

A GLOBAL ECOLOGICAL SIGNAL OF EXTINCTION RISK
IN MARINE RAY-FINNED FISHES

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF
HAWAI'I AT HILO IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF

MASTER OF SCIENCE

IN

TROPICAL CONSERVATION BIOLOGY AND ENVIRONMENTAL SCIENCE

MAY 2022

By

Trevor Bak

Thesis Committee:

Matthew Knope, Chairperson

Rebecca Ostertag

John Burns

Keywords: Extinction Risk, Marine Fishes, Global, Modern Biodiversity Crisis

ACKNOWLEDGEMENTS

I thank Maya Munstermann for all her help with getting my project off the ground and for providing guidance and R code to help complete this project.

I thank Jeff Regalario, Angela Colon, Lily Gavagan, Syndey Lewis, Christina Wine, and Natalia Zelaya for all their help with building the dataset and keeping a positive spirit as we navigated the massive upheavals brought about by Covid.

I thank Patrick Hart for helping to support me financially during my graduate school career, allowing me to focus on developing my thesis and doing the best science I could without the distraction and stress of having to work a side job. I additionally thank Doreen Koizumi for her help in administering this grant.

I thank Jon Payne, Noel Heim, Douglas McCaulley, and Rick Camp for their support with manuscript revision, suggestions for research directions, and help with understanding and improving my statistical approach for the project.

I thank Matt Knope for all his support and guidance throughout this project and for taking a chance on me as I transitioned into a new field of research.

I thank all my friends and family for all the love and support they have shown as I worked to complete this research during a difficult time for every last one of us.

ABSTRACT

The Earth is potentially entering a sixth mass extinction event comparable to the previous “big five” mass extinctions. Many marine fish species are currently facing rapid population declines from a broad range of threat types, but their extinction risk profiles are largely under-studied in comparison to their terrestrial counterparts. Selective extinction of increasing numbers of marine fish species may result in rapid alteration of global ocean ecosystem structure and function. In this study, we compiled a data set of 9,040 species of marine ray-finned fishes (class Actinopterygii) from global databases and used phylogenetic generalized linear models to examine which ecological traits are associated with increased extinction risk, based on the International Union for the Conservation of Nature (IUCN) Red List. We also assessed which threat types are driving these species towards greater extinction risk, if threatened species face a greater average number of total threat types than non-threatened species, and possible biases in the assignment of extinction risk status by the IUCN for each ecological variable. Further, we examined whether controlling for phylogenetic non-independence alters the general conclusions drawn from our study. We found that species with larger body size, longer population doubling times, life-history strategies that involve movement into brackish and/or freshwater, and pelagic species are all at elevated extinction risk. However, we found no significant difference in extinction risk based on trophic level. Commercial harvesting threatens the greatest number of species followed by pollution, development, and then climate change. We also found that threatened species, on average, simultaneously face a significantly greater total number of threat types than non-threatened species. We did identify relatively minor biases in the assignment of extinction risk status by the IUCN Red List across all traits and we further determined that controlling for phylogenetic non-independence does not strongly affect our general conclusions.

Collectively, these results point to which ecological traits place marine ray-finned fishes at higher risk of extinction and which threat types most urgently need to be addressed if we are to curtail rapid alteration of global marine ecosystems.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS	ii
ABSTRACT.....	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
INTRODUCTION	1
METHODS	3
Taxonomy.....	3
Predictor Variables.....	4
Extinction Risk.....	4
Phylogenetic Generalized Linear Models	5
Threat Types.....	6
Data Bias	6
RESULTS	7
Predictor Variables and Extinction Risk.....	7
Incorporation of Phylogenetic Data	9
Threat Types.....	10
Predictor Variables and Top Four Threat Types.....	11
Data Coverage.....	13
DISCUSSION.....	15
Traits Associated with Extinction Risk.....	15
Threats Faced by Species	18
Threats and Predictor Variables	20
IUCN Data Coverage	22
Phylogenetic Methods.....	23
Implications for Ecosystems	24
Conclusion.....	25
REFERENCES	26

LIST OF TABLES

Table 1: GLM and PhyloGLM Results for Predictor Variables and Extinction Risk..... 10

Table 2: PhyloGLM Results for Predictor Variable and Threat Types..... 12

Table 3: PhyloGLM Results for Predictor Variable and IUCN Extinction Risk Coverage..... 15

LIST OF FIGURES

Figure 1: Distribution of Coefficient Values for Predictor Variables and Extinction Risk	8
Figure 2: Total Length and Extinction Risk	9
Figure 3: Most Common Threat Types Driving Extinction Risk	11
Figure 4: IUCN Extinction Risk Data Coverage by Predictor Variable	14

INTRODUCTION

The current rate of species extinction in many clades is so high that the modern biodiversity crisis is often referred to as the 6th mass extinction (e.g., Barnosky et al. 2011), in reference to the “big five” mass extinctions first identified in the marine animal fossil record (Raup & Sepkoski 1982). The modern rate of extinction in some clades has been estimated to be as much as a 1000 times higher than their background rate known from the fossil record (De Vos et al. 2015).

Marine fishes in particular are under intense pressure from overharvesting, in addition to a range of other local and global threats (McCauley et al. 2015; IPBES 2019). Among commercially fished species, three quarters of marine fish stocks are considered either fully exploited, over exploited, or depleted (IPBES 2019), with many species showing as much as 90% reduction in their historical ranges (McCauley et al. 2015; Newsome et al. 2020). Although there has been relatively few documented marine fish extinctions, these trends suggest marine fishes may start going extinct at higher rates in the near future (Hutchings & Reynolds 2004; Monte-Luna et al. 2007; Ceballos et al. 2017) and the loss of marine fishes to extinction has profound implications for the structure and function of marine ecosystems globally (Worm et al. 2006). While the rate and magnitude of population declines has been well-studied, the complete picture of extinction selectivity in the modern biodiversity crisis for marine fishes remains understudied.

Understanding extinction selectivity, or the traits associated with extinction, in addition to extinction rate and magnitude, is key to understanding how the current biodiversity crisis will reshape the biotic composition of marine life in the near future (Bush et al. 2020). Exploring if extinction selectivity is present is especially critical as nonrandom extinctions tends to lead to greater loss of evolutionary history than extinctions that are random (Purvis et al. 2000a; Vamosi

& Wilson 2008). Additionally the potential loss of phylogenetic diversity may be so impactful that the time for fish biodiversity to recover may be on the scale of many millions of years (Davis et al. 2018).

To assess extinction risk status among ray-finned marine fishes (class Actinopterygii), we used the International Union for Conservation of Nature's (IUCN) Red List (IUCN 2019). Previous studies have examined modern extinction selectivity, but prior studies have not focused on the ray-finned fishes at the species level with the breadth of ecological traits examined here (Purvis et al. 2000b; Olden et al. 2007; Jager et al. 2008; Payne et al. 2016; Ripple et al. 2017; Munstermann et al. 2022). We also capitalize on recently available large-scale and species-level phylogenetic hypotheses (Rabosky et al., 2018) to address possible phylogenetic non-independence of species traits. Few prior studies have incorporated phylogenetic data into their analyses, which may potentially give rise to misleading results if the predictor and response variables are phylogenetically nested together (Purvis et al. 2000b; Harnik et al. 2012; Finnegan et al. 2015). In addition, leveraging IUCN Red List data with vastly greater coverage than in recent years (McCauley et al. 2015), we are uniquely able to provide an updated and improved analysis from previous assessments. We also analyze the association of threat types and predictor variables to contextualize our results, a method also only used in a limited number of previous studies (Arthington et al. 2016; Munstermann et al. 2022). We further examine our results for data biases in the IUCN assessment of risk for the ray-finned fishes, and we test if correcting for phylogenetic non-independence alters general study conclusions, which to our knowledge, has not been performed within a trait-extinction risk framework before.

