



A tangled web: global review of fishing interactions with rhino rays

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Abstract Rhino rays (Order Rhinopristiformes) are one of the most threatened vertebrate groups. Despite overfishing being recognised as the greatest threat to this group, a comprehensive assessment of the fisheries and types of fishing gear that rhino rays interact with is lacking. We reviewed published and grey literature ($n=116$ references) to evaluate interactions between rhino rays and fisheries, determine gear types most responsible for their capture, and species for which most interactions occur by region. Interactions ($n=420$) were reported from 37 of 88 range states, for 52 of 68 known species. Combined, 59% of the literature reported interactions from trawlers and gillnets. Wedgefishes (Rhinidae) were the most reported family (29%) and bowmouth guitarfish (*Rhina ancylostomus*)

the most reported species (9.5%). Asia accounted for half of interactions ($n=211$), with 67% of the literature from unspecified gear (e.g., mixed landings), masking gear-specific interactions. Data quality was variable, with the highest resolution in countries with lower species diversity and where species are least imperiled (e.g., Australia). Discard mortality and physiological effects of capture are poorly known with data available for 25% of species (almost exclusively from Australia and the Americas). While additional data are urgently required to quantify the true extent of rhino ray catch globally, reducing fisheries mortality is a priority and key to address declining populations. Recommendations include prioritizing spatial management in critical habitats (e.g., nursery areas), expansion in the use of proven bycatch reduction devices, encouraging safe

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release and handling, and addressing drivers of retention and trade.

Keywords Bycatch · Conservation · Sawfishes · Wedgefishes · Guitarfishes · Banjo rays

Introduction

Fisheries, both target and bycatch (i.e., the discards and landings of non-target catch), impact a diverse range of taxa globally and are driving population declines in marine megafauna (e.g., sea turtles, marine mammals, seabirds, sharks, and rays) (Alverson et al. 1994; Senko et al. 2014; Bonanomi et al. 2017; Dulvy et al. 2021). Marine megafauna are generally characterized by life history parameters that include slow growth, late sexual maturity, and low natural mortality, making them particularly susceptible to overexploitation and depletion from fishing pressure (Musick 1999; Senko et al. 2014). Fisheries interactions with marine mammals and seabirds have been widely studied (e.g., Anderson et al. 2011; Jog et al. 2022), however, other species susceptible to fisheries driven mortality have received less attention.

Nearly all species of the class Chondrichthyes (sharks, rays, and chimaeras) are captured as bycatch in fisheries (99%; 1082/1093 evaluated species; Dulvy et al. 2021). For many elasmobranchs (sharks and rays), global fishing mortality likely exceeds their rebound potential (Pardo et al. 2016). This limits the ability of these species to sustain current levels of catch and recover from population depletion (Musick 1999; Stevens et al. 2000; Pardo et al. 2016). Research and data collection on fisheries interactions have largely focused on pelagic species which are regularly caught in industrial longline or purse seine fisheries but represent a small proportion of sharks and rays ($n=31$ species; Pacoureau et al. 2021). Many other groups of sharks and rays are highly threatened, with fisheries driving population declines, yet available data to aid management are scarce (e.g., Kyne et al. 2020; Dulvy et al. 2021). Indeed, the lack of data on catch and bycatch levels for many sharks and rays presents a serious barrier to understanding the scale of the issue and effectively addressing it. Research and conservation efforts have increasingly focused on sharks, while less attention has been paid to rays (Molina and Cooke 2012; Ferrette et al. 2019;

D’Alberto et al. 2022). This is despite the increasing proportion of rays in global catches (e.g., White et al. 2013; Bonanomi et al. 2017), reports of expanding targeted ray fisheries (e.g., D’Alberto et al. 2022; Tyabji et al. 2022), and data highlighting they have an elevated risk of extinction (Dulvy et al. 2021). Rays face a higher level of extinction risk than sharks with 36% and 31%, respectively assessed as threatened according to the IUCN Red List of Threatened Species™ (‘IUCN Red List’) (Dulvy et al. 2021). Improved information on fishery interactions with the most threatened species is urgently needed to understand the scale of interactions and to develop and implement mitigation measures.

The order Rhinopristiformes (herein ‘rhino rays’) are a group of shark-like rays, comprising five families: sawfishes (Pristidae), wedgefishes (Rhinidae), guitarfishes (Rhinobatidae), giant guitarfishes (Glaucostegidae), and banjo rays (Trygonorrhinidae). The level of global extinction risk for rhino rays is extremely high. At the order level, 72% of the 65 evaluated species fall within IUCN Red List threatened categories (Critically Endangered, Endangered, Vulnerable; IUCN 2023). Extinction risk at the family level is variable but all families have a higher proportion of threatened species than chondrichthyans as a whole (32% threatened): sawfishes (100% threatened), wedgefishes (90% threatened), guitarfishes (66% threatened), giant guitarfishes (100% threatened), and banjo rays (38% threatened) (IUCN 2023). This places three families (sawfish, wedgefish, giant guitarfish) amongst the most threatened vertebrates globally. Interactions with and mortality of rhino rays in fisheries is a major concern especially since their occupancy of estuarine, coastal, and continental shelf benthic habitats make them extremely susceptible to capture by multiple fishing gear in subsistence, artisanal, and industrial fisheries (Moore 2017; Jabado et al. 2018; Kyne et al. 2020).

A substantial increase in fishing effort throughout the distribution of rhino rays has added to pressures on populations (Moore 2017; Jabado 2018; Kyne et al. 2020; Kyne and Jabado 2021). Despite documented population declines linked to the incidental capture of rhino rays (White et al. 2013; Newell 2017; Kyne et al. 2020; Larre et al. 2021), there has been no attempt to collate available information to understand the potential impacts of various fishing gear on these species, highlight knowledge gaps, and determine conservation priorities. Here, we aim to address

this data paucity by reviewing the available literature to understand fisheries interactions and: (1) determine the fishing gears that rhino rays are reported as most susceptible to capture in; (2) identify the species most at risk from target and incidental captures and the regions where high levels of interactions are reported; (3) evaluate research into the effectiveness of mitigation measures for this group; (4) describe fishing-related mortality rates and known physiological consequences from capture stress; and (5) provide recommendations for priority conservation actions.

Methods

We present a contemporary (1989 onwards) review of primary (i.e., peer-reviewed publications) and gray literature (i.e., technical reports, theses), discussing major fishing gear commonly cited as interacting with rhino rays. This timeframe reflects the available information that could be extracted from online sources, our ability to evaluate the accuracy of the data, and ensures that our review is of contemporary relevance for management. We focus specifically on trawls, gillnets (and trammel nets), and line fishing methods (e.g., benthic longlines and hook-and-line). However, to provide a comprehensive picture of likely impacts of fisheries on rhino rays, we also review data on other gears that generally have lower levels of interaction, such as seine nets and bather protection programs. We also present information collected from market or landing site surveys where gear type may not be known with certainty (i.e., multi-gear fisheries). To best understand gear interactions among species in this group, information deriving from both target fisheries and bycatch is reported. We excluded information derived from scientific or research surveys as well as directed sampling, to focus on fishing interactions. Further, data collected through citizen science or interview surveys are not reported since they often do not contain quantitative data and/or are self-reported. On the other hand, results presented in the sections concerning mitigation measures, and mortality and physiological considerations, incorporate data from scientific cruises and laboratory experiments when rhino rays were specifically considered.

Searches were first conducted on the Web of Science in English. Each search began by targeting

general literature on marine megafauna interactions with fisheries, using search terms such as ‘target’, ‘fishery’, ‘landings’, ‘incidental’, ‘bycatch’, ‘megafauna’, ‘threatened’, and ‘non-target catch’. We then refined searches by using the Boolean search terms: discard*; non-target*; elasm*; shark*; ray*; rhino ray*; wedgefish*; guitarfish*; sawfish*; banjo ray*; as well as all species-, genus-, and family level scientific names. The same search terms were also entered into Google Scholar and Google Chrome. A snowball method gathered references from peer-reviewed articles and technical reports. Though searches were conducted in English, non-English sources were included based on accessibility and ability to extract information accurately. From each study/reference, we extracted data to the lowest taxonomic level and recorded where available, gear type, mesh size, depth, soak time, location of study, year(s), duration of monitoring or data collection, size ranges, and if animals were retained or discarded. Each of these data points are referred to as ‘interactions’ and therefore, there may be multiple interactions reported from one study. For example, a study with observations from gillnets that reported on three species, would represent three interactions. Likewise, three species each observed from two gear types represents six interactions. In cases of uncertainty, we took the more conservative number, therefore, interactions are likely to represent lower limits in our study, rather than upper.

We define fishing gear types as per Kyne and Jabado (2021), and first present catch information (target catch and bycatch) according to fishing gear (benthic trawl [since rhino rays are demersal species]), gillnet, line, mixed gear, bather protection gear, and recreational fishing, with regional subsections provided within each gear type. The following five regions were considered: North America (Canada to Mexico on the Pacific and Atlantic coast), Central and South America (Guatemala to Chile on the Pacific coast and Belize to Argentina on the Atlantic coast), Mediterranean Sea and Africa (Atlantic and Indian Ocean coasts), Asia (Middle East to Southeast Asia), and Oceania (Australasia and Melanesia). This is followed by a section on available mitigation measures, which covers technical modifications to gear that have been successful at reducing catch rates of rhino rays, and a section on physiological considerations (e.g., discard fate, sublethal considerations). These two sections are arranged according

to gear type. We acknowledge that various input and output controls exist in fisheries management that can be successful at reducing fisheries interactions, but that was not the focus here, and therefore these have not been included.

Scientific names used reflect the most recent taxonomic revisions (Eschmeyer's Catalog of Fishes; Fricke et al. 2023) and common names follow those used by the IUCN Red List (IUCN 2023). We note that nomenclature used might differ from the source because of taxonomic revisions (e.g., species formerly in the genus *Rhinobatos* but now placed in *Pseudobatos* are referred to as the latter). These synonyms and changes are noted in Online Resources 1 and 2, respectively.

