HAL open science

Threatened fish species in the Northeast Atlantic are functionally rare

Noémie Coulon, Martin Lindegren, Eric Goberville, Aurèle Toussaint, Aurore Receveur, Arnaud Auber

To cite this version:

Noémie Coulon, Martin Lindegren, Eric Goberville, Aurèle Toussaint, Aurore Receveur, et al.. Threatened fish species in the Northeast Atlantic are functionally rare. Global Ecology and Biogeography, 2023, 10.1111/geb.13731 . hal-04162009

HAL Id: hal-04162009

https://hal.science/hal-04162009

Submitted on 13 Jul 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

Check for updates

Received: 8 June 2022 | Revised: 2 June 2023 | Accepted: 25 June 2023

DOI: 10.1111/geb.13731

RESEARCH ARTICLE

Global Ecology and Biogeography A Journal of Macroecology WILEY

Threatened fish species in the Northeast Atlantic are functionally rare

Noémie Coulon[1,2] | Martin Lindegren[3] | Eric Goberville[4] | Aurèle Toussaint[5] | Aurore Receveur[6] | Arnaud Auber[2]

[1]Laboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (BOREA) MNHN, CNRS, IRD, SU, UCN, UA, Dinard, France

[2]IFREMER, Unité Halieutique Manche Mer du Nord, Laboratoire Ressources Halieutiques, Boulogne-sur-Mer, France

[3]Centre for Ocean Life, c/o National Institute of Aquatic Resources, Technical University of Denmark, Kgs. Lyngby, Denmark

[4]Laboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (BOREA) MNHN, CNRS, IRD, SU, UCN, UA, Paris, France

[5]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

[6]CEntre de Synthèse et dAnalyse sur la Biodiversité (CESAB), Fondation pour la recherche sur la biodiversité (FRB), Montpellier, France

Correspondence
Noémie Coulon, Laboratoire de Biologie des Organismes et Ecosystèmes Aquatiques (BOREA) MNHN, CNRS, IRD, SU, UCN, UA, 38 Rue du Port Blanc, Dinard 35800, France.
Email: noemie.coulon@mnhn.fr

Funding information
Electricité de France; Estonian Ministry of Education and Research; Fondation pour la Recherche sur la Biodiversité; France Filière Pêche; Muséum National d'Histoire Naturelle

Handling Editor: Ines Martins

Abstract

Aim: The criteria used to define the International Union for Conservation of Nature (IUCN) Red List categories are essentially based on demographic parameters at the species level, but they do not integrate species' traits or their roles in ecosystems. Consequently, current IUCN-based protection measures may not be sufficient to conserve ecosystem functioning and services. Some species may have a singular combination of traits associated with unique functions. Such functionally distinct species are increasingly recognized as a key facet of biodiversity since they are, by definition, functionally irreplaceable. The aim of this study is to investigate whether threatened species are also functionally rare and to identify which traits determine extinction risk.

Location: European continental shelf seas.

Time period: 1984–2020.

Major taxa studied: Marine fish.

Methods: Using newly compiled trait information of 425 marine fish species in European waters, and more than 30 years of scientific bottom trawl surveys, we estimated the functional distinctiveness, restrictedness and scarcity of each species and cross-referenced it with their IUCN conservation status.

Results: In European continental shelf seas, 38% of the species threatened with extinction (9 out of 24 species) were identified as the most functionally distinct. By mapping extinction risk in the multidimensional species trait space, we showed that species with the greatest risk of extinction are long-lived and of high trophic level. We also identified that the most functionally distinct species are sparsely distributed (4% of the total area on average) and have scarce abundances (<1% of the relative mean abundance of common species).

Main Conclusions: Because a substantial proportion of threatened species are functionally distinct and thus may play unique roles in ecosystem functioning, we stress that species traits—especially functional rarity—should become an indispensable step in the development of conservation management plans.

KEYWORDS
distinctiveness, extinction risk, functional rarity, IUCN, marine fish, species trait, threatened

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.
© 2023 The Authors. *Global Ecology and Biogeography* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

Global changes and increasing anthropic pressures are causing a rapid and unprecedented loss of biodiversity (Ceballos et al., 2015; IPBES, 2019). This so-called '*biodiversity crisis*' not only threatens unique habitats and biota worldwide, but also the provisioning of key goods and services for human well-being (Halpern et al., 2008; Pecl et al., 2017). To ensure that biodiversity is preserved and that natural resources are used in an equitable and sustainable manner, the International Union for Conservation of Nature (IUCN) encourages and assists societies to preserve the integrity and diversity of nature. This includes providing assessments of the extinction risk of species across the globe to define the IUCN Red List used as a benchmark to support policymakers, government agencies, wildlife departments and nongovernmental organizations in the elaboration of conservation actions and priorities (Alaniz et al., 2019). Red List categories are defined according to quantitative thresholds using five criteria that incorporate the geographical range of the species and population size/trends, known for only a few well-monitored species (IUCN, 2022). The IUCN Red List does not currently integrate species traits that provide insights into their contribution to ecosystems through physiological, morphological, reproductive or behavioural characteristics (Tilman, 2001; Violle et al., 2017), making it difficult to integrate ecosystem functioning into conservation plans.

Traits provide a mechanistic understanding of species responses to environmental forcing and their effects on ecosystem functioning (Gagic et al., 2015; McGill et al., 2006). Trait-based indexes can detect community responses earlier than indexes based on taxonomic characteristics (McLean et al., 2019; Mouillot, Bellwood, et al., 2013; Pécuchet et al., 2017), allowing more efficient conservation plans. Moreover, trait-based approaches are helpful to anticipate which species are the most sensitive to climatic (Jones & Cheung, 2018), and/or anthropogenic (e.g. fishing; Cheun et al., 2005) pressures, to implement targeted protection measures, even before species are impacted (Hare et al., 2016). For example, the use of trait-based metrics has shown that seabirds with narrow habitat breadths, and fast reproduction strategies, are impacted by human-induced habitat degradation worldwide (Richards et al., 2021). Species traits can serve as a valuable tool in assessing species extinction risk (Carmona et al., 2021), especially when demographic data are lacking (Luiz et al., 2016; Walls & Dulvy, 2020). By incorporating species traits, it becomes easier to align species richness hotspots with functional concerns (Grenié et al., 2018), an approach more in line with a precautionary attitude (Dulvy et al., 2021; Lyons et al., 2005). This is especially evident for marine fish such as skates, classified as non-threatened or data deficient species, but identified as highly sensitive to trawling based on their life-history parameters, body shape and habitat (Rindorf et al., 2020). Using different scenarios based on the IUCN species' extinction risk assessments, a recent study projected a global erosion of the functional spectra of larger species with slower pace of life (Carmona et al., 2021). Although considering functional trait information for more than 75,000 species worldwide, marine fishes were not included despite their important ecological and socio-economical roles and benefits to human health and well-being, from protein supply to climate regulation to recreation (Guerry et al., 2010). Many of these services rely—to some extent—on the presence of only a few functionally distinct species that provide pivotal functions within ecosystems (Bracken & Low, 2012; Dee et al., 2019; Leitão et al., 2016).

These key functions are generally achieved through a combination of traits that provide species-specific capabilities: while some combinations are widespread in marine ecosystems (e.g. invertivorous diet, demersal water-column position, diurnal active period, solitary behaviour and small-to-medium body size; McLean et al., 2021), other trait compositions are more distinct and supported predominantly by species with no functional equivalent; this results in low functional redundancy (Violle et al., 2017). The classical approach that consists of using biomass or total productivity as an indicator of ecosystem functioning, where dominant species are assumed to drive ecological processes and low-abundant species are assumed to contribute weakly (Grime, 1998), has led to disregarding low-abundant species that may be functionally distinct. Nevertheless, it is generally accepted that even when they are low in abundance, top predators can have a disproportionate impact on ecosystem functioning. Therefore, it should be acknowledged that the loss of species with unique functional traits (i.e. functionally distinct species; Violle et al., 2017), can have major impacts on ecosystem stability and functioning if no other species can compensate for the potentially lost functions (Mouillot et al., 2013a, 2013b). Shifts in energy and/or nutrient inputs in ecosystems or disequilibrium in the structure of trophic webs have already been documented in response to the loss of these species (Carmona et al., 2021; Colares et al., 2022; McLean et al., 2019).

Functionally distinct species are under-represented in the IUCN categories because of a lack of species trait information, including distinctiveness, in the classification (Loiseau et al., 2020), which may lead to mismatches between hotspots of functional fish distinctiveness and the implementation of protection measures such as marine protected areas (Grenié et al., 2018; Trindade-Santos et al., 2022). When functionally distinct species are also spatially restricted or poorly abundant, ecosystem stability may be even more fragile in the sense that stability depends on a few key species having disproportionate impacts on the ecosystem relative to their biomass (i.e. functionally rare species; Violle et al., 2017). For example, the giant moray eel (*Gymnothorax javanicus*) is a large sedentary nocturnal benthic specialized predator, with few potential challengers to this role in coral reef ecosystems (Mouillot, Bellwood, et al., 2013). This species is no longer just functionally distinct, it is also functionally rare within communities (Violle et al., 2017), as are most predators. Unfortunately, distinctiveness is thought to be an evolutionary response to a spatially and temporally stable environment, so functionally distinct species—especially species with specific dietary needs—may be more vulnerable to abrupt environmental and anthropogenic changes than those carrying more common traits (Clavel et al., 2011). Protecting functionally rare species is therefore

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

crucial to maintaining the ecological integrity of ecosystems while helping to identify which sites to prioritize for conservation. It should also allow for the protection of a large assemblage of species, by focussing efforts on only a few, which can be a considerable advantage in establishing management plans (Astudillo-Scalia & de Albuquerque, 2019).

Based on approximately four decades of scientific bottom trawl surveys in European seas, we first identified which species are functionally distinct and what are the traits that characterize them. We then quantified to what degree threatened species are the most functionally rare by assessing their functional distinctiveness, restrictedness and scarcity. Finally, we argue for greater integration of traits in the assessment of species extinction risk, as the use of traits also allows the identification of functionally distinct species which, by definition, contribute to vulnerable functions performed by few species (Violle et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study area and bottom trawl surveys

The study area covers most of the European continental shelf seas, including the Baltic Sea, the North Sea, the English Channel, the Scottish west coast, the Celtic Sea, Rockall and Porcupine Banks, the Irish Sea, Bay of Biscay and the Portuguese coast and is divided into 1° longitude by 0.5° latitude grid cells (hereafter 'rectangles') as defined by the International Council for the Exploration of the Sea (ICES) (Figure 1). Abundance data were collated from 20 scientific bottom trawl surveys (see Supporting Information Appendix S1—Table S1) during the last four decades, from 1984 to 2020. Sampling was carried out during daylight at an average speed of 4 knots for at least 20 min. Although gears and sampling schemes differ between surveys (see Supporting Information Appendix S1—Table S1), all captured individuals were identified at the finest taxonomic level possible and reported in a standardized number of individuals per species caught per hour of trawling, including potadromous species that may be caught in brackish water (Kawamura, 2008). The abundance dataset we used was obtained from the ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark. (https://datras.ices.dk) and includes 425 species across 536 standard ICES rectangles. Due to the absence of reporting on non-commercial species from Spanish surveys, we did not include these surveys. Since the total number of hauls per rectangle is spatially heterogeneous (from 3 to 1070; see Supporting Information Appendix S2—Figure S1a), we standardized sampling effort by means of species accumulation curves (SACs) (Chao, 1987) for each rectangle, considering each haul as a sampling unit, using the *'vegan'* R package (Oksanen et al., 2008). Nonlinear Michaelis–Menten curves were fitted to each of the SACs. When the total number of hauls was lower than the estimated number of hauls necessary to achieve 65% of the asymptotic species richness, we discarded the rectangle (59 rectangles out of 536) following the approach of Maureaud et al. (2019) (see Supporting Information Appendix S2—Figure S1b).

2.2 | Species traits and gap filling

We selected traits that reflect habitat use, life-history and trophic ecology of species expected to be implicated in the response of species to environmental changes and ecosystem functioning (see Supporting Information Appendix S1—Table S2 for reasoning; Beukhof, Dencker, Pecuchet, & Lindegren, 2019; McLean et al., 2019, Murgier et al., 2021). Among the selected traits, eight are continuous (trophic level, age at sexual maturity, length at sexual maturity, fecundity, offspring size, Von Bertalanffy growth coefficient K, maximum length and length infinity) and three are categorical (position in the water column, feeding mode and spawning type). Trait data for the 425 species were initially collected by extracting trait values from the North Atlantic and Northeast Pacific shelves dataset collated by Beukhof, Dencker, Palomares, and Maureaud (2019). Our obtained trait dataset had 38% missing trait values (1289 out of 3386), explained by the presence of missing data in Beukhof, Dencker, Palomares, and Maureaud (2019) and because some species we studied were not in Beukhof et al. (2019b). We filled missing values by following the procedure undertaken by Beukhof, Dencker, Palomares, and Maureaud (2019) and by using the predictive life-history model developed by Thorson et al. (2017).