In this study we specifically focus on the traits body size, minimum population doubling time, trophic level, euryhaline status (ability to tolerate salinity), and general habitat association and

explore how they are associated with extinction risk and top extinctions threats. We address five research questions in this study: 1) Is there an association between these ecological traits and extinction risk? 2) Does correcting for phylogenetic non-independence influence inferred relationships among these variables? 3) Is there an association between ecological traits and threat types? 4) Do threatened species have a greater number of threats assigned on average than non-threatened species? 5) Is there an association between ecological traits and being assigned an IUCN Red List extinction risk status?

METHODS

Taxonomy

All marine species from the World Register of Marine Species (WoRMs) were downloaded with permission in November 2019, which produced a dataset comprising 192,973 marine species. This list was then matched to species with an IUCN Red List assignment, and species without an assignment were removed. The dataset was then filtered to the ray-finned fishes (class Actinopterygii) by creating a subset filtering out all non-Actinopterygii Linnaean classes (“IUCN data set”). A separate dataset with predictor variables was created by extracting data from Fishbase.org, resulting in a dataset of 16,530 species. The Fishbase.org dataset was then matched with the IUCN dataset and species without an IUCN assignment were removed, resulting in a total of 9,040 species that were listed in WoRMS and contained both trait data from Fishbase.org and an IUCN Red List assignment. Out of the 9,040 species, 7,206 species were classified as non-threatened, 385 species were classified as threatened, and 1,438 species were data deficient, which were removed from downstream analyses.

Predictor Variables

The predictor variables with available data from Fishbase.org that we chose to examine were: body size, minimum population doubling time, habitat tiering, euryhaline status, and trophic level. Body size (N = 4,146 species) was measured as total length in (log10) millimeters. In addition to testing how body size was associated with extinction risk, we also examined the proportion of species threatened among a range of categorical body sizes. Minimum population doubling time was based on Froese et al. (2017) and categorized by Fishbase.org into less than 15 months (N = 3,604 species), 1.4 - 4.4 years (N = 2,367 species), 4.5 – 15 years (N = 542 species), or more than 15 years (N = 160 species). Habitat tiering was converted to binomial categories as either benthic (N = 2,417 species) or pelagic (N = 1,168 species) from a range of classifications (such as demersal, pelagic-oceanic, bathypelagic, etc.), to increase statistical power. Euryhaline status was based on a binary categorization by Fishbase.org indicating whether they were or were not marine, brackish, or freshwater. A species could be classified as “marine only” (N = 6,049 species), “marine and brackish” (N = 720 species), or “marine, brackish, and freshwater” (N = 658 species). Trophic level (N = 6,946 species) was defined as 1 + mean trophic level of the food items the species eats (Froese & Pauly, 2000).

Extinction Risk

The IUCN’s Red List categorizes extinction risk into a hierarchy of categories of seven categories (from least- to most-threatened): least concern (LC), near threatened (NT), vulnerable (VU) endangered (EN), critically endangered (CR), extinct in the wild (EW), or extinct (EX). Species lacking sufficient data to make a categorization are assigned data deficient (DD). Following previous work, (Ripple et al. 2017; Atwood et al. 2020), extinction risk status was collapsed to binomial threatened and non-threatened to increase statistical power, with

vulnerable (VU), endangered (EN), and critically endangered (CR) classified as “Threatened” and near threatened (NT) and least concern (LC) classified as “Non-threatened” and both Extinct in the Wild (EW) and Extinct (EX) species were not included.

Phylogenetic Generalized Linear Models

Phylogenetic Generalized Linear Models (PhyloGLMs) were used to analyze associations among our five predictor variables and both IUCN threat status and threat types, while accounting for statistical non-independence due to shared evolutionary history (Felsenstein, 1985). Species-level molecular phylogenetic trees for the Actinopterygii were downloaded from the data supplement in Rabosky et al. (2018) and all analyses were completed in R 4.1.1 (R Core Team 2021) using the PhyloLM package (Tung Ho & Ané 2014). Trees were initially built using 24 nuclear and mitochondrial loci from five sources (see Rabosky et al. 2018 table S1 for details) utilizing a Bayesian analysis framework, with species missing molecular data added according to known taxonomic relationships. This estimation was repeated 100 times to generate 100 trees and produce a distribution of fully sampled Actinopterygii (Rabosky et al. 2018). For minimum population doubling time, the extinction risk reference category was set to the fastest doubling interval (less than 15 months) to test if increased population doubling time influenced extinction risk. For Euryhaline status, ‘marine only’ was set as the reference to explore test if coming into contact with fresh or brackish water influenced extinction risk. For tiering, pelagic was set as the reference to test if benthic species were at significantly different extinction risk. Reference categories were kept the same for both the data bias and threat type analyses for consistency. For each trait, a PhyloGLM was run on each of the 100 phylogenetic trees to produce a distribution of 100 results. To examine if accounting for phylogenetic relationships affected our general

conclusions, we ran each predictor-extinction risk analysis as both a PhyloGLM and as a simple Generalized Linear Model (GLM) for comparison.

Threat Types

Extinction threat types were downloaded with permission in February 2021 using the IUCN Application Programming Interface (API). The twelve primary IUCN Red List threat types are: 1) Development, 2) Aquaculture and Agriculture, 3) Energy Production and Mining, 4) Transportation, 5) Harvesting, 6) Human Disturbance, 7) Natural System Modification, 8) Invasive Species and Disease, 9) Pollution, 10) Geological Events, 11) Climate Change, and 12) Other. A total of 3,897 of the 7591 species in our final dataset had one or more threats assigned to them. We determined what the most common threats were across all of these species using the IUCN assignments, and we tested if threatened species had a greater average number of assigned threats compared to non-threatened species using Wilcoxon rank-sum tests. Lastly, we explored how each predictor variable was associated with each of the four most common threat types using PhyloGLMs.

Data Bias

For each of the five predictor variables we assessed if biases were present in whether or not species were assigned an extinction risk status. Species were classified as either reviewed (having an IUCN status assigned) or unreviewed (no IUCN status assigned). Data deficient species were not included in this analysis. PhyloGLMs were used to test for an association between predictor variable and reviewed vs. unreviewed status. Additionally, we examined the number and percentage of species that had IUCN coverage by each predictor variable.

RESULTS

Predictor Variables and Extinction Risk

We found a statistically significant relationship between body size, minimum population doubling time, euryhaline status, tiering, and extinction risk. The distribution of coefficients for each predictor variable shows how each variable is associated with threatened status across the 100 phylogenetic trees. Coefficient distributions that fall completely above or completely below zero indicate a statistically significant association ($P < 0.01$; Munstermann et al. 2021). Larger body size was positively associated with extinction risk (Fig. 1A), however, a histogram of percentage of species threatened revealed a modestly bimodal distribution with some smaller species also threatened (Fig. 2). For habitat tiering, benthic fishes were at significantly greater risk relative to pelagic fishes (Fig. 1B). For minimum population doubling time, species categorized as taking longer than 15 months doubling time were at significantly higher extinction risk. We found no significant difference in extinction risk across trophic levels (Fig. 1C). For euryhaline status, “marine and brackish” and “marine, brackish, and freshwater” species were at significantly greater extinction risk than marine only species (Fig. 1D).

