Original Article

Projecting climate-driven shifts in demersal fish thermal habitat in Iceland's waters

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As climate change shifts marine species distribution and abundance worldwide, projecting local changes over decadal scales may be an adaptive strategy for managers and industry. In Iceland, one of the top fish-producing nations globally, long-term monitoring enables model simulations of groundfish species habitat distribution. We used generalized additive models to characterize suitable thermal habitat for 51 fish species in Iceland's waters. We projected changes in suitable thermal habitat by midcentury with an ensemble of five general circulation models from the Coupled Model Intercomparison Program 6 (CMIP6) and NOAA (CM2.6) and two scenarios (SSP 5-8.5 and SSP 2-4.5). We found a general northward shift in suitable thermal habitat distribution, with variable regional dynamics among species. Species thermal bias index was a weak predictor of projected thermal habitat change, with warmer-water species more likely to see increases in thermal habitat and southern warm-edge range expansions. While these results isolate the effects of future changes in temperature, providing an indication of suitable thermal habitat, low model explanatory power suggests that additional variables may improve distribution projections. Such projections might serve as guideposts to inform long-term management decisions about regional and species-specific suitability for Iceland's fisheries, infrastructure investment, and risk evaluation under climate change.

Keywords: climate change, generalized additive model, global climate model, species distribution modelling, suitable thermal habitat.

Introduction

Climate change is shifting marine species distribution and abundance worldwide (Parmesan, 2006; Poloczanska et al., 2013). These shifts are projected to continue as climate change intensifies (Molinos et al., 2016), with complex and unevenly distributed social–ecological consequences (Sumaila et al., 2011; Golden et al., 2016; Lam et al., 2016; Pinsky et al., 2018). Alongside the urgent need for bold action to reduce greenhouse gas emissions is the need for

adaptive management approaches to maintain desired fishery outcomes under changing and novel conditions. Researchers project that implementing management that accounts for changes in fish species productivity and distribution can improve outcomes for fishery catches and profits under most climate scenarios (Gaines et al., 2018; Free et al., 2020). For fisheries with adequate scientific and technical capacity, conducting forecasts and incorporating future climate scenarios into management decisions is a key aspect of climate-adaptive management (Pinsky and Mantua, 2014;

Holsman *et al.*, 2019; Karp *et al.*, 2019; Free *et al.*, 2020). While seasonal and interannual forecasts may be of most immediate use for management and industry, climate-scale projections allow managers and practitioners to evaluate risk, plan for future losses or gains in suitability, and inform longer term decision-making processes such as national legislation or international negotiations (Hobday *et al.*, 2018; Holsman *et al.*, 2019).

In Iceland, the economic and cultural importance of fisheries and the sophistication of its management and scientific systems mean that projecting future change in fish stocks could be a key priority for achieving climate-adaptive fisheries (Kleisner *et al.*, 2021). Consistently ranking among the top 20 marine fish capture producing countries worldwide (FAO, 2020), Iceland is located in a highly productive transition zone between warm Atlantic and cold Polar currents. The interactions of these currents create high spatial and temporal oceanographic variability within Iceland's waters, and the ecosystem is highly sensitive to their dynamics (Astthorsson *et al.*, 2007). Environmental conditions have fluctuated over the past century in relation to multidecadal oscillations and local atmospheric dynamics with profound ecological and economic consequences: Relatively warm periods were associated with fishery booms that drove the development of Iceland's commercial fisheries and economy, and cooler-water periods (in combination with overfishing) associated with devastating fishery crashes (Ogilvie and Jónsdóttir, 2000; Astthorsson *et al.*, 2007; Valtýsson and Jónsson, 2018).

Recently, a warm anomaly from the mid-1990s to late-2010s drove substantial changes in fish abundance and distribution around Iceland, including documentation of new species and increases of warmer-water species (Astthorsson and Palsson, 2006; Valdimarsson *et al.*, 2012; Valtýsson and Jónsson, 2018). Particularly notorious was the abrupt expansion of Atlantic mackerel (*Scomber scombrus*) into Iceland's waters (Astthorsson *et al.*, 2012; Olafsdottir *et al.*, 2019) that quickly became an economic boon for Iceland, but led to international political conflict over the fishing of the stock (Spijkers and Boonstra, 2017). Researchers also noted significant shifts in groundfish distribution and community assemblage, with heterogeneous regional trends associated with oceanographic conditions and the influence of coastal fjord systems on predator–prey dynamics (Stefánsdóttir, 2008; Jónsdóttir *et al.*, 2019; Stefánsdóttir, 2019).

Given these past temperature-related changes, a logical next step might be to project how future change might affect fish species abundance and distribution. Global studies have projected that Iceland, like other high-latitude countries, could be a climate "winner," potentially experiencing increased biodiversity and fisheries catch potential as warmer waters move fish poleward (Cheung *et al.*, 2009; Molinos *et al.*, 2016). However, given the highly local and variable dynamics of Iceland climatic conditions and differing ecological, economic, and cultural importance of its fish species, higher resolution projections indicating specific species and regional dynamics could be more applicable for fisheries managers and industry. Campana *et al.* (2020) used Iceland's bottom trawl survey data to model fish habitat and projected that a uniform 1°C increase in bottom temperature would drive a general northward shift in habitat distribution, with significant variation across species and quadrants of the exclusive economic zone (EEZ). The authors noted a high level of regional and temporal variation in past warming trends and warned that future warming is unlikely to be homogenous nor linear.

Iceland's fishery managers have collected standardized fisheries independent and fisheries dependent data since the 1980s,

allowing for detailed analyses of species abundance and distribution in relation to environmental conditions that can inform future projections. These long-term monitoring data are ideal for a common but data-intensive approach to anticipating regional or global species distribution shifts: pairing statistical models of species suitable habitat with global climate model outputs (Stock *et al.*, 2011). Given the uncertainty inherent to projecting both the dynamics of the global climate and the human actions and policies that influence those dynamics, using an ensemble of climate models across different scenarios is advised (Morley *et al.*, 2018, 2020). Here, we use long-term fisheries independent trawl data and an ensemble of the newest generation of global climate models from the Coupled Model Intercomparison Project (CMIP6) to project how future climate change will affect suitable thermal habitat of 51 species in Iceland's waters at a 0.25° x 0.25° resolution. These spatially explicit climate projections can more directly inform Iceland's fishing industry and fisheries management's needs for adapting to climate-driven changes in fish distribution and illustrate to other nations and regions how these projections might be considered in long-term climate-adaptive management.

