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Recommended Citation

Birge, Tiffany L.. "Global Conservation Status and Threat Patterns of the World's Most Prominent Forage Fishes (Teleostei, Clupeiformes)" (2019). Master of Science (MS), Thesis, Biological Sciences, Old Dominion University, DOI: 10.25777/8m64-bg07 [https://digitalcommons.odu.edu/biology_etds/109](https://digitalcommons.odu.edu/biology_etds/109?utm_source=digitalcommons.odu.edu%2Fbiology_etds%2F109&utm_medium=PDF&utm_campaign=PDFCoverPages)

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GLOBAL CONSERVATION STATUS AND THREAT PATTERNS OF THE WORLD'S MOST

PROMINENT FORAGE FISHES (TELEOSTEI, CLUPEIFORMES)

by

Tiffany L. Birge A.S. May 2014, Tidewater Community College B.S. May 2016, Old Dominion University

A Thesis Submitted to the Faculty of Old Dominion University in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

BIOLOGY

OLD DOMINION UNIVERSITY December 2019

Approved by:

Kent E. Carpenter (Advisor)

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ABSTRACT

GLOBAL CONSERVATION STATUS AND THREAT PATTERNS OF THE WORLD'S MOST PROMINENT FORAGE FISHES (TELEOSTEI, CLUPEIFORMES)

Tiffany L. Birge Old Dominion University, 2019 Advisor: Dr. Kent E. Carpenter

Conserving biodiversity is one of the greatest ethical responsibilities and challenges humans face. Understanding the conservation status of taxonomic groups provides a systematic way to prioritize efforts to combat biodiversity loss. The 405 species within the order Clupeiformes are the herrings, shads, sardines, anchovies, menhadens and relatives that include many of the most important marine forage fishes. These small, schooling fishes are economically, ecologically and culturally significant globally. Despite their contribution to global fisheries and our increasing reliance on these fishes for food and industrial commodities, they are generally poorly known with limited information regarding basic biology and population trends. I applied IUCN Red List methodology, a comprehensive and systematic approach to assessing extinction risk of species, to all clupeiform species. I then used these assessments to synthesize and address their global conservation status and to highlight the potential for improvements to conservation and fisheries management. The best estimate of nearly 11% of species are of elevated conservation concern, although this could be as high as 34% if Data

Deficient species are all threatened. The Caribbean and the Indo-Malay-Philippine Archipelago both have high concentrations of either threatened or Data Deficient species and are areas of particular conservation concern. Major threats include exploitation, pollution and habitat modification for human use although the intensity of a specific threat differs between freshwater, estuarine and marine environments. Life history and ecological traits of threatened and Near Threatened species were characterized between primary habitat systems. Immediate conservation priorities include: 1) the evaluation of current fisheries management strategies, with a strong recommendation toward ecosystem-based management protocols that incorporate group-specific life history traits, and 2) local, intensive habitat restoration to reduce pollution and remove dams. These extinction risk assessments and subsequent analyses should be used to monitor conservation progress and as an informative tool for fisheries and conservation managers.

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This thesis is dedicated to my father, Bruce P. Birge and to my mother, Jaqueline R. Birge for always inspiring and encouraging my sense of adventure by putting up with my many childhood

experiments and for providing continual love and support.

ACKNOWLEDGEMENTS

This research would not have been possible without the continuous support and encouragement from many important people. First, and foremost, I would like to thank my advisor, Dr. Kent Carpenter, for providing me with this incredible opportunity and for showing me that great things can be accomplished without taking life too seriously. I also thank my committee members, Dr. Thomas Munroe and Dr. Sara Maxwell, each of whom provided great insight throughout this process. Tom, thank you for constantly challenging me and for pushing me to think outside of the box. Sara, thank you for always reminding me to take a step back and to enjoy the ride. A special and heartfelt thank you to my mentor and dear friend Dr. Gina Ralph, whom without her support and guidance, I would not be where I am today.

Thanks also to the main funding sources: Toyota Motor Corporation provided the funding for this research and the Philippines' Bureau of Fisheries and Aquatic Resources (BFAR) provided funding and logistical aid for the clupeiform workshop in 2017.

Many thanks are extended to Rob Bullock for the facilitation of species assessments and for his invaluable friendship throughout this process. To my current and previous lab mates, C. Linardich, M. Harvey, C. Gorman, J. Buchannan, E. Stump, A. Ackiss, E. Biesack, B. Stockwell, J. Whalen, J. Baldisimo, M. Kenton, I. Lopez and E. Garcia, thanks for all the advice and laughs you've provided me with. To the members of the BGSO, you have become my biology family; thank you for helping me navigate the roller coaster that is graduate school. My deepest gratitude goes to my family, Dad, Mom, Courtney, Corbin, Brian, Dustin and Aunt Sharon; thank you for the many sacrifices you have made for me and for your uplifting support during this journey.

Special thanks for the 132 experts who made these assessments possible: M. Santos, D. Gaughan, W. Mohd Arsaad, G. Allen, R. Raghavan, N. Boguskaya, I.G. Priede, D.J. Allen, H. Larson, L.R. Casten, M.N. Alava, N. Richman, A. Beresford, A. Chenery, M. Ram, R. Reis, F. Lima, D. Grubbs, J. Simons, J. Caruso, J. Brenner, L. Tornabene, J. Brown, J. Freyhof, M. Kottelat, L. Grijalba Bendeck, T. Iwamoto, W. Eschmeyer, J. Alvarado, R. Wagner, W. Bussing, B. Collette, P. Chakrabarty, J. Carlson, J.D. McEachran, G.A. Hammerson, C. Vidthayanon, T. Moelants, S. Chaudhry, B.R. Jha, N.C. Datta, R. Britz, S.C. Dey, M. Entsua-Mensah, P. Laléyé, T.A. Adeofe, K. Camara, Y.H. Camara, K. Cissoko, L. de Morais, R. Djiman, E. Mbye, A. Sidibe, P. Tous, A. Sagna, M. Sylla, J.G. Nielsen, F. Kaymaram, J. Bishop, M. Al-Husaini, S. Hartmann, S. Alam, K. Al-Kalaf, Q. Alghawzi, A. Salarpouri, J. Quilang, J. Torres, D. Milton, A. Cotto, E. Medina, O. Bernal, M. Loeb, C. van der Lingen, P. Borsa, E. Abdulqader, H. Al-Nazry, M. Al-Muktar, K. Nedreaas, A.-B. Florin, R. Cook, P. Fernandes, P. Lorance, K.A. Aiken, A. Ali, B. Collen, K.R. Devi, F. Pezold, R. Robertson, K. Cleary, T. Sandell, D. Hay, R. Gustafson, J. Williams, H. Palla, R. Deligero, M. Alcantara, M. Doyola, L. Gatlabayan, M. Villarao, A. Tambihasan, G. Lopez, J. Villanueva, F. Buccat, L. Parido, N. Lanzuela, P. Belga, A. Gapuz, A.K. Acosta, M. Casini, P. Henderson, H.H. Ng, K.E. Carpenter, G. Ralph, J.S., Sparks, A.J. Crivelli, R. Bills, B. Smith-Vaniz, D. Herdson, S. Molur, N. Dahanukar, G. Ntakimazi, L. de Costa, B.D. Olaosebikan, T. Ravelomanana, P.C. Heemstra, J. Tyler, M. Pal and A. Sidibé. Specific recognition and thanks go to Dr. Fabio Di Dario, Dr. Thomas Munroe and Dr. Harutaka Hata, whose collaboration, dedication and extensive review of many species assessments greatly improved this research.

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CHAPTER 1

INTRODUCTION

Global biodiversity is under threat. From grasses and dragonflies to sharks and mangroves, and nearly all taxa in between, there is growing concern regarding the survival status of biodiversity. Population declines have been documented in such diverse taxa as mammals (Davidson et al., 2009; Ripple et al., 2016), birds (Dunn et al., 2002), large predatory fishes (Myers and Worm, 2005), amphibians (Bielby et al.*,* 2008), flying insects (Hallmann et al., 2017) and plants (Willis, 2017), leading to local extirpations and global extinctions (Young et al., 2016). Although up to 100 million species are estimated as extant (May, 1992; Mace et al.*,* 2005), with the best working estimate between 8 – 9 million species (Chapman, 2009; Hilton-Taylor et al., 2009; Mora et al., 2011), only around 2 million species have been described to date (Hilton-Taylor et al., 2009). As a result, there is risk that species will disappear before we are aware they exist. Given that current rates of extinction are over 1000 times that of the background rate of extinction (Pimm et al., 2014), the future of biodiversity is bleak.

Despite the dominant aquatic global surface area (\sim 71% of earth's surface) and even larger inhabitable volume (Polidoro et al., 2009; Darwall et al., 2009), our knowledge of and concern for these ecosystems lags far behind that of terrestrial systems. Historically, active conservation of aquatic resources lags behind terrestrial conservation effort. This is partly due to proximity and ease of study of terrestrial systems, but also because the aquatic realm is a

vast environment, whose size alone was thought to be a buffer to impacts (Myers and Worm, 2005). As a result, global species conservation status is heavily biased towards terrestrial vertebrates and plants (Hilton-Taylor et al., 2009; Polidoro et al., 2009). Presently, major anthropogenic threats to marine and freshwater species are recognized (Young et al., 2016), particularly from the fishing sector (e.g., Atlantic cod: Shelton et al., 2006).

Fisheries are important to the financial and nutritional security of billions of people globally (FAO, 2018). Capture fisheries generate substantial local and national revenue (total estimated at USD 130 billion in 2016: FAO, 2018), mostly from landings of marine fisheries (FAO, 2018). These landings play a vital role in global nutritional security by providing a valuable source of protein and micronutrients (FAO, 2018). Fish provide over 3.2 billion people with about 20% of their average per capita animal protein intake (FAO, 2018) and consumption has steadily grown in developing regions and low-income food-deficit countries (FAO, 2018). However, overharvesting of our fish stocks has resulted in population declines up to 90% for pelagic fish species (Sadovy, 2001; Myers and Worm, 2003; Pauly et al., 2005; Sadovy et al., 2013). Taxa- and region-specific studies increasingly express that exploitation is the most prominent threat and is of growing concern as our reliance on fishery resources continues to expand (Sadovy et al., 2013; Lynch et al., 2016; FAO, 2018).

