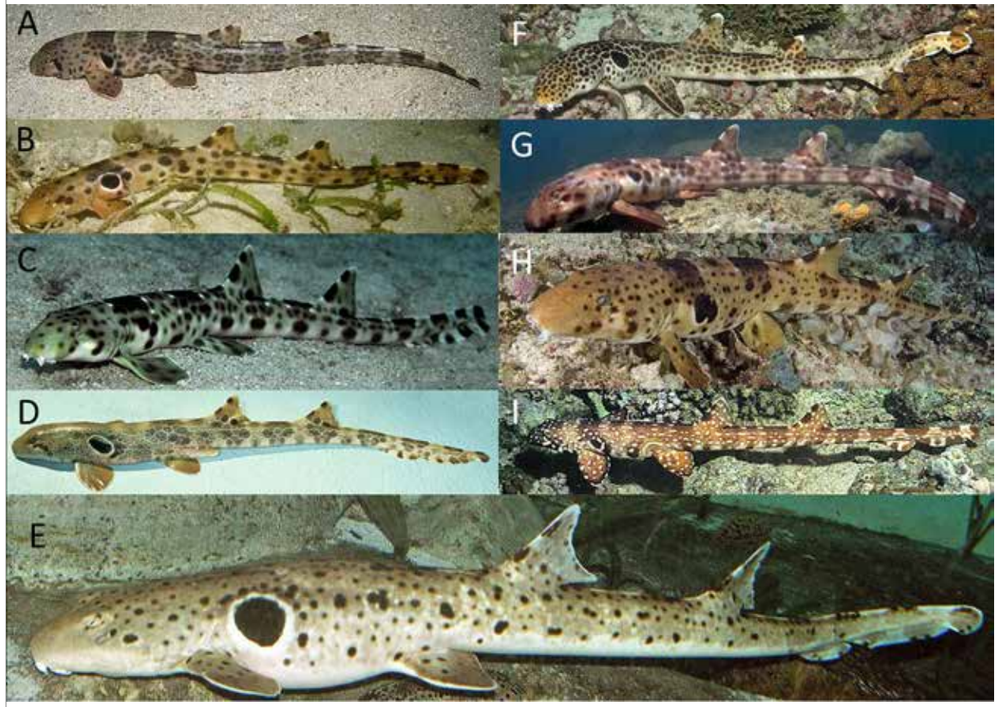

Figure 1: A comparison of the body markings of the nine species of Hemiscyllium. A) The Raja Ampat Epaulette Shark, B) Papuan Epaulette Carpetshark, C) Gale's Epaulette Shark, D) Speckled Carpetshark, E) Epaulette Shark, F) Michael's Epaulette Shark, G) Halmahera Epaulette Shark, H) Henry's Epaulette Shark, and I) Hooded Carpet Shark. | Photos (A–F) by G.R. Allen, (G) by M.V. Erdmann, (H) by B. Jones, and (I) by S. Michael. Reprinted with permission from Allen et al. (2016) Journal of the Ocean Science Foundation

