



Partitioning climate uncertainty in ecological projections: Pacific oysters in a hotter Europe

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ABSTRACT

Projections of the range expansions of marine species are critical if we are to anticipate and mitigate the impacts of climate change on marine ecosystems. However, most projections do not assess the level of uncertainty of future changes, which brings their usefulness for scenario planning and ecosystem management into question. For the overall climate system, these uncertainties take three forms: scenario uncertainty, climate model uncertainty and internal climate variability. Critically, internal variability, a measure of how natural variability affects future climate projections, has largely been ignored in ecological studies. Here we use an ensemble modelling approach for the non-native Pacific oyster in Europe to understand the impact of these uncertainties. Future Pacific oyster recruitment was projected using a model that relates recruitment to cumulative and instantaneous heat exposure. Model projections were carried out for four climate change scenarios: SSP1 2.6, SSP2 4.5, SSP3 7.0 and SSP5 8.5. In each scenario an ensemble of over twenty climate models was used. The impact of internal variability in climate models was assessed by using five climate models which were available with multiple pre-industrial starting points. We find that model uncertainty within SSP1 2.6 is higher than the differences between SSP1 2.6 and SSP 4.5, but it is unclear if overall scenario uncertainty is greater than climate model uncertainty due to its subjective nature. Comparisons of scenario projections indicate that future recruitment areas of Pacific oysters under the SSP5 8.5 scenario could be more than twice as high as in the low emissions SSP1 2.6 scenario. Importantly, the ensemble showed that near-term changes in Pacific oysters are highly uncertain due to internal variability, which is of a similar magnitude to climate model uncertainty on a 20-year timescale. Our results show that it is critical to think about the future in terms of potential scenarios and not individual projections.

1. Introduction

Species distribution models can play a key role by indicating to ecosystem managers and policymakers what future changes will occur in marine ecosystems, so that they can assess whether current or future management regimes are “climate-smart” (Queirós et al., 2021). A critical component of such assessments is an understanding of the level of uncertainty in future projections, which is still absent from most studies. This paper addresses how uncertainty in future climate change impacts our ability to accurately project future biogeographic expansions of species, using the non-native Pacific oyster in Europe as a target species. In particular, we consider how internal climate variability (a measure of how the chaotic nature of the climate system and natural oscillations make future predictions uncertain) could influence

ecological projections.

Climate change is likely a key driver of the ongoing northward expansion of wild Pacific oyster populations in recent decades across northern Europe (Diederich et al., 2005; Thomas et al., 2018). Rising temperatures will increase invasion risk for three key reasons: 1) it will increase the viability of Pacific oyster aquaculture (Palmer et al., 2021), which will increase the frequency of population seeding to wild locations; 2) increasing temperatures will result in more rapid development (Mann, 1979); and 3) it will increase the number of regions where water temperatures exceed the apparent temperature threshold for spawning to occur (Dutertre et al., 2009; Mann, 1979). Factors 2) and 3) will gradually alter the number of regions where areas neighbouring aquaculture sites remain sink populations in a future climate.

The introduction of Pacific oysters from Japan to Europe began in the

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mid-1960s, and since this time Pacific oyster *Crassostrea gigas* aquaculture has expanded dramatically. It is now the European Union's second most important aquaculture species by economic value, with an annual production of over 100,000 t (Nielsen and Motova, 2014). However, the geographic pattern of production is set to change in a warmer future as the productivity of more northern regions improves (Callaway et al., 2012). This will likely result in positive economic benefits for these regions (Callaway et al., 2012), but there will also be complex impacts on ecosystems (Herbert et al., 2016) and on native species (Markert et al., 2010; Nehls et al., 2006; Reise, 1998) due to the spread of this species to new habitats. Furthermore, a northward expansion of Pacific oysters may bring into question the ecological sustainability of some aquaculture sites and the restoration potential of native oysters, which may see competition from this newly invasive species.

The introduction of Pacific oysters quickly resulted in their spread to wild sites in northern France (Grizel and Heral, 1991). However, until the 1990s, it was thought that Pacific oysters were mostly incapable of spawning in countries north of France due to cold waters, and they were therefore incapable of becoming invasive (Drinkwaard, 1998; Wehrmann et al., 2000). However, from the 1990s there was an increasing number of observations of Pacific oyster populations in parts of Scandinavia (Wrangé et al., 2010), the Dutch coast (Troost, 2010), Wadden Sea (Wehrmann et al., 2000), and the southern English coast (Spencer et al., 1994) that could not be explained purely by accidental releases from aquaculture sites or ballast water.

Projecting future climate change impacts on Pacific oysters is therefore necessary if we are to understand both their ecosystem impacts and to understand the future ecological sustainability of Pacific oyster aquaculture. The impacts of climate change on species distributions are typically projected using statistical or mathematical models that are driven by global or regional climate or biogeochemistry models under a future greenhouse gas emissions scenario. These projections have three main sources of climate uncertainty: scenario uncertainty, climate model uncertainty and internal climate variability (Hawkins and Sutton, 2009). Scenario uncertainty reflects how uncertainty in future greenhouse gas emissions will create uncertainty in future climate and thus the ecology of species. Climate model uncertainty represents how the sometimes wide spread of projections from climate models can impact ecology. Scenario uncertainty and climate model uncertainty have been addressed in multiple ecological studies (e.g. Buisson et al., 2010), and their importance is widely understood. A further source of uncertainty is ecological uncertainty, which can be addressed by using multiple ecological models, but this aspect is not addressed here.

Internal variability refers to the level of uncertainty in future climate projections due to natural variability, which is a result of the complex and chaotic behaviour of climate systems, and it is typically viewed as being largely irreducible (Hawkins et al., 2016). The importance of internal variability in climate models is an issue that has largely been ignored by scientists studying climate change impacts, even though it has been shown to be important in many cases (Schwarzwald and Lenssen, 2022). Multiple analyses of global models have shown that this can be a major source of uncertainty at a regional scale (Frölicher et al., 2016). Critically, for ecosystem management, which often considers short timescales, internal variability is often a dominant source of uncertainty for climate projections over short-term periods (Lehner et al., 2020).

The central aim of this study is to project future climate change impacts on recruitment of Pacific oysters across the north-west European shelf and to assess how much the following contribute to its uncertainty: climate model uncertainty, climate scenario uncertainty, and internal variability within climate models. Pacific oyster was chosen both because of its growing ecological and economic importance in Europe but also because its recruitment, which largely determines its geographic distribution, can be projected with a model that is not computationally intensive.

2. Methods

Due to its life cycle, Pacific oyster is a species that is challenging to model with a typical statistical species distribution model, which uses statistical methods to relate the observed occurrences of species with environmental variables. This is primarily due to the fact that its northern distribution in the observational record is contaminated by the occurrence of organisms that have escaped from aquaculture sites. We therefore chose to use recruitment as a proxy for the potential occurrence of sustainable wild Pacific oyster populations. Recruitment is understood to be the critical determinant of whether wild Pacific oyster populations are sustainable because the temperature requirements for growth are lower than for recruitment (Syvret et al., 2008). This often enables aquaculture to occur with a low risk of wild population sustainability after accidental release. The geographic shift in regions where recruitment can occur should provide a meaningful indicator of the impact of climate change on this species.

2.1. Degree-days model of Pacific oyster recruitment

Pacific oyster recruitment (i.e. conditioning of eggs, spawning of larvae and metamorphosis to spat) are here modelled following an approach outlined by previous work (Syvret et al., 2008), where heat exposure determines the occurrence and timing of recruitment. First, biological development is assumed to only occur above a biological zero temperature of 10.55 °C (Mann, 1979). Second, the model assumes that cumulative heat exposure determines if adult oysters are capable of spawning. Heat exposure is defined in terms of cumulative degree-days relative to the biological zero of 10.55 °C, with the total degree-days between the start of the year and day of year d calculated as $\int_0^d \max(T_d - 10.55, 0)$, where T_d is daily temperature (°C). For adults to spawn, the cumulative heat exposure must exceed 600°-days, and in addition the model assumes that water temperatures must exceed 18 °C for spawning to occur, in line with existing modelling methods and field evidence (Dutertre et al., 2009; Gourault et al., 2019; Thomas et al., 2016; Thomas and Bacher, 2018). Once spawning has occurred, the model assumes that there is a further development period required for metamorphosis, i.e. for larvae to develop fully and to settle to spat. A further 225°-days of heat exposure for the completion of recruitment following spawning is therefore required. Finally, Pacific oysters reside on the seafloor in shallow regions that are permanently mixed. We therefore assumed that sea surface temperature (SST) represents the water temperatures experienced by oysters. Modelling, analysis and visualization were carried out using the Python package nctoolkit (Wilson and Artioli, 2023) and the R package suite "tidyverse" (Wickham et al., 2019).

