



Direct effects of climate change on productivity of European aquaculture

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Abstract

Aquaculture managers and industry must take into account the impact of climate change on production and environmental quality to ensure that sector growth is sustainable over the coming decades, a key requirement for food security. The potential effects of climate change on aquaculture range from changes to production capacity in existing cultivation areas to changes in the areas themselves, which may become unsuitable for particular species, but also suitable for new species. The prediction of where and how such changes may occur is challenging, not least because the cultivated species may themselves exhibit plasticity, which makes it difficult to forecast the degree to which different locations and culture types may be affected. This work presents a modelling approach used to predict the potential effects of climate change on aquaculture, considering six key finfish and shellfish species of economic importance in Europe: Atlantic salmon (*Salmo salar*), gilthead seabream (*Sparus aurata*), sea bass (*Dicentrarchus labrax*), Pacific oyster (*Crassostrea gigas*), blue mussel (*Mytilus edulis*) and Mediterranean mussel (*Mytilus galloprovincialis*). The focus is on effects on physiology, growth performance and environmental footprint, and the resultant economic impact at the farm scale. Climate projections for present-day conditions; mid-century (2040–2060) and end-of-century (2080–2100) were extracted from regionally downscaled global climate models and used to force bioenergetic models. For each of those time periods, two different carbon concentration scenarios were considered: a moderate situation (IPCC RCP 4.5) and an extreme situation (IPCC RCP 8.5). Projected temperature changes will have variable effects on growth depending on the species and geographic region. From the case studies analysed, gilthead bream farmed in sea cages in the western Mediterranean was the most vulnerable, whereas offshore-suspended mussel culture in SW Portugal was least affected. Most of the marine finfish simulated were projected to have decreased feeding efficiency in both mid-century and end-of-century climate scenarios. Bivalve shellfish showed a decreasing trend with respect to most productivity parameters as climate change progresses, under both emission scenarios. As a general trend across species and regions, economic uncertainty is expected to increase under all future projections.

Keywords Aquaculture · Climate change · IPCC · Modelling · Productivity · Management

Introduction

In 2017, European aquaculture production was just short of three million tonnes (META 2020), about 54% of which came from non-EU countries, mainly Norway and Turkey. Overall, European aquaculture contributes less than 4% to the world total of 80 Mt (FAO 2018), which partly explains why the European Union currently imports about 68% of the aquatic products it consumes (European Commission 2018).

Policymakers and citizens alike recognize the need for greater aquatic food security in the EU, which means increasing aquaculture production (see European Parliament resolution P8_TA(2018)0248), given that capture fisheries for most species are stagnant or declining (e.g. Vasilakopoulos et al. 2014; Froese et al. 2018). Sustainable growth of the aquaculture sector will also benefit employment, trade balance and food safety, given the high standards EU producers must comply with.

In order to achieve sustainable growth, investors and industry need information on the multiple challenges an expanding aquaculture sector must deal with; these include (Ferreira et al. 2020): (i) licencing and competing uses of space; (ii) market dynamics, including global markets and (iii) environmental hazards and constraints. The first class of issues is regulatory and governance related, and the second class is difficult to predict given market uncertainty both in supply and pricing—nevertheless, given the current burden of imports and the increasing tendency of major world producers to satisfy domestic markets (Lopes et al. 2017), there is a strong case for expansion in the EU.

Although there are a number of environmental constraints, by far the most important over the medium (20–30 years) to long (50–100 years) term is climate change. Anthropogenic-induced warming of aquatic habitats (marine and freshwater), as well as altered precipitation patterns, is expected to have direct and indirect effects on aquaculture such as changes in disease occurrence, physiology, growth performance and/or feed conversion efficiency and reproduction of farmed fish and shellfish (Catalán et al. 2019; Reid et al. 2019; Dahlke et al. 2020). These direct and indirect effects may result in favourable, unfavourable or neutral changes in aquaculture, in the short or long term and at different spatial scales (Barange et al. 2018).

Water temperature is a key factor influencing the physiology and ecology of fish (Pörtner and Peck 2010; Frost et al. 2012; Neubauer and Andersen 2019) and shellfish (e.g. Bayne 2017) species, but the effects of increases in temperature are not necessarily negative; higher temperatures may be associated with longer growing seasons, faster growth rates and lower natural winter mortality depending on region, farm and species (Li et al. 2016; Weatherdon et al. 2016).

Potential negative aspects include changes in (i) cultivation range for particular species depending on temperature thresholds; (ii) dissolved oxygen in the water column; (iii) biomass and species composition of algal blooms; (iv) intensity and/or frequency of storms (Seneviratne et al. 2012; Bouwer 2019), increasing damage to farm infrastructure (Reid et al. 2019), escapees, and introgression and (v) the host-pathogen overlap window, which can change the nature and frequency of disease events (Jennings et al. 2016).

In order to assess the effects of climate change on cultivated organisms, models must be applied to predict (a) the changes in the driving variables that determine the performance of aquaculture farms and (b) the consequences of those changes on the performance of the farms using three key performance indicators (KPI): production, environmental effects and profitability.

In order to assess changes to driving variables in the ocean, global climate models must be used, such as those included in the Fifth Coupled Model Intercomparison Project (Taylor et al.

2011) and used by the Intergovernmental Panel on Climate Change. Outputs of these models can then provide the forcing for models that downscale to the regional level and simulate transfers of carbon and nutrients through marine systems. A few examples of this coupling are the Proudman Oceanographic Laboratory Coastal Ocean Modelling System coupled to the European Regional Seas Ecosystem Model (POLCOMS-ERSEM) (Butenschön et al. 2016; Holt et al. 2001) or the Regional Ocean Modelling System (ROMS) (Shchepetkin and McWilliams 2005) coupled to the NORWegian ECOlogical Model system (NORWECOM) (Skogen et al. 2014).

The simulation of aquaculture at specific test sites requires local-scale models—a wide variety of these are available, including models to simulate production (Gangnery et al. 2004; Ferreira et al. 2008; Larsen et al. 2014), environmental impacts (Cromey et al. 2002; Fabi et al. 2009) and economic optimisation (Ferreira et al. 2012) of both finfish and bivalve aquaculture (Brigolin et al. 2009; Ferreira et al. 2012).

The most useful models for analysing response provide a deterministic simulation of physiology for the species of interest—e.g. Scope For Growth models (Brigolin et al. 2009), Dynamic Energy Budget models (Fuentes-Santos et al. 2019; Kooijman 2010) or the species-specific ecophysiological model (Scholten and Smaal 1998, 1999)—and scale individual processes to a typical farm (e.g. Cubillo et al. 2016; Føre et al. 2016). In addition, outputs for the relevant KPI are essential in order to analyse the consequences of different climate change scenarios for the sustainable development of aquaculture.

In this work, we selected and applied a set of models to address both the driving forces and the response of aquaculture farms to the direct effects of different climate change scenarios. Where appropriate, individual models were calibrated based on experiments designed to quantify key parameters such as effects of multiple stressors (e.g. changes in temperature and dissolved oxygen) on feeding or growth rates. Details of experimental work are given in CERES (2020a, 2020b).

In parallel with the work reported herein, quasi-deterministic models were developed, using the same physiological basis as used for this study, to address the indirect effects of climate change, with an emphasis on host-pathogen dynamics (Ferreira et al. 2019, 2021).

The modelling framework applied in the present work considered six species (3 fish and 3 bivalves), which together account for about 80% of European production. The main aims of this study were to:

1. Develop and implement a multi-model framework to address direct effects of climate change on growth performance and aquaculture production;
2. Apply this framework to key marine finfish and shellfish species farmed in Europe;
3. Inform industry and policymakers about effects of these climate change-related stressors;
4. Propose adaptation responses and measures for risk mitigation and sustainable development of aquaculture.

Material and methods

Modelling approach

This article addresses the projected changes in suitability and productivity due to direct effects of climate change on cultivated finfish and bivalve shellfish species of economic importance in Europe by coupling climate models, bioenergetic models and suitability maps.

We used regionally downscaled climate models to simulate future climate change projections under two different carbon concentration scenarios, a moderate and a worst-case scenario, based on the IPCC Representative Concentration Pathways (van Vuuren et al. 2011).

The outputs of these models provided the forcing variables for individual growth and local-scale production models. These local-scale models were used to simulate the impacts of direct effects of climate change on the productivity of farming systems representative for each species and country.

This study includes marine species of primary economic or regional speciality interest which, together, cover most marine aquaculture production within the EU28 (Table 1). The local-scale production models are based on individual growth models developed for each of these species, which allows the evaluation of the effects of climate change on the growth and physiology of cultured animals.

Modelling results obtained for present-day conditions (2000–2019) were compared with projections for the mid-twenty-first century (2040–2059) and the end-of-century (2080–2099) under both moderate and extreme carbon concentration scenarios, following the steps in Fig. 1.