One extremely important, but often underappreciated, component of fisheries are the forage fishes. These highly numerous small- and medium-sized, pelagic species support global economies through direct fisheries exploitation and also by serving as a major food source for higher predators that are important to these economies as well (Pikitch et al., 2014). Forage fishes comprise over 30% of the total global marine fish catch (Alder et al., 2008; Smith et al.,

2011). Species of the order Clupeiformes, including herrings, shads, menhadens, sardines, anchovies, and their relatives, make up a major component of forage fishes and dominate worldwide forage fish landings (Tacon and Metian, 2009a). Three distinct contributions of forage fishes have been recognized, including: 1) ecological support for predators as a vital food resource, 2) economic value to forage fisheries, and 3) support for the catch and value of other commercially targeted predators, such as fishes, mammals and squid (Cury et al., 2011; Smith et al., 2011; Pikitch et al., 2014; Hilborn et al., 2017).

Clupeiform fisheries have a long history of nutritional, cultural and economic importance (Whitehead, 1985; Alder, et al., 2008). Their presence has been associated with persistent human settlement, growth and survival for thousands of years (Finney et al., 2002; Bassett, 2014) and is well documented in the northeastern Pacific (Thornton et al., 2010; Levin et al., 2016), the northwestern (Bassett, 2014) and northeastern Atlantic (Bloch, 1809; Coull, 2003) and the tropical western Pacific (Ruddle and Ishige, 2010). Due to their overall importance and abundance, some have been considered as cultural keystone species and have been given local nicknames like 'silver of the sea' and 'silver darlings' (Coull, 2003; Smyllie, 2004; Murray, 2015; Levin et al., 2016) to reflect the important status of these species.

Today, many millions of people rely on clupeiform catches across the world for food, industrial commodities, and everyday items. The majority of clupeiform resources are 'reduced' or processed and turned into fishmeal and related products (van der Meer et al., 2015), which makes them one of the largest species groups targeted for non-food uses (Tacon and Metian 2009a, 2009b). Currently, the largest consumer of reduced fish product is the aquaculture sector (Tacon and Metian, 2009b), which is rapidly increasing to keep pace with the growing

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demand for fish products (FAO, 2018). Aside from aquaculture, agricultural industries use reduced material as fertilizer and as fishmeal or fish oil to support livestock in direct or compound animal feed (Tydemers, 2004; Tacon and Metian, 2009a; Pikitch et al., 2012; FAO, 2016a). Fish oil is also used in a wide array of industrial applications including fuel, glue production, paint manufacture, and as a vitamin supplement (Tydemers, 2004).

To keep up with the high demand for these products, clupeiforms comprise some of the world's largest fisheries and continue to be the principal group of non-domesticated vertebrates harvested by man (Whitehead, 1985; Tacon and Metian, 2009a, 2009b; FAO, 2018). In general, the largest fisheries exploit cold-water clupeoids, such as species of *Sardinops* and *Clupea* (Whitehead, 1985; FAO, 2018). Historically, the largest fishery by volume was the famous Peruvian anchoveta (*Engraulis ringens*), which contributed an annual estimated 16 million tonnes during peak harvest years (Castillo and Mendo, 1987; Tsukayama and Palomares, 1987; Pikitch et al., 2012).

Of growing concern to fisheries and conservation managers is the tendency, particularly of the cold-water species that support large fisheries, to exhibit highly variable, albeit natural, population fluctuations (Whitehead, 1985; McKechnie et al., 2013). The episodic trends in population fluctuations are thought to be heavily influenced by environmental conditions (Pikitch et al., 2014), such as long-term, decadal-scale physical processes (e.g., El Niño: Alheit et al., 2009). Knowledge is limited on how the excessive removal of these species by fisheries may impact aquatic ecosystems (Alder et al., 2008). However, heavy industrial fishing pressure is known to exacerbate the population flux and has recently been shown to increase the

likelihood of population collapse in small pelagic fishes that have been exploited by long-term fisheries (Pinsky et al., 2011).

The overwhelming importance of cold-water clupeoid fisheries often overshadows the contributions of tropical and freshwater clupeiform fisheries (Whitehead, 1985). These warmwater fisheries tend to dominate the landings of artisanal and subsistence sectors, rather than the industrial sector (Whitehead, 1985). When reported in fisheries landings, multiple species are often lumped in landings data (e.g., *Stolephorus* spp., FAO, 2018), making analysis of species-specific trends problematic.

Aside from most cold-water species that tend to represent the landings of the larger fisheries, we know very little about clupeiforms globally despite our overwhelming reliance on them and their known importance in nearly every aquatic ecosystem (Whitehead, 1985). Research has been hindered by confusing taxonomy and challenging identifications (Whitehead, 1985). Overall, it is relatively easy to distinguish clupeiforms from other fish groups because nearly all lack a visible lateral line on the body; however, it is difficult to tell them apart from each other, particularly in regions where clupeiform species richness is high (Whitehead, 1985). Ironically, these areas coincide with the fastest growing human populations and their reliance on fisheries, and often these ecosystems represent regions most in need of conservation (Darwall et al., 2009).

The Clupeomorpha (Greenwood et al., 1966), along with Alepocephali and Ostariophysi make up the Otocephala, one of four extant lineages of Teleostei (Nelson et al., 2016). Representatives of the Order Clupeiformes are characterized within two suborders: the

Denticipitoidei, a monotypic group with only one extant representative, *Denticeps clupeoides* Clausen 1959*,* and the Clupeoidei which comprises all other extant species in the Order Clupeiformes (Whitehead, 1985; Grande, 1985; Di Dario, 2004; Di Dario and de Pinna, 2006; Lavouè et al., 2014; Bloom and Egan, 2018). Since Fowler's attempt to list all valid clupeoid species (Fowler, 1973), Whitehead (1985) and Whitehead et al., (1988) have been the only comprehensive works to compile species-specific information on valid species in the suborder Clupeoidei, representing nearly the entire Order Clupeiformes.

Historically, clupeiform systematics largely relied on morphometric, meristic, and other morphological characters, which sometimes classified taxa based more on overall similarity or geographical convenience rather than on rigorous scientific support (Bloom and Egan, 2018). Grande's (1985) five proposed subfamilies of Clupeidae (Alosinae, Clupeinae, Pellonulinae, Dorosomatinae and Dussumieriinae), and the description of what is now considered to be a species-complex of the genus *Sardinops* (Whitehead, 1985), are examples of such taxonomic convenience. Further, given that numerous and often similar species are known in many genera, some valid species may have long been obscured within the synonymies of others, and many more proposed names exist than are needed (Whitehead, 1985).

Current advancement of molecular and genetic methods and recent morphological analyses aided in the description of several species and rearrangement of groups (e.g., Loeb et al., 2017; Li and Ortí, 2007; Lavouè et al., 2014; Di Dario, 2009; Hata and Motomura, 2018; Bloom and Egan, 2018). However, some systematic relationships remain unresolved (Malabara and Di Dario, 2016; Bloom and Egan, 2018). Given this taxonomic and systematic uncertainty, for the purposes of this thesis, I followed the family group names outlined in the study by Van

der Laan et al., (2014) that recognizes seven families (Denticipitidae, Clupeidae, Engraulidae, Pristigasteridae, Chirocentridae, Dussumieriidae and Sundasalangidae). Recent and ongoing analyses, including the reassignment of the Sundasalangidae within the Clupeidae (Lavoué et al., 2014), elevation of the subfamily Spratelloidinae to the family Spratelloididae (Bloom and Egan, 2018) and re-examinations of genera (e.g., revision of *Sardinella* and *Stolephorus* by Hata and Motomura, 2017, 2018, and 2019; revision of *Anchoviella* by Loeb et al., 2017) will likely improve our understanding of the taxonomic and systematic relationships within the Order Clupeiformes.

Given the taxonomic challenges presented by the clupeiforms, species-specific threats can go undocumented particularly in face of overexploitation and in their dependence on often degraded coastal ecosystems. Information about which species are at risk and what factors are most threatening is particularly important to successfully and strategically plan and implement conservation management policies (Venter et al., 2006). Therefore, to evaluate the conservation status of clupeiform fishes, I used the most widely accepted standard for assessing the symptoms of extinction risk, the International Union for Conservation of Nature (IUCN) Red List Criteria (Hoffman et al., 2008). This thesis analyzes the conservation status of the clupeiforms, accounting for species-specific characteristics and population trends. In Chapter 2, I evaluated the global extinction risk for all species using the IUCN Red List methodology. I hypothesized that major threats would vary by family group and by the primary habitat type occupied by the species. In Chapter 3, I used data and results from the Red List Assessments to test the influence of habitat type and natural history traits on susceptibility to threats. I hypothesized that species can be characterized into groups based on these ecological

and natural history traits, and that such analyses could be used to inform management measures.

CHAPTER 2

GLOBAL CONSERVATION STATUS OF THE WORLD'S MOST PROMINENT FORAGE FISHES (TELEOSTEI: ORDER CLUPEIFORMES)

INTRODUCTION

Forage fishes directly link primary production to keystone predators in marine environments (Pikitch et al., 2014). These small- to medium-sized, typically very numerous pelagic species also support the global economy by directly and indirectly sustaining many fisheries (Pikitch et al., 2014). Forage fishes make up over 30% of the global marine catch (Alder et al., 2008; Smith et al., 2011). They also play a key role as prey for many commercially targeted predators, such as fishes, mammals and squids (Cury et al., 2011; Smith et al., 2011; Pikitch et al., 2014; Hilborn et al., 2017).

Species of the order Clupeiformes, including herrings, shads, menhadens, sardines, anchovies, and their relatives, are a major component of forage fishes and dominate worldwide forage fish landings (Tacon and Metian, 2009a). Additional to providing ecological and economic support, clupeiforms contribute to food security worldwide given their abundance, access and exceptionally high nutrient content (FAO, 2018); in some communities, clupeiforms make up the major or the sole protein source (Mohan Dey et al., 2005; Alder et al., 2008; Kawarazuka and Béné, 2011; Mohanty et al., 2019). Historically, clupeiform presence has been associated with persistent human settlement, growth and survival for thousands of years

(Bloch, 1809; Coull, 2003; Thornton et al., 2010; Ruddle and Ishige, 2010; Bassett, 2014; Levin et al., 2016). To meet the needs of a projected rising human global population (United Nations, Department of Economic and Social Affairs, Population Division, 2017), demand for fisheries resources is expected to continue to grow (FAO, 2018). Given the overall ecological, cultural, nutritional, and economic importance of clupeiforms worldwide, their conservation status warrants greater attention.