Results

From 116 studies, we recorded 420 fishing interactions with rhino rays from 37 of the 88 countries rhino ray distribution is reported from (i.e., range states; Fig. 1). Trawls and unspecified gear (e.g., from data collected at landing sites) each represented roughly one-third of the studies, but the latter was attributed to the highest proportion of interactions (Table 1 and Online Resource 2). Although instances where records were not species-specific may mask higher diversity, interactions at the species level were reported for 52 species; by region and [known] gear, species coverage was highest from Asia ($n=27$), in trawls ($n=35$), and gillnets ($n=27$). All families were observed from both trawls and gillnets, while gillnets accounted for the widest range of observed inter- and intraspecific

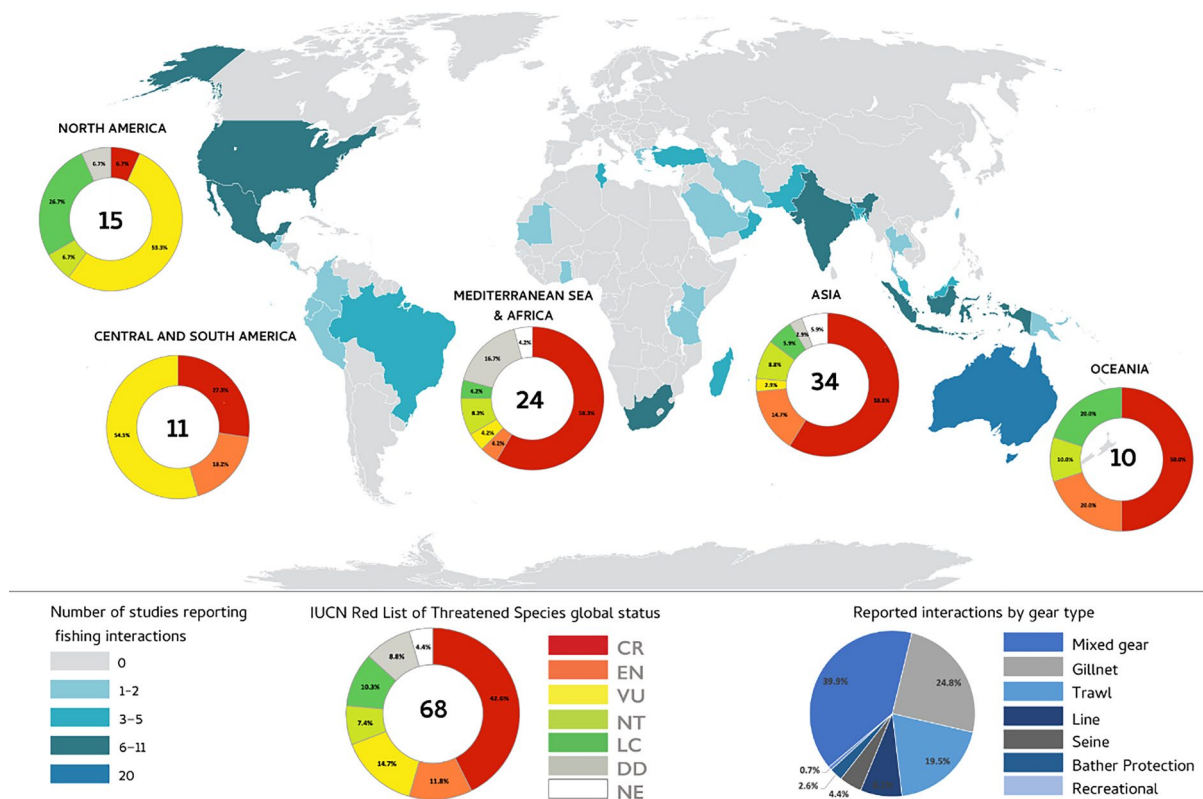


Fig. 1 Global fisheries interactions with rhino rays. Colored countries are those where interactions with at least one species of rhino ray have been reported. Donut charts indicate the proportion of species globally and in each of the five major regions by IUCN Red List category (CR, Critically Endan-

gered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated). The number of species recorded from each region is given in the center of the chart. Note that some wide-ranging species have been included in more than one chart

Table 1 Number and proportion of interactions with rhino rays covered in this review ($n=116$ references) in each region by type of fishery and family interaction reported. NR indicates studies were not available, or not considered (see Meth-

ods). Interactions and coverage are provided in detail in Online Resources 2 (meta-data) and 3. BPG, bather protection gear

Gear type	Overall $N=420$ (100%)	Mixed $N=183$ (44%)	Gillnet $N=101$ (24%)	Trawl $N=78$ (19%)	Line $N=26$ (6.2%)	Seine $N=19$ (4.5%)	BPG $N=11$ (2.6%)	Recreational $N=2$ (0.5%)
<i>Region</i>								
Asia	211 (50)	132 (72)	22 (22)	32 (41)	11 (42)	14 (74)	NR	NR
Oceania	88 (21)	13 (7.1)	43 (43)	16 (21)	5 (19)	5 (26)	6 (55)	NR
Mediterranean Sea and Africa	66 (16)	18 (9.8)	21 (21)	12 (15)	8 (31)	NR	5 (45)	2 (100)
North America	41 (9.8)	18 (9.8)	10 (9.9)	11 (14)	2 (7.7)	NR	NR	NR
Central and South America	14 (3.3)	2 (1.1)	5 (5.0)	7 (9.0)	NR	NR	NR	NR
<i>Family/Order</i>								
Rhinidae	120 (29)	65 (36)	22 (22)	15 (19)	6 (23)	8 (42)	3 (27)	1 (50)
Rhinobatidae	107 (25)	54 (30)	17 (17)	26 (33)	8 (31)	1 (5.3)	0 (0)	1 (50)
Glaucoptegidae	96 (23)	41 (22)	26 (26)	16 (21)	6 (23)	7 (37)	0 (0)	0 (0)
Pristidae	60 (14)	16 (8.7)	26 (26)	8 (10)	2 (7.7)	0 (0)	8 (73)	0 (0)
Trygonorrhinidae	30 (7.1)	5 (2.7)	7 (6.9)	12 (15)	3 (12)	3 (16)	0 (0)	0 (0)
Rhinopristiformes	7 (1.7)	2 (1.1)	3 (3.0)	1 (1.3)	1 (3.8)	0 (0)	0 (0)	0 (0)

sizes, 13–600 and 90–550 cm total length (TL), respectively (Online Resource 2). Instances from line capture were less common and captured larger sizes.

Benthic trawls

North America

In the United States (US) West Coast Ground fisheries, recorded discards (2002–2014) of rhino rays included the banded guitarfish (*Zapteryx exasperata*) and shovelnose guitarfish (*Pseudobatos productus*) (Jannot et al. 2021). During the observed commercial operations, both species interacted with the nearshore California Halibut Bottom Trawl fishery, with at-sea discards of *P. productus* estimated at ~20.1 metric tons (mt) (Jannot et al. 2021).

From 2007 to 2016, observer coverage from the southeastern US shrimp fishery reported freckled guitarfish (*Pseudobatos lentiginosus*) from the Gulf of Mexico, comprising <0.001% of total recorded catch weight, and smalltooth sawfish (*Pristis pectinata*;

$n=12$) from the Atlantic Ocean off the coast of Florida, as bycatch (Scott-Denton et al. 2012, 2020). Between 2017 and 2018, observers reported one *P. lentiginosus* as bycatch from 169 hauls (Moncrief-Cox et al. 2021).

In the Gulf of California, Mexico, the speckled guitarfish (*Pseudobatos glaucostigmus*) is among the most common bycatch species in the prawn trawl fishery (Garcés-García et al. 2020). A total of 4774 sharks and rays were recorded from 486 tows from 2011 to 2017 with *P. glaucostigmus* recorded in 35.6% of trawls. Trawling depths ≥ 12 m caught a greater number of *P. glaucostigmus* ($n=342$) than trawls < 12 m ($n=190$) (Garcés-García et al. 2020). Southern banded guitarfish (*Z. xyster*) were present in 7.6% of trawls (Garcés-García et al. 2020).

Central and South America

Along the Pacific coast of Costa Rica, Clarke et al. (2016) reported *Z. xyster* as the fourth most abundant elasmobranch species from 127 commercial shrimp trawl and 219 scientific hauls from 2008 to 2012.

Of total reported elasmobranch catch ($n=4564$), *Z. xyster* and whitesnout guitarfish (*P. leucorhynchus*) contributed 9% ($n=393$; 379 from commercial hauls) and 2% ($n=90$; all from commercial hauls), respectively. Immature rays were most abundant (73%) at < 50 m depth, whereas 57% of animals were mature at 50–100 m depth (Clarke et al. 2016). Between 2010 and 2011, 62% of *Z. xyster* ($n=208$) sampled from the bycatch of benthic shrimp trawls were immature (Azofeifa-Solano et al. 2021).

Off the Pacific coast of Colombia, a single *P. prahli* was reported from the catch of a benthic prawn trawler in August 2007 (Payan et al. 2010).

Off southeastern Brazil, between 2014 and 2015, Brazilian guitarfish (*P. horkelii*; $n=43$), shortnose guitarfish (*Z. brevirostris*; $n=12$), and chola guitarfish (*P. percellens*; $n=5$) were recorded from 37 shrimp trawl hauls with all life stages represented (Rodrigues et al. 2019). Individuals of *P. horkelii* included neonates ($n=22$) and juveniles ($n=21$). All *P. percellens* and 83% of *Z. brevirostris* were adults.

Mediterranean Sea and Africa

Landing site surveys in the Gulf of Gabès, Tunisia between 2004 and 2008 recorded common guitarfish (*Rhinobatos rhinobatos*) and blackchin guitarfish (*Glaucostegus cemiculus*) from shrimp trawls (Enajarr et al. 2015).

From 2009 to 2010, in Iskenderun Bay, Türkiye, benthic trawlers were surveyed during commercial operations (Yaglioglu et al. 2015). Hauls ($n=61$) across seasons recorded 11 species of elasmobranch which comprised 23% of the total catch biomass. *Rhinobatos rhinobatos* and *G. cemiculus*, pooled as *Rhinobatos* spp., comprised 11% of overall elasmobranch biomass (Yaglioglu et al. 2015).

In Mauritanian shrimp fisheries, from 2004 to 2006, observers recorded *R. rhinobatos* as discards in 14.9% ($n=121$) of shrimp trawls (Goudswaard and Meissa 2006).

In South Africa, 169 trawls targeting prawns were observed from 1989 to 1992, recording rhino rays ($n=49$; 5.4%) in 20% of trawls, including: greyspot guitarfish (*Acroteriobatus leucospilus*; $n=23$; 2.5%), lesser guitarfish (*Acroteriobatus annulatus*; $n=9$; 1%), whitespotted wedgfish (*Rhynchobatus djiddensis*; $n=15$; 1.6%), and bowmouth guitarfish (*Rhina ancylostomus*; $n=2$; 0.2%) (Fennessy 1994).

From 1996 to 2000 off the south coast of South Africa, observers sub-sampled discards from benthic trawls. *Acroteriobatus annulatus* were reported from 294 inshore sole and 139 offshore hake trawls and contributed 1.5% and 7% to the average abundance of the fisheries, respectively (Walmsley et al. 2007).

From 2003 to 2006, 3570 commercial trawls were observed from inshore benthic trawlers in South Africa (Attwood et al. 2011). From an estimated annual catch estimate of 17,434 tonnes (t), annual catch composition of *A. annulatus* was estimated at 0.1% (18.3 t) based on unsorted samples, while contributing 0.6% to the actual discard composition from all years combined (Attwood et al. 2011).

Asia

From 1987 to 1990, discards of ‘mixed guitarfish’ comprised 3% of the annual discards from the Kuwaiti shrimp fishery (Ye et al. 2000).

From 1993 to 1994, 60 hauls from benthic shrimp trawlers recorded 366 elasmobranchs in the Hormoz Strait, Iran (Vossoughi and Vosoughi 1999). Five rhino ray species were recorded comprising sharpnose guitarfish (*Glaucostegus granulatus*; $n=11$), *Rhynchobatus djiddensis* ($n=4$), brown guitarfish (*Rhinobatos schlegelii*; $n=2$), narrow sawfish (*Anoxypristis cuspidata*; $n=1$), and Bengal guitarfish (*Rhinobatos annandalei*; $n=1$) (Vossoughi and Vosoughi 1999). Over two shrimp trawling seasons (2001–2002) in the northern Arabian/Persian Gulf (Iran), bycatch of *R. annandalei* and *R. djiddensis* represented < 0.01% and < 0.2%, respectively, of the combined total of target and bycatch (Paighambari and Daliri 2012).

Off the coast of Oman, Salalah guitarfish (*Acroteriobatus salalah*; $n=26$) were recorded from benthic trawls (Henderson and Reeve 2011).

Monthly samples of bycatch trash heaps (i.e., for use as fish manure) from surveyed commercial trawls off southern India from 2018 to 2019 recorded stripenose guitarfish (*Acroteriobatus variegatus*; $n=446$; 12%) and *R. annandalei* ($n=887$; 24%) from eleven ray species ($n=3680$) (Bhagyalekshmi and Kumar 2021). A higher relative abundance of juveniles and sub-adults (70%) than adults was observed for *A. variegatus*, while similar relative abundances between juvenile and adult *R. annandalei* bycatch was observed (Bhagyalekshmi and Kumar 2021).

