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Pacific oyster (*Crassostrea gigas*) growth modelling and indicators for offshore aquaculture in Europe under climate change uncertainty

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ABSTRACT

Aquaculture development in Europe, while critical to the European Union (EU) Blue Growth strategy, has stagnated over the past decades due largely to high competition for space in the nearshore coastal zone among potential uses and the lack of clear priorities, policy, and planning at EU and national scales. Broad Marine Spatial Planning, including the designation of Allocated Zones for Aquaculture, requires spatial data at the corresponding broad spatial scale, which has not been readily available, as well as model projections to assess potential impacts of climate change. Here, daily chlorophyll-a, water temperature, salinity, and current speed outputs from a marine ecosystem model encompassing the coastal North East Atlantic, the North Sea, and the Mediterranean Sea (the pan-European POLCOMS-ERSEM model configuration) are used to drive a Dynamic Energy Budget growth model of Pacific oyster (*Crassostrea gigas*). Areas broadly suitable for growth were identified using threshold tolerance range masking applied using the model variables mentioned above, as well as bathymetry data. Oyster growth time series were transformed into simplified indicators that are meaningful to the industry (e.g., time to market weight) and mapped. In addition to early-century indicator maps, modelling and mapping were also carried out for two contrasting late-century climate change projections, following representative concentration pathways 4.5 and 8.5. Areas found to have good oyster growth potential now and into the future were further assessed in terms of their climate robustness (i.e., where oyster growth predictions are comparable between different future climate scenarios). Several areas within Europe were highlighted as priority areas for the development of offshore Pacific oyster cultivation, including coastal waters along the French Atlantic, the southern North Sea, and western Scotland and Ireland. A large potential growth hot spot was also identified along northwestern Africa, associated with a cool, productive upwelling coastal zone. The framework proposed here offers a flexible approach to include a large range of ecological input data, climate and ecosystem model scenarios, aquaculture-related models, species of interest, indicator types, and tolerance thresholds. Such information is suggested to be included in more extensive spatial assessments and planning, along with further socioeconomic and environmental data.

1. Introduction

A diverse marine aquaculture sector has been linked with achieving a more sustainable food system, with both environmental and human health benefits when best practices and appropriate site selection are applied (Schubel and Thompson 2019). Although Europe is one of the largest markets for seafood globally, it remains highly dependent upon international sources to meet demand. Over 60% of seafood consumed by European Union member states are supplied by non-European imports (STECF 2018). At the same time, the proportion of European seafood supplied by aquaculture remains much lower than ratios observed internationally, at approximately 20% compared with over 50%, and with much lower growth rates (FAO, 2018; STECF 2018). Throughout Europe, a major bottleneck in issuing new licenses has

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constrained the aquaculture industry for over a decade. This results in large part from the lack of clear prioritization, planning, and management, as well as the high level of competition for space in the already-overcrowded coastal zones (Hofherr et al. 2015). For Europe to achieve its desired "Blue Growth" strategy, of which aquaculture development is a key component (European Commission 2017), such issues need to be addressed.

Offshore cultivation has been cited as potentially having the means to overcome space limitations in nearshore areas in Europe and around the world (European Commission 2017; Gentry et al. 2017). Technological advances (Buck and Langan 2017; Landmann et al. 2019), as well as experimental results (e.g., Pogoda et al. 2011, 2012, 2013), indicate the increasing feasibility of cultivating various species in the offshore realm, which in most cases is exposed to strong waves, high current velocities, and strong winds, among other challenges. The potential to combine aquaculture with, for example, offshore wind energy generation in coproduction scenarios (Buck et al. 2008; Jansen et al. 2016; Buck and Langan 2017; Buck et al. 2018) and within multi-species facilities offshore, including integrated multi-trophic aquaculture (Troell et al. 2009; Korzen et al. 2016; Buck and Langan 2017), further adds to the appeal with respect to dual purpose investments or leveraging existing resources. Furthermore, recent studies point to a suite of additional benefits of offshore aquaculture, ranging from reduced pathogen and pollutant exposure (Buck et al. 2005; Pernet et al. 2018) to greater production and carrying capacity (Di Trapani et al. 2014).

Pacific oyster (*Crassostrea gigas*) has been considered for offshore farming in several European countries (e.g., France (Palmer et al. 2020; Glize et al. 2010; Mille et al. 2008), Germany (Buck and Langan 2017; Pogoda et al. 2011; Buck et al. 2006), and the UK (Ferreira et al. 2009)). Although offshore cultivation remains experimental at these sites, results to date have been promising, with a growth rate often outpacing that in nearby coastal farms. At several French Atlantic sites, *C. gigas* growth was found to be more than 15% and as much as 100% higher offshore than at a reference intertidal site, varying between animal ploidy and life stage (i.e., spat versus adults) considered (Mille et al. 2008; Glize et al. 2010). Likewise, similar or higher survival rates and oyster quality indices (ratio of flesh to total animal weight) have also been documented from oysters grown in offshore cages in Germany (Pogoda et al. 2011; Buck et al., 2020), in France (Glize et al. 2010), as well as in New Zealand (Heasman et al. 2020 under review). Despite such promise, substantial investments would be required to install and maintain infrastructure, as well as for ongoing operations, and the offshore environment remains largely uncharted territory from an aquaculture industry perspective (Gentry et al. 2017).

Adequate planning and policy, including the designation of Allocated Zones for Aquaculture (AZAs) based on state-of-the-art science, have been recognized as being crucial to the success and sustainability of such investments and to the aquaculture industry in general (e.g., European Commission 2013; Macias et al. 2019). Spatialized data, across a range of scales and for various parameters, is needed to inform Marine Spatial Planning (MSP), including the identification of potential AZAs and for farm site selection therein (Lester et al. 2018; Falconer et al. 2019). To assist policy and planning endeavors at the European scale, broad, large-scale tools and information can provide insight for high-level planning and policy stages and must complement and inform more local site-specific work. Nonetheless, there is a general lack of relevant international-scale studies and data at the corresponding spatial scale needed for broad, long-term policy and planning decisions (Falconer et al. 2019).

For sustainable decision making by the aquaculture industry, it is also crucial to consider the challenges and ongoing impacts of climate change on the coastal ocean (FAO, 2018; Bindoff et al. 2019). There is much uncertainty surrounding what climate change will look like where and when, as well as how ecosystems and society will respond, and the numerous possible related feedbacks (Moss et al. 2010; Gattuso et al. 2015; Freer et al. 2018). Satellite remote sensing offers a rich, spatiotemporal component to study ecosystem processes in the ocean and coastal zone, and has been usefully applied to aquaculture in several instances (e.g. Radiarta and Saitoh 2009; Thomas et al. 2011; Kapetsky et al. 2013; Thomas et al. 2016; Aura et al. 2016; Brigolin et al. 2017; Snyder et al. 2017; Barillé et al. 2020; Palmer et al. 2020; Porporato et al. 2020). However, long-term planning and zone or site selection also benefits from the consideration of what future conditions might look like, impossible through the use of remote sensing data alone, and requiring the coupling of climate and ecosystem models to investigate the influence of predicted future environmental changes on aquaculture-related indicators. Modelling that considers multiple, diverse scenarios can help us to understand the potential magnitude of future climate change impacts and uncertainty (Bindoff et al. 2019), in addition to providing rich spatial datasets necessary for MSP as described above, and has therefore been chosen for use in this work.

The present study offers a framework for decision support in planning aquaculture zoning by comparing the potential for offshore Pacific oyster growth across the Northeast Atlantic, North Sea, and Mediterranean Sea under conditions representative of the early 21st century and two contrasted end-of-century climate change scenarios. Areas characterized by good growth and likely to be more stable under climate change uncertainties are highlighted for priority consideration by the industry. An ecophysiological oyster growth model driven by ecosystem model outputs was used to map growth potential in offshore areas identified to be within the bivalve's tolerance range. The use of coarse spatial resolution (0.1°) data over a large, continental-scale geographic region allows the identification of broad spatial trends and hot spots for industry planning and policy purposes, within which more fine-resolution, detailed work could be undertaken for specific site selection.

2. Materials and methods

2.1. Input data: POLCOMS-ERSEM

The Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS; Holt and James 2001) and the European Regional Seas Ecosystem Model (ERSEM; Butenschön et al. 2016) are coupled to model the three-dimensional hydrodynamic-biogeochemical conditions of the coastal and shelf zones of the North East Atlantic, the North Sea, and the Mediterranean Sea. The former provides the physical drivers to the latter, biogeochemical model. In addition to POLCOMS-ERSEM-modelled chlorophyll-a concentrations (chl-a) from the three largest of the four possible phytoplankton functional types (picoplankton (< 2 μm) are not filtered by Pacific oyster and were therefore not included), current speed, salinity, water temperature, and the bathymetry of the model domain were also used for the selection of areas where offshore oyster aquaculture would be feasible (see 2.2).

All POLCOMS-ERSEM data were at a 0.1° spatial and a daily temporal resolution, for the specific years for which in situ oyster growth data were also available, and for an early-century (2000–2004) reference period and two contrasted climate change scenarios for a late-century (2090–2099) period (CERES, 2018). Future climate change scenarios considered here are based on two of the Representative Concentration Pathways (RCPs) in standard use by the Intergovernmental Panel on Climate Change (IPCC), RCP 4.5 and RCP 8.5, and driven using the global climate Max-Planck-Institute Earth System Model, Low Resolution (MPI-ESM-LR). Meteorological conditions at the sea surface were taken from the 0.11° regional model Rossby Centre Regional Atmospheric Model, version 4, driven by the Max-Planck-Institute Earth System Model, Low Resolution (MPI-ESM-LR-RCA4) and river inputs were taken from the European domain of the HYdrological Predictions for the Environment (*E*-HYPE), also driven by MPI-ESM-LR. The model outputs were compared to satellite measurements of sea surface temperature and chlorophyll concentration for the period 1998–2015 (CERES, 2018). Temperature outputs corresponded well with satellite observations and were 0.5–1 °C higher in the North Sea and western

Mediterranean, less than satellite observations by a similar amount elsewhere, and with Spearman correlation of greater than 0.9 in all regions. Modelled chlorophyll values exceeded satellite observations by up to 2 mg m^{-3} in spring, but showed good agreement in other seasons; the model captures the spatial and temporal variation of chlorophyll concentration, with Spearman correlation 0.6 overall, and 0.5 in the North Sea (CERES, 2018).