Continuous traits were supplemented with information extracted from FishBase (Froese & Pauly, 2020) restricted to the Northeast Atlantic and completed by scientific literature as undertaken by Beukhof, Dencker, Palomares, and Maureaud (2019). For 'trophic level', 'offspring size' and 'fecundity' traits not available at the species levels, we averaged the trait values at the genus level or family level if genus was not available, following Beukhof, Dencker, Palomares, and Maureaud (2019). Additionally, 'age at maturity', 'size at maturity', 'Von Bertalanffy's growth coefficient K' and 'infinite size' traits were completed (171 values) using the data-integrated predictive life-history model (Thorson et al., 2017) made available in the '*FishLife*' R package. This model estimates life-history parameters by incorporating existing data and life-history correlations between related species into a multivariate random walk model. Three life-history traits per species must be known to accurately predict the remaining life-history variables. Predictions are more accurate for species with many measurements than those for which only a few measurements were made. Therefore, we were unable to predict all of the missing life-history traits and applied the note accompanying the FishBase 'Growth' table advising to keep species life-history parameters only when the predicted infinite size is not more or less than one-third different from the maximum reported size for the species. For categorical traits, missing traits were extracted from FishBase, completed by scientific literature and finally assigned according to the trait values of a species of the same genus or family when information was available. After completion, only 4% of the values (i.e. 139 of the 3386) were missing and scattered

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

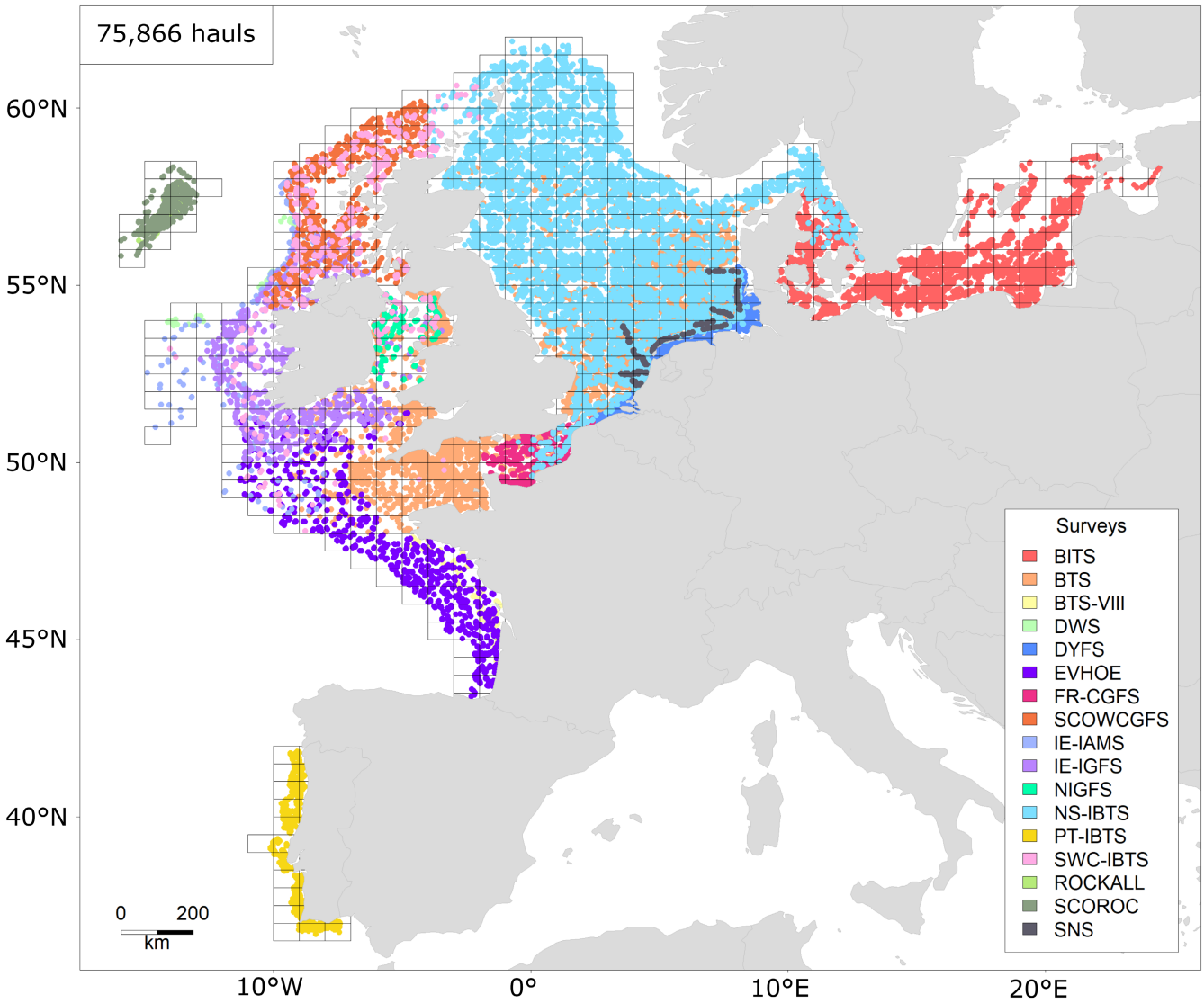

FIGURE 1 Map of the available bottom trawl surveys of demersal fish communities across northwest European continental shelf seas obtained from the International Council for the Exploration of the Sea data portal (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). Coloured dots locate the individual hauls, with one colour per survey. ICES rectangles (1° longitude by 0.5° latitude grid cells) are represented. See Supporting Informatioin Appendix S1—Table S1 for detailed information about bottom trawl surveys and their acronyms.

within the different trait types with less than 10% missing values, at most, per trait. Our final database contains 339 species fully informed. The resulting trait database is openly available at Figshare public data repository 10.6084/m9.figshare.19833304.v1 (see also Appendix 1—Data sources).

2.3 | Functional distinctiveness, restrictedness and scarcity

The functional rarity framework developed by Violle et al. (2017) provided a definition and quantification of functional rarity that considers both trait distinctiveness, species abundance and species distribution. According to this concept, functionally rare species have low abundances and are the most distinct and spatially restricted in local areas, while functionally common species have the highest abundances, common trait values and larger spatial distributions. The functional distinctiveness D_i of species i is an index calculated independently of species abundance, quantifying how a species i is functionally dissimilar to all other species in the community (Violle et al., 2017), considering one combination of traits:

$$D_i = \frac{\sum_{j=1, j\neq i}^{S} d_{ij}}{S-1} \quad (1)$$

with S the total number of species within the study area and d_{ij} the dissimilarity between species i and j. A species with a high D_i value is considered functionally distinct compared with the rest of the pool (Violle et al., 2017). Because identifying the relevant number of traits to correctly describe ecological functions is difficult and subjective

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(Lepš et al., 2006; Petchey & Gaston, 2002), we computed an integrative version of the functional distinctiveness index (IntDi) that not only considers one combination of traits (i.e. the combination of all available traits) but all possible combinations of available traits. This index therefore provides a more robust assessment of species distinctiveness (see Supporting Information Appendix S1—Table S3) and a more objective ranking between species according to their functional distinctiveness; it ensures that a species has a high distinctiveness value not because of a single extreme trait value but because it has several uncommon trait values (Grenié et al., 2017). The R code is freely available at Figshare public data repository 10.6084/m9.figshare.22317643.v1 (see also Appendix 1—Data sources). We calculated the dissimilarity matrix (i.e. dissimilarities between species based on their traits) of each possible combination of traits among the 11 traits selected for this study, considering that a minimum of 4 is needed to characterize the difference between species (Petchey & Gaston, 2002). This procedure therefore provides a total of 1816 dissimilarity matrices. We then calculated the IntDi value of each species from the integrated dissimilarity matrix itself computed as the average between the 1816 matrices (see Supporting Information Appendix S2—Figure S2 for example). Additionally, to prevent any disproportionate contribution of categorical traits in dissimilarity matrices and thus on distinctiveness computation, we applied the approach developed by de Bello et al. (2021) using the '*gawdis*' package. Functional distinctiveness was standardized so that it ranges between 0 and 1. We followed the same procedure for the resulting trait database, the database with no missing data, and the database with missing data predicted with the R package '*missForest*' (Stekhoven & Buehlmann, 2012). We developed two linear models (Supporting Information Appendix S2—Figure S3; R_1^2=0.9954 & R_2^2=0.9982) and calculated the percentage of variation between the rankings to ensure the robustness of the ranking made from the integrated distinctiveness calculation (refer to Supporting Information Appendix S1—Table S4). The 425 species were then grouped on the basis of their IntDi values: the first group (D1, the most functionally common species) was defined according to the first decile of IntDi, while the last group (D10, the most functionally distinct species) was defined according to the last decile. This division into deciles was done a posteriori according to the number of groups allowing to best isolate the most functionally distinct species according to the distribution of distinctiveness values (Figure 2). We then performed Spearman correlation tests to assess the relationship between each continuous trait and species distinctiveness. For categorical traits, differences in functional distinctiveness between trait modalities were computed using Wilcoxon post hoc tests.

A Principal Coordinate Analysis (PCoA) was performed on the average dissimilarity matrix to summarize interspecific dissimilarities in a biplot referred to as a 'trait space'. We calculated the functional dissimilarity between the species of a functional distinctiveness group (e.g. D2) and all other species from all other groups (for this example: all groups without D2) to test for the difference between functional distinctiveness groups (D1 to D10 distribution deciles), according to their dissimilarities. We then tested whether this functional dissimilarity was lower or higher than expected by chance given the number of species in each functional distinctiveness group. The functional dissimilarity between the species of a functional distinctiveness group and all other species was calculated using the R function '*dissim*' of the package '*TPD*' (Carmona et al., 2019). It reflects the degree of functional dissimilarity between the probabilistic distributions of species in the trait space between the two assemblages and ranges from 0 (complete overlap) to 1 (no overlap). We used a TPD (Trait probability density; '*TPD*' package; Carmona et al., 2019) approach—estimation of the probabilistic distribution of the species within the trait space—by performing multivariate kernel density estimations. We divided the 2-dimensional space into 40,000 cells, that is, 200 per dimension. For each species, the kernel was a multivariate normal distribution centred in the coordinates of the species in the trait space and bandwidth was chosen using unconstrained bandwidth selectors from the '*Hpi*' R function in the '*ks*' package (Chacón & Duong, 2018). We then compared the

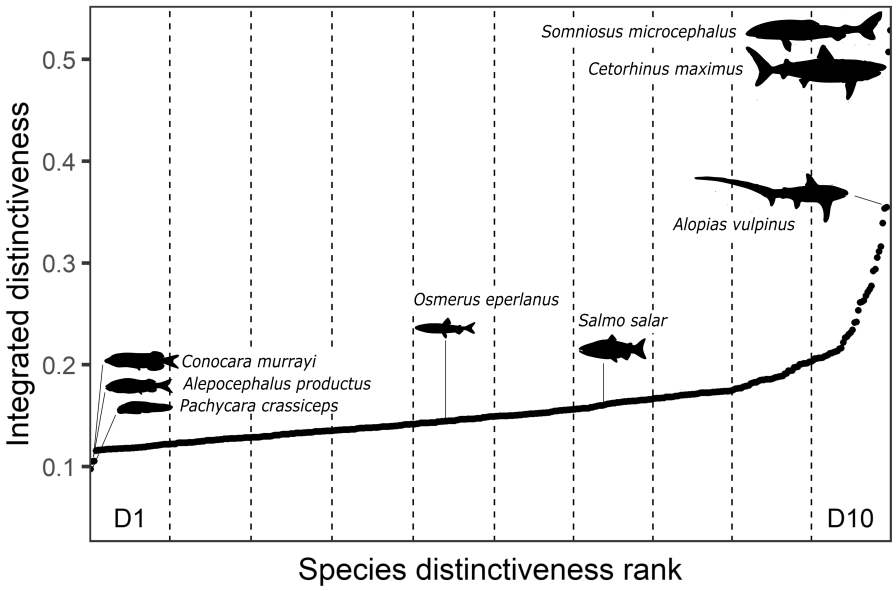

FIGURE 2 Integrated distinctiveness index per species showing that most species are rather functionally common and only a few are very distinct. The grey dotted lines separate species according to distinctiveness deciles, from D1 (the most functionally common species) to D10 (the most functionally distinct species).

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

observed functional dissimilarity to a null model where the functional distinctiveness groups were randomly assigned to species, keeping the number of species in each group constant. We drew 999 simulated assemblages and compared simulated and observed functional dissimilarities. We calculated standardized effect sizes (SES) as the difference between the observed value and the mean of the simulated values after standardization by their standard deviations: *p*-values higher (lower) than 0.975 (0.025) indicate that the observed functional dissimilarity is significantly lower (higher) than expected by chance (using a 5% threshold), given the number of species in each group.

We then turned to the complementary components of functional distinctiveness to define functional rarity, that is, the scarcity and spatial restrictedness of species in the study area. Although initially defined at local and regional spatial scales, the indexes can be calculated at the same study scale to capture both aspects of functional rarity: being low in abundance and being spatially poorly distributed (Grenié et al., 2017; Ricotta et al., 2016). This is because both range size and local abundance influence extinction risk; species with small ranges can avoid extinction if their local abundance is high, while species with low local abundance can avoid extinction if they are widespread; species with both small ranges and low local abundance should be at high risk (Johnson, 1998). For a given species, we compared its geographical range with the geographical extent of the entire study area. The spatial restrictedness R_i is an index between 0 and 1 based on species occurrence (Violle et al., 2017) (weakly impacted by gear selectivity) and is computed as follows:

$$R_i = 1 - \frac{K_i}{K_{tot}} \tag{2}$$

with K_i the number of ICES rectangles where species *i* occurs and *Ktot* the total number of ICES rectangles in the dataset. R_i nearly equals one when a species is present in a single site and 0 when the species is present in all sites (Grenié et al., 2017). Because there are differences in sampling effort between the 536 ICES rectangles, we computed the restrictedness to prevent under or overestimation. The restrictedness was computed for each grid cell by randomly selecting the minimum number of hauls to catch 65% of the asymptotic number of species with enough sampling effort (477 rectangles out of 536). For a given species, the procedure was repeated 100 times. The integrated restrictedness (IntRi) was calculated as the average of restrictedness values.

The scarcity index Sc_i, which ranges between 0 and 1, measures the relative abundance of species *i* in the community (Violle et al., 2017):

$$Sc_i = \left(-S \times \ln(2) \times Ab_i \right) \tag{3}$$

with *S* the total number of species in the study area and Ab_i the relative abundance of species *i* (i.e. the mean abundance of the species divided by the mean abundance of all species in the Northeastern community). A species with a low relative abundance will have a scarcity value close to 1, while dominant species will tend toward 0. Since scientific bottom trawl surveys are conducted with bottom trawls and not pelagic trawls, we also calculated the scarcity index excluding the 24 pelagic species. For both restrictedness and scarcity, a unilateral Welch's *t*-test was performed to compare the restrictedness/scarcity between the most functionally common and distinct species (D1 and D10, respectively). We also implemented two Generalized Linear Mixed Models (GLMM) using the *'lme4'* R package (Bates et al., 2015) using the restrictedness/scarcity index as a response, the deciles (D1 and D10) as predictors and the species family as a random factor.

