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Extinction risk and conservation of marine bony shorefishes of the Greater Caribbean and Gulf of Mexico

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Abstract

1. Understanding the conservation status of species is important for prioritizing the allocation of resources to redress or reduce biodiversity loss. Regional organizations that manage threats to the marine biodiversity of the Caribbean and Gulf of Mexico seek to delineate conservation priorities.
2. This process can be usefully informed by extinction risk assessments conducted under the International Union for Conservation of Nature (IUCN) Red List criteria: a widely used, objective method to communicate species-specific conservation needs. Prior to the recent Red List initiatives summarized in this study, the conservation status was known for just one-quarter of the 1360 Greater Caribbean marine bony shorefishes. During 10 Red List workshops, experts applied data on species' distributions, populations, habitats, and threats in order to assign an extinction risk category to nearly 1000 shorefishes that range in the Greater Caribbean. As conservation is mostly implemented at national and local levels, two more workshops assessed the Gulf of Mexico populations of 940 shorefishes using the regional Red List guidelines.
3. About 5% of these shorefishes are globally or regionally threatened, including 6% of Greater Caribbean endemics and 26% of Gulf endemics. About 9% of the species are Data Deficient. Species-richness analyses show that the highest numbers of threatened species endemic to the Greater Caribbean are found in Belize, Panama, and the Cayman Islands. The most pervasive threats to the threatened and Near Threatened species are overexploitation, habitat degradation, and predation by the invasive lionfish. Half of the threatened species are experiencing multiple threats that are likely to amplify extinction risk.
4. Recommended actions, in addition to conducting diversity surveys in lesser explored areas, include improving fishery management, reducing habitat degradation, and controlling lionfish populations.

KEYWORDS
coastal, conservation evaluation, fish, ocean, Red List

1 | INTRODUCTION

A loss of marine biodiversity directly degrades the ability of the ocean environment to produce food and other resources, and reduces marine ecosystem resilience (Worm et al., 2006). It is now clearly recognized that marine species face many extinction risks (Dulvy, Sadovy, & Reynolds, 2003; Hutchings & Reynolds, 2004; Roberts & Hawkins, 1999; Webb & Mindel, 2015). Obtaining information essential for defining the actions needed for effective marine conservation has been slower than has occurred for terrestrial systems, but this is now at the forefront of many international and national-level conservation planning agendas (Edgar, 2011). Consequently, best practice for identifying area-specific priorities and the placement of reserves has undergone considerable exploration by marine conservation biologists (Agardy, Notarbartolo di Sciara, & Christie, 2011).

Completing the first two stages of systematic conservation planning, which are to map biodiversity distribution patterns and identify conservation needs and goals, requires a large dataset on the distributions, population status, habitats, and threats of entire faunas (Margules & Pressey, 2000). Estimating extinction risk via the International Union for Conservation of Nature (IUCN) Red List of Threatened Species fulfills these data needs, and subsequently informs priorities for biological surveys and for mitigating the impact of specific threats (Vié, Hilton-Taylor, & Stuart, 2009). The open-access platform of the Red List is beneficial to a variety of stakeholders that seek to prevent biodiversity loss by identifying at-risk species within a certain geographic area or taxonomic group. These species-specific data can inform the prioritization of conservation actions that address the most pervasive threats or knowledge gaps (Brooks et al., 2006; Hoffmann et al., 2006; Rodrigues, Pilgrim, Lamoreux, Hoffmann, & Brooks, 2006).

The Greater Caribbean has the highest richness of marine species in the Atlantic Ocean and is a global biodiversity hot spot for tropical reef species (Roberts et al., 2002). This biogeographic area extends from Cape Hatteras, North Carolina, USA, southwards at least to French Guiana, and includes Bermuda, the Gulf of Mexico, the Caribbean Sea, and the Antilles (Robertson & Cramer, 2014). Geopolitically, the region includes 45 exclusive economic zones (EEZs) governed by 28 different countries. Fisheries for Caribbean reef fishes are a major source of food for coastal communities in over 25 countries, with annual net benefits estimated at US $395 million (Burke, Reytar, Spalding, & Perry, 2011). Many of these are insular countries with domestic economies currently strongly dependent on subsistence from marine resources and tourism (Mumby et al., 2014).

Throughout the Greater Caribbean, reduced shorefish diversity as a result of habitat degradation, overfishing, and predation by the invasive Indo-Pacific lionfish, diminishes nearshore ecosystem function (Albins & Hixon, 2013; Jackson, Donovan, Cramer, & Lam, 2014; Micheli et al., 2014; Paddack et al., 2009). In addition to these threats, the Gulf of Mexico, a semi-enclosed water body that includes the USA, Mexico, and north-western Cuba, is also affected by oil spills from extensive offshore oilfields in the northern and south-west sectors (Karnauskas, Schirripa, Kelble, Cook, & Craig, 2013). Greater Caribbean fishes are also subject to climate-change effects that manifest in various biophysical manners (Busch et al., 2016). To redress these issues, several regional and national-level initiatives are working to improve the established marine protected areas (MPAs), delineate new MPAs, and implement cross-boundary fisheries management.

The lack of open-access species databases impedes efforts to prevent biodiversity loss, however. For example, the disaster response to the 2010 Deepwater Horizon oil spill lacked comprehensive, baseline information on most of the marine species that were likely to encounter the spill and clean-up effort (Campagna et al., 2011). Sub-global level Red List assessments produce finer-resolution information for developing site and species-level conservation plans and the efficient maximization of limited funding sources (Vié et al., 2009). Prior to the Greater Caribbean and Gulf of Mexico Red List initiatives, only one-quarter of the 1360 marine bony shorefishes had been assessed under Red List criteria. Completing these initiatives resulted in the recent publication on the Red List website of 1000 global-level and 940 Gulf of Mexico regional-level assessments, which has greatly reduced a once substantial knowledge gap. The results of these efforts were summarized in a recent report published by the IUCN (Linardich et al., 2017), which concluded that 5% of Greater Caribbean marine bony shorefishes have been listed at an elevated risk of extinction as a result of overexploitation, habitat degradation, and predation by the invasive lionfish, and that the region's highest species richness occurs in south Florida and the Mesoamerican Reef region.

The purpose of the present paper is to compare this Greater Caribbean dataset that resulted from the global-level Red List assessment process with a similar dataset of regional-level assessments in the Gulf of Mexico. The biogeographic richness patterns of species were analysed by overlaying distribution maps, and major threats affecting species listed as Critically Endangered, Endangered, Vulnerable, or Near Threatened, and the factors that contributed to species being listed as Data Deficient, were quantified.

2 | METHODS

For the purpose of this study a shorefish was considered to be any marine bony fish with an upper depth range limit that was shallower than 200 m, and that primarily uses habitats found between estuaries and the continental shelf edge. This includes demersal or pelagic species occurring over the continental shelf that sometimes extend into deeper oceanic water. Sharks, rays, and chimaeras were not included because their conservation status has been addressed previously (Dulvy et al., 2014). A list of 1360 shorefishes was compiled in 2014 based on the best available data at that time, according to scientific literature and consultation with ichthyologists. At least 11 Greater Caribbean shorefishes have been described since the list was finalized (Linardich et al., 2017). All taxonomy was standardized against the *Catalog of Fishes* (Eschmeyer, 2015). The list of 940 Gulf of Mexico shorefishes was derived from the list of Greater Caribbean shorefishes by selecting species with geographic ranges that include the Gulf.

Our definition of the Greater Caribbean followed the conclusions of analyses of the biogeography of shorefishes reported by Robertson and Cramer (2014), with the southern extent at French Guiana and with the northern limit in the USA at Cape Hatteras (North Carolina). The Gulf of Mexico was defined according to the geopolitical

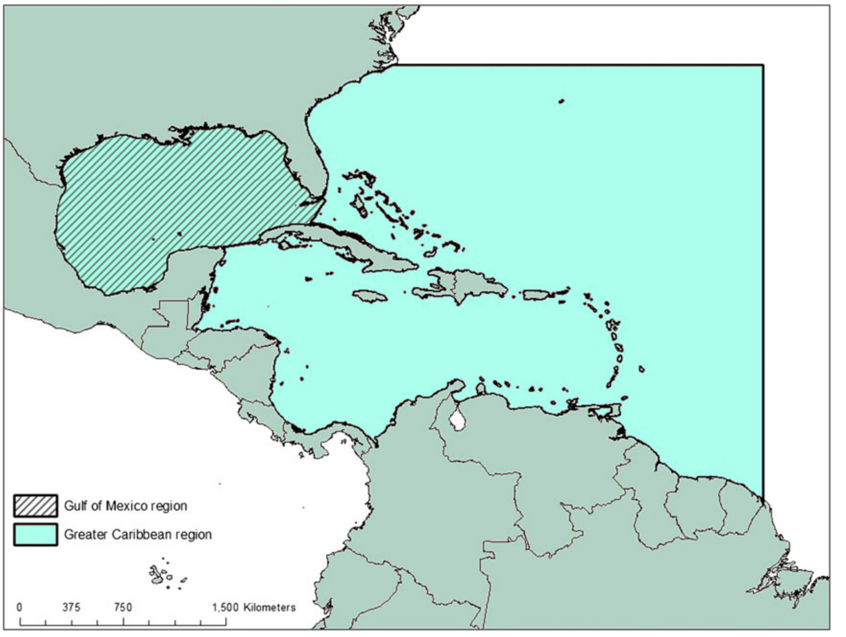

FIGURE 1 Map of Greater Caribbean and Gulf of Mexico regions. The Gulf of Mexico region is depicted in the map in stripes, and the Greater Caribbean is in blue. The Greater Caribbean also includes the entirety of the Gulf of Mexico

boundaries set by Felder, Camp, and Tunnell (2009), which includes the north-west coast of Cuba (Figure 1). The term 'endemic' refers to species that have their range entirely within the boundaries of the Greater Caribbean and/or Gulf of Mexico, or that have no more than very minor range extensions along the continental shelf (Robertson & Cramer, 2014). For example, if a species was distributed in a large part of the region but only extended slightly beyond French Guiana into the Brazilian State of Amapá, at the Amazon River mouth, it was considered a Greater Caribbean endemic.

