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Contribution to the Special 'Global status of wedgefish and guitarfish'

REVIEW

Global status and research priorities for rhino rays

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ABSTRACT: Global biodiversity continues to decline in the terrestrial and aquatic realms. Across animal groups, threatened species are at risk of extinction if not managed effectively and permitted to recover. The cartilaginous fish order Rhinopristiformes (rhino rays) comprises 5 families: sawfishes, wedgefishes, guitarfishes, giant guitarfishes, and banjo rays. While the global plight of sawfishes, which are heavily depleted and have undergone range contraction unprecedented in cartilaginous fishes, has drawn attention to their status, the other families have received less focus to date. To highlight research on the non-sawfish rhino rays, the American Elasmobranch Society held the inaugural Global Wedgefish & Guitarfish Symposium in 2021. This Special Issue of *Endangered Species Research* presents a series of papers from that symposium. Rhino rays (68 species globally) face an extremely elevated risk of extinction, with nearly three-quarters of species threatened (72.7%; Critically Endangered, Endangered, or Vulnerable on the IUCN Red List of Threatened Species) and nearly half (48.5%) of all species classified as Critically Endangered. This level of critical endangerment is amongst the highest of all 136 vertebrate orders, with rhino rays ranking only below sturgeons and paddlefishes (order Acipenseriformes) and coelacanths (Coelacanthiformes). Recommendations for research priorities were developed through an expert-elicitation approach in the fields of status, taxonomy, life history, habitat, molecular ecology, fisheries, trade, and *ex situ* breeding. Only significant investment in research priorities will strengthen the information base upon which to make conservation and management decisions and secure a future without extinctions for rhino rays.

KEY WORDS: Banjo rays · Extinction risk · Guitarfish · Rhinopristiformes · Threatened species · Wedgefish

1. INTRODUCTION

The global biodiversity crisis continues, with current extinction rates estimated to be 1000 times the natural background level (De Vos et al. 2015). Species at risk of extinction globally number more than 45 000 (those listed as Critically Endangered, Endangered, or Vulnerable on the IUCN Red List of Threatened

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Species; IUCN 2024). These species represent potential future extinctions if their recovery is not facilitated by strong conservation and management measures underpinned by sound scientific research. Documented global extinctions since 1500 (the timestamp for assessing human-induced extinctions; IUCN Standards and Petitions Committee 2024) have numbered at least 908 species (IUCN 2024). These include species prominent in the public sphere (e.g. dodo *Raphus cucullatus*; Hume 2006) and those less charismatic taxa that sound the alarm on ongoing anthropogenic threats (e.g. Bramble Cay melomys *Melomys rubicola*; Fulton 2017). Extinctions represent an irreplaceable loss of biodiversity, and future loss is expected to continue given elevated extinction risk facing many taxa groups.

In the aquatic realm, unsustainable exploitation is a major threat to biodiversity. Strong management frameworks can result in sustainable fisheries which are underpinned by sound knowledge of species biology, stock structure, and abundance. Conversely, where effective management is lacking, fisheries can drive species to overexploited levels. There is a growing divergence between these 2 scenarios (Worm & Branch 2012). One major lineage that is facing an elevated threat status primarily driven by overfishing, both targeted and incidental (bycatch), is the cartilaginous fishes (class Chondrichthyes: sharks, rays, and chimaeras). This relatively diverse group of ~1250 species is of high conservation concern, with one-third of species at risk of extinction (IUCN 2024). Cartilaginous fishes generally exhibit 'slow' life history (e.g. late age-at-maturity, low fecundity, low natural mortality) and, subsequently, limited population growth rates (Musick 1999), which limits their ability to sustain exploitation or recover from population depletion. This class comprises 8 orders of sharks, 4 orders of rays, and 1 order of chimaeras. The cartilaginous fishes occur primarily in marine waters, with only ~5% occupying non-marine environments (Lucifora et al. 2015). This group occurs from inshore coastal waters, across continental and insular shelves and pelagic waters of the open ocean, to deepwater habitats of slopes, seamounts, and plateaus (although they are absent from the deepest oceans; Priede et al. 2006).

Cartilaginous fishes inhabiting nearshore waters are particularly susceptible to human activities given the increased levels of fishing pressure and coastal development (Knip et al. 2010). The first documented modern extinction of a cartilaginous fish occurred within nearshore waters subject to these pressures (Java stingaree *Urolophus javanicus*; Constance et al. 2023). The chondrichthyan order Rhinopristiformes (rhino rays) also largely occupies the shallow coastal zone. The order comprises sawfishes, wedgefishes, guitarfishes, giant guitarfishes, and banjo rays. All are characterised by a ray-like anterior, a shark-like posterior, and an elongated snout, most prominent in the tooth-studded rostra of sawfishes (Last et al. 2016). Severe global declines and range contractions in the sawfishes led to a concerted research and management focus on this family (Poulakis & Grubbs 2019). Subsequently, concern was raised for rhino rays more broadly due to the effects of targeted fishing, bycatch, and largely unregulated trade across geographic ranges with little refuge from these processes (Moore 2017, Jabado 2019, Kyne et al. 2020, Kyne & Jabado 2021, Pytka et al. 2024).

