# Extinction Risk and the Small Population Paradigm in the Micro-Endemic Radiation of Epaulette Sharks

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## Abstract

The Epaulette sharks (or walking sharks) in the genus *Hemiscyllium* comprise nine species, of which two are classified as Near Threatened and five as Vulnerable on the IUCN Red List. Here, we summarize the current taxonomy, biology, IUCN Red List status, threats, and conservation status of the Epaulette sharks. We find that the Epaulette sharks are facing direct threats from local, small-scale fisheries and indirect threats of habitat loss and degradation from climate change, coastal development, and industrial effluents. Many species benefit from protection in the extensive Marine Protected Areas in the Raja Ampat region. But in order to effectively conserve this unique radiation of sharks, priority must be placed on protecting the shallow near-shore habitats where they live and carefully managing the small-scale fisheries that have the potential to cause local extinction due to low population numbers and extremely restricted geographic ranges.

## Introduction

The word "shark" conjures an image of an iconic apex predator typified and popularized by the Hollywood movie portrayal of the White Shark (*Carcharodon carcharias*) in "Jaws," though White Sharks can hardly be considered the archetypal shark. The Class Chondrichthyes arose around 420 million years ago and sharks, rays, and ghost sharks are one of the largest vertebrate radiations, spanning many of the world's ocean habitats and some freshwater ones as well (Stein et al., 2018). There is an incredible diversity of morphologies, adaptations and lifestyles, ranging from dorso-ventrally flattened sit-and-wait predators like the Angel sharks (Squatinidae) to the small-bodied snake-like morphology that has evolved convergently in both the Catsharks (Scyliorhinidae) within the order Carcharhiniformes and also in the Bamboo sharks (Hemiscylliidae) within the order Orectolobiformes (Compagno, 1990; Dudgeon et al., 2020; Ebert et al., 2013).

Just as science is mostly focused on the more conventional requiem sharks (Carcharhinidae) and mackerel sharks (Lamniformes) (Shiffman et al., 2020), so too is our understanding of threats, extinction risk and conservation for sharks as a whole. The emerging paradigm is that the largest bodied species with slow life histories most accessible to fisheries (i.e., distributed in shallow, coastal waters), are likely to be declining due to overfishing and have an elevated risk of extinction (Field et al., 2009; Dulvy et al., 2014; Walls and Dulvy, 2020). This intrinsic sensitivity arises because the largest species tend to have late maturation, long lifespans, and particularly low fecundity, which results in some of the lowest intrinsic population growth rates among vertebrates (Hutchings et al., 2012; Cortés, 2016; Pardo et al., 2016a, 2016b). Such low population growth rates, combined with largely uncontrolled fishing mortality result in steep population reductions, exceeding the thresholds of the IUCN A criterion which categorizes the extinction risk of relatively large populations based on the rate of decline over a period of three generations (Porszt et al., 2012; d'Eon-Eggertson et al., 2015; Sherley et al., 2019). As such most sharks exemplify the "declining population paradigm" in which they are at risk of extinction not because populations are small, but instead because mortality rates exceed population growth rates, which if allowed to continue unabated, can only lead to extinction (Caughley, 1994; Mace and Lande, 1991).

It is increasingly clear that it is a "useful" fallacy that large population sizes and large geographic ranges can buffer such species from extinction (Hutchings, 2001; Sadovy, 2001; Kindsvater et al., 2016); "useful" in that this myth enables continued exploitation with minimal monitoring and management. Empirical evidence bears this out with increasingly concrete documentation of local, regional and global extinctions of wide-ranging and formerly abundant marine fishes due to overexploitation (Dulvy and Yan, 2020; Lawson et al., 2020; Yan et al., 2021). By contrast, most terrestrial taxa classified as threatened are at risk of extinction due to the "small population paradigm," with most species assessed using those criteria of the IUCN Red List Categories and Criteria which focus upon small geographic range (criterion B) and small population sizes (criteria C and D) and declines (criterion C) (Collen et al., 2016). While there has been much focus on extinction risk and conservation of wide-ranging sharks and rays, here we focus attention on the emergence of elevated extinction risk in smaller-bodied chondrichthyans that have narrow habitat requirements and geographic ranges, and by implication, smaller population sizes. Specifically, we focus upon the Epaulette sharks of the genus *Hemiscyllium*. We first describe the biology and the threats facing the nine species in the genus, and then describe the current conservation status of each of the Epaulette shark species.

## Biology

### Taxonomy and geographic distribution

There are nine recognized species in the genus *Hemiscyllium*, commonly known as Epaulette or Walking sharks. Together with the seven Indo-Pacific species of *Chiloscyllium*, they comprise the family Hemiscylliidae in the order Orectolobiformes.

The nine *Hemiscyllium* species are endemic to New Guinea, its satellite islands (including Halmahera, Aru and the Raja Ampat islands), and northern Australia: *H. freycineti*, *H. galei*, *H. hallstromi*, *H. halmahera*, *H. henryi*, *H. micheali*, *H. ocellatum*, *H. strahani*, and *H. trispeculare*. Four of the nine species have been recently described, including *H. galei* and *H. henryi* (Allen and Erdmann, 2008), *H. michaeli* (Allen and Dudgeon, 2010), and *H. halmahera* (Allen et al., 2013).