In Chennai, India, from 2002 to 2006, rhino ray landings from trawl capture averaged 110.6 t/year out of an average elasmobranch production of 841.8 t/year (Mohanraj et al. 2009). Rhino ray landings (reported by weight) decreased from a peak of 278.7 t in 2002 to 38.3 t in 2006 (Mohanraj et al. 2009). Of the four rhino ray species recorded, *R. djiddensis* accounted for the highest average proportion annually (42.1%), followed by *R. ancylostomus* (35.6%), *G. granulatus* (26.5%), and widenose guitarfish (*Glaucostegus obtusus*; 1.8%) (Mohanraj et al. 2009). Relative to the total average weight composition of all elasmobranchs from 2002 to 2006, *R. djiddensis* accounted for 5.5%, followed by *R. ancylostomus* (4.2%) (Mohanraj et al. 2009).

In Malvan, India, landing sites were surveyed over three sampling periods from 2018 to 2020 and sampled all boats with elasmobranch landings (Kottillil et al. 2023). Benthic and pelagic trawls accounted for 65% of 13,189 elasmobranchs recorded, and rhino rays included *Glaucostegus granulatus* ($n=34$) which was primarily reported from trawls (62% of records), and *G. obtusus* ($n=21$), *R. ancylostomus* ($n=2$), and one unidentified *Glaucostegus* species (Kottillil et al. 2023). Also reported from Malvan trawlers, *G. granulatus* and *G. obtusus* ($n=17$ combined) were observed during 2018 and 2019 (Gupta et al. 2020).

Between 2013 and 2014, rhino rays accounted for 10.7% of rays ($n=6,191$) sampled from landings of otter trawls in Ranong and Satun, Thailand: *R. schlegelii* ($n=440$; 7.1%); spotted guitarfish (*Rhinobatos punctifer*; $n=89$; 1.4%); bottlenose wedgefish (*Rhynchobatus australiae*; $n=78$; 1.3%); *R. ancylostomus* ($n=50$; 0.8%); *G. cf. granulatus* ($n=6$; 0.1%); broadnose wedgefish (*R. springeri*; $n=1$; 0.02%); and *G. obtusus* ($n=1$; 0.02%) (BOBLME 2015).

During surveys of fisheries in Indonesian waters, *R. australiae* was reported in unspecified quantities from the Java Sea trawl fishery (D'Alberto et al. 2022).

Oceania

Interaction reports from Australia's Northern Prawn Fishery (NPF) covering 2012–2022 include data on dwarf sawfish (*Pristis clavata*), green sawfish (*P. zijsron*), largetooth sawfish (*P. pristis*), and *A. cuspidata* (as listed threatened species these are the only rhino rays for which interactions are reported in this

fishery). The category 'sawfishes' was also included when species-level identification was not possible. For consistency and accuracy, we pooled all species into a single category, and included interactions only from commercial NPF operations (i.e., removed scientific surveys and commercial records from the Torres Strait and Blood Tiger Prawn Fisheries which were not as consistent). Interactions ranged from a low of 307 records in 2015 to a high of 1344 in 2021, representing 3.8% and 9.1% of total protected species interactions respectively from the fishery (AFMA 2022). Overall, sawfish comprised 6.2% (6,884 of 110,423) of protected species interactions (AFMA 2022).

In New South Wales, eastern fiddler rays (*Trygonorrhina fasciata*) are common bycatch of commercial trawlers. From 2015 to 2016, 171 *T. fasciata* were surveyed from an unquantified number of hauls (Reis and Figueira 2020).

Western shovelnose rays (*Aptychotrema vincentiana*) and southern fiddler rays (*Trygonorrhina dumerilii*) are regular components of the elasmobranch bycatch in southwest Western Australian commercial prawn and scallop trawl fisheries (Marshall et al. 2007; Jones et al. 2010). Unquantified bycatch of *T. dumerilii* was recorded monthly from 2002 to 2004 (excluding May–September) (Marshall et al. 2007). Between 2002 and 2008, *A. vincentiana* ($n=237$), *T. dumerilii* ($n=220$), and one *R. australiae* were recorded as bycatch of commercial trawl vessels during observer trips (Jones et al. 2010). The two banjo rays comprised 8% and 7% of the elasmobranch catch, respectively (Jones et al. 2010). Izzo and Gillanders (2008) collected *T. dumerilii* ($n=43$) from commercial prawn trawls from South Australian waters (unspecified sampling period).

In the eastern Australian stout whiting (*Sillago robusta*) trawl fishery during 2009–2010, the combined catch of rhino rays constituted 63% of discarded elasmobranch bycatch from otter trawls (Rowse and Davies 2012). Eastern shovelnose rays (*Aptychotrema rostrata*; 54%; $n=735$) dominated the rhino ray bycatch composition and accounted for 0.1% of total catch biomass (Rowse and Davies 2012). 'Guitarfishes' ($n=114$; 8.2%; described as Rhinobatidae) and two *T. fasciata* comprised the remaining rhino rays.

Trawls monitored by White et al. (2019) in the Gulf of Papua prawn trawl fishery (Papua New

Guinea, PNG) from 2014 to 2015, recorded eyebrow wedgfish *Rhynchobatus palpebratus* ($n=60$; 3%), *A. cuspidata* ($n=11$; 0.5%), *G. typus* ($n=5$; 0.2%), *R. ancylotomus* ($n=2$; 0.1%), and *P. pristis* ($n=1$; 0.1%) (White et al. 2019).

Gillnets

North America

From 1998–2017, one incidental catch of *P. pectinata* in shark-targeted drift nets was reported in the US Southeast Gillnet Fishery (NMFS 2009; Kroetz et al. 2020). Bycatch records from 12 US east coast commercial gillnet fisheries indicated that *P. pectinata* is only reported from nets targeting sharks (Zollett 2009).

In Mexico from 1998 to 1999, *P. productus* ($n=4510$) comprised 78% of reported total catches from benthic gillnet fisheries (Márquez-Farias 2005). During landing surveys of artisanal gillnet fisheries, 79,375 elasmobranchs were observed in Sonora (1998, $n=14$; 1999, $n=77,825$) and Baja California (1998, $n=150$; 1999, $n=1386$) (Bizzarro et al. 2007, 2009). In 1999, *P. productus* comprised 33% ($n=25,443$) and 12% ($n=165$) of total elasmobranch catch in Sonora and Baja California, respectively; in 1998, one individual was recorded only in Sonora (Bizzarro et al. 2007, 2009). *Zapteryx exasperata* (Sonora $n=1324$; Baja California, $n=347$) were reported only in 1999 in Sonora (Bizzarro et al. 2007, 2009). From 2013 to 2015, 244 *Z. exasperata* were recorded; landings were highest during April and August (Cervantes-Gutiérrez et al. 2018).

Central and South America

From 2015 to 2017, surveys of gillnets from two fishing communities in Guatemala recorded one *P. percellens* from 688 chondrichthyans (Hacohen-Domené et al. 2020). In Guatemalan fisheries from 2017 to 2020, *P. leucorhynchus* represented <3% ($n=25$) of elasmobranchs ($n=669$) recorded from benthic and midwater gillnets (Castillo and Morales 2021). Consistent with low maturity rates of overall catch (6–7%), 100% of *P. leucorhynchus* were immature (Castillo and Morales 2021).

From 2018 to 2020, *P. horkelii* ($n=136$) were recorded from ~44 surveys of commercial benthic trammel nets in southern Brazil (Larre et al. 2021).

In Peru between 2015 and 2016, Pacific guitarfish (*Pseudobatos planiceps*; $n=167$) were sampled from commercial benthic and surface gillnets (Gonzalez-Pestana et al. 2021).

Mediterranean Sea and Africa

A single *G. cemiculus* was recorded in 1995 in Greek waters in a fishing net (Corsini-Foka 2009).

In the Gulf of Gabès, Tunisia, *G. cemiculus* and *R. rhinobatos* are targeted in a benthic gillnet ('Garracia') fishery which operates March to July/August (Echwikhi et al. 2013; Enajjar et al. 2015). During 2007–2008, *G. cemiculus* represented 52% of catches ($n=313$) and *R. rhinobatos* 6.8% of catches ($n=41$) from 45 fishing sets (Echwikhi et al. 2013). The majority of *G. cemiculus* (92%) and *R. rhinobatos* (83%) were retained (Echwikhi et al. 2013). From 2004 to 2008, *G. cemiculus* ($n>833$) were observed from 'Garracia' (Enajjar et al. 2015). Pooled data from commercial surveys and landings sites found unquantified numbers of *R. rhinobatos* in trammel nets (Enajjar et al. 2015).

In April 2013, two *G. cemiculus* were observed as catch from trammel nets in Izmir Bay, Türkiye (Akyol and Capape 2014).

Eighteen ray species, including two rhino ray species, were recorded at processing and landing sites in Ghanatown in The Gambia between 2010 and 2018. *Rhinobatos rhinobatos* were regularly recorded, though in small numbers, in contrast to the high quantities of *G. cemiculus* caught in a benthic gillnet fishery (Moore et al. 2019). The latter were observed as dominant among elasmobranch landings and frequently processed upon landing, making quantification difficult (Moore et al. 2019). From two separate survey days in 2014, head sections ($n=314$) of *G. cemiculus* were measured, and 26 whole individuals were observed on a sampling day in 2018 (Moore et al. 2019).

From 2020 to 2021, landed guitarfishes ($n=537$) were recorded from 80 survey days of market and landing sites in four Ghanaian communities from benthic and drift gillnets (Seidu et al. 2022a). The spineback guitarfish (*Rhinobatos irvinei*; $n=383$)

was the most frequent, followed by *R. albomaculatus* ($n=86$), *R. rhinobatos* ($n=34$), and *G. cemiculus* ($n=34$) (Seidu et al. 2022a).

From 2014 to 2015 in Kenya, *R. djiddensis* ($n=8$) were caught in various mesh sizes and constituted 0.6% of species caught, including six juveniles (Osuka et al. 2021).

From 2016 to 2017, landing sites in Tanzania were monitored for marine megafauna landings and reported Zanzibar guitarfish (*Acroteriobatus zanzibarensis*) in unspecified quantities (Temple et al. 2019).

In Madagascar from 2001 to 2004, Robinson and Sauer (2013) surveyed benthic set nets over 116 fishing trips. *Rhynchobatus* spp. ($n=23$) and *R. ancylostomus* ($n=4$) were recorded from 640 elasmobranchs.

A survey of small-scale (non-motorised) shark (including rhino ray) fisheries in Madagascar recorded a minimum of 498 rhino rays in benthic nets consisting of *R. djiddensis*, *R. ancylostomus*, smoothnose wedgefish (*Rhynchobatus laevis*), greyspot guitarfish (*Acroteriobatus andysabini*), and *A. annulatus* (Humber et al. 2017). All observed rhino rays were pooled and catch-specific data were only available when in the top three landed taxa. Over the whole study (which included line gear, see *Lines*), scalloped hammerhead (*Sphyrna lewini*), slit-eye shark (*Loxodon macrorhinus*), and rhino rays (pooled) together accounted for >75% (8637 of 11,428) of recorded landings (Humber et al. 2017).

Asia

In the Hormoz Strait, one *A. cuspidata* was observed from a drift gillnet (Vossoughi and Vosoughi 1999).

Landings surveyed by Kottillil et al. (2023) in Malvan, India from 2018 to 2020 recorded 6351 elasmobranchs from non-motorised and motorised vessels operating gillnets. Observed rhino rays included *G. obtusus* ($n=137$), *G. granulatus* ($n=9$), and *R. ancylostomus* ($n=2$) (Kottillil et al. 2023).

