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Ghosts of the deep – Biodiversity, fisheries, and extinction risk of ghost sharks

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Abstract

Ghost sharks (subclass Holocephali) remain a largely data-poor group of cartilaginous fishes. The general paucity of attention may partially be related to identification and unresolved taxonomic issues, occurrence in the deep oceans, and their low value and interest in fisheries (which some notable exceptions). Here, we synthesize and assess the extinction risk of all known extant ghost sharks (52 species) by applying the IUCN Red List of Threatened Species Categories and Criteria. Ghost sharks have a low proportion of threatened (8%) and Near Threatened (8%) species, with most species (69%) assessed as Least Concern. The group still exhibits some data deficiency (15%), and biological information is lacking for most species. Endemism is high, with 37% of species known from only one location or one country. Species richness was highest in the Northeast Atlantic, off the northwest coast of Africa (Morocco to Mauritania), the East China Sea, New Zealand and off the northwest coast of South America (Ecuador and Peru). Ghost sharks are predominately taken as by-catch, but some targeted fishing and/or retention for the liver oil trade occurs. Species-specific reporting, monitoring and management are required to assess population trends, and further investigation is needed on trade and use, particularly for higher risk species including the sicklefin chimaeras (genus *Neoharriotta*) and the American Elephantfish (*Callorhynchus callorhynchus*, Callorhinidae).

KEYWORDS

by-catch, chimaera, chondrichthyan, data deficiency, holocephali, IUCN Red List, liver oil, sustainable fisheries

1 | INTRODUCTION

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There is an increasing urgency to better understand and monitor anthropogenic impacts on the marine environment and marine species as reliance on marine resources continues to grow and species status worsens (Visbeck, 2018). Chondrichthyans (sharks, rays and ghost sharks) are no exception, and there is an ever-growing body of scientific literature and public interest dedicated to understanding, conserving, and managing this class of fishes (Simpfendorfer et al., 2011). In recent decades, interest in chondrichthyans and concern for their plight and the paucity of conservation has resulted in the implementation of some regional and global trade and fisheries management, and conservation measures (Friedrich et al., 2014). However, of the ~1,250 cartilaginous species (Fricke, Eschmeyer, & Fong, 2020), research efforts have largely focused on a select number of larger and more charismatic shark and ray species (Shiffman et al., 2020). This lack of attention is especially true for species that live in the deep ocean, where most species are data poor (Kyne & Simpfendorfer, 2007).

One oft-overlooked group is the ghost sharks (subclass Holocephali) that, together with the Elasmobranchii (sharks and rays), comprise the class Chondrichthyes—one of the three taxonomic classes of fishes. Ghost sharks are the oldest radiation of fishes and vertebrates, with a median evolutionary distinctiveness of 40 million years (compared to an average of 26 million years across all chondrichthyans) (Stein et al., 2018). They are referred to by a range of common names, including ghost shark, chimaera, rabbitfish, ratfish or spookfish. Ghost sharks comprise three families, distinguished by their snout morphology: Callorhinchidae (plow-nosed chimaeroids), Chimaeridae (short-nosed chimaeroids) and Rhinochimaeridae (long-nosed chimaeroids) (Figure 1). Ghost sharks are globally distributed with the exception of the highest latitudes. Despite their widespread global occurrence, many have surprisingly restricted geographic ranges and the lineage has a high degree of endemism (Didier et al., 2012). Ghost sharks are mostly deepwater species apart from members of the family Callorhinchidae, which are found along the coastal waters of southern Africa, South America and Australia and New Zealand (hereafter called Australasia) (Kyne & Simpfendorfer, 2007). They inhabit depths down to 3,000 m and hence are among the deepest recorded chondrichthyans (Priede & Froese, 2013). Almost half (23 of 52) of ghost shark species have been described since 2002 and these have been mostly from the Indo-Pacific Oceans (Didier et al., 2012; Last & Stevens, 2009; White & Kyne, 2010). Additional species continue to be described due to renewed interest, continued exploration of the deep ocean and increased taxonomic resolution (e.g. Clerkin et al., 2017).

The deep-dwelling and offshore distributions of ghost sharks have meant they have not been readily accessible to fisheries to the same extent as shelf-dwelling sharks and rays. Ghost sharks were estimated to make up <1% of the total global chondrichthyan catch between 1950 and 2009 (Dulvy et al., 2014). Nevertheless, ghost sharks are increasingly captured, as both targeted catch and by-catch, in many coastal and deepwater fisheries (e.g. da Silva et al., 2015; Jabado et al., 2017; White et al., 2009). They are increasingly retained and processed for their flesh, liver oil and fishmeal, and very low quantities of ghost shark fins are also present in the fin trade (Fields et al., 2018). The species in this trade identified by genetic analyses are species with active fisheries management, suggesting these fins are most likely a by-product of retention for meat/flesh and liver oil.

The potential for overfishing is considerable in some cases. Ghost sharks can contribute to a considerable proportion of unintentional catch of deepwater and coastal fisheries. For example, Rabbitfish (*Chimaera monstrosa*, Chimaeridae) accounted for up to 15% of discards in deepwater trawls off Ireland (Calis et al., 2005), and the White-spotted Chimaera (*Hydrolagus colliei*, Chimaeridae) was reported in 70% of inshore tows in the groundfish fishery of the U.S. west coast between 2002 and 2009 (Heery & Cope, 2014). Ghost sharks are caught in artisanal, industrial and recreational demersal gears including longlines, trawls, trammel nets and gillnets (e.g. Braccini et al., 2009; ICES-WGEF, 2018; White et al., 2009). Three ghost shark fisheries, the Australian and New Zealand Elephantfish (*Callorhinchus milii*, Callorhinidae) and the New Zealand Pale Ghostshark (*Hydrolagus bemisi* Chimaeridae), have been recognized globally as some of the more sustainable and well-managed shark fisheries (Simpfendorfer & Dulvy, 2017). For most species, however, catches are discarded, not reported or reported under a generic fisheries code (e.g. *Hydrolagus* spp.) (Bustamante, 1997; ICES-WGEF, 2018). Consequently, this lack of catch reporting reduces our ability to assess population trends at the species level and implement management actions where required. A lack of species-specific

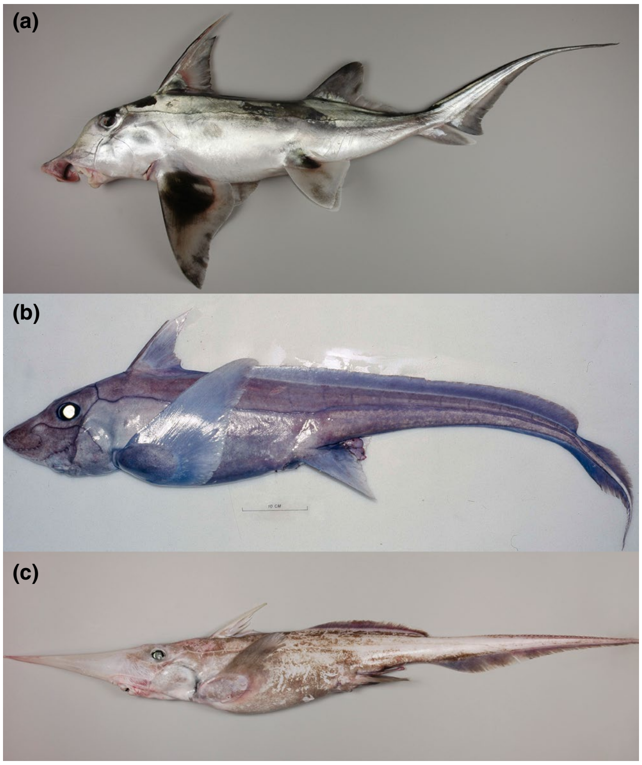

FIGURE 1 Representative species from each ghost shark family: (a) Elephantfish (*Callorhinchus milii*, Callorhinchidae); (b) Pointy-nosed Blue Chimaera (*Hydrolagus trolli*, Chimaeridae); and (c) Pacific Longnose Chimaera (*Rhinochimaera pacifica*, Rhinochimaeridae). Photo credits to P. Marriott/NIWA [Colour figure can be viewed at wileyonlinelibrary.com]

catch reporting data can mask declines, and even local extinctions as has been well-characterized in skates (family Rajidae) of the North Atlantic (Dulvy et al., 2000).

Compared to many other at-risk chondrichthyan lineages, ghost sharks have been considered among the least threatened species group but also the most data deficient (~60% of ghost sharks assessed; Dulvy et al., 2014). This high level of data deficiency raises the concern that species may be at some risk of local overfishing and global extinction, and this risk is going unnoticed, unmonitored and unmanaged. Here, we assess the threat status based on the combination of distribution, habitat and ecology, population trends, threats, and use and trade of all ghost sharks. We present the first Red List reassessment for an entire subclass of chondrichthyans, including a global synthesis of major threats and the revised extinction risk statuses for all holocephalan species. We present future research and management directions to: address priority knowledge gaps, promote sustainable fisheries, while ensuring the long-term survival of the oldest extant radiation of fishes.

2 | MATERIALS AND METHODS

We define the species to be included in this synthesis and the data collation process, the application of the IUCN Red List of Threatened Species Categories and Criteria in assessing extinction risk, and the mapping of species distributions.

2.1 | Species list and data collation

A two-day workshop was held in June 2018 in João Pessoa, Brazil and conducted by four experts and members of the IUCN Species Survival Commission Shark Specialist Group (IUCN SSC SSG) to review and assess the status of ghost shark species. We reviewed all available information on taxonomy, geographic range, population, habitat and ecology, use and trade, threats, and conservation actions for each species. This information was collated from scientific journal publications, published reports (e.g. fisheries-independent research surveys, stock assessments, indicator analyses), government and agency reports (e.g. National Plan of Action-Sharks, FAO guidebooks), unpublished fisheries data and expert observations. Thirty-four of the 52 recognized species were assessed at the workshop in Brazil (D.A. Ebert, unpublished data). Additional species, recently assessed as part of regional workshops focusing on the Northeast Pacific held in 2014–2015 (one species, Ebert et al., 2017), the European Union in 2014 (three species, Fernandes et al., 2017), Australia in 2015 (10 species, Simpfendorfer et al., 2017), the United Arab Emirates in 2017 (one species, Jabado et al., 2017) and New Zealand in 2017 (three species, Finucci et al., 2019) were incorporated into the global synthesis described here. Of these, the statuses of three species were reassessed to ensure consistency in the application of the IUCN Red List Categories and Criteria.