Under RCP 4.5, radiative forcing is projected to stabilize at 4.5 W m^{-2} by ~2050, corresponding to a moderate, roughly business-as-usual scenario. Under RCP 8.5, radiative forcing is projected to be more extreme, exceeding 8.5 W m^{-2} by 2100 (Moss et al. 2010). These two scenarios were chosen to give a range of possible future climate response: RCP 8.5 is at the upper end of plausible carbon concentrations, while RCP 4.5 is more moderate, while still showing a clear climate signal. Projected global temperature rise under RCP 4.5 is approximately 2 °C (IPCC 2013), in line with the goal set in the 2015 Paris Agreement.

A representative year from each of the three periods or scenarios was produced for oyster tolerance range masking and growth modelling, described below, by taking the average of all years for the given period/scenario.

2.2. Tolerance range-based masking of unsuitable areas

As for a number of other cultivated species (e.g., Gentry et al. 2017; Kapetsky et al. 2013), tolerance thresholds and ranges of certain variables and conditions have been reported in the literature, within which Pacific oyster can typically thrive. Prior to mapping growth potential and related indicators, areas identified through such criteria as being unsuitable for Pacific oyster growth were masked out and not included in further mapping. Only areas for which associated POLCOMS-ERSEM data values were within the oyster tolerance ranges of chlorophyll-a, water temperature, salinity, and current speed, as well as the technical bathymetry limitations for mooring infrastructure, reported in Table 1 for at least 95% of the given year were retained (as per Kapetsky et al. 2013). This was done for each period (early- and late-century) and scenario (RCP 4.5 and 8.5) considered. An example of combining the criteria for these variables to produce the overall suitability masking is provided for the early-century reference period in Fig. 5.

2.3. Dynamic energy budget (DEB) modelling

Dynamic Energy Budget (DEB) theory (Kooijman 2010) provides a generic (i.e., non-species-specific) approach to mechanistically model the flow of energy through individual organisms, from the ingestion and assimilation of food, through somatic maintenance and growth, to reproduction. Here, we make use of the original parameterization for Pacific oyster (*Crassostrea gigas*) put forth by Pouvreau et al. (2006), and further updated by Bernard et al. (2011) and Thomas et al. (2016), whereby water temperature influences energy flow and allocation at all stages, and food abundance further impacts ingestion according to a calibrated coefficient (the half-saturation ingestion coefficient; X_k). In the offshore environments considered in the current work, the oysters are always submerged in the water (i.e., 100% immersion time). The impact of turbidity on oyster growth is assumed to be negligible offshore (Gernez et al. 2014), and the half-saturation ingestion coefficient through which high concentrations of inorganic sediment modulate ingestion, as put forth by Thomas et al. (2016), X_{ky}, is therefore not included in the current modelling. A DEB model schematic can be found in the supplementary information of this article (Fig. S1), and parameterization (except for X_k) and equations are those reported in the supplementary information of Thomas et al. (2016).

Here, two datasets reporting the results of rare in situ offshore Pacific oyster growth experiments were used to calibrate the X_k coefficient and to validate the model outputs. The first dataset was compiled over two separate growing seasons (2008 and 2010) from the offshore Bourgneuf Bay, France, through experiments performed by a regional aquaculture organization (*Syndicat Mixte pour le Développement de l'Aquaculture et de la Pêche en Pays de la Loire, SMIDAP)* (Glize and Guissé, 2009; Glize et al. 2010). The second, reported in Pogoda et al. (2011), is from three sites and two years (2004 and 2007) in the German Bight area of the south-eastern North Sea (Fig. 1). French data for adult and spat oysters from 2010 (for which most data were available) were used in the optimization-calibration process, and all other data were used to validate calibration results using the metrics of mean bias (Eq. 1) and absolute and relative root mean square error (RMSE; Eqs. 2, 3). In each, *M* refers to the DEB-modelled shell length, *O* to the in situ-observed shell length, and *n* to the number of observations.

$$\text{Mean bias} = \frac{1}{n}\sum_{1}^{n}(M-O) \tag{1}$$

$$\text{RMSE} = \sqrt{\frac{\sum_{1}^{n}(M-O)^2}{n}} \tag{2}$$

$$\text{Rel.RMSE}\ (\%) = \text{RMSE}/(max(O)-min(O)) \times 100 \tag{3}$$

Model outputs are dry flesh mass (DFM) and shell length, which is then transformed to total weight for use in the current work using a robust empirical relationship (Palmer et al. 2020) between the two variables obtained from the IFREMER in situ monitoring network, *Réseau d'observations conchylicoles* database (RESCO; Fleury et al. 2018). Outputs were generated for the same daily time step as the input chl-a and water temperature data, and mapped on the same spatial grid (i.e., 0.1°). For each of the three periods/scenarios, models were initialized to begin on April 1 of that year, with adult DFM = 0.3 g and shell length = 5.7 cm, and spat DFM = 0.05 g and shell length = 1.9 cm.

2.4. Oyster growth aquaculture indicators

Aquaculture industry-relevant information was then extracted from each of the adult and spat oyster total weight growth curves output from the DEB modelling described above for each pixel. The three-dimensional data (latitude, longitude, time) was thereby transformed into two-dimensional (latitude, longitude) indicator maps for each of the periods and scenarios considered. Two types of adaptable indicator are presented here as examples: (1) the date at which a target weight is reached for a given production year, and (2) the total weight achieved by a date of interest. Although any target weight and date of interest can be selected, we have chosen to demonstrate the date at which minimum market weight for an adult Pacific oyster (30 g) is achieved, the date at which spat reach size T20/T25 (14 g, a popular size for resale to grow out to market weight; Palmer et al. 2020), and the total adult weight achieved by December 1, which is the main European market, corresponding to the French tradition of eating oysters as part of Christmas and New Year celebrations. Mapped indicators, or combinations of indicators, can then be used to assess which areas have the highest growth potential.

Table 1
Pacific oyster tolerance thresholds and ranges, and corresponding references, for several variables used to constrain the area suitable for cultivation, within which relative growth potential was assessed.

Variable	Documented tolerance/feasible range	Reference
Bathymetry	< 200 m	Gentry et al. (2017)
Chl-a	> 1 mg m^{-3}; > 2 μm particles	Barillé et al. (1993)
Current speed	Current 0.1–1 m s^{-1}	Kapetsky et al. (2013)
Salinity	15–45 psu	Nell and Holliday (1988)
Water temperature	3–35 °C	Bayne (2017)

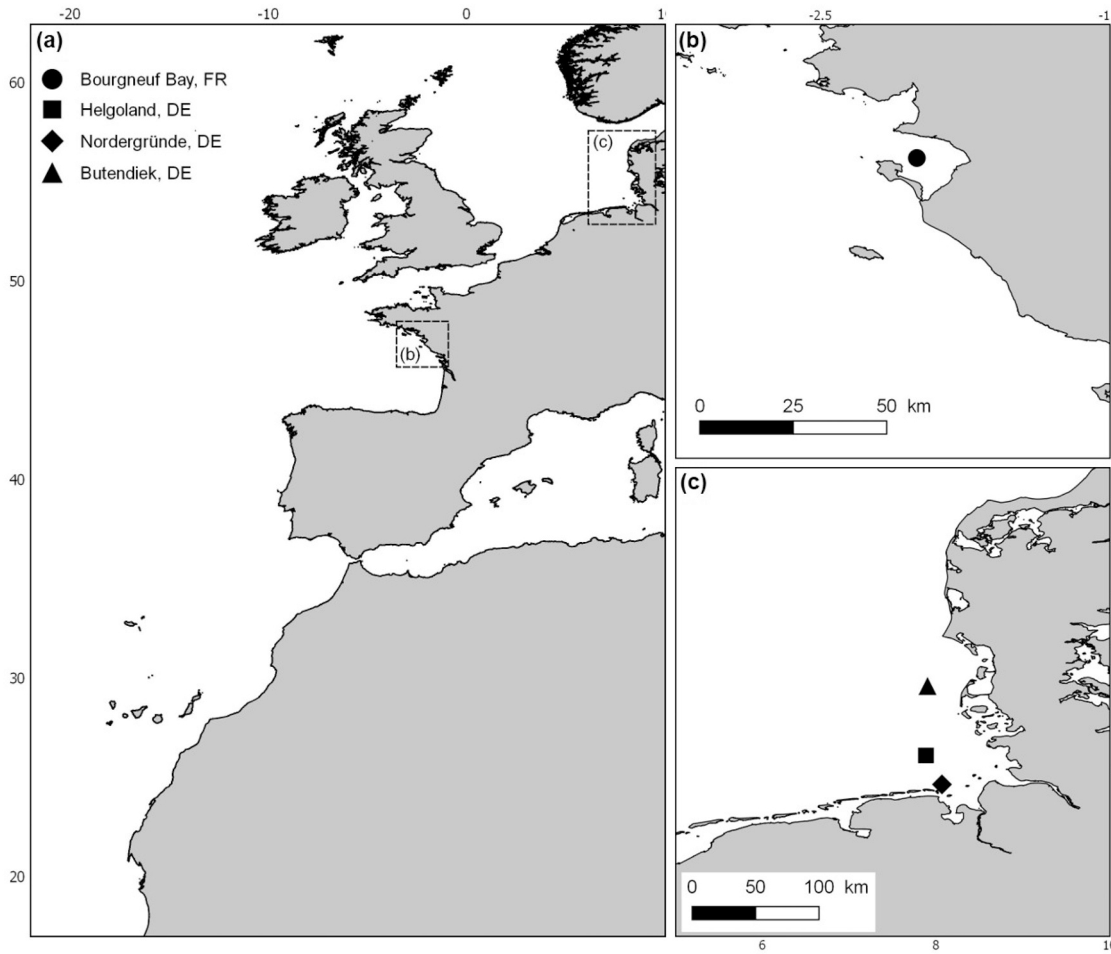

Fig. 1. Model domain (a) and locations of offshore Pacific oyster growth data used for Dynamic Energy Budget model calibration ((b) Bourgneuf Bay, France) and validation ((b) Bourgneuf Bay, and (c) German sites, Helgoland, Nordergründe, and Butendiek).