2.1 | Red List methods

The extinction risk was estimated for each species under quantitative methods developed by the IUCN (IUCN, 2012a; Mace et al., 2008). Supporting data included distribution maps, population status, habitats, life history, use and trade, threats, and conservation measures. Ten Red List workshops held between 2009 and 2013 facilitated global assessments for about 1000 shorefishes, with the participation of local and regional experts in fish taxonomy, biology, populations, and potential anthropogenic threats (Linardich et al., 2017). Two additional workshops attended by 22 experts in 2014 (Corpus Christi, Texas, USA) and 15 experts in 2015 (Mérida, Yucatán, Mexico) completed regional assessments for 940 Gulf of Mexico shorefishes. At these workshops, a group of facilitators trained in the Red List methods guided small groups of participants through the process of assigning an appropriate extinction risk category to each species. Each assessment was reviewed after the workshop by one or more researchers experienced in applying the Red List methods. Prior to publication on the Red List website, a final review was completed by a Red List expert at IUCN to check for concordance with the guidelines and formatting rules (IUCN, 2013). All resulting species data, literature cited, maps, and extinction risk categories for all species discussed here were made freely available on the Red List website (www.iucnredlist.org) from June 2016.

Species were listed in one of the three threatened categories, ordered by increasingly higher extinction risk as Vulnerable (VU), Endangered (EN), and Critically Endangered (CR), when they met the quantitative thresholds associated with either one or more of the five criteria (A–E). Wide-ranging species experiencing population declines as a result of exploitation were assessed under Criterion A when quantified population data were available for three generations or 10 years, whichever was longer. Restricted range species affected by a known major threat, often some type of habitat degradation, were assessed under Criterion B according to area estimations of its extent of occurrence (EOO) and/or area of occupancy (AOO). A category of Near Threatened was applied only if quantified estimates of population decline or AOO/EOO were very close to meeting the criteria for a threatened category. Data Deficient (DD) was applied to species that were poorly known (e.g. taxonomic uncertainty and/or unknown distribution extent), as well as to species where declines were likely to have occurred as a result of some major threat affecting a substantial part of its population, but for which quantified data were insufficient (e.g. fishing pressure). Species that did not reach the thresholds for Criteria A–E and/or for which there were no known major threats were assessed as being of Least Concern (LC), and were considered to have a lower risk of extinction. The Gulf of Mexico regional assessments followed the same methodology as the global assessments, except for the consideration of the status of populations outside the region and the possibility that immigration from outside the region could affect the extinction risk within the region (IUCN, 2012b). Further documentation on Criteria C–E can be accessed at www.iucnredlist.org (IUCN, 2012a), and a detailed explanation of how the Red List methods were applied to these shorefishes is provided in the supporting information (Appendix S1).

2.2 | Distribution mapping methods

Each distribution map was drawn as a polygon that encompassed the known occurrence of the species based on scientific literature, expert comments during Red List workshops, and vetted point records compiled by fish researchers at the Smithsonian Tropical Research Institute (Robertson & Van Tassell, 2015). Records of known vagrancy were excluded as they do not represent the existence of a resident population. Generalized distribution maps of marine species for use in Red List assessments are drawn with two strategic considerations: (i) the ability to visualize distributions on a variety of spatial scales; and (ii) the ability to analyse generalized distributions in concert with other data layers (e.g. habitat or depth). Clipping nearshore distributions to the continental shelf break (typically at a depth of around 200 m) can prevent an accurate visualization of the distribution of a species at large spatial scales because many islands and some continental areas have very narrow shelf areas. Thus, distributions were standardized by clipping to a 100 km shoreline buffer or a maximum depth of 200 m, whichever was further from the coastline. For the occasional situation where a species significantly extended beyond the continental shelf onto the slope, the distribution was clipped to a maximum depth of 300 m. These exaggerated buffers should be removed when analysing geographic patterns at finer spatial scales. The distributions of open-ocean species (e.g. certain tunas, flyingfishes, etc.) were not clipped to a buffer.

2.3 | Species richness analyses

Maps of overall richness, richness of Greater Caribbean endemics, richness of DD species, richness of threatened species, and richness of threatened Greater Caribbean endemics were created for both the Greater Caribbean fauna and the Gulf of Mexico fauna. All distribution map shape files were transformed into the World Cylindrical Equal Area Projected Coordinate system and converted into a square grid raster of 5 × 5 km cell size using the 'polygon to raster' tool. The decision to use this cell size was based on the size of the smallest distribution polygon in the data set (Rahbek, 2005), which is 32 km^2. The cell assignment type was set to maximum combined area, so that a value of '1' was assigned to each grid cell that the distribution polygon overlapped with, regardless of the amount of overlap. The rasters were then added together using the 'cell statistics' tool so that the result was expressed as the number of species that occupy each grid cell. All symbology on the maps was classified by Jenks natural breaks into six classes with a colour scheme of blue to red, where the highest scoring cells (class 6) are red. Error sources that may be associated with these spatial analyses are further discussed in the supporting information (Appendix S2).

To complement the richness analyses and inform conservation at the country level, the number of species, Greater Caribbean endemics, threatened species, threatened Greater Caribbean endemics, and Data Deficient species within each EEZ was compared with the total number in each category across the entire Greater Caribbean. For example, the number of species in Belize was divided by the total number of species (1360) to get the relative number of species in Belize. The 45 individual EEZs were identified by clipping a spatial layer of the global EEZs sourced from http://marineregions.org (VLIZ, 2016) to the Greater Caribbean boundaries, and the area (km^2) within each EEZ was calculated based on this layer. Corrections were made in 816 species distributions that eliminated tiny overlaps with EEZs where the species is not known to occur. These overlaps were present because the distributions were not drawn according to EEZ boundaries and the configuration of EEZs in the Caribbean is particularly complex. The numbers of species that occur within each EEZ were then calculated by applying the 'identity' tool, which identified the EEZs that a species distribution overlapped.

2.4 | Reporting summary statistics, major threats, and data deficiency

In the IUCN Red List assessment methodology, the true number of threatened species, e.g. those listed as CR, EN, or VU, is uncertain because any species listed as DD has the potential to be threatened (Butchart & Bird, 2010). Consequently, the proportion of these shorefishes listed as threatened was presented as both a midpoint and a range, where the upper bound represents the scenario that all DD species are threatened, and the lower bound represents the scenario where no DD species are threatened. According to the IUCN (2011), the equation used to calculate the midpoint is as follows: (CR + EN + VU)/(total assessed – DD).

Major threats were quantified across all species listed as Near Threatened or in one of the threatened categories globally and regionally. The threats were identified by reviewing the extinction risk assessment, which was compiled via published literature and/or expert knowledge (that may not be in the published literature) during the Red List process. Four primary threats (overexploitation, habitat degradation, invasive-lionfish predation, and competition with other invasive species) were identified. Habitat degradation was further divided into seven subcategories because the underlying degradation processes varied widely. This finer-resolution presentation of an indirect threat (i.e. habitat loss caused by anthropogenic activities then causing population decline) is more informative to developing specific conservation goals related to habitat protection and/or restoration. Overexploitation was not treated similarly because it is caused by a single process: the direct take of individuals from the population.

The number of threatened and Near Threatened species affected by each of the primary and secondary threats were considered separately for the global (83 species, 10 threats) and regional (44 species, 7 threats) analyses. Multivariate species-threat matrices, with threats coded as binary variables, were inputs to calculate the Bray–Curtis dissimilarity measure. Canonical analysis of principal coordinates was used to visualize the species in a multivariate framework; this constrained ordination method maximizes differences between groups (Anderson & Willis, 2003), and has been used in a similar analysis of imperilled Canadian species (McCune et al., 2013). The threats were then correlated with three categorical variables: Red List category, position in the water column (demersal or pelagic), and maximum body size (small, <20 cm total length; medium, 21–80 cm total length; and large, > 80 cm total length). All multivariate analyses were run in PRIMER 6 with PERMANOVA+ (Clark & Gorley, 2006).

Contributing factors that led to DD listings were also summarized similar to the identification of major threats. In addition, intrinsic characteristics that can cause a species to be poorly known, such as diminutive size, deep-living, and cryptic behaviour, were quantified across the DD species known from limited specimens and/or localities according to the text within the Red List assessment.