Simulating future conditions/scenarios definition

The EU H2020 project CERES (Climate change and European aquatic RESources) used regionally downscaled climate models to produce future climate projections of the physical and biogeochemical environment and the lower trophic level ecosystem for European seas in the twenty-first century.

The northeast Atlantic, including the North Sea and the Mediterranean Sea where most species of this study are farmed, was modelled as a single domain of the POLCOMS-ERSEM modelling system that has been successfully applied for these regions (Butenschön et al. 2016; Holt et al. 2001, 2012; Kay and Butenschön 2016). The Norwegian and Barents Sea (where the main production of Norwegian Salmon is located) were modelled using the ROMS model coupled to the physical, chemical and biological NORWECOM model (Kay et al. 2018).

The future climate is strongly dependent on the future emissions of greenhouse gases, and two different representative concentration pathways (RCPs) were used to describe two alternative greenhouse gas concentration trajectories up to 2100, as adopted by the Intergovernmental Panel on Climate Change (IPCC): (i) a moderate situation (RCP 4.5), in which carbon concentrations rise until mid-century and then stabilize around 650 ppm, and (ii) an extreme situation (RCP 8.5) in which carbon concentrations rise throughout the century reaching more

Table 1 CERES species location pairs, type of culture and annual production in tonnes (economic importance)

Region	Species	Country	Annual production ¹ per country/Europe	Culture system
Northeast Atlantic	Atlantic salmon	Ireland	18,342/1,442,889	Circular cages
Northeast Atlantic	Atlantic salmon	Norway	1,233,619/1,442,889	Circular cages
Eastern Mediterranean	European seabass	Turkey	99,971/178,993	Circular cages
Western Mediterranean	Gilthead seabream	Spain	17,005/156,026	Circular cages
North Sea coast	Blue mussel	Denmark	2414/110,378	Longlines
North Sea coast	Blue mussel	Netherlands	43,969/110,378	Bottom culture
North Sea coast	Pacific oyster	Netherlands	2323/95,664	Off-bottom trestles
Southwest Europe (Atlantic)	Mediterranean mussel	Portugal	1746/334,193	Longlines offshore

¹ Country and European totals from Eurostat, sourced from <https://longline.co.uk/meta>

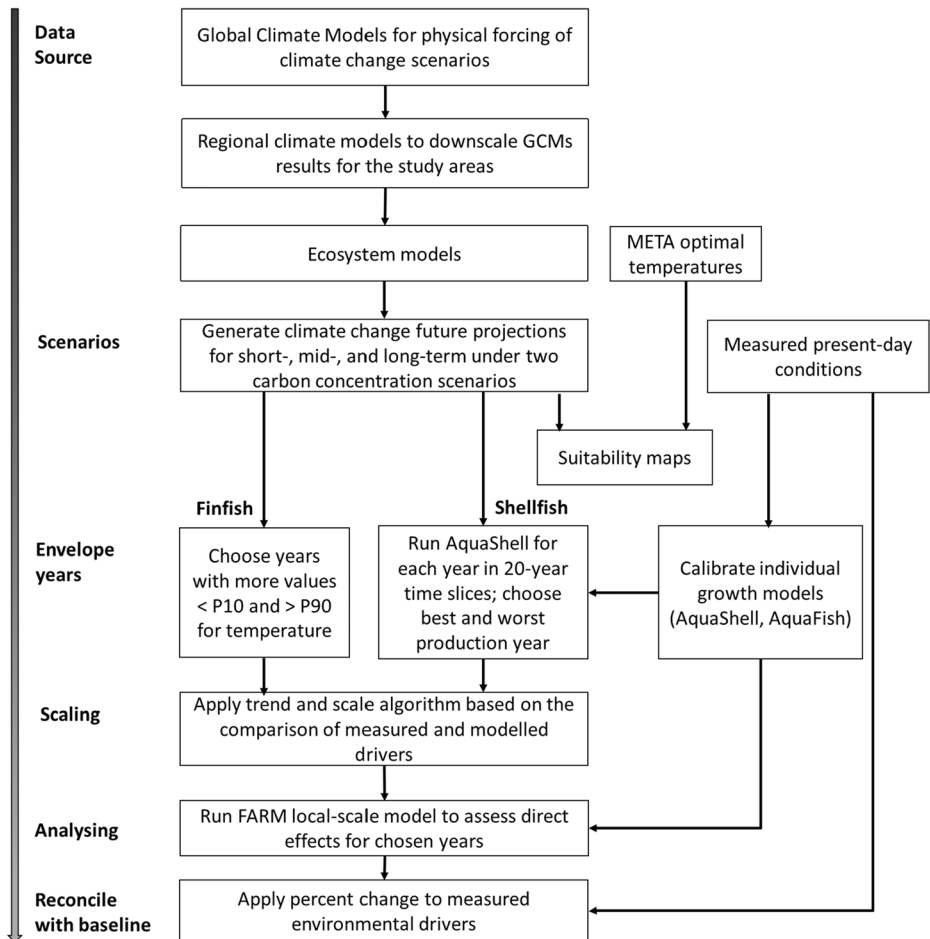


Fig. 1 Sequence of work followed in the present study that includes the adaptation of outputs from regionally downscaled climate models as inputs for individual growth models and local-scale population models

than 1370 ppm in 2100 (van Vuuren et al. 2011). The exception is the Norwegian Sea, where projections are limited to RCP 4.5 up to 2070. These future climate projections were obtained from two global climate models: MPI-ESM-LR for POLCOMS-ERSEM and NorESM for NORWECOM.

The regionally downscaled climate models provided projections for daily mean temperature, salinity, chlorophyll and other biogeochemical variables, which were used as drivers by individual growth models and local-scale production models.

The model's skill was assessed by comparing to satellite values of sea surface temperature and chlorophyll (Kay et al. 2018). Monthly mean sea surface temperature was in good agreement with satellite observations for 1985–2015, with bias less than 0.5 °C and correlation higher than 0.9 in all regions. The model reproduces the temporal and spatial patterns of chlorophyll concentration seen in satellite observations for 1997–2015, though with summer values higher than observed. Projected change in sea surface temperature is consistent with that from a range of global climate models in all regions (Peck et al. 2020, Chapter 2).

Downscaling drivers from regional to farm-scale level

The environmental drivers generated by the regional-scale physical and biogeochemical models were adapted due to discrepancies in scale between these large-scale models and farm-scale aquaculture models.

All the locations selected for the aquaculture population modelling are either in estuarine and fjordic systems or at the inner shelf, where mesoscale oceanographic features need to be resolved in order to properly characterise the main environmental drivers. The POLCOMS-ERSEM and the NORWECOM models have an approximately 10×10 km (100 km^2) spatial resolution, which is too coarse to resolve cultivation in embayments or coastal waters.

In addition, the large-scale models simulate the twenty-first century continuously and produce daily, weekly or monthly averages. For the study of direct and indirect effects of climate change on aquaculture, our methodology required a time-slice approach using 20-year intervals to characterize the short- (2000–2020), mid- (2040–2060) and long-term (2080–2100) responses to climate change.

To reproduce the distribution of possible outcomes within each of the 20-year interval time slice, the model must be run twenty times for each element of the combinatorial triplet (time slice, species location, RCP). To overcome the logistical constraints while delivering this distribution, we opted for the calculation of two extreme years for each combination, i.e. the envelope years that cover the possible range of the drivers, leading to a ten-fold reduction in the number of model runs (Fig. 1, more details in Ferreira et al. 2019).

In order to set baselines and perform the validation of the population model, at least a single year of measurements of the main environmental drivers was required for each of the target locations. The projection of these years into the future or into days when there are no measurements was done by combining the measured value and the trend between measurement instants—anchor points—with the fluctuation of the large-scale model between those points. These transformations were applied at each segment between the anchor points and have the following assumptions and simplifications:

- For the observation year, the resulting value should be equal to the measurements for all anchor points;
- The slope between large-scale model results at the anchor points is not relevant but the fluctuation from the anchor points is;
- The slope between two anchor points is calculated based on the measurements and maintained in all scenarios;
- Zero or negative results are considered invalid;
- In the absence of a modelled variable, linear interpolation of the measured values is used in all runs. An exception to this is total particulate matter (TPM), absent in the large-scale model, which is assumed to vary with particulate organic matter (POM).