2.4 | Relationship between extinction risk, functional distinctiveness and traits

Regional IUCN Red List statuses of species were obtained using the *'rredlist'* R package (Chamberlain & Salmon, 2018) and manually verified thanks to the IUCN Red List of Threatened Species (IUCN, 2022). Only species with IUCN status (and not 'Data Deficient' status; 362 out of 425 species) and complete trait information (294 out of 425 species) were selected for the rest of the study. We converted IUCN status into two threat categories: (i) 'not threatened', which grouped together 'least concern' (LC) and 'near-threatened' (NT) species, and (ii) 'threatened', that encompassed 'vulnerable' (VU), 'endangered' (EN) and 'critically endangered' (CR) species. A unilateral Welch's *t*-test was performed to assess whether species assigned as 'threatened' have a higher distinctiveness than 'non-threatened' species. We then mapped species conservation status in trait space using a trait probability density approach, following Carmona et al. (2021): we set up a Generalized Additive Model (GAM), using the species conservation status as a response, the corresponding position in the different dimensions of the trait space (PCoA axes) as predictors. Model predictions (i.e. the probability of species being threatened) were done for the different PCoA axes without extrapolation. By representing predictions on the different axis, we mapped the complete functional space and therefore offer a visualization of how extinction risk was distributed across trait combinations.

We finally performed a down-sampled Random Forest classification (RF; *'randomForest'* R package, Breiman, 2011), recommended when classes are unbalanced (Freeman et al., 2012) to assess the contribution of individual traits on species conservation status. Instead of a bootstrap sample from the entire dataset, each tree of the forest during down-sampling is built from a bootstrap sample from the rare class, along with a sub-sample of the same size from the more common class (Chen et al., 2004). Species threat (1: threatened, 24 species; 0: not threatened, 270 species) was the response variable, and species trait values were the predictors.

The flowchart of the methodology developed for our analyses is presented in Supporting Information Appendix S2—Figure S4.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

3 | RESULTS

3.1 | Functionally rare species and their traits

Species rank based on distinctiveness is very robust to missing data, in particular for defining the ranks of the most common and distinct species (see Supporting Information Appendix S1—Table S4), but the absolute value of the distinctiveness decreases more for the most distinct species (see Supporting Information Appendix S2—Figure S3; $R_1^2 = 0.9954$ & $R_2^2 = 0.9982$). The integrated distinctiveness (IntDi; Figure 2; see SupportingInformation Appendix S1—Table S5) of Northeastern Atlantic marine fish ranges from 0.10 for *Pachycara crassiceps* to 0.51 and 0.53 for Basking Shark (*Cetorhinus maximus*) and Greenland Shark (*Somniosus microcephalus*), respectively, followed by Thresher Shark (*Alopias vulpinus*) with a IntDi value of 0.35. With a median integrated distinctiveness value of 0.14, most species of the European continental shelf are quite functionally common and only a few species are very functionally distinct. The first functional distinctiveness group (D1; 42 species), defined according to the first decile of the integrated distinctiveness indexes distribution, encompasses the most functionally common species with IntDi values ranging from 0.10 to 0.12. Almost all D1 species are 'non-guarder' (one value is missing) and 'demersal' (40 out of 43 species). They spawn a very large number of tiny eggs (median offspring size = 0.96 mm; median fecundity = 50,000) (see Supporting Information Appendix S2—Figure S5). On the opposite part of the distribution (Figure 2), D10 species (42 species, of which 41% are elasmobranchs with 16 sharks and one skate, and a significant number of deep-sea species) groups together the most functionally distinct species with IntDi values between 0.20 and 0.53.

Species that belong to D10 represent between 0 and 17% of the total number of species per ICES rectangle, the maximum number being observed on Porcupine Bank (see Supporting Information Appendix S2—Figure S6). They present particularly high restrictedness values (IntRi = 0.960 ± 0.097), indicating a spatial restriction with significantly more limitations than for D1 species (IntRi = 0.860 ± 0.219; unilateral Welch's *t*-test; $p = 0.003$; see Supporting Information Appendix S1—Table S5). At the scale of the European continental shelf seas, D10 species are present on average in 4% of the ICES rectangles, the most common species being present on average in 14% of the rectangles. Functionally distinct species (D10 species) also present very high scarcity values (Sci = 0.863 ± 0.278), which is significantly higher (unilateral Welch's *t*-test; $p = 0.011$; see Supporting Information Appendix S1—Table S5) than for functionally common species (D1 species; Sci = 0.590 ± 0.450): the relative mean abundance of functionally distinct species corresponds to 0.86% of the relative mean abundance of common species. When pelagic species are removed from the calculation of the scarcity index, the same conclusions are reached (unilateral Welch's *t*-test; $p = 0.003$). In addition, the variance of the family random effect is less than the residual variance of each GLMM showing that significant differences in restrictedness/scarcity between D1 and D10 species are not due to a family effect. In other words, this means that whatever the family, functionally distinct species are also scarce and geographically restricted, resulting in functionally rare species.

The first two axes of the PCoA (57.3% of the total variance; Figure 3a), and tests for the relationship between each trait and the species integrated distinctiveness (see Supporting Information Appendix S2—Figure S5), show that functionally rare species are mainly characterized by slow individual growth, large body size (i.e. length at infinity and maximal length), high trophic level, late sexual maturity, low fecundity and that they provide high parental investment to their progeny in comparison to functionally common species. These species are also mainly not demersal.

3.2 | Extinction risk and functional distinctiveness

Thirty species have not yet been assigned a European IUCN status and 33 species have a 'Data-Deficient' status. These species are distributed in each of the functional distinctiveness groups (see Supporting Information Appendix S2—Figure S7). Of the 294 species considered in this section, 24 are classified as 'threatened' (see Supporting Information Appendix S1—Table S5). Using a unilateral Welch's *t*-test to test whether 'threatened' and 'nonthreatened' species have distinct IntDi values, we show that 'threatened' species have a significantly higher distinctiveness ($p = 0.003$) than 'non-threatened' species (see Supporting Information Appendix S2—Figure S8). Indeed, 37.5% of the 'threatened' species are functionally rare species (D10 species) and this percentage increases further (58.3%) if we include D9 species, the second most functionally distinct group. These correspond to elasmobranchs (D9 and D10 species) classified as 'vulnerable', 'endangered' and 'critically endangered' on the IUCN Red List; European Sturgeon (*Acipenser sturio*) classified as 'critically endangered' (D10 species) and Beaked Redfish (*Sebastes mentella*) classified as 'endangered' (D9 species); 100% of the most common species (D1 species) are 'non-threatened' species. However, some threatened species are classified into the rather common functional groups (D2, D3 and D4 species): Sandy Ray (*Leucoraja circularis*; EN), Shagreen Ray (*Leucoraja fullonica*, VU), European Eel (*Anguilla anguilla*, CR), European Whitefish (*Coregonus lavaretus*, VU) and Roundnose Grenadier (*Coryphaenoides rupestris*, EN).

Species with the greatest risk of extinction belong to the group with the highest dissimilarity in trait space (SES = 0.78; Supporting Information Appendix S1—Table S6), a dissimilarity greater than that expected by chance (SES = 14.78, $p = 1$). The subspace they occupy is mostly characterized by slow pace-of-life species (i.e. slow individual growth, late sexual maturity, low fecundity, high parental care and larger offspring size; Figure 3b), large maximum size and high trophic levels with a piscivorous feeding mode. These traits are also the most important for assessing the risk of extinction of species according to the down-sampled random forest (error rate = 7.14%; see Supporting Information Appendix S2—Figure S9) with species in the 'threatened'

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

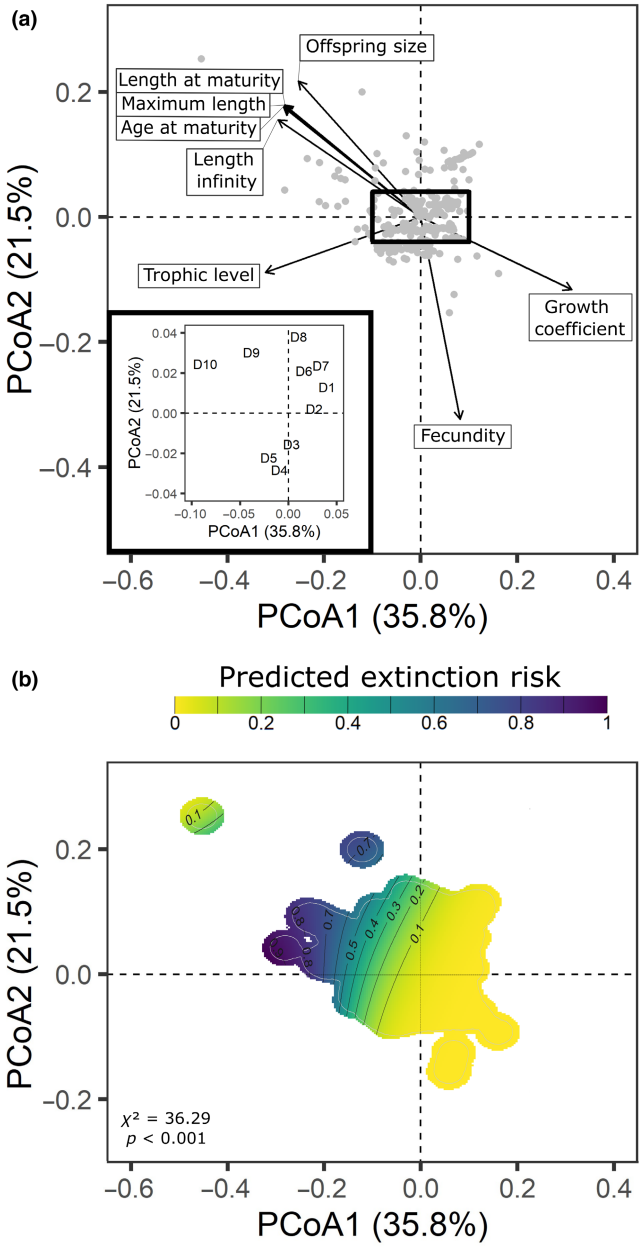

FIGURE 3 Sorting of species along the two principal axes of the principal coordinate analysis (PCoA) of the Northeastern Atlantic marine fish trait data. (a). Functionally rare species are long-lived species. Annotations from D1 (the most common species) to D10 (the most distinct species) refer to the centroids of each functional group. Categorical factors are not represented for convenience and given their low explanatory power. (b). Threatened fish species are functionally rare. Extinction risk in the trait space of the Northeastern Atlantic marine fish. Probability of species being classified as threatened according to the Generalized additive model (GAM) (with binomial distribution; χ^2 and p-values are shown), using the position of species in the functional space as predictors. Yellow tones indicate a low risk of extinction. Purple tones indicate a high risk of extinction. The grey line indicates the 0.99 quantile of the spectra of each group, considering only species with known extinction risk and traits (294 out of 425).

category having larger maximum length and much larger offspring size (see Supporting Information Appendix S2—Figure S10), followed by body size coefficients, fecundity and trophic level.

4 | DISCUSSION

Our aim was to evaluate whether threatened fish species are functionally rare and identify traits that make them vulnerable. To do so, we used IUCN species status, species traits and abundance data from bottom trawl surveys to define the functional rarity of 425 fish species in the European seas. Here we both demonstrate that (i) a substantial proportion (38%) of threatened fish are functional distinct, spatially restricted and present high abundance scarcity and (ii) that the functional distinctiveness of these species is primarily associated with slow pace-of-life strategies. Our results are analogous to similar studies on freshwater fishes (Su et al., 2019), or on terrestrial mammals and birds (Loiseau et al., 2020), demonstrating a general trend to devote efforts to protect species with unique functional traits and supporting key functions within ecological processes (Dee et al., 2019; Leitão et al., 2016; Mouillot, Bellwood, et al., 2013).

The most functionally distinct species identified in our analysis tend to occupy a higher trophic position in the food web to the extent that some, such as Porbeagle (*Lamna nasus*) that feeds mainly on teleost fish and cephalopods (Stevens, 2010), are known to be apex predators (Wallach et al., 2015). Because top predators exert top-down regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013), their decline or disappearance may destabilize ecosystems functioning through cascade reactions (Leitão et al., 2016; Mouillot, Graham, et al., 2013; Murgier et al., 2021; Violle et al., 2017). Top predators may also be linked to other ecosystem functions, such as transporting nutrients and carbon through the layers of the ocean (Atwood et al., 2018; Higgs et al., 2014; Williams et al., 2018). For example, Swordfish (*Xiphias gladius*) feed near the surface at night (0–90 m) and up to 650 m depth during the day on myctophid fish and squid (Chancollon et al., 2006). Species with a high trophic level may also facilitate the acquisition of organic matter for other species both during their lifetime through their feeding practices (e.g. bioturbation of skates; O'Shea et al., 2012) and after their death when the sinking of their carcass provides food for mobile scavengers over extended periods of time ranging from several weeks to months (e.g. Porbeagle or Thresher Shark; Higgs et al., 2014). Species, such as Turbot (*Scophthalmus maximus*), Brill (*Scophthalmus rhombus*) and Blue Shark (*Prionace glauca*), can also support ecosystem services including food supply (Simpfendorfer et al., 2011) and tourism (Cisneros-Montemayor et al., 2013; Gonzáles-Mantilla et al., 2022). Associating the extinction risk to the impact of a given species on the entire food web—like the complexity of its interactions with other species—would be relevant to move toward efficient ecosystem conservation plans.

Functionally distinct species (D10 species) also reach sexual maturity later, at a larger size, and carry few larger eggs or offspring to which they provide parental care, thus having an overall slower pace of life. Among these species, there are 16 external brooding and internal live-bearing sharks whose new-born pups are very large (28–175 cm), such as Blue Shark that has evolved placentae with gestation lasting from 9 to 12 months (Dulvy & Reynolds, 1997). The 'bearer' type (i.e. external brood and internal live-bearer type) occurs

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

when the benefits of increased offspring survival outweigh the costs of reduced fertility, mobility and increased metabolic demands of carrying offspring through development (Goodwin et al., 2002). Two teleost species (Ribbonfish: *Trachipterus arcticus* and European Sturgeon), distinguished by very high fecundity in contrast to older ages at maturity are also among the most functionally distinct species. Similarly, by studying more than 75,000 species of vascular plants, mammals, birds, reptiles, amphibians and freshwater fish, Carmona et al. (2021) showed that species with long-lived functional strategies, living in stable environments in which investment in juvenile survival is more effective in maintaining the population, are more likely to be threatened with extinction.

