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ORIGINAL ARTICLE

Highly mixed impacts of near-future climate change on stock productivity proxies in the North East Atlantic

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Abstract

Impacts of climate change on ocean productivity sustaining world fisheries are predominantly negative but vary greatly among regions. We assessed how 39 fisheries resources—ranging from data-poor to data-rich stocks—in the North East Atlantic are most likely affected under the intermediate climate emission scenario RCP4.5 towards 2050. This region is one of the most productive waters in the world but subjected to pronounced climate change, especially in the northernmost part. In this climate impact assessment, we applied a hybrid solution combining expert opinions (scorings)—supported by an extensive literature review—with mechanistic approaches, considering stocks in three different large marine ecosystems, the North, Norwegian and Barents Seas. This approach enabled calculation of the directional effect as a function of climate exposure and sensitivity attributes (life-history schedules), focusing on local stocks (conspecifics) across latitudes rather than the species in general. The resulting synopsis (50–82°N) contributes substantially to global assessments of major fisheries (FAO, The State of World Fisheries and Aquaculture, 2020), complementing related studies off northeast United States (35–45°N) (Hare et al., PLoS One, 2016, 11, e0146756) and Portugal (37–42°N) (Bueno-Pardo et al., Scientific Reports, 2021, 11, 2958). Contrary to prevailing fisheries forecasts elsewhere, we found that most assessed stocks respond positively. However, the underlying, extensive environmental clines implied that North East Atlantic stocks will develop entirely different depending upon the encountered stressors: cold-temperate stocks at the southern and Arctic stocks at the northern fringes appeared severely negatively impacted, whereas warm-temperate stocks expanding from south were found to do well along with cold-temperate stocks currently inhabiting below-optimal temperatures in the northern subregion.

KEYWORDS
climate vulnerability assessment, downscaled climate models, harvestable resources, high latitudes, large marine ecosystems, population dynamics

1 | INTRODUCTION

Climate fluctuations and change (Bindoff et al., 2019; IPCC, 2013, 2021) affect ecosystems by altering regional productivity (Free et al., 2019; Lehodey et al., 2006) and typically displacing species polewards (Poloczanska et al., 2013), though predicted shifts are less and more mixed with the RCP4.5 compared with the RCP8.5 scenario (Morley et al., 2018). Such responses are constrained by stock-specific habitat availability, ocean circulation patterns and bathymetry (Brander, 2007; Gullestad et al., 2020) and by physiological features like metabolic processes restricted to tolerable thermal windows (Cheung et al., 2013; Payne et al., 2021; Pörtner & Peck, 2010). Therefore, different stocks may respond in many ways to regional climate change. The North East Atlantic stands out as a specially interesting biogeographic realm (Paasche et al., 2015) for contrasting responses as the living resources, representing annual landings of several million tonnes (FAO, 2020), extend over considerable areas where the impacts of the warming scenarios are manifested differently (Figure 1) (Drinkwater, 2005; Gullestad et al., 2020; Payne et al., 2021; Peck & Pinnegar, 2018; Simpson et al., 2011). Several studies in temperate waters have recognized effects of climate fluctuation and change on stock productivity parameters in both southern (Beaugrand et al., 2003; Perry et al., 2005; Simpson et al., 2011) and northern subregions (Hollowed & Sundby, 2014; Kjesbu et al., 2014). However, the ecological and commercial importance along with the lengthy list of North East Atlantic stocks demands a consistent assessment of the effects of climate change to project trends in their productivity and resilience. Our article—with an extensive Supplementary Information (Appendix S1, including also List of Abbreviations and Consulted Geographical Locations)—aims at contextualizing the near-future stock responses in three large marine North East Atlantic ecosystems: the North, Norwegian and Barents Seas (Appendix S1, Figures S1 and S2).

So-called Climate Vulnerability Assessments ultimately aim to inform stakeholders on how measures of productivity of targeted resources may (or might) develop in decades to come. A major US National Oceanic and Atmospheric Administration (NOAA) initiative, Hare et al. (Hare et al., 2016), assessed North West Atlantic species by scoring sensitivity attributes, expressing life-history trait-based adaptive capacity and climate exposure, highlighting the corresponding role of climate stressors. These species-specific expert scorings were undertaken to conclude on the directional effect, that is whether projecting a negative, neutral or positive trend in productivity (Hare et al., 2016). Here, we used this NOAA approach as a baseline but opted for the term Climate Impact Assessment (CIA) to further emphasize the existence of both positive (Kjesbu et al., 2014) and negative (Fossheim et al., 2015) effects of climate change on stock productivity indices. Also, we produced Stock Narratives (Appendix S1, Stock Narratives) rather than Species Narratives (Hare et al., 2016) as local stocks of the same species might fare highly differently under climate

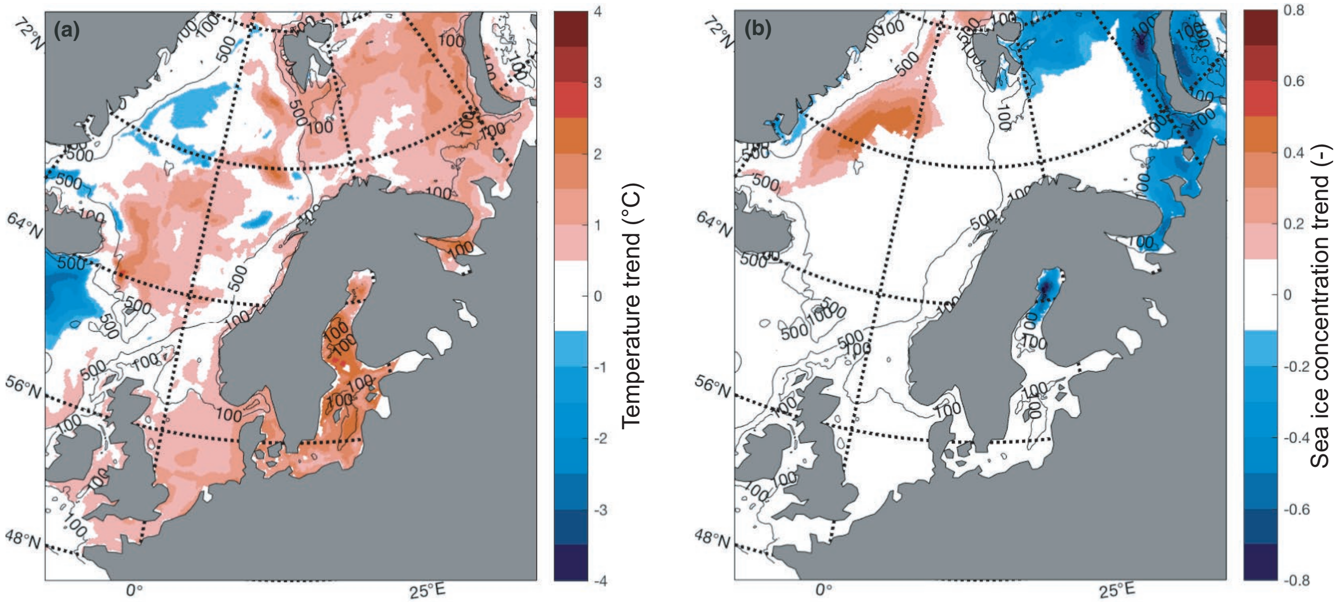


FIGURE 1 Projected change in (a) sea surface temperature and (b) sea ice concentration from 2010 to 2041 during wintertime (January–March) in the North East Atlantic. The simulation is downscaled with the regional ocean modelling system (ROMS) from the Norwegian Earth System Model (NorESM1-M) for the RCP4.5 emission scenario. Contours refer to 100 and 500 m depth

change, depending upon their habitats (Drinkwater, 2005; Grant & Bowen, 1998; Peck & Pinnegar, 2018; Simpson et al., 2011). We realized, as concluded earlier (Bueno-Pardo et al., 2021), that stock assessors commonly have congruent views regarding sensitivity attributes scorings (Appendix S1, Stock Narratives) (see also below), underlining the appropriateness of the present route to include both data-poor and data-rich stocks in a coherent fashion (Hare et al., 2016). Our analyses were advanced mechanistically by the exceptionally long and dedicated history of research in the North East Atlantic on environmental influences on stock productivity (Gullestad et al., 2020; Hjort, 1914; Paasche et al., 2015; Simpson et al., 2011; Skern-Mauritzen et al., 2016). Hence, this CIA is founded on a review of unique breadth and depth (Appendix S1, Supplementary References (*N* = 799)). However, despite that about 80% of the North East Atlantic harvested stocks are currently managed sustainably (FAO, 2020), any unaccounted effects of fishing pressure should be bore in mind. This issue is exemplified by changing spatial distributions with warmer waters, which challenge international agreements on quota sharing but especially for widely distributed stocks (Gullestad et al., 2020). We labelled our route of investigation a "hybrid solution," that is, combining expert opinions (scorings)—supported by the above-mentioned extensive literature—with in-depth mechanistic approaches, though where an overriding principle within the CIA was to analyse all stocks in a coherent fashion. Based on the above considerations and literature insights, we hypothesized that the directional effect—the cornerstone of the present assessment—would display large variability across latitudes and cold, warm temperate and Arctic stocks.