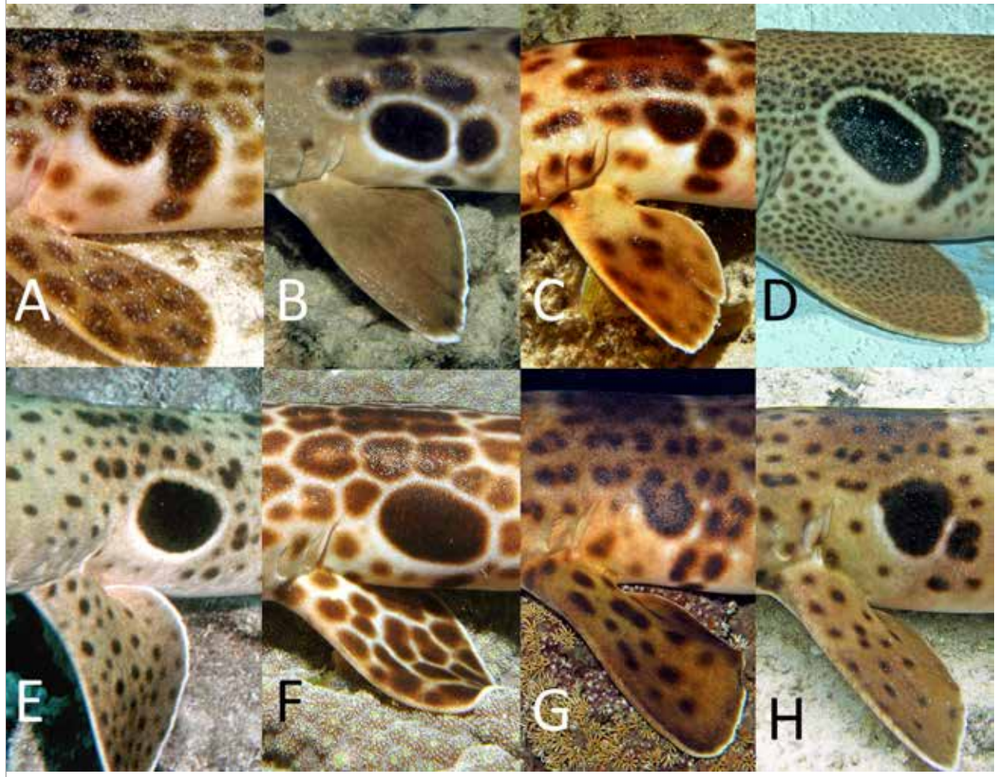

Figure 2: A comparison of the post cephalic markings ('epaulettes') of eight of the nine species of Hemiscyllium. A) The Raja Ampat Epaulette Shark, B) Papuan Epaulette Carpetshark, C) Gale's Epaulette Shark, D) Speckled Carpetshark, E) Epaulette Shark, F) Michael's Epaulette Shark, G) Halmahera Epaulette Shark, and H) Henry's Epaulette Shark. | Photos (A–D, F) by G.R. Allen, (E) by R. Steene, and (G) by M.V. Erdmann. Reprinted with permission from Allen et al. (2016) Journal of the Ocean Science Foundation

needed to survey areas including the Gulf of Carpentaria, the Gulf of Papua north of Port Moresby, the Casuarina Coast between Merauke and Etna Bay on the south of New Guinea, the Huon Gulf region between Lae and Tufi, and the south eastern tip of New Guinea between Milne and Orangerie Bays (and over to the Torres Strait) (Allen et al., 2016; Dudgeon et al., 2020). Knowledge on distribution limits of each species is needed to determine whether there are any hybridization zones or possibly even additional undescribed species awaiting discovery in these regions. Within species, highly limited dispersal has been shown in the Epaulette Shark, which demonstrated strong population genetic structuring based on single nucleotide polymorphisms along the length of the Great Barrier Reef and between reefs separated by as little as 110 km (Shackelton, 2022).

The rather unique situation of a genus of sharks with such restricted and non-overlapping species distributions, likely due to extremely limited dispersal capabilities, invariably raises a suite of questions about the underlying evolutionary processes that led to speciation in the group and resulted in the current distributions. Using a dated molecular phylogeny, Dudgeon et al. (2020) explored the likely sequence of events that resulted in the radiation of walking sharks. These authors conclude that *Hemiscyllium* represents a very recent radiation that began in the late Miocene and accelerated through the Pliocene, with the most recently derived species being Gale's Epaulette Shark and The Raja Ampat Epaulette Shark, which split a mere two million years ago. They show Hooded Carpet Shark from northern New Guinea to be the most basal taxon and hypothesise that this species gradually moved south and east to eventually cross the Torres Strait into northern Australia, giving rise to a clade that now includes Papuan Epaulette Carpetshark, Michael's Epaulette Shark, Epaulette Shark, and Speckled Carpetshark. They further hypothesised that the ancestors of the Halmahera Epaulette Shark may have in fact 'hitched a ride' on island arc fragments that were originally in contact with the northern coast of New Guinea, but which gradually moved to the north and west before colliding and forming present day Halmahera Island, which now sits about 130 km to the northwest of the western tip of New Guinea. That 'founder population' may then have given rise to the second major radiation that formed the clade (now spread across the Bird's Head region of northwest New Guinea) including Halmahera Epaulette Shark (the most basal taxon in this clade), Raja Ampat Epaulette Shark, Gale's Epaulette Shark, and Henry's Epaulette Shark. Divergence between these species was likely caused by a combination of founder events and vicariance caused by eustatic changes and tectonic movements that both created new habitat as well as caused new barriers to dispersal. In summary, Dudgeon et al. (2020) provided a compelling argument that *Hemiscyllium* represents one of the most recent evolutionary radiations of sharks, driven by a combination of vicariance and founder modes of speciation mediated by tectonic and oceanographic processes.