Methods

Projecting future temperature changes in Iceland's waters

We used a suite of global climate models to project future ocean surface and bottom temperatures in Iceland's waters, including a high-resolution global climate model (CM2.6 from the National Oceanic and Atmospheric Administration Geophysical Fluid Dynamics Laboratory, NOAA GFDL) and four coarser global climate models from the CMIP6. Researchers have found that CM2.6 (10-km ocean resolution) resolves the ocean circulation in the Northwest Atlantic more realistically than coarser models (Saba *et al.*, 2016). However, this model has a cold bias in sea surface and bottom temperature in Iceland's waters in the historical period from 1982 to 2012, so we selected the highest resolution CMIP6 models that have a range of cold and warm biases to complement the higher resolution CM2.6. These were GFDL CM4 (25-km ocean resolution) from the NOAA GFDL, USA; CNRM-CM6 (25-km ocean resolution) from the Centre National de Recherches Meteorologiques and Centre Europeen de Recherche et de Formation Avancee en Calcul Scientifique, France; HadGEM3-GC31 (100-km ocean resolution) from the Met Office Hadley Centre, UK; and IPSL-CM6A-LR (100-km ocean resolution) from L'Institut Pierre Simon Laplace, France. We downloaded CMIP6 data using the *xarray* package (version 0.15.1) in Python (version 3.7.6; Hoyer and Hamman, 2017).

The CMIP6 models use future scenario simulations that combine the Representative Concentration Pathways (RCPs) of radiative forcings used in the Intergovernmental Panel on Climate Change's Fifth Assessment Report (IPCC AR5) with Shared Socioeconomic Pathways (SSPs) of societal development (Eyring *et al.*, 2016; O'Neill *et al.*, 2017). We examined two future scenarios for the years 2015–2100: SSP 2-4.5, a "middle of the road" scenario where countries continue along historical social, economic, and technological development trajectories as they strive toward sustainable development goals; and SSP 5-8.5, a "fossil-fueled development" scenario where accelerated economic growth emphasizes fossil fuels (O'Neill *et al.*, 2017). The CM2.6 projects an idealized transient climate response (1% per year increase in atmospheric CO_2) simulation over 80 years, where the last 20 years are comparable to years
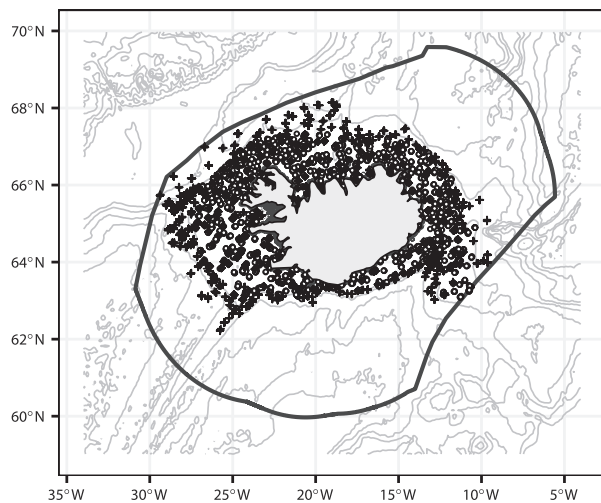
Figure 1. Study region indicating bottom trawl survey points in spring (circles) and autumn (+). Thin lines indicate 500 m isobaths and thick line indicates Iceland's EEZ.

2061–2080 of SSP 5-8.5. We, thus, focused on this 2061–2080 period for our future projections.

We standardized the models using the "delta method," where we calculated the difference between each model's monthly projections and modelled historical control (mean of 1985–2015), and then added these deltas to a standard climatology (Anandhi *et al.*, 2011; Kleisner *et al.*, 2017; Morley *et al.*, 2018). We used a sea surface temperature (SST) climatology from daily NOAA Optimum Interpolated Sea Surface Temperature (OISST) data from 1982 to 2012 and a bottom temperature climatology from the NOAA Greenland–Iceland–Norwegian Seas Regional Climatology version 2 (GINS RC v2) from 1985 to 2012 (Seidov *et al.* 2013). All projections were interpolated to a standard 0.25° x 0.25°grid to match the OISST resolution. We ran a monthly SST and bottom temperature hindcast for the years 2000–2018 using the Mercator Ocean Global Reanalysis (GLORYS) dataset from the Copernicus Marine Environment Monitoring Service and a projection for the years 2061–2080 for each the five models and two scenarios on a projection grid of the 2312 0.25° cells in Iceland's EEZ.

Modelling species suitable thermal habitat

The Icelandic Marine and Freshwater Research Institute (MFRI) conducts annual standardized bottom trawl surveys in the spring and autumn to inform groundfish stock assessments. The spring survey has been conducted since 1985 at about 590 fixed stations covering Iceland's continental shelf to a depth of 500 m (Solmundsson *et al.*, 2020). The autumn survey, initiated in 1996 and expanded in 2000, covers about 400 fixed stations that additionally include deeper waters along the continental slope (400–1500 m; Campana *et al.* 2020). Fish lengths and standard weight conversions are used to calculate biomass (kg) per nautical mile. Surface temperature and bottom temperature are also measured *in situ*. We used surveys through March 2020, excluding the autumn survey before it was expanded in 2000 and 2011 when a labour strike interrupted the survey, for *n* = 27524 total survey tows (Figure 1). We combined the spring and autumn surveys to better account for the full thermal envelope each species experiences throughout the year (Kleisner *et al.*, 2017).

We modelled individual species abundance and distribution with generalized additive models (GAMs), using the *mgcv* package (version 1.8.33) in R (version 4.0.2; Wood, 2011). Because the purpose of this analysis was to predict suitable thermal habitat, we tested a limited number of models based on ecological hypotheses and selected the final model based on predictive performance as measured by Akaike's Information Criterion (AIC) and prediction error in out-of-sample validation (Tredennick *et al.*, 2021). Further, we did not include model terms that would constrain prediction, such as year or latitude and longitude. We modelled biomass density (kg per nautical mile, as calculated by MFRI) of each species as the response variable, with a suite of static and dynamic environmental variables as the predictor variables. We used a Tweedie distribution on the observations with a log-link function between the predictors and the response variable and power-parameter $1 < p < 2$ estimated during fitting (Shono 2008).

The predictor variables for the final model included the observed depth of the trawl survey tow and rugosity as static habitat variables and five temperature metrics as dynamic environmental variables. We calculated rugosity as the mean of the absolute differences in depth of a cell and its eight surrounding cells (the terrain ruggedness index; Wilson *et al.* 2007). We downloaded gridded bathymetry data from the NOAA ETOPO1 1 Arc-Minute Global Relief Model at a 3-minute resolution (0.05° x 0.05° cells) using the *marmap* package (version 1.0.4) in R. We determined that this resolution was appropriate to the spatial scale of ridge and valley bathymetric features along Iceland's shelf, and that models with this resolution performed better than those with 1-minute or 6-minute resolution rugosity. We included *in situ* surface and bottom temperature from the survey tows and used GLORYS temperature data to calculate the annual minimum and maximum surface and bottom temperature at each survey point (that is, the minimum or maximum temperature over the preceding 12 months in the 0.25° x 0.25° cell where the tow was conducted), as these annual extremes may also influence species distribution (Morley *et al.*, 2018). We removed the annual minimum bottom temperature as a predictor variable because it was highly correlated with the survey in situ bottom temperature (Spearman's rho = 0.77) and did not perform as well as *in situ* bottom temperature in model selection.

