Title: Temperature change effects on marine fish range shifts: a meta-analysis of ecological and methodological predictors

Running title: Meta-analysis of range shifts in marine fish

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Abstract

The current effects of global warming on marine ecosystems are predicted to increase, with species responding by changing their spatial distributions. Marine ectotherms such as fish experience elevated distribution shifts, as temperature plays a key role in physiological functions and delineating population ranges through thermal constraints. Distributional response predictions necessary for population management have been complicated by high heterogeneity in magnitude and direction of movements, which may be explained by both biological as well as methodological study differences. To date, however, there has been no comprehensive synthesis of the interacting ecological factors influencing fish distributions in response to climate change and the confounding methodological factors that can affect their estimation. In this study we analyzed published studies meeting criteria of reporting range shift responses to global warming in 115 taxa spanning all major oceanic regions, totaling 569 three-dimensional population responses (latitudinal, longitudinal and depth), with temperature identified as a significant driver. Overall, studies on marine fish distributional responses have generally been of limited spatial and temporal scope, with comparisons among studies being complicated by large variation in methodology. We identified varying degrees of heterogeneity in latitudinal range shifts (km year^{-1}) across ecological and methodological predictors, with multivariate regression analysis revealing response rate differences due to niche affinity, depth changes, as well as methodological biases due to different approaches in estimating and reporting latitudinal range shifts. Finally, we found strong geographical publication bias and limited taxonomical scope, highlighting the need for more representative and standardized research in order to address heterogeneity in distribution responses and improve predictions in face of changing climate.

Key words: range shift, distribution changes, temperature, climate change, marine, meta-analysis, fish, methodological bias

Author contributions

C.D. and S.K. conceived the project. C.D. collected the data and performed the analyses with help by S.K. C.D. wrote the first version of the manuscript with input from S.K. All authors contributed to the final version.

Conflict of Interest Statement

All authors declare that they have no conflicts of interest.

Introduction

Over the last century, global warming has had substantial impacts on marine ecosystems, with species locally extirpating (Pinsky et al. 2019), changing distributions in depth and latitude (Poloczanska et al., 2013; Chen et al., 2011; Kortsch et al., 2012), or in some cases shifting phenotypes in response to climatic pressures (Manhard et al., 2017; Perry et al., 2005; Ryu et al., 2020). In marine ectotherms such as fish, population distributional limits are influenced by physiological thermal constraints, as temperature affects critical functions such as metabolism, growth and reproduction (Addo-Bediako et al., 2000; Angilletta et al., 2002; Roessig et al., 2004). Accordingly, species' range changes in response to climate change have been up to seven-fold faster in the ocean as compared to on land (Poloczanska et al., 2013). As marine temperatures are forecasted to continue rising, the ability to predict fish redistributions will be vital to protect ecosystem functions, maintain food security and other contributors to human well-being (Bonebrake et al., 2018; Pecl et al., 2017). A central challenge in predictive species range modeling has been the observation that, although many ranges have displayed anticipated poleward shifts in response to warming (Chen et al., 2011), a substantial number of range shifts have not followed projections and show significant variation in rate and direction of movements (Urban, 2015; Poloczanska et al., 2013), complicating population response predictions and conservation management. A key development in addressing this variation has been the acknowledgement that a suite of other non-temperature associated biotic factors, including species interactions (Louthan et al., 2015; Ellingsen et al., 2020), ecological and life history traits (MacLean and Beissinger, 2017) and eco-evolutionary dynamics (Cacciapaglia and van Woesik, 2018; Fredston et al., 2021; Nadeau and Urban, 2019), can also affect a population's ability to colonize and establish in novel environments, and should thus be incorporated into forecasts. However, an often overlooked factor in predicting and synthesizing climate change responses are differences in methodological approaches to measuring population distribution changes over time (Wolkovich et al., 2012; Brown et al., 2016), which might explain part of the observed variation in direction and velocity of responses to temperature, even within the same geographical and taxonomic context. For example, for some marine fish species within the same geographic regions seemingly contradictory responses are being reported. In the North Atlantic, for example, some studies suggest rapid environmental tracking at a rate corresponding to the local climate velocity (the pace and direction of climate shift across landscape; Frainer et al., 2017; Perry et al., 2005), while other multidecadal studies on range shifts suggest that only few are completely keeping pace with changing climate (Fredston-Hermann et al., 2020) and report significantly slower distribution responses (Campana et al., 2020). Addressing this variation will be key to improved response predictions informing conservation management, particularly as the magnitude of range shifts is likely to increase under climate change forecasts. To date, however, there has been no comprehensive synthesis of the interacting ecological factors influencing fish distributions in response to climate change and the confounding methodological factors that can affect their estimation.

The lack of attention to methodological biases in marine range shift research is surprising considering the wide range of methods for data acquisition, processing and modeling, resulting in high heterogeneity of research quality and results. While some methodological details need to be tailored to be suitable for specific taxa, ecosystems and geographical conditions, large heterogeneity in other variables potentially affecting accuracy such as population sampling effort, temporal resolution and statistical approaches remain. For example, redistribution inferences may be affected by sampling methods including choice of proxy for distribution measurement (Brown et al., 2011; Wernberg et al., 2012), including the ‘center of distribution’ (COD) which constitutes the mean latitude of the spatial extent (e.g., Li et al., 2019; Hsieh et al., 2009; Husson et al., 2022), or a population’s most extreme boundaries of longitude, latitude or depth, inferred, for example, by presence-absence data (e.g., Fredston-Hermann et al., 2020). How these distribution indices are obtained also affects the predictions that are produced (Brown et al., 2016): popular data sources include abundance data from survey trawls by long term fisheries or research programs (Perry et al., 2005; Yemane et al., 2014), tagging-recapture data (Hammerschlag et al., 2022; Neat and Righton, 2007), historical records (Kumagai et al., 2018), or genetic-molecular methods (Knutsen et al., 2013; Spies et al., 2020). Each of these methods has various costs and benefits, tradeoffs associated with monetary expense, sampling effort and feasibility on the one hand, and the likelihood of observing specific species or species types, achieving adequate sample sizes, and spatial-temporal resolution on the other. Variation also exists in the data analysis stage, including the decision of whether to report movement estimates for a single species or cumulative inferences for whole assemblages reflecting changes in community traits and composition (e.g., Dulvy et al., 2008; Frainer et. al., 2017). Response estimates in marine taxa were also shown to be affected when other climatic predictors than temperature, such as salinity (Champion et al., 2021), oscillation indexes (Nye et al., 2009; Han et al., 2020), bathymetry (Li et al., 2019; Hammerschlag et al., 2022), or non-climatic drivers such as food availability (Smith et al., 2021) or exploitation by fishing (Engelhard et al., 2014; Bell et al., 2015), were included (Brown et al., 2016). Nevertheless, robust data from wild marine fish populations incorporating both biotic and abiotic drivers of climate responses remain scarce (but see Adams et al., 2019), with potential differential effects on response estimates between single and multi-predictor models remaining unexplored. Overall, while this methodological variation is known to exist, it remains unclear whether it has generated any systematic biases in the existing literature which may distort estimates of geographical shifts across fish species.

This review aims to summarize the current state and remaining gaps of knowledge on ecological and methodological factors influencing range shifts in response to ocean warming in marine fish. The scope of this review is limited to dynamics at the leading edge of range shifts, where expansion velocities are most frequently outpacing contraction speeds at trailing edges (Poloczanska et al., 2013). First, we carried out a systematic literature review to gather data from existing original articles meeting criteria of measuring range shifts due to sea temperature. The aim was to investigate trends between rate of temperature change and range shifts across different niches, habitats and other ecological factors such as life stage and marine exclusivity. Second, we summarized the current state of methodology prevalent across these studies, such as data acquisition and analysis methods, temporal and spatial resolution, and estimated the effects of study methods on population redistribution inferences.

Methods

Literature search and eligibility criteria

The methodology of this review and meta-analysis was guided by the Preferred Reporting Items for Systematic reviews and Meta-analyses (PRISMA; Page et al., 2021).

Only original research papers documenting latitudinal or depth responses to temperature in marine fish were considered. The terms range and distribution shifts are used in this study interchangeably and refer to, based on definitions used by Parmesan et al. (2005) and Sorte et al. (2010), a change in the distribution of native species' boundaries from their historical boundaries, including relocations, expansions, contractions along range edges. For a study to be included in the analysis, it had to have a minimum sample size of 30 marine fish per investigated species, discuss temperature as a likely driver of distributional range changes (preferably by statistical association) and have a span of at least five years, as fewer temporal sampling points may increase bias of short-term responses to climate fluctuations rather than long-term redistribution trends (Poloczanska et al., 2013). Studies looking at seasonal distribution responses or being only concerned with response predictions were excluded as this review is focused on historical long-term range changes. This review was limited to studies reporting quantified measurements of spatial change, for example in centers of distribution (COD), range edges (mean latitude in degrees or kilometers) or depth changes (in meters) over a defined time span, excluding reports of community compositional changes. Studies were included if their methodology included presence-absence data, abundance data combined with another type of data, molecular methods or long-term tagging studies (at least 10 years with at least 10 individuals). Public science-based studies were only included if steps to reduce bias and false reporting were taken, such as verifying sightings by taxonomic experts. Reports based on new sightings only were excluded, as this type of data usually has low sample sizes and is prone to extreme outliers or misidentification.

Studies were identified by performing a literature search on the electronic database Web of Science in June 2022 with different combinations of the keywords '*fish geograph*'*,

’distribution’, ‘range’, ‘shift’, ‘contract’, ‘expan*’* on studies dating until present, and were limited to articles in the research area of Zoology published in English language (Table 1). Additionally, suitable articles were identified further by scanning reference lists and review articles on related topics. Authors of four studies were contacted via email to obtain missing information on results and methodology. Of these, co-investigator Dr. Maria Fossheim provided species-wise raw data of latitudinal changes in distribution in February 2022 from the paper by Husson et al. (2022).

Table 1. Search strategy and information sources. *Six searches were performed in the online database Web of Science (WoS) including different combinations of the search terms ‘fish geograph*’, ’distribution’, ‘range’, ‘shift’, ‘contract*’, ‘expan*’ with no date limitation for English original articles within the Zoology research area in June 2022; with results showing number of hits for each search term.*

Search Number	Search Engine	Search Term	Results	Type	Research Area
1	WoS	fish geograph* distribution contract* temperature	45	articles	Zoology
2	WoS	fish geograph* range shift temperature	210	articles	Zoology
3	WoS	fish geograph* range expan* temperature	149	articles	Zoology
4	WoS	fish geograph* range contract* temperature	44	articles	Zoology
5	WoS	fish geograph* distribution shift temperature	280	articles	Zoology
6	WoS	fish geograph* distribution expan* temperature	168	articles	Zoology

Study selection

Records retrieved from the database were screened for duplicates and manually checked for the first round of eligibility, according to which abstracts had to confirm the study focus to include marine fish and distributional range changes in response to temperature. Further four rounds of filtering were performed according to inclusion and exclusion criteria (Table 2). This process was performed independently by one reviewer, while the second reviewer randomly selected a sample of five studies in every stage to assess, with disagreements between reviewers being resolved by consensus. Articles extracted from references were simultaneously screened for eligibility in the same manner.