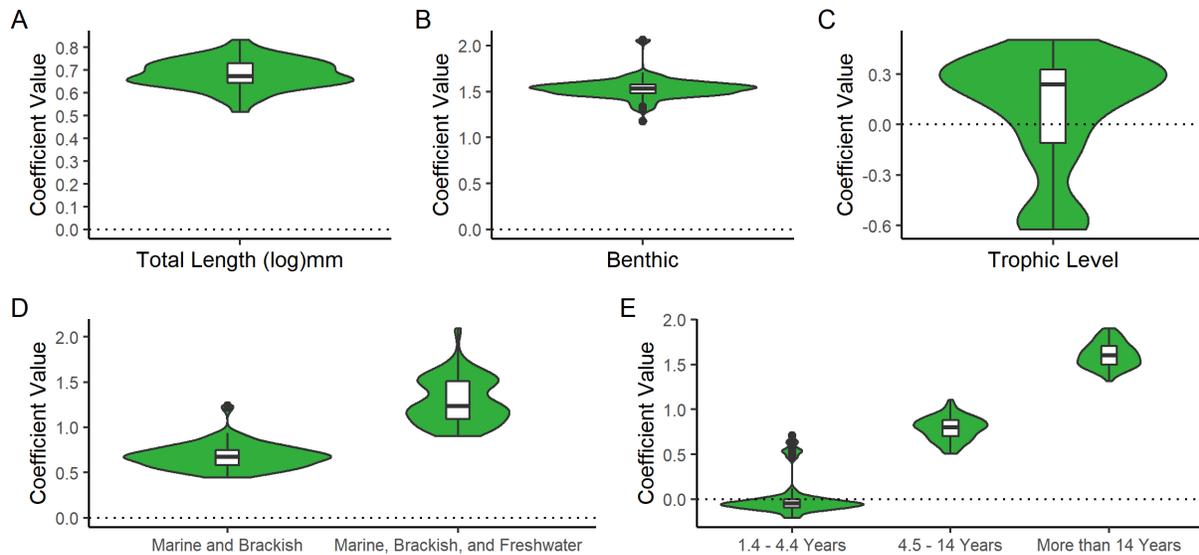


Figure 1. Results for ecological coefficient values from all 100 trees in the PhyloGLMs. The zero line represents the reference category, coefficients following completely above or completely below zero are statistically significant ($p < 0.01$; Munstermann et al., 2021). The green violin plot shows the spread of coefficient values with width indicating the number of coefficient values, and boxplots are drawn within the violin showing the median and interquartile range. A) Greater total length is positively associated with higher extinction risk. B) Benthic species are at elevated extinction risk as compared to the pelagic reference category. C) Trophic level shows no significant relationships with extinction risk. D) Euryhaline species (species that move between marine and brackish and/or freshwater) are at significantly greater extinction risk than marine only species. E) Increasing minimum population doubling time is associated with greater extinction risk, although 1.4 - 4.4 years is not statistically significant as compared to reference category less than 15 months.

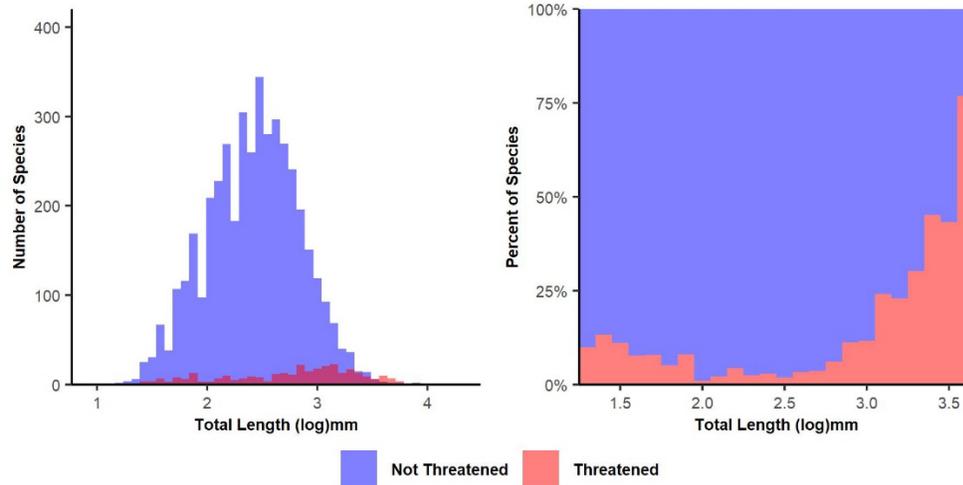


Figure 2. Number of species and percentage of species threatened as a function of body size (total length in log₁₀ mm). A weakly bimodal distribution in which the largest and smallest fishes are at higher percent threatened. However, overall, threatened fishes are on average larger (*t*-test: Mean Non-Threatened = 2.42 log(mm), Mean Threatened = 2.77 (log)mm, *t*-stat = -9.9, *df* = 341.23, *P*<0.0001).

Incorporation of Phylogenetic Data

Across the variables body size, trophic level, euryhaline status, and habitat tiering, incorporating phylogenetic information led to small variations in results but did not change the pattern of significance and directionality of association (Table 1). *Z*-value scores did increase when incorporating phylogenetic data for minimum population doubling time, but the pattern of significance remained the same. Estimates are presented as log odds, which is the log of the odds ratio.

Table 1. Results for PhyloGLMs and GLMs, statistically significant results are in italics.

Variable, Levels of Variable	GLM				PhyloGLM			
	Estimate	Std. Error	Z Value	P Value	Estimate	Std. Error	Z Value	P Value
Total Length								
	<i>0.83</i>	<i>0.2</i>	<i>4.57</i>	<i><0.0001</i>	<i>0.74</i>	<i>0.19</i>	<i>3.87</i>	<i><0.001</i>
Trophic Level								
	-0.14	0.11	-1.36	0.18	-0.15	0.11	-1.46	0.14
Minimum Population Doubling Time								
1.4 – 4.4 years	-0.21	0.13	-1.61	0.11	-0.6	0.13	-0.45	0.65
4.5 – 14 years	<i>0.55</i>	<i>0.18</i>	<i>3.13</i>	<i><0.01</i>	<i>0.95</i>	<i>0.17</i>	<i>5.77</i>	<i><0.0001</i>
More than 14 years	<i>1.58</i>	<i>0.21</i>	<i>7.3</i>	<i><0.0001</i>	<i>1.83</i>	<i>0.21</i>	<i>8.54</i>	<i><0.0001</i>
Euryhaline Status								
Marine and Brackish	<i>1.26</i>	<i>0.13</i>	<i>9.43</i>	<i><0.0001</i>	<i>1.27</i>	<i>0.14</i>	<i>8.81</i>	<i><0.0001</i>
Marine Brackish and Freshwater	<i>0.38</i>	<i>0.17</i>	<i>2.23</i>	<i>0.03</i>	<i>0.53</i>	<i>0.16</i>	<i>3.29</i>	<i><0.01</i>
Tiering								
Benthic	<i>1.12</i>	<i>0.21</i>	<i>5.33</i>	<i><0.0001</i>	<i>1.51</i>	<i>0.28</i>	<i>5.37</i>	<i><0.0001</i>

Threat Types

The most common threat type across all species was harvesting, which was followed by pollution, development, and then climate change (Fig. 3A). Comparing the total number of threats facing a given species, threatened species had, on average, a greater number of total threats than non-threatened species ($W = 297719$, mean non-threatened: 1.71 threats, mean threatened: 2.23 threats, $p < 0.0001$) (Fig. 3B).

