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Conservation status of the world's hagfish species and the loss of phylogenetic diversity and ecosystem function

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ABSTRACT

1. Hagfishes represent an ancient and unique evolutionary lineage that plays an important role in the cycling of organic matter and other nutrients to maintain the overall health of the ecosystems they inhabit.
2. Fisheries worldwide directly profit from the harvesting of hagfishes for leather and food, as well as from the positive habitat effects hagfishes provide for other target species. Overexploitation and destructive fishing practices are major threats to several hagfish species, especially those with restricted or small distributions.
3. In order to evaluate the effect of these threats on populations, the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria were applied to assess the probability of extinction for all of the world's known hagfish species.
4. Nine of the 76 hagfish species (12%) were determined to be in threatened categories, indicating an elevated risk of extinction. Particular areas and species of concern include southern Australia where 100% of hagfish species present were determined to be at an elevated risk of extinction and the coast of southern Brazil where up to 50% of hagfish species present are at an elevated risk of extinction. Also of concern, are the species found in the East China Sea, Pacific coast of Japan, and coastal Taiwan where as many as 50% of hagfish species are threatened with extinction.
5. The loss of hagfish species will have detrimental effects on ecosystems as a whole as well as the fisheries that depend on them, especially in the many areas around the world that have low hagfish species diversity.
6. Better information, data, regulation and management of hagfish fisheries and other threats to hagfish populations are urgently needed to ensure the survival of these important species.

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INTRODUCTION

Hagfishes are evolutionarily significant organisms that are phylogenetically unique. These species represent the most ancient lineage of fishes and are one of only two groups of living jawless fishes (Nelson, 2006). Their morphology is enigmatic and a new subphylum, the Craniata, was created to account for the hypothesis that they may not belong to Vertebrata because they do not possess the metamerically arranged endoskeletal elements flanking the spinal cord and other features that characterize vertebrates (Donoghue *et al.*, 2000; Janvier, 2007). Nevertheless, molecular evidence suggests that hagfishes are sister to the other living jawless fishes, the lampreys (Yu *et al.*, 2008; Near, 2009). If that hypothesis is correct, then the absence of vertebrae in hagfishes is a secondary loss during their evolution (Janvier, 2007). Regardless of the phylogenetic controversy, hagfishes represent a unique line of evolution that holds special relevance for conservation of biodiversity (Crozier, 1997). Phylogenetic distinctiveness is an important criterion in conservation effort and has been used to target living fossils such as the Coelacanth for conservation priority (Bowen, 1999). Hagfishes represent an even more ancient and

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phylogenetically distinct lineage than coelacanths and under this criterion warrant high priority.

In addition, hagfishes are of high ecological importance in the areas they inhabit. They play a key role in substrate turnover, nutrient cycling, and as detritus feeders (Martini, 1998). The ecological niche occupied by hagfish species has been well documented (Martini, 1998; St Martin, 2001). By consuming the dead and decaying carcasses that have fallen to the benthic zone, hagfishes clean the ocean floor creating a rich environment for other species including commercial ground fish such as codfish, haddock, and flounder (Martini, 1998; St Martin, 2001). The presence of detritus feeders is especially important in areas of intense fishing, because there are large excesses of detritus due to bycatch discards (Martini, 1998). Hagfishes are also prey for many species of pinnipeds as well as some major fisheries species such as codfish, white hake, and halibut (Martini, 1998). For example, the Cape hagfish, *Myxine capensis*, accounted for 14.4% of the diet of 90 specimens of *Octopus magnificus* (Cephalopoda) caught off Namibia and South Africa (Villanueva, 1993). However, the beneficial ecological effects hagfish provide for other species have not been studied in detail and for this reason it is not fully understood what impact the loss of hagfish species will have on their habitat. In order to fully understand the role hagfishes play in the benthic community, better research is needed on individual species' distribution, biology and ecology, as well as the impacts of targeted and trawling fisheries on hagfish populations and the ecosystems they support.

The whale-fall community, which is the environment with the highest species richness of any known hard substrate community, is facilitated by hagfishes. The first of at least three successional stages in the colonization of whale carrion is implemented by mobile scavengers such as hagfishes. In this stage, hagfishes feed on and remove the soft tissue, dispersing tissue particles and heavily enriching the area within 1–3 m of the skeleton with organic matter. This allows heterotrophic bacteria and opportunistic polychaetes, molluscs and crustaceans to colonize the site (Smith and Baco, 2003; Smith, 2007). After the carcass has been completely stripped and only bone is left, sulfide-based chemoautotrophic bacteria inhabit the area, both free-living and endosymbiotic within the tissues of mussels, clams, and vestimentiferan polychaetes (Smith, 2007). These sulfophilic organisms comprise most of the species richness of these unique whale-fall sites.

Hagfish populations are threatened by targeted and bycatch fisheries harvesting, as well as by habitat degradation caused by fishing gear. With the recent emergence of the 'eel skin' market in Korea for the production of leather from hagfish skin, several fisheries have emerged that target hagfishes primarily (Gorbman *et al*., 1990; Barrs, 1993). Exploitation of hagfishes also affects other commercial species. Without the presence of hagfishes the ocean floor would be riddled with fallen carrion, reducing the amount of suitable habitat in local environments. For example, in certain locations in the north-western Atlantic when fishing pressure was focused on hagfishes the stock of other commercial species such as flounder plummeted (St Martin, 2001). Additionally, hagfish inhabit the superficial layer of soft, flocculent, muddy sediments that blankets the substrata of the ocean floor (Lesser *et al*., 1996). Recent studies also have indicated that at least three species (*Eptatretus eos*, *E. lakeside* and *E. lopheliae*) are closely associated with deep coral reefs or rocky habitats (Fernholm and Quattrini, 2008). Bottom trawling gear not only tears through this superficial layer and destroys the natural environment hagfishes inhabit, but also harvests hagfishes as bycatch (Wayte *et al*., 2004). Most fisheries that obtain hagfishes as bycatch discard them onto the surface of the water (Lesser *et al*., 1996; Wayte *et al*., 2004; Bromhead and Bolton, 2005). Here, almost none of the hagfishes survive because of the disorientation and physiological stressors such as salinity and temperature changes associated with the altering of their natural depth (Lesser *et al*., 1996).

