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RESEARCH ARTICLE

Northeast Atlantic elasmobranch community on the move: Functional reorganization in response to climate change

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Abstract

While spatial distribution shifts have been documented in many marine fishes under global change, the responses of elasmobranchs have rarely been studied, which may have led to an underestimation of their potential additional threats. Given their irreplaceable role in ecosystems and their high extinction risk, we used a 24-year time series (1997–2020) of scientific bottom trawl surveys to examine the effects of climate change on the spatial distribution of nine elasmobranch species within Northeast Atlantic waters. Using a hierarchical modeling of species communities, belonging to the joint species distribution models, we found that suitable habitats for four species increased on average by a factor of 1.6 and, for six species, shifted north-eastwards and/or to deeper waters over the past two decades. By integrating species traits, we showed changes in habitat suitability led to changes in the elasmobranchs trait composition. Moreover, communities shifted to deeper waters and their mean trophic level decreased. We also note an increase in the mean community size at maturity concurrent with a decrease in fecundity. Because skates and sharks are functionally unique and dangerously vulnerable to both climate change and fishing, we advocate for urgent considerations of species traits in management measures. Their use would make it better to identify species whose loss could have irreversible impacts in face of the myriad of anthropogenic threats.

KEYWORDS
climate change, community, elasmobranch, joint species distribution modeling, range shift, species traits

1 | INTRODUCTION

Climate change is an intensifying pressure affecting all marine organisms that may lead to irreversible ecological transformations such as biodiversity loss, decreased ocean productivity, and altered food webs (Henson et al., 2021; Hoegh-Guldberg & Bruno, 2010; Worm & Lotze, 2021). Increasing temperatures are responsible for shifting the distribution of marine species to more offshore, deeper, or colder waters (Dulvy et al., 2008; Punzón et al., 2016), as well as to higher latitudes (Cheung et al., 2013). Furthermore, ocean acidification is known to have turned calcified coastal habitats into non-calcified ones, reducing benthic complexity and reshaping nursery communities (Cattano et al., 2020; Zunino et al., 2019). While climate change effects on teleost fishes have been extensively documented (Pörtner

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& Peck, 2010), fewer studies have been carried out in elasmobranchs (sharks, rays, and skates; Rummer et al., 2022), whose lineage includes more than three times as many species threatened with extinction (IPBES, 2019; Stein et al., 2018). Since elasmobranchs had lived in periods with higher atmospheric CO_2 concentrations than today, it was thought that they should be able to tolerate such conditions in the future (Rummer & Munday, 2017). However, since the late 2010s, a growing number of experimental studies show that elasmobranchs are sensitive to ocean acidification and warming (Rummer et al., 2022). Population-level changes in response to climate change have also been observed in recent decades, such as changes in the range and/or migratory timing of the Tiger Shark (Hammerschlag et al., 2022), or increased use of breeding habitat by the Bull Shark (Bangley et al., 2018) and White Shark (Tanaka et al., 2021). Future shifts are also expected for the 21st century, with both gains and losses of suitable habitats depending on the species (e.g., Grieve, et al., 2020, and requiem and mackerel sharks, Birkmanis et al., 2020; Diaz-Carballido et al., 2022; Lezama-Ochoa et al., 2023).

Climate change may equally exacerbate fisheries-related risks by increasing the strength and frequency of extreme events (Cheung et al., 2021; Yan et al., 2021). For example, the risk of extinction of the Short-tailed Nurse Shark (*Pseudoginglymostoma brevicaudatum*) increased in the southwestern Indian Ocean due to the combination of overfishing, destructive fishing practices, rising temperatures, and increased frequency and severity of coral bleaching (Pollom et al., 2022). This is of particular concern in the Northeast Atlantic, where the English Channel and North Sea have been identified as hot spots for global warming (Dulvy et al., 2008; Simon et al., 2023) and where bycatch, habitat loss, and degradation are driving almost half of sharks and their relatives to extinction (56 out of 136 species, Dulvy et al., 2021; Walls & Dulvy, 2021). Shallow-distributed, slow-growing, low reproductive capacity species are the most likely to experience a decline in status (Coulon et al., 2023; Pimiento et al., 2023; Stein et al., 2018; Walls & Dulvy, 2021).

Elasmobranchs contribute to ecosystem functioning with unique combinations of physiological, morphological, reproductive, or behavioral traits (Tilman, 2001) that have no functional equivalent (i.e., functionally distinct species; Coulon et al., 2023; Leitão et al., 2016; Mouillot et al., 2013; Violle et al., 2017). They are known for exerting top-down regulation (Barley et al., 2017a, 2017b; Ruppert et al., 2013) but they are also linked to other ecosystem functions such as promoting energetic connectivity between neritic, oceanic, and deep-sea ecosystems (Shipley et al., 2023). Simulated extinction scenarios within various taxonomic groups (e.g., vascular plants, mammals, birds, reptiles, amphibians, and freshwater fish) revealed extensive changes in species trait composition within communities when functionally distinct species were lost (Carmona et al., 2021; Colares et al., 2022; McLean et al., 2019). Consequently, coupled with the human-induced reduction in population size, elasmobranch range shifts in the Northeast Atlantic could lead to profound and irreversible ecosystem reorganizations.

Using 24 years (1997–2020) of scientific bottom trawl surveys in the Northeast Atlantic, we first evaluated the sensitivity of five skate and four shark species to pH and temperature gradients. Then, we investigated whether the habitat suitability of these populations has been altered by ongoing climate change. Lastly, we studied how the trait composition of the elasmobranch community has changed over the last three decades.

2 | MATERIALS AND METHODS

2.1 | Study area and bottom trawl surveys

The study area covers the Greater North Sea, Celtic Seas, and Bay of Biscay (Figure 1). Spanning 24 years (1997–2020), the dataset is part of the time series of scientific bottom trawl surveys collated by the International Council for the Exploration of the Sea (ICES) expert groups conducted to examine changes in fish stock abundance and distribution (Appendix S1—Table S1). Species abundance data were downloaded from ICES Database on Trawl Surveys (DATRAS), 2023, ICES, Copenhagen, Denmark.

Only fishing gear types with homogeneous spatiotemporal coverage and hauls made in the first 200 m depth were used to reduce spatiotemporal capture bias. All abundance data were converted to presence–absence to reduce biases of gear catchability. Only species present in more than 2% of the total number of trawls were

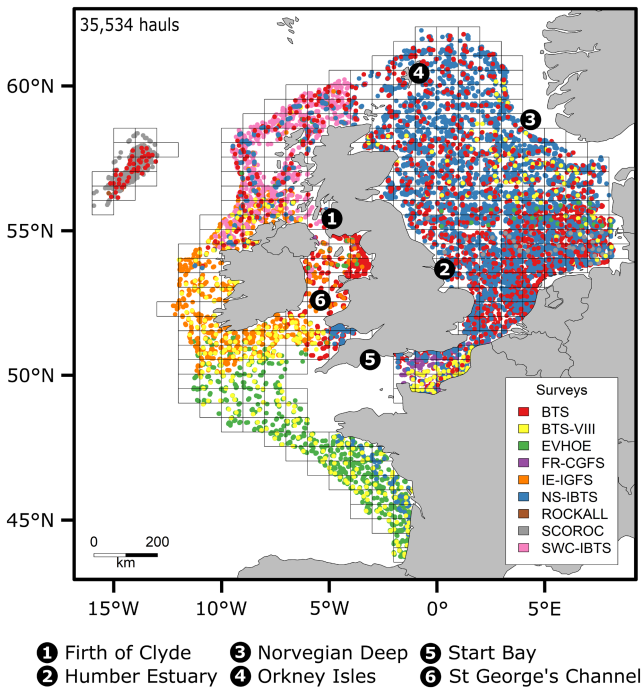


FIGURE 1 Map of the available bottom trawl surveys of elasmobranch communities across northwest European continental shelf seas obtained from the International Council for the Exploration of the Sea data portal (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx). Colored dots locate the individual hauls, with one color per survey. ICES rectangles (1° × 0.5° grid cells) are represented. Table S1 for detailed information about bottom trawl surveys and their acronyms. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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selected (minimal thresholds defined according to model prediction accuracy). This was to reduce the imbalance between presence and absence data that can limit the model's ability to effectively learn the characteristics of the minority class (i.e., the class of presences), leading to biased predictions and reduced accuracy in identifying suitable habitats (Appendix S1—Table S1 and Appendix S2—Figures S1–S4). Some parts of our study area (e.g., the North Sea) are sampled at multiple seasons (i.e., quarters) within a year which implies a greater number of presences per year in these subareas. Therefore, the study area was gridded with cells of 0.111°×0.134° in which only one species occurrence per year was kept to limit bias model training (Feng et al., 2019; Appendix S2—Figure S5).

The final selected community is composed of four sharks (Spurdog, *Squalus acanthias*; Large-spotted Dogfish, *Scyliorhinus stellaris*; Small-spotted Catshark, *Scyliorhinus canicula*; Starry Smooth-hound, *Mustelus asterias*) and five skates (Spotted Ray, *Raja montagui*; Thornback Ray, *Raja clavata*; Blonde Ray, *Raja brachyura*; Cuckoo Ray, *Leucoraja naevus*; Thorny Ray, *Amblyraja radiata*).

2.2 | Environmental drivers

Depth (positive values) and slope, descriptors of relief and complexity were obtained from GEBCO Bathymetric Compilation Group (2020) and "MARSPEC: ocean climate layers for marine spatial ecology" (Sbrocco & Barber, 2013), respectively (Appendix S2—Figure S6). Habitat types were obtained from the EUSeaMap 2021–EUNIS 2019 habitat types (European Marine Observation and Data Network) and grouped into seven broader categories based on their grain size composition (Appendix S1—Table S2), then used to calculate a Shannon substrate diversity index, reflecting habitat diversity.

