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1 For submission to *Aquaculture; Sustainability and Society* section

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

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14

15 **Abstract**

16 Aquaculture development in Europe, while critical to the European Union (EU) Blue Growth
17 strategy, has stagnated over the past decades due largely to high competition for space in the
18 nearshore coastal zone among potential uses and the lack of clear priorities, policy, and
19 planning at EU and national scales. Broad Marine Spatial Planning, including the designation
20 of Allocated Zones for Aquaculture, requires spatial data at the corresponding broad spatial
21 scale, which has not been readily available, as well as model projections to assess potential
22 impacts of climate change. Here, daily chlorophyll-a, water temperature, salinity, and current
23 speed outputs from a marine ecosystem model encompassing the coastal North East Atlantic,
24 the North Sea, and the Mediterranean Sea (the pan-European POLCOMS-ERSEM model
25 configuration) are used to drive a Dynamic Energy Budget growth model of Pacific oyster
26 (*Crassostrea gigas*). Areas broadly suitable for growth were identified using threshold
27 tolerance range masking applied using the model variables mentioned above, as well as
28 bathymetry data. Oyster growth time series were transformed into simplified indicators that
29 are meaningful to the industry (e.g., time to market weight) and mapped. In addition to early-
30 century indicator maps, modelling and mapping were also carried out for two contrasting late-
31 century climate change projections, following representative concentration pathways 4.5 and
32 8.5. Areas found to have good oyster growth potential now and into the future were further
33 assessed in terms of their climate robustness (i.e., where oyster growth predictions are
34 comparable between different future climate scenarios). Several areas within Europe were
35 highlighted as priority areas for the development of offshore Pacific oyster cultivation,
36 including coastal waters along the French Atlantic, the southern North Sea, and western
37 Scotland and Ireland. A large potential growth hot spot was also identified along northwestern
38 Africa, associated with a cool, productive upwelling coastal zone. The framework proposed
39 here offers a flexible approach to include a large range of ecological input data, climate and
40 ecosystem model scenarios, aquaculture-related models, species of interest, indicator types,
41 and tolerance thresholds. Such information is suggested to be included in more extensive
42 spatial assessments and planning, along with further socioeconomic and environmental data.

43

44 **Keywords**

45 bivalve; Pacific oyster; Dynamic Energy Budget (DEB); Marine Spatial Planning (MSP);
46 offshore aquaculture; site selection, climate change

47

48 **Highlights**

- 49 - Aquaculture-relevant oyster growth indicators modelled and mapped across Europe
- 50 - Large-scale hot spots highlighted as potential zones for industry development
- 51 - Contrasted climate change scenarios considered to assess future uncertainty

52

53 **1. Introduction**

54 A diverse marine aquaculture sector has been linked with achieving a more sustainable food
55 system, with both environmental and human health benefits when best practices and
56 appropriate site selection are applied (Schubel and Thompson, 2019). Although Europe is one
57 of the largest markets for seafood globally, it remains highly dependent upon international
58 sources to meet demand. Over 60% of seafood consumed by European Union member states
59 are supplied by non-European imports (STECF, 2018). At the same time, the proportion of
60 European seafood supplied by aquaculture remains much lower than ratios observed
61 internationally, at approximately 20% compared with over 50%, and with much lower growth
62 rates (FAO, 2018; STECF, 2018). Throughout Europe, a major bottleneck in issuing new
63 licenses has constrained the aquaculture industry for over a decade. This results in large part
64 from the lack of clear prioritization, planning, and management, as well as the high level of
65 competition for space in the already-overcrowded coastal zones (Hofherr et al., 2015). For
66 Europe to achieve its desired “Blue Growth” strategy, of which aquaculture development is a
67 key component (European Commission, 2017), such issues need to be addressed.

68 Offshore cultivation has been cited as potentially having the means to overcome space
69 limitations in nearshore areas in Europe and around the world (European Commission, 2017;
70 Gentry et al., 2017). Technological advances (Buck and Langan, 2017; Landmann et al.
71 2019), as well as experimental results (e.g., Pogoda et al., 2011; 2012; 2013), indicate the
72 increasing feasibility of cultivating various species in the offshore realm, which in most cases
73 is exposed to strong waves, high current velocities, and strong winds, among other challenges.
74 The potential to combine aquaculture with, for example, offshore wind energy generation in
75 coproduction scenarios (Buck et al., 2008; Jansen et al., 2016; Buck and Langan, 2017; Buck
76 et al., 2018) and within multi-species facilities offshore, including integrated multi-trophic
77 aquaculture (Troell et al., 2009; Korzen et al., 2016; Buck and Langan, 2017), further adds to
78 the appeal with respect to dual purpose investments or leveraging existing resources.
79 Furthermore, recent studies point to a suite of additional benefits of offshore aquaculture,
80 ranging from reduced pathogen and pollutant exposure (Buck et al., 2005; Pernet et al., 2018)
81 to greater production and carrying capacity (Di Trapani et al., 2014).

82 Pacific oyster (*Crassostrea gigas*) has been considered for offshore farming in several
83 European countries (e.g., France (Palmer et al., 2020; Glize et al., 2010; Mille et al., 2008),
84 Germany (Buck and Langan, 2017; Pogoda et al., 2011; Buck et al., 2006), and the UK
85 (Ferreira et al., 2009)). Although offshore cultivation remains experimental at these sites,
86 results to date have been promising, with a growth rate often outpacing that in nearby coastal
87 farms. At several French Atlantic sites, *C. gigas* growth was found to be more than 15% and
88 as much as 100% higher offshore than at a reference intertidal site, varying between animal
89 ploidy and life stage (i.e., spat versus adults) considered (Mille et al., 2008; Glize et al.,
90 2010). Likewise, similar or higher survival rates and oyster quality indices (ratio of flesh to
91 total animal weight) have also been documented from oysters grown in offshore cages in
92 Germany (Pogoda et al., 2011; Buck et al., 2020), in France (Glize et al., 2010), as well as in
93 New Zealand (Heasman et al., under review). Despite such promise, substantial investments
94 would be required to install and maintain infrastructure, as well as for ongoing operations, and
95 the offshore environment remains largely uncharted territory from an aquaculture industry
96 perspective (Gentry et al., 2017).

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

108 For sustainable decision making by the aquaculture industry, it is also crucial to consider the
109 challenges and ongoing impacts of climate change on the coastal ocean (FAO, 2018; Bindoff
110 et al., 2019). There is much uncertainty surrounding what climate change will look like where
111 and when, as well as how ecosystems and society will respond, and the numerous possible
112 related feedbacks (Moss et al., 2010; Gattuso et al., 2015; Freer et al., 2018). Satellite remote
113 sensing offers a rich, spatiotemporal component to study ecosystem processes in the ocean
114 and coastal zone, and has been usefully applied to aquaculture in several instances (e.g.
115 Radiarta and Saitoh, 2009; Thomas et al., 2011; Kapetsky et al., 2013; Thomas et al., 2016;
116 Aura et al., 2016; Brigolin et al., 2017; Snyder et al., 2017; Barillé et al., 2020; Palmer et al.,
117 2020; Porporato et al., 2020). However, long-term planning and zone or site selection also
118 benefits from the consideration of what future conditions might look like, impossible through
119 the use of remote sensing data alone, and requiring the coupling of climate and ecosystem
120 models to investigate the influence of predicted future environmental changes on aquaculture-
121 related indicators. Modelling that considers multiple, diverse scenarios can help us to
122 understand the potential magnitude of future climate change impacts and uncertainty (Bindoff
123 et al., 2019), in addition to providing rich spatial datasets necessary for MSP as described
124 above, and has therefore been chosen for use in this work.

