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Nutrient extraction and ecosystem impact by suspended mussel mitigation cultures at two contrasting sites

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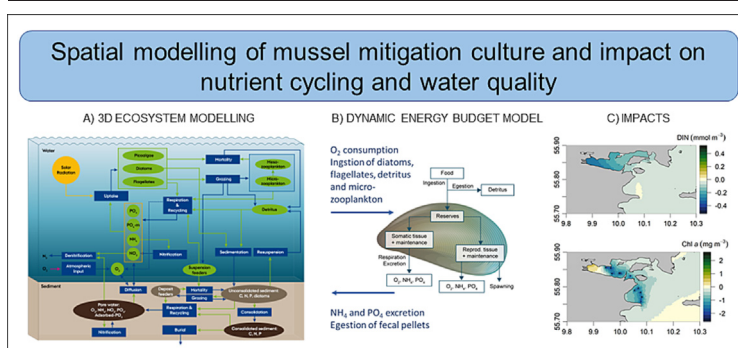
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HIGHLIGHTS

- The net effect of bivalve culture on ecosystem nutrient cycling is uncertain.
- 3D high-resolution ecosystem-mussel farm modeling was applied at two contrasting sites.
- Water quality showed higher improvement in a restricted fjord than in an exposed bay.
- Mussel mitigation culture showed a high net extraction of nitrogen at ecosystem scale.
- Important for further development, site selection, and monitoring of mussel culture.

GRAPHICAL ABSTRACT



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ABSTRACT

Mussel mitigation culture is increasingly recognized as a tool to extract nutrients from eutrophic systems by harvesting mussel biomass and nutrients contained therein. The net effect of mussel production on the nutrient cycling in the ecosystem is, however, not straightforward due to the interaction with physical- and biogeochemical processes regulating ecosystem functioning. The aim of the present study was to evaluate the potential of using mussel culture as a tool to mitigate eutrophication at two contrasting sites: a semi-enclosed fjord and a coastal bay. We applied a 3D coupled hydrodynamic-biogeochemical-sediment model combined with a mussel eco-physiological model. The model was validated against monitoring data and research field data on mussel growth, sediment impacts, and particle depletion from a pilot mussel farm in the study area. Model scenarios with intensified mussel farming in the fjord and/or the bay were conducted. The results showed that mussel mitigation culture still has a high net N-extraction when including ecosystem effects, such as changes in biodeposition, nutrient retention, denitrification, and sediment nutrient fluxes in the model. Mussel farms located in the fjord were more effective in directly addressing excess nutrients and improving water quality due to the relative vicinity to primary nutrient sources (riparian) and physical characteristics of the fjord system. The results will be important to consider in other systems concerning site selection, development of bivalve aquaculture, and associated sampling strategies for monitoring the farming impacts.

1. Introduction

Coastal eutrophication is a worldwide problem that was first recognized in the 1970s and is characterized by an excess of nutrients, hypoxia, harmful algae blooms, turbid water, and loss of benthic flora and fauna (Nixon, 1995; Cloern, 2001; Conley et al., 2011). After three decades of efforts on

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reducing nutrient loads, some coastal systems are starting to show signs of recovery in the Baltic Sea, the North Sea, and some North American bays (Dolch et al., 2013; Riemann et al., 2016; Boesch, 2019). However, the ecosystem responses to nutrient reductions do not always lead to full recovery due to complex feedback mechanisms (e.g., internal nutrient loads, loss of biodiversity, and functional habitat) and shifting baselines (Duarte et al., 2009a). In addition, climate change increases the pressure on coastal ecosystems, through warming and decline in oxygen content, offsetting the expected effect of nutrient reductions (Friedland et al., 2012; Breitburg et al., 2018; Boesch, 2019). Hence, additional intervention options are desirable to accelerate nutrient reductions and recover ecosystems from eutrophication (Duarte and Krause-Jensen, 2018; Kotta et al., 2020).