2.2 | IUCN Red List Categories and Criteria

The IUCN Red List Categories and Criteria (Version 3.1) (IUCN, 2012; IUCN Standards & Petitions Subcommittee, 2017) were applied to each ghost shark at the global level. Each species was assessed against each of five quantitative criteria A-E: Criterion A, population size reduction; B, geographic range; C, small population size and decline; D, very small or restricted population; and E, quantitative analysis (e.g. a population viability analysis indicating a probability of extinction). Ghost sharks did not meet any of the Criteria B, C, D or E, and we were unable to provide evidence of restricted geographic range, a small population size, presence of a very small or restricted population or to support a fully quantitative assessment. Some species did meet the geographic range threshold for Criteria B, but did not meet any two of the three sub-criteria. Thus, species were assessed only against Criteria A, where the rate of population size reduction was determined over the longer time frame of 10 years or three generations ("generation length" is defined as the average age of parents of the current cohort, i.e. newborn individuals in the population; IUCN Standards & Petitions Subcommittee, 2017). Generation lengths were estimated between 15 and 21.7 years (see Table 1), calculated from growth parameters from species-specific

TABLE 1 Summary of all ghost sharks assessed against the IUCN Red List of Threatened Species Categories and Criteria

Family	Species name	Authority	Common name	Red List Assessment	Depth range (m)	Maximum size (cm)	Female age-at-maturity; Longevity (years)*	Generation Length (years)	Source(s)
Callorhinchidae	*Callorhinchus callorhynchus*	(Linnaeus, 1758)	American Elephantfish	VU A2d	0–481	102	5–9; 28	17.5	Alarcón et al., 2011; Weigmann 2016
	Callorhinchus capensis	Duméril, 1865	St. Joseph	LC	0–600	120	4.2; 10	–	Freer & Griffiths, 1993; Weigmann 2016
	Callorhinchus milii	Bory de Saint-Vincent, 1823	Elephantfish	LC	0–227	125	4.5; 19	–	Francis, 1997; Weigmann 2016
Chimaeridae	*Chimaera argiloba*	Last, White & Pogonoski, 2008	Whitefin Chimaera	LC	370–520	91.2		–	Weigmann 2016
	Chimaera bahamaensis	Kemper, Ebert, Didier & Compagno, 2010	Bahamas Chimaera	LC	732–1,506	88.1		–	Weigmann 2016; FLMNH, 2019
	Chimaera buccanigella	Clerkin, Ebert & Kemper, 2017	Dark-mouth Chimaera	DD	495–960	86		–	Clerkin et al., 2017
	Chimaera carophila	Kemper, Ebert, Naylor & Didier, 2014	Brown Ghostshark	LC	846–1,350	103.5		–	Weigmann 2016
	Chimaera cubana	Howell Rivero, 1936	Cuban Chimaera	LC	180–1,050	80.3		–	Benavides et al., 2014; Weigmann 2016
	Chimaera didierae	Clerkin, Ebert & Kemper, 2017	Falkor Chimaera	DD	1,000–1,100	82.5		–	Clerkin et al., 2017
	Chimaera fulva	Didier, Last & White, 2008	Southern Chimaera	LC	780–1,095	118.7	18; 37	–	Bell, 2012; Weigmann 2016
	Chimaera jordani	Tanaka, 1905	Jordan's Chimaera	DD	716–780	93		–	Nakabo 2013
	Chimaera lignaria	Didier, 2002	Carpenter's Chimaera	LC	400–1,800	142	33; 40	–	Bell, 2012; Weigmann 2016
	Chimaera macrospina	Didier, Last & White, Didier, Last & White 2008	Longspine Chimaera	LC	435–1,300	103.4		–	Weigmann 2016
	Chimaera monstrosa	Linnaeus, 1758	Rabbitfish	VU A2bd	50–1,742	119	11.2; 30	21.7	Calis et al., 2005; Weigmann 2016
	Chimaera notafricana	Kemper, Ebert, Compagno & Didier, 2010	Cape Chimaera	LC	680–1,000	93		–	Kemper et al. 2010; Weigmann 2016
	Chimaera obscura	Didier, Last & White 2008	Shortspine Chimaera	LC	450–1,080	95.1		–	Didier, Last & White 2008; Weigmann 2016

(Continues)

TABLE 1 (Continued)

Family	Species name	Authority	Common name	Red List Assessment	Depth range (m)	Maximum size (cm)	Female age-at-maturity; Longevity (years)*	Generation Length (years)	Source(s)
	Chimaera ogilbyi	Waite 1898	Ogilby's Ghostshark	NT	139–872	104	28; 41	18.6	Bell, 2012; Finucci, White, et al., 2018
	Chimaera opalescens	Luchetti, Iglésias & Sellos, 2011	Opal Chimaera	LC	800–1,975	109.8		–	Weigmann 2016; Freitas et al. 2017
	Chimaera orientalis	Angulo, López, Bussing & Murase, 2014	Eastern Pacific Black Chimaera	DD	560–1,138	85.8		–	Weigmann 2016
	Chimaera owstoni	Tanaka, 1905	Owston's Chimaera	DD	650–900	80		–	Nakabo 2013
	Chimaera panthera	Didier, 1998	Leopard Chimaera	LC	327–1,020	129		–	Weigmann 2016
	Chimaera phantasma	Jordan & Snyder, 1900	Silver Chimaera	VU A2d	20–962	110		18.6	Weigmann 2016
	Chimaera willwatchi	Clerkin, Ebert & Kemper, 2017	Seafarer's Ghostshark	DD	89–1,365	97		–	Clerkin et al., 2017
	Hydrolagus affinis	(de Brito Capello, 1868)	Smalleyed Rabbitfish	LC	293–2,909	147		–	Weigmann 2016
	Hydrolagus africanus	(Gilchrist, 1922)	African Rabbitfish	LC	303–1,570	98.4		–	Weigmann 2016
	Hydrolagus alberti	Bigelow & Schroeder, 1951	Gulf Chimaera	LC	328–1,470	100	9–19; 12–23	–	Weigmann 2016; Hannan, 2016
	Hydrolagus alphus	Quaranta, Didier, Long & Ebert, 2006	Whitespot Ghostshark	LC	630–907	48		–	Weigmann 2016
	Hydrolagus barbouri	(Garman, 1908)	Ninespot Chimaera	DD	250–1,100	86		–	Weigmann 2016
	Hydrolagus bemisi	Didier, 2002	Pale Ghostshark	LC	400–1,100	111.5	Attempted but no estimates given	–	Francis & Ó Maolagáin, 2000; Weigmann 2016
	Hydrolagus colliei	(Lay & Bennett, 1839)	White-spotted Chimaera	LC	0–1,029	60	14; 21	–	King & McPhie, 2015; Weigmann 2016
	Hydrolagus erithacus	Walovich, Ebert & Kemper, 2017	Robin's Ghostshark	DD	470–1,000	140		–	Walovich et al., 2017
	Hydrolagus homonycteris	Didier, 2008	Black Ghostshark	LC	400–1,450	108.5		–	Weigmann 2016

(Continues)

TABLE 1 (Continued)

Family	Species name	Authority	Common name	Red List Assessment	Depth range (m)	Maximum size (cm)	Female age-at-maturity; Longevity (years)*	Generation Length (years)	Source(s)
	Hydrolagus lusitanicus	Moura, Figueiredo, Bordalo-Machado, Almeida & Gordo, 2005	Portuguese Chimaera	LC	1,600	117.7		–	Weigmann 2016
	Hydrolagus macrophthalmus	de Buen, 1959	Bigeye Chimaera	LC	300–1,370	63.6		–	Jew et al. 2019
	Hydrolagus marmoratus	Didier, 2008	Marbeled Ghostshark	LC	548–995	80.1		–	Weigmann 2016
	Hydrolagus matallanasi	Soto & Vooren, 2004	Striped Rabbitfish	VU A2d	416–736	69.5		18.6	Weigmann 2016
	Hydrolagus mccoskeri	Barnett, Didier, Long & Ebert, 2006	Galapagos Ghostshark	LC	396–506	38.1		–	Weigmann 2016
	Hydrolagus melanophasma	James, Ebert, Long & Didier, 2009	Eastern Pacific Black Ghostshark	LC	30–1,800	128		–	James et al. 2009; Araya et al. 2020
	Hydrolagus mirabilis	(Collett, 1904)	Large-eyed Rabbitfish	LC	450–2,058	84		–	Weigmann 2016
	Hydrolagus mitsukurii	(Jordan & Snyder, 1904)	Mitsukuri's Chimaera	NT	325–830	79	15 (longevity)	15	Tseng, 2011; Weigmann 2016
	Hydrolagus novaezealandiae	(Fowler, 1911)	New Zealand Chimaera	LC	25–950	96	Attempted but no estimates given	–	Francis & Ó Maolagáin, 2000; Weigmann 2016
	Hydrolagus pallidus	Hardy & Stehmann, 1990	Pale Chimaera	LC	883–2,650	137.6		–	Weigmann 2016
	Hydrolagus purpurescens	(Gilbert, 1905)	Purple Chimaera	LC	920–1,951	138		–	Weigmann 2016
	Hydrolagus trolli	Didier & Séret, 2002	Pointy-nosed Blue Chimaera	LC	612–2,000	120.4		–	Weigmann 2016
Rhinochimaeridae	*Harriotta haeckeli*	Karrer, 1972	Smallspine Chimaera	LC	1,114–2,603	74		–	Weigmann 2016
	Harriotta raleighana	Goode & Bean, 1895	Narrownose Chimaera	LC	350–2,600	120		–	Weigmann 2016
	Neoharriotta carri	Bullis & Carpenter, 1966	Caribbean Chimaera	NT	90–600	120		15	Weigmann 2016; García et al. 2017; O. Lasso-Alcalá, unpubl. data, 2019

(Continues)

TABLE 1 (Continued)

Family	Species name	Authority	Common name	Red List Assessment	Depth range (m)	Maximum size (cm)	Female age-at-maturity; Longevity (years)*	Generation Length (years)	Source(s)
	Neoharriotta pinnata	(Schnakenbeck, 1931)	Sicklefin Chimaera	NT	150–760	147		15	Weigmann 2016; Diez & Mugerza, 2017
	Neoharriotta pumila	Didier & Stehmann, 1996	Dwarf Chimaera	LC	100–1,120	72.8		–	Weigmann 2016
	Rhinochimaera africana	Compagno, Stehmann & Ebert, 1990	Paddlenose Chimaera	LC	430–1,450	150		–	Weigmann 2016
	Rhinochimaera atlantica	Holt & Byrne, 1909	Atlantic Longnose Chimaera	LC	400–1,849	141		–	Weigmann 2016
	Rhinochimaera pacifica	(Mitsukuri, 1895)	Pacific Longnose Chimaera	LC	191–1,290	130	21; 25	–	Bell, 2012; Weigmann 2016

age and growth estimates (American Elephantfish, *Callorhinchus callorhynchus*, Callorhinchidae) or derived from Calis et al. (2005) and scaled to species' size.