Furthermore, we show that distinct species (D10 species) are mostly poorly geographically distributed and low in abundance. Unfortunately, species that have small population sizes, restricted geographical ranges (or habitat extent) and, often, narrow environmental niches, are especially vulnerable to extinction (Casey et al., 2021; Davies et al., 2004; Harnik et al., 2012; Johnson, 1998; Loiseau et al., 2020). Some of the most spatially restricted species (see restrictedness index) are evolving at great depths (e.g. *Melanostigma atlanticum*; *Maulisia microlepis*; *Benthocometes robustus*; *Normichthys operosus)*, including deep-sea sharks (e.g. sharpnose sevengill shark (*Heptranchias perlo)* and *Somniosus* sp.), therefore having a low probability of being encountered on the continental shelf due to biological constraints. Large pelagic species such as Thresher Shark and Swordfish rank among the least abundant species in European seas, as indicated by the scarcity index. By contrast, seven small pelagic fishes (out of a total of 29 pelagic species in our dataset) including European Sprat (*Sprattus sprattus)*, Atlantic Horse Mackerel (*Trachurus trachurus)*, Atlantic Mackerel (*Scomber scombrus)* and European Anchovy (*Engraulis encrasicolus*) are among the most abundant species. The International Bottom Trawl Survey (IBTS) has been previously shown effective for examining the temporal dynamics of both demersal and pelagic fishes (Hiddink & Ter Hofstede, 2008; McLean et al., 2018). Furthermore, bottom trawl surveys, including the IBTS surveys, are reliably used for pelagic stock assessment (HAWG, 2022; Heessen et al., 1997; ICES, 2007, 2022; Monnahan et al., 2021). Therefore, other species traits such as size and body shape or behaviour must be considered to further explain differences in abundance (Walker et al., 2017). What is certain is that less abundant species are less resilient to abrupt environmental changes (Bell & Gonzalez, 2011), and anthropogenic pressure such as habitat degradation and overfishing—that we can be related to the anthropogenic Allee effect; for example, Courchamp et al. (2006)—due to a limited supply of beneficial mutations and interspecific competition with more common species that have already undergone such beneficial mutation (Bell, 2017; van Eldijk et al., 2020) and competitive exclusion as they are less able to exploit their habitat (Segre et al., 2014). Here, we reveal that the abundance of the most functionally distinct species is low across the Northeast Atlantic, with maximum richness and abundance being found on the Porcupine Bank (see Supporting Information Appendix S2—Figure S5), although this region is one of the less well sampled of the European seas. Specific surveys conducted in this region between 2006 and 2009, O'Hea et al. (2020) sampled 21 species of deep-sea sharks (we counted seven deep-sea sharks in our datasets), the greatest number of individuals being constrained in deep habitats (~ 500 m depth). Porcupine Bank and adjacent areas support an important European demersal fishery, which makes these deep-sea species highly vulnerable to bottom trawl bycatch (Oliver et al., 2015), especially those for which abundance data do not support the implementation of management measures (ICES, 2021).

Our study reveals that the species facing the greatest risk of extinction are frequently functionally distinct species (D10 species), often contributing to unique niches and functions in the ecosystem (Hammerschlag et al., 2019). We showed that 38% of the species threatened with extinction according to the IUCN Red List in European seas (9 out of 24 species) are the most functionally distinct species (D10 species) with eight sharks belonging to both. If the second most functionally distinct group of species is added, the number of species increases up to 58% (14 species out of 24) and also includes one skate and one ray. Already alarming, this result is certainly underestimated because of the 'Data Deficient' classification of six D10 species (e.g. Forkbeard, *Phycis phycis*; Ocean Sunsfish, *Mola mola*; Arrowhead Dogfish, *Deania profundorum*; Sharpnose Sevengill Shark; Little Sleeper Shark, *Somniosus rostratus* and Atlantic Torpedo Ray, *Tetronarce nobiliana*) (Dulvy et al., 2021). Dulvy et al. (2021) estimated that one-third of chondrichthyan fishes worldwide were threatened with extinction, the largest sharks and rays being in the most peril, especially those living in shallow waters that are more accessible to fisheries, and more impacted by habitat degradation and pollution (Dulvy et al., 2021; Pacoureau et al., 2021). This risk is mainly related to their greater body size—a determining trait in the rate of extinction of animal species since the Pleistocene—(Cardillo et al., 2005; Carmona et al., 2021) and may result from a higher hunting pressure, a higher requirement for resources and a slower response to changes in conditions; nuances exist, however (see review by Chichorro et al., 2019). Moreover, sharks and skates are especially threatened in the Northeast Atlantic due to non-selective fishing techniques (Smith & Garcia, 2014; Walls & Dulvy, 2020) that may have led to local extinctions, such as occurred with Common Skate (*Dipturus batis*) (Brander, 1981) and angel sharks *Squatina* spp. (Lawson et al., 2020). If functionally rare species were to disappear, we could see significant changes in the functioning of ecosystems in connection with irreparable losses of functions (Carmona et al., 2021). Looking back to the unique functions already mentioned, such as highly specialized predation (Mouillot, Bellwood, et al., 2013), top-down trophic regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013), transfer of matter through the ocean layers (Atwood et al., 2018; Higgs et al., 2014; Williams et al., 2018), access facilitation to organic matter (Higgs et al., 2014; O'Shea et al., 2012), protein supply (Simpfendorfer et al., 2011) and ecotourism (Gonzáles-Mantilla et al., 2022), we realize that entire ecosystems are at stake, from coral reefs to abyssal plains to the continental shelves on which our marine resource

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

exploitation relies. We also should highlight that several non-threatened species were functionally distinct, such as deep-sea lizardfish (*Bathysaurus ferox*), Alepocephaliformes, Stomiiformes, that can perform vertical migrations (e.g. *Vinciguerria poweriae*). Species expressing this behaviour influence ecological processes (e.g. grazing and predation pressure) in the upper water column by altering the composition of assemblages between day and night, and also participate in the organic matter transport from the surface to the seafloor (Angel & Pugh, 2000), thus enhancing the efficiency of the biological pump (Bianchi et al., 2013). Certainly ecologically unique—yet overlooked in conservation strategies—functionally distinct deep-sea species deserve greater attention for their conservation (Davies et al., 2007), especially in the context of climate change and carbon sequestration (Birch et al., 2016; De Stasio et al., 1993; Pinti et al., 2023).

The way we identify functionally distinct species is independent of species selectivity but can be influenced by both the selection of traits and the initial set of studied species (Legras et al., 2020). This means that whether a species is distinct or not is context and area dependent, conditioned by the regional species pool and their prevailing set of traits and adaptations. We therefore caution that our conclusions are limited to the spatial scale, species pool and trait combination we used. The inclusion of traits related to species' ecological versatility, such as thermal preference or range and vulnerability to acidification, could have been relevant to identifying species whose narrow ecological niches may make them particularly vulnerable to climate change (Jones & Cheung, 2018), with global declines observed in functionally distinct species predicted by niche theory (Clavel et al., 2011). For example, some functionally distinct but abundant and widely distributed species that were not identified as functionally rare in this study may become so if they exhibit increased sensitivity to environmental variation. Conversely, some species identified as low abundant and sparsely distributed but functionally common and therefore redundant in the ecosystem could become functionally rare if other species collapse. Second, highly specific life-history traits, such as amphidromy, could have been used to define distinct species (e.g. European Eel; European Whitefish; Salmon, *Salmo salar*), with amphidromic recruitment leading to movement of biomass from marine to freshwater systems, which may have important ramifications for riverine and estuarine trophic ecology and production (Jenkins et al., 2010). The inclusion of amphidromia would also be of particular interest as amphidromous species are at risk of extinction, mainly due to stream alteration (e.g. in-stream barriers, Cooney & Kwak, 2013; flow modifications, Kwak et al., 2013). Although there are many examples of very low abundance species having a disproportionate impact on their ecosystems (e.g. Canadian Beaver, *Castor canadensis*; bass, *Micropterus* spp.; gophers, *Geomys bursarius*, *Thomomys bottae* and Snow Geese, *Chen caerulescens*, as documented by Power et al., 1996), it should be noted that functionally distinct species are not always scarce. Neither are they always threatened, as evidenced for Brill (*Scophthalmus rhombus*): classified as a functionally distinct species (D10), Brill is present in over 38% of our study area, is one of the 100 most abundant species and belongs to the 'least concern' category. It is important to distinguish functional distinctiveness from functional rarity, which encompasses both the concept of functional distinctiveness and the notion of low abundance and spatial distribution. Lastly, we cannot reject a null effect of the selectivity of the trawling gears on scarcity results. The gears used during scientific surveys, primarily designed to sample commercial fish species, have varied over time with the improvement of fishing techniques; and they vary spatially at the scale of the different surveys, which may bias the assessment of spatial diversity patterns (O'Neill & Mutch, 2017).

Further research is needed to better understand the responses of functionally distinct species to past and current environmental changes and anthropogenic stressors. This will allow us to anticipate ecosystem responses and to develop management plans and strategies tailored to the responses of distinct species that will almost certainly determine future ecosystem structure and function. Such work should include understanding their responses to pressures in both recent (Osgood et al., 2021) and past periods (e.g. paleontological studies; Paillard et al., 2021; Stein et al., 2018). Identifying sustainable fishing strategies that reduce the impacts on functionally distinct species, for example, by limiting disturbance on critical life stages/areas, is also an essential prerequisite.

Our study highlights the importance of considering the conservation significance of functionally distinct species with unique combinations of ecological traits known to preserve ecosystem structure and function, a too often-overlooked facet of biodiversity. The life-history strategy of the most functionally rare species makes them particularly vulnerable to both natural variability and the drivers of global change, increasing the need for adaptive conservation efforts. In the context of the biodiversity crisis, there is an urgent need to complement the indicators used to guide species management and conservation policies, such as the IUCN Red List. Including the functional component of biodiversity would help better identify species that deserve special conservation attention due to their functional role, with respect to ecosystem functioning and balance.

ACKNOWLEDGEMENTS

This research is supported by the Fondation pour la Recherche sur la Biodiversité (FRB) and Electricité de France (EDF) in the context of the CESAB project 'Causes and consequences of functional rarity from local to global scales' (FREE), by FRB and FFP (France Filière Pêche) in the context of the CESAB project 'Climate change effects on exploited marine communities' (MAESTRO) and by FRB, the Canadian Institute of Ecology and Evolution (CIEE), and the French Embassy in Canada in the context of the CESAB project 'Fish biodiversity under global change: a worldwide assessment from scientific trawl surveys' (FISHGLOB). AT was supported by the Estonian Ministry of Education and Research (PSG505). NC was supported by the Muséum National d'Histoire Naturelle (MNHN). We especially acknowledge Matthew McLean for proofreading.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The trait dataset that supports the fundings of this study is openly available at Figshare public data repository 10.6084/m9.figshare.19833304.v1. The abundance data that support the findings of this study are available on the ICES Database of Bottom Trawl Surveys (DATRAS) at https://datras.ices.dk. IUCN statutes that support the findings of this study are available on The IUCN Red List of Threatened Species (Version 2022–2) at https://iucnredlist.org. The R code used to calculate the integrated distinctiveness index that supports the fundings of this study is openly available at Figshare public data repository 10.6084/m9.figshare.22317643.v1.

ORCID

Noémie Coulon https://orcid.org/0000-0002-3408-4084
Martin Lindegren https://orcid.org/0000-0002-9185-951X
Eric Goberville https://orcid.org/0000-0002-1843-7855
Aurèle Toussaint https://orcid.org/0000-0002-5738-4637
Aurore Receveur https://orcid.org/0000-0003-0675-4172
Arnaud Auber https://orcid.org/0000-0002-8415-1652

REFERENCES

Alaniz, A. J., Perez-Quezada, J. F., Galleguillos, M., Vásquez, A. E., & Keith, D. A. (2019). Operationalizing the IUCN Red List of Ecosystems in public policy. *Conservation Letters*, *12*, e12665. https://doi.org/10.1111/conl.12665

Angel, M. V., & Pugh, P. R. (2000). Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic. In M. B. Jones, J. M. N. Azevedo, A. I. Neto, A. C. Costa, & A. M. F. Martins (Eds.), *Island, ocean and deep-sea biology. Developments in hydrobiology* (Vol. *152*). Springer. https://doi.org/10.1007/978-94-017-1982-7_16

Astudillo-Scalia, Y., & de Albuquerque, F. S. (2019). Evaluating the performance of rarity as a surrogate in site prioritization for biodiversity conservation. *Global Ecology and Conservation*, *18*, 2351–9894. https://doi.org/10.1016/j.gecco.2019.e00639

Atwood, T. B., Madin, E. M. P., Harborne, A. R., Hammill, E., Luiz, O. J., Ollivier, Q. R., Roelfsema, C. M., Macreadie, P. I., & Lovelock, C. E. (2018). Predators shape sedimentary organic carbon storage in a coral reef ecosystem. *Frontiers in Ecology and Evolution*, *6*, 110. https://doi.org/10.3389/fevo.2018.00110

Barley, S. C., Meekan, M. G., & Meeuwig, J. J. (2017a). Species diversity, abundance, biomass, size and trophic structure of fish on coral reefs in relation to shark abundance. *Marine Ecology Progress Series*, *565*, 163–179. https://doi.org/10.3354/meps11981

Barley, S. C., Meekan, M. G., & Meeuwig, J. J. (2017b). Diet and condition of mesopredators on coral reefs in relation to shark abundance. *PLoS One*, *12*, e0165113. https://doi.org/10.1371/journal.pone.0165113

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bell, G. (2017). Evolutionary rescue. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 605–627.