A recent phylogenetic analysis by Dudgeon et al. (2020) sheds light on the history and evolution of the Epaulette sharks. When the genetic maximum likelihood tree is examined with biogeographic reconstruction of the New Guinea region, a narrative of speciation is apparent. *Hemiscyllium strahani* appears to be the oldest taxon of the genus and was likely present on the northern coast of what is now New Guinea more than 9 million years ago (Ma). Individuals of *H. strahani* are hypothesized to have gradually moved east and south around New Guinea to cross the Torres Strait and colonize the northern coast of Australia, giving rise to *H. michaeli*, *H. hallstromi*, *H. trispeculare*, and *H. ocellatum*. At the same time, individuals may have colonized the island fragments which now comprise Halmahera, as these were once much farther east than where they are now. Over time, as the island fragments comprising modern day Halmahera moved west and the Bird's Head region of western Papua was being formed, individuals on Halmahera became more isolated and began to colonize the new habitat around the Bird's Head region, giving rise to *H. halmahera*, *H. henryi*, *H. galei*, and *H. freycineti* between 4 and 2 Ma (Fig. 1).
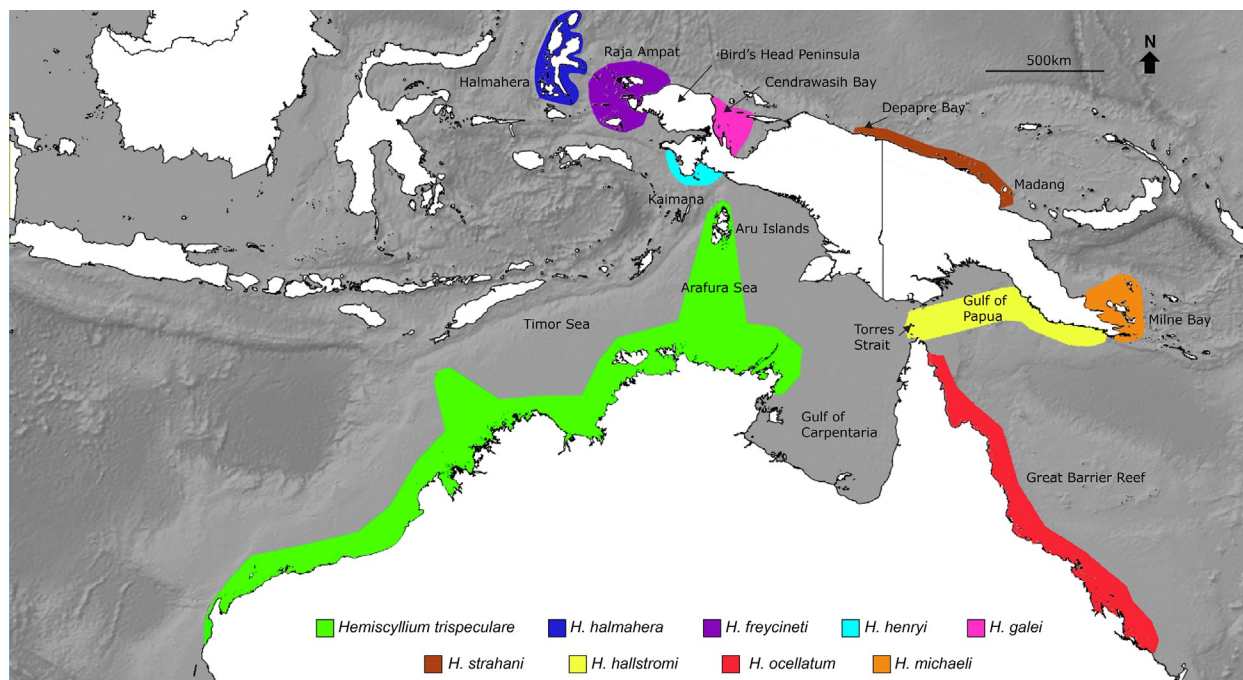


**Fig. 1**  Map of *Hemiscyllium* species geographic distributions. Note these are not cropped to depth, but in the analysis of Area of Occupancy these maps were cropped to the species depth distribution. This map is adapted from Dudgeon CL, Corrigan S, Yang L, Allen GR, Erdmann MV et al. (2020) Walking, swimming or hitching a ride? Phylogenetics and biogeography of the walking shark genus *Hemiscyllium*. *Marine and Freshwater Research*. 71: 1107–1117 with the addition to the distribution of *H. halmahera* around North Maluku and Morotai Island, Indonesia.

**Table 1**    Distribution descriptions of the Epaulette sharks.

| Species | Distribution |
|---|---|
| *Hemiscyllium freycineti*, (Quoy and Gaimard, 1824) | Endemic to the Raja Ampat Islands, West Papua, Indonesia (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. galei*, Allen and Erdmann, 2008 | Endemic to Cendrawasih Bay, West Papua Province, Indonesia (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. hallstromi*, Whitney, 1967 | Endemic to the south-east coast of Papua New Guinea, from the Torres Strait to the southernmost reach of Milne Bay (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. halmahera*, Allen et al., 2013 | Endemic to Halmahera, Indonesia (Allen et al., 2016; Dudgeon et al., 2020; Jutan et al., 2018). |
| *H. henryi*, Allen and Erdmann, 2008 | Endemic to the southern Bird's Head region (Fakfak and Kaimana), West Papua Province, Indonesia (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. michaeli*, Allen and Dudgeon, 2010 | Endemic to eastern Papua New Guinea in the vicinity of Milne Bay (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. ocellatum*, (Bonnaterre, 1788) | Found on the northern coast of Australia, east of the Torres Strait in Queensland (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. strahani*, Whitney, 1967 | Endemic to the north coast of New Guinea from Jayapura, Indonesia to Madang, Papua New Guinea (Allen et al., 2016; Dudgeon et al., 2020). |
| *H. trispeculare*, Richardson, 1843 | Found on the northern coast of Australia from Western Australia to the Northern Territory, west of the Gulf of Carpentaria, and north into the Arafura Sea at the island of Aru (Allen et al., 2016; Dudgeon et al., 2020). |

