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Research article

Impacts of climate change on water quality, benthic mussels, and suspended mussel culture in a shallow, eutrophic estuary

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ABSTRACT

Climate change is a global problem that causes severe local changes to marine biota, ecosystem functioning, and ecosystem services. The Limfjorden is a shallow, eutrophic estuary influenced by episodic summer hypoxia with an important mussel fishery and suspended mussel culture industry. Three future climate change scenarios ranging from low greenhouse gas emissions (SSP1-2.6), to intermediate (SSP2-4.5) and very high emissions (SSP5-8.5) were combined with nutrient load reductions according to the National Water Plans to investigate potential impacts on natural benthic mussel populations and suspended mussel culture for the two periods 2051–2060 and 2090–2099, relative to a reference period from 2009 to 2018. The FlexSem model combined 3D hydrodynamics with a pelagic biogeochemical model, a sediment-benthos model, and a dynamic energy budget - farm scale model for mussel culture. Model results showed that the Limfjorden was sensitive to climate change impacts with the strongest responses of physics and water quality in the worst case SSP5-8.5 scenario with no nutrient reductions. In the two low emissions scenarios, expected improvements of bottom oxygen and Chlorophyll *a* concentrations due to reduced nutrient loads were counteracted by climate change impacts on water physics (warming, freshening, stronger stratification). Hence, higher nutrient reductions in the Water Plans would be needed to reach a good ecological status under the influence of climate change. Suspended mussel culture was intensified in all scenarios showing a high potential harvest, whereas the benthic mussels suffered from reduced food supply and hypoxia. Provided the environmental changes and trends in social demands, in the future, it is likely that suspended mussel cultivation will become the primary source of mussels for the industry. Model scenarios can be used to inform managers, mussel farmers, fishermen, and the local population on potential future changes in bivalve harvesting and ecosystem health, and to find solutions to mitigate climate change impacts.

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1. Introduction

Climate change is a global problem that has led to ocean warming, increased freshwater input, lower surface salinity, and altered levels of stratification, as observed in the Baltic Sea during the last decades [1–5]. These drivers have affected the biogeochemical environment through de-oxygenation, acidification, reduced water clarity, and more frequent harmful algal blooms [1,6–8]. The climate change-related impacts are expected to be intensified further in the future, and heavily affect marine life and the provided marine ecosystem services for humans (e.g., food provisioning, nutrient regulation) [9–11]. In addition, the geographical distributions, seasonality, and productivity of plants and animals are likely to change under climate change, either directly due to physiological responses or indirectly from changes in their habitats [12,13]. Hence, these climate related changes in marine ecosystems are anticipated to have long-term and direct consequences for fisheries and aquaculture, and thereby on future food security [14–16].

Climate change impacts can interact with other stressors such as excess nutrient loads and overfishing making marine life even more vulnerable to change [13]. Eutrophication is a leading factor causing hypoxia, harmful algae blooms, turbid water, and loss of benthic flora and fauna in many estuaries worldwide [17–19]. The European Water Framework Directive (WFD) requires good ecological status achieved by 2027 and land-based nutrient reductions are under implementation by the member states [20,21]. However, the planned nutrient reductions may not be enough when considering climate change impacts and lag-time in the ecosystem responses due to complex feedback mechanisms (e.g., internal nutrient loads, loss of biodiversity, and functional habitat) and shifting baselines [22–24].

Low-trophic aquaculture (e.g., suspended mussel culture) is considered environmentally sustainable because it relies on naturally present food (phytoplankton and detritus) and provides high-quality protein food products with a low-carbon footprint compared to land-based protein sources [25–27]. Hence, a shift in people's diets to low-carbon ocean-based proteins has the potential to benefit the

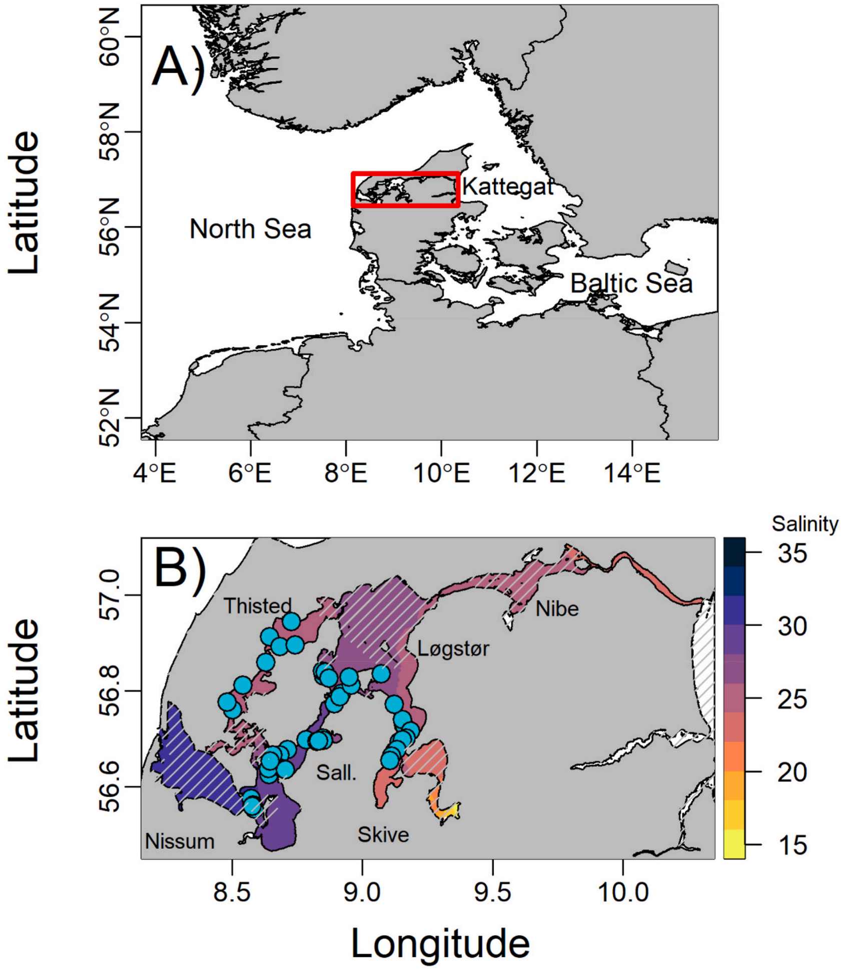


Fig. 1. Map showing A) the location of the Limfjorden (red box) and B) surface salinity (color bar), mussel farms (cyan points), and names of the main basins; Nissum Broad (Nissum), Sallingsund (Sall.), Thisted Broad (Thisted), Løgstør Broad (Løgstør), Skive Fjord (Skive), and Nibe Broad (Nibe). Grey hatched lines are the Natura 2000 areas where mussel farming is not allowed. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

climate [28] and support the growing global food demand [29]. In addition, mussel filtration of phytoplankton and detritus, incorporation of ingested nutrients into biomass, and subsequent harvesting of mussels can be used as a tool to extract nutrients and improve the water quality of eutrophic marine ecosystems [30–32]. However, as climate change progresses, mussel culture may be less productive in the future due to physiological stress from altered temperature, salinity, food levels, oxygen levels, and ocean acidification [16]. Likewise, benthic mussel populations are expected to diminish from climate change impacts and eutrophication, being exposed to increasing periodicity of hypoxia and euxinia; as well as poor sediment substrates [33]. The mussel fishery, on the other hand, is often considered less environmentally sustainable than suspended mussel culture in sensitive habitats [34]. Dredging causes sediment resuspension, increasing oxygen consumption from exposure of carbon and nutrients to the water column, suppression of wild stocks, and damage to non-target species [35,36].