2.2. Environmental data

Climate change uncertainties were assessed by projecting future Pacific oyster recruitment using the above model and bias-corrected temperature projections from a large ensemble of global climate models. We utilized the hierarchy of simulations available in the Coupled Model Intercomparison Project 6 (CMIP6). Within CMIP6, a large number of global climate models provided projections of future climate under at least one future greenhouse gas emissions scenario. This enables a large ensemble of climate models to be used to estimate the influence of climate uncertainty within scenarios and between scenarios. Furthermore, a small number of models are available with different pre-industrial starting points. The variability in projections from individual models with different starting points is viewed as a reliable indicator of the level of uncertainty to internal variability in a climate model (Hawkins et al., 2016).

We used four Shared Socioeconomic Pathways (SSPs) in the future projections of SST and thus Pacific oyster recruitment, which in order of

Table 1

List of CMIP6 models used for Pacific oyster projections. The SSP columns indicate whether data was available for the specific SSP. Models with the superscripts 1–5 were available either at multiple spatial resolutions or with different sub-models, and a multi-model average was used for those models. 5 of the models had at least 10 variants (i.e. runs with different pre-industrial initial conditions). These models have numbers within brackets in the SSP columns indicating how many variants were used.

| Model | SSP1 2.6 | SSP2 4.5 | SSP3 7.0 | SSP5 8.5 | Reference |
|--------------------------------|-------------|-------------|-------------|-------------|--------------------------|
| ACCESS-CM2 | Y | Y | Y | Y | Bi et al., 2020 |
| ACCESS-ESM1–5 | Y (40) | Y (40) | Y (40) | Y (40) | Ziehn et al., 2020 |
| BCC-CSM2-MR | Y | Y | Y | Y | Wu et al., 2019 |
| CanESM5 | Y (10) | Y (10) | Y (10) | Y (10) | Swart et al., 2019 |
| CESM2 | Y | Y | Y | Y | Danabasoglu et al., 2020 |
| CMCC-CM2-SR5 | Y | Y | Y | Y | Cherchi et al., 2019 |
| CMCC-ESM2 | Y | Y | Y | Y | Lovato et al., 2022 |
| CNRM-CM6–1 ¹ | Y | Y | Y | Y | Voltaire et al., 2019 |
| CNRM-CM6–1-HR ¹ | Y | Y | Y | Y | Voltaire et al., 2019 |
| CNRM-ESM2–1 | Y | Y | Y | Y | Séférian et al., 2019 |
| EC-Earth3 ² | Y | Y (20) | Y | Y | Döscher et al., 2022 |
| EC-Earth3-AerChem ² | N | N | Y | N | van Noije et al., 2021 |
| EC-Earth3-CC ² | N | Y | N | Y | Döscher et al., 2022 |
| EC-Earth3-Veg ² | Y | Y | Y | Y | Döscher et al., 2022 |
| EC-Earth3-Veg-LR ² | Y | Y | Y | Y | Döscher et al., 2022 |
| GFDL-ESM4 | Y | Y | Y | Y | Dunne et al., 2020 |
| HadGEM3-GC31-LL ³ | Y | Y | N | Y | Roberts et al., 2019 |
| HadGEM3-GC31-MM ³ | Y | N | N | Y | Roberts et al., 2019 |
| IPSL-CM6A-LR | N | Y | N | N | Boucher et al., 2020 |
| MIROC6 | Y | Y | Y | Y | Tatebe et al., 2019 |
| MPI-ESM1–2-HR ⁴ | Y | Y | Y | Y | Mauritsen et al., 2019 |
| MPI-ESM1–2-LR ⁴ | Y (30) | Y (30) | Y (30) | Y (30) | Müller et al., 2018 |
| NESM3 | Y | Y | N | Y | Yang et al., 2020 |
| NorESM2-LM ⁵ | Y | Y | Y | Y | Seland et al., 2020 |
| NorESM2-MM ⁵ | Y | Y | Y | Y | Seland et al., 2020 |
| UKESM1–0-LL | Y (30) | Y | Y (30) | Y | Sellar et al., 2019 |

increasing future greenhouse gas emissions were: SSP1 2.6, SSP2 4.5, SSP 3.7 and SSP5 8.5. For details about the SSPs, see Riahi et al. (2017). The model ensemble (Table 1) was created by extracting all available CMIP6 models with daily SST from 1995 to 2099 for each scenario from the Earth System Grid Federation database (Cinquini et al., 2014). This resulted in an ensemble with 16 models for SSP1 2.6, 17 for SSP2 4.5, 15 for SSP3 7.0 and 16 for SSP5 8.5. Models that were available with multiple spatial resolutions or with multiple sub-models, e.g. differing vegetation models, were treated as single models and the multi-model mean was taken in those cases.

Global climate models can have large biases in temperature, and a model of Pacific oyster recruitment using raw temperature values will result in present-day maps of recruitment that are not comparable between models. We therefore bias-corrected daily SST from the global models using the change-factor approach (Ekstrom et al., 2015). This bias correction approach requires a change-factor, defined as the difference between the observed and modelled SST, to be calculated for a baseline historical period and for each day and model grid cell. This daily change factor is then added to the projected model values, resulting in corrected values that will have a historical climatology that

matches observations. The change factors were derived by calculating daily climatologies for the period 1995–2014. Historical daily mean SST (at a horizontal resolution of 0.05 by 0.05°) for bias correction was acquired from the Operational Sea Surface Temperature and Sea Ice Analysis system (OSTIA) (Good et al., 2020) provided by the United Kingdom Met Office. Data was downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS: marine.copernicus.eu; <https://doi.org/10.48670/moi-00168>). Finally, the CMIP6 model change factors were regridded from their native model grids (which are typically close to 1° in resolution) to 0.05 by 0.05° resolution and added to the historical climatology to derive the bias-corrected future SST. This regridding used bilinear interpolation with spatial infilling using nearest neighbour in coastal regions, and resulted in model grids that had identical wet areas across all simulations.

High resolution bathymetry data was acquired from the General Bathymetric Chart of the Oceans. (GEBCO_2019 grid; Weatherall et al., 2015). Exclusive Economic Zone data was acquired from <http://www.marineregions.org/>.

Internal variability was assessed by using available climate models with multiple variants which have different pre-industrial initial conditions. In total there were five of these models: ACCESS-ESM1–5, CanESM5, EC-Earth3, MPI-ESM1–2-LR, UKESM1–0-LL. The use of multiple pre-industrial conditions, which arise naturally in the CMIP6 pre-industrial spin-up period, is the typical approach to understanding how internal variability influences future projections (Hawkins and Sutton, 2009).

2.3. Assessing relative contribution of scenario, model and internal variability to total uncertainty

We estimated the relative contribution of climate model uncertainty and internal variability to the overall uncertainty using a similar approach to that outlined by Hawkins and Sutton (2009). In this approach uncertainties in projected future changes are defined in terms of the intra-ensemble variances. For example, if the projections from a single model, when run with different pre-industrial starting points, typically show greater variance than the spread across models then we can conclude that internal variability is a greater source of variability, and vice versa. Calculating uncertainty due to internal variability requires a large ensemble, and we therefore only used the models ACCESS-ESM1–5, CanESM5, EC-Earth3 and UKESM1–0-LL, which had at least 10 ensemble members available. The relative contribution of internal variability was calculated for each climate model separately. The variables analysed were mean SST and oyster recruitment areas. For conciseness we only show the United Kingdom EEZ in the results section, as this has the largest area and is broadly representative of the study region.