Species that are not endemic to the Gulf of Mexico received both a global and a regional Red List category, which created an opportunity to compare the status of populations inside the Gulf versus outside the Gulf. All species that were assigned a regional category that differed from their global category were identified (*n* = 102). To further examine the result that species with differing categories were more commonly listed at a lower threat level in the Gulf of Mexico and at a higher threat level in their global population, chi-square tests of independence were conducted. In addition, we considered if the species was fished at the global level, or not, as a potential factor contributing to the differing regional and global Red List categories. All chi-square tests were two-tailed with $P < 0.05$ considered significant; however, there were many cells with fewer than five species, so results must be interpreted with caution (McDonald, 2014). Analyses were run in R 3.2.2 (R Core Team, 2015).

3 | RESULTS

3.1 | Summary statistics

Across all Greater Caribbean species, all Gulf of Mexico species, and Greater Caribbean endemics, the proportions of threatened species range from 4 to 6% and the proportions of NT species are between 1 and 2% (Table 1). The midpoint, which accounts for the uncertainty introduced by species listed as DD, diverges from the straight proportion threatened by only 1 to 3 percentage points. The proportions of DD species range between 8 and 13%, with the highest proportion observed in Greater Caribbean endemics. The 46 Gulf of Mexico endemics have the highest proportion of threatened species, at 26%.

3.2 | Species richness

Overall, high richnesses of Greater Caribbean shorefishes are found in the following areas: south Florida (USA), Colombia and Venezuela, Panama, from Belize to Honduras, and Puerto Rico and the Virgin Islands (Figure 2a). The distribution of areas with high richness for the 725 Greater Caribbean endemics is similar to that for the overall richness, except for the inclusion of the Bahamas and the exclusion of Trinidad and Tobago (Figure 2b). Areas of overall low species richness are primarily found throughout the offshore oceanic waters, and are secondarily found in the Cayman Islands, French Guiana, Bermuda, from North Carolina to South Carolina (USA), and in the north-western Gulf of Mexico, from Louisiana (USA) to Tamaulipas (Mexico) (except the Flower Garden Banks).

No clear spatial patterns in the richness of the 65 threatened species occur (Figure 2c), most likely because about 37% of these species range widely throughout the region. The lowest richnesses of threatened species occur in areas where there is also low overall species richness, which includes offshore oceanic areas, from Guyana to French Guiana and along the north-western coast of the Gulf of Mexico. The highest richnesses in the 45 threatened Greater Caribbean endemics are in the Florida Keys (USA), the Bahamas, the Cayman Islands, from Puerto Rico to Dominica, Panama, and from along the northern Yucatán (Mexico) to Honduras (Figure 2d). Notably, the Cayman Islands also has a relatively low overall species richness (Figure 2a).

High richnesses of DD species occur along Venezuela, followed by Curaçao, Belize, and northern Colombia (Figure 2e). Very small geographic areas, such as Navassa Island (near Haiti), Arrowsmith Bank off Caribbean Mexico, and Exuma Sound in the Bahamas also have relatively high numbers of DD species. Lowest DD richness occurs in the Gulf of Mexico and along much of the US Atlantic coast.

In relation to EEZs, the highest relative numbers of Greater Caribbean threatened species are found in Mexico and the USA (Figure 3a), whereas high relative numbers of threatened Greater Caribbean endemics occur in Mexico, Belize, and the USA (Figure 3b), and high relative numbers of DD species are found in Venezuela and Colombia (Figure 3c). Mexico, Colombia, and Belize rank in the top five countries for relative numbers of DD species, threatened species, and threatened Greater Caribbean endemics (Table S6). Across the 45 Greater Caribbean EEZs, the USA, Mexico, the Bahamas, Venezuela, Colombia, and Honduras rank within the top 10 largest EEZs, as well as within the top five for highest relative numbers of threatened species, threatened Greater Caribbean endemics, or DD species. There are at least two notable exceptions, however: (i) Belize, which has a relatively small EEZ (ranked 29th out of 45) and high numbers of species; and (ii) Bermuda, which has a large EEZ (ranked sixth out of 45) and low numbers of species.

The Florida Keys, where more than 650, or 69%, of the 940 Gulf of Mexico shorefishes are found, is the primary area of high richness in the Gulf (Figure 4a). Secondary areas are in US waters from coastal south-west Florida and the Flower Garden Banks, and in Mexico from Campeche Bank. The lowest richness occurs in the offshore pelagic

TABLE 1 Numbers of marine bony shorefishes by Red List category. The percentage of species in each category is given in parentheses. The midpoint and the range of percentage threatened accounts for the uncertainty introduced by species listed as being Data Deficient. The midpoint is calculated as (CR + EN + VU)/(total assessed − DD). The lower bound of the range of percentage threatened is (CR + EN + VU)/(total assessed), and the upper bound, which assumes that all DD species are threatened, is (CR + EN + VU + DD)/total assessed. Abbreviations: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient

	Total species	Threatened	NT	DD	Midpoint	Range of % threatened	LC
Greater Caribbean	1360	65 (5%)	18 (1%)	114 (8%)	5%	5–13%	1163 (86%)
Greater Caribbean endemics	725	45 (6%)	6 (1%)	94 (13%)	7%	6–19%	580 (80%)
Gulf of Mexico	940	34 (4%)	10 (1%)	86 (9%)	4%	4–13%	810 (86%)
Gulf of Mexico endemics	46	12 (26%)	1 (2%)	4 (9%)	29%	26–35%	29 (63%)

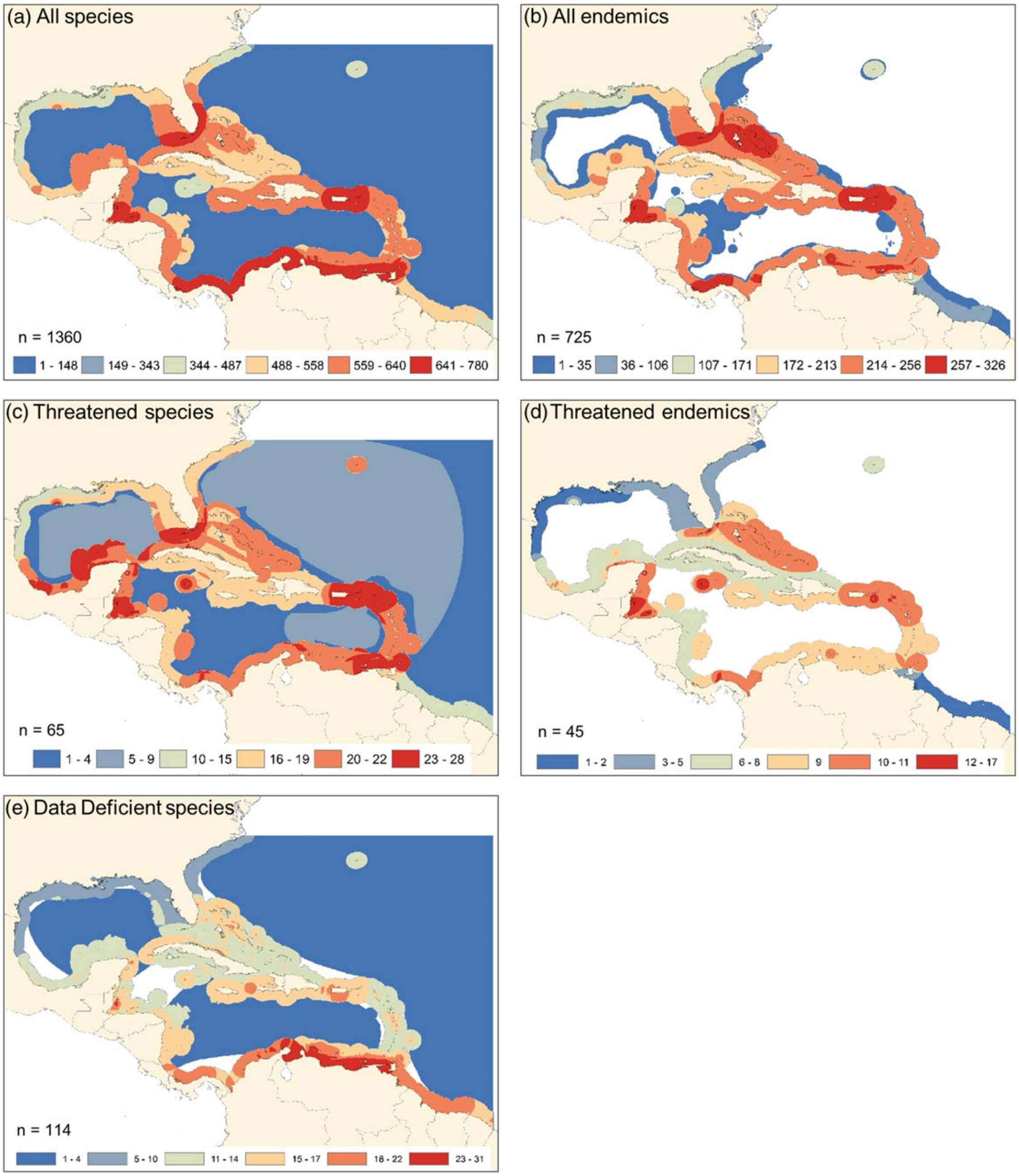

FIGURE 2 Richness of Greater Caribbean shorefishes. Maps of (a) all species richness, (b) all Greater Caribbean endemics richness, (c) threatened species richness, (d) Greater Caribbean threatened endemics richness, and (e) Data Deficient species richness. Each map shows the number of species per 25 km^2 grid cell (5 × 5 km). The total number of species is displayed at the bottom left of each map

zone and in coastal Louisiana and Texas, USA, and Tamaulipas, Mexico. Only 5% of Gulf shorefishes are endemic and the richness of these 46 species is highest along the northern US Gulf coast and is lowest in south Florida and the Campeche Bank, which is about the reverse of the richness pattern of overall Gulf species (Figure 4b). Interestingly, the Flower Garden Banks and Veracruz, Mexico, have high richnesses of overall species as well as Gulf endemics. High richnesses of species regionally listed as threatened occur in the southern Gulf from Veracruz, Mexico, to the Florida Keys and Cuba, and the lowest levels occur along coastal Louisiana, USA, to Tamaulipas, Mexico (Figure 4c). Species regionally listed as DD occur generally homogeneously throughout the Gulf, except for somewhat higher numbers in Cuba and the Florida Keys (Figure 4d).