2 | MATERIALS AND METHODS

2.1 | Species and stocks

The current synopsis considered 30 North East Atlantic marine species, including 24 teleosts, 3 elasmobranchs and 3 crustaceans. The overall selection of study candidates was undertaken to cover as far as possible different lifestyles as well as habitat areas, within realistic workloads and available expertise. To address local environmental impacts, species were in several cases represented by both their southern and northern component, if such conspecifics (stock) structuring was in place. Altogether, this analysis comprised 39 stocks. We used this term rather than population to reflect that this investigation focused on harvestable resources, though including also stocks where members only appear in bycatches, or stocks currently protected from exploitation (IMR, 2021). These conservation measures referred particularly to the red-listed basking shark (*Cetorhinus maximus*, Cetorhinidae), European eel (*Anguilla anguilla*, Anguillidae) and golden redfish (*Sebastes norvegicus*, Sebastidae) but also spurdog (*Squalus acanthias*, Squalidae) and porbeagle (*Lamna nasus*, Lamnidae) with no targeted fishery in recent years (Appendix S1, Stock Narratives). A special case was the northern stock of Norway pout (*Trisopterus esmarkii*, Gadidae) with no systematic landing reports but forming an important contrast to the southern stock located in North Sea waters. Stock classification schemes were in accordance with International Council for the Exploration of the Sea (ICES) practice (ICES, 2021), providing also their living areas (ICES, 2017).

2.2 | Area of interest and thermal zones

The focal geographical region was the North East Atlantic (Figure S1)—split into the North Sea (Figure S2), Norwegian Sea and Barents Sea—a total area of about 3.4 million km^2 (Gullestad et al., 2020). Note that some of the considered species are more extensively distributed, foremost basking shark with a transatlantic and trans-equatorial migration pattern but also European eel spawning in the Northwest Atlantic (Sargasso Sea). To further place single CIAs results into a synthesis framework, species were split into being either warm temperate, cold temperate or Arctic following traditional definitions in the literature. However, this characterization—based on the underlying geographical reference from mid- to the northernmost part of high latitudes—was not always straightforward. Complex species to classify in this respect were basking shark considered a (cold-adapted) warm-temperate species in the present region, as well as Barents Sea capelin (*Mallotus villosus*, Osmeridae) feeding in Arctic waters—near the Polar front—but spawning in cold-temperate waters along the Norwegian coast. In the latter respect, we used the cold-temperate species category rather than the Arctic species category to emphasize that the encountered temperatures might be well above those seen in Arctic waters. Operationally, this thermal zone scheme implied that, for example, stocks located in the North Sea could be regarded as cold temperate instead of warm temperate. Furthermore, whether the stocks under consideration was local, regional or widely distributed (Gullestad et al., 2020) was a central element in the CIA.

2.3 | Work execution plan and expertise involved

This article was the outcome of a series of workshops, ranging from introductory courses to in-depth discussions. Stock Narratives (Appendix S1, Stock Narratives) were produced by stock assessors focusing on the dynamics of the stock in question in their daily work—thus considered to be true experts, all named for any further correspondence (Appendix S1, Table S1). Rather than including more members with less expertise, high-level expertise was emphasized, even though this in a few situations implied one-author contributions, especially for Stock Narratives referring to stocks with minor commercial interest. For major stocks, three experts were typically involved. Across-expert variability in the following sensitivity attributes scoring by stock (Table 1) was ignored as no clear relevance could be detected in pilot tests (Bueno-Pardo et al., 2021). This baseline work, including the Stock Narrative as such, was subsequently quality-assessed by a review panel with three members (Appendix S1, Table S1). The below-addressed downscaled climate projections as well as forcing of the regional biogeochemical model were undertaken by specialists on North East Atlantic biophysics. The dedicated 5-member group scoring climate exposure and finally calculating the resulting directional effect (Table 1) covered climate research, biophysical interactions, marine ecology, population dynamics and physiology (Appendix S1, Table S1).

2.4 | Scoring analysis

In our concerted practices, we successively passed through sensitivity attribute (for further definition, see Appendix S1, Table S2), climate exposure scorings and directional effect calculations (Table 1). Data produced by stock during this CIA were aggregated in tabular form to provide a simplified overview and ease any updates in the future studies (Appendix S1, Table S3).

More specifically, we started off by consulting templates and principles presented by Hare et al. (2016) followed by method revisions principally defined by the significantly larger study area, different biophysical forcing, stock structuring and the aim of de facto calculating the directional effect (Table 1). All sensitivity attributes were principally adopted, the exception being Sensitivity to Ocean Acidification which was revised to consider effects on the species instead of its prey and Species Interaction which was added to the list ($N = 13$; Table 1). Regarding climate exposure factors, air temperature, precipitation and sea-level sensitivity were presently left out whereas temperature influences were further specified as either referring to surface temperature, temperature at 100, 500 m or bottom temperature. However, depending on the typical depth of the stock in the water column (Appendix S1, Stock Narratives) only one of these four temperature options were applied in each stock-specific case. This restriction was made to avoid overexpressing the role of temperature during scoring. We kept pH and O_2 on the original climate exposure list developed by Hare et al. (2016). Importantly, gross primary (Bueno-Pardo et al., 2021) and secondary production and sea ice abundance were introduced as additional climate exposure criteria (Table 1). Anyhow, as in Hare et al. (2016), we used the 5-point scoring system with four levels (low = 1; moderate = 2; high = 3, and very high = 4) to thereafter estimate the weighted average of each sensitivity attribute and climate exposure (Table 1). Any dominating factors, defined as a weighted average ≥3.0, were simultaneously noticed (Appendix S1, Table S3). This scoring schemes ended by presenting the grand mean (and associated *SD*) for all relevant sensitivity attributes and climate exposures per species or stock (Table 1). As the route for expressing the directional effect routine deviated from Hare et al. (2016)—though adopting −1, 0 and 1 as direction indicator—any accumulated directional effect (Table 1) between ± 1 was classified as a neutral effect, and a value below and above these thresholds considered a negative and positive effect, respectively. The fact that the direction indicator was multiplied with the strength of each single climate exposure (Table 1) provided the opportunity to systematically account for dominating factors but also largely reduce the impact of trivial factors, when being an issue. The accumulated directional effect, as used, is a relative index indicating which path the stock productivity is expected to follow in the future. Associated simple regression analyses were undertaken, albeit not for climate exposure against directional effect due to violation of the assumption of independence.

TABLE 1 Template for sensitivity attributes and climate exposure scoring, and calculation of the accumulated directional effect. A virtual stock is used as an example, displaying generally low figures for sensitivity attributes and climate exposure, and a neutral accumulated directional effect. NEW or REVISED refers to adjustments in the template originally developed by Hare et al. (2016), N/A under usage reflects that this factor is not applicable for this stock, and Remark is for pertinent notes (such as "no species-specific data"). Within each sensitivity attribute and climate exposure, the available 5 points (tallies) should be distributed across low (L), moderate (M), high (H) and very high (VH) (Hare et al., 2016), as exemplified for sensitivity attributes Habitat Specificity and Spawning Cycle, and climate exposure Bottom Temperature. Sensitivity attribute and climate exposure scoring: L = 1; M = 2; H = 3; VH =4. Accumulated directional effect criteria: negative (red) < −1; neutral (yellow) ≥ −1 and ≤1; positive (green) >1. The formulae in questions are given at the bottom of the template

STOCK (Lat. name) in ...							
Sensitivity attributes	**L**	**M**	**H**	**VH**	**Mean$_w$***	**Usage**	**Remark**
Habitat Specificity	**3**	**2**	0	0	1.4		
Prey Specificity	5	0	0	0	1.0		
Species Interaction NEW	5	0	0	0	1.0		
Adult Mobility	5	0	0	0	1.0		
Dispersal of Early Life Stages	5	0	0	0	1.0		
ELH Survival and Settlement Requirements	5	0	0	0	1.0		
Complexity in Reproductive Strategy	5	0	0	0	1.0		
Spawning Cycle	**1**	**1**	**3**	0	2.4		
Sensitivity to Temperature	5	0	0	0	1.0		
Sensitivity to Ocean Acidification REVISED	5	0	0	0			No species-specific data
Population Growth Rate	5	0	0	0	1.0		
Stock Size/Status	5	0	0	0	1.0		
Other Stressors	5	0	0	0	1.0		
Grand mean					1.2		
Grand mean *SD*					0.4		
Climate exposure	**L**	**M**	**H**	**VH**	**Mean$_w$***	**Usage**	**Directional effect**
Surface Temperature	5	0	0	0	1.0	N/A	
Temperature 100 m NEW	5	0	0	0	1.0	N/A	
Temperature 500 m NEW	5	0	0	0	1.0	N/A	
Bottom Temperature NEW	0	0	**3**	**2**	3.4		−1
O_2 (Surface)	5	0	0	0	1.0		0
pH (Surface)	5	0	0	0	1.0		0
Gross Primary Production NEW	4	1	0	0	1.2		1
Gross Secondary Production NEW	0	3	2	0	2.4		1
Sea Ice Abundance NEW	5	0	0	0	1.0	N/A	
Grand mean					1.4		
Grand mean *SD*					0.9		
Accumulated Directional Effect** NEW					–		0.2
Accumulated Directional Effect: Neutral							0.2

*Mean$_W$ = ((L × 1 + M × 2 + H × 3 + VH ×4))/(L + M + H + VH) (Hare et al., 2016), with Mean$_w$ (Weighted Mean) rounded off to the nearest 0.1,
**Accumulated directional effect =Sum (Mean$_{W,1}$ × DE$_1$ + Mean$_{W,2}$ × DE$_2$ + ... + Mean$_{W,9}$ × DE$_9$), with Mean$_W$ here referring to climate exposure.