In light of this concern, the American Elasmobranch Society (AES), a professional non-profit organization 'that seeks to advance the scientific study of living and fossil sharks, skates, rays, and chimaeras, and the promotion of education, conservation, and wise utilization of natural resources' (https://elasmo.org/about/), held a Global Wedgefish & Guitarfish Symposium in 2021. The symposium aimed to showcase contemporary research on the non-sawfish rhino rays (wedgefishes, guitarfishes, giant guitarfishes, and banjo rays). Sawfish had previously been the subject of an earlier symposium in 2016 (Poulakis & Grubbs 2019), with the Global Wedgefish & Guitarfish Symposium aiming to highlight the relatively less-studied remaining rhino ray families.

Here, an overview of the AES Global Wedgefish & Guitarfish Symposium is presented, along with an up-to-date assessment of global rhino ray diversity and status and a series of research priorities based on topics presented at the symposium. Acknowledging the concern already raised for this group (e.g. Moore 2017, Jabado 2019, Kyne et al. 2020), we provide a contemporary perspective on status, diversity, and topics ranging from taxonomy to trade. The primary focus is on the non-sawfish rhino rays, although sawfishes are included in the assessment of species diversity and status.

2. MATERIALS AND METHODS

2.1. AES Global Wedgefish & Guitarfish Symposium

The symposium was held online over 2 days in November 2021. Prior to this, a call out was made to the chondrichthyan research community to submit abstracts for consideration in the symposium. The symposium was advertised widely through the AES, social media, and research networks, with an open invitation to attend the online sessions (through an online registration). Symposium presenters were later invited to submit manuscripts for consideration in a Special Issue of *Endangered Species Research*.

2.2. Diversity and status

Species diversity was collated from Last et al. (2016) and Fricke et al. (2024), encompassing all currently accepted taxonomic concepts and binomial names. Several new species have been described since the publication of Last et al. (2016) in the families Rhinidae (*Rhynchobatus mononoke*), Rhinobatidae (*Acroteriobatus andysabini*, *A. stehmanni*, *Pseudobatos buthi*, *Rhinobatos austini*, *R. manai*, *R. ranongensis*), and Glaucostegidae (*G. younholeei*). These species are included in Fricke et al. (2024). Two species listed as valid by Fricke et al. (2024) but not considered valid by Last et al. (2016) and IUCN (2024) are not included here (*G. microphthalamus*, which is considered a synonym of *G. typus*, and *G. spinosus*, whose validity is questionable; see Weigmann 2016). Lastly, the name *Rhynchobatus compagnoi* is used in error for *R. cooki* in Last et al. (2016). The species list and IUCN Red List categories (see below) were valid as of 23 September 2024 (IUCN Red List Version 2024-1; IUCN 2024).

Extinction risk categories were taken from the IUCN Red List of Threatened Species, the world's most comprehensive and accepted source of status (IUCN 2012, 2024). Species can be assessed as Extinct (EX; 'no reasonable doubt that the last individual has died'), Extinct in the Wild (EW; 'known only to survive in cultivation, in captivity or as a naturalized population [or populations] well outside the past range'), Critically Endangered (CR; 'facing an extremely high risk of extinction in the wild'), Endangered (EN; 'facing a very high risk of extinction in the wild'), Vulnerable (VU; 'facing a high risk of extinction in the wild') (collectively, CR, EN, VU species are referred to as threatened species), Near Threatened (NT; 'does not qualify for CR, EN or VU now, but is close to qualifying for or is likely to qualify for a threatened category in the near future'), Least Concern (LC; species that do not qualify for CR, EN, VU, or NT), and Data Deficient (DD; 'inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status') (IUCN 2012).

To compare the extinction risk profile of rhino rays with other taxa, the status of all 136 vertebrate orders was extracted from the IUCN Red List using the 'Advanced Search' tool (IUCN 2024). Search parameters were set at: 'Taxonomy' = (1) 'Animalia', (2) 'Chordata'; 'Geographical scope' = 'Global'; 'Red List Category' = 'Critically Endangered' + 'Endangered' + 'Vulnerable'; with 'Include' set to 'Species'. The search covered all orders of the classes Actinopterygii (ray-finned fishes; n = 48 orders), Amphibia (amphibians; n = 3), Aves (birds; n = 36), Chondrichthyes (cartilaginous fishes; n = 13), Mammalia (mammals; n = 27), Myxini (hagfishes; n = 1), Petromyzonti (lampreys; n = 1), Reptilia (reptiles; n = 4), and Sarcopterygii (lobe-finned fishes; n = 3). Extinction risk by order was calculated as (1) the proportion of extant species assessed as threatened (CR, EN, and VU) and (2) the proportion of extant species assessed as CR ('extremely high risk of extinction').