Estuaries are important for humans due to the many economic (e.g., aquaculture, fishing, shipping) and recreational (e.g., swimming, angling, boating) activities but they are also sensitive to the cumulative pressures from the many human activities, pollution from land, and climate change impacts [37]. Future scenarios considering combined effects of climate change, nutrient loads on bivalve aquaculture in temperate coastal ecosystems are few [38–40]. Hence, more studies are needed in those systems to inform managers, aquaculture farmers, and local communities on potential future changes in ecosystem health and bivalve biomass and harvesting potential. The Intergovernmental Panel on Climate Change (IPCC) has developed two types of complementary scenarios [14]. The first type, so-called Representative Concentration Pathways (RCPs), describes how the concentration of CO_2 and other greenhouse gasses may rise or fall in the future [41]. The second type of scenarios consists of five so-called Shared Socio-economic Pathways (SSP1-SSP5), which describe how future changes in society (population growth, gross domestic product, international cooperation, etc.) can influence how easy it is for countries to enact climate adaptation or climate mitigation policies. The SSPs (social-economic, geo-political) and RCPs (levels of radiative forcing in CMIP6) were designed to be used together but should be adapted to local conditions (e.g., type of fishery and aquaculture, nutrient load) [15,42,43].

The present study aims to test the impact of three future scenarios based on different combinations of climate change impacts and nutrient load reductions in a shallow, eutrophic estuary. The objectives were to i) design localized scenarios for the Danish Limfjorden, ii) perform model projections for the periods 2051–2060 and 2090–2099, iii) evaluate the impact on physical properties (temperature, salinity, stratification) and water quality (oxygen, Chl *a*), and iv) the subsequent consequences for benthic mussels and suspended mussel culture in the three selected scenarios. This is to our knowledge the first attempt to make climate change scenarios for a shallow coastal system in this region, whereas several model studies have assessed the open water, basin-scale impacts in the Baltic Sea [8,23,44].

2. Methods

2.1. Study area

The Limfjorden is a micro-tidal, shallow estuary with a mean depth of 4.8 m, which consists of several smaller basins connected by narrow straits (Fig. 1B). It is located in the northern part of Denmark with connections to the saline North Sea (west) and the brackish Kattegat (east) (Fig. 1A). Accordingly, a salinity gradient ranges from 32 to 34 g kg^{-1} in the west to 19–24 g kg^{-1}in the east (Fig. 1B). Further, the high supply of fresh water from rivers reduces the salinity, especially in the innermost part, Skive Fjord, with salinities of 15–20 g kg^{-1}. The main current direction is from west to east modified by the wind direction and a weak tidal signal [45]. The Limfjorden is eutrophic with seasonal hypoxia and high-standing stock of blue mussels (*Mytilus edulis*) [46,47]. The system receives a high nutrient load from the catchment dominated by agriculture and is in a poor ecological condition according to the EU Water

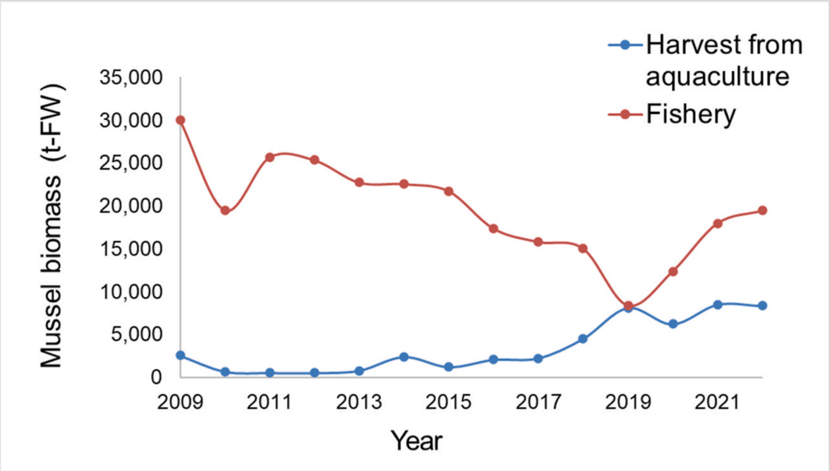


Fig. 2. Mussel harvest from aquaculture and mussel landings from fishery in the Limfjord area (Data from the Fishery Agency).

Framework Directive [48,49]. Mussel dredging is currently the most crucial fishery [50] since the finfish fishery collapsed in the 1990ies [51]. Since then fished mussel landings have decreased from a maximum of approximately 122 Kt fresh-weight (FW) in 2001, to 19.5 Kt FW in 2022 (Data from Danish Fisheries Agency). The mussel harvest from commercial farms, on the other hand, has increased from less than 2.5 Kt FW in 2009–2017 to 8.4 Kt FW in 2022 (Fig. 2) due to higher technological expertise and profit [32,52,53]. The number has nevertheless not increased over the past couple of years due to the ban on new permits, but the number of applications is around the same number of current farms, so when the government approves new permits, growth should be expected.

2.2 Model set-up.

We applied the FlexSem model framework for setting up a 3D coupled hydrodynamic-biogeochemical-sediment model for the Limfjorden [54,55]. The model framework was previously applied to study the impacts of intensified mussel farming [32], mussel transplantation to mitigate hypoxia [46], mussel dredging [34], dispersal of mussel larvae [56], and drivers of hypoxia [47] in the Limfjorden. The model used an unstructured mesh with 6686 elements with a total area of 1502 km^2. The area of the elements varied from 20,368 m^2 (length = 143 m) to 314,297 m^2 (length = 1773 m) with an average of 224,579 m^2 (length = 474 m). The vertical resolution was 1.5 m in the flexible surface layer followed by nine 1 m depth layers, and three 5 m layers, with a maximum water depth of 30 m. The hydrodynamic model solved the Navier-Stoke equations for velocities and the advection-diffusion equations for the transport of tracers (e.g., heat, salinity, nutrients). The turbulent part of the hydrodynamic solution was modeled by a *k*-epsilon model in the vertical [57,58] and a Smagorinsky model in the horizontal [59]. For this study, a surface radiation model was added to the setup, which calculated the heat transfer through the ocean surface and modifies the water temperature by calculating the short-wave radiation, the long wave radiation, the sensible heat flux, and the latent heat flux. The latter three are surface layer effects, whereas the short-wave radiation penetrates the surface and attenuates throughout the upper water column [54]. The addition of a surface radiation model enables running scenarios to model water temperature under predicted future meteorological forcing SSP1-2.6. The model was described and validated in a previous study demonstrating good performance [32,45].