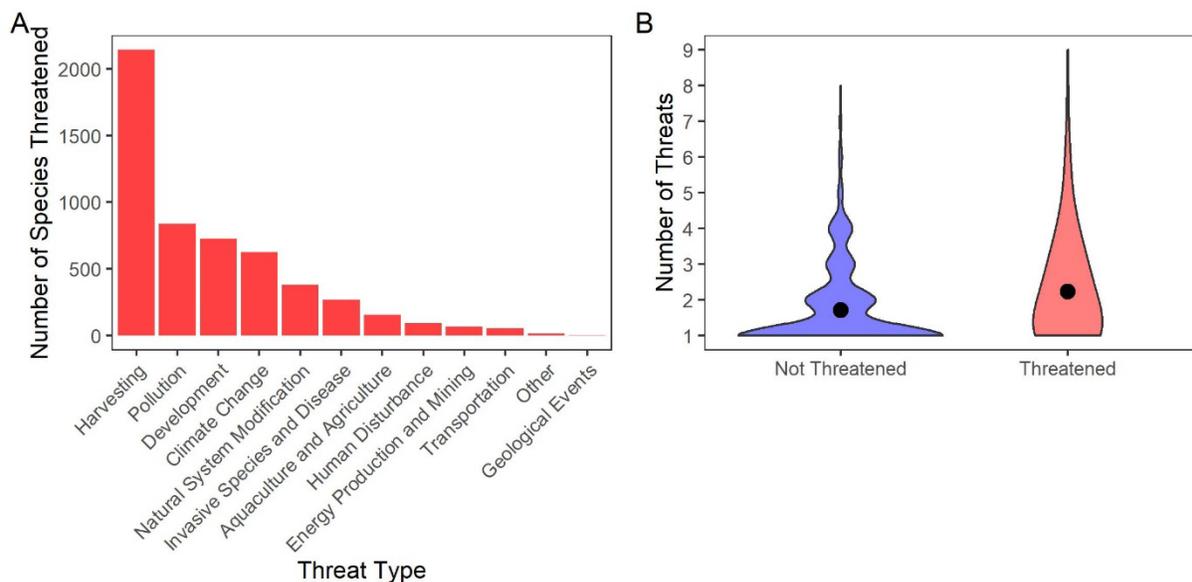


Figure 3. A) Number of species threatened by each threat type, across all species in the analyses with threat types assigned ($n = 2,992$). B) Distribution of the number of threats for non-threatened and threatened species (Mean non-threatened: 1.71 threats, mean threatened: 2.23 threats; $W = 297719$, $p < 0.0001$); black dots represent the mean for each category.

Predictor Variables and Top Four Threat Types

We tested for an association between each predictor variable and the top four threat types: harvesting, pollution, development, and climate change (Table 2). For body size, larger fishes were more likely to be significantly associated with harvesting, while smaller fishes were more likely to be significantly associated with development, climate change, and pollution. For minimum population doubling time, fishes that have the longest population doubling times (more than 14 years) had the strongest positive association with harvesting, while having the strongest negative association with pollution. Further, fishes that have the shortest population doubling times (less than 15 months) had the strongest negative association with pollution. Higher trophic level species were positively associated with harvesting and pollution while lower trophic level

species were positively associated with climate change and development. For euryhaline status, “Marine Brackish and Freshwater” had the strongest negative association with harvesting and climate change, and the strongest positive association with pollution, and development. Lastly, for tiering, benthic species were most strongly negatively associated with harvesting and most strongly positively associated with pollution, climate change, and development.

Table 2. PhyloGLM results for each predictor variable and the four most common threat types across all species included in the analysis. Statistically significant results are in italics.

Italicized = reference

Threat Type	Level	Coefficient	Std Error	Z Value	P Value
Body Size					
<i>Harvesting</i>	<i>n/a</i>	<i>2.08</i>	<i>0.20</i>	<i>10.56</i>	<i><0.0001</i>
<i>Pollution</i>	<i>n/a</i>	<i>-0.70</i>	<i>0.15</i>	<i>-4.57</i>	<i><0.0001</i>
<i>Climate Change</i>	<i>n/a</i>	<i>-0.98</i>	<i>0.18</i>	<i>-5.47</i>	<i><0.0001</i>
<i>Development</i>	<i>n/a</i>	<i>-1.32</i>	<i>0.19</i>	<i>-6.90</i>	<i><0.0001</i>
Minimum Population Doubling Time					
Harvesting	<i>1.4 – 4.4 Years</i>	<i>1.07</i>	<i>0.12</i>	<i>9.12</i>	<i><0.0001</i>
	<i>4.5 – 14 Years</i>	<i>1.46</i>	<i>0.20</i>	<i>7.36</i>	<i><0.0001</i>
	<i>More Than 14 Years</i>	<i>1.82</i>	<i>0.38</i>	<i>4.81</i>	<i><0.0001</i>
Pollution	<i>1.4 – 4.4 Years</i>	<i>-0.59</i>	<i>0.10</i>	<i>-5.70</i>	<i><0.0001</i>
	<i>4.5 – 14 Years</i>	<i>-0.66</i>	<i>0.16</i>	<i>-4.11</i>	<i><0.0001</i>
	<i>More Than 14 Years</i>	<i>-0.16</i>	<i>0.22</i>	<i>-0.74</i>	<i>0.46</i>
Climate Change	<i>1.4 – 4.4 Years</i>	<i>-0.86</i>	<i>0.13</i>	<i>-6.67</i>	<i><0.0001</i>
	<i>4.5 – 14 Years</i>	<i>-0.95</i>	<i>0.21</i>	<i>-4.50</i>	<i><0.0001</i>
	<i>More Than 14 Years</i>	<i>-1.08</i>	<i>0.37</i>	<i>-2.94</i>	<i>0.003</i>
Development	<i>1.4 – 4.4 Years</i>	<i>-0.81</i>	<i>0.12</i>	<i>-6.63</i>	<i><0.0001</i>
	<i>4.5 – 14 Years</i>	<i>-0.84</i>	<i>0.19</i>	<i>-4.42</i>	<i><0.0001</i>
	<i>More Than 14 Years</i>	<i>-1.47</i>	<i>0.40</i>	<i>-3.67</i>	<i><0.001</i>
Trophic Level					
Harvesting	<i>n/a</i>	<i>0.82</i>	<i>0.10</i>	<i>8.31</i>	<i><0.0001</i>
Pollution	<i>n/a</i>	<i>0.35</i>	<i>0.09</i>	<i>3.73</i>	<i><0.0001</i>
Climate Change	<i>n/a</i>	<i>-0.53</i>	<i>0.11</i>	<i>-4.91</i>	<i><0.0001</i>

Development	<i>n/a</i>	<i>-0.69</i>	<i>0.11</i>	<i>-6.42</i>	<i><0.001</i>
Euryhaline Status					
Harvesting	<i>Marine, Brackish, and Freshwater</i>	<i>-0.94</i>	<i>0.15</i>	<i>-6.45</i>	<i><0.0001</i>
	<i>Marine and Brackish</i>	<i>0.09</i>	<i>0.12</i>	<i>0.73</i>	<i>0.47</i>
Pollution	<i>Marine, Brackish, and Freshwater</i>	<i>1.59</i>	<i>0.15</i>	<i>10.64</i>	<i><0.0001</i>
	<i>Marine and Brackish</i>	<i>0.11</i>	<i>0.12</i>	<i>0.91</i>	<i>0.36</i>
Climate Change	<i>Marine, Brackish, and Freshwater</i>	<i>-0.81</i>	<i>0.18</i>	<i>-4.51</i>	<i><0.0001</i>
	<i>Marine and Brackish</i>	<i>-0.57</i>	<i>0.15</i>	<i>-3.70</i>	<i><0.001</i>
Development	<i>Marine, Brackish, and Freshwater</i>	<i>0.77</i>	<i>0.15</i>	<i>5.09</i>	<i><0.0001</i>
	<i>Marine and Brackish</i>	<i>0.74</i>	<i>0.13</i>	<i>5.79</i>	<i><0.0001</i>
Habitat Tiering					
Harvesting	<i>Benthic</i>	<i>-1.36</i>	<i>0.28</i>	<i>-4.79</i>	<i><0.0001</i>
Pollution	<i>Benthic</i>	<i>1.53</i>	<i>0.25</i>	<i>6.15</i>	<i><0.0001</i>
Climate Change	<i>Benthic</i>	<i>1.3</i>	<i>0.35</i>	<i>3.67</i>	<i><0.001</i>
Development	<i>Benthic</i>	<i>1.5</i>	<i>0.30</i>	<i>5.10</i>	<i><0.0001</i>

Data Coverage

We found significantly different levels of IUCN Red List coverage for each predictor variable. For body size (total length), unreviewed species tended to be slightly smaller than reviewed species (Fig. 4A, Table S1, $P < 0.0001$). Lower trophic level species had a greater association with being unreviewed than higher trophic level species (Fig. 4B, Table S1, $P < 0.0001$). A slightly greater percentage of species with faster population doubling times (less than 15 months) were unreviewed relative to the other categories with slower doubling times (Fig. 4C, Table S1, $P < 0.0001$). Marine only species had a greater percentage of unreviewed compared to “marine and brackish” and “marine, brackish, and freshwater” species (Fig. 4D, Table S1, $P < 0.0001$).