The Tweedie GAM was defined as follows:

$$Y \sim TW(\mu, \sigma^2, p)$$

$$E(Y) = \mu = g^{-1}(\eta)$$

$$\mathrm{Var}(Y) = \sigma^2 \mu^p$$

$$g(\mu) = \eta = intercept + s(towdepth) + s(rugosity) + s(SST)$$
$$+ s(BT) + s(minSST) + s(maxSST) + s(maxBT),$$

where *Y* is the random variable representing survey tow biomass in kg per nautical mile, μ is the expected value of *Y* under the Tweedie distribution with σ^2 as the dispersion parameter, and *p* as the power-parameter with $1 < p < 2$, and *g(.)* representing the log link function, the inverse of which is an exponential. The additive function *s(.)* reflects the smoothing basis, namely a thin plate regression spline, with input values as defined previously with sea surface temperature denoted as *SST* and bottom temperature as *BT*. A restricted maximum likelihood (REML) approach was used to fit the models.

The GLORYS data were available from 1993 to 2018, so we trained the final model on data from 1993 to 2013 (approximately 75% of the tows, $n = 15049$ observations) and tested predictions on the tows from 2014 to 2018 ($n = 4710$). To assess model performance, we calculated AIC and Mean Absolute Error (MAE):

$$MAE = \frac{1}{n} \sum_{i=1}^{n} |f_i - y_i|,$$

where f_i is the suitable thermal habitat prediction value for survey tow i, y_i is the observed biomass for survey tow i, and n is the total number of survey tows in the testing data.

We further assessed the predictive performance of a temperature-based model by comparing the model MAE with that of a "naïve" model with temperature variables removed (i.e. just tow depth and rugosity as predictors) for each species. We considered the temperature-based model unsuitable for predicting thermal habitat of a species if the ratio of the full model MAE to naïve model MAE was > 1, and removed two species (dogfish, *Squalus acanthias* and twohorn sculpin, *Icelus bicornis*) from analysis based on this ratio test. Because the ratio was close to 1 for several species, we supplemented the ratio test with the Diebold–Mariano test on model forecasts using the *forecast* package (version 8.13) in R (Hyndman *et al.*, 2021), with the time-step (h) parameter set to 1 (see Kleisner *et al.*, 2017). A total of two additional species (moustache sculpin, *Triglops murrayi* and roundnose grenadier, *Coryphaenoides rupestris*) had a MAE ratio > 1 and a Diebold–Mariano p-value > 0.05. We, thus, included these species in our results for completeness but do not discuss them in depth here. We also provide MAE ratios and Diebold–Mariano test results in the supplemental information. We report results for 51 demersal fish species that had been recorded at the species level and had sufficient observations for the GAM parameters. A table indicating scientific, common, and Icelandic names for each species is available in the supplemental information.

Finally, we explored the contribution of temperature variables to deviance explained in the models by comparing the percent deviance explained of the full model and the naïve model. Although, less relevant to evaluating model predictive power, this analysis was to aid interpretation of the results and indicate which species may be most—or least—responsive to temperature. We also explored the contribution of each individual predictor variable to model deviance explained by comparing the percent deviance explained from the full model and a model with that covariate dropped for each species.

By fitting these models with temperature variables as the only dynamic predictors, we sought to isolate temperature effects in exploring distribution and abundance trends due to projected climate change by mid-century. Both demersal fish habitat and the projected impacts of climate change in Iceland's waters are more complex than changing temperature, and solely temperature-based models may be insufficient to fully characterize fish species climate vulnerability (McHenry *et al.* 2019). Further, these models do not account for changes in physiology, behaviour, species interactions, or fishing pressure, all of which could influence species abundance and distribution in response to changing environmental conditions. We, therefore, refer to the model outputs and projections as "suitable thermal habitat" rather than biomass or distribution, as they represent potential suitable habitat and species density based on temperature, with all else held constant (Kleisner *et al.*, 2017; Morley *et al.*, 2018).

Projecting future suitable thermal habitat

We calculated the amount of available suitable thermal habitat as the sum of all modelled suitable thermal habitat values in the full EEZ projection grid (Morley *et al.*, 2018). We compared the median suitable thermal habitat in the historical period (2000–2018) with the future period (2061–2080) for each species. Because some changes were quite large (orders of magnitude), we present log10-fold change [log (median future suitable thermal habitat/median historical suitable thermal habitat)] so that relative increases and decreases can be compared. For rabbitfish (*Chimaera monstrosa*), the North Atlantic codling (*Lepidion eques*), Vahl's eelpout (*Lycodes gracilis*), and the three *Sebastes* species (*Sebastes marinus*, *Sebastes mentella*, and *Sebastes viviparus*), large model error at deep depth values resulted in uninterpretable prediction values in the eastern edge of the EEZ; for these species we cropped predictions at 1200 m depth and present comparative results on those cropped values. We calculated the centroid of distribution for each species as mean latitude and longitude weighted by the modelled suitable thermal habitat value, and calculated the distance (km) and direction (degrees) shifted between the historical and future period with the *geosphere* package (version 1.5.10) in R (Hijmans, 2019). Additionally, we calculated the shifts in cold and warm edges of species distributions as the difference in the 5th and 95th respective percentile latitude of thermal habitat values > 0.05 (Fredston-Hermann *et al.*, 2020).

We grouped species by three habitat indices outlined in Campana *et al.* (2020), based on bottom temperatures and depths from the trawl surveys. We calculated thermal bias index as the difference in median biomass-weighted bottom temperature of tows in which each species was observed and the median bottom temperature of all survey tows, stenothermal index as the range of 5th and 95th percentiles of those biomass-weighted observed bottom temperatures for each species, and depth index as the biomass-weighted median observed tow depth for each species. Because the spring and autumn surveys sample different areas and depths, we calculated separate index values for each season and took a weighted mean based on the number of observations in each season. Following Campana *et al.* (2020), we categorized species into warm water (positive thermal bias), cool water (−3–0°C thermal bias), and cold water (< −3°C thermal bias) niches for visualization and discussion. We tested associations between habitat indices and projected shifts in total suitable thermal habitat and the shifts in bearing and distance of centroid of distribution with ordinary least squares regression.