In Goa, India, 122 *G. cf. granulatus* were sampled from fish landing centres between 2014 and 2018, landed as bycatch from benthic gillnets (Sreekanth et al. 2022). From 2002 to 2006 (excluding November), rhino ray landings from mechanised gillnets targeting sharks and tunas in Chennai, India averaged 1.2 t/year (Mohanraj et al. 2009). Of the four reported rhino ray species, *R. djiddensis* constituted an average

of 58.4% of total rhino ray composition annually, followed by *R. ancylostomus* (25%), *G. granulatus*, and *G. obtusus* (8.3% each) (Mohanraj et al. 2009).

From 2001 to 2005, surveys at Muara Angke in Indonesia recorded landings of 1,559 elasmobranchs from the tangle net fishery (benthic gillnets) in 15 of 53 survey days (D'Alberto et al. 2022). Rhino rays comprised 20.8% of the observed elasmobranch catch, including *R. australiae* (15.3%; $n=238$), the most abundant rhino ray, and main target of the fishery, *R. ancylostomus* ($n=57$), and *R. palpebratus* ($n=30$). Additionally, *P. pristis* ($n=2$), *G. typus* ($n=14$), and unquantified clubnose guitarfishes (*Glaucostegus thouin*) were recorded (D'Alberto et al. 2022). *Rhynchobatus australiae* were also landed as bycatch of small mesh gillnets (D'Alberto et al. 2022).

Oceania

In the Queensland Gulf of Carpentaria, Australia, the commercial shark and bony fish set net fishery was opportunistically observed between 2000 and 2002 (Peverell 2005). *Anoxypristis cuspidata* were recorded in offshore ($n=74$) and inshore ($n=37$) nets. Catches of *P. pristis* ($n=62$), *P. clavata* ($n=24$), and *P. zijsron* ($n=19$) were only observed inshore (Peverell 2005).

Observer data from the commercial gillnet sector of eastern Queensland (2007–2009), found *A. cuspidata* to be the most frequently caught rhino ray species ($n=55$), followed by *Rhynchobatus* spp. ($n=49$; likely *R. australiae* and/or *R. palpebratus* based on local species occurrence), and *G. typus* ($n=19$) (White et al. 2013). Observers in the commercial gillnet fishery within the Great Barrier Reef World Heritage Site, recorded 180 occurrences of rhino rays ($n=6,828$ total elasmobranch catch) from 2006 to 2009 (Harry et al. 2011). *Anoxypristis cuspidata* ($n=75$) and *Rhynchobatus* spp. ($n=68$) were the most frequently caught, each representing 1% of total catch. *Glaucostegus typus* ($n=27$) and *P. zijsron* ($n=7$) comprised <1% of the catch (Harry et al. 2011).

From 1993 to 2020, observer data from 2,932 commercial shark gillnet sets in Western Australia reported discards of *R. australiae* ($n=8$) and 'guitarfish and shovel-nose rays' ($n=318$) but the proportion was relatively low at <0.1 and 0.35%,

respectively (Braccini and Murua 2022). In the shark fishery of southwest Western Australia, small numbers of *A. vincentiana* ($n=6$) and *T. dumerilii* ($n=5$) were recorded as bycatch of gillnets on observer trips from 2002 to 2008 (Jones et al. 2010).

Limited observer coverage (52 days) of the Northern Territory Barramundi Fishery during 2002–2008, which deploys gillnets in estuarine and coastal areas, recorded *A. cuspidata* ($n=37$), *P. clavata* ($n=20$), *G. typus* ($n=2$), *P. zijsron* ($n=12$), and *Rhynchobatus* spp. ($n=15$) as bycatch (recorded as 13 *R. djiddensis* and 2 *R. australiae*, but likely to be *R. australiae* and/or *R. palpebratus* based on local species occurrence) (Field et al. 2013).

Between 2017 and 2020, monitoring of shark and ray catch of small-scale fishers using gillnet in northern PNG reported *A. cuspidata* ($n=13$; 7.4% of catch), *P. pristis* ($n=13$; 7.4%), *G. typus* ($n=2$; 1.1%), and *R. australiae* ($n=1$; 0.6%) (Grant et al. 2021). In southern PNG, monitoring reported *P. pristis* ($n=34$), *A. cuspidata* ($n=49$; ~8% of catch), *R. palpebratus* ($n=10$; 1.6%), *P. clavata* ($n=9$; 1.5%), *G. typus* ($n=9$; 1.5%), and *P. zijsron* ($n=1$; 0.2%) (Grant et al. 2021).

Line fisheries

North America

In the US bottom shark longline fishery, Brame et al. (2019) reported 40 *P. pectinata* incidentally caught since 2005 until 2018.

Mediterranean Sea and Africa

A single *R. rhinobatos* was recorded off Rhodes, Greece, from longline capture in 2008 (Corsini-Foka 2009).

In the Gulf of Gabès, Tunisia, observers onboard commercial longline boats from 2007–2008, recorded two species of rhino rays from 30 benthic longline sets: *G. cemiculus* ($n=123$; 31.3% of total elasmobranch catch) and *R. rhinobatos* ($n=44$; 11.2%) (Echwikhi et al. 2014).

Observations of 35 pelagic longline trips (96 sets) in the Gulf of Gabès during 2016 and 2017 were dominated by elasmobranchs (94%) (Saidi et al. 2019). *Glaucostegus cemiculus* accounted for 0.25% ($n=3$) of all landings (Saidi et al. 2019).

During commercial benthic longline operations in Tunisia, observations of 162 sets from 2016–2017 reported a catch rate of 49% ($n=1437$) for elasmobranchs (Saidi et al. 2023). Reported catch rates of *G. cemiculus* contributed 19% ($n=274$) to observed elasmobranch catch rates. Retention rate of this species was reported as 100%, of which 70% of females and 43% of males were reportedly juvenile (Saidi et al. 2023).

One *G. cemiculus* was caught on a benthic longline in 2015, in Kuşadası Bay, Türkiye (Filiz et al. 2016).

Surveys of commercial benthic longlines along the Lebanese coast recorded 67 *R. rhinobatos* from 2012 to 2014 (Lteif et al. 2016). Fishing depths were between 15 and 110 m and over 90% of individuals were fished from depths < 50 m (Lteif et al. 2016).

In Madagascar, 108 unspecified guitarfish were recorded from landings of small-scale hook-and-line shark fisheries between 2007 and 2012 (Humber et al. 2017).

Asia

In Malvan, India, *G. granulatus* ($n=2$) and one *G. obtusus* were reported captured from hook-and-line fisheries (Kottillil et al. 2023).

In Bangladesh during 2017, 13 *R. ancylotomus* were observed from artisanal hook-and-line (Haque et al. 2021a).

Images of elasmobranch bycatch from Indonesian snapper-grouper fisheries identified 64 elasmobranch species ($n=3172$) from 1446 images from January 2017 to December 2018 (Lindfield and Jaiteh 2019). Rhino ray bycatch comprised *R. australiae* ($n=73$), *R. springeri* ($n=8$), *Rhinobatos* spp. ($n=8$), *R. ancylotomus* ($n=5$), and Jimbaran guitarfish (*R. jimbaranensis*; $n=2$) (Lindfield and Jaiteh 2019).

Oceania

In 2013, in New South Wales, bycatch data from 17 commercial benthic longliners included *A. rostrata* ($n=2$) and *R. australiae* ($n=8$) (Broadhurst et al. 2014). In the shark fishery of southwest Western Australia, *T. dumerilii* ($n=32$) and *A. vincentiana* ($n=3$) were recorded as bycatch of longlines between 2002 and 2008 (Jones et al. 2010).

In southern PNG, seven *P. pristis* were reported from 2017 to 2020 during surveys of longlines from small-scale fisheries (Grant et al. 2021).

Seine

Asia

In Malvan in 2019, rhino rays represented <4% (*G. obtusus*, $n=4$; *G. granulatus*, $n=1$) of elasmobranchs ($n=132$) from 39 randomly sampled beach seine hauls (Gupta et al. 2022). A separate study in Malvan, conducted between 2018 and 2020, reported 20 *G. obtusus* and one unidentified guitarfish from seine (Kottillil et al. 2023).

Haque et al. (2021a) recorded one *G. typus* from purse seine landings in Bangladesh in 2017.

In 2019, data from 1,470 rhino rays were collected at three ports (Tegalsari, Bajomulyo, and Tasik) in Java, Indonesia comprising *R. australiae* ($n=660$), *R. laevis* ($n=329$), *R. springeri* ($n=245$), *R. ancylostomus* ($n=126$), *G. typus* ($n=59$), and *G. thouin* ($n=51$) (Yuwandana et al. 2020). Bycatch data from 2233 rhino rays from ‘cantrang’ (similar to Danish seine gear) collected at Tegalsari Port (2019–2020) indicate that *R. australiae* were least frequent ($n=585$; 26%), with *R. laevis* and *R. springeri* each representing 37% of the rhino ray catch (Wulandari et al. 2021).

Oceania

From 2009 to 2010, *A. rostrata* accounted for 2340 of 2790 elasmobranchs observed from Danish seines in Queensland’s stout whiting fishery (Rowell and Davies 2012). Grouped ‘guitarfishes’ accounted for <4% ($n=102$), including one *R. ancylostomus* (Rowell and Davies 2012). From April 2016–2017, a subset of 142 *A. rostrata* were recorded from seines in Queensland (Campbell et al. 2021).

Mixed gear

This section presents data derived from mixed landings where no single primary fishing gear is reported or where landings likely originate from a variety of fishing gear.

North America

Artisanal landing sites in Baja California, Baja California Sur, Sonora, and Sinaloa, Mexico were surveyed seasonally from March 1998–November 1999, totalling 445 survey days. *Pseudobatos productus* ($n=23,099$), *Z. exasperata* ($n=298$), *P. glaucostigmus* ($n=541$), *P. leucorhynchus* ($n=1$), and 69 *Pseudobatus* (unspecified species) were recorded (Bizzarro et al. 2007, 2009).

Central and South America

Between April 2013 and January 2015, *P. leucorhynchus* ($n=1024$) were sampled from artisanal gillnet and beach seine fisheries in Ecuador (Romero-Caicedo and Carrera-Fernandez 2015).

From September 2009–August 2010, 36 *P. planiceps* were collected from Chorrillos Fish market, Peru, caught by fishers <2 km from the coast (Iannacone et al. 2011).

Mediterranean Sea and Africa

From 2000 to 2001, one *R. rhinobatos* was reported from the southern Aegean Sea, Türkiye (Öğretmen et al. 2005).

Landing sites in Ghana were visited 108 times in 2020, recording 2,157 elasmobranchs from 34 species (Seidu et al. 2022b). Three rhino ray species made up <3% ($n=52$) of landings and consisted of *R. irvinei* ($n=30$), *G. cemiculus* ($n=11$), and *R. rhinobatos* ($n=11$) (Seidu et al. 2022b).

From 2020–2022, 23 elasmobranch species ($n=102$) from landings, fish markets, and artisanal processors were surveyed along the Tanzanian coast (Rumisha et al. 2023). Rhino rays comprised 17% of records, including *R. australiae* (13%), *A. variegatus* (2%, likely to be Zanzibar guitarfish (*A. zanzibarensis*) based on local species occurrence), *R. ancylostomus* (1%), and *R. annandalei* (1%).

On Unguja Island, Zanzibar, in 2015, elasmobranchs were reported from landing sites ($n=208$) and merchant stalls ($n=150$) selling meat or whole specimens (Barrowclift et al. 2017). *Rhina ancylostomus* ($n=3$) and *R. australiae* ($n=2$) were observed from landings, and *A. zanzibarensis* ($n=8$) were reported from meat merchants (Barrowclift et al. 2017).