The pelagic biogeochemical model in FlexSem was two-way coupled to a sediment biogeochemical model and a Dynamic Energy Budget (DEB)-population model [32]. The pelagic model simulated the cycling of nitrogen (N) and phosphorous (P) using Redfield ratios [60,61]. The 11 state variables described concentrations of inorganic nutrients (NO_3, NH_4, PO_4), PO_4 adsorbed by metals in particles ($PO_{4\text{-metal}}$), three functional groups of phytoplankton (diatoms, flagellates, picoplankton), micro- and mesozooplankton, detritus, and oxygen (Figure A1). The model considered the processes of nutrient uptake, growth, grazing, respiration, recycling, mortality, and settling of detritus and diatoms. Chl *a* concentrations were used as a proxy for phytoplankton biomass using a conversion factor of 2 mg Chl *a* $(\text{mmol-N})^{-1}$ [63]. The sediment model comprised an unconsolidated layer (Redfield ratios) exposed to resuspension, a consolidated layer with variable CNP-ratios, settled diatoms and mussel pellets, pore-water inorganic nutrients (NO_3, NH_4, PO_4, and $PO_{4\text{-metal}}$), deposit feeders, microphytobenthos, and oxygen. The DEB model described mussel growth as a function of temperature, salinity, and food levels and was previously parameterized and validated for the Limfjorden and the Baltic Sea [64,65]. The DEB model was coupled with the population model describing the abundance of mussels in the farms over time which was set to decrease exponentially over time due to self-thinning [66].

2.2. Model scenarios

The reference scenario (REF) used historical (2009–2018) atmospheric forcing, open boundary conditions (OBC), and river run-off and NP load data (Table 1). There were 14 active commercial mussel farms with a density of 35 mussels per farm-m^{-3} representing the mean production during this period [32]. Daily OBC of salinity and temperature and hourly OBC of water level and velocities were obtained from the HIROMB-BOOS-HIRLAM model for the 10-year reference period 2009 to 2018 [67]. Monthly OBC of nutrients, Chl *a* (distributed in the three phytoplankton groups), and oxygen were obtained from monitoring data near the boundaries (www.odaforalle.dk). OBC of zooplankton were extracted from a station within the Limfjorden, whereas detritus and $PO_{4\text{-metal}}$ were set to a constant value of 0.5 mmol m^{-3} due to missing observations. Atmospheric deposition of nitrogen was applied as a constant value

Table 1

Overview of localized model scenarios with atmospheric forcing, time-slices, number and type of mussel farms, reduction of nutrient loads as % of the REF, and scenario description. For the SSP1-2.6 scenario, two sensitivity studies were conducted assuming i) no increase in mussel farms compared to REF and ii) no implementation of the Water Plans.

Scenario	Time-slice Years	Mussel farms	N-load reduction	Description
REF	2009–2018	14 commercial farms	–	Reference period
SSP1-2.6	2051–2060 2090–2099	52 commercial farms	36 %	Global Sustainability, best case with strongly mitigated responses
SSP2-4.5	2051–2060 2090–2099	52 commercial farms	36 %	Local Stewardship, middle of the road
SSP5-8.5	2051–2060 2090–2099	52 commercial farms	0 %	World Markets, worst case with unmitigated system responses
Sensitivity studies				
SSP1-2.6-MF	2051–2060 2090–2099	14 commercial farms	36 %	Global Sustainability, sensitivity study with few mussel farms
SSP1-2.6-WP	2051–2060 2090–2099	52 commercial farms	0 %	Global Sustainability, sensitivity study with no implementation of the Water Plans

(1504 t-N year^{-1} corresponding to 16 % of total N-load) to the sea surface [32,68]. More details about model initialization, parameterization, configuration, and validation for the Limfjorden set-up can be found in Maar et al. [32]. Run-off and nutrient loads (diffuse and point sources) were obtained from the SWAT catchment model with 79 sources with daily resolution [69].

The three future climate change scenarios (SSP1-2.6, SSP2-4.5, and SSP5-8.5), are named after the shared socioeconomic pathway and the level of radiative forcing in the year 2100 they represent relative to pre-industrial conditions (2.6, 4.5, and 8.5 W m^2, respectively). The choice of scenarios allows for a representation of the range of potential future responses to climate change corresponding roughly to strongly mitigated, middle of the road, and unmitigated system responses, respectively [15]. SSP1-2.6 is broadly consistent with the maximum atmospheric CO_2 concentration required under the Paris Climate Agreement, which sets the ambition to "substantially reduce global greenhouse gas emissions to limit the global temperature increase in this century to 2 °C while pursuing efforts to limit the increase even further to 1.5 °C". Greenhouse gas emissions are intermediate in SSP2-4.5 while they continue to increase throughout the 2100 century in SSP5-8.5 [15]. The scenarios were conducted for the time-slices 2051–2060 and 2090–2099. Each 10-year time-slice used a spin-up of 10 years (same forcing period as the scenario) to reach semi-steady state conditions for water column and sediment (Figure A2). Due to the reduced spatial extend and the shallow bathymetry of the region spin-up times for the system are on the order of months for the water column and less than 10 years for the sediment (Figure A3). We applied 10-year time