To ensure we were assessing uncertainties in climatological changes, variables were first converted to 20-year rolling means and the change in the variable since the 1995–2014 climatological period was calculated. For each time-period t , scenario s and climate model m , we defined total uncertainty as follows:

$$T(t, s, m) = M(t, s) + I(t, s, m)$$

where $M(t, s)$ is the model uncertainty and $I(t, s, m)$ is the uncertainty due to internal variability. $M(t, s)$ was defined as the inter-model variance in the projected change for the scenario s . $I(t, s, m)$ was defined as the intra-model variance in the projected change for the scenario s . The fraction of variability due to internal variability was thus defined as $I(t, s, m)/T(t, s, m)$.

We chose to not explicitly assess the relative importance of scenario uncertainty as defined in prior studies (Hawkins and Sutton, 2009). This measure can be understood or misunderstood as a measure of whether uncertainty in future greenhouse gas emissions is more or less important than uncertainty in climate models. This can be assessed by calculating

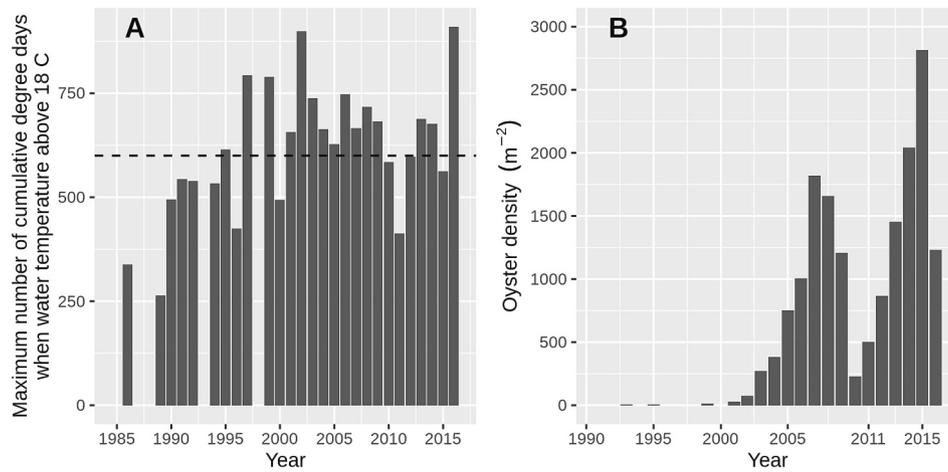


Fig. 1. A) Modelled hindcast time-series of Pacific oyster spawning occurrence. The bars represent maximum cumulative degree days attained by days when water temperature exceeded the spawning threshold of 18 °C near Sylt, Wadden Sea. The dashed line shows the 600°-days limit assumed to be required for spawning. Years without bars are those where temperatures never exceed 18 °C. In years with 600°-days when temperature exceeds 18C organisms can complete development and thus recruitment can occur. B) Pacific oyster density in Sylt, digitized from [Reise et al., 2017](#). The rapid expansion of oyster density followed the modelled transition from rare to frequent recruitment.

the variability across scenarios. However, this measure gives each scenario equal weighting, which can be interpreted as meaning equal likelihood. This appears unlikely, and the high emissions scenario SSP-5 8.5 is now viewed by many as improbable ([Hausfather and Peters, 2020](#)). Furthermore, the measure is highly sensitive to the number of scenarios used, how they are defined and the emissions levels in the lowest and highest emissions scenarios. Given scenario uncertainty can only be subjectively compared with model and internal variability uncertainty we did not explicitly compare them. However, for each scenario we calculated the standard deviation of the multi-ensemble, which can be compared with differences between scenarios to provide a subjective assessment of the relative importance of scenario uncertainty.

2.4. Aggregation to exclusive economic zones

Recruitment area in the exclusive economic zones (EEZ) of the United Kingdom, Ireland, the Netherlands, Germany, and Denmark are likely to increase across the 21st Century. We therefore aggregated modelled recruitment area for each projected year. Pacific oysters have habitat requirement of a bathymetry of less than 40 m, and they prefer hard seabed substrate. In the study region, suitable bathymetric areas can be mapped with high confidence; however there is insufficient data for hard substrate to be mapped confidently ([Wilson et al., 2018](#)). While recruitment of Pacific oysters is influenced by substrate type ([Carrasco et al., 2019](#)), there is evidence of Pacific oysters living in a broader range of habitats ([Lejart and Hily, 2011](#); [Mortensen et al., 2017](#)). We therefore

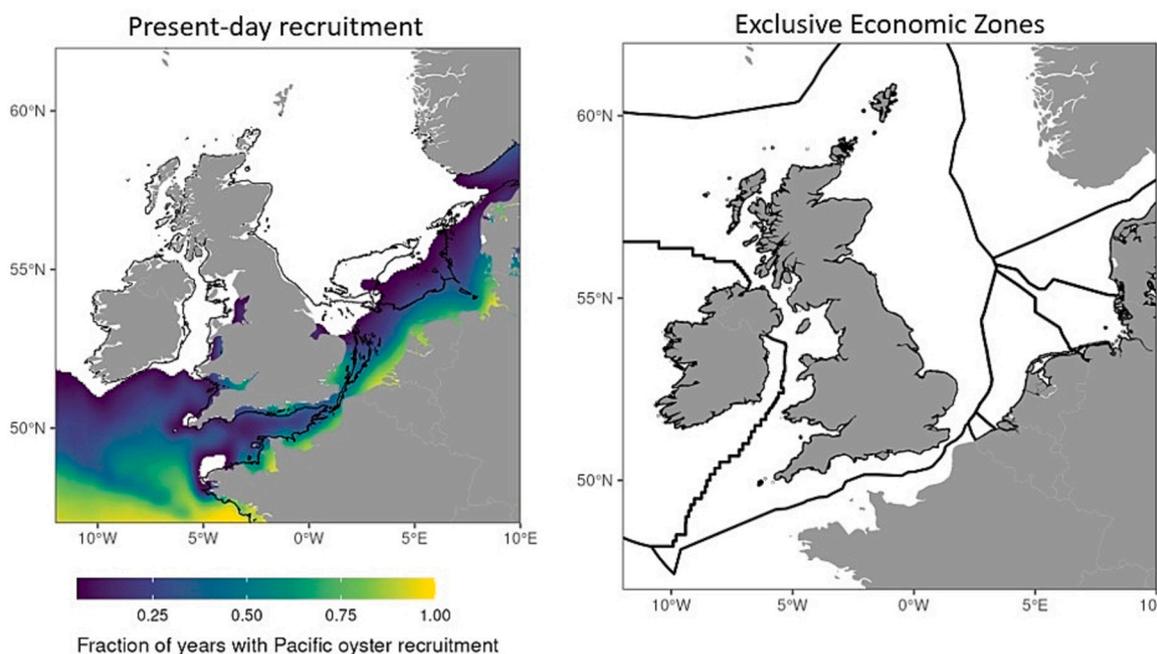


Fig. 2. Left: Baseline (1995–2014) proportion of years when the temperature conditions can lead Pacific oyster recruitment to occur. Recruitment was modelled using a temperature-dependent development model. Regions where predicted recruitment did not occur are displayed in white. It is assumed that the recruitment occurs where the bathymetry is shallower than 40 m. The 40 m isobaths are shown with black lines. Deeper regions are only shown to make future changes more legible. Right: map of Exclusive Economic Zones on the north westEuropean shelf. EEZs are outlined with black lines.

