REVIEW

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

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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 595 three-dimensional population responses (latitudinal, longitudinal, and depth), with temperature identified as a significant driver. We found that latitudinal shifts were the fastest in non-exploited, tropical populations, and inversely correlated with depth shifts which, in turn, dominated at the trailing edges of population ranges. While poleward responses increased with rate of temperature change and latitude, niche was a key factor in predicting both depth (18% of variation) and latitudinal responses (13%), with methodological predictors explaining between 10% and 28% of the observed variance in marine fish responses to temperature change. 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.

KEYWORDS
climate change, distribution changes, fish, marine, meta-analysis, methodological bias, range shift, temperature

1 | 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 (Brown et al., 2016; Chen et al., 2011; Kortsch et al., 2012; Lenoir et al., 2020; Poloczanska et al., 2013), 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), and are restricted by narrower thermal safety margins (Pinsky et al., 2020). Accordingly, species' range changes in response to climate change have been up to sevenfold faster in the ocean as compared to on land (Poloczanska et al., 2013). As marine temperatures are forecasted to continue rising (Pörtner et al., 2019), 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 (Poloczanska et al., 2013; Urban, 2015), complicating population response predictions and conservation management. A key development in addressing this variation has been the acknowledgment that a suite of other non-temperature associated biotic factors, including species interactions (Ellingsen et al., 2020; Louthan et al., 2015), ecological and life history traits (MacLean & Beissinger, 2017), and ecoevolutionary dynamics (Cacciapaglia & van Woesik, 2018; Fredston et al., 2021; Nadeau & 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 (Brown et al., 2016; Wolkovich et al., 2012), 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. Some syntheses

have indeed highlighted the complexity of interacting functional and taxonomic predictors of climate responses in marine taxa (Lenoir et al., 2020), with Brown et al. (2016) demonstrating higher importance of methodological biases in marine range shift estimates than previously thought. To date, however, no recent synthesis with a focus on marine fish exists. As such, there is a need to build upon this initial work and to summarize the most recent literature to test an extended scope of interacting ecological factors influencing both the latitudinal and depth changes of marine fish species in response to climate change, and the confounding methodological factors that can affect their estimation.

The scarcity of analyses of 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 remains. 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., Hsieh et al., 2009; Husson et al., 2022; Li et al., 2019), or a population's most extreme boundaries of longitude, latitude, or depth, inferred, for instance, 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): common 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 & 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, such as tradeoffs associated with monetary expense, sampling effort, and feasibility in contrast to the likelihood of observing specific species or species types, achieving adequate sample sizes, and spatial–temporal resolution. 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 climatic predictors, other than temperature, such as salinity (Champion et al., 2021), oscillation indexes (Han et al., 2021; Nye et al., 2009), bathymetry (Hammerschlag et al., 2022; Li et al., 2019), or non-climatic drivers, such as food availability (Smith et al., 2021) or exploitation by fishing (Bell et al., 2015; Engelhard et al., 2014), 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., 2018), 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 latitudinal and depth shifts in response to ocean warming in marine fish. First, we carried out a systematic literature review to gather data from existing original articles meeting criteria of measuring range shifts in response to temperature change. 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.

2 | METHODS

2.1 | Literature search

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).

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, Dr. Maria Fossheim and Dr. Raul Primicerio provided species-wise raw data of latitudinal changes in distribution from the paper by Husson et al. (2022). The three remaining studies, for which no data were received, were dropped from analyses.

2.2 | Study selection

Records retrieved from the database were screened for duplicates, and for the first round of eligibility abstracts were manually checked to confirm the study focus included marine fish and distributional range changes in response to temperature (Figure 1). Four further 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.

Only original research papers documenting latitudinal or depth responses to temperature in marine fish were considered (Table 2). 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 discuss temperature as a likely driver of distributional range changes (preferably by statistical association) and have a span of at least 5 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 in mean latitude, either of centers of distribution (COD), or range edges (mean maximum and minimum latitudes, or lower and upper 5th latitudinal percentile), or estimates of depth changes (in meters) over a defined time span. The final step (Table 2) selected studies based on reliability of implemented methodologies. Studies were included if their methodology included presence–absence data, abundance data combined with another type of data, or molecular
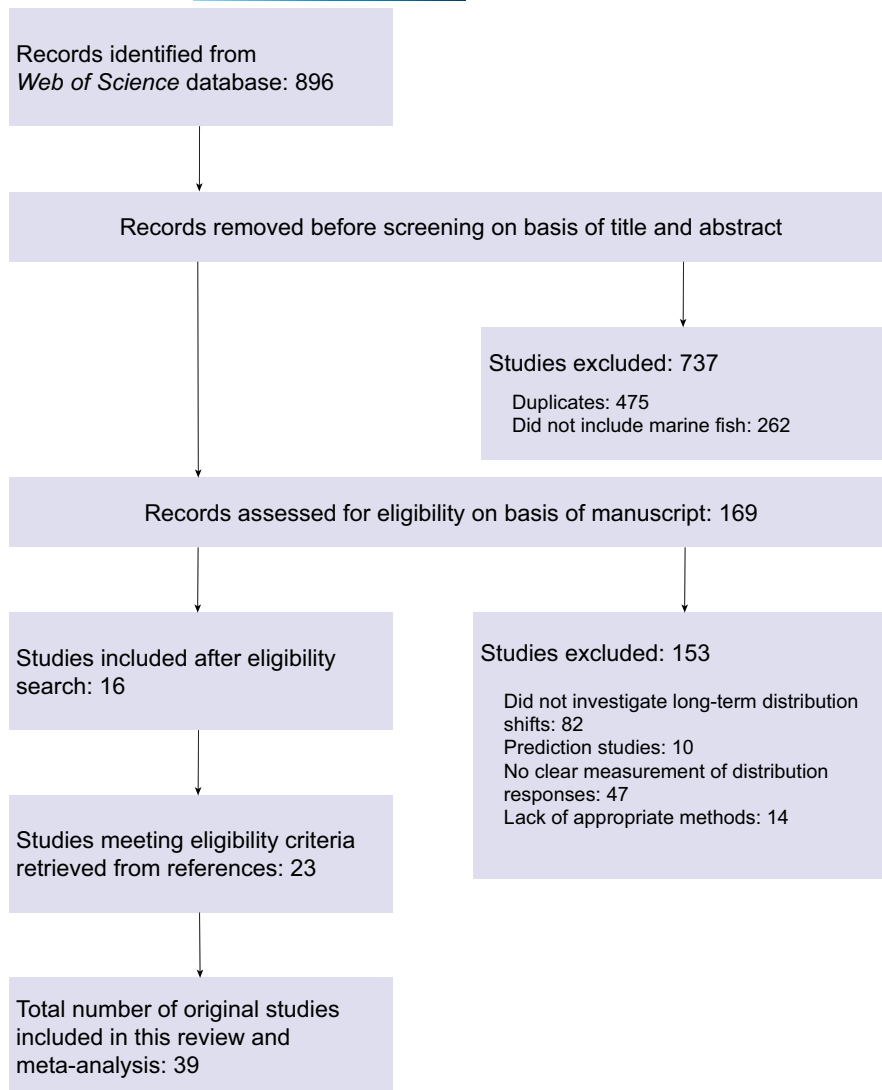
TABLE 1 Search strategy and information sources. Six searches were performed in the online database Web of Science (WoS) including different combinations of the search terms 'fish geograph*', 'distribution', 'range', 'shift', 'contract*', 'expan*' with no date limitation for English original articles 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