In light of the important ecological roles hagfishes play in the benthic community, some populations may be compromised by overexploitation and habitat decline. To determine the impact of potential threats on hagfish species on a global scale, species-specific data were collated and used to determine the probability of extinction for all 76 known species of hagfish under the Categories and Criteria of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species.

METHODS AND MATERIALS

The IUCN Red List Categories and Criteria were applied to the world's known 76 species of hagfish, which are all included in the Myxinidae (Fernholm and Mincarone, 2010; Kuo *et al*., 2010). Data on the taxonomy, distribution, population status, habitat and ecology, major threats, and conservation measures of each species were collected, and used to apply the IUCN Red List Categories and Criteria during an IUCN Red List Assessment Workshop in Manaus, Brazil in 2009. During this workshop, leading experts met to share and synthesize species-specific data, and to collectively apply the IUCN Red List Categories and Criteria (IUCN, 2001). The IUCN Red List Categories and Criteria are the most widely accepted system for classifying extinction risk at the species level (De Grammont and Cuarón, 2006; Hoffmann *et al*., 2008; Mace *et al*., 2008). The assessment process consolidates the most current and highest quality data available, and ensures peer-reviewed scientific consensus on the probability of extinction for each species (Stuart *et al*., 2004; Carpenter *et al*., 2008; Schipper *et al*., 2008; Polidoro *et al*., 2010). All species data and results of Red List assessments are freely and publicly available on the IUCN Red List of Threatened Species (IUCN, 2011).

The IUCN Red List Categories comprise eight different levels of extinction risk: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). A species qualifies for one of the three Threatened categories (CR, EN, or VU) by meeting the quantitative threshold for that Category in one of the five different available Criteria (A-E).

Hagfish species determined to be Threatened or Near Threatened were primarily assessed under Criterion A and Criterion B. A species qualifies for a threatened category under Criterion A when it meets the threshold of population decline (30% for Vulnerable, 50% for Endangered, and 80% for Critically Endangered) over a timeframe of three generation lengths, a measure of reproductive turnover rate, in the recent past. Under Criterion A, generation length is the average age of the reproducing adult (IUCN, 2001), and is generally unknown for hagfish species. For the two species assessed under Criterion A, generation length was conservatively estimated to be 8 years based on estimated maturation by age 1 or 2 years and a maximum longevity of approximately 17 years from aquarium specimens. For the vast majority of hagfish species that are fished or caught as bycatch, there are no available data to quantify population decline under Criterion A. However, the two species assessed under Criterion A are present in the East China Sea, where significant decreases in the hagfish landed are considered to be the result of overfishing (Honma, 1998). For these species, aggregated hagfish catch landings from 1980–1995 and information on fishing effort in the East China Sea (Gorbman *et al*., 1990; Honma, 1998) were combined with the estimated proportion of the species' global range that contains this fishery and conservatively used as a surrogate to estimate population decline over time. A species qualifies for a threatened category under Criterion B when it meets the threshold for a small geographic range size (maximum extent of occurrence <20 000 km^2 or area of occupancy <2000 km^2 to meet the lowest threshold for Vulnerable) and has a continued decline in population or habitat quality and/or habitat fragmentation. Using GIS, extent of occurrence was calculated based on the minimum convex polygon created by connecting known localities (IUCN, 2001). Area of occupancy was not known nor used for species assessed under Criterion B.

A category of Near Threatened is assigned to species that come close to but do not fully meet all the thresholds or conditions required for a threatened category under any given criterion. A category of Least Concern is assigned if available species information and data fall well below any given criterion threshold, indicating a relatively low risk of extinction. A species can be assessed as Data Deficient when extinction risk or population status cannot be evaluated due to insufficient knowledge. This latter category does not necessarily mean that the species is not threatened. On the contrary, when data become available, numerous Data Deficient species often prove to be at risk.

RESULTS

Of the 76 species of hagfishes, nine (12%) qualified for one of the three Red List Categories of Threatened Critically Endangered (1 sp.), Endangered (2 spp.), or Vulnerable (6 spp.) (Table 1), and two species qualified for a listing of Near Threatened. Owing to an extensive lack of species knowledge (e.g. only known from type specimens) or the absence of quantifiable fisheries data, 30 of the 76 species (39%) were categorized as Data Deficient. For example, many boats that capture hagfish bycatch either report all species as one general species or do not report any catch data at all (Gorbman *et al*., 1990). Also, the demersal, muddy habitat colonized by hagfishes is one that is not often sampled in many areas, especially those areas that are in extremely deep waters. Eight of the species listed as Data Deficient are known only from a single type specimen, and major threats to five of these eight species are unknown. Twenty-three of the 30 (77%) Data Deficient species were considered to have significant major threats such as trawling, bycatch, targeted fisheries, or habitat degradation operating within their depth and distribution range, but the impact of these threats could not be adequately quantified. These Data Deficient species should be reassessed as new information becomes available, as they may qualify for a threatened category in the near future. Almost half of all species were assessed as Least Concern, 35 of 76 (46%), either because there were no known major threats or known threats were not thought to be severely affecting the global population of the species throughout its geographic and depth ranges.

The genus with the highest proportion of Threatened species is *Paramyxine* (Figure 1). Of the 14 species in this genus, four (29%) qualified under one of the three Threatened categories, four are listed as Least Concern, and six are Data Deficient. *Paramyxine* species are mainly endemic to specific regions in the north-west Pacific with the exception of two species endemic to the coast of Colombia and one species endemic to the Gulf of Mexico. All of the four Threatened species in this genus have a very small estimated extent of occurrence (Table 1), and are exposed to significant threats from heavy fishing within their restricted range, including harvest as bycatch and continuous habitat degradation. The majority of species in the two largest genera of hagfish, *Eptatretus* (37 spp.) and *Myxine* (21 spp.), were listed as either Least Concern or Data Deficient. The three smaller genera, *Nemamyxine* (2 spp.), *Neomyxine* (1 sp.) and *Notomyxine* (1 sp.), are represented mainly by Data Deficient species (Figure 1), with the exception of *Nemamyxine kreffti*, which was listed as Near Threatened. This species has an extent of occurrence less than 30,000 km^2, is the target of fisheries, and local fisheries are causing the degradation of its habitat.