For each segment between the n and $n+1$ anchor points, the resulting downscaled variable C is:

$$C(t)_{n:n+1} = s C'_{LS}(t) + C_{ED}(t)|_n + t \left(\frac{\Delta C_{ED}}{\Delta t} \right) \Big|_n^{n+1}$$

where the fluctuation between the large-scale (subscript *LS*) model result at *n* and all results in the segment is:

$$C'_{LS}(t)_{n:n+1} = C_{LS}(t) - C_{LS}|_n$$

scaled to the range of the environmental drivers (subscript *ED*) by:

$$s = \frac{\max[C_{LS}] - \min[C_{LS}]}{\max[C_{ED}] - \min[C_{ED}]}$$

In summary, (i) the fluctuation between anchor points is used to interpolate between observations or project the fluctuations into the future; (ii) the measured trend is applied to this fluctuation and (iii) the fluctuation is scaled by the relation between the large-scale results and the observations to translate the oceanic type ranges into estuarine/near-shore type ranges. In the case of TPM, the fluctuation of modelled POM was used to project changes from measured TPM anchor points and scaled by the relation between the ranges of modelled POM and measured TPM.

While this algorithm fills in the gaps for the measurement years and is able to project these years into the past and future based on the large-scale model results, it has some limitations: (i) fewer measured anchor points decrease the robustness of the algorithm and (ii) the final results tend to converge around the anchor points making the method somewhat rigid in terms of the changes in the phase of the maxima and minima in relation to the measured year.

The forcing functions obtained from the climate models to drive the physiological models were temperature, salinity and seston concentration (Chl-a and detritus) for shellfish species and seawater temperature for finfish species. For each of the forcing functions, we considered depth-averaged values for the surface mixed layer, which can encompass the first 10 to 200 m depending on the location and time of year. For all locations, the models take into account the whole range of depths where finfish and shellfish are cultivated.

For bivalve shellfish species, each individual growth model was run for the full combination of scenarios (each of the twenty years within each time-slice and emission scenario) to approximate the extreme values by choosing the years that yield the highest and lowest harvestable biomass. The environmental drivers from those years were used to drive the farm-scale model.

For the finfish species, a selection procedure was devised to choose the pair of years which would capture the range of effects of future temperature variability, the key driver for the finfish models, within each 20-year time slice. Several routes may be taken to choose the two envelope years for temperature, e.g. (i) yearly mean; (ii) seasonal mean for the given season (e.g. coldest winter, hottest summer) and (iii) extreme warm and cold events. Any of these options will have drawbacks such as smoothing out extremes (year or season means); hiding shifts and duration of the season (year mean or extreme events). Due to the current emphasis on the projected increase in extreme events as one of the main outcomes of climate change on aquaculture, we opted to choose years which contained either more extreme cold weather or extreme hot weather events. To determine this, for each of the locations and time slices, a daily sea temperature percentile 10 (p10) and percentile 90 (p90) was calculated. Two years were chosen for each of the (location, time slice) pair to drive the farm-scale model: an extremely cold year with the larger number of days below p10 and an extremely hot year with the larger number of days above p90.

Individual growth models

The individual Net Energy Balance models used in this work are based on the generic AquaShell™ and AquaFish™ framework for shellfish and finfish species, respectively. These bioenergetic models have been parameterized for several bivalve and finfish species and used to predict their growth, reproductive effort and overall mass balance for the whole culture cycle at the individual level (e.g. Ferreira et al. 2010, 2012, 2014). Individual growth models were calibrated and validated against present-day conditions for each species and production region using experimental growth data obtained from CERES partners.

Individual models for finfish

The individual growth models (AquaFish) simulate fish growth and physiology through a mechanistic representation of feeding and feeding regulation; energy transfers (input and loss) through harvestable products, wastes and biological processes; oxygen consumption through anabolic and catabolic processes; and mass balance equations to account for the inputs and outputs to the production system. By contrast to organically extractive shellfish aquaculture, finfish are fed (typically dry feed pellets in the EU), and one of the key indicators of finfish aquaculture is the feed conversion ratio (FCR), meaning the feed supplied must be accounted for in the model. The mechanism controlling feeding regulation was adapted from feed tables which were used to derive equations relating feed intake to allometry and temperature.

The gilthead seabream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*) models used in this work are described in Ferreira et al. (2012), and the salmon (*Salmo salar*) model in Cubillo et al. (2016).

Individual models for shellfish

The shellfish growth models (AquaShell) are driven by allometry and relevant environmental variables. The clearance rate is a function of water temperature, salinity, seston concentration (Chl-a and detritus) and allometry. Oxygen consumption rate is a function of temperature and allometry. The models simulate changes in individual weight, expressed as tissue dry weight and shell weight, and scales to total fresh weight and shell length. These models additionally provide environmental feedback for particulate organic waste (faeces and pseudofaeces) and excretion of dissolved substances.

In order to predict direct climate change impacts on shellfish, existing formulations (i.e. functional responses to changes in temperature, salinity and available food) were taken or adapted from the literature and were parameterized based on physiological experiments developed under CERES (CERES 2020a, 2020b).

Local-scale production models

All the validated individual growth models were integrated into the FARM local-scale production model to simulate production, economic performance and environmental effects of finfish and shellfish aquaculture in the European Union. The general characteristics and implementation of the FARM model have been described in Ferreira et al. (2007a) and have been widely applied to multiple systems for the shellfish (e.g. Ferreira et al. 2007b, 2008, 2009) and finfish species (e.g. Ferreira et al. 2012, 2014) considered in the present study.

FARM was fed with an accurate description of the culture practice used at the “typical farm” following Lasner et al. (2016), which is considered to be representative for each species and region (Table 2 for shellfish and Table 3 for finfish). The local-scale models were validated against measured production at each farm using measured environmental drivers for present-day conditions provided by CERES partners.

The validated FARM model was then used to simulate different climate change scenarios, using mid- and end-of-century projections from regionally downscaled climate models (NORWECOM for Norwegian salmon and POLCOMS-ERSEM for the other species and locations), under two different carbon concentration scenarios: RCP 4.5 and RCP 8.5—RCP 4.5 for Norway (Kay et al. 2018)—which are further downscaled to the farm level.

Reconciliation with measured baseline results

In order to reduce linear errors, and given that the individual and population models were calibrated against present-day growth and environmental conditions, we applied the percent change of each scenario to these empirical results. For this, the results for each scenario were scaled by large-scale model results for the measured year. This percent change was then applied to population model results forced with empirical drivers measured at each farm.

We compared model results for present-day conditions (2000–2020) against mid-twenty-first century (2040–2060) and end-of-century (2080–2100) results, within each emission scenario. We assumed a symmetric behaviour of the data and the results for the two extreme years to represent the possible interval/range for the response. We calculated the average value of these two extreme years. If the mean value for a certain interval fell within (outside) the response range of another time-slice/emission scenario, the effects of climate change are

Table 2 Culture practice data for the typical shellfish farms in the different EU production regions. This data was used to run the FARM model under present-day conditions and climate change scenarios. *TFW*, total fresh weight

	Blue mussel Denmark	Blue mussel Netherlands	Pacific oyster Netherlands	Med mussel Portugal
Culture area (ha)	10.13	8.0	0.5	10.1
Culture structures	Suspended longlines	Subtidal—bottom culture	Intertidal—trestles	Suspended longlines
Seed cost (€ kg ⁻¹)	n.a. ¹	1.0	50	1.0
First-sale price (€ kg ⁻¹)	1.1	0.8	4.7	0.65
Stocking density (ind m ⁻²)	296	5,000	800	312
Mortality (% cycle ⁻¹)	17	98	76	10
Seed weight (g TFW)	3.74	0.2	0.14	1.0
First seeding day	291	120	90	150
Culture period (days)	365	794	900	550
Harvest weight (g TFW)	> 14	>16	>50	10–20

¹ Mussel seed in Denmark is typically obtained from collector ropes instead of hatcheries

Table 3 Culture practice data for the typical finfish farms in the different EU production regions. This data was used to run the FARM model under present-day conditions and climate change scenarios and test different climate change scenarios. *LW*, live weight

	Gilthead bream Spain	Sea bass Turkey	Atlantic salmon Ireland	Atlantic salmon Norway
Leased area (ha)	85.76	3.75	17.0	4.05
Culture area (ha)	0.84	0.98	1.9	0.8
Culture structures	Circular cages	Circular cages	Circular cages	Circular cages
Feed cost (€ kg ⁻¹)	1.00	0.66	1.51	1.11
Juvenile cost (€ per thousand fish)	275	168	797	1250
First-sale price (€ kg ⁻¹)	5.44	2.8	6.0	5.5
Stocking density (ind m ⁻²)	519.5	210.5	21.5	78.3
Mortality (% cycle ⁻¹)	8	3	30	5
Juvenile weight (g LW)	38	40	80	77
First seeding day	195	90	Late March	Late August
Culture period (days)	510	500	529	590
Harvest weight (g LW)	400–500	400–600	5000	5000

considered to be similar (different). When they are different and the intervals do not overlap, these differences are considered to be significant.