Benthic species had a significantly greater percentage of unreviewed species than pelagic species (Fig. 4E, Table S1, $P < 0.0001$).

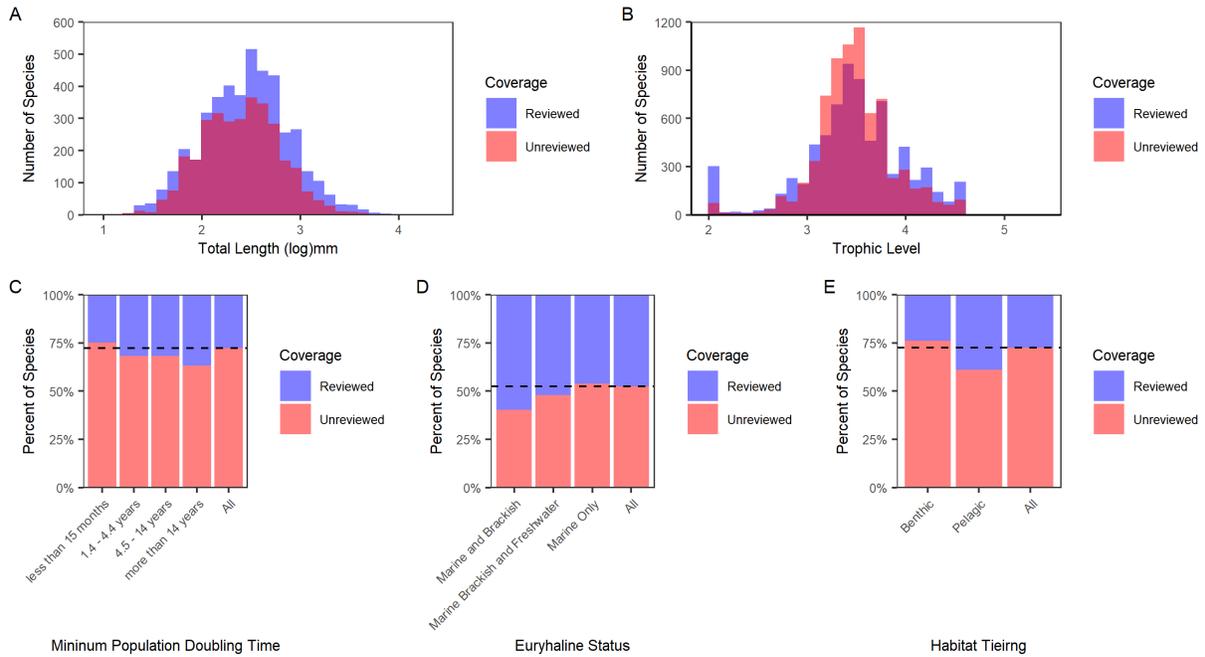


Figure 4. Data bias trends showing how data coverage is distributed across variables. Data deficient species are not included in either category. Number of species are shown for continuous variables to better show distribution of data while percentage is used for categorical variables for ease of comparison. Purple color indicates where reviewed and unreviewed species overlap. Dashed line in C, D, and E represent the overall percentage of data coverage across all levels of the variable.

Table 3. Results for PhyloGLMs testing for predictor variable association with IUCN coverage. Negative estimate numbers indicate an association with being reviewed. Statistically significant results are in italics.

Variable, Levels of Variable	Estimate	Std Error	Z Value	P Value
Total Length	<i>-0.95</i>	<i>0.06</i>	<i>-16.02</i>	<i><0.0001</i>
Trophic Level	<i>-0.75</i>	<i>0.033</i>	<i>-22.83</i>	<i><0.0001</i>
Minimum Population Doubling Time				
1.4 – 4.4 Years	<i>-0.65</i>	<i>0.04</i>	<i>-15.43</i>	<i><0.0001</i>
4.5 – 14 Years	<i>-0.74</i>	<i>0.06</i>	<i>-11.55</i>	<i><0.0001</i>
More Than 14 Years	<i>-0.93</i>	<i>0.11</i>	<i>-8.70</i>	<i><0.0001</i>
Euryhaline Status				
Marine and Brackish	<i>-1.51</i>	<i>0.09</i>	<i>-17.11</i>	<i><0.0001</i>
Marine, Brackish, and Freshwater	<i>-1.68</i>	<i>0.12</i>	<i>-14.16</i>	<i><0.0001</i>
Tiering				
Benthic	<i>1.31</i>	<i>0.14</i>	<i>9.07</i>	<i><0.0001</i>

DISCUSSION

Our study provides novel insights into the well documented declines in marine ray-finned fishes by examining ecological extinction threat profiles, utilizing a phylogenetically informed approach. To our knowledge, this is the first study to examine this combination of core ecological traits and to perform a threat-based analysis to suggest which broad level extinction threats are contributing the most to extinction risk. We also provide a new analysis of assignment bias by the IUCN Red List and test the utility of tree-based comparative methods to control for evolutionary and statistical non-independence. Together, these new results illuminate which types of marine ray-finned fish species are most likely to be go extinct in the near future and which threat types most urgently need to be ameliorated to potentially prevent these extinctions.

Traits Associated with Extinction Risk

Humans have been selectively harvesting larger-sized fish species for at least the past 50,000 years (Jackson et al. 2001) and this trend continues into the present. In line with this, we find that

larger fishes were at greater extinction risk confirming the results of previous studies (Olden et al. 2007; Pinsky et al. 2011; Ripple et al. 2017). This higher extinction risk among larger fishes appears that it may be unlike that of previous mass extinction events; in the “big five” mass extinctions (Raup and Sepkoski, 1982) either no size bias was detected or smaller marine vertebrate genera had a higher likelihood of extinction (Payne et al. 2016; Puttick et al. 2017). Further, Pinsky et al. (2011) and Ripple et al. (2017) have demonstrated the body size extinction risk relationship in the modern oceans is bimodal for bony fishes and our results generally support this finding (Figure 4), although we did not find that smaller fishes are at significantly greater risk.

Slower life history species have been found to be less able to recover after adverse environmental events, perhaps driving them towards higher extinction risk (Purvis et al. 2000b; Jager et al. 2008). Indeed, we find that species with slower minimum population doubling times (4.5-14 years and greater than 14 years) are at higher extinction risk relative to those species with faster doubling times (less than 15 months). Slower life history species being at higher extinction risk may also reflect covariance between body size and population doubling time, given that larger species tend to have slower life histories (Fisher & Owens 2004) and are at greater risk (Fig. 1E). While some evidence suggests that faster life history species are now being targeted by fisheries under the assumption they are more sustainable, this appears to also be driving greater depopulation trends for these taxa (Pinsky et al. 2011). However, it is important to note that Pinsky et al. (2011) examined fisheries collapse rather than extinction risk, and only examined commercially fished species, potentially explaining the divergence from our results.

While some studies have provided evidence of fishing down trophic levels (i.e., “fishing down the food web” a la Pauly et al. (1998)) with the average trophic level of fishes caught by fisheries declining over time, we did not find a statistically significant association between trophic level and extinction risk. Further, it is unclear if the decline in the trophic level of fishes caught in commercial fisheries is the result of changing fishing practices driven by advances in technology that enable greater harvesting of benthic species or changing population levels by trophic level (Caddy & Garibaldi 2000). Regardless, there has been large decline in predator populations for marine fishes (Myers & Worm 2005), but predator population trends were not compared to non-predator population trends, making it unclear if the decline is unique to predators or common across all trophic levels. Christensen et al. (2014) found evidence for the decline of higher trophic level species in their study, in which they used modeling techniques to compare predator (trophic level 3.5 and higher) and prey (trophic level 2.0 and lower) populations over the past century. They found over the past 100 years predator populations have declined by 66%, but prey populations have increased, potentially due to predator release (Christensen et al. 2014). The apparent discrepancy in results between our study and these previous studies (Caddy & Garibaldi 2000; Christensen et al. 2014) may be due to the use of different analytical models and/or treating trophic level as continuous variable rather than a categorical variable (e.g., predator and prey).