A wide range of parameters may be affected by climate forcing and are likely to restrict sharks and skates distribution (e.g., temperature, dissolved oxygen, chlorophyll *a*, pH; Rummer et al., 2022; Schlaff et al., 2014). To correctly estimate species' responses to environmental variables, we built the most parsimonious model possible (Merow et al., 2014). We retained only temperature and pH that were not highly correlated with all the other variables (i.e., were unique in terms of signal; $R^2 < .75$). For example, we did not include dissolved oxygen because it was strongly correlated with temperature, meaning that the oxygen signal was already included in the temperature variable. While temperature influences key metabolic and physiological processes in ectothermic species and drives seasonal (Dunbrack & Zielinski, 2003; Hopkins & Cech, 2003; Vaudo & Heithaus, 2013) and diurnal movements (Matern et al., 2000; Papastamatiou et al., 2015; Vaudo et al., 2016), pH can markedly affect organismal physiology and behavior (Green & Jutfelt, 2014; Rummer et al., 2020) and enhanced temperature-induced effects (Rummer et al., 2022). Moreover, the effects of pH on the distribution of species remain unclear. Surface parameters were used in preference to bottom parameters, as bottom pH data were not available and most of the study area is relatively shallow, resulting in a close relationship between surface and bottom parameters (Young & Holt, 2007). Similarly, the monthly summer maximum of sea surface temperature (SST) and surface pH were selected in preference to winter values or annual averages. In addition, summer values are more likely to exert pressure on species that reach the upper limit of their thermal niche. For example, some oviparous species spawn during summer along the coast (e.g., *Scyliorhinus canicula*, Ellis & Shackley, 1997). Data were obtained from E.U. Copernicus Marine Service Information for each year (Appendix S1—Table S2). Monthly Atlantic Multidecadal Oscillation (AMO) indexes were obtained from the NOAA-PSL and averaged per year (Enfield et al., 2001; Appendix S1—Table S3) to disentangle the effects of ongoing climate change and the potential effects of long-term natural climate oscillations (Edwards et al., 2013; Faillettaz et al., 2019).

All drivers were downloaded at the finest resolution, then scaled down to presence–absence data cells (i.e., 0.111°×0.134°) and kept in the absence of strong correlations (threshold = 0.85; Appendix S2—Figure S7).

2.3 | Species traits

We selected six species traits reflecting trophic ecology, life history, and ecological versatility that are expected to be implicated in the species' response to environmental changes (McLean et al., 2018; Murgier et al., 2021) and geographic range shifts (Albouy et al., 2015; Sunday et al., 2015; Appendix S1—Table S5 for reasoning). Species traits were collected by extracting traits values from Coulon et al. (2023) and Ocean Biodiversity Information System (OBIS, 2022). From the OBIS data, the geographic range was calculated as the difference between the highest and lowest latitudes in the distribution, given the spatial extent of the study area and after removing the first and last percentiles of the latitude distribution, to limit false presences due to species misidentification. The depth preference was calculated as the mean value of the depth distribution (Appendix S1—Table S5).

2.4 | Joint species distribution modeling

We used an hierarchical modeling of species communities (HMSC; Ovaskainen et al., 2017), belonging to the joint species distribution models (jSDM) class (Warton et al., 2015) to model species-specific changes in response to environmental variations and capture changes in species trait composition (Maioli et al., 2023; Montanyès et al., 2023; Weigel et al., 2023), using the "*Hsmc*" R package (Tikhonov et al., 2020; version 3.0-1). Each grid cell (29,193) was considered as a sampling unit (matrix S). We included species occurrence as a response variable in the HMSC analysis (matrix Y) and modeled presence–absence with a probit link function (Ovaskainen & Abrego, 2020), assuming the default prior distributions. Six continuous environmental drivers were included (matrix X), estimating a second-order polynomial term for sea surface temperature and pH (Appendix S2—Figure S8). We also included six species traits (matrix T) and a phylogenetic tree of elasmobranch species from VertLife.org (matrix C; Stein et al., 2018). Finally, we included a random effect to account for

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spatially structured samplings (i.e., fishing gears- types and quarters; matrix Π) and potential year-to-year variation not captured by the climatic covariates (i.e., years).

Two Markov Chains Monte Carlo (MCMC) simulations were run to generate 1000 posterior samples using a thinning interval of 50 following a burn-in period of 25,000 (Jönsson et al., 2022; Ovaskainen & Abrego, 2020). The effective sample sizes were very close to the actual sample sizes (mean difference < 6%), indicating that there is very little autocorrelation between consecutive samples. The potential scale reduction factors were very close to one (mean difference < 0.3%), which indicates that the two chains gave consistent results, as was also suggested by visual inspection of the trace plots (Appendix S3). The model was evaluated using area under the receiver operating curve (ROC) score (AUC = 0.83 ± 0.05; Appendix S1—Table S6), and examining the positive predictive value (PPV = 0.98 ± 0.04; Appendix S1—Table S6) and negative predictive value (NPV = 0.04 ± 0.07; Appendix S1—Table S6) using a random subset of 75% of the dataset used for parameter estimation and the remaining 25% of observations for validation (Elliott, Carpentier, et al., 2020). Thresholds were defined per species to maximize the Percentage of Correct Classification (PCC) using the R function "*optimal. threshold*" in the "*PresenceAbsence*" R package (Cantor et al., 1999; Manel et al., 2001; Wilson et al., 2004).

2.5 | Species responses to pH and temperature

We evaluated the species sensitivity to pH and temperature gradients by estimating second-order polynomial terms following Antão et al. (2022). Species were considered nonresponsive if the calculated range of probability (referred to as the posterior distribution) for a species' response included zero with more than 10% probability. Nonzero responses were then classified as positive, negative, or bell-shaped, depending on the sign of the derivative. A positive response corresponds to a species at the lower end of its niche (i.e., occurrences increasing along the environmental gradients), a bell-shaped response (derivative is positive or negative over at most 60% of the environmental gradient; Antão et al., 2022) corresponds to a species at the optimum of its niche (i.e., occurrences peaking within the gradients), and a negative response corresponds to a species at the upper end of its niche (i.e., occurrences decreasing along the gradients) (Antão et al., 2022).

2.6 | Shift in habitat suitability

We determined habitat suitability-weighted areas using annual jSDM projections from 1997 to 2020, calculating the sum of the cell areas weighted by the habitat suitability of each species (from 0 to 1), subsequently referred to as habitat suitability areas (A_{Hs}), as follows:

$$A_{Hs;j} = \sum_{i=1}^{N} a_{Hs;i} \times Hs_i \quad (1)$$

where j is the year considered, $a_{Hs;i}$ is the area of the spatial cell i in km^2 calculated using the *"area"* function of the *"raster"* R package, Hs_i is the habitat suitability in the cell, and N is the total number of cells. This weighted calculation limits threshold selection bias and is a more conservative approach, given the different range of habitat suitability between species (Lezama-Ochoa et al., 2023; Rubenstein et al., 2023).

Along the same lines, we calculated habitat suitability-weighted centroids (C) and centroids of the first and last decile of the habitat suitability based on longitudinal, latitudinal, and depth components for each species, subsequently referred to centroids, as follows:

$$C_{X,j} = \frac{\sum_{i=1}^{N} X_i \times Hs_i}{\sum_{i=1}^{N} Hs_i} \quad (2)$$

where j is the year considered, X_i is the latitude, longitude, or depth at the center of spatial cell i, Hs_i is the habitat suitability in the cell i, and N is the total number of cells (Weinert et al., 2016).

Then, we looked for trends in changes in habitat suitability-weighted areas, centroids, and habitat suitability in each cell for each species over time, based on Kendall's tau using the *"trend"* R package (Hipel & McLeod, 1994; Mann, 1945; Sen, 1968).

2.7 | Temporal change in species traits composition

Community weight mean (CWM) provides information about the average value of a species trait within the community, considering species abundance. Rather than assigning a weight to each species based on its abundance per cell, we assigned a weight to each species corresponding to the rate of change in the habitat suitability to examine changes in species trait composition for each trait in each cell over time. CWM values provide an overview of temporal changes but do not allow the strength and direction of the factors behind their variation to be quantified. For example, CWM increases when (i) the habitat suitability of species with higher species traits than the community increases, and (ii) the habitat suitability of species with lower species traits than the community decreases, while the CWM decreases when the opposite occurs. Therefore, we also decomposed the four underlying processes that cause CWMs to change (McLean et al., 2021). We calculated the difference between each species' traits and the mean of the community, multiplied this value by each species' change in habitat suitability, and took the sum of the resulting values for all species within each process (McLean et al., 2021):

$$PS_{k,i} = \sum_{s=1}^{N} (ST_s - CWM_{k,i}) \times \Delta Hs_i \quad (3)$$

where ST is the mean trait value of the species s, CWM is the community-weighted mean of the trait k in the cell i in all years, ΔPresence is the species' change in presence (i.e., Sen's slope), and N the total number of species. We evaluated the accuracy of this approach by comparing the value of the process strengths to the

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rate of change in CWM for each grid cell and for each trait (McLean et al., 2021; Appendix S2—Figure S9).

3 | RESULTS

3.1 | Species responses and pH & temperature

The three factors having the greatest influence on habitat suitability according to jSDM are SST (mean variance explained = 28.7), quarters and gears (mean variance explained = 24.8), and pH (mean variance explained = 18.4). Seafloor parameters (Appendix S2—Figure S10), and AMO had the lowest influence (mean variance explained = 0.1). The random effect of quarters and gears is spatiotemporally structured and reflects the different environmental conditions in the study area as well as the different distribution of species. While temperature explained more than 50% of the variance in habitat suitability for *L. naevus*, *R. montagui*, and *S. acanthias*, pH explained more than 50% in habitat suitability for *M. asterias* and more than 40% for *S. stellaris* (Appendix S2—Figure S10).

By estimating a second-order polynomial term for pH and temperature, we were able to state that all species, with the exception of *S. stellaris*, were in the optimal part of their pH niche from 1997 to 2020 (Figure 2; Appendix S1—Table S7), with no change over time. While four species (*A. radiata*, *M. asterias*, *R. clavata*, *S. stellaris*) were in the optimal part of their thermal niche, five (*L. naevus*, *R. brachyura*, *R. montagui*, *S. canicula*, *S. acanthias*) were at the higher end (Figure 2; Appendix S1—Table S7), meaning that during the warming period of 1997–2020, these species were present in temperature conditions in which their habitat suitability decreases when temperature increases.

3.2 | Shift in habitat suitability

Four of the nine species habitat suitability area increased with an annual rate of 2620 km^2 for *M. asterias* ($p < .001$), 1886 km^2 for *R. clavata* ($p < .01$), 1419 km^2 for *R. brachyura* ($p < .001$), and 1410 km^2 for *S. stellaris* ($p < .001$) (Appendix S1—Table S8). It extended approximately to 6% of the study area for *M. asterias*, 4% for *R. clavata* and *R. brachyura*, and 3% for *S. stellaris* from 1997 to 2020.

