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Policy analysis

Global conservation status of the world's most prominent forage fishes (Teleostei: Clupeiformes)

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ABSTRACT

Understanding the extinction risk of taxonomic groups increases our ability to prioritize efforts to address biodiversity loss. Over 400 species of herrings, shads, sardines, anchovies, menhadens, and relatives belong to the Order Clupeiformes and include many of the most important forage fishes. These small, schooling fishes are ecologically, economically, and culturally significant. However, despite their global contribution to fisheries and our increasing reliance on them for food and modern commodities, we lack critical information regarding basic biology and population trends for most species. We applied the IUCN Red List methodology, a comprehensive and systematic approach to assess extinction risk, to all clupeiform species. The best estimate suggests nearly 11% of species are of elevated conservation concern, although this could be as high as 36%. Two regions, the Caribbean and the Indo-Malay-Philippine Archipelago have high concentrations of threatened and Data Deficient species and are areas of conservation concern. Major threats include overexploitation, pollution, and habitat modification. Immediate conservation priorities include: 1) increasing research and mitigative action directed toward species assessed as threatened or Data Deficient; 2) improving fisheries management regulations for the understudied but heavily exploited species, and 3) promoting local, intensive habitat restoration to reduce pollution and remove dams. These extinction risk assessments and subsequent analyses should be used as an informative tool for fisheries and conservation managers and to monitor conservation progress.

1. Introduction

Forage fishes are a crucial link between primary production and keystone predators in aquatic environments (Pikitch et al., 2014). These typically abundant small- to medium-sized pelagic species feed at the base of the food web and serve as a predominate prey source for numerous predators, such as piscivorous fishes, mammals, squids, and seabirds, many of which are also commercially important (Cury et al., 2011; Smith et al., 2011; Pikitch et al., 2014; Hilborn et al., 2017). Forage fishes include a diverse array of bony fishes and invertebrates such as krill and squid (Pikitch et al., 2014; Rountos, 2016). Many species also support the global economy by directly and indirectly sustaining many fisheries (Pikitch et al., 2014) and contribute 20–30% to the annual global marine catch (Alder et al., 2008; Smith et al., 2011; Pikitch et al., 2014).

Species of the Clupeiformes (Teleostei), commonly known as herrings, shads, menhadens, sardines, anchovies, and their relatives, are a major component of forage fishes in coastal ecosystems and dominate worldwide forage fish landings (Tacon and Metian, 2009; FAO, 2020). Additional to providing ecological and economic support, clupeiforms

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contribute to global food security given their abundance, easy access, and exceptionally high nutrient content (FAO, 2018). In some human communities, clupeiforms comprise the major or the sole protein source (Alder et al., 2008; Mohanty et al., 2019). Historically, clupeiform presence has been associated with persistent human settlement, growth, and survival (e.g., Bloch, 1809; Thornton et al., 2010; Levin et al., 2016). To meet the needs of a rising human population (United Nations, Department of Economic and Social Affairs, Population Division, 2017), demand for fisheries resources is expected to continue growing (FAO, 2018). Given the overall ecological, cultural, nutritional, and economic importance of clupeiforms worldwide, their conservation status warrants greater attention.

The Clupeiformes includes 415 species that are globally distributed with tropical, temperate, and sub-Arctic representatives (Whitehead, 1985; Whitehead et al., 1988; Lavoué et al., 2013). Clupeiform fishes are ecologically diverse and span all aquatic habitats, including coastal and open marine environments, oceanic islands, estuaries, and freshwater rivers and lakes (Whitehead, 1985; de Pinna and Di Dario, 2003; Lavoué et al., 2013; Bloom and Egan, 2018). Species can be restricted to marine, estuarine, or fresh waters, or they can be euryhaline, where a subset exhibit diadromy (Whitehead, 1985). Strictly marine clupeiforms (33.7% of all species) are distributed in every ocean, except for the Southern Ocean (Whitehead, 1985), while strictly freshwater species (17.8% of all species) are found on every continent except for Antarctica (Bloom and Lovejoy, 2012, 2014; Bloom and Egan, 2018).

Despite the global importance of clupeiforms, basic biological information, fisheries data, and management efforts are severely deficient compared to those of other commercially important fishes, such as tunas and billfishes. This disparity may be due in part to perception of extinction resistant traits or may result from the taxonomic complexity of clupeiforms (Whitehead, 1985; Alder et al., 2008). Value per pound for clupeiforms is also far less than that for other commercial fishes, which may further disincentivize the contribution of resources to research and conservation for the clupeiforms. For example, the average commercial landed value of all tunas in the U.S. for 2017 was about USD $2.8/pound, while the average value for clupeiforms was roughly USD $0.09/pound (NOAA Fisheries, 2019). The paradox between worldwide clupeiform importance and lack of available resources and reliable data reinforces the need to invest effort into understanding the current conservation status of the members of this group.