2.5 | Climate projections

The currently undertaken climate projections covered 2010–2070 (RCP4.5) (Figure 2), whereas the CIA as such was limited to 2010–2041. For comparison, the time window of consideration in Hare et al. (2016) was 2005–2055 (RCP8.5).

2.5.1 | Modelled temperature by depth and sea ice concentration

The future climate strongly depends on future emissions of climate gases released to the atmosphere. The Coupled Model Intercomparison Project Phase 5 (Taylor et al., 2012) offers many

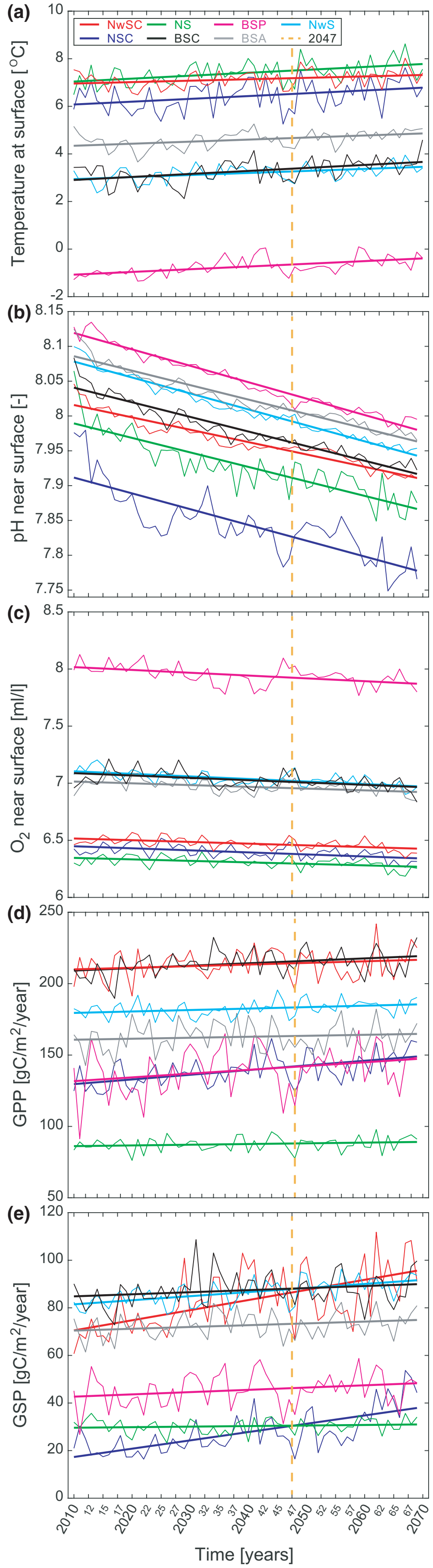


FIGURE 2 Time series (2010–2070) of key, projected (RCP4.5) climate exposure parameters—represented by the mean (thin line) and overall trend (thick line)—consulted in this study, split by geographical polygon area (Appendix S1, Figure S5): (a) winter temperature at surface; (b) pH near surface (0.2% of local bottom depth); (c) O_2 near surface (0.2% of local bottom depth); (d) annual gross primary production (GPP) integrated over all layers; and (e) annual gross secondary production (GSP) integrated over all layers in North Sea Coast (NSC, blue), North Sea (NS, green), Norwegian Sea Coast (NwSC, red), Norwegian Sea (NwS, cyan), Barents Sea Polar (BSP, magenta), Barents Sea Atlantic (BSA, grey) and Barents Sea Coast (BSC, black) (Figure S5). This CIA specifically consulted projections until 2041, that is prior to the sudden drop in several of these climate exposure factors near 2047 (vertical line)

global climate models that each deliver different projections of the future climate following different greenhouse gas representative concentration pathways. These climate models are global and run with relatively low horizontal resolution. To provide projections with more detailed and realistic circulation and hydrographic properties in the Nordic Seas, these climate models can be downscaled with regional models. In this analysis, we have used Regional Ocean Model System—ROMS (Sandø et al., 2014; Shchepetkin & McWilliams, 2005) to downscale the Norwegian Earth System Model—NorESM (Bentsen et al., 2013) forced with the RCP4.5 scenario. The emissions in this scenario peak around 2040, decline and stabilize at an increased radiative forcing of 4.5 W/m^2 in 2100 relative to preindustrial time. This downscaled projection covers the North Atlantic Ocean, the Nordic and Barents Seas, and the Arctic Ocean and has been evaluated and used in previous studies on effects of climate change on the marine ecosystem (Sandø et al., 2020, 2021; Skogen et al., 2018). However, in addition to the warming due to anthropogenic emissions of greenhouse gases, there is a considerable contribution of natural variability in the climate system. This natural variability can dominate the climate variability on interannual to decadal timescales differently from the contribution from anthropogenic emissions that is small but positive every year and are expected to dominate on centennial time scales (Hawkins & Sutton, 2009). Finally, it should be emphasized that the years with extremes related to natural variability occur randomly in climate projections and that extreme years in the ensemble member downscaled here is not a prediction of when these will happen in the future. In other words, the extremes are statistically random in time, resulting from natural variability anomalies on top of global warming.

We produced winter temperature trends and variability in a potential future climate by extracting output from January to March and sea ice concentration from April. Time series of average temperature from different polygons (Appendix S1, Figure S5) are used to show the characteristics for different ocean basins and corresponding coastal regions, whereas maps of trends and standard deviations are included to show the spatial variability (see below as well as Appendix S1, Climate Projections). The ocean basins are, as mentioned above, the North Sea, Norwegian Sea and Barents Sea, where the Barents Sea has also polygons based on characteristic Atlantic and Polar water masses (Appendix S1, Figure S5). The trends in the time series within the period of interest are expressed in terms of the slope of the corresponding regression. Notably, the sea surface temperature time series show large interannual variability (Appendix S1, Figure S6), and in the early 2040s, there is a substantial and sudden decline until the mid-2040s (Figure 2a) which is also reflected as an increase in sea ice concentration (Appendix S1, Figure S7). To see how this decline influences the long-term trend, these sea surface temperatures are calculated both for the period 2010–2041 and 2010–2046. The numbers (Appendix S1, Table S5) show that the trend during this decline is reduced in all regions, except in the Barents Sea Polar region. It should be noted that the time series are spatial mean values within the polygons and that trends can be larger in some smaller areas (Figure 1). The strongest trends until the mid-2040s at the surface are found in the Barents Sea Polar and North Sea regions, and the mean trends here range from 0.6 to 0.8°C (Appendix S1, Table S5). The largest losses in sea ice in the Barents Sea take place in the northern and eastern parts (Figure 1b). At 100 m the temperature trend in the Barents Sea Polar is still in this range while the other regions range from 0.2 to 0.5°C (Appendix S1, Figure S9; Table S6). The bottom trends are similar to surface trends with maximum values in the Barents Sea Polar and North Sea (Appendix S1, Figure S15; Table S7). Despite small trends in the Norwegian coastal regions at 100 m and at bottom, the spatial plots show high values in the Lofoten area (Appendix S1, Figures S10 and S16). The strongest temperature variability is found along the Polar Front southeast of Svalbard, in the eastern part of the Barents Sea, and along the rim in the Norwegian Sea. There is also strong variability in the Skagerrak coastal area at the surface and in the Lofoten area below the surface (Appendix S1, Figures S6, S11 and S17). Likewise, the variability in sea ice is strongest along the Polar Front and in the eastern parts of the Barents Sea (Appendix S1, Figure S8).

2.5.2 | Modelled pH, oxygen, primary and secondary production

For pH, oxygen and primary and secondary production, the NorESM1-ME/ROMS downscaling forced a biogeochemical model (The NORWegian ECOlogical Model system End-To-End; NORWECOM.E2E) for the Barents and Nordic Seas. NORWECOM.E2E is a coupled physical–chemical–biological model, developed to study primary production, nutrient budgets and dispersion of particles such as fish larvae and pollution. The model has been successfully validated by comparison with field data in the Nordic and Barents Seas (Hjøllo et al., 2012; Skaret et al., 2014; Skogen et al., 2007, 2018). Any additional influences due to benthic–pelagic coupling (Stock et al., 2017) was presently left out in the light of analytic consistency and relevance; the North Sea and Barents Sea are shelf seas, but not the Norwegian Sea (Figure 1). Ocean acidification was projected by consulting the embedded module (Skogen et al., 2014). In the present study, the model is run in offline mode. Physical ocean fields (velocities, salinity, temperature, water level and sea ice) from the ROMS downscaling were interpolated from 5-daily means and used as physical forcing together with daily atmospheric (wind and short-wave radiation) fields from the NorESM1-ME simulation. In the biochemical model, the prognostic variables are dissolved inorganic nitrogen, phosphorous and silicate, two different types of phytoplankton (diatoms and flagellates), two detritus (dead organic matter) pools (nitrogen and phosphorous), diatom skeletal (biogenic silica) and oxygen. Two types of zooplankton (meso- and micro-zooplankton) are included. The processes included are primary and secondary production, grazing by zooplankton on phytoplankton and detritus, respiration, algae mortality, remineralization of inorganic nutrients from dead organic matter, self-shading, turbidity, sedimentation, resuspension, sedimental burial and denitrification. Time series for the same polygons as for temperature (Appendix S1, Figure S5) was produced (Figure 2b-e, Appendix S1, Tables S8–11); the variables are annual mean surface pH and oxygen, as well as annual gross primary and secondary production, with the corresponding linear trends and standard deviations. As above for temperature, the trends in the time series within the period of interest are expressed in terms of the slope of the corresponding regression.