This extension is correlated with a centroids northward shift for *M. asterias* and *R. clavata* (respectively, 0.3 km $decade^{-1}$; $p < .02$ and .5 km $decade^{-1}$; $p < .05$) as well as deepening (0.02 m $decade^{-1}$ and 0.03 m $decade^{-1}$; $p < .001$) (Appendix S1—Table S9). While the depth range of *M. asterias* has narrowed, with a deeper upper limit and a shallower lower limit, *R. clavata* upper longitudinal range extends to the east (Appendix S1—Table S10). Although the habitat suitability areas for *S. canicula* and *A. radiata* have not changed in size over time (Appendix S1—Table S8), their centroids have shifted

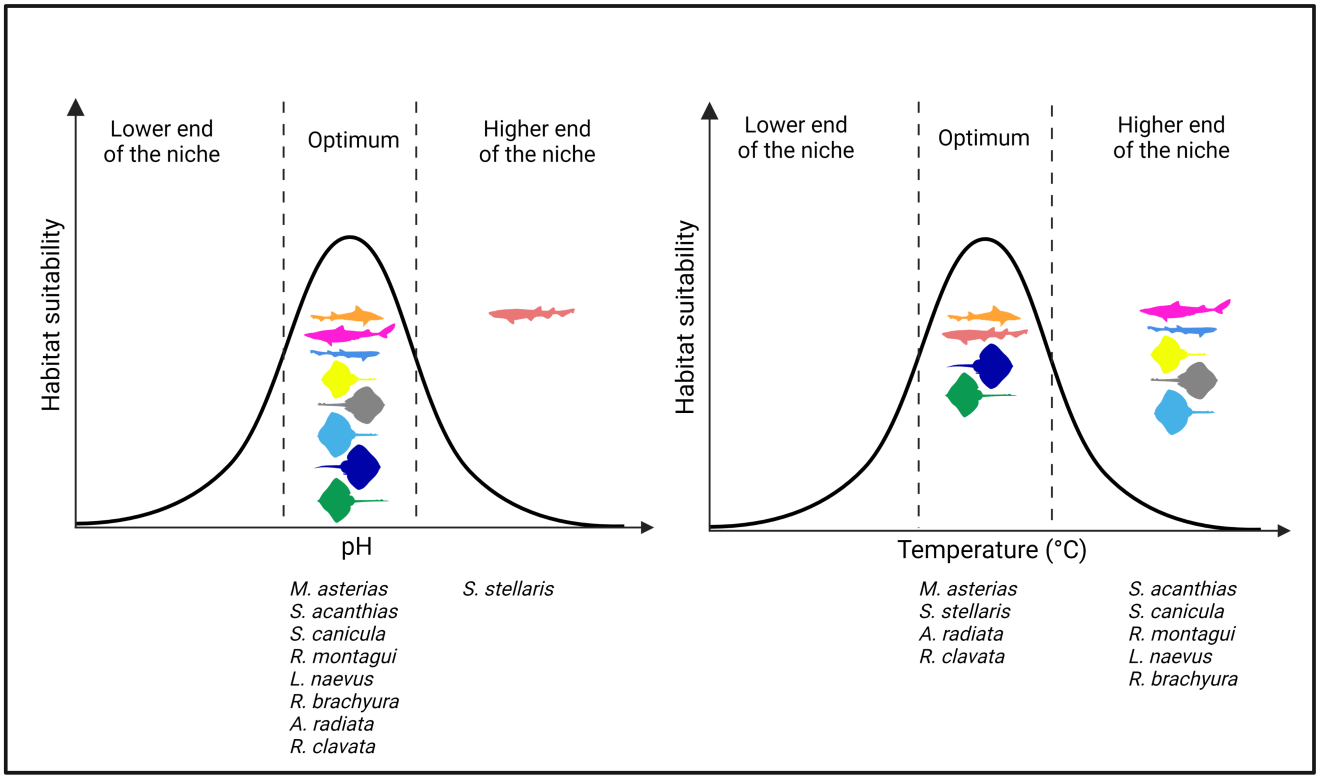


FIGURE 2 Species at the lower, optimal, or upper end of their pH and thermal niche with at least 90% posterior support for the effect of pH in the joint species distribution models between 1997 and 2020. Non-zero responses were classified as "bell-shaped," "increasing" or "decreasing" based on the sign of the derivative of the response over the observed pH gradient. The colors refer to the different species studied. Created with BioRender.com.

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northward (0.1 km decade^{-1}; $p < .01$), and in depth (0.01 m decade^{-1}; $p < .03$) for *S. canicula* and westward (0.5 km decade^{-1}; $p < .01$) for *A. radiata* (Appendix S1—Table S9). Although no change in the centroids for *R. brachyura* could be detected, the upper and lower limits of its range have shifted eastwards and extended northwards (Appendix S1—Table S10). *R. montagui* has also expanded eastwards (Appendix S1—Table S10).

L. naevus occupied the northwestern part of the study area to the North Channel (Appendix S4) and its habitat suitability decreased in the Irish Sea, English Channel, and the southern North Sea (Figure 3). *R. montagui* habitat suitability increased moderately in the Irish Sea, St. George's Channel, Scottish Sea, and around the Orkney Isles (+ 9% decade^{-1} cell^{-1}, Figure 3). *A. radiata* and *S. acanthias* are closely associated with deeper and cooler waters (50–200 m; Appendix S4) with increased habitat suitability along the Norwegian Deep (+5% and +4% decade^{-1} cell^{-1}, respectively, Figure 3), and along the continental shelf north of the British Isles and in the trough of the Firth of Clyde though. The habitat

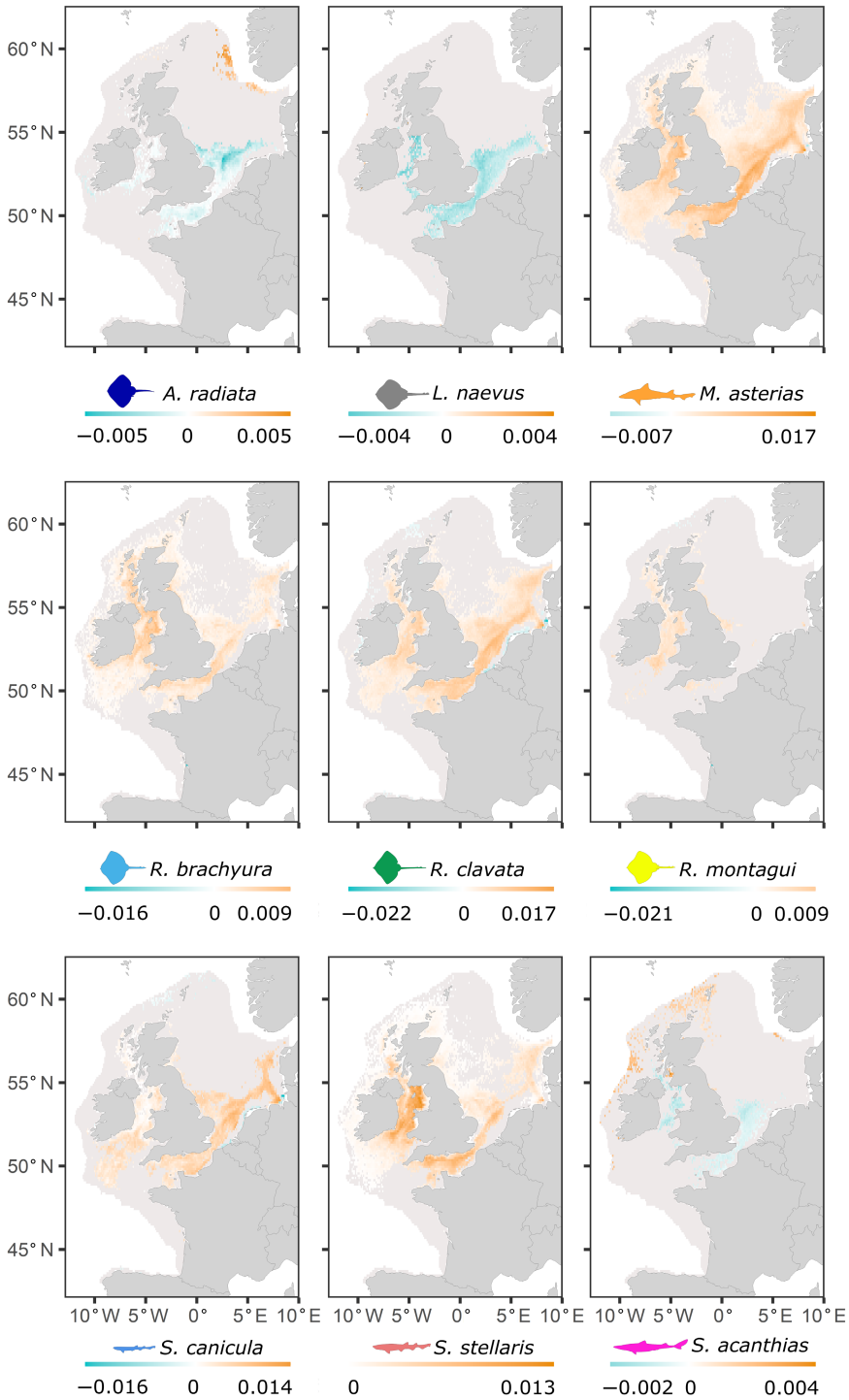


FIGURE 3 Estimates of the habitat suitability regression coefficient over time in each cell (0.111° × 0.134°) based on Kendall's tau. Gray cells show no trend in the variation of the habitat suitability while orange tones indicate an increase in habitat suitability, and light blue tones a decrease ($p < .05$). Each map depicts trends for one species. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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suitability of *R. clavata* and *S. canicula* increased in the Western Channel, the southern and eastern North Sea reaching a rate of +10% and +20% decade^{-1} cell^{-1}, respectively, and to a lesser extent in the Irish Sea and the Celtic Sea (Figure 3). In contrast, the decrease in their habitat suitability is maximal along the German, Dutch, and Belgian coasts (both at a rate of −20% decade^{-1} cell^{-1}, Figure 3). Habitat suitability of *M. asterias* and *S. stellaris* has increased sharply in the Irish Sea, St George's Channel, in the southern and eastern North Sea, reaching rates of +20% decade^{-1} cell^{-1} and +10% decade^{-1} cell^{-1}, respectively (Figure 3). For *R. brachyura*, habitat suitability increased in the Irish Sea and west of Scotland up to 10% decade^{-1} cell^{-1} (Figure 3).

3.3 | Changes in species traits composition

The CWM of trophic level has decreased in the southern North Sea, especially in the Dogger Bank due to increased habitat suitability for low trophic level species (Figure 4) (e.g., *M. asterias*; Figure 3). The CWM length at maturity increased (+6 cm decade^{-1} cell^{-1}) due to an increase in the habitat suitability of late maturing species (Figure 4) (e.g., *M. asterias*, *R. brachyura*; Figure 3) and this was true up to the southern and eastern North Sea. Meanwhile, a decrease in the CWM fecundity was also detected in the Eastern English Channel, the Irish Sea and St. Georges Channel (up to −4 offsprings decade^{-1} cell^{-1}) due to an increase in the habitat suitability of low fecundity species (Figure 4) (e.g., *M. asterias*, *S. stellaris*; Figure 3). Finally, the CWM latitudinal range around the British Isles has decreased (−0.3° decade^{-1} cell^{-1}) due to an increase in the habitat suitability of species with a narrow latitudinal distribution (Figure 4) (e.g., *R. montagui*; Figure 3). In the North Sea, the British Isles, and in the western part of Celtic Sea, the CWM depth preference decreased (i.e., became shallower) by −4 m decade^{-1} cell^{-1} due to an increase in the habitat suitability of shallow water species (Figure 4; e.g., *M. asterias*, *R. clavata*; Figure 3). These changes mainly took place in areas of greater depth, which ultimately translates into a shift of shallow communities toward deeper waters.