Eptatretus octatrema is the only Critically Endangered species of hagfish, the IUCN Red List Category corresponding to the highest probability of extinction. One of the rarest species of hagfish, *E. octatrema* has only been confirmed once from the examination of two type specimens in the South African Museum, both captured over 100 years ago. This species is considered to inhabit an area of less than 100 km^2 off Cape Saint Blaize, South Africa, a region that is both heavily fished and scientifically surveyed with nets capable of its capture (Scott, 1949). Three other species of hagfish have been collected by scientific surveys conducted within this species' habitat. *E. octatrema* has a relatively shallow water distribution, and its native habitat is heavily affected by extensive trawling (Scott, 1949; Wayte *et al*., 2004). Coastal development and dredging of the coastal waters in the area are also major threats for the species. Owing to the extremely low incidences of occurrence, further surveys to determine if this species is still extant should be considered a high priority.

Two species, *Myxine paucidens* and *Paramyxine taiwanae*, were listed as Endangered. These species have particularly small distributions, each with an extent of occurrence estimated to be less than 3000 km^2. *Myxine paucidens* is known only from four museum specimens with the last known record of the species dating back to 1972. The species is probably endemic to the Hyalonema ground and Sagami Nada, Honshu, Japan, where all known specimens were collected. Although this area is heavily studied, no other accounts of this species have ever been recorded. The area is heavily trafficked by trawling vessels, whose activities most likely result in continual habitat degradation. Since no specimens have been recorded in the last 35 years, scientific surveys of the area to verify the presence of this species are urgently needed. *Paramyxine taiwanae* is found off the coast of north-western Taiwan and is known from approximately 150 specimens. This species is affected by habitat loss and is collected as bycatch by extensive trawling and trapping within its restricted distributional and depth ranges. If populations of other hagfish species in the region of Taiwan continue to decline it is possible that *P. taiwanae* will become a target species for the food and leather industry. There

Table 1. Red List categories and criteria, depth range, region of occurrence, and major threats for all hagfish species known to date (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient)

Species	Redlist category	Criterion applied	Population decline (%)	Maximum extent of occurrence (km^2)	Depth range (m)	Region of occurrence	Major threats
Eptatretus alastairi	LC				380 to 550	endemic to Australia	none known
Eptatretus astrolabium *	DD				to 500	endemic to Papua New Guinea	none known
Eptatretus bischoffii	DD				6 to 50	endemic to Chile	target of fisheries, bycatch, habitat degradation
Eptatretus burgeri	NT	A	23		5 to 270	Yellow Sea and East China Sea	target of fisheries
Eptatretus caribbeaus	LC				365 to 500	endemic to Caribbean Sea	none known
Eptatretus carlhubbsi	LC				481 to 1574	central North Pacific	none known
Eptatretus cirrhatus	LC				1 to 1100	south-eastern Oceana	none known
Eptatretus deani	DD				107 to 2743	eastern Pacific	target of fisheries
Eptatretus eos *	DD				991 to 1013	endemic to Tasman Sea	none known
Eptatretus fernholmi *	DD				to 563	endemic to Luzon Island, Philippines	none known
Eptatretus fritzi	LC				183 to 2743	endemic to Guadalupe Island, Mexico	none known
Eptatretus goliath *	DD				to 811	endemic to New Zealand	potentially impacted by deep-sea trawling
Eptatretus gomoni	LC				260 to 705	endemic to Western Australia	none known
Eptatretus grouseri	LC				648 to 722	endemic to Galapagos Archipelago	none known
Eptatretus hexatrema	LC				12 to 400	endemic to Namibia and South Africa	bycatch, habitat degradation
Eptatretus indrambaryai	LC				267 to 400	endemic to Andaman Sea	potentially impacted by offshore bottom trawling
Eptatretus lakeside *	DD				to 762	endemic to Galapagos Archipelago	none known
Eptatretus laurahubbsae	LC				to 2400	endemic to Juan Fernández Island, Chile	none known
Eptatretus longipinnis	VU	B		15000	14 to 40	endemic to South Australia	bycatch, habitat degradation
Eptatretus lopheliae	DD				382 to 700	endemic to eastern Central U.S.	habitat degradation
Eptatretus mcconnaugheyi	DD				43 to 415	endemic to south-western U.S. and Mexico	potentially impacted by trawling and other fisheries
Eptatretus mccoskeri *	LC				to 201	endemic to Galapagos Archipelago	none known
Eptatretus mendozai	LC				720 to 1100	endemic to Puerto Rico, Dominican Republic, and Haiti	none known
Eptatretus menezesi	LC				250 to 600	endemic to southern Brazil	bycatch
Eptatretus minor	DD				300 to 400	endemic to Gulf of Mexico	bycatch
Eptatretus multidens	LC				239 to 770	western Central and South Atlantic	bycatch
Eptatretus nanii	DD				100 to 470	endemic to Chile	recently impacted by trawling and other fisheries
Eptatretus octatrema	CR	B		100	49 to 66	endemic to South Africa	habitat degradation, coastal development
Eptatretus okinoseanus	LC				300 to 1020	Japan and Taiwan	bycatch
Eptatretus polytrema	DD				10 to 350	endemic to Chile	none known
Eptatretus profundus	LC				490 to 1150	endemic to South Africa	potentially impacted by trawling and other fisheries
Eptatretus rubicundus *	DD				to 800	endemic to north-eastern Taiwan	none known
Eptatretus sinus	LC				198 to 1330	endemic to Gulf of California, Mexico	none known
Eptatretus stoutii	DD				16 to 966	eastern North Pacific	target of fisheries
Eptatretus strahani	DD				189 to 430	Philippines and Western Australia	habitat degradation
Eptatretus strickrotti *	LC				to 2211	endemic to East Pacific Rise vent site	none known
Eptatretus wisneri	LC				512 to 563	endemic to Galapagos Archipelago	none known
Myxine affinis	LC				3 to 146	endemic to southern Chile and Argentina	potentially impacted by trawling and other fisheries
Myxine australis	LC				4 to 146	southern coast of South America	habitat degradation
Myxine capensis	LC				88 to 675	southern Africa	bycatch, habitat degradation