The modelling framework proposed here also considers the variability between late century RCP scenarios to identify climate robust zones. Porporato et al. (2020) demonstrated the interest of adding an uncertainty analysis to assess the robustness of site selection for finfish cultivation in the Mediterranean. In this work, we propose a simple metric to assess the areas where growth potential will remain consistent in the future. A stability index was calculated here as the absolute difference between indicator values for the two future scenarios normalized to the indicator value itself (Eq. 4):

$$\Delta X_{RCP}\text{stability index} = |X_{RCP\ 8.5} - X_{RCP\ 4.5}| / max(X_{RCP\ 8.5}, X_{RCP\ 4.5}) \quad (4)$$

where $X_{RCP\ 8.5}$ is the resulting indicator value under the RCP 8.5 end-of-century scenario and $X_{RCP\ 4.5}$ is the value of the indicator obtained under the RCP 4.5 end-of-century scenario.

We used five classes to map the variability in future oyster growth: 0.00–0.05 (very stable), 0.05–0.10 (stable), 0.10–0.15 (medium stability), 0.15–0.20 (low stability), and > 0.20 (very low stability). The most “climate robust” areas were those with stability index values of between 0.00 and 0.10, corresponding to both high and consistent growth projections in light of the uncertainties inherently associated with climate prediction and ecosystem modelling. This chosen threshold value could be adjusted by the user depending on their needs and the indicator in question.

Future stability was determined for areas already exhibiting good growth potential for the early-century reference period. In the current example, for total adult oyster weight attained by December 1, this means that future growth variability was only determined for areas where adults reach at least the 30 g minimum market weight in the 2000–2004 reference period. A framework for decision-making based on current and future oyster growth indicators is proposed in Fig. 2. The first step considers whether an area corresponds to good growth (according to user-defined criteria depending on the indicator) under current environmental conditions. The second step identifies areas for which growth either remains good or improves relative to current conditions in at least one of the future scenarios. The last step uses the stability index (eq. 4) to identify areas that are similar under the two distinct climate change scenarios. These can be given further priority in selecting zones for industry development (Fig. 2).

In addition to maps of current and future growth potential for the full study area, the future growth potential of several example areas within the Biscay Bay on the French Atlantic coast is compared statistically with current growth potential through ANOVA (by rank when normality and equal variance assumptions fail) and subsequent Tukey (or Mann-Whitney, if following Kruskall-Wallis ANOVA by rank) pairwise comparison.

3. Results

3.1. Biogeochemical climate change scenarios

The future changes in chl-a and water temperature predicted by the model POLCOMS-ERSEM in the two climate change scenarios are presented in Figs. 3 and 4 respectively. Both RCP 4.5 and 8.5 scenarios consistently predict an overall warming trend, which is nonetheless

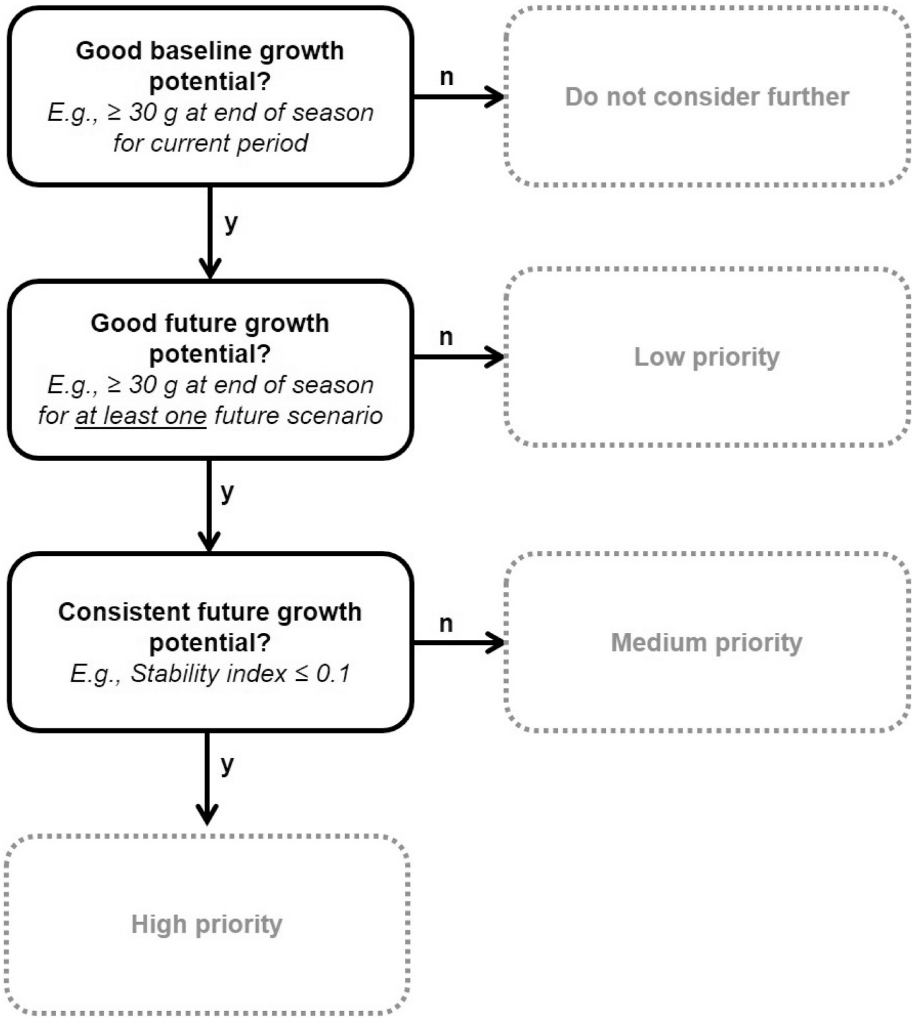

Fig. 2. Schematic of decision-making framework incorporating maps of current and future oyster growth indicators to identify climate-robust hot spots as potential AZAs. As an example, criteria based on one indicator, the adult weight attained by December 1st, are shown at each step.

higher under the more extreme RCP 8.5 scenario. Furthermore, in areas currently characterized by warmer waters (e.g., lower latitudes; the Mediterranean Sea; Fig. 3a), we see greater warming, particularly under RCP 8.5 (Fig. 3c).

Chl-a concentration is, unsurprisingly, generally higher in the near-coastal areas, with certain regions standing out as being exceptionally productive in this sense (e.g., off the coasts of Western Sahara and Mauritania in Africa; Fig. 4a). Unlike the consistent trend observed for water temperature, however, whereas mean annual chl-a concentration is projected to increase under climate change in some areas, it is also projected to decrease over large regions of the study area, notably from the Bay of Biscay on the French Atlantic coast northward (Fig. 4b, c). Furthermore, the change in the mean annual chl-a is not always greater under the more extreme RCP 8.5 scenario than under the RCP 4.5 scenario. Rather, for some areas (e.g., the west coast of Portugal) the area or magnitude of increasing chl-a is greater under RCP 4.5 than under RCP 8.5, and vice versa (e.g., the coasts of Western Sahara and Mauritania and the Mediterranean).

3.2. Delimitation of tolerance range

The results of the binary, threshold-based masking of unsuitable area for the early-century reference period are presented in Fig. 5. Very similar results were also obtained and used for each of the two late-century climate change scenarios. Although water temperature (3–35 °C; Bayne 2017) and salinity (15–45 psu; Nell & Holliday,1988) were also considered, these were not found to limit the suitable area in terms of Pacific oyster tolerance ranges for any of the periods or scenarios considered here. Further narrowing the salinity range to 25–40 psu was likewise not found to limit the suitable area. We see that, although current speed is the primary limiting factor for much of the study area (Fig. 5c), bathymetry (Fig. 5a) and chl-a concentration (Fig. 5b) ranges also serve to limit some areas. This is notably the case in the Mediterranean Sea, with bathymetry alone found to further limit the potential of offshore Pacific oyster cultivation along the north coast of Spain and northern and western Portugal at the coarse spatial resolution of the data used in this exercise. Areas where conditions fall within all tolerance ranges are highlighted in the cumulative constraint mask (Fig. 5d). Within these areas, the growth potential was simulated and mapped by using the DEB model.