Perhaps unsurprisingly, the unique combination of features of epaulette sharks - striking colour patterns, intriguing behaviours such as 'walking' and the ability to crawl between isolated tide pools, highly restricted endemic distributions that make them perfect icons of a given region's unique marine life, and their status as some of the 'youngest of all shark species' - has imbued the walking sharks in the genus *Hemiscyllium* with a charisma that has made them important tourism attractions across their range. Particularly in regions of New Guinea (and its satellite islands) with burgeoning marine tourism industries including Milne Bay, Cendrawasih Bay, Raja Ampat, Halmahera, Fakfak, and Kaimana, the respective walking sharks found in each of those regions are now highly sought after by snorkellers and divers. Walking sharks have even been credited with driving a resurgence of interest in night diving and snorkelling. Dive resorts across the region advertise the chance to see walking sharks as a major attraction for tourists, and some have even incorporated them into their business logos. The economic value of walking sharks as living marine tourism assets was indeed a primary driver for the Indonesian government to confer full protected species status on all walking sharks found in Indonesian waters (see 'Conservation and Management' section).

MAJOR DRIVERS OF LOSS

All nine species of *Hemiscyllium* have been assessed for the IUCN Red List of Threatened Species, with two species considered to be Near Threatened (NT) and five species Vulnerable (VU; Table 1). Only the two species occurring in northern Australia, with the broadest of all epaulette sharks' distributions, are considered Least Concern (LC). A comprehensive discussion of the threats walking sharks face and their current conservation status, as well as a summary of the criteria used to assess their IUCN Red List status is covered in VanderWright et al. (2022). The authors highlighted that the underlying factor which resulted in VU and NT listings for seven of the nine walking sharks were their small geographic ranges (IUCN Red List B Criterion), and in particular their small Area of Occurrence (AOO; measured by mapping all known points of occurrence and then overlaying 2x2 km grid cells, with the sum of the area of the cells that that species occurs within being the AOO). In the case of walking sharks, the five species now listed as VU have AOO's of less than 2,000 km^2, with Hooded Carpet Shark having the smallest AOO at only 720 km^2 of suitable habitat along the northern coast of New Guinea. By comparison, the two species assessed to be of LC, Epaulette Shark and Speckled Carpetshark, both have AOO's that exceed 10,000 km^2 in northern Australia.

The range of threats most pertinent to walking sharks included a combination of direct threats from local, small-scale fisheries (and targeted capture for the marine ornamental trade for some species), and indirect threats of habitat loss and degradation due to coastal development, sedimentation, pollution, and climate change (VanderWright et al., 2022). As small-bodied sharks, epaulette sharks are generally of no value in the shark fin trade, and there is similarly no known commercial fishery for their meat, skin, or body parts. However, artisanal fishers around New Guinea and the satellite islands where walking sharks occur generally keep and consume any walking sharks they may catch with handlines, and in some places target walking sharks during night-time gleaning on reef flats (VanderWright et al., 2022). The relatively fast rate of growth and reproduction of walking sharks is likely sufficient to keep pace with the moderate fishing pressures exerted by the low human population densities occurring around New Guinea. However, there is increasing concern that targeted collection of walking sharks for the marine ornamental trade (well-documented by Jutan et al., 2018, for Halmahera Epaulette Shark, but likely also affecting other epaulette sharks as well) may be adding significant pressure on their populations.