The teleost fish order Clupeiformes includes 405 species that are globally distributed with tropical, temperate and sub-Arctic representatives (Whitehead, 1985; Blaber et al., 1996; Wongratana et al., 1999; Munroe et al., 1999; Lavoué et al., 2013; Pikitch et al., 2014). Members of this Order are ecologically diverse and span all aquatic habitats, including freshwater rivers and lakes, estuaries, coastal marine areas, and the open ocean (Whitehead, 1985; Lavoué et al., 2013; Bloom and Egan, 2018). Clupeiform species can be restricted to fresh, estuarine, or marine waters, or they can exhibit diadromy (Whitehead, 1985). This ability to navigate between marine and freshwater habitats is shared with other groups such as stingrays, needlefishes, silversides, drums and pufferfishes (Lovejoy et al., 2006; Bloom and Lovejoy, 2017; Bloom and Egan, 2018). Strictly marine clupeiforms (32% of all species) are distributed in every ocean, except for the Southern Ocean (Whitehead, 1985), strictly freshwater species (18% of all species) are found on every continent except for Antarctica (Bloom and Lovejoy, 2012, 2014; Bloom and Egan, 2018).

In general, life history traits such as high fecundity, widespread distributions, adaptability to diverse habitats, and high dispersal ability are features that are thought to increase survivability in face of anthropogenic stresses (Stearns, 1992; Hutchins, 2000; Sadovy, 2001; Denney et al., 2002; Reynolds et al., 2005; Alder et al., 2008; Comeros-Raynal et al., 2016). In contrast, slow growth, large body size, and high longevity are life history features thought to increase a species' vulnerability to extinction (Roberts and Hawkins, 1999; Reynolds et al., 2005; Harnik et al., 2012; Juan-Jorda et al., 2015; Comeros-Raynal et al., 2016). These innate traits have also been used to determine a species' ability to cope with, and recover from, human-induced and environmental disturbances (Cardillo et al., 2005, 2008; Reynolds et al., 2005). However, high fecundity, early age at maturation and similar demographic traits do not reliably predict a species' vulnerability to, or ability to recover from, overexploitation (Jennings et al., 1998; Kindsvater et al., 2016; Sadovy, 2001; Juan-Jorda et al., 2012, Comeros-Raynal et al., 2016).

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 and taxonomic complexity of clupeiforms (Whitehead, 1985; Alder et al., 2008). Clupeiform value per pound is also far less than that for other commercial fishes, which may further disincentivize the contribution of resources to research and conservation for the clupeiform fishes. 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 study resources and reliable data reinforces the need to invest effort into understanding the current conservation status of species within the Order. The International

Union for Conservation of Nature Red List of Threatened Species provides an ideal starting point for highlighting and addressing conservation needs for fish species, including the clupeiforms (Mace et al., 2008).

The IUCN Red List is a comprehensive repository of open-access, species-specific assessments that conveys a species' symptoms of extinction (Rodrigues et al., 2006; Vié et al., 2009). Red List assessments are the most widely accepted standard for species-level risk evaluations (Hoffman et al., 2008). By illuminating knowledge gaps regarding the conservation status of species (e.g., Carpenter et al., 2008; Schipper et al., 2008; Polidoro et al., 2010; Short et al., 2011), the 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 information on the conservation status of clupeiforms hampers our ability to proactively manage and conserve these essential components of aquatic food webs. Therefore, the extinction risk of all 405 species within the Order was evaluated following the IUCN Red List methodology to provide a baseline from which to monitor changes. The resulting information was then used to evaluate: 1) variability in the proportion of species at an elevated risk of extinction as a function of family (Denticipitidae, Pristigasteridae, Engraulidae, Chirocentridae, Clupeidae, Dunssumieriidae, Sundasalangidae), and as a function of habitat (freshwater, marine and euryhaline); 2) major threats to all species; and 3) spatial trends in clupeiform species richness.

METHODS

Red List Methods

A comprehensive species list was compiled based on the online version of the Catalog of Fishes (Eschmeyer et al., 2017) and in consultation with taxonomic experts. Individual clupeiform species assessments were collated from information on the geographic distribution, population status, life history, utilization and quality of habitat, potential threats and the conservation measures of each species. The assessment process required input and involvement from 132 international experts from more than 20 countries who systematically evaluated extinction risk indicators for all 405 species. Three nominal species recently described after December 2018 as new or elevated as distinct from synonymy with another species are not included within these analyses, but Red List assessments have been completed for these species (Appendix A).

The IUCN Red List includes eight levels of extinction risk (Fig. 1): 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 species can qualify for a threatened category (CR, EN, VU) by meeting at least one of the five quantitative thresholds that fall 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).

Fig. 1. The nine extinction risk categories from the IUCN Red List of Threatened Species.

A category of NT can be applied if the quantified estimates of population decline or range size nearly meet the thresholds for assigning a threatened category under at least one of the criteria. The DD category is applied if a species is only known from few specimens, lacks available information to assess under any of the criteria, or if there is uncertainty regarding its taxonomic status. This category can also be applied if declines are likely due to a known threat (e.g., fishing pressure), but the threat could not be quantified, such that a more appropriate category could be applied.

All five Red List Criteria were considered during the assessment process; however, almost all species were assessed under criteria A (population decline) or B (restricted range). Data required to assess a species under the remaining criteria (C, D or E) were often unavailable given the difficulty of quantifying the number of mature individuals present in fish populations. As of July, 2019, all species are published on the Red List website (www.iucnredlist.org), where species data, maps and extinction risk categories are freely available.

Quantifying Threats

As part of the Red List process, threats were identified for each species based on the published literature and in consultation with experts. Threats were quantified within the Red List assessments using a hierarchal process by coding an individual threatening event to the finest resolution level possible (IUCN, 2016). Major threats were then summarized and the proportion of threatened and near threatened species was explored for all species, as well as by clupeiform family and major habitat system. The proportion of threatened and NT species is expressed using both a midpoint and a range to address the uncertainty surrounding the true status of a DD species. The midpoint was calculated by removing the species listed as DD, whereas the lower and upper bound were calculated by either excluding or including the DD species with the threatened species, respectively. The lower bound assumes that none of the DD species are threatened, while the upper bound assumes that all DD species are threatened.

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, I modified the IUCN Red List 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 known to occupy only freshwater environments and the marine system includes species restricted to marine waters. I added a third, euryhaline category that includes estuarine species, diadromous species, and species known or suspected to tolerate changes in salinity.

Distribution Mapping Methodology

Maps were created for each species using ArcMAP 10.3 by compiling data from published and grey literature, expert knowledge, and online databases (e.g., FishNet2; OZCAM; GBIF) on known occurrence along with habitat and depth limits. 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 bathyline or 100 km from the shore, whichever is further from the coast. Bathymetric layers were extracted from two global level sources, the National Geophysical Data Center's ETPO1 (Amante and Eakins, 2008) 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 then combined to encompass the entirety of the species' range.

Global maps of overall species richness, Data Deficient richness, and richness of elevated concern species were created using ArcMap 10.3 based on two biogeographic systems. Species with a freshwater extent (n = 74) were summarized within the Global HydroBASINS (Leher and Grill, 2013), using Level 3, the largest river basins of each continent. Species with a marine extent (n = 130) 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. Freshwater and marine layers were merged to summarize species with both a freshwater and marine extent ($n = 201$).

RESULTS

Global IUCN Red List status of clupeiforms

The best estimate of the proportion of elevated concern for clupeiforms species is 11% (n = 33), which includes those assessed as threatened or Near Threatened. Given the uncertainty of an appropriate Red List Category for all Data Deficient (DD) species, the true proportion of elevated concern species could lie between 8 – 34%. Of all species (n = 405), three (0.7%) are listed as Critically Endangered (CR), 11 (2.7%) as Endangered (EN), 13 (3.2%) as Vulnerable (VU) and six species (1.5%) as Near Threatened (NT) (Fig. 2). Species are primarily listed as threatened or Near Threatened due to a restricted range size with an ongoing threat (criterion B; n = 18) or due to population decline (criterion A; n = 10); two species (*Sardinella tawilis* and *Alosa vistonica*) are listed as threatened under both criteria A and B (Appendix A).

Three species are listed as Vulnerable (VU) given that they have a very restricted range and a serious plausible future threat (criterion D). Of the remaining 372 species, 266 (65.7%) are categorized as Least Concern (LC) and another 106 (26.2%) are considered as Data Deficient (DD).

Fig. 2. Proportion of species (n = 405) listed in each Red List Category. Abbreviations of Red List Categories are as follows: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern and DD = Data Deficient.

Among the families of clupeiform fishes, the family Denticipitidae consists of only one species (*Denticeps clupeoides*), which is listed as VU; as such, it is the family with the highest proportion of elevated concern overall (Fig. 3). However, excluding *D. clupeoides*, the Clupeidae (26 of 195 species; midpoint = 16.6%) has the highest proportion of elevated concern species, followed by the Engraulidae (5 of 154 species; midpoint = 4.9%) and the Pristigasteridae (1 of 36 species; midpoint = 3.8%). None of the Chirocentridae (n = 2), Dussumieriidae (n = 10) or Sundasalangidae (n = 7) are considered threatened. However, the high proportion of DD species, especially within the Sundasalangidae, may be obscuring trends in threat patterns and compromising the accuracy of the overall conservation status estimated for these species.

Fig. 3. Proportion of species listed in each Red List Category separated by family. The total number of species in each family is represented by the number at the top of each bar. Abbreviations of Red List Categories are as follows: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern and DD = Data Deficient. The midpoint is represented by the black bar and was calculated by the following equation: $(CR + EN + VU) / (Total - DD)$.

Species classified as euryhaline (i.e., diadromous or estuarine) constituted nearly half of the species within the order ($n = 201$; 49.6%), followed by marine ($n = 130$; 32.1%) and freshwater species (n = 74; 18.3%) (Fig. 4). Euryhaline species have the largest proportion of Least Concern species ($n = 147$; 73.1%) followed by marine ($n = 80$; 61.5%), and then by freshwater species (n = 39; 52.7%). Overall, despite having the lowest number of representatives, the freshwater inhabitants have the highest proportion of elevated concern species ($n = 16$; 21.6%), more than double that of the species inhabiting marine and euryhaline habitats combined (5.4% and 5.0%, respectively). Additionally, all species assessed as CR, the highest threat level, are found in freshwater habitats.