Results

Projected climate change

The projected climate model deltas resulted in a mean increase in surface temperatures in Iceland's EEZ of 1.96°C for SSP 2-4.5 (ranging from 0.76°C, CNRM to 2.40°C, MOHC) and 2.40°C for SSP 5-8.5 (ranging from 1.00°C, CM2.6 to 3.40°C, IPSL) by 2061–2080. For bottom temperatures, the mean projected increase for 2061–2080 was 0.06°C for SSP 2-4.5 (ranging from −1.5°C, GFDL to 1.21°C, IPSL) and 0.20°C for SSP 5-8.5 (ranging from −1.35°C, GFDL to 1.47°C, IPSL) in 2061–2080 (see Supplemental information for time series of individual climate model projections). Spatially, surface warming was projected throughout Iceland's EEZ and most pronounced in offshore northeast waters for both scenarios (Figure 2a). The variation among climate model surface
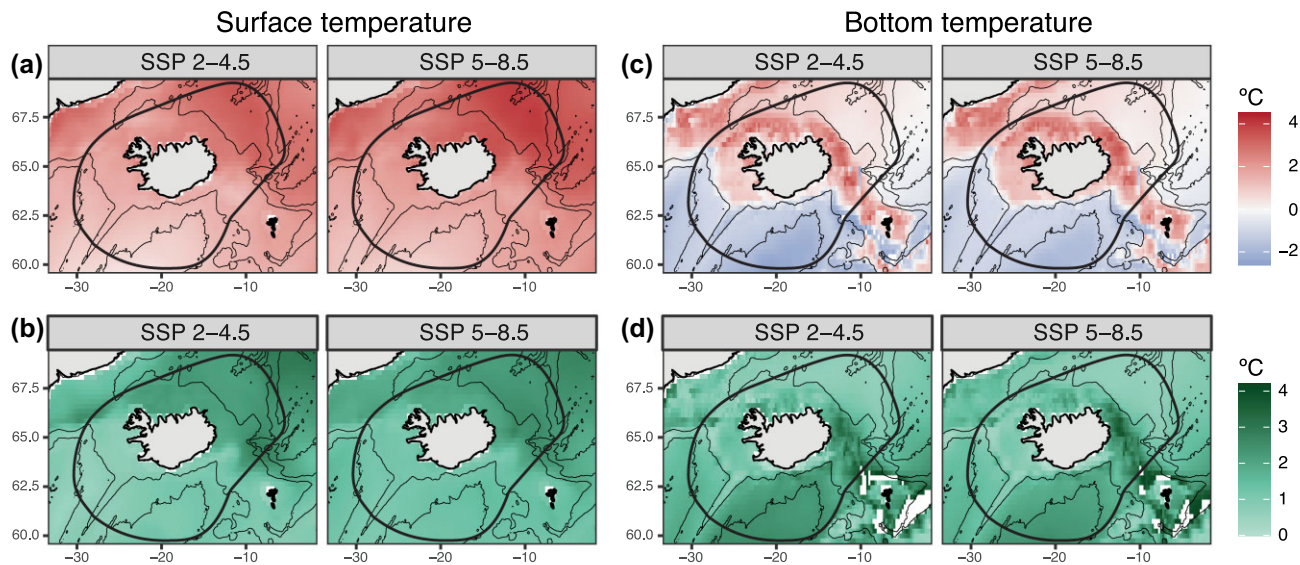
Surface temperature

Bottom temperature

Figure 2. Projected ensemble means (a and c) and standard deviation (b and d) for sea surface and bottom temperature deltas for the years 2061–2080 for the middle of the road (SSP 2-4.5) and fossil-fueled development (SSP 5-8.5) scenarios. Thin lines indicate 1000 m isobaths and thick lines indicate Iceland's EEZ.

temperature projections was also highest in Iceland's northern waters, which likely reflects uncertainty in the mixing dynamics between Atlantic and polar waters (Figure 2b). Bottom temperature deltas showed cooling in Iceland's southern waters beyond the continental shelf, and concentrated warming along the northern shelf and east along the Iceland–Faroes ridge in the southeast (Figure 2c). Variation among models was highest in the east where warming is most pronounced, as well as offshore southern waters (Figure 2d).

Model performance and temperature variable contribution to deviance explained

The GAMs explained on average 59% of deviance (*SD* 20; range 21–96) across the 51 species. The contribution of temperature variables to deviance explained (the difference in percent deviance explained between the full model and naïve model for each species) was mean 22% (*SD* 12, range 5–55). Temperature variables contributed more than 30% deviance explained for 12 species: megrim (*Lepidorhombus whiffiagonis*), Norway pout (*Trisopterus esmarkii*), Norway haddock (*S. viviparus*), blue ling (*Molva dypterygia*), grey gurnard (*Eutrigla gurnardus*), ling (*Molva molva*), monkfish, (*Lophius piscatorius*), silvery pout (*Gadiculus argenteus*), Vahl's eelpout, (*L. gracilis*), whiting (*Merlangius merlangus*), rabbitfish (*C. monstrosa*), and Atlantic poacher (*Leptagonus decagonus*). A total of five species had temperature contribute < 10% deviance explained: roundnose grenadier (*C. rupestris*), jelly cat (*Anarhichas denticulatus*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), and Atlantic wolffish (*Anarhichas lupus*). For these species, projections should be interpreted more carefully, and additional non-temperature variables would be necessary to better characterize distribution. In examining the contribution of individual variables to percent deviance explained (the difference in deviance explained between the full model and a model with that covariate dropped for each species), depth contributed mean 9%; bottom temperature, minimum surface temperature, and annual maximum bottom temperature contributed mean 1.5–2%; and rugosity, annual maximum surface tem-

perature, and surface temperature contributed approximately mean 1% (Figure 3). Moderate correlation among the predictor variables (0.2–0.7) impacts these calculations of contribution to deviance explained, making the grouped temperature contributions likely overestimates and the individual variable contributions likely underestimates. We present the values here as context for interpreting the appropriateness of suitable thermal habitat as a proxy for species distribution, rather than detailed characterization of the role of temperature variables in these models. Full model performance and variable contribution for all species is available in the supplemental information.

Projected changes in suitable thermal habitat

Warmer water species were generally projected to see an increase in suitable thermal habitat in 2061–2080 relative to 2000–2018, while cold and cool water species were generally projected to see a decrease in suitable thermal habitat (Figure 4). While the patterns were largely similar across the two scenarios, SSP 5-8.5 could incur more extremes in species suitable thermal habitat increases, with seventeen species projected to see increased suitable thermal habitat availability in all five climate models in SSP 5-8.5 vs. ten species for SSP 2-4.5. Only moustache sculpin (*T. murrayi*) had a different direction of projected median suitable thermal habitat change between the two scenarios, with a projected increase in suitable thermal habitat in SSP 2-4.5 and a decrease in SSP 5-8.5 (Figure 4).