3 | RESULTS AND DISCUSSION

3.1 | Study stocks and their habitats

Altogether, 31 of the 39 North East Atlantic stocks considered are cold temperate, the remaining number being warm temperate (*N* = 6) and Arctic (*N* = 2) (Appendix S1, Stock Narratives). In 2018—with the most recent, complete statistics—these stocks contributed 84% to all fisheries landings in the North East Atlantic, with, as expected (Gullestad et al., 2020), a substantial variation in landed tonnes across stocks (Appendix S1, Table S4). A recent hazard metric analysis, based on the negative impact of exceeding a stock-specific thermal safety margin, concluded that European fishing fleets operating in the North Sea, English Channel and Celtic and Irish Seas are particularly at high climate risk, that is encountering adverse consequences (Payne et al., 2021).

The warm Atlantic Current extends the cold-temperate climate far into the North East Atlantic, towards the edge of the Polar Basin (80°N), with ice-free conditions during summer (Ingvaldsen et al., 2021; Stroeve et al., 2007). Contrarily, in the north-western North Atlantic, the Labrador Current extends the cold Arctic waters equatorwards causing ice conditions to occur towards Newfoundland (50°N) (Drinkwater, 1996). In the north-easternmost North East Atlantic, the extreme light cycle with summer midnight sun and winter dark compels an overwintering strategy of planktivores and subsequent spring spawning (Sundby et al., 2016). Piscivores may skip such an overwintering strategy, but need to synchronize their spawning cycle, if oviparous, with the spring bloom to provide enough food for their planktivorous offspring (Ferreira et al., 2020). These strict life cycle adaptations are omnipresent north of ≈64°*N* (Sundby et al., 2016). The presently investigated >30-degree latitudinal coverage from 50 to 82°N corresponds to about 3,700 km. Across this considerable sea distance, the temperature of the upper ocean layer—represented by the climatological mean at 50 m depth (Garcia et al., 2019)—varies seasonally between 7.0 and 11.0°C at the northern entrance of the North Sea to between −1.0 and 2.0°C in the northern Barents Sea. In the southernmost part of the study area, cold-temperate stocks overlap with warm-temperate ones (Gullestad et al., 2020), whereas in the northernmost region, they overlap with Arctic stocks (Fossheim et al., 2015).

3.2 | Climate stressors

Although the downscaled climate projection under emission scenario RCP4.5 covered 2010–2070, we focused on the interval 2010–2041 as there was a substantial decline in sea surface temperature in the mid-2040s, though thereafter quickly returning to the same trajectory (Figure 2a). The simulation showed increased sea surface temperature in the North East Atlantic, especially in the North and Barents Seas (and in the Baltic Sea which was beyond the present CIA) (Figure 1). Projected sea surface temperatures also increased in the Norwegian Sea but decreased in the Greenland Sea and particularly south of Iceland, the latter coinciding with the northern extension of the Subpolar Gyre (Hátún et al., 2005) (Figure 1). The trend at 100-m depth reflected sea surface temperature, although the amplitude decreased with depth (Figure 2a, Appendix S1, Figures S9, S10, S12, S13). Overall, temperature was the dominant climate exposure factor within the CIA (Appendix S1, Table S3), further outlined below.

The following forcing of the regional biogeochemical model by the above-referenced climate model system projected a series of parametric changes in potential climate stressors and drivers other than temperature, though mostly minor. The outputs spoke for a decline in pH of about 0.1 over the next three decades (Figure 2b, Appendix S1, Table S8) and a corresponding decline of about 0.15 and 0.20 ml/L in oxygen content in the Norwegian Sea and the Barents Sea Polar, respectively (Figure 2c, Appendix S1, Table S9). Decreasing trends (slope) within ocean basins were markedly smaller than the contrast in absolute values (intercept) across basins: about 0.2 for pH and about 1.5 ml/L for oxygen content. The ongoing decrease in sea ice concentration in the Barents Sea (Appendix S1, Figure S7) resulted in diverging stock responses—increased feeding area and heightened productivity for Northeast Arctic cod (*Gadus morhua*, Gadidae) (Kjesbu et al., 2014) whereas severely impaired habitat conditions for polar cod (*Boreogadus saida*, Gadidae) (Appendix S1, Table S3) (Gjøsæter et al., 2020). Factors underlying variations in gross primary production (diatoms and flagellates) are multifaceted (Boyd et al., 2014), thus the current forcing projected high variability, both locally and interannually, but, despite these intrinsic dynamics, an overall, weak positive trend (Figure 2d, Appendix S1, Table S10), supported by other, recent gross primary production assessments (Holt et al., 2016; du Pontavice et al., 2021; Pörtner et al., 2014). A broadly similar picture was seen for gross secondary production, except an adverse pattern in the North Sea, besides the overall low value in this ocean basin (Figure 2e, Appendix S1, Table S11). Hence, gross secondary production (Beaugrand et al., 2003) along with temperature at 100 m was dominating, negative climate exposures for North Sea cod (Appendix S1, Table S3). The future status of *Calanus finmarchicus* (Calanidae) constituted an important background for our work as *C. finmarchicus* is a key prey for many of the studied stocks or their early life stages, besides being increasingly harvested (Appendix S1, Stock Narratives). Hence, our conclusions are dependent upon the status of this crustacean, which is projected to respond positively to climate change by expanding in the north and with the core distribution still in the Norwegian Sea, despite a clear retraction in the south (cf. North Sea) (Appendix S1, Stock Narrative) (Beaugrand et al., 2002).

3.3 | Climate impacts on stock productivity

Scoring of sensitivity attributes indicated that the 39 North East Atlantic stocks assessed (Figure 3, Appendix S1, Table S3), provided considered at the aggregated (grand mean) level, apparently were not that sensitive to climate change, seen by the lack of relationship with grand mean climate exposure ($p = .94$) (Figure 3a) and the weak, though significant and negative relationship with accumulated directional effect ($r^2 = .23$, $p = .02$) (Figure 3b). Altogether, grand mean sensitivity attributes scores were centred around moderate vulnerability (score 2; Figure 3a), assumingly reflecting an overall, adaptive capacity to local, natural environmental conditions (Pörtner & Farrell, 2008). Likewise, variation (*SD*) in grand mean sensitivity attributes was scattered with no obvious trend when regressed on accumulated directional effect ($p = .16$) (Figure 3c).

However, further in-depth examinations revealed that 32 out of 39 stock showed presence of individual sensitivity attributes with high or very high scores, that is with mean values between 3 and 4 (Figure 4, Appendix S1, Figures S3 and S4, Table S3)—factors that might become critical or even more critical if greenhouse gas emissions are not reduced in the future. Furthermore, a given grand mean climate exposure could relate to opposite accumulated directional effects (Figure 3d). This contrasting response reflects stocks that thrive under climate change and, conversely, stocks that suffer under climate change. In addition to this depiction are stocks that are apparently unaffected by climate change, creating altogether a trifurcation (Figure 3d).

In view of the high importance of issues related to reproductive ecology (Dahlke et al., 2020; Pörtner & Farrell, 2008) (Figure 4), the biophysical attributes of spawning sites were further explored (Figure 5a). Related phenology issues were presently not pursued, though potentially important to better understand climate-induced changes in recruitment success (Ferreira et al., 2020). Due to the closed gyre circulation pattern in the North Sea, spawning and adult