Table 2. Study selection criteria. *After removal of duplicates from the database search, five rounds of screening were performed according to criteria concerning study focus and appropriate methodology, with the number of unique articles left after each selection round shown.*

Filtering number	Study selection criterium	Criterium description	No. of unique studies
1	Fish and marine ecotype	Sampling marine fish	169
2	Range shift criteria	Change in range over latitudes, distribution changes, long-term (min 5 years) not seasonal, no first sightings	89
3	No projections	Exclude prediction studies	81
4	Clear measurement	Calculated shift in latitude (by degrees or kilometers), e.g. of center of distribution or range edges	67

5	Appropriate data type	Abundance data combined with presence absence data (or clear measurement provided), or other methods such as long-term studies, tagging or genetic molecular methods	15

Data collection process

After the filtering process, an extraction sheet with variables of interest was created. We pilot-tested five records and refined the sheet accordingly. In cases where variables were provided only in graphical rather than numerical representations, numeric data was extracted manually from graphs using WebPlotDigitizer version 4.5 (Rohatgi, 2021). For temperature, yearly temperature values were extracted from graphs: a) for longitudinal studies, annual temperature rate (°C year^{-1}) was calculated as the difference between temperature estimate at the beginning and end of sampling period, divided by total duration; b) for studies comparing cold versus warm periods, from yearly estimates mean values for each period were calculated, to then compare the difference in cold periods relative to the warm periods. For graphical representations of distribution responses over time (reported for every year or usually per decade in raster maps) and where no numerical values could be obtained (either not provided or authors were unresponsive to requests), latitudinal changes were calculated as the difference in mean latitude of species presence data (from the sum of all latitude coordinates where species was recorded to be present, usually in 5° windows) between start and end of sampling period.

Data items

Information from each study was extracted covering the following:

(1) Species name (scientific and common) and their habitat and niche affinity, as provided by the study or otherwise sourced from the online fish catalog fishbase.org (version 02/2022);

(2) Whether a latitudinal redistribution was observed and the type (range shift, expansion or contraction) and direction (north, east, south, west-wards and whether this constituted a poleward direction);

(3) Whether depth changes were recorded and if changes were significant and according to temperature predictions with deeper or shallower depth changes;

(4) Temperature and its measurement type (sea surface or bottom water temperature), whether temperature was statistically tested for association with range shifts and whether it was a significant predictor of the changes; as well as yearly temperature change, as reported for sampling locations or approximate study area. If temporal temperature data was not provided, mean sea surface temperature (SST) estimates were derived from the NOAA Physical Sciences Laboratory data of annual SST averages in 5° resolution within approximate sampling location coordinates, accessed at (https://psl.noaa.gov/cgi-bin/data/timeseries/timeseries1.pl).

(5) Other significant predictors of distribution changes identified by the study;

(6) Methods of measurement which were classified into five categories: center of distribution (COD), shifts in range edges (RG), mean depth changes (MD), and genetic molecular methods (GM), and a category for all other methods (O) such as the less frequent approach of long-term citizen science studies or tagging/tracking studies.

(7) Overall size of shift (OSS), i.e., total distance moved in depth and longitudinally/latitudinally over the study period; whether OSS was provided in a quantifiable form (e.g., °latitudes, kilometers year^{-1} or kilometers °C^{-1}). Some studies provided only combined averages for grouped species (such as by habitat affinities) either for latitudinal and depth or latitudinal changes only and were marked appropriately (OSS_C, OSS_{C*}, respectively) to further treat with caution as these may reduce accuracy and statistical power in further

meta-analyses. Studies were further divided into two categories: those which measured distributional and temperature changes longitudinally in succession every year, and others which divided the study period into cold and warm years according to yearly temperature anomaly estimates and based further analyses on the comparison between cold and warm years.

(8) Amount of change in horizontal range shifts and depth, with estimates standardized into kilometers year^{-1} and meters year^{-1}, respectively, by dividing the total change by study period. Where range shifts were reported in degrees, the result was converted into kilometers by the approximate conversion of 1 °latitude ≈ 110.574 km. While many studies reported shifts along the West-East axis, it was mostly not feasible to extract separate shift rates, and thus the OSS values taken here represent the sum of all movements of all directions, with North-South movements being significant in all cases where range shifts were confirmed. Annual latitudinal range shift (LRS) rates were represented relative to poleward direction, where positive values represent poleward shifts and negative values represent negative shifts.

(9) Data on sampling are size (in km^2): where not provided, approximate estimates were extracted according to sampling map coordinates;

(10) Information on life stage, e.g., whether sampled individuals were eggs, juveniles or adults; and whether fish were marine exclusive or anadromous;

(11) Location (continent, sea or ocean) and duration (in years) of the respective study. All data items were extracted separately where studies subdivided sampling location and time periods. For example, in the case when studies divided population distributions within an ecoregion into different areas, e.g., round fish areas in the North Sea (Bluemel et al., 2022) or subregions in the Eastern Pacific based on fishing management areas or local oceanographic conditions (e.g., Li et al., 2019). Separate data entry points for analyses in this study also

constituted instances of divided study periods, reflecting relevant temporal trends in biomass or (seasonal) water temperature fluctuations (e.g., Bluemel et al., 2022; Bell et al., 2015).

(12) Type of data used to calculate distribution location (e.g., COD or range edges) - abundance data, presence-absence data, tagging data (T), observations from long-term sightings (S) or information from genetic-molecular analyses (G). For the study by Husson et al. (2022), of which raw data was obtained for 29 species, two sets of LRS estimates were included in this study - one set of COD estimates weighted by abundance data and another weighted by presence-absence data, totaling 58 entries included in further analyses.

(13) Depending on type of data collection method, the number of individuals collected, such as in tagging-recapture studies (e.g., Neat and Righton, 2006; Hammerschlag et al., 2022), reports based on long-term sighting records (e.g., Kumagai et al. 2018) or using population genetic techniques (e.g., Knutsen et al., 2013); and the yearly average of stations fished, such as in studies relying on abundance data from trawling surveys, were extracted. All data are provided in Supporting Dataset 1.

Summary measures

The aim was to estimate standardized responses of latitudinal and depth shifts in marine fish distributions over time from studies that used a diversity of measurement methods. In most cases, the shifts were measured as the spatial change of the center of distribution of a given species (sometimes multiple species forming an assemblage) for every study year, or between cold and warm years. Some studies also measured mean latitude changes of the leading range edge (e.g., Fredston et al., 2021) or tested the effect of interactions between multiple environmental factors including chlorophyll-a concentrations, ocean currents, pH and oxygen concentrations in addition to water temperature on the probability of species presence. Due to many cases of non-compatible forms of reported data across studies, data transformations and extractions were performed to calculate *ΔTemperature* °C, the difference in temperature between end and start of sampling periods divided by the number of study years, and the total amount of range change over the study period.

The meta-analyses were performed by selecting multivariate models with random effects, with the best models chosen according to likelihood ratio tests. We included 'Study' as a random effect to account for multiple estimates derived from the same paper. The primary analytical unit was the estimate for a given species or group of species of distance in latitude moved per year (LRS; km year^{-1}) in response to temperature.

Additionally, summary statistics of implemented methods across studies, geographical study distribution and other identified significant LRS predictors were reported, as described in the 'Assessment of methodology' section.

Model selection

Factors which may affect LRS in response to *ΔTemperature* (°C year^{-1}) and were tested in linear mixed effect models included:

a) methodological factors. *OSS reporting* (per species (1) or group of species (*C/C**)), *Data type* (single or combinations of abundance (A), presence-absence (P), genetic (G), long-term sightings (S), tagging (T) or other (O) data), Study span (duration of sampling time; years), *Area size* (geographical area of sampling locations; km^2) and *Non-temperature predictors*, a binomial factor indicating whether any other non-temperature predictors were identified;

b) ecological predictors: *Niche* (four categories: deep-water, polar, temperate, tropical), *Depth change* (whether depth change occurred as predicted by temperature change

(Yes/No)), *Habitat* (seven categories: bathydemersal, bathypelagic, benthopelagic, demersal, pelagic-neritic, reef-associated) and their interactions. Interactions between depth change and habitat or niche might reflect disproportional depth responses, where some habitats and niches might be less or more able to change depth. *ΔTemperature* and *Depth change* interaction might reflect heterogenous depth responses depending on the rate of warming, where fish in faster warming waters might be more likely to shift depth. To investigate the effect of vertical distribution shifts on latitudinal range changes, initially *Yearly depth change* rates (m year^{-1}) were included, however, the former yielded small model sample size ($n = 41$) and thus was replaced by the binomial *Depth change* predictor ($n = 136$), as many studies investigated depth changes without estimating rates.

The best model was selected by a back- and forward-ward selection process, starting with the 'full' model (Equation 1) and reducing predictors until the best configuration was identified based on the lowest Akaike Information Criterion (AIC), calculated in the *lmerTest* package (v3.1-3, Kuznetsova et al., 2017) by maximum likelihood method. A more complex model was deemed significantly better than the simpler one when $\Delta AIC > 4$.

From the full model, one outlier identified with a Bonferroni outlier test (*car* package v.3.1, ref) was removed (Bonferroni $p < 0.001$), which significantly improved model fit ($\Delta AIC = 32$). Log-transformations to improve data normality were used for each numerical predictor one by one and included if model fit was improved according to AIC. For each model (Supplementary Table S2), log-likelihoods, p-values were calculated using Satterthwaite's approximations and three-way ANOVAS were performed for model comparison in the *lmerTest* package. The assumption of residual normality was determined to be satisfactory by visually inspecting residual and QQ plots. Concerns about any potential violation of this assumption should be alleviated by the fact that mixed-effect models are known to be generally robust to violations of model assumptions.

For the best fitting model, marginal and conditional effect sizes (R^2) for mixed-effect models were calculated in the *MuMIn* package (v.1.46.0, Barton and Barton, 2015) according to Eq. 1 and Eq. 2, respectively. The marginal R^2 represents variance explained by fixed predictors, while the conditional statistic shows the variance explained by both fixed and random effects, f representing the variance of fixed effects, α the variance of random effects, and ε the observation-level variance (Nakagawa and Schielzeth, 2013). Relative contributions of predictors to explained variation in range shift rates were compared by calculating partial marginal R^2 estimates (Nakagawa and Schielzeth, 2013).

$$R^2_{\text{marginal}} = \frac{\sigma^2_f}{\sigma^2_f+\sigma^2_\alpha+\sigma^2_\varepsilon} \qquad \text{(Equation 1)}$$

$$R^2_{\text{conditional}} = \frac{\sigma^2_f+\sigma^2_\alpha}{\sigma^2_f+\sigma^2_\alpha+\sigma^2_\varepsilon} \qquad \text{(Equation 2)}$$

Assessment of methodology

Summary statistics for the frequency of publication years, mean study period, mean study area size with standard deviations were calculated. Aspects of methods used across investigated studies, such as how and what type of data to calculate range shifts was obtained, how and if LRS was reported are summarized in Table 3.