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species provides a key starting point for highlighting and addressing conservation needs for species (Mace et al., 2008). The IUCN Red List, an open-access repository of species-specific assessments, categorizes a species conservation status by interpreting its risk to extinction (Rodrigues et al., 2006; Vié et al., 2009). Red List assessments are the most widely accepted standard for species-level risk evaluations (Hoffmann et al., 2008). By illuminating gaps in conservation knowledge for species, assessments can be used to inform and influence decisions regarding biodiversity conservation (Rodrigues et al., 2006; Mace et al., 2008; Vié et al., 2009).

Limited species-specific conservation information on clupeiforms hampers our ability to proactively manage and conserve these essential components of aquatic food webs. To address this gap, we applied the IUCN Red List methodology to assess the extinction risk of the 415 valid clupeiform species. The assessments and accompanying data were used to evaluate: 1) variability in the proportion of species at an elevated risk of extinction as a function of family, and habitat; 2) major threats; and 3) spatial patterns in species richness. These analyses provide a baseline from which to monitor changes in conservation status and are used to identify conservation priorities and research needs.

2. Methods

2.1. Taxonomic scope

Phylogenetic relationships among the main groups of the Clupeiformes are contentious, resulting in different proposals of taxonomic classifications (e.g., Di Dario, 2002, 2009; Miyashita, 2010; Lavoué et al., 2014). Overall, the order is divided into the Denticipitoidei, with a single living representative (*Denticeps clupeoides*) in the Denticipitidae, and the Clupeoidei (Grande, 1985), which includes all remaining 414 species of the Clupeiformes assessed here. The Clupeoidei has been traditionally divided into four families: the Chirocentridae, Pristigasteridae, Engraulidae, and the Clupeidae (e.g., Whitehead, 1985). However, morphological characters and molecular evidence indicates that the Clupeidae, which includes about half of all currently valid species of the Clupeiformes (Nelson et al., 2016), is not a monophyletic group (summarized in Lavoué et al., 2014). To partially acknowledge that, we provisionally accept the classification of Lavoué et al. (2014), which includes *Dussumieria*, *Etrumeus*, *Spratelloides*, and *Jenkinsia*, in a distinct family (Dussumieriidae). *Sundasalanx* is a paedomorphic genus of freshwater clupeiforms of unknown relationships within the Clupeoidei (Siebert, 1997; Lavoué et al., 2013, 2014). The genus is generally regarded as a member of the Clupeidae (Siebert, 1997; Lavoué et al., 2014; Nelson et al., 2016), but given its controversial position in the Clupeoidei, the Sundasalangidae is also provisionally recognized as a distinct family (Van der Laan et al. 2014). In this arrangement, the Clupeidae includes 188 species. Therefore, for the purposes of this study, seven families of the Clupeiformes are recognized: Denticipitidae (1 species), Pristigasteridae (37 species), Engraulidae (161 species), Chirocentridae (2 species), Clupeidae (188 species), Dussumieriidae (19 species), and Sundasalangidae (7 species).

2.2. Quantifying extinction risk

We compiled a species list based on the online version of the Catalog of Fishes up to March 2020 (Fricke et al., 2020) and in consultation with taxonomic experts. Individual clupeiform species' assessments were based on available information from published and grey literature regarding geographic distribution, population status, life history, utilization and quality of habitat, potential threats, and known conservation measures. The assessment process included involvement from 132 international experts from more than 20 countries with regional or species expertise. We identified potential experts to be involved in the assessments from the authors of peer-reviewed publications, FAO fisheries identification guides, and through the IUCN Species Survival Commission network. All 415 species were assessed against the IUCN Red List Criteria (Mace et al., 2008; IUCN, 2012) at workshops and through online collaborations. Draft assessments go through multiple rounds of review by species experts and the Red List process prior to publication. As of July 2020, all species assessments included in this analysis are published on the Red List website (www.iucnredlist.org).

The IUCN Red List includes eight global 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: IUCN, 2012). A taxon is considered EX when there is no reasonable doubt the last individual has died or is EW if it is only known to survive in cultivation, captivation, or in naturalized populations outside of its historic range (IUCN, 2012). A species can reasonably be presumed EX or EW when exhaustive surveys fail to report it (IUCN, 2012). To qualify for a threatened category (CR, EN, VU) a species must meet at least one of the five quantitative thresholds under IUCN Criteria (A–E: Mace et al., 2008). The criteria evaluate population decline (A), restricted geographic distribution (B), small population size and decline (C), very small or restricted population size (D), and the high probability of potential extinction (E: Akçakaya et al., 2000; Mace et al., 2008).