Some species were assessed for the first time and were considered Not Evaluated (NE) prior to the workshop. At the workshop, species were assigned to one of eight IUCN Red List categories: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU) (collectively, CR, EN and VU are the "threatened" categories), Near Threatened (NT), Least Concern (LC), or Data Deficient (DD) (for definitions, see IUCN, 2012). Under Criteria A2, where the cause of population reduction (for ghost sharks this is fishing) has not ceased, is not understood, or may not be reversible, threatened categories are designated as follows: population reduction 30%–49% (Vulnerable); population reduction 50%–79% (Endangered); population reduction >80% (Critically Endangered) (IUCN, 2012). Near Threatened species exhibited some population reduction (20%–29%) and Least Concern species were those species where no population reduction was suspected or where population reduction was not approaching these thresholds.

The terms *observed*, *estimated*, *projected*, *inferred*, and *suspected* are used in the IUCN Red List of Threatened Species Categories and Criteria to describe the degree of uncertainty of the evidence used for specific criteria (IUCN Standards & Petitions Committee, 2017). These terms essentially describe the quality of data used to arrive at the assessments. Where population trend data are lacking, trend can be *inferred* based on changes in catch, landings or trade data, or *suspected* based on circumstantial evidence. An example of the latter is the qualitative degree of overlap between a species' geographic and depth range and the level of fishing effort; the premise being that complete overlap leaves little refuge from fishing-induced mortality, and "actual levels of exploitation" (from either directed fishing or by-catch) will drive the population to decline if mortality is greater than the population growth rate. See IUCN Standards and Petitions Committee (2017) for definitions and descriptions. This approach is similar to various forms of ecological risk assessment (Hobday et al., 2011).

The Data Deficient (DD) category is applied to taxa where there is inadequate information available to make an assessment of extinction risk (IUCN, 2012). If a species qualified for a change in status from a previously published assessment (a "down-listing" or "up-listing" in status), changes were classified as genuine (a change in extinction risk) or non-genuine (e.g. due to new information, or an error in the previous assessment) (IUCN Standards & Petitions Subcommittee, 2017). A precautionary attitude was considered as recommended for global assessments and the downstream consequences of species status were ignored to ensure an unbiased scientific determination of status without concern for subsequent management consequences (IUCN Standards & Petitions Subcommittee, 2017). Red List assessments were submitted to the IUCN Red List Unit for publication on the IUCN Red List of Threatened Species (http://www.iucnredlist.org/).

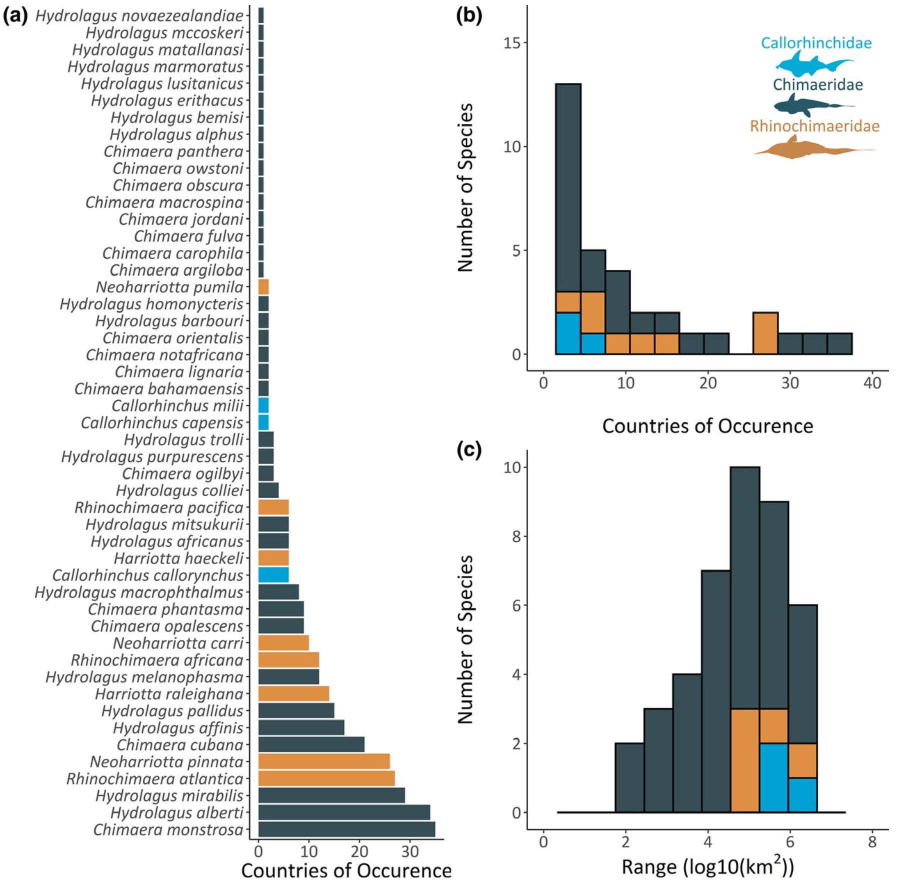

FIGURE 2 (a) The number of countries of occurrence by ghost shark species; (b) frequency of species occurrence by country, grouped by ghost shark family; and (c) frequency of species range (log10 (km^2)), grouped by ghost shark family. Ghost shark families: Callorhinchidae (blue), Chimaeridae (grey) and Rhinochimaeridae (brown). The three species of ghost sharks found in areas beyond national jurisdictions (Falkor Chimaera, [*Chimaera didierae*, Chimaeridae], Dark-mouth Chimaera [*Chimaera buccanigella*, Chimaeridae] and Seafarer's Ghost Shark [*Chimaera willwatchi*, Chimaeridae] are not included in (a) or (b). Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

2.3 | Species distribution and richness mapping

Individual distribution maps were refined from the previously published IUCN Red List Assessment or created for each ghost shark species. The geographic distribution of each species was refined to their known depth range based on the highest-resolution bathymetry dataset available at a global extent (15 arc seconds; GEBCO, 2019). A map of species richness counts (i.e. total number of species) was generated by overlaying each of the 52 species distribution maps and summing the number of extant species found in any one area of the global mapping region. We also mapped the individual distributions for the threatened (CR, EN, VU only) and NT species. All maps were created used ArcGIS Desktop 10.6 (ESRI, 2018).

3 | RESULTS AND DISCUSSION

We provide a global synthesis of contemporary knowledge of ghost sharks, with an updated revision of all IUCN Red List of Threatened Species assessments. There are 52 recognized ghost shark species across six genera, representing ~5% of chondrichthyan diversity. Ghost sharks have a low proportion of threatened (8%) and NT (8%) species, but still exhibit some data deficiency (15%). Several global ghost shark hotspots were identified, some of which also correspond to areas where ghost sharks are most threatened from fishing activities (e.g. East China Sea). We expand on the following key issues here, including (i) biodiversity, (ii) life-history traits and population connectivity, (iii) global spatial and depth distributions and hotspots, (iv) fisheries and international trade, (v) fisheries data availability and improving management, (vi) improving spatial protection, (vii) climate change, (viii) extinction risk and (ix) recommendations for future research focus.

3.1 | Taxonomic diversity

There has been considerable effort in recent years to describe new species and increase our understanding of ghost shark diversity but much needs to be done. Revisions of outdated taxonomic descriptions are required for those species where holotypes have been lost (e.g. *Chimaera monstrosa*), where detailed morphometric descriptions are not available (e.g. the Purple Chimaera *Hydrolagus purpurescens*, Chimaeridae), or where species complexes are suspected (e.g. Mitsukuri's Chimaera *Hydrolagus mitsukurii*¸ Chimaeridae). Ultimately, such revisions may change the recorded diversity of the group. To date, there are three species belonging to the family Callorhinchidae, 41 species belong to Chimaeridae, and eight species belong to Rhinochimaeridae. Taxonomic resolution is essential to reduce misidentification, a pattern observed regularly by the authors while producing this work. Improved identification will assist