(*Continues*)

Table 1. (Continued)

Species	Redlist category	Criterion applied	Population decline (%)	Maximum extent of occurrence (km^2)	Depth range (m)	Region of occurrence	Major threats
Myxine circifrons	LC				700 to 1860	eastern Pacific	potentially impacted by trawling and other fisheries
Myxine debueni	DD				300 to 302	endemic to Strait of Magellan	potentially impacted by fishing activity
Myxine fernholmi	LC				135 to 1480	Falkland Islands and northern Chile	potentially impacted by trawling and other fisheries
Myxine formosana	DD				588 to 1500	endemic to Taiwan	recently targeted in commercial fisheries
Myxine garmani	VU	A	35		200 to 1100	endemic to Japan	target of fisheries
Myxine glutinosa	LC				40 to 1100	eastern and western North Atlantic	target of fisheries
Myxine hubbsi	LC				1100 to 2440	eastern Pacific	potentially impacted by trawling and other fisheries
Myxine hubbsoides	DD				735 to 880	endemic to Central Chile	unknown
Myxine ios	LC				614 to 1625	eastern Atlantic	potentially impacted by trawling and other fisheries
Myxine jespersenae	LC				752 to 1556	central North Atlantic	bycatch
Myxine knappi	DD				to 650	endemic to southern Argentina and Falkland Islands	potentially impacted by trawling and other fisheries
Myxine kuoi *	DD				to 595	endemic to Taiwan	bycatch and a possible target of fisheries
Myxine mccoskeri	LC				439 to 1174	southern Caribbean Sea	potentially impacted by trawling and other fisheries
Myxine mcmillanae	LC				603 to 1500	Caribbean Sea and north-eastern Gulf of Mexico	potentially impacted by trawling and other fisheries
Myxine paucidens	EN	B		3000	450 to 631	endemic to central eastern Honshu, Japan	habitat degradation
Myxine pequenoi	DD				185 to 251	endemic to Chile	potentially impacted by trawling and other fisheries
Myxine robinsorum	LC				783 to 1768	southern Caribbean Sea	unknown
Myxine sotoi	VU	B		20000	690 to 810	endemic to southern Brazil	bycatch, habitat degradation
Nemamyxine elongata	DD				to 132	endemic to New Zealand	potentially impacted by fishing activity
Nemamyxine kreffti	NT	B		30000	80 to 800	western South Atlantic	target of fisheries, habitat degradation
Neomyxine biniplicata	DD				6 to 1095	endemic to New Zealand	potentially impacted by trawling and other fisheries
Notomyxine tridentiger	DD				6 to 143	southern coast of South America	potentially impacted by trawling and other fisheries
Paramyxine ancon	DD				470 to 488	endemic to Colombia	potentially impacted by trawling and other fisheries
Paramyxine atami	DD				300 to 536	endemic to Japan	bycatch
Paramyxine cheni	VU	B		6000	156 to 268	endemic to Taiwan	bycatch, habitat degradation
Paramyxine chinensis	DD				500 to 600	northern South China Sea and Taiwan	target of fisheries
Paramyxine fernholmi	VU	B		6000	200 to 412	endemic to Taiwan	bycatch, habitat degradation
Paramyxine moki *	DD				to 100	endemic to Sagami Bay, Japan	habitat degradation
Paramyxine nelsoni	VU	B		6000	50 to 250	endemic to Taiwan	bycatch, habitat degradation
Paramyxine sheni	LC				200 to 800	endemic to Taiwan	potentially impacted by trawling and other fisheries
Paramyxine springeri	LC				400 to 730	endemic to Gulf of Mexico	bycatch
Paramyxine taiwanae	EN	B		3750	120 to 427	endemic to Taiwan	bycatch, habitat degradation
Paramyxine walkeri	DD				75 to 120	endemic to Japan	potentially impacted by fishing activity
Paramyxine wayuu	DD				300 to 306	endemic to Colombia	potentially impacted by trawling and other fisheries
Paramyxine wisneri	LC				330 to 412	endemic to Taiwan	none known
Paramyxine yangi	LC				120 to 547	endemic to Taiwan	bycatch

* species known only from a single specimen.

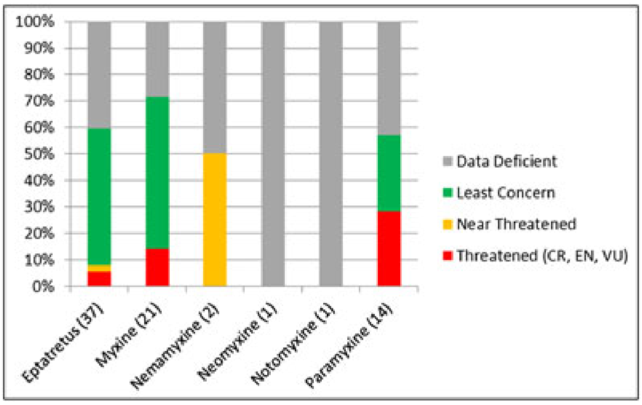

Figure 1. Percentage of species in each Red List Category in each genus and the number of species per genus.

are no current conservation measures in place for either of these two Endangered species. In order to protect the survival of both populations more information is needed on their status, life history, and the effects of trawling activities on their native habitat.

Six species are listed as Vulnerable. All six are heavily affected by bycatch and habitat degradation from fisheries activities throughout their restricted ranges, and five of them have an extent of occurrence estimated to be less than 20 000 km^2. One commercial species, *Myxine garmani*, is listed as Vulnerable because of the impact of targeted fisheries throughout its relatively restricted range in Japan. In half of its range, in an area along the south-eastern coast of Japan, mixed hagfish landings between 1980 and 1995 show a 70% decline in total hagfish catch (Gorbman *et al*., 1990; Honma, 1998) with assumed consistent effort. As this species is the most common species in this area, it is inferred that the majority of the catch is composed of *M. garmani*. Assuming no decline has occurred in the other half of this species' range, a minimum of a 35% decline in the population of *M. garmani* is estimated to have occurred in the past 25 years.