To identify geographical publication biases, studies were grouped into locations (North Sea, Barents Sea, Northwest Atlantic, East Pacific, Bering Sea, Yellow Sea, Southwest Atlantic, central Indian Ocean, central Atlantic and central Pacific) based on their central coordinates of sampling area and visualized on a map with frequencies representing number of studies per location. Study locations in central Indian, central Atlantic and central Pacific originated from a single study (Worm and Tittensor, 2011) which had large sampling areas. Total numbers of type of range changes (shift, expansion or contraction) across data entries of populations analyzed (n = 569) and direction of shift (North, South, West, East) of species per location were calculated, with trends of shift directions shown as proportion of species per location moving in either of the four directions.

To assess risk of study publication bias, a funnel plot and regression of the effect sizes (reported LRS estimates) on sample sizes (N) was computed. As studies either did not report sample size or had no uniform unit, depending on the study method, N was either the total number of fish sampled per population or average number of stations per year trawled. Symmetry of the funnel shape was inspected visually and tested with a regression of effect sizes (y) on $1/\sqrt{N}$ (Tang and Liu, 2000), where p-values below significance threshold ($\alpha = 0.05$) suggest potential publication bias (Supplementary Fig. S2A-B). While for funnel plot regression analyses most commonly the weighted standard error of effect sizes are used (e.g., Egger's test; Egger et al. 1997), this measure was not available for most studies and was replaced by sample size in Tang and Liu's test (2000), which addresses the inflated false positive rates associated with the former regression test (Jin et al., 2015).

Average LRS estimates across different predictors were expressed in medians and respective interquartile ranges (IQR), i.e., the difference between the upper lower quartile range of the data, due to the tendency for the data to have skewed distributions and outliers. Data was analyzed and plots were created in the software R (version 4.2.1; R Core Team, 2018).

Table 3: Assessment of methodology of reviewed literature. *Questions regarding methodology aspects potentially affecting effect size of LRS (latitudinal range shift) of reviewed studies (n = 37) and how they were answered are shown. Studies were divided into types (longitudinal or cold vs. warm period comparisons), OSS (overall shift size) reporting (individual or grouped values for range shift rates), data types (abundance, presence-absence data or other), with their differences tested in the selection process of mixed-effect linear models.*

Methodology aspect investigated		**Method**
Depth change	*How many studies investigated vertical range shifts?*	Count data
	Did depth change affect effect size?	Multivariate regression model
Was temperature effect statistically tested?		Count data
Were other significant explanatory variables identified? What were they?		Count data
Prevalent data types	*What were they?*	Frequencies of data categories
	Did they differentially affect effect sizes?	Multivariate regression model
Study location	*Were there biases in publication location?*	Summary of distribution of publication locations
	Did location affect effect sizes?	Visual assessment
How was OSS reported?	*What was the prevalence of estimates reported for species or groups of species?*	Count data
	Did differences in OSS influence affect effect sizes?	Multivariate regression model
Did study type affect effect sizes?		Multivariate regression model

Results

Study selection

A total of 37 studies were identified for inclusion in the review (Supplementary Table S1). The search of Web of Science databases provided a total of 896 records. After adjusting for duplicates and studies which do not include marine fish 169 remained. Of these, another 153 studies were discarded during the filtering process through reviewing the abstracts and examining article methods in detail. An additional 22 studies that met the criteria for inclusion were identified by checking the references of relevant papers and searching for studies that have cited these papers (Fig. 1).

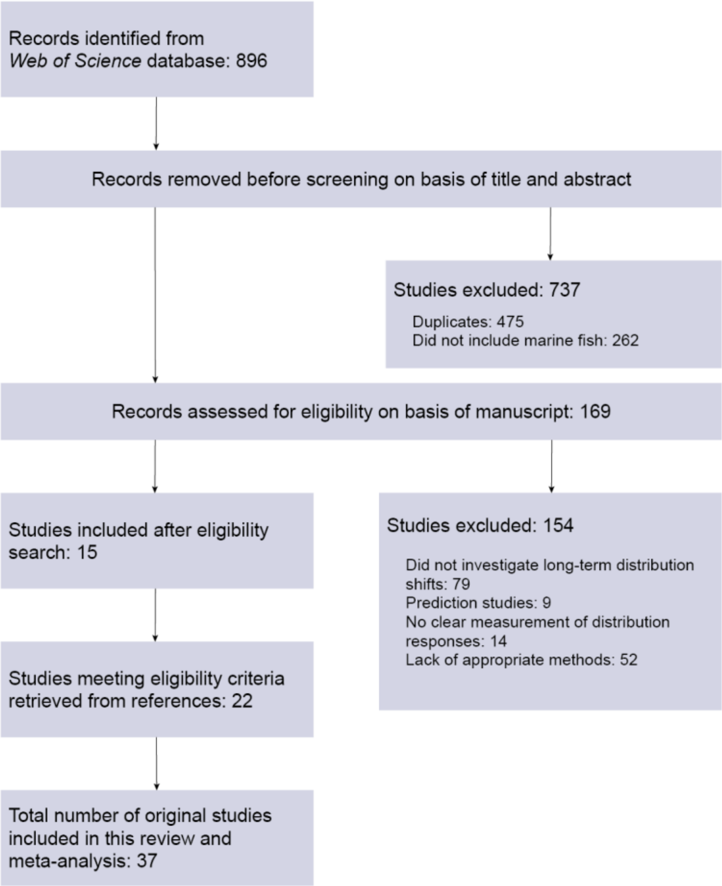

Figure 1: Flow Chart representing stages of the study selection process*. From the original 896 records found in the bibliographic database Web of Science with search terms shown in Table 1, studies were scanned first by title and abstract for eligibility, and further filtered by*

criteria concerning methodology (see Table 2). Additional 22 studies meeting criteria were retrieved from relevant references, totaling a final of 37 articles included in this analysis.

Geography

The average sample size across the 11 major locations was 51.7 (±37.1) species per location, with more than half (67%) of all populations displaying a range shift, of which 13% expanded range, and 8% contracted their range, when excluding multi-species LRS estimates (Fig. 2). Most populations showing range shifts moved northward (42%) while a quarter moved south, with only 7% and 9% moving east or west, respectively. Overall, more than half (54%) of the populations moved poleward, particularly in Asia (4 out of 4), Australia (50 out of 55), the North Sea (53 out of 80), the Bering Sea (41 out of 56) and the Barents Sea (49 out of 59).

In the East Pacific, central Atlantic and Indian oceans movement was less directional and more proportional across all directions, with 68%, 64% and 50% of populations, respectively, not showing any significant horizontal shifts (Fig. 2). While some populations were classified as moving into multiple directions depending on the specific study, e.g., northeast or southwest which here were calculated as separate counts for each of the four major directions, many studies investigated movements only across the north-south axis, which could have biased lower frequencies of shifts on the east-west axis.

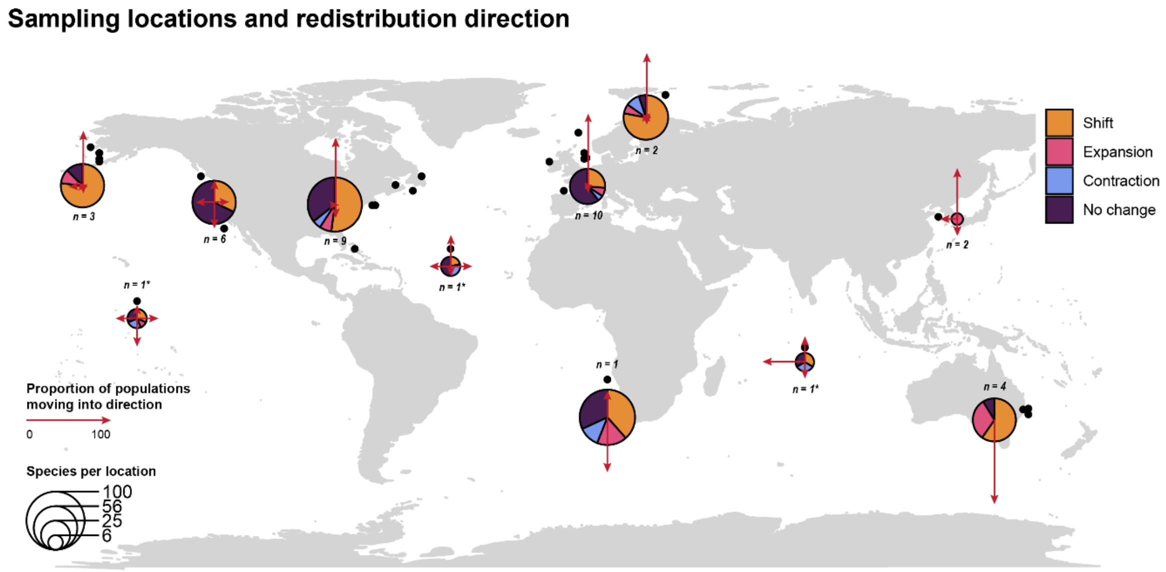

Figure 2: Map of sampling locations and sizes with type of range shift. *From articles included in this review (n = 37), study locations were grouped into 11 locations which are represented by pie charts. Cumulative number of species sampled per location is shown as pie chart circle size, with number of studies per location denoted as n. Type of range change is color-coded: range shift (orange), range expansion (pink), range contraction (blue), no change (purple), and shown in proportions from total counts of sampled populations per location. Arrows indicate proportions of populations per location moving along four directions (north, east, south and west). Black points represent the center of individual study sampling locations. Range shift estimates from multi-species estimates (n = 92) were excluded. Asterisks (*) indicate the same single study by Worm and Tittensor (2011) covering most of the Pacific, Atlantic and Indian oceans.*

When comparing individual LRS rates among major geographical locations, the southwest Pacific (Australian coast) had by far the fastest latitudinal range changes ($\text{median}_{\text{LRS}}$ = 20.7 km year^{-1}; IQR = 12.4), followed by South African population ($\text{median}_{\text{LRS}}$ = 7.4 km year^{-1}; IQR = 16.6), the North Atlantic ($\text{median}_{\text{LRS}}$ = 5.7 km year^{-1}; IQR = 17.9; Supplementary Figure 5). In the Northeast Pacific, marine fish shifted around 0.8 km year^{-1} (IQR = 0.2; n = 5), while the Bering Sea saw shifts of 1.3 km year^{-1} (IQR = 2, n = 46).