Major threats

Of the 405 species, 144 have at least one coded threat; the remaining 261 species either have no major threats causing significant impacts or threats are unknown for these species. Overall, the most prominent threat by a significant margin impacting all clupeiforms, is exploitation (Fig. 5). Pollution and natural system changes (e.g., dams) impact nearly the same number of species (47 and 42, respectively). Despite having the highest proportion of LC species, euryhaline species are disproportionately impacted by pollution and natural system modifications relative to freshwater and marine species. For example, the number of euryhaline species impacted by one of these threats is more than 1.5 times the number of fresh and marine species combined. Likewise, euryhaline species impacted by both threats (pollution and natural system modifications) is double that of the combined number of marine and freshwater species impacted by these factors. Climate change and invasive species make up the fourth and

fifth most common threat to all species, respectively. However, invasive species impact more threatened and NT species than climate change.

Spatial Analyses

Global species richness follows two general distribution patterns; a longitudinal gradient, where the highest tropical richness is within the Indo-West Pacific, and a latitudinal gradient where richness decreases with an increasing latitude from the tropics. The highest global species richness of all 405 clupeiforms is located along the coast of India and throughout the Indo-West Pacific from the eastern Andaman Sea, east to the Philippines, Indonesia and northeastern Papua New Guinea (Fig. 6A). 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 southern and northernmost limits of the global range for species of this order (e.g., the Arctic and sub-Arctic region, and north of the Southern Ocean), further inland (e.g., the rivers of China, Australia, and parts of Africa), and off Polynesian Islands in the central and south Pacific (e.g., Hawaii, New Zealand, Society Islands, etc.).

Fig. 4. Proportion of species listed in each Red List Category by major habitat (fresh, euryhaline or marine). The total number of species is represented by the number at the top of each bar. Abbreviations of Red List Categories are as follows: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern and DD = Data Deficient. The midpoint is represented by the black bar and was calculated by the following equation: $(CR + EN + VU)/(Total - DD)$.

Fig. 5. Number of species impacted by major threats. Each threat is represented by the number of species listed in each Red List category. Threats that impact less than five species (Human intrusion and Transportation) are excluded. Abbreviations of Red List Categories are as follows: $CR = Critically$ Endangered, $EN = End$ angered, $VU = V$ ulnerable, NT = Near Threatened, LC = Least Concern and DD = Data Deficient.

In general, richness of DD species closely follows that of the total species richness (Fig. 6C). However, the richness of DD species 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.

B - Threatened and NT species

C-DD species

Fig. 6. Number of clupeiforms in each Large Marine Ecoregion (LME) and freshwater hydrobasin for A) All species, B) all species of elevated concern (CR, EN, VU, NT), and C) all Data Deficient species. Colors correspond to the number of species listed at the bottom of each map. The Marine Ecosystems of the World (MEOW) at the province level was used for marine species, Hydrobasins of the world at level three was used for freshwater species. The freshwater and marine extents were created separately and merged to represent the total global extent for euryhaline species.

Conversely, the highest richness of species of elevated concern (threatened and NT, $n =$ 33) occurs within the greater Caribbean (Fig. 6B). Other areas of high richness of species of elevated concern are along the western Pacific continental coast (Russia south to Indonesia), and inland areas including the Caspian Sea, rivers of Croatia to Greece and Bulgaria, the Congo River in Central Africa, and the rivers of Borneo. A low richness of species of elevated concern is found along the northeastern United States, within Central America, along the eastern and southern coasts of South America, the western coast of Africa, parts of Europe including the Mediterranean and Black Seas, southern Australia, and within some freshwater areas in China and Russia.

DISCUSSION

When compared to other economically and ecologically important fish groups globally assessed using the IUCN Red List methodology (e.g., Collette et al., 2011; Sadovy de Mitcheson et al., 2013; Comeros-Raynal et al., 2016), clupeiforms have the lowest percentage of threatened and Near Threatened (NT) species overall. Just over 8% are currently known to be at high risk of potential future extinction as compared to roughly 18% of tunas and billfishes (Collette et al., 2011), 26% of groupers (Sadovy de Mitcheson et al., 2013) and 17% of sparids (Comeros-Raynal et al., 2016). However, major threats to clupeiforms are nearly identical to those found in previous analyses of the conservation status of other fishes (e.g., Roberts and Hawkins, 1999; Reynolds et al., 2005; Dulvy et al., 2009; Harnik et al., 2012), with exploitation as the leading threat for all clupeiforms in all habitats. While exploitation may be the most prolific threat by impacting the highest number of clupeiforms, pollution may be the most

detrimental, as it affects a greater number of species assessed as Critically Endangered (CR) (Fig. 5).

The lower proportion of threatened species in clupeiforms compared to other bony fishes may be a function of uncertainty of conservation status and is likely an underestimate of the true threatened status. The high percentage of data deficiency in clupeiforms (26.2%) surpasses that of the tunas and billfishes (Collette et al., 2011) and sparids (Comeros-Raynal et al., 2016), which have less than 20% of species that are 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 occur within the clupeiforms.

For individual species, the paucity of data on distribution, status, ecology and threats may be a consequence of taxonomic uncertainty (IUCN, 2017). For example, *Alosa curensis* is DD because it was previously recognized as a synonym of *Alosa brashnikowi* and is known only from a few specimens. Thus, information associated with what was previously thought to be the single global population of the nominal *A. brashnikowi*, may not also be applicable to *A. curensis*. Challenges associated with taxonomic uncertainty or recent revision, such as estimating decline or geographic range, may allow species-specific threats to go undocumented.

The high proportion of DD clupeiform species coincides with geographic areas of both dense clupeiform biodiversity and areas of depressed economic status. 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). This pattern is reflected in clupeiforms. 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). 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 clupeiforms.

In many parts of the world, particularly in highly biodiverse areas, stock assessments and fishery effort data are lacking or unreported for many clupeiforms. 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 often include many species lumped together because many clupeiforms that co-occur look very similar, are difficult to identify taxonomically, and are known to school together in some cases (e.g. sardines and anchovies: Bakun and Cury, 1999). Teasing apart landings from multi-species fisheries is a difficult task and when identifications contain many errors can lead to a false estimation of species-specific catch data (Gaichas et al., 2012). Exploitation is a major threat to over 25% of clupeiform species and this may be an underestimate given uncertainties in catch data and the population status of DD species (26.2%). 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 lumped 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) and ultimately impacting the efficacy of conservation or management decisions.

The highest concentration of threatened species in this analysis is centered in the Caribbean region, but this estimate does not take into consideration uncertainty concerning species listed as DD. The highest species richness and number of species listed as DD is concentrated in the central Indo-West Pacific region. Given that the Caribbean and the Indo-West Pacific are both areas of high species richness, but that about one-tenth of the Caribbean species are assessed as DD compared to roughly one-third of Indo-West Pacific species, we therefore know more about the species in the Caribbean in general. Currently, clupeiforms in the Caribbean would benefit most from threat mitigation as this region has the highest number of threatened and NT species present. It has been noted that the most diverse areas often have the highest number of threatened species (Baille et al., 2004). As data become available to adequately assess species currently listed as DD, it is possible that we may find a higher proportion of threatened and NT species within the Indo-West Pacific rather than within the Caribbean. However, currently clupeiforms in the Indo-West Pacific region may benefit most from emergent research to fill in our knowledge gaps presented by the high number of DD species.

In addition to the high proportion of DD species, traditional perceptions of intrinsic life history traits have been an impediment to the conservation concerns of clupeiforms overall. Their typical high fecundity, multiple spawning, and early age at maturation are regarded as resilience factors even though these traits often do not reflect vulnerability to extinction

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(Jennings et al., 1998; Kindsvater et al., 2016; Sadovy, 2001; Juan-Jorda et al., 2012; Comeros-Raynal et al., 2016). For example, the Pacific herring (*Clupea pallasii*) is a widely distributed species that is exploited to a varying degree 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, the intrinsic life history characteristics of many clupeiforms may be providing them with a buffer against extinction relative to other 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, a freshwater or euryhaline species is threatened by both pollution and natural system modifications, indicating a potential cumulative effect between threats. This interaction was not explored in this study. Genera with many anadromous representatives such as *Alosa* and *Tenualosa* appear to be most negatively impacted by one or both threats (e.g., Freyhof and Kottelat, 2008b; NatureServe, 2013; Di Dario, 2018b; Mohd Arshaad et al., 2018). In line with previous studies of other freshwater fishes (e.g., Collen et al., 2014), freshwater clupeiforms have over double the proportion of threatened and NT species compared with marine and euryhaline clupeiform species combined (% threatened and NT = 21.6% of FW, 5.4% for marine, and 5.0% for euryhaline). Given that all species listed as Critically Endangered (CR) are freshwater clupeids, the responses of these fishes to stresses should be examined more closely.

Given the overall importance of clupeiform fishes and their ubiquity as an important fishery resource, there should be concern regarding these species despite the lower percentage of threatened species compared to other fish groups of higher economic value. Many species threatened with exploitation have monitoring in place, which may not be sufficient; therefore, it is urgent that the efficiency of current management measures is evaluated. An increase in species-specific landings and catch statistics would also further improve our abilities to assess exploitation as a threat for a larger number of species. Additionally, a few large-scale industrial fisheries, such as those for the Peruvian anchoveta (*Engraulis ringens*) and for the Pacific herring (*Clupea pallasii*), may benefit from increased multi-national cooperative regulations. Species listed as an elevated conservation concern should be monitored more closely and anthropogenic pressure strictly managed although prioritizing research and conservation initiatives in areas of high biodiversity can be difficult given limited resources. Fishery managers in areas with a large proportion of exploited DD species should prioritize research initiatives to fill gaps in our understanding of these species. At a local level, species with limited ranges, such as *Alosa killarnensis* (Freyhof and Kottelat, 2008) and *Sardinella tawilis* (Santos et al., 2018), should be a priority for stringent protection, especially regarding habitat quality, which impacts mainly freshwater and estuarine species.