For each assessment, experts evaluated the species-specific data available against all five Red List Criteria (IUCN, 2001, 2012). Almost all species were assessed under criteria A (population decline) or B (restricted geographic range). Data required to assess a species under the remaining criteria (C, D or E) were often unavailable. Species were assigned to the highest threat category for which the available data met or exceeded the associated thresholds and conditions (IUCN, 2001, 2012; IUCN Standards and Petitions Subcommittee, 2017). A category of NT was applied if the quantified estimates of population decline or geographic range size nearly meet the thresholds for assigning a threatened category under at least one of the criteria. A species was listed as LC if it did not qualify for a threatened or NT listing based on the available data. Finally, the DD category was applied if a species is known from few specimens, lacks information to assess under any of the criteria, or there is uncertainty regarding its taxonomic status (IUCN, 2001, 2012; IUCN Standards and Petitions Subcommittee, 2017). This category was also applied if declines were likely due to a known but unquantified threat (e.g., fishing pressure), such that a more appropriate category could not be assigned.

Direct threats impacting each species were identified from using information available in the published literature (peer-reviewed and grey), verified by species or regional experts, and categorized within each species assessment using the standardized IUCN Threat Classification Scheme (version 3.2: IUCN-CMP, 2016). These coded threats and full bibliographies are available as part of the assessment for each species. Major threats were summarized across species as a function of primary habitat system (marine, euryhaline, freshwater). The proportion of species listed as threatened (CR, EN, VU) and NT, herein referred to as species of elevated concern, was also explored as a function of family and major habitat system. The proportion of species of elevated concern is expressed using both a midpoint and a range to address the uncertainty surrounding the true status of DD species. The midpoint was calculated by removing the species listed as DD, whereas the lower and upper bounds were calculated by excluding or including the DD species with the threatened and NT, respectively. The lower boundary assumes that none of the DD species are of an elevated concern, while the upper boundary assumes that all DD species are of an elevated concern (IUCN, 2016).

A species was assigned a major habitat category using the information in the Red List assessments. Given the known or suspected tolerance for salinity fluctuations exhibited by many clupeiforms, we modified the IUCN Red List system classification scheme from two aquatic categories (freshwater, including inland estuarine waters; and marine, including coastal estuarine waters) to three categories. Therefore, the freshwater system includes those species known to occupy only freshwater environments and the marine system includes species restricted to marine waters. The third, euryhaline category includes estuarine species, diadromous species, and species known or suspected to tolerate changes in salinity.

2.3. Distribution maps and spatial analyses

Maps were created for each species using ArcMap 10.3 based on occurrence records, habitat preferences, and depth limits and were reviewed by species experts. As marine clupeiforms are primarily coastal, the distribution polygons for strictly marine species were standardized using a base map that represents either the 200 m bathymetric line or 100 km from the shore, whichever was further from the coast. Bathymetric layers were extracted from two global level sources, the National Geophysical Data Center's ETPO1 (Amante and Eakins, 2009) and the General Bathymetric Chart of the Oceans (GEBCO: IOC et al., 2003). Maps for freshwater species were created using hydrobasins, because these areas are considered as minimum management units for freshwater conservation (Lévêque et al., 2008; Carrizo et al., 2013). For species that utilize both marine and freshwater habitats (e.g., diadromous species), maps separately followed the marine and freshwater protocols, and were combined to encompass the entirety of the species' range.

Global maps of overall species richness, DD richness, and richness of elevated concern species were also created using ArcMap 10.3. Species with a freshwater distribution were summarized within the Global HydroBASINS (Lehner and Grill, 2013), using the largest river basins of each continent. Species with a marine distribution were summarized within the Marine Ecosystems of the World at the province level (Spalding et al., 2007). This shapefile was modified to include a region for the Caspian Sea, as it is excluded from the Global HydroBASINS and Marine Ecosystems of the World.

3. Results

3.1. Global IUCN Red List status of clupeiforms

The best estimate of the proportion of clupeiforms of elevated concern is 11%. Given the uncertainty of an appropriate Red List Category for all DD species, the true proportion of elevated concern species could lie between 8 and 36%. Of all species (n = 415), three (0.7%) are listed as CR, 11 (2.7%) as EN, 13 (3.1%) as VU, and five (1.2%) as NT. No species were listed as EX or EW. Species are primarily listed as elevated concern either due to a restricted range size with an ongoing threat (criterion B; n = 17) or due to population decline (criterion A; n = 10); two species (*Sardinella tawilis* and *Alosa vistonica*) are listed under both criteria A and B. Three species are listed as VU given a very restricted range and a serious plausible future threat (criterion D). Of the remaining 383 species, 267 (64.3%) are categorized as LC, and 116 (28.0%) are considered DD.