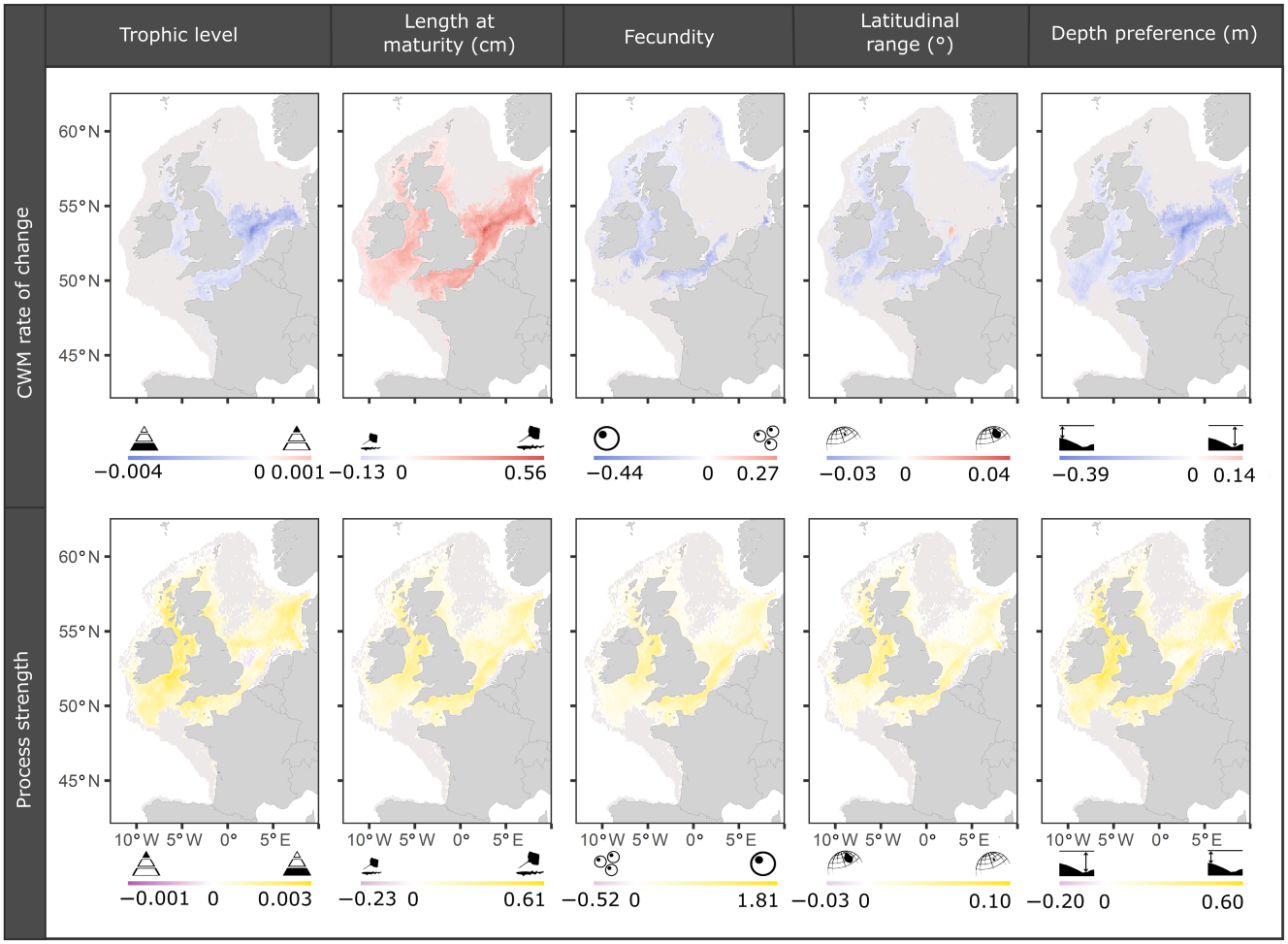


FIGURE 4 Rate of change in community-weighted mean (CWM) of trophic level, length at maturity, fecundity, latitudinal range, and depth preference for the period 1997–2020 in each cell (0.111° × 0.134°) and strengths of the processes leading to changes in the CWMs. Gray cells show no trend in the variation of the CWMs ($p > .05$). Red tones indicate a positive CWM rate of change, while dark blue tones indicate a negative. Yellow tones indicate a process with a positive force, while violet tones indicate a process with a negative force. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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4 | DISCUSSION

Despite a relatively short period of survey (1997–2020), it appears that climate change has contributed to change in elasmobranch communities in the Northeast Atlantic. Our results are analogous to similar studies conducted in the Northeast Atlantic on teleost fishes (Gordó-Vilaseca et al., 2023), cephalopods (Oesterwind et al., 2022), zooplankton (Ratnarajah et al., 2023), and diatoms (Edwards et al., 2022), demonstrating that the ongoing climate changes are affecting all marine organisms without exception. We found that, of the nine species of skates and sharks studied, five are at the upper limit of their thermal niche. Furthermore, six of the nine species experienced a change in their habitat suitability through an increase in size and/or a shift northward, eastward, or deeper. We found that the changes in the species' suitable habitat led to changes in the species trait assemblage. We detected a decrease in the mean trophic level, as well as an increase in size at maturity, correlated to a lesser extent with a decrease in fecundity. Communities have also been altered by the shift of species habitat suitability toward deeper waters. Finally, species with low latitudinal distribution experienced a shift in their suitable habitat to tight areas defined by high depths.

Although *L. naevus* and *R. montagui* were at their upper thermal limit, there was no change in their habitat suitability areas over time, despite the measured sea warming. Since *L. naevus* occupied the northwestern part of the European sea shelf and its habitat suitability decreased with increasing temperature, it is therefore questionable whether the species is currently undergoing a shift or whether the study area is not suitable for detection, knowing *L. naevus* has previously undergone deep-sea shifts in response to warming (Perry et al., 2005; Poulard & Blanchard, 2005). This dataset covers the European continental shelf and is not representative of the time series available worldwide (Maureaud et al., 2021). This raises concerns about the ability to monitor deep-sea and offshore species and justifies the need to adopt a precautionary approach to the exploitation of the ecosystems in which they depend (e.g., deep-sea mining and offshore fishing).

Within more coastal areas, we detected increased habitat suitability of *R. montagui* off the Humber Estuary and Start Bay but not throughout the Greater North Sea (Ellis et al., 2004; Sguotti et al., 2016). It could be hypothesized that although remaining adults could currently withstand the environmental conditions faced in estuaries (Ashcroft, 2010), eggs and juveniles may not have the same ability (Di Santo, 2015; Elliott, Bearup, et al., 2020; Musa et al., 2020; Rosa et al., 2014), thereby impeding the recolonization process that has been underway since the 1990s (Amelot et al., 2021). This also highlights the importance of long-term monitoring of spawning and nursery sites (Kinney & Simpfendorfer, 2009; McLean et al., 2018).

We show that *A. radiata* and *S. acanthias* are closely associated with deeper and cooler waters. While their habitat suitability at the southern edge of their distribution decreased, it increased in the north and on the continental slope. Although *A. radiata* shift was expected because it is already at the edge of its distribution (Ellis et al., 2004; Sguotti et al., 2016; Townhill et al., 2023), changes in the habitat suitability of *S. acanthias* were not expected (Ellis et al., 2004), suggesting a greater sensitivity to temperature increased and potential concomitant factors that have led to a sharp decline in its abundance since 1980 in the southern North Sea (Murgier et al., 2021; Sguotti et al., 2016). Continental slope can currently provide a climate change refuge for these species (Ashcroft, 2010; Morelli et al., 2016), but it is a restricted habitat and the dispersal capacity and population dynamics of these species limit their ability to adapt and colonize new potentially suitable areas.

The habitat suitability of *S. canicula* and *R. clavata* increased in the western English Channel, southern and eastern North Sea while it decreased along the German, Dutch, and Belgian coasts. We depicted the continuous northward shift pattern of *S. canicula* previously stated in several studies (Ellis et al., 2004; Rindorf et al., 2020; Sguotti et al., 2016; Townhill et al., 2023), coupled with a shift in depth. Before population depletion in the 1990s (Amelot et al., 2021), *R. clavata* was historically widespread around the British Isles (Ellis et al., 2004) and across the southern North Sea (Sguotti et al., 2016). After the 2000s, abundance increased in the North Sea (Rindorf et al., 2020) and in the eastern English Channel (Elliott, Bearup, et al., 2020), particularly with the fisheries ban on Undulate Ray (*Raja undulata*; 2009–2015), since *R. undulata* has a similar niche as *R. clavata* (Elliott, Bearup, et al., 2020; Elliott, Carpentier, et al., 2020). Therefore, while the decrease in the *R. clavata* habitat suitability could be mostly attributed to environmental changes, its increase could be attributed both to the current suitable environmental conditions and to the beneficial effects of *R. undulata* fishery regulation (Elliott, Bearup, et al., 2020).

Concerning *M. asterias*, the pH is the first factor explaining the variance in its occurrence. The direct effect of acidification on elasmobranchs is limited to oviparous species (Rummer et al., 2022) with the exception of the Blacktip Reef Shark (*Carcharhinus melanopterus*) neonates (Bouyoucos et al., 2020; Bouyoucos & Rummer, 2020; Rummer et al., 2020). Because experimental studies are limited by available facilities, we propose studying in situ behavior (e.g., foraging, activity levels) or physiological (e.g., hematology, metabolic rates, hypoxia tolerance) responses of viviparous sharks with a wide distribution (e.g., *C. melanopterus*), including areas where seawater is naturally more acidic due to volcanic carbon dioxide vents (e.g., coral studies, Comeau et al., 2022; Hall-Spencer et al., 2008). We also stress the need to consider the indirect effects caused by the increased sensitivity of calcifying benthic invertebrates on which benthivorous species such as *M. asterias* depend (Ellis et al., 1996; Marshall et al., 2017), whose habitat has greatly increased toward the northeast of the North Sea. While there were limited historical records of *Mustelus* spp. in the southern North Sea until the 1980s (Ellis et al., 2004), their abundance then increased exponentially after 2000 in close relation to warming surface (Rindorf et al., 2020).