CHAPTER 3

CHARACTERIZING CLUPEIFORM THREATS, LIFE HISTORY TRAITS, AND HABITAT PREFERENCE TO INFORM MANAGEMENT OF DATA DEFICIENT SPECIES

INTRODUCTION

Aquatic biodiversity supports ecosystem health and the ecosystem services we rely upon (Brooks et al., 2006). Covering more than 71% of the Earth's surface and even more inhabitable space by volume, freshwater, estuarine and marine environments supply more than 40 million jobs with an estimated contribution of several trillion dollars annually to the global economy (Darwall et al., 2011; FAO, 2018). The services provided by our aquatic ecosystems include food provisioning, climate and atmospheric regulation, carbon sequestration, flood control, storm protection, nutrient cycling and waste removal (Aladin et al., 2005; Worm et al., 2006; Palumbi et al., 2009). Despite our reliance on aquatic resources, conservation initiatives have lagged far behind those of the terrestrial realm (Hilton-Taylor et al., 2009; Polidoro et al., 2009; Darwall et al., 2011). Resource limitation and exigent needs have resulted in prioritized conservation within marine and freshwater environments to support species groups such as mammals (Freeman, 2008), sharks (Dulvy et al., 2008) and turtles (Seminof and Shanker, 2008), or regions of most concern such as the Mediterranean Sea (Smith and Darwall, 2006; Abdul Malak et al., 2011). However, the conservation and management dilemmas of priority species cannot be solved without also incorporating the complexities and trade-offs of the ecosystem,

including the effects of predator-prey interactions. Thus, recent interest has shifted toward ecosystem-based management to account for ecological, economic and societal challenges associated with fisheries management (Link, 2002; Pikitch et al., 2004, 2012, 2014; Palumbi et al., 2009).

Clupeiforms, including herrings, shads, sardines, anchovies and their relatives make up the bulk of what we consider to be forage fishes (Whitehead, 1985) as they are a major food source for many aquatic predators (Pikitch et al., 2012). In addition to providing support for many other, often commercially important species, clupeiforms make up lucrative fisheries on every continent where they are distributed (Whitehead, 1985). They have supported the world's largest fishery in history (the Peruvian anchoveta, *Engraulis ringens*: Whitehead, 1985) and continue to support substantial fisheries worldwide (FAO, 2018). Clupeiform fisheries make major contributions to international industrial commodities and provide nutritional security for billions of people globally each year (Alder, 2008; Tacon and Metian, 2009).

Management and conservation regulations for clupeiforms are often lacking in the places where needed most, such as in tropical areas of highest biodiversity with the lowest capacity to fund such initiatives (Worm and Branch, 2012). Current management efforts are often species-specific for the well-known or heavily exploited species of clupeiforms. Management objectives using Maximum Sustainable Yield, biomass cutoff limits, or gear restrictions have worked well for managing and rebuilding some stocks including, for example, the Pacific herring, *Clupea pallasii* (WDFW, 2018) which is in a low biodiversity temperate region. However, regions of high biodiversity of clupeiforms generally lack species-specific management capabilities.

In tropical regions with high biodiversity, multispecies catches of clupeiforms are often very difficult to identify to the species level (Whitehead, 1985; FAO, 2018) confounding fishery management efforts. Instead, species are categorized with variable resolution into taxonomic groups by genus or family, or into functional groups such as 'forage fishes' or 'small-to mediumsized pelagics', with similar management strategies applied to all species in the group (Beverton, 1990; Patterson, 1992). However, clupeiforms express an extensive spectrum of diversity of life history features among species (Whitehead, 1985; Bloom and Egan, 2018). For example, maximum known lengths vary from about 2 cm in species of *Sundasalanx* (Roberts, 1981) to 100 cm in *Chirocentrus nudus* and *C. dorab* (Munroe et al., 1999) with known longevities spanning from less than one year in *Spratelloides gracilis* (Milton et al., 1991; Meekan et al., 2006) to up to 25 years in *Sardinops sagax* (Whitehead, 1985). Total geographic distributions extend from a single small lake as in the case of *Alosa killarensis* (Freyhof and Kottelat, 2008) to the entire Indo-West Pacific in *Sardinella gibbosa* (Whitehead, 1985). Clupeiforms span maximum depths from less than 10 meters in *Anchoa analis* (Whitehead et al., 1988) to more than 400 meters in *Clupeonella grimmi* (Aliasghari et al., 2017). Habitat preference and tolerance of ecological conditions also vary widely in species throughout the order with representatives from freshwater, estuarine, marine and diadromous groups (Whitehead, 1985).

The highly variable life history traits of clupeiforms suggests that diverse management approaches that account for this variation may help solve management hurdles in data poor fisheries (Siple et al., 2018). Identifying differences and similarities among species to group them based on shared life history, ecological characteristics, and response to threats may

provide tractable management strategies. Particularly in areas of high clupeiform diversity where ecological and biomass data are relatively limited, traditional management strategies are challenged by data limitation (Smith et al., 2009; Carruthers et al., 2014). Methods dealing with data-poor fisheries are often in the form of a 'Robin-hood' approach, where borrowed information from a similar, well-known species is used to make decisions for the lesser known species (Smith et al., 2009). However, given the diversity of clupeiforms, (Whitehead, 1985; Bloom and Egan, 2018) information from many of the well-known species may not be applicable to those that are data limited. Therefore, an alternative 'basket' approach, where similar, data-poor species are binned and managed together (Smith et al., 2009), may prove to be the more useful management approach.

METHODS

The IUCN Red List is a globally recognized standard for assessing species-level extinction risk and acts as a baseline from which to monitor change (Vié et al., 2009). IUCN Red List assessments were conducted for the 405 valid clupeiform species following Eschmeyer et al., (2017) and taxonomic expertise (Appendix A). Four nominal species were described as new or elevated from synonymy since December 2018; species Red List assessments for these taxa have been completed, but the information from these assessments is not included in this analysis. Each assessment includes expert-vetted information on geographic distribution, population trends, ecology, potential threats and existing conservation measures (for detailed Red List methodology, see Ch. 2 and Appendix B).

Multivariate analyses are widely used in ecology to address increasingly complex questions and are used here to explore patterns within available clupeiform data. These sophisticated ordination techniques are required to reduce dimensionality and visualize patterns in multivariate data (Anderson and Willis, 2003). Analysis options include unconstrained methods such as principal component analysis, principal coordinate analysis and nonmetric multidimensional scaling, whereas constrained methods include such analyses as canonical discriminant analysis, canonical correlation analysis and canonical analysis of principal coordinates (Anderson and Willis, 2003). Unconstrained methods are typically used to discover unknown or suspected patterns in data (Anderson and Willis, 2003). In general, constrained ordinations use *a priori* hypotheses from which to produce a plot so that a matrix of response variables such as community or species data can be related to some predictor variable or variables, such as measured ecological data. Canonical analysis of principal coordinates (CAP) is a flexible constrained method that allows the use of any distance or dissimilarity measure and accounts for underlying correlation structuring among response variables (Anderson and Willis, 2003).

To explore which known characters from well-studied species can be used to help bin together and possibly improve conservation measures for poorly-known species, two CAP analyses were conducted. Species-specific data were exported from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species open-sourced database (available at: www.iucnredlist.org) and organized into matrices. These matrices of species data were then imported into PRIMER-*e* with PERMANOVA+, a multivariate statistical software for ecological sciences (Anderson et al., 2008; Clarke and Gorley, 2015). A Bray-Curtis similarity test was then

run on the matrix data to quantify the similarities between species relative to the input variables. I tested for significance between groups in *a priori* hypotheses using a permutational multivariate analysis of variance (PERMANOVA). Finally, CAP was used to visually compare species assemblages and to ascertain which axes in a multivariate space effectively discriminate between *a priori* groups. A unit circle and vectors of the response variables were overlaid on the CAP figure to determine which variables most influence the observed patterns.

Additionally, I explored the effects of habitat on the maximum size of 394 exploited and non-exploited species (all species for which maximum size data were available). I used a twoway analysis of variance (ANOVA), followed by a Tukey HSD post-hoc test for pairwise comparisons. Analyses were completed using the R Project version 3.4.3 (R Core Team, 2017) and RStudio.

To determine how major threats vary as a function of the primary occupied habitat system (freshwater, marine or euryhaline), the species with major threats identified as part of the IUCN Red List assessments (n=144) were included in a CAP analysis. The remaining 261 species have either no major threats identified, or threats are suspected but unconfirmed. The threats identified for each species were organized based on the IUCN threat classification hierarchy (IUCN, 2012) and include exploitation, climate change, mining, human disturbance, invasive species, natural system modifications, which primarily refers to dam placement or water abstraction, pollution, residential and commercial development, and transportation corridors.

I included two explanatory variables: the IUCN Red List categories and the primary occupied habitat system (freshwater, marine, euryhaline). The IUCN Red List categories include Data Deficient (DD), Least Concern (LC), Near Threatened (NT) and the threatened categories: Vulnerable (VU), Endangered (EN), Critically Endangered (CR) Extinct in the Wild (EW) and Extinct (EX) (IUCN, 2012; Chapter 2, Fig. 1). Given the high degree of plasticity in salinity tolerance that is known or suspected for many clupeiforms, I modified the habitat system classification used in the IUCN Red List methodology. Instead of including just two aquatic categories (freshwater, including inland, brackish and upper estuarine waters, and marine, including coastal or lower estuarine waters: IUCN, 2013), I added a third, euryhaline category that separates the estuarine component from the Red List classifications. Therefore, the freshwater system refers to species currently known to occupy freshwater habitats with no documented tolerance of an increased salinity; marine species are known to tolerate only marine waters. The euryhaline category comprises a variety of species including strictly estuarine species, diadromous species and those known or presumed to tolerate wide salinity fluctuations. Separating estuarine and diadromous groups was problematic as several species could not be easily classified into one of these two groups. For example, a species may be known to tolerate a wide range in salinity with records from both marine and freshwaters, but diadromy is unconfirmed. Therefore, a single, euryhaline category was implemented to account for all estuarine species and those known to withstand salinity fluctuations to a varying degree.

To address which life history characteristics are most important in determining clustering of species of elevated conservation concern, life history and ecological traits of all threatened and NT species (n=33) were included in a second CAP analysis. I included the

following as response variables: maximum standard length, number of coded threats, habitat system preference (freshwater, marine or euryhaline), habitat specificity (generalist or specialist) and proxies for distribution and relative clupeiform richness in an area where a species is found. Habitat system preference and habitat specificity (generalist or specialist) are numerical variables coded within the input matrix. Habitat system data were carried over from the species-threat matrix. Within Red List assessments, the number and type of habitats occupied by a species are coded based on information from available literature; this information was pulled from assessments and used to assign a species as either a habitat generalist or specialist. The attribution of a species to one of the two categories follows Stump et al., (2018); if a species occupies only one coded habitat type (i.e., freshwater lakes/rivers) it was considered a specialist and if it occupies more than one habitat type (i.e., freshwater rivers and coastal marine waters), it was considered a generalist. A numerical estimate of total geographic distribution area was measured by determining the number of countries where a species is known, inferred or suspected to occur. Using the distribution shapefiles of each species, estimated clupeiform diversity in an area where a species is found was measured in ArcMAP 10 by adding the number of other clupeiforms that have an overlapping distribution with an individual species.