3.3 | Major threats

In both the Greater Caribbean and the Gulf of Mexico, the most common threats for NT and threatened species are habitat degradation and overexploitation (Figure 5). Within habitat degradation, coral/hard-bottom degradation ranked highest (31% of the NT and threatened species). Invasive-lionfish predation, often concurrent with reef-habitat degradation (coral/hard-bottom), is affecting almost 25% of the threatened and NT species. Dams and/or freshwater diversion and competition with invasive species affect nine species that use freshwater, brackish, and marine habitats. Two very specific threats are anchialine-cave degradation that affects three Caribbean cavefishes (*Lucifuga* spp.) and the construction of a pier complex in the habitat of the small range of the

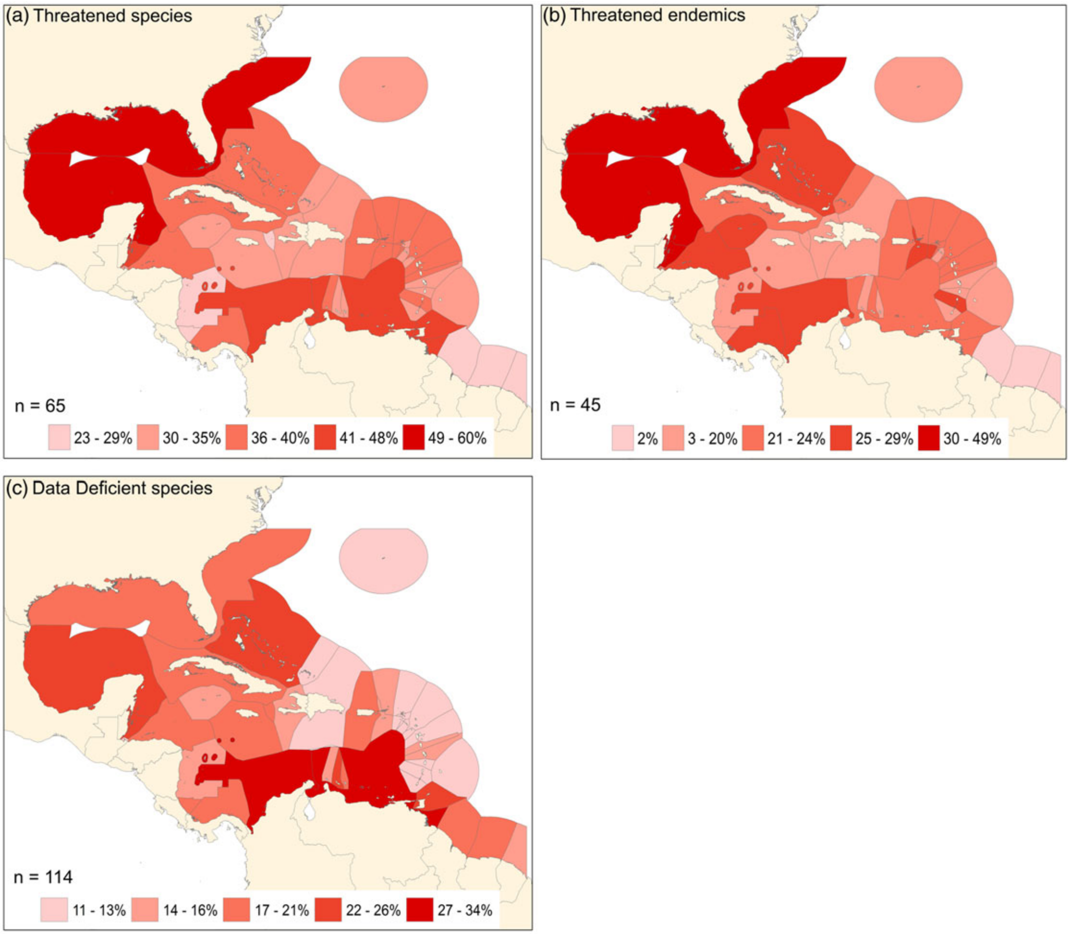

FIGURE 3 Relative numbers of Greater Caribbean shorefishes by exclusive economic zone (EEZ). Maps of (a) relative numbers of threatened species by EEZ, (b) relative numbers of threatened Greater Caribbean endemics by EEZ, and (c) relative numbers of DD species by EEZ

Mexican-endemic reticulate toadfish, *Sanopus reticulatus*. In general, the same threat types were recorded at the global and regional levels, with the exception that mangrove, anchialine-cave degradation, and competition with invasive species were not recorded in the Gulf of Mexico.

At both the global and the regional levels, the multivariate threat analysis revealed a clear separation in threats as a function of maximum body size. The primary threat to small-bodied species was habitat degradation, whereas the primary threat to medium- and large-bodied species was overexploitation (Figure 6). Only two small-bodied species had overexploitation recorded as a threat: *Anchoa choerostoma*, the Bermuda anchovy, and *Hippocampus erectus*, the lined seahorse, the latter of which also had habitat degradation recorded. All large-bodied species (n = 30) and most (10 out of 14) medium-bodied species were overexploited, with 40% (n = 16) of these also affected by habitat degradation. Similar patterns were documented in the regional analysis, where 20 of the 22 medium- and large-bodied species, and only two of the 22 small-bodied species, had overexploitation recorded as a threat. No clear patterns were revealed between threats and the position of species in the water column or Red List category (results not shown).

3.4 | Factors contributing to Data Deficient listings

Seventy-two percent (n = 82) of the 114 Greater Caribbean species assessed as DD globally, and 84% (n = 72) of the 86 species assessed as DD in the Gulf of Mexico, are only known from a few records, and as a result, their true range sizes remain unknown (Figure 7). The majority, or 83%, of the 82 poorly known Greater Caribbean DD species are diminutive, and over half have some combination of being diminutive, cryptic, and/or deep-living (Table 2). At times, taxonomic uncertainty also contributed to an unknown range size. The most common DD factor related to threat was the lack of data on habitat degradation, and the second most common factor was a lack of fishery data, especially for heavily exploited species (Figure 7). Some DD species with plausible threats, but unknown impact, also had relatively limited ranges, including several that exhibited traits of being a preferred lionfish prey item. Four DD deep-living eels and one cusk-eel known from very few records have only been collected within the vicinity of the Gulf of Mexico Deepwater Horizon oil spill. Like the major threat types, the factors contributing to DD listings do not notably differ between the Greater Caribbean assessments and the regional Gulf of Mexico assessments.

3.5 | Comparing global and Gulf of Mexico regional Red List categories

Out of the 940 species that range in the Gulf of Mexico, 894 are not endemic to that region, and therefore received both a global and a