Methodology

The mean study duration was 41 (±49) years, at a sampling area size of 356,628 (±358,127) km^2 on average. Strong geographical bias of study location was observed - half of the studies originated from North America, with almost a third (31%) performed in Europe. Australia, Asia and Africa had even less representation with 11%, 6% and 3% of the identified research articles, respectively. No eligible reports from South America and Antarctica were identified in study.

Most frequently investigated taxa were classified as tropical (n = 62), followed by temperate (n = 48), deep-water (n = 37) and 19 polar populations (Supplementary Fig. S1). The most frequently studied fish families included *Pleuronectidae* (n = 78, particularly *Microstomus*, *Atheresthes, Eopsetta* and *Pleuronectes* spp.), *Gadidae* (n = 51, *Gadus*, *Melanogrammus*, *Pollachius* spp.), *Scombridae* (n = 28, *Scomber* and *Thunnus* spp.), *Rajidae* (n = 21, including *Amblyraja radiata* and *Leucoraja* spp.), *Sebastidae* (n = 19 such as *Helicolenus dactylopterus*, *Sebastes* spp.).

Out of 37 reviewed studies 26 provided sample size estimates, of which 13 reported total number of fish samples per population (median_N = 1172; IQR = 3384) and 17 provided average stations fished per year (median_N = 117; IQR = 246). From eye-balling the resulting funnel plots of regressed LRS effect sizes on sample sizes, there was little evidence for risk of publication bias, particularly when the N proxy was individuals sampled per population (Supplementary Fig. S2A). Although a regression test suggested significantly asymmetrical funnel shape ($F_{1,152}$ = 396; p = 0.048) when expressing N as mean yearly rate of stations trawled, this proxy provided significantly less resolution of effect size distribution due to sampling of multiple populations with high heterogeneity in LRS across the same fishing stations (Supplementary Fig. S2B).

Nearly 80% of studies implemented statistical tests to investigate range shift association with temperature changes, and over a third investigated depth changes and the trailing front of distribution ranges. The majority of studies were longitudinal, i.e., assessed range changes across successive years, as opposed to comparing seasonal thermal variation and. From those studies confirming range shifts, most reported LRS sizes for individual species (77%), with four reporting combined shift sizes for groups of at least two species (Table 4). The most common types of data used across studies included abundance (78%) and presence-absence data (64%), which in some studies were used together.

Table 4. Methodology aspects of reviewed studies. *Percentages of the total (n = 37) included studies corresponding to the listed criteria are shown, with total counts in brackets.*

Tested association with temperature statistically		76% (29)
Investigated depth changes		42% (16)
Investigated trailing edge		34% (13)
Study span ≥20 years long		68% (26)
Compared cold to warm periods		10% (4)
Overall shift magnitude provided (from 35 confirming range shifts)	*Yes*	77% (27)
	No	17% (6)

	Combined (for both latitudinal and depth or only latitudinal changes)	11% (4)
Type of data	*Abundance*	78% (28)
	Presence-absence	64% (23)
	Genetic molecular	5.5% (2)
	Tagging	5.5% (2)
	Long-term sightings	5.5% (2)
	Other	11% (4)

Factors affecting range-shift estimation

The best model, according to both AIC (AIC = 257) and ANOVA tests, included log-transformed LRS and the predictors *ΔTemperature*, *OSS reporting*, *Niche* and *Depth change,* of which all but *ΔTemperature* were significant ($p < 0.05$, Supplementary Tables S3-4). The model had an intermediate effect size when considering only fixed effects ($R^2_{marginal} = 0.43$), with *OSS reporting* explaining 39% of the variance in range shifts and the ecological factors *Depth change* and *Niche* accounting for 25% and 10%, respectively (due to shared variances, individual predictors did not add up to total marginal variance).

From the filtered dataset for outliers, from which the highest likelihood model was fitted, 270 individual population-wise LRS estimates were retained, while 92 entries provided LRS estimates for grouped populations, such as species combined into assemblages according to niche or temperature affinity (e.g., Dulvy et al., 2008; Li et al., 2019; Pinsky et al., 2013). Median LRS was higher among studies which reported range shift sizes for individual populations (median$_{LRS}$ = 4.14; IQR = 6.55), as compared to those that grouped populations (median$_{LRS}$ = 0.3; IQR = 1.13; Fig. 3).

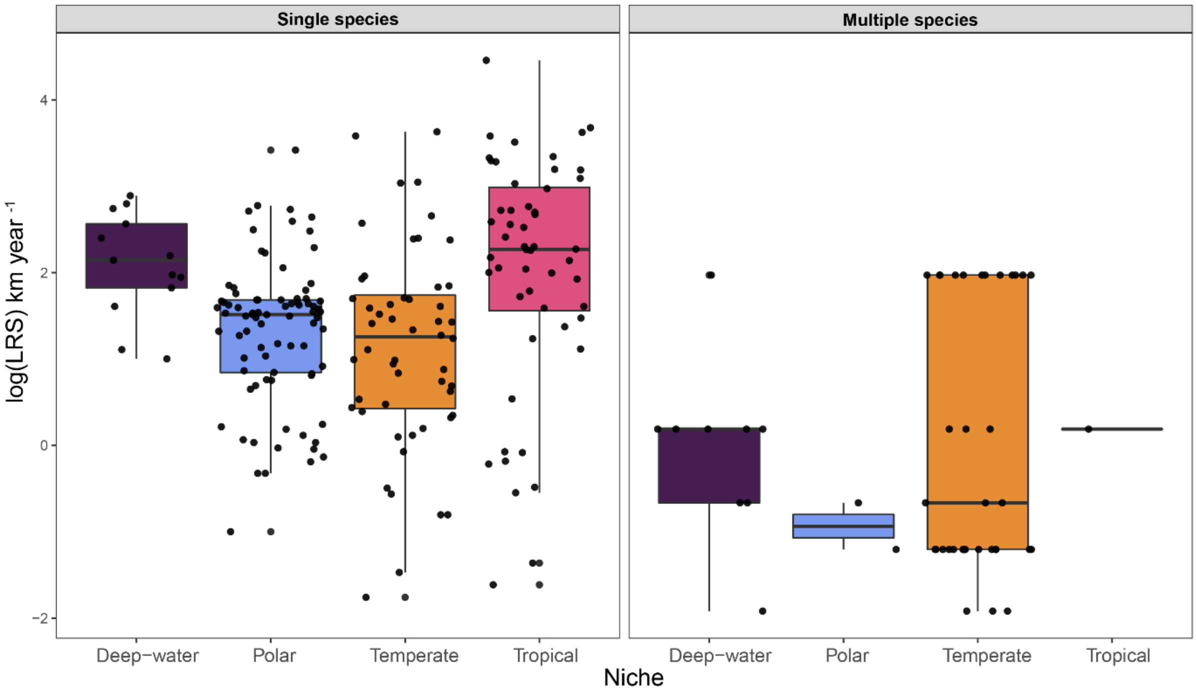

Figure 3: Latitudinal range shift vs. OSS reporting method. *Log-transformed latitudinal range shift (LRS; km year* $^{-1}$*) means across niche categories (denoted in colors) are shown with individual data points (black dots), for fish for which overall shift size (OSS) was reported individually per population (n = 270) and those for which only group-wise estimates were provided (n = 92). LRS are calculated in relation to poleward shift, where positive values indicate shift poleward and negative non-poleward movements.*

For individual estimates, the rate of latitudinal shifts was greater in populations which did not change mean depth (n = 80, median$_{LRS}$ = 5.0 km year^{-1}; IQR = 9.42), compared to populations which were reported to shift their depth distribution (n = 58, median$_{LRS}$ = 3.46 km year^{-1}; IQR = 5.36). Whether a population changed their distribution in depth also affected the relationship between annual temperature change and rate of range shift. Specifically, in depth shifting populations, the correlation between LRS and temperature change was negative among all niches, while for polar and tropical fish with no depth shift this relationship was positively correlated regardless of the OSS method (Fig. 4).

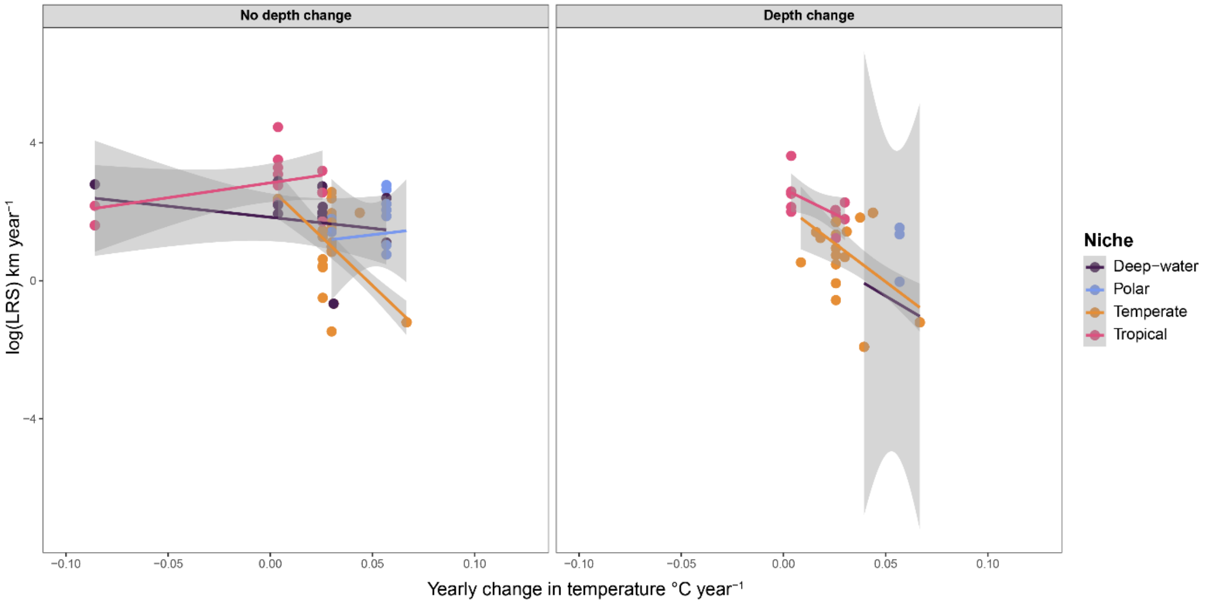

Figure 4: Latitudinal range shift vs. temperature change. *Log-transformed latitudinal range shift (LRS; km year^{-1}) values in relation to temperature change (ΔTemperature, °C year^{-1}) across niche categories are shown, for populations which changed depth (n = 133) and those with no significant depth change (n = 167). Fitted regressions are plotted with 95% confidence intervals (gray). According to temperature change estimates from included studies, tropical populations experienced the slowest yearly temperature increase (0.01 ±0.03 °C year^{-1}), followed by deep-water (0.02 ±0.04 °C year^{-1}), temperate (0.04 ±0.03 °C year^{-1}) and polar taxa (0.06 ±0.1 °C year^{-1}). LRS are reported in relation to poleward direction, where negative estimates represent non-poleward shifts and positive estimates mean poleward shifts.*

Out of 75 estimated depth shift responses, the majority (73%) shifted in the direction as expected from temperature changes (i.e., to cooler waters), which constituted greater increases in depth than those moving against expectations (Fig. 5B). From individual depth shift estimates (n = 286), tropical populations (n = 68) exhibited the most rapid increase in depth ($\text{median}_{\Delta\text{depth}}$ = -0.8 m year^{-1}; IQR = 1.85), followed by polar populations ($\text{median}_{\Delta\text{depth}}$ = -0.05 m year^{-1}; IQR = 0.5; n = 99), while deep-water (n = 36) and temperate populations (n

= 83) mainly moved to shallower depths (2.8 m year^{-1}; IQR = 2.4 and 0.5 m year^{-1}; IQR = 0.6, respectively).