RESULTS

For clupeiforms with at least one identified threat (n = 144), the CAP analysis revealed a separation of species assemblages as a function of habitat system, specifically between threats

impacting freshwater and marine species (Fig. 7). The euryhaline species assemblage overlaps with both the freshwater and marine species clusters. This partitioning is supported by a significant difference between habitat systems (PERMANOVA, p = 0.001, 999 permutations). A pair-wise comparison indicates that threats experienced by marine species are significantly different from those of both freshwater ($p = 0.001$) and euryhaline species ($p = 0.001$), but euryhaline and freshwater threats are not significantly different from each other ($p = 0.432$).

Three of the nine major threats identified were highlighted as the most pervasive by examining the vector length of explanatory variables: exploitation, pollution and natural system modifications. In general, the primary threat to marine species is exploitation, impacting 34 out of 38 species (89.5%) impacted by a threat. Comparatively, freshwater species tend to be more collectively impacted by pollution and natural system modifications than marine species (Fig. 7), both of which individually affect 37.5% of the freshwater species that are impacted by at least one major threat. However, exploitation is the most prevalent threat to freshwater clupeiforms, impacting 62.5% (20 of 32 species) of those with a recorded threat. Euryhaline species are impacted by all three major threats. Exploitation impacts the largest proportion of euryhaline species (70.3%), while the proportion affected by pollution and natural system modifications (41.9% and 36.5%, respectively) rivals that of the freshwater species. Of the marine species with a recorded threat, only two, *Harengula jaguana* and *Sardinella maderensis*, are impacted by pollution (Tous et al., 2015; Munroe et al., 2019). Both species occur at or near estuary mouths and are impacted by various sources of pollution, such as agricultural and industrial effluents. Likewise, an additional two marine species, *Anchoa helleri* and *Nemalosa*

japonica, are impacted by natural system modifications that include heavy coastal land reclamation and water diversions (Iwamoto et al., 2010; Di Dario, 2018a).

Seven distinct groups have been identified among the clupeiforms with major known threats based on the string of threats impacting each species (Fig. 7). Except for group 7, at least one species from each primary habitat (freshwater, euryhaline or marine) is represented in every group. All species within a group share similar threats. For example, groups 1, 3, and 6 represent 14, 64, and 12 species, respectively that are all impacted by one of the most prominent threats (natural habitat system changes, exploitation, or pollution). Species within group 1 are primarily only impacted by changes to the natural habitat such as dams and water abstraction. Group 3 represents species that are all primarily threatened by exploitation and group 6 represents those mostly impacted by pollution. Groups 2 and 7 are characterized by species likely impacted by two of the most prominent threats, pulling them in between the two threat vectors in space. For example, group 2 represents 11 species threatened by both exploitation and natural system modifications, whereas species in group 7 are impacted by natural system changes and pollution. Groups 4 and 5 include species threatened by two of the most prominent threats and by at least one of the less influential threats, such as climate change or mining.

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Fig. 7. Canonical Analysis of Principal Coordinates (CAP) ordination of species with known threats in multivariate threat space by primary habitat system (n = 144). Habitat system abbreviations are $E = E$ uryhaline, $F = F$ reshwater and $M = M$ arine. The three most prominent threats – Exploitation, Pollution and Natural system modifications are labelled; major threats including climate change, mining, human disturbance, invasive species, residential/commercial development and transportation corridors impact a smaller proportion of species and are not labelled. Each species is represented by a single symbol; however, as there is substantial overlap, symbol transparency was set at 50% to indicate where overlaps occur. Thus, symbols that appear darker in color represent more species than lighter symbols. Each group of species, indicated by the numerical value above the group, represents a different number of species: group $1 - 14$ species (E = 7, F = 6, M = 1); group 2 – 11 species (E = 6, F = 4, M = 1); group 3 – 64 species (E = 25, F = 9, M = 30); group $4 - 21$ species (E = 16, F = 2, M = 3); group $5 - 18$ species (E = 10, F = 6, M = 2); group $6 - 12$ species (E = 7, F = 4, M = 1); group 7 – 4 species (E = 3, F = 1, M = 0). The direction and length of the vectors represent the relationship between the ordination axes and threat type.

Results of the CAP analysis on known life history characteristics of elevated concern species (n = 33) show slight partitioning between the three habitat systems (freshwater, marine, euryhaline), but is most notable between marine and freshwater fishes (Fig. 8). A significant difference occurs between characteristics of species within the three habitat systems (PERMANOVA, p = 0.001, 999 permutations). Based on a pair-wise comparison, characters exhibited by freshwater species are significantly different from those of both euryhaline ($p =$ 0.001) and marine (p = 0.002) species, whereas marine and euryhaline species are not significantly different from each other ($p = 0.079$).

Two explanatory variables, maximum standard length and relative clupeiform diversity, have the most influence on the species assemblage pattern. In general, freshwater species of concern tend to have smaller maximum standard lengths compared to euryhaline and marine species. *Clupeonella grimmi, Anchoa choerostoma* and *Opisthonema berlangai* are the only three marine species that cluster with the freshwater species, likely because they are some of the smallest marine species included in the study and are also those with the lowest number of other clupeiforms present in their ranges.

Fig. 8. Canonical Analysis of Principal Coordinates (CAP) ordination of threatened and Near Threatened species-specific life history and ecological traits in multivariate space by primary habitat system (n = 33). Habitat system abbreviations are E = Euryhaline, F = Freshwater and M = Marine. The two most prominent traits – maximum size in cm (MaxSL) and number of other clupeiforms within a species distribution (Richness) are labeled; additional traits represented by the unlabeled vectors include habitat requirements (e.g., generalist or specialist), the number of country waters a species is distributed within and total number of threats known to impact a species. Individual symbols represent a single species; symbol transparency was set a 50% to indicate where species are overlapping. The direction and length of the vectors represent the relationship between the ordination axes and the life history and ecological characters.

Fig. 9. Mean maximum standard length (cm) of clupeiforms (n = 394) as a function of primary habitat system (marine, euryhaline, freshwater) and exploitation status (exploited or not exploited). Grey bars indicate mean size of exploited species; white bars represent mean size of unexploited species. Standard error is indicated by the black vertical lines.

Table 1

Tukey HSD pair-wise comparisons of exploited vs. non-exploited species within each primary habitat system. Difference is the difference in means of standard length, Lower bound and Upper bound refer to the lower and upper confidence intervals, and p-adjusted indicates the adjusted p-values for the possible pairs. The marine and euryhaline systems show a significant difference between the size of exploited vs. non-exploited species; the difference in size between exploited and non-exploited freshwater species is not significant.

DISCUSSION

Marine, freshwater and euryhaline clupeiforms are influenced by threats differently. Additionally, life history characteristics influencing susceptibility to threats also differ according to these major habitat types. In general, marine and freshwater species exhibited different responses to threats, and were influenced by different life history characteristics. Euryhaline species had similar responses to threats as freshwater species but were more similar to marine species in susceptible life history characteristics. Some shared threats such as exploitation affect species differently among these habitat systems.

Within each habitat system, size can influence how threats impact species. While exploitation affects species of all sizes within each habitat system, larger-bodied species are more impacted in marine and euryhaline systems (Fig. 8 and 9). For example, large-scale commercial fisheries often target the larger-bodied marine and euryhaline species (e.g., Atlantic herring, *Clupea harengus*) or multi-species groups and genera (e.g., *Stolephorus* spp.). Some of the largest-bodied exploited clupeiforms tend to be diadromous species in euryhaline waters where the passage through narrow estuaries makes them easily harvestable and increases their vulnerability as many are purposely targeted throughout various stages of ontogeny (McDowall, 1999). For example, the anadromous *Tenualosa macrura* (NT) and *T. toli* (VU) are a delicacy in Malaysia and Indonesia where small males are fished in marine waters and large ripe females are targeted for roe during spawning runs (Di Dario, 2018b; Mohd Arshaad et al., 2018) limiting their ability to repopulate. In contrast, freshwater species tend to be exploited based on geographic availability instead of size; the smallest known exploited clupeiform, *Nannothrissa stewarti*, is a freshwater species with a maximum known standard

length of 2.3 cm. Freshwater and inland fisheries typically support small-scale commercial, artisanal and subsistence fisheries of clupeiforms for food rather than reduction-type fisheries.

For clupeiforms, exploitation is the most important threat in all three habitats both in terms of numbers of species listing fisheries as the most prominent threat (Chapter 1) and in numbers of species corresponding to the exploitation axis in the CAP analysis (Fig. 7). However, 30 out of 38 (79%) marine species with a known threat are only or mostly impacted by exploitation (group 3 in Fig. 7) making this group proportionately the most heavily impacted by fisheries among the three habitats, compared to less than 40% of euryhaline species and less than 30 % of freshwater species in group 3. Fishery collapse of low trophic-level species has been linked to high fishing mortality and a long history of a developed fishery (Pinsky et al., 2011), as is the case for many clupeiforms. For example, the Pacific herring, *Clupea pallasii,* a temperate marine species widely distributed in the northern Pacific Ocean, has a complex population structure with multiple spawning stocks that have been fished for millennia and have supported industrial fisheries since the early 1900s (Hay et al., 2001). Despite long-term management and monitoring throughout most of its range, some spawning stocks are increasing in abundance (e.g., Quilicene Bay stock: WDFW, 2018), while a neighboring stock may be in a critically low state even after long periods of closed fisheries (e.g., Cherry Point stock: WDFW, 2018). In contrast, the world's only freshwater sardine (Bombon sardine, *Sardinella tawilis*) is a tropical species endemic to a single lake in the Philippines (Whitehead, 1985; Papa et al., 2008) and is one of the most commercially important fish in the country (Mutia, 2015) with limited monitoring and regulation until relatively recently (Villanueva et al., 1996; Willette et al., 2011; Mutia, 2015). Illegal and over-fishing practices have resulted in

declining catches of *S. tawilis* since the late 1990s (Marmaril, 2001; Mutia et al., 2004, 2015). An example of estuarine species that also appear to by heavily exploited with inadequate management are the anadromous species of *Tenualosa* in Malaysia and Indonesia (Di Dario, 2018b; Mohd Arshaad et al., 2018). These three ecologically different species (*C. pallasii, S. tawilis* and *Tenuolosa spp.*) have responded similarly to exploitation with apparently unsustainable population declines in some cases, both with and without long-term complex fisheries management. It is suspected that the response of other, lesser-known clupeiforms to high fishing pressure across habitat systems is comparable.