Bell, G., & Gonzalez, A. (2011). Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science*, *1327*, 1327–1331. https://doi.org/10.1126/science.1203105

Beukhof, E., Dencker, T., Pecuchet, L., & Lindegren, M. (2019). Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. *Marine Ecology Progress Series*, *610*, 205–222. https://doi.org/10.3354/meps12826

Beukhof, E., Dencker, T. S., Palomares, M. L. D., & Maureaud, A. (2019). A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas. *Pangaea*. https://doi.org/10.1594/PANGAEA.900866

Bianchi, D., Stock, C., Galbraith, E. D., & Sarmiento, J. L. (2013). Diel vertical migration: Ecological controls and impacts on the biological pump in a one-dimensional ocean model. *Global Biogeochemical Cycles*, *27*, 478–491. https://doi.org/10.1002/gbc.20031

Birch, H. S., Coxall, H. K., Pearson, P. N., Kroon, D., & Schmidt, D. N. (2016). Partial collapse of the marine carbon pump after the Cretaceous-Paleogene boundary. *Geology*, *44*(4), 287–290. https://doi.org/10.1130/G37581.1

Bracken, M. E., & Low, N. H. (2012, May). Realistic losses of rare species disproportionately impact higher trophic levels. *Ecology Letters*, *15*(5), 461–467. https://doi.org/10.1111/j.1461-0248.2012.01758.x

Brander, K. (1981). Disappearance of common skate Raia batis from Irish Sea. *Nature*, *290*, 48–49. https://doi.org/10.1038/290048a0

Breiman, L. (2011). Random forests. *Machine Learning*, *45*, 5–32.

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D., & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, *309*, 1239–1241.

Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2019). Trait probability density (TPD): Measuring functional diversity across scales based on TPD with R. *Ecology*, *100*(12), e02876. https://doi.org/10.1002/ecy.2876

Carmona, C. P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González-M, R., González-Suárez, M., Salguero-Gómez, R., Vásquez-Valderrama, M., & Toussaint, A. (2021). Erosion of global functional diversity across the tree of life. *Science Advances*, *7*(13), eabf2675. https://doi.org/10.1126/sciadv.abf2675

Casey, M. M., Saupe, E. E., & Lieberman, B. S. (2021). The effects of geographic range size and abundance on extinction during a time of "sluggish" evolution. *Paleobiology*, *47*, 54–67. https://doi.org/10.1017/pab.2020.52

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*, e1400253. https://doi.org/10.1126/sciadv.1400253

Chacón, J. E., & Duong, T. (2018). *Multivariate kernel smoothing and its applications* (1st ed.). Chapman and Hall/CRC. https://doi.org/10.1201/9780429485572

Chamberlain, S., & Salmon, M. (2018). Rredlist R package: 'IUCN' red list. version 0.7.0. https://CRAN.Rproject.org/package=rredlist

Chancollon, O., Pusineri, C., & Ridoux, V. (2006). Food and feeding ecology of Northeast Atlantic swordfish (*Xiphias gladius*) off the Bay of Biscay. *ICES Journal of Marine Science*, *63*, 1075–1085. https://doi.org/10.1016/j.icesjms.2006.03.013

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, *43*, 783–791. https://doi.org/10.2307/2531532

Chen, C., Liaw, A., & Breiman, L. (2004). *Using random forest to learn unbalanced data*. Technical Report 666. Statistics Department, University of California at Berkeley.

Cheun, W. W. L., Pitcher, T. J., & Pauly, D. (2005). A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biological Conservation*, *124*, 97–111. https://doi.org/10.1016/j.biocon.2005.01.017

Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*, 220–229. https://doi.org/10.1016/j.biocon.2019.07.001

Cisneros-Montemayor, A. M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., & Sumaila, U. R. (2013). Global economic value of shark ecotourism: Implications for conservation. *Oryx*, *47*, 381–388. https://doi.org/10.1017/S0030605312001718

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, *9*, 222–228. https://doi.org/10.1890/080216

Colares, L. F., Lobato, C. M. C., Montag, L. F. D. A., & Dunck Oliveira, B. (2022). Extinction of rare fish predicts an abrupt loss of ecological function in the future of Amazonian streams. *Freshwater Biology*, *67*, 263–274. https://doi.org/10.1111/fwb.13839

Cooney, P. B., & Kwak, T. J. (2013). Spatial extent and dynamics of dam impacts on tropical Island freshwater fish assemblages. *Bioscience*, *63*, 176–190.

Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signoret, L., Bull, L., & Meinard, Y. (2006, November). Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biology*, *4*(12), e415. https://doi.org/10.1371/journal.pbio.0040415

Davies, A. J., Roberts, J. M., & Hall-Spencer, J. (2007). Preserving deep-sea natural heritage: Emerging issues in offshore conservation and management. *Biological Conservation*, *138*(3–4), 299–312. https://doi.org/10.1016/j.biocon.2007.05.011

Davies, K. F., Margules, C. R., & Lawrence, J. F. (2004). A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology*, *85*, 265–271. https://doi.org/10.1890/03-0110

de Bello, F., Botta-Dukát, Z., Lepš, J., & Fibich, P. (2021). Towards a more balanced combination of multiple traits when computing functional differences between species. *Methods in Ecology and Evolution*, *12*, 443–448. https://doi.org/10.1111/2041-210X.13537

De Stasio, B. T., Jr., Nibbelink, N., & Olsen, P. (1993). Diel vertical migration and global climate change: A dynamic modeling approach to zooplankton behavior. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *25*(1), 401–405. https://doi.org/10.1080/03680770.1992.11900148

Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When do ecosystem services depend on rare species? *Trends in Ecology & Evolution*, *34*, 746–758. https://doi.org/10.1016/j.tree.2019.03.010

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., … Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, *31*(22), 5118–5119. https://doi.org/10.1016/j.cub.2021.08.062

Dulvy, N. K., & Reynolds, J. D. (1997). Evolutionary transitions among egg-laying, live- bearing and maternal inputs in sharks and rays. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, *264*, 1309–1315. https://doi.org/10.1098/rspb.1997.0181

Freeman, E. A., Moisen, G. G., & Frescino, T. S. (2012). Evaluating effectiveness of down-sampling for stratified designs and unbalanced prevalence in Random Forest models of tree species distributions in Nevada. *Ecological Modelling*, *233*, 1–10. https://doi.org/10.1016/j.ecolmodel.2012.03.007

Froese, R., & Pauly, D. (Eds.). (2020). FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2020)

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-Dewenter, I., Emmerson, M., Potts, S. G., Tscharntke, T., Weisser, W., & Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B*, *282*, 20142620. https://doi.org/10.1098/rspb.2014.2620

Gonzáles-Mantilla, P. G., Gallagher, A. J., León, C. J., & Vianna, G. M. S. (2022). Economic impact and conservation potential of shark-diving tourism in the Azores Islands. *Marine Policy*, *135*, 104869. https://doi.org/10.1016/j.marpol.2021.104869

Goodwin, N. B., Dulvy, N. K., & Reynolds, J. D. (2002). Life-history correlates of the evolution of live bearing in fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*, 259–267. https://doi.org/10.1098/rstb.2001.0958

Grenié, M., Denelle, P., Tucker, C. M., Munoz, F., & Violle, C. (2017). Funrar: An R package to characterize functional rarity. *Diversity and Distributions*, *23*, 1365–1371. https://doi.org/10.1111/ddi.12629

Grenié, M., Mouillot, D., Villéger, S., Denelle, P., Tucker, C. M., Munoz, F., & Violle, C. (2018, October). Functional rarity of coral reef fishes at the global scale: Hotspots and challenges for conservation. *Biological Conservation*, *226*, 288–299. https://doi.org/10.1016/j.biocon.2018.08.011

Grime, J. P. (1998). Benefits of plant diversity to ecosytems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Guerry, A. D., Plummer, M. L., Ruckelshaus, M. H., & Harvey, C. (2010). Ecosystem service assessments for marine conservation. In P. Kareiva, H. Tallis, T. Ricketts, G. Daily, & S. Polasky (Eds.), *Natural capital: Theory and practice of mapping ecosystem services* (pp. 296–322). Oxford University Press.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, *319*, 948–952. https://doi.org/10.1126/science.1149345

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., Gallagher, A. J., Irschick, D. J., Skubel, R., & Cooke, S. J. (2019). Ecosystem function and services of aquatic predators in the Anthropocene. *Trends in Ecology & Evolution*, *34*, 369–383. https://doi.org/10.1016/j.tree.2019.01.005

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., Scott, J. D., Alade, L., Bell, R. J., Curti, K. L., Curtis, T. H., Kircheis, D., Kocik, J. F., Lucey, S. M., McCandless, C. T., Milke, L. M., Richardson, D. E., Robillard, E., … Griswold, C. A. (2016). A Vulnerability Assessment of Fish and Invertebrates to Climate Change on the Northeast U.S. Continental Shelf. *PLOS ONE*, *11*(2), e0146756. https://doi.org/10.1371/journal.pone.0146756

Harnik, P. G., Simpson, C., & Payne, J. L. (2012). Long-term differences in extinction risk among the seven forms of rarity. *Proceedings of the Royal Society B*, *279*, 4969–4976. https://doi.org/10.1098/rspb.2012.1902

HAWG. (2022). Herring Assessment Working Group for the Area South of 62°N (HAWG) report. https://ices-library.figshare.com/articles/report/Herring_Assessment_Working_Group_for_the_Area_South_of_62_N_HAWG_/19249010?file=38181423

Heessen H.J.L., Dalskov J. & Cook R.M. (1997). The international bottom trawl survey in the North Sea, the Skagerrak and Kattegat. ICES CM 1997/Y:31. International Council for the Exploration of the Sea, Copenhagen.

IPBES. (2019). Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. In E. S. Brondízio, J. Settele, S. Díaz, & H. T. Ngo (Eds.), *IPBES secretariat* (p. 1144). Bonn, Germany.

Simpfendorfer, C. A., Heupel, M. R., White, W. T., & Dulvy, N. K. (2011). The importance of research and public opinion to conservation management of sharks and rays: A synthesis. *Marine and Freshwater*, *62*, 518–527. https://doi.org/10.1071/MF11086

Hiddink, J., & Ter Hofstede, R. (2008). Climate induced increases in species richness of marine fishes. *Global Change Biology*, *14*, 453–460. https://doi.org/10.1111/j.1365-2486.2007.01518.x

Higgs, N. D., Gates, A. R., & Jones, D. O. B. (2014). Fish food in the Deep Sea: Revisiting the role of large food-falls. *PLoS One*, *9*, e96016. https://doi.org/10.1371/journal.pone.0096016

ICES. (2007). *Regional abundance surveys with input to the ICES fisheries advice for the CFP* (p. 21). ICES Publications.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ICES. (2021). *Working group on elasmobranch fishes (WGEF)*. ICES Scientific Reports. https://doi.org/10.17895/ices.pub.8199

ICES. (2022). *ICES survey protocols*. ICES Publications. Collection. https://doi.org/10.17895/ices.pub.c.6315609.v1

IUCN. (2022). The IUCN red list of threatened species. Version 2022-2. https://www.iucnredlist.org

Jenkins, A. P., Jupiter, S. D., Qauqau, I., & Atherton, J. (2010). The importance of ecosystem-based management for conserving aquatic migratory pathways on tropical high islands: A case study from Fiji. *Aquatic Conservation*, *20*, 224–238. https://doi.org/10.1002/aqc.1086

Johnson, C. (1998). Species extinction and the relationship between distribution and abundance. *Nature*, *394*, 272–274. https://doi.org/10.1038/28385

Jones, M. C., & Cheung, W. W. L. (2018). Using fuzzy logic to determine the vulnerability of marine species to climate change. *Global Change Biology*, *24*, e719–e731. https://doi.org/10.1111/gcb.13869

Kawamura, K. (2008). Handbook of European freshwater fishes" by M. Kottelat & J. Freyhof (2007). *Ichthyological Research*, *55*, 99. https://doi.org/10.1007/s10228-007-0012-3

Kwak, T. J., Smith, W. E., Buttermore, E. N., Cooney, P. B., & Cope, W. G. (2013). Fishery population and habitat assessment in Puerto Rico streams: Phase 2 final report. Federal aid in sport fish restoration project F-50 final report. Submitted to marine resources division, Puerto Rico Department of Natural and Environmental Resources, San, Juan, Puerto Rico. (Available from: T. J. Kwak, Box 7617, North Carolina State University, 100 Eugene Brooks Avenue, Raleigh, North Carolina 27695 USA.).

Lawson, J. M., Pollom, R. A., Gordon, C. A., Barker, J., Meyers, E. K. M., Zidowitz, H., Ellis, J. R., Bartolí, Á., Morey, G., Fowler, S. L., Alvarado, D. J., Fordham, S. V., Sharp, R., Hood, A. R., & Dulvy, N. K. (2020). Extinction risk and conservation of critically endangered angel sharks in the Eastern Atlantic and Mediterranean Sea. *ICES Journal of Marine Science*, *77*(1), 12–29. https://doi.org/10.1093/icesjms/fsz222

Legras, G., Loiseau, N., Gaertner, J.-C., Poggiale, J.-C., & Gaertner-Mazouni, N. (2020). Assessing functional diversity: The influence of the number of the functional traits. *Theoretical Ecology*, *13*, 117–126. https://doi.org/10.1007/s12080-019-00433-x

Leitão, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortunel, C., Mendonça, F. P., & Mouillot, D. (2016). Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society B*, *283*, 20160084. https://doi.org/10.1098/rspb.2016.0084

Lepš, J., de Bello, F., Lavorel, S., & Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: Practical considerations matter. *Preslia*, *78*, 481–501 ⟨halsde-00293183⟩.

Loiseau, N., Mouquet, N., Casajus, N., Grenié, M., Guéguen, M., Maitner, B., Mouillot, D., Ostling, A., Renaud, J., Tucker, C., Velez, L., Thuiller, W., & Violle, C. (2020). Global distribution and conservation status of ecologically rare mammal and bird species. *Nature Communications*, *11*, 5071.