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

136

137 **2. Materials and methods**

138 2.1 Input data: POLCOMS-ERSEM

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

150 All POLCOMS-ERSEM data were at a 0.1° spatial and a daily temporal resolution, for the
151 specific years for which *in situ* oyster growth data were also available, and for an early-
152 century (2000-2004) reference period and two contrasted climate change scenarios for a late-
153 century (2090-2099) period (CERES, 2018). Future climate change scenarios considered here
154 are based on two of the Representative Concentration Pathways (RCPs) in standard use by the
155 Intergovernmental Panel on Climate Change (IPCC), RCP 4.5 and RCP 8.5, and driven using
156 the global climate Max-Planck-Institute Earth System Model, Low Resolution (MPI-ESM-
157 LR). Meteorological conditions at the sea surface were taken from the 0.11° regional model
158 Rossby Centre Regional Atmospheric Model, version 4, driven by the Max-Planck-Institute
159 Earth System Model, Low Resolution (MPI-ESM-LR-RCA4) and river inputs were taken
160 from the European domain of the HYdrological Predictions for the Environment (E-HYPE),
161 also driven by MPI-ESM-LR. The model outputs were compared to satellite measurements of
162 sea surface temperature and chlorophyll concentration for the period 1998-2015 (CERES,
163 2018). Temperature outputs corresponded well with satellite observations and were 0.5-1°C
164 higher in the North Sea and western Mediterranean, less than satellite observations by a
165 similar amount elsewhere, and with Spearman correlation of greater than 0.9 in all regions.
166 Modelled chlorophyll values exceeded satellite observations by up to 2 mg m⁻³ in spring, but

167 showed good agreement in other seasons; the model captures the spatial and temporal
168 variation of chlorophyll concentration, with Spearman correlation 0.6 overall, and 0.5 in the
169 North Sea (CERES, 2018).

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

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

180

181 2.2 Tolerance range-based masking of unsuitable areas

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

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

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

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199 2.3 Dynamic Energy Budget (DEB) modelling

200 Dynamic Energy Budget (DEB) theory (Kooijman, 2010) provides a generic (i.e., non-
201 species-specific) approach to mechanistically model the flow of energy through individual

202 organisms, from the ingestion and assimilation of food, through somatic maintenance and
 203 growth, to reproduction. Here, we make use of the original parameterization for Pacific oyster
 204 (*Crassostrea gigas*) put forth by Pouvreau et al. (2006), and further updated by Bernard et al.
 205 (2011) and Thomas et al. (2016), whereby water temperature influences energy flow and
 206 allocation at all stages, and food abundance further impacts ingestion according to a calibrated
 207 coefficient (the half-saturation ingestion coefficient; X_k). In the offshore environments
 208 considered in the current work, the oysters are always submerged in the water (i.e., 100%
 209 immersion time). The impact of turbidity on oyster growth is assumed to be negligible
 210 offshore (Gernez et al., 2014), and the half-saturation ingestion coefficient through which
 211 high concentrations of inorganic sediment modulate ingestion, as put forth by Thomas et al.
 212 (2016), X_{ky} , is therefore not included in the current modelling. A DEB model schematic can
 213 be found in the supplementary information of this article (Fig. S1), and parameterization
 214 (except for X_k) and equations are those reported in the supplementary information of Thomas
 215 et al. (2016).

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

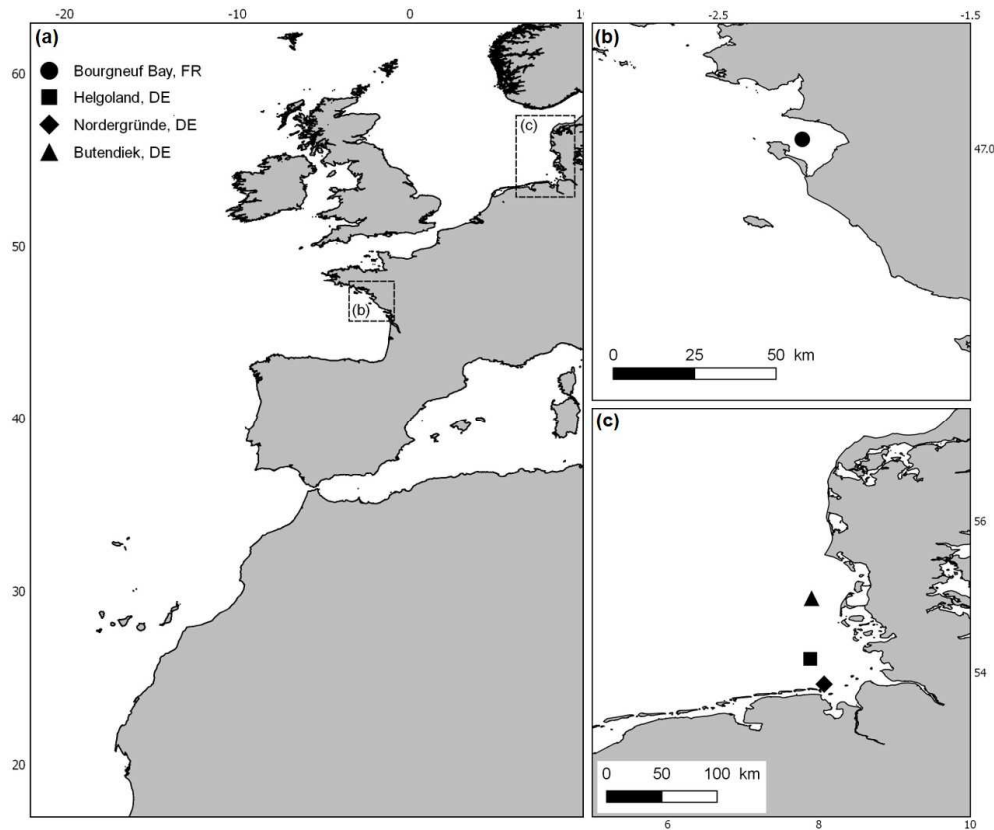
$$229 \quad \text{Mean bias} = \frac{1}{n} \sum_1^n (M - O) \quad \text{eq. 1}$$

$$230 \quad \text{RMSE} = \sqrt{\frac{\sum_1^n (M - O)^2}{n}} \quad \text{eq. 2}$$

$$231 \quad \text{Rel. RMSE (\%)} = \text{RMSE} / (\max(O) - \min(O)) \times 100 \quad \text{eq. 3}$$

232

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



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Figure 1. (a) Model domain 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).

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246 2.4 Oyster growth aquaculture indicators

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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.