Records identified from
Web of Science database: 896

Records removed before screening on basis of title and abstract

Studies excluded: 737

Duplicates: 475
Did not include marine fish: 262

Records assessed for eligibility on basis of manuscript: 169

Studies included after eligibility search: 16

Studies excluded: 153

Did not investigate long-term distribution shifts: 82
Prediction studies: 10
No clear measurement of distribution responses: 47
Lack of appropriate methods: 14

Studies meeting eligibility criteria retrieved from references: 23

Total number of original studies included in this review and meta-analysis: 39

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). 23 additional studies meeting criteria were retrieved from relevant references, totaling a final of 39 articles included in this analysis.

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	87
3	No projections	Exclude prediction studies	77
4	Clear measurement	Calculated shift in latitude (by degrees or kilometers), e.g., of center of distribution or range edges	30
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	16

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. 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. To avoid biases due to local population abundance changes, we excluded estimates based on changes in relative community composition and species richness or stemming solely from abundance data with sparse time points (less than 5 years).

2.3 | Data collection process

After the filtering process, an extraction sheet with variables of interest (described under *Data Items*) was created (Supporting Data S1). We pilot-tested five records and refined the sheet accordingly. In cases where variables were provided only in graphical rather than numerical representations (either not provided or authors were unresponsive to requests), numeric data were extracted manually from graphs using WebPlotDigitizer version 4.5 (Rohatgi, 2021). Numerical values of distribution responses over time, obtained by digitizing raster maps, were used to calculate latitudinal changes by fitting simple regression models between yearly mean latitude of species presence data and sampling years. For temperature, yearly temperature values were extracted from available graphs and fitted into linear regression models to obtain estimates of annual temperature change (°C year^{-1}) if not provided in the original articles; for studies comparing cold versus warm periods, yearly estimated mean values for each period were calculated, to then compare the difference in cold periods relative to the warm periods.

2.4 | Data items

Information from each study was extracted covering the following:

1. Species name (scientific and common), their habitat (demersal, pelagic, or reef associated) and niche affinity (deep-water, polar, temperate, or tropical), and commercial exploitation status, as provided by the study or otherwise sourced from the online fish catalog fishbase.org (version 02/2022); information on taxa and life stage, for example, whether sampled individuals were bony or non-bony fish and life stage (eggs, larvae, juveniles, or adults); and whether fish were marine exclusive or diadromous;

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 were not provided, monthly sea surface temperature (SST) estimates in 1° resolution for each sampled raster grid within each study's duration were derived from the Hadley Centre Global Sea Ice and Sea Surface Temperature dataset (Rayner et al., 2003);

5. Whether other significant predictors of distribution changes, such as chlorophyll-*a* concentrations, ocean currents, pH, and oxygen concentrations in addition to water temperature, were identified by the study;

6. Methods of measurement which were classified into three categories: observations based on abundance data (A), presence–absence data (P), or a combination of both (AP), where we expect abundance-only data to bias toward lower range shift estimates as it is less influenced by potential outliers as in occurrence data. For the study by Husson et al. (2022), of which raw data were 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. We also considered which portion of a species' range was measured—the center (usually as the mean latitude or abundance weighed centroid), the leading or trailing edge (the upper and lower percentiles of a species distribution range), as we expect faster response rates at the leading front and center compared to the trailing edge;

7. If and how the overall size of shift (OSS) in depth and longitude/latitude was provided in a quantifiable form (e.g., °latitudes, km year^{-1}, or km °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), which may reduce accuracy and statistical power in further meta-analyses. Distinguishing between different OSS reporting approaches (single or multi-population averages) allowed to test for their potential effect on reported distribution responses, as averages from multiple taxa are expected to be less accurate. Studies were further divided into three categories according to sampling frequency: those which measured distributional and temperature changes annually, irregularly (e.g., excluding some years during the study period), or between two points in time, such as studies 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. Yearly rate of change in latitudinal, longitudinal range and depth, with estimates standardized into km year^{-1} and m year^{-1}, respectively, by extracting means from manuscripts or fitting linear regressions of yearly shift estimates if not provided. 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, only six separate longitudinal response estimates

could be extracted, thus further analysis focused on latitudinal and depth shifts. Annual latitudinal range shift (LRS) rates were represented relative to poleward direction, where positive values represent poleward shifts and negative values represent shifts toward the equator. Positive depth shift estimates represent increasing depth and negative decreasing depth;

9. Data on the mean coordinates and sampling area size (in km^2): where not provided, approximate estimates were estimated based on extracted sampling map coordinates;

10. Location (continent, sea, or ocean) of the respective study and the number of sampled years. 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, for example, 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., Bell et al., 2015; Bluemel et al., 2022);

11. Type of sampling method used to calculate distribution location, either from fisheries, such as through trawling, or from cameras and diving records, tagging studies, observations from long-term sightings, revision of historical records or information from genetic molecular analyses. Methods were grouped into trawl (486 observations), historical records (64), diving surveys (snorkel or camera, 9), tagging (3), or other fishing methods (33); and

12. The number of species per study investigated; and, depending on type of data collection method, the sample size in number of individuals collected, such as in tagging–recapture studies (e.g., Hammerschlag et al., 2022; Neat & Righton, 2007), 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 S1.

2.5 | 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. 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. As the dataset to which the full model was fitted was reduced to 179 data points (which had estimates of both LRS and presence or absence of depth shifts), not all collected variables could be tested to avoid

overfitting. We separately tested the effect of rate of depth change (m year^{-1}, 72 estimates), sampling method (trawl, historical records, diving surveys, and other fishing methods), and geographical location (the ocean basin of study site) on LRS estimates by fitting simple mixed-effect models with study as a random effect.