Finally, we showed an increase in the habitat suitability of *S. stellaris*. This trend can reflect the potential increase in the abundance of *S. stellaris* as reported by Rindorf et al. (2020) and ICES (2022) but can also be attributed to improved identification of *S. stellaris* in scientific surveys, as suggested by the increase in

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landings that is mainly due to the improved species identification in fish markets in recent years (ICES, 2022). We therefore insist on eliminating misidentifications that may currently limit studying the responses of some species that look similar but have very different species traits (e.g., *Dipturus* spp. complex; Iglésias et al., 2010), and the need to be very careful with species identification when working with time series. *S. stellaris* trend can also be explained by the colonization of the southwestern part of the North Sea at depths of 20–50 m while it was very rare from 1967 to 2002 (Ellis et al., 2004). We found that *R. brachyura* was at the upper limit of its thermal niche, with habitat suitability increasing northward. Therefore, the contraction of its habitat to the south could be expected in the future.

Since we detected a decrease in the trophic level of the elasmobranch communities, which includes some of the highest trophic level species in the Northeast Atlantic (Coulon et al., 2023), food web dynamics under environmental change, from primary producers to top predators, should be investigated to detect potential food web imbalances (Albouy et al., 2014; Halouani et al., 2016; Nagelkerken et al., 2020; Sagarese et al., 2017). Similarly, the community deepening, a direct response to climate change (Dulvy et al., 2008; Punzón et al., 2016), may have altered ecosystem functioning, particularly in the southern North Sea (Murgier et al., 2021) and Celtic Sea. We also noted that species redistribution may currently be limited by depths beyond 50 m in the North Sea due to recruitment failure (Nicolas et al., 2014). Although linear trends are currently being observed, a threshold could be expected, with an abrupt change in community composition (Couce et al., 2020; Monaco & Helmuth, 2011; Townhill et al., 2023). Concerning life-history traits, we found an increase in size at maturity associated, to a lesser extent, with a decrease in fecundity. While in the Irish Sea, this is mainly attributed to the increased habitat suitability of *S. stellaris*, which is also the main species that led to the decrease in the mean latitudinal range of the communities, the dynamics are less clear in the Celtic and North Sea, where we can however reasonably attribute a strong effect of the presence of *M. asterias*. Since elasmobranchs have a slower pace of life compared to most teleost fishes, large-bodied endemic species (e.g., *D. intermedius*, Garbett et al., 2023) are even more vulnerable to climate change (Jones & Cheung, 2018). Nonetheless, some species such as *M. asterias* may currently benefit from ongoing changes (Sguotti et al., 2016). Furthermore, we cannot exclude a time lag between observed climate changes and their effects on communities, given their long lifespan and slow population turnover (Thompson & Ollason, 2001). As a result, a decline could occur in the decades to come, notably due to a failure of reproduction or recruitment.

The trends currently observed could be found in sympatric species and/or species sharing common traits (Barnett et al., 2019; Coulon et al., 2023), especially endangered species. This means that species found along the continental shelf, such as the Sandy Ray (*Leucoraja circularis*) and the Shagreen Ray (*Leucoraja fullonica*), can respond at least as much as *L. naevus* and therefore deserve special conservation attention. Similarly, it is reasonable to argue that coastal species such as the Small-eyed Ray (*R. microocellata*) and *R. undulata* have also been impacted by ongoing climate change in some way because of their lower ecological versatility than most of the species studied. It would be interesting to study a larger number of species, including teleost fishes with numerous and diverse traits, to identify the most sensitive combinations of traits to climate change. This will allow us to focus our conservation efforts without the need for individual species assessments.

We chose pH and temperature to study changes in habitat suitability over time. Additional drivers likely to be affected by climate forcing (e.g., dissolved oxygen) were not included in the model because they were highly correlated with temperature and/or depth. We acknowledge that they may have concomitantly contributed to the modification of species habitat suitability. For example, some studies showed that dissolved oxygen could influence the distribution of elasmobranchs over small spatial and temporal scales (Carlisle & Starr, 2009; Coffey et al., 2017; Drymon et al., 2013) and be responsible for increased mortality in the *S. canicula* embryos (Musa et al., 2020). Furthermore, we focused on maximum temperatures in summer because we were concerned with the upper limit of the species' thermal niche. However, losses of suitable habitat in summer could potentially be offset by gains in suitable habitat in winter and/or spring. These environmental changes are likely to cause phenological changes (e.g., in spawning periods, Rogers & Dougherty, 2019). For migratory species (e.g., *Mustelus asterias*), modifications in spatial sex differentiation during circannual migration could also be expected (Brevé et al., 2016, 2020).

We emphasize caution, since although the habitat suitability of species is related to the environmental parameters, it is not synonymous with presence probability. Changes in presence probability may be constrained by changes in environmental conditions but also by biotic interactions (Elliot et al., 2016; Preston et al., 2008), such as prey availability (Aebischer et al., 1990; Frederiksen et al., 2006). While we can consciously consider that interspecific relationships have been intrinsically taken into account where sampling has been conducted, we cannot reject that they may limit the probability of species presence where sampling has not. Fishing activity is also one of the main concerns in the Northeast Atlantic (Pimiento et al., 2023; Walker et al., 2019). In the Greater North Sea, the three main landed Rajidae species are *R. clavata*, *L. naevus*, and *R. montagui* (Amelot et al., 2021); hence, we cannot neglect an effect of fishing that we could not test in this study given the temporal range and spatial resolution of the fishing data available. Furthermore, our study did not test the possible degradation of essential habitats due to human pressures (e.g., the effect of bottom trawling on the productivity of marine fish; Collie et al., 2017). We can only stress the potential concomitant effects of climate change, fishing and habitat degradation. It is crucial to consider this new factor when implementing management measures, knowing species' sensitivity to both overfishing and climate change is higher at their range boundaries (Fredston-Hermann et al., 2020; Predragovic et al., 2023; Yan et al., 2021).

Long neglected in environmental matters, a growing number of studies, including this one, tend to demonstrate the vulnerability of elasmobranchs to climate change in addition to their vulnerability to

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anthropogenic pressures. As they are keystone species for ecosystem functioning, it is urgent to review our operating modes, from our habits to the management measures in place. These changes would then allow the necessary rebound of elasmobranchs to converge toward more resilient ecosystems.

AUTHOR CONTRIBUTIONS

Noémie Coulon: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft. **Sophie Elliott:** Conceptualization; methodology; supervision; validation; writing – original draft. **Nils Teichert:** Conceptualization; methodology; supervision; validation; writing – review and editing. **Arnaud Auber:** Methodology; resources; validation; writing – review and editing. **Matthew McLean:** Methodology; software; validation; writing – review and editing. **Thomas Barreau:** Methodology; resources; validation; writing – review and editing. **Eric Feunteun:** Funding acquisition; project administration; supervision; validation; writing – review and editing. **Alexandre Carpentier:** Conceptualization; funding acquisition; project administration; supervision; validation; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The abundance data that support the findings of this study are openly available on the ICES Database of Bottom Trawl Surveys (DATRAS) at https://datras.ices.dk. Species traits were collected by extracting traits values from Coulon et al. (2023) openly available on https://doi.org/10.6084/m9.figshare.19833304.v1 and using occurrence data from Ocean Biodiversity Information System (OBIS, 2022) openly available on https://obis.org/. Depth and slope data are openly available on the GEBCO Bathymetric Compilation Group 2019 (2019). The GEBCO_2019 Grid—a continuous terrain model of the global oceans and land. British Oceanographic Data Centre, National Oceanography Centre, NERC, United Kingdom (doi: 10.5285/836f016a-33be-6ddc-e053-6c86abc0788e). The relief and complexity data are openly available on MARSPEC: ocean climate layers for marine spatial ecology. https://doi.org/10.1890/12-1358.1. Seabed habitat data are openly available on European Marine Observation Data Network (EMODnet) (https://emodnet.ec.europa.eu/en/seabed-habitats). The pH and temperature data are openly available on E.U. Copernicus Marine Service Information (https://doi.org/10.48670/moi-00058: https://doi.org/10.48670/moi-00059). The Atlantic Multidecadal Oscillation data are openly available on the NOAA PSL (https://www.psl.noaa.gov/data/timeseries/AMO/). Phylogeny subset is openly available on the Global Phylogeny of Sharks (https://vertlife.org/sharktree/). The R code used for this study is openly available on https://github.com/ncoulon9/Coulon-et-al.-2024.

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REFERENCES

Aebischer, N. J., Coulson, J. C., & Colebrookl, J. M. (1990). Parallel long-term trends across four marine trophic levels and weather. *Nature*, *347*(6295), 753–755. https://doi.org/10.1038/347753a0

Albouy, C., Lasram, F. B. R., Velez, L., Guilhaumon, F., Meynard, C. N., Boyer, S., Benestan, L., Mouquet, N., Douzery, E., Aznar, R., Troussellier, M., Somot, S., Leprieur, F., Le Loc'h, F., & Mouillot, D. (2015). FishMed: Traits, phylogeny, current and projected species distribution of Mediterranean fishes, and environmental data: *Ecological archives* E096-203. *Ecology*, *96*(8), 2312–2313. https://doi.org/10.1890/14-2279.1

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., & Gravel, D. (2014). From projected species distribution to food-web structure under climate change. *Global Change Biology*, *20*(3), 730–741. https://doi.org/10.1111/gcb.12467

Amelot, M., Batsleer, J., Foucher, E., Girardin, R., Marchal, P., Poos, J. J., & Sys, K. (2021). Evidence of difference in landings and discards patterns in the English Channel and North Sea Rajidae complex fishery. *Fisheries Research*, *242*, 106028. https://doi.org/10.1016/j.fishres.2021.106028

Antão, L. H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Opedal, Ø. H., Heliölä, J., Henttonen, H., Huitu, O., Korpimäki, E., Kuussaari, M., Lehikoinen, A., Leinonen, R., Lindén, A., Merilä, P., Pietiäinen, H., Pöyry, J., Salemaa, M., … Laine, A.-L. (2022). Climate change reshuffles northern species within their niches. *Nature Climate Change*, *12*(6), 587–592. https://doi.org/10.1038/s41558-022-01381-x

Ashcroft, M. B. (2010). Identifying refugia from climate change: Identifying refugia from climate change. *Journal of Biogeography*, *37*(8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Bangley, C. W., Paramore, L., Shiffman, D. S., & Rulifson, R. A. (2018). Increased abundance and nursery habitat use of the bull shark (*Carcharhinus leucas*) in response to a changing environment in a warm-temperate estuary. *Scientific Reports*, *8*(1), 6018. https://doi.org/10.1038/s41598-018-24510-z

Barley, S. C., Meekan, M. G., & Meeuwig, J. J. (2017a). Diet and condition of mesopredators on coral reefs in relation to shark abundance. *PLoS One*, *12*(4), e0165113. https://doi.org/10.1371/journal.pone.0165113

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Barley, S., Meekan, M., & Meeuwig, J. (2017b). 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

Barnett, L. A. K., Jacobsen, N. S., Thorson, J. T., & Cope, J. M. (2019). Realizing the potential of trait-based approaches to advance fisheries science. *Fish and Fisheries*, *20*(5), 1034–1050. https://doi.org/10.1111/faf.12395

Birkmanis, C. A., Freer, J. J., Simmons, L. W., Partridge, J. C., & Sequeira, A. M. M. (2020). Future distribution of suitable habitat for pelagic sharks in Australia under climate change models. *Frontiers in Marine Science*, *7*, 570. https://doi.org/10.3389/fmars.2020.00570

Bouyoucos, I. A., & Rummer, J. L. (2020). Improving "Shark Park" protections under threat from climate change using the conservation physiology tool box. In S. J. Cooke, C. L. Madliger, O. P. Love, & C. E. Franklin (Eds.), *Conservation physiology: Integrating physiology into animal conservation and management* (pp. 185–204). Oxford University Press.