Each of the Epaulette shark species have a unique, non-overlapping range "tiled" with its congeners (Fig. 1, Table 1). The distributions range from Northern Australia to Halmahera, Indonesia with patches around Papua New Guinea and West Papua (Fig. 1). The hypothesized sequence of speciation of the genus *Hemiscyllium* helps to explain the "tiled" distributions, which have very little overlap (save for possibly the Torres Strait). With low dispersal potential and close association with shallow coral reef and associated habitats, the ranges of the Epaulette sharks seem to be driven largely by geographic changes in the region, leading to the creation of both barriers and new habitat.

## Morphology

The nine species of *Hemiscyllium* are morphologically similar, with only slight variation recorded among species. These sharks do not generally exceed 85 cm total length (TL), and most are smaller than 75 cm TL. They have slender bodies that taper towards the posterior, with elongated precaudal tails (Compagno, 1990). They typically have short, rounded snouts with short nasal barbels, their mouth is positioned below the eyes, they have two similarly sized dorsal fins that are posterior to the pelvic fins, and they all have a long slender tail (Allen et al., 2016; Fig. 2A). Subtle differences in adult color patterns (including the size, shape and spacing of the spots that cover the dorsal surfaces of the sharks) are the primary character used to distinguish the nine species; the juvenile color pattern is only known for a few of the species and consists of broad brown and white banding (Ebert et al., 2013; Allen et al., 2016).

This long and slender body type is common among the benthic reef-dwelling sharks and has evolved convergently across other families of sharks. One example is the Coral Catsharks (genus *Atelomycterus*) in the family Scyliorhinidae of the order Carcharhiniformes, which has very similar external morphology and habitat associations to *Hemiscyllium* (Fig. 2B).

## Habitat

The Epaulette sharks are commonly encountered on shallow coral reefs and associated seagrass and mangrove habitats in depths of 0–20 m, though some individuals are occasionally found as deep as 30–40 m. These sharks are well-camouflaged and can be observed foraging over reef flats and tide pools even at low tide. The main activity pattern is affected by a combination of suitable tidal and light conditions. They are more active after dark and particularly around dawn or dusk. The Epaulette sharks are tolerant of hypoxia and able to survive in anoxic waters (Routley et al., 2002). This trait is important as these sharks are often found in shallow (~15 cm deep), warm (~30 °C) waters that become severely hypoxic during the night due to the depletion of oxygen by the respiration cycle of primary producers. This trait may enable this species to survive in areas of poor water quality as is typical of poorly flushed sunlit tidepools (Allen et al., 2016).

## Reproduction

Our knowledge of reproduction in the Epaulette sharks is limited to data from *H. halmahera* and especially *H. ocellatum*, with very little known from the other species. All members of the genus *Hemiscyllium* are presumed to be oviparous with a size-at-birth estimated as ~15 cm TL, based on *H. ocellatum* (West and Carter, 1990). The size-at-maturity is estimated to range from 48 to 68 cm TL depending on the species. Age data was used from the Halmahera Epaulette Shark (*H. halmahera*) and the Epaulette Shark (*H. ocellatum*) which have estimates for age-at-maturity of 2 and 4 years respectively (Heupel, 1999; Jutan et al., 2018). Maximum age of these sharks can range from 6 to 10 years (Heupel, 1999, Jutan et al., 2018). This equates to an average generation length of 5.5 years that can be inferred to be similar for other members of the genus.
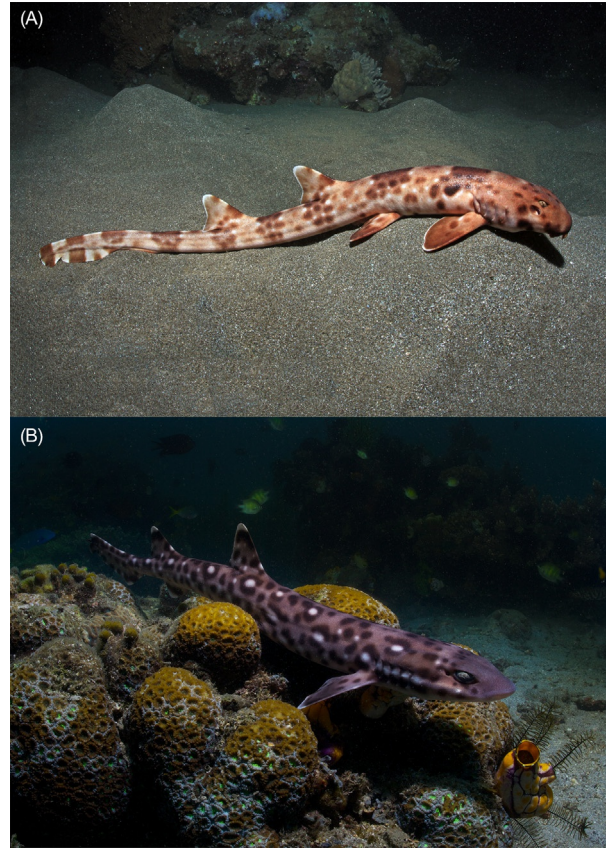
**Fig. 2**    (A) Photographs of a Halmahera Epaulette Shark (*Hemiscyllium halmahera*) and (B) a Spotted-belly Catshark (*Atelomycterus erdmanni*) in their natural habitat. Photograph credits: M.V. Erdmann.