From 2016 to 2017, surveys of 21 small-scale fisheries reported Halavi guitarfish (*Glaucostegus halavi*) and *R. ancylostomus* from Kenya, *R. australiae* from Kenya and Tanzania, and *A. zanzibarensis* from Tanzania (Temple et al. 2019). In Madagascar, *R. djiddensis* and *A. andysabini* were recorded with the latter prevalent in the catch composition of rays (Temple et al. 2019).

Asia

Market surveys in Jeddah, Saudi Arabia from 2011 to 2013 recorded 2,724 elasmobranchs (Spaet and Berumen 2015). Four species of rhino rays accounted for ~1.5% of records: *R. ancylostomus* ($n=4$), *G. halavi* ($n=12$), and two potentially undescribed species of *Rhynchobatus* ($n=25$) (Spaet and Berumen 2015).

From 2008 to 2011, landing surveys were conducted in Kuwait, Qatar, and Abu Dhabi (United Arab Emirates [UAE]) with rhino rays comprising ~4% of 4649 individuals recorded (Moore et al. 2012). Five species were recorded: *G. granulatus* (Kuwait, $n=143$), *R. djiddensis* (Kuwait, $n=17$; Qatar, $n=2$), *G. halavi* (UAE, $n=13$), *R. cf. punctifer* (Qatar, $n=3$; Kuwait, $n=1$), and *R. ancylostomus* (UAE, $n=1$) (Moore et al. 2012; Moore 2012).

Rhino rays composed 3% of recorded sampling from Bahrain in April 2012, fished from Bahraini, Saudi Arabian, and Qatari waters (Moore and Peirce 2013). Observed rhino ray landings included *R. punctifer* ($n=18$), *R. cf. djiddensis* ($n=14$), and *G. halavi* ($n=5$) (Moore and Peirce 2013).

From 2016 to 2020, 135 landing surveys in Saudi Arabia (Arabian/Persian Gulf) recorded 848 elasmobranchs (Hsu et al. 2022). Rhino rays comprised 3% of observations, including *R. laevis* ($n=10$), *G. halavi* ($n=6$), *R. australiae* ($n=5$), *Rhinobatos* sp. ($n=2$), *Rhynchobatus* sp. ($n=1$), and *R. punctifer* ($n=1$) (Hsu et al. 2022).

From 2010 to 2012, surveys of four UAE landing sites recorded 442 rhino rays (Jabado 2018). *Rhynchobatus* spp. comprised >55% of rhino rays ($n=246$), followed by *G. halavi* ($n=65$), *R. ancylostomus* ($n=54$), *R. annandalei* ($n=42$), *R. punctifer* ($n=27$), *Rhinobatos* sp. ($n=4$), and one each of *P. zijssron*, *G. granulatus*, Oman guitarfish (*Acroteriobatus omanensis*), and *A. salalah* (Jabado 2018).

From 2002 to 2003, surveys at Omani landing sites recorded six rhino ray species from 44 elasmobranch species: *A. omanensis*, *R. djiddensis*, *G. halavi*, *R. ancylostomus*, *R. punctifer*, and one undescribed species (Henderson et al. 2007). Total quantities were unspecified, though *G. halavi* occurred at a high relative frequency at one site (Henderson et al. 2007). In Oman (Seeb Fish Market), two male *A. salalah* were recorded in February 2010 (Henderson and Reeve 2011). One *Rhynchobatus* sp. was reported from landings in Oman in 2011, potentially representing *R. djiddensis* (Moore 2012).

In Balochistan, Pakistan, surveys from 2007 to 2010 reported unspecified quantities of *R. ancylostomus*, *G. granulatus*, *R. annandalei*, *G. halavi*, and unidentified species of *Pristis* and *Rhynchobatus* (Gore et al. 2019). Surveys in Karachi recorded 27 elasmobranch species during 2015–2016, including four rhino ray species: *G. halavi* and *G. granulatus* ($n < 10$ combined), *R. annandalei* ($n=4$), and *R. punctifer* ($n=4$) (Fatima et al. 2016). Seven rhino ray species from Karachi Fish Harbour were reported from 2019–2020 in unspecified quantities (Moazzam and Osmany 2020). Relative composition rates showed *G. granulatus* as dominant (61.7%), followed by *G. obtusus* (23.3%), *R. annandalei* (7.3%), *R. ancylostomus* (6%), and a combined 1.7% comprised of *R. punctifer*, *G. halavi*, and *A. salalah* (Moazzam and Osmany 2020).

Between 2012–2016, rhino rays accounted for 41.1% of the total weight of rays (37,387 kg) landed as bycatch of commercial trawls, gillnets, and dol nets (i.e., bag nets) operating off Maharashtra, India (Purushottama et al. 2020). Recorded rhino rays included: *R. annandalei* ($n=593$), *R. ancylostomus*, *Rhynchobatus* spp., *R. australiae*, *R. laevis*, *G. granulatus*, *G. halavi*, *G. obtusus*, and *P. pristis*. *Rhinobatos annandalei* were recorded each month, excluding during the annual fishing ban from June to July (Purushottama et al. 2020).

From 2016 to 2019, Purushottama et al. (2022) collected *R. ancylostomus* ($n=36$) from gillnetters and trawlers operating off Karnataka, India. Landing surveys by Kottillil et al. (2023) reported in sections above, recorded a further 37 guitarfishes (*G. obtusus*, $n=33$; *G. granulatus*, $n=1$; *Glaucostegus* spp., $n=3$) from pooled gears, likely from shore seine or hook-and-line.

Landing site surveys in Bangladesh recorded 162,888 (398.7 MT) elasmobranchs between 2006 and 2007 (Roy et al. 2007). Four rhino ray species were recorded: *G. granulatus* ($n=1,062$; 0.7%), *R. djiddensis* ($n=524$; 0.3%), *R. ancylostomus* ($n=44$; <0.01%), and *A. cuspidata* ($n=3$; <0.01%) (Roy et al. 2007).

Artisanal catches from the Bay of Bengal, Bangladesh were surveyed at landing and processing centers during 2017 (Haque et al. 2021a). Of 1689 rhino rays, identification to the species level consisted of: *G. granulatus* and *G. cf. granulatus* ($n > 897$; ~53.1%), Ranong guitarfish (*Rhinobatos ranongensis*) ($n > 300$; ~18%), *G. obtusus* ($n=182$; 16.6%), *R. ancylostomus* ($n=113$; 6.7%), *R. annandalei* ($n=35$; 2.1%), *G. typus* ($n=28$; 1.7%), *P. pristis* ($n=32$; 1.9%), and one each of *P. zijsron* and smoothback guitarfish (*Rhinobatos lionotus*). During surveys with artisanal Bangladeshi fishers and traders between 2018 and 2019, Haque et al. (2021b) opportunistically documented 336 rhino rays from five species: *G. granulatus*, *G. obtusus*, *G. typus*, *R. ancylostomus*, and *R. annandalei*. In 2021, the Bangladeshi guitarfish (*Glaucostegus younholeei*; $n=13$) was described for the first time from a landing center in Cox's Bazar (Habib and Islam 2021).

Surveys in Sarawak, Malaysian Borneo recorded 4,823 elasmobranchs, of which 132 were rhino rays: *R. australiae* ($n=58$), *R. springeri* ($n=43$), *G. thouin* ($n=14$), *R. ancylostomus* ($n=10$), *R. laevis* ($n=3$), *G. typus* ($n=2$), and *Rhynchobatus* sp. ($n=2$) (Booth et al. 2021).

In Perak (Peninsular Malaysia) and Sabah (Malaysian Borneo), 7,253 rays from 609 landings were recorded between 2016 and 2017, including *Rhynchobatus australiae* ($n=142$), *R. cf. jimbaranensis* ($n=185$), and *R. ancylostomus* ($n=1$) (Abd Haris Hilmi et al. 2020).

Surveys of ray landings in eastern Indonesia recorded 28,385 batoids between 2001 and 2006 (White and Dharmadi 2007). Rhinobatidae were the second most abundant family after Dasyatidae (stingrays), though there was a large disparity between the two families at 5% and 89%, respectively (White and Dharmadi 2007). Seven species of rhino rays were recorded, of which Indonesian guitarfish (*Rhinobatos penggali*; 3.1% of total landings), *Rhinobatos jimbaranensis* (1.7%), and *R. australiae* (1.4%) were the dominant species (White and

Dharmadi 2007). The remaining species (*P. pristis*, *G. thouin*, *G. typus*, *R. ancylostomus*) collectively represented <1% of total examined landings. From 2017 to 2019, landings were surveyed at five ports landing catches from western Indonesian waters and comprised *R. australiae* ($n=2064$) and *R. ancylostomus* ($n=334$) (Kurniawan et al. 2021). In Lampung Province, Indonesia, one fishing port was selectively sampled for elasmobranchs in 2022 (Yudha et al. 2022). Individuals of an unidentified *Rhynchobatus* species ($n=80$; 22.6%) and one *R. ancylostomus* were recorded from 354 rays.

Visits to Singapore fishing ports in 2019 recorded 590 rhino rays, 215 at the species level ($n=6$ species; Choy et al. 2022) comprising *R. australiae* ($n=142$; 66%), *R. laevis* ($n=30$), *G. typus* ($n=21$), *R. palpebratus* ($n=11$), *R. springeri* ($n=10$), and clown wedgefish (*Rhynchobatus cooki*; $n=1$). Interviews with merchants suggested that 77% of identified individuals were caught in Indonesia, including all *G. typus* and the *R. cooki* with only four *R. australiae* reportedly caught in Singapore (Choy et al. 2022). A separate study conducted in Singapore in 2019 recorded *R. australiae* ($n=4$) and *G. typus* ($n=1$) at fishing ports (Choo et al. 2021).

Between 2005 and 2006, opportunistic sampling from a fish market on the Penghu Islands of Taiwan recorded 13 mature *R. schlegelii* (Schluessel et al. 2015).

Oceania

The Northern Territory Offshore Net and Line Fishery deploys both pelagic gillnets and longlines. Limited observer coverage (49 days) during 2002–2007 recorded *A. cuspidata* ($n=8$), *R. australiae* ($n=3$), and one each of *G. typus* and *P. zijsron* as bycatch (Field et al. 2013). Recorded interactions with listed threatened species between 2014–2015 and 2018–2019 included 119 *A. cuspidata*, 80 *P. zijsron*, 13 *P. pristis*, and 2 *P. clavata* (NTG 2020).

Grant et al. (2021) reported *P. pristis* ($n=19$), *A. cuspidata* ($n=3$), and one unidentified sawfish from unspecified gear (likely gillnets) while monitoring small-scale fisheries in southern PNG from 2017 to 2020.

Bather protection gear

Mediterranean Sea and Africa

Modified conventional drumlines ('SMART drumline') were deployed on Reunion Island from 2014 to 2017, capturing 12 *R. djiddensis* out of 269 elasmobranchs (Guyomard et al. 2019).

The KwaZulu-Natal (KZN) Sharks Board (South Africa) maintains data from bather protection nets which includes records of 91 sawfish catches since 1964 (Everett et al. 2015). A small number of these were from the 1990s ($n=8$) with the last being an unspecified *Pristis* species in 1999 (Everett et al. 2015). From 1981 to 2017, 2,856 *R. djiddensis* were reported from KZN bather protection nets (Daly et al. 2021).