Among families of the Clupeiformes, the Denticipitidae consists of only one species, *Denticeps clupeoides*, which is listed as VU. As such, this family has the highest proportion of elevated concern species overall (Fig. 1). Excluding *D. clupeoides*, the Clupeidae has the highest proportion of elevated concern species (25 of 188 species; midpoint = 16.7%), followed by the Engraulidae (5 of 161 species; midpoint = 4.9%), and the Pristigasteridae (1 of 37 species; midpoint = 3.8%). None of the Chirocentridae (n = 2), Dussumieriidae (n = 19) or Sundasalangidae (n = 7) are listed as threatened. However, the high proportion of DD species, especially within the Sundasalangidae, may be obscuring the actual conservation status of these families.

Species classified as euryhaline (i.e., diadromous or estuarine) constituted nearly half of all clupeiforms (n = 201; 48.4%), followed by marine (n = 140; 33.7%) and freshwater species (n = 74; 17.8%) (Fig. 2). Euryhaline habitats harbor the largest proportion of LC species (n = 147; 73.1%) followed by marine habitats (n = 80; 57.1%), and then freshwater habitats (n = 40; 54.1%). Despite having the lowest number of representatives, freshwater clupeiforms have the highest proportion of elevated concern species (16 of 74 species; midpoint = 28.6%), more than three times the proportion in marine environments (7 of 140 species; midpoint = 8.0%), and four times the proportion of elevated concern species found in euryhaline environments (9 of 201 species; midpoint = 5.7%). Additionally, all species assessed as CR (n = 3), the highest threat level, are found in freshwater habitats.

3.2. Major threats

Of the 415 species, 144 have at least one identified threat. The remaining 271 species have either no major threats causing significant impacts, or threats to these species are unknown. The most prominent threat to clupeiforms in all habitats is overexploitation, impacting 107 species overall (Fig. 3). Pollution and natural system changes (e.g., dams) impact nearly the same number of species (47 and 42, respectively). However, despite having the highest proportion of LC species (Fig. 2), the majority of species impacted by pollution or natural system changes are euryhaline (Fig. 3). Of the species impacted by at least one threat, roughly the same proportions of freshwater and euryhaline

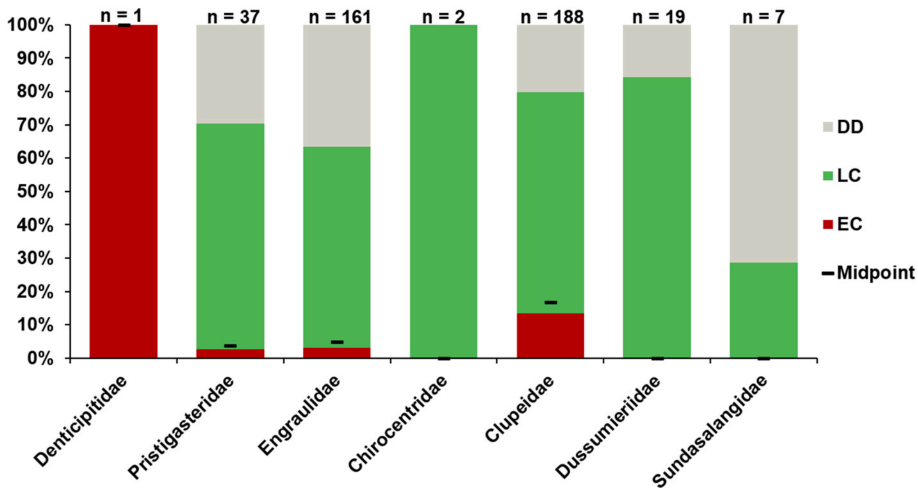

Fig. 1. Proportion of species listed in Red List Categories partitioned by family. Abbreviations of Red List Categories are as follows: EC = elevated concern (includes species evaluated as Critically Endangered, Endangered, Vulnerable, or Near Threatened), LC = Least Concern and DD = Data Deficient. The total number of species in each family is represented by the number at the top of each bar. The midpoint is represented by the black bar and was calculated by the following equation: (CR + EN + VU + NT) / (Total − DD).