Based on *H. ocellatum* at Heron Island, mating probably occurs between July and November though periodicity for other species could be different. Females have been observed carrying egg cases in the wild between August and December (Heupel et al., 1999), although in captivity it has been observed to breed continuously throughout the year (West and Carter, 1990). Two egg capsules are produced and deposited among coral heads at night. A pair of egg capsules may be produced every 14 days, resulting in up to about 20 potential offspring per year. Growth of neonates is initially slow, but reaches approximately 5 cm per year after about 3 months (West and Carter, 1990).

### Maximum population growth rate

Maximum population growth rate ($r_{max}$) is calculated as a function of age of maturity, maximum age, fecundity, and somatic growth rate ($k$ from von Bertalanffy growth function; Musick, 1999). The maximum population growth rate reflects the productivity of a population where density-dependence is absent (i.e., depleted populations; Myers et al., 1997) and comparisons of $r_{max}$ among species can help inform overexploitation risk when population data may be lacking (Dulvy et al., 2014; Pardo et al., 2016a; Dillingham et al., 2016). For our purposes, we estimated the $r_{max}$ for Epaulette sharks using methods outlined by Pardo et al., 2016a. We used:

$$l_{\alpha_{mat}} b = e^{r_{max} \cdot \alpha_{mat}} - e^{-M}(e^{r_{max}})^{\alpha_{mat} - 1}$$

where $l_{\alpha mat}$ is the survival to maturity, $b$ is the annual reproductive output of daughters, $\alpha_{mat}$ is the age of maturity, and $M$ is the natural mortality. For the Epaulette sharks, we set $b$ to ten using estimates for *H. ocellatum* (West and Carter, 1990) as they produce 20 offspring annually and we assumed 1:1 sex ratio. Age at maturity ($\alpha_{mat}$) was set to a uniform distribution ranging from two to four based on *H. halmahera* and *H. ocellatum* (Heupel, 1999; Jutan et al., 2018). Natural mortality ($M$) was estimated as $1/\omega$ where $\omega$ is the average lifespan ([age of maturity + maximum age]/2). Maximum age was explored using a uniform distribution ranging from 6 to 10 based on *H. halmahera* and *H. ocellatum*, resulting in an average lifespan of 5.5 years (Heupel, 1999, Jutan et al., 2018).
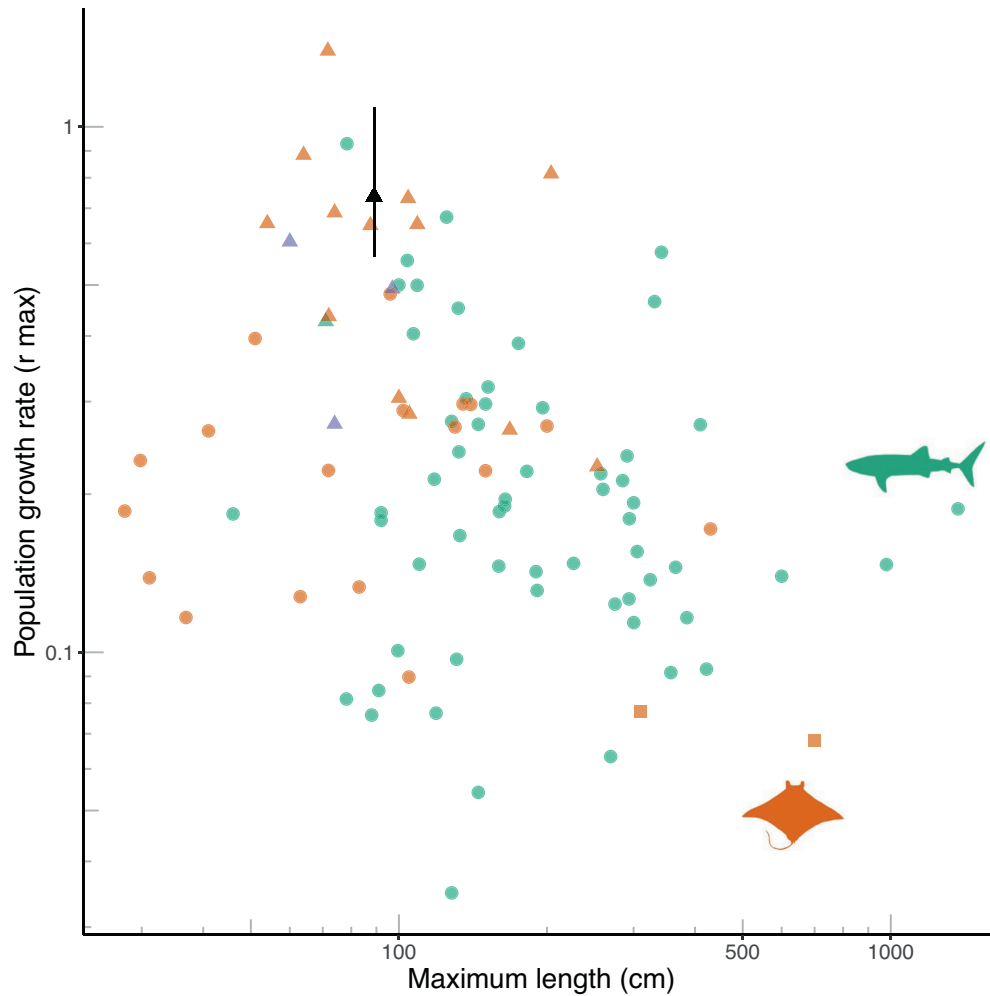
**Fig. 3** Maximum population growth rates, $r_{max}$, for 97 sharks, rays, and ghostsharks adapted from Pardo SA, Kindsvater HK, Cuevas-Zimbrón E, Sosa-Nishizaki O, Pérez-Jiménez JC and Dulvy NK (2016a) Growth, productivity, and relative extinction risk of a data-sparse devil ray. *Scientific Reports* **6**: 1–10. Epaulette sharks are represented by the black triangle and the vertical bar represents the 95% confidence interval. Key: Sharks: green; rays: red; ghostsharks: blue; circles: viviparous species; triangles: oviparous species; squares: Mobulidae.