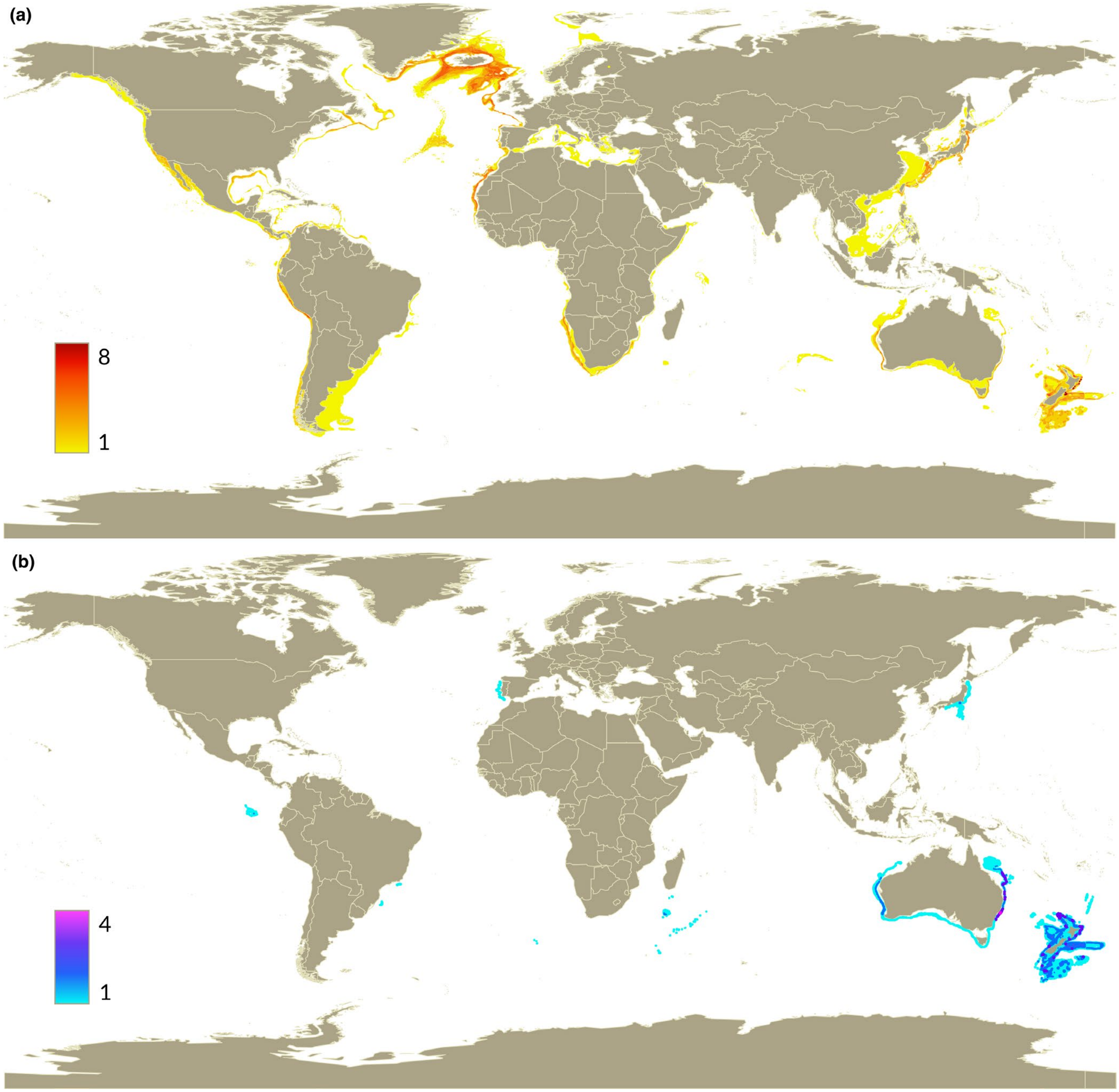

FIGURE 3 (a) Global ghost shark species richness (i.e. total number of individual species); and (b) global ghost shark endemic species richness [Colour figure can be viewed at wileyonlinelibrary.com]

in reporting fisheries catches to the species level which could ultimately give more reliable indications of population trends over time.

3.2 | Life-history traits and population connectivity

Very basic biological knowledge is often lacking for ghost sharks, allowing plenty of scope to increase research in this field. However, the often-cryptic nature of ghost sharks, coupled with inaccessibility of the deep sea or remote locations, and lack of commercial value, has limited the number of studies on ghost shark life history. Life-history studies on deepwater species in particular have been limited to a handful of species commonly caught as by-catch in regional fisheries (e.g. Barnett et al., 2009; Finucci et al., 2017; Finucci et al., 2017). These studies have indicated ghost sharks are likely more productive than other chondrichthyans, for example *Chimaera monstrosa* has been shown to have a high intrinsic rebound potential relative to other deepwater chondrichthyans (Kyne & Simpfendorfer, 2007). This may explain, in part, as to why some ghost shark species appear to be able to withstand considerable exploitation (e.g. Dark Ghostshark [*Hydrolagus novaezealandiae*, Chimaeridae], Fisheries New Zealand, 2019).

TABLE 2 Management implementations for ghost sharks where species-specific management is available. Country codes: Argentina (ARG), Chile (CHL), South Africa (ZAF), Australia (AUS) and New Zealand (NZL)

Management action	*Callorhinchus callorhynchus*	*Callorhinchus capensis*	*Callorhinchus milii*	*Hydrolagus bemisi*	*Hydrolagus novaezealandiae*
Gear restrictions	X (ARG, CHL)	X (ZAF)			
Temporal closures	X (ARG)				
Recreational (daily) catch limits	X (ARG)	X (ZAF)	X (AUS, NZL)		
Commercial (operational) catch limits	X (ARG)				
Total applied effort (TAE)		X (ZAF)			
Limited entry	X (CHL)	X (ZAF)			
Spatial closures		X (ZAF)			
Individual transferable quotas (ITQs)			X (AUS, NZL)	X (NZL)	X (NZL)

Age and growth estimations have been attempted for a quarter of species (see Table 1), yet there are significant challenges in ageing ghost sharks. Ghost sharks lack hard internal structures (e.g. vertebrae) used for ageing other chondrichthyans and attempts have been made to assess the feasibility of other three other characters, including eye lens (Francis & Ó Maolagáin, 2000), band counts in dorsal fin spines (Barnett et al., 2009; Calis et al., 2005; Francis, 1997; Moura et al., 2004) and tritor ridges on tooth plates (Bell, 2012; Hannan, 2016; King & McPhie, 2015; Tseng, 2011). Maximum age estimates of 40+ years have been suggested from these methods, but results are either unreliable or not validated (Bell, 2012). The use of tritor ridges produces vastly different results depending on if the formation of tritor ridges is assumed to be annual or biannual, a similar assumption for vertebral band counts widely used in shark and ray demography (Hannan, 2016). The length and base width of dorsal fin spines is positively correlated with fish length (Bell, 2012), but the mineral density gradients normally indicative of growth zones were not found in dorsal fin spines of *Hydrolagus colliei* (Barnett, Ebert, et al., 2009). Growth rings observed in dorsal fin spines of *Callorhinchus milii* have been shown to be uncorrelated to age and instead are simply layers of material deposited aperiodically to strengthen the spine (Francis & Ó Maolagáin, 2019). Maximum age estimates for ghost sharks are scarce, although an Australian tagging study in 1973–1976 recaptured a male *Callorhinchus milii* estimated to be more than 19 years old (Coutin, 1992; Francis, 1997). Age and growth parameters are essential inputs for national and international management and conservation, including stock assessments (longevity, mortality, biomass estimates), risk assessments and estimating extinction risk (intrinsic population growth and generation length). Without species-specific age and growth data, a representative species must be used to estimate generation lengths so that population trends can be scaled over time to produce the population reduction required for the application of the IUCN Criterion A. Here, data from *Chimaera monstrosa* were used to estimate generation lengths for chimaerids and rhinochimaerids as this species is found in the deep sea and is of similar size to many other ghost sharks. These generation length estimates should be used with caution, however, until species-specific age, growth and longevity data become available and validated.

Virtually nothing is known of ghost shark population structure or movement. For those species assessed by fisheries management, populations are presumed to be one stock (e.g. Fisheries New Zealand, 2019). Given the lack of embryonic dispersal, and assumed limited juvenile and adult dispersal, ghost shark population structure may be more complex than assumed (Barnett et al., 2012). Recent genetic analysis showed that there are two populations of *Chimaera monstrosa*, the Atlantic and Mediterranean Sea, separated by the shallow depth of the Strait of Gibraltar (Catarino et al., 2017). This remains, however, the only published molecular analysis of population structure on ghost sharks. On the west coast of the United States, differences in temporal trends of *Hydrolagus colliei* abundance suggested at least two distinct stocks in the regional stock structure (Barnett et al., 2012). With acoustic tracking, *Hydrolagus colliei* was shown to have a range of spatial patterns dependent on where the animal was tagged; some individuals remained in one general location, while others showed regular movement patterns of >90 km over a nine-month period (Andrews & Quinn, 2012). It was suggested site fidelity was correlated to high prey density access, and this hypothesis could be indicative of deepwater species distributions known from areas of high productivity (e.g. seamounts). Such observations could have implications for management, as ghost sharks have been shown to aggregate near highly productive areas also associated with high levels of fishing (e.g. Finucci et al., 2018; Marsac et al., 2020), and limited movement may increase susceptibility to fishing mortality.

Mark–recapture studies are recommended to better understand ghost shark age, growth, longevity and movement patterns. With advancements in technology that have successfully tagged and tracked deepwater chondrichthyans (e.g. Daley et al., 2015), future studies could investigate the feasibility of such methods in deepwater ghost sharks. Alternative methods, such as parasite community structure as a predictor of host population structure has also been trialled in a ghost shark (St. Joseph, *Callorhinchus capensis*, Callorhinchidae), and could be a useful tool to compliment other means of assessing population structure (Morris et al., 2019). Further molecular studies are a higher priority to delineate population structure.

3.3 | Global distribution, species richness and endemism

Ghost sharks have a high degree of endemism; 37% of species (*n* = 19) are currently known from only one location or one country (Figure 2a,c). Of these, three species (Falkor Chimaera [*Chimaera didierae*; Chimaeridae], Dark-mouth Chimaera [*Chimaera buccanigella*, Chimaeridae] and Seafarer's Ghost Shark [*Chimaera willwatchi*, Chimaeridae]) are known only from areas beyond the jurisdiction of any Exclusive Economic Zone (EEZ). Species range by family was largest for rhinochimaerids (71,593–3,768,491 km^2, mean range = 892,552 km^2) and smallest for the chimaerids (224–2,420,847 km^2, mean range = 349,928 km^2) (Figure 2b). No ghost shark has been described from the Arctic and Antarctic FAO Major Marine Fishing Areas (Ebert & Winton, 2010).