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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

265 where growth potential will remain consistent in the future. A stability index was calculated
266 here as the absolute difference between indicator values for the two future scenarios
267 normalized to the indicator value itself (eq. 4):

$$268 \quad \Delta X_{\text{RCP stability index}} = |X_{\text{RCP 8.5}} - X_{\text{RCP 4.5}}| / \max(X_{\text{RCP 8.5}}, X_{\text{RCP 4.5}}) \quad \text{eq. 4,}$$

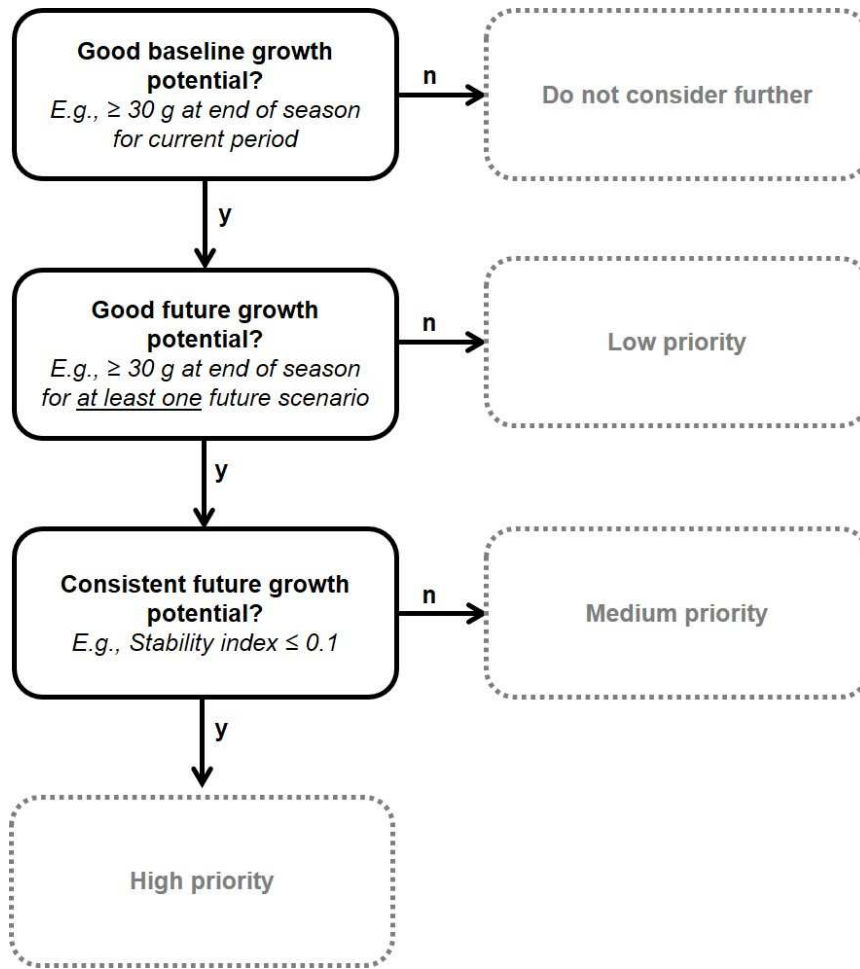
269 where $X_{\text{RCP 8.5}}$ is the resulting indicator value under the RCP 8.5 end-of-century scenario and
270 $X_{\text{RCP 4.5}}$ is the value of the indicator obtained under the RCP 4.5 end-of-century scenario.

271 We used five classes to map the variability in future oyster growth: 0.00 – 0.05 (very stable),
272 0.05 – 0.10 (stable), 0.10 – 0.15 (medium stability), 0.15 – 0.20 (low stability), and > 0.20
273 (very low stability). The most “climate robust” areas were those with stability index values of
274 between 0.00 and 0.10, corresponding to both high and consistent growth projections in light
275 of the uncertainties inherently associated with climate prediction and ecosystem modelling.
276 This chosen threshold value could be adjusted by the user depending on their needs and the
277 indicator in question.

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

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

297

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

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305 3. Results

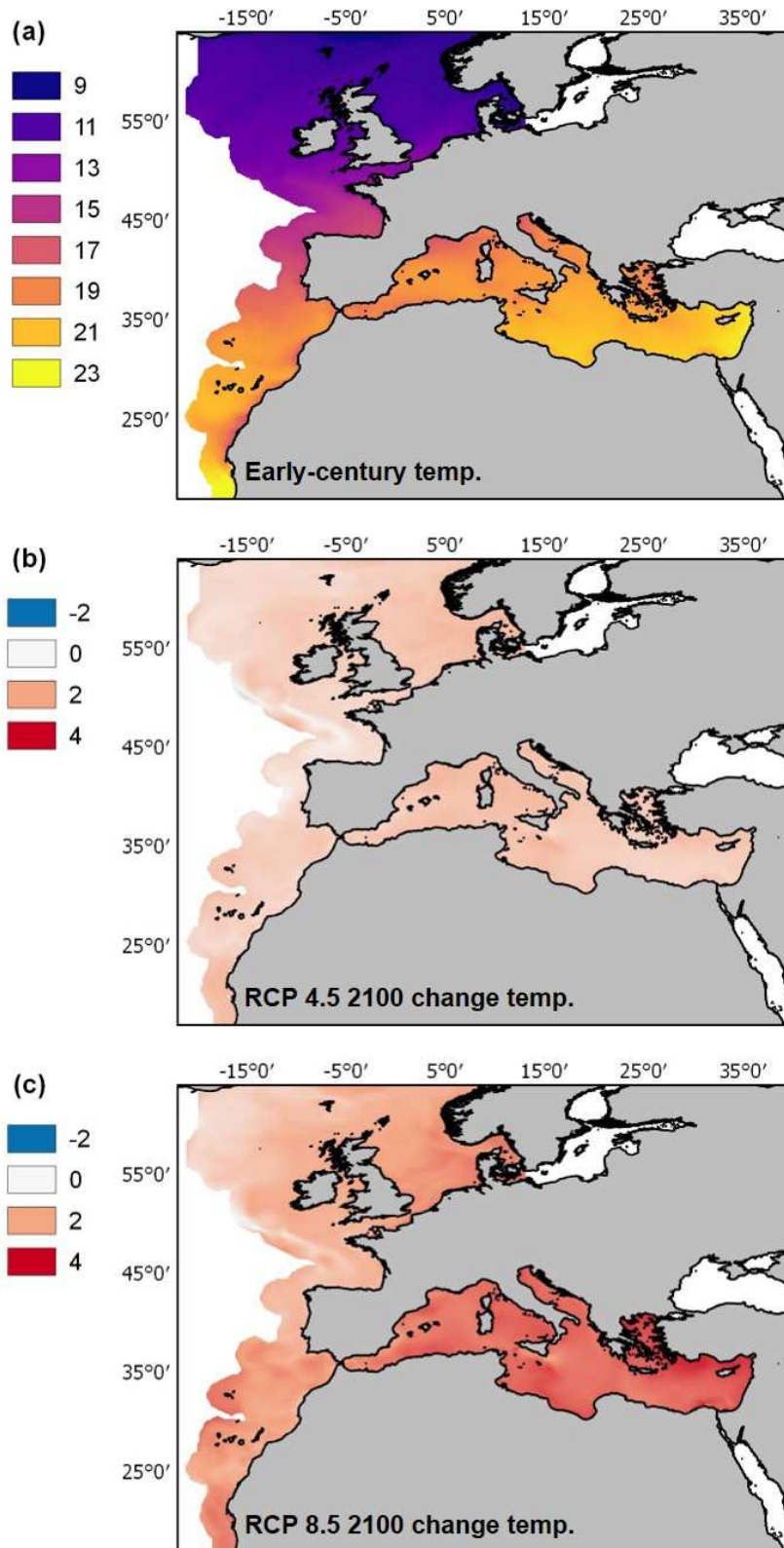
306 3.1 Biogeochemical climate change scenarios

307 The future changes in chl-a and water temperature predicted by the model POLCOMS-
 308 ERSEM in the two climate change scenarios are presented in Figures 3 and 4 respectively.
 309 Both RCP 4.5 and 8.5 scenarios consistently predict an overall warming trend, which is
 310 nonetheless higher under the more extreme RCP 8.5 scenario. Furthermore, in areas currently

311 characterized by warmer waters (e.g., lower latitudes; the Mediterranean Sea; Fig. 3a), we see
312 greater warming, particularly under RCP 8.5 (Fig. 3c).