2.3. Research priorities

Research priorities were identified through an expert-elicitation approach. Lead authors of manuscripts included in the Special Issue were invited to recommend 4–5 research priorities for each topic covered by the manuscript subject matter: status, taxonomy, life history, habitat, molecular ecology, fisheries, trade, and *ex situ* breeding. Research priorities were reviewed and agreed upon by all authors. Priorities are unranked, that is, no one priority in a field is deemed more important than another. The final list of research priorities is not exhaustive, but represents those which experts currently consider important to improve knowledge, management capacity, and conservation of rhino rays.

3. RESULTS & DISCUSSION

3.1. AES Global Wedgefish & Guitarfish Symposium

The symposium comprised 27 presentations on research, conservation, and management of non-sawfish rhino rays. Presenters were affiliated with 18 countries across all continents except for Antarctica. The symposium had 280 registered attendees from 37 countries. The 15 countries with the most registered participants were the United States (n = 84; 30.0%), Australia (31; 11.1%), Brazil (24; 8.6%), Peru (12; 4.3%), United Kingdom (12; 4.3%), South Africa (11; 3.9%), India (9; 3.2%), Thailand (8; 2.9%), Singapore

(7; 2.5%), Sri Lanka (7; 2.5%), Canada (6; 2.1%), Germany (6; 2.1%), Indonesia (6; 2.1%), Bangladesh (5; 1.9%), and France (5; 1.9%).

As part of the Symposium, the Beyond Jaws podcast hosted 8 episodes dedicated to rhino rays (https://elasmo.org/podcast/). Twenty-nine symposium presentation authors joined the podcast to share their personal rhino ray research story, with each podcast episode having multiple guests. This synergistic approach provides an oral history as told by the researchers themselves for future generations researching this enigmatic group. Other outputs related to the symposium were a dedicated homepage (https://elasmo.org/conferences/global-wedgefish-guitarfish-symposium-2021/), a YouTube channel showcasing 26 presentations (https://www.youtube.com/wedgefish-guitarfish-symposium), and a summary report containing all presentation abstracts (Ebert et al. 2021). The symposium web homepage (and associated links) and YouTube Channel are open access and are maintained by the American Elasmobranch Society. This unique, first of its kind, complementary approach can serve as a template for future symposia to support the public dissemination of information, helping to promote research and raise awareness.

This *Endangered Species Research* Special Issue 'Global status of wedgefish and guitarfishes' presents papers on taxonomy (Aitchison et al. 2024), life history (D'Alberto et al. 2024), habitat (Al Hameli et al. 2024), molecular ecology (Groeneveld et al. 2024), fisheries (Gonzalez-Pestana et al. 2024), trade (Karnad et al. 2024), and *ex situ* breeding (Hanna et al. 2024). A variety of taxa are covered, namely, wedgefishes (bottlenose wedgefish *Rhynchobatus australiae*, D'Alberto et al. 2024; whitespotted wedgefish *R. djiddensis* and *R. australiae*, Groeneveld et al. 2024; bowmouth guitarfish *Rhina ancylostomus*, Hanna et al. 2024), giant guitarfishes (Halavi guitarfish *Glaucostegus halavi*, Al Hameli et al. 2024), guitarfishes (Pacific guitarfish *Pseudobatos planiceps*, Gonzalez-Pestana et al. 2024; Austin's guitarfish *Rhinobatos austini*, slender guitarfish *R. holcorhynchus*, bareback guitarfish *R. nudidorsalis*, Aitchison et al. 2024), and rhino rays collectively (Karnad et al. 2024).

3.2. Diversity and status

Rhino rays comprise 5 families consisting of 68 species: sawfishes (Pristidae; 5 species), banjo rays (Trygonorrhinidae; 8 species), giant guitarfishes (Glaucostegidae; 7 species), wedgefishes (Rhinidae; 11 species), and guitarfishes (Rhinobatidae; 37 species) (Table 1). Extinction risk is high across the family, with 72.7% of assessed species threatened (100% of sawfishes; 37.5% of banjo rays; 100% of giant guitarfishes; 90.9% of wedgefishes; 65.7% of guitarfishes; Table 1).

Rhino rays (72.7% threatened) are among the top 10 most threatened vertebrate orders of animals on earth, after sturgeons and paddlefishes (Acipenseriformes), mesites (Mesitornithiformes), pangolins (Pholidota), sea cows (Sirenia), elephants (Proboscidea), coelacanths (Coelacanthiformes), and Australian lungfishes (Ceratodontiformes), all of which are 100% threatened, and odd-toed ungulates (Perissodactyla; 75% threatened) (Table 2).