Luiz, O. J., Woods, R. M., Madin, E. M., & Madin, J. S. (2016). Predicting IUCN extinction risk categories for the World's data deficient groupers (Teleostei: Epinephelidae). *Conservation*, *9*, 342–350. https://doi.org/10.1111/conl.12230

Lyons, K. G., Brigham, C. A., Traut, B. H., & Schwartz, M. W. (2005). Rare species and ecosystem functioning. *Conservation*, *19*, 1019–1024. https://doi.org/10.1111/j.1523-1739.2005.00106.x

Maureaud, A., Hodapp, D., van Denderen, P. D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T., Beukhof, E., & Lindegren, M. (2019). Biodiversity–ecosystem functioning relationships in fish communities: Biomass is related to evenness and the environment, not to species richness. *Proceedings of the Royal Society B*, *286*, 20191189. https://doi.org/10.1098/rspb.2019.1189

Mcgill, B., Enquist, B., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and & Evolution*, *21*, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McLean, M., Mouillot, D., Lindegren, M., Engelhard, G., Villéger, S., Marchal, P., Brind'Amour, A., & Auber, A. (2018). A climate-driven functional inversion of connected marine ecosystems. *Current Biology*, *28*(22), 3654–3660. https://doi.org/10.1016/j.cub.2018.09.050

McLean, M., Mouillot, D., Lindegren, M., Villéger, S., Engelhard, G., Murgier, J., & Auber, A. (2019). Fish communities diverge in species but converge in traits over three decades of warming. *Global Change Biology*, *25*, 3972–3984. https://doi.org/10.1111/gcb.14785

McLean, M., Stuart Smith, R. D., Villéger, S., Auber, A., Edgar, G., MacNeil, M. A., Loiseau, N., Leprieur, F., & Mouillot, D. (2021). Trait similarity in reef fish faunas across the world's oceans. *Proceedings of the National Academy of Sciences*, *118*(12), e2012318118. https://doi.org/10.1073/pnas.2012318118

Monnahan, C. C., Thorson, J. T., Kotwicki, S., Lauffenburger, N., Ianelli, J. N., & Punt, A. E. (2021). Incorporating vertical distribution in index standardization accounts for spatiotemporal availability to acoustic and bottom trawl gear for semi-pelagic species. *ICES Journal of Marine Science*, *78*(5), 1826–1839. https://doi.org/10.1093/icesjms/fsab085

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J., & Thuiller, W. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, *11*, e1001569. https://doi.org/10.1371/journal.pbio.1001569

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Murgier, J., McLean, M., Maire, A., Mouillot, D., Loiseau, N., Munoz, F., Violle, C., & Auber, A. (2021). Rebound in functional distinctiveness following warming and reduced fishing in the North Sea. *Proceedings of the Royal Society B*, *288*, 20201600. https://doi.org/10.1098/rspb.2020.1600

O'Hea, B., Davie, S., Johnston, G., & O'Dowd, L. (2020). Assemblages of Deepwater shark species along the north east Atlantic continental slope. *Deep Sea Research*, *157*, 103207. https://doi.org/10.1016/j.dsr.2019.103207

Oksanen, J., Roeland, K., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2008). Vegan R package: 'IUCN' Red List. Version 2.5-7. http://cran.r-project.org/, http://vegan.r-forge.r-project.org/

Oliver, S., Braccini, M., Newman, S. J., & Harvey, E. S. (2015). Global patterns in the bycatch of sharks and rays. *Marine Policy*, *54*, 86–97. https://doi.org/10.1016/j.marpol.2014.12.017

O'Neill, F. G., & Mutch, K. (2017). Selectivity in trawl fishing gears. *Scottish Marine and Freshwater Science*, *8*(1), 85.

Osgood, G. J., White, E. R., & Baum, J. K. (2021). Effects of climate-change-driven gradual and acute temperature changes on shark and ray species. *The Journal of Animal Ecology*, *90*, 2547–2559. https://doi.org/10.1111/1365-2656.13560

O'Shea, O. R., Thums, M., van Keulen, M., & Meekan, M. (2012). Bioturbation by stingrays at Ningaloo Reef, Western Australia. *Marineand Freshwater Research*, *63*, 189. https://doi.org/10.1071/MF11180

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., Fordham, S. V., Barreto, R., Fernando, D., Francis, M. P., Jabado, R. W., Herman, K. B., Liu, K. M., Marshall, A. D., Pollom, R. A., Romanov, E. V., Simpfendorfer, C. A., Yin, J. S., Kindsvater, H. K., & Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, *589*, 567–571. https://doi.org/10.1038/s41586-020-03173-9

Paillard, A., Shimada, K., & Pimiento, C. (2021). The fossil record of extant elasmobranchs. *Journal of Fish Biology*, *98*, 445–455. https://doi.org/10.1111/jfb.14588

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi,

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, eaai9214. https://doi.org/10.1126/science.aai9214

Pécuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., Punzón, A., Sólmundsson, J., & Payne, M. R. (2017). From traits to life-history strategies: Deconstructing fish community composition across European seas. *Global Ecology and Biogeography*, *26*, 812–822. https://doi.org/10.1111/geb.12587

Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, *5*, 402–411. https://doi.org/10.1046/j.1461-0248.2002.00339.x

Pinti, J., DeVries, T., Norin, T., Serra-Pompei, C., Proud, R., Siegel, D. A., Kiørboe, T., Petrik, C. M., Andersen, K. H., Brierley, A. S., & Visser, A. W. (2023). Model estimates of metazoans' contributions to the biological carbon pump. *Biogeosciences*, *20*, 997–1009. https://doi.org/10.5194/bg-20-997-2023

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the quest for keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience*, *46*(8), 609–620. https://doi.org/10.2307/1312990

Richards, C., Cooke, R. S. C., & Bates, A. E. (2021). Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. *Global Ecology and Biogeography*, *30*, 973–986. https://doi.org/10.1111/geb.13279

Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B. E., & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: A quantitative guide. *Methods in Ecology and Evolution*, *7*, 1386–1395. https://doi.org/10.1111/2041-210X.12604

Rindorf, A., Gislason, H., Burns, F., Ellis, J. R., & Reid, D. (2020). Are fish sensitive to trawling recovering in the Northeast Atlantic? *Journal of Applied Ecology*, *57*, 1936–1947. https://doi.org/10.1111/1365-2664.13693

Ruppert, J. L. W., Travers, M. J., Smith, L. L., Fortin, M.-J., & Meekan, M. G. (2013). Caught in the middle: Combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PLoS One*, *8*, e74648. https://doi.org/10.1371/journal.pone.0074648

Segre, H., Ron, R., De Malach, N., Henkin, Z., Mandel, M., Kadmon, R., & Vellend, M. (2014). Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecology Letters*, *17*(11), 1400–1408. https://doi.org/10.1111/ele.12343

Smith, A. D. M., & Garcia, S. M. (2014). Fishery management: Contrasts in the Mediterranean and the Atlantic. *Current Biology*, *24*(17), 810–812. https://doi.org/10.1016/j.cub.2014.07.031

Stein, R. W., Mull, C. G., Kuhn, T. S., Aschliman, N. C., Davidson, L. N. K., Joy, J. B., Smith, G. J., Dulvy, N. K., & Mooers, A. O. (2018). Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nature Ecology and Evolution*, *2*, 288–298. https://doi.org/10.1038/s41559-017-0448-4

Stekhoven, D. J., & Buehlmann, P. (2012). MissForest—Nonparametric missing value imputation for mixed-type data. *Bioinformatics*, *28*(1), 112–118. https://doi.org/10.1093/bioinformatics/btr597

Stevens, J. D. (2010). Epipelagic oceanic elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *The biology of sharks and their relatives* (Vol. *2*, pp. 3–35). CRC Press.

Su, G., Villéger, S., & Brosse, S. (2019). Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread. *Global Ecology and Biogeography*, *28*, 211–221. https://doi.org/10.1111/geb.12843

Thorson, J. T., Munch, S. B., Cope, J. M., & Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, *27*, 2262–2276. https://doi.org/10.1002/eap.1606

Tilman, D. (2001). Functional diversity. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (pp. 109–120). Academic Press. https://doi.org/10.1016/B0-12-226865-2/00132-2

Trindade-Santos, I., Moyes, F., & Magurran, A. E. (2022). Global patterns in functional rarity of marine fish. *Nature Communications*, *13*, 877. https://doi.org/10.1038/s41467-022-28488-1

van Eldijk, T. J. B., Bisschop, K., & Etienne, R. S. (2020). Uniting community ecology and evolutionary rescue theory: Community-wide rescue leads to a rapid loss of rare species. *Frontiers in Ecology and Evolution*, *8*, 552268. https://doi.org/10.3389/fevo.2020.552268

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., Livingstone, S. W., & Mouillot, D. (2017). Functional rarity: The ecology of outliers. *Trends in Ecology & Evolution*, *32*, 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Walker, N. D., Maxwell, D. L., Le Quesne, W. J. F., & Jennings, S. (2017). Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*, *74*(5), 1448–1457. https://doi.org/10.1093/icesjms/fsw250

Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J., & Shanas, U. (2015). What is an apex predator? *Oikos*, *124*, 1453–1461. https://doi.org/10.1111/oik.01977

Walls, R. H. L., & Dulvy, N. K. (2020). Eliminating the dark matter of data deficiency by predicting the conservation status of Northeast Atlantic and Mediterranean Sea sharks and rays. *Biological Conservation*, *246*, 108459. https://doi.org/10.1016/j.biocon.2020.108459

Williams, J. J., Papastamatiou, Y. P., Caselle, J. E., Bradley, D., & Jacoby, D. M. P. (2018). Mobile marine predators: An understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B*, *285*, 20172456. https://doi.org/10.1098/rspb.2017.2456

SUPPORTING INFORMATION

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

How to cite this article: Coulon, N., Lindegren, M., Goberville, E., Toussaint, A., Receveur, A., & Auber, A. (2023). Threatened fish species in the Northeast Atlantic are functionally rare. *Global Ecology and Biogeography*, *00*, 1–19. https://doi.org/10.1111/geb.13731

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

APPENDIX 1

DATA SOURCES

A.1 | THREATENED FISH SPECIES IN THE NORTHEAST ATLANTIC ARE FUNCTIONALLY RARE

Trait dataset

The sources used to build the dataset of traits for marine fish taxa observed during international scientific bottom-trawl surveys in the Northeast Atlantic are listed here. This dataset, which completes the one presented by Beukhof et al. (2019), is freely available at the Figshare public data repository (https://doi.org/10.6084/m9.figshare.19833304.v1).

Aasen, O. (1963). Length and growth of the Porbeagle (Lamna nasus, Bonnaterre) in the North West Atlantic, *Environmental Science*, *21*(13), 20–37.

Abou Shabana, N. M., Abd El Rahman, S. H., Al Absawy, M. A., & Assem, S. S. (2012). Reproductive biology of *Argyrosomus regius* (Asso, 1801) inhabiting the south eastern Mediterranean Sea, Egypt. *Egyptian Journal of Aquatic Research*, *38*, 147–156.

Allain, V. (1999). Fecundity of the deep-sea fish in the north-east Atlantic *Alepocephalus bairdii* (Pisces: Alepocephalidae). *Journal of the Marine Biological Association of the UK*, *79*, 765–767.

Baker, K. D., Devine, J. A., & Haedrich, R. L. (2009). Deep-sea fishes in Canada's Atlantic: Population declines and predicted recovery times. *Environmental Biology of Fishes*, *85*, 79–88.

Banon, R., Alonso-Fernandez, A., Barros-Garcia, D., Rios, M-B., & de Carlos, A. (2018). Geographic expansion of *Ephippion guttifer* (Tetrodontidae) in the north-eastern Atlantic. *Journal of Fish Biology*, *93*, 733–737.

Banon, R., Caballero-Huertas, M., Alonso-Fernandez, A., Barros-Garcia, D., Otero, J., & de Carlos, A. (2020). Signals of changes in the ichyofauna composition of Galician waters (NW Iberian Peninsula). *Regional Studies in Marine Science*, *39*, 101435.

Bottari, T., Dimech, M., Nardone, G., Rinelli, P., & Ragonese, S. (2010). Distribution and biological features of the African Armoured Searobin, *Peristedion cataphractum* (Actinopterygii: Scorpaeniformes: Peristediidae), off the southerne coasts of Sicily (Mediterranean Sea). *Acta ichthyologica et piscatoria*, *40*, 113–127.

Bulman, C., & Koslow, J. (1995). Development and depth distribution of the eggs of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae). *Marine and Freshwater Research*, *46*, 697.

Cabral, H. N. (2000). Distribution and abundance patterns of flatfishes in the Sado Estuary, Portugal. *Estuaries*, *23*, 351–358.

Calis, E., Jackson, E. H., Nolan, C. P., & Jeal, F. (2005). Preliminary age and growth estimates of the rabbitfish, *Chimaera monstrosa*, with implications for future resource management. *Journal of Northwest Atlantic Fishery Science*, *35*, 15–26.

Camhi, M. D., Pikitch, E. K., & Babcock, E. A. (Eds.). (2008). Sharks of the open ocean: Biology, fisheries and conservation. Blackwell Science.

Carpenter, K. E., & De Angelis, N. (Eds.). (2002). The living marine resources of the Western Central Atlantic. Volume 3: Bony fishes part 2 (Opistognathidae to Molidae), sea turtles and marine mammals (Vol. 3). FAO FishFinder.

Carrasson, M., & Matallanas, J. (2002). Feeding strategies of *Polyacanthonotus rissoanus* (Pisces: Notacanthidae) in the deep western Mediterranenan. *Journal of the Marine Biological Association of the United Kingdom*, *82*, 665–671.

Casadevall, M., Bonet, S., & Matallanas, J. (1993). Description of different stages of oogenesis in *Ophidion barbatum* (Pisces, Ophidiidae). *Environmental Biology of Fishes*, *36*(2), 127–133. https://doi.org/10.1007/BF00002791

Castle, P. H. J. (1978). Ovigerous Leptocephali of the Nettastomatid Eel Genus Facciolella. *Copeia 1978*, 29.