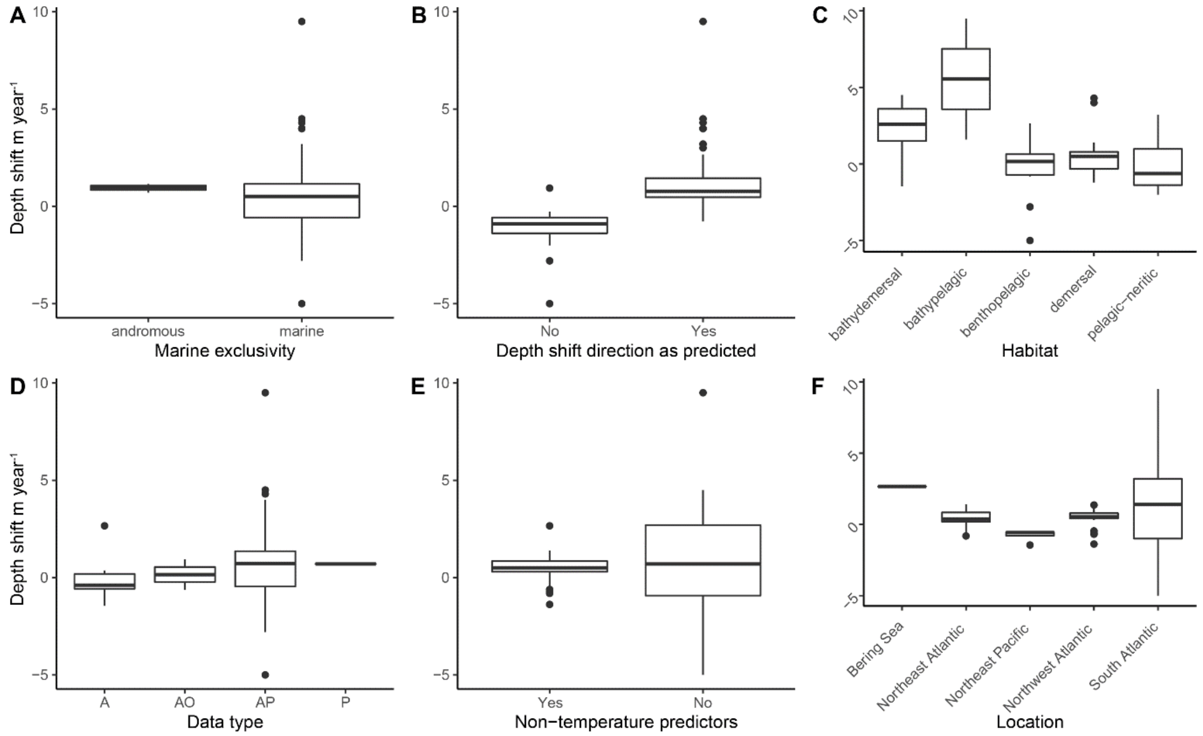

Figure 5: Depth responses across ecological and methodological factors. *Boxplots show median and quartile ranges of yearly rates of depth shift estimates (n = 77) for:* ***A****. whether populations are anadromous (n = 11) or marine exclusive (n = 258);* ***B****. whether depth shift was in the direction as predicted by thermal clines. Most of the time this meant increase in depth;* ***C****. Habitat affinity;* ***D****. Data type including abundance data (A), presence-absence data (P), or other sources (O) and their combinations;* ***E****. whether other non-temperature predictors (Table 5) were identified;* ***F****. Location of sampling sites, which were grouped into eleven major regions according to study coordinates. Positive values represent an increase in depth, while negative estimates mean shifts to shallower waters.*

For other ecological factors not included in the maximum likelihood model, different magnitudes of heterogeneity in LRS rates were observed. When comparing individual estimates between adult (n = 256) and non-adult fish (juveniles, larvae or eggs; n = 14), the latter seemed to shift almost five times slower (Fig. 6A). For migration at spawning, anadromous and marine exclusive populations were shifting at similar rates (4.3 - 3.6 km year^{-}

^{1} Fig. 6B). Among fish residing in different habitats, reef-associated fish shifted ranges at the fastest rates (median$_{LRS}$ = 11 km year^{-1}; IQR = 13.5). Pelagic fish had generally higher LRS estimates (4.7-6.9 km year^{-1}) than demersal species which moved at generally lower rates (0.7-5 km year^{-1}; Fig. 6C).

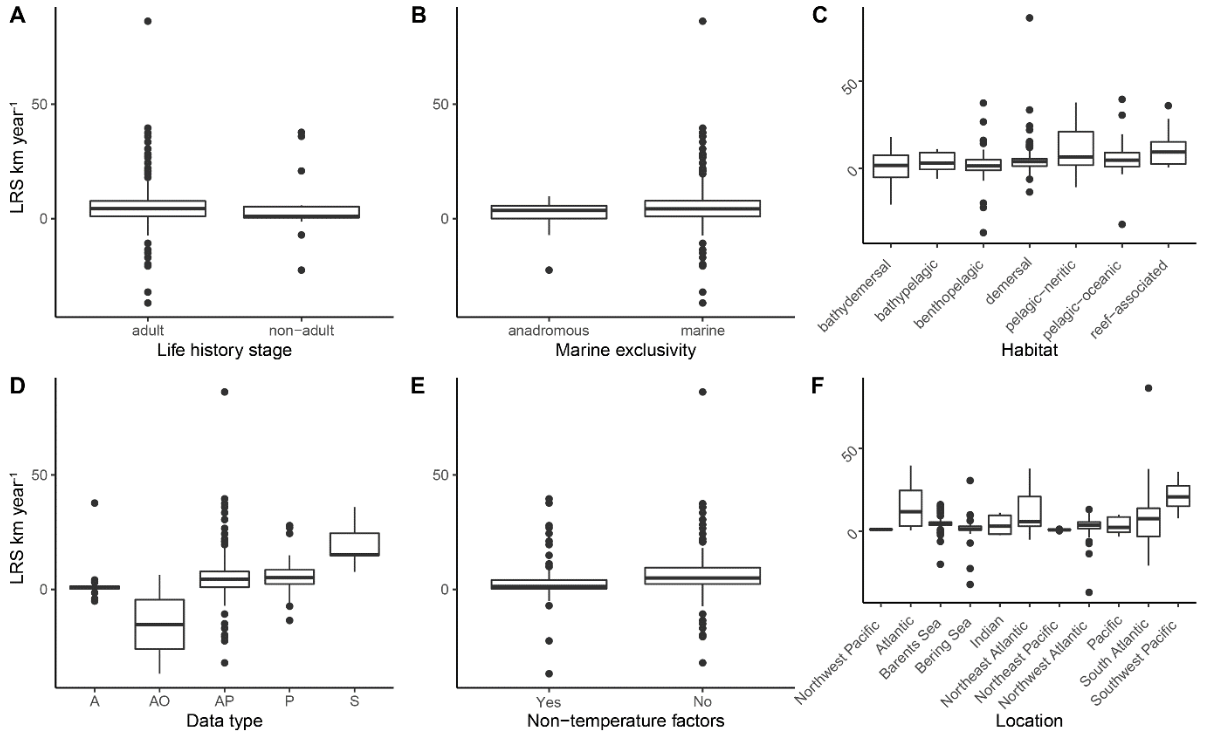

Figure 6: Summary statistics for predictors excluded from the highest-likelihood model. *boxplots show median and quartile ranges of latitudinal range shift (LRS) estimates for each aspect:* ***A****. life stage categorized into adult (n = 256) and non-adult (eggs, larvae, juveniles, n = 14);* ***B****. whether populations are anadromous (n = 11) or marine exclusive (n = 258);* ***C****. Habitat affinity;* ***D****. Data type including abundance data (A), presence-absence data (P), data from long-term sightings (S) or other sources (O) and their combinations;* ***E****. whether other non-temperature predictors (Table 5) were identified;* ***F****. Location of sampling sites, which were grouped into eleven major regions according to study coordinates. LRS is expressed in respect to poleward direction, where negative values indicate anti-poleward range shifts. 93 multi-species estimates were excluded.*

Besides temperature, the most common explanatory variable for changes in marine fish ranges included oceanic oscillation indexes such as from the Atlantic and Pacific oceans, and was reported nine times across reviewed studies (Table 5). Other factors included abiotic marine factors such as ocean currents, salinity, depth and chlorophyll-a concentration (n = 9), as well as exploitation by fishing (n = 7). Density dependence was mentioned five times, which in some cases had larger effect sizes than temperature.

Table 5. Frequency of other significant predictors of range changes. *Predictors other than temperature with significant effects on redistribution in the reviewed studies (n = 37) were summarized into the shown categories, and counted as unique occurrences across studies (n).*

Other identified predictors	***n***
Oceanic oscillation indexes	9
Other oceanic variables (currents, salinity, depth, chlorophyll-a concentration)	9
Fishing pressure	7
Population abundance/density dependence	5
Reproductive (recruitment, spawning stock biomass, buoyancy)	3
Food availability	1

Discussion

We found that the majority of fish populations have responded to thermal warming with a poleward change in their geographical distribution (Fig. 2), which is consistent with forecasts for future responses to further climate change (García Molinos et al., 2015; Schickele et al., 2020). Importantly, however, we also found substantial heterogeneity in degree and direction of biogeographical shifts (Champion et al., 2021), which was influenced by both ecological factors such as niche and depth changes, and methodological factors associated with data collection and reporting (Supplementary Fig. S3).

Ecological factors influencing distribution responses

Niche affinity was a key factor affecting LRS rates globally, confirming expectations that tropical species shift faster in response to warming than other marine fishes (Fig. 3) across inhabited study locations (Fig. 6F). Tropical populations showed a disproportionately poleward movement (Fig.1, Fig. 2), and had a positive correlation between rate of LRS and ΔTemperature, as was the case for polar taxa (Fig. 4). This is consistent with high sensitivity to temperature change in stenothermic species with narrow thermal tolerance limits and restricted spatial ranges, such as tropical species inhabiting shallow waters close to their tolerance limits (Storch et al., 2014). Indeed, we found that reef-associated fish tended to display the most rapid latitudinal shifts compared to other habitat-affinities, although this trend was not significant (Fig. 6C). Other studies have shown that, in comparison to temperate fish, tropical species may have increased sensitivity and lower adaptability to thermal increase (Comte and Olden, 2017; Nati et al., 2021) and may thus be more likely to shift distributions to track suitable thermal habitat.