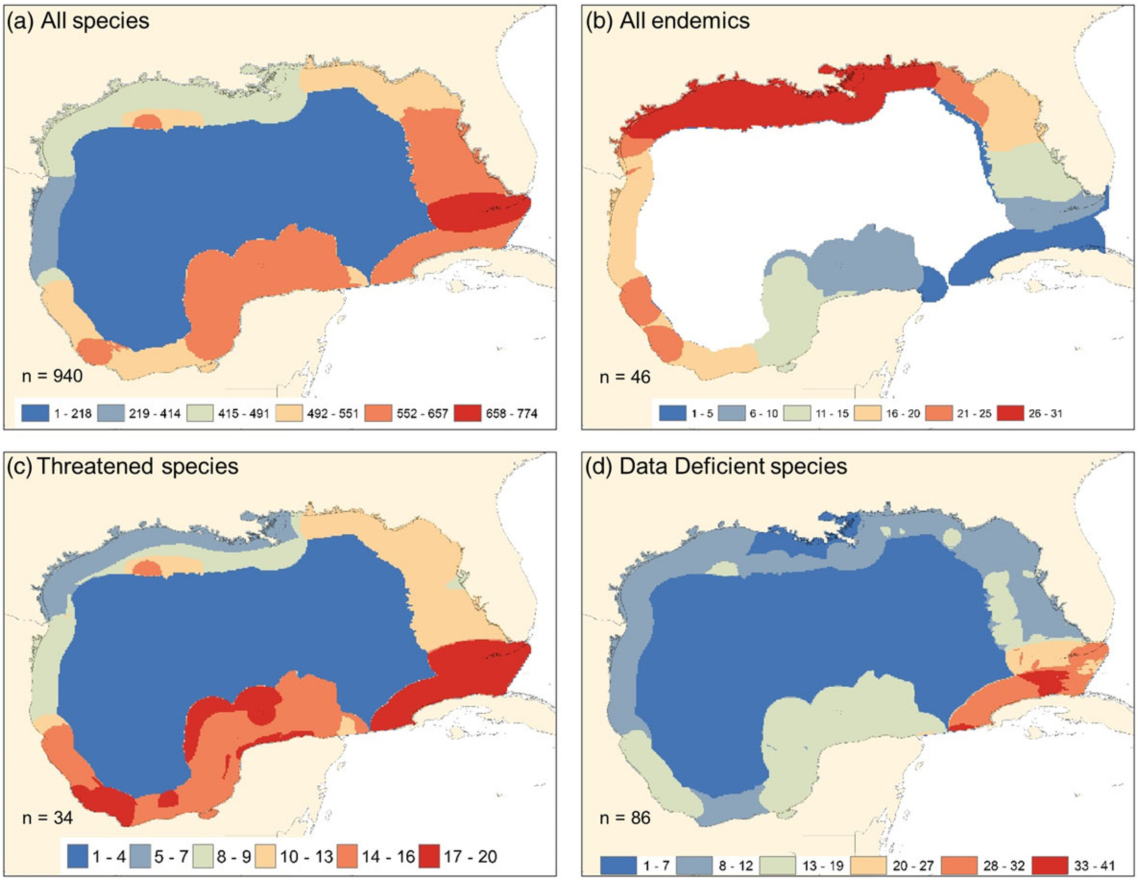

FIGURE 4 **Richness of Gulf of Mexico shorefishes.** Number of marine bony shorefishes in the Gulf of Mexico per 25 km^2 grid cell for (a) all species, (b) all Gulf endemics, (c) regionally threatened species, and (d) regionally Data Deficient species. The total number of species is displayed at the bottom left of each map

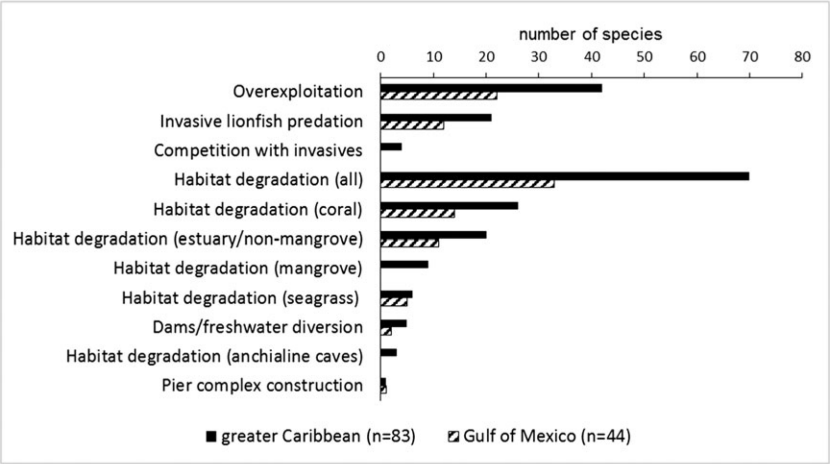

FIGURE 5 The threat types contributing to Near Threatened and threatened listings in the entire fauna and in the Gulf of Mexico fauna. Some species are affected by more than one threat type

regional Red List category. Of these Gulf non-endemics, 11% (n = 102) have regional Red List categories that differ from their global category (Table 3), meaning that the status of their population within the Gulf differs from their population considered at a global level. The majority (65%) of these species are listed as DD in the Gulf and LC globally. Twenty-four species were not listed as DD either globally or regionally; of those, about two-thirds were listed at a higher risk globally than regionally, and one-third were listed at a lower risk globally. The chi-square analysis shows a significant relationship between the global and regional Red List categories (χ^2 = 206.4, df = 25, P << 0.05).

As the true conservation status of species listed as DD is unknown, there are four possible levels for the difference between the global and regional Red List categories: (i) global threat status is higher than the regional status (n = 16); (ii) global threat status is lower than the regional status (n = 8); (iii) global threat status is DD (n = 10);

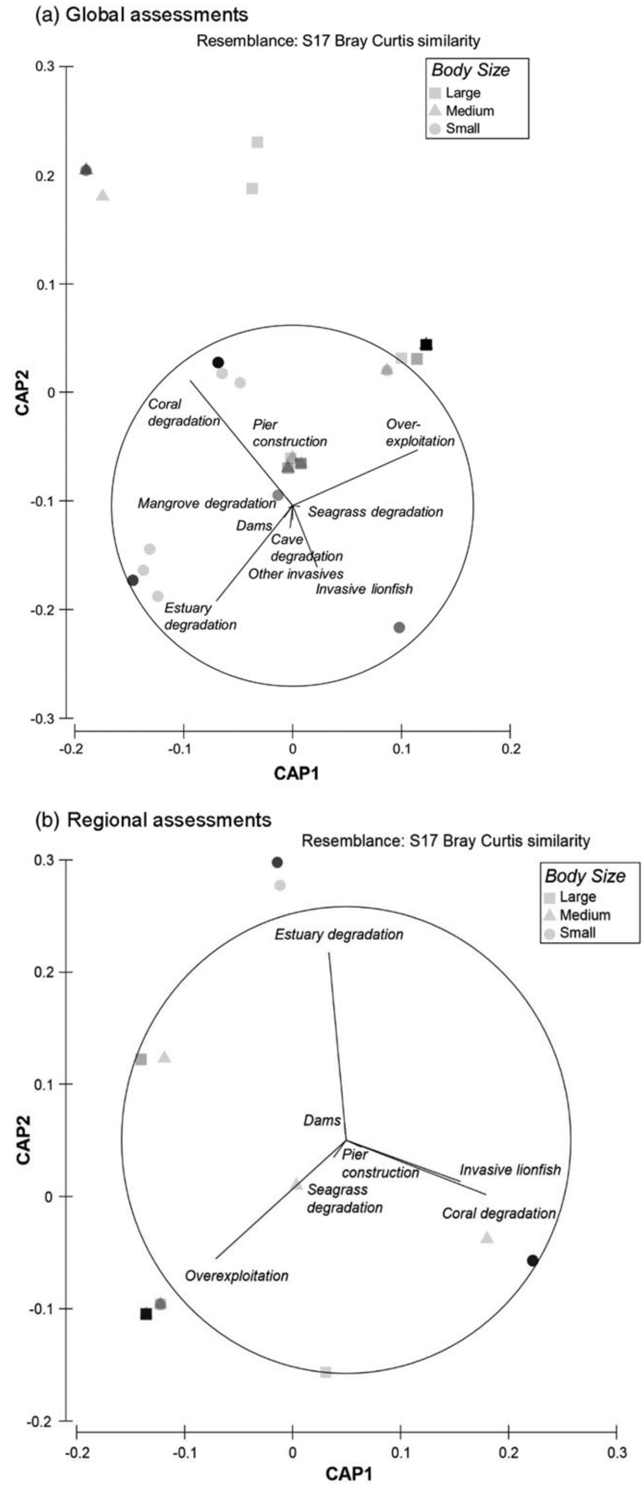

FIGURE 6 Constrained ordination (canonical analysis of principal coordinates) of threats. Threats to threatened and Near Threatened species in relation to maximum body size (small, <20 cm total length; medium, 21–80 cm total length; and large, >80 cm total length). (a) Greater Caribbean global assessments (83 species, 10 threats); (b) Gulf of Mexico regional assessments (44 species, seven threats). Individual symbol transparency was set to 0.15 to indicate where species are overlapping

and (iv) regional threat status is DD (n = 68). This distribution of species across these levels was significantly affected by whether or not the species was fished at the global level (χ^2 = 59.3, df = 3, P << 0.05). All 16 of the species listed at a higher threat status globally than regionally support fisheries in some capacity within their global range.

4 | DISCUSSION

About 53% of Greater Caribbean bony shorefishes are endemic, compared with 33% of all Eastern Central Atlantic bony fishes found in waters of less than 300 m depth (Polidoro et al., 2017) and 79% of all Eastern Tropical Pacific shorefishes (Robertson & Cramer, 2009). Five percent of Greater Caribbean marine bony shorefishes are threatened, as compared with 9% in the Eastern Tropical Pacific (Polidoro et al., 2012) and about 6% of all bony fishes found in waters of less than 300 m depth in the Eastern Central Atlantic (Polidoro et al., 2017). The rate of endemism is much higher in Eastern Tropical Pacific shorefishes (Robertson & Cramer, 2009), where several species restricted to small, insular areas have an elevated extinction risk, which is likely to explain the higher number of threatened species in that region. Between 8 and 9% of Greater Caribbean and Gulf of Mexico shorefishes, 16% of Eastern Tropical Pacific shorefishes (Polidoro et al., 2012), and 10% of Eastern Central Atlantic bony fishes occurring in water shallower than 300 m are listed as DD in some part because of a lack of fishery data (Polidoro et al., 2017). In the European region, where shorefish diversity is better studied than in the Greater Caribbean, DD richness patterns in fishes may largely be driven by the abundance of heavily exploited species for which fishery data are not available (Nieto et al., 2015). In comparison with other parts of the world, Dulvy et al. (2014) identified the Greater Caribbean region as an area with relatively high numbers of DD sharks and rays, as a result of the lack of general rather than specific (i.e. fishery-data) information about them.