When we solve the above equation for $r_{max}$ with random draws from the parameter ranges, we obtain an average maximum population growth rate estimate of 0.736 for Epaulette sharks (95% CI: 0.565–1.089, Fig. 3). The population doubling time is estimated as $T_d = \ln(2)/\ln(1 + r_{max})$, therefore $T_d = 1.22$ years (CI 1.55–0.89) for Epaulette sharks, which is fast compared to a typical carcharhinid shark, such as the Night Shark (*C. signatus*) in the Atlantic which usually have an $r_{max}$ of ~0.2 resulting in a doubling time of 35 years (Pardo et al., 2016a, 2018). This estimate of Epaulette shark $r_{max}$ is high compared to other sharks, but unsurprising given that they are small meso-predators that reach maturity quickly and lay many eggs per year. The relatively high maximum population growth rate may be a key reason that the Epaulette sharks persist in their current distributions in the face of a number of important threats, described below.

## Threats

### Small geographic ranges and habitat loss

Due to the seemingly heavy reliance on shallow reef habitats and possibly low dispersal, the Epaulette sharks exhibit generally small range sizes compared to other shallow reef-dwelling sharks. With the majority of Epaulette sharks not being observed deeper than 20 m, they are limited to reside on the very upper shelf and may be unable to traverse boundaries of depths greater than 50 m. With small range sizes, any loss in habitat will very likely cause declines in mature individuals and increases the likelihood of local extinction events.

Two species of *Hemiscyllium* are classified as Near Threatened (NT), while five species are now classified as Vulnerable (VU) to extinction on the IUCN Red List of Threatened Species (Table 1, Fig. 4). Of these seven species, all of them are assessed using the
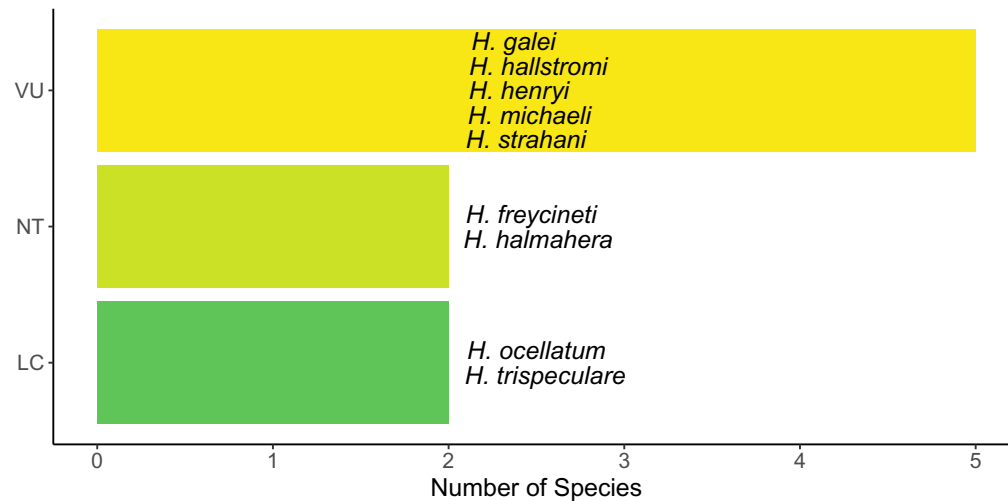
**Fig. 4**    The number of species in each IUCN Red List status category; LC: Least Concern; NT: Near Threatened; VU: Vulnerable.