Exploitation is a much more prevalent threat for marine clupeiforms than freshwater and estuarine clupeiforms even though exploitation is the most ubiquitous threat in all three major habitat types. In IUCN Red List assessments, exploitation threats are essentially nullified if the population is managed sustainably. Typical fisheries management practices such as those based on Maximum Sustainable Yield, fishing effort, or gear restrictions may not be appropriate for some exploited clupeiforms, particularly data-limited species that are targeted in un- or poorly regulated fisheries. Instead, simple strategies based on what is known about species such as primary habitat type and other easily recognizable traits such as body size may be a useful approach to manage clupeiforms. This may allow management measures to be tailored to species groups with limited data if the response to threats within the group is similar to what we observe for other data-rich clupeiforms within the same habitat.

Grouping species for management purposes using readily available traits as I show here in an exploratory CAP approach is consistent with existing fisheries management schemes. Recent proposed management methods are shifting from single-species to multi-species and

ecosystem-based management which would better support the trophic interactions of forage fishes and their predators (Coll et al., 2008; Pikitch et al., 2012, 2014; Essington et al., 2015; Siple et al., 2018). However, the complex data needed to implement these strategies is only available for data-rich forage fishes. Recent work by Siple et al., (2018) suggests that the best management strategies for forage fishes incorporate species-specific life history traits. Given that life history data are limited for the majority of clupeiforms, this exploratory CAP analysis shows that groups can be separated as a function of habitat system and available natural history traits. By binning the data-limited clupeiforms into simple, discrete groups based on what we currently know, our ability to efficiently manage and conserve these species may improve. Similar approaches may also be useful for other 'small pelagic' taxa characterized by high ecological diversity and data-limitations.

Aside from the threat of exploitation, pollution and natural system modifications that degrade habitats and their ecosystem services are most detrimental to freshwater, euryhaline, and some nearshore marine species. Neither of these threats show size-specificity; however, larger euryhaline species likely experience threats differently than smaller freshwater species. For example, dams indiscriminately impact freshwater and euryhaline species of all sizes by fragmenting suitable habitat and preventing migration away from a threat (van Puijenbroek et al., 2019). However, typically large diadromous species would be heavily impacted by dams during spawning runs (McDowall, 1999; Marmulla et al., 2001). For example, severe reductions in population abundance and local extirpations were observed in the American shad, *Alosa sapidissima* because of damming (Haro and Castro-Santos, 2012). Similar trends have been reported for the Pontic (*Alosa pontica*) and Allis (*Alosa alosa*) shads in Europe (van Puijenbroek et al., 2019) as well as for the tropical Hilsa shad (*Tenualosa ilisha*) in the Indian Ocean (Hossain et al., 2019). Dam modifications (e.g., fish passages) to accommodate shad spawning migrations have existed for more than 250 years (Haro and Castro-Santos, 2012); however, these mitigations do not help spawning populations already driven away from natal streams (Sprankle, 2005; Monk et al., 1989).

Maximizing differences among groups using CAP (Anderson and Willis, 2003) helps examine conservation questions of clupeiforms; however, it is not without its limitations. This method has been used previously in conservation studies of a regional assemblage of all threatened and NT shallow water bony fishes (Linardich et al., 2019) and a variety of imperiled Canadian species (McCune et al., 2013). Here it was applied to a single Order of predominantly forage fishes with a more limited variability of natural history characteristics than what is observed in a diverse regional group of species. In addition, data is limited by information compiled in the IUCN Red List species accounts. Common life history traits used to assess population trends in the Red List assessments (e.g., age or size at maturity, fecundity, longevity, etc.) are unknown for many clupeiforms. Therefore, only widely available natural history traits were used, such as maximum length, number of threats, habitat system preference, habitat specialization, and proxies for distribution and relative clupeiform diversity.

Assigning habitat system categories was also challenging, particularly when distinguishing between true diadromous and salinity-tolerant species. Many species were lumped into a single euryhaline category because the existence of diadromy is possible, but unknown for many clupeiforms. Additional research on habitat requirements and basic biology would greatly benefit our ecological understanding of this group and improve future analyses of threats and conservation needs. A high degree of local knowledge is suspected to be sequestered in unpublished and gray literature. Efforts to make local and indigenous knowledge accessible to the public would also work to expand our understanding of the conservation status of this group.

Threats to clupeiform fishes will continue to worsen without comprehensive mitigation and improved fisheries management should be highest priority given its prevalence while remaining cognizant of other threats. While more information is needed regarding the negative impacts of processes like climate change, this analysis suggests that short-term conservation efforts should also focus on minimizing localized threats in all habitats. Specifically, national and local measures should be taken to reduce the impact of habitat degradation on freshwater, euryhaline, and nearshore marine fishes. By mandating local pollution mitigation and dam removals, suitable habitat can be restored, which can substantially contribute to the local economy by increasing recreational use and ecotourism. Compounding strategies that limit pollution and remove multiple dams have shown to restore natural fish populations in the Cuyahoga River, Ohio after many years of severe degradation (State of Ohio Environmental Protection Agency, 2008) and may also prove successful for clupeiform fishes.

Given that our reliance on clupeiform fishery resources is expected to increase, future work should build upon the CAP results by refining the characters used as an approach to develop new or improve existing management of similar data-limited fisheries. A broad management scheme that provides at least somewhat effective regulation to many similar species is preferred over a complete lack of management or monitoring, as is currently the case for many of these clupeiform fisheries. Following this approach, we may also inch closer to the goal of ecosystem-based fisheries management.

CHAPTER 4

DISCUSSION AND CONCLUSIONS

This thesis represents the first evaluation of the global conservation status of all members of the Order Clupeiformes and the first attempt to characterize known threats and life history traits by preferred habitat system. Despite many recent morphological, phylogenetic and group-specific works (e.g., Di Dario, 2004; Lavoué et al., 2013, 2014; Hata and Motomura 2017; Loeb et al., 2018; Bloom and Egan, 2018), the compiled species-specific IUCN Red List assessments represent the first review of all species since Whitehead (1985) and Whitehead et al., (1988) assembled taxonomic and biological information on all valid clupeoid species.

This also represents the first initiative to synthesize conservation information from IUCN Red List assessments for a single aquatic taxonomic group with representatives of all habitat types and a particularly high number of diadromous species. Many Red List assessments exist for diadromous species, including representatives of sturgeons, salmons, lampreys, anguillid eels and now, clupeiforms. However, except for the global conservation status of the mostly catadromous, anguillid eels (n = 13: Jacoby et al., 2015), diadromous species are often included within regional freshwater initiatives (e.g., Freyhof and Brooks, 2011; Kottelat et al., 2008), even if they are anadromous and spend most of their life cycle in marine waters. While this method may work to address major regional and system-wide conservation issues, it can

undermine the true conservation status of specific taxonomic groups by excluding part of their range from analyses. For example, because all anadromous lampreys were assessed with the European freshwater fishes (Freyhof and Brooks, 2011), the respective European marine fishes initiative did not include them (Nieto et al., 2015), despite that their marine ranges were excluded from freshwater analyses (Freyhof and Brooks, 2011—Appendix 4). The addition of clupeiforms to the IUCN Red List increases the representation of diadromous species within global analyses of overall species conservation.

Highlighting large-scale species patterns from a conservation perspective is a beneficial tool that can answer broad questions with more certainty. By looking at these patterns across an entire taxonomic group, underlying relationships have been uncovered (e.g., widespread major threats, geographic areas of most concern). Ultimately, this synthesized information may be used to influence management and implement better informed conservation measures with a higher probability of success. For example, we now know which threats are the most pervasive to all clupeiforms globally – exploitation, pollution and natural system modifications, and that the impacts of these threats are heavily influenced by primary habitat system and the size of the species. This highlights strategies to address specific threats within each habitat system.

The geographic areas of most concern for clupeiforms (e.g., the Caribbean and the Indo-Malay-Philippine Archipelago) were also identified in this study and support the findings of other Red List syntheses of taxonomic groups, including the groupers (Sadovy de Mitcheson et al., 2013), coastal sharks and rays (Dulvy et al., 2013), freshwater fishes (Collen et al., 2014),

and bonefishes (Adams et al., 2014). Across all assessed taxa, it is becoming increasingly apparent that these large regions with the highest biodiversity warrant management prioritization, especially given that these areas are also where cumulative human impacts are increasing (Halpern et al., 2015). Resources are needed both in research, because of the high number of species and subsequent large proportion of Data Deficient species, and for conservation planning, due to the high number of threatened and Near Threatened species. These emphasized patterns and subsequent increases in our knowledge base will allow us to direct attention to overexploited stocks, heavily degraded waterways and regions most in need of conservation.

Piecing together patterns at a global scale can be extremely useful in assessing broad consistencies but is not without its challenges. Limited by the underlying data, results are subject to shift in response to an increase in available information. Aside from missing data, a plethora of relevant and potentially useful information remains sequestered in unpublished or gray literature. An increase in open-access knowledge regarding geographic distribution, habitat utilization (specifically for spawning and migratory behavior), and total catches would elevate our understanding of clupeiform conservation status. Also, increased impact assessments of local threats on biodiversity would provide opportunity to better quantitatively assess threats to the clupeiforms present in those areas. Additional to insufficient data for many species, the methodology and level of detail, length and consistency of monitoring available are sources of variation both within and between countries, which can make an accurate synthesis of conservation status difficult.

As with many taxonomic groups, clupeiforms have long been plagued with unresolved taxonomy (Whitehead, 1985), hindering biological assessments. Despite recent attempts to untangle taxonomic relationships, some species-level distinctions are still questioned, such as those within the genus *Sardinops* (Whitehead, 1985; Parrish, 1989) and new species continue to be described such as within the genera *Sardinella* and *Stolephrous* (Hata and Motomura, 2018, 2019a, 2019b). While taxonomic changes advance our understanding of a species group, they can have implications within extinction risk assessments. For example, the two most important criteria of distribution and population size often change with information provided in taxonomic revisions and decreases in either of these criteria may result in an increase of risk of extinction.