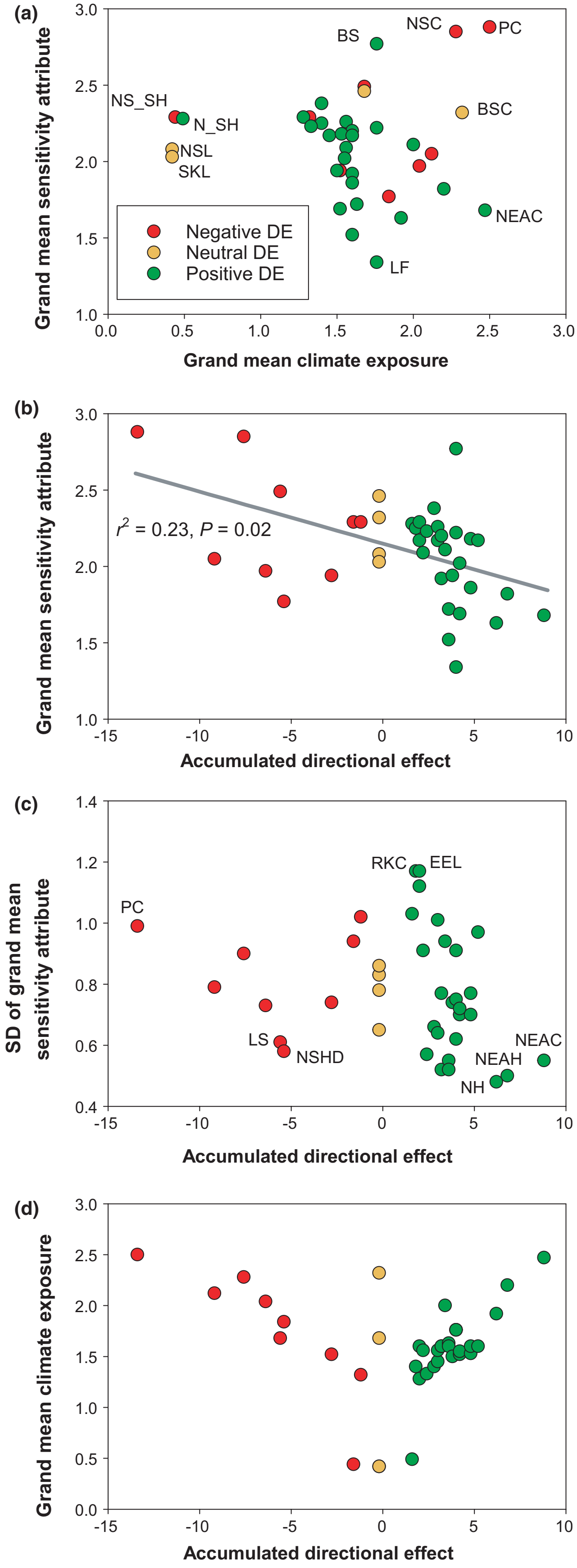


FIGURE 3 Relationships between climate impact measures applied on 39 North East Atlantic stocks. Grand mean sensitivity attributes and climate exposures (RCP4.5, 2010–2041) are visualized by the resulting accumulated directional effect (DE). (a) Sensitivity attribute versus. climate exposure; (b) sensitivity versus. directional effect; (c) standard deviation (*SD*) of sensitivity attribute versus. directional effect; and (d), climate exposure versus. directional effect. Sensitivity attribute and climate exposure scoring: 1 = low; 2 = moderate; 3 = high; 4 = very high, the latter undetected at the grand mean level. Accumulated directional effect criteria: negative (red) < -1; neutral (yellow) ≥ -1 and ≤ 1; positive (green) >1. "Outlier stocks" are exemplified, with their abbreviations explained in Figure 5

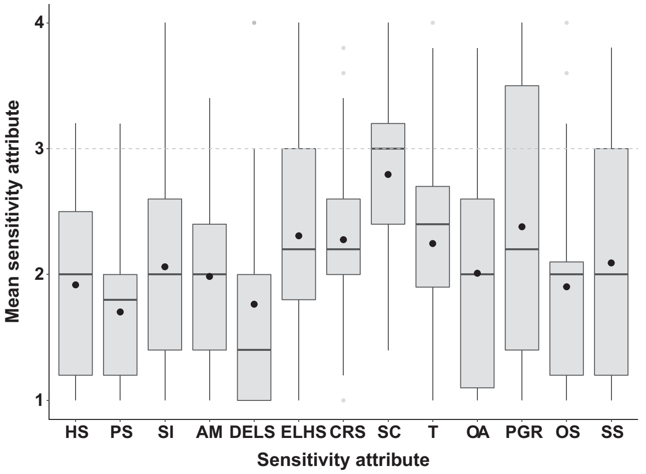


FIGURE 4 Statistical overview of scoring of individual sensitivity attributes. The grey dashed line at a mean score = 3.0 represents the limit above which an individual sensitivity attribute is considered as a dominating factor. Scoring: 1 = low; 2 = moderate; 3 = high; 4 = very high. Applied sensitivity attributes abbreviations are as follows: HS = Habitat Specificity; PS = Prey Specificity; SI = Species Interaction; AM = Adult Mobility; DELS = Dispersal of Early Life Stages; ELHS = ELH Survival and Settlement Requirements; CRS = Complexity in Reproductive Strategy; SC = Spawning Cycle; T = Sensitivity to Temperature; OA = Sensitivity to Ocean Acidification; PGR = Population Growth Rate; SS = Stock Size/Status; OS = Other Stressors. Boxplots are in the style of Tukey (median = 50% quantile; upper and lower hinges = 75 and 25% quantile, respectively; whiskers, for example upper whisker = largest observation less than or equal to upper hinge +1.5 × interquartile range). Grey and black dots represent outliers and statistical mean, respectively

feeding areas are largely overlapping (Sundby et al., 2017). In the Norwegian and Barents Seas, the life cycles of the various stocks are steered by the combined effect of (i) the strong north-eastward-flowing currents and (ii) strict adaptations to spring–bloom dynamics (see above). As a result, the seasonal life cycle of Barents Sea stocks is structured by summer–autumn feeding in the Barents Sea, counter-current spawning migration to coastal areas in winter–spring, return migration of adults, and, finally, pelagic offspring drifting back to the Barents Sea (Bergstad et al., 1987). The Northeast Arctic cod is an extreme example of this migration triangle (Harden Jones, 1968), with a spawning migration of >1,500 km (Sundby & Nakken, 2008). The spawning areas for the Barents Sea stocks, all cold temperate, are found along the Norwegian coast (Figure 5a). The only presently studied species with specialized adaptation to spawn in the Barents Sea as such are polar cod, an Arctic species, and snow crab (*Chionoecetes opilio*, Oregoniidae), a new species to the sub-Arctic community (Appendix S1, Stock Narratives).

The currently outlined directional effect patterns characterizing the 39 assessed North East Atlantic stocks with either declining, neutral or increasing productivity (Figure 5b) appeared closely linked to their thermal window of tolerance (Appendix S1, Stock Narratives):

3.3.1 | Mixed responses within the same species

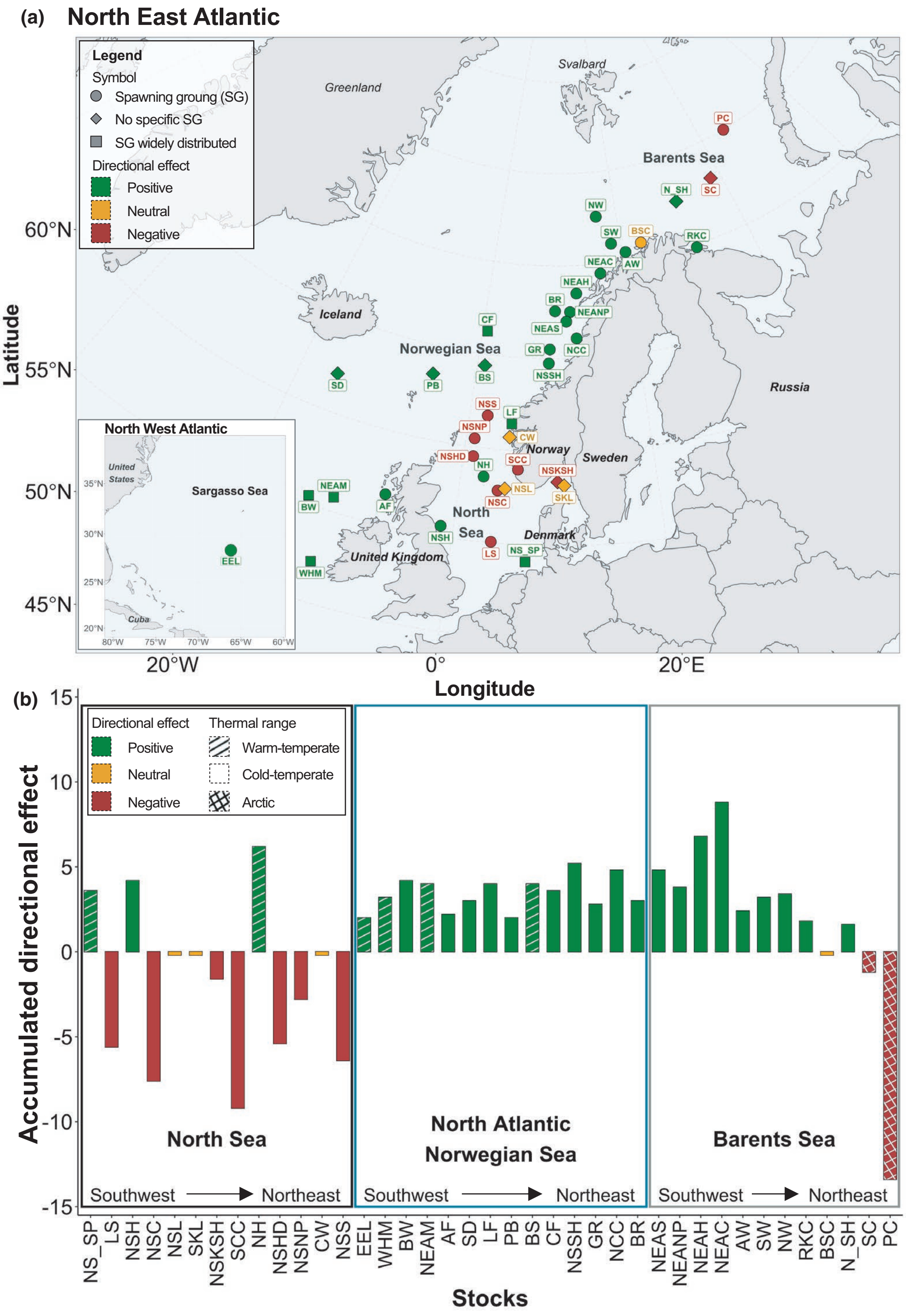
Cold-temperate stocks in the North Sea are presently living near the upper limit of temperature adaptation. Under onward climate change, these stocks will continue to decline, with local extinction as the ultimate result of temperature increases beyond the present assessment time limit of the mid-21st century (Appendix S1, Stock Narratives). The North Sea circulation pattern, with a prevailing southward current from the spawning areas in the northern North Sea (Sundby et al., 2017), creates a “trap” for cold-temperate stocks under climate change as their offspring are advected into warm waters during summer and autumn. Only a smaller fraction of these offspring, entrained in the northward-flowing Norwegian Coastal Current, escape into colder water masses (Sundby et al., 2017). Therefore, a prominent and largely generic feature among the North Sea cold-temperate stocks is that they are assessed to develop negatively, whereas in the Barents Sea, stocks of the same species are assessed to develop positively (Figure 5b). These stock-specific and contrary directional effects are most clearly demonstrated for conspecifics in the North and Barents Seas, for example, the four gadoid species cod, haddock (*Melanogrammus aeglefinus*, Gadidae), saithe (*Pollachius virens*, Gadidae) and Norway pout that have an opposite response to increasing temperature in different ocean basins (Figure 5). The long spawning migration outlined for Northeast Arctic cod is seemingly an adaptation to avoid an extended offspring advection into Arctic areas hostile even for cold-temperate stocks. However, as the ice retracts and gross primary production as well as gross secondary production apparently increase (Figure 2), the feeding area for cold-temperate stocks in the Barents Sea increases and amplifies the positive effects of climate change (Gullestad et al., 2020; Kjesbu et al., 2014). Contrarily, in the North Sea the transport of the offspring is exposed to mesoscale eddies with less net advection (Sundby et al., 2017)—and mainly into warmer waters—where the preferred prey *C. finmarchicus* retracts northwards (Appendix S1, Stock Narratives), accelerating the negative impact of global warming. Moreover, the North Sea shallows considerably southwards, diminishing the habitat extent of many cold-water stocks (Engelhard et al., 2014) and reducing species diversity (Sundby et al., 2017). The two Northern shrimp (*Pandalus borealis*, Pandalidae) stocks also respond oppositely to climate change (Figure 5b), although with less amplitude, because of their deeper distribution in the water column where the thermal increase is far less than in the upper layers (see above).