IUCN Red List B criterion. The B criterion is applied to species with a small geographic range as well as two of the following three conditions: (a) is also fragmented or found in few locations, and/or (b) is undergoing continuing decline and/or (c) extreme fluctuations. Most species are rare and have small geographic ranges, so having a small geographic range is not enough to meet this criterion (Gaston, 1994; Mace et al., 2008). This area-based occurrence metric can work on two scales. The first and larger scale is referred to as the Extent of Occurrence (EOO) in the B1 criterion. The EOO is calculated by drawing a polygon around the known distribution of the species and measuring the area of the drawn polygon. Critically and counterintuitively this polygon can include unsuitable habitat (such as the land between islands and deepwater separating islands). This is because these measures capture the spatial extent of a threatening process and the likely high spatial autocorrelation in population dynamics at small spatial scale (Joppa et al., 2015). If the EOO is less than 20,000 km$^2$, the species is considered to be in one of the threat categories if it also meets two of the three subcriteria including: (a) severely fragmented or low number of locations, (b) continuing decline in (i) extent of occurrence, (ii) area of occupancy and/or habitat quality, (iv) number of locations or subpopulations, or (v) number of mature individuals, and (c) extreme fluctuations in area, number of locations, or number of mature individuals. The second scale that the B2 criteria works on is referred to as the Area of Occurrence (AOO). The AOO is measured by mapping all known points of occurrence and then overlaying 2 × 2 km grid cells. The sum of the area of the cells that the species occurs within is the AOO. If the AOO is less than 2000 km$^2$, then the species is considered to be in one of the threat categories (if it also meets the same subcriteria defined above).

Six of the seven Near Threatened or threatened Epaulette sharks were assessed using the AOO B criterion. This was possible due to the heavy reliance of these sharks on their reef habitat. When the 2 × 2 km grid cells were overlaid with the known reef habitat in each species distribution, it was possible to calculate the AOO for each species (Table 2).

*H. strahani* exhibits the smallest AOO with an estimated 720 km$^2$ of suitable habitat along the coast of northern New Guinea. The Epaulette sharks with the largest AOO are *H. trispeculare* and *H. ocellatum*, each with more than 10,000 km$^2$ of usable habitat on the northern coast of Australia. The mosaic of these species' ranges is intriguing, with no known overlap of any 2 species save for possibly the Torres Strait, where *H. hallstromi* and *H. ocellatum* may co-occur.

**Table 2**    List of Epaulette shark species and their IUCN Red List Status.

| Species | IUCN Red List Status and Criteria | References |
| --- | --- | --- |
| *Hemiscyllium freycineti*, (Quoy and Gaimard, 1824) | Near Threatened B2ab (ii, iii, v) | VanderWright et al. (2020b) |
| *H. galei*, Allen and Erdmann, 2008 | Vulnerable B2ab (ii, iii ,v) | VanderWright et al. (2020d) |
| *H. hallstromi*, Whitney, 1967 | Vulnerable B1ab (iii) | Dudgeon et al. (2016) |
| *H. halmahera*, Allen et al., 2013 | Near Threatened B2ab (ii, iii, v) | VanderWright et al. (2020e) |
| *H. henryi*, Allen and Erdmann, 2008 | Vulnerable B2ab (ii, iii, v) | VanderWright et al. (2020c) |
| *H. michaeli*, Allen and Dudgeon, 2010 | Vulnerable B2ab (ii, iii, v) | VanderWright et al. (2020a) |
| *H. ocellatum*, (Bonnaterre, 1788) | Least Concern | Bennett et al. (2015) |
| *H. strahani*, Whitney, 1967 | Vulnerable B2ab (ii, iii, v) | VanderWright et al. (2020f ) |
| *H. trispeculare*, Richardson, 1843 | Least Concern | Heupel (2015) |

### Fishing as a threat

Large (>30 cm Standard Length, SL) coral reef fishes that are targeted by fishers have exhibited declines in abundance even in areas with low human population in Papua New Guinea (Drew et al., 2015). This pattern of steep decline of predatory fishes as a result of subsistence fishing is found throughout the western Pacific (Dulvy et al., 2004a, 2004b; Newton et al., 2007). Even apparently unfished species (<30 cm SL) also show declines, but less than that of the targeted species (Drew et al., 2015). The Epaulette sharks present in New Guinea are taken by artisanal fishing by gleaning (collecting by hand or hand spear on intertidal reef flats, generally at night), extensive gill netting down to 20 m depths (using a 10 cm mesh size), and hand-lining which is prevalent throughout most of their range at 5–15 m depths.

These species are also targeted for the aquarium trade. *H. halmahera* is collected for the aquarium trade with larger individuals (>60 cm TL) collected for local aquaria and smaller individuals (<60 cm TL) are targeted for export to European aquaria, with up to 60 individuals per shipment (Jutan et al., 2018; VanderWright et al., 2020e). A recent online search uncovered a website that offers live individuals for USD $88 each that are labelled Indonesian Bambooshark (*C. hasselti*) but showed pictures of *H. galei* in the description (Marine World Aquatics, 2020). This finding, as well as anecdotal reports from fishers in eastern Indonesia, suggests that other members of Hemiscylliidae could be targeted and might be marketed as bamboo sharks, walking sharks or Epaulette sharks. Based on observations of the authors and the results of fisher interviews, we conclude that if Epaulette sharks are caught, they are always retained for artisanal consumption or for the aquarium trade. They are not generally sold or seen in fish markets.