4.1 | Species richness patterns: Greater Caribbean

Despite our gradually increasing knowledge of fish distributions, the results of these richness analyses probably include some bias because of gaps in the sampling effort (Gotelli & Colwell, 2001). In an analysis of Caribbean-only marine biodiversity, Miloslavich et al. (2010) reported that the location of richness hot spots to some extent reflects areas where sampling effort has been disproportionately high: i.e. Belize, Puerto Rico–Virgin Islands, Colombia, and Tobago. Robertson and Cramer (2014) also pointed out that the lack of records from certain areas is likely to have arisen from a lack of comprehensive marine biodiversity surveys, rather than from low diversity, as those areas have a range of habitats that are typical of the Caribbean. Those areas include much of Cuba, Hispaniola, the large shelf off Honduras and Nicaragua, and the banks between Nicaragua and Jamaica (Miloslavich et al., 2010; Robertson & Cramer, 2014). In the present study, the overall richness of Greater Caribbean shorefishes (Figure 2a) does show these areas as having relatively low richnesses. In contrast, three areas of high richness – the Florida Keys, Puerto Rico, and St Croix – all fall under US jurisdiction, which has the financial resources to fund high levels of sampling effort. Furthermore, Belize and central Panama are home to Smithsonian research facilities

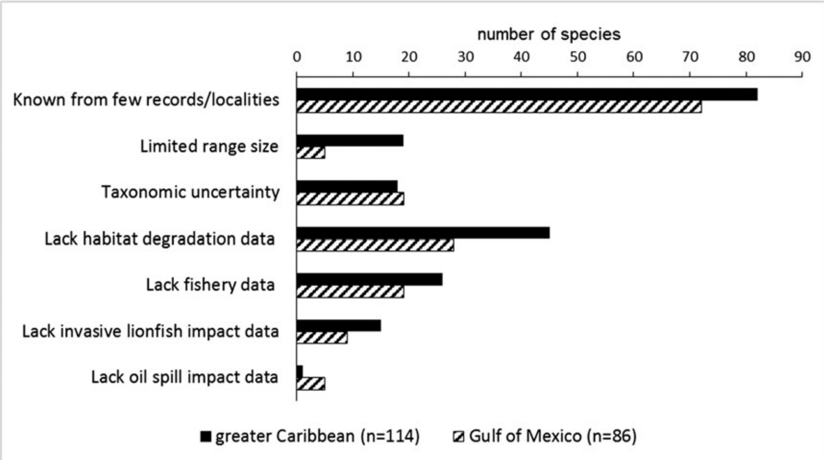

FIGURE 7 The contributing factors to Data Deficient (DD) listings in the entire fauna and in the Gulf of Mexico fauna. Some species are listed as DD for more than one factor

TABLE 2 Characteristics of Greater Caribbean Data Deficient (DD) species known from limited specimens. Diminutive is defined as having an adult maximum length of less than 15 cm. Cryptic species are those often not recorded because they tend to remain completely within the structure or the benthos, and/or are active only at night. Deep-living species mostly inhabit depths of greater than 30 m

Characteristic	No. of poorly known DD species (*n* = 82)
Diminutive	68
Cryptic	25
Deep-living	13
Diminutive and cryptic	16
Diminutive and deep-living	13
Deep-living and cryptic	9
Diminutive, deep-living, and cryptic	8

TABLE 3 Contingency table for 102 species with differing regional and global Red List categories. The global category evaluated the entire population, whereas the regional category evaluated the population in the Gulf of Mexico alone. Abbreviations: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient

	Regional Red List category						
Global Red List category	CR	EN	VU	NT	LC	DD	Total
CR	0	1	0	1	1	0	3
EN	1	0	0	0	0	0	1
VU	0	2	0	2	4	2	10
NT	0	1	1	0	7	0	9
LC	0	0	1	2	0	66	69
DD	0	1	0	1	8	0	10
Total	1	5	2	6	20	68	102

that specialize in cataloguing biodiversity, including that of reef fishes. Survey work by Colombia's Institute of Marine and Coastal Research and effort in Venezuela by the ichthyologist Fernando Cervigón may have also contributed to these areas having high reported species richness. Curaçao's high richness is also likely linked to the collecting efforts by Smithsonian ichthyologists that included recent discoveries of new species via specialized deep sampling that has been rarely employed elsewhere in the region (e.g. Baldwin & Johnson, 2014).

Of the 1360 Greater Caribbean bony shorefishes assessed for this study, 53% are endemic. Both Robertson and Cramer (2014) and Miloslavich et al. (2010) reported a lower rate of endemics at 45%, with this difference likely to have been influenced by their inclusion of elasmobranchs, few of which are endemic. Most of the Greater Caribbean shorefishes, including the endemics, are widely distributed, presumably because of the relatively high level of connectivity within the region, facilitated by an abundance of offshore island chains (Robertson & Cramer, 2014). This is likely to drive the somewhat indistinct patterns in Greater Caribbean shorefish richness; however, the Caribbean is not entirely lacking in complexity of subregional connectivity (Cowen, Paris, & Srinivasan, 2006).

Besides sampling effort, the following biotic factors also drive spatial variation in shorefish richness patterns: (i) the abundance of widely distributed species; (ii) geographic isolation; (iii) prevailing currents and water temperature; (iv) the availability of complex habitats; and (v) overlap of biogeographic zones. South Florida, which has the highest shorefish richness, has characteristics that fit several richness drivers. It is well studied, contains a relatively large area of reef habitat, is influenced by currents flowing through the nearby Florida Straits, which are likely to amplify the settlement of propagules originating in the Caribbean Sea, and is located where several subregional biogeographic zones abut: the Gulf of Mexico, the east coast of the USA, and the Bahamas. Belize and the Bay Islands of Honduras, also with high species richness, is an area with substantial mangrove, seagrass, and coral reef habitats that is somewhat isolated to the north and south (Cowen et al., 2006; Robertson & Cramer, 2014). Continental Venezuela and Colombia have high richness, but, rather than being the result of habitat complexity, this is likely to be linked to the abundance of rocky shorelines, upwelling areas, and large river outflow that dominate the area (Robertson & Cramer, 2014). A nearby strong gyre somewhat isolates the reef systems of Panama and Colombia (Cowen et al., 2006), and this may contribute to this region having high richness in both overall species and Greater Caribbean endemics. The Bahamas, which is geographically isolated from much of the

Caribbean, has a relatively high richness of Greater Caribbean endemics, but not of overall species (Cowen et al., 2006). The resource-poor environment of the offshore oceanic zone is used by relatively few shorefishes, and thus has low overall species richness. Low nearshore richness is found in areas with limited habitat complexity and a paucity of coral reefs, such as the north-western Gulf of Mexico, the Carolinas (USA), and French Guiana (Robertson & Cramer, 2014). Contributors to low richness in the Cayman Islands may be driven by its small area and simplified habitats, resulting from a constricted reef profile, and a lack of both extensive backreef habitat and freshwater. Of the three Cayman Islands, only Grand Cayman has a substantial lagoon and large area of mangroves.

Richness patterns in the threatened species are not geographically variable to any marked degree, as about half of the 65 species are widely distributed throughout the region, and the threats impacting most of them (i.e. overexploitation, coral degradation, and the invasive lionfish) also occur widely throughout the region at varying levels. On the contrary, richness patterns are more defined in the threatened Greater Caribbean endemics, as most (33 out of the 45) have a limited range. The relatively high richness of threatened Greater Caribbean endemics off Panama may partly relate to the occurrence of limited-range species potentially affected by the localized threat from the Panama Canal. Similarly, localized coastal development is a threat to sensitive habitats that support limited-range fishes in Belize. The high richness of threatened Greater Caribbean endemics in the Cayman Islands is influenced by the recent discovery of three Cayman-endemic gobies (Victor, 2014) that were listed as threatened.

The Greater Caribbean is a region where both basic diversity knowledge as well as fishery data availability varies widely by country. Specialized sampling methods targeting deep and/or cryptic species commonly result in the discovery of new or poorly known species. The implementation of such methods, however, has been rare and opportunistic across the Greater Caribbean (Baldwin & Johnson, 2014; Smith-Vaniz, Jelks, & Rocha, 2006; Williams et al., 2010). Given that 72% of the DD species are known from limited records, the distribution of sampling effort may drive richness patterns in DD species. Most of the DD species that have well-known distributions occur widely throughout the region, which further contributes to the ambiguity in DD richness patterns.