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

324



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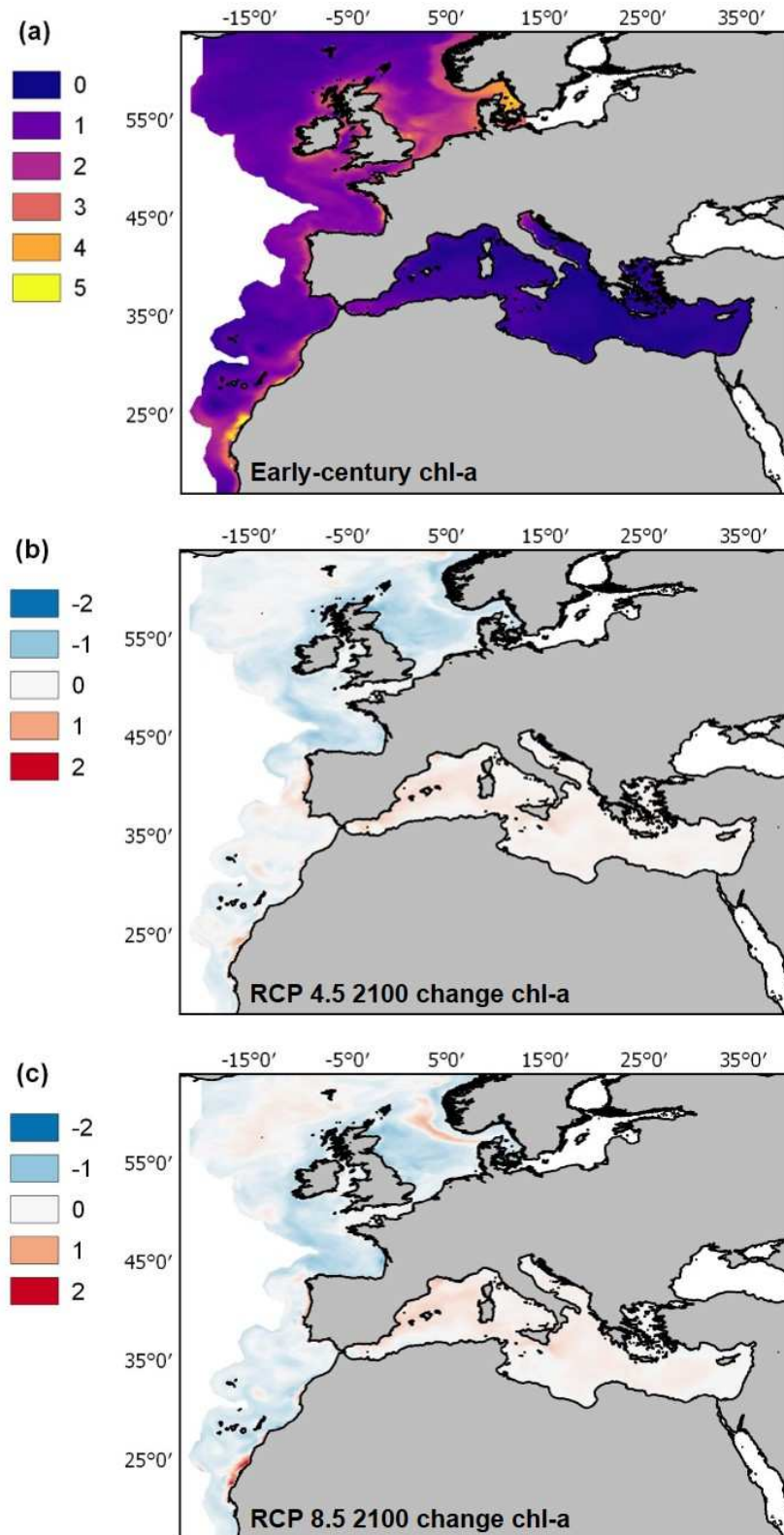
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Figure 3. (a) Mean annual water temperature ($^{\circ}\text{C}$) for the early-century reference period, 2000-2004, and changes in mean annual water temperature ($^{\circ}\text{C}$) under the emissions scenarios (b) RCP 4.5 and (c) 8.5 by late-century (2090-2099). The white areas are outside the model domain.



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Figure 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.

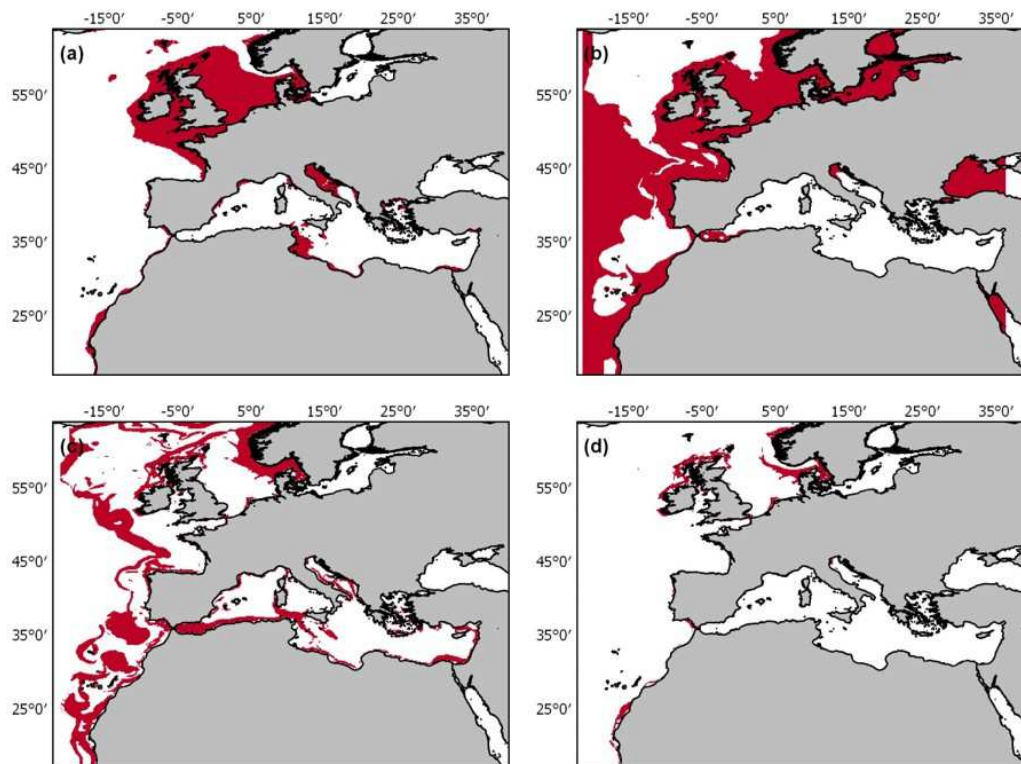
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336

337 3.2 Delimitation of tolerance range

338 The results of the binary, threshold-based masking of unsuitable area for the early-century
339 reference period are presented in Figure 5. Very similar results were also obtained and used
340 for each of the two late-century climate change scenarios. Although water temperature (3-
341 35°C; Bayne, 2017) and salinity (15-45 psu; Nell & Holliday,1988) were also considered,
342 these were not found to limit the suitable area in terms of Pacific oyster tolerance ranges for
343 any of the periods or scenarios considered here. Further narrowing the salinity range to 25-40
344 psu was likewise not found to limit the suitable area. We see that, although current speed is
345 the primary limiting factor for much of the study area (Fig. 5c), bathymetry (Fig. 5a) and chl-a
346 concentration (Fig. 5b) ranges also serve to limit some areas. This is notably the case in the
347 Mediterranean Sea, with bathymetry alone found to further limit the potential of offshore
348 Pacific oyster cultivation along the north coast of Spain and northern and western Portugal at
349 the coarse spatial resolution of the data used in this exercise. Areas where conditions fall
350 within all tolerance ranges are highlighted in the cumulative constraint mask (Fig. 5d).
351 Within these areas, the growth potential was simulated and mapped by using the DEB model.