Bouyoucos, I. A., Watson, S.-A., Planes, S., Simpfendorfer, C. A., Schwieterman, G. D., Whitney, N. M., & Rummer, J. L. (2020). The power struggle: Assessing interacting global change stressors via experimental studies on sharks. *Scientific Reports*, *10*(1), 19887. https://doi.org/10.1038/s41598-020-76966-7

Brevé, N. W. P., Winter, H. V., Van Overzee, H. M. J., Farrell, E. D., & Walker, P. A. (2016). Seasonal migration of the starry smoothhound shark *Mustelus asterias* as revealed from tag-recapture data of an angler-led tagging programme. *Journal of Fish Biology*, *89*, 1158–1177. https://doi.org/10.1111/jfb.12994

Brevé, N. W. P., Winter, H. V., Wijmans, P. A. D. M., Greenway, E. S. I., & Nagelkerke, L. A. J. (2020). Sex differentiation in seasonal distribution of the starry smooth-hound *Mustelus asterias*. *Journal of Fish Biology*, *97*, 1870–1875. https://doi.org/10.1111/jfb.14548

Cantor, S. B., Sun, C. C., Tortolero-Luna, G., Richards-Kortum, R., & Follen, M. (1999). A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. *Journal of Clinical Epidemiology*, *52*(9), 885–892.

Carlisle, A., & Starr, R. (2009). Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Marine Ecology Progress Series*, *380*, 213–228. https://doi.org/10.3354/meps07907

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

Cattano, C., Agostini, S., Harvey, B. P., Wada, S., Quattrocchi, F., Turco, G., Inaba, K., Hall-Spencer, J. M., & Milazzo, M. (2020). Changes in fish communities due to benthic habitat shifts under ocean acidification conditions. *Science of the Total Environment*, *725*, 138501. https://doi.org/10.1016/j.scitotenv.2020.138501

Cheung, W. W. L., Frölicher, T. L., Lam, V. W. Y., Oyinlola, M. A., Reygondeau, G., Sumaila, U. R., Tai, T. C., Teh, L. C. L., & Wabnitz, C. C. C. (2021). Marine high temperature extremes amplify the impacts of climate change on fish and fisheries. *Science Advances*, *7*(40), eabh0895. https://doi.org/10.1126/sciadv.abh0895

Cheung, W. W. L., Watson, R., & Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, *497*(7449), 365–368. https://doi.org/10.1038/nature12156

Coffey, D. M., Carlisle, A. B., Hazen, E. L., & Block, B. A. (2017). Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark. *Scientific Reports*, *7*(1), 10434. https://doi.org/10.1038/s41598-017-11059-6

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

Collie, J., Hiddink, J. G., Van Kooten, T., Rijnsdorp, A. D., Kaiser, M. J., Jennings, S., & Hilborn, R. (2017). Indirect effects of bottom fishing on the productivity of marine fish. *Fish and Fisheries*, *18*(4), 619–637. https://doi.org/10.1111/faf.12193

Comeau, S., Cornwall, C. E., Shlesinger, T., Hoogenboom, M., Mana, R., McCulloch, M. T., & Rodolfo-Metalpa, R. (2022). pH variability at volcanic CO_2 seeps regulates coral calcifying fluid chemistry. *Global Change Biology*, *28*(8), 2751–2763. https://doi.org/10.1111/gcb.16093

Couce, E., Engelhard, G. H., & Schratzberger, M. (2020). Capturing threshold responses of marine benthos along gradients of natural and anthropogenic change. *Journal of Applied Ecology*, *57*(6), 1137–1148. https://doi.org/10.1111/1365-2664.13604

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*, *32*(10), 1827–1845. https://doi.org/10.1111/geb.13731

Di Santo, V. (2015). Ocean acidification exacerbates the impacts of global warming on embryonic little skate, *Leucoraja erinacea* (Mitchill). *Journal of Experimental Marine Biology and Ecology*, *463*, 72–78. https://doi.org/10.1016/j.jembe.2014.11.006

Diaz-Carballido, P. L., Mendoza-González, G., Yañez-Arenas, C. A., & Chiappa-Carrara, X. (2022). Evaluation of shifts in the potential future distributions of carcharhinid sharks under different climate change scenarios. *Frontiers in Marine Science*, *8*, 745501. https://doi.org/10.3389/fmars.2021.745501

Drymon, J. M., Carassou, L., Powers, S. P., Grace, M., Dindo, J., & Dzwonkowski, B. (2013). Multiscale analysis of factors that affect the distribution of sharks throughout the northern Gulf of Mexico. *Fishery Bulletin*, *111*(4), 370–380. https://doi.org/10.7755/FB.111.4.6

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, K. 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*(21), 4773–4787. https://doi.org/10.1016/j.cub.2021.08.062

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Dunbrack, R., & Zielinski, R. (2003). Seasonal and diurnal activity of six-gill sharks (*Hexanchus griseus*) on a shallow water reef in the strait of Georgia, British Columbia. *Canadian Journal of Zoology*, *81*(6), 1107–1111. https://doi.org/10.1139/z03-087

Edwards, M., Beaugrand, G., Helaouët, P., Alheit, J., & Coombs, S. (2013). Marine ecosystem response to the Atlantic multidecadal oscillation. *PLoS One*, *8*(2), e57212. https://doi.org/10.1371/journal.pone.0057212

Edwards, M., Beaugrand, G., Kléparski, L., Hélaouët, P., & Reid, P. C. (2022). Climate variability and multi-decadal diatom abundance in the Northeast Atlantic. *Communications Earth & Environment*, *3*(1), 162. https://doi.org/10.1038/s43247-022-00492-9

Elliot, S. A. M., Milligan, R. J., Heath, M. R., Turrell, W. R., & Bailey, D. M. (2016). Disentangling habitat concepts for demersal marine fish management. In R. N. Hughes, D. J. Hughes, I. P. Smith, & A. C. Dale (Eds.), *Oceanography and marine biology: An annual review* (Vol. *54*, 1st ed.). CRC Press. https://doi.org/10.1201/9781315368597

Elliott, S. A. M., Bearup, D., Carpentier, A., Larivain, A., Trancart, T., & Feunteun, E. (2020). Evaluating the effectiveness of management measures on skates in a changing world. *Biological Conservation*, *248*, 108684. https://doi.org/10.1016/j.biocon.2020.108684

13652486, 2024, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17157 by Content Fulfillment, Wiley Online Library on [08/12/2025]. 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

Elliott, S. A. M., Carpentier, A., Feunteun, E., & Trancart, T. (2020). Distribution and life history trait models indicate vulnerability of skates. *Progress in Oceanography*, *181*, 102256. https://doi.org/10.1016/j.pocean.2019.102256

Ellis, J. R., Cruz-Martínez, A., Rackham, B. D., & Rogers, S. I. (2004). The distribution of chondrichthyan fishes around the British Isles and implications for conservation. *Journal of Northwest Atlantic Fishery Science*, *35*, 195–213. https://doi.org/10.2960/J.v35.m485

Ellis, J. R., Pawson, M. G., & Shackley, S. E. (1996). The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-East Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, *76*(1), 89–106. https://doi.org/10.1017/S0025315400029039

Ellis, J. R., & Shackley, S. E. (1997). The reproductive biology of *Scyliorhinus canicula* in the Bristol Channel, U.K. *Journal of Fish Biology*, *51*(2), 361–372. https://doi.org/10.1111/j.1095-8649.1997.tb01672.x

Enfield, D. B., Mestas-Nunez, A. M., & Trimble, P. J. (2001). The Atlantic multidecadal oscillation and its relationship to rainfall and river flows in the continental U.S. *Geophysical Research Letters*, *28*, 2077–2080.

Faillettaz, R., Beaugrand, G., Goberville, E., & Kirby, R. R. (2019). Atlantic multidecadal oscillations drive the basin-scale distribution of Atlantic bluefin tuna. *Science Advances*, *5*(1), eaar6993. https://doi.org/10.1126/sciadv.aar6993

Feng, X., Park, D. S., Walker, C., Peterson, A. T., Merow, C., & Papeş, M. (2019). A checklist for maximizing reproducibility of ecological niche models. *Nature Ecology & Evolution*, *3*(10), 1382–1395. https://doi.org/10.1038/s41559-019-0972-5

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, *75*(6), 1259–1268. https://doi.org/10.1111/j.1365-2656.2006.01148.x

Fredston-Hermann, A., Selden, R., Pinsky, M., Gaines, S. D., & Halpern, B. S. (2020). Cold range edges of marine fishes track climate change better than warm edges. *Global Change Biology*, *26*(5), 2908–2922. https://doi.org/10.1111/gcb.15035

Garbett, A., Loca, S. L., Barreau, T., Biscoito, M., Bradley, C., Breen, J., Clarke, M., Ellis, J. R., Griffiths, A. M., Hannon, G., Jakobsdóttir, K., Junge, C., Lynghammar, A., McCloskey, M., Minos, G., Phillips, N. D., Prodöhl, P. A., Roche, W., Iglésias, S. P., … Collins, P. C. (2023). A holistic and comprehensive data approach validates the distribution of the critically endangered flapper skate (*Dipturus intermedius*). *Journal of Fish Biology*, *103*(3), 516–528. https://doi.org/10.1111/jfb.15466

Gordó-Vilaseca, C., Stephenson, F., Coll, M., Lavin, C., & Costello, M. J. (2023). Three decades of increasing fish biodiversity across the northeast Atlantic and the Arctic Ocean. *Proceedings of the National Academy of Sciences*, *120*(4), e2120869120. https://doi.org/10.1073/pnas.2120869120