3.3.2 | Species that thrive

Not surprisingly, there do exist stocks that thrive well in a warmer climate, as seen by their historically peaked prevalence during warm phases of long-term climate fluctuations (Barcelo et al., 2016; Gullestad et al., 2020). These stocks are well-adapted to temperatures above those typically encountered, exemplified by North Sea sprat (*Sprattus sprattus*, Clupeidae), with major spawning areas in the southern part of the North Sea (Figure 5a), and Northern hake (*Merluccius merluccius*, Merlucciidae), for which feeding and spawning areas have been displaced northwards west of Ireland during the last two decades (Gullestad et al., 2020; Sundby et al., 2017). Hake spawning areas are also currently found in the northern North Sea (Figure 5a), and intensified spawning is occurring along the coast of mid-Norway (62–63°N) (Werner et al., 2016). However, farther poleward displacement of hake spawning areas might be challenged by the above-outlined extreme spring–bloom dynamics north of 64°*N* (Sundby et al., 2016). A third group is principally doing well, that is, those stocks with their northernmost distribution in the Nordic Seas. These members include basking shark, porbeagle, spurdog and European eel, with the latter being catadromous and spawning far outside the study area, in the Sargasso Sea (Figure 5a). All four were assessed to have extended their distributions towards the northeast and to potentially become more abundant, though provided current strict rebuilding plans are maintained (Appendix S1, Stock Narratives). Horse mackerel (*Trachurus trachurus*, Carangidae) and North East Atlantic mackerel (*Scomber scombrus*, Scombridae) spawn over vast areas, both in oceanic and in coastal areas (Appendix S1, Stock Narratives). Blue whiting (*Micromesistius poutassou*, Gadidae) and mackerel together with the endemic Norwegian spring-spawning herring (*Clupea harengus*, Clupeidea) together constitute the “pelagic complex” in the Norwegian Sea that utilizes *C. finmarchicus* as their major food (Huse et al., 2012). This CIA projected the pelagic complex to respond favourably to warming (Figure 5b), with strengthened northward feeding migration of adult mackerel (Nøttestad et al., 2016) (Appendix S1, Stock Narratives). However, this increased prey field may intensify mackerel predation on Norwegian spring-spawning herring larvae reducing subsequent recruitment success (Allan et al., 2021).

3.3.3 | Species that suffer

Stocks assessed to do poorly under ongoing climate change include polar cod and snow crab in the Barents Sea (Figure 5b). However,



Abbreviation	Stock name
AF	Anglerfish
AW	Atlantic wolffish
BR	Beaked redfish
BS	Basking shark
BSC	Capelin, Barents Sea
BW	Blue whiting
CF	*Calanus finmarchicus*
CW	Corkwing wrasse
EEL	European eel
GR	Golden redfish
LF	Lumpfish
LS	Lesser sandeel
N_SH	Shrimp, Northern
NCC	Cod, Norwegian Coastal - North
NEAC	Cod, North East Arctic
NEAH	Haddock, North East Arctic
NEAM	Mackerel, North East Atlantic
NEANP	Norway pout, North East Arctic
NEAS	Saithe, North East Arctic
NH	Hake, Northern
NS_SP	Sprat, North Sea
NSC	Cod, North Sea
NSH	Herring, North Sea
NSHD	Haddock, North Sea
NSKSH	Shrimp, North Sea - Northern, Skagerrak - Kattegat
NSL	Norway lobster, Norway Deep
NSNP	Norway pout, North Sea
NSS	Saithe, North Sea
NSSH	Herring, Norwegian spring-spawning
NW	Northern wolffish
PB	Porbeagle
PC	Polar cod
RKC	Red kring crab
SC	Snow crab
SCC	Cod, Norwegian Coastal - South
SD	Spurdog
SKL	Norway lobster, Skagerrak - Kattegat
SW	Spotted wolffish
WHM	Horse mackerel, Western

FIGURE 5 Accumulated directional effect (RCP4.5, 2010–2041) for 39 North East Atlantic stocks. (a) Geographical positions show spawning ground of each stock, referring either to the existence of a main spawning ground (SG), no specific SG, or SG widely distributed. Inset applies to European eel; (b) numerical scores of accumulated directional effects split by ocean area—from southwest to northeast ranked by assumed general SG location—and the physiologically adapted thermal regime, that is, whether the stock in question is warm, cold temperate or Arctic. Accumulated directional effect criteria: negative (red) <−1; neutral (yellow) ≥−1 and ≤1; positive (green) >1. All stock names are abbreviated

a series of native, non-commercial Arctic stocks, not assessed in this analysis, inhabit the ice-covered region in the Barents Sea (Fossheim et al., 2015). They are evidently decimated as they are severely challenged by cold-temperate (boreal) stocks, both as prey and during competition for food, a process labelled “borealization” (Fossheim et al., 2015). This ecosystem alteration relates to that the physical characteristics of the Artic water masses are becoming more similar to those of the Atlantic water masses due to the strengthened influx of the warmer Atlantic Current (Ingvaldsen et al., 2021). Thus, the resulting species take-over in the Barents Sea resembles that of the North Sea, but the effect on commercial species is largely positive in the Arctic (Appendix S1, Stock Narratives).

4 | CONCLUSION

Although the implementation plan of a CIA resembles the one commonly used within stock assessment (data collation, analysis, simulation, synthesis and quality assessment), a main difference in the analysis is that it is principally based on expert scorings rather than model outcomes. The latter approach would, in the present setting, be challenged by cases of co-linearity, for example the sensitivity attribute on "Early Life History Survival and Settlement Requirements" and "Complexity in Reproductive Strategy" (Appendix S1, Table S2) are fundamentally linked (Wright & Trippel, 2009). Consequently, any consistent, sophisticated model approach for analysing multiple stocks under a series of environment stressors and drivers and varying habitat conditions seems lacking, at least so far: some approaches will characteristically consider only a few environmental factors, or focus on single, extremely data-rich species. In this article, we adopted a "hybrid solution" where expert opinions were stringently placed within a mechanistic, biophysical framework, as detailed above, followed by the actual calculations of the accumulated directional effect. For the present climate projection, we found that trends and standard deviations for the period until 2041 are largely analogous to those for the extended simulation to 2070 and include a contribution from natural variability that adds to that of global warming. These plots represent a potential extreme warm event at most sea locations within a couple of decades.

It should be noted that using only one realization from one global model and one specific future scenario is a limitation, which should be taken into consideration when interpreting the present findings. That said, there is considerably less spread between the different scenarios before the mid-2040s than towards the end of this century (Drinkwater et al., 2021; IPCC, 2013), so the trends in climate exposure factors for the period studied in this CIA as such (2010–2041) should be reasonable representative. Nevertheless, it should be emphasized that our assessments of gross primary production are not only based on the above downscaled projections, but also on the earlier mentioned downscaled results of Holt et al. (Holt et al., 2016) and on the projections by Pörtner et al. (Pörtner et al., 2014).

IPCC assessments highlight a wide variety of responses to climate change among the world ocean's ecosystems (Hoegh-Guldberg et al., 2014). The present North East Atlantic study considered temperate-to-Arctic spring–bloom ecosystems (<10°C), whereas the North West Atlantic study (Hare et al., 2016) covered subtropical to temperate ecosystems (22–9°C) and the Portuguese coast study (Bueno-Pardo et al., 2021) a temperate, seasonal upwelling system (17–15°C). The differences in methodological approaches reflected the need to tailor approaches to the specific ecosystem's structure and functioning, but also to the basic knowledge accumulated for each. In view of the North West Atlantic study (Hare et al., 2016), one might speculate that North East Atlantic species are, to a larger extent, evolutionarily adapted to climate fluctuations due to the regional occurrence of inter-glacial periods in the North East Atlantic (Bigg et al., 2008). However, the main issue is the asymmetry in environmental clines, abrupt in the North West Atlantic and gradual in the North East Atlantic (Sundby, 2000). The present large coverage in latitudes (Figure 1) necessitated contrasting species and conspecifics across distant waters finding marked difference in their productivity scenarios represented by the accumulated directional effect (Figure 5). Climate projections extended farther into the future and using RCP8.5 instead of RCP4.5 would undoubtedly (Bindoff et al., 2019) have reduced the number of stocks with foreseen increased productivity. This viewpoint is underlined by that most stocks showed presence of high or very high scores for some individual sensitivity attributes, expected to play a strengthened negative role if greenhouse gas emissions are not curtailed. Our work diverts from related investigations by focusing on stock-specific CIAs across multiple marine ecoregions, clarifying that the robustness of marine organisms to climate change is not an attribute developed in isolation from species with which they interact or from the encountered abiotic habitat.