When ranked by the proportion of CR species, rhino rays (48.5% CR) rank third only after sturgeons and paddlefishes (68% CR) and coelacanths (50%, represented by a single CR species since there are only 2 extant coelacanths) (Table 3). CR species face 'an extremely high risk of extinction' (IUCN 2012), and on the scale of endangerment, are positioned just above Extinct and Extinct in the Wild, making rhino rays one of the most at-risk animal groups on the planet.

3.3. Research priorities

The following sections outline research priorities in the fields of status, taxonomy, life history, habitat,

Table 1. Rhino ray diversity and extinction risk status by family. IUCN Red List of Threatened Species status is summarized by percentage of Critically Endangered (CR) and threatened species (CR, Endangered, and Vulnerable) (IUCN 2024). See Table S1 in the Supplement at www.int-res.com/articles/suppl/n055p129_supp.pdf for a full list of species and status

Family	Species diversity	IUCN Red List status
Pristidae (sawfishes)	5 (7.4%)	CR: 100% Threatened: 100%
Trygonorrhinidae (banjo rays)	8 (11.8%)	CR: 0% Threatened: 37.5%
Glaucostegidae (giant guitarfishes)	7 (10.3%)	CR: 100% Threatened: 100%
Rhinidae (wedgefishes)	11 (16.2%)	CR: 90.9% Threatened: 90.9%
Rhinobatidae (guitarfishes)	37[a] (54.4%)	CR: 28.6% Threatened: 65.7%
Total	68	CR: 48.5% Threatened: 72.7%

[a]Two rhinobatid species have not yet been evaluated against the IUCN Red List Categories and Criteria

Table 2. The world's top 10 most at-risk orders of vertebrate animals by percentage of assessed extant species listed as threatened (Critically Endangered, Endangered, Vulnerable) on the IUCN Red List of Threatened Species (IUCN 2024). Numbers of species include those that are extant and that have been assessed against the IUCN Red List Categories and Criteria. Therefore, the number of species may be lower than the total species richness (e.g. 2 rhino rays have not yet been assessed, giving 66 assessed species versus 68 total species; **bold** row). A full list of the status of all vertebrate orders can be found in Table S2

Rank	Class	Order	Number of assessed extant species	Number (%) of threatened species
1	Actinopterygii (ray-finned fishes)	Acipenseriformes (sturgeons and paddlefishes)	25	25 (100%)
2	Aves (birds)	Mesitornithiformes (mesites)	3	3 (100%)
3	Mammalia (mammals)	Pholidota (pangolins)	8	8 (100%)
4	Mammalia (mammals)	Sirenia (sea cows)	4	4 (100%)
5	Mammalia (mammals)	Proboscidea (elephants)	3	3 (100%)
6	Sarcopterygii (lobe-finned fishes)	Coelacanthiformes (coelacanths)	2	2 (100%)
7	Sarcopterygii (lobe-finned fishes)	Ceratodontiformes (Australian lungfishes)	1	1 (100%)
8	Mammalia (mammals)	Perissodactyla (odd-toed ungulates)	16	12 (75.0%)
9	**Chondrichthyes (cartilaginous fishes)**	**Rhinopristiformes (rhino rays)**	**66**	**48 (72.7%)**
10	Mammalia (mammals)	Primates (primates)	523	349 (66.7%)

Table 3. The world's top 10 most at-risk orders of vertebrate animals by percentage of assessed extant species listed as Critically Endangered (CR; at an 'extremely high risk of extinction') on the IUCN Red List of Threatened Species (IUCN 2024). Numbers of species include those that are extant and that have been assessed against the IUCN Red List Categories and Criteria. Therefore, the number of species may be lower than the total species richness (e.g. 2 rhino rays have not yet been assessed, giving 66 assessed species versus 68 total species; **bold** row). A full list of the status of all vertebrate orders can be found in Table S2

Rank	Class	Order	Number of assessed extant species	Number (%) of CR species
1	Actinopterygii (ray-finned fishes)	Acipenseriformes (sturgeons and paddlefishes)	25	17 (68.0%)
2	Sarcopterygii (lobe-finned fishes)	Coelacanthiformes (coelacanths)	2	1 (50.0%)
3	**Chondrichthyes (cartilaginous fishes)**	**Rhinopristiformes (rhino rays)**	**66**	**32 (48.5%)**
4	Mammalia (mammals)	Monotremata (monotremes)	5	2 (40.0%)
5	Mammalia (mammals)	Pholidota (pangolins)	8	3 (37.5%)
6	Chondrichthyes (cartilaginous fishes)	Squatiniformes (angel sharks)	23	8 (34.8%)
7	Mammalia (mammals)	Proboscidea (elephants)	3	1 (33.3%)
8	Reptilia (reptiles)	Crocodylia (crocodiles)	23	7 (30.4%)
9	Reptilia (reptiles)	Testudines (turtles)	264	68 (25.8%)
10	Mammalia (mammals)	Perissodactyla (odd-toed ungulates)	16	4 (25.0%)

molecular ecology, fisheries, trade, and *ex situ* breeding. Key recommendations for each topic are provided in Table 4.