### Habitat loss and degradation from coastal development and mining

In Papua New Guinea, many of the major rivers have been degraded by land clearing and pollution from mining operations (Fowler et al., 2005). The downstream effects of these practices may have dire consequences for nearby reef communities. In the Gulf of Papua, threats to reefs include river-borne pollutants and sedimentation from mining run-off (Kirsch, 1996), dynamite fishing, oil exploration and pipeline development, and localized sewage effluent from Port Moresby (Convention on Biological Diversity, 2010).

In eastern PNG there has been habitat degradation of reef flats due to nearby road construction and land conversion for palm oil throughout ~20% of its range over the last 10 years (Fig. 5; VanderWright et al., 2020a). Cendrawasih Bay, West Papua Province, Indonesia also exhibits habitat loss and degradation of the reef flats resulting from road construction and extensive land conversion for palm oil in the coastal area over the past 5 years.

Habitat degradation of reef flats occurs in approximately 20% of the Raja Ampat Island region due to a combination of tourism and coastal development (VanderWright et al., 2020b). Resort or homestay construction not only generates sedimentation, it also



Fig. 5    Example of coastal development present in New Guinea (Mayalibit Bay, Raja Ampat, West Papua). Photograph credit: C. Hufford, Conservation International.

involves the collection of large rocks and dead coral heads or "bommies" from the intertidal zone that were favored daytime sheltering sites for Epaulette sharks. There is also frequent disturbance of shallow reef flats and seagrass beds by speedboats and longboats accessing beaches in the region.

In Halmahera, Indonesia there is habitat degradation of reef flats due to dynamite fishing and open-pit mining in coastal zones throughout its range. The mining in the area also poses a threat of heavy metal pollution. A study of mercury in *H. halmahera* shows exposure of 6.50 µg/g creatinine, which is above the safe threshold of 1 µg/g creatinine suggesting renal stress from heavy metal exposure (Jutan et al., 2019).

### Climate change

Global climate change has already resulted in large-scale coral bleaching events at increasing frequency, causing worldwide reef degradation since 1997. Almost all warm-water coral reefs are projected to suffer significant losses of area and local extinctions, even if global warming is limited to 1.5 °C (IPCC, 2019). With the heavy reliance of Epaulette sharks on their shallow reef habitats, any significant loss or shifts in reef distribution would result in the loss of mature individuals and could lead to local extinction events that may not be easily reversible given their likely limited dispersal capability. Other threats from climate change include higher sea surface temperatures and reduced dissolved oxygen, which fortunately the Epaulette sharks have been shown to be rather resilient to (Wise et al., 1998; Routley et al., 2002; Heinrich et al., 2014).

### Conservation

Many of the Epaulette sharks occur inside marine protected areas (MPAs) with varying levels of protection and enforcement. *Hemiscyllium freycineti* is afforded significant conservation protection, with the majority of its home range included within a network of nine separate MPAs totaling 2,031,878 ha and covering 80% of the species' range (VanderWright et al., 2020b). *Hemiscyllium freycineti* is a favored species for viewing by the booming dive and snorkel marine tourism industry in Raja Ampat, and it is fully protected throughout its full range by Raja Ampat Regency Law No. 9/2012 that provides full protection to all sharks and rays within the 45,000 km$^2$ Raja Ampat regency, as well as providing full protection to all Raja Ampat endemic fish species (no possession, no trade). Despite these protections, some gleaning pressure still exists.

*Hemiscyllium henryi* is afforded some conservation protection over some of its known range (~25%) by three MPAs: Kaimana MPA (122,586 ha), Buruway MPA (240,493 ha) and Teluk Nusalasi Van Den Bosch (248,270 ha)—though enforcement is generally weak and there is no explicit protection for sharks in this region (VanderWright et al., 2020c). Moreover, the use of gillnets is very common over this species' range. The MPAs do prevent wholesale habitat destruction and commercial fisheries however.

*Hemiscyllium galei* is afforded some conservation protection over much of its known range (80%) by the Teluk Cendrawasih National Marine Park (1,453,500 ha)—though enforcement is generally weak and there is no explicit protection for sharks within the park (VanderWright et al., 2020d). The park does prevent habitat destruction and commercial fisheries. There is a growing marine tourism industry in the region that values this species as a tourism asset.

In eastern Papua New Guinea, there is a growing marine tourism industry that values reef species as tourism assets. There are some small community-based MPAs in the Milne Bay region that may offer some protection for *H. michaeli*, and there is a local marine tourism industry which values this species on the reefs.

*Hemiscyllium ocellatum* is protected in parts of the Great Barrier Reef Marine Park, Queensland and *H. trispeculare* is protected in Ningaloo Marine Park, Western Australia (Bennett et al., 2015; Heupel, 2015). There are currently no known conservation measures in place for *H. halmahera*, *H. strahani*, or *H. hallstromi*, though a number of MPAs are now being gazetted around Halmahera and Morotai Islands that should provide some protection to *H. halmahera*.

Importantly, the Indonesian Ministry of Marine Affairs and Fisheries has designated the six species which occur in Indonesian waters (*H. halmahera*, *H. freycineti*, *H. henryi*, *H. trispeculare*, *H. galei* and *H. strahani*) as priority species for conservation action, and is considering protected species status for the group.