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

a. Methodological factors: *OSS reporting*—whether shifts were reported per species (1) or groups of species for latitude and depth (C) or latitude only (C*); *Data type*—abundance (A), presence–absence (P), or their combination (AP); *Years sampled*—number of study years for which data were obtained; *First study year*; *Area size* (geographical area of sampling locations in km^2); *Marine exclusivity*—whether the taxa were diadromous or exclusively marine-dwelling; *Number of species*; *Study sampling frequency*—if data were collected every year (yearly), not for every year within the study period (irregular), or compared between two time periods; and *Non-temperature predictors*, a binomial factor indicating whether the study identified any other non-temperature predictors (which were not tested separately in this study due to low sample sizes);

b. Ecological predictors: *ΔTemperature*, the annual rate of temperature change (°C year^{-1}), to investigate whether degrees of distribution responses correlate with rates of temperature changes, as one might expect higher rates of temperature warming to provoke increased range shift responses; *Niche* (four categories: deep-water, polar, temperate, tropical); *Depth change* (binomial factor indicating whether depth change occurred or not); *Commercial exploitation status*, *Mean study latitude* and *Habitat*—seven categories (bathydemersal, bathypelagic, benthopelagic, demersal, pelagic–neritic, reef associated) grouped into pelagic, demersal, and reef associated. *Taxonomy* included five groups: bony fish, bony fish(eggs), bony fish (juvenile), bony fish (larval), and non-bony fish; *Range location* was either center, trailing, or leading edge of a distribution range. Testing of additional variables or interactions, such as between *Depth change* and *Niche* or *ΔTemperature* was limited by number of data points included ($n=179$) after filtering for both estimated LRS and presence or absence of depth change. To investigate the effect of depth changes on latitudinal range changes, initially annual depth change rates (m year^{-1}) were included, however, the former yielded small model sample size ($n=72$) and was thus replaced by the binomial *Depth change* predictor ($n=179$), as many studies investigated the occurrence of depth changes without estimating rates.

The best model was selected by a back-ward selection process, starting with the "full" model (Equation 1) and reducing predictors until the best configuration was identified based on the lowest Bayes information criterion (BIC), calculated in the *lmerTest* package (v3.1-3, Kuznetsova et al., 2017) by maximum likelihood method.

From the full model, one outlier (i.e., one population's response estimate) identified with a Bonferroni outlier test was removed

(Bonferroni $p < .001$), which improved model likelihood (Δlog-Lik = 5). Log-transformations to improve data normality were included for numerical predictors if model fit was improved. For each model (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.

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 & Barton, 2015) according to Equations (1) and (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 & Schielzeth, 2013). Relative contributions of predictors to explained variation in range shift rates were compared by calculating partial marginal R^2 estimates (Nakagawa & Schielzeth, 2013).

$$R^2_{marginal} = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_\alpha + \sigma^2_E}, \tag{1}$$

$$R^2_{conditional} = \frac{\sigma^2_f + \sigma^2_\alpha}{\sigma^2_f + \sigma^2_\alpha + \sigma^2_E}. \tag{2}$$

The same model selection procedure was performed to identify the best model for depth change responses. After removing two outliers we fitted the full model to 104 observations, which included *ΔTemperature*, *Data type*, *Niche*, *Habitat*, *Commercial exploitation status*, *Sampled years*, *Mean study latitude*, and *Range location*. For the significant predictors according to BIC partial effects were estimated and plotted, estimates are reported in Table S4.

2.6 | Effect size estimation by correlation coefficients

The relationship between temperature change and LRS was quantified by extracting correlation coefficient (r) values from retrieved studies. Where coefficients were not reported, numerical values were obtained by digitizing figures when available and performing linear regressions. We used Fisher's z transformation to calculate a standardized effect size for each individual observation, where $z = 0.5 \times \log[(1+r)/(1-r)]$. The variance of z was calculated as $1/\sqrt{(n-3)}$ (Borenstein et al., 2009), where n corresponds to sample sizes which were normalized, as they originated from studies reporting either the number of individual fish caught or trawled stations and constituted different value ranges.

The overall significance of the temperature–LRS relationship was assessed by a random-effects model in R package *metafor* v.3.8-1 (Viechtbauer, 2010) using the transformed effect sizes. We assessed the heterogeneity within significant predictors with identified by the best multivariate model by an inverse-variance-weighted hierarchical mixed-effects meta-regression of z, including Study as a random effect to account non-independence of multiple observations within a single study. Among categorical predictors from the best fitting model, only Data type and Niche category had sufficient data (>1 r estimates per level). All parameters were calculated using maximum likelihood, which is preferred when fitting hierarchical mixed-effects models (Zuur et al., 2009).

We combined effect sizes across all studies for each Data type and Niche affinity to obtain the mean effect sizes which represent the weighted average of relationships between temperature and LRS. As the conditional variance is inversely related to n, studies with larger sample sizes had a greater weight. Effects were considered statistically significant if the 95% confidence interval (CI) did not include zero. Back-transformed z values to correlation coefficients were plotted for each data type and niche, where positive r values indicate increasing latitudinal change (km year^{-1}) per °C year^{-1}.

2.7 | Assessment of methodology

Summary statistics for the frequency of publication years, mean study period, and mean study area size with standard deviations were calculated. Methodological aspects of investigated studies, such as the type of data used to calculate range shifts, and how and if LRS was reported, were summarized.

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 & Tittensor, 2011) which had large sampling areas. Total numbers of each type of range change (shift, expansion, or contraction), and direction of shift (north, south, west, and east) of retained population responses ($n = 595$) were calculated. Trends of shift directions were reported as the proportion of populations per location moving in either of the four directions.

To assess potential publication bias, a funnel plot and regression of the effect sizes (reported LRS estimates) on sample sizes (n) was computed. 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 & Liu, 2000), where p-values below significance threshold ($\alpha = 0.05$) suggest potential publication bias (Figure S2a,b). While for funnel plot regression analyses the weighted standard error of effect sizes is most commonly 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).
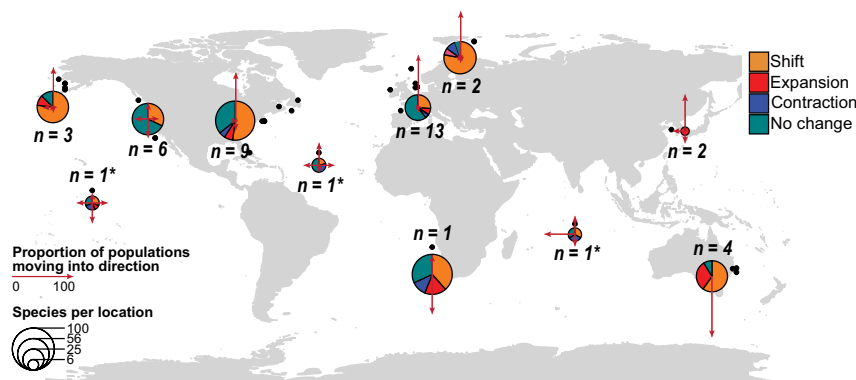
Sampling locations and redistribution direction

FIGURE 2 Map of sampling locations and sizes with type of range shift. From articles included in this review (n = 39), 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 (red), range contraction (blue), no change (green), 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.