3.3. Dynamic energy budget (DEB) calibration and validation

Only one parameter of the DEB model was required to be tuned. The half-saturation coefficient (X_k) was determined through the regression-based optimization using data on offshore adult and spat growth in Bourgneuf Bay, France, in 2010. The resulting value was found to reasonably model adult and spat oyster growth observed in situ for a separate year (2008) in Bourgneuf Bay, as well as that measured in situ at three German sites in 2004 and 2007 (Pogoda et al. 2011), across the

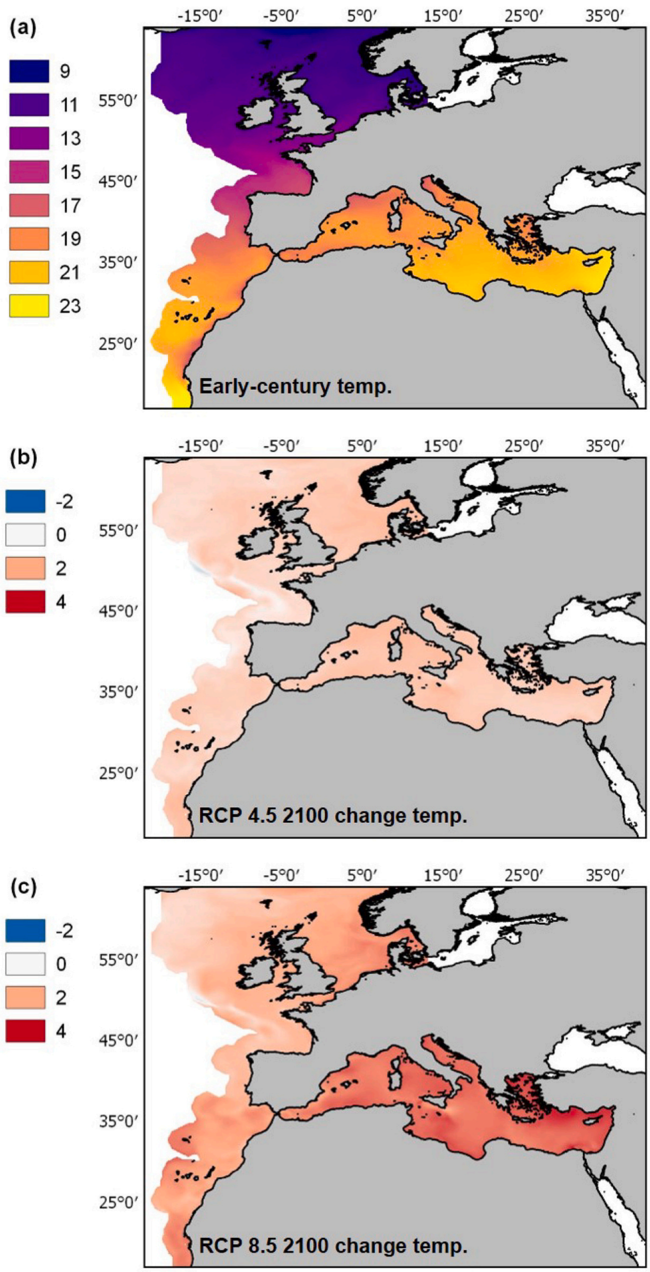

Fig. 3. (a) Mean annual water temperature (°C) for the early-century reference period, 2000–2004, and changes in mean annual water temperature (°C) under the emissions scenarios (b) RCP 4.5 and (c) 8.5 by late-century (2090–2099). The white areas are outside the model domain.

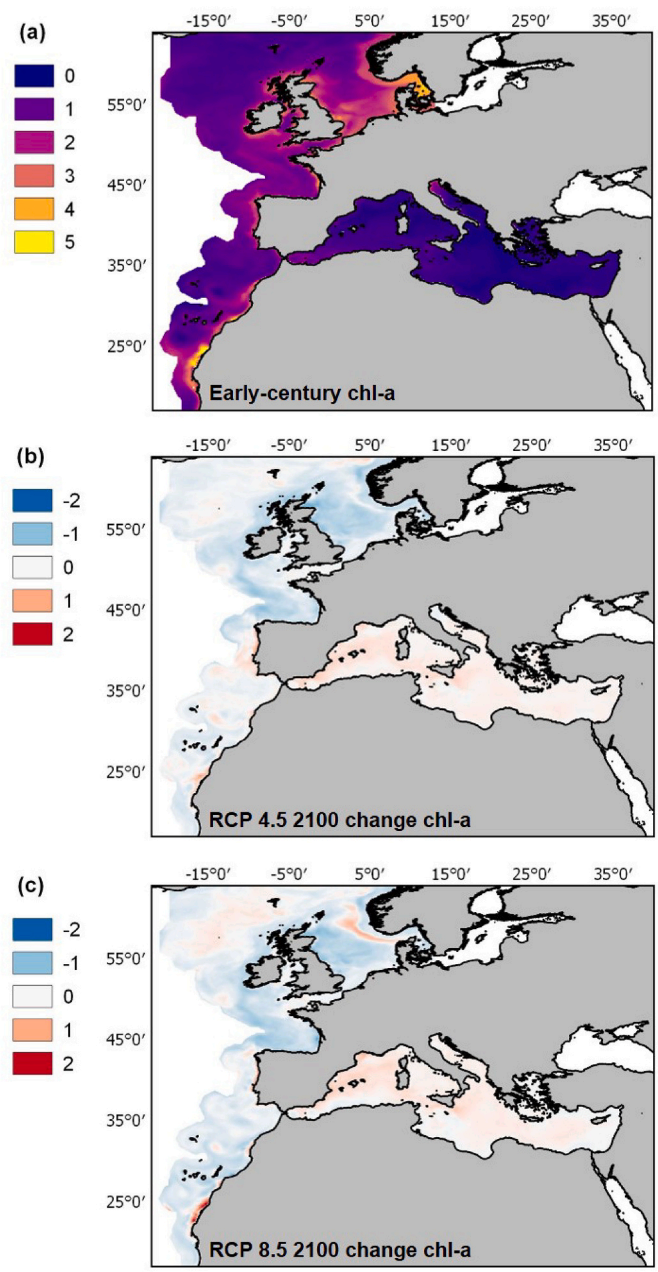

Fig. 4. (a) Mean annual chlorophyll-a (mg m^{-3}) for the early-century reference period, 2000–2004, and changes in mean annual chlorophyll-a (mg m^{-3}) under the emissions scenarios (b) RCP 4.5 and (c) 8.5 by late-century (2090–2099). The white areas are outside the model domain.

full in situ size range (Fig. 6). Shell length measurements ranged from less than 3 to almost 10 cm, corresponding to total weights ranging between approximately 2 and 75 g. Note that in situ measurements from the start of the growing seasons were used to initialize the DEB model, and so are not included in Fig. 6.

3.4. Oyster growth indicator mapping

3.4.1. Current spatial trends and hot spots

Within the suitable area determined through tolerance range masking (Fig. 5), oyster growth potential was found to be highly variable for each of the three indicators. Total adult weight obtained for the main European market (i.e., December 1, Fig. 7), shows many areas of low growth (in red) where only ~6 g were gained over the entire growing season (from the initial total weight of 14 g on April 1), and end-of-season weight remains below the market minimum (i.e., 30 g). A number of areas, especially close to the coast, mapped in orange, yellow, or green, were found to achieve minimum market weight under current (i.e., early-century reference period) conditions, with several along the French Atlantic coast of the Biscay Bay (Fig. 7d), as well as off western Africa (Fig. 7e). These areas resulted in hot spots of exceptional growth, with large oysters (46–65 g, corresponding to the French caliber 4; Palmer et al. 2020) growing from the initial 14 g spat within a single season. The two other indicators determined the date on which a target total weight was achieved (i.e., 30 g for adults (Fig. S2) and 14 g for spat (Fig. S3)). For both of these, the mapped area of the indicator is less than the total suitable area and less than the area mapped for adult weight on December 1, because the target weight will not be reached everywhere