### Conclusions

Overall, the Epaulette sharks are a unique clade endemic to northern Australia and New Guinea, with over two-thirds of the species threatened or Nearly Threatened. Two of the nine species present on the north coast of Australia (*H. trispeculare* and *H. ocellatum*) are of Least Concern and are somewhat protected from many of the threats present in New Guinea and the surrounding islands. Being shallow reef-associated species, the Epaulette sharks are experiencing a myriad of threats, with little or no depth refuge to escape them. Human activity, both on land and in the ocean, is causing the known threats that these sharks experience. There is direct exploitation and extraction of these species as well as indirect stress and mortality from coastal development (Fig. 6).

The Epaulette sharks appear to be limited to shallow depths and both their global and local distribution is limited to reef habitats and associated seagrass and mangroves. Their dispersal may be limited by their inability to traverse long distances or deep channels. This is compounded by their egg-laying reproductive mode which does not provide any additional dispersal ability.
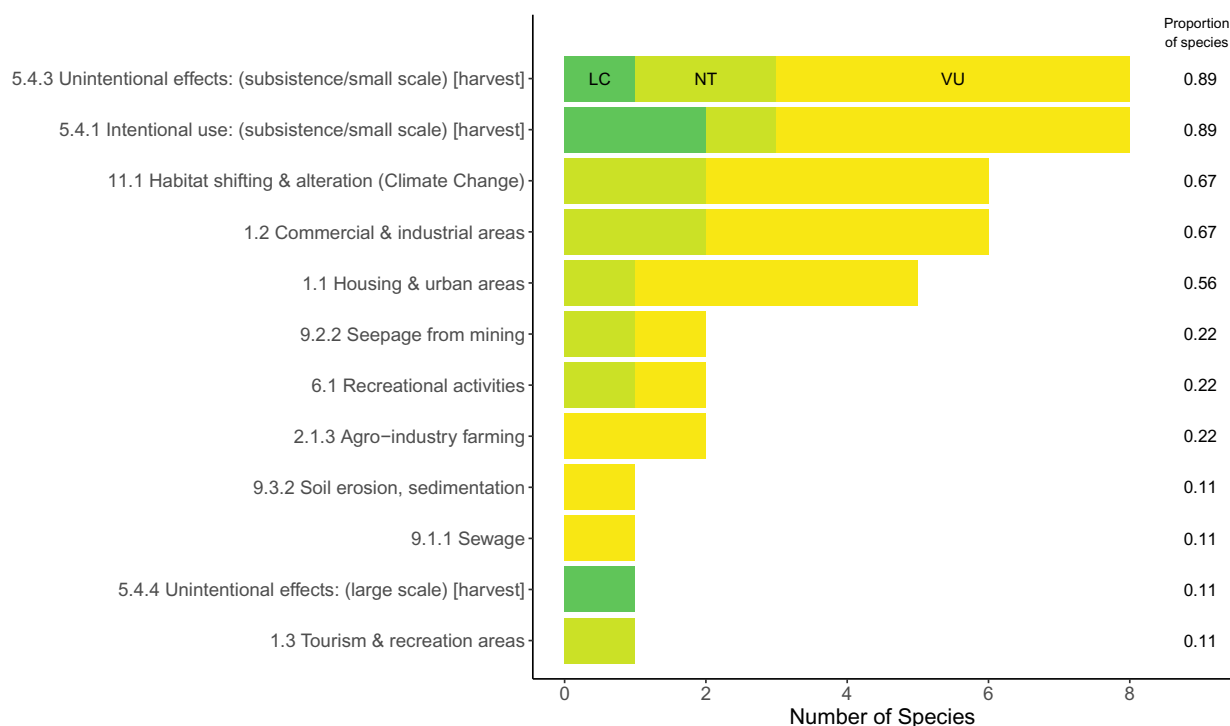
**Fig. 6** The number of Epaulette shark species coded each IUCN-defined threat category, with the proportion of Epaulette shark species threatened by that category listed on the right of each bar.

Habitat degradation has a disproportionately large effect on these sharks as they rely on coastal reefs and associated seagrass and mangrove habitats and are unable to move to a new area when habitat is lost. The reefs in New Guinea are being degraded by multiple processes that may compound each other. Climate change has led to warmer temperatures and increased ocean acidification, which has triggered multiple coral bleaching events in the region since the late 1990s (IPCC, 2019). Coastal development in New Guinea for housing and industry such as mining and palm oil plantations, has changed the sediment flow in the area, which can degrade the nearby reefs (VanderWright et al., 2020a). These agriculture and mining activities also generate runoff effluents which can be detrimental to the reefs in the area as well as the organisms associated with them. Fishing is an omnipresent threat that is present throughout the world's coral reefs (Newton et al., 2007; MacNeil et al., 2015, 2020). The Epaulette sharks are easily targeted as a shallow water species associated with reefs, seagrass beds and mangroves. In New Guinea, they are caught in multiple fishing gears and are used for subsistence food and exported for the marine ornamental trade. The seven species present in New Guinea and the adjacent islands are exposed to at least 10 categories of threats, with small-scale (artisanal) fishing, habitat degradation from climate change, and commercial and industrial development happening homogeneously across the region. With many of the Epaulette sharks exhibiting rather small Areas of Occurrence, conservation of reef habitat should be a top priority, particularly in New Guinea and the adjacent islands, where range sizes are the smallest and coastal development is advancing rapidly.

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