Average LRS estimates were expressed in medians and respective interquartile ranges (IQRs), that is, the difference between the upper lower quartile range of the data, due to the tendency for the data to have skewed distributions and outliers. For predictors from mixed-effect models, marginal effects (β) were reported with 95% confidence intervals (package *marginaleffects* v.0.9.0, Arel-Bundock, 2023). Data were analyzed and visualized in R (version 4.2.3; R Core Team, 2023).

3 | RESULTS

3.1 | Study selection

A total of 39 studies were identified for inclusion in the review (Table S1; Alheit et al., 2012; Bell et al., 2015; Bluemel et al., 2022; Champion et al., 2021; Chust et al., 2019; Dulvy et al., 2008; Engelhard et al., 2011, 2014; Fossheim et al., 2015; Fowler et al., 2017; Fredston-Herman et al., 2020; Hammerschlag et al., 2022; Han et al., 2021; Hsieh et al., 2008, 2009; Hughes et al., 2014; Hurst et al., 2012; Husson et al., 2022; Kotwicki & Lauth, 2013; Kumagai et al., 2018; Last et al., 2011; Li et al., 2019; Mueter & Litzow, 2008; Neat & Righton, 2007; Nicolas et al., 2011; Nye et al., 2009; Olafsdottir et al., 2018; Overholtz et al., 2011; Perry et al., 2005; Pinsky et al., 2013; Rose et al., 2000; Sabatés et al., 2006; Smith et al., 2018; Swain & Benoit, 2006; van Hal et al., 2010; Vestfals et al., 2016; Worm & Tittensor, 2011; Yasumiishi et al., 2020; Yemane et al., 2014). The search of Web of Science databases provided a total of 896 records. After adjusting for duplicates and studies which did not include marine fish, 169 studies remained. Of these, another 153 studies were discarded during

the filtering process through reviewing the abstracts and examining article methods in detail. An additional 24 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 (Figure 1).

3.2 | Geography

The average sample size across the 11 major locations was 54.1 (±39.3) species per location, with more than half (77%) of all populations displaying a range shift, of which 16% expanded range, and 9% contracted their range, when excluding multi-species LRS estimates (Figure 2). Overall, more than half (54%) of the populations moved poleward, particularly in Asia (4 of 4), Australia (50 of 55), the North Sea (52 of 80), the Bering Sea (40 of 56), and the Barents Sea (49 of 59). Regarding longitudinal shifts, populations shifted overall eastwards (median = 1.7 km year^{-1}; IQR = 11.8, n = 6). While in some regions such as in the East Pacific, central Atlantic and Indian oceans responses were less significant or multidirectional (Figure 2), many studies investigated movements only across the north–south axis, which could have biased lower frequencies of shifts on the east–west axis.

When comparing individual LRS rates among major geographical locations, the southwest Pacific (Australian coast) had by far the fastest latitudinal range changes (median$_{LRS}$ = 20.7 km year^{-1}; IQR = 11.9), followed by the North Atlantic (median$_{LRS}$ = 8.5 km year^{-1}; IQR = 18.4) and South African populations (median$_{LRS}$ = 7.6 km year^{-1}; IQR = 17.0). In the Northeast Pacific, marine fish shifted around 0.8 km year^{-1} (IQR = 0.1; n = 5), while the Bering Sea saw shifts of 1.0 km year^{-1} (IQR = 2.5, n = 57), and the Northwest Atlantic 3.2 km year^{-1} (IQR = 3.9, n = 61).

3.3 | Methodology

The mean study duration was 41 ($\pm$49) years, at a sampling area size of 356,628 ($\pm$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 less representation with 11%, 6%, and 3% of the identified research articles, respectively. No eligible reports from South America and Antarctica were identified.

Most frequently investigated taxa were classified as tropical ($n=65$), followed by temperate ($n=52$), deep-water ($n=37$), and 19 polar populations (Figure S1). The most frequently studied fish families included *Pleuronectidae* ($n=80$, particularly *Microstomus*, *Atheresthes*, *Eopsetta*, and *Pleuronectes* spp.), *Gadidae* ($n=52$, *Gadus*, *Melanogrammus*, *Pollachius* spp.), *Scombridae* ($n=28$, *Scomber* and *Thunnus* spp.), *Rajidae* ($n=21$, including *Amblyraja radiata* and *Leucoraja* spp.), and *Sebastidae* ($n=18$ such as *Helicolenus dactylopterus*, *Sebastes* spp.).

Nearly 80% of studies implemented statistical tests to investigate range shift association with temperature changes, and assessed range changes annually (Figure 3), with only few studies measuring changes irregularly or comparing two time periods. 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. The most common types of data used across studies included abundance (81%) and presence–absence data (67%), which in some studies were used in combination. Most samples originated from trawling (74%) or other fishing data, while 10% and 5% of studies revised historical occurrence records from literature and carried out tagging–recapture experiments, respectively.

From visual inspection of funnel plots of regressed LRS effect sizes on sample sizes, there was little evidence for risk of publication bias, particularly when the sample size proxy was individuals sampled per population (Figure S2a). Although a regression test suggested significantly asymmetrical funnel shape ($F_{1,152}=396$; $p=.048$) when expressing n as mean yearly rate of stations trawled, this proxy provided considerably less resolution of effect size distribution due to sampling of multiple populations with high heterogeneity in LRS across the same fishing stations (Figure S2b).

3.4 | Factors affecting range shift estimation

The best model (ΔBIC $=53.4$ compared to full model) included ecological predictors *ΔTemperature*, *Niche*, *Depth change*, and *Mean study latitude* and methodological variables *OSS reporting*, *Data type*, *First study year*, and *Other predictors* (Table S2). The model had an intermediate effect size when considering only fixed effects ($R^2_{marginal}=0.30$), with methodological factors explaining 10% of the variance in range shifts, and combined ecological factors accounting for 7%, while niche affinity had the highest single proportion of 13% (Table S5; 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, 179 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). LRS was on average higher among studies which reported range shift sizes for individual populations as compared to those that grouped populations (Figure 4c); and lower when based on occurrence data compared to those derived from abundance data or a combination of the two (Figure 4d). Moreover, estimates tended to be lower if studies started in earlier years (Figure 4h). As sea temperature significantly increased over the years (ANOVA test: $F_{1,340}=9.81$, $p=.002$) and was positively correlated with LRS, this effect might be rather due to methodological biases, driven by significantly earlier study start among the fastest shifting temperate and tropical species, as study timing differed significantly among niche affinities (ANOVA: $F_{3,38}=34.8$, $p<.001$).

Range shift estimates were lower in studies which found significant effects of other non-temperature predictors (Figure 4e). 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, which was reported nine times across reviewed studies (Table 3). Other factors included abiotic marine factors such as ocean currents, salinity, depth and chlorophyll-a concentration ($n=9$), and exploitation by fishing ($n=7$). Density dependence was mentioned five times, which in some cases had larger effect sizes than temperature.