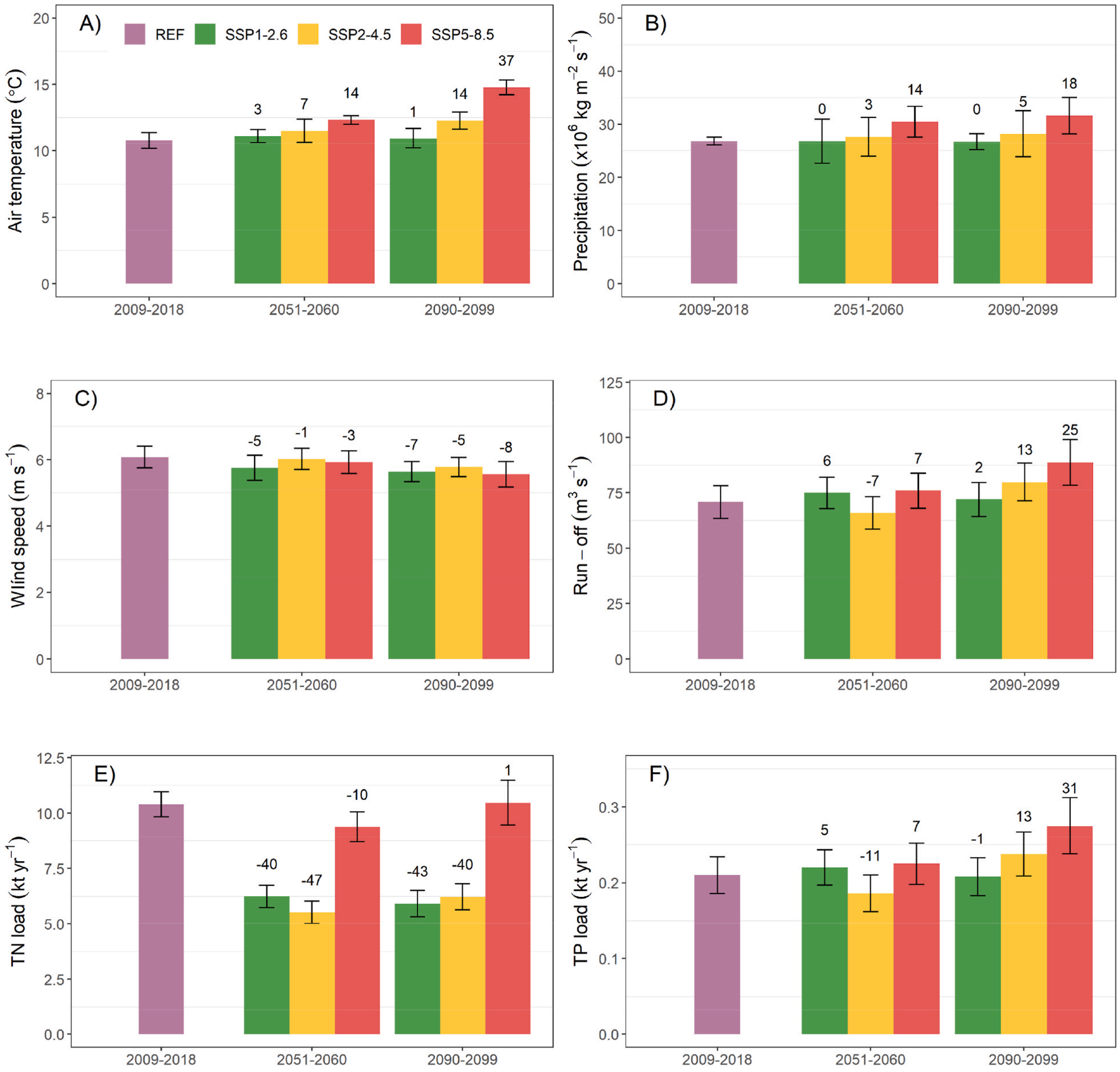


Fig. 3. Forcing data showing annual means (±SD) for each period of A) air temperature, B) precipitation, C) summer wind speed, D) run-off, E) TN river load, and F) TP river load. Values above the columns are the percentage differences from the reference period 2009–2018.

slices to reduce computational costs. Further, we needed realistic current velocities and surface heights at the open boundaries that only could be obtained for 10 years in the reference period (2009–2018) from the two-way nested HBM model provided by DMI [67].

In the SSP1-2.6 and SSP2-4.5 scenarios, land-based nutrient load reductions are expected to be implemented according to the Danish Water Plans (36 % reduction of current N-load, no P reduction required) [49]. In the SSP5-8.5 scenario, it was assumed that the National Water Plans were not implemented due to the growth of the agriculture sector with little concern for the environmental impacts (Table 1). Mussel culture was assumed to be intensified to meet the global market's demand for protein food with a low carbon footprint in all scenarios after consultation with stakeholders in the EU FutureMARES project. The number of commercial mussel farms was set to 52 (density of 70 mussels m^{-3}, production cycle from July to June next year) aimed for food production corresponding to the maximum number of farms in a previous carrying capacity study [32]. Fishing mortality was not changed in the scenarios. A sensitivity study was conducted for the SSP1-2.6, where i) mussel culture was at the same level as the reference period and ii) Water Plans were not implemented (Table 1).

2.3. *Applied model forcing in the scenarios*

Atmospheric boundary conditions to force the model simulations were taken from the EC-Earth CMIP6 simulations (three-hourly resolution) for the historical and future periods. The single model approach was chosen over an ensemble approach to preserve extremes (e.g., storms, heat waves) and physical consistency of the dynamics. Physical features such as gyres or fronts that appear in individual models in different locations in space and time can easily get disrupted or blurred by the statistical operation of building an ensemble. The issue is further complicated by the loss of the mechanistic links across variables that exist in the dynamic models but may not be conserved by the ensemble averages. Two other climate model outputs were assessed over the region of interest. NorESM data was only available as daily values and wind speed was not available at the standard surface level (10 m), thus lacking the necessary temporal variability for correct mixing of the fjord. The CMCC-ESM2 data was available with three-hourly resolution but the scenarios all gave very similar results for the Limfjorden area (not shown). This pattern disagrees with results emerging for the sea surface conditions for the North Sea of the statistical downscaling ensemble used for the lateral boundary conditions which suggests warming trends similar to the evolution of the global means [70,71]. Hence, we preferred the EC-Earth model which captures a wider range of scenario uncertainty.

In the climate change scenarios, OBC of water level, velocities, nutrients, zooplankton, and detritus were reused from REF [32] because they were not stored as output by the regional climate model projections [72]. Multiple (4–6) CMIP6 models were downscaled for the ocean to produce ensemble averages for the North Sea region across climate scenarios SSP1-2.6, SSP2-4.5, and SSP5-8.5. These data provided monthly OBC values for temperature, salinity, Chl *a*, and oxygen at 5, 25, and bottom depth levels [72].

The river runoff for the reference period and the future scenario periods is simulated with the SWAT model [73,74]. The SWAT set up and calibration is the same as in Molina-Navarro, Andersen [69], using 17 and 12 monitoring stations for the calibration of discharge and nutrients, respectively. The reference (baseline) period is 2009–2018, with a 9-year spin-up period 2000–2008. The climate data is the observed daily values from the Danish Meteorological Institute, precipitation (10 km grid), min. and max. temperature, wind speed, relative humidity (20 km grid), solar radiation (20 km grid). The precipitation is corrected for gauge under catch [75]. The future scenarios are run as "delta change" scenarios, where the mean monthly difference between the climate model precipitation and temperature for the reference period and the future periods are forced upon the observed climate time series [76]. Precipitation is changed as a percent change and temperature with the absolute change relative to the reference period. Wind speed, solar radiation and relative humidity were not changed for the future scenarios. All scenario runs include the 9 years spin-up period. The model delineation is constructed to ensure that areas in reality drained by streams smaller than the threshold for creating subbasins are pooled together and are included in the model [77].

2.4. *Forcing patterns in the scenarios*

Overall, the SSP5-8.5 scenario showed the strongest changes in forcing data for the last time-slice 2090–2099, whereas SSP1-2.6 and SSP2-4.5 showed weaker and more similar changes (Fig. 3). Air temperature increased (Fig. 3A) and wind speed decreased in all scenarios (Fig. 3C). Precipitation and run-off increased up to 20–25 % in SSP5-8.5 by the end of the century (Fig. 3B–D). TN load decreased considerably in SSP1-2.6 and SSP2-4.5 due to the implementation of the Water Plans, whereas SSP5-8.5 showed little change. TP followed the run-off patterns with highest increases in SSP5-8.5 for each time-slice (Fig. 3F). OBC showed a gradual increase in seawater temperature, a gradual decrease in salinity, and oxygen, but no change in Chl *a* concentration over time [72].

2.5. *Data analysis*

The strength of water column stratification was estimated as the Potential Energy Anomaly (PEA) [78]. Water quality (surface Chl *a* concentrations and bottom oxygen) were estimated for the summer period (May to September) with highest production and strongest hypoxia [47]. Future changes were estimated as the reference period subtracted from each scenario (10-years means).