Suitability mapping

Suitability maps were based on the known optimal growing temperatures for each farmed species (<https://longline.co.uk/meta/>) and were used to compare the suitability of present-day temperature conditions with projected suitability in the mid-century (2040–2060) under RCP 4.5 and 8.5. Datasets containing monthly average sea surface temperatures (°C) from physical short-, medium- and long-term projections representing the North East Atlantic and the Mediterranean were compiled from the POLCOMS-ERSEM model. The present-day output layer covered average monthly temperatures within a 2000–2019 time slice and projected future temperature outputs covered a 2040–2059 time slice for each RCP. The layers consisted of a matrix of raster grid cells (0.1° resolution, approximately 10 km) each assigned an average temperature.

The mean, minimum and maximum temperature values for each month of the year were calculated for each grid cell of the spatial domain, using the raw temperature data for each time slice and scenario. The daily temperatures for the average year were then estimated using the equation below:

$$\text{Daily Temp} = \text{mean} + \frac{(\text{max} + \text{min})}{2} \times \cos(\text{Day} + 150) \times \frac{2\pi}{360}$$

where, for each grid cell in the spatial domain, mean is the mean monthly temperature for the average year, max is the maximum monthly temperature for the average year, min is the minimum monthly temperature for the average year and Day is the day number of the year (i.e. 1st January = 1 and 31st December = 365). The function is offset by 150 days as peak temperatures occur in the UK around August.

To calculate the species suitability score for each spatial point, the total number of days in the average year that fell within the optimum temperature ranges for each species was

calculated. This value was then converted into a proportion of the year by dividing by 365 days. All analyses were carried out in R Studio (R Core Team 2020).

Results

Model calibration and validation

Shellfish validation curves for measured versus simulated shell length and live weight are presented in Fig. 2. Model predictions predominantly fell within the range of observed values at each time step and represented shellfish growth patterns at all tested locations. The shellfish individual growth models also accurately predicted end-point biomass values at harvest.

The individual finfish models led to correct end-point growth estimates for all species and regions tested. In those cases where the harvest size prediction fell outside the observed range, the deviation was small (Table 4).

The outputs of the FARM local-scale model were validated against harvest weight and production yield reported by the farmers for the measured year (Table 5). FARM results showed good agreement with end-point growth and production values across all species and regions (see Table 5 and Fig. 3 as an example for Atlantic salmon in Norway).

As can be seen in Table 5, modelled salmon production for Ireland and Norway only exceeds reported production values by 8.7% and 7.6%, respectively. The sea bass population model was validated against available production for six cultivation sites in three Turkish provinces (Izmir, Muğla and Mersin). Modelled sea bass biomass production oscillates between 858 tons farm⁻¹ for Muğla and 1088 tons farm⁻¹ for Mersin, i.e. a 10.2% lower and 8.8% greater than the reported 1000 tons farm⁻¹, respectively. Modelled gilthead seabream biomass production in the Spanish Mediterranean coast was 1677 and 1688 ton farm⁻¹ for

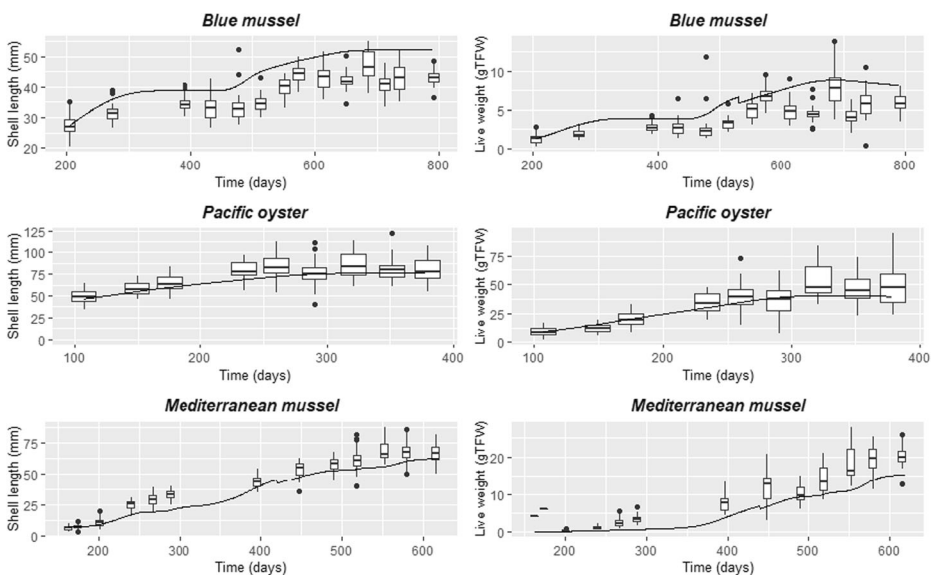


Fig. 2 Validation curves showing measured growth (box plots) and predicted growth (lines) in shell length and live weight for the three shellfish species at different cultivation sites using the WinShell individual model

Table 4 Individual model WinFish calibration results for harvest weight in the different species and regions

Location	Species	Reported harvest weight (g LW)	Modelled harvest weight (g LW)
Italy	Sea bass	300–400	377
Italy	Gilthead bream	300–400	405
Ireland	Atlantic salmon	≥ 5000	5002
Norway	Atlantic salmon	≥ 5000	5683
Cyprus	Gilthead bream	300–400	388
Cyprus	Sea bass	400–500	478
Scotland	Atlantic salmon	4500–5000	4856
Israel	Gilthead bream	350–400	411
Israel	Sea bass	350–500	477
Spain	Sea bass	400–600	464–532
Spain	Gilthead bream	400–500	438–449

2015 and 2016 drivers, respectively, that is 7.9 and 7.3% less than reported production at the Spanish typical farm.

Modelled production of suspended blue mussels at the Danish farm and mussel bottom culture in the Netherlands was 9.1% and 2.9% lower than the reported yields, respectively. Predictions for Mediterranean mussel production in offshore suspended longlines in Portugal matched the production reported at the Sagremarisco farm (Table 5).

Projected changes in suitability and productivity of farmed fish and shellfish

This section addresses projected changes in suitability and productivity due to direct effects of climate change on finfish (seawater temperature) and bivalve shellfish (seawater temperature, chlorophyll a and salinity) species of economic importance in Europe (Table 1). Results of the biological modelling of future climate-driven changes in these stressors on growth performance and economic parameters are presented in Tables 6 and 7.

Table 5 FARM validation results for harvest weight across species and regions

Location	Species	Reported harvest weight (g LW)	Modelled harvest weight (g LW)	Reported production (tons farm ⁻¹)	Modelled production (tons farm ⁻¹)
Ireland	Atlantic salmon	> 5000	6134	1666	1811
Norway	Atlantic salmon	> 5000	5863	3239	3482
Turkey	Sea bass	400–600	428–542	1000	898–1088
Spain	Gilthead bream	400–500	420–423	1820	1677–1688
Netherlands	Pacific oyster	50–100	66.4	Not available	55.4
Netherlands	Blue mussel	16–25	25	160	155.3
Denmark	Blue mussel	14–20	19.5	240 ¹	267
Portugal	Med mussel	10–20	12.2–18.9	450	451.5

¹ Predicted blue mussel production for 2017 which was a low-production year as culture practice was not optimized. Typically, production range between 225 and 405 t per farm (4.7–8.4 t per line)