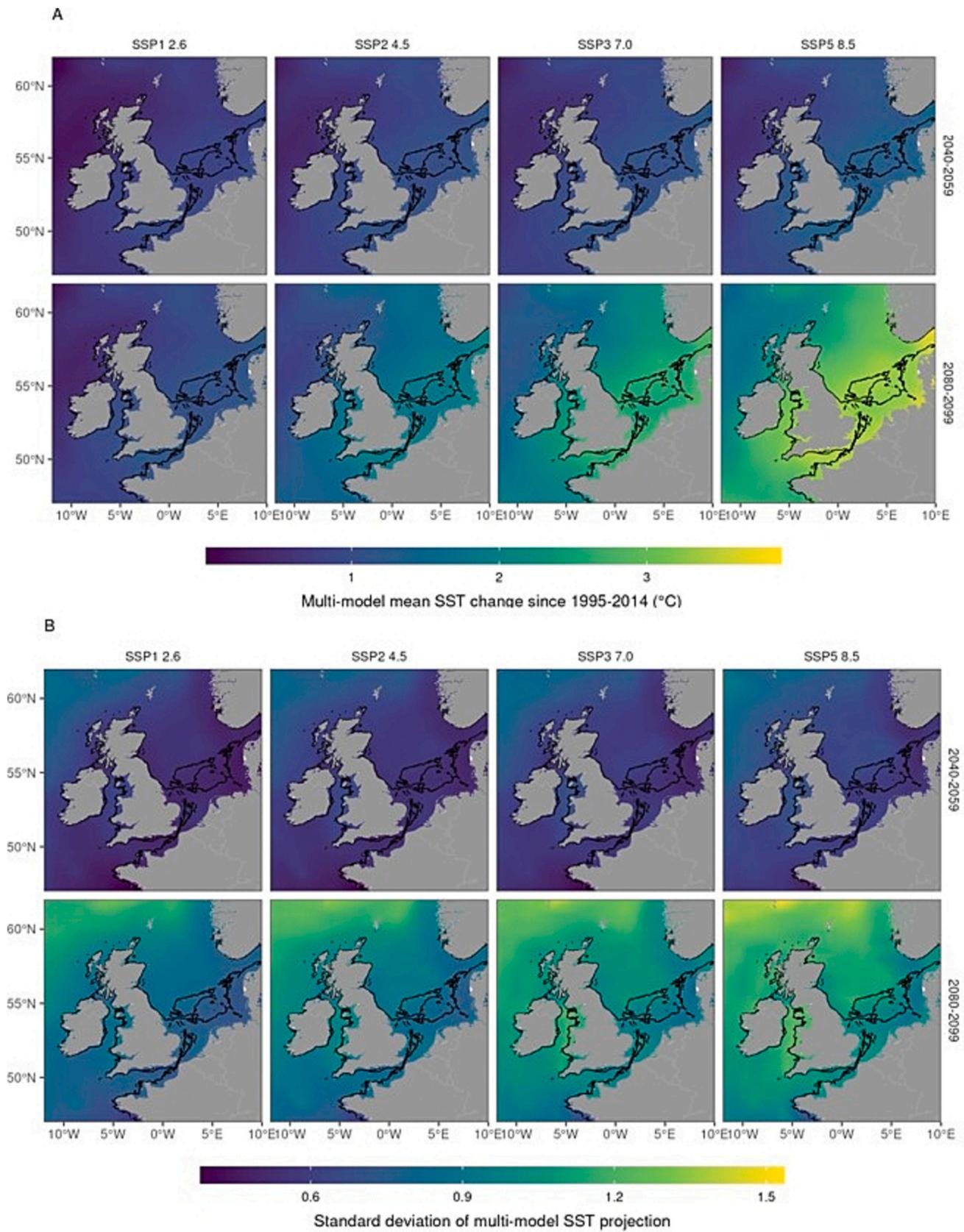


Fig. 3. A) Projected change of the multi-model ensemble mean of annual SST across the CMIP6 ensemble between 1995 and 2014 with respect to the middle (first row) and the end (second row) of the 21st Century. B) Standard deviation of the projected SST from the multi-model ensemble for the middle and end of the 21st Century.

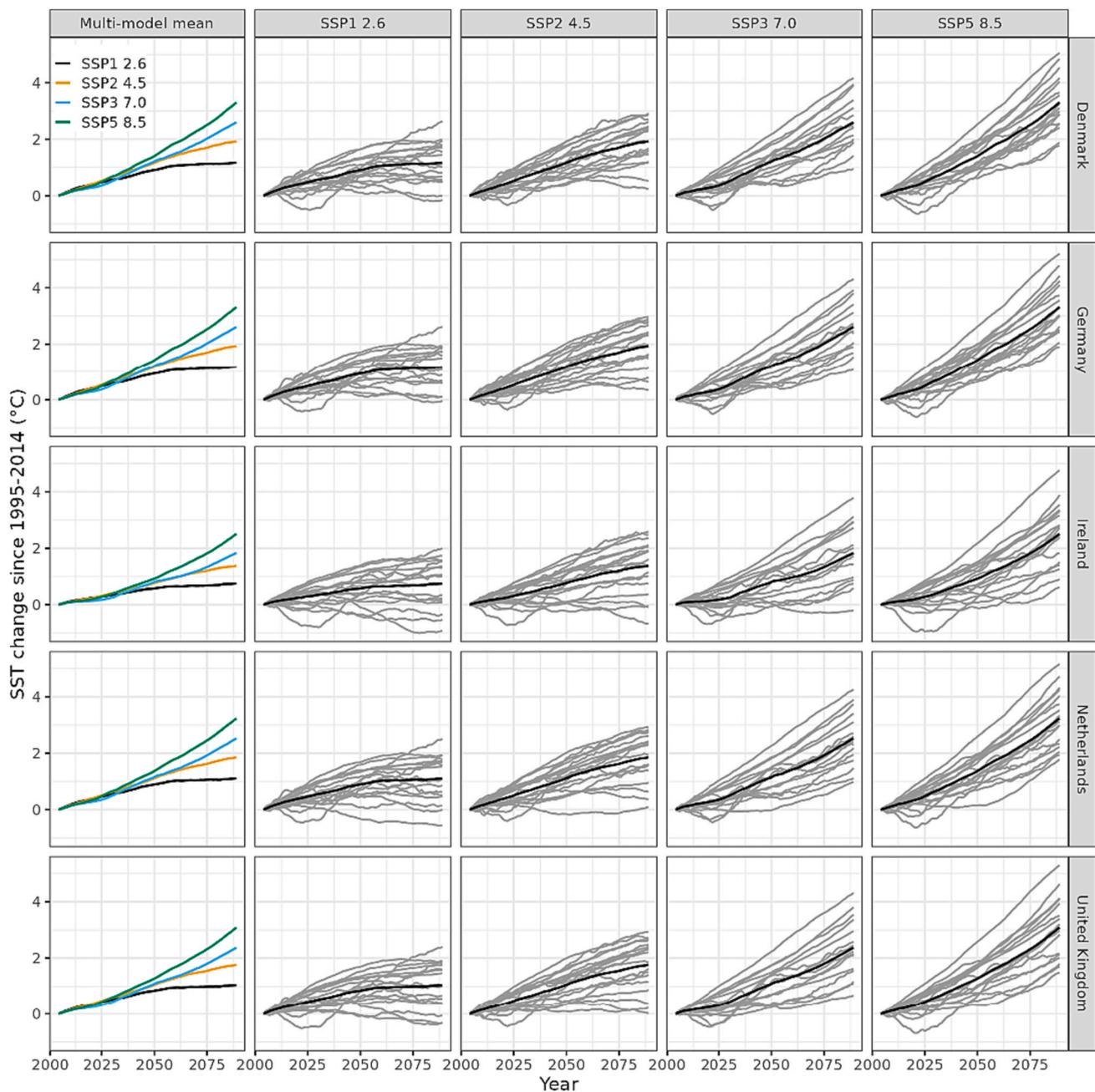


Fig. 4. Multi-model ensemble projections of change in SST in EEZs since 1995–2014 using a 20-year rolling average temperature. Each grey line represents the mean change projected by a single CMIP6 model, averaged over the EEZ. The solid black line represents the multi-model average. The middle year of the 20-year period is used, i.e. the final year shown is 2090 and this represents the years 2080–2099.

simplified the habitat requirements to only relate to bathymetry. We defined the recruitment area in each EEZ for each year as the total area of sea shallower than 40 m that has temperature conditions that permit recruitment in that year.