For individual estimates, the rate of latitudinal shifts was greater in populations which did not change mean depth ($\beta=9.68$ km year^{-1}; 95% CI (6.54–12.82); $p<.001$), compared to populations which were reported to shift their depth distribution ($\beta=6.58$ km year^{-1}; 95% CI (3.47–9.69); $p<.001$; Figure 4b). The deeper populations moved, the less latitudinal change was observed ($\beta=-3.95$ km year^{-1} for every meter in depth increase, $p<.001$, Figure 5e). LRS increased with annual temperature change, with tropical taxa moving the fastest at 18.46 km C^{-1} (95% CI (14.62–22.3); $p<.001$), while deep-water populations were the slowest at 8.23 km C^{-1} (95% CI (4.95–11.5); $p<.001$; Figure 4a), the latter having the highest proportion of non-poleward shifts (43% of responses). Responses also varied with a population's geographical location, as LRS estimates were highest among high-latitude taxa (Figure 4g).

The positive correlation between LRS and temperature change was supported by weighted means of correlation coefficients, with a grand mean effect size of 0.29 (95% CI (0.16–0.43)). The effect of temperature on climate responses varied as a function of niche and the type of data used by studies, with polar taxa showing nearly a twofold larger correlation coefficient ($r=.53$) compared to temperate counterparts (Figure S3).

Although not included in the final model, differences in responses between range locations were observed with leading edge populations moving poleward the fastest (median-$_{LRS}=7.2$ km year^{-1}) compared to trailing and center populations (4.2 and 1.6 km year^{-1}, respectively; Figure 5a); and exploited
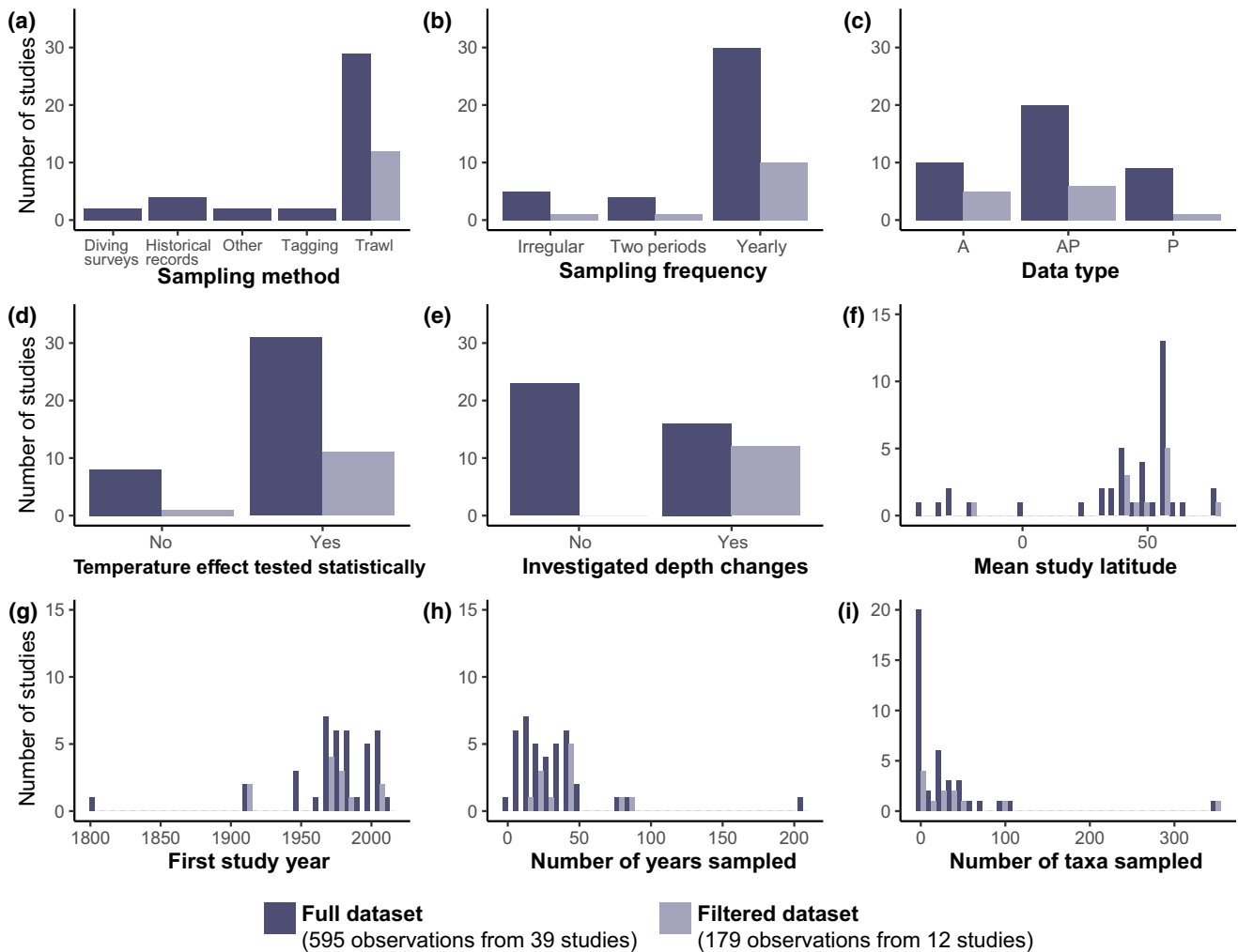
FIGURE 3 Frequency of methodological aspects across studies. Colors indicate counts for the complete dataset (dark) from 39 retained studies yielding 595 range shift responses to temperature change, or the data included in multivariate models (light) to test latitudinal range shift responses (12 studies with 179 observations). The reduction from 342 latitudinal shift estimates was due to only 179 observations investigating depth changes (e). Plots show (a) data acquisition method; (b) sampling frequency: whether sampling every year, sporadically or comparing two time points; (c) data type: based on abundance (a), presence–absence data (P) or a combination of the two (AP); (d) whether the study performed statistical analyses to confirm temperature effects on range shifts; (f) mean current latitude of sampling area; (g) first year of study period; number of sampled years (h) and taxa (i).

populations moving slightly less (2.1 km year^{-1}) than non-exploited counterparts (3.0 km year^{-1}; Figure 5c). Bony juvenile fish shifted poleward faster (15.2 km year^{-1}) than adults (2.8 km year^{-1}), while non-bony fish on average moved equatorward by 0.2 km year^{-1} (Figure 5j).