Geographic areas of concern

Hagfish species richness is naturally low across the globe, with only a single species of hagfish present along the vast majority of coastlines (Figure 2). For this reason, the loss of even a single species in any given region may have unforeseen ecological effects on local ecosystems.

Southern Australia

The coast of South Australia, for example, boasts a rich environment for the fish that inhabit the area, providing a highly profitable region for fisheries to operate (Wayte *et al*., 2004). Throughout the entire southern coastline of Australia and its deeper waters, only one hagfish species, *Eptatretus longipinnis*, listed as Vulnerable, has ever been reported and is found between Robe and Port MacDonnel (Figures 1 and 2) (Mincarone and Fernholm, 2010). This species inhabits coastal shallow waters between 14 and 40 m depth, which makes it susceptible to accidental harvesting by a range of different fisheries. Across the small distributional range of this species there has been extensive scientific surveying and commercial trawling which has produced only eight museum specimens to date and has confirmed its extent of occurrence to be less than 15 000 km^2. *Eptatretus longipinnis* is reported to be part of the discarded bycatch in the gillnet, hook, and trap fisheries (Bromhead and Bolton, 2005). In addition, the quality of the habitat of this species in its narrow distributional range is declining steadily because of heavy commercial fishing activities (Wayte *et al*., 2004).

South-west Brazil and Uruguay

Off the coast of Brazil and Uruguay, between 33% and 67% (1 or 2 of 3 species) of hagfishes present in different overlapping areas along the coast are listed in Threatened or Near Threatened categories (Figure 3). Following the launch of a deep-water fishing development programme in 1998, the continental slope of southern Brazil and Uruguay has become a highly profitable region for deep-water fisheries (Perez and Wahrlich, 2005; Pezzuto *et al*., 2006). The fisheries that have emerged in recent years mainly target species within a depth range of 200–900 m, which directly overlaps with the distribution of all known species of hagfish in this region. For example, *Myxine sotoi*, listed as Vulnerable, is found off the coast of south central Brazil at depths between 690–810 m (Mincarone, 2001), an area that is regularly trawled by deep-sea fisheries, some of which record this species as bycatch. This species shares its northerly limit at Rio de Janeiro, Brazil with *Eptatretus menezesi*, a Least Concern species (Mincarone, 2000, 2001). *Nemamyxine kreffti*, a Near Threatened species, extends across the southern distribution of *M. sotoi* and south to Uruguay, making two out of three (67%) hagfish species present in this area either Near Threatened or Vulnerable. *M. sotoi* is not found in southern Brazil, where *E. menezesi* and *N. kreffti* are the only hagfishes known to occur until slightly north of the Brazil/Uruguay border. At the Brazil/Uruguay border and southward, *N. kreffti* and *E menezesi* are joined by *Myxine australis*, another Least Concern species, making just one in three species present (33%) in Threatened or Near Threatened categories in this region. Off southern Uruguay and northern Argentina, *E. menezesi* is replaced by another Least Concern species, *Notomyxine tridentiger*.

North-west Pacific

The north-western Pacific (including the East China Sea, Yellow Sea, and coast of Taiwan) boasts the highest diversity of hagfishes on the globe. Eighteen of 76 (24%) known species of hagfish occur in this region, with the greatest diversity in any one area off the south-western coast of Taiwan where nine species might be found in a single location. Seven (39%) of the 18 known species in the north-western Pacific region are in threatened or Near Threatened categories comprising anywhere from 33–100% of the hagfish species present in a given area (Figure 3). Hagfishes are of significant economic importance in this region primarily for their leather, which is harvested for the eel-skin industry, and also as a source of food (Gorbman *et al*., 1990; Honma, 1998). In the past, the value of manufactured eel-skin products in the Korean eel-skin industry was estimated to be approximately $100 million per year and has probably risen since (Gorbman *et al*., 1990). As a consequence, many of the endemic species of the region are targeted by fisheries to be shipped to Korean manufacturers (Gorbman *et al*., 1990; Honma, 1998). Non-target hagfish