Changes in depth in response to warming influenced the relationship between LRS and ΔTemperature (Fig. 4), with depth shifting taxa on average moving latitudinally 0.46 km year^{-1} less per °C year^{-1}, as compared to those not changing depth (Supplementary Table S2). This suggests that fish populations might not need to shift horizontally if they can adjust their depth to track their favorable temperature niche (Hollowed et al., 2007), which was demonstrated in groundfish finding thermal refuge across rugged seabeds and canyons in the Western Gulf of Alaska (Li et al., 2019). In line with predicted narrow temperature tolerance limits of stenotherms (Storch et al., 2014), we found polar and tropical species to experience the fastest increase in depth, particularly when moving to colder waters (Fig. 5B), such as in the Bering Sea and South Atlantic (Fig. 5F). It is well established that polar fish communities can experience rapid and disruptive community structure changes, due to arrivals of poleward shifting boreal species (Fossheim et al., 2015; Frainer et al., 2017). Experiencing the fastest temperature increase (Stocker, 2014), but being limited in poleward expansion due to the edge of the sea shelf (Wassmann et al., 2006), arctic fish species might depend on moving to deeper waters as a last resort to avoid extirpation (Fossheim et al., 2015). On the other hand, deep-water species showed some of the lowest depth changes which might indicate that these populations are mostly within their thermal tolerance window, which is also supported by the assumed environmental stability at greater oceanic depths (Campana et al., 2020; Yasuhara and Danovaro 2016). However, deep-water fish species are more difficult and costly to sample and require alternative sampling methods due to their habitat fragility (Mallet and Pelletier, 2014), and as a result are frequently data deficient under their IUCN categorization or have inaccurate depth distribution records (Wellington et al., 2021), which would be essential to robustly discern effects of temporal and spatial temperature changes in the deep sea (Emblemsvåg et al., 2020; Yasuhara and Danovaro, 2016).

Other factors, such as life stage, were not found to significantly affect range shift response, even though sensitivity to warming is thought to be partly dictated by thermal tolerances changing throughout the marine fish life cycle (Killen et al., 2007; Pörtner and Farrell, 2008; Whitney et al., 2013). Early life stages, embryos in particular, are most sensitive with their thermal limit being on average 8 °C lower than in other stages (Dahlke et al., 2020), and are likely a major predictor of population responses to warming (Dahlke et al., 2020). Although we found slower range shifts for larvae, eggs and juveniles compared to adult fish, this difference was not significant, though our inferences might have been affected by limited statistical power and unequal sample sizes (15 and 254 population responses, respectively). Similarly, the number of responses for anadromous marine species was limited ($n_{populations}$ = 14, mostly *Oncorhynchus* spp. (n = 8); Fredston-Hermann et al., 2021; Mueter et al., 2006; Nye et al., 2009; Yasumiishi et al., 2020), yielding an LRS estimate close to marine exclusive species responses (Fig. 6B). Thus, robust empirical data of more diverse marine life stages or life cycles could facilitate important hypotheses on non-adult temperature response outside laboratory settings (but see Barbeaux and Hollowed 2018) or inferences of potential range shift limitations in diadromous fish species due to affinity to natal homing grounds (Hare et al., 2016).

The effects of variable study methods

OSS reporting was identified as a significant factor affecting LRS estimates, with group-wise estimates being lower than those derived from individual species estimates. This could be due to random bias due to lower sample size ($n_{populations}$ = 93) and method-specific bias in the four studies from which all group-wise estimates were obtained (Dulvy et al., 2008; Li et al., 2019; Perry et al., 2005; Pinsky et al., 2013). Nevertheless, inclusion of the OSS predictor in the highest likelihood model suggests that other methodological differences across studies could affect range shift calculations to a certain degree, even if not identified as significant in the current analysis.

Overall, there was large variation in reviewed study methods, which are difficult or arguably impossible to standardize and compare. Most notably, the different data types, from which all subsequent range shift estimates are calculated, have numerous varying characteristics. Abundance data, mostly obtained from fishery or research trawl data, such as from the

Nansen Survey Program in Namibia and Angola (Yemane et al., 2014), has been widely used across population distribution literature as it is thought to represent the whole population range, and be less sensitive to search effort and misleading outliers (Brown et al., 2016). While fishery survey data can provide temporally and spatially high-resolution data, and decade-long records can be conveniently retrieved for new analyses, its frequent usage has created publication bias towards commercially important fish species in the northern hemisphere (Supplementary Fig. S1). Alternatively, recent studies measuring changes in range limits, such as by Fredston-Hermann et al. (2020), use only presence-absence data to infer changes in leading and trailing edges in the Northwest Atlantic, arguing that abundance data does not truly reflect potential changes of species ranges, but is rather confounded by density dependence effects through abundance changes caused by non-climatic factors such as fishing (Quinn and McCall, 1991). However, abundance and climate driven distribution shifts should be possible to distinguish by direction of shift: the former should be unselective in direction while the latter is expected to move along the temperature gradient. In a study on arctic fish by Husson et al. (2022), abundance measures were weighted by either biomass or presence-absence data producing different centers of distribution estimates, which were also observed across our study synthesis. Specifically, studies implementing abundance data had substantially lower range shift estimates than those using presence-absence data or a combination of the two (Fig. 6D), which is in line with findings by Brown et al. (2016) that presence-absence data is more sensitive to outliers. Others, such as Bluemel et al. (2021), account for bias in LRS estimates due to abundance changes by dividing the study period according to biomass trends (e.g., low or high abundance period).

Other data types include long-term sightings and tagging studies, which normally include low sample sizes using costly satellite or data storage tags (Hammerschlag et al., 2022; Neat and Righton, 2007), although cost-effectiveness may be increased through citizen science initiatives, such as the decadal-long tagging program in cooperation with Australian recreational anglers (NSW DPI 2019) applied by Champion et al., (2021). While sightings, including new sightings outside of previously known population limits, have been suggested to confirm range shifts or expansions (Fogarty et al., 2017), such measurements should be treated with particular caution due to increased chance of detection bias and representing outliers (Brown et al., 2016). Accordingly, due to their reduced spatial and temporal resolution, many studies based on sightings failed to meet the minimum selection criteria. Ultimately, future syntheses or research creating new time series should consider associated advantages and potential biases associated with every data type to make response estimates more comparable.

Another source of variation is the geographical scope of each study, with spatial sampling extents varying widely, and often spanning across whole oceans (e.g., Worm and Tittensor, 2011). The common assumption of marine ecosystems being almost barrier-free with species generally occupying all thermally suitable areas (Sunday et al., 2011) has been challenged by accumulating evidence of local population subdivision due to a wide range of biotic and abiotic factors (Baker and Hollowed, 2014; Barbeaux and Hollowed, 2018; Sandoval-Huerta et al., 2019; Sherman et al., 2008) which likely causes variation in exposure and responses to water temperature changes (Poloczanska et al., 2013). Only few studies have accounted for sub-regional differences in topography and oceanic factors such as currents or salinity gradients, which all might delineate divisions across marine species distributions (Kleisner et al., 2016; Marshall et al., 2016; Momigliano et al., 2019). For example, a study in the Northeast Pacific by Liu et al. (2019) demonstrated significant heterogeneity in marine fish responses to marine warming due to sub-regional topography and geography characteristics. Other studies have measured shifts separately for identified central population areas based on ecologically relevant locations, such as known breeding grounds (Bluemel et al., 222). A promising tool to investigate heterogeneity in range shift responses are genetic molecular techniques which help delineate cryptic diversity (Jokinen et al., 2019) and estimate dispersal velocity of locally adapted genotypes (Jonsson et al., 2018) for improved response predictions, and infer historic range changes and migration routes for both ancient and contemporary distribution responses (Knutsen et al., 2013; Robalo et al., 2020; Spies et al., 2020), yet such genetic application to climate range shift studies is still scarce.

The variation in species' responses to climate change has been addressed through various predictors such as local adaptation (Johnsson et al., 2018), phenotypic plasticity (Donelson et al., 2019; Reusch 2014), species interactions (Figueira et al., 2019; Torres et al., 2008), food availability (Fossheim et al. 2015) and even social behavior (Smith et al., 2018). In some marine fishes, the likelihood of successful range expansions and colonization of new habitats was explained by species-level traits such as dispersal ability and being a generalist (Sunday et al., 2015), although trait-based range shift forecasts seem to have generally little explanatory power (Angert et al., 2011). Whilst significant response variation is likely explained by a multitude of climatic and biotic factors (McHenry et al. 2019), the majority of reviewed studies investigated only temperature as a predictor (in some cases only by suggestion rather than empirical testing). For example, some studies suggest that range shifts may be driven by abundance changes, as density dependence may lead to range expansions during high abundance and *vice versa* (Kotwicki et al., 2013; Olafsdottir et al., 2019; Swain et al., 2006; Worm and Tittensor 2011; Yasumiishi et al., 2020). Nevertheless, it is still unknown how marine range shift estimates from single-predictor studies compare to multi-factor estimates. From analyzed studies, those which focused solely on temperature had generally higher LRS estimates (median = 5; IQR = 7.1 km year^{-1}) than those which identified at least one additional driver to temperature (median = 1.2; IQR = 3.8 km year^{-1}), possibly due to the confounding effects of additional variables explaining part of the LRS variation. While some studies found significant effects of fishing pressure (Bell et al., 2015; Engelhard et al., 2014; Worm and Tittensor, 2011; Rose et al., 2000; Neat et al., 2006), recruitment level (Hurst et al., 2012) and spawning stock biomass (Hughes et al., 2014), marine studies including multiple climatic and non-climatic effects into climate response models are generally scarce. The multi-factor approach was shown to have elevated phenology response estimates in marine organisms when compared to inferences from studies including temperature as the sole predictor (Brown et al., 2016). Thus, further research is needed to explore interactions between climatic and other ecological factors, and to test how these compare to single-predictor response estimates.

Opportunities for future improvement

Our conclusions might have been affected by multiple statistical issues and biases associated with meta-analysis (Gurevitch and Hedges, 1999). First, the identified studies mostly originate in the northern hemisphere, particularly Northern Europe and North America with a limited number of fish species ($n_{species}$ = 345) of the estimated ~30 000 fish species present globally (Froese and Pauly, 2022). This suggests a significant research bias and limited taxonomic scope in marine fish climactic research. A common paradox in ecological research is observed whereas taxonomically rich ecoregions, such as the tropics, are strongly underrepresented (Hansen and Cramer, 2015). Very few or no studies could be identified from some of the most biodiverse regions such as Southeast Asia, South America and Africa – highlighting the pressing need to expand research on climate responses in marine fish in face of increasing climate change pressures.