Variance in depth changes was best explained by niche affinity (18% of variation), commercial exploitation status (7%), position within the range distribution and rate of temperature change (3% each), as well as data type (28% of variance), according to the best model which explained overall 47% of the variance in depth responses (ΔBIC = 12.6 between full and final model). Depth shifting populations ($n = 104$) moved to overall shallower depths with higher rates of temperature change (Figure 6b), while non-exploited species deepened their distributions significantly faster ($\beta = 1.96$ m year^{-1}; 95% CI: 1.3–2.6) than exploited taxa (0.59 m year^{-1}; 95% CI: 0.9–3.4; Figure 5d).

Studies estimating depth changes based on abundance data found overall decreasing depth responses, while abundance–occurrence data tended to suggest increasing depths (Figure 6c). Individuals at the trailing edge of population distributions were showing the largest move toward deeper waters (Figure 6a), particularly among deep-water species. Tropical taxa showed the slowest depth responses, with shallowing trends at the center and leading edge (Figure 5a). Out of 104 estimated depth shift responses, the majority (73%) shifted in the direction as expected from temperature changes (i.e., to cooler waters).

4 | DISCUSSION

We found that the majority of fish populations have responded to thermal warming with a poleward change in their geographical
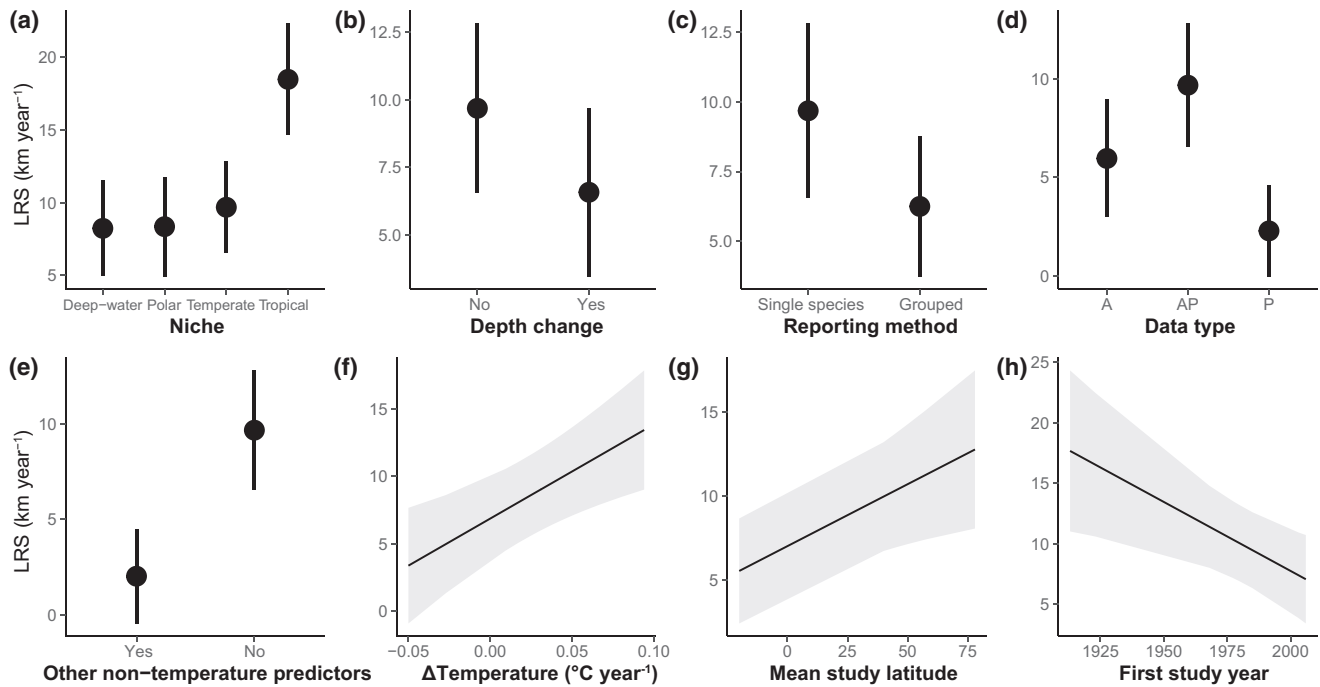
FIGURE 4 Latitudinal range shift predictors. Partial effects of fixed predictors included in the final mixed-effect model ($\Delta BIC_{\text{full-final model}} = 53.4$) explaining latitudinal range shift (LRS; km year^{-1}) in response to temperature in marine fish. Points indicate predicted means, and bars and grey shading the 95% confidence intervals. Positive LRS estimates indicate poleward shifts, while negative estimates represent equatorward movements. OSS reporting method had two categories for studies reporting LRS either for taxa individually (single) or the mean of multiple taxa (grouped). Data type was either abundance (A), presence–absence data (P) or a combination of the two (AP). According to temperature change estimates from included studies, tropical populations experienced the slowest yearly temperature increase (0.02 ± 0.02°C year^{-1}), followed by deep-water (0.03 ± 0.03°C year^{-1}), temperate (0.04 ± 0.03°C year^{-1}) and polar taxa (0.05 ± 0.1°C year^{-1}).

TABLE 3 Frequency of other significant predictors of range changes. Predictors other than temperature with significant effects on redistribution in the 39 reviewed studies 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

distribution (Figure 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 (Figure S3).