Of the three habitat indices, thermal bias was a weak predictor of change in projected suitable thermal habitat, with the relationship $y = 0.07x + 0.04$ (adjusted $r^2 = 0.17$, $p < 0.001$) for SSP 2-4.5 and $y = 0.10x + 0.09$ (adj. $r^2 = 0.23$, $p < 0.001$) for SSP 5-8.5. Stenothermic index and depth index were very weak predictors (adj. $r^2 < 0.1$) or did not show a significant relationship with projected suitable thermal habitat change in either scenario (stenothermic index: $p = 0.42, 0.12$; depth index: $p = 0.15, 0.03$).

These projected suitable thermal habitat suitability were spatially heterogeneous within Iceland's waters, with most species
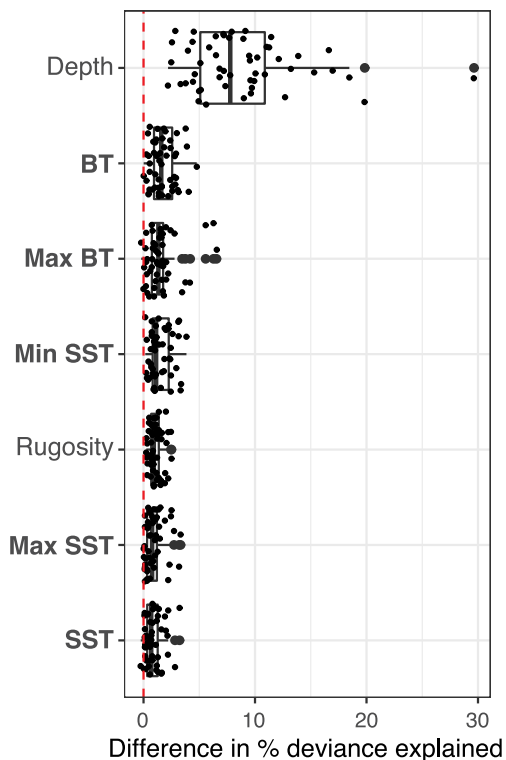
Figure 3. Variable contributions to percent deviance explained, calculated as the difference in percent deviance explained between the full model and a model with that covariate dropped for each species. Variables are ordered by median contribution to deviance explained and bolded variables indicate dynamic temperature variables. SST is sea surface temperature and BT is bottom temperature.

showing relatively localized increases and/or decreases (Figure 5). Cod (*Gadus morhua*), saithe (*Pollachius virens*), and tusk (*Brosme brosme*), all commercialized species, showed increases along Iceland's northern continental shelf and decreases along the southern coast (Figure 5a). The projected increases suitable thermal habitat for cod were farther offshore, especially in SSP 5-8.5, while projected increases for saithe and tusk were more coastal, with projected decreased thermal habitat suitability at the northern shelf margins. Norway pout (*T. esmarkii*), a key prey species, along with warm-water whiting (*M. merlangus*) and witch (*Glyptocephalus cynoglossus*), showed suitable thermal habitat increases along Iceland's southern and western continental shelf (Figure 5b). A similar pattern was projected for warm-water monkfish (*L. piscatorius*), megrim (*L. whiffiagonis*), skate (*Dipturus batis*), fourbeard rockling (*Rhinonemus cimbrius*), and Norway haddock (*S. viviparus*), with additional dynamics along the southeast Iceland–Faroes ridge (Figure 5c). Cool-water lumpfish (*Cyclopterus lumpus*) and Atlantic wolffish (*A. lupus*) showed inshore suitable thermal habitat decreases, concentrated in the northwest fjords and east coast for lumpfish and west and northwest coasts for wolffish (Figure 5d). Starry ray (*Amblyraja radiata*) showed decreases in projected suitable thermal habitat across Iceland's shelf while ling (*M. molva*) showed increased projected suitable habitat. Haddock (*Melanogrammus aeglefinus*) showed southern increases and northern decreases in projected suitable thermal habitat, roughly the opposite pattern to cod, saithe, and tusk. Maps indicating projected

suitable thermal habitat changes for all analyzed species and all projection periods 2021–2100 are available in the supplemental information.

Taken together, these projected shifts in species suitable thermal habitat showed general northward movement. The centroid of suitable thermal habitat was projected to shift north for cold- and cool-water species and more northwest for warm-water species in SSP 2-4.5 and more northwest for cold-and cool-water species and north for warm-water species in SSP 5-8.5 (Figure 6). Warm-water species saw a mean projected shift in centroid of suitable thermal habitat of 73 km in SSP 2-4.5 (*SD* 52; range 56, GFDL CM4 to 109, HadGEM3-GC31) and 77 km in SSP 5-8.5 (*SD* 60, range 64, GFDL CM4 to 115, HadGEM3-GC31). Cool-water species saw a mean projected centroid shift of 72 km in SSP 2-4.5 (*SD* 55, range 64, IPSL-CM6A-LR to 86, HadGEM3-GC31) and 78 km in SSP 5-8.5 (*SD* 59, range 64, CM 2.6 to 94, HadGEM3-GC31). Cold-water species saw the largest mean projected centroid shift of 87 km in SSP 2-4.5 (*SD* 77, range 58, CNRM-CM6 to 117, GFDL CM4) and 104 km in SSP 5-8.5 (*SD* 79, range 78, CM 2.6 to 132, HadGEM3-GC31).

The habitat indices were all insignificant or very weak (adjusted $r^2 < 0.1$) predictors of change in the distance or bearing of the centroid of suitable thermal habitat in both scenarios. Thermal bias index was a weak predictor of the distance of southern movement of the warm edge of suitable thermal habitat ($y = -0.09x + 0.20$, adj. $r^2 = 0.15$, $p < 0.001$ for SSP 2-4.5; $y = -0.11x + 0.23$, adj. $r^2 = 0.21$, $p < 0.001$ for SSP 5-8.5), but was a very weak predictor of the distance of northward movement of the cold edge of suitable thermal habitat (adj. $r^2 < 0.1$). Stenothermic index and depth index were very weak predictors (adj. $r^2 < 0.1$) or did not show a significant relationship with projected shifts in cold or warm edges of suitable thermal habitat for either scenario.