Australasia had the greatest species richness; combined, these two countries account for 35% of global ghost shark diversity (*n* = 18). Species richness was highest in the Northeast Atlantic, off the northwest coast of Africa (Morocco to Mauritania), followed by the East China Sea, New Zealand and off the northwest coast of South America (Ecuador and Peru) (Figure 3a). Patterns of ghost shark richness follow similar patterns to that of chondrichthyan total species richness and evolutionarily distinct species richness (Derrick et al., 2020). A notable exception is the Northeast Atlantic region where ghost shark richness was relatively high, but relatively low for all chondrichthyans. Ghost shark endemic species richness patterns were also very similar to chondrichthyan endemic species richness, with the highest regions of ghost shark endemism off Australasia, Japan, South Africa (Madagascar Ridge), Brazil and the Galapagos Islands (Figure 3b). Some ghost shark endemism was also reported off Portugal (Portuguese Chimaera, *Hydrolagus lusitanicus*, Chimaeridae), a finding not observed in all chondrichthyan endemic species richness.

Collectively, absolute reported depth ranges for ghost sharks ranged from 0 to 2,909 m (mean maximum depth = 1,290 m, $SD \pm 590$ m) (Table 1). By family, depth range was 0–600 m (mean = 218 ± 95 m) for callorhinchids, 0–2,909 m (mean = 889 ± 330 m) for chimaerids and 90–2,603 m (mean = 943 ± 521 m) for rhinochimaerids. The Smalleyed Rabbitfish (*Hydrolagus affinis*, Chimaeridae) had the deepest recorded depth of 2,909 m, and along with the Smallspine Chimaera (*Harriotta haeckeli*, Rhinochimaeridae), these species had the greatest reported depth ranges (293–2,909 m and 1,114–2,603 m, respectively).

3.4 | Ghost shark fisheries and trade

Ghost sharks are predominately by-catch species with little to no commercial value. They may be discarded, or retained and utilized for human consumption, fish meal, fertilizer or liver oil, predominately within local communities. The international market comprises primarily of the meat of inshore callorhinchids (and to a lesser extent *Hydrolagus bemisi* and *Hydrolagus novaezealandiae*), which are often marketed under names such as pearl fish, silver fish and smoothhound fillets to markets in Australia, China, Japan and Brazil (Nibam, 2011; Seafood NZ, 2018; SUBPESCA, 2020). As coastal human populations rise and pressure on already depleted coastal fisheries increases, fishing effort has shifted into deeper and previously unexploited waters, exposing some deeper-dwelling ghost sharks to new fishing pressures. This effort expansion is revealed by new species and new records in recent years in regions including the Caribbean Sea and Andaman Sea (e.g. Kumar et al., 2018; Polanco-Vásquez et al., 2017). In the Caribbean Sea, interest in developing deepwater fisheries has grown (e.g. Paramo et al., 2017; Wehrtmann et al., 2017), and some small-scale fishing across the region operate to depths where cartilaginous fishes are occasionally caught (Baremore et al., 2016; Hacohen-Domené et al., 2020). The Caribbean Chimaera (*Neoharriotta carri*, Rhinochimaeridae) was one of the most abundant deepwater chondrichthyans sampled from demersal trawl surveys off the Caribbean coast of Central America at depths up to 1,500 m, accounting for 16% (*n* = 62) of chondrichthyan catch (Benavides et al., 2014). This species is not known to be targeted in industrial fisheries, but is caught as by-catch in demersal trawl, trammel net, gillnet and longline fisheries and has particularly high distribution overlap with fisheries operating from Venezuela (Benavides et al., 2014; Oscar Lasso Alcalá, personal communication). In eastern Indonesia, artisanal deepwater longline fisheries operate to depths of up to 800 m, and Ogilby's Chimaera (*Chimaera ogilbyi*, Chimaeridae) accounted for nearly 10% of chondrichthyan landings at some fish landing sites (Prihatiningsih & Chodrijah, 2018; White et al., 2009). One exploratory Peruvian Patagonian Toothfish (*Dissostichus eleginoides*, Nototheniidae) fishery reported the Eastern Pacific Black Ghostshark (*Hydrolagus melanophasma*, Chimaeridae) comprising 35% of the total fish catch by weight (Bustamante, 1997); the species is regularly reported from fisheries operating along western South America in Ecuador, Peru and Chile (D.A. Ebert, unpublished data; Ñacari et al., 2020). Deepwater chondrichthyan fisheries predominately target species which can be utilized for their oil-rich livers, such as dogfishes (*Squalus* spp.) and gulper sharks (*Centrophorus* spp.) (Akhilesh, 2014; White et al., 2009), but fishing effort is often indiscriminate, and ghost sharks are often utilized when caught. These fisheries generally emerge in regions where there is high artisanal fishing effort and limited capacity to manage or enforce sustainable use of fisheries resources (Pomeroy, 2012).

There appears to be an increasing global interest in ghost shark liver oil, often marketed as ratfish oil. Chondrichthyans have long been utilized for their liver oil (e.g. Francis, 1998), in which extracted squalene is used for fuel, cosmetic and pharmaceutical purposes, dyes and sunscreens. Little is known of contribution of ghost shark liver oil to the squalene industry, apart from the target fishery for the Sicklefin Chimaera (*Neoharriotta pinnata*, Rhinochimaeridae) in India where its liver oil is considered high quality and is the second-most

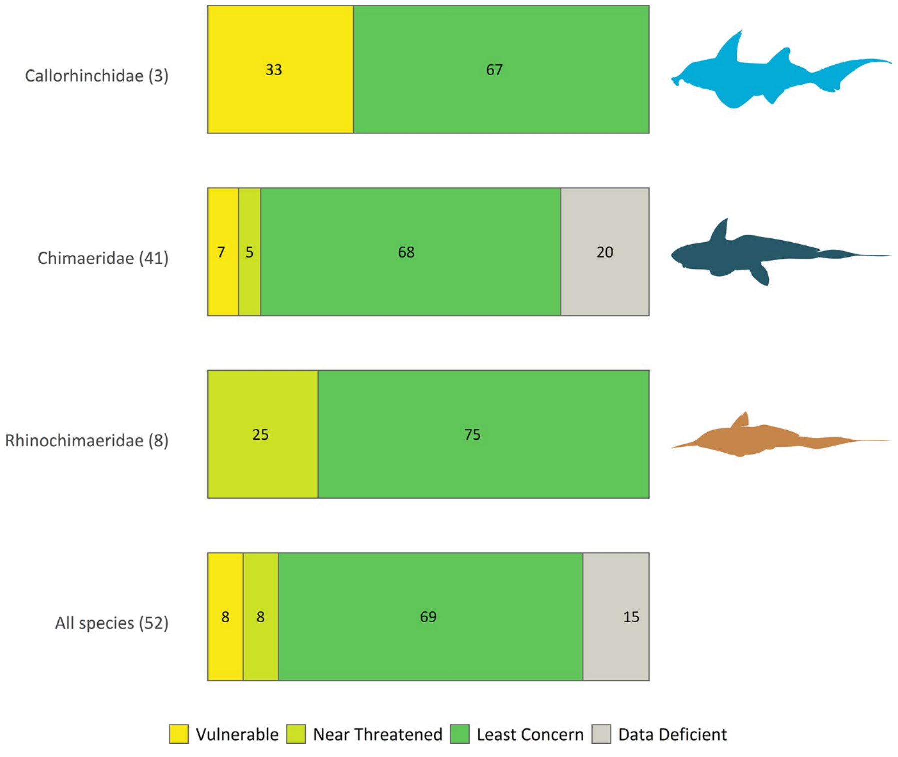

FIGURE 4 Percentage of species in each of the IUCN Red List of Threatened Species categories, by ghost shark family. Number of species in each family reported in brackets [Colour figure can be viewed at wileyonlinelibrary.com]

valuable liver oil (after gulper shark) (K.K. Bineesh, personal communication). Liver oil may be processed locally or shipped overseas for processing before being sold on the international market to places such as Japan and the European Union. *Neoharriotta pinnata*, known from the Southeast Atlantic Ocean (west coast of Africa) and Northern Indian Ocean (Gulf of Aden to Sri Lanka), is one of the few ghost sharks with a known targeted fishery. In Cochin, India, intensive targeted fishing effort of the species resulted in a 90% decline in landings of from 57.9 to 5.8 t between 2008 and 2011 (Akhilesh, 2014; Akhilesh et al., 2011). Catch records are sparse elsewhere across its distribution, although fishing effort from distant water fleets along West Africa has grown considerably since the 1960s (Alder & Sumaila, 2004). In the North Atlantic, noticeable increases in the retention of ghost sharks may be a response to compensate for the zero-total allowable catch (TAC) for deepwater sharks (ICES-WGEF, 2018). Since 1991, estimated landings of ghost sharks (*Chimaera monstrosa*, and *Hydrolagus* spp.) show no trends, however, official landings from countries reporting to the International Council for the Exploration of the Sea (ICES) have increased by over twofold during 2006–2014 (ICES-WGEF, 2018). Norway, in particular, has seen increases in retention of *Chimaera monstrosa*, from 114 t in 2012 to 217 t in 2017 as deepwater sharks—the traditional source of liver oil—have come under zero-retention regulations (ICES-WGEF, 2018). Ghost shark liver oil products are readily available for online purchase, and while there is a wealth of knowledge available on its application, there is virtually nothing known on trade or species affected. If new fisheries were to develop for ghost shark liver oil, targeted species will likely be susceptible to rapid population reduction.

There is very little fisheries data on ghost sharks; available information comes from catch and effort or landings data, and fisheries-independent and fisheries-dependent surveys. However, reporting of ghost shark catch may or may not be obligatory, and if reported, species are often lumped under a generic fisheries code, such as "*Hydrolagus* sp.", "silver shark" or the "rabbitfish (*Chimaera monstrosa* and *Hydrolagus* spp)" code used by nations reporting to the ICES advisory body. The abundance of species records ranged from one known individual (*Chimaera didierae*) to considerable annual fisheries catch records, for example 1,363 tonnes of *Hydrolagus novaezealandiae* reported landings in 2017–2018 New Zealand commercial catches (Fisheries New Zealand, 2019). Without species-specific information, it is difficult to determine the effect of fishing, if any, on individual species. For fisheries management, the absence of species-specific information on catch, life history and migration reduces the ability to measure abundance trends and can result in undetected local extinctions (Dulvy et al., 2000). For IUCN Red List assessments and other conservation-based measures, trends in population abundance must then be inferred from related species or fishing effort ("actual levels of exploitation").