In this study, the challenges stemming from data limitation and taxonomic uncertainty resulted in many clupeiform species assessed as Data Deficient. The resulting uncertainty in the overall threat status of clupeiforms presents faults in our understanding of conservation status for these species. Uncertainty may result in an underestimate of the true risk of extinction, leading to missed opportunities to apply appropriate mitigation (Davidson et al., 2012; Bland et al., 2014; Dulvy et al., 2014). Therefore, threatened and DD species impacted by multiple threats, particularly those that migrate between habitat systems, should take priority for future research and re-assessments similar to what was determined for the porgies (Comeros-Raynal et al., 2016).

This study represents the current picture of conservation status of clupeiforms based on the best available data. It is a starting point and will provide a more comprehensive

representation as more data are funneled into the species-specific re-assessments. By monitoring changes in conservation status of many taxa and continuing to add whole taxonomic groups onto the IUCN Red List, we can refine and enrich our understanding of biodiversity conservation and redress the declining state of biodiversity across the globe by providing better information for making more informed decisions. Outside of the scientific community, the IUCN Red List assessments and subsequent analyses may inform all stakeholders and end-users, including, fishers, processers, and consumers. Embracing biodiversity conservation will allow us to see maximum benefits for all parties, including the long-term sustainable use of our aquatic resources as well as helping to maintain or replenish the balance of the ecosystem.

Addition of this group to the Red List acts as further evidence in support of overarching conservation dilemmas and as a catalyst for change such as decreasing local human impact on aquatic ecosystems and resources. For example, a common finding among these speciesspecific initiatives is that the major threats most prevalent to clupeiforms are also those that negatively impact many other taxa. While the individual effects and the intensity of the threat may vary by species and locality, the overall outcomes tend to be similar, further supporting the need for local as well as multinational threat mitigation. It will not only benefit clupeiforms to revisit management protocols as well as water use and waste removal protocols, but it will also benefit many other important freshwater, estuarine and marine taxa and fishery resources.

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APPENDIX A

LIST OF ALL CLUPEIFORM IUCN RED LIST CATEGORIES

Table A1: List of all 405 clupeiforms alphabetical by family and then by species name. The global IUCN Red List categories and criteria are listed: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient, NE = Not Evaluated. Criterion A = population decline in the past, present or future, B = restricted range, C = small population size and decline, D = very small or restricted population, E = quantitative analysis of extinction probability. For further information available on categories and criteria, visit the IUCN Red List website (www.iucnredlist.org). The preferred habitat system is also listed; $F = F$ reshwater, M = Marine, E = Euryhaline which includes estuarine species and diadromous species.

APPENDIX B

IUCN RED LIST METHODS AND DATA USE

To supplement the Red List methods described in Chapter 2, further information on important terminology, threat classifications, distribution mapping methodology and the estimation of declines used in the Red List assessments and the thesis are outlined. Further information regarding the uncertainty within the Red List assessments is also expressed below.

Red List terminology

Within the scope of the Red List methodology, specific definitions are used. The term population refers to the total number of individuals of a species throughout its global distribution, while population size is the total number of mature individuals (e.g., those capable of reproduction). Both terms, population and population size, are required for criteria A, C and D (IUCN Standards and Petitions Subcommittee, 2017). Generation length is applicable to criteria A, C1 and E, and is the average age of parents of the current cohort (i.e., recruited individuals in the population) and serves as a measure of the turnover rate of breeding individuals within the population (IUCN Standards and Petitions Subcommittee, 2017). The predisturbance generation length was used to account for potential variation under threat such as exploitation (IUCN Standards and Petitions Subcommittee, 2017). Declines must be calculated over a period of time equal to three generation lengths or ten years, whichever is longer (IUCN, 2012). The equation used in the assessments to calculate generation length is as follows:

Generation Length =

Age at first reproduction $+$ (age at last reproduction – age at first reproduction) / 2

Location defines a geographically or ecologically distinct area where a single threatening event can rapidly impact all individuals of the taxon present and is necessary for the application of criteria B and D (IUCN Standards and Petitions Subcommittee, 2017). The known geographic extent of a species is quantitatively expressed in two ways: Extent of Occurrence (EOO) used for criteria A and B and Area of Occupancy (AOO) used for criteria A, B and D (IUCN Standard and Petitions Subcommittee, 2017). The EOO is defined by the smallest, continuous imaginary boundary that can be drawn around the area where the species is known, inferred or suspected to be present. It is also referred to as the 'minimum convex polygon' and represents the degree to which threatening factors are spatially spread across a taxon's geographic range. The AOO is the area within the species' EOO that is actually occupied, accounting for the fact that the EOO likely contains unoccupied or unsuitable habitat. A 2x2 km grid is used to standardize estimates of AOO (IUCN, 2017).

Threat classifications

Major threats used in analyses follow the hierarchal threat schematic provided by the IUCN Red List. Major threats were coded within a species assessment only if confirmation of impact on the species or locality within its range exists. Many clupeiform species have limited data available regarding their conservation status. Therefore, for threats that were only suspected to impact a species, the threat was neither coded within the species assessment, nor included in the analyses.

Major threats known to impact clupeiforms include biological resource use ($n = 106$), pollution (n = 47), natural system modifications (n = 42), climate change (n = 23), invasive species and diseases ($n = 15$), energy production ($n = 7$), residential or commercial development $(n = 5)$, human intrusions $(n = 1)$ and transportation service corridors $(n = 1)$. Within these major threats, sub-threats were also coded to specify the source of the major threat (IUCN, 2019). For clupeiforms, biological resource was coded for species impacted by bycatch, subsistence, artisanal, recreational, commercial and industrial exploitation. Pollution as a major threat is sourced from agricultural, domestic, industrial and/or military effluents but also includes sedimentation. Large and small dams as well as water management/use (e.g., water abstraction) are included under natural system modifications. Climate change is broken down into specific impacts, which include droughts, habitat shifting and temperature extremes. The invasive species and diseases category include both native, and non-native problematic species or diseases. Energy production exclusively refers to impacts from mining and quarrying for this taxa. Threats known to impact five or less species but ultimately may disturb critical habitats include residential and commercial development (e.g., commercial, industrial or housing development projects), transportation corridors (e.g., shipping lanes) and human intrusions which stem from recreational activities. For further detailed information regarding IUCN Red List threat schemes, see the IUCN Red List website (www.iucnredlist.org).

Distribution maps

A species-specific distribution map is a depiction of a taxon's native geographic range or limits of distribution and can be helpful in communicating and/or addressing conservation

planning. These maps are used for visualization and spatial analyses and can also be used in different types of analyses that can identify gaps in knowledge and conservation priority areas by, for example, highlighting areas with a high number of threatened or Data Deficient species. However, the polygons neither depict the potential spread of extinction risk nor do they represent that a species is uniformly distributed throughout. They can be used to support the estimate of AOO or EOO, but do not represent either parameter.

Estimates of decline

Time series data of spawning stock biomass (SSB), catch-per-unit effort (CPUE), total landings reported to the FAO (FAO, 2016) and reconstructed catches (Pauly and Zeller, 2016a), where available, were used as indices of abundance to estimate population decline. If available, estimated biomass (e.g., SSB) from fishery stock assessments took priority over other data types, such as landings, when calculating declines. Fishery-dependent data (e.g., reported landings or reconstructed catches) were reported to the species, genus or family level.

Uncertainty within Red List data

Data were often pieced together from various sources to determine the species' conservation status; it is understood that there is inherent uncertainty within the available data and thus, the resulting conclusions. Uncertainty may arise from factors including natural variation, vagueness of terms and definitions or measurement error (Akçakaya et al., 2000; IUCN, 2012) and can be managed by using parameter estimates from expert knowledge and data to produce a range of plausible categories (Mace et al., 2008; IUCN, 2012; Collen et al., 2016; IUCN, 2017). The level of uncertainty within the data was expressed using the terms

observed, estimated, inferred or suspected, following guidelines defined by the Red List (IUCN Standards and Petitions Subcommittee, 2017).

APPENDIX C

LIST OF ALL SPECIES WITH KNOWN THREATS USED IN CAP ANALYSIS

List of all 144 clupeiform species with known threats alphabetical by family and then by species name. Threats are coded with 1 if impacted by the threat and 0 if not impacted. The primary habitat system (SYS) is listed; F = Freshwater, M = Marine, and E = Euryhaline, which include estuarine species as well as anadromous species. The global IUCN Red List categories (RL CAT) are also listed; EC = elevated conservation concern and include all threatened (Critically Endangered, Endangered and Vulnerable) and Near Threatened species, LC = Least Concern, DD = Data Deficient.

APPENDIX D

LIST OF ALL SPECIES OF ELEVATED CONSERVATION CONCERN USED IN CAP ANALYSIS

List of the 33 clupeiform species assessed as threatened (Critically Endangered, Endangered and Vulnerable) or Near Threatened alphabetical by family and then by species name. The primary habitat system is coded with 0's and 1's for marine and freshwater species; euryhaline species are characterized by a 1 in both columns. Habitat refers to whether a species is a habitat generalist, coded with a 1 or a specialist, coded with a 0. The maximum known standard length (MaxSL) in centimeters, number of countries a species is known to be distributed within (COO) as a proxy for geographic distribution and the number of other clupeiforms within an individual species range as a proxy for relative diversity are listed. The number impacting a species and the global categories are also listed: CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient.

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EDUCATION

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Research Assistant, August 2016 – Present, International Union for Conservation of Nature's Global Species Programme Marine Biodiversity Unit, Old Dominion University, Norfolk, Virginia

Phytoplankton Laboratory and Field Technician Intern, May 2016 – August 2016, Old Dominion University, Norfolk, Virginia

THESIS-RELATED PRESENTATIONS

March 2019. Oral presentation: The fast life of forage fishes: conservation status of the world's clupeiforms (Order Clupeiformes). Biology Graduate Student Organization Spring Symposium, Old Dominion University

March 2017. Poster presentation: The global extinction Risk of forage fishes of the order Clupeiformes. $31st$ Annual Meeting of the American Fisheries Society – Tidewater Chapter Meeting, Virginia Beach, Virginia