Discussion

These results corroborate previous projections that future climate change could result in significant shifts in fish species abundance and distribution in Iceland's waters, and further illustrate potential variability in responses among species and regions. Consistent with global hypotheses and the analyses of Campana *et al.* (2020), our results indicate an overall northward shift in center of suitable thermal habitat distribution for Iceland's demersal fish species, with warmer water species more likely to expand the southern warm edge of their range. Species thermal bias was a more significant, albeit weak, predictor of future suitable thermal habitat change than stenothermic index or depth preference, results also similar to the findings of Campana *et al.* (2020). In general, our analyses suggest similar trends to those observed during the mid-1990s warming period (Valtýsson and Jónsson, 2018) could be expected by mid-century, with many warmer water species likely to experience overall increases in suitable thermal habitat in Iceland's EEZ. However, these patterns are localized and may be accompanied by regional decreases. Projected patterns both of warming and of species suitable thermal habitat changes were similar across the two scenarios, although the high-CO_2 emissions scenario potentially represents both greater opportunities in increased suitable thermal habitat for warm-water commercial species and greater losses for commercially or culturally important cooler-water species, as well as more uncertainty in the direction of change for key species including cod. Below we discuss potential economic, cultural, and ecological consequences of these projected suitable thermal habitat shifts, as well as caveats.
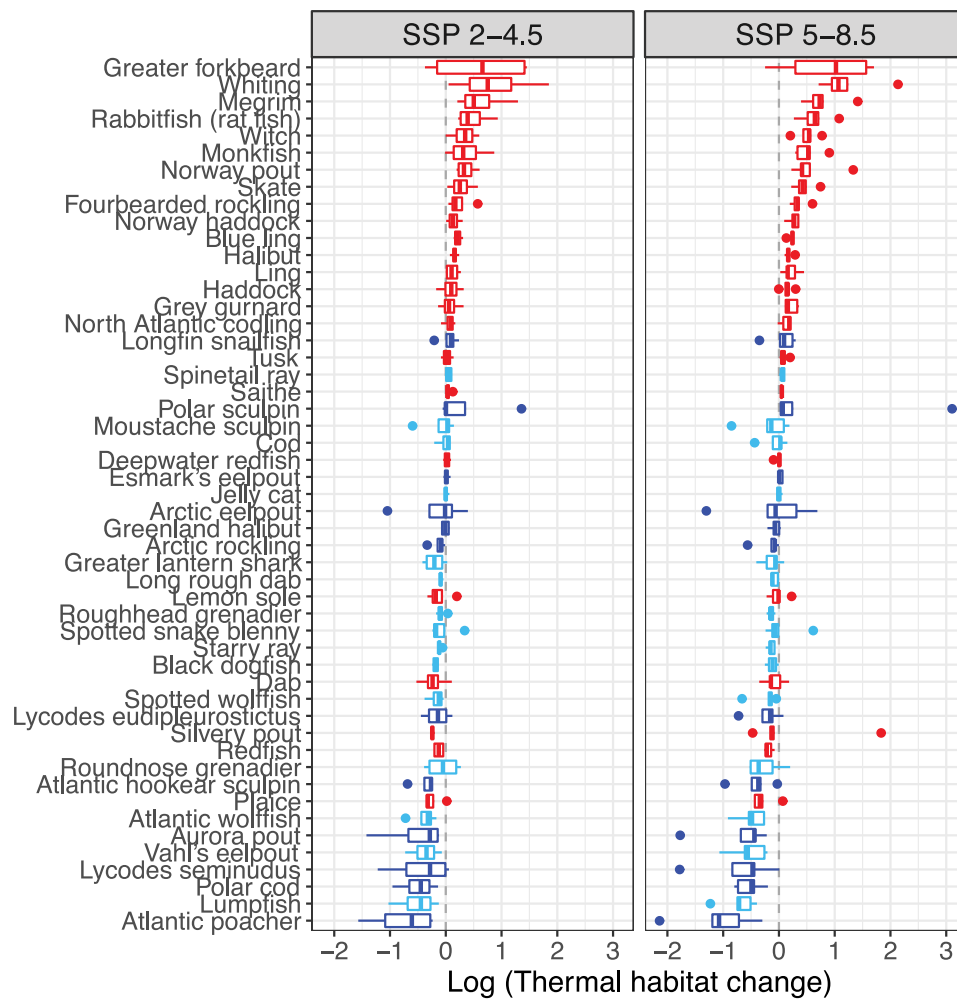
Figure 4. Projected changes in suitable thermal habitat for modelled species for 2061–2080 relative to 2000–2018 for middle of the road (SSP 2-4.5, left) and fossil-fuelled development (SSP 5-8.5, right) scenarios. Boxplots represent the distribution of suitable thermal habitat projections from each of the climate models. Colours represent categories of species thermal bias index: red species are warm water, light blue are cool water, and dark blue are cold water (see methods and Campana *et al.*, 2020 for classifications). Note that *x*-axis is on a log10 scale, so a species with a value of −1 would have 10% of the total projected suitable thermal habitat in 2061–2080 relative to 2000–2018.

It is encouraging for Iceland that many commercially important species are projected to see increases in suitable thermal habitat within its EEZ. However, regional heterogeneity in suitable thermal habitat changes may be of interest to managers and the fishing industry. For example, the overall median increase in suitable thermal habitat for cod, a flagship commercial species for Iceland, is largely along the north and northeastern shelf; inshore waters, particularly in the southeast and southern Westfjords, are predicted to see decreases in suitable thermal habitat, with further decreases in the north and northeast under SSP 5-8.5. Potential future decreased suitable thermal habitat for cod under some climate models and scenarios may represent a major concern for the fishing industry and Iceland's economy, as cod contributes nearly half of marine products export value (Statistics Iceland, 2021). Meanwhile, the projected increase in suitable thermal habitat for high-value monkfish along the south and southwest coasts may represent a commercial opportunity for those regions. The distribution of this species around Iceland is thought to be particularly sensitive to temperature changes, as its northern habitat edge is generally in Ice-