3.3.1. Status

Assessments of extinction risk provide an understanding of the vulnerabilities of species and help to identify conservation priorities. A comparison between all 136 vertebrate orders shows that rhino rays rank in the top 10 orders in terms of proportion of threatened species, and in the top 3 in terms of proportion of CR species. In most cases, threatened assessments for rhino rays are based on Red List Criterion A (the population reduction criterion), which requires some measure of population trend (this can be observed, estimated, inferred, or suspected) and a generation length of the species over which trend can be measured (IUCN 2012). Such details are generally lacking for most rhino rays (e.g. Kyne et al. 2020).

Priority research areas to accurately assess the status of rhino rays include the collection of time-series data to estimate trend, which should be species-specific and long-term, and ageing studies to determine generation length (see Section 3.3.3). Six rhino rays are currently assessed as DD (Table S1 in the Supplement at www.int-res/articles/suppl/n055p129_supp.pdf), where there is insufficient information available to accurately assess status (IUCN 2012).

Table 4. Research priority recommendations across 8 key fields of rhino ray research. SNPs: single nucleotide polymorphisms

Field of research	Recommendations
Status	• Collect species-specific data on population trends • Estimate generation lengths for applying the IUCN Red List population decline criterion • Gather data on Data Deficient and Not Evaluated rhino rays to allow an accurate assessment of extinction risk • Reassess the status of all species regularly (every 10 yr)
Taxonomy	• Clarify unresolved taxonomy, especially amongst the genera *Acroteriobatus*, *Glaucostegus*, *Pseudobatos*, *Rhinobatos*, and *Rhynchobatus* • Describe new species as they are identified • Revise historical species descriptions to incorporate sexual dimorphism and changes with ontogenetic growth, where necessary • Improve species-specific identification, especially defining key diagnostic characters to separate morphologically similar species (including in the field)
Life history	• Collect species-specific life history information across size classes (where not detrimental to the population) • Ensure accurate species identification (using molecular tools) to avoid confounding effects of species complexes on biological parameters • Verify the periodicity of growth band pair formation and validation of age estimates • Investigate the use of non-lethal sampling techniques for reproductive examination and emerging techniques for ageing
Habitat	• Identify critical habitats for different life stages, prioritizing key reproductive habitats (e.g. nursery areas) • Employ tagging and telemetry studies to understand habitat use and movement ecology • Understand benthic fauna composition in critical habitats to identify prey sources including their seasonality • Assess rhino ray use of poorly known habitats particularly shallow flat habitats of the intertidal zone, sandbanks, sandy and muddy substrates, and seagrass beds
Molecular ecology	• Prioritize collaborative sample collection to build comprehensive sample sets for research projects • Utilize next-generation sequencing technologies, SNPs, and multi-marker approaches to assess population genetics • Include environmental variables in assessments of adaptive molecular variation • Adopt multidisciplinary strategies that integrate direct approaches with genetic methods, including using traditional morphological taxonomy alongside molecular-based methods
Fisheries	• Improve fisheries data collection by increasing taxonomic resolution to species level and accurately quantifying fishing effort • Implement science-based species-specific regulations (i.e. limiting fishing effort or catch in directed fisheries and releasing catch in bycatch fisheries) • Develop safe release methods and assess post-release survivorship through tagging and physiological studies • Improve the selectivity of fishing practices and/or implement bycatch mitigation measures, especially in coastal gillnet and trawl fisheries • Identify critical habitats to prioritize area-based fisheries management
Trade	• Describe species-specific trade using multi-disciplinary approaches integrating social science, biological, and economic methods along with product tracking technology • Understand drivers of demand (e.g. consumption) of rhino ray products • Identify and characterize domestic and international supply/value chains and how these change in response to variation in supply/value chains of other resources (e.g. sharks) • Define the socio-economic and geo-political contexts in which trade is undertaken, including livelihood values
Ex situ breeding	• Investigate the potential role of aquaria in *ex situ* breeding of the most at-risk rhino ray species • Develop husbandry protocols to assist in future collection, transport, housing, and release needs • Characterize gestation periods through ultrasonography and endocrinology • Identify breeding seasonality and frequency (e.g. annual or biennial) to understand reproductive potential • Develop standardized protocols for artificial insemination procedures including semen collection, transportation, and storage

Based on the global status of conspecific species, it is to be expected that some of these species are threatened. Research and data collection specific to these DD species is therefore a priority so that they can accurately be assessed. A further 2 species (Malagasy blue-spotted guitarfish *Acroteriobatus andysabini* and Socotra blue-spotted guitarfish *A. stehmanni*) have not yet been assessed against the IUCN Red List Categories and Criteria, and undertaking research to understand and accurately assess their status is a priority. Lastly, IUCN Red List assessments are valid for 10 yr, such that timely reassessments are required for all species on an ongoing basis. This will serve to monitor status, detect where species are becoming more at risk, and identify where conservation successes are resulting in improvements in status (although it is acknowledged that recovery may be prolonged in rhino rays; e.g. D'Alberto et al. 2019).