3. Results

3.1. Changes in environmental variables

Physical variables showed the strongest responses to future conditions in the SSP5-8.5 scenario for the second time-slice (2090–2099) in agreement with forcing data (Fig. 4A–C). The SSP1-2.6 and SSP2-4.5 scenarios showed in general similar and lower responses than SSP5-8.5 for the two time-slices. Sea surface salinity decreased by 0.5–2.2 g kg^{-1} corresponding to 2–8 % change (Fig. 4A), whereas sea surface summer temperature increased gradually over time and across scenarios with 1–5 °C (5–27 %) (Fig. 4B). Salinity decreased due to higher run-off (Fig. 5A–C) and temperature increased in all parts of the estuary (Fig. 5D–F). Water column stratification (PEA) did not change much in the first time-slice but increased in the second time-slice mostly in SSP5-8.5 (Fig. 4C). Highest changes of PEA were found in Skive Fjord and in the eastern Channel towards the Kattegat (Fig. 5G–I). Heat waves (>25 °C) occurred <1 day per year in SSP1-2.6 and SSP2-4.5, whereas in SSP5-8.5 there were on average 1.3 and 6.2 days per year during 2051–2060 and 2090–2099, respectively (Figure A3). The warmest areas were found in the Nibe Broad and the inner parts of Skive Fjord outside the mussel farming sites. The warmest year was 2097 in SSP5-8.5.

Hypoxic conditions became worse over time in the SSP5-8.5 scenario and slightly better in the SSP2-4.5 scenario, whereas there were small changes in the SSP1-2.6 scenario (Fig. 4D). Oxygen concentrations increased slightly in Thisted Broad, Løgstør Broad, and Skive Fjord and decreased in the other parts in SSP1-2.6 and SSP2-4.5 (Fig. 6A and B), whereas oxygen decreased all over the Limfjorden in SSP5-8.5 (Fig. 6C). Chl *a* concentrations decreased with 8 %–17 % in the scenarios SSP1-2.6 and SSP2-4.5 in contrast to

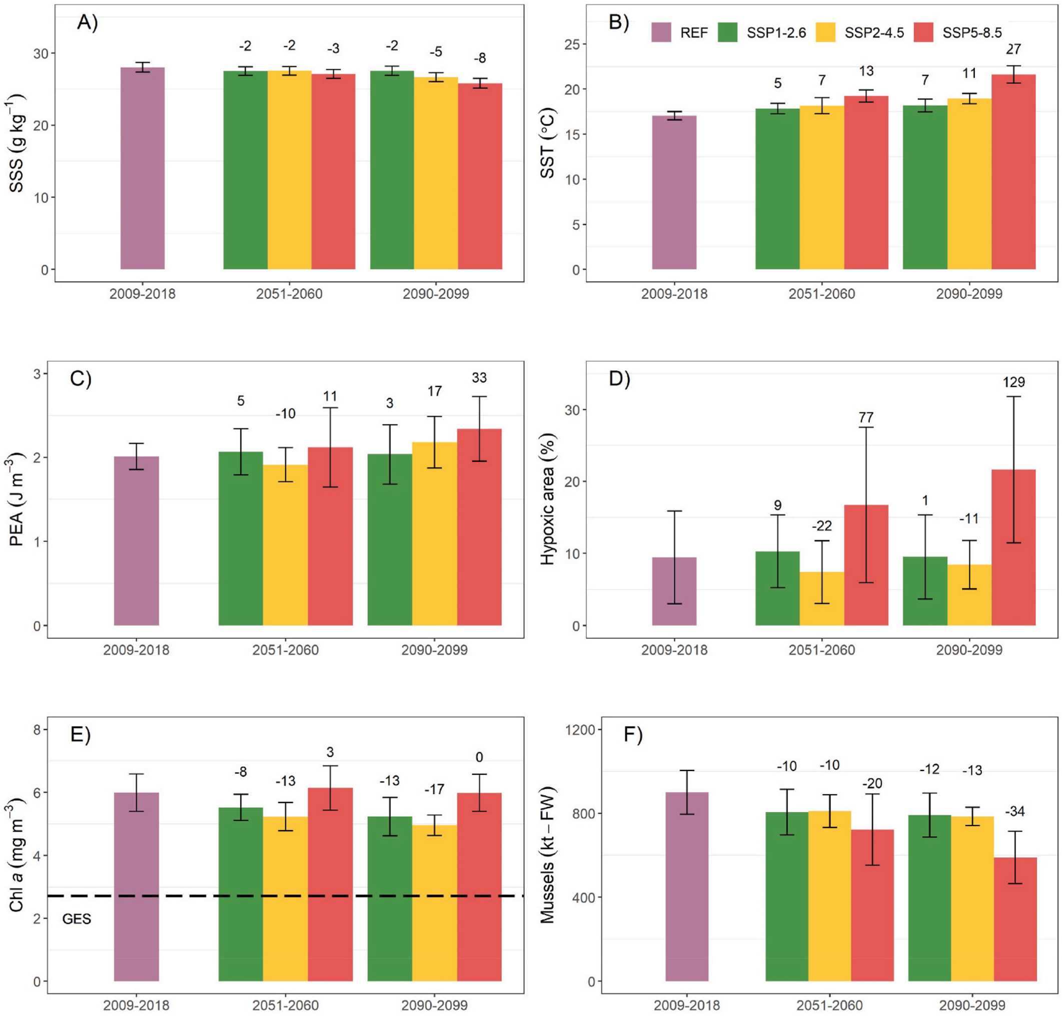


Fig. 4. Summer (June to September) means (±SD) of A) sea surface salinity (SSS), B) sea surface temperature (SST), C) stratification index (PEA), D) hypoxic area (<4 mg l^{-1}) as percentage of total area, E) surface Chl *a* concentration, and F) benthic mussel biomass for the reference period (2009–2018) and the three scenarios and the two time-slices 2051–2060 and 2090–2099. The values above the columns are the percentage deviations from the reference period. The horizontal dashed line in E) indicates the thresholds for a good ecological status (GES).