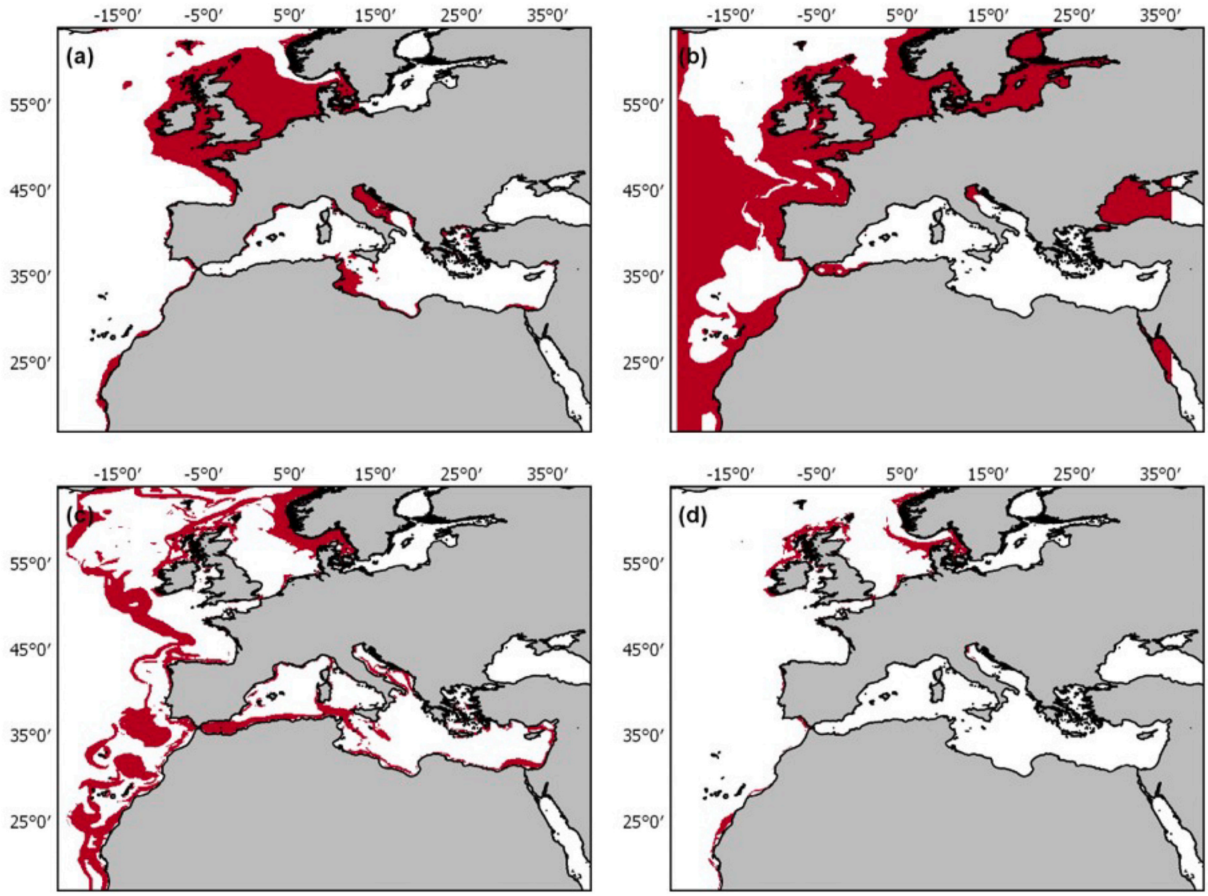

Fig. 5. Ranges within which Pacific oyster cultivation is considered to be suitable (in red), based on (a) bathymetry, (b) chlorophyll-a, and (c) current speed masks used to define (d) the overall suitable area for Pacific oyster cultivation and within which DEB modelling was carried out, for the early-century reference period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

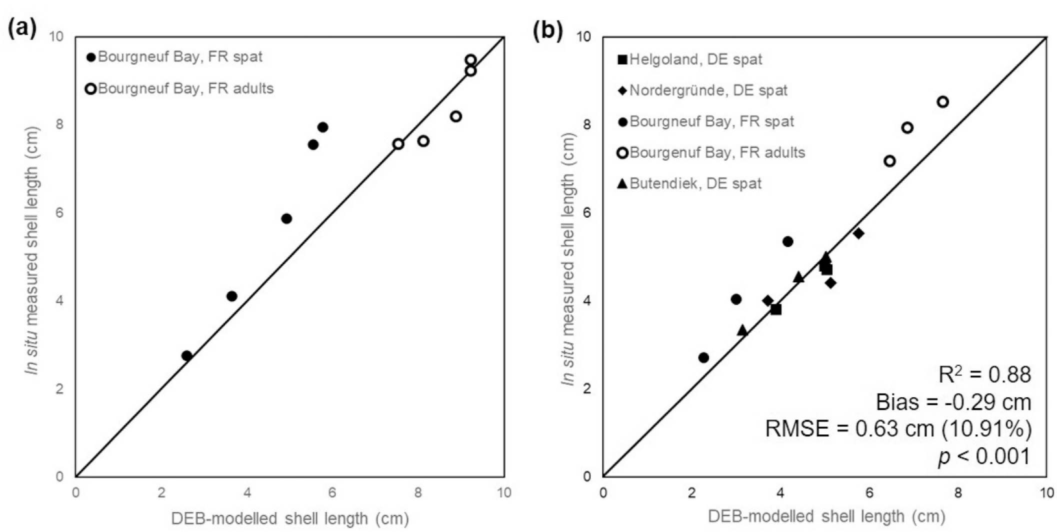

Fig. 6. (a) Calibration and (b) validation of the DEB half-saturation coefficient (X_k).

(e.g., the red areas of Fig. 7 are <30 g by the end of the growing season). However, where the target weights are achieved, similar growth hot spots are identified, notably in western France and Africa.

3.4.2. Climate robust zones

Future growth potential was also considered by mapping the indicators for each of the climate change scenarios, to assess where investments to the industry and related policy decisions might be the most sustainable, as well as have the most impact currently. Fig. 8 shows the example of adult growth (total weight by Dec. 1) for several potential zones off western France, near areas where Pacific oyster is currently cultivated, and compares current growth and spatial variability (Fig. 8a)

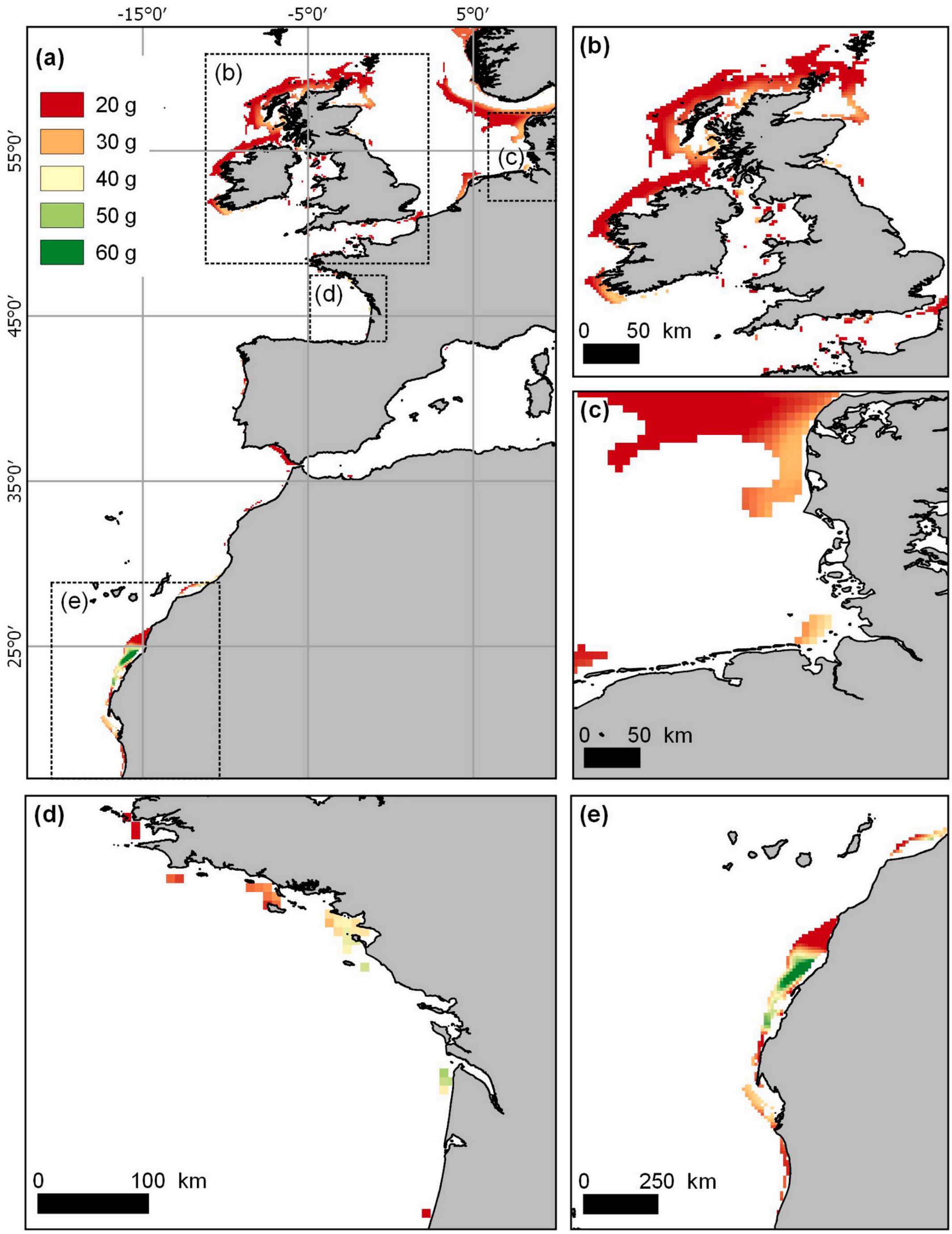

Fig. 7. Pacific oyster total adult weight obtained by Dec. 1 (from an initial weight of 14 g on April 1) for the early-century reference period, for the full model domain (a) and indicated close-ups: (b) the United Kingdom, (c) the southeastern North Sea, (d) the Bay of Biscay, and (e) the west coast of Western Sahara and Mauritania.

with those under RCP 4.5 (Fig. 8b) and RCP 8.5 (Fig. 8c). An area of relatively poor and decreasing growth potential is observed in South Brittany (Fig. 8d). ANOVA and Tukey pairwise comparisons indicate decreasing growth potential under both future climate scenarios compared with current conditions in this area (Tukey $p < 0.001$ for both RCP 4.5 and RCP 8.5). This contrasts with an area of moderate and stable growth in coastal waters close to the Loire Estuary (Fig. 8e). Kruskall-Wallis ANOVA by ranks indicates no significant difference between current and future scenarios there ($p = 0.122$). Another area with very good growth potential is observed in the coastal waters south of the Gironde Estuary (Fig. 8f). Here, the growth potential was projected to remain reasonable in both scenarios, with marketable product achieved within the average projected future season, despite the potential decrease under both future RCP scenarios compared to the reference period.