As expected, the size of the EEZ partly drives the relative number of species that are in each EEZ, with large EEZs likely to have more species than small EEZs; however, highly biogeographically and geopolitically separated countries like Bermuda have a large EEZ, but relatively low numbers of species. Regardless of EEZ size, the number of species can also be high in EEZs that contain a well-connected network of complex habitats. For example, Belize has a much smaller EEZ compared with others with high numbers of total species, Greater Caribbean endemics, and threatened species (e.g. the USA, Mexico, and the Bahamas), but it also has high numbers of species. In addition, regardless of EEZ size, there is a need for species-specific conservation action, but Belize could potentially preserve a relatively large number of imperilled species by promoting action over a smaller total area than is required in other countries to accomplish the same goal.

4.2 | Species richness patterns: Gulf of Mexico

The highest richnesses in the Gulf of Mexico are in areas with reef habitat, including the Florida Keys, the Flower Garden Banks, Alacranes Reef, north-west Cuba, and the hard-bottom areas off south-west Florida (e.g. Pulley Ridge). Other Mexican reefs exist in offshore areas on the Campeche Bank, but are considerably less-studied (Robertson, Perez-España, Lara, Itza, & Simoes, 2016). Contributing to low richness in the northern Gulf are the presence of large river systems, cooler winter temperatures, very little shallow coral reef, and a predominance of soft bottom along the shoreline, which is a combination of conditions found nowhere else in the Greater Caribbean region (Robertson & Cramer, 2014). The nearest equivalent is the northern Gulf of California, which is an area of low shorefish richness in the tropical eastern Pacific, also with low temperatures and dominated by soft bottom (Mora & Robertson, 2005).

Only 5% of the 940 shorefishes are endemic to the Gulf of Mexico. The richness pattern of these 46 Gulf endemics contrasts with that of the overall species richness: whereas the highest richness of endemics is along the northern Gulf coast, the lowest richness is in the south-eastern Gulf. This pattern reflects results reported by Smith, Carpenter, and Waller (2002) and Robertson and Cramer (2014). Based on the presence of sister species along the US Atlantic coast, Smith et al. (2002) hypothesized that endemism in the northern Gulf could have resulted from speciation that followed climate-induced vicariance sometime prior to the establishment of the Florida peninsula. In the southern Gulf, Mexico's Veracruz Reef System is only weakly connected to reefs elsewhere in the region through the northward flow of the Loop Current (Johnston & Bernard, 2017; Sanvicente-Añorve, Zavala-Hidalgo, Allende-Arandía, & Hermoso-Salazar, 2014), and has only relatively recently become known as an area of Gulf endemism after survey efforts resulted in the discovery of several undescribed reef fishes (Del Moral-Flores et al., 2013).

The highest richness of the 34 threatened Gulf species occurs in areas with coral reef habitat, as the majority are reef-associated. Many of the DD species in Cuba and the Florida Keys are known from limited records, which suggests two possible scenarios: that these records represent waifs deposited from currents originating in the Caribbean, and therefore viable populations of these species do not occur within the Gulf, or that they could represent established populations that are not generally observed because of natural rarity or cryptic behaviour.

4.3 | Major threats

At-risk species begin to decline towards extinction often as a result of synergistic impacts from secondary threats (Brook, Sodhi, & Bradshaw, 2008), which is of particular concern as half of the NT and threatened Greater Caribbean and Gulf of Mexico shorefishes (44 out of 88) are affected by more than one threat. In general, of the threatened and NT species, the smaller species tend to be more restricted in range and affected by localized threats such as habitat degradation and/or invasive species, whereas larger species tend to be more widely distributed and affected by overexploitation. For example, the threatened Mardi Gras wrasse (*Halichoeres burekae*) and social wrasse

(*Halichoeres socialis*) are two restricted-range, reef-associated species that are susceptible to predation by the invasive lionfish, and inhabit areas where serious reef degradation has been documented (Rocha, Rocha, Baldwin, Weigt, & McField, 2015). Two threatened marine catfishes (*Notarius neogranatensis* and *Sciades parkeri*) and the NT southern flounder (*Paralichthys lethostigma*) also face threats from overexploitation as well as estuarine degradation. Although few anadromous species occur in this region, four (e.g. the VU blueback herring, *Alosa aestivalis*) have declined considerably as a result of exploitation and river modification.

Half of the NT and threatened species are heavily targeted by commercial and/or recreational fisheries (mostly pelagic and reef based). Red List studies on European fishes, all sharks and rays, all groupers, and all tunas and billfishes, also recorded overexploitation as a key major threat (Collette et al., 2011; Dulvy et al., 2014; Nieto et al., 2015; Sadovy de Mitcheson et al., 2013). Scientific stock assessments and strict management has allowed several fished populations to recover or to begin to recover in US waters (National Oceanic and Atmospheric Administration, NOAA, 2015); however, fishing is insufficiently monitored or regulated in less developed countries, where declines continue (Worm & Branch, 2012). For example, the overexploited goliath grouper (*Epinephelus itajara*) and red snapper (*Lutjanus campechanus*) have been increasing in US waters, but are listed as threatened, largely because of long-term declines and the lack of effective fisheries management in the remainder of their ranges.

The severe decline in Caribbean coral cover (Jackson et al., 2014), and the continued deterioration of reef and hard-bottom complexity (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Lindeman & Snyder, 1999) is particularly concerning to Greater Caribbean shorefishes, many of which are reef-associated (Robertson & Cramer, 2014). For example, of the 11 coralbrotulas (Bythitidae), small, cryptic fishes that inhabit interstitial spaces in coral reef, one is threatened because of susceptibility to reef complexity loss and four are DD through a lack of information. Many Greater Caribbean reef specialists, especially small-bodied species, use coral reefs for shelter and food, and are likely to undergo population declines because of the region-wide loss of coral cover and changes in coral assemblages (Alvarez-Filip, Paddack, Collen, Robertson, & Côté, 2015; Newman et al., 2015; Rogers, Blanchard, & Mumby, 2014). Nearshore marine habitats such as hard bottom, which can support coral reef development, also support juveniles of many reef species that ontogenetically distribute across the shelf with development, and are designated as Essential Fish Habitat and Habitat Areas of Particular Concern according to the US South Atlantic Fishery Management Councils. These include economically valuable snappers, grunts, groupers, drums, and others, some of which are DD, NT, or threatened. Large coastal construction projects (e.g. extensive dredge-and-fill projects, cruise ship, and other port infrastructure projects) impact these habitats via direct burial, removal, and short-term or often cumulative long-term sedimentation (Lindeman & Snyder, 1999; Miller et al., 2016).

The non-native Pacific lionfish (*Pterois volitans*), which is now established throughout the Greater Caribbean, has been shown to cause significant declines in small reef fish biomass and diversity when present in high densities (Albins, 2015; Côté & Smith, 2018; Green, Akins, Maljković, & Côté, 2012). Preferred lionfish prey have shallow bodies, diminutive size, and behaviour that includes hovering above reef substrate (Green & Côté, 2014), and lionfish diet studies frequently list species of squirrelfishes, cardinalfishes, gobies, blennies, basslets, damselfishes, and small labrids. Eight gobies in the genus *Coryphopterus*, which are typically reef specialists and some of the most frequently consumed prey fishes, are listed as VU, except for one species listed as DD. As these assessments were finalized between 2011 and 2015, the literature pertaining to invasive lionfish predation has grown considerably. It is likely that new information will inform our knowledge on the impact of lionfish predation on Greater Caribbean fishes, and this will be used to update the assessments of these species in the future.

Estuarine habitats are susceptible to removal for land development, and degradation by pervasive run-off pollution and river flow alteration (e.g. dams), which negatively affect downstream estuaries by altering salinity gradients (Lotze et al., 2006). As a result, estuary specialists, especially anadromous fishes, frequently experience range reductions, spawning habitat loss, and decreasing egg survivability (Pringle, Freeman, & Freeman, 2000). Estuary degradation affects six diminutive, limited-range, Gulf of Mexico endemics that are listed as NT or threatened. Mangroves and seagrasses, which are typically associated with estuaries, provide essential habitat for Greater Caribbean fishes, but have also declined as a result of eutrophication via nutrient run-off and direct removal (Matheson, Camp, Sogard, & Bjorgo, 1999; Mumby et al., 2004). For example, two seagrass specialists, the dwarf seahorse (*Hippocampus zosterae*) and the dusky pipefish (*Syngnathus floridae*), are listed as NT on the regional level in the Gulf of Mexico.

Anchialine caves, which are partial marine/fresh environments that occur within the terrestrial landscape, and connect to saltwater via subterranean passages, are present in the Greater Caribbean only from Cuba and the Bahamas. A limited number of these caves support three species of live-bearing, nearly blind fishes in the genus *Lucifuga* (family Bythitidae). These highly restricted species were listed as threatened because some of these caves have become dumps for trash and sewage, been disturbed by hydrological manipulation, or freshwater species have been introduced that compete with the *Lucifuga* spp. for limited resources (García-Machado et al., 2011; Proudlove, 2001). A single Bahamian locality, the Lucayan Caverns, is relatively well protected through its inclusion in the Lucayan National Park, but conservation actions for the other caves are unknown.