If fisheries are known to overlap with species' spatial and/or depth distributions, but the degree of threat cannot be assessed with certainty, then species cannot be assessed beyond Data Deficient. Two regions had a number of Data Deficient species because trend data were unavailable. The first area, the Northwest Pacific Ocean, where three species are known to occur, Jordan's Chimaera (*Chimaera jordani*, Chimaeridae), Owston's Chimaera (*Chimaera owstoni*, Chimaeridae) and Ninespot Chimaera (*Hydrolagus barbouri*, Chimaeridae). These ghost sharks are not known to be targeted but may be caught as by-catch in industrial demersal trawl or recreational set net fisheries and are likely discarded at sea or landed under a generic "shark" code (H. Ishihara, personal communication).

The second region, the Southwest Indian Ocean, included four species [*Chimaera buccanigella*, *Chimaera didierae*, *Chimaera willwatchi*, and Robin's Ghostshark (*Hydrolagus erithacus* Chimaeridae)] where, since the 1970s, relatively recent fisheries rapidly developed on the high seas for commercially important deepwater stocks such as Orange Roughy (*Hoplostethus atlanticus*, Trachichthyidae), Alfonsino (*Beryx* spp.) and *D. eleginoides* (Bensch et al., 2009; Marsac et al., 2020). Deepwater sharks have been both targeted and taken incidentally in a number of gear types including demersal trawl, midwater trawl, demersal longline and demersal gillnet (Marsac et al., 2020; Georgeson et al., 2019), but there are no data available for ghost sharks from this region. It is not known if fishing activities are driving population reductions.

3.5 | Species-specific fisheries management: can ghost shark fisheries be sustainable?

The majority of ghost sharks (90%) have no species-specific management. However, four of the five species that are managed appear to be able to withstand some levels of fishing pressure. Of the five ghost sharks where species-specific management action was found, four of these species were assessed as LC (Table 2). Three species, *Callorhinchus milii* (Australia and New Zealand), *Hydrolagus bemisi* and *Hydrolagus novaezealandiae* (both New Zealand), have been identified as some of the most sustainable shark fisheries in the world (Simpfendorfer & Dulvy, 2017). Species-specific management tools for ghost sharks include Individual Transferable Quotas (ITQs), recreational bag limits, spatial and temporal fisheries closures, limited entry and gear restrictions for target fisheries (e.g. AFMA, 2020; da Silva et al., 2015; Fisheries New Zealand, 2019). Without management, however, ghost sharks are prone to population reduction, as observed for *Callorhinchus milii* in New Zealand. By 1986, *Callorhinchus milii* was considered overfished in parts of New Zealand after decades of increasing commercial exploitation dating back to the early 1900s (Francis, 1998). This species was introduced to the New Zealand Quota Management System (QMS) that year and a conservative Total Allowable Commercial Catch (TACC) was introduced to promote stock rebuilding. Within a decade the stock was rebuilt (Francis, 1998), providing evidence that ghost sharks are capable of rebounding from population reduction, even after periods of intense fishing effort (Barnett et al., 2012; Fisheries New Zealand, 2019).

3.6 | Ghost shark hotspots and marine protection

The Southwest Pacific is a global hotspot for ghost shark diversity, where over a third of species have been documented. This Australasian region is known for its high levels of marine endemism; nearly a quarter of Australian fish fauna and a quarter of New Zealand coastal fish fauna are endemic to their respective countries (Eschmeyer

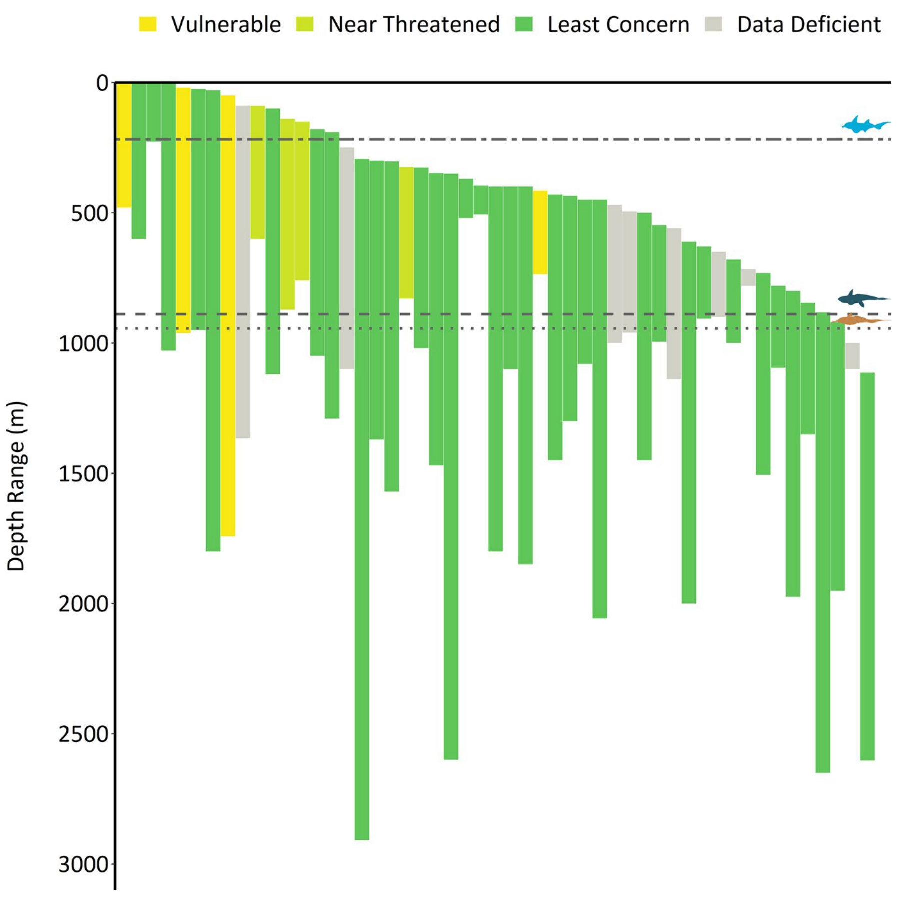

FIGURE 5 Depth range (m) for each ghost shark, ranked by decreasing mean depth (m). Species coloured according to extinction risk (Vulnerable [yellow], Near Threatened [pale green], Least Concern [green] and Data Deficient [grey]). Horizontal line refers to mean depth of each ghost shark family (Callorhinchidae [blue], Chimaeridae [grey] and Rhinochimaeridae [brown]). Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

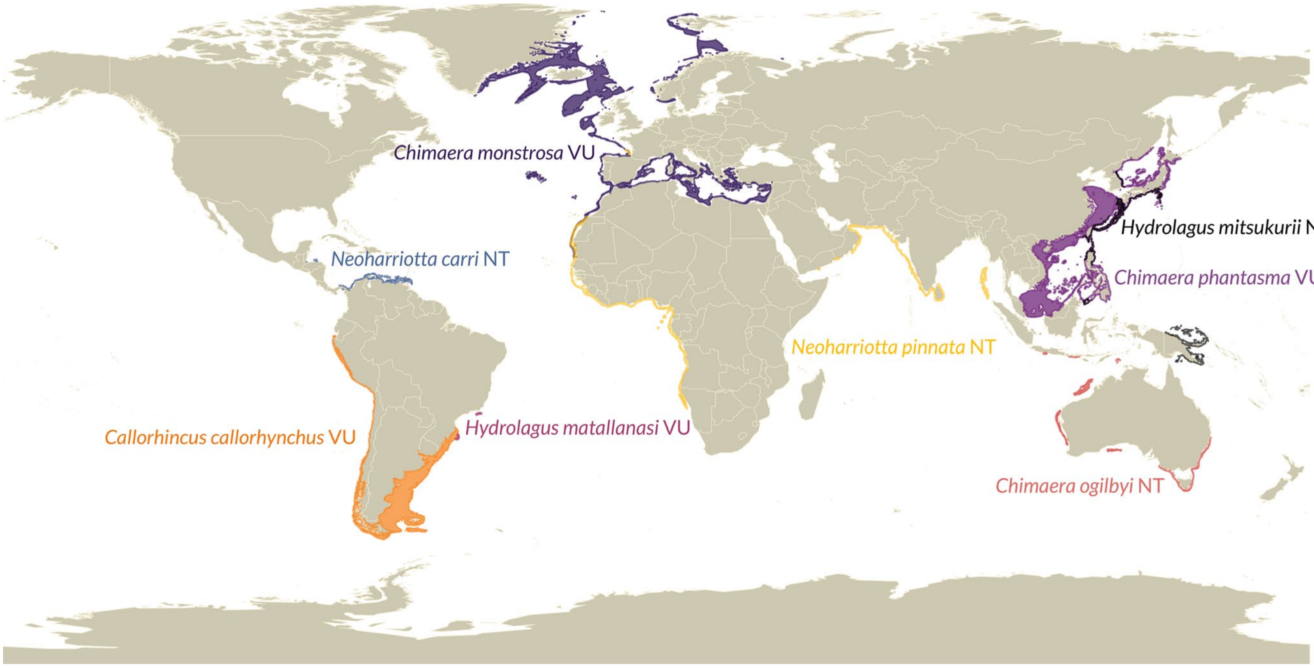

FIGURE 6 Distribution of Vulnerable (VU) (*Callorhincus callorhynchus* [orange], *Chimaera monstrosa* [dark purple], *Chimaera phantasma* [purple], *Hydrolagus matallanasi* [maroon]) and Near Threatened (NT) (*Chimaera ogilbyi* [pink], *Hydrolagus mitsukurii* [black], *Neoharriotta carri* [blue], *Neoharriotta pinnata* [yellow]) ghost sharks globally. Figure appears in colour in the online version only [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2010; Walrond, 2009). Both Australia and New Zealand display a high degree of chondrichthyan endemism with 25% and 20% of species, respectively (Finucci et al., 2019; Simpfendorfer et al., 2017). At present, there are few accounts of ghost sharks from Pacific Islands (e.g. Pointy-nosed Blue Chimaera *Hydrolagus trolli*, Chimaeridae, from New Caledonia). The lack of records may reflect limited deepwater fishing activity and surveys in the region, and additional species and species records are expected with increased deepwater exploration.