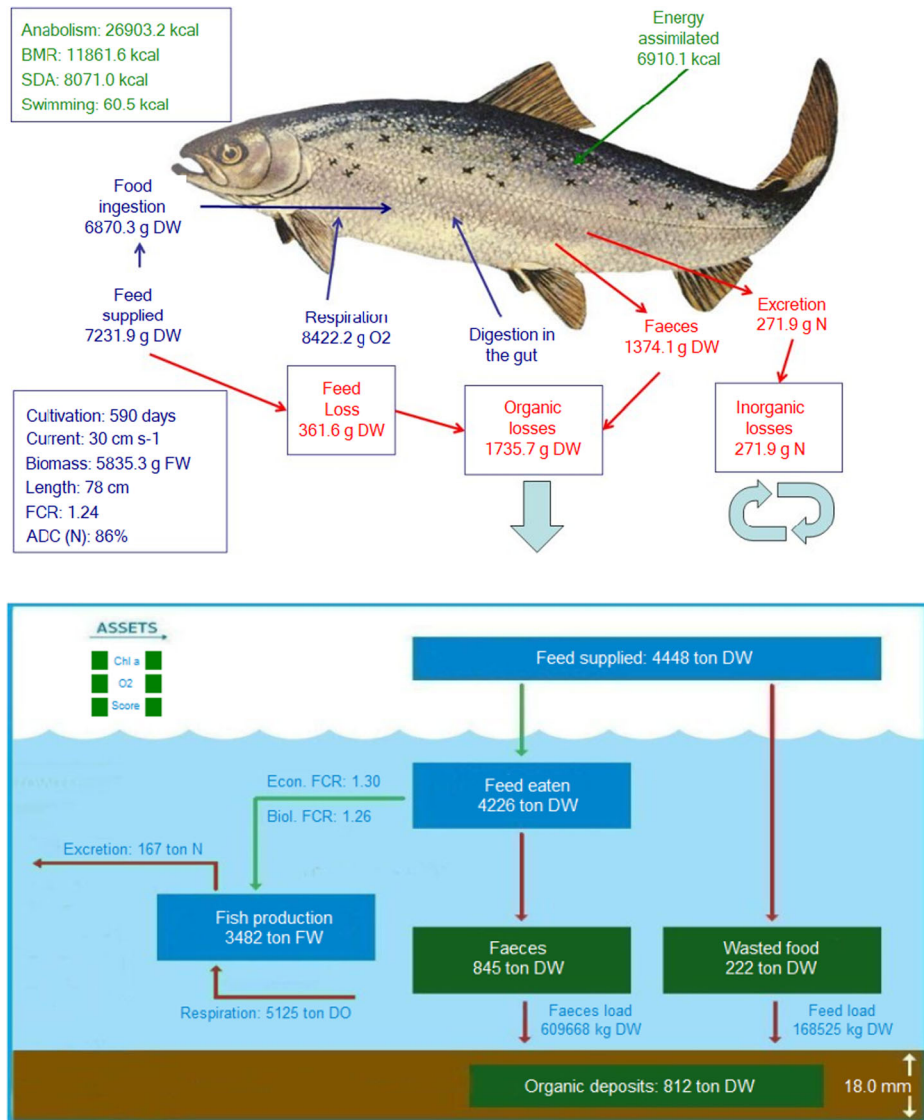


Fig. 3 Above: WinFish mass balance results for an individual Atlantic salmon over a full growth cycle at the typical open water farm in Norway. Below: FARM model annualized mass balance for Atlantic salmon culture in net pens at the typical Norwegian farm. DO, dissolved oxygen; DW (FW), dry (fresh) weight; BMR, basal metabolic rate; SDA, specific dynamic action; FCR, feed conversion ratio

The final harvest weight (g live weight) and production (tonnes) attained at the end of the standard production cycle at the typical farm were chosen as indicators for growth and farm performance. The feed conversion ratio (FCR, no units) measures the animal efficiency in converting feed mass into increased body mass and was estimated for the grow-out production period as feed mass (in dry weight) divided by the increase in animal weight (in wet weight). The average physical product (APP), estimated as the ratio between the biomass produced and

Table 6 Projected changes in productivity in the mid-century scenario across regions and species, when compared to current conditions. The range bars represent the variability of the results: small = low variability, medium = moderate variability and large = high variability. APP, Average Physical Product; FCR, Feed Conversion Ratio

Country	Species	Harvest weight			Production			APP			Revenue			Profit			FCR		
		RCP	8.5	4.5	RCP	8.5	4.5	RCP	8.5	4.5	RCP	8.5	4.5	RCP	8.5	4.5	RCP	8.5	4.5
Ireland	Salmon	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Norway	Salmon	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Turkey	Sea bass	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Spain	Gilthead bream	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Denmark	Blue mussel	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Netherlands	Blue mussel	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Netherlands	Pacific oyster	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Portugal	Med mussel	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I

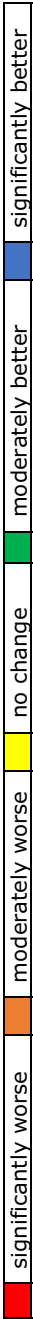
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significantly worse	moderately worse	no change	moderately better	significantly better
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Table 7 Projected changes in productivity and economic externalities in the end-of-century scenario across regions and species, when compared to current conditions. The range bars represent the variability of the results: small = low variability, medium = moderate variability and large = high variability. *APP*, average physical product; *FCR*, feed conversion ratio

Country	Species	Harvest weight			Production			APP			Revenue			Profit			FCR		
		RCP	4.5	8.5	RCP	4.5	8.5	RCP	4.5	8.5	RCP	4.5	8.5	RCP	4.5	8.5	RCP	4.5	8.5
Ireland	Salmon	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Norway	Salmon	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Turkey	Sea bass	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Spain	Gilthead bream	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Denmark	Blue mussel	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Netherlands	Blue mussel	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Netherlands	Pacific oyster	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Portugal	Med mussel	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I

Legend:



the biomass seeded, was used to measure farm productivity. As economic indicators, we used the first-sale revenue and the profit obtained by the farmer.

Direct effects on finfish aquaculture

Most of the finfish species were projected to have increased FCR (i.e. decreased feeding efficiency¹) in both mid-century and end-of-century scenarios, i.e. fish will need more feed to reach harvest size and feed costs will be higher, although only Irish salmon and gilthead bream profits would be negatively affected (Tables 6 and 7). This is particularly clear in the end-of-century scenario.

Gilthead seabream is the fish most affected by temperature-related changes projected at mid- and end-of-century. Our models predict that this species would need significantly longer to reach minimum commercial size—most gilthead bream will not reach harvest size in the end-of-century projection under any emission scenario. This is also the only fish where growth, yield at harvest and return on investment (measured as APP) worsens as climate change progresses.

The modelled weight obtained with the FARM model for gilthead bream under current conditions was about 420 g (Table 5). Weight decrease is observed for both RCP 4.5 and RCP 8.5 in the mid-century projection, and further decrease occurs for both RCPs in the end-century projection. RCP 8.5 shows a higher range than RCP 4.5 (Tables 6 and 7), i.e. farmers can expect greater variability in the harvest and will therefore face greater uncertainty in their business—risk mitigation strategies will thus become increasingly important.

The projections for the end-century scenarios show worse productivity for all finfish species except for Norwegian salmon, which presented similar results in both time slices but greater variability (i.e. greater economic uncertainty) in the end-of-century scenario. In the long term, the profitability of Irish salmon farming appears to be more negatively impacted by direct effects of climate change than that of Norwegian salmon (Tables 6 and 7).

Average Irish salmon size at harvest increased over time, meaning that projected temperature gets closer to optimum values for salmon growth, except for the late-century high-emission scenario when the temperature would be too high for salmon and growth slowed down (results not shown). This improvement in growth is not reflected in the economic aspect as profit diminishes over time; this decline is especially important in the end-of-century high-emission scenario. Irish farmers will get lower profits as climate change progresses, particularly under the high-emission scenario.

In Norway, due to colder baseline (current) temperatures and the absence of RCP 8.5 scenarios, the temperature does not reach such high values as to observe a negative effect on salmon growth. In fact, growth and profit increased in both mid- and end-of-century scenarios when compared to present-day results (Tables 6 and 7), although there is no significant difference between mid- and end-of-century results.

In the analysis of direct effects of climate change, not only the average values were considered but also the range or variability of simulation results obtained, as an indicator of the economic uncertainty of the farmer.

There is lower economic uncertainty in RCP 4.5 results than in the present-day situation for all species in the mid-century projection (Table 6). At the end-of-century, there is greater uncertainty of RCP 4.5 results for Norwegian salmon and Turkish sea bass (i.e. the farmer will

¹ Feeding efficiency is considered to be $1/\text{FCR}$.

potentially get bigger or smaller animals than at present and thus greater or lower benefit), and less uncertainty for Irish salmon and Spanish gilthead bream when compared to the present-day situation (Table 7).

In both mid- and late-century projections, there is more uncertainty in RCP 8.5 productivity results for gilthead bream and sea bass (and less for Irish salmon), when compared to present-day results.

In general, modelling results for both time slices presented a greater range of potential responses (uncertainty) in RCP 8.5 than in RCP 4.5 scenarios for all species analysed. Uncertainty also increased throughout time under both emission scenarios.

Direct effects on bivalve shellfish aquaculture

Mediterranean mussels cultivated on offshore longlines appear to be the least adversely affected by climate-driven projections of changes in temperature, salinity and food availability (Tables 6 and 7). The productivity of Mediterranean mussel aquaculture in Portugal was projected to remain similar or improve slightly under both emission scenarios when compared to the present-day situation; the worst results were predicted for the end-of-century high-emission scenario.

Conversely, the longline culture of blue mussel in Denmark and off-bottom culture of Pacific oyster in the Netherlands were projected to be most deleteriously impacted, showing poorer results for all production parameters at the late-century scenario in both RCP 4.5 and RCP 8.5 projections. At mid-century, blue mussel bottom culture in the Netherlands was similar to present-day but was predicted to decrease in production (and increase in economic uncertainty) at the end-of-century scenario.

Shellfish bivalve species showed a decreasing trend in relation to most productivity parameters (e.g. average harvest size, production and profit) as climate change progressed under both emission scenarios, with the exception of Mediterranean mussel that presents similar values across time slices. As a general trend across species and regions, economic uncertainty is expected to increase under all future projections (Tables 6 and 7) and the differences between low- and high-emission scenarios were not significant (results not shown).