Despite these known threats from direct capture of walking sharks, it is suspected that the loss and degradation of the shallow

Figure 3: Photographs showing the distinctly different juvenile (upper image) and adult (lower image) body coloration patterns of the Michael's Epaulette Shark. Though the juvenile pattern is unknown for several walking sharks, for those where it is, the juvenile shows a black and white or brown and white banding pattern similar to juvenile Chiloscyllium *species. | M.V. Erdmann*

coral reef and associated habitats where walking sharks occur is likely a bigger concern to the long-term persistence of these species (VanderWright et al., 2022). A specific threat identified is sedimentation and eutrophication from poorly planned coastal development; this ranges from construction of coastal roads to tourism accommodations with insufficient wastewater management, as well as collection of the larger coral boulders - under which walking sharks shelter during the day - for use in building foundations. Land conversion for palm oil, sugar cane, and other industrial-scale plantations in the coastal zone is another threat. Sedimentation and toxic effluent from coastal strip mining is also a significant threat to the habitat of some species of walking sharks in New Guinea and Halmahera.

Climate change is an ever-present concern as well, with ongoing degradation of shallow water coral reef and seagrass bed habitats predicted throughout the range of walking sharks as sea surface temperatures continue to rise. A more direct impact of climate change on walking sharks has been identified (Wheeler et al., 2021); in laboratory experiments they showed that growth and metabolic performance of Epaulette Shark becomes sub-optimal as water temperatures increase from 27°C (considered 'normal' for their habitat on the Great Barrier Reef; GBR) to 29–31°C (elevated temperatures which are nonetheless well within the range of expected temperature rise on the GBR). On the contrary, The Raja Ampat Epaulette Shark, Gale's Epaulette Shark, and Henry's Epaulette Shark are regularly (often daily) exposed to significantly higher temperatures of 34–36°C during daytime at low-tide exposures of the reef flat environments where they shelter, with no apparent ill effects (Erdmann, unpublished data). As such, it is not clear that the findings of Wheeler et al. (2021) are relevant to most walking sharks, nor if they might not be an artefact of experimental design in laboratory conditions.

Overall, it is the small geographic ranges of most walking sharks that is the root cause of concern for their susceptibility to extinction risk. Despite their quick growth and reproduction, and thus high population growth rate, their relatively tiny distributions, combined with limited potential to actively move away from degraded habitats or even seek refuge in depth, means walking sharks are particularly susceptible to any major perturbations to their habitat. Because of these factors, walking sharks are an interesting counterexample to the 'normal' situation facing many threatened sharks (VanderWright et al., 2022). The 'declining population paradigm' explains this more commonly seen situation, whereby intensive and pervasive fishing pressure threatens many slow growing/slow reproducing large sharks, despite range sizes that may span entire ocean basins. Instead, walking sharks present a situation more typical of the 'small population paradigm' that threatens many terrestrial species – while they may grow and reproduce fast and are not subject to intensive direct harvest, they are susceptible simply due to their relatively small populations that are in turn a result of their small geographic ranges.

CONSERVATION AND MANAGEMENT

Fortunately, at least seven of the nine species of walking sharks receive partial protection because of Marine Protected