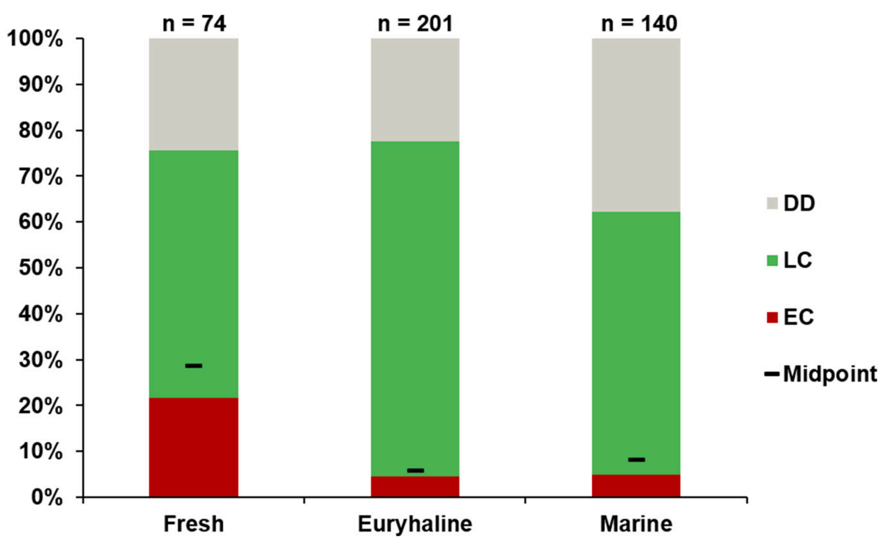

Fig. 2. Proportion of species listed in Red List Categories by major habitat system (freshwater, euryhaline, or marine). Abbreviations of Red List Categories are as follows: EC = elevated concern (includes species evaluated as Critically Endangered, Endangered, Vulnerable, or Near Threatened), LC = Least Concern and DD = Data Deficient. The total number of species in each family is represented by the number at the top of each bar. The midpoint is represented by the black bar and was calculated by the following equation: (CR + EN + VU + NT) / (Total − DD).

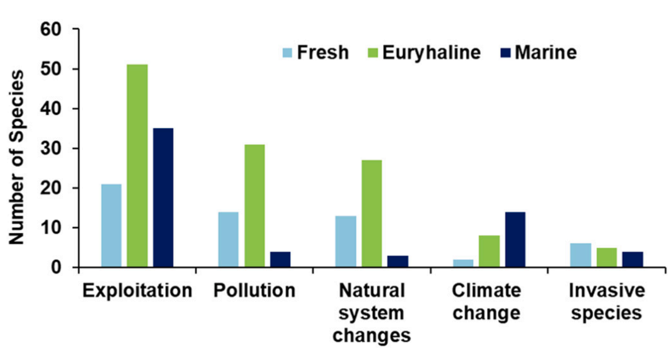

Fig. 3. Number of clupeiform species impacted by major threats. Each threat is represented by the number of species impacted separated by major habitat system (freshwater, euryhaline, or marine). Threats impacting less than ten species (Mining, Development, Human intrusion, and Transportation) are excluded.

species are impacted by pollution and natural system changes overall (84 and 76%, respectively). The proportion of marine species impacted by climate change (36%) is more than two times the proportion of euryhaline (11%) and freshwater (6%) species, while invasive species impact a higher proportion of freshwater species (18%) relative to the proportion of marine and freshwater species (11% and 7%, respectively).

3.3. Spatial analyses

Global species richness of clupeiforms follows two distribution patterns; a longitudinal gradient, where the highest tropical richness is within the Indo-West Pacific, and a latitudinal gradient where richness decreases with increasing distance from the tropics. The highest species richness of all clupeiforms is along coastal India and throughout the Indo-West Pacific from the eastern Andaman Sea, east to the Philippines, Indonesia, and northeastern Papua New Guinea (Fig. 4A). High richness also occurs in the central eastern Pacific from Mexico to northern Peru, and the central western Atlantic from the greater Caribbean to northern Brazil. Areas of lowest species richness are within the northern and southernmost limits of the global range for clupeiforms (e.g., the Arctic and north of the Southern Ocean), in inland rivers, and off Polynesian Islands.

In general, DD species richness closely follows that of the total species richness (Fig. 4B). However, DD species richness is higher in northern Australian rivers relative to the total species richness. In contrast, the high species richness in Europe, eastern United States, and South American rivers is not mirrored by high DD species richness.