Sample sizes were low for some geographic regions, such as in the northwest Pacific where only two studies (Kumagai et al., 2018; Han et al., 2020) were retrieved, representing four species with an average sample size of 106 (±46) individuals per taxa. In other regions, disproportionate species sample sizes could have influenced interpretations, such as in the East Pacific, where contrasting, multidirectional range shift averages are mainly driven by one large study by Li et al. (2019), measuring depth and horizontal distribution shifts of ten fish species in nine subregions. The latter example additionally illustrates the need for improved standardization in marine LRS measurement methods to improve comparability of results.

Large variation in publication of LRS and temperature estimates across studies also complicated our interpretations. For example, very few studies presented supporting numeric data of both yearly population center or range edge estimates and high-resolution water temperature data, and if they did, these were often in different units, with LRS unit measures ranging from °latitude year^{-1} to km year^{-1}. While some estimates for either of these measures were not possible to extract, others were derived from figures within published papers, which could have affected the accuracy of estimates. Mean SST estimates extracted from NOAA databases for studies failing to report temperature were of reduced resolution (5° resolution within approximate sampling area), which may have exacerbated inherent biases inaccurate water temperature estimates (Chan, 2021). Improved temporal and spatial resolution of water temperature estimates, including lagged effects, or implementing tags storing individually experienced water conditions (e.g., Hammerschlag et al., 2022) would likely improve response predictions to climate changes.

Implications and recommendations

While no single formula for inferring marine fish distribution responses to warming exists, the local ecological factors as well as the extent of current methodological variation biases highlighted here will be key to improving the accuracy and usefulness of research comparing historical distribution data, creating new time series in the future, and synthesizing literature findings. To facilitate future climate impact research, increased standardization and robustness of range shift measurement methods could be achieved by identifying population structure shaped by relevant ecological variables, such as separate spawning grounds or timing (Oomen and Hutchings, 2015; Petrou et al., 2021) and larval retention (Sinclair and Power, 2015), as well as abiotic barriers due to bathymetry, geology, oceanography (Morgan et al., 2009), and genetic factors, such as cryptic diversity and shared local adaptations (DuBois et al., 2022). For underrepresented habitats such as deep-water or tropical niches, improved spatial and temporal resolution (i.e., robust sample sizes of sampled individuals and spatial and temporal sampling frequency in long-term studies), with measurement in all three dimensions (i.e., depth, latitude and longitude) will be needed to identify vulnerable species and populations. Bias in LRS comparisons over time could be reduced by controlling for locally relevant confounding factors, such as density dependencies, or phenomena such as the Southern Oscillation affecting temperature trends in the tropics (Jakovlev et al., 2021). There is an urgent need to expand geographical and taxonomic representation of marine fish range shift responses to climate change. Particularly in the highly biodiverse tropics and global south where marine taxa have been identified as the most vulnerable to warming (Comte and Oden, 2017), marine research and long-term fisheries monitoring programs are less established than in the northern hemisphere, and thus robust accounts of whether and how marine fish populations track their temperature niche are lacking.

Addressing the observed variation in marine range shifts will be fundamental for improving response predictions crucial to inform effective fisheries and conservation management strategies, particularly as the magnitude of distribution responses and extinction risk are likely to increase under climate change forecasts (Penn and Deutsch, 2022). In some of the most vulnerable marine ecosystems, such as the arctic, where species have limited thermal tolerance, food web structure and native biodiversity are already rapidly changing due to arrivals of invasive species from lower latitudes (Bartley et al., 2019; Fossheim et al., 2015; Kortsch et al., 2015). Globally, more frequent invasions and resulting novel community structures and interspecific interactions in temperate and arctic latitudes will have likely ecosystem-wide ramifications of yet unknown magnitude (Kortsch et al., 2015; Nadeau and Urban, 2019; Sorte et al., 2010). Therefore, addressing the natural complexity of distributional responses should rely on innovative and robust methods to allow assessment and comparison of findings.

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Supplementary Data

Supplementary Table S1: Studies from literature review retained in analyses. *After the screening and selection process of search results based on inclusion criteria (see methods), 37 studies were identified for analyses. For each record, citation, number of populations included in this study (N), niche(s) of reported species in descending order of corresponding proportions are shown: temperate (TM), tropical (TR), deep-water (DW) and polar (P). Years of sampling start and end, as well as location of studies are reported. Numbers of populations identified as shifting or not moving horizontally (Yes/No); method of reporting overall shift size (OSS): individually (1), combined for groups of species for both vertical and horizontal (C) or combined only for horizontal distribution shifts (C*); and data type: abundance (A), presence-absence (P), tagging (T), genetic-molecular (G) data, or observations from long-term sightings (S). *While 29 unique populations were retained from Husson et al. (2022), two sets of entries corresponding to two types of weighted abundance data (biomass and presence-absence-weighted data) for each population (n = 58) were included in the analyses.*

Citation	**N**	**Niche**	**Start**	**End**	**Location**	**Range shift (Yes/No)**	**OSS**	**OSS units**	**Data type**
(Alheit et al., 2012)	2	TM	1990	2000	North Sea, Baltic Sea	2/0	1	°latitude	AP
(Champion et al., 2021)	4	TR	1998	2018	Southwestern Pacific	4/0	1	km decade^{-1}	P
(Chust et al., 2019)	1	TR	1981	2017	Northeast Atlantic	1/0	1	km decade^{-1}	P
(Dulvy et al., 2008)	28	TM, DW	1980	2004	North Sea	28/0	C	km decade^{-1}	AP
(Engelhard et al., 2011)	4	TM,DW	1924	1947	North Sea	3/1	1	km	A
(Engelhard et al., 2014)	2	TM,DW	1920	1930	North Sea	2/0	1	km	A
(Fossheim et al., 2015)	1	P	2004	2012	Barents Sea	0/1	1	km	AP
(Fowler et al., 2017)	7	TR	2006	2016	Southeast Pacific	7/0	1	km year^{-1}	S
(Fredston-Hermann et al., 2020)	43	TM, TR, DW, P	1968	2017	Northwest Atlantic	24/19	1	km year^{-1}	P
(Hsieh et al., 2009)	29	DW, TM, TR	1951	1998	Northeast Pacific	9/20	1	km °C^{-1}	AP
(Hsieh et al., 2008)	23	TM, TR, DW	1951	1998	Northeast Pacific	5/18	1	°latitude	AP

(Hughes et al., 2014)	1	TM	1977	2010	Northeast Atlantic	1/0	1	km °C^{-1}	A
(Hurst et al., 2012)	1	P	2004	2009	Bering Sea	0/1	N/A	N/A	AP
(Husson et al., 2022)	29*	P, DW	2004	2017	Barents Sea	56/2	1	km	AP
(Knutsen et al., 2013)	1	TM	1980	2012	North Atlantic	1/0	0	N/A	G
(Kotwicki and Lauth, 2013)	20	P, TM, DW	1982	2011	Bering Sea	20/0	1	km	A
(Kumagai et al., 2018)	3	TR	1970	2013	Northwest Pacific	3/0	1	km year^{-1}	P
(Last et al., 2011)	42	TR, TM	1800	2009	Southwestern Pacific	37/5	0	N/A	S
(Li et al., 2019)	51	TM, DW, P	1995	2015	Northeast Pacific	51/0	C*	N/A	A
(Mueter and Litzow, 2008)	18	P, TM	1982	2006	Bering Sea	18/0	1	km	AP
(Neat and Righton, 2007)	1	TM	1999	2005	North Sea	0/1	N/A	N/A	T
(Nye et al., 2009)	36	TM, TR, DW, P	1968	2007	Northwest Atlantic	21/15	1	km year^{-1}	AP
(Olafsdottir et al., 2018)	1	TM	1997	2006	Northeast Atlantic	1/0	1	km	AP
(Overholtz et al., 2011)	1	TM	1968	2008	Northwest Atlantic	1/0	1	km	AO
(Perry et al., 2005)	37	TM, DW, P	1977	2001	North Sea	16/21	C,1	km	AP
(Pinsky et al., 2013)	2	TM, DW, P	1968	2011	Northwest Atlantic	1/1	C	°latitude year^{-1}	AP
(Han et al., 2021)	1	TM, DW, P	2001	2017	Yellow Sea	1/0	1	km	AP
(Bell et al., 2015)	4	TM, TR	1972	2008	Northwest Atlantic	3/1	1	km year^{-1}	AP
(Rose et al., 2000)	1	P	1981	1992	Northwest Atlantic	1/0	1	°latitude	AO
(Smith et al., 2021)	2	TM, TR	2002	2018	Southwestern Pacific	2/0	0	N/A	AP
(Swain and Benoit, 2006)	1	P	1971	2003	North Atlantic	1/0	0	N/A	AO

(Vestfals et al., 2016)	2	P	1982	2013	Bering Sea	2/0	0	N/A	A
(Worm and Tittensor, 2011)	32	TR	1960	1999	Pacific	15/17	1	°latitude	AP
(Yasumiishi et al., 2020)	15	P	2002	2018	Bering Sea	9/6	1	km	AP
(Yemane et al., 2014)	91	DW, TR	1985	2010	South Atlantic	62/29	1,0	km year^{-1}	AP
(Hammerschlag et al., 2022)	2	TM	2010	2019	Northwest Atlantic	2/0	1	°latitude °C^{-1}(SST.anomaly)	T
(Bluemel et al., 2022)	1	TM	1978	2020	North Sea	1/0	1	km	AP

Supplementary Table S2: Estimated LRS models*. For each model, predictors and model fit represented by Akaike Information Criterion (AIC), log-likelihood (LL) with respective degrees of freedom (df) are reported. For performed Likelihood Ratio Tests (LRT) between the model and the nested models, df, chi-square (X^2) and p-value estimates are reported, with significant results denoted in bold.*

Model name	**Compared with**	**Fixed effects**	**Random effects**	**Model fit**			**LRT against nested**		
			Study	**AIC**	**LL**	**df**	**df**	**X^2**	***p***
Full model	-	ΔTemperature + OSS + Data type + Niche + log(Span) + log(Area size) + Depth change + Habitat + Niche:Depth change + ΔTemperature:Depth change + Habitat:Depth change + Non-temperature predictors	Intercept	262.8	-104.4	27	-	-	-