Cengiz, Ö., Ismen, A., & Ozekinci, U. (2014). Reproductive biology of the spotted flounder, *Citharus linguatula* (Actinopterygii: Pleuronectiformes: Citharidae), from Saros Bay (northern Aegean Sea, Turkey). *Acta Ichthyologica et Piscatoria*, *44*, 123–129.

Childress, J. J., Taylor, S. M., Cailliet, G. M., & Price, M. H. (1980). Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. *Marine Biology*, *61*, 27–40.

Christiansen, J. S., Fevolden, S. E., Karamushko, O. V., & Karamushko, L. I. (1998). Maternal output in polar fish reproduction. In G. Di Prisco, E. Pisano, & A. Clarke (Eds.), Fishes of Antarctica: A biological overview (pp. 41–52). Springer Milan.

Clarke, M. W., Connolly, P. L., & Bracken, J. J. (2001). Aspects of reproduction of the deep water sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. *Journal of the Marine Biological Association of the United Kingdom*, *81*, 1019–1029.

Coggan, R. A., Gordon, J. D. M., & Merrett, N. R. (1999). Aspects of the biology of *Nezumia aequalis* from the continental slope west of the British Isles. *Journal of Fish Biology*, *54*, 152–170.

Çoker, T., Akyol, O., Özaydın, O., Leblebici, S., & Tosunoğlu, Z. (2008). Determination of batch fecundity in *Uranoscopus scaber* Linnaeus, 1758 from the Aegean Sea, Turkey. *Journal of Applied Ichthyology*, *24*, 85–87.

Collins, S. P. (1981). Littoral and Benthic investigations on the West Coast of Ireland: XIII. The Biology of *Gobiusculus flavescens* (Fabricius) on the Connemara Coast. *Proceeding of the Royal Irish Academy*, *81B*.

Compagno, L. J. V. (1984). Sharks of the world: An annotated and illustrated catalogue of shark species known to date. United Nations Development Programme.

Correia, A. T., Manso, S., & Coimbra, J. (2009). Age, growth and reproductive biology of the European conger eel (*Conger conger*) from the Atlantic Iberian waters. *Fisheries Research*, *99*, 196–202.

Cotton, C. F., Dean Grubbs, R., Dyb, J. E., Fossen, I., & Musick, J. A. (2015). Reproduction and embryonic development in two species of squaliform sharks, *Centrophorus granulosus* and *Etmopterus princeps*: Evidence of matrotrophy? *Deep-Sea Research II*, *115*, 41–54.

Cowx, I. G. (1983). The biology of bream, *Abramis brama* (L), and its natural hybrid with roach, *Rutilus rutilus* (L), in the River Exe. *Journal of Fish Biology*, *22*, 631–646.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Cox, G. J., & Francis, M. P. (1997). Sharks and rays of New Zealand. Canterbury University Press.

Crabtree, R. E., Sulak, K. J., & Musick, J. A. (1985). Biology and distribution of species of Polyacanthonotus (Pisces: Notacanthiformes) in the western North Atlantic. *Bulletin of Marine Science*, *36*, 235–248.

da Silva, H. N. (1988). and reproduction of Kitefin shark *Dalatias lici* (Bonn, 1788) in Azorean waters. International Council for the Exploration of the Sea ICES C.M.

Deniel, C. (1990). Comparative study of the growth of flatfishes on the west coast of Brittany. *Journal of Fish Biology*, *37*, 149–166.

D'Onghia, G., Sion, L., Maiorano, P., Mytilineou, Ch., Dallessandro, S., Carlucci, R., & Desantis, S. (2006). Population biology and life strategies of *Chlorophthalmus agassizii* Bonaparte, 1840 (Pisces: Osteichthyes) in the Mediterranean Sea. *Marine Biology*, *149*, 435–446.

Ebert, D. A. (2002). Some observations on the reproductive biology of The sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) from southern African waters. *South African Journal of Marine Science*, *24*, 359–363.

Ebert, D. A. (2005). Reproductive biology of skates, Bathyraja (Ishiyama), along the eastern Bering Sea continental slope. *Journal of Fish Biology*, *66*, 618–649.

Ebert, D. A., Compagno, L. J. V., & Cowley, P. D. (2006). Reproductive biology of catsharks (Chondrichtyes: Scyliorhinidae) off the west coast of southern Africa. *ICES Journal of Marine Science*, *63*, 1053–1065.

Ebert, D. A., & Stehmann, M. (2013). Sharks, batoids and chimaeras of the North Atlantic. Food and Agriculture Organization of the United Nations.

Fanelli, E., Papiol, V., Cartes, J. E., & Rodriguez-Romeu, O. (2014). Trophic ecology of *Lampanyctus crocodilus* on north-west Mediterranean Sea slopes in relation to reproductive cycle and environmental variables. *Journal of Fish Biology*, *84*, 1654–1688.

Faria, C., Borges, R., Gil, F., Almada, V. C., & Gonçalves, E. J. (2002). Embryonic and larval development of *Lipophrys pholis* (Pisces: Blenniidae). Scientia Marina, *66*, 21–26.

Fernandez-Arcaya, U., Recasens, L., Murua, H., Ramirez-Llodra, E., & Rotllant, G. (2012). Population structure and reproductive patterns of the NW Mediterranean deep-sea macrourid *Trachyrincus scabrus* (Rafinesque, 1810). *Marine Biology*, *159*, 1885–1896.

Fernandez-Arcaya, U., Ramirez-Llodra, E., Rotllant, G., Recasens, L., Murua, H., Quaggio-Grassiotto, I., & Company, J. B. (2013). Reproductive biology of two macrourid fish, *Nezumia aequalis* and *Coelorinchus mediterraneus*, inhabiting the NW Mediterranean continental margin (400–2000 m). *Deep-Sea Reasearch II*, *92*, 63–72.

Fernandez-Arcaya, U., Drazen, J. C. Murua, H., Ramirez-Llodra, E., Bahamon, N., Recasens, L., Rotllant, G., & Company, J. B. (2016). Bathymetric gradients of fecundity and egg size in fishes: A Mediterranean case study. *Deep Sea Research Part I: Oceanographic Research Papers*, *116*, 106–117.

Filer, K. R., & Sedberry, G. R. (2008). Age, growth and reproduction of the barrelfish *Hyperoglyphe perciformis* (Mitchill) in the western North Atlantic. Journal of Fish Biology, 72, 861–882.

Finucci, B., Dunn, M. R., Jones, E. G., Anderson, J. (2017). Reproductive biology of the two deep-sea chimaerids, longnose spookfish (*Harriotta raleighana*) and Pacific spookfish (*Rhinochimaera pacifica*). Deep-Sea Reasearch I, 120, 76–87.

Follesa, C., & Carbonara, P. (2019). Atlas on the maturity stages of Mediterranean fishery resources. Food and Agriculture organization of the United Nation.

Froese, R., Binohlan, C. (2003). Simple methods to obtain preliminary growth estimates for fishes. *Journal Applied Ichthyology*, *19*, 376–379.

Froese, R., & FishBase, P. D. (2018). World Wide Web electronic publication. https://fishbase.mnhn.fr/search.php

Froese, R., & FishBase, P. D. (2020). World Wide Web electronic publication. https://fishbase.mnhn.fr/search.php

García, V. B., Lucifora, L. O., & Myers, R. A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings: Biological Sciences*, *275*, 83–89.

Gennari, E., & Scacco, U. (2007). First age and growth estimates in the deep water shark, *Etmopterus Spinax* (Linnaeus, 1758), by deep coned vertebral analysis. *Marine Biology*, *152*, 1207–1214.

Gibson, R. N., & Ezzi, I. A. (1980). The biology of the scaldfish, *Arnoglossus laterna* (Walbaum) on the west coast of Scotland. *Journal of Fish Biology*, *17*, 565–575.

Glamuzina, B., Jug-Dujakovic, J., & Katavic, I. (1989). Preliminary studies on reproduction and larval rearing of common Dentex, *Dentex dentex* (Linnaeus, 1758). *Aquaculture*, *77*, 75–84.

Gordon, J. D. M, Merret, N. R., Bergstad, O. A., & Swan, S. C. (1987). Deep-sea bottom-living fishes at two repeat stations at 2,200 and 2,900 m in the Rockall Trough, norteastern Atlantic Ocean. *Marine Biology*, *96*, 217–238.

Gordon, J. D. M. (2005). Biological parameters of deepwater fishes. In R. Shotton (Ed.), *Deep Sea 2003: Conference on the Governance and Management of Deep-sea Fisheries. Part 2: Conference poster papers and workshop papers. FAO Fisheries Proceedings*.

Greenstreet, S. P. R., Rossberg, A. G., Fox, C. J., Le Quesne, W. J. F., Blasdale, T., Boulcott, P., Mitchell, I., Millar, C., & Moffat, C. F. (2012). Demersal fish biodiversity: Species-level indicators and trends-based targets for the Marine Strategy Framework Directive. *ICES Journal of Marine Science*, *69*, 1789–1801.

Gurkan, S., Taskavak, E., & Hossucu, B. (2009). The reproductive biology of the Great Pipefish Syngnathus acus (Family: Syngnathidae) in the Aegean Sea. *North-Western Journal of Zoology*, *5*, 179-190. https://www.researchgate.net/publication/26636801_The_reproductive_biology_of_the_Great_Pipefish_Syngnathus_acus_Family_Syngnathidae_in_the_Aegean_Sea

Gutowsky, L. F. G. (2012). Intra-population variability of life-history traits and growth during range expansion of the invasive round goby, *Neogobius melanostomus*. *Fisheries Management and Ecology*, *19*, 78–88.

Heessen, H. J., Daan, N., & Ellis, J. R. (Eds.). (2015). *Fish atlas of the Celtic Sea, North Sea and Baltic Sea: based on international research-vessel surveys*. Academic Publishers, KNNV Publishing.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hutchings, K., Griffiths, M. H., & Field, J. G. (2006). Regional variation in the life history of the canary drum *Umbrina canariensis* (Sciaenidae), in South African waters. *Fisheries Research*, *77*, 312–325.

ICES. (1982). *Preliminary results of Norwegian investigations on the greater silver smelt, Argentina silus (Ascanius).*

ICES. (1994). *Some aspect of biology of non-target fish species in the Barents Sea*.

ICES. (1998). *Age, maturity and other biological parameter of two Morid species Lepidion eques (Gunther, 1887) and Antimora rostrata Gunther, 1878, in Icelandic Waters*.

ICES. (2009). *Report of the Herring Assessment Working Group for the Area South of 62 N*.

ICES. (2015). *Report of the Workshop on Egg staging, Fecundity and Atresia in Horse mackerel and Mackerel (WKFATHOM)*.

ICM-CSIS. (2013). *Scientific report supporting the management plan for Boat Seine*.

Iglesias, S. M., Du Buit, M-H., & Nakaya, K. (2002). Egg capsules of deep-sea catsharks from eastern north Atlantic with first descriptions of the capsules of *Galeus murinus* and *Apristurus aphyodes* (Chondrichthyes: Scyliorhinidae). *Cybium: International Journal of Ichthyology*, *26*, 59–63.

Ilkyaz, A. T., Metin, G., Soykan, O. & Kinacigi̇l, H. T. (2018). Spawning Season, First Maturity Length and Age of 21 Fish Species from the Central Aegean Sea, Turkey. *Turkish Journal of Fisheries and Aquatic Sciences*, *18*, 211–216.

Irvine, S. B., Stevens, J. D., & Laurenson, L. J. (2006). Surface bands on deepwater squalid dorsal-fin spines: an alternative method for ageing *Centroselachus crepidater*. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 617–627.

Isbert, W., Péres-del-Olmo, A., Montero, F. E., & Carrasson, M. (2019). Seasonal and depth related variation of parasite communities of Notacanthus bonaparte Risso, 1840 (Notacanthiformes: Notacanthidae) over the northwest Mediterranean slope. *Deep-Sea Research I*, *153*. 103103.

Ismen, A. (2003). Age, growth, reproduction and food of common stingray (*Dasyatis pastinaca* L., 1758) in İskenderun Bay, the eastern Mediterranean. *Fisheries Research*, *60*, 169–176.

Kabasacal, H. (1998). Confirmation of the presence of Gadella maraldi (RISSO, 1810) in the seas of Turkey. *Biljeske – Notes*, *80*, 1–9.

Kawaguchi, K., Mauchline, J. (1982). Biology of Mictophid Fishes (Family Mitophidae) in the Rockall Trough, Northeartern Atlantic Ocean. *Biological Oceanography*, *4*, 337–373.

Kennedy, M., & Fitzmaurice, P. (1974). Biology of the Rudd *Scardinius erythrophthalmus* (L.) in Irish Waters. *Proceedings of the Royal Irish Academy*, *74*, 245–303.

Ketchen, K. S. (1972). Size at Maturity, Fecundity, and Embryonic Growth of the Spiny Dogfish (*Squalus acanthias*) in British Columbia Waters. *Journal of the Fisheries Research Board of Canada*, *29*, 1717–1723.

Kitagawa, D., Kuroda, K., & Tsuruta, Y. (1985). Description and distribution of eggs and larvae of the brown hakeling *Physiculus maximowiczi* in Japanese waters. *Nippon Suisan Gakkaishi*, *51*, 1627–1630.

Kunzlik, P. A. (1988). The basking shark. Department of Agriculture and Fisheries, Scottich Fisheries Information Pamphlet (14), 21 p.

Linkowski, T. B., Radtke, R. L., & Lenz, P. H. (1993). Otolith microstructure, age and growth of two species of Ceratoscopelus (Osteichthyes: Myctophidae) from the eastern North Atlantic. *Journal of Experimental Marine Biology and Ecology*. *167*, 237–260.

Linlokken, A. N., & Sandlund, O. T. (2016). Recruitment of sympatric vendace (*Coregonus albula*) and whitefish (*C. lavaretus*) is affected by different environmental factors. *Ecology of Freshwater Fish*, *25*, 652–663.

Liu, K.-M., Lin, C.-P., Joung, S.-J., & Wang, S.-B. (2011). Age and growth estimates of the blacktip sawtail catshark *Galeus sauteri* in northeastern waters of Taiwan. *Zoological Studies*, *50*, 284–295.