Conversely, the highest richness of species of elevated concern (n =

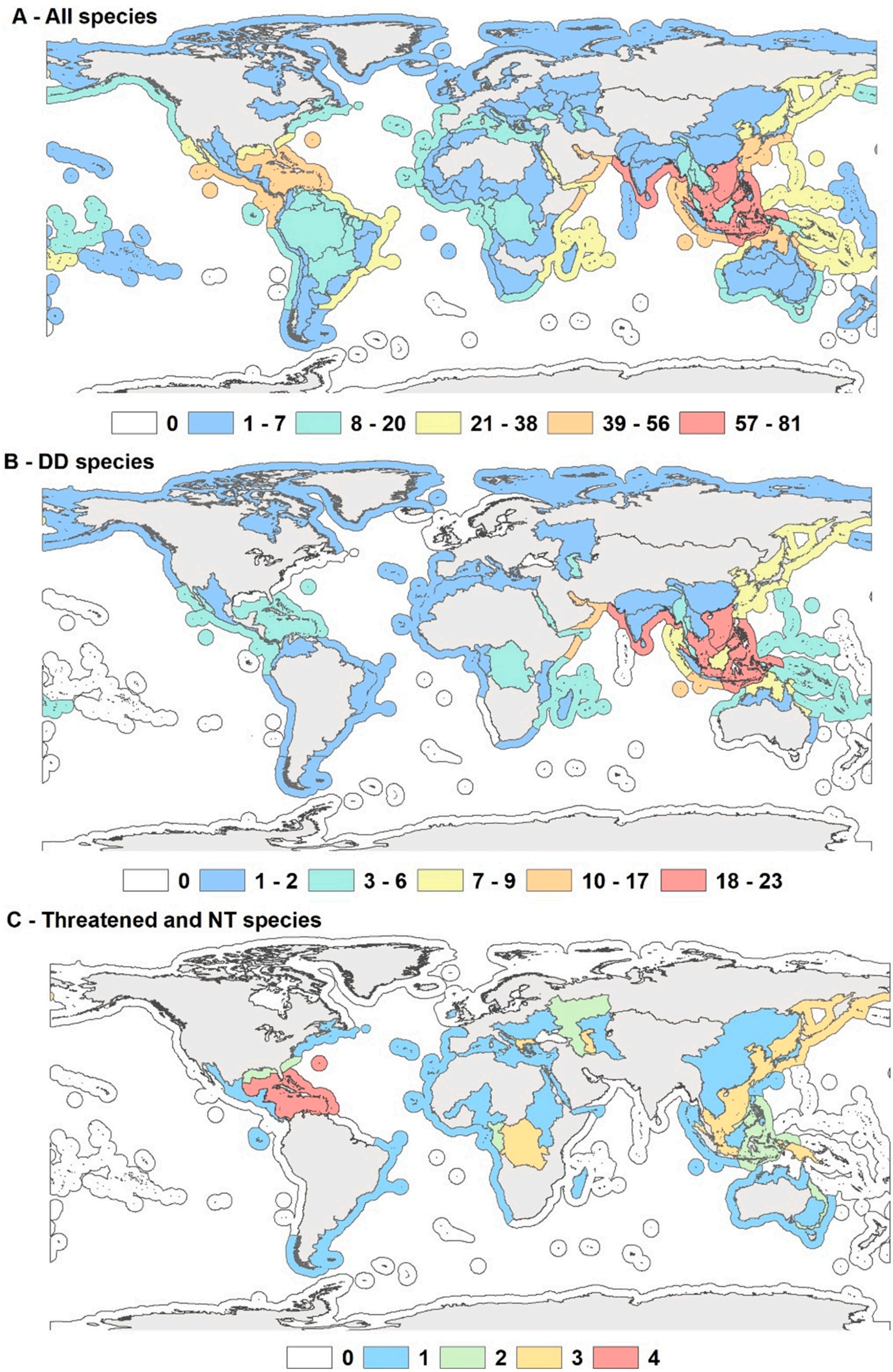

Fig. 4. Number of clupeiform species in each Large Marine Ecoregion and freshwater hydrobasin for A) all species, B) all Data Deficient species, and C) all species of elevated concern (Critically Endangered, Endangered, Vulnerable, Near Threatened). Colors correspond to numbers of species listed at the bottom of each map. The Marine Ecosystems of the World at the province level (Spalding et al., 2007) was used for marine species, Global HydroBASINS at level three (Lehner and Grill, 2013) was used for freshwater species. The freshwater and marine extents were created separately and merged to represent the total global extent for euryhaline species.

32) occurs within the greater Caribbean (Fig. 4C). Other areas of high richness for species of elevated concern are along the western Pacific continental coast (Russia south to Indonesia), and inland areas including the Caspian Sea and the Congo River in Central Africa. A low richness of elevated concern species is scattered along regions such as the northeastern United States, the eastern and southern coasts of South America, western Africa, and parts of Europe and Asia.