3.3.2. Taxonomy

Taxonomic issues, including misidentification and unidentified species, can severely hinder conservation and management efforts (Johri et al. 2020). Rhino rays can be especially difficult to distinguish from one another, and several undescribed species likely exist (Jabado 2018). In the southwestern Indian Ocean specifically, 3 species of *Rhinobatos* were often misidentified and confused, hindering efforts to study their life history and limiting species-specific monitoring in fisheries (Ebert & Gon 2017, Aitchison et al. 2024). Clarification of the taxonomic status of these species will aid in identification, leading to improvements in fisheries monitoring and management (Aitchison et al. 2024). Several species, for example in the genera *Acroteriobatus*, *Glaucostegus*, and *Rhynchobatus*, remain poorly understood with vague original descriptions, hindering species-specific identification and management.

A concerted effort is required to clarify the taxonomic status of rhino rays, including describing new species. Priority should be given to species in need of taxonomic revision with the greatest extinction risk (CR species, e.g. *R. djiddensis*) with specimens of both sexes incorporated to capture sexual dimorphism, and changes associated with ontogenetic growth, which is present in some rhino ray species, but generally poorly understood within the order (Last et al. 2019, Aitchison et al. 2024). In addition, key characteristics should be determined to aid rapid field identification at landing sites and fish markets, including where only part of the fish may be available for examination. Some characteristics that appear promising include nasal lamellae counts, coloration, and thorn patterns (Aitchison et al. 2024). Complementary morphological and molecular tools can be used alongside each other to aid identification, although for the latter, the importance of verified reference material is critical (Giles et al. 2016). Comprehensive species descriptions and reliable field diagnosis would not only improve identification of these species relative to one another for monitoring and management, but also provide a taxonomic foundation for life history, habitat, and molecular studies.

3.3.3. Life history

An understanding of basic life history (age, growth, and reproduction) is lacking for many rhino rays, and there is a need for better life history information across the group. For *R. australiae* in Southeast Asia, slow growth and an estimated extended theoretical longevity (to 47 yr) (D'Alberto et al. 2024) highlights the 'conservative' life history pattern generally characteristic of cartilaginous fishes (Musick 1999). Generating life history information for threatened and rare species, such as many rhino ray species, can be difficult. Studies rely on lethal techniques to assess reproductive state and obtain vertebrae for ageing, but the removal of individuals for scientific research may pose a threat to some populations (Heupel & Simpfendorfer 2010, Awruch et al. 2021). Collection of samples for threatened species often relies on opportunistic sampling, such as from fish markets, which can be biased due to the size selectivity of the fishing gear (e.g. White & Dharmadi 2007). Further, exact collection locations of examined specimens (i.e. the fishing grounds) are not readily available. Regardless, accurate life history estimates and the quantifiable uncertainty around them is critical to understand rhino ray species biology and population dynamics, and ultimately for developing effective science-based management and conservation strategies.

Priority research areas to accurately generate life history information for rhino rays include the collection of species-specific age, growth, and reproductive data, particularly across all size classes. When undertaking life history studies, species identification should be confirmed through genetic analysis due to potential misidentification (see Section 3.3.2). Verification of growth band periodicity and/or validation of ages should be important priorities and will assist with the confirmation of age estimates, thereby reducing uncertainty in growth rate estimates (Cailliet et al. 2006). Crucial reproductive information, particularly for larger size classes, is missing for most species, including estimated length- and/or age-at-maturity, litter size, gestation period, and reproductive periodicity. The feasibility of applying non-lethal techniques for assessing reproductive information (e.g. concentrations of sex steroids and ultrasonography) (Matsumoto et al. 2023) and development of emerging ageing techniques such as epigenetic ageing (Mayne et al. 2019) should be investigated for rhino rays.

3.3.4. Habitat

Understanding rhino ray habitat can assist in identifying threatening processes and priority areas for conservation. The majority of species occupy inshore waters of the coastal zone and the continental shelf at depths of <100 m, with smaller numbers occurring on the outer continental shelf and upper slope, and in estuarine and riverine environments (Last et al. 2016). Rhino rays are predominantly benthic, although a few reports have documented rhino rays swimming in mid-water (Forget & Muir 2021, Bruns et al. 2024). They are mostly associated with sandy or muddy substrates, seagrass beds, mangroves, and coral reefs, and often occupy different habitats at different life stages. Their inshore habitats can be subject to degradation and loss, for example, in Abu Dhabi, UAE, where a notable abundance of *G. halavi* were recorded in an area undergoing intense development (Al Hameli et al. 2024).