Green, L., & Jutfelt, F. (2014). Elevated carbon dioxide alters the plasma composition and behaviour of a shark. *Biology Letters*, *10*(9), 20140538. https://doi.org/10.1098/rsbl.2014.0538

Grieve, B. D., Hare, J. A., & McElroy, W. D. (2020). Modeling the impacts of climate change on thorny skate (*Amblyraja radiata*) on the northeast US shelf using trawl and longline surveys. *Fisheries Oceanography*, *30*, 300–314. https://doi.org/10.1111/fog.12520

Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M., Rowley, S. J., Tedesco, D., & Buia, M.-C. (2008). Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature*, *454*(7200), 96–99. https://doi.org/10.1038/nature07051

Halouani, G., Lasram, B. R., Frida Shin, Y.-J., Velez, L., Verley, P., Hattab, T., Oliveros-Ramos, R., Diaz, F., Ménard, F., Baklouti, M., Guyennon, A., Romdhane, M. S., & Le Loch, F. (2016). Modelling food web structure using an end-to-end approach in the coastal ecosystem of the Gulf of Gabes (Tunisia). *Ecological Modelling*, *339*, 45–57. https://doi.org/10.1016/j.ecolmodel.2016.08.008

Hammerschlag, N., McDonnell, L. H., Rider, M. J., Street, G. M., Hazen, E. L., Natanson, L. J., McCandless, C. T., Boudreau, M. R., Gallagher, A. J., Pinsky, M. L., & Kirtman, B. (2022). Ocean warming alters the distributional range, migratory timing, and spatial protections of an apex predator, the tiger shark (*Galeocerdo cuvier*). *Global Change Biology*, *28*(6), 1990–2005. https://doi.org/10.1111/gcb.16045

Henson, S. A., Cael, B. B., Allen, S. R., & Dutkiewicz, S. (2021). Future phytoplankton diversity in a changing climate. *Nature Communications*, *12*(1), 5372. https://doi.org/10.1038/s41467-021-25699-w

Hipel, K. W., & McLeod, A. I. (1994). *Time series modelling of water resources and environmental systems*. Elsevier Science.

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the World's marine ecosystems. *Science*, *328*(5985), 1523–1528. https://doi.org/10.1126/science.1189930

Hopkins, T. E., & Cech, J. J. (2003). The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environmental Biology of Fishes*, *66*(3), 279–291. https://doi.org/10.1023/A:1023907121605

ICES. (2022). *Working group on elasmobranch fishes (WGEF)* (p. 90228362 Bytes). ICES Scientific Reports. https://doi.org/10.17895/ICES.PUB.21089833

Iglésias, S. P., Toulhoat, L., & Sellos, D. Y. (2010). Taxonomic confusion and market mislabelling of threatened skates: Important consequences for their conservation status. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*(3), 319–333. https://doi.org/10.1002/aqc.1083

IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. In E. S. Brondizio, J. Settele, S. Díaz, & H. T. Ngo (Eds.), (p. 1148). IPBES Secretariat. https://doi.org/10.5281/zenodo.3831673

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*(2), e719–e731. https://doi.org/10.1111/gcb.13869

Jönsson, M., Perhans, K., Appelgren, L., & Gustafsson, L. (2022). Bryophytes of conservation concern decline and traits change in retention patches during two decades following forest harvest. *Biological Conservation*, *273*, 109647. https://doi.org/10.1016/j.biocon.2022.109647

Kinney, M. J., & Simpfendorfer, C. A. (2009). Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters*, *2*(2), 53–60. https://doi.org/10.1111/j.1755-263X.2008.00046.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: Biological Sciences*, *283*(1828), 20160084. https://doi.org/10.1098/rspb.2016.0084

Lezama-Ochoa, N., Brodie, S., Welch, H., Jacox, M. G., Pozo Buil, M., Fiechter, J., Cimino, M., Muhling, B., Dewar, H., Becker, E. A., Forney, K. A., Costa, D., Benson, S. R., Farchadi, N., Braun, C., Lewison, R., Bograd, S., & Hazen, E. L. (2023). Divergent responses of highly migratory species to climate change in the California current. *Diversity and Distributions*, *00*, 1–14. https://doi.org/10.1111/ddi.13800

Maioli, F., Weigel, B., Chiarabelli, E., Manfredi, C., Anibaldi, A., Isailović, I., Vrgoč, N., & Casini, M. (2023). Influence of ecological traits on spatio-temporal dynamics of an elasmobranch community in a heavily exploited basin. *Scientific Reports*, *13*(1), 9596. https://doi.org/10.1038/s41598-023-36038-y

Manel, S., Williams, H. C., & Ormerod, S. J. (2001). Evaluating presence-absence models in ecology: The need to account for prevalence. *Journal of Applied Ecology*, *38*, 921–931.

Mann, H. B. (1945). Non-parametric test against trend. *Econometrica*, *13*, 245–259. https://doi.org/10.2307/1907187

13652486, 2024, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17157 by Content Fulfillment, Wiley Online Library on [08/12/2025]. 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

Marshall, K. N., Kaplan, I. C., Hodgson, E. E., Hermann, A., Busch, D. S., McElhany, P., Essington, T. E., Harvey, C. J., & Fulton, E. A. (2017). Risks of ocean acidification in the California current food web and fisheries: Ecosystem model projections. *Global Change Biology*, *23*(4), 1525–1539. https://doi.org/10.1111/gcb.13594

Matern, S. A., Cech, J. J., & Hopkins, T. E. (2000). Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: Evidence for behavioral thermoregulation? *Environmental Biology of Fishes*, *58*(2), 173–182. https://doi.org/10.1023/A:1007625212099

Maureaud, A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M. L., Amador, K., Anderson, S. C., Arkhipkin, A., Auber, A., Barri, I., Bell, R. J., Belmaker, J., Beukhof, E., Camara, M. L., Guevara-Carrasco, R., Choi, J., Christensen, H. T., Conner, J., … Thorson, J. (2021). Are we ready to track climate-driven shifts in marine species across international boundaries?—A global survey of scientific bottom trawl data. *Global Change Biology*, *27*(2), 220–236. https://doi.org/10.1111/gcb.15404

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., Mouillot, D., Maureaud, A. A., Hattab, T., MacNeil, M. A., Goberville, E., Lindegren, M., Engelhard, G., Pinsky, M., & Auber, A. (2021). Disentangling tropicalization and deborealization in marine ecosystems under climate change. *Current Biology*, *31*(21), 4817–4823. https://doi.org/10.1016/j.cub.2021.08.034

McLean, M. J., Mouillot, D., Goascoz, N., Schlaich, I., & Auber, A. (2018). Functional reorganization of marine fish nurseries under climate warming. *Global Change Biology*, *25*(2), 660–674. https://doi.org/10.1111/gcb.14501

Merow, C., Smith, M. J., Edwards, T. C., Guisan, A., McMahon, S. M., Normand, S., Thuiller, W., Wüest, R. O., Zimmermann, N. E., & Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, *37*(12), 1267–1281. https://doi.org/10.1111/ecog.00845

Monaco, C. J., & Helmuth, B. (2011). Tipping points, thresholds and the keystone role of physiology in marine climate change research. In M. Lesser, (Ed.). *Advances in marine biology* (Vol. *60*, pp. 123–160). Elsevier. https://doi.org/10.1016/B978-0-12-385529-9.00003-2

Montanyès, M., Weigel, B., & Lindegren, M. (2023). Community assembly processes and drivers shaping marine fish community structure in the North Sea. *Ecography*, *2023*(10), e06642. https://doi.org/10.1111/ecog.06642

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing climate change refugia for climate adaptation. *PLoS One*, *11*(8), e0159909. https://doi.org/10.1371/journal.pone.0159909

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*(5), e1001569. https://doi.org/10.1371/journal.pbio.1001569

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: Biological Sciences*, *288*(1942), 20201600. https://doi.org/10.1098/rspb.2020.1600

Musa, S. M., Ripley, D. M., Moritz, T., & Shiels, H. A. (2020). Ocean warming and hypoxia affect embryonic growth, fitness and survival of small-spotted catsharks, *Scyliorhinus canicula*. *Journal of Fish Biology*, *97*(1), 257–264. https://doi.org/10.1111/jfb.14370

Nagelkerken, I., Goldenberg, S. U., Ferreira, C. M., Ullah, H., & Connell, S. D. (2020). Trophic pyramids reorganize when food web architecture fails to adjust to ocean change. *Science*, *369*(6505), 829–832. https://doi.org/10.1126/science.aax0621

Nicolas, D., Rochette, S., Llope, M., & Licandro, P. (2014). Spatio-temporal variability of the North Sea cod recruitment in relation to temperature and zooplankton. *PLoS One*, *9*(2), e88447. https://doi.org/10.1371/journal.pone.0088447

OBIS. (2022). *Ocean biodiversity information system*. Intergovernmental Oceanographic Commission of UNESCO. www.obis.org

Oesterwind, D., Barrett, C. J., Sell, A. F., Núñez-Riboni, I., Kloppmann, M., Piatkowski, U., Wieland, K., & Laptikhovsky, V. (2022). Climate change-related changes in cephalopod biodiversity on the north East Atlantic shelf. *Biodiversity and Conservation*, *31*(5–6), 1491–1518. https://doi.org/10.1007/s10531-022-02403-y

Ovaskainen, O., & Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Cambridge University Press. https://doi.org/10.1017/9781108591720

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*(5), 561–576. https://doi.org/10.1111/ele.12757

Papastamatiou, Y. P., Watanabe, Y. Y., Bradley, D., Dee, L. E., Weng, K., Lowe, C. G., & Caselle, J. E. (2015). Drivers of daily routines in an ectothermic marine predator: Hunt warm, rest warmer? *PLoS One*, *10*(6), e0127807. https://doi.org/10.1371/journal.pone.0127807

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912–1915. https://doi.org/10.1126/science.1111322

Pimiento, C., Albouy, C., Silvestro, D., Mouton, T. L., Velez, L., Mouillot, D., Judah, A. B., Griffin, J. N., & Leprieur, F. (2023). Functional diversity of sharks and rays is highly vulnerable and supported by unique species and locations worldwide. *Nature Communications*, *14*(1), 7691. https://doi.org/10.1038/s41467-023-43212-3

Pollom, R., Cheok, J., Pacoureau, N., Gledhill, K. S., Kyne, P. M., Ebert, D. A., Jabado, R. W., Herman, K. B., Bennett, R. H., Silva, C., Fernando, S., Kuguru, B., Leslie, R., McCord, M. E., Samoilys, M., Winker, H., Fennessy, S., Pollock, C. M., Rigby, C. L., & Dulvy, N. K. (2022). Overfishing and climate change elevate extinction risk of endemic sharks and rays in the Southwest Indian Ocean hotspot and adjacent waters [preprint]. In Review. https://doi.org/10.21203/rs.3.rs-984080/v2