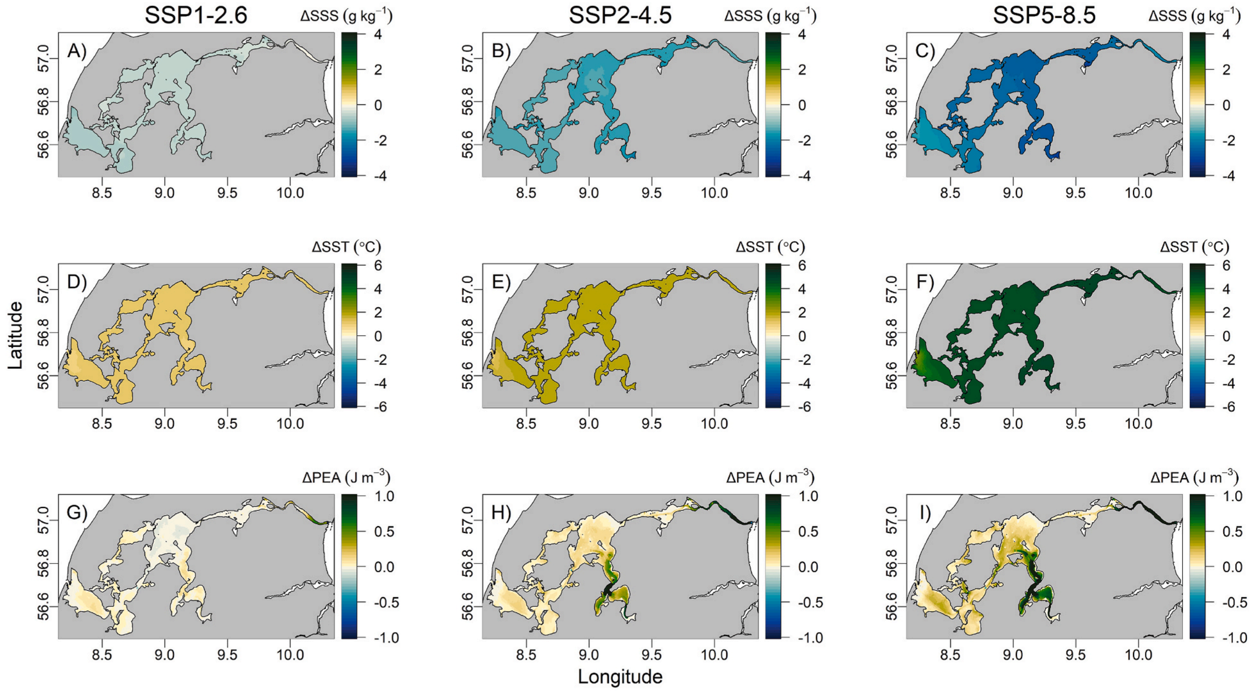


Fig. 5. Spatial plots showing the difference of physical variables between the three scenarios (years 2090–2099) and the reference (years 2009–2018) for the summer period. A-C) surface salinity, D-F) surface temperature, and G-I) stratification index for the scenarios SSP1-2.6 (1st column), SSP2-4.5 (2nd column), and SSP5-8.5 (3rd column).

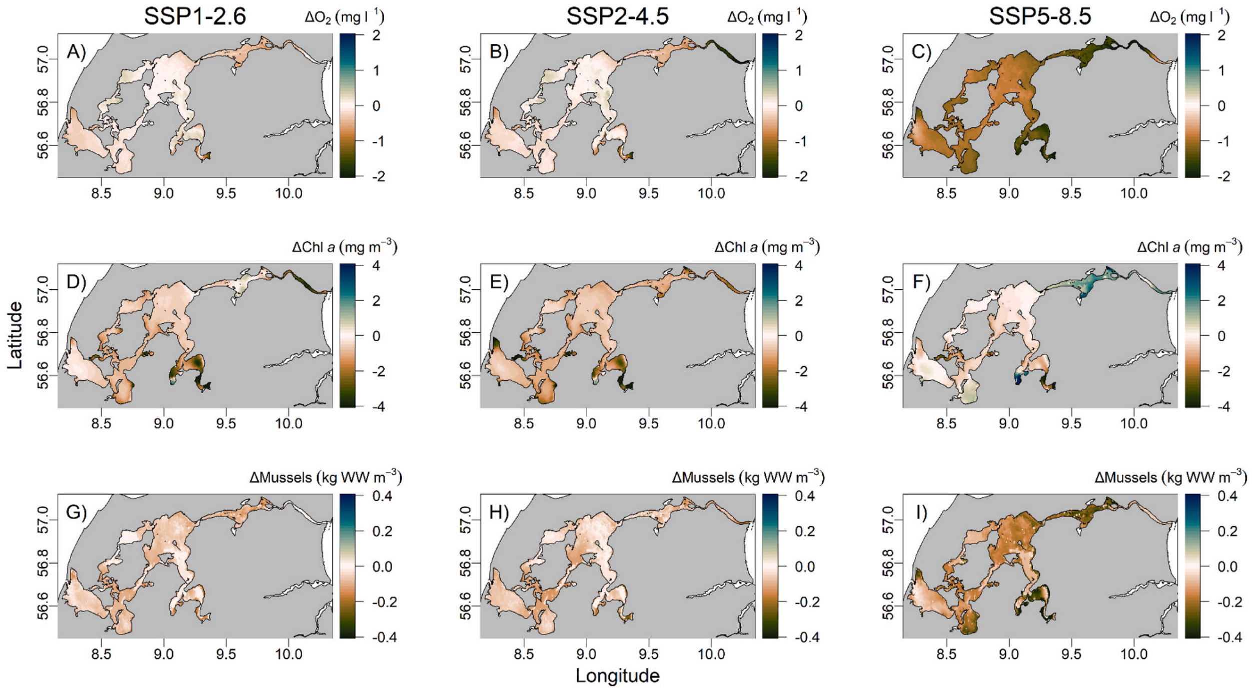
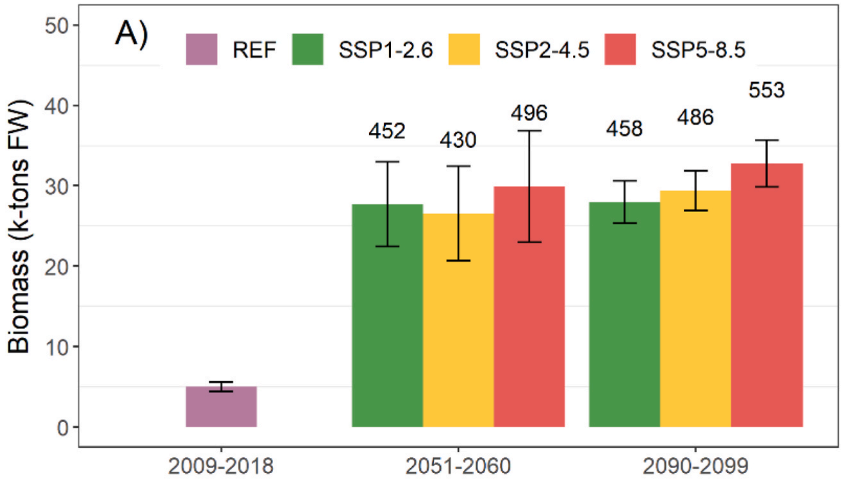


Fig. 6. Spatial plots showing the difference of ecosystem variables between the three scenarios (years 2090–2099) and the reference (years 2009–2018) for the summer period bottom. A-C) bottom oxygen, D-F) surface Chl *a* concentrations, and G-I) benthic mussel biomass for the scenarios SSP1-2.6 (1st column), SSP2-4.5 (2nd column), and SSP5-8.5 (3rd column).