Oceania

In New South Wales, bather protection nets captured *R. australiae* ($n=14$) from a reported catch of 420 marine megafauna individuals during 2016–2018 (Broadhurst and Cullis 2020). Sawfish catch analysis in the Queensland Shark Control Program (QSCP) between 1963 and 2016, includes 1,450 sawfish captures (Wueringer 2017). Species-specific data are limited but from 88 sawfish recorded since 1996, *A. cuspidata* represented 59% of catch, *Pristis* spp. 39%, with only a single each of *P. clavata* and *P. zijsron* identified (Wueringer 2017).

Recreational

Mediterranean Sea and Africa

Long-term data (1977–2017) from 41,519 angling competitions (268,988 anglers) in KZN recorded 7703 *R. djiddensis* (Daly et al. 2021). From 2015 to 2017, 659 fish were recorded from 269 anglers during national angling competitions in the Eastern and Western Cape, including 78 *A. annulatus* (Butler et al. 2017; Mannheim et al. 2018).

Bycatch mitigation approaches

Here we provide an overview of available information on bycatch mitigation of rhino rays. Approaches to

bycatch mitigation often involve considerations of gear selectivity to exclude size classes based on life-history stage. For rhino rays however, this can be a poor proxy as size ranges are so varied that size-at-maturity for one species can be closer to a minimum observed size of another. Further, one factor to consider in relation to the effectiveness of bycatch mitigation is snout morphology. This varies from the long-toothed rostrum of sawfishes, the pointed snout of wedgefishes and guitarfishes, and the rounded snout of some banjo rays. Snout morphology can impact both entanglement in fishing gear and escape from bycatch mitigation devices.

Benthic trawls

The application of Turtle Exclusion Devices (TEDs) or Bycatch Reduction Devices (BRDs) in trawl nets has proven very effective at reducing the bycatch of sharks and rays. Sawfishes are, however, susceptible to rostral entanglement in nets before reaching the TED (which is usually placed around the entrance of the net codend). A study to assess the performance of TEDs and other BRDs (fish-eye, big-eye, square mesh panel) in Australia's NPF found neither had a significant difference on number of sawfishes caught ($n=33$), however, there was a significant difference in the number of *A. cuspidata* caught in nets with a TED ($n=4$) versus without ($n=15$) (Brewer et al. 2006).

As a result of their relatively small size, TEDs had no impact on bycatch of *A. rostrata* in penaeid and stout whiting sectors of the Queensland East Coast Trawl Fishery (a multi-species fishery with different sectors targeting different species) (Campbell et al. 2021). Nets fitted with TEDs in the scallop sector of this fishery did however have a lower probability of catching *A. rostrata* (Courtney et al. 2008). Amongst elasmobranchs, this species is the most common bycatch across this fishery (Kyne et al. 2002; Rowsell and Davies 2012; Campbell et al. 2021).

Manipulating grid orientation (i.e., upward vs. downward) offers conflicting evidence of impact on rhino rays. Brewer et al. (2006) found no impact, although their analysis grouped rhino rays with other rays. Wakefield et al. (2016) found top-shooter devices (grids oriented upwards) resulted in a 20–30% increase in rhino ray escapement, with higher proportions of escape at shallower depths. The percentage of rhino rays observed escaping in three BRDs ranged ~25% in

square mesh and downward devices to 55% in upward devices. However, 58.5% of rhino rays (excluding sawfish entangled at the net entrance) passed through to the codend (Wakefield et al. 2014, 2016).

Trawl speed contributes to bycatch composition where slower speeds are likely to catch smaller individuals unable to outswim the trawl (Garcés-García et al. 2020; Campbell et al. 2021). Raising ground gear in benthic trawls was recently found to reduce bycatch of *R. rhinobatos* to 8% compared to standard ground gear [(catch per unit effort: 0.67 kg CI 0.26–1.21)], likely a result of their tendency to stay close to the seabed (Fakioğlu et al. 2022).

Gillnets

The impact of gillnet illumination with green LED lights has had mixed results with rhino rays. Senko et al. (2022) used paired illuminated bottomset nets with control nets (non-illuminated). Results indicate that elasmobranch biomass was reduced from 14% (control) to 1% (illuminated), a 95% reduction. *Pseudobatos productus* and *Z. exasperata* were recorded during the study, but logistical constraints precluded the ability to collect species-specific elasmobranch data (J. Senko, personal communication, February 25, 2022). Green LED lights were found to reduce bycatch of green turtles (*Chelonia mydas*) but had no impact on the target species, *P. planiceps* (Ortiz et al. 2016).

Gillnet mesh size can impact the size selectivity of catches. For example, Indonesia's tangle net fishery uses mesh size > 50 cm to catch rhino rays > 130 cm TL (D'Alberto et al. 2022). Aspects of net-setting can also affect selectivity. A taught net can make mesh size more selective, whereas a looser net reduces selectivity and creates more entanglement. Variations in catch rates between the morphologically similar guitarfish and wedgearfish observed in Queensland net fisheries could reflect a difference in net tautness, suggesting that tendency for nets to drop when the tops are submerged contributed to a difference in size classes when compared to nets with the same mesh size but stayed taut in the water (White et al. 2013). In the case of sawfishes, these considerations are largely redundant due to the susceptibility of entanglement by their rostrum (White et al. 2013; Lemke and Simpfendorfer 2023).

The position of 67 sawfish captured by QSCP gillnets was recorded, finding 94% were caught closer to the bottom of the net (Wueringer 2017). This suggests that raising gear could reduce capture in some cases, although larger sawfishes have been observed swimming mid-water, which can make them susceptible to nets other than those that are benthic set (Kroetz et al. 2020).

Electrical deterrents

Relying on the sensitive electroreceptors (Ampullae of Lorenzini) of elasmobranchs, the use of electric pulses or fields have been tested as non-lethal deterrents. This technology may have application to multiple gear types. *Pristis pristis* were used as a test subject and overall fleeing behaviour did not occur until the animal was close to the electric field, and therefore entry to a net would not be prevented (Abrantes et al. 2021). Raoult et al. (2023) trialed electrical deterrents to reduce batoid predation in oyster farms. Interactions with *A. rostrata* ($n=43$) and *T. fasciata* ($n=34$) demonstrated 60% and 100% efficacy rates, respectively. There is consensus that more research is needed to test stronger wavelengths (Molina and Cooke 2012; Patterson et al. 2014; Abrantes et al. 2021; Raoult et al. 2023). However, scaling to the levels needed remains a costly and impractical solution (Abrantes et al. 2021; Raoult et al. 2023). Other non-lethal deterrents, such as magnets and rare earth metals have been effective in some elasmobranch species but inter-specific differences present conflicting results (Patterson et al. 2014; Raoult et al. 2023).

Mortality and physiological response to capture stress

Beyond immediate mortality, the negative effects of capture in sharks and rays can include post-capture and post-release mortality, and potential sub-lethal effects associated with capture stress (Horodysky et al. 2015, 2016; Ellis et al. 2017). These aspects are little known for rhino rays. Rhino rays are buccal pumpers, and it is therefore expected that the reduction in ventilatory rates while trapped is not as harmful as observed for ram ventilator species (Ellis et al. 2017; Broadhurst and Cullis 2020). However, since many rhino rays tend to get trapped by the

snout during fishing interactions, the lactate buildup up from extenuating exercise coupled with reduced respiratory efficiency can lead to rapid, and possibly irreversible systemic acidosis (Wosnick et al. 2023). Impacts of capture stress may be more severe during reproductive periods, resulting in lower neonate body mass, capture induced abortions, and higher mortality rates (Guida et al. 2017; Wosnick et al. 2019; Finotto et al. 2021, 2023).

Benthic trawls

Data on at-vessel-mortality (AVM) are available for 13 rhino ray species caught in trawl fisheries (Table 2). Off South Africa, AVM varied greatly for four guitarfish species caught in trawl operations: *A. leucospilus* (52.6%), *R. djiddensis* (18.2%), *A. annulatus* (~11%), and *R. ancylostomus* (0%; $n=1$ and therefore not necessarily representative) (Fennessy 1994). In northern Australia's NPF, AVM for *R. palpebratus* and *R. djiddensis* was estimated at 10% (Stobutzki et al. 2002) while for *A. cuspidata* estimated mortality rates were ~90% (Salini et al. 2007). The higher mortality of *A. cuspidata* is related to their entanglement in the nets which means having to be brought on deck (Salini et al. 2007). AVM rates were high for *A. cuspidata* (88%) and *P. clavata* (100%; $n=2$ and therefore not necessarily representative) upon trawl capture in the Great Barrier Reef World Heritage Area (Tobin et al. 2010).

Negative reproductive consequences from capture stress have been reported for pregnant *T. dumerilii* that have been subjected to trawl simulation and air exposure (Finotto et al. 2021, 2023). During simulated capture trials, neonate *T. dumerilii*, born from mothers that underwent capture stress, showed lower nutritional condition and immune response impairment, as well as reduced growth and altered behaviors (Finotto et al. 2021). The physiological effects of trawl capture also affect maternal oxygen uptake rates, leading to a reduction in oxygen and energy allocation to pregnancy and embryonic respiration in the species (Finotto et al. 2023). Data from both studies were derived under research conditions (i.e., simulated capture).

In addition to crushing-related injuries sustained in the codend, contusion-related injuries may also occur as a result of behavior related to morphology (Rodrigues et al. 2019). Of nine ray species sampled from

artisanal trawls in Brazil, snout contusions were only noticeable on *P. percellens* and *P. horkelli*, species distinguishable by relatively long, thin snouts. The trauma caused by the contusions could explain the higher capture mortality rate exhibited by *P. percellens* (20%) and *P. horkelli* (30%) (Table 2) compared to the overall mortality rate of 10.6% (Rodrigues et al. 2019). Only juveniles and neonates died from capture, suggesting ontogenetic resistance to in-net mortality. Mortality (10%) in *Z. brevirostris* was also only recorded for neonates and juveniles (Rodrigues et al. 2019).

Gillnets

Data for commercial gillnet catches of *A. vincentiana* in southern Australia recorded a 20% AVM rate, though sample size was limited to five individuals (Walker et al. 2005). Capture mortality of sawfishes in gillnets of the Northern Territory Barramundi Fishery recorded by observers in 2007–2008 were 51% for *A. cuspidata*, 45% for *P. clavata*, and 55% for *P. zijron* (Field et al. 2013).

Information on physiological responses or sublethal effects are limited, though analysis of stress responses indicates that average lactate concentrations of juvenile *P. pectinata* ($n=46$) from scientific gillnets in Florida were lower than averages reported for some gillnet-caught sharks (Prohaska et al. 2018). In contrast, potassium concentrations were elevated relative to other elasmobranchs. Mark-recapture and tracking data did not suggest post-release mortality, but potassium may not be a reliable indicator of stress (Prohaska et al. 2018).

In southern Brazil, *Z. brevirostris* caught in gillnets during the reproductive period suffer consecutive abortions followed by maternal mortality (up to 60%), along with physiological disruption leading to loss of homeostatic balance and lactic acidosis (Wosnick et al. 2019). The same occurs for males during the copulation period, with increased mortality (up to 70%) and lethal physiological alterations associated with commercial capture (Prado et al. 2022). Survival rates outside the reproductive period are extremely high for both sexes (AVM of 2–5%) (Wosnick et al. 2019; Prado et al. 2022).