Habitat occupancy and use can be evaluated by descriptive habitat assessments, tagging and telemetry studies, and species distribution modelling. Habitat information for most non-sawfish rhino rays is rudimentary and generally broad. The identification of critical habitats is a priority for most species including documenting nursery areas, which can be inshore and overlap with fishing and development pressures. The identification of potential hotspots through landing site surveys can direct research towards where critical habitats may occur (e.g. African wedgefish *R. luebberti*; Doherty et al. 2023). Tagging and telemetry studies can be employed to understand habitat use and movement ecology including seasonal and ontogenetic changes in habitat use. Understanding benthic fauna composition in critical habitats can identify prey sources, ensuring an ecosystem-level picture of habitat. Finally, some key habitats have had little research into their use by rhino rays, particularly shallow flat habitats of the intertidal zone, sandbanks, sandy and muddy substrates, and seagrass beds.

3.3.5. Molecular ecology

Molecular analyses can underpin studies on taxonomy, genetic diversity, population structure, trade monitoring, and surveys (e.g. environmental DNA or eDNA). The application of genetic methods to the non-sawfish rhino rays has been fairly limited to date (e.g. Giles et al. 2016), with considerable opportunities and needs in the above-mentioned topics. Molecular studies often encounter sampling bias, may be limited by sample size, or are based on single genetic markers while a multi-marker approach is preferred (Aschliman et al. 2012). In the western Indian Ocean, a biodiverse region for rhino rays, a dual marker approach (mitochondrial and nuclear) was applied to *R. australiae* and *R. djiddensis* which aided in taxonomic classification, identifying areas with higher-risk populations (i.e. low levels of genetic diversity) and unique genetically distinct conservation units (Groeneveld et al. 2024).

Future studies should focus on acquiring an extensive sample size and consider leveraging collaborative sample-sharing platforms to improve statistical robustness. The use of next-generation sequencing technologies can further enhance the resolution of studies involving non-model organisms, such as rhino rays (Maduna et al. 2017, Pearce et al. 2021). There is a shift towards using single nucleotide polymorphisms (SNPs) for assessing population genetics due to their superior reproducibility (DeFaveri et al. 2013, Zimmerman et al. 2020), highlighting the need to develop SNP panels for rhino rays. Some marine species are displaying shifts in geographic range, and these are projected to increase due to climate change (Blamey et al. 2015). Genome-wide assessments of adaptive variation would be beneficial to better understand the influence of environmental variables on rhino ray molecular profiles, which can aid in predicting responses to new selective challenges. A multidisciplinary strategy that integrates direct approaches, such as movement studies, with genetic methods is imperative to thoroughly understand species distributions and processes that shape patterns of genetic variation. Lastly, the persistent issue of taxonomic uncertainty also necessitates the combined use of traditional morphological taxonomy alongside molecular-based methods (see Section 3.3.2).

3.3.6. Fisheries

The main threat to rhino rays is overexploitation through generally unregulated and undermanaged targeted and incidental fisheries (Moore 2017, Jabado 2018, Pytka et al. 2024). Rhino rays mainly occur in shallow coastal and continental shelf waters (see Section 3.3.4). Thus, they are accessible to small-scale (i.e. artisanal) and large-scale (i.e. industrial) fisheries. Due to their primary distribution in tropical regions, most rhino ray species occur in countries with high levels of poverty and low levels of food security. Therefore, rhino rays can represent a valuable resource for coastal communities, although intensification of fishing coupled with limited management place this resource at risk. In many parts of the tropical oceans, fishing effort has been increasing through time, yet landings or catch rates have been decreasing, resulting in severe population reductions for some species (Kyne et al. 2020, Gonzalez-Pestana et al. 2024). Rhino rays may be consumed locally or exported to foreign markets (see Section 3.3.7), with local or international consumption being a driver of retention when caught. International trade is now regulated through the listing of sawfishes, wedgefishes, giant guitarfishes, and guitarfishes on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which, if effectively implemented, may improve status. However, CITES does not manage domestic exploitation or trade. For example, in Peru, *P. planiceps* is severely depleted due to historical local consumption with no evidence of international trade (Gonzalez-Pestana et al. 2024).

Data collection at the species level can improve the sustainable management of target and bycatch species. Catch monitoring at the finest possible taxonomic resolution is essential to estimate abundance and trends (for which data on fishing effort is also needed). This information can feed into stock assessments for exploited species to guide catch quotas and other regulations. For threatened species, safe release after capture is imperative to permit recovery. Research is therefore needed on safe release methods that improve both survivorship and crew safety, and on post-release survivorship through tagging and physiological studies. As most rhino rays are captured by gillnet and trawl (Pytka et al. 2024), researching more selective fishing practices and/or bycatch mitigation measures is vital. For area-based fisheries management, identifying critical habitats (see Section 3.3.4) can guide the delineation of important areas for the conservation of species (e.g. Important Shark and Ray Areas; Hyde et al. 2022).