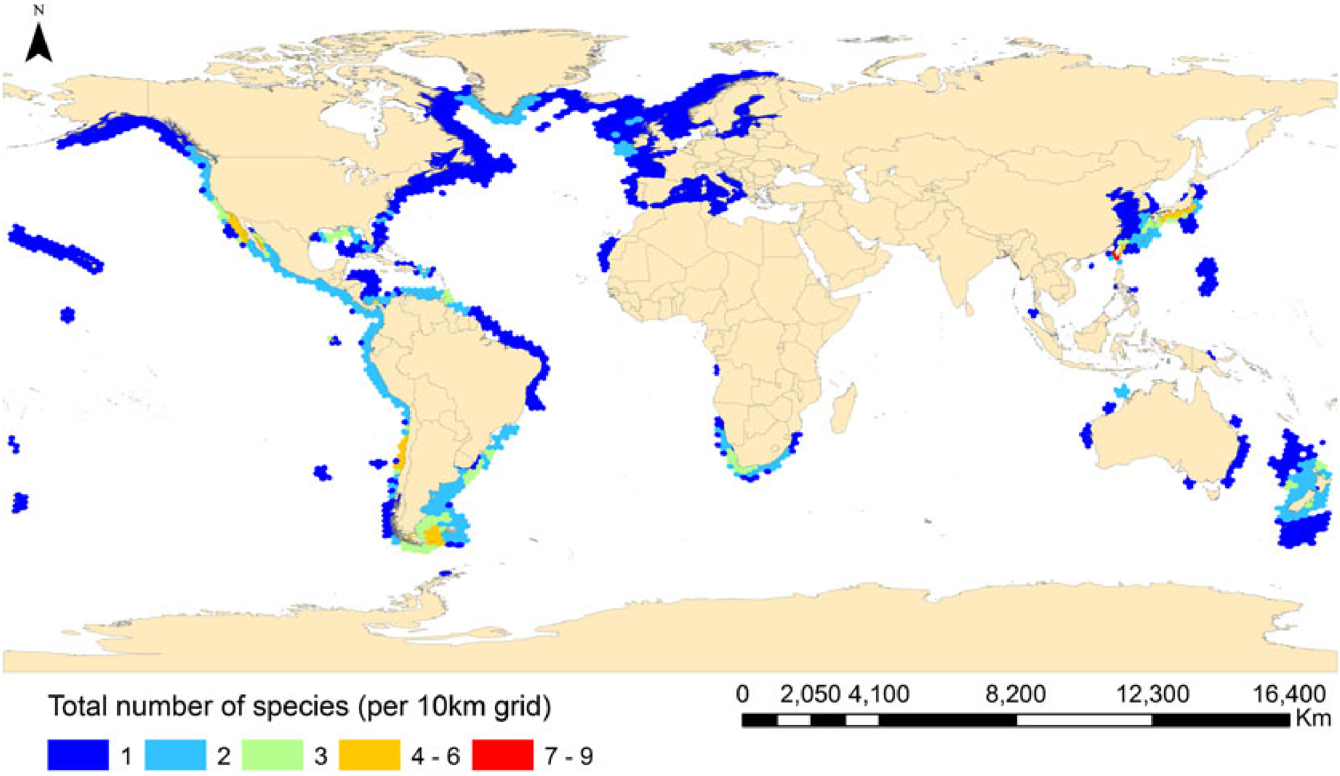

Figure 2. Hagfish species richness.

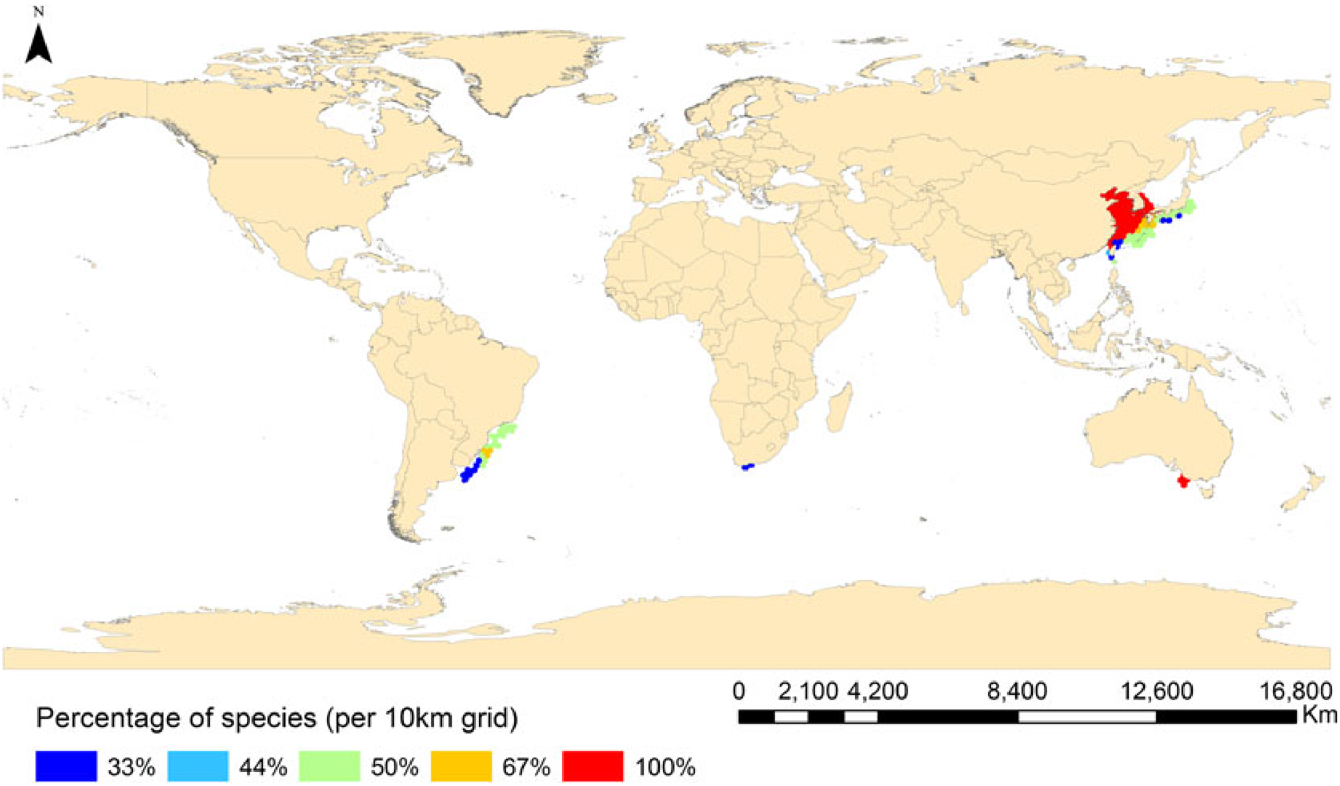

Figure 3. Proportion of threatened (CR, EN, VU) and Near Threatened (NT) species of hagfishes occurring in major regions of the World.

bycatch in the north-western Pacific is not discarded like it is in many other regions, but is instead sold in local fishing markets as a food source (Mok and Chen, 2001).

The area including the Yellow Sea, East China Sea and north-western Taiwan Strait has the highest proportion of Threatened or Near Threatened species, with the two species of hagfish (100%) in the area, excluding the waters surrounding the Ryukyu Islands, listed in Threatened or Near Threatened categories (Figure 3). In all of the Yellow Sea, north-western Taiwan Straight, and the majority of the East China Sea, only two hagfish species are found, *Eptatretus burgeri* and *Myxine garmani*. These species were assigned categories of Near Threatened and Vulnerable, respectively, and in consequence 100% of the species in this area have an elevated risk of extinction (Figure 3). The distribution of *M. garmani* includes all the surrounding waters of the middle and northern Ryukyu Islands (with the exception of the southern islands between Miyakojima and Yonakuni Islands) and overlaps the distribution of *Eptatretus okinoseanus*, listed as Least Concern. *Eptatretus burgeri* is found only around the northernmost of the Ryukyu Islands together with *M. garmani* and *E. okinoseanus*, and therefore two of the three species (67%) of hagfish are either Threatened or Near Threatened in this area. In the middle Ryukyu Islands only *M. garmani* and *E. okinoseanus* are found, making 50% of the hagfish species present threatened. All of the Threatened or Near Threatened species in the north-western Pacific have relatively small ranges and are heavily affected by both targeted and non-targeted fisheries.