Preliminary data for *P. horkelii* and *P. percellens* captured in gillnets in southern Brazil indicate that AVM is higher (30%) than for *Z. brevirostris* (2–5%)

Table 2 Fishing-related mortality by family, species, gear type, and country. Proportion recorded as dead and sample size are reported. In studies where fate was unknown for the whole sample size, the proportion dead from the total sample size is first reported, followed by [adjusted %] where proportion dead is reported from a sub sample [adjusted *n*] where fate was known. BPG, bather protection gear. Refer to Online Resource 2 for detailed study information

Family/Species	Gear	Country	Mortality %[%]	Sample size <i>n</i> [<i>n</i>]	Reference
Glaucostegidae					
<i>Glaucostegidae cemiculus</i>	Line	Tunisia	0	123	Echwikhi et al. (2014)
<i>Glaucostegidae obtusus</i>	Seine	India	25	4	Gupta et al. (2022)
<i>Glaucostegus granulatus</i>	Seine	India	0	1	Gupta et al. (2022)
Pristidae					
Pristidae	Trawl	Australia	32	6,884	AFMA 2012–(2022)
<i>Anoxypristis cuspidata</i>	Trawl	Australia	88	75	Tobin et al. (2010)
<i>Pristis clavata</i>	Trawl	Australia	100	2	Tobin et al. (2010)
<i>Pristis pectinata</i>	Trawl	USA	20	5	Scott-Denton et al. (2012)
<i>Anoxypristis cuspidata</i>	Gillnet	Australia	51	37	Field et al. (2013)
<i>Pristis clavata</i>	Gillnet	Australia	45	20	Field et al. (2013)
<i>Pristis zijsron</i>	Gillnet	Australia	55	11	Field et al. (2013)
<i>Pristis zijsron</i>	Line	Australia	0	2	Braccini and Waltrick (2019)
<i>Pristis pectinata</i>	Line	USA	2.5	40	Brame et al. (2019)
Pristidae	BPG	Australia	5	1,450	Wueringer (2017)
Pristidae	BPG	South Africa	14[57]	91[36]	Everett et al. (2015)
Rhinidae					
<i>Rhina ancylostomus</i>	Trawl	South Africa	0	1	Fennessy (1994)
<i>Rhynchobatus djiddensis</i>	Trawl	South Africa	18	11	Fennessy (1994)
<i>Rhynchobatus palpebratus</i>	Trawl	Australia	10	59	Stobutzki et al. (2002)
<i>Rhynchobatus australiae</i>	Line	Australia	0	15	Braccini and Waltrick (2019)
<i>Rhynchobatus australiae</i>	Line	Australia	75	8	Butcher et al. (2015)
<i>Rhina ancylostomus</i>	Seine	Australia	0	1	Rowell and Davies (2012)
<i>Rhynchobatus australiae</i>	BPG	Australia	29*	14	Broadhurst and Cullis (2020)
<i>Rhynchobatus djiddensis</i>	BPG	South Africa	28	2,856	Daly et al. (2021)
Rhinobatidae					
<i>Acroteriobatus leucospilus</i>	Trawl	South Africa	53	19	Fennessy (1994)
<i>Acroteriobatus annulatus</i>	Trawl	South Africa	11	9	Fennessy (1994)
<i>Pseudobatos perellens</i>	Trawl	Brazil	20	5	Rodrigues et al. (2019)
<i>Pseudobatos horkelii</i>	Trawl	Brazil	30	43	Rodrigues et al. (2019)
Rhinobatidae	Trawl	Australia	79[83]	114[108]	Rowell and Davies (2012)
<i>Rhinobatos rhinobatos</i>	Line	Tunisia	0	44	Echwikhi et al. (2014)
Rhinobatidae	Seine	Australia	5	102	Rowell and Davies (2012)
Trygonorrhinidae					
<i>Aptychotrema vincentiana</i>	Trawl	Australia	99[93]	735[696]	Rowell and Davies (2012)
<i>Trygonorrhina fasciata</i>	Trawl	Australia	0	2	Rowell and Davies (2012)
<i>Zapteryx brevirostris</i>	Trawl	Brazil	10	12	Rodrigues et al. (2019)
<i>Aptychotrema vincentiana</i>	Gillnet	Australia	20	5	Walker et al. (2005)
<i>Zapteryx brevirostris</i>	Gillnet	Brazil	68	50	Prado et al. (2022)**
<i>Aptychotrema rostrata</i>	Line	Australia	0	2	Butcher et al. (2015)
<i>Aptychotrema rostrata</i>	Seine	Australia	8[29]	2,340[601]	Rowell and Davies (2012)
<i>Trygonorrhina fasciata</i>	Seine	Australia	0	2	Rowell and Davies (2012)

* 2 deaths were a result of depredation. ** Physiological analysis performed

(Leite 2022), possibly due to the distinct snout morphology between genera. In benthic gillnet operations, *Pseudobatos* species are brought on board alive, and increased AVM seem to be associated with poor handling by fishers and thermal shock experienced on warmer days (Wosnick N, pers. obs.). Physiological analysis indicated that there is no difference in the magnitude of the stress imposed by capture between species (Leite 2022). Physiological disruption appears to be associated with lactic acidosis and subsequent rupture of membranes, leading to systemic allostatic overload.

Line

In longline operations, AVM rates were 0% when *R. australiae* are hooked for 7 h and 25% when hooked for 14 h (Butcher et al. 2015). In the case of *A. rostrata*, a single individual remained alive after 14 h hooking (Butcher et al. 2015). In Florida, blood parameter analysis of *P. pectinata* ($n=33$) sampled from shallow and deep scientific longlines suggested physiological resilience (Prohaska et al. 2018).

Recreational

There was no difference between the concentrations of stress markers (lactate and glucose) in *A. annulatus* before and after handling improvement at angling competitions in South Africa (Mannheim et al. 2018). However, there was a significant improvement in condition scores for the species ($n=10$), suggesting chances of post-release survival increased with interventions (Butler et al. 2017; Mannheim et al. 2018).

Discussion

We present the first global review of fishing interactions with rhino rays. Despite being one of the most threatened marine groups globally, reports of catches or landings have only been published from 37 of 88 range states. Our results highlight that fishing data on this group are severely lacking, especially considering that our review does not account for unreported discards. By approaching the available information regionally and by gear type, we demonstrate where reported interactions are highest

(Asia and Oceania) and in which gears (gillnets and trawls). Data derived from Central and South America, the Mediterranean Sea and Africa, and Asia are primarily based on the monitoring of landing sites, while data from observer coverage are largely restricted to Oceania and North America. Both data collection methods provide important insights into retained catch and commercially exploited species, but also have limitations with respect to data accuracy including gear associated with catches and landings, discards vs releases, fishing-related mortality, and species identification. We acknowledge that by only considering English sources (or some limited references in other languages included within references), we are likely to have underestimated the available data for some regions (e.g., Central and South America in Spanish or Portuguese). We also note that some studies pooled data from scientific and observer coverage. Despite representing important contributions, they were excluded from results (e.g., Stobutzki et al. 2002). Our results are discussed through the following themes: (1) interactions by region and gear; (2) physiological considerations; (3) drivers of retention; and (4) options for minimizing bycatch.

Interactions by region and gear

Information on interactions varied across regions and were likely influenced by fishing effort, species richness, identification challenges, fishing practices (e.g., mixed gear), data availability, and size selectivity. While data on relative catch levels and the frequency of interactions in different fishing gear can be informative, information on fishing effort to produce standardised catch rates (e.g., catch-per-unit-effort; CPUE) is more useful. In most cases, fishing effort data were not included in published literature. Since Asia and Africa account for the highest species richness of rhino rays, the number of species reported from studies in these regions was also high. However, 42% of rhino ray species known to occur in Africa were not covered in the literature compared with only 12% of species occurring in Asia. For many countries in these regions (especially Africa), reports of interactions were not available despite being range states for several rhino ray species. This could also explain the lower-than-expected species coverage. In Asia,

the overwhelming majority of reported interactions were from landings and usually mixed gear with little information on overall catch composition, discards, and relative landings. Given that these regions are often characterized by limited fisheries governance or management capacity (e.g., Jabado 2018), and high levels of fishing pressure (Kyne and Jabado 2021), our review clearly underestimated interaction levels. These regions would benefit from increased resources and capacity to improve established fisheries monitoring programs and ensure rhino rays are prioritized in data collection protocols. This is critical to understand the status of species and assess trends in catches over time.

Identification can be challenging for many rhino ray species, both as whole specimens and processed products (e.g., White et al. 2013; Jabado 2018). This has been exacerbated by recent and ongoing changes in the taxonomy of this group (e.g., Last et al. 2016a, b). The most frequently reported species in our review was *R. ancylostomus*. Critically Endangered, it is the widest ranging of the wedgefishes and is susceptible to catch and retention in fisheries across its range. It is a morphologically distinct and recognizable species, and this may explain a reporting bias. Reporting of species that have similar characteristics (i.e., look-alikes) and overlap in distribution, likely results in a poorer level of species-specific data availability (e.g., amongst *Rhynchobatus* spp.). Improved identification of rhino rays requires readily available identification guides (both for whole animals and processed parts) in local languages and training to accurately characterize species composition in catches and landings. Molecular identification has been applied to identify derivative products (e.g., fins, meat) at the point of landing and in trade, including to differentiate between legally and illegally captured or traded specimens (De-Franco et al. 2012; Cardenosa et al. 2018; Bernardo et al. 2020; Asbury et al. 2021). However, the widespread use of molecular techniques remains limited and their uptake will require access to specialized equipment, training, and capacity building.

Rhino rays interacted with a variety of gear types, although trawl and gillnet were predominant. Uncertainty in gear (i.e., ‘mixed gear’) was significant and masked true counts of gear type responsible for catches. In many cases however, mixed catches and landings were commonly attributed to gillnets or trawls based on fisheries operating in study regions

(e.g., Enajjar et al. 2015; Fatima et al. 2016; Grant et al. 2021; Hsu et al. 2022; Seidu et al. 2022b). Coastal trawls are recognized as one of the biggest threats to rhino rays (Jabado et al. 2017) and trawls were reported from more publications than gillnets (36 and 32, respectively). However, gillnets were responsible for a higher number of interactions (101 to 78) but lower species coverage (gillnet, 26 species; trawl, 34). Reported interactions, sample sizes, and species coverage did not always have a positive correlation. In Oceania, gillnets were responsible for the highest interactions, but sample sizes and species richness were highest from trawls. In contrast, interactions and numbers captured were highest from trawls while species richness was higher from gillnets in Asia. Some species may be subject to capture in various gear types in the same region with varying levels of risk. For example, shrimp trawl captures pose the most risk to large juvenile and adult *P. pectinata* within three US fisheries (shrimp trawl, gillnet, bottom longline) (Graham et al. 2022). In other cases, both trawl and gillnet were responsible for high catches of rhino rays in the same areas but across different seasons (Bizzarro et al. 2007, 2009).

Limited information was available on interactions in recreational fisheries, which can form a substantial component of unreported elasmobranch interactions (Coll et al. 2014). Available published information was restricted to two range states (South Africa, Brazil). Rhino rays are known to interact with recreational fisheries, but information availability is mostly limited to data sources such as citizen science. In the US for example, recreational fisheries are a major interaction source with *P. pectinata* with high reported release rates. These interactions are managed through legislative protection as well as education and outreach programs (Carlson et al. 2007; NMFS 2009; Wiley and Simpfendorfer 2010). Across most rhino ray range states however, recreational fisheries are not managed (Potts et al. 2019). Here, species-specific best-handling guides and outreach programs are key resources for mitigating mortality from interactions with recreational fishing.