We find that fishes that came into contact with brackish or freshwater are at elevated extinction risk relative to marine-only fishes, in line with previous research that has found diadromous fishes are at heightened extinction risk (Grant et al. 2019). “Marine, brackish, and freshwater” fishes being at a higher risk than the other two categories indicates that diadromous fishes are subjected to stressors not faced by exclusively marine species. There has been pronounced

documented declines in diadromous fish populations in the past century from overfishing with some species experiencing declines of over 90% (Limburg & Waldman 2009). Annual Atlantic salmon catches have declined to near zero from a high of 6000 tons (Chaput 2012) while Chinook salmon runs in Oregon are down to 11-19% of their estimated historical level (Meengs & Lackey 2005). A genetic analysis of Pacific salmon indicates the century-long decline of these species may be greater than previously estimated (Price et al. 2019). The situation for diadromous fishes may continue to worsen as climate change is predicted to pose significant challenges by altering hydrological patterns, which could change stream and river flow volumes and/or seasonality, further threatening diadromous fishes (Schröter et al. 2005). We also found benthic fishes were at higher extinction risk than pelagic fishes. This finding differs from one of the few studies to examine extinction risk and habitat tiering in the modern (Payne et al. 2016) that found no association between extinction risk and this binary habitat tiering designation. However, their study combined marine molluscs and vertebrates at the genus level in aggregate, which may explain the discrepancy in our findings.

Threats Faced by Species

The total number of species impacted by each threat type shows that commercial harvesting is the most common extinction threat for marine ray-finned fishes, followed by pollution, development, and then climate change (Fig. 3). Fisheries have long been recognized as exerting significant stress by over-harvesting fish populations and many commercially fished species are depleted far below their historical baseline (Hutchings & Reynolds 2004; McCauley et al. 2015; Arthington et al. 2016). The effects of ocean pollution on marine fish mortality and population trends are not as clear as the effects of harvesting. Oil spills can have negative impacts on fish stocks, especially in their damage to embryos and larvae, but even the effects of oil spills remain

understudied (Sørhus et al. 2015; Langangen et al. 2017). Studies have also demonstrated that pollution can lead to lower species richness among fishes in a given ecosystem (Johnston & Roberts 2009). However, the overall effects of pollution on extinction risk and population declines for marine fishes remains understudied. Rapid development, such as that occurring in the Persian Gulf region for example, can lead to massive loss of suitable habitat, as coastal land is taken over for homes, industry, and shipping, driving declines in fish species (Sheppard et al. 2010; Cavalcante et al. 2011). The projected impacts of climate change on marine fishes is still a matter of ongoing research, but some results suggest climate change will have its biggest impact on tropical fishes and will be latitudinally selective in its impacts (Comte & Olden 2017).

We also found that threatened species have a greater average number of threats than non-threatened species, in line with other studies that have tested for the difference of average number of threats for threatened and non-threatened species (González-Suárez & Revilla 2014; Ducatez & Shine 2017; Munstermann et al. 2021). Among terrestrial vertebrates, Munstermann et al. (2021) found on average 2.66 threat types for threatened species and 2.37 threat types for non-threatened species. We also found that threatened species face a greater average number of threat types, but we find a lower average number of threats for both threatened (2.23) and non-threatened (1.71), but a greater difference in means between the two categories. Ducatez & Shine (2017) found the number of threats assigned varied based on research effort, perhaps explaining why terrestrial species have more assigned threats on average, given the under-studied nature of marine ray-finned fishes in comparison to terrestrial vertebrates. Collectively, these findings demonstrate that as the number of threat types increases beyond two, species are more likely to be at higher extinction risk supporting that the “death by a thousand cuts” scenario is now a

consistent signal across multiple vertebrate groups (González-Suárez & Revilla 2014; Ducatez & Shine 2017; Munstermann et al., 2021).

Threats and Predictor Variables

The association of body size with the top four threat types may help explain why larger sized fishes are at greater extinction risk. We found a positive association between increased body size and harvesting as a threat type, in line with prior studies (Olden et al. 2007; Genner et al. 2010). On the other hand, we find that smaller fishes are more likely to have pollution, development, and climate change as a threat type, suggesting exposure to these threats is driving the heightened percentage of threatened smaller species. Genner et al. (2010) also found the smallest fish species were the most likely to be threatened by climate change. Smaller fishes tend to utilize smaller geographic ranges during their life history (Kramer & Chapman 1999; Luiz et al. 2013), and perhaps small range size is driving the relationship of the smaller fishes being more threatened by pollution, climate change, and development that may not simultaneously impact all regions of a large ranging species in the same way. However, as noted above, Pinsky et al. (2011) found higher likelihood of fisheries collapse among the smallest fishes, due to fisheries management targeting these fishes under the assumption that the smaller, faster reproducing fishes can better withstand fishing pressure. Minimum population doubling time followed the same pattern as body size with species exhibiting slower population doubling time being more likely to be threatened by harvesting, and faster doubling time species were more likely to be threatened by pollution, development, and climate change.

While our study did not find an association between trophic level and extinction risk, we did find that the harvesting threat type is more common for higher trophic level species, in line with prior

studies (Caddy & Garibaldi 2000; Myers & Worm 2005). In addition, pollution as a threat type was positively associated with higher trophic level, possibly suggesting bioaccumulation of pollutants from lower to higher trophic levels (Le Croizier et al. 2016). On the other hand, the climate change and development threat types were negatively associated with higher trophic level, perhaps due to covariation with body size and/or motility allowing these often larger, more motile, higher trophic level species to relocate away from these stressors.

We also find that species that come into contact with brackish and freshwater are significantly more likely to have pollution or development as a threat type. Pollution can adversely impact diadromous fishes, with raw and lightly treated sewage creating oxygen dead zones, and other contaminants such as polychlorinated biphenyls (PCBs), may also cause sublethal issues that reduce diadromous fish survivability (Limburg & Waldman 2009). Further, dams are often associated with human development and there are estimated to be ~80,000 dams of six feet or taller in the rivers of the United States alone, that are well-documented to impede the natural life history migrations of salmonids and other fishes (Jackson & Marmulla 2001). Additionally, diadromous fishes often travel such long distances that they cross multiple political boundaries, impeding coordinated protection policies (McIntyre et al. 2015).

We find that pelagic fishes are more likely to be threatened by harvesting as a threat type than benthic fishes, potentially explaining why they are at elevated extinction risk, with increased fishing pressure driving depopulation trends. This is despite pelagic fishes having larger ranges on average than benthic fishes (Macpherson 2003), and larger range size has been shown to be protective against extinction across geological time intervals (Finnegan et al. 2015). Benthic

species are more likely to have pollution, development, and climate change as threat types, which may reflect benthic species having smaller ranges on average (Macpherson 2003).

Caution is warranted however when interpreting the results for threat types, as the IUCN assigns threat types in a non-systematic manner. In contrast to the assignment to levels of extinction risk, which are determined using extensive quantitative criteria (IUCN Species Survival Commission 2012), there appears to be no consistent criteria used to determine whether a threat applies to a given species (Hayward 2009; Cassini 2011). Deficiencies can be present, such as highly threatened species with clearly defined threats not being assigned any threats (Hayward 2009). For the climate change threat type in particular, assignment of climate change deviates from other methods used to assess species' susceptibility to climate change (Trull et al. 2018). Nonetheless, there is general agreement between IUCN threat types and other assessments of threat types, such as harvesting being the greatest threat for marine fishes and the well documented decline in commercially fished species caused by fisheries (McCauley et al. 2015). Further improvement could be made by developing a more systematic and rigorous framework for assigning threat types, such as the one proposed by Cassini (2011), that calls for species assessors identifying threats to work with specialists in species distribution to define objective values to measure threat and match threats with geographic region.