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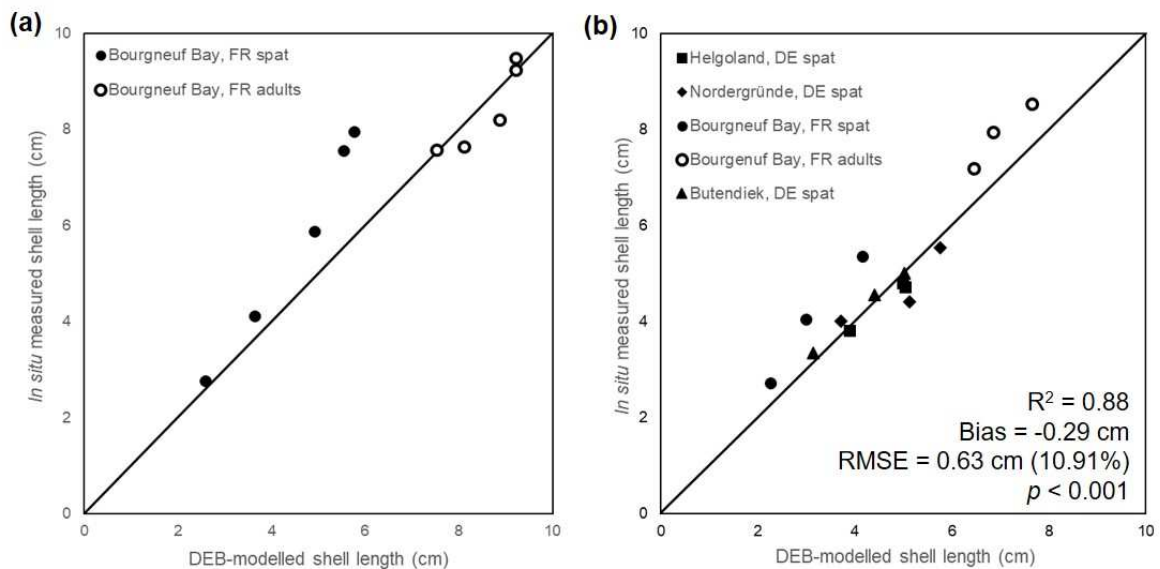


353

354 Figure 5. Ranges within which Pacific oyster cultivation is considered to be
355 suitable (in red), based on (a) bathymetry, (b) chlorophyll-a, and (c) current speed
356 masks used to define (d) the overall suitable area for Pacific oyster cultivation and
357 within which DEB modelling was carried out, for the early-century reference
358 period.

360 3.3 Dynamic Energy Budget (DEB) calibration and validation

361 Only one parameter of the DEB model was required to be tuned. The half-saturation
 362 coefficient (X_k) was determined through the regression-based optimization using data on
 363 offshore adult and spat growth in Bourgneuf Bay, France, in 2010. The resulting value was
 364 found to reasonably model adult and spat oyster growth observed *in situ* for a separate year
 365 (2008) in Bourgneuf Bay, as well as that measured *in situ* at three German sites in 2004 and
 366 2007 (Pogoda et al. 2011), across the full *in situ* size range (Fig. 6). Shell length
 367 measurements ranged from less than 3 to almost 10 cm, corresponding to total weights
 368 ranging between approximately 2 and 75 g. Note that *in situ* measurements from the start of
 369 the growing seasons were used to initialize the DEB model, and so are not included in Fig. 6.