Such information can also be considered and mapped in terms of a decision-making framework, such as that proposed in Fig. 2. After determining areas where the user-defined criteria of "good" growth potential is currently achieved (the 30 g minimum market weight is applied in this example), areas where this is also achieved in the future for at least one of the climate change scenarios were identified, and further refined to areas where "good" growth potential was consistent between climate change scenarios (i.e., ΔX_{RCP}, as defined in Eq. 4). These areas are mapped for our example indicator (adult weight on

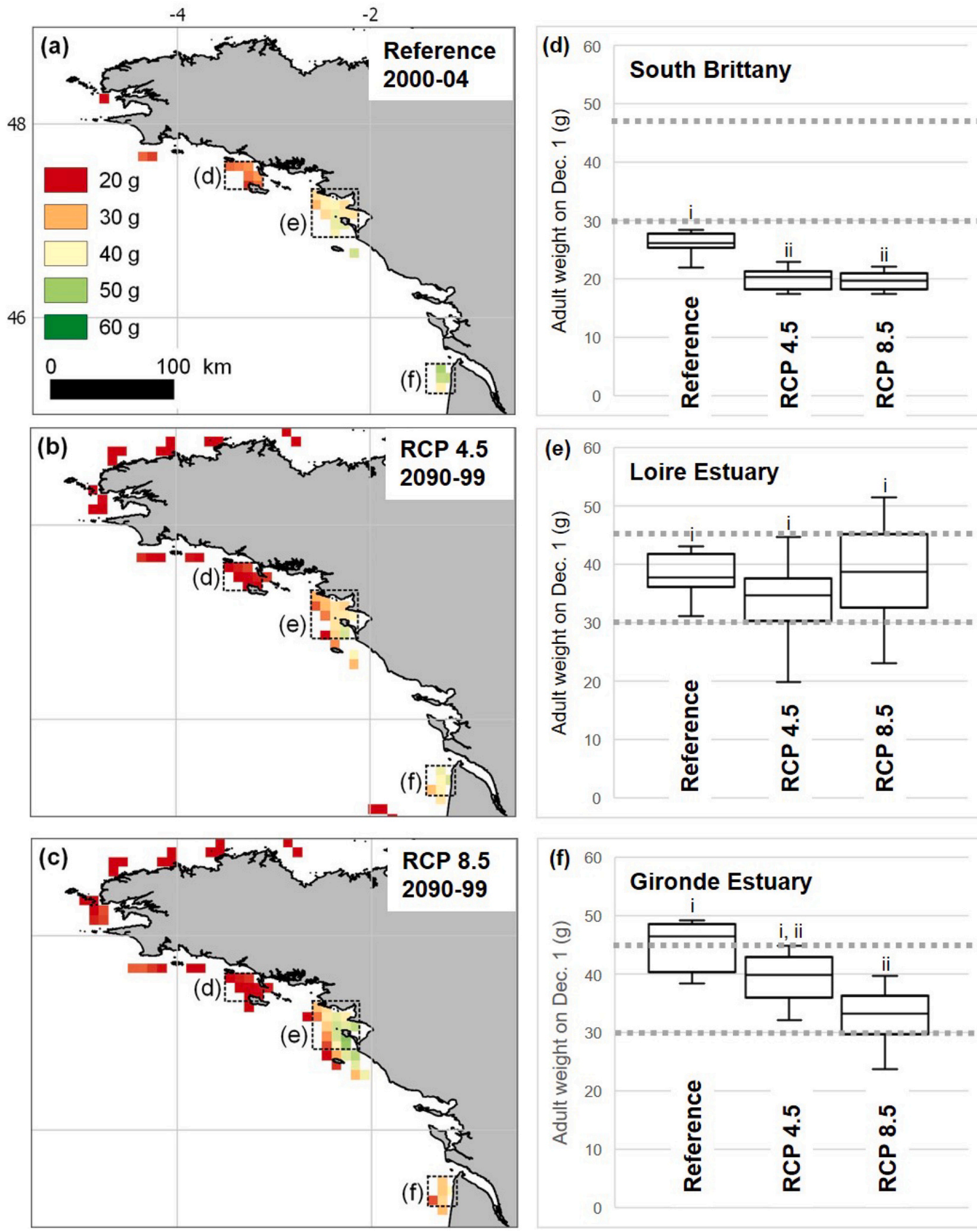

Fig. 8. Pacific oyster total adult weight obtained by December 1 (from an initial weight of 14 g on April 1) in the Bay of Biscay for (a) the early-century reference period and (b, c) two future climate change scenarios considered (RCPs 4.5, 8.5). (d-f) Data from each period and scenario have been extracted from three potential zones of interest along the coast to consider spatial (within-box) and between-scenario (between-box) variability: (d) South Brittany, (e) coastal waters close to the Loire Estuary, and (f) coastal waters south of the Gironde Estuary. Grey dashed lines indicate minimum market weight (30 g) and Caliber 4 total weight (45 g) for the French market (Palmer et al. 2020). Boxes sharing a common superscript are not statistically different (Tukey $p < 0.05$).

December 1) in Fig. 9, and include the Loire Estuary area identified in Fig. 8e discussed above, with most climate-robust (i.e., most consistent future conditions, also characterized by good current and future growth potential) in green, and indicate the interest of certain areas from a climate change perspective. This further constrains areas to be targeted for investment, such as off the coasts of Scotland, Ireland, Germany, Denmark, France, and western Africa (Fig. 9). These areas are fewer and smaller than the current areas of good growth potential in Fig. 7, as growth potential decreases under at least one climate change scenarios for many areas. Similarly, the most "climate robust" areas (lowest ΔX_{RCP}) highlighted in Fig. 9 are not necessarily those with the highest current growth potential highlighted in Fig. 7, since this is instead an indicator of future change and stability between climate scenarios (i.e., off the coast of Germany in Figs. 7c and 9c versus off the coast of western Africa in Figs. 7e and 9e). It is therefore recommended to include both of these respective absolute and relative indicators in policy and investment considerations.

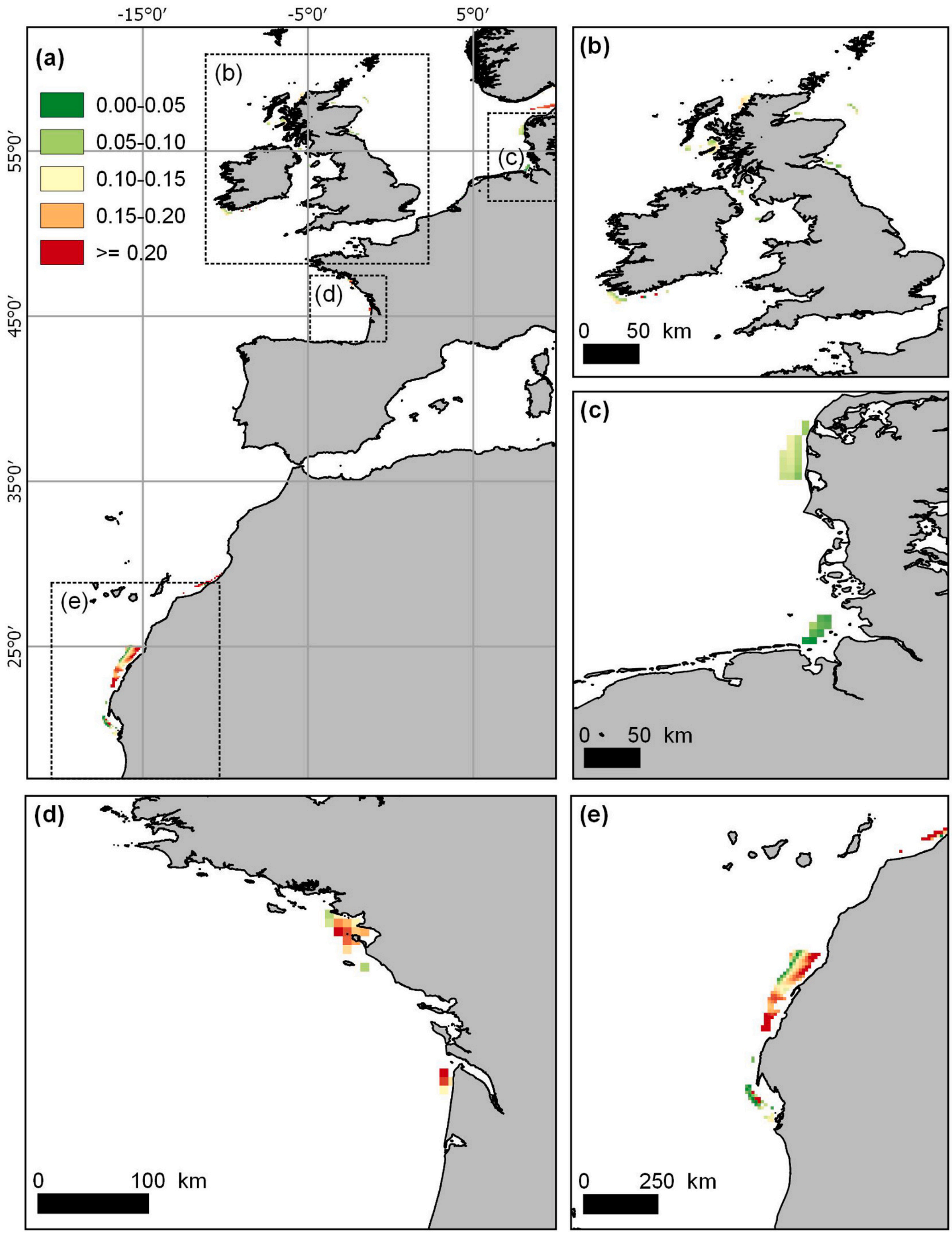

Fig. 9. ΔX_{RCP} stability index results for future oyster growth (total adult weight by Dec. 1) between two climate change scenarios considered (RCP 4.5 and 8.5) (difference normalized to the maximum absolute total weight between the two scenarios) for the full model domain (a) and close-ups of (b) the United Kingdom, (c) the southeastern North Sea, (d) the Bay of Biscay, and (e) the west coast of Western Sahara and Mauritania. More climate-robust areas are considered to be those with lower future, between-scenario normalized variability. These areas are shown in green, and have normalized variability of less than 0.1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Spatial trends and areas of interest identified

Several broad zones of European and northwestern African waters have been identified as having significant Pacific oyster aquaculture potential, now and into the future under different climate change scenarios, through the use of modelled growth indicators. These allowed us to recognize areas where offshore aquaculture zones, and eventually farms, may be best situated to optimize oyster growth. Generally, across the model domain, water temperature follows a latitudinal gradient, decreasing poleward (Fig. 3a). Chl-a, on the other hand, follows a more near- to offshore gradient, with higher concentrations typically observed nearer the coastline (Fig. 4a). The influence of these parameters on oyster growth potential is clear in the similar spatial patterns observed between, for example Figs. 4a and 7a.