IUCN Data Coverage

Data coverage biases are a well-documented issue in biology, for example “charismatic megafauna” receiving more research attention and funding (Hosey et al. 2020). However, we generally find only negligible differences across levels for each of our ecological categories between reviewed and unreviewed species (Fig. 4). An exception to this being that we did find

that larger species were more likely to have an IUCN Red List assignment, which is in agreement with previous findings that among cartilaginous fishes (Chondrichthyes) larger species are positively associated with research effort (Ducatez 2019). Further, we did not find any significant relationship between IUCN Red List coverage and trophic level. This is in contrast to Chondrichthyes, which appear to have higher research effort for higher trophic level species (Ducatez 2019). Fast population doubling time species (less than 15 months) were more likely to be unreviewed. Marine only fishes were less well covered compared to species that came into contact with brackish and/or freshwater and benthic species were less well covered compared to pelagic. To our knowledge this is the first study to examine IUCN data coverage for these variables for Actinopterygii. However, despite finding differences in coverage, all differences were small. For total length, difference in means is < 0.35 (log)mm and for categorical variables differences are less than 12% (relative to all). Nonetheless, biases in the distribution of missing data are important and can lead to errors such as an increase in type I errors and incorrect imputation values (Ducatez 2019; Etard et al. 2020), so future studies should continue to check for IUCN coverage when doing trait extinction risk analyses.

Phylogenetic Methods

Comparative phylogenetic methods have been commonly used since the mid-1980s (Felsenstein 1985) to address possible violations of statistical model assumptions that can occur when performing analyses on closely related species, as species are not statistically independent of each other due to their shared evolutionary history (Felsenstein 1985; Ives & Garland 2010). Over the past four decades, an array of approaches to addressing phylogenetic non-independence have been developed and routinely utilized (Pennell & Harmon 2013; Revell & Harmon 2022). However, it is not yet clear if accounting for phylogeny is always necessary when studying the

association between traits and extinction risk, and incorporation of well-constrained phylogenetic relationships is not always possible or practical for all taxa in question, often further limiting sample sizes. We find only marginal and non-significant differences between results based on phylogenetic GLMs versus GLMs without phylogenetic data (Table 1). Further, we find no instance where the directionality of an association changed between the two analytical approaches (Table 1). The lack of significant difference suggests incorporating phylogenetic relationships may not be necessary, at least for this specific data set, but this finding calls for further investigation into when incorporating phylogenetics is necessary for trait-based extinction risk analyses.

Implications for Ecosystems

The heightened extinction risk of species with these functional traits may adversely impact global ecosystems. For example, larger bodied fishes are at higher extinction risk and generally have larger home ranges and biomass intake (McCauley et al. 2015), and the selective removal of larger species may reduce nutrient movement and ecosystem connectivity (McCauley et al. 2015; Ripple et al. 2017). Slower growing fishes are at greater risk and take longer to recover after population collapses, suggesting losing these species may impede population recovery after disturbances (Jennings et al. 1998; Jager et al. 2008). Species inhabiting marine, brackish, and freshwater habitats (i.e., diadromous species) are at heightened extinction risk and are critical for connecting marine and inland habitats and releasing nutrients into inland environments, especially through decomposition (Limburg & Waldman 2009).

Conclusion

Given both magnitude of species that are threatened and the current rates of species loss (McCauley et al. 2015; Ceballos et al. 2017; IPBES 2019) in the modern biodiversity crisis, large-scale systematic analyses are necessary to pinpoint which ecological traits make species the most vulnerable to extinction and which threat types are most strongly associated with these species. By leveraging the combination of newly available ecological, phylogenetic, and extinction risk profile data for a large proportion of marine ray-finned fishes, we demonstrate that species with larger body size, longer population doubling times, life-history strategies that involve movement into brackish and/or freshwater, and pelagic species are all at elevated extinction risk. Further, we find that commercial harvesting is currently the greatest threat to marine ray-finned fishes, followed by pollution, development, and then climate change and that threatened species are simultaneously exposed to a greater number of threats supporting a “death by a thousand cuts” scenario, which appears to now be a common signature across marine and terrestrial vertebrates. Failure to quickly address and ameliorate these threats may lead to global consequences for marine ecosystem structure and function.

REFERENCES

- Arthington AH, Dulvy NK, Gladstone W, Winfield IJ. 2016. Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* **26**:838–857.
- Atwood TB, Valentine SA, Hammill E, McCauley DJ, Madin EMP, Beard KH, Pearse WD. 2020. Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances* **6**:eabb8458. American Association for the Advancement of Science.
- Barnosky AD et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471**:51–57.
- Bush AM, Wang SC, Payne JL, Heim NA. 2020. A framework for the integrated analysis of the magnitude, selectivity, and biotic effects of extinction and origination. *Paleobiology* **46**:1–22. Cambridge University Press.
- Caddy JF, Garibaldi L. 2000. Apparent changes in the trophic composition of world marine harvests: the perspective from the FAO capture database. *Ocean & Coastal Management* **43**:615–655.
- Cassini MH. 2011. Ranking threats using species distribution models in the IUCN Red List assessment process. *Biodiversity and Conservation* **20**:3689–3692.
- Cavalcante G, Marquis E, Benedetti L, Trick C, Kjerfve B, Sale PF. 2011. Managing the growing impacts of development on fragile coastal and marine ecosystems: Lessons from the Gulf. Page 100.
- Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences* **114**:E6089.
- Chaput G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science* **69**:1538–1548.
- Christensen V, Coll M, Piroddi C, Steenbeek J, Buszewski J, Pauly D. 2014. A century of fish biomass decline in the ocean. *Marine Ecology Progress Series* **512**.
- Comte L, Olden JD. 2017. Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change* **7**:718–722.
- Davis M, Faurby S, Svenning J-C. 2018. Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proceedings of the National Academy of Sciences* **115**:11262–11267. National Academy of Sciences.
- De Vos JM, Joppa LN, Gittleman JL, Stephens PR, Pimm SL. 2015. Estimating the normal background rate of species extinction. *Conservation Biology* **29**:452–462.
- Ducatez S. 2019. Which sharks attract research? Analyses of the distribution of research effort in sharks reveal significant non-random knowledge biases. *Reviews in Fish Biology and Fisheries* **29**:355–367.
- Ducatez S, Shine R, Shine R, Shine R. 2017. Drivers of Extinction Risk in Terrestrial Vertebrates. *Conservation Biology* **10**:186–194. John Wiley & Sons, Inc.
- Etard A, Morrill S, Newbold T. 2020. Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography* **29**:2143–2158.
- Felsenstein J. 1985. *Phylogenies and the Comparative Method*. The American Naturalist **125**:1–15. [University of Chicago Press, American Society of Naturalists].