land's southern waters (MFRI, 2021a). A sudden geographic expansion around Iceland in the 2000s associated with warmer temperatures created a spike in local fisheries and investments in monkfish gillnets, but populations and distribution have since declined and gillnetting operations have largely halted since 2016 (MFRI, 2021a). With projected temperature increases and suitable thermal habitat, this fishery could see a resurgence. Conversely, projected nearshore declines in Atlantic wolffish suitable thermal habitat could detrimentally impact the small-scale fishing sector, as this species is primarily commercialized by smaller vessels in shallow waters of the north and northwest (MFRI, 2021b). Thus, the economic impacts of these projected suitable thermal habitat shifts may unevenly affect different regions and sectors of the fishing industry, as larger vessels with more technological capacity are less dependent on proximity to fishing grounds than smaller vessels (Edvardsson *et al.* 2018). Projections on this multidecadal scale could, therefore, inform long-term planning not only for fishery development but also broader infrastructure policy, as investment in energy transmission and roads is critical for the competitiveness
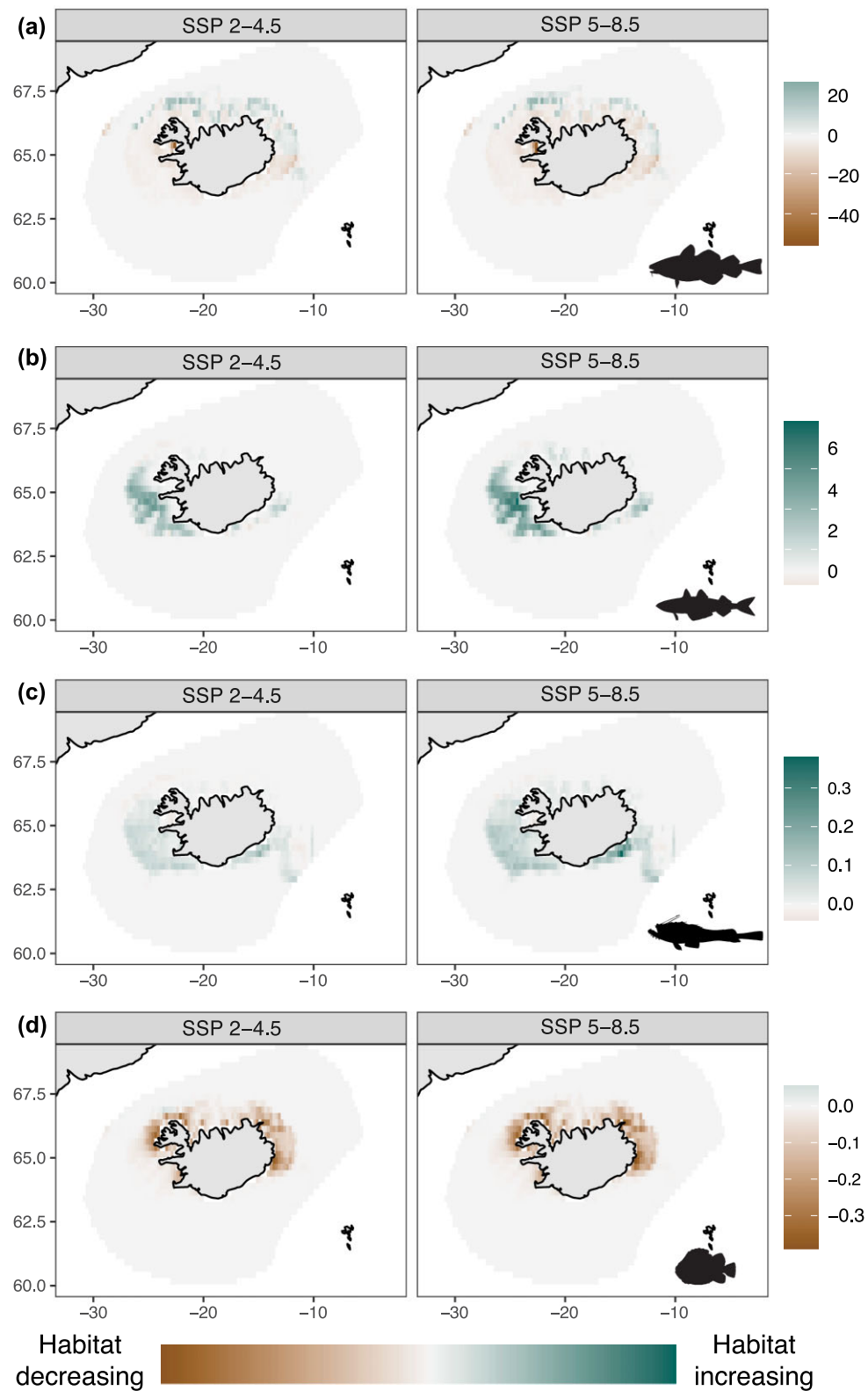
Figure 5. Maps demonstrating patterns of projected changes in future suitable thermal habitat, typified by cod (a), Norway pout (b), monkfish (c), and lumpfish (d) in 2061–2080 relative to 2000–2018 under the middle of the road (SSP 2-4.5, left) and fossil-fuelled development (SSP 5-8.5, right) scenarios. Habitat change is defined as the difference between the projected future and baseline suitable thermal habitat values. Green regions indicate increases in suitable thermal habitat whereas brown regions indicate decreases in suitable thermal habitat.
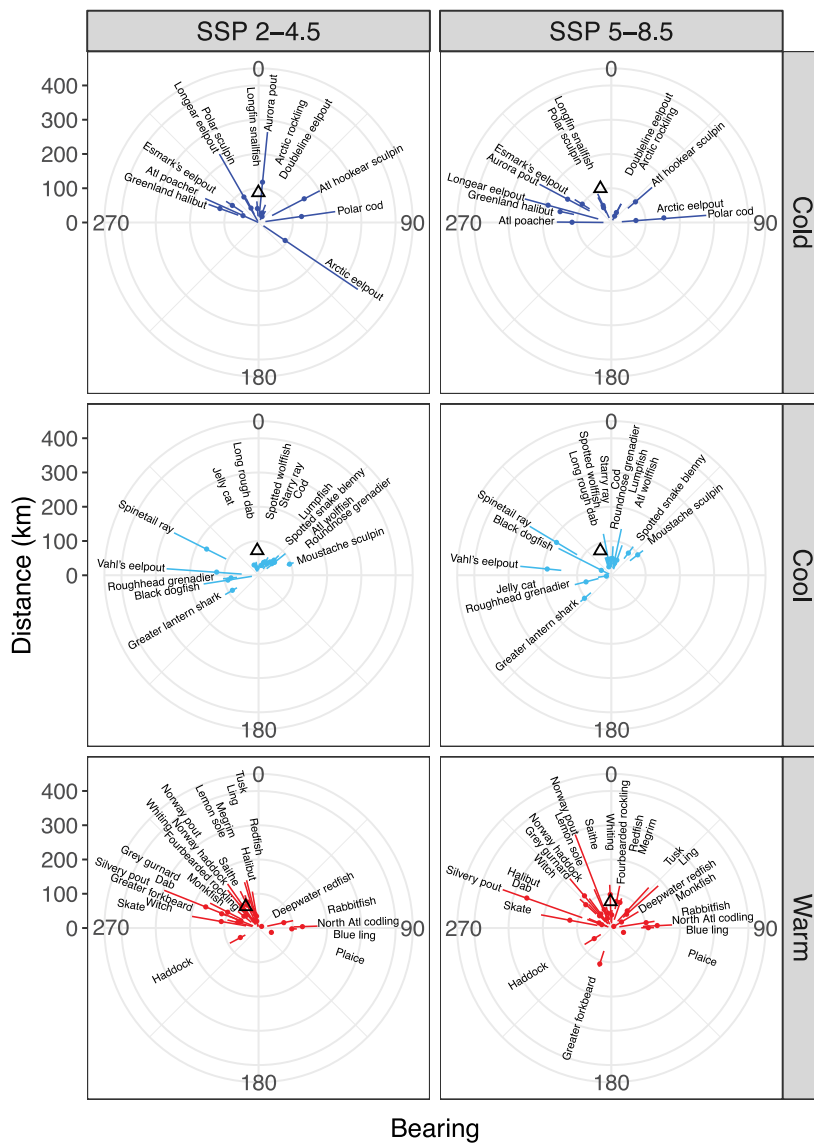
Figure 6. Projected distance (km) and direction (bearing, 0–360°) of shifts in the centroid of suitable thermal habitat distribution between 2000–2018 and 2061–2080 under the middle of the road (SSP 2-4.5, left) and fossil-fuelled development (SSP 5-8.5, right) scenarios. Line segment lengths span the minimum and maximum projected shifts in distance among the five climate models, with circles indicating the median projection. Colours represent species thermal bias category (see Figure 4). Triangles indicate the circular average value for the change in bearing, grouped by thermal bias category.

of smaller and more remote processing facilities (Reynisson *et al.* 2012).