3. Model validation

The primary aim of the study is to assess the role of uncertainty in future climate influences ecological projections with Pacific oysters used as an example species. We argue above that invasions of species can be projected using a model that relates recruitment to temperature alone, and a similar approach was used by King et al. (2021). While the model acts in a similar way to a typical species distribution model, the validation of the model cannot be carried out in a similar fashion due to the

existence of “false positives” in distribution records of Pacific oysters. For example, Pacific oysters have been observed as far north as the Shetland Islands in the United Kingdom. However, it appears implausible that these observations are from sustainable wild populations given the environmental conditions in the region. This is clear given that Pacific oysters were absent in the Wadden Sea in the 1990s when environmental conditions were much more conducive to Pacific oyster growth than in the present-day Shetlands.

We therefore chose to validate by asking whether it can explain historical invasions of Pacific oysters. This was carried out using the extensive time series of Pacific oyster abundance in Sylt. Using data covering the years 1991 to 2016, Reise et al. (2017) showed that Pacific oyster density was very low prior to 2000, with a rapid expansion in the years that followed. This was potentially caused by a sharp transition

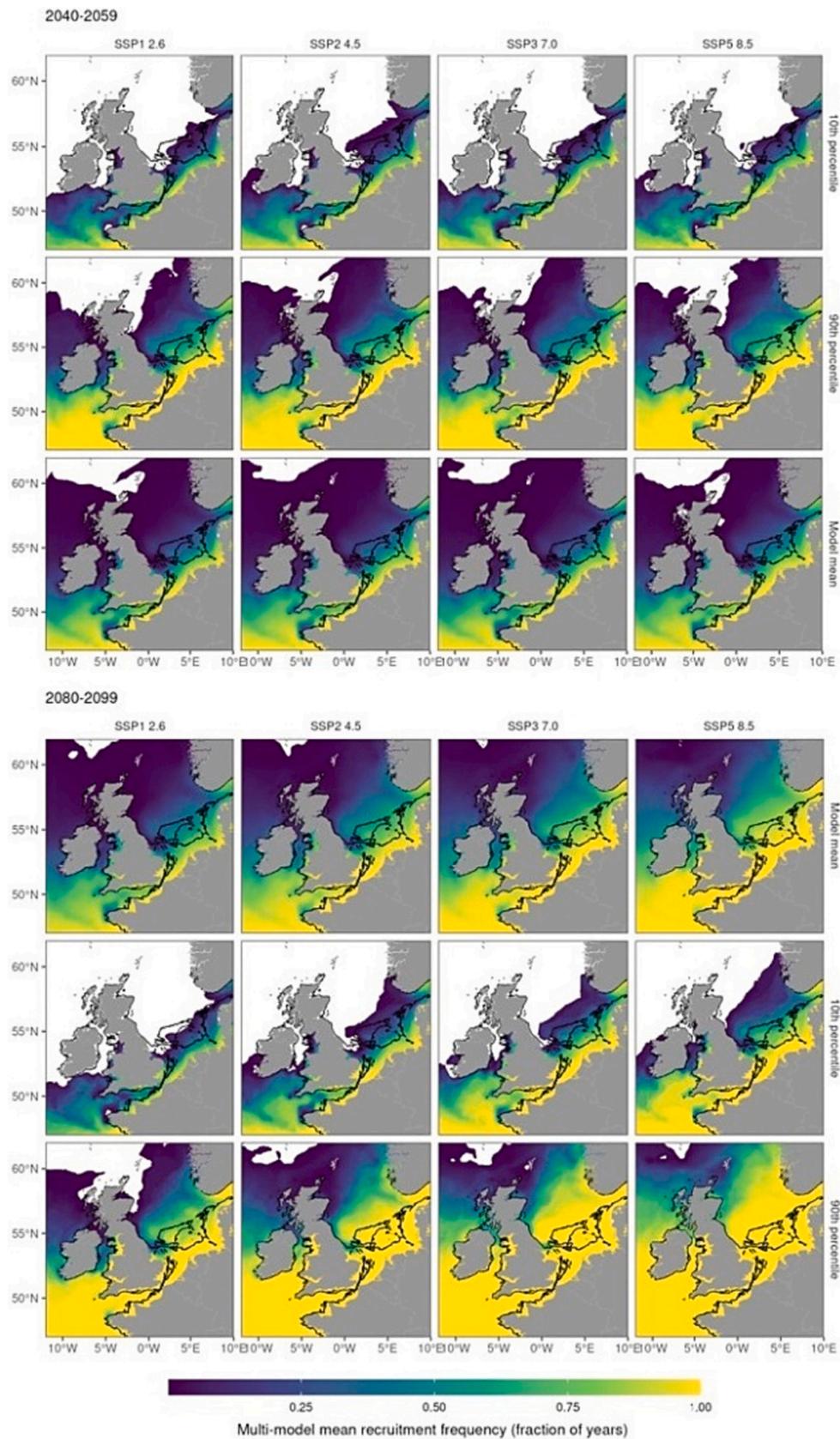


Fig. 5. Projected multi-model ensemble mean, 10th and 90th percentiles of recruitment frequency of Pacific oyster in the middle and end of the 21st Century in four climate scenarios; regions where simulated recruitment did not occur are displayed with white, as in Fig. 2 for the baseline (1995–2014) recruitment frequency.

Table 2

Summary of projected changes in Pacific potential oyster recruitment area (10,000 km²) exclusive economic zones (EEZs) across four climate change scenarios. The table summarizes changes between the baseline period 1995–2014 and the future periods 2040–2059 and 2080–2099. For each scenario the average projected change from a multi-model ensemble is shown, with the 5th to 95th percentile shown in brackets.

| EEZ | Period | SSP1 2.6 | SSP2 4.5 | SSP3 7.0 | SSP5 8.5 |
|----------------|---------|----------------|----------------|-----------------|-----------------|
| Total Shelf | 2040–59 | 56.4 (25.1) | 62.9 (23.8) | 57.9 (26.1) | 69.2 (25.4) |
| | 2080–99 | 72.3 (40.3) | 99.1 (33.1) | 110.2 (25.5) | 122.7 (17.2) |
| Denmark | 2040–59 | 10.3 (5) | 12.6 (5) | 12.8 (6) | 14.6 (5.1) |
| | 2080–99 | 12.5 (7.8) | 17.7 (6.2) | 20.9 (3.3) | 22.3 (1.3) |
| Germany | 2040–59 | 9.5 (3.2) | 10.7 (2.8) | 10.5 (3.4) | 11.5 (2.2) |
| | 2080–99 | 9.8 (4.7) | 12.6 (2.9) | 13.7 (1.3) | 14.1 (0.7) |
| Ireland | 2040–59 | 0.8 (0.7) | 1.1 (0.9) | 1.1 (1.1) | 1.5 (1.3) |
| | 2080–99 | 1.4 (1.4) | 3 (2.1) | 3.7 (2.2) | 4.9 (1.9) |
| Netherlands | 2040–59 | 13.8 (6.5) | 16.1 (5.5) | 15.9 (6.1) | 17.7 (4.2) |
| | 2080–99 | 14.6 (8.3) | 19.6 (4.8) | 21.7 (1.9) | 22.5 (0.9) |
| United Kingdom | 2040–59 | 21.7 (11.2) | 25.6 (12) | 25.9 (13.5) | 30.3 (12) |
| | 2080–99 | 26.4 (17.8) | 39.8 (16.8) | 48 (11.1) | 55.1 (6.8) |

from rare to frequent Pacific oyster recruitment. We therefore tested whether the recruitment model used here predicted such a transition. We did this by tracking the number of degree-days experienced by Pacific oysters each year from 1991 to 2016, and assessing whether the cumulative total exceeded 600°-days and temperature exceeded 18 °C, thus enabling spawning. While, our model requires a further 225°-days for full recruitment, we found that this always occurred in the region once spawning had occurred. This enabled us to develop a time series which showed whether temperatures exceeded 18 °C and the maximum number of cumulative degree days animals were exposed to when this temperature threshold was exceeded. Daily temperatures were interpolated to the Sylt location using interpolated values from the OSTIA SST product listed above.