- Finnegan S et al. 2015. Paleontological baselines for evaluating extinction risk in the modern oceans. *Science* **348**:567–570. American Association for the Advancement of Science.
- Fisher DO, Owens IPF. 2004. The comparative method in conservation biology. *Trends in Ecology & Evolution* **19**:391–398.
- Froese R, Demirel N, Coro G, Kleisner K, Winker H. 2017. Estimating fisheries reference points from catch and resilience. *Fish and Fisheries* **18**:506–526.
- Froese R, Pauly D. 2000. *FishBase 2000: Concepts, Design and Data Sources*. ICLARM, Los Ban Os. Laguna.
- Genner MJ, Sims DW, Southward AJ, Budd GC, Masterson P, Mchugh M, Rendle P, Southall EJ, Wearmouth VJ, Hawkins SJ. 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology* **16**:517–527.
- González-Suárez M, Revilla E. 2014. Generalized Drivers in the Mammalian Endangerment Process. *PLoS ONE* **9**:e90292.
- Grant MI, Kyne PM, Simpfendorfer CA, White WT, Chin A. 2019. Categorising use patterns of non-marine environments by elasmobranchs and a review of their extinction risk. *Reviews in Fish Biology and Fisheries* **29**:689–710.
- Harnik PG et al. 2012. Extinctions in ancient and modern seas. *Trends in Ecology & Evolution* **27**:608–617.
- Hayward MW. 2009. The need to rationalize and prioritize threatening processes used to determine threat status in the IUCN Red List. *Conservation Biology: The Journal of the Society for Conservation Biology* **23**:1568–1576.
- Hosey G, Melfi V, Ward SJ. 2020. Problematic animals in the zoo: The issue of charismatic megafauna. Pages 485–508 in Angelici FM, Rossi L, editors. *Problematic wildlife II: new conservation and management challenges in the human-wildlife interactions*. Springer International Publishing, Cham. Available from https://doi.org/10.1007/978-3-030-42335-3_15 (accessed March 9, 2022).
- Hutchings JA, Reynolds JD. 2004. Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk. *BioScience* **54**:297–309.
- IPBES. 2019. IPBES (2019): Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Bonn, Germany. Available from <https://doi.org/10.5281/zenodo.3831673>.
- IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-3. Available from <https://www.iucnredlist.org>.
- IUCN Species Survival Commission. 2012. *IUCN Red List Categories and Criteria: Version 3.1* Second. Gland, Switzerland and Cambridge, UK.
- Ives AR, Garland T Jr. 2010. Phylogenetic logistic regression for binary dependent variables. *Systematic Biology* **59**:9–26.
- Jackson D, Marmulla G. 2001. Dams, fish and fisheries: Opportunities, challenges and conflict resolution. Food & Agriculture Org.
- Jackson JBC et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems.
- Jager HI, Rose KA, Vila-Gispert A. 2008. Life history correlates and extinction risk of capital-breeding fishes. Pages 15–25 in Dufour S, Prévost E, Rochard E, Williot P, editors. *Fish and Diadromy in Europe (ecology, management, conservation): Proceedings of the symposium held 29 March – 1 April 2005, Bordeaux, France*. Springer Netherlands, Dordrecht. Available from https://doi.org/10.1007/978-1-4020-8548-2_2 (accessed October 10, 2021).

- Jennings S, Reynolds JD., Mills SC. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**:333–339.
- Johnston EL, Roberts DA. 2009. Contaminants reduce the richness and evenness of marine communities: A review and meta-analysis. *Environmental Pollution* **157**:1745–1752.
- Kramer DL, Chapman MR. 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* **55**:65–79.
- Langangen Ø, Olsen E, Stige LC, Ohlberger J, Yaragina NA, Vikebø FB, Bogstad B, Stenseth NC, Hjermann DØ. 2017. The effects of oil spills on marine fish: Implications of spatial variation in natural mortality. *Marine Pollution Bulletin* **119**:102–109.
- Le Croizier G et al. 2016. Trophic ecology influence on metal bioaccumulation in marine fish: Inference from stable isotope and fatty acid analyses. *Science of The Total Environment* **573**:83–95.
- Limburg KE, Waldman JR. 2009. Dramatic declines in north Atlantic diadromous fishes. *BioScience* **59**:955–965.
- Luiz OJ, Allen AP, Robertson DR, Floeter SR, Kulbicki M, Vigliola L, Becheler R, Madin JS. 2013. Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings of the National Academy of Sciences* **110**:16498–16502.
- Macpherson E. 2003. Species range size distributions for some marine taxa in the Atlantic Ocean. Effect of latitude and depth. *Biological Journal of the Linnean Society* **80**:437–455.
- McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR. 2015. Marine defaunation: Animal loss in the global ocean. *Science* **347**: 1255641-1- 1255641-7.
- McIntyre PB, Liermann CR, Childress E, Hamann EJ, Hogan JD, Januchowski-Hartley SR, Koning AA, Neeson TM, Oele DL, Pracheil BM. 2015. Conservation of migratory fishes in freshwater ecosystems. Pages 324–360 in Closs GP, Olden JD, Krkosek M, editors. *Conservation of Freshwater Fishes*. Cambridge University Press, Cambridge.
- Meengs CC, Lackey RT. 2005. Estimating the size of historical Oregon salmon runs. *Reviews in Fisheries Science* **13**:51–66.
- Monte-Luna P del, Lluch-Belda D, Serviere-Zaragoza E, Carmona R, Reyes-Bonilla H, Auriolles-Gamboa D, Castro-Aguirre JL, Prío SAG del, Trujillo-Millán O, Brook BW. 2007. Marine extinctions revisited. *Fish and Fisheries* **8**:107–122.
- Munstermann M, Heim N, McCauley D, Payne J, Upham N, Wang S, Knope M. 2022. A global ecological signal of extinction risk in terrestrial vertebrates. *Conservation Biology*.
- Myers RA, Worm B. 2005. Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360**:13–20.
- Newsome TM, Wolf C, Nimmo DG, Kopf RK, Ritchie EG, Smith FA, Ripple WJ. 2020. Constraints on vertebrate range size predict extinction risk. *Global Ecology and Biogeography* **29**:76–86.
- Olden JD, Hogan ZS, Zanden MJV. 2007. Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography* **16**:694–701.
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F. 1998. Fishing down marine food webs. *Science* **279**:860–863.
- Payne JL, Bush AM, Heim NA, Knope ML, McCauley DJ. 2016. Ecological selectivity of the emerging mass extinction in the oceans. *Science* **353**:1284–1286.

- Pennell MW, Harmon LJ. 2013. An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. *Annals of the New York Academy of Sciences* **1289**:90–105.
- Pinsky ML, Jensen OP, Ricard D, Palumbi SR. 2011. Unexpected patterns of fisheries collapse in the world's oceans. *Proceedings of the National Academy of Sciences* **108**:8317–8322.
- Price MHH, Connors BM, Candy JR, McIntosh B, Beacham TD, Moore JW, Reynolds JD. 2019. Genetics of century-old fish scales reveal population patterns of decline. *Conservation Letters* **12**:e12669.
- Purvis A, Agapow PM, Gittleman JL, Mace GM. 2000a. Nonrandom extinction and the loss of evolutionary history. *Science* **288**:328–330.
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM. 2000b. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**:1947–1952.
- Puttick MN, Kriwet J, Wen W, Hu S, Thomas GH, Benton MJ. 2017. Body length of bony fishes was not a selective factor during the biggest mass extinction of all time. *Palaeontology* **60**:727–741.
- Rabosky DL et al. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**:392–395.
- Raup DM, Sepkoski JJ. 1982. Mass extinctions in the marine fossil record. *Science* **215**:1501–1503. American Association for the Advancement of Science.
- Revell L, Harmon L. 2022. *Phylogenetic Comparative Methods in R*. Available from <https://press.princeton.edu/books/paperback/9780691219035/phylogenetic-comparative-methods-in-r> (accessed April 19, 2022).
- Ripple W, Wolf C, Newsome T, Hoffmann M, Wirsing A, McCauley D. 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences* **114**:201702078.
- Schröter D et al. 2005. Ecosystem Service Supply and Vulnerability to Global Change in Europe. *Science* **310**:1333–1337.
- Sheppard C et al. 2010. The Gulf: a young sea in decline. *Marine Pollution Bulletin* **60**:13–38.
- Sørhus E, Edvardsen RB, Karlsen Ø, Nordtug T, Meeren T van der, Thorsen A, Harman C, Jentoft S, Meier S. 2015. Unexpected Interaction with Dispersed Crude Oil Droplets Drives Severe Toxicity in Atlantic Haddock Embryos. *PLOS ONE* **10**:e0124376.
- Trull N, Böhm M, Carr J. 2018. Patterns and biases of climate change threats in the IUCN Red List. *Conservation Biology* **32**:135–147.
- Tung Ho L si, Ané C. 2014. A linear-time algorithm for gaussian and non-gaussian trait evolution models. *Systematic Biology* **63**:397–408.
- Vamosi JC, Wilson JR. 2008. Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecology Letters* **11**:1047–1053.
- Worm B et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**:787–790.