These projections could have cultural implications as well as economic ones. Projected declines in inshore suitable thermal habitat for lumpfish may be challenging for communities where the fishery is a "cultural keystone:" although not one of the major commercialized species in terms of volume or value, it plays an outsize role in community heritage and local identity (Chambers, 2016). Starry ray, while not commercialized, has historically been utilized when brought in as bycatch and consumed as a festive delicacy on the December 23rd Mass of St. Thorlak. Projected declines in suitable thermal habitat throughout Iceland's continental shelf may reduce the availability of this species, contributing to ongoing declines in this holiday tradition (MMR, 2020).

Further, these projected changes in fish species suitable thermal habitat could have implications for food web structure and function within Iceland"s waters and in the broader North Atlantic. Consistent with studies in the Barents Sea, these results indicate a borealization of North Atlantic marine ecosystems, with increases in abundance and northward expansions of warmer-water Atlantic species relative to colder-water Arctic species (Fossheim *et al.*, 2015; Kortsch *et al.*, 2015). Expansion of generalist predators such as cod, haddock, and whiting could compound temperature-related suitable habitat decreases for colder-water species through predation and competition. Their predation across wide environmental niches, in combination with projected suitable thermal habitat declines for several species thought to have important structural roles as food web connectors such as eelpouts (Lycodes spp.), wolffishes

(Anarhichus spp.), and polar cod (*Boreogadus saiga*), could contribute to a more homogenous and less modular food web structure in Iceland and in more northern waters, which could be more vulnerable to climate and other disturbances (Kortsch *et al.*, 2015). Incorporating further study of food web dynamics and predator–prey interactions into species distribution projections would be key for informing management decisions under warming conditions. Predator–prey interactions have already been a dominant ecological driver in Iceland's waters: During the mid-1990s warming period, increasing cod and other gadoid stocks along Iceland's northern coast is believed to have triggered the decline of a commercially important shrimp fishery, as these fish preyed heavily on northern shrimp and other species in closed fjord systems (Jónsdóttir *et al.*, 2019). More recently, mackerel predation has been associated with declines in other warm-water species despite continued warming (Valtýsson and Jónsson, 2018).

Overall, these results explore a range of potential outcomes for species distribution based on future temperature change as a starting point for discussion and planning. We focused on suitable thermal habitat based on data availability and to build on previous work predicting temperature effects (e.g. Campana *et al.* 2020), but in interpreting these results it is important to note that temperature alone is likely insufficient for making predictions of species abundance and distribution (Hollowed *et al.*, 2013; McHenry *et al.*, 2019; Husson *et al.*, 2020). Indeed, low explanatory power of the models, and for some species very low contribution of temprature variables to deviance explained, suggest that additional variables would be needed for better characterization of distribution for many species. In a study of a similar suite of species in the Barents Sea, Husson *et al.* (2020) found that while depth and temperature were important limiting factors of habitat suitability, salinity was also a key predictor. They further found that for many species, static variables including sediment type were more influential in determining habitat suitability. Mesoscale oceanographic dynamics such as the subpolar gyre have also been demonstrated to influence fish abundance in Greenland, and would likely affect Icelandic stocks as well (Post *et al.*, 2021). Exploring these additional variables, as well as potential interactions between them, may improve model explanatory power and predictive performance.

Species-specific behaviour and life-history traits are also key factors determining responses to environmental change (Hollowed *et al.*, 2013). While fitting these general models allowed us to explore overall trends in a wider range of species, a more tailored, species-specific approach would be useful for both for improving predictions and interpreting how our suitable thermal habitat projections may relate to actual distribution. The habitat indices we used here as indicators of species life history or behaviour did not have strong predictive power for change in projected suitable thermal habitat or distance or direction of centroid shifts, so other life history traits such as site fidelity and reproductive dynamics would be considerations for further study (Hollowed *et al.*, 2013). Additionally, temperature may variably affect species at different life stages or among subpopulations. Cod, for example, exhibit ontogenetic regional shifts that follow the clockwise flow of currents around Iceland (Astthorsson *et al.*, 2007), as well as behavioural ecotypes with separate temperature and depth niches (Grabowski *et al.*, 2011). Considering life history traits also highlights caveats with the trawl survey methods for characterizing the distribution of some species. The demersal trawls are thought to inadequately cover the shallow distribution of plaice, for example (MFRI, 2021c). Plaice also spawn during the early spring, concurrent with the spring surveys

(Solmundsson *et al.*, 2005), which may result in aggregations that could bias the survey. The surveys were designed to sample common commercial species, particularly cod, so projections for non-commercialized or rarer species should be interpreted with more caution.

Finally, management decisions are likely to be more significant determinants of fish abundance and distribution than long-term climate trends, particularly for the next few decades (Mullon *et al.*, 2016). Our suitable thermal habitat projections can provide an idea of regions or species that could be important to develop or to protect, but the future outcomes will depend largely on human actions—both in terms of fisheries management and climate mitigation. This study demonstrates the value of using global climate models to make spatially explicit projections of fish suitable thermal habitat, which may serve as guideposts for long-term scenario planning, investment in fisheries and infrastructure, and risk evaluation. For Iceland and other regions with available data to support habitat modelling, such forward-looking studies could be a valuable strategy for achieving climate-adaptive fisheries.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

NOAA High Resolution SST data were provided by the NOAA/OAR/ESRL PSL, Boulder, CO, USA, from their website at https://www.ncdc.noaa.gov/oisst. GLORYS data were provided by the Copernicus Marine Environmental Monitoring Service at https://resources.marine.copernicus.eu/?option = com_csw&view = details&product_id = GLOBAL_REANALYSIS_PHY_001_031.

Code for downloading climate data and performing these analyses is available at https://github.com/juliagmason/iceland_climate_resilient_fisheries.

Acknowledgements

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Handling Editor: Rebecca Selden