370

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

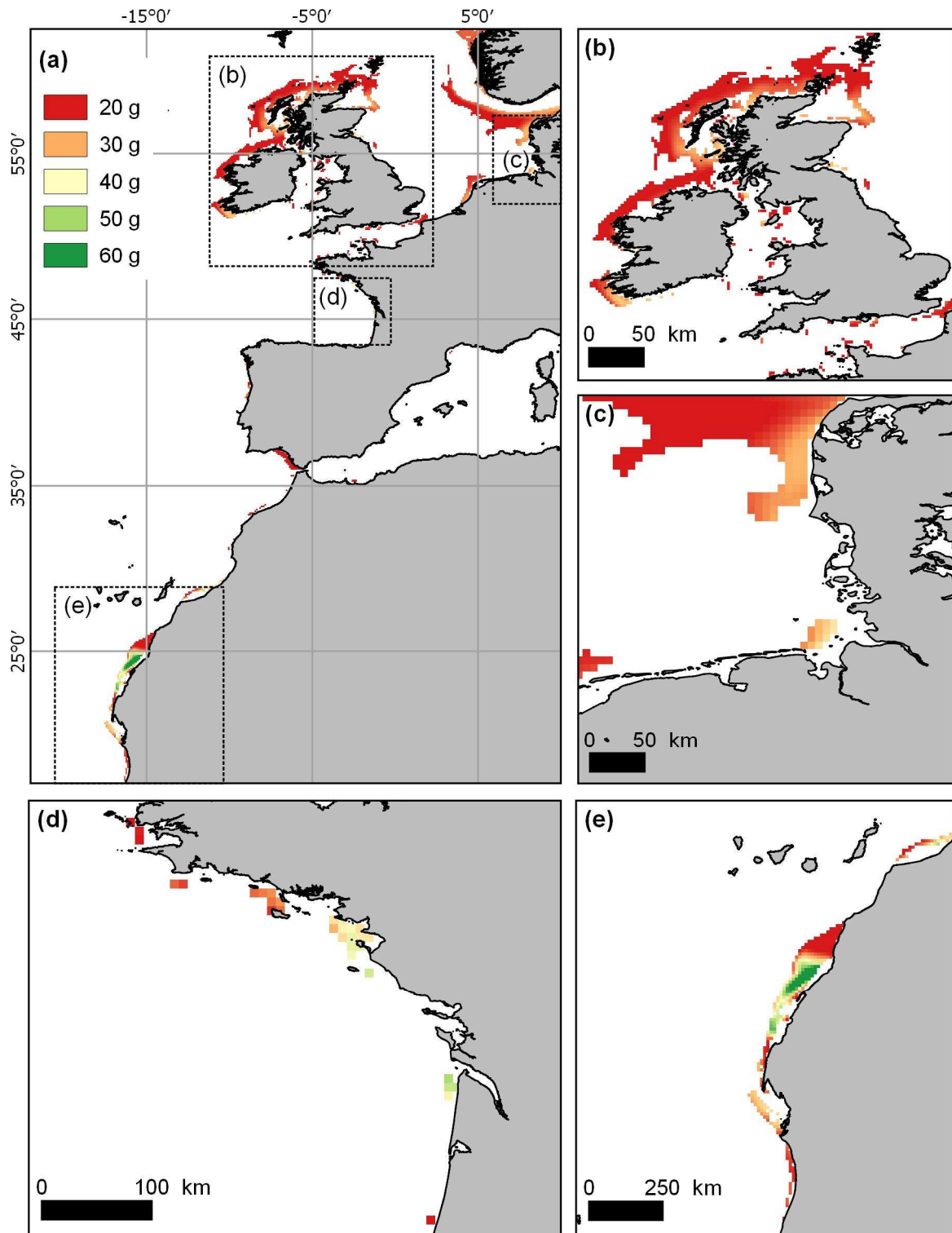
373

374 3.4 Oyster growth indicator mapping

375 *Current spatial trends and hot spots*

376 Within the suitable area determined through tolerance range masking (Fig. 5), oyster growth
 377 potential was found to be highly variable for each of the three indicators. Total adult weight
 378 obtained for the main European market (i.e., December 1, Fig. 7), shows many areas of low
 379 growth (in red) where only ~6 g were gained over the entire growing season (from the initial
 380 total weight of 14 g on April 1), and end-of-season weight remains below the market
 381 minimum (i.e., 30 g). A number of areas, especially close to the coast, mapped in orange,
 382 yellow, or green, were found to achieve minimum market weight under current (i.e., early-
 383 century reference period) conditions, with several along the French Atlantic coast of the
 384 Biscay Bay (Fig. 7d), as well as off western Africa (Fig. 7e). These areas resulted in hot spots
 385 of exceptional growth, with large oysters (46 – 65 g, corresponding to the French caliber 4;
 386 Palmer et al. 2020) growing from the initial 14 g spat within a single season. The two other

387 indicators determined the date on which a target total weight was achieved (i.e., 30 g for
388 adults (Fig. S2) and 14 g for spat (Fig. S3)). For both of these, the mapped area of the
389 indicator is less than the total suitable area and less than the area mapped for adult weight on
390 December 1, because the target weight will not be reached everywhere (e.g., the red areas of
391 Fig. 7 are < 30 g by the end of the growing season). However, where the target weights are
392 achieved, similar growth hot spots are identified, notably in western France and Africa.

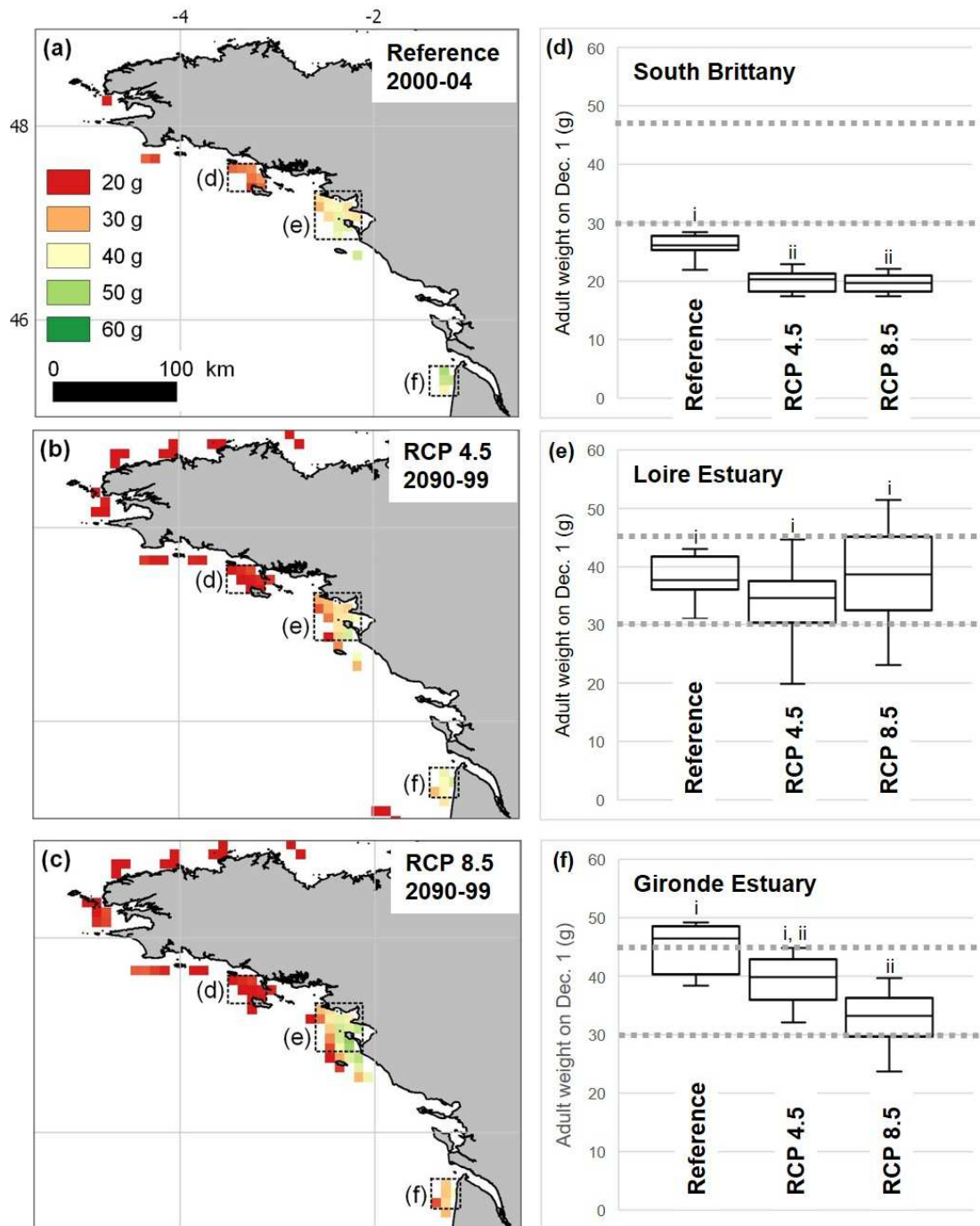


394 Figure 7. Pacific oyster total adult weight obtained by Dec. 1 (from an initial
395 weight of 14 g on April 1) for the early-century reference period, for the full
396 model domain (a) and indicated close-ups: (b) the United Kingdom, (b) the
397 southeastern North Sea, (c) the Bay of Biscay, and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

399

400 *Climate robust zones*

401 Future growth potential was also considered by mapping the indicators for each of the climate
402 change scenarios, to assess where investments to the industry and related policy decisions
403 might be the most sustainable, as well as have the most impact currently. Figure 8 shows the
404 example of adult growth (total weight by Dec. 1) for several potential zones off western
405 France, near areas where Pacific oyster is currently cultivated, and compares current growth
406 and spatial variability (Fig. 8a) with those under RCP 4.5 (Fig. 8b) and RCP 8.5 (Fig. 8c). An
407 area of relatively poor and decreasing growth potential is observed in South Brittany (Fig.
408 8d). ANOVA and Tukey pairwise comparisons indicate decreasing growth potential under
409 both future climate scenarios compared with current conditions in this area (Tukey $p < 0.001$
410 for both RCP 4.5 and RCP 8.5. This contrasts with an area of moderate and stable growth in
411 coastal waters close to the Loire Estuary (Fig. 8e). Kruskal-Wallis ANOVA by ranks
412 indicates no significant difference between current and future scenarios there ($p = 0.122$).
413 Another area with very good growth potential is observed in the coastal waters south of the
414 Gironde Estuary (Fig. 8f). Here, the growth potential was projected to remain reasonable in
415 both scenarios, with marketable product achieved within the average projected future season,
416 despite the potential decrease under both future RCP scenarios compared to the reference
417 period.