4.4 | Data Deficient species

Studies by taxonomists repeatedly confirm that many Greater Caribbean fishes remain undiscovered, especially diminutive and/or cryptic taxa that inhabit depths beyond recreational scuba limits (Baldwin & Johnson, 2014; Collette, Williams, Thacker, & Smith, 2003; Smith-Vaniz et al., 2006). Eighteen of the DD species were described only within the past decade (2005–2015), mostly via DNA barcoding (e.g. Victor, 2013) or discovery during deep-diving research (e.g. Baldwin & Johnson, 2014). More than half of all the DD assessments in this study mention at least one potential threat to the species, and 13 DD species are known to have relatively limited ranges. For example, the DD Trinidad anchovy (*Anchoa trinitatis*) is a mangrove specialist harvested in bait fisheries that occurs only from Cartagena, Colombia to Trinidad. The DD hornless blenny (*Emblemariopsis randalli*) has a potentially restricted range in Venezuela and exhibits characteristics of preferred lionfish prey. The uncertainty caused by species assessed as DD restricts our understanding of threat patterns (Bland, Collen, Orme, & Bielby, 2012). For example, Venezuela has an overall high DD richness, with at least six DD species that have ranges mostly restricted to that country; therefore, Venezuela may be an undetected area of high threatened species richness (Linardich et al., 2017).

The lack of long-term catch data in large portions of the broad ranges of the Greater Caribbean snappers and grunts (*Lutjanidae* and *Haemulidae*) resulted in eight species being globally listed as DD. As these fishes, such as the DD black margate (*Anisotremus surinamensis*), are often exploited in mixed-catch fisheries, the species-specific data required to quantify population decline can be difficult to obtain (Claro, Sadovy de Mitcheson, Lindeman, & García-Cagide, 2009). Recreational catch data are even less accessible than commercial landings data, which is of particular concern for sportfishes (Cooke & Cowx, 2004). For example, the greater amberjack (*Seriola dumerili*) is NT in the Gulf, based on declines in the estimated total biomass found in US waters, which represents half of its Gulf range. This species supports a valuable sportfishery in Mexico, which comprises the other half of the range, but no formal data are available from this region. The potential is high that this species could qualify for a threatened category in the Gulf, but the lack of data prohibits any estimation of decline beyond what is available in the US stock assessment.

4.5 | Comparing global and Gulf of Mexico regional assessments

Red List assessments conducted at the subglobal or regional level are more appropriate for informing conservation priorities in large areas with low fish endemism, such as the Gulf of Mexico, because the chance for identifying false-positive priorities is reduced. Analysing the regional and global status of Gulf shorefishes separately also revealed that 25% of Gulf endemics are threatened with extinction, mostly through estuarine, hard bottom, and coral habitat degradation.

Species listed as DD in the Gulf and LC globally represent the majority of differences between the regional and global Red List categories. These are primarily widely distributed species with very few Gulf records available, resulting in poorly known distributions within the Gulf. For example, the quillfin blenny (*Gobioclinus filamentosus*) is only known in the Gulf from a few records taken from two Campeche Bank reef localities, but elsewhere occurs through much of the Caribbean Sea. It is plausible that additional sampling could reveal that these species are more widely distributed in the Gulf, and thus should be listed as LC, or that they are restricted in range and could qualify for a threatened status.

Some species not endemic to the Gulf were listed at a higher threat category or as DD in the Gulf because of regional threats from coral or estuary degradation. For example, the regionally VU leopard goby (*Tigrigobius saucrus*), which is dependent on live coral heads, and is likely to be susceptible to lionfish predation, has a range in the Gulf restricted to areas with documented coral declines (i.e. Veracruz, the Florida Keys, and Cuba). At the global level it is listed as LC because of its wide distribution. *Stegastes otophorus*, a damselfish that inhabits only brackish waters near river mouths, and ranges between Cuba and Colombia, has a Gulf distribution restricted to polluted areas near Havana, Cuba, and is listed as EN in the Gulf, but DD globally. Four deep-living snake eels, one of which may be endemic to the Gulf (*Gordiichthys ergodes*), and one cusk-eel are only known from records taken in the north-eastern Gulf from localities near the 2010 Deepwater Horizon oil spill. These benthic-oriented species were listed as DD at the regional level in part because of the potential threat from interaction with contaminated sediment (Snyder, Pulster, Wetzel, & Murawski, 2015).

Fisheries and overexploitation affect the global and regional Red List categories in a variety of ways. Thirty-six of the species with different global and regional categories are fished globally, and 16 have a lower regional Red List status. For these species, the Gulf population is declining at a lower rate than globally, primarily through the effective regulation of fishing mortality, mostly in US waters, and the lack of directed fisheries in the Gulf. The lack of high-resolution fishery data, especially in Mexico and Cuba, where funding for fishery data collection, stock assessments, or regulation enforcement is mostly insufficient, also impacts the assessments: for example, the Atlantic tarpon (*Megalops atlanticus*) and cubera snapper (*Lutjanus cyanopterus*) are VU on the global level but are DD in the Gulf because of limited quantitative data on population trends.

5 | CONCLUSIONS

This study documents the fact that marine fishes of all functional roles face a litany of growing threats that, by acting concurrently, often amplify extinction risks, reinforcing the need for systematic conservation planning that addresses multi-threat scenarios (Côté, Darling, & Brown, 2016). Our awareness of extinction risk in Greater Caribbean shorefishes has grown considerably with the recent availability of at least 1000 new assessments, including 47 species listed as threatened. In addition, regional Red List assessments of these species in the Gulf of Mexico highlight potential region-specific conservation priorities for widely distributed fishes, as well as restricted range Gulf endemics. Ultimately, factors besides Red List status, such as economics, cultural values, and the practicality of conservation action must also be considered (IUCN, 2012a), but these assessments will be integral to nominating the first Caribbean marine Key Biodiversity Areas (IUCN, 2016), as well as informing conservation initiatives such as the Gulf of Mexico Large Marine Ecosystem Project, the Caribbean Challenge Initiative, the Specially Protected Areas and Wildlife (SPAW) List of Protected Areas, and the Aichi Biodiversity Targets. For example, the distribution of 18 threatened shorefishes intersects with the Belize Barrier Reef Reserve System, which is also a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage site. Eight of these species are endemic to Belize or have most of their ranges in that country; four of them are affected by the invasive lionfish and all of them are affected by habitat degradation. Given these new data, priority actions within management plans can be updated.

Strengthening our understanding of threatened diversity is dependent on the reconciliation of DD species, especially those with identified threats (Bland, Collen, Orme, & Bielby, 2015). In the face of increasing threats to marine species, the lack of fundamental biodiversity data increases the possibility that species could be lost prior to description (Mora, Tittensor, & Myers, 2008); therefore, supporting specialized sampling efforts will expand our ability to identify at-risk biodiversity (Tornabene & Baldwin, 2017). A major issue is the lack of even basic fishery catch-and-effort statistics by species from the incredibly diverse array of regions within the Greater Caribbean. These gaps inhibit our capacity to manage populations and allows for overexploitation. The benefits of properly managed fisheries on local economies and marine ecosystem health are well known, and therefore, action to regulate unsustainable fishing effort should be prioritized (Botsford, Castilla, & Peterson, 1997). Investing in standardized, long-term fishery population and/or habitat monitoring would facilitate this while also improving our awareness of non-targeted threatened and DD species, including those susceptible to lionfish predation.

Identifying conservation priorities that aim to prevent biodiversity loss at the species level is a key product of IUCN Red List assessments. The species of concern examined in this study include several examples across different habitat types within the Greater Caribbean, for which there are specific conservation action recommendations. The endangered Nassau grouper (*Epinephelus striatus*) is an economically important reef species that has experienced large-scale declines through the heavy exploitation of seasonal spawning aggregations. Other Greater Caribbean grouper species with similar behaviours have also declined, including the yellowfin grouper (*Mycteroperca venenosa*), the black grouper (*Mycteroperca bonaci*), and the tiger grouper (*Mycteroperca tigris*), which highlights the importance of reducing fishing on aggregation sites.

Overexploited open-ocean species, including the bigeye tuna (*Thunnus obesus*), bluefin tuna (*Thunnus thynnus*), white marlin (*Kajikia albida*), and blue marlin (*Makaira nigricans*), have some of the largest distributions in this study, and their conservation requires improvements in the implementation of fishing regulation via regional fisheries management organizations. Two threatened, restricted-range species, the seafan blenny (*Emblemariopsis pricei*) and the ferocious coralbrotula (*Ogilbichthys ferocis*), inhabit interstitial space in live coral reefs, which has degraded through the loss of coral cover and reef complexity.

The causes of Caribbean coral system declines are complex and can vary widely by locality, but recommendations for conservation action include minimizing impacts from coastal development projects, addressing climate change, reducing fishing of threatened species, including key herbivores (e.g. parrotfish), and the direct restoration of corals where feasible. Many other systems have complex stories that suggest species management actions. For example, three threatened estuary-dependent killifishes that are endemic to the Gulf of Mexico – the giant killifish (*Fundulus grandissimus*), saltmarsh topminnow (*F. jenkinsi*), and Yucatán killifish (*F. persimilis*) – would benefit from the restoration of vegetated wetland habitats and reductions in freshwater pollution.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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