Taiwan

The highest hagfish species diversity of any area is found off the coast of Taiwan, with 13 species of hagfish present (Figure 2). Five of these species are in Threatened or Near Threatened categories (38%). The five species in Threatened or Near Threatened categories are believed to be endemic to Taiwan, except *Eptatretus burgeri*, which is also found off the coast of southern Japan and the northern Ryukyu Islands, the western East China Sea, and the Yellow Sea. *Eptatretus burgeri*, listed as Near Threatened, is heavily harvested throughout its range for the eel-skin industry in Korea and as a food source in Taiwan, Japan, and China (McMillan and Wisner, 2004). Catch data in one third of the range of *E. burgeri* show a 70% decline between 1980 and 1995 (Gorbman *et al*., 1990; Honma 1998) with effort assumed to be low but consistent through this period. Assuming no decline in the other portions of the range of this species or in more recent years, it is conservatively estimated that there has been at least a 23% decline in *E. burgeri* since 1980. Despite such alarming catch data, this species continues to be harvested at high levels even as the size of individuals has decreased in the last decade (McMillan and Wisner, 2004).

Chile and Argentina

Chile and Argentina host the highest number of Data Deficient species (Figure 4), even though the southern central coasts of South America have the second highest hagfish biodiversity in the world (Figure 2). Of the combined 14 species that inhabit this area including the Falkland Islands, eight (57%) have been assessed as Data Deficient. These eight species account for between 33% (1 in 3 species) and 100% of the hagfish species present along different overlapping areas in the region (Figure 4). The highest proportion of Data Deficient species occurs along the coast of central Chile where *Eptatretus bischoffii, Eptatretus polytrem*, and *Myxine pequenoi* comprise 100% of the hagfish population (Figure 4). The coastline to the north of central Chile is mainly inhabited by four species of hagfishes (*E. bischoffii*, *E. nanii*, *E. polytrema* and *Myxine circifrons*). All *Eptatretus* species found in the area are also listed as Data Deficient, while *M. circifrons* is listed as Least Concern, making 75% of the species present Data Deficient (Figure 4). *E. bischoffii* has the most northerly distribution of any of the *Eptatretus* species and it combines in its northern distribution with *M. circifrons* to make 50% of the species present Data Deficient. *Myxine fernholmi*, a Least Concern species, has been recorded from one specimen in northern Chile, and it overlaps with *E. bischoffii* and *M. circifrons* in this area to give 33% of hagfishes present Data Deficient categories. The only other hagfish species found in this area, *Myxine hubbsoides*, is known only from three type specimens collected off the coast of central Chile, and was therefore listed as Data Deficient. West of central Chile, *E. polytrema* is found around the eastern Juan Fernández Islands in relatively shallow waters (10 to 350 m). It is listed as Data Deficient because it is only known from a few specimens, and it is not known if any fishing or other threats are affecting its population or relatively shallow water habitat. The western Juan Fernández Islands are inhabited by *E. laurahubbsae*, which is a Least Concern species. Although *E. laurahubbsae* is also only known from a few specimens, it is found in very deep waters (to 2400 m), and there are no suspected threats to this species.

The coasts of Argentina and the Falkland Islands (including the eastern Strait of Magellan) are inhabited by seven species of hagfish, comprising the most diverse region of the south-west Atlantic (Figure 2). However, knowledge of the hagfishes that occur in this area is still insufficient and the proportion of Data Deficient species in the south-west Atlantic is relatively high (Figure 4). The entirety of the coastline of Argentina is inhabited by *M. australis* and *N. tridentiger*, which are assessed as Least Concern and Data Deficient respectively. Along the northern half of the Argentine coastline on the continental shelf and slope near the La Plata River, only one other species, *N. kreffti*, which is listed as Near Threatened, is found. The north-eastern and southern Falkland Islands are inhabited exclusively by *Myxine fernholmi*, a Least Concern species, and *Myxine knappi*, a Data Deficient species, while in the north-western portion of the Falkland Islands only *M. knappi* and *N. tridentiger* are found. Bottom finfish trawlers operate extensively around the Falklands Islands and within the depth range of both of these species (Moore, 1999), although the majority of demersal trawlers in the region are restricted to operating over shelf waters (<200 m depth), and the number of boats operating within the 200 nautical mile Falklands Conservation Zone is limited to about 200 vessels per year (Coggan *et al*., 1996). However, the impact of trawling on these Data Deficient species populations is not known. On the western side of the islands, both *M. knappi* and *N. tridentiger* have a distribution stretching to the coast of Argentina where they overlap with *M. australis* on the eastern coast. In the combined Pacific and Atlantic waters surrounding Tierra del Fuego, *N. tridentiger* is sympatric in most locations with two Least Concern species, *M. affinis* and *M. australis*, to give this region 33% Data Deficient hagfish species. In the Straight of Magellan, these three species combine with *Myxine dubueni*, a Data Deficient Species only known from the type locality, which makes 50% of hagfishes present Data Deficient. Both *M. australis* and *M. affinis* are considered to be relatively widespread and common where found.

North-west USA and Canada

Another region with a high proportion of Data Deficient species is the north-west coast of the USA and Canada, where