4. Discussion

Major threats to clupeiforms are similar to those found for other groups of fishes (e.g., Roberts and Hawkins, 1999; Reynolds et al., 2005; Dulvy et al., 2009; Harnik et al., 2012), with overexploitation as the leading threat for all clupeiforms in all habitats. While overexploitation may be the most prolific threat by impacting the highest number of clupeiforms, pollution may be the most detrimental, as it affects greater numbers of CR species. When compared to other economically and ecologically important fish groups globally assessed using the IUCN Red List methodology, clupeiforms have the lowest estimated percentage of threatened and NT species overall. Using the midpoint of species evaluated as elevated concern, roughly 11% are currently at high risk compared to approximately 22% of tunas and billfishes (Collette et al., 2011), 19% of sparids (Comeros-Raynal et al., 2016), and 19% of groupers (Sadovy de Mitcheson et al., 2020).

The lower proportion of threatened species in clupeiforms may be a function of uncertainty and is likely an underestimate of the true conservation status for many of these species. The high percentage of DD clupeiforms (28%) surpasses that of the tunas and billfishes (Collette et al., 2011), sparids (Comeros-Raynal et al., 2016), and groupers (Sadovy de Mitcheson et al., 2020), each with less than 20% of those species evaluated as DD. A DD listing is most often related to taxonomic uncertainty, low number of known specimens, unknown geographical range, or inability to quantify a threat or decline in population (IUCN, 2012), all of which are common within the clupeiforms. Continued taxonomic research will likely identify additional cryptic species (e.g., recent revisions of species of *Sardinella*, *Stolephorus* and *Encrasicholina* – Thomas et al., 2014; Hata and Motomura, 2019a, 2019b, 2019c), clarifying our current understanding of the complex taxonomy and biodiversity of this group and influencing the assessments of some species.

If the DD species were evenly distributed relative to total richness, we would expect that all areas would have about 28% DD species. Instead, we found high variation in both the numbers and proportion of DD species. For example, a few freshwater river basins (in eastern and northwestern Africa; southern United States and northern Mexico; and Borneo) are, or are nearly 100% DD. However, these areas are characterized by low clupeiform richness, with only one or two species occurring in each of these regions. The highest number of clupeiform species evaluated as DD generally coincides with geographic areas of both high clupeiform biodiversity and areas of low per-capita income. For example, the Coral Triangle is the epicenter of marine biodiversity (Carpenter and Springer, 2005; Sanciangco et al., 2013) and is a hotspot for clupeiform species (up to 81), which are heavily relied on for subsistence in local fisheries.

In general, global biodiversity is unevenly distributed; the most biodiverse places are often areas of high human populations of relatively low per capita income (Baille et al., 2004; Brooks et al., 2006) and tend to have the highest number of threatened species (Hoffmann et al., 2010; Baille et al., 2004). Countries with high human populations and high biodiversity are less likely to have financial resources available for research and conservation purposes (Baille et al., 2004), and may rely more heavily on local marine resources for livelihood (Creel, 2003; Ferrol-Schulte et al., 2015). In contrast, countries such as those in the advanced economies of Europe invest substantially in conservation research and management and have few globally threatened species (Baille et al., 2004), including those among the clupeiforms where both the number and proportion of threatened and DD are very low.

In many parts of the world, particularly in highly biodiverse areas, clupeiform stock assessments and fishery effort data are lacking or are unreported. Where data are available, it is often in the form of raw fishery landings (FAO, 2016) or reconstructed catches (Pauly and Zeller, 2016a). These landings frequently aggregate several species together because those that co-occur often school together and are difficult to identify (e.g., species of sardines and anchovies: Bakun and Cury, 1999). Teasing apart landings from multi-species fisheries is a difficult task and identifications that contain many errors can lead to false estimations of species-specific catch data (Gaichas et al., 2012). Overexploitation is a major threat to over 25% of clupeiform species, but this likely underestimates the impact given uncertainties in landings and the population status of species evaluated as DD. Clupeiforms also contribute to many unreported artisanal fisheries (Whitehead, 1985; Whitehead et al., 1988), represent a significant portion of bycatch in other industrial trawl fisheries (e.g., Stobutzki et al., 2001), and are taken in illegal, unreported and unregulated fisheries (IUU: Agnew et al., 2009). Accidental and IUU fishing, along with aggregated landings, adversely affect our ability to quantify global fishing pressure on these species. It can further impact conclusions drawn regarding population trends by underestimating true catches (Pauly and Zeller, 2016b), which ultimately impacts the efficacy of conservation or management decisions.