There are no marine protected areas (MPAs) designated specifically to benefit ghost sharks, although some established efforts may indirectly provide partial refuge from anthropogenic impacts. The distributions of the Whitespot Ghostshark (*Hydrolagus alphus*, Chimaeridae) and Galapagos Ghostshark (*Hydrolagus mccoskeri*, Chimaeridae) fall entirely within the Galapagos Marine Reserve. The Punta Bermeja Natural Protected Area (Rio Negro Province) in Argentina, originally designated in 1971 to protect one of the largest colonies of the South American Sea Lion (*Otaria flavescens*, Otariidae), now limits most fishing and forbids the retention of any chondrichthyan (Venerus & Cedrola, 2017). In New Zealand, the Banks Peninsula Marine Mammal Sanctuary bans most industrial gillnet and trawl fisheries to protect Hector's dolphins (*Cephalorhynchus hectori*, Delphinidae) from by-catch (Dawson & Slooten, 1993). Both protected areas likely offer refuge from fishing effort for regional callorhinchid species. The combination of the extensive Australian Marine Park network (Parks Australia, 2020) and spatial fisheries management arrangements may provide refuge for several Australian species. This includes the closure of most southeastern Australian waters deeper than 700 m to trawling (Patterson et al., 2019).

Habitat use of ghost sharks is largely unknown, thus impeding the ability to identify and protect areas of importance to these species. Particular patterns of habitat use or requirements may increase ghost shark exposure to anthropogenic impacts. Some species have been documented to aggregate in large numbers (Finucci, Dunn, et al., 2018; Holt et al., 2013). The reasoning for these occurrences is unclear but we speculate they are for reproduction. Ghost sharks are oviparous but egg-laying grounds and possible nursery areas have not been identified for most species and may prove difficult to find if egg capsules are buried in the sediment (Freer & Griffiths, 1993). Large numbers of egg capsules and/or juveniles have been identified from seven locations: the Mernoo Bank on the Chatham Rise (*Hydrolagus bemisi* and *Hydrolagus novaezealandiae*) and Canterbury Bight and Marlborough Sounds (*Callorhinchus milii*) off New Zealand (Francis, 1997; Horn, 1997); the Gulf of San Matías in Argentina (*Callorhinchus callorhynchus*) (Di Giácomo & Perier, 1994); the Gulf of Mannar off India (rhinochimaerid, identified as the Atlantic Longnose Chimaera *Rhinochimaera atlantica*, Rhinochimaeridae, but more likely to be *Neoharriotta pinnata*) (Chembian, 2007); and Saint Helena Bay off South Africa (*Callorhinchus capensis*) (Freer & Griffiths, 1993). In Western Port, Australia, large concentrations of *Callorhinchus milii* eggs and neonates were found on the outer margins of subtidal areas on sandy sediment and seagrass meadows, suggesting this is an important region for early life-history stages of the species (Braccini et al., 2009). This area has also undergone extensive habitat loss and modification with urbanization, resulting in increased turbidity, loss of seagrass and mangrove habitat, and high nutrient and contamination loading (May & Stephens, 1996). Effects of these environmental changes were suspected to result in considerable reductions in adult stock size or recruitment failure (Braccini et al., 2009; Walker & Hudson, 2005). There are a number of coastal habitats off Tasmania, Australia, declared as shark refuge areas (SRAs) where fishing for elasmobranchs is prohibited (Barnett et al., 2019). Despite recent efforts showing these areas also provide essential habitat for *Callorhinchus milii* reproduction, ghost sharks are not included in this current management scheme (Barnett et al., 2019).

For many deepwater ghost sharks, protecting species-specific areas of importance may not be an option, particularly for those species in Areas Beyond National Jurisdiction (ABNJ). However, some general management measures are available. Three ghost sharks (*Chimaera buccanigella*, *Chimaera didierae*, *Chimaera willwatchi*) are "key species of concern" within the international fisheries agreement, Southern Indian Ocean Fisheries Agreement (SIOFA), because of their restricted distributions (SIOFA, 2019). In the Northeast Atlantic where 10 ghost shark species occur, the North East Atlantic Fisheries Commission (NEAFC) implemented fisheries management measures including the banned use of gill, entangling and trammel nets in depths >200 m, fisheries closures along the Mid-Atlantic Ridge and Rockall Hatton Bank, and prohibited targeting of deepwater chondrichthyans, including ghost sharks (NEAFC, 2017). The establishment of the South African offshore multi-use Prince Edward Islands Marine Protected Area includes limited fishing effort (WWF, 2013) and may provide some refuge for the recently described *Hydrolagus erithacus*. Other MPAs inclusive of seamounts, such as the Motu Motiro Hiva Marine Park off Easter Island, where unidentified ghost shark species have been reported (Friedlander et al., 2013), are also likely to minimize some impacts of human activities for ghost sharks in the region.

Ghost sharks have been captured or observed in areas such as deep-reefs on the continental slope (Soto & Vooren, 2004; Quaranta et al., 2006), which may be at risk of anthropogenic impact. In the deep ocean, ghost shark egg-laying or foraging habitat may be at risk from damage caused by demersal trawling and exploratory mineral mining. The effects of fishing on the demersal marine environment are well-studied (Clark & Rowden, 2009; Jones, 1992), but the impact of new industries with growing interest, such as deepwater mining, are still relatively unknown. Large clusters of egg cases from other oviparous chondrichthyans have been located near cold seeps (Treude et al., 2011), cold-water coral reef habitat (Henry et al., 2013) and various discreet locations of the outer and middle shelf and upper slope of canyons (Hoff, 2016). Most recently, hydrothermal vents have been identified as natural egg-case incubators for the Pacific White Skate (*Bathyraja spinosissima*, Arhynchobatidae) along the Galapagos Rift in the Pacific (Salinas-de-León et al., 2018). While it is unknown if ghost sharks also engage in this behaviour, deepwater video imaging analysis has revealed ghost sharks associated with hydrothermal vents, feeding on the demersal fauna (Cuvelier et al., 2009). Hydrothermal vents are also of particular interest for resource extraction (Boschen et al., 2013). Habitat preference and usage are likely to be species-specific, as different species have been observed across specific habitat types (e.g. soft bottom substrate, high rock relief; see Ebert, 2016). Identifying these areas of importance for various life-history stages is essential for the spatial and temporal management of such deepwater features before they are impacted by human activities (Clark & Dunn, 2012).

3.7 | Future threat: changing oceans

Analyses of on the impacts of climate change on chondrichthyans have largely been limited to estuarine, inshore and reef-associated species (e.g. Chin et al., 2010). Preliminary and anecdotal evidence suggest inshore ghost sharks may also be subject to changes in the environment associated with climate. Expected responses to climate change in marine species include changes in behaviour, life history and habitat use (Hollowed et al., 2013). In South Africa, where changes in sea temperature and upwelling intensity have been documented in recent decades (Rouault et al., 2010), *Callorhinchus capensis* was identified to be among the most sensitive species assessed to regional climate change impacts (Ortega-Cisneros et al., 2018). Ghost sharks deposit multiple pairs of egg capsules on the seafloor where embryos develop over an incubation period of up to six months before hatching (Didier & Rosenberger, 2002). This prolonged incubation period leaves egg capsules vulnerable to environmental disturbances. Stranded *Callorhinchus capensis* egg capsules have been reportedly dislodged during storms (Freer & Griffiths, 1993), and increased storm frequency as a result of climate change may influence population recruitment due to a loss of eggs reaching hatching stage (Ortega-Cisneros et al., 2018).

Ghost sharks may also undergo changes in distributions with increasing sea temperatures. An evaluation of species distributions from trawl survey effort between 1985 and 2010 estimated that *Callorhinchus capensis* could experience a latitudinal range contraction in Namibian waters of up to 60 km/year; this rate of contraction corresponded with warming sea temperatures (Yemane et al., 2014). Off the east coast of New Zealand's South Island, relative fish abundance indices for *Callorhinchus milii* were strongly correlated with increasing sea surface temperature and sea surface height (Dunn et al., 2009). The mechanisms for this correlation are unknown and cannot be determined whether increases in abundance indices were indicative of true population increase. As sea temperatures rise, demersal species have been shown to shift to deeper waters (Dulvy et al., 2008). Such movement could displace inshore ghost sharks from shallower, protected or less-fished areas into deeper waters which may increase species' catchability, and thus, susceptibility to fishing.

3.8 | Extinction risk

Overall, 16% (n = 8) of ghost sharks were threatened (VU) or NT worldwide (Figure 4, Table 1): four species (8%) were VU and four species (8%) were NT. None of the species were assessed as EX, EW, CR or EN. A total of 36 species (69%) were LC and eight (15%) as DD, where there was insufficient information to make an accurate assessment of extinction risk. Seven species were assessed for the first time (13%; previously NE); five were classified as DD (9%), and two as LC (4%). By family, one (33%) callorhinchid and three (7%) chimaerids were threatened. Twenty-five per cent of rhinochimaerids were NT (n = 2) which included two of the three species of *Neoharriotta*. VU and NT species met Criterion A (the population reduction criterion) with suspected population reductions over three generations of 30%–49% and 20%–29%, respectively (Figure 4). From previous assessments, 21 species (40%) changed status and all changes were considered non-genuine (i.e. there was not a genuine improvement or deterioration in extinction risk). One species, the Large-eyed Rabbitfish (*Hydrolagus mirabilis*, Chimaeridae), was down-listed in status from NT to LC. The species was previously listed as NT because deepwater fishing pressure was anticipated to increase, and with no management in place, future population reduction was suspected. However, economic forces including volatile fuel prices deterred fishing effort from materializing further into deeper waters (e.g. Abernethy et al., 2010). Since its initial assessment, there are no data to infer or suspect *Hydrolagus mirabilis* has exhibited any population reduction. All updated assessments can be found on the IUCN Red List of Threatened Species website, https://www.iucnredlist.org/.