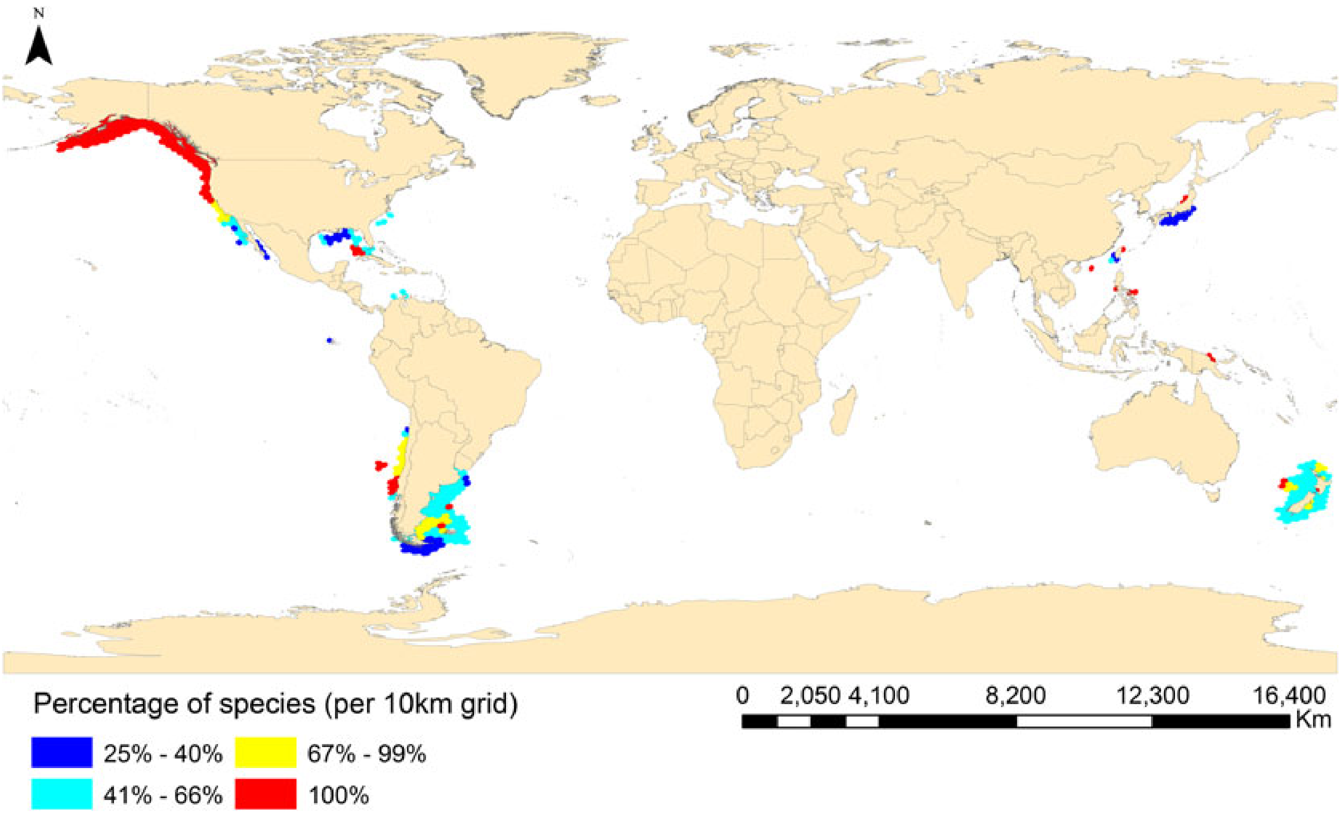

Figure 4. Proportion of Data Deficient (DD) species of hagfishes occurring in major regions of the World.

the only hagfish species present, *Eptatretus stoutii* and *Eptatretus deani*, are heavily targeted for the Asian eel skin leather market (Barrs, 1993). Reported landings for these species are mixed and have been quite variable in both total catch and effort over the past 20 years (Barrs, 1993; FAO, 2009). The causes of the variability in catch and effort trends in this region are not completely understood and for this reason both species could not be assigned a Red List category other than Data Deficient.

Indian Ocean

Hagfish are not known to be present in the Indian Ocean. This is probably attributable to insufficient sampling in the area, which has produced almost no specimens to date.

CONCLUSIONS AND RECOMMENDATIONS

Knowledge of known hagfish species is lacking in several areas of the world due to the cryptic nature of the fishes and the lack of research and sampling in the various areas they inhabit. In order to understand hagfish species better, their distribution, population trends, habitat and ecology need to be studied in much greater detail. The decline of hagfish species, especially in areas of intense fishing and with already low hagfish species diversity, is thought to result in ecosystem alterations that could have detrimental effects on the trophic dynamics of benthic habitat (St Martin, 2001). When fishing pressure shifts to hagfishes in certain areas, other commercial ground fish have shown declines in catch numbers (St Martin, 2001). Operating unchecked, the hagfishery industry has been able to thrive, boasting profits of over $100 million per year (Gorbman *et al*., 1990). Several fisheries now exist to satisfy the demand for eel-skin in Korea, which continues to be a lucrative business (Gorbman *et al*., 1990; Barrs, 1993; Keith, 2006). However, the multiple beneficial effects hagfishes have on their habitats and wider ecosystems have yet to be studied in detail, and overharvesting of hagfishes may have lasting ecological damage, especially in the many areas with low hagfish diversity. More research is therefore urgently needed not only on individual hagfish species to determine their distribution, biology and ecology, but also on the impacts of targeted and trawling fisheries on hagfish populations and the ecosystems they support.

No current conservation measures or legislation exist to protect the survival of hagfish populations throughout the world's oceans. Even in areas where hagfishes are heavily targeted and highly profited from, there are no restrictions or guidelines in place for acceptable harvesting practices. The only protection afforded to any hagfish species is general trawling and fishing restrictions put in place for a region where that species is found. A species might be fortunate if it inhabits a region that has established marine protected areas, but since many hagfishes are deepwater species, these shallow water areas do not cover the majority of the hagfish species' distribution in many cases. *Myxine glutinosa* is the one species of hagfish that is in the process of having its catch numbers regulated as the Gulf of Maine Hagfish Fishery has established plans to regulate their catch (Keith, 2006). In addition, the National Marine Fisheries Service (NMFS) has proposed a data collection programme that requires seafood dealers to acquire permits and report on the purchase of hagfishes made from commercial fishing vessels in order to aid in the future management of the species (Keith, 2006).

More legislation and protection is required in order to ensure the long-term survival of hagfish species, with a focus on those species that are targeted for harvest. In particular, better fisheries statistics including catch landings and recorded bycatch of hagfish species is needed to determine not only the impact of extensive trawling on hagfish populations, but also to better determine species distribution and population trends. Research is also needed on the impact of trawling on hagfish ecology and habitat. More awareness needs to be raised on the ecological importance of these species that play such an important role in nutrient cycling worldwide, but are relatively few in number. With a broader knowledge of hagfishes both individually and as a whole, more effective conservation measures can be put in place to limit the impact that human activity is having on a relatively understudied part of marine biodiversity that should not be overlooked.

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