The highest concentration of threatened species is centered in the Caribbean region; however, the highest species richness overall and of DD species is concentrated in the central Indo-West Pacific region. Therefore, only about one-tenth of the Caribbean species are assessed as DD compared to roughly one-third of Indo-West Pacific species, highlighting our increased knowledge of Caribbean species. Currently, clupeiforms in the Caribbean would benefit most from threat mitigation, while emergent research to fill in our knowledge gaps in the Indo-West Pacific region should be prioritized. As more data become available to adequately assess species currently listed as DD, it is likely that we may find a higher proportion of elevated concern species within the Indo-West Pacific, relative to that reported from the Caribbean.

In addition to the high proportion of DD species, traditional perceptions of intrinsic life history traits have impeded the conservation of clupeiforms. Their typically high fecundity, multiple spawning, and early age of maturation are regarded as resilience factors, even though these traits often do not reflect lower vulnerability to extinction (Jennings et al., 1998; Kindsvater et al., 2016; Sadovy, 2001; Juan-Jorda et al., 2012; Comeros-Raynal et al., 2016). For example, the widely distributed Pacific herring (*Clupea pallasii*) is exploited to varying degrees throughout a large portion of its range. In some regions where this species has experienced drastic declines, subpopulations have not recovered even decades after fishing pressure has ceased (see Hay et al., 2001 for description of Yellow Sea and Hokkaido – Sakhalin herring). Overall, intrinsic life history characteristics of many clupeiforms and likely other important forage groups may provide a buffer against extinction (compared to long-lived taxa such as sharks, rays, tunas, billfishes, and groupers), but this buffer does not hold for all clupeiform subpopulations.

Synergistic influences of threats can be detrimental to the survival of a population (Brook et al., 2008). Often, freshwater and euryhaline clupeiforms are threatened by both pollution and natural system modifications, indicating a potential for increased cumulative effects. Many anadromous representatives in genera such as *Alosa* and *Tenualosa* appear to be most negatively impacted by one or both threats (e.g., Freyhof and Kottelat, 2008a; NatureServe, 2013; Di Dario, 2018; Mohd Arshaad et al., 2018). In line with previous studies of other freshwater fishes (e.g., Collen et al., 2014), freshwater clupeiforms have roughly four times the proportion of elevated concern species compared with that among marine and euryhaline representatives within the group. Given that all species listed as CR are freshwater clupeids, the responses to multiple stresses by all freshwater clupeids should be examined more closely. Additionally, the freshwater denticle herring, *Denticeps clupeoides*, is the only member of the Denticipitoidei, a very distinct and presumably old (ca. 126–121 Mya) lineage of clupeiform fishes (Malabarba and Di Dario, 2017). This species is a relict that inhabits a few isolated coastal streams of West Africa (Teugels, 2003), a region heavily impacted by agricultural and urban developments (Lalèyè et al., 2010). Immediate implementation of strategies aimed at the conservation of *D. clupeoides* and other threatened freshwater clupeiforms is highly recommended.

5. Conclusion

Despite the relatively lower percentage of threatened species compared to that of other fish groups of similar economic value, the overall ecological importance of clupeiform fishes and their ubiquity as an essential fishery resource warrants conservation concern. At a local level, species with limited ranges, such as *Alosa killarnensis*, *Denticeps clupeoides*, and *Sardinella tawilis*, may require stringent protection and improvement of habitat quality (Freyhof and Kottelat, 2008b; Lalèyè et al., 2010; Santos et al., 2018). Additionally, though some species threatened with overexploitation have localized management and monitoring in place, such as *Sardinella lemuru* in the southern Philippines (Rola et al., 2018), the efficacy of current measures need to be evaluated. An increase in species-specific landings and catch statistics, coupled with effort data, would also further improve future assessments of exploited species, especially in developing countries. Large-scale industrial fisheries, such as those for the Peruvian anchoveta (*Engraulis ringens*) and the Pacific herring (*Clupea pallasii*), may benefit from increased multi-national cooperative regulations. Species of elevated conservation concern are also potential targets for improved and more stringent monitoring. Given the limited resources available, research and conservation prioritization can be difficult in areas of high biodiversity; however, mitigation of anthropogenic stressors in these areas where elevated concern species are distributed is critical. Fishery managers and funding agencies in regions with large proportions of exploited DD species may also consider prioritizing research initiatives to fill gaps in our understanding of these species.

CRediT authorship contribution statement

Tiffany Birge: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – Original draft, Visualization. **Gina Ralph:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – Review & editing, Visualization. **Fabio Di Dario:** Writing – Review & editing. **Thomas Munroe:** Conceptualization, Writing – Review & editing. **Rob Bullock:** Investigation, Writing – Review & editing. **Sara Maxwell:** Conceptualization, Writing – Review & editing. **Mudjie Santos:** Writing – Review & editing. **Harutaka Hata:** Writing – Review & editing. **Kent Carpenter:** Conceptualization, Writing – Review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108903.

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