3.3.7. Trade

Trade in rhino ray products has been documented extensively across the world and reported from several continents including the Americas (e.g. Brazil; Alvarenga et al. 2021), Asia (e.g. Singapore; Choy et al. 2022), and Africa (e.g. Ghana; Seidu et al. 2022). International trade is now regulated for all rhino ray families except banjo rays through their CITES listings, while domestically, only a few countries have implemented national protections for some species (e.g. Bangladesh; see Haque et al. 2021). Domestic trade, particularly to meet food security needs in impoverished coastal communities, needs to be examined within the larger context of declining marine fisheries. As larger-bodied rhino ray species are depleted, retention and trade has increased amongst smaller-bodied species, such as guitarfishes. While a variety of rhino ray products are traded, including fins, meat, and emerging products (e.g. jewellery made from *Rhina ancylostomus* thorns; Pytka et al. 2023), trade is poorly documented with little traceability. India, for instance, does not report rhino ray trade and fishing statistics to the UN Food and Agriculture Organization (FAO), possibly because rhino rays are considered bycatch and are primarily used for local consumption rather than global trade (Karnad et al. 2024). In countries such as India, sawfishes, wedgefishes, and giant guitarfishes used to be targeted for trade, but with steep population declines, catches and trade have reportedly decreased (Karnad et al. 2024).

Rhino ray products such as meat, fins, and skin traverse a diversity of supply chains (including online marketplaces) in local and international trade (Haque & Spaet 2021, Seidu et al. 2022, Gupta et al. 2023, Pytka et al. 2023). Much of the research on rhino ray trade has been qualitative and restricted to limited geographic case studies. Further research is needed to examine exactly which species continue to be most affected by trade, the drivers of this trade, and what trade pathways/supply chains the products traverse in order to develop species- and context-specific conservation strategies. This research should utilize multidisciplinary approaches, including integrating social science, biological, and economic methods with product tracking technologies (e.g. forensics, monitoring of online trade including tracking of the black market) or tools to describe and understand trade. Understanding the underlying drivers behind trade, particularly where rhino rays are integrally part of local socio-economic systems or used for subsistence-level trade, are key to inform more participatory conservation approaches.

3.3.8. *Ex situ* breeding

Conservation-based breeding programs managed by the international zoo and aquarium industry are well-recognized methods for supporting the future viability of threatened species. Establishing a species-specific breeding program is a multifaceted endeavour which relies upon an in-depth understanding of the reproductive biology and breeding behaviour of species. The majority of chondrichthyan reproductive behaviours reported in the literature have been observed and characterized *ex situ* rather than *in situ* (Henningsen et al. 2004). Ethograms (a catalogue of behaviours) characterizing a species' reproductive actions can serve as the foundational knowledge for the establishment of a successful breeding program. Current *ex situ* management of *R. ancylostomus* has allowed for the observation and identification of this species' otherwise rarely witnessed reproductive behaviours (Hanna et al. 2024). Almost 5 yr of *ex situ* ethogram data on the breeding behaviours of this species have been collected and analyzed in support of a global initiative on *ex situ* conservation of the species ('Shark Ray 360'; Abel et al. 2024, Hanna et al. 2024).

Zoos and aquaria are well placed to support future *ex situ* breeding of the most at-risk rhino ray species. To facilitate this, standardized husbandry and reintroduction protocols are needed to assist future collection, transport, housing, and release needs. Further research utilizing ultrasonography and endocrinology to characterize gestational periods within rhino rays is also a priority. The identification of breeding seasonality and gestational periods would aid in the understanding of reproductive cycles, *ex situ* breeding, and animal care procedures concerning delivery and care of pups. The use of artificial insemination (AI) with large animal species has been successfully undertaken in sharks and rays (e.g. Adams et al. 2022) and has been identified as a region for further development for large rhino rays such as *R. ancylostomus*. Clarification of best practices for collection and storage of semen is an identified need in this area. Eventually, in combination with other data from ultrasonography, endocrinology, and seasonality, this research can inform successful AI reproduction. These research aspects are some of the necessary components to successfully manage and ensure the genetic diversity of a species where the ultimate goal is *in situ* reintroduction.

4. CONCLUSION

Rhino rays are among the most threatened groups of vertebrates on the planet. The proportion of Critically Endangered species (those facing an 'extremely high risk of extinction'; IUCN 2012) ranks only below sturgeons and paddlefishes, and coelacanths. Rhino rays as a group are at higher extinction risk levels than many charismatic animal groups, such as primates, carnivores (order Carnivora), and penguins (order Sphenisciformes) (Table S2), yet the deficiency in rhino ray research, monitoring, and management investment is likely to lead to species loss. Managing the complexities of high intrinsic susceptibility, under-regulated and under-managed exploitation and trade, and the livelihood needs of coastal communities, will require a significant commitment to rhino ray conservation and management. The papers published in this Special Issue are examples of the type of research needed across this group. Future investment in these types of studies and the research priority recommendations put forward in this overview article will strengthen the information base upon which to make conservation and management decisions.

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