Documented declines based on abundance data were found for only two species: *Chimaera monstrosa* (VU) and *Chimaera ogilbyi* (NT). *Chimaera monstrosa* has a widespread distribution across the Northeast Atlantic Ocean and Mediterranean Sea where there is an extensive history of fishing (ICES-WGEF, 2018; Romas & Fernández-Peralta, 1995). It is caught as by-catch in deepwater trawl, longline, and gillnet fisheries (ICES-WGEF, 2018). In the Tyrrhenian Sea (western Mediterranean Sea), a decline of 91% in relative abundance of *Chimaera monstrosa* was estimated from commercial and research trawl surveys from 1972 to 2004 (Ferretti et al., 2005). Surveys in the central Aegean Sea (eastern Mediterranean Sea) failed to detect the species during a 10-year study period (1995–2000 and 2003–2006, Damalas & Vassilopoulou, 2011). These reports may be an artefact of survey limitations (e.g. not sampling the entire species' depth range), and however, large declines (>90%) or the disappearance of slope species have been widely reported across the Mediterranean Sea (Aldebert, 1997; Ferretti et al., 2013). Regional fishing pressure in the Mediterranean Sea is expected to continue into the future as fishing effort shifts to non-European waters, including areas previously regarded as refugia (Colloca et al., 2017). In Sweden, *Chimaera monstrosa* is listed as nationally Endangered (ICES-WGEF, 2018). While often discarded, post-release mortality rates for *Chimaera monstrosa* are estimated to be high (Moura et al., 2018). Post-release mortality is likely to be persistent amongst all ghost sharks given the poor condition individuals are in (if alive at all) when hauled on deck (e.g. Braccini et al., 2012).

In the Indo-Pacific, *Chimaera ogilbyi* is arguably the only ghost shark where species-specific population reduction as a result of fishing is well-documented. Between 1976–1977 and 1996–1997, mean catch rate of *Chimaera ogilbyi* from the upper slope trawl fishery off New South Wales, Australia declined from 8.3 to 0.3 kg/hr (Graham et al., 2001), equating to a population reduction of >99.9% over three generation lengths (~56 years). This region is estimated to include approximately 10% of the species' known distributional range, which extends throughout Australia, Indonesia and Papua New Guinea (Finucci et al., 2018). The steep decline in this small part of its range was offset by low mortality throughout the rest of its range. Previous assessments for Ogilby's Ghostshark (*Hydrolagus ogilbyi*, Chimaeridae) and the Blackfin Ghostshark (*Hydrolagus lemures*, Chimaeridae) were VU and LC, respectively. Taxonomic resolution of this group synonymized *Hydrolagus lemures* with *Hydrolagus ogilbyi* and clarified generic placement (Finucci, White, et al., 2018); *Chimaera ogilbyi* was assessed as NT.

Where species-specific abundance trends were unavailable, the statuses of other VU and NT ghost sharks were based on the high degree of intersection between geographic distribution range and intensive fishing pressures ("actual levels of exploitation" in IUCN Criterion A). A qualitative ecological risk assessment-style approach was applied, whereby both spatial overlap and the level of fishing effort was considered to assess "levels of exploitation" and the resultant *suspected* population reduction. The Striped Rabbitfish ([*Hydrolagus matallansi*, Chimaeridae], VU) is endemic to a small part of southern Brazil (states of Rio de Janeiro and Santa Catarina), where rapid and intense deepwater fisheries developed in the late 1990s to reduce pressure on depleted coastal stocks (Alvarez Perez et al., 2009). These fisheries have operated across the entire known geographical and bathymetrical range of *Hydrolagus matallansi* (e.g. Perez et al., 2013), where the species was caught in fisheries and by-catch monitoring programmes (Rincon et al., 2017). Fishing activities mostly ceased in 2006 but may return at any point in the future due to the dynamic nature of Brazilian fisheries (Alvarez Perez et al., 2009).

Data were most limited for ghost sharks in the Northwest Pacific. Here, the Silver Chimaera ([*Chimaera phantasma*, Chimaeridae], VU) has a relatively shallow distribution (most records < 500 m) and is commonly observed as landed catch from the trawl fisheries in the East China Sea (A. Yamaguchi, personal communication; Ebert et al., 2013), where fishing intensity is high (Szuwalski et al., 2017). Its distribution extends across the South China Sea where there has been a 52% decline in all shark species landings in Taiwan between 1953 and 2015 (Liao et al., 2019), and reconstructed catches of sharks, rays and skates from China have declined by 67% (90,000–30,000 t annually) since the 1950s (Zeller & Pauly, 2016). In the Philippines, where fishing of deepwater chondrichthyans dates to the 1960s (Flores, 2004), unidentified ghost sharks, also referred to as "silversharks" and may include *Chimaera phantasma*, have been collected from local landing sites (BFAR, 2017). *Hydrolagus mitsukurii* (NT) is also known from this region, but its range also extends to Papua New Guinea where there are currently no known deepwater fisheries. In Taiwanese fish markets, *Hydrolagus mitsukurii* is not nearly as common as *Chimaera phantasma*, but as fishing effort expanded into deeper waters, observations of the species have increased in the past 20 years (Ebert et al., 2013).

Deepwater species often receive less attention than their inshore and pelagic counterparts due to the perceived notion that these species are out of sight and out of mind—existing at depths beyond the reach of current fishing activities and thus, face a lesser degree of threat (Dulvy et al., 2014). No explicit relationship was observed between threat level and mean depth distribution, although VU and NT species generally had shallower mean depth distributions (Figure 5,

Table 1). The mean depth distributions of all threatened and NT species were <600 m (246–576 m), with the exception of *Chimaera monstrosa* (932 m). The co-occurrence of threatened or NT species could reveal higher than average deepwater fishing mortality (Dulvy et al., 2014; Jabado et al., 2017). However, there was little spatial distributional overlap of VU and NT species (Figure 6). Some limited overlap of VU and NT species occurred off the coast of Mauritania (*Chimaera monstrosa* and *N. pinnata*), Japan, and in the East and South China Seas (*Chimaera phantasma* and *Hydrolagus mitsukurii*). The Bay of Biscay also has overlap of *Chimaera monstrosa* and *N. pinnata*, where one specimen of *N. pinnata* was recently found (Diez & Mugerza, 2017).

3.9 | Recommendations

Ghost sharks remain poorly understood as a result of little public appeal, no apparent commercial value, and limited accessibility due to their distribution and cryptic nature. Past, present and future human activities are likely to impact some species. Species-specific reporting, monitoring and management are needed to assess population trends at the species level and to ensure ghost sharks do not undergo similar population reductions observed in many of their cartilaginous cousins. IUCN Red List status is not a statement of conservation priority (IUCN Standards & Petitions Subcommittee, 2017) but by assessing species using the IUCN Red List of Threatened Species Categories and Criteria, this process can assist in identifying knowledge gaps and where research efforts should be focused. While all ghost sharks warrant further research as outlined above, we have identified several species that are most in need of immediate monitoring and management. These species face high levels of exploitation across most, if not all, of their known distribution, have limited refuge from fishing activities and have little to no species-specific management. The genus *Neoharriotta*, comprising three species, are amongst the larger of the ghost sharks (reaching at least 127 cm total length), utilized for their flesh and oil-rich livers, and are readily accessible to near-shore fisheries. Two of the three *Neoharriotta* spp were assessed as NT. As mentioned previously, *N. pinnata* is currently targeted intensively off the coast of India for its liver oil, and much of its known distribution around Africa overlaps with intensive, and often illegal, fishing efforts from distant water fleets (Belhabib, 2017). In the Caribbean, *N. carri* is increasingly being observed in developing deepwater fisheries across the southern Caribbean Sea, where a number of fisheries using multiple gear types reach depths of 800 m, covering the entire known depth range of the species (Benavides et al., 2014; Polanco-Vásquez et al., 2017; Oscar Lasso Alcalá, personal communication). Catch rates and utilization of the species are not well known. The third species, the Arabian Sicklefin Chimaera (*Neoharriotta pumila*, Rhinochimaeridae), was listed as Least Concern, as its depth distribution is largely beyond the depth range of regional fisheries off Somalia and Yemen (Jabado et al., 2017). However, increasing interest from foreign fisheries fishing fleets and high rates of illegal, unreported and unregulated (IUU) fishing off the coast of Somalia (Glaser et al., 2019), as well as reports of large shipments of shark liver oil exported from the region (K.K. Bineesh, personal communication), suggest this species may soon be a risk from intensive fishing pressure, if not already. An investigation into the global liver oil trade and its uses is needed to fully understand the ecological impacts on these species, as well as the economic and social impacts on communities and industries that rely and/or profit on them.

Callorhynchus callorhynchus was one of a few ghost sharks assessed as threatened. Its widespread, inshore distribution off the coast of South America in the Southwest Atlantic and Southeast Pacific Oceans subjects the species to intensive fishing pressure throughout the year across most of its depth and spatial distribution (Aedo et al., 2010; Alarcón et al., 2011; Bernasconi et al., 2015). It is utilized for its flesh and fins in local and international trade (SUBPESCA, 2020). As by-catch, it is often recorded in industrial fisheries targeting shrimp species and Argentine Hake (*Merluccius hubbsi*, Merlucciidae) and is one of the most recorded and landed chondrichthyans in the region (e.g. Núñez et al., 2016). Species-specific trends are difficult to assess. In Argentina, increases in landings and large fluctuations in catch-per-unit-effort (CPUE) are thought to reflect fleet dynamics rather than true population abundance (Bernasconi et al., 2015). In Chile, large declines in biomass (~24,000 to ~3,000 t) were estimated between 1986 and 2008 in fishing Regions IV to X (accounting for 99% of landings) (Aedo et al., 2010). While some species-specific and general management arrangements are available (e.g. gear restrictions, daily catch limits, limited entry, see Table 2), much of the species' distribution occurs where fisheries have been characterized by declining catches and a shift to species of lower trophic levels (e.g. Villasante et al., 2015). In Chile, widespread artisanal fisheries account for nearly half of all fish and crustacean landings, however, monitoring of landings is poor and thought to be under-reported (Van der Meer et al., 2015). Given that callorhinchids can exhibit population decline when sufficient fisheries management is not available, we recommend that quotas are set to ensure fishing activities become sustainable and any population declines are stabilized and reversed. As a wide-ranging species across South America, transnational co-operation will likely be necessary to encourage sustainable management of this locally important marine resource.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study. All updated assessments can be found on the IUCN Red List of Threatened Species website, https://www.iucnredlist.org/.

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