4.1 | Ecological factors influencing distribution responses

We found a significant positive correlation between rate of LRS and latitude which bolsters previous findings by Lenoir et al., 2020, confirming the expectation of faster poleward movements in the Northern Hemisphere where oceans have been warming at faster rates than in the South (Friedman et al., 2013). However, mean current latitude explained only 2% of the variance in LRS, while niche affinity was a more important predictor of latitudinal and depth shifts globally. Results also show that tropical species shift latitudinally more rapidly (Chaudhary et al., 2021; McLean et al., 2021) in response to warming than other marine fishes (Figure 4a), with disproportionate poleward movements (Figure 2). 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 (Figure 5b). Other studies have shown that, in comparison to temperate fish, tropical species may have increased sensitivity and lower adaptability to thermal increase (Comte & Olden, 2017; Nati
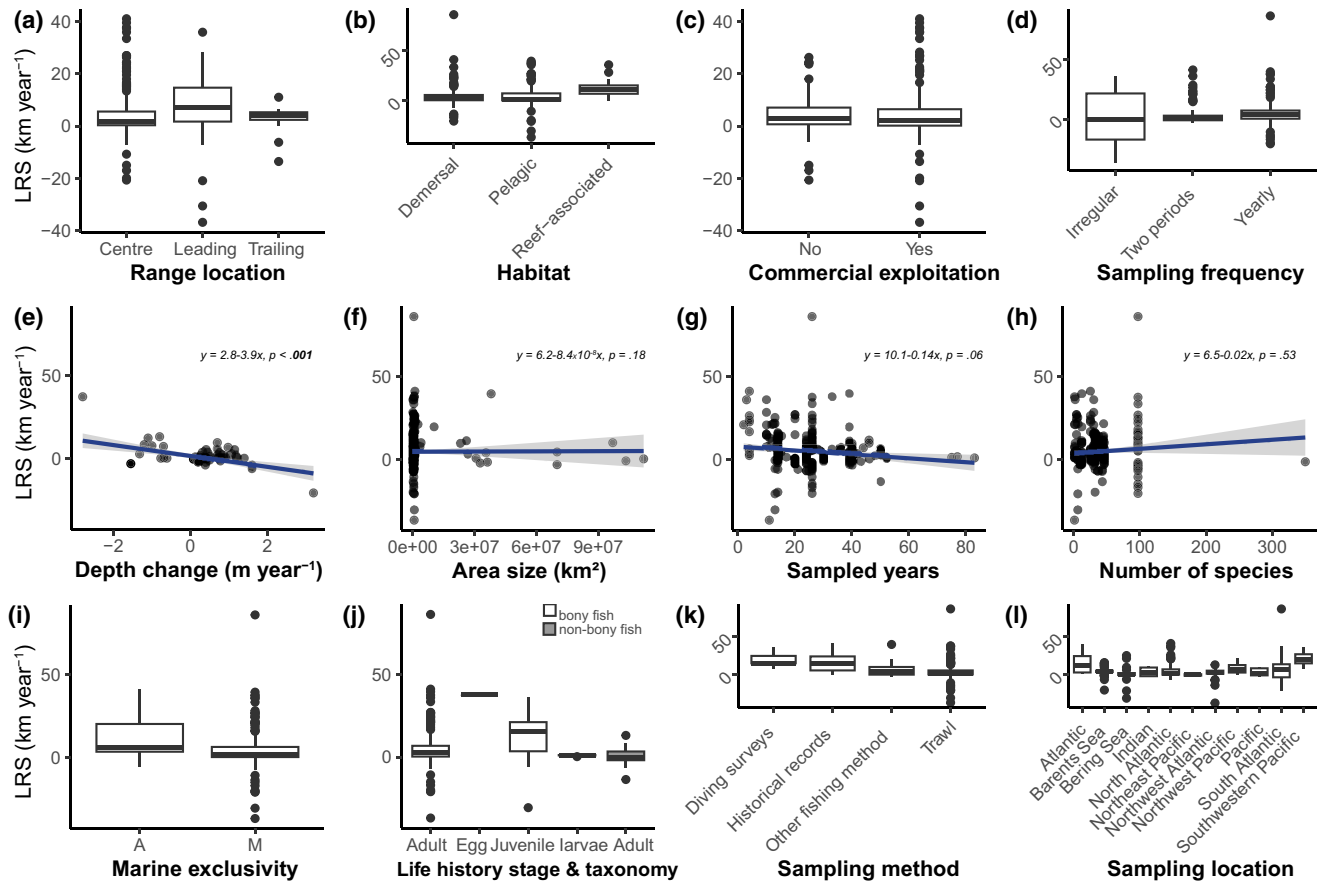
FIGURE 5 Non-significant latitudinal range shift predictors. Effects of excluded predictors from simple mixed-effect models with Study as a random effect. Rate of depth change (e, 72 estimates), sapling method (k) and location (l) were tested separately and were not included in the models to avoid overfitting due to limited data. Depth change showed a significantly negative correlation with LRS ($p < .001$). Positive LRS estimates indicate poleward shifts, while negative values indicate equatorward movements.

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 rate of LRS, with depth shifting taxa on average moving latitudinally by 3.95 km year^{-1} less for every meter in depth increase per year. 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) and illustrated by tropical species having the slowest and shallowing depth changes (Figure 6a). In line with predicted narrow temperature tolerance limits of stenotherms (Storch et al., 2014), we found polar species to experience some of the fastest increases in depth of occurrence. 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). Although leading edges showed faster poleward LRS rates compared to the trailing edge and center (Figure 5a), this difference was not significant, which is in line with previous findings suggesting similar warming sensitivities at opposite distribution fronts (Brown et al., 2016; Lenoir et al., 2020; Sunday et al., 2012), but in contrast to other reports (Poloczanska et al., 2013). Interestingly, faster depth increases were observed at the trailing edge across all niches (Figure 6a), despite similar rates of warming at the trailing and leading edges (mean$_{\Delta temperature} = 0.03°C$ year^{-1}), suggesting that depth responses at contracting range fronts may be a response to other drivers. While additional drivers such as habitat and prey availability or resource competition for these responses were not investigated by studies, we found that commercially exploited species changed their mean depths at lower rates than non-target counterparts (Figure 6d). Restricted responsiveness to climate change in exploited populations might be due to reduced ability to establish in new areas due to localized effects of fishing pressure on abundance and age structure (Rindorf & Lewy, 2006), which has been observed in fish stocks globally (Engelhard et al., 2014; Hsieh et al., 2008; Last et al., 2011).
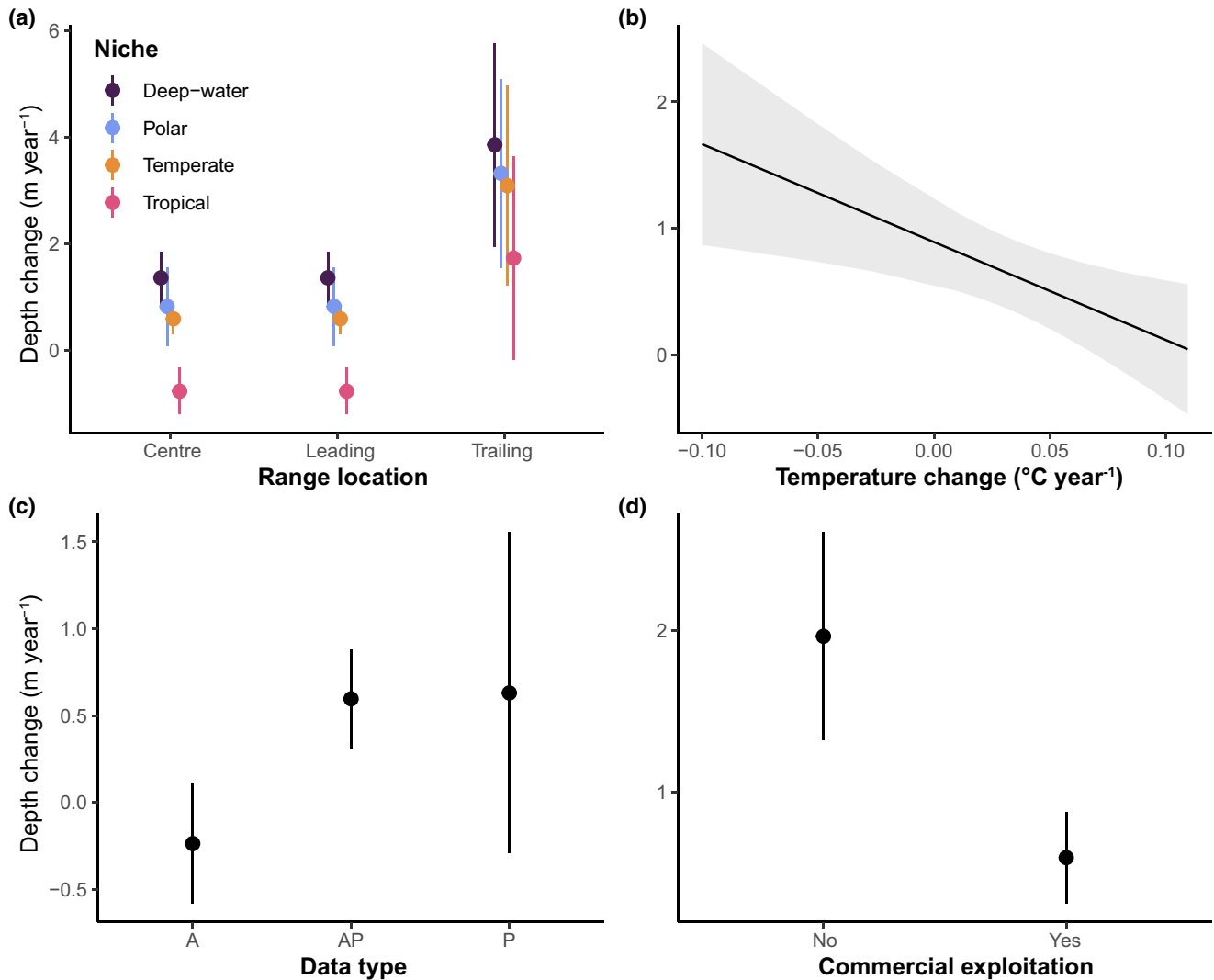
FIGURE 6 Depth shift predictors. Term plots of fixed predictors included in the final model (selected according to BIC) explaining changes in average depth (m year^{-1}) in response to temperature change. Points indicate predicted marginal means, and bars and grey shading the 95% confidence intervals. Data type was either abundance (A), presence–absence data (P) or a combination of the two (AP). Positive depth change values represent deepening, while negative values indicate distribution changes to shallower waters.