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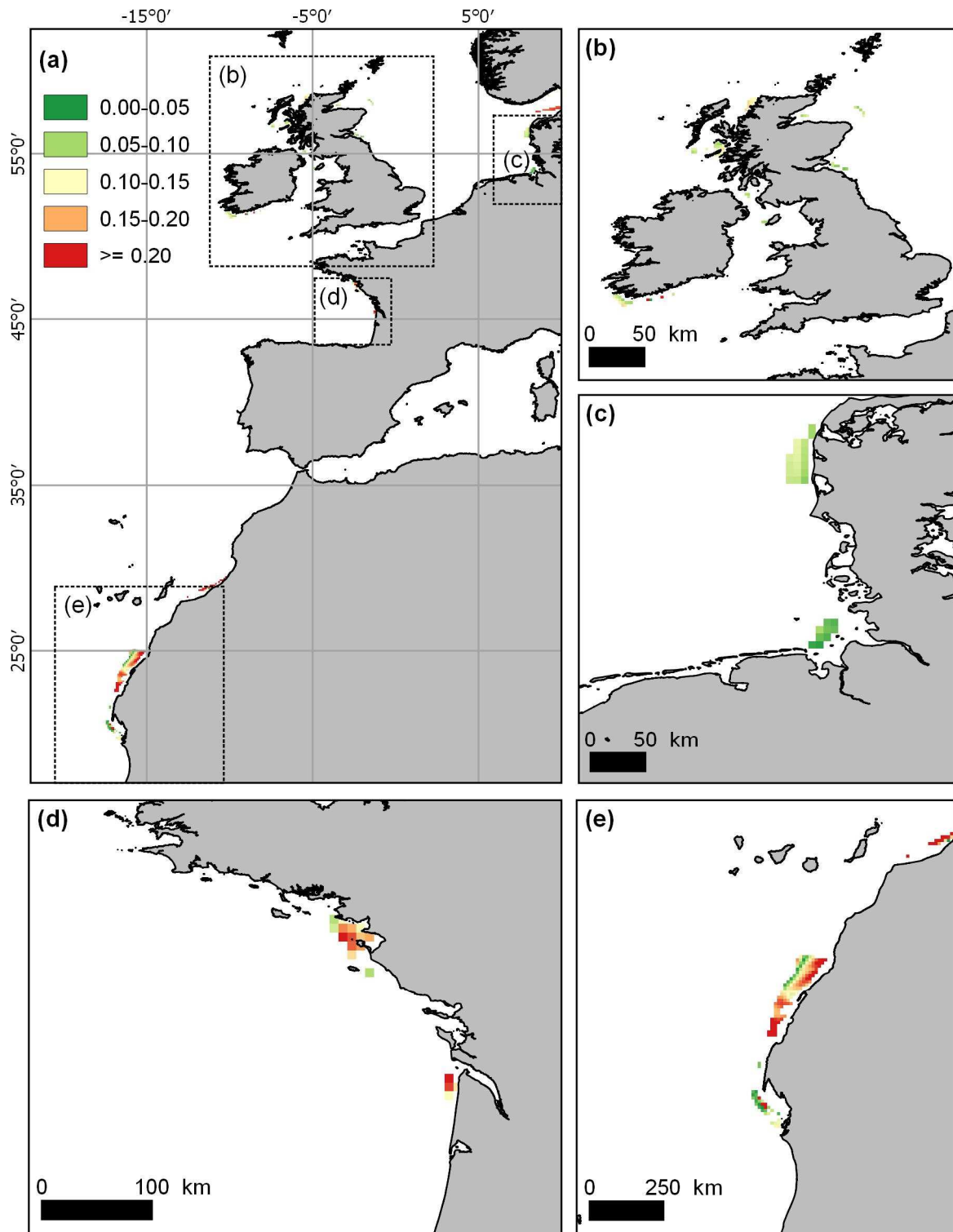
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429

Figure 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 Calibre 4 total weight (45 g) for the French market (Palmer et al. 2020). Boxes sharing a common superscript are not statistically different (Tukey $p < 0.05$).

430 Such information can also be considered and mapped in terms of a decision-making
431 framework, such as that proposed in Figure 2. After determining areas where the user-
432 defined criteria of “good” growth potential is currently achieved (the 30 g minimum
433 market weight is applied in this example), areas where this is also achieved in the future
434 for at least one of the climate change scenarios were identified, and further refined to
435 areas where “good” growth potential was consistent between climate change scenarios
436 (i.e., ΔX_{RCP} , as defined in eq. 4). These areas are mapped for our example indicator
437 (adult weight on December 1) in Figure 9, and include the Loire Estuary area identified
438 in Fig. 8e discussed above, with most climate-robust (i.e., most consistent future
439 conditions, also characterized by good current and future growth potential) in green, and
440 indicate the interest of certain areas from a climate change perspective. This further
441 constrains areas to be targeted for investment, such as off the coasts of Scotland,
442 Ireland, Germany, Denmark, France, and western Africa (Fig. 9). These areas are fewer
443 and smaller than the current areas of good growth potential in Figure 7, as growth
444 potential decreases under at least one climate change scenarios for many areas.
445 Similarly, the most “climate robust” areas (lowest ΔX_{RCP}) highlighted in Figure 9 are
446 not necessarily those with the highest current growth potential highlighted in Figure 7,
447 since this is instead an indicator of future change and stability between climate
448 scenarios (i.e., off the coast of Germany in Figs. 7c and 9c versus off the coast of
449 western Africa in Figs. 7e and 9e). It is therefore recommended to include both of these
450 respective absolute and relative indicators in policy and investment considerations.

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Figure 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). 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.

459 4. Discussion

460 4.1 Spatial trends and areas of interest identified

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

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

481 This corresponds to the general spatial trends in productivity and magnitude of chl-a
482 concentrations observed here by others over the past decades (Demarcq and Somoue, 2015).
483 Furthermore, we see both climate change scenarios corresponding to further increases in
484 annual mean chl-a relative to the early-century reference period (Fig. 4b,c), with even more
485 productive conditions under more extreme climate change (i.e., RCP 8.5). It is therefore
486 unsurprising to see this area also highlighted as an area of exceptional potential in the future,
487 and several large areas (totalling > 6000 km²) where this is expected to be the case under both
488 climate change scenarios considered are highlighted (in green) as relatively climate robust in
489 Fig. 9a,e.

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

500 Typically, for example near the calibration-validation site of Bourgneuf Bay, France, adult
501 grow-out from spat of a similar size will take at least two (and up to four) growing seasons in

502 the nearshore intertidal environment where oyster farms are currently located (note that these
503 areas cannot be observed at the spatial resolution of this work), due to particular challenges
504 encountered there (i.e., much higher turbidity; substantially lower immersion time; Palmer et
505 al., 2020). Although the nearshore-offshore difference in growth rates will certainly be less
506 substantial in areas where these factors are not as contrasted from one setting to the other (i.e.,
507 nearshore oyster cultivation in fjords or lochs where tidal gradients and inorganic turbidity are
508 lower), and further experimental results are needed to evaluate this, faster growth may be a
509 primary incentive to moving cultivation offshore. This is in addition to existing space
510 constraints already highlighted as a barrier to European aquaculture expansion nearer shore
511 (Hofherr et al., 2015).

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

520

521 4.2 Advantages and limitations of the modelling approach and data used

522 The advantage of combining dynamic, ecophysiological growth modelling with the binary
523 tolerance range threshold approach employed elsewhere (e.g., Gentry et al. 2017; Kapetsy et
524 al., 2013) is clear in terms of the additional information and insight provided. Within areas
525 identified to fall within the Pacific oyster tolerance range for a number of variables (Fig. 5d),
526 there is a great deal of variability in oyster growth potential. Such an approach has also been
527 used to identify suitable areas for finfish cultivation in the Mediterranean (Porporato et al.,
528 2020) and North Africa (Brigolin et al., 2015) and for shellfish cultivation in the Adriatic
529 (Brigolin et al., 2017) and western France (Thomas et al., 2011, 2016; Barillé et al., 2020),
530 where good modelled growth is considered with other advantageous factors in more thorough
531 spatial multi-criteria evaluation.