Size classes of rhino rays that interact with different gear are influenced by factors such as species life history (e.g., if a fishery operates within a nursery area), animal behaviour (e.g., aggregations), size selectivity of the gear (particularly relevant for gillnet), and the use of BRDs which may exclude certain

size classes from capture. The size of animals caught was reported from 53% of reports and the widest size range was recorded from gillnets. Neonates and juveniles were reported from most gears (Online Resources 2). Gillnets and lines were also associated with targeted elasmobranch fisheries (D'Alberto et al. 2022) and interactions with lines occurred most frequently in areas which target large-bodied rhino rays such as in the Mediterranean Sea (Tunisia, Türkiye), Bay of Bengal (Bangladesh, India), and Indonesia (Echwiki et al. 2014; Haque et al. 2021a; Saidi et al. 2023). Distinguishing between gear used to target rhino rays and gear that incidentally catches species will contribute to informed decisions regarding fisheries regulations including gear specifications, size limits, or safe release practices. This is particularly important at the country level and a priority focus should be on regulating targeted rhino ray fisheries where they are currently known to exist such as in Tunisia, Ghana, and Indonesia (e.g., Enajjar et al. 2015; D'Alberto et al. 2022; Seidu et al. 2022a).

Physiological considerations

A severe lack of knowledge on the physiological effects and mortality associated with capture for rhino rays was noted. Although there is information for at least one species for each fishing gear covered in the present study, the amount and quality of available data are insufficient to extrapolate across the group. Reported mortality rates varied significantly, which may be a result of the fishing gear and its deployment, species-specific susceptibility, or a combination of both. The largest portion of literature was focused on sawfish and guitarfish, with five species from each family (100% and 14% of species, respectively) assessed for physiological effects and/or capture mortality rates. Species-specific data were available for three banjo rays (38% of species), three wedgefishes (27%), and two giant guitarfishes (29%), highlighting limited coverage (26%) across these families.

Evolutionary factors are likely to play a role on the susceptibility of rhino rays to capture mortality. Phylogeny has been shown to explain some of the AVM patterns observed for sharks and rays caught in pelagic longlines (Gilman et al. 2022). Due to the lack of AVM data for rhino rays, only *G. cemiculus* was included in the meta-analysis, so the influence of evolutionary factors on rhino ray capture susceptibility could not

be assessed. Future predictions based on phylogenetic proximity and shared phenotypes may shed light on susceptibility to mortality and physiological effects. It is recommended that alternative methods and technologies (e.g., electronic monitoring/machine learning), that can play a role in enhancing data collection and estimating species-specific mortality (Poisson et al. 2014, 2022; Mangi et al. 2015), should be used to allow for more robust predictive analyses.

Individuals captured within their reproductive period or in the early life stages are most sensitive to capture mortality (Prohaska et al. 2018; Wosnick et al. 2019; Finotto et al. 2021, 2023; Prado et al. 2022;). Appropriate management measures should therefore focus on seasonal closures around key life history stages and events. Such critical habitats and areas can be identified through various approaches including Important Shark and Ray Areas (ISRA; Hyde et al. 2022; Kyne et al. 2023). Given the overall data paucity on capture mortality rates and physiological effects identified in our review, further research is required not only to fill species knowledge gaps but also to assess ontogenetic and sex-related responses to capture stress. Most studies available on capture stress and mortality were carried out through scientific research or laboratory experiments. Physiological effects or mortality rates may therefore be underestimated due to differences in capture and handling in fishing versus scientific settings (Musyl et al. 2009). Collaborative research with the fishing sector will be essential to provide accurate data, establish visual and behavioural proxies for assessing capture stress (Wosnick et al. 2023), and provide samples for developing physiological assays and indicators (Moyes et al. 2006). Working with the fishing industry will be critical as it can improve the uptake of handling and safe release manuals and training, which can significantly increase survival rates after release.

Drivers of retention

Rhino rays are retained in fisheries for a variety of uses and trade which can support food security and livelihoods (Kyne and Jabado 2021). The fins of rhino rays such as wedgefishes are considered high value, fetching up to USD 964 per kilogram (Hau et al. 2018; Jabado 2019). This has driven target fisheries (e.g., D'Alberto et al. 2022) and retention when captured (Jabado 2018). In the past, demand

was restricted to the larger wedgefishes and giant guitarfishes, but the trade has expanded to include smaller animals and species (i.e., guitarfishes) in international trade (Fields et al. 2018; Cardeñosa et al. 2020). The meat of rhino rays as a source of protein is also increasingly reported with wedgefishes considered to have high quality meat (Barrowclift et al. 2017; Cervantes-Gutiérrez et al. 2018; Haque et al. 2021a, b) although smaller-sized and lower quality rhino rays can also be retained for use as fish meal (Bhagyalekshmi and Kumar 2021). Beyond the fin and meat trade, there are also emerging markets for several products which include skin, snouts, thorns, and jaws (Haque et al. 2018, 2021b; Choy et al. 2022; Pytka et al. 2023). Trade in these products, which can drive target fisheries, remain largely undocumented and unregulated (e.g., Haque et al. 2018, 2021b).

Understanding the drivers of retention and trade can help inform management of fisheries interactions and measures aimed at reducing mortality. Drivers can differ geographically and/or by species and require an understanding of cultural context (Tyabji et al. 2022), as well as economic and subsistence values. Working with fishing communities to understand what drives retention or release will contribute to designing appropriate interventions aimed at behavioural change (Mannheim et al. 2018). For example, animals <60 cm TL are discarded in some fisheries due to their small sizes (e.g., Castillo and Morales 2021; Gupta et al. 2022), offering an opportunity for safe release initiatives. Domestic policies and implementation of legislation to manage fishery input (e.g., fishing effort) and fishery output (e.g., catch quotas) controls will need to be implemented to sustainably manage exploitation. In many cases though, species-level protection will be essential for highly threatened species (i.e., Critically Endangered and Endangered species). Until recently, domestic level protection was primarily limited to sawfishes (e.g., Australia, USA), however, in recent years, Brazil, Bangladesh, Pakistan, and the UAE have fully protected rhino rays (in addition to several countries that have banned all shark and ray fishing within their waters). Yet, with limited monitoring and enforcement, fishing continues in both target and bycatch fisheries across most range states (e.g., Larre et al. 2021). Further, in some countries, protected species lists do not accurately reflect current taxonomy and require updating (e.g., Tyabji et al. 2020). At the international level, trade of four families of rhino rays

(sawfishes, wedgefishes, giant guitarfishes, and guitarfishes) is regulated through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Other treaties like the Convention on the Conservation of Migratory Species of Wild Animals (CMS) or the CMS Sharks Memorandum of Understanding also list several species on their Appendices such as *R. rhinobatos* (Kyne and Jabado 2021). If implemented, these listings have the potential to reduce fisheries interactions and improve traceability in trade, but this requires resources, species-specific data collection, and an understanding and identification of the above products in the supply chain. It is, however, important to recognize the relevance of rhino ray meat and by-products in domestic markets, especially in the Global South, pointing to a need for improved legislation, monitoring at various scales, and considerations of food security and livelihood alternatives.

Options for minimizing bycatch

Technical modifications to fishing gear provide options for reducing rhino ray bycatch in fisheries where utilization and trade do not necessarily drive retention or where legislative requirements prohibit retention. Our review showed that research on options to minimize interactions with rhino rays is generally limited and has largely focused on sawfishes. There are however several measures that have proven successful for bycatch reduction that may have applicability to rhino rays. In trawl fisheries, TEDs have proven very effective at reducing shark and ray bycatch including demonstrated reduction in rhino ray bycatch (Brewer et al. 2006; Campbell et al. 2021). While mandated in prawn/shrimp trawl fisheries in some rhino ray range states (e.g., Australia, USA), programs to expand uptake of these measures to tropical regions where rhino ray diversity is high and where trawl fisheries operate in high numbers, would be highly beneficial. Other technological advances have recently demonstrated reductions in shark and ray interaction levels in gillnet and line fisheries. Net illumination with simple LED lights significantly reduced catches of sharks in a Gulf of California gillnet fishery (Senko et al. 2022) while the electric deterrent SharkGuard, reduced catch levels on pelagic longlines (Doherty et al. 2022). Trialling these devices in rhino ray specific contexts should be a research priority.

The unique rostral morphology of sawfishes presents some challenges for reducing interactions in net fisheries. Although TEDs have shown some success in reducing *A. cuspidata* capture in a northern Australian prawn trawl fishery (Brewer et al. 2006), entanglement often occurs well before the position of the TED. Testing of electric deterrents showed some promise in eliciting a behavioural response with a limited number of sawfish ($n=2$) but this was not currently considered transferable to fishing operations (Abrantes et al. 2021). This is a research area that requires further development and testing. Simpler modifications or adjustments to fishing practices may also reduce interactions not only of sawfishes but rhino rays more broadly. This may include raising gear off the benthos as rhino rays are primarily benthic species (e.g., Fakioglu et al. 2022) or increasing the tension of gillnets (White et al. 2013). The introduction of any technical bycatch mitigation requires fishery-dependent testing to ensure effectiveness at bycatch reduction while maintaining the catch of target species (e.g., raising ground gear may be impractical in trawl or some net fisheries targeting benthic species). Understanding behavioural, physiological, and ecological aspects (including habitat use and movement patterns; Molina and Cooke 2012) of species captured incidentally is important in developing and trialling mitigation strategies. Finding strategies that work to mitigate bycatch for multiple gears from multiple taxa while ensuring adequate levels of capture of target species should be a research priority.

Given that some level of interaction will be inevitable as fishing continues, proper handling and release are essential next steps. This is especially important for rhino rays given evidence of high survival among buccal pumpers in various gear in general, and exhibited by rays in gillnets after extended soak times (Ellis et al. 2017, 2018; Wosnick et al. 2019; Prado et al. 2022). In many countries of the world, rhino rays are landed alive, and processing begins before they die (Jabado unpubl. data for UAE, India, Senegal, Mauritania, and The Gambia). Given the high levels of interactions across a range of size classes documented here, we advise increasing policies towards safe release and the development of context-specific safe-release guides (e.g., Grant et al. 2023). Equally, proper handling of animals is critical to prevent injury, reduce stress and potentially capture-induced

parturition in females (e.g., Adams et al. 2018), or avoid mortality of the captured animal (e.g., dragging an animal by the tail can tear connective tissue and/or damage internal organs).

Conclusion

Fishing interactions are continuing to impact rhino rays and retention of previously discarded species is increasing. Food security, dynamic and complex trade, and high levels of threat where management capacity is lowest requires a diversity of conservation and management planning and action. In the Global South, where the highest rhino ray diversity has been reported, most coastal communities heavily rely on fish for animal protein (Chuenpagdee et al. 2006) with shark and ray fishing (including rhino rays) forming an integral part of livelihoods (e.g., Yulianto et al. 2018; Haque et al. 2022). In some areas, bans or limitations on landings may not pose a burden to livelihoods (Gupta et al. 2023) although effectiveness of measures will vary depending on regulatory capacities and financial constraints (Komoroske and Lewison 2015). Incorporating the human dimensions of rhino ray fishing is key to proposing effective mitigation strategies that acknowledge the socioeconomic and subsistence value of rhino rays for traditional fishing communities.

Paramount is the need for continued and improved data collection to fill the many gaps highlighted in this review. Essential parameters to be incorporated in research and monitoring include accurate species identification (and defining target vs bycatch species), size compositions of catches, fishing gear characteristics (e.g., mesh or hook size), discard and release rates, and mortality/survivorship rates. Beyond that, reducing interactions and mortality is the most urgent need given their imperilled status and will require the implementation and uptake of a diverse range of measures. Priorities include domestic level species protections and enforcement for the most threatened species, domestic fishing management regulations for sustainable exploitation (where this is possible), implementation and monitoring of international trade measures, and incorporation of area-based management considerations (i.e., protected areas). While this will require a commitment to resourcing, capacity, enforcement, and monitoring,

together, this suite of measures can help to secure and recover rhino ray populations.

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Data availability All data generated or analysed during this study are included in this published article [and its supplementary information files, available online].

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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