Finfish suitability maps

In terms of near coastal suitability, temperature suitability maps (Fig. 4) showed that for salmon under present-day conditions, the greatest proportion of optimal growing days were predicted off the southwest coast of Ireland and between the southwest tip of England and northwest of France. The coasts of the rest of Ireland, Northern Ireland, Scotland, Norway and the east coast of England also showed high suitability in terms of the proportion of days within a year that are in the optimal growing range for Atlantic salmon. Suitability in these areas was also predicted to increase proportionately by the greatest amount under both RCPs 4.5. and 8.5. The lowest proportion of optimal growing days was observed in the southern region of the mapped area where temperatures generally exceeded those deemed optimal for Atlantic salmon. Despite already showing the lowest suitability in the present day, the southern areas within the maps were also predicted to show the highest proportional decrease in suitability under both RCPs.

Analysis of cells proximal to the typical salmon farms on which this study focused showed that under present-day conditions, on average, 64% of days per year in the cells around the Irish farm compared to 53% around the Norwegian farm were in the optimal growing

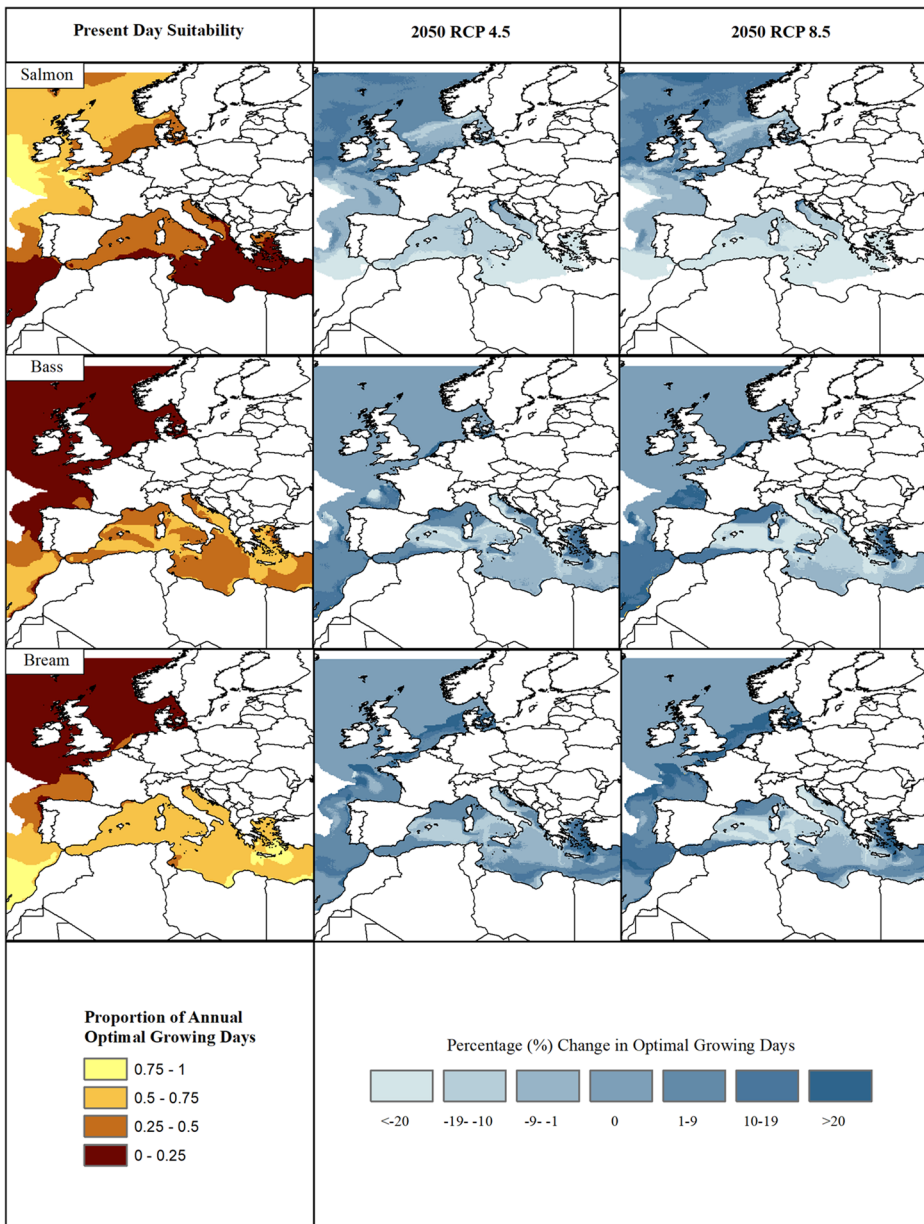


Fig. 4 Temperature suitability maps for three finfish species showing the percentage change in optimal growing days under present-day temperatures and projected mid-century temperatures (2050) under RCP 4.5 and RCP 8.5 scenarios

temperature range. Under RCP 4.5 and 8.5 respectively, this was predicted to increase to 69% and 68% for the typical Irish farm and 55% and 57% for the typical Norwegian farm. The average present-day temperature in the proximity of the Irish typical farm was 11.4 °C, which was predicted to rise to 11.9 °C and 12.0 °C under RCP 4.5 and 8.5 respectively. The average

present-day temperature in the proximity of the Norwegian typical farm was 10.5 °C, which was predicted to rise to 10.9 °C or 11.1 °C under RCP 4.5 and 8.5 respectively.

For both sea bass and gilthead bream, the proportion of optimal growing days was highest in the southern region of the mapped range, throughout the Mediterranean (Fig. 4). Temperature suitability was generally greater for gilthead bream than sea bass, with higher suitability across the Mediterranean Sea, along the coast of Portugal, Spain and southwest of France. For both species, suitability was predicted to reduce throughout the Adriatic Sea, the coast of Italy and Eastern coast of Spain. Along almost the entire coast of Spain, France and Greece suitability was predicted to improve, with increases in suitability generally being greater for bream than bass. Within the Mediterranean Sea, the greatest increases in suitability were predicted in the waters between Greece and Turkey followed by the northern coasts of Africa, the south coast of Spain and France and the north-west coast of Italy, under both RCPs. Outside of the Mediterranean Sea, suitability in terms of optimal growing days was predicted to increase for both species along the north-western edge of Africa and along the western and northern coasts of Portugal, Spain, France, Belgium, the Netherlands, Germany, Denmark and South Coast of England. These increases and their range were predicted to be higher for gilthead bream than bass.

Focussing on mapped cells in the region of the typical sea bass and gilthead seabream farms in the western (Spain) and eastern (Turkey) the Mediterranean showed that for both species, on average, 64% of days were in the optimal growing range in the eastern farm compared to 61% in the western farm. Under RCP 4.5 and 8.5 respectively, this was predicted to remain at 64% and reduce to 61% for the eastern farm and increase to 62% for the western farm under both RCPs. The average temperature around the eastern farm was predicted to be 20.3 °C under present-day conditions, rising to 21.1 °C or 21.4 °C under RCPs 4.5. and 8.5 respectively. The average temperature around the western farm was predicted to be 18.4 °C under present-day conditions, rising to 18.8 °C or 19.1 °C under RCPs 4.5. and 8.5 respectively.

Shellfish suitability maps

Blue mussels have a physiological temperature range of 2 to 27 °C, but optimal growing temperatures of between 8 and 18 °C based on experimental work developed under the CERES project (CERES 2020a). Maps (Fig. 5) showing the proportion of growing days per year in the optimal temperature range show that the northwest region of the mapped area encompassing Ireland, Northern Ireland and much of the west coast of England, Wales and Scotland was most suited to blue mussel growth under present-day conditions. Suitability throughout the northern half of the mapped range was predicted to increase under both RCP 4.5 and 8.5. Average seawater temperatures across the North Sea study region in the vicinity of the Dutch and Danish typical farm sites were estimated at 11 °C but were predicted to increase by 0.45 °C and 0.64 °C under RCPs 4.5 and 8.5, respectively. On average, 73% of days per year in the North Sea region were predicted to be in the optimal temperature range for blue mussel growth. Under RCPs 4.5 and 8.5, the proportion of days per year within the optimal growing temperature range was predicted to increase to 78% of days and 80% of days, respectively. Conversely, suitability throughout the Mediterranean Sea and the area south of Portugal was found to be relatively low under present-day conditions and was predicted to reduce in suitability in the future under both RCPs. On average, only 51% of days in the Mediterranean region were predicted to be in the optimal temperature range for blue mussel growth, and this was predicted to reduce to 47% and 43% under RCPs 4.5 and 8.5, respectively.