Within the total model domain (i.e., Fig. 7a), the area off northwestern Africa (Fig. 7e) stands out in particular. This corresponds to a large upwelling area that is part of the Canary Upwelling Current, flowing southward from the Iberian Peninsula to Senegal, whereby north-easterly winds move the warmer surface waters further offshore to be replaced by cooler, deeper, more nutrient rich waters (Pelegrí and Benazzouz 2015). Indeed, following only the Benguela Current (from southern South Africa to Angola), the Canary Upwelling Current is the second most productive system in the world (Demarcq and Somoue 2015). Superimposed upon the general latitudinal water temperature gradient observed in Fig. 3a, we see waters approximately 1–3 °C cooler in this zone (annual mean), similar to temperatures typically observed 15–20° further north, as well as higher chl-a concentration (Fig. 4a), corresponding to the enhanced productivity enabled by these very nutrient-rich upwelling waters.

This corresponds to the general spatial trends in productivity and magnitude of chl-a concentrations observed here by others over the past decades (Demarcq and Somoue 2015). Furthermore, we see both climate change scenarios corresponding to further increases in annual mean chl-a relative to the early-century reference period (Fig. 4b,c), with even more productive conditions under more extreme climate change (i.e., RCP 8.5). It is therefore unsurprising to see this area also highlighted as an area of exceptional potential in the future, and several large areas (totalling >6000 km^2) where this is expected to be the case under both climate change scenarios considered are highlighted (in green) as relatively climate robust in Fig. 9a,e.

Several European areas were also found to have a high and climate-robust growth potential (Fig. 7b-d), although this is somewhat lower compared with that of the northwestern African hot spot, due to the combined influence of overall lower temperatures and chl-a concentrations. In Fig. 7a-d, a dominant latitudinal gradient in oyster growth potential was also mapped, similar to general trends in water temperature, with less rapid growth observed to the northwest of Scotland and Ireland (Fig. 7b) and in the North Sea (Fig. 7c) than in the more southerly Biscay Bay (Fig. 7d). However, although lower, many of these more northerly areas also achieve minimum market weight (30 g) within the single growing season considered here (Figs. 9, S2). Relative to the current status quo of nearshore Pacific oyster cultivation, this should be regarded as exceptionally good growth.

Typically, for example near the calibration-validation site of Bourgneuf Bay, France, adult grow-out from spat of a similar size will take at least two (and up to four) growing seasons in the nearshore intertidal environment where oyster farms are currently located (note that these areas cannot be observed at the spatial resolution of this work), due to particular challenges encountered there (i.e., much higher turbidity; substantially lower immersion time; Palmer et al. 2020). Although the nearshore-offshore difference in growth rates will certainly be less substantial in areas where these factors are not as contrasted from one setting to the other (i.e., nearshore oyster cultivation in fjords or lochs where tidal gradients and inorganic turbidity are lower), and further experimental results are needed to evaluate this, faster growth may be a primary incentive to moving cultivation offshore. This is in addition to existing space constraints already highlighted as a barrier to European aquaculture expansion nearer shore (Hofherr et al. 2015).

These more northern case sites are also characterized by more climate-robust good growth potential in the future (Fig. 9), whereby growth between the two scenarios is more similar. However, this indicator should be interpreted while also taking into account the absolute growth under the different climate change scenarios. Given the definition of the climate-robustness indicator, there may be good projected growth (e.g., 30 g) under one scenario, and exceptional growth (e.g., 90 g) under the other, which leads to less stable results (i.e., 0.67) than simply good growth (i.e., 30 g) under both scenarios (i.e., 0.0). This highlights the need to combine more than one indicator for a fuller picture in effective decision-making.

4.2. Advantages and limitations of the modelling approach and data used

The advantage of combining dynamic, ecophysiological growth modelling with the binary tolerance range threshold approach employed elsewhere (e.g., Gentry et al. 2017; Kapetsy et al. 2013) is clear in terms of the additional information and insight provided. Within areas identified to fall within the Pacific oyster tolerance range for a number of variables (Fig. 5d), there is a great deal of variability in oyster growth potential. Such an approach has also been used to identify suitable areas for finfish cultivation in the Mediterranean (Porporato et al. 2020) and North Africa (Brigolin et al. 2015) and for shellfish cultivation in the Adriatic (Brigolin et al. 2017) and western France (Thomas et al. 2011, 2016; Barillé et al. 2020), where good modelled growth is considered with other advantageous factors in more thorough spatial multi-criteria evaluation.

Under the same DEB model initialization (i.e., oyster size, start and end dates) and parameterization, total adult weight at the end of the growing season ranges from <20 g to >60 g across the full model domain (Fig. 7a), and ranges by as much as 50 g over as little a distance as 100 km, notably off the coast of northwestern Africa (Fig. 7e), but also by as much as 20 g over the same distance along the French Atlantic (Fig. 7d) and western Scottish coast (Fig. 7b), and even by as much as 10–15 g over just 30 km for parts of all of the areas of interest (Fig. 7). Without this information to further optimize aquaculture zoning and site selection, we would simply know that Pacific oyster aquaculture should be feasible across this area (Fig. 5).

While the coarse spatial resolution of the input data (0.1°) is an inherent limitation of such broad scale studies, it makes it possible to provide general assessment of trends and scenarios using a cohesive approach and methodology at multi-national scale, to support decision-making and planning, and identify hot spots for potential development or further consideration (Falconer et al. 2019). However, the inability of studies at such large scales to account for environmental heterogeneity on finer spatial and temporal scales, documented as being important to organismal physiology, is a notable limitation and highlights the need for complementary studies across scales (Helmuth et al. 2014). In many instances, anomalies and extreme events (for example in water temperature), as well as the dynamic and heterogeneous nature of the "ocean weather" (Bates et al. 2018), which could substantially affect growth, reproduction, and mortality of Pacific oyster and many other species, may not be detected when using such coarse input data. Instead, the signal is averaged out over the larger spatial and temporal timestep and extremes are dampened. Although the offshore environment investigated here is expected to be much less sensitive and heterogeneous compared with the highly variable nearer-shore and intertidal environments (i.e. Gernez et al. 2017; Choi et al. 2019), the importance of local climatic and non-climatic stressors should not be neglected in site selection and should be included in the finer-scale site selection activities recommended to follow broad zoning initiatives.

The reliability of such modelling results is also limited by the availability of in situ data for calibration and validation. As offshore aquaculture remains relatively novel and experimental, in situ data are likewise rare, as has been noted elsewhere and for other species (e.g., Brigolin et al. 2017). In our case, we were fortunate to have two spatially disparate sites for DEB model calibration and validation, representing two oyster-producing zones in Europe (the French Atlantic and German North Sea) and substantial latitudinal and longitudinal gradients, as well as from four different years. Although at an even greater spatial distance, Monaco et al. (2019) reported the inability to predict Mediterranean mussel (*Mytilus galloprovincialis*) growth at a South African site using calibration parameterization from a native Mediterranean site. Such inability was speculated to be due to unaccounted for differences in environmental variables and phenotypic plasticity. The inclusion of additional environmental parameters (e.g., suspended particulate matter; Thomas et al. (2016)) and other approaches to address issues of environmental variability over large spatial scales have been proposed elsewhere (Thomas and Bacher 2018; Alunno-Bruscia et al. 2011).

Validation results (Fig. 6) here were found to be satisfactory across both sites and multiple years. However, in situ data remain relatively sparse given the coverage of the model domain. Despite this limitation, our results demonstrated the added value of the methodology and framework applied in revealing general trends and hot spots. Further in situ data acquisition is recommended to support and complement modelling studies allowing fuller spatial coverage at all scales. Our work can help to justify and optimize the investment in carrying out additional field studies, through the identification of promising potential zones.

Many facets of the methodology and approach presented are flexible, in that they could be applied using other models, for other species, different production stages (e.g., spat and adult cultivation demonstrated here), or different indicators (whether new ones, or by simply adjusting the weight and/or timing thresholds for the indicators demonstrated here) and definitions of resulting "good" potential and zones (e.g., Figs. 2, 9). Multiple indicators and selection criteria could be combined to assess the sensitivity thereof, as well as to strengthen the support for highlighted areas. Likewise, any spatiotemporal input data of choice could foreseeably be used, provided that its appropriateness is demonstrated via successful growth model validation.