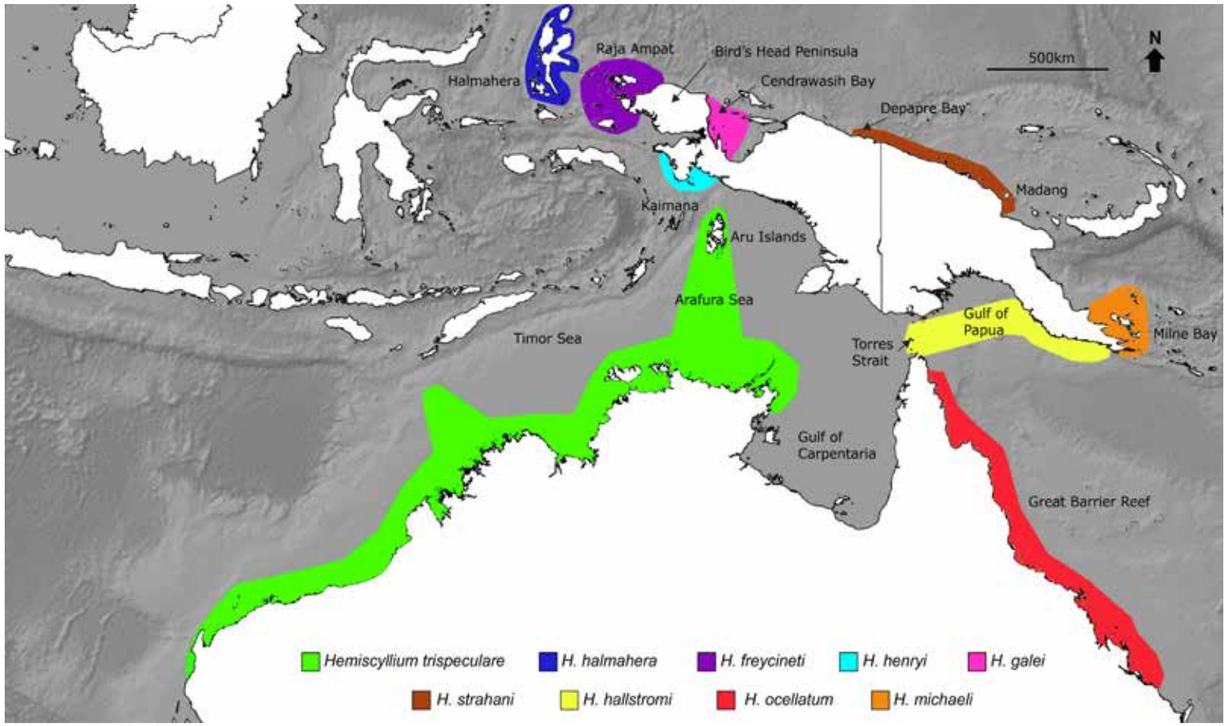

Figure 4: Map of the known geographic distributions of the nine species of Hemiscyllium | Map by C. Dudgeon; reprinted with permission from VanderWright et al. (2022) Imperilled: The Encyclopaedia of Conservation.

Halmahera Epaulette Shark, *Hemiscyllium halmahera*, in Halmahera, Indonesia | Mark Erdmann

Michael's Epaulette Shark, *Hemiscyllium michaeli*, in Milne Bay, Papua New Guinea | Gerry Alen

Hooded Carpet Shark
Hemiscyllium strahani from
Jayapura, Indonesia |
Mark Erdmann

Areas (MPAs). While MPAs cover significant percentages of their respective ranges, these MPAs vary widely in terms of their size, level of protection, and degree of effective enforcement (VanderWright et al., 2022). Those perhaps receiving the highest level of protection through MPAs are Epaulette Shark and Speckled Carpetshark, the two Australian species assessed as LC on the IUCN Red List, with parts of their ranges included within the Great Barrier Reef Marine Park and Ningaloo Marine Park, respectively.

Similarly, The Raja Ampat Epaulette Shark in Raja Ampat, West Papua, is afforded abundant protection through inclusion of over 80% of its distributional range within a network of nine well-patrolled MPAs covering 2,031,878 ha (VanderWright et al., 2022). Moreover, this species is fully protected throughout its entire range by the Raja Ampat Regency Law No. 9/2012 that provides full protection to all sharks and rays within their 45,000 km^2 marine area. With a booming marine tourism industry that highly values its sharks and rays, as evidenced by its now actively growing Reef Manta Ray (*Mobula alfredi*) population (Setyawan et al., 2022a, b), walking sharks in Raja Ampat are generally very well-protected.

Henry's Epaulette Shark, found along the Fakfak and Kaimana coastlines of the southern Bird's Head Peninsula in West Papua, has approximately 25% of its range included within three MPAs (Kaimana MPA – 122,856 ha; Buruway MPA – 240,493 ha; and Teluk Nusalasi Van Den Bosch MPA – 248,270 ha), though these MPAs are not yet as well-managed and enforced as those in Raja Ampat (VanderWright et al., 2022). Likewise, Gale's Epaulette Shark has over 80% of its known range protected within the Teluk Cenderawasih National Marine Park, though enforcement is again not at the same level of Raja Ampat or Australia.

Halmahera Epaulette Shark is afforded at least some protection by the local MPAs around Halmahera and Morotai islands, while Michael's Epaulette Shark may also receive some protection of its habitat from a network of small community based MPAs in Milne Bay (VanderWright et al., 2022). In both areas, there are marine tourism operators that place a high value on their endemic walking sharks, which may also encourage local conservation efforts. The remaining two species, Hooded Carpet Shark and Papuan Epaulette Carpetshark, appear to have the fewest formal protection measures in place of all the walking sharks, though Hooded Carpet Shark may receive some protection from a local MPA that has been declared in the northernmost reaches of its distribution in Depapre Bay, Papua, Indonesia.