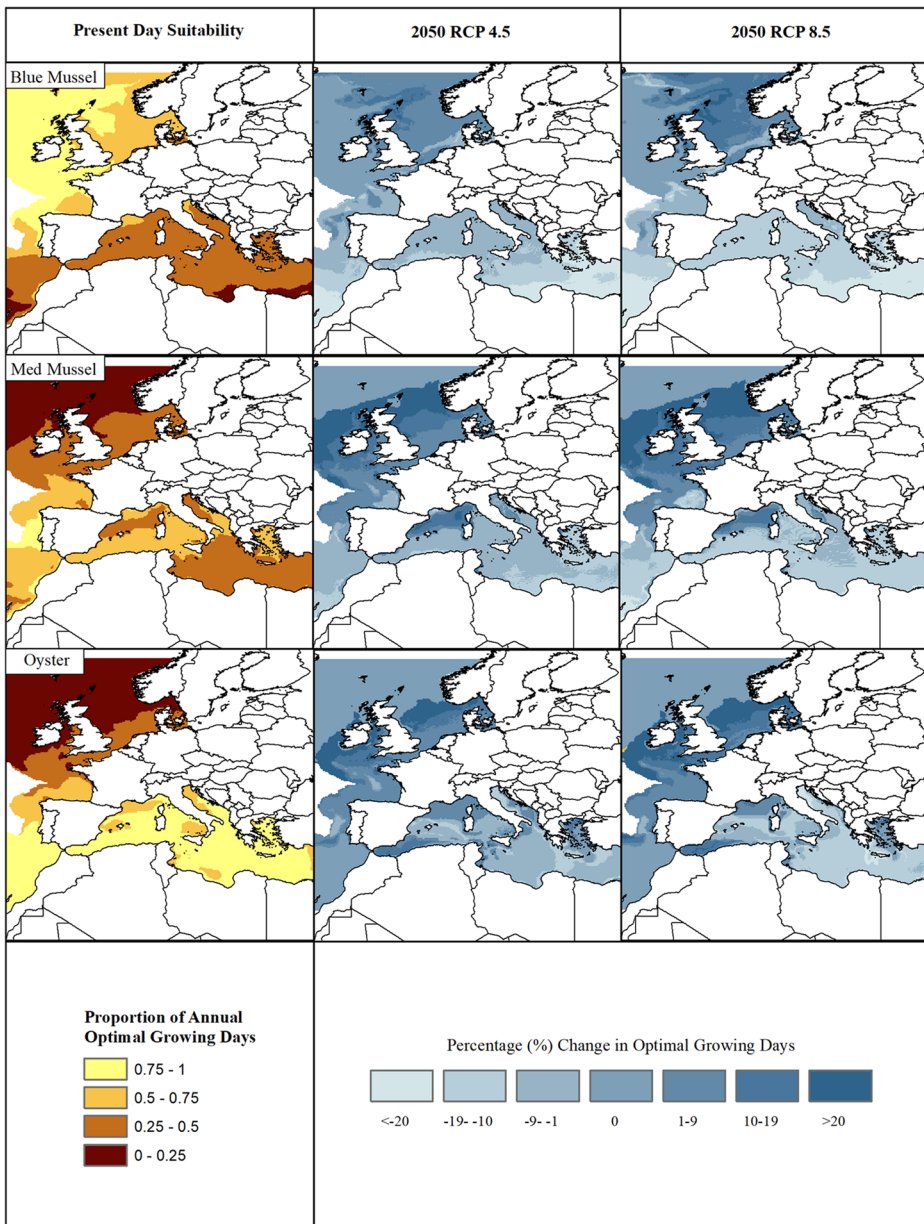


Fig. 5 Temperature suitability maps for three shellfish species showing the percentage change in optimal growing days under present-day temperatures and projected mid-century temperatures (2050) under RCP 4.5 and RCP 8.5 scenarios

Optimal temperatures for the growth of Mediterranean mussel is 14 to 20 °C (van Erkom and Griffiths 1992); therefore, temperature suitability for this species under present-day conditions was predicted to be distributed in a pattern broadly opposite to that predicted to be most suitable for blue mussel growth. The areas highest in suitability were predicted to be in the southwest of the mapped range, the western Mediterranean and waters between Greece and

Turkey. These regions were predicted to remain similar in terms of suitability under both RCPs with most areas changing by $< \pm 10\%$. Conversely, the northern region of the mapped range was found to be least suited to Mediterranean mussel growth, with suitability being predicted to further improve under both RCPs.

Optimal temperatures for the growth of Pacific oyster range between 15 and 25 °C according to CERES experiments (CERES 2020b); consequently, the pattern over which areas of optimal temperature suitability was predicted for this species is similar to that of the Mediterranean mussel. However, due to their higher temperature tolerance, areas of high suitability were calculated to extend further into the eastern Mediterranean Sea. As with the Mediterranean mussel, under both RCPs 4.5 and 8.5, suitability was predicted to increase in the northern half of the mapped range and remain roughly similar in the southern half with most areas in this region changing by $< \pm 10\%$. It should be noted that the predicted areas of highest suitability for Pacific oyster growth do not correspond with the main growing regions across Europe. This is likely a consequence of the spatial scale of the data used which is predicting offshore temperatures that may not be reflective of the temperatures in the intertidal zone where oysters are often farmed.

Discussion

Outputs from the regionally downscaled global climate model showed the variable incidence of extreme temperatures among the selected aquaculture locations. Accordingly, these future climate-related changes would have variable effects on species growth and farm productivity, both spatially and interspecifically. Steeves et al. (2018) also found different spatial and seasonal rates of seawater warming in coastal waters and suggested these will create risks and opportunities in growth and phenology for different species due to species-specific thermal physiologies. The projected temperature-related changes of climate change observed in this study had a different impact on each aquaculture species, with gilthead seabream in sea cages in the western Mediterranean and offshore suspended Mediterranean mussel culture in SW Portugal as the most and least vulnerable, respectively.

Dahlke et al. (2020) observed that vulnerability to climate change depends on the most temperature-sensitive life stages of a species, with spawning adults and embryos having narrower tolerance ranges than larvae and non-reproductive adults. In aquaculture, this effect is mitigated because both the hatchery and nursery stages are usually carried out under temperature-controlled conditions in indoor facilities. In this study, we focused on the grow-out stage because this typically takes place under natural conditions at the sea, where the effects of climate change will be more evident. During this stage, we will just have non-reproductive adults as the industry interest is that the animals allocate the highest amount of energy into growth, but this higher vulnerability of sensitive life stages may be a concern for those farmed species that rely on natural recruitment of seed, such as some shellfish species.

Poikilothermic animals such as fish or shellfish have specific temperature limits and tolerance ranges, which were considered in the physiological models used in the present study, which determine their latitudinal distribution limits and sensitivity to climate change (Sunday et al. 2012). A logarithmic inverse correlation between the temperature dependence of physiological rates and thermal tolerance range is proposed by Dahlke et al. (2020) to reflect a fundamental, energetic trade-off in thermal adaptation.

The impact of direct effects of climate change such as ocean warming will mostly depend on (i) the thermal tolerance window and adaptation capacity of each species and (ii) how close the tolerance and optimal temperature windows for each species are from the present-day temperature range at each farm. This agrees with the approach followed by Montalto et al. (2016) and Falconer et al. (2020) who looked at differences in the time spent within the estimated species' thermal tolerance and thermal optima to determine their future suitability.

Accordingly, climate change-driven temperature/salinity/Chl-a shifts are more likely to negatively affect those species cultivated closer to their distribution limits (Helmuth 1998; Helmuth et al. 2006; Petes et al. 2007; Beukema et al. 2009). In our study, this may be the case for Atlantic salmon which was more affected by seawater warming in Ireland than in Norway. In the case of shellfish, this could also be a plausible explanation for Mediterranean mussels in SW Portugal being less affected than blue mussels in the Netherlands or Denmark, although the wider tolerance range to temperature of Med mussels cannot be discarded. We did not find water temperatures exceeding the lethal limit of any of the examined species at any time slice or emission scenario, which is in agreement with Montalto et al. (2016).

As an example, the mean sea surface temperature in southwest Portugal is $\sim 17^{\circ}\text{C}$, although it is highly dependent on upwelling/downwelling events, ranging from 13.1 to 25.2°C (Fragoso and Icelly 2009). This range is roughly the same as the optimum temperature range for the Mediterranean mussel (van Erkom and Griffiths, 1992, 1993) and thus, we could expect any temperature shift to be non-desirable. Climate change projections in this study suggest that waters around the Portuguese coast will warm by up to 1 and 2°C by the end of the century under RCP 4.5 and RCP 8.5 respectively, with the largest increase being reported in the south. On the other hand, projected changes in net primary production suggest a general trend of marginal increases in production under both RCP 4.5 and RCP 8.5 which could potentially boost bivalve growth (Kay et al. 2018).