Other factors, such as life stage and taxonomy, were not found to significantly affect latitudinal 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 & 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 faster range shifts for larvae and juveniles compared to adult fish, 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., 2020; Mueter & Litzow, 2008; Nye et al., 2009; Yasumiishi et al., 2020). 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 & Hollowed, 2018) or inferences of potential range shift limitations in diadromous fish species due to affinity to natal homing grounds (Hare et al., 2016).

4.2 | The effects of variable study methods

Both LRS and depth responses were greater when estimated from both abundance and presence–absence data together than from abundance data alone (Figures 4d and 6c). Abundance data, mostly obtained from fishery or research trawling 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 to 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 toward commercially important fish species in the northern hemisphere (Figure 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 do 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 & 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 line with findings by Brown et al. (2016), we observed that studies incorporating occurrence-based data had substantially higher range shift estimates than those using abundance data only, suggesting that presence–absence data may be more sensitive to outliers. Although response estimates from presence–absence data only were lower than estimates derived from a combination of occurrence and presence–absence data, all former observations originated from one single study and should thus be interpreted with caution.

Previous climate response syntheses have argued that single-species studies confirming range shifts consistent with warming may be more likely to be published and thus bias meta-analyses (Parmesan, 2007). While we did not identify publication bias due to low numbers of investigated species or sampled years, we found that range shift estimates reported as the average of multiple taxa were lower than those derived from individual species estimates. This could be due to random bias due to lower sample size 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) or indeed indicate that single-taxa studies are over-represented (Figure 3i). Unexpectedly, estimates of LRS decreased with date of the first study year (Figure 4h), which likely reflects methodological biases of earlier and longer reporting history of faster shifting temperate and tropical taxa. This also highlights that climate response studies for deep-water and polar species encompass shorter and more recent time periods, possibly biasing climate response estimations.

Contrary to expectations, we found only a weak negative effect of study area size on LRS values (Figure 5f). A plausible source of distributional response variation is the geographical scope of each study, with spatial sampling extents varying widely, and often spanning across whole oceans (e.g., Worm & 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 & Hollowed, 2014; Barbeaux & 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 a few studies have accounted for subregional 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 Li et al. (2019) demonstrated significant heterogeneity in marine fish responses to marine warming due to subregional 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., 2022). A promising tool to investigate heterogeneity in range shift responses is genetic molecular techniques which help delineate cryptic diversity (Jokinen et al., 2019) and estimate dispersal velocity of locally adapted genotypes (Jonsson et al., 2018). These techniques may improve 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), although such genetic applications to climate range shift research are still scarce.

The variation in species' responses to climate change has been addressed through various predictors such as local adaptation (Jonsson 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). While the majority of reviewed studies investigated (but not always statistically tested) temperature as the sole predictor, a significant proportion of climate response variation is likely explained by a multitude of climatic and biotic factors instead of temperature alone (McHenry et al., 2019). 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 & Lauth, 2013; Olafsdottir et al., 2018; Swain & Benoit, 2006; Worm & Tittensor, 2011; Yasumiishi et al., 2020). Our results suggest that marine range shift estimates from single-predictor studies focusing solely on temperature were higher than those originating from studies which identified at least one additional driver to temperature (Figure 4e), possibly due to the confounding effects of additional variables explaining part of the LRS variation. While some studies found effects of fishing pressure (Bell et al., 2015; Engelhard et al., 2014; Neat & Righton, 2007; Rose et al., 2000; Worm & Tittensor, 2011), 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 only (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.

4.3 | Opportunities for future improvement

Our conclusions might have been affected by multiple statistical issues and biases associated with meta-analysis (Gurevitch & 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 & 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 & 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 (Han et al., 2021; Kumagai et al., 2018) 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, multi-directional range shift averages are mainly driven by one large study by Li et al. (2019), measuring depth and horizontal distribution shifts of 10 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. 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. 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.

4.4 | 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 & Hutchings, 2015; Petrou et al., 2021) and larval retention (Sinclair & 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, including phenomena such as the Southern Oscillation affecting temperature trends in the tropics (Jakovlev et al., 2021), or density dependencies, such as in Bluemel et al. (2022) who accounted for biases by temporal biomass trends. There is an urgent need to expand geographical and taxonomic representation of marine fish range shift responses to climate change. In particular, expansion is needed in the highly biodiverse tropics and global south where marine taxa have been identified as the most vulnerable to warming (Comte & Olden, 2017). As in these regions marine research and long-term fisheries monitoring programs are less established than in the northern hemisphere, 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 & 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 & 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.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.7937671, reference number 7937671.

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