4. Results

The model hindcast of recruitment frequency at Sylt indicates that a pronounced shift occurred at the start of the 20th Century (Fig. 1). Spawning only occurred in 3 of the years between 1985 and 1999. In contrast, it occurred in 8 consecutive years from 2001 to 2008. This modelled shift coincides with the historical timing of the observed large increase of abundance in the region. This indicates that the model can credibly be used to project shifts in recruitment and distribution.

The historical baseline (1995–2014) for the model runs is shown in Fig. 2. Modelled present-day recruitment is largely restricted to the southern North Sea and a portion of the southern coast of the United Kingdom. The multi-model ensemble shows that rising temperatures are likely to cause a large northward shift in Pacific oyster recruitment.

The multi-model ensemble shows that SST is projected to increase in the study region between the historical baseline and the end of the 21st century (2080–2099) (Fig. 3 and Fig. 4). There is high agreement between models that SST will increase across the study region under the SSP2 4.5, SSP3 7.0 and SSP5 8.5 scenarios, by the multi-model ensemble spread (Fig. 4). Warming is not geographically uniform across the ensemble. The north-west Atlantic portion of the domain, including the western coast of Ireland and the northwestern United Kingdom, sees visibly lower warming. Notably there is less agreement between models that that SST will rise in the Irish EEZ and the expected temperature rise is also slightly lower. This is reflected by the much larger standard

deviation in projected SST across models in the north-west of the model domain (Fig. 3). Projected increases of SST from multi-model means in the EEZ typically vary from 1 °C in SSP1 2.6 to 3 °C in SSP5 8.5; however, under the high emissions scenario SSP5 8.5 there is a spread of approximately 3 °C in the temperature increase.

The projected warming across scenarios causes large projected increases in Pacific oyster recruitment area across the EEZs (Fig. 5, Table 2). Under all scenarios, the majority of the southern North Sea, along with the southern and western coast of England and Wales, will see oyster spawning occurring in the majority of years by the end of the 21st Century. Recruitment is projected to become frequent, i.e. occurring in the majority of years, on the southern Irish coast by the end of the century under each scenario but it is only expected to become frequent on the northern coast under the higher emissions scenarios SSP3 7.0 and SSP5 8.5. In contrast to the other regions, Pacific oyster recruitment is projected to remain infrequent on the Scottish coast, even under the more extreme climate change scenario SSP5 8.5. Projected infrequency of recruitment in the northwest part of the region is due to lower projected increase in temperature (Fig. 3), but also to their lower temperatures in the present-day.

As expected, the Pacific oyster recruitment is highly scenario-dependent (Fig. 6). The total increase in recruitment area, i.e. the total area where recruitment is projected to occur, in the United Kingdom EEZ is approximately two times higher under the high-emissions scenarios SSP5 8.5 than in the low-emissions scenario SSP1 2.6 in the United Kingdom's and Danish EEZ's, while for the Irish EEZ it is approximately four times higher.

Truly objective comparisons of scenario uncertainty with model uncertainty are not possible for multiple reasons. The relative importance of scenario uncertainty is highly influenced by what we deem to be a plausible range of future emissions. Assessments of historical predictions of future energy consumption and emissions make it clear that the probability of future emissions scenarios cannot be quantified in a credible way (Smil, 2000). However, we can make approximate comparisons if we make assumptions about the likely range, say the 95% percent confidence interval. This can tell us the standard deviation, i.e. 0.5 times the difference between lower and upper value in the interval, under the assumption possibilities are normally distributed. This allows us to compare the standard deviations from the multi-model ensemble with our assumed credible ranges for scenarios. If we assume that future emissions will probably be between SSP1 2.6 and SSP2 4.5, i.e. there is a 95% probability of emissions being between these scenarios, then we can conclude that climate model uncertainty is more important than scenario uncertainty. Across the full region and most EEZs, the difference between recruitment areas in 2080–99 is smaller than the inter-model standard deviation in either SSP1 2.6 or SSP2 4.5. However, if we assume that we cannot place credible possibilities on future emissions, and assumed that there is a 95% probability of future emissions between SSP1 2.6 and SSP5 8.5, scenario uncertainty would be comparable to model uncertainty.

Analysis of intra-model differences in the recruitment projections indicate that climate model internal variability can have a large influence, as shown by Fig. 7, which displays the intra-model spread in how much recruitment area will change across the north west European shelf. The total range of projections for the mid-century shows a large spread for most of the models, with the intra-model range in the projected change in recruitment area varying by more than a factor of two for four out of six of the models assessed. This intra-model spread reflects that seen in SST (Supporting Materials Fig. S1–24), which has high uncertainty in mid-century due to internal variability. For example, under SSP3 7.0 the range in projected SST increase is similar or larger to the average projected increase for most of the models for the United Kingdom EEZ (Fig. S18).

The comparison of variability due to climate model uncertainty and internal climate variability shows that internal variability is a highly important source of variability at the start of the time series and becomes

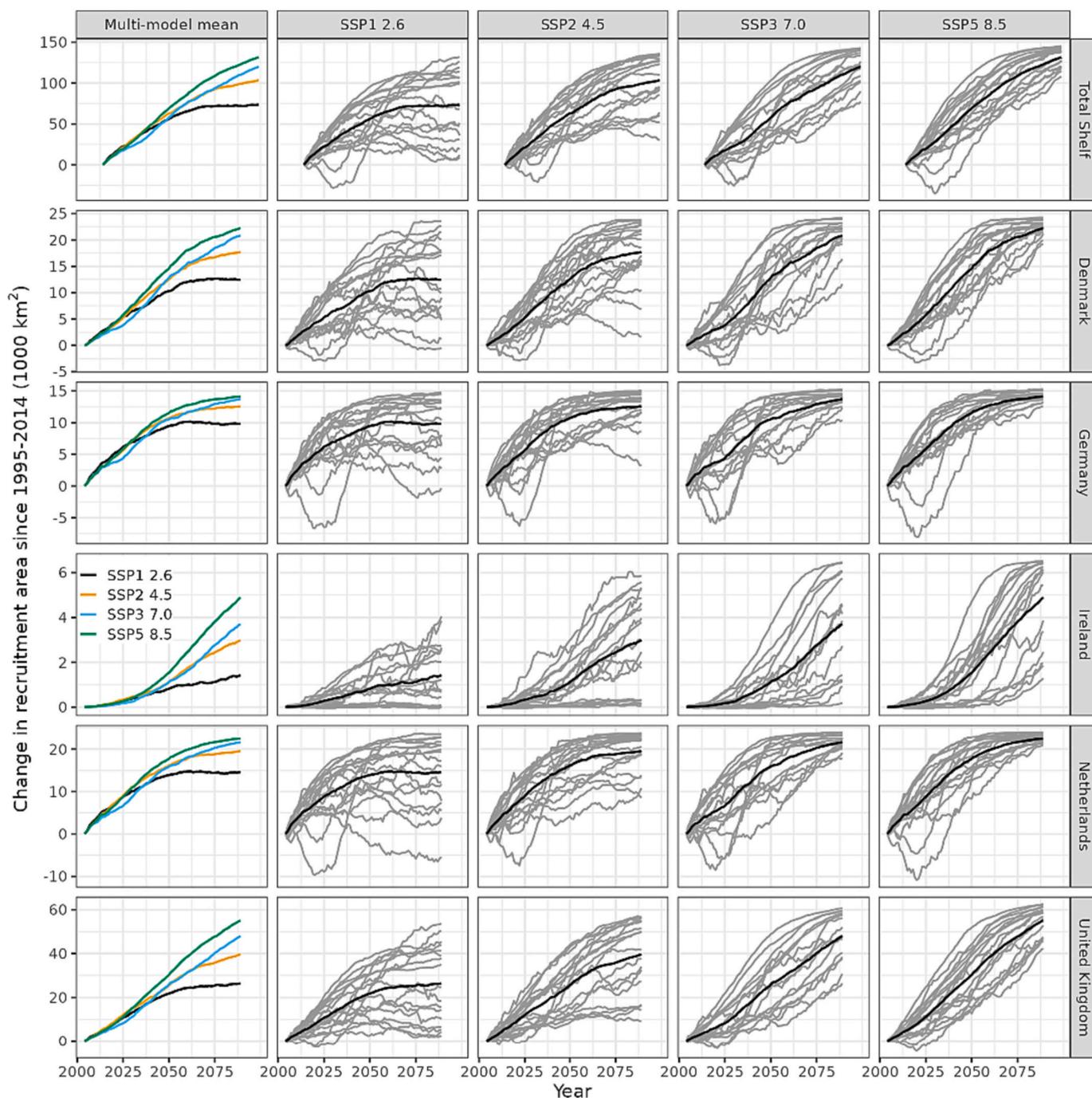


Fig. 6. Multi-model ensemble projections of change in Pacific oyster recruitment area in EEZs since 1995–2014. Recruitment area is defined as the area where Pacific oyster recruitment occurs. Each grey line represents the model-mean recruitment area for the recruitment model using an individual CMIP6 model. The solid black line represents the multi-model average.