SSP5-8.5 showing small changes (<3 %) (Fig. 4E). The average Chl *a* concentrations were never below the threshold for a good ecological status of the Limfjorden. Spatially, Chl *a* concentrations decreased mostly in the Skive and Sallingsund areas in SSP1-2.6 and SSP2-4.5 (Fig. 6D and E), whereas the pattern was more complex for SSP5-8.5 with some local increases e.g., in Nibe Broad (Fig. 6F). Benthic mussel biomass decreased in all scenarios, most severely in SSP5-8.5 (Fig. 4F), and in all areas of the Limfjorden (Fig. 6G–I).

3.2. *Suspended mussel culture*

Suspended mussel culture harvest potential increased in all scenarios and time-slices compared to the reference, although slightly higher in SSP5-8.5, due to the higher number of mussel farms (Fig. 7A). Mussel shell length at harvest time decreased less than 6 % in all scenarios and time-slices, mostly in SSP1-2.6 and SSP2-4.5 scenarios (Fig. 7B). Sensitivity studies were conducted to disentangle the effects of nutrient reductions and mussel farming from climate change. The sensitivity tests showed that intensified mussel farming and implementation of the Water Plans both had a positive effect on bottom oxygen (increase) and surface Chl *a* concentrations (decrease) in the SSP1-2.6 scenario (Table A1). The response was stronger for nutrient reductions than for mussel farming. Hence, if the Water Plans were not implemented or mussel farming was status quo, the water quality would be worse in SSP1-2.6. Benthic mussel biomass decreased similarly in SSP1-2.6 and the sensitivity studies (Table A1).



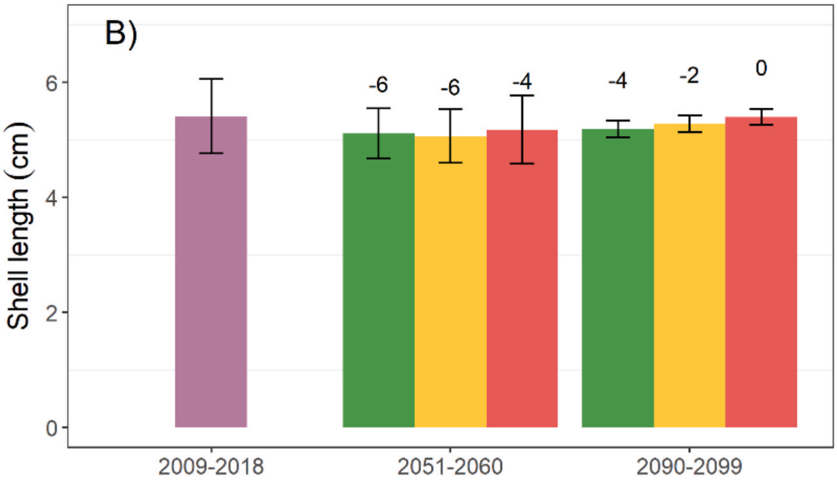


Fig. 7. Annual means (±SD) of A) mussel harvest from suspended farms and B) mussel shell length in the scenarios indicated with percentage changes from the reference period 2009–2018. See Fig. 4 for further explanation.

4. Discussion

4.1. Changes in physics and bottom oxygen

The Limfjorden is a shallow estuary where the physical properties were found to be sensitive to climate change impacts due the influence of many freshwater sources and a complex geomorphology restricting the water exchange with the North Sea (west entrance) and the Baltic Sea (east entrance) (Fig. 5). Sea surface temperatures were projected to increase by 1–5 °C and salinity to decrease with up to 2.2 g kg^{-1} over the next 30–60 years in the three scenarios. Similar results for temperature and salinity were found for the shallow Curonian Lagoon influenced by large river discharges and low water exchange with the Baltic Sea [79]. Model projections of the Baltic Sea and North Sea likewise showed a sea water warming of 2–5 °C by the end of 2100 [80,81]. Salinity is similarly predicted to decrease in the North Sea, whereas the change in salinity is uncertain for the Baltic Sea depending on the global sea level rise and intrusion of salt water from the North Sea [5,72,80]. Water column stratification increased over time in the Limfjorden due to warming, increased precipitation and run-off, and less wind mixing (Figs. 2 and 3C). In the Baltic Sea and the North Sea, a shallower and more intense thermocline was also found during summer in the warming scenarios [80,81]. Stronger stratification can limit the exchange of oxygen, nutrients, and phytoplankton between the bottom and the surface layers with consequences for water quality and productivity [82].

Hypoxia occurs as episodic summer events during stratified periods interrupted by wind mixing in the Limfjorden [82]. The main drivers of short-term hypoxia were previously found to be sea water temperature combined with wind patterns, whereas the high biological activity sustained the hypoxia development [47]. In the two most optimistic future scenarios, SSP1-2.6 and SSP2-4.5, the bottom area affected by oxygen depletion changed little compared to REF (Fig. 4D) because the implementation of nutrient reductions according to the National Water Plans cancelled out the negative effects from higher seawater temperatures and stronger stratification (Fig. 3D). In the worst-case scenario, SSP5-8.5, oxygen conditions were reduced in all the Limfjorden (Fig. 6C). Stronger water column stratification (less ventilation), increased discharge of nutrients, and increased nutrient cycling during climate warming was also found to amplify oxygen depletion and partially counteract the planned nutrient abatement strategies in the Baltic Sea [24,44,80]. The sensitivity study confirmed that without implementation of the Water Plans, oxygen depletion would be even stronger (Table A1). Hypoxia is known to cause mass mortality of benthic mussels [46], loss of eelgrass [83], and higher nutrient fluxes from the sediment stimulating summer phytoplankton blooms [84] thereby worsening the ecological conditions of the estuary.

4.2. Changes in Chl a concentrations and benthic mussels

Summer Chl *a* concentrations are often used as an indicator of the ecological status [20]. In the Limfjorden, the threshold for a good ecological status was never reached in any of the scenarios despite some decreases in the two most optimistic scenarios (SSP1-2.6 and SSP2-4.5). However, the sensitivity study showed that the nutrient reductions did have some effect, but not enough to fully compensate for the other negative effects (Table A1). The nutrient reduction from land was not effective during summer due to higher nutrient recycling in the pelagic food web and higher nutrient fluxes from the sediment under climate warming facilitating phytoplankton blooms [32,84]. Chl *a* concentrations decreased slightly more in SSP2-4.5 compared to SSP1-2.6 because of the higher temperatures facilitating higher nutrient fluxes and denitrification in the sediment and thereby a faster reduction of the internal sediment load over the study period. Hence, the sediment N-pool decreased over time in the future scenarios due to a combination of decreasing N-load and warming (Figure A2). The sensitivity study also showed that mussel farming contributed to reduced Chl *a* concentrations (Table A1). Suspended mussel culture contributes to higher water quality due to the removal of nutrients by biomass harvesting, filtration of phytoplankton and detritus, and lower sedimentation on the basin scale [30,32,85].

Benthic mussels were projected to experience a lower food supply in all scenarios and, in some cases, less oxygen that caused lower future biomass in all scenarios (Fig. 6G–I). The current mussel fishery varies from 8.4 to 30.0 Kt FW per year and has declined over time (Fig. 2). The fishery is highly regulated and monitored to avoid overfishing of the population and imposition of unacceptable cumulative effects on ecosystem components [50]. A further decrease of the standing stock by 10–36 % would have detrimental impact on the fishing quota, which in combination with likely poorer mussel condition due to reduced food and increased stress, would further diminish the fishery's economic viability. Additionally, as regulators have increasingly limited fishing to deeper areas to accommodate eelgrass habitat, mussels in deeper areas will be exposed to the more adverse conditions in the Limfjorden.