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AUTHOR CONTRIBUTIONS

O.S.K., S.S. and G.H. formulated hypotheses and approach, with A.B.S, F.V., M.F., E.O., M.S.-M., S.S.H and Ja.E.S; O.S.K., S.S., A.B.S, S.S.H and G.H. wrote the main manuscript; O.S.K., M.A. and M.T. reviewed stock narratives; M.A. and M.T. revised Supplementary Information; A.B.S., S.S.H. and M.S.M. performed climate projections; O.S.K. and M.S.-M. considered statistics; M.S.-M. introduced stock interaction attribute; M.S. revised ocean acidification attribute; S.S., C.J., C.T.B., Gu.S., F.Z., K.N., E.E., H.H., A.M.H., C.K., Y.R., A.A., O.T.A., E.B., B.B., C.D., K.T.H., Å.H., C.H., Ed.J., Es.J., H.K., E.M., L.N., Ge.S., M.S.-M., Jo.E.S., Ari.S., Arv.S., E.K.S. and J.H.S. wrote Stock Narratives and scored sensitivity attributes; S.S. and G.H. scored climate exposure; S.S., G.H., O.S.K, A.B.S and M.A. scored directional effect; G.H. and F.V. provided funding; O.S.K led the project. All authors attended workshop discussions and commented upon earlier manuscript drafts.

DATA AVAILABILITY STATEMENT

All data consulted are accessible in the online Supporting Information file.

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REFERENCES

Allan, B. J. M., Ray, J. L., Tiedemann, M., Komyakova, V., Vikebø, F., Skaar, K. S., Stiasny, M. H., Folkvord, A., Nash, R. D., & Stenevik, E. K. (2021). Quantitative molecular detection of larval Atlantic herring (*Clupea harengus*) in stomach contents of Atlantic mackerel (*Scomber scombrus*) marks regions of predation pressure. *Scientific Reports*, *11*(1), 1–11. https://doi.org/10.1038/s41598-021-84545-7

Barcelo, C., Ciannelli, L., Olsen, E. M., Johannessen, T., & Knutsen, H. (2016). Eight decades of sampling reveal a contemporary novel fish assemblage in coastal nursery habitats. *Global Change Biology*, *22*(3), 1155–1167. https://doi.org/10.1111/gcb.13047

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, *426*(6967), 661–664. https://doi.org/10.1038/nature02164

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., & Edwards, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, *296*(5573), 1692–1694. https://doi.org/10.1126/science.1071329

Bentsen, M., Bethke, I., Debernard, J. B., Iversen, T., Kirkevåg, A., Seland, Ø., Drange, H., Roelandt, C., Seierstad, I. A., Hoose, C., & Kristjánsson, J. E. (2013). The Norwegian Earth System Model, NorESM1-M - Part 1: Description and basic evaluation of the physical climate. *Geoscientific Model Development*, *6*(3), 687–720. https://doi.org/10.5194/gmd-6-687-2013

Bergstad, O. A., Jørgensen, T., & Dragesund, O. (1987). Life-history and ecology of the gadoid resources of the Barents Sea. *Fisheries Research*, *5*(2–3), 119–161. https://doi.org/10.1016/0165-7836(87)90037-3

Bigg, G. R., Cunningham, C. W., Ottersen, G., Pogson, G. H., Wadley, M. R., & Williamson, P. (2008). Ice-age survival of Atlantic cod: Agreement between palaeoecology models and genetics. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1631), 163–172. https://doi.org/10.1098/rspb.2007.1153

Bindoff, N. L., Cheung, W. W., Kairo, J. G., Arístegui, J., Guinder, V. A., Hallberg, R., Hilmi, N. J. M., Jiao, N., Karim, M. S., & Levin, L. (2019). Changing ocean, marine ecosystems, and dependent communities. IPCC special report on the ocean and cryosphere in a changing climate, 477–587.

Boyd, P. W., Sundby, S., & Pörtner, H.-O. (2014). Cross-chapter box on net primary production in the ocean. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change* (pp. 133–136). Cambridge University Press.

Brander, K. M. (2007). Global fish production and climate change. *Proceedings of the National Academy of Sciences*, *104*(50), 19709–19714. https://doi.org/10.1073/pnas.0702059104

Bueno-Pardo, J., Nobre, D., Monteiro, J. N., Sousa, P. M., Costa, E. F. S., Baptista, V., Ovelheiro, A., Vieira, V. M. N. C. S., Chícharo, L., Gaspar, M., Erzini, K., Kay, S., Queiroga, H., Teodósio, M. A., & Leitão, F. (2021). Climate change vulnerability assessment of the main marine commercial fish and invertebrates of Portugal. *Scientific Reports*, *11*(1), 2958. https://doi.org/10.1038/s41598-021-82595-5

Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frolicher, T. L., Lam, V. W. Y., Palomares, M. L. D., Watson, R., & Pauly, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, *3*(3), 254–258. https://doi.org/10.1038/nclimate1691

Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H. O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, *369*(6499), 65–70. https://doi.org/10.1126/science.aaz3658

Drinkwater, K. (1996). Atmospheric and oceanic variability in the Northwest Atlantic during the 1980s and early 1990s. *Journal of Northwest Atlantic Fishery Science*, *18*, 77–97. https://doi.org/10.2960/J.v18.a6

Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, *62*(7), 1327–1337. https://doi.org/10.1016/j.icejms.2005.05.015

Drinkwater, K. F., Harada, N., Nishino, S., Chierici, M., Danielson, S. L., Ingvaldsen, R. B., Kristiansen, T., Hunt, G. L., Mueter, F., & Stiansen, J. E. (2021). Possible future scenarios for two major Arctic Gateways connecting Subarctic and Arctic marine systems: I. Climate and physical–chemical oceanography. *ICES Journal of Marine Science*, *78*(9), 3046–3065. https://doi.org/10.1093/icesjms/fsab182

du Pontavice, H., Gascuel, D., Reygondeau, G., Stock, C., & Cheung, W. W. (2021). Climate-induced decrease in biomass flow in marine food webs may severely affect predators and ecosystem production. *Global Change Biology*, https://doi.org/10.1111/GCB.15576

Engelhard, G. H., Righton, D. A., & Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Global Change Biology*, *20*(8), 2473–2483. https://doi.org/10.1111/gcb.12513

FAO (2020). *The State of World Fisheries and Aquaculture 2020*. Sustainability in Action.

Ferreira, A. S. A., Stige, L. C., Neuheimer, A. B., Bogstad, B., Yaragina, N., Prokopchuk, I., & Durant, J. M. (2020). Match-mismatch dynamics in the Norwegian-Barents Sea system. *Marine Ecology Progress Series*, *650*, 81–94. https://doi.org/10.3354/meps13276

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*(7), 673–677. https://doi.org/10.1038/nclimate2647

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, *363*(6430), 979–983. https://doi.org/10.1126/science.aau1758

Garcia, H., Boyer, T., Baranova, O., Locarnini, R., Mishonov, A., Grodsky, A., Paver, C., Weathers, K., Smolyar, I., & Reagan, J. (2019). World Ocean Atlas 2018: Product documentation. A. Mishonov, Technical Editor.

Gjøsæter, H., Huserbråten, M., Vikebø, F., & Eriksen, E. (2020). Key processes regulating the early life history of Barents Sea polar cod. *Polar Biology*, *43*(8), 1015–1027. https://doi.org/10.1007/s00300-020-02656-9

Grant, W. S., & Bowen, B. W. (1998). Shallow population histories in deep evolutionary lineages of marine fishes: Insights from sardines and anchovies and lessons for conservation. *Journal of Heredity*, *89*(5), 415–426. https://doi.org/10.1093/jhered/89.5.415

Gullestad, P., Sundby, S., & Kjesbu, O. S. (2020). Management of transboundary and straddling fish stocks in the Northeast Atlantic in view of climate-induced shifts in spatial distribution. *Fish and Fisheries*, *21*(5), 1008–1026. https://doi.org/10.1111/faf.12485

Harden Jones, F. R. (1968). *Fish Migration*. Edward Arnold.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., Scott, J. D., Alade, L., Bell, R. J., Chute, A. S., Curti, K. L., Curtis, T. H., Kircheis, D., Kocik, J. F., Lucey, S. M., McCandless, C. T., Milke, L. M., Richardson, D. E., … Griswold, C. A. (2016). A vulnerability assessment of fish and invertebrates to climate change on the Northeast U.S. Continental Shelf. *PLoS One*, *11*(2), e0146756. https://doi.org/10.1371/journal.pone.0146756

Hátún, H., Sandø, A. B., Drange, H., Hansen, B., & Valdimarsson, H. (2005). Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science*, *309*(5742), 1841–1844. https://doi.org/10.1126/science.1114777

Hawkins, E., & Sutton, R. (2009). The potential to narrow uncertainty in regional climate predictions. *Bulletin of the American Meteorological Society*, *90*(8), 1095–1108. https://doi.org/10.1175/2009bams2607.1

Hjøllo, S. S., Huse, G., Skogen, M. D., & Melle, W. (2012). Modelling secondary production in the Norwegian Sea with a fully coupled physical/primary production/individual-based *Calanus finmarchicus* model system. *Marine Biology Research*, *8*(5–6), 508–526. https://doi.org/10.1080/17451000.2011.642805

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in light of biological research. Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 20, 1–228.