increasingly unimportant over time (Fig. 8). The ensemble indicates that internal climate variability may be approximately 40% of that due to climate model uncertainty on a 20-year time scale. However, this declines significantly over the 21st Century with a value of approximately 25% by mid-century. By the 2080–99 period, climate model uncertainty dominates, climate internal variability is less than 10% of climate model uncertainty. Notably, internal variability varies significantly across models, with its importance varying by more than a factor of two across models. This highlights that the uncertainty within individual models can be similar or greater than that from a multi-model ensemble when predicting mid-century changes in temperature or recruitment area.

5. Discussion

We have shown that future climate change is expected to cause sea temperatures to rise across the northwest European shelf, which will result in the continued northward expansion of the non-native Pacific oyster. However, the inherent uncertainties in these projections will pose multiple challenges for ecosystem management. Importantly, we have highlighted that an ensemble and scenario approach is critical if we are to assess climate impacts on future distributions of species and that natural climate variability places significant limits on our ability to make confident and accurate medium-term predictions.

This is the first work to partition climate uncertainty in projections of

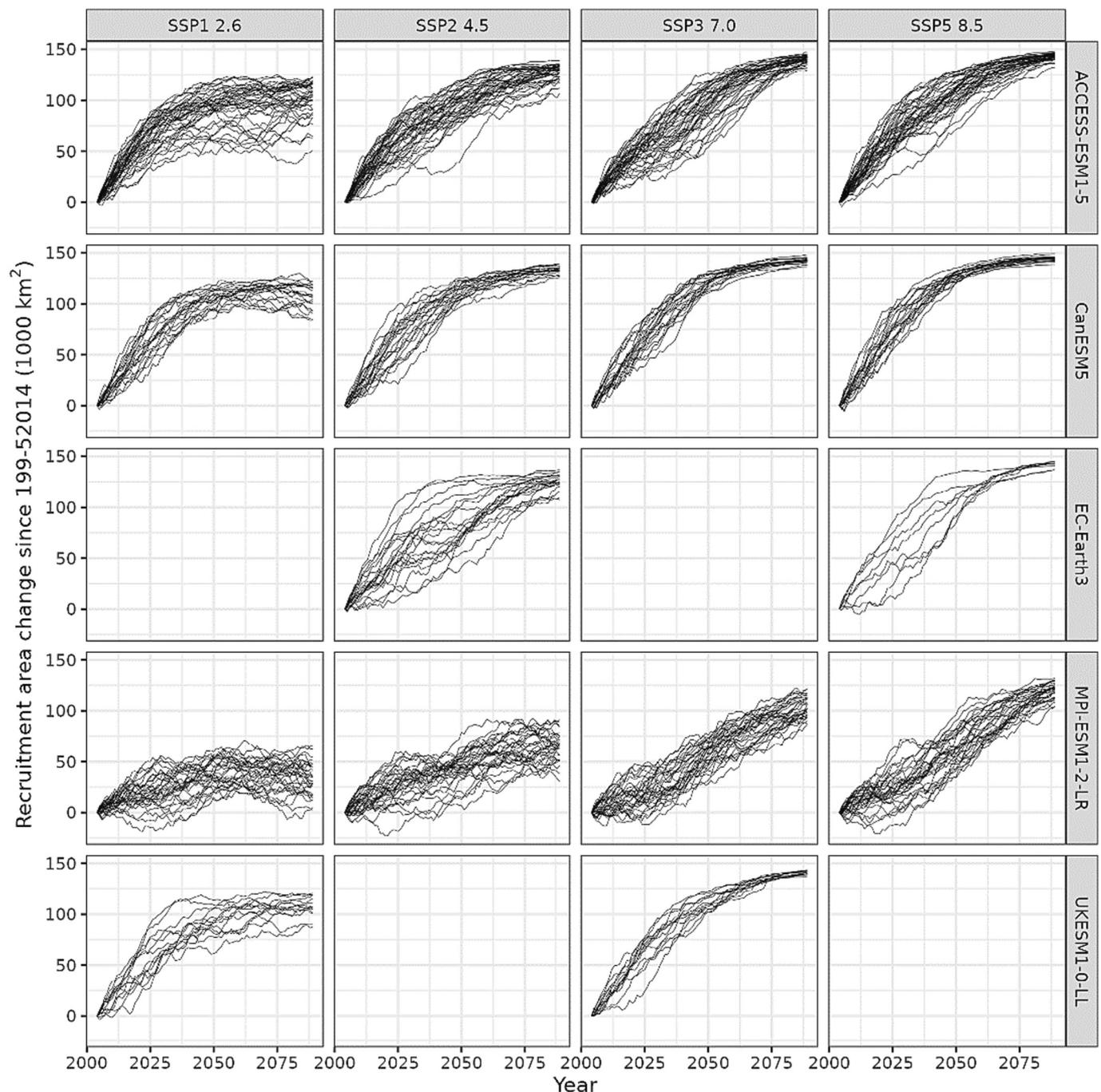


Fig. 7. Multi-model ensemble projections of change in Pacific oyster recruitment area across the NW European Shelf. Rows represent separate models, and columns represent different climate change scenarios. Each line represents a projection where the ecological model is driven by a different variant, i.e. a model run with different pre-industrial starting conditions, of the named global climate model.

either sea surface temperature or Pacific oyster recruitment in the region. However, we can compare our results with previous work partitioning uncertainty in projections of air temperature (Hawkins and Sutton, 2009), which should be comparable due to the close coupling of air and sea surface temperature (Liss and Duce, 2005). In line with our work, uncertainty due to internal variability is approximately the same as that due to model uncertainty using a 20-year lead time (Hawkins and Sutton, 2009). Similarly, model uncertainty dominates internal variability when projecting air temperatures in the United Kingdom by the end of the century. The close coupling of air temperature and sea surface temperature means that marine scientists can draw on the now relatively extensive literature assessing the role of internal variability in air

temperature when considering whether it should be considered for their study area and species. For example, Lehner et al. (2020) mapped the relative contribution of internal variability, model uncertainty and scenario uncertainty based on CMIP6 output.