4.3. Mussel harvesting

Intensified mussel farming was beneficial in all scenarios yielding a much higher harvest without decreasing the mussel shell length more than 6 % compared to the present situation (Fig. 7). Shell length is important for the mussel farmers because the market generally demands a shell length >4.5 cm [64]. For a full year production cycle, shell lengths were >5 cm in all scenarios, and harvest could occur earlier and expand the market supply period. Mussel spat recruitment in the mussel farms was assumed to be the same in all scenarios and time-slices despite a decrease in the benthic mussel population. However, a recent particle tracking study showed that mussel populations in the Limfjorden are highly connected across basins [56]. Only extreme changes in the pelagic larvae duration or severe hypoxia causing mass mortality of mussels would change the overall dispersal patterns and potentially reduce the connection to the Skive area [86]. Furthermore, previous studies have shown that spat recruitment mainly is limited by substrate availability and predation, and not by larvae density in Danish waters [87,88].

Heat waves have been observed to cause mortality and reduced growth of mussels in low salinity environments (around 7 g kg^{-1})

posing an additional physiological stress [64]. In the Limfjorden, salinity is above the critical level for reduced growth at the farm sites [89] even under future change where salinity is predicted to decrease (Fig. 3A). Hence, the mussels in the Limfjorden would probably be less sensitive to heat waves than in low salinity environments [64]. The measured temperature response of blue mussel growth is dome-shaped with optimal temperatures varying from 8 to 20 °C depending on food conditions and local adaptation [90]. At 30 °C, the mortality was 100 % after four days in lab experiments with blue mussels from the Limfjorden [90]. Hence, heat waves above 25 °C may have deleterious effects on mussels and increase summer mortality [39,90]. In the applied DEB model, optimal temperature for food assimilation was 20 °C followed by a strong decline at higher temperatures, whereas maintenance costs continue to increase with increasing temperatures [64,91]. The temperature increase was up to 5 °C in the SSP5-8.5 scenario (Fig. 3B) and the number of days with heat waves increased up to 6.2 days per year on average and 14 days as maximum (Figure A3). However, the warmest areas were found outside the mussel production sites and we did not see a severe reduction in mussel growth. Hence, harvest potential was highest in the SSP5-8.5 scenario due to the combination of higher temperatures (Fig. 3B) and no change in Chl *a* concentrations compared to the SSP1-2.6 and SSP2-4.5 scenarios showing a decrease in Chl *a* levels (Fig. 3E). Model scenarios of theoretical bay ecosystems, varying in morphology and freshwater input, likewise found that blue mussel aquaculture will benefit from climate change impacts due to increasing temperatures and the concomitant increase in metabolic rates within their thermal tolerance range [40].

Ocean acidification was not considered in the Limfjorden model although blue mussel growth can be reduced at pH below 7.4 [92]. The regional models providing the open boundary data predicted a decrease in pH from around 8.1 to 7.6 in the SSP5-8.5 by year 2100 [72]. If we assume a similar decrease in the Limfjorden, blue mussel growth would not be negatively affected by ocean acidification within the study period. However, it is not clear how a lower pH will affect recruitment and early life-stages [93] or potentially cancel out the positive effects of increasing temperatures on mussel clearance rate and growth [94].

4.4. Model considerations

We only used one set of meteorological Earth System Model projections as atmospheric climate change forcing for each scenario instead of a model ensemble. For the considered area, regional dynamic downscaling products from CMIP6 are few and, hence a statistical downscaling approach was applied at the open ocean boundaries that showed realistic results within the predicted range of outcomes for each scenario. Whereas the tendencies could be analyzed with the current approach, it was not possible to fully assess the uncertainties involved in this study which focuses mainly on the scenario uncertainty. Model uncertainty and internal variability and uncertainties in initial conditions and model forcings would require a multi-model and multi-realization ensemble. Sea level rise was not considered at the two open boundaries and could change the inflow of salt water from the North Sea into the Limfjorden. However, the future global sea level rise is very uncertain and more knowledge is needed before implementation [80], particularly at regional to local level. Nutrient input from the atmosphere and the open boundaries were not changed in the scenarios due to limited data availability. However, the freshwater discharge accounts for 81 % of the total external nitrogen input to the Limfjorden [32], and were changed in the scenarios based on the applied catchment model and the National Water Plans (Fig. 3E).

5. Conclusions

In summary, a 3D numerical ecosystem model was used to make future scenarios of climate change and nutrient reductions on physical properties and water quality and associated consequences for the benthic and cultured mussels in a shallow estuary. The system showed strong responses of physical properties and water quality to climate change that partly counteracted the planned nutrient reductions from land. Hence, higher nutrient reductions in the coming Water Plans would be needed to reach a good ecological status under the influence of climate change. Benthic mussels were predicted to suffer from limited food supply and also hypoxia in the worst case, whereas suspended mussel culture showed a high harvest potential in all three scenarios. Reflecting the past two decades' trends and considering the regulatory and social trends related to mussel fisheries, it is likely that there will be a shift in total production from the mussel fishery to suspended mussel culture provided permits will be assigned for new farms, and that spat recruitment continues to be sufficient. Relay of suspended mussels onto the seafloor as artificial mussel beds is a new production mode, but it is not clear to what extent this will expand to support the future fishery. Previous studies have shown that system responses to climate change are more variable in coastal systems than for open waters due to the more complex geomorphology and influence by freshwater sources [5,40,79]. Hence, localized model set-ups and scenarios are needed for coastal ecosystems to achieve more realistic outcomes with higher relevance for the local community. However, to fully assess the uncertainties involved in the model results, future applications should use different atmospheric climate forcing for each scenario [44]. The conducted model scenarios can be used to inform managers, mussel farmers, fishermen, and the local population on potential future changes in bivalve harvesting and ecosystem health to find solutions to mitigate climate change impacts.

Software availability statement

The FlexSem source code and precompiled source code for Windows (GNU General Public License) can be downloaded at https://marweb.bios.au.dk/Flexsem. The specific code for the model set-up can be downloaded from Zenodo.org: https://doi.org/10.5281/zenodo.7124459 [95] and https://doi.org/10.5281/zenodo.10071986 [55].

Data availability statement

Climate forcing data (atmospheric forcing) can be downloaded from https://doi.org/10.5194/gmd-15-2973-2022 [70] and lateral open boundary data from https://doi.org/10.5281/zenodo.6523926 [72]. River runoff and nutrient loads can be downloaded from https://doi.org/10.5281/zenodo.10159527.

CRediT authorship contribution statement

Marie Maar: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Janus Larsen:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Momme Butenschön:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Trond Kristiansen:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Hans Thodsen:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Daniel Taylor:** Writing – review & editing, Validation, Methodology, Investigation, Data curation. **Vibe Schourup-Kristensen:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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