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*, *77*, 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x

Poulard, J.-C., & Blanchard, F. (2005). The impact of climate change on the fish community structure of the eastern continental shelf of the Bay of Biscay. *ICES Journal of Marine Science*, *62*(7), 1436–1443. https://doi.org/10.1016/j.icesjms.2005.04.017

Predragovic, M., Cvitanovic, C., Karcher, D. B., Tietbohl, M. D., Sumaila, U. R., Horta, E., & Costa, B. (2023). A systematic literature review of climate change research on Europe's threatened commercial fish species. *Ocean & Coastal Management*, *242*, 106719. https://doi.org/10.1016/j.ocecoaman.2023.106719

Preston, K. L., Rotenberry, J. T., Redak, R. A., & Allen, M. F. (2008). Habitat shifts of endangered species under altered climate conditions: Importance of biotic interactions: Biotic interactions, altered climate and habitat. *Global Change Biology*, *14*(11), 2501–2515. https://doi.org/10.1111/j.1365-2486.2008.01671.x

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J. M., & López-López, L. (2016). Response of a temperate demersal fish community to global warming. *Journal of Marine Systems*, *161*, 1–10. https://doi.org/10.1016/j.jmarsys.2016.05.001

Ratnarajah, L., Abu-Alhaija, R., Atkinson, A., Batten, S., Bax, N. J., Bernard, K. S., Canonico, G., Cornils, A., Everett, J. D., Grigoratou,

13652486, 2024, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17157 by Content Fulfilment, Wiley Online Library on [08/12/2025]. 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

M., Ishak, N. H. A., Johns, D., Lombard, F., Muxagata, E., Ostle, C., Pitois, S., Richardson, A. J., Schmidt, K., Stemmann, L., … Yebra, L. (2023). Monitoring and modelling marine zooplankton in a changing climate. *Nature Communications*, *14*(1), 564. https://doi.org/10.1038/s41467-023-36241-5

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*(10), 1936–1947. https://doi.org/10.1111/1365-2664.13693

Rogers, L. A., & Dougherty, A. B. (2019). Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Global Change Biology*, *25*(2), 708–720. https://doi.org/10.1111/gcb.14483

Rosa, R., Baptista, M., Lopes, V. M., Pegado, M. R., Ricardo Paula, J., Trübenbach, K., Leal, M. C., Calado, R., & Repolho, T. (2014). Early-life exposure to climate change impairs tropical shark survival. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1793), 20141738. https://doi.org/10.1098/rspb.2014.1738

Rubenstein, M. A., Weiskopf, S. R., Bertrand, R., Carter, S. L., Comte, L., Eaton, M. J., Johnson, C. G., Lenoir, J., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A., & Thompson, L. M. (2023). Climate change and the global redistribution of biodiversity: Substantial variation in empirical support for expected range shifts. *Environmental Evidence*, *12*(1), 7. https://doi.org/10.1186/s13750-023-00296-0

Rummer, J. L., Bouyoucos, I. A., Mourier, J., Nakamura, N., & Planes, S. (2020). Responses of a coral reef shark acutely exposed to ocean acidification conditions. *Coral Reefs*, *39*(5), 1215–1220. https://doi.org/10.1007/s00338-020-01972-0

Rummer, J. L., Bouyoucos, I. A., Wheeler, C. R., Pereira Santos, C., & Rosa, R. (2022). Chapter 25: Biology of sharks and their relatives. In J. C. Carrier, C. A. Simpfendorfer, M. R. Heithaus, & K. E. Yopak (Eds.), *Climate change and sharks* (3rd ed.). CRC Press. https://doi.org/10.1201/9781003262190

Rummer, J. L., & Munday, P. L. (2017). Climate change and the evolution of reef fishes: Past and future. *Fish and Fisheries*, *18*(1), 22–39. https://doi.org/10.1111/faf.12164

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*(9), e74648. https://doi.org/10.1371/journal.pone.0074648

Sagarese, S. R., Lauretta, M. V., & Walter, J. F. (2017). Progress towards a next-generation fisheries ecosystem model for the northern Gulf of Mexico. *Ecological Modelling*, *345*, 75–98. https://doi.org/10.1016/j.ecolmodel.2016.11.001

Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: Ocean climate layers for marine spatial ecology. *Ecology*, *94*, 979. https://doi.org/10.1890/12-1358.1

Schlaff, A. M., Heupel, M. R., & Simpfendorfer, C. A. (2014). Influence of environmental factors on shark and ray movement, behaviour and habitat use: A review. *Reviews in Fish Biology and Fisheries*, *24*(4), 1089–1103. https://doi.org/10.1007/s11160-014-9364-8

Sen, P. K. (1968). Estimates of the regression coefficient based on Kendall's tau. *Journal of the American Statistical Association*, *63*, 1379–1389.

Sguotti, C., Lynam, C. P., García-Carreras, B., Ellis, J. R., & Engelhard, G. H. (2016). Distribution of skates and sharks in the North Sea: 112 years of change. *Global Change Biology*, *22*(8), 2729–2743. https://doi.org/10.1111/gcb.13316

Shipley, O. N., Matich, P., Hussey, N. E., Brooks, A. M. L., Chapman, D., Frisk, M. G., Guttridge, A. E., Guttridge, T. L., Howey, L. A., Kattan, S., Madigan, D. J., O'Shea, O., Polunin, N. V., Power, M., Smukall, M. J., Schneider, E. V. C., Shea, B. D., Talwar, B. S., Winchester, M., … Gallagher, A. J. (2023). Energetic connectivity of diverse elasmobranch populations – Implications for ecological resilience. *Proceedings of the Royal Society B: Biological Sciences*, *290*(1996), 20230262. https://doi.org/10.1098/rspb.2023.0262

Simon, A., Poppeschi, C., Plecha, S., Charria, G., & Russo, A. (2023). Coastal and regional marine heatwaves and cold spells in the north-eastern Atlantic. *Ocean Science*, *19*, 1339–1355. https://doi.org/10.5194/os-19-1339-2023

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 & Evolution*, *2*, 288–298. https://doi.org/10.1038/s41559-017-0448-4

Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R. A., Smale, D. A., Fulton, E. A., Slawinski, D., Feng, M., Radford, B. T., Thompson, P. A., & Bates, A. E. (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, *18*(9), 944–953. https://doi.org/10.1111/ele.12474

Tanaka, K. R., Van Houtan, K. S., Mailander, E., Dias, B. S., Galginaitis, C., O'Sullivan, J., Lowe, C. G., & Jorgensen, S. J. (2021). North Pacific warming shifts the juvenile range of a marine apex predator. *Scientific Reports*, *11*(1), 3373. https://doi.org/10.1038/s41598-021-82424-9

Thompson, P. M., & Ollason, J. C. (2001). Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, *413*(6854), 417–420. https://doi.org/10.1038/35096558

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., Jonge, M. M. J., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the R-package H MSC. *Methods in Ecology and Evolution*, *11*(3), 442–447. https://doi.org/10.1111/2041-210X.13345

Tilman, D. (2001). Functional diversity.

Townhill, B. L., Couce, E., Tinker, J., Kay, S., & Pinnegar, J. K. (2023). Climate change projections of commercial fish distribution and suitable habitat around north western Europe. *Fish and Fisheries*, *24*, 848–862. https://doi.org/10.1111/faf.12773

Vaudo, J., Wetherbee, B., Wood, A., Weng, K., Howey-Jordan, L., Harvey, G., & Shivji, M. (2016). Vertical movements of shortfin mako sharks *Isurus oxyrinchus* in the western North Atlantic Ocean are strongly influenced by temperature. *Marine Ecology Progress Series*, *547*, 163–175. https://doi.org/10.3354/meps11646

Vaudo, J. J., & Heithaus, M. R. (2013). Microhabitat selection by marine mesoconsumers in a thermally heterogeneous habitat: Behavioral thermoregulation or avoiding predation risk? *PLoS One*, *8*(4), e61907. https://doi.org/10.1371/journal.pone.0061907

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*(5), 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Walker, N. D., García-Carreras, B., Le Quesne, W. J. F., Maxwell, D. L., & Jennings, S. (2019). A data-limited approach for estimating fishing mortality rates and exploitation status of diverse target and non-target fish species impacted by mixed multispecies fisheries. *ICES Journal of Marine Science*, *76*(4), 824–836. https://doi.org/10.1093/icesjms/fsy205

Walls, R. H. L., & Dulvy, N. K. (2021). Tracking the rising extinction risk of sharks and rays in the Northeast Atlantic Ocean and Mediterranean Sea. *Scientific Reports*, *11*(1), 15397. https://doi.org/10.1038/s41598-021-94632-4

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology & Evolution*, *30*, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Weigel, B., Kotamäki, N., Malve, O., Vuorio, K., & Ovaskainen, O. (2023). Macrosystem community change in lake phytoplankton

13652486, 2024, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17157 by Content Fulfilment, Wiley Online Library on [08/12/2025]. 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

and its implications for diversity and function. *Global Ecology and Biogeography*, *32*(2), 295–309. https://doi.org/10.1111/geb.13626

Weinert, M., Mathis, M., Kröncke, I., Neumann, H., Pohlmann, T., & Reiss, H. (2016). Modelling climate change effects on benthos: Distributional shifts in the North Sea from 2001 to 2099. *Estuarine, Coastal and Shelf Science*, *175*, 157–168. https://doi.org/10.1016/j.ecss.2016.03.024

Wilson, K. A., Westphal, M. I., Possingham, H. P., & Elith, J. (2004). Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biological Conservation*, *22*(1), 99–112.

Worm, B., & Lotze, H. K. (2021). Chapter 21—Marine biodiversity and climate change. In T. M. Letcher (Ed.), *Climate change* (Vol. *2021*, 3rd ed., pp. 445–464, ISBN 9780128215753). Elsevier. https://doi.org/10.1016/B978-0-12-821575-3.00021-9

Yan, H. F., Kyne, P. M., Jabado, R. W., Leeney, R. H., Davidson, L. N. K., Derrick, D. H., Finucci, B., Freckleton, R. P., Fordham, S. V., & Dulvy, N. K. (2021). Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. *Science Advances*, *7*(7), eabb6026. https://doi.org/10.1126/sciadv.abb6026

Young, E. F., & Holt, J. T. (2007). Prediction and analysis of long-term variability of temperature and salinity in the Irish Sea. *Journal of Geophysical. Research*, *112*, C01008. https://doi.org/10.1029/2005JC003386

Zunino, S., Canu, D. M., Zupo, V., & Solidoro, C. (2019). Direct and indirect impacts of marine acidification on the ecosystem services provided by coralligenous reefs and seagrass systems. *Global Ecology and Conservation*, *18*, e00625. https://doi.org/10.1016/j.gecco.2019.e00625

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