Model 2	Full model	ΔTemperature + OSS + Data type + Niche + log(Span) + log(Area size) + Depth change + Habitat + Niche:Depth change + Habitat:Depth change + Non-temperature predictors	Intercept	260.9	-104.5	26	1	0.21	0.65
Model 3	2	ΔTemperature + OSS + Niche + log(Span) + log(Area size) + Depth change + Habitat + Niche:Depth change + Habitat:Depth change + Non-temperature predictors	Intercept	260.2	-107.1	23	3	5.26	0.15
Model 4	3	ΔTemperature + OSS + Niche + log(Area size) + Depth change + Habitat + Niche:Depth change + Habitat:Depth change + Non-temperature predictors	Intercept	259.8	-107.9	22	1	1.54	0.21
Model 5	4	ΔTemperature + OSS + Niche + log(Area size) + Depth change + Habitat + Niche:Depth change + Habitat:Depth change	Intercept	258.9	-108.4	21	1	1.1	0.29
Model 6	5	ΔTemperature + OSS + Niche + log(Area size) + Depth change + Habitat + Niche:Depth change	Intercept	260.7	-111.3	19	2	5.77	0.056
Model 7	6	ΔTemperature + OSS + Niche + log(Area size) + Depth change + Niche:Depth change	Intercept	256.5	-114.3	14	5	5.85	0.32
Model 8	7	ΔTemperature + OSS + Niche + log(Area size) + Depth change	Intercept	254.9	-116.5	11	3	4.42	0.22

Model 9	8	ΔTemperature + OSS + Niche + Depth change	Intercept	256.7	-118.4	10	1	3.8	0.05
Model 10	9	ΔTemperature + Niche + Depth change	Intercept	260.7	-122.4	8	2	8.0	**0.018**
Model 11	9	ΔTemperature + OSS + Depth change	Intercept	266.9	-126.4	7	3	9.83	**0.001**

***Supplementary Table S3: Predictor estimates of the best performing LMM**. Fixed effect estimates, standard error (SE), 95% Confidence Intervals, t and p-value estimates are reported. For the random effect intercept of 'Study' the explained variance and standard error (SD) are shown, with marginal (Eq. 1) and conditional (Eq. 2) model effect sizes calculated below. The p-values for fixed effects were calculated using Satterthwaite's approximations. Confidence Intervals have been calculated using the lme4 package. Model equation: log(LRS) ~ ΔTemperature + OSS reporting + Niche + Depth change + (1|Study)*

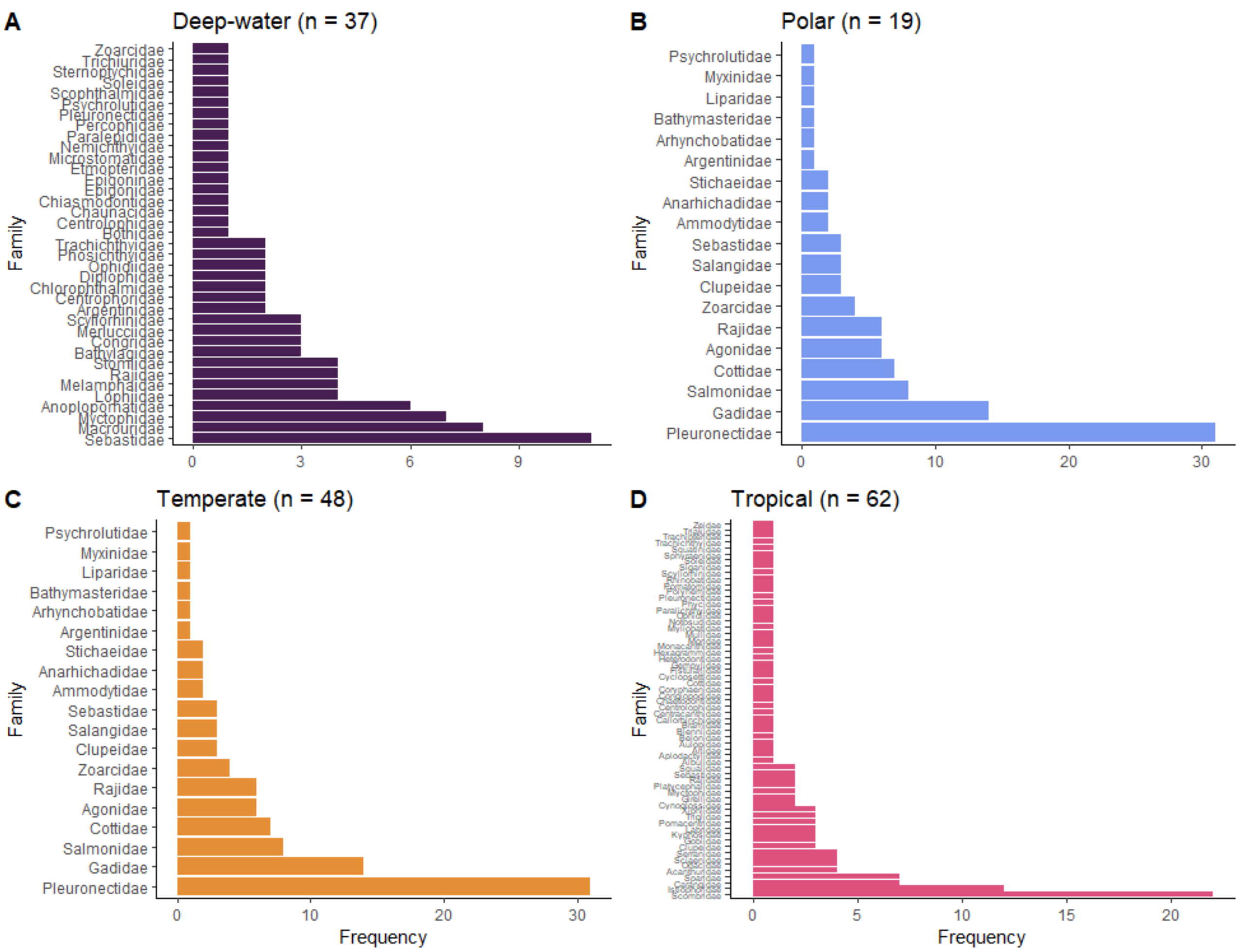
Fixed Effects					
	Est/Beta	SE	95% CI	t	p
Intercept	2.22	0.53	1.12 – 2.46	4.17	**0.001**
ΔTemperature	3.99	2.84	-0.88 – 8.42	1.41	0.162
OSS reporting(C)	-2.16	0.95	-2.87 – -0.57	-2.28	**0.046**
OSS reporting(C*)	-1.74	0.97	-2.49 – 0.12	-1.8	0.099
Niche(Polar)	-0.099	0.25	-0.52 – 0.31	-0.39	0.69
Niche(Temperate)	-0.23	0.17	-0.53 – 0.04	-1.33	0.18
Niche(Tropical)	0.59	0.19	0.27 – 0.91	3.01	**0.003**

Depth change(yes)	-0.46	0.13	-0.68 – -0.23	-3.39	**0.0009**
Random Effects					
			Variance	S.D.	
Study (Intercept)			0.88	0.94	
Residual			0.28	0.53	
Model fit					
R^2			Marginal	Conditional	
			0.43	0.86	

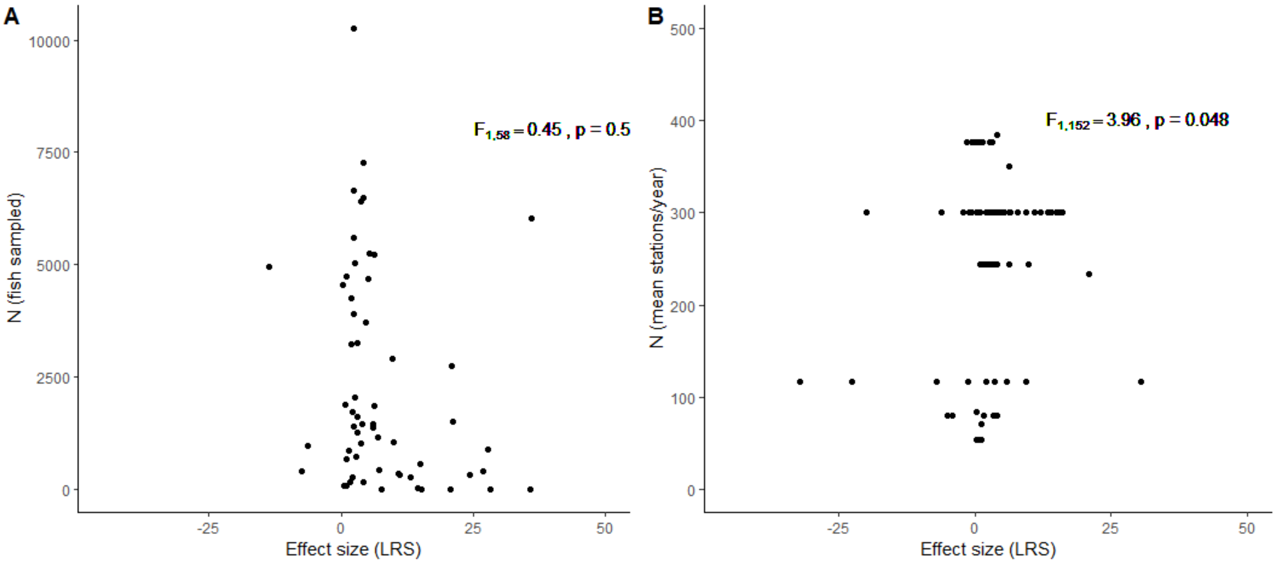
Supplementary Table S4. Fixed effect estimates. *Summary statistics (sum of squares, mean square, degrees of freedom (df), denominator df, F-ratio (F) and p-values) from a three-way ANOVA test using Satterthwaite's method of the highest likelihood model with mixed effects (log(LRS) ~ ΔTemperature + OSS reporting + Niche + ΔTemperature:Depth change + (1|Study)). Significant effects are in bold (p < 0.05).*

Type III Analysis of Variance Table with Satterthwaite's method						
Fixed effect	Sum Sq	Mean Sq	df	dfDen	F	p-value
∆Temperature	0.5	0.5	1	124.98	1.81	0.18
OSS reporting	2.54	1.27	2	19.81	4.56	**0.02**
Niche	4.79	1.59	3	124.39	5.75	**0.001**
Depth change	3.24	3.24	1	125.87	11.65	**0.0008**

Supplementary Figures



Supplementary Figure S1. Frequency plots of species families retained for analysis. *Taxa investigated in retrieved studies were grouped according to niche - deep-water, polar, temperate and tropical - with numbers of unique taxa per niche shown in brackets. From the dataset of 569 population responses to temperature change, most originated from temperate species (n = 212), followed by tropical (n = 139), polar (n = 125), and deep-water (n = 93).*



Supplementary Figure S2: Funnel plots based on sample size. A: Effect size of LRS (latitudinal range shift rate in km year^{-1}) regressed on sample size N (number of fish sampled per population; median$_N$ = 1172, IQR = 3384) for populations where both sample sizes and shift estimates were provided (n = 60). Symmetry of funnel plot was confirmed ($p > 0.05$). **B:** Effect size of LRS regressed on sample size N expressed as average sampled fishery stations per year (n = 154; median$_N$ = 117, IQR = 246). Funnel shape was slightly asymmetrical ($p < 0.05$) suggesting potential publication bias, based on a regression test regressing effect sizes (*y*) on 1/√N (Tang and Liu, 2000).