For the Mediterranean Sea, MPI-ESM projections suggest a rising trend of 0.02°C per year in SST (2°C over a century). This trend is in contrast to observations showing a decline in temperatures over the past 2000–4000 years (e.g. Margaritelli et al. 2020, and references therein) but is in line with a much faster rise in the past century (Margaritelli et al. 2020; von Schuckmann et al. 2020). The controversial temperature predictions for the Mediterranean Sea, depending on the GCM used, may add an associated degree of uncertainty to the farm-scale production results.

Due to the coarse spatial resolution of downscaled climate model predictions, the modelling results of the present study should be interpreted with caution, particularly with respect to shellfish farming, although they do provide useful insights into the levels of spatial variability we might expect in species' responses to climate change in coming decades, and the importance of considering local-scale impacts (Montalto et al. 2016). Although the downscaling method takes into account the ranges and annual shape of the local scale, it assumes that changes at the local scale follow linearly changes at the regional scale. Changes in coastal and estuarine processes such as upwelling and increase in river-borne suspended solids may be misrepresented by the method used. Furthermore, the formulation used for downscaling the regional models tends to follow the same phase of the reference observed data, hiding eventual season shifts in the resulting drivers. The availability of finer scale near-shore data than those provided by the available regional climate and biogeochemical models would improve the prediction capacity of the present modelling approach, as other authors have suggested (Montalto et al. 2016; Falconer et al. 2020; Thomas et al. 2016).

Farm management and aquaculture practices—particularly the seeding period, culture length, stocking density and the seed/harvest size—will also need to adapt to the new conditions of climate change. Current production systems will have to evolve, requiring new approaches to management that are based on potential changes in behavioural and physiological responses as abiotic and biotic conditions change (D'Abramo and Slater 2019). There are many options for aquaculture adaptation to climate change, from simple management changes (such as changes in the stocking densities or the diet) to complex engineering or biotechnology solutions (e.g. selective breeding programmes for stressor-resistant traits or molecular selection techniques) that can be applied at the farm management level or at a wider scale (Reid et al. 2019). Engineering and management solutions can reduce exposure to stressors or mitigate stressors through environmental control (Reid et al. 2019). The timing of seasonal changes is also important for the aquaculture industry as it influences many important aspects of production from stocking strategies to product quality (Mørkøre and Rørvik 2001).

Previous studies have shown heterogeneous effects of global warming on the growth of finfish (e.g. Eide and Heen 2002; Falconer et al. 2020; Klinger et al. 2017) and shellfish (e.g. Montalto et al. 2016; Steeves et al. 2018), depending mostly across species and regions, with growth rates and reproductive scope likely to decline once critical temperature thresholds are reached (Potts et al. 2015). As climate change progresses, most shellfish case studies analysed here showed a decreasing trend in relation to most growth and productivity parameters under both emission scenarios. Due to this impaired growth, farmers will need to extend production cycles that may in turn affect the profitability and the seasonality of the sales.

Similarly, most finfish case studies were projected to show greater growth but decreased feeding efficiency under both emission scenarios when compared to present-day conditions, i.e. fish will need more feed to reach harvest size and feed costs will be higher, resulting in negative consequences in farm profits. This was particularly clear in the end-of-century scenario where all finfish species showed worse feeding efficiencies.

As a general trend across species and regions, economic uncertainty of farming operations (estimated here as the response range of simulation results) is expected to increase under all future projections when compared to the present-day situation, especially at the end of the century and under the high-emission scenario. Kreiss et al. (2020) suggested that in addition to changes in water quality and temperature that can directly influence fish production by altering health status, growth performance and/or feeding efficiency, the aquaculture sector also faces an uncertain future in terms of production costs and returns, which will determine in great extent future farm profitability.

The farming practice and cultivation structures employed seem to be key factors in the level of exposure of species to direct effects of climate change. Mediterranean mussels cultivated in offshore longlines appear to be the least adversely affected by climate-driven changes in physical conditions. In offshore-suspended cultivation systems, the effects of climate change seem to be ameliorated by oceanic conditions. In fact, the European Union is promoting the development of aquaculture toward the offshore areas which is being supported financially by the European Maritime and Fisheries Fund² since 2012 (European Commission 2012) and the Norwegian salmon sector is already investing in moving production systems offshore (e.g. “Havfarm”). Steeves et al. (2018) also concluded that offshore aquaculture should be considered as a cultivation method to avoid increased temperature-related mortality of *M. edulis* from thermal stress.

² COM/2011/0804

In the same line, suspended culture instead of intertidal bottom culture or floating cages would be highly recommended in areas where the temperature is expected to rise, because the intertidal is more exposed to changes in temperature than subtidal environments (Helmuth 1998; Sarà et al. 2011). This is in agreement with Montalto et al. (2016) who found larger predicted rates of phenological advance by 2050 (averaged across three bivalve species at 51 sites in the Mediterranean Sea) for subtidal (3.8 days) than intertidal habitats (7.6 days) per decade. They suggest that at the intertidal, these species would be affected by changes in both the terrestrial and marine environments.

While aquaculture is expected to play a critical role in meeting growing global food demands in the future (FAO 2018), climate change is altering coastal and marine environments at an unprecedented rate (FAO 2017; IPCC 2014) and impacting seafood aquaculture production in complex ways (Barange et al. 2018; Merino et al. 2012). Through direct and indirect pathways, climate change will have implications at both the individual and production levels: implications for animal physiology, growth and feeding efficiency and thus on farm production and profitability.

This study focused on the projected changes in productivity due to direct effects of climate change: seawater temperature, chlorophyll *a*, seston concentration and salinity. It did not consider indirect stressors that may potentially affect these cultivated species, such as hypoxia or ocean acidification, or the consequences on farm profitability associated with changes in disease risks or harmful algal blooms, increased storminess or the appearance of non-indigenous species. Even in the cases where future temperature development had a positive effect on Atlantic salmon growth, as predicted for sites in northern Norway, changes in temperature may also increase the prevalence of the disease, due to higher temperatures (Falconer et al. 2020). The combination of these direct and indirect effects of climate change will ultimately determine the change in productivity and profitability of the different aquaculture species at each farming site and may also create opportunities for new species and alternative farming practices.

Conclusions

Research to understand how climate change affects aquaculture will benefit most from a combination of empirical studies, modelling approaches and observations at the farm level (Reid et al. 2019).

In order to contribute to this goal, our study applied a multi-model framework, including atmospheric models, water circulation, biogeochemistry and physiology and population dynamics of cultivated species, to explore and predict impacts of future climate change projections on the productivity of the European aquaculture sector. The combination of bioenergetic models with environmental data from in situ, satellite or climate models has been used to investigate the effect of projected future temperature scenarios on the performance and distribution of organisms—this has been shown to be a valuable tool for ecosystem studies (Sarà et al. 2011, 2013; Thomas et al. 2016; Klinger et al. 2017; Steeves et al. 2018).

This multi-model approach helps understand to what extent the direct effects of climate change will present challenges (or opportunities) for different aquaculture species and geographical regions. The findings of this study are relevant for medium-term aquaculture planning, as the local impact of climate-related changes on physiology and growth will create

species-specific risks and opportunities in terms of growth efficiency, productivity and profitability.

The use of suitability maps helped determine which areas will become less attractive for aquaculture and which will potentially become more suitable.

The different production systems, species and regions analysed herein illustrate the generality of this modelling approach for the aquaculture sector, allow the identification of potential winners and losers and support the deployment of mitigation and adaptation measures.

Global population and seafood demand are both increasing, while fisheries decline during this period of rapid climate change. Aquaculture is well positioned to help meet the world's future demand for protein and food security needs but is also heavily dependent on the environment and thus highly vulnerable to climate change effects since it relies on specific species that are sufficiently domesticated and takes place at fixed locations. There are, however, opportunities for adaptation. Key indicators obtained by modelling growth, production and environmental effects in response to climate change will help quantify the challenges ahead. These will be met in various ways, including technological improvements to finfish cages, changes in feed composition and use of land-based facilities where temperature and other environmental variables can be better controlled.

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Code availability Not applicable.

Author contributions All authors contributed to the conception and design of the study; S.K. provided the outputs from the global and regionally downscaled climate models; J.L. downscaled the drivers generated by the regional-scale models to be used by the local-scale models; A.C. and J.F. developed the individual shellfish and finfish growth models; A.C. conducted the local-scale modelling; N.T., J.G. and A.K. provided the suitability maps. A.C. wrote the first draft of the manuscript; J.F., N.T., A.K. and J.G. wrote sections of the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

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Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval Not applicable.

Consent to participate All authors consented to participate in all aspects of this research and publication.

Consent for publication All authors agree to the publication of this manuscript in Aquaculture International.

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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