Hoegh-Guldberg, O., Cai, R., Poloczanska, E. S., Brewer, P. G., Sundby, S., Hilmi, K., Fabry, V. J., Jung, S., Skirving, W., & Stone, D. A. (2014). The ocean. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate Change 2014: Impacts, adaptation, and vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1655–1731). Cambridge University Press.

Hollowed, A. B., & Sundby, S. (2014). Change is coming to the northern oceans. *Science*, *344*(6188), 1084–1085. https://doi.org/10.1126/science.1251166

Holt, J., Schrum, C., Cannaby, H., Daewel, U., Allen, I., Artioli, Y., Bopp, L., Butenschon, M., Fach, B. A., Harle, J., Pushpadas, D., Salihoglu, B., & Wakelin, S. (2016). Potential impacts of climate change on the primary production of regional seas: A comparative analysis of five European seas. *Progress in Oceanography*, *140*, 91–115. https://doi.org/10.1016/j.pocean.2015.11.004

Huse, G., Holst, J. C., Utne, K., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., Fenchel, T., & Uiblein, F. (2012). Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea – results of the INFERNO project. *Marine Biology Research*, *8*(5–6), 415–419. https://doi.org/10.1080/17451000.2011.653372

ICES (2017). Ecoregions including ICES statistical areas. www.ices.dk/data/Documents/Maps/ICES-Ecoregions-hybrid-statistical-areas.png

ICES (2021). Fisheries overviews. https://www.ices.dk/advice/Fisheries-overviews/Pages/fisheries-overviews.aspx

IMR (2021). Bestandstabell (Stock Table). https://www.hi.no/radgivning/bestandsoversikt/nb/

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, https://doi.org/10.1038/s43017-021-00228-x

IPCC (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC (2021). Summary for policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. In press).

Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjøsæter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D. M., & Skjæraasen, J. E. (2014). Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(9), 3478–3483. https://doi.org/10.1073/pnas.1316342111

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J. M., Hare, S. R., Ottersen, G., Perry, R. I., Roy, C., Van der Lingen, C. D., & Werner, F. (2006). Climate variability, fish, and fisheries. *Journal of Climate*, *19*(20), 5009–5030. https://doi.org/10.1175/jcli3898.1

Morley, J. W., Selden, R. L., Latour, R. J., Frölicher, T. L., Seagraves, R. J., & Pinsky, M. L. (2018). Projecting shifts in thermal habitat for 686 species on the North American continental shelf. *PLoS One*, *13*(5), e0196127. https://doi.org/10.1371/journal.pone.0196127

Nøttestad, L., Utne, K. R., Óskarsson, G. J., Jonsson, S. T., Jacobsen, J. A., Tangen, O., Anthonypillai, V., Aanes, S., Vølstad, J. H., Bernasconi, M., Debes, H., Smith, L., Sveinbornsson, S., Holst, J. C., Jansen, T., & Slotte, A. (2016). Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014. *ICES Journal of Marine Science*, *73*(2), 359–373. https://doi.org/10.1093/icesjms/fsv218

Paasche, Ø., Österblom, H., Neuenfeldt, S., Bonsdorff, E., Brander, K., Conley, D. J., Durant, J. M., Eikeset, A. M., Goksøyr, A., Jónsson, S., Kjesbu, O. S., Kuparinen, A., & Stenseth, N. C. (2015). Connecting the Seas of Norden. *Nature Climate Change*, *5*(2), 89–92. https://doi.org/10.1038/nclimate2471

Payne, M. R., Kudahl, M., Engelhard, G. H., Peck, M. A., & Pinnegar, J. K. (2021). Climate risk to European fisheries and coastal communities. *Proceedings of the National Academy of Sciences*, *118*(40), e2018086118. https://doi.org/10.1073/pnas.2018086118

Peck, M., & Pinnegar, J. K. (2018). Climate change impacts, vulnerabilities and adaptations: North Atlantic and Atlantic Arctic marine fisheries. In M. Barange, T. Bahri, M. C. M. Beveridge, K. L. Cochrane, S. Funge-Smith, & F. Poulain (Eds.), *Impacts of Climate Change on Fisheries and Aquaculture: Synthesis of Current Knowledge, Adaptation and Mitigation Options* (Vol. *627*, pp. 87-111). FAO.

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

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919–925. https://doi.org/10.1038/nclimate1958

Pörtner, H. O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, *322*(5902), 690–692. https://doi.org/10.1126/science.1163156

Pörtner, H.-O., Karl, D. M., Boyd, P. W., Cheung, W., Lluch-Cota, S. E., Nojiri, Y., Schmidt, D. N., Zavialov, P. O., Alheit, J., & Aristegui, J. (2014). Ocean systems. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi,

Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part a: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 411–484). Cambridge University Press.

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*, *77*(8), 1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x

Sandø, A. B., Johansen, G. O., Aglen, A., Stiansen, J. E., & Renner, A. H. H. (2020). Climate change and new potential spawning sites for Northeast Arctic cod. *Frontiers in Marine Science*, *7*, 28. https://doi.org/10.3389/fmars.2020.00028

Sandø, A. B., Melsom, A., & Budgell, W. P. (2014). Downscaling IPCC control run and future scenario with focus on the Barents Sea. *Ocean Dynamics*, *64*(7), 927–949. https://doi.org/10.1007/s10236-014-0731-8

Sandø, A. B., Mousing, E. A., Budgell, W. P., Hjøllo, S. S., Skogen, M. D., & Ådlandsvik, B. (2021). Barents Sea plankton production and controlling factors in a fluctuating climate. *ICES Journal of Marine Science*, *78*(6), 1999–2016. https://doi.org/10.1093/icesjms/fsab067

Shchepetkin, A. F., & McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, *9*(4), 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002

Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schon, P. J., Sims, D. W., & Genner, M. J. (2011). Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology*, *21*(18), 1565–1570. https://doi.org/10.1016/j.cub.2011.08.016

Skaret, G., Dalpadado, P., Hjøllo, S. S., Skogen, M. D., & Strand, E. (2014). *Calanus finmarchicus* abundance, production and population dynamics in the Barents Sea in a future climate. *Progress in Oceanography*, *125*, 26–39. https://doi.org/10.1016/j.pocean.2014.04.008

Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., & Kjesbu, O. S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries*, *17*(1), 165–175. https://doi.org/10.1111/faf.12111

Skogen, M. D., Budgell, W. P., & Rey, F. (2007). Interannual variability in Nordic Seas primary production. *ICES Journal of Marine Science*, *64*(5), 889–898. https://doi.org/10.1093/icesjms/fsm063

Skogen, M. D., Hjøllo, S. S., Sandø, A. B., & Tjiputra, J. (2018). Future ecosystem changes in the Northeast Atlantic: A comparison between a global and a regional model system. *ICES Journal of Marine Science*, *75*(7), 2355–2369. https://doi.org/10.1093/icesjms/fsy088

Skogen, M. D., Olsen, A., Børsheim, K. Y., Sandø, A. B., & Skjelvan, I. (2014). Modelling ocean acidification in the Nordic and Barents Seas in present and future climate. *Journal of Marine Systems*, *131*, 10–20. https://doi.org/10.1016/j.jmarsys.2013.10.005

Stock, C. A., John, J. G., Rykaczewski, R. R., Asch, R. G., Cheung, W. W. L., Dunne, J. P., Friedland, K. D., Lam, V. W. Y., Sarmiento, J. L., & Watson, R. A. (2017). Reconciling fisheries catch and ocean productivity. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(8), E1441–E1449. https://doi.org/10.1073/pnas.1610238114

Stroeve, J., Holland, M. M., Meier, W., Scambos, T., & Serreze, M. (2007). Arctic sea ice decline: Faster than forecast. *Geophysical Research Letters*, *34*(9), https://doi.org/10.1029/2007GL029703

Sundby, S. (2000). Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, *85*(4), 277–298. https://doi.org/10.1080/00364827.2000.10414580

Sundby, S., Drinkwater, K. F., & Kjesbu, O. S. (2016). The North Atlantic spring-bloom system – where the changing climate meets the winter dark. *Frontiers in Marine Science*, *3*, 12. https://doi.org/10.3389/fmars.2016.00028

Sundby, S., Kristiansen, T., Nash, R., & Johannessen, T. (2017). Dynamic mapping of North Sea spawning – Report of the KINO Project. *Fisken og Havet*, *2*, 195.

Sundby, S., & Nakken, O. (2008). Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, *65*(6), 953–962. https://doi.org/10.1093/icesjms/fsn085

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, *93*(4), 485–498. https://doi.org/10.1175/bams-d-11-00094.1

Werner, K. M., Staby, A., & Geffen, A. J. (2016). Temporal and spatial patterns of reproductive indices of European hake (*Merluccius merluccius*) in the northern North Sea and Norwegian coastal areas. *Fisheries Research*, *183*, 200–209. https://doi.org/10.1016/j.fishres.2016.06.008

Wright, P. J., & Trippel, E. A. (2009). Fishery-induced demographic changes in the timing of spawning: Consequences for reproductive success. *Fish and Fisheries*, *10*(3), 283–304. https://doi.org/10.1111/j.1467-2979.2008.00322.x

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