This is especially important in using modelled data to drive models (as in the current case, where climate model data are used to drive ecological models, the output of which is used to drive oyster growth modelling), as error propagates at each stage. Notably, many other climate change models and scenarios are available, including models that better take internal climate variability into account (Freer et al. 2018; Thomas et al. 2018). Here, the purpose was to show results from two contrasting future projections, as the greatest unknown in current climate change predictions is the pace of anthropogenic greenhouse gases emissions rather than modelling uncertainties (Thomas et al. 2018). While this gets at some of the uncertainty in future climate change, and demonstrates a framework to include this in choosing AZAs, it is by no means intended to be an exhaustive or complete assessment. However, as mentioned above, different input data based on other climate scenarios and/or models, as well as other ecological models, could be used as of interest. This would also give more understanding of the uncertainty in the model results. The source model used here (MPI-ESM-LR) gives a lower projected rise than some other global climate models and so greater future change than projected here could be possible.

4.3. Additional considerations in establishing allocated zones for aquaculture

A number of biogeochemical and physical variables output from the POLCOMS-ERSEM ecosystem model were used here to delineate and highlight areas that should be given priority consideration for offshore Pacific oyster aquaculture, as well as to indicate areas not likely to be suitable, successful, or sustainable in this respect. Although framed here within Pacific oyster tolerance ranges and growth modelling, the considered variables (chl-a, water temperature, salinity, current speed, bathymetric depth) are broadly relevant to many farmed, as well as unfarmed species, in addition to underlying countless ecological processes in the marine environment. However, many other variables and factors that were beyond the scope of this work and were not explicitly considered here are known or expected to also be important determinants of Pacific oyster and other aquaculture potential at a given location.

Some factors are known to currently preclude the installation of offshore infrastructure in some locations that might otherwise be productive (e.g., wave height, which may impact organism growth potential as well as accessibility of offshore structures to undertake operations and maintenance (Buck and Langan 2017)). Some are likely to intensify in some locations or generally under climate change conditions (e.g., frequency of storms (Feser et al. 2015), ocean acidification (Kroeker et al. 2010; Barton et al. 2012), frequency of wintertime seawater temperature anomalies (Thomas et al. 2018), and drop in pH levels (Law et al. 2018), as well as the cumulative effects of combinations of these parameters). These stressors will have a direct impact on the potential for offshore as well as nearshore aquaculture into the future. Others (e.g., storm surges (Vousdoukas et al. 2016) and sea level rise (Grinsted et al. 2015)) may not be as detrimental to infrastructure and cultivation in the offshore environment itself, but may be important to consider in terms of their projected increasing impact on the coast and related damage to infrastructure necessary to support offshore production there (e.g., ports; grading, packing, and distribution facilities). Likewise, interaction between and among climatic and non-climatic stressors, and potential adaptation and acclimatization may be substantial (Helmuth et al. 2014).

As different species are expected and documented to respond differently to the impacts of climate change (e.g., Filgueira et al. 2016; Steeves et al. 2018; Thomas and Bacher 2018), this should also be considered in selecting species to farm. For the Atlantic Canadian site investigated by Steeves et al. (2018), although the growth of both species was found to be enhanced overall, the greater thermal tolerance of the eastern oyster, *Crassotrea virginica*, allowed it to outperform the blue mussel, *Mytilus edulis*. Modelling by Filgueira et al. (2016) found similar results favouring *C. virginica* over *M. edulis* in warming scenarios, and also suggests that bivalve aquaculture may enhance ecological resilience under some climate change scenarios and coastal geomorphologies (e.g., bays with large rivers). Likewise, the negative environmental impacts accruing from the aquaculture of different species are also not expected to be uniform in space and time under different climate scenarios and for different species. This has been demonstrated for the Mediterranean seabass, *Dicentrarchus labrax*, in the Mediterranean and Black seas in terms of organic loading as well as animal growth, whereby the trade-off between fish growth and farm pollution was found to become increasingly difficult to optimize under their modelled climate change scenarios (Sarà et al. 2018). In the Mediterranean, the growth, mortality, and phenology of three different commercial mussel species has been forecasted to respond variably and non-linearly by species and site in response to modelled warming (Montalto et al. 2016). Pacific oyster results from the northeast Atlantic suggest that climate change has a positive impact on oyster growth and reproduction (due to chl-a and SST increase; Thomas et al. 2016) and that phytoplankton dynamics, more than temperature directly, underlie modelled climate-driven phenological shifts in this species in terms of spawning event timing (Gourault et al. 2019b). On the other hand, warming is also likely to result in a higher risk of adult oyster mortality due to an increase in the occurrences of positive wintertime temperature anomalies (Thomas et al. 2018).This highlights the need for modelling across trophic levels, and to consider seasonal dynamics and interannual climate variability in addition to more binary tolerance ranges.

Further variables to consider relate more to alternative and conflicting uses of the space from a socioeconomic perspective, notably related to capture fisheries, the existence of other industries (e.g., windfarms; oil and gas platforms), transportation and militarized zones, and environmentally protected areas (Barillé et al. 2020; Porporato et al. 2020). The presence of sufficient coastal infrastructure to support offshore aquaculture (e.g., harbours or ports within a reasonable distance) is another crucial consideration. Some of these will result in the absolute preclusion of aquaculture from some areas (i.e., marine protected areas, or if there is not a port within, for example, 25 nm (Kapetsky et al. 2013), offshore aquaculture cannot be considered), whereas others will need to be considered in terms of finding a balance with aquaculture (e.g., fishing type (Barillé et al. 2020)).

Existing examples of spatial multi-criteria evaluation (SMCE) and multi-criteria decision analysis (MCDA) offer frameworks for how a multitude of variables of different types can be integrated to further improve information provided for planning and policy, as well as site selection (Falconer et al. 2019). Whereas most assess conditions for a current or recent scenario, the consideration of future climate change uncertainty, via the inclusion of different RCP scenarios in the stability index proposed here, represents a novel adaptation of such a SMCE approach, and is key to supporting sustainable decision-making for long-term industry investments and development.

Although it is likely that not all data that would be beneficial to include are available at the appropriate spatial resolution and broad spatial coverage demonstrated here (Falconer et al. 2019), such data could be added upon considering specific identified hot spots at the smaller regional scale to further assess a proposed AZA, or at the even smaller local scale, as part of the farm site selection step. In this work, our aim is to demonstrate the added benefit and utility of using such a dynamic, growth modelling-based approach to identify areas of interest from a biological perspective, and we recommend the integration of such results and indicators as produced here into a fuller SMCE or MCDA.

In addition to considering the biological potential of a cultured species of interest (i.e., Pacific oyster here) along with factors likely to restrict potential areas for aquaculture, areas where additional benefit may be possible should also be sought out. Co-production with other sectors, notably energy, can also be targeted as a means to make dual use of shared infrastructure. Co-production of shellfish with offshore wind energy has received a great deal of attention, and, albeit less-so, co-production with active or decommissioned offshore oil and gas platforms has also been noted, with a few small-scale demonstration projects having taken place (Buck and Langan 2017). Although each of these activities is complex and controversial in its own right, the idea is that existing physical infrastructure, as well as processes related to site selection and permitting, might be leveraged to the benefit of new, related aquaculture developments (Buck and Langan 2017). Likewise, this would represent a more efficient use of space in the marine environment, which, even offshore, is limited and multiple potential uses must be balanced.

Areas where the biological potential is high for several potential species could likewise be prioritized in the designation of general AZAs within economic exclusive zones of a country. This has been done to a certain extent using a binary thresholding approach (e.g., Gentry et al. 2017), but could be improved upon by making use of DEB modelling of other shellfish or finfish of interest. In fact, such parameterization has already been undertaken for a suite of relevant species (e.g., blue mussel (*Mytilus edulis*; Filgueira et al. 2011), Mediterranean mussel (*Mytilus galloprovincialis*; Sarà et al. 2012), great scallop (*Pecten maximus*; Gourault et al. 2019a), European seabass (*Dicentrarchus labrax*; Stavrakidis-Zachou et al. 2019), and white and gilthead seabream (*Diplodus sargus* and *Sparus aurata*; Serpa et al. 2013)), noting that, of course, not all species will be of interest or feasible for all countries.

Such areas of added benefit, where different species or different commodities have the potential to be produced, should be identified and included positively in MSP activities, such as SMCE or MCDA. As discussed in Palmer et al. (2020), issues of Pacific oyster carrying capacity and stocking density were not considered here, and are implicitly excluded from the in situ datasets upon which modelled results are based. If farms were established offshore, with inherently greater numbers of farming structures, growth potential and carrying capacity would be expected to be affected, and the environmental impact would need to be considered.

5. Conclusions

Several large (>1000 km^2) areas have been highlighted as current hot spots for offshore Pacific oyster cultivation across Europe and northwestern Africa. These are found to be associated with continued good production into the coming century under distinct climate change scenarios according to the input data, model results, and framework presented here. Pacific oyster and/or other bivalve cultivation is already practiced in the more nearshore environment for several highlighted regions, including the intertidal zone of the French Atlantic, the southern North Sea, southwestern Ireland, and lochs of western Scotland, indicating the promise for facilitated industry and expertise transfer to the offshore environment in these areas. A large area off the coasts of Western Sahara and Mauritania is also highlighted, corresponding to a major upwelling zone, which could indicate a promising new industry for this region. Such climate-robust areas of exceptional Pacific oyster growth are recommended for prioritization in subsequent zoning or higher-resolution site selection. A suite of flexible indicators and a framework to integrate results into decision making have been demonstrated, which may be adapted to the specific decision-making need or to uptake similar modelling results for other species of interest.

Author contributions

SP, PG, LB, and SC designed the study. SC and SK generated POLCOMS-ERSEM data, and SP generated the DEB outputs. PG and LB contributed to in situ data collection and compilation. SP, SC, and SK contributed to data analysis. SP, PG, LB, SC, SK, and BB contributed to data interpretation. SP wrote the manuscript. All authors contributed to writing and revision and gave their approval to the manuscript final version.

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Declaration of Competing Interest

None

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2020.736116.

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