We have only considered climate uncertainty in this study. However, ecological uncertainty should be considered by future work. A key ecological uncertainty in understanding the present and future geographic distribution of Pacific oysters is the temperature threshold for spawning, which we assumed to be 18 °C. The experimental work of Mann (1979) and field observations (Dutertre et al., 2009) make it clear that spawning threshold is likely to be at most 18 °C, but there is some evidence it could be as low as 16 °C (Ruiz et al., 1992). Future

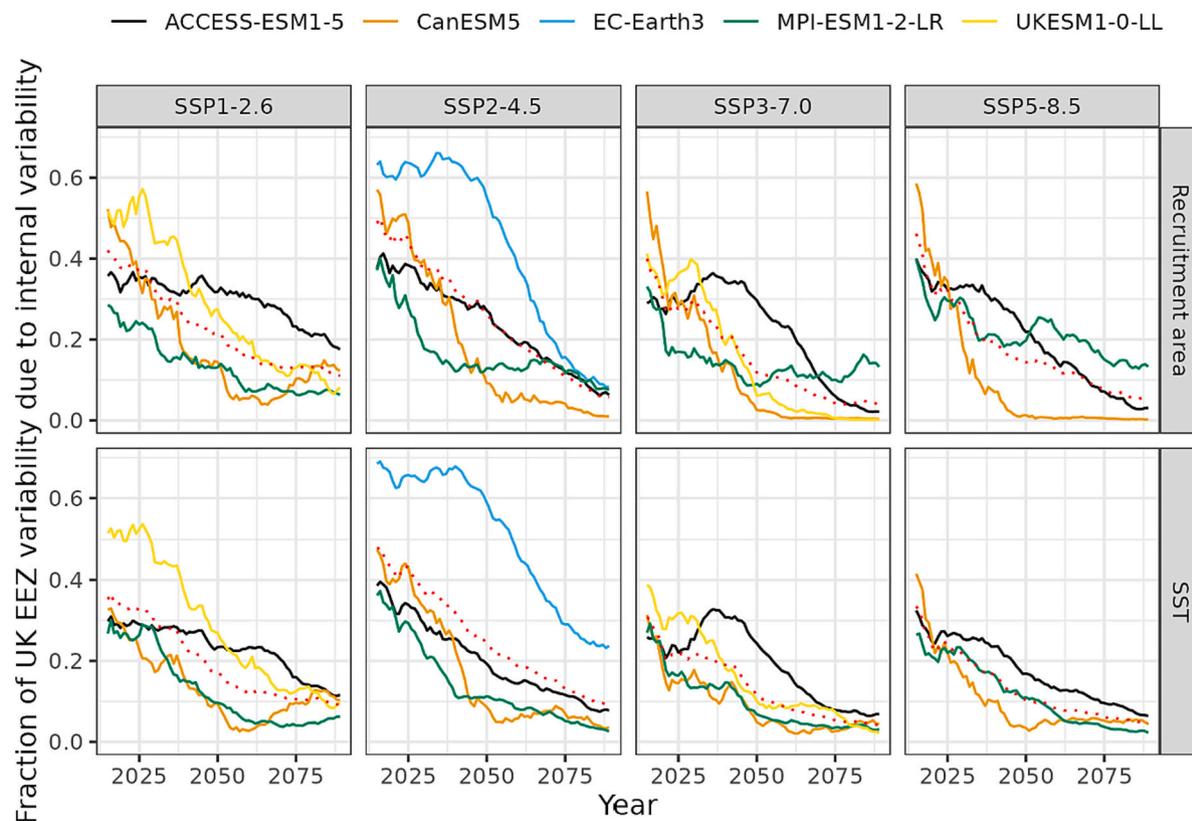


Fig. 8. Fraction of variability in projected Pacific oyster recruitment area and SST in the United Kingdom EEZ due to internal climate variability. For each scenario and time-period, total variability was defined as the sum of the between-model variance and the intra-model variance for each time-period. Variances were calculated using 20-year rolling averages of area and SST. The dashed red-line indicates the mean fraction across the models assessed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

experimental work is therefore critical if we are to map present-day spawning regions with higher confidence. Ecological uncertainty has partly been considered by Jones et al. (2013), who used a multi-model ensemble of presence-based species distribution models to project changes in Pacific oyster occurrence. However, statistical modelling approaches based on occurrence data have potentially insurmountable problems due to the false positives that result from escapes from aquaculture sites, as indicated by the very high northern limit modelled by Jones et al. (2013) who used this approach. A notable result of our analysis is that modelled Pacific oyster recruitment is not expected to be possible on the northern Scottish coast in future, even under the most extreme climate change scenario. Recent work has found this species occurring in the Firth of Forth on the east coast of Scotland (Smith et al., 2015), with an occurrence at a surprisingly high latitude in the Shetland Islands (Shelmerdine et al., 2017). However, whether these populations were introduced and are sustainable has not been established. Our modelling results question whether such populations could ever be viable, in particular for the Shetland Islands where present day SST never exceeds 14 °C.

An open question is whether uncertainties in regional ecological projections can be reduced in future through improvements in global climate models (Séférian et al., 2020) or the use of regional general circulation models (Giorgi and Gutowski Jr, 2015) or biogeochemistry models (Holt et al., 2016). Global climate models currently have low spatial resolution (approximately 1° by 1°), but improvements to this should result in more credible projections across Europe (Iles et al., 2020). Furthermore, this low spatial resolution can result in a poor representation of river flows and interconnection between water bodies such as the Baltic and North Seas, which can be partly resolved by using what are called dynamically downscaled regional models (Flaounas et al., 2013; Hermans et al., 2020). Dynamical downscaling works by

forcing a higher-resolution and more complex regional model by boundary conditions from a global model. While dynamical downscaling of global can add significant value, in the case of the model used here or any model that is strongly influence by sea surface temperature, they are likely to provide similar results to global models due to methodological issues. Dynamical downscaling typically is carried out by forcing regional ocean models with air temperature from a global climate model (Holt et al., 2016). Sea surface temperature in a dynamically downscaled model will therefore be strongly correlated with air temperature in the global climate model, and therefore the global climate model's sea surface temperature.

The approach taken by this study was to understand the uncertainties that exist within a large ensemble of global climate models and how they cause uncertainties in future Pacific oyster recruitment trends, and we did not aim to account for climate model skill when assessing uncertainties. However, analysis of the latest-generation of climate models has identified the existence of a “hot-model” problem, wherein many models are thought to be warmer than plausible, and therefore multi-model projections should account for climate model-skill (Hausfather et al., 2024). Future work should therefore consider how to weight climate models for ecological projections based on regional performance, which has the potential to reduce the uncertainty shown here.

Our work highlights the importance of internal variability of climate models for medium-term ecological projections. It is commonly argued that this type of uncertainty is irreducible (Hawkins et al., 2016; Marotzke, 2019) because of the challenges of assessing whether global climate model runs with different pre-industrial starting points are more or less credible than each other. This must be considered when assessing the implications of medium-term projections, as the uncertainty due to internal variability is additive to that from model and scenario uncertainty. While the role of internal variability has been discussed in prior

work on ecological projections (e.g. Freer et al., 2018), this is, to our knowledge, the first study to quantitatively assess the impact of internal variability on projections for marine species, and future work needs to expand to other species and geographic regions. Critically, the model used here only considers temperature, and it is unclear how important internal variability is in projections of critical parameters such as primary production, which typically display higher overall uncertainty than temperature in global models (Kwiatkowski et al., 2020; Tagliabue et al., 2021).

This work points towards a more robust approach to assessing the ecological sustainability of Pacific oyster aquaculture development. It has been previously argued that the model used here can be used to assess whether Pacific oyster aquaculture sites pose a risk of leading to successful invasions of wild sites (Syvret et al., 2008). A more robust approach would account for potential future increases in temperature on relevant timescales, which would cover the development and sustained growth of aquaculture in areas of concern. This would fit in the developing paradigm of “climate-smart” marine spatial planning and regulation where marine spatial plans are not only effective in the present-day but are also effective in potential future climates (Queirós et al., 2021). Critically, highly accurate forecasts or predictions at a 20-year time scale are not possible, and ecosystem managers should anticipate a range of credible scenarios, from one where temperatures potentially decline slightly to one where they by over 1 °C in this time scale. Given the probabilistic nature of future warming demonstrated here, regulators will need to consider whether they need to take a cost-benefit or a precautionary approach to regulation.

6. Conclusions

It is essential to think about the future of species' geographic distributions in terms of potential scenarios and not individual predictions where possible. While it is currently not plausible to construct highly credible confidence intervals for future ecological changes, we can get clear indications of them by using multiple climate models and by assessing the extent to which internal variability, i.e. natural climate variability exhibited by the model, limits our ability to make confident projections. If ecological projections shift to this approach, we can increase both our confidence in the direction of change expected in future, but also what magnitude of change we may realistically have to adapt to.

CRedit authorship contribution statement

Robert J. Wilson: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Susan Kay:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Stefano Ciavatta:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2024.102537>.

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