Spurred by the updated IUCN Red Listings, strong support of conservation organisations, and marine tourism industry, the Indonesian government's Ministry of Marine Affairs and Fisheries passed Ministerial Decree #30/2023. This decree granted full protected species status to all six species of walking shark that occur within Indonesian territorial waters (The Raja Ampat Epaulette Shark, Gale's Epaulette Shark, Halmahera Epaulette Shark, Henry's Epaulette Shark, Hooded Carpet Shark, and Speckled Carpetshark). As of 2023, plans are in place to develop a National Plan of Action for the management of each of these six newly protected species.

Other than the two formal walking shark protections mentioned above for Indonesian species (Raja Ampat Regency Law #9/2012 and Indonesian Ministry of Marine Affairs and Fisheries Ministerial Decree #30/2023), there are no further formal protections in place for walking sharks. As of 2023, they are not covered by trade controls under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), though this may warrant consideration if the marine ornamental trade in walking sharks shows signs of increasing. Additionally, walking sharks do not qualify for protections under the Convention for the Conservation of Migratory Species of Wild Animals (CMS) as they are not migratory species.

It is apparent that the two species of walking shark found in southeastern Papua New Guinea - Michael's Epaulette Shark and Papuan Epaulette Carpetshark (both of which are assessed as VU) - should be prioritised for concerted conservation efforts. This might include formal protection regulations, designation of MPAs that protect significant areas of their distribution or a focus on policies designed to limit impacts of coastal development, mining, and land conversion to palm oil production on their limited shallow water habitat. It is perhaps worth mentioning that there is still a fair bit of uncertainty over the limits of distribution of these two species, including whether they establish a zone of secondary contact or hybridisation in the region between Milne Bay and Orangerie Bay near the southeastern tip of Papua New Guinea. Determining these distributions with more precision will be critical to designing conservation strategies to protect these two species.

Overall, the conservation outlook for the nine species of walking sharks is relatively bright and was made even more so with the rapid and forward-thinking move of the Indonesian government to fully protect all six species found in its waters shortly after their Red List assessments (completed in 2020) indicated five of these six species were either VU or NT. Nonetheless, with such small populations and restricted ranges, walking sharks will remain highly susceptible to disturbances and especially to habitat loss. This situation underscores the importance of focusing on the protection of shallow water habitats where walking sharks exist, and particularly on increasing efforts to limit land-based impacts from mining, palm oil conversion, road development, and poor coastal development practices in general. It is also important to manage the small-scale fisheries that still regularly catch walking sharks for local consumption, carefully monitor trends in the marine ornamental trade, and take action to limit or control exports of live animals if there are indications of overexploitation.

Table 1: List of walking sharks and their IUCN Red List status | Source: adapted from VanderWright et al. (2022)

SPECIES AND AUTHORITY	COMMON NAME	IUCN RED LIST STATUS
Hemiscyllium freycineti (Quoy & Gaimard, 1824)	The Raja Ampat Epaulette Shark	Near Threatened
Hemiscyllium galei Allen & Erdmann, 2008	Gale's Epaulette Shark	Vulnerable
Hemiscyllium hallstromi Whitley, 1967	Papuan Epaulette Carpetshark	Vulnerable
Hemiscyllium halmahera Allen, Erdmann & Dudgeon, 2013	Halmahera Epaulette Shark	Near Threatened
Hemiscyllium henryi Allen & Erdmann, 2008	Henry's Epaulette Shark	Vulnerable
Hemiscyllium michaeli Allen & Dudgeon, 2010	Michael's Epaulette Shark	Vulnerable
Hemiscyllium ocellatum (Bonnaterre, 1788)	Epaulette Shark	Least Concern
Hemiscyllium strahani Whitley, 1967	Hooded Carpet Shark	Vulnerable
Hemiscyllium trispeculare Richardson, 1843	Speckled Carpetshark	Least Concern

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Top: Hooded Carpet Shark *Hemiscyllium strahani* from Jayapura, Indonesia | Mark V. Erdmann

Bottom: Gale's Epaulette Shark *Hemiscyllium galei* from Cendrawasih Bay, Indonesia | Gerry Allen