532 Under the same DEB model initialization (i.e., oyster size, start and end dates) and
533 parameterization, total adult weight at the end of the growing season ranges from < 20 g to >
534 60 g across the full model domain (Fig. 7a), and ranges by as much as 50 g over as little a
535 distance as 100 km, notably off the coast of northwestern Africa (Fig. 7e), but also by as
536 much as 20 g over the same distance along the French Atlantic (Fig. 7d) and western Scottish
537 coast (Fig. 7b), and even by as much as 10-15 g over just 30 km for parts of all of the areas of
538 interest (Fig. 7). Without this information to further optimize aquaculture zoning and site
539 selection, we would simply know that Pacific oyster aquaculture should be feasible across this
540 area (Fig. 5).

541 While the coarse spatial resolution of the input data (0.1°) is an inherent limitation of such
542 broad scale studies, it makes it possible to provide general assessment of trends and scenarios
543 using a cohesive approach and methodology at multi-national scale, to support decision-
544 making and planning, and identify hot spots for potential development or further

545 consideration (Falconer et al., 2019). However, the inability of studies at such large scales to
546 account for environmental heterogeneity on finer spatial and temporal scales, documented as
547 being important to organismal physiology, is a notable limitation and highlights the need for
548 complementary studies across scales (Helmuth et al., 2014). In many instances, anomalies and
549 extreme events (for example in water temperature), as well as the dynamic and heterogeneous
550 nature of the “ocean weather” (Bates et al., 2018), which could substantially affect growth,
551 reproduction, and mortality of Pacific oyster and many other species, may not be detected
552 when using such coarse input data. Instead, the signal is averaged out over the larger spatial
553 and temporal timestep and extremes are dampened. Although the offshore environment
554 investigated here is expected to be much less sensitive and heterogeneous compared with the
555 highly variable nearer-shore and intertidal environments (i.e. Gernez et al., 2017; Choi et al.,
556 2019), the importance of local climatic and non-climatic stressors should not be neglected in
557 site selection and should be included in the finer-scale site selection activities recommended
558 to follow broad zoning initiatives.

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

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

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

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

604

605 4.3 Additional considerations in establishing Allocated Zones for Aquaculture

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

616 Some factors are known to currently preclude the installation of offshore infrastructure in
617 some locations that might otherwise be productive (e.g., wave height, which may impact
618 organism growth potential as well as accessibility of offshore structures to undertake
619 operations and maintenance (Buck and Langan, 2017)). Some are likely to intensify in some
620 locations or generally under climate change conditions (e.g., frequency of storms (Feser et al.,
621 2015), ocean acidification (Kroeker et al., 2010; Barton et al., 2012), frequency of wintertime
622 seawater temperature anomalies (Thomas et al., 2018), and drop in pH levels (Law et al.
623 2018), as well as the cumulative effects of combinations of these parameters). These stressors
624 will have a direct impact on the potential for offshore as well as nearshore aquaculture into
625 the future. Others (e.g., storm surges (Vousdoukas et al., 2016) and sea level rise (Grinsted et
626 al., 2015)) may not be as detrimental to infrastructure and cultivation in the offshore
627 environment itself, but may be important to consider in terms of their projected increasing
628 impact on the coast and related damage to infrastructure necessary to support offshore
629 production there (e.g., ports; grading, packing, and distribution facilities). Likewise,
630 interaction between and among climatic and non-climatic stressors, and potential adaptation
631 and acclimatization may be substantial (Helmuth et al., 2014).

632 As different species are expected and documented to respond differently to the impacts of
633 climate change (e.g., Filgueira et al., 2018; Steeves et al., 2018; Thomas and Bacher, 2018),
634 this should also be considered in selecting species to farm. For the Atlantic Canadian site
635 investigated by Steeves et al. (2018), although the growth of both species was found to be
636 enhanced overall, the greater thermal tolerance of the eastern oyster, *Crassostrea virginica*,
637 allowed it to outperform the blue mussel, *Mytilus edulis*. Modelling by Filgueira et al. (2018)
638 found similar results favouring *C. virginica* over *M. edulis* in warming scenarios, and also
639 suggests that bivalve aquaculture may enhance ecological resilience under some climate
640 change scenarios and coastal geomorphologies (e.g., bays with large rivers). Likewise, the
641 negative environmental impacts accruing from the aquaculture of different species are also
642 not expected to be uniform in space and time under different climate scenarios and for
643 different species. This has been demonstrated for the Mediterranean seabass, *Dicentrarchus*
644 *labrax*, in the Mediterranean and Black seas in terms of organic loading as well as animal
645 growth, whereby the trade-off between fish growth and farm pollution was found to become
646 increasingly difficult to optimize under their modelled climate change scenarios (Sarà et al.,
647 2018). In the Mediterranean, the growth, mortality, and phenology of three different
648 commercial mussel species has been forecasted to respond variably and non-linearly by
649 species and site in response to modelled warming (Montalto et al., 2016). Pacific oyster
650 results from the northeast Atlantic suggest that climate change has a positive impact on oyster
651 growth and reproduction (due to chl-a and SST increase; Thomas et al., 2016) and that
652 phytoplankton dynamics, more than temperature directly, underlie modelled climate-driven
653 phenological shifts in this species in terms of spawning event timing (Gourault et al., 2019).
654 On the other hand, warming is also likely to result in a higher risk of adult oyster mortality
655 due to an increase in the occurrences of positive wintertime temperature anomalies (Thomas
656 et al., 2018). This highlights the need for modelling across trophic levels, and to consider
657 seasonal dynamics and interannual climate variability in addition to more binary tolerance
658 ranges.

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

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

677 Although it is likely that not all data that would be beneficial to include are available at the
678 appropriate spatial resolution and broad spatial coverage demonstrated here (Falconer et al.,
679 2019), such data could be added upon considering specific identified hot spots at the smaller
680 regional scale to further assess a proposed AZA, or at the even smaller local scale, as part of
681 the farm site selection step. In this work, our aim is to demonstrate the added benefit and
682 utility of using such a dynamic, growth modelling-based approach to identify areas of interest
683 from a biological perspective, and we recommend the integration of such results and
684 indicators as produced here into a fuller SMCE or MCDA.

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

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

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

715

716 **5. Conclusions**

717 Several large (> 1000 km²) areas have been highlighted as current hot spots for offshore
718 Pacific oyster cultivation across Europe and northwestern Africa. These are found to be
719 associated with continued good production into the coming century under distinct climate

720 change scenarios according to the input data, model results, and framework presented here.
721 Pacific oyster and/or other bivalve cultivation is already practiced in the more nearshore
722 environment for several highlighted regions, including the intertidal zone of the French
723 Atlantic, the southern North Sea, southwestern Ireland, and lochs of western Scotland,
724 indicating the promise for facilitated industry and expertise transfer to the offshore
725 environment in these areas. A large area off the coasts of Western Sahara and Mauritania is
726 also highlighted, corresponding to a major upwelling zone, which could indicate a promising
727 new industry for this region. Such climate-robust areas of exceptional Pacific oyster growth
728 are recommended for prioritization in subsequent zoning or higher-resolution site selection. A
729 suite of flexible indicators and a framework to integrate results into decision making have
730 been demonstrated, which may be adapted to the specific decision-making need or to uptake
731 similar modelling results for other species of interest.

732

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744 **Author contributions**

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

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