Lloret, J., Serrat, A., Thordarson, G., Helle, K., Jadaud, A., Bruno, I., Ordines, F., Sartor, P., Carbonara, P., & Rätz, H.-J. (2020). The poor health of deep-water species in the context of fishinf activity and a warming climate: will popoulation of Mola species rebuild or collapse? *Journal Fish of Biology*, *98*, 1–13.

Lyczkowski-Shultz, J. (2003). Preliminary guide to the identification of the early life history stages of tetraodontid fishes of the Western Central North Atlantic. NOAA Technical Memorandum NMFS-SEFSC-494,9 p.

Magnússon, J. V. (2001). Distribution and some other biological parameters of two morid species *Lepidion eques* (Günther, 1887) and *Antimora rostrata* (Günther, 1878) in Icelandic waters. *Fisheries Research*, *51*, 267–281.

Mann, R. H. K., & Mills, C. A. (1985). Variations in the sizes of gonads, eggs and larvae of the dace, *Leuciscus leuciscus*. *Environmental Biology of Fishes*, *13*, 227–287.

Marconato, A., & Bisazza, A. (1988). Mate choice, egg cannibalism and reproductive success in the river bullhead, *Cottus gobio* L. *Journal of Fish Biology*, *33*, 905–916.

Marks, A. D., Kerstetter, D. W., Wyanski, D. M., & Sutton, T. T. (2020). Reproductive Ecology of Dragonfishes (Stomiiformes: Stomiidae) in the Gulf of Mexico. *Frontiers in Marine Science*, (101), 1–17. https://nsuworks.nova.edu/occc_fac_articles/1089

Marliave, J. B. (1987). The life history and captive reproduction of the Wolf-eel *Anarrhichthys ocellatus* at the Vancouver Public Aquarium. *International Zoo Yearbook*, *26*, 70–81.

Martins, R. S., & Schingel, P. R. (2012). Biological aspect of the Sailfin dory Zenopsis conchifer (Lowe, 1852) caught by deep-sea trawling fishery off southern Brazil. *Brazilian Journal of Oceanography*, *60*, 171–179.

Matic-Skoko, S., Antolic, B., & Kraljevic, M. (2004). Ontogenetic and seasonal feeding habits of the annular seabream (*Diplodus annularis* L.) in Zostera sp. beds, eastern Adriatic Sea. *Journal of Applied Ichthyology*, *20*, 376–381.

McEachran, J. D. (1977). Variation in Raja garmani and the status of *Raja lentiginosa* (Pisces: Rajidae). *Bulletin of Marine Science*, *27*, 423–439.

Mehanna, S. (2006). Fisheries regulations based on yield per recruit analysis for the spotted seabass *Dicentrarchus punctatus*

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

(Moronidae) at Barwadil llagoon, Mediterranean coast of sinal, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries*, *10*, 129–145.

Merrett, N. R., Domanski, P. A. (1985). Observations on the ecology of deep-sea bottom-living fishes collected off the Northwest Africa: II. The Moroccan Slope (27°–34°N), with special reference to *Synaphobranchus kaupi*. *Biological Oceanography*, *3*, 349–399.

Mindel, B. L., Neat, F. C., Trueman, C. N., Webb, T. J., & Blanchard, J. L. (2016). Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea. *PeerJ*, *4*, e2387.

Moreno, T., Castro, J. J., & Socorro, J. (2005). Reproductive biology of the sand smelt *Atherina presbyter* Cuvier, 1829 (Pisces: Atherinidae) in the central-east Atlantic. *Fisheries Research*, *72*, 121–131.

Moura, T., Figueiredo, I., Machado, P. B., & Gordo, L. S. (2004). Growth pattern and reproductive strategy of the holocephalan *Chimaera monstrosa* along the Portuguese continental slope. *Journal of the Marine Biological Association of the UK*, *84*, 801–804.

Munos-Chapuli, R., & Perez Ortega, A. (1985). Resurrection of Galeus atlanticus (Vaillant, 1888), as a valid species from the NE-Atlantic Ocean and the Mediterranean Sea. *Bulletin du Museum national d'Histoire naturelle de Paris*, *7*, 219–233.

Murry, B. A., Farrell, J. M., Schulz K. L., & Teece, M. A. (2008). The effect of egg size and nutrient content on larval perforfance: implication to protracted spawning in northerne pike (*Esox lucius* Linnaeus). *Hydrobiologia*, *601*, 71–82.

Muss, B. J., Nielsen, J., Dahlstrom, P., Olesen Nystrom, B. (2014). *Poissons de mer et de pêche Europe Occidentale*. Delachaux et Niestlé.

Nakaya, K. (1998). Taxonomic review of Apristurus laurussonii (Saemundsson, 1922) from the eastern North Atlantic (Elasmobranchii : Scyliorhinidae). *Cybium*, *22*, 1–9.

Neves Santos, M., Costa Monteiro, C., Erzini, K., & Lasserre, G. (1998). Maturation and gill-net selectivity of two small sea breams (genus Diplodus) from the Algarve coast (south Portugal). *Fisheries Reasearch*, *36*, 185–194.

Nielsen, J. G., Bertelsen, E., & Jespersen, A. (1989). The biology of *Eurypharynx pelecanoides* (Pisces, Eurypharyngidae). *Acta Zoologica*, *70*, 187–197.

Nielsen, J. G. (1999). A review of the genus Neobythites (Pisces Ophidiidae) in the Atlantic, with three new species. *Bulletin of Marine Science*, *64*, 335–372.

OBIS. (2018). *Ocean biogeographic information system*. Intergovernmental Oceanographic Commission of UNESCO.

O'Connell, M., & Fives, J. M. (1995). The biology of the Lesser Sand-Eel *Ammodytes tobianus* L. In the Galway Bay Area. *Biology and Environment: Proceedings of the Royal Irish Academy*, *95*, 87–98.

Pajuelo, J. G., Socorro, J., Gonzalez, J. A., Lorenzo, J. M., Pérez-Penalvo, A., Martinez, I., & Hernandez-Cruz, C. M. (2006). Life history of the red-banded seabream *Pagrus auriga* (Sparidae) from the coasts of the Canarian archipelago. *Journal of Applied Ichthyology*, *22*, 430–436.

Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., Esteban, A., Fock, H. O., Gil de Sola, L., Punzon, A., Solmundsson, J., & Payne, M. R. (2017). From traits to life-history strategies: Deconstructing fish community composition across European seas. *Global Ecology and Biogeography*, *26*, 812–822.

Peres, M. B., & Klippel, S. (2003). Reproductive Biology of Southwestern Atlantic Wreckfish, *Polyprion americanus* (Teleostei: Polyprionidae). *Environmental Biology of Fishes*, *68*, 163–173.

Porcu, C., Follesa, M. C., Gastoni, A., Mulas, A., Pedoni, C., & Cau, A. (2013). The reproductive cycle of dee-sea eel, *Nettastoma melanurum* (Nettastomatidae: Anguilliformes) from the south-eastern Sardinian Sea (central-western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom*, *93*, 1105–1115.

Pulliainen, E., & Korhonen, K. (1990). Seasonal changes in condition indices in adult mature and non-maturing burbot, *Lota lota* (L.), in the north-eastern Bothnian Bay, northern Finland. *Journal of Fish Biology*, *36*, 251–259.

Raju, S. N. (1974). Three new species of the genus Monognathus and the Leptocephali of the order Saccopharyngiformes. *Fishery Bulletin*, *72*, 547–562.

Retzer, M. E. (1991). Life-history aspects of four species of Cusk-Eels (Ophidiidae: Ophidiiformes) from the Northern Gulf of Mexico. *Copeia*, *1991*, 703–710.

Rey, J., Coelho, R., Lloris, D., Séret, B., de Sola, L. G. (2010). Distribution pattern of Galeus atlanticus in the Alboran Sea (south western Mediterranean) and some sexual character comparison with *Galues melastomus*. *Marine Biology Research*, *6*, 364–372.

Rodríguez, J. M., Alemany, F., & García, A. (2017). *A guide to the eggs and larvae of 100 commons Western Mediterranean Sea bony fishes species*. Food and Agriculture Organization of the United Nations.

Rosecchi, E., & Crivelli, A. J. (1992). Study of a sand smelt (Atherina boyeri Risso 1810) population reproducing in fresh water. *Ecology of Freshwater Fish*, *1*, 77–85.

Sayer, M. D. J., Gibson, R. N., & Atkinson, R. J. A. (1996). Growth, diet and condition of corkwing wrasse and rock cook on the west coast of Scotland. *Journal of Fish Biology*, *49*, 76–94.

Silverberg, N., Edenborn, H. M., Ouellet, G., & Béland, P. (1987). Direct evidence of a mesopelagic fish, *Melanostigma atlanticum* (Zoarcidae) spawning within bottom sediments. *Environmental Biology of Fishes*, *20*, 195–202.

Sley, A., Hadj Taeib, A., Jarboui, O., Ghorbel M., & Bouain A. (2015). Annual reproductive cycle, spawning periodicity and sexual maturity of false scad Caranx rhonchus (Geoffroy Saint-Hilaire, 1817) (Pisces, Carangidae) from the South-Eastern Mediterranean (Gulf of Gabès, Tunisia). *Journal of Applied Ichthyology*, *31*, 437–441.

Sousa, R., Ferreira, S., Chada, T., Delgado, J., & Carvalho, D. (2009). First approach to the biology of the deepwater shark *Deania profundorum* (Chondrichthyes: Centrophoridae). *Marine Biodiversity Records*, *2*, E44.

Stehmann, M. F. W., & Merrett, N. R. (2001). First records of advanced embryos and egg capsules of Bathyraja skates from the deep north-eastern Atlantic. *Journal of Fish Biology*, *59*, 338–349.

Stequert, B., Menard, F., & Marchal, E. (2003). Reproductive biology of Vinciguerria nimbaria in the equatorial waters of the eastern Atlantic Ocean. *Journal of Fish Biology*, *62*, 1116–1136.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Stergiou, K. I. (1999). Intraspecific variations in size- and age-at-maturity for Red Bandfish, Cepola macrophthalma. *Environmental Biology of Fishes*, *54*, 151–160.

Sulak, K. J., Wenner, C. A., Sedberry, G. R., & Guelpen, L. V. (1985). The life history and systematics of deep-sea lizard fishes, genus Bathysaurus (Synodontidae). *Canadian Journal of Zoology*, *63*, 623–642.

Thorson, J. T., Munch, S. B., Cope, J. M., & Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, *27*, 2262–2276.

Tojeira, I., Faria, A. M., Henriques, S., Faria, C., & Gonçalves, E. J. (2012). Early development and larval behaviour of two clingfishes, *Lepadogaster purpurea* and *Lepadogaster lepadogaster* (Pisces: Gobiesocidae). *Environmental Biology of Fishes*, *93*, 449–459.

Tsikliras, A. C., & Stergiou, K. I. (2014). Age at maturity of Mediterranean marine fishes. *Mediterranean Marine Science*, *16*, 5–20.

Van Der Veer, H. W. (1990). On the ecology of the dragonet *Callionymus lyra* L. in the southern North Sea. *Netherlands Journal of Sea Research*, *26*, 139–150.

Vassilopoulou, V., Siapatis, A., Christides, G., & Bekas, P. (2005). The biology and ecology of juvenile pilotfish (*Naucrates ductor*) associated with Fish Aggregating Devices (FADs) in eastern Mediterranean waters. *Mediterranean Marin Science*, *5*, 61–70.

Vedishcheva, E. V., Orlov, A. M., Orlova, S. Y., & Trofimova, A. O. (2016). First data on the age, growth processes, and otoliths of snub-nosed spiny eel *Notacanthus chemnitzii* (Notacanthidae). *Journal of Ichthyology*, *56*, 890–898.

Wheeler, A. (1993). The distribution of Gobius cobitis in the British Isles. *Journal of Fish Biology*, *43*, 652–655.

Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., & Tortonese, E. (1986). *Fishes of the North-Eastern Atlantic and Mediterranean*. United Nations Educational Scientific and Cultural.

Wiedmann, M. A., Primicerio, R., Dolgov, A., Ottesen, C. A. M., & Aschan, M. (2014). Life history variation in Barents Sea fish: Implications for sensitivity to fishing in a changing environment. *Ecology and Evolution*, *4*, 3596–3611.

Wienerroither, R., Johannesen, E., Dolgov, A.V., Byrkjedal, I., Bjelland, O., Drevetnyak, K., Eriksen, K.B., Høines, Å.S., Langhelle, G., Langøy, H., & Murashko, P.A. (2011). Atlas of the Barents Sea Fishes based on the winter survey. IMR/PINRO Joint Report Series.

Yano, K. (1995). Reproductive biology of the Black Dogfish, *Centroscyllium Fabricii*, Collected from waters off Western Greenland. *Journal of the Marine Biological Association of the United Kingdom 75*, 285.

Abundance dataset

The Database of Trawl Surveys (DATRAS) is a repository for data collected primarily from bottom trawl fish surveys coordinated by ICES expert groups. These surveys cover a wide range of areas, including the Baltic Sea, Skagerrak, Kattegat, North Sea, English Channel, Celtic Sea, Irish Sea, Bay of Biscay, and the eastern Atlantic from the Shetlands to Gibraltar. The current dataset includes more than 45 years of continuous time series data, which is continuously updated by national institutions. Users can freely download both data products (such as CPUE) and raw data in accordance with the ICES Data Policy on the ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark, via the DATRAS website at https://datras.ices.dk.

IUCN statutes

The IUCN Red List Categories and Criteria were developed for assessing the extinction risk of species. This system provides information on a variety of factors, including range, population size, habitat and ecology, use and/or trade, threats, and conservation actions. This information can inform conservation decisions and actions. The IUCN Red List of Threatened Species provides free access to the latest IUCN Red List Categories and Criteria. Users can download the most recent version of the IUCN Red List at the following website: https://www.iucnredlist.org, Version 2022-2.

Integrated distinctiveness R code

The R code is freely available at Figshare public data repository https://doi.org/10.6084/m9.figshare.22317643.v1.

14668238, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/geb.13731 by Cochrane France, Wiley Online Library on [12/07/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License