Mussel mitigation culture is increasingly recognized as a tool to extract nutrients from eutrophic systems by harvesting mussel biomass and nutrients contained therein (Smaal and van Duren, 2019; Taylor et al., 2019; Timmermann et al., 2019). Mussels have a high filtration capacity and remove plankton and detrital particles efficiently from the water column (Petersen et al., 2013). The ingested nutrients are bound in mussel biomass with some fractions lost to respiration and biodeposition, while there is a net removal of nutrients from the ecosystem by harvest (Ferreira and Bricker, 2016; Nielsen et al., 2016). Mussel mitigation culture is designed for maximizing nutrient extraction with high mussel densities in a given area, but the mussels are therefore smaller and of lower quality than in conventional commercial farms (Petersen et al., 2014; Nielsen et al., 2016). The harvested mitigation mussels can be used as organic animal feedstuff, substituting conventional terrestrial (e.g., soy) or marine (e.g., anchovy) feed products (Jönsson and Elwinger, 2009; van der Heide et al., 2021). A previous field study in a Danish eutrophic estuary demonstrated high nutrient extraction potential with the harvest of up to 2 t-N ha⁻¹ and 0.12 t-P ha⁻¹ in standard farms of 18 ha (Taylor et al., 2019), whereas the mitigation potential has been reported lower in the Baltic Sea due to lower salinity hampering growth (Buer et al., 2020; Kotta et al., 2020).

The net effect of mussel production on the nutrient cycling in the ecosystem is, however, not straightforward due to the interaction with biogeochemical processes regulating ecosystem functioning (Guyondet et al., 2022). Filtration by suspended mussel aquaculture can improve water clarity (Taylor et al., 2021), but at the same time change abundance and size composition of the plankton community with implications for food web dynamics (Strohmeier et al., 2012; Sonier et al., 2016). Settling of mussel biodeposits can cause the accumulation of organic matter underneath the culture units leading to local hypoxia, inhibition of denitrification, and increased nutrient fluxes (Nizzoli et al., 2011; Holmer et al., 2015; Hylén et al., 2021a). Furthermore, bio-deposits sink faster than food particles (phytoplankton and detrital particles) and can increase the retention of nutrients at the farm site (Cranford et al., 2007), whereas the removal of particles by mussel filtration can decrease basin scale sedimentation (Timmermann et al., 2019). The excretion of nutrients by mussels can, on the other hand, lead to faster export of nutrients from the system, whereas the uptake of excreted nutrients by phytoplankton can lead to higher nutrient retention (Guyondet et al., 2022).

The hydrodynamic regime (e.g., current speed, flushing) is important for mussel nutrient extraction and retention (Maar et al., 2020; Taylor et al., 2021). Bivalve aquaculture has been shown to provide a net nutrient extraction in idealized model systems with different flushing levels, but without explicit descriptions of sediment chemistry (Guyondet et al., 2022). Another model study likewise showed a net nutrient extraction with intensified mussel aquaculture, but also lower basin-scale denitrification due to reduced sedimentation (Maar et al., 2023b). Hence, the efficacy of mussel mitigation culture for nutrient extraction and retention depends on many complex feed-back ecosystem processes that are difficult to predict under varying hydrodynamic regimes, environmental conditions, and spatial-temporal scales. To resolve the role of mussel mitigation culture, 3D coupled hydrodynamic-ecosystem models that are two-way coupled to a mussel farm module are ideal to simulate complex environmental interactions (Ferreira et al., 2014; Maar et al., 2020; Guyondet et al., 2022).

The aim of the present study was to evaluate the potential of using mussel culture as a tool to mitigate eutrophication at two contrasting sites: a semi-enclosed fjord and a coastal bay. We applied a 3D coupled hydrodynamic-biogeochemical-sediment model combined with a mussel eco-physiological model. The model system was used to estimate the amount of extracted nutrients and the ecosystem impacts of the mussel mitigation farms at the two sites compared to baseline conditions without mussel culture. The experience from this study has broader relevance for other areas concerning optimal site selection of bivalve aquaculture with the aim to extract nutrients as a tool to mitigate eutrophication as suggested e.g., the Baltic Sea (Buer et al., 2020; Kotta et al., 2020), Northeastern America (Rose et al., 2014), Canada (Clements and Comeau, 2019), the Mediterranean, and some Chinese bays (Rose et al., 2015b).

2. Methods

2.1. Study area

The study area is in southwestern Kattegat, Denmark, which is the transition zone between the North Sea and the Baltic Sea (Fig. 1A). Two contrasting sites were analyzed, the semi-enclosed fjord “Horsens Fjord” and “As Vig” - an exposed bay just outside the mouth of Horsens Fjord (Fig. 1C). The area is eutrophic and in a ‘bad ecological status’ according to the EU Water Framework Directive (WFD). The catchment area is dominated by agriculture and Horsens Fjord hosts five fish farms. The nutrient load for the whole study area is 4000 t-N year⁻¹ and 143 t-P year⁻¹ from agriculture and 61 t-N year⁻¹ and 7 t-P year⁻¹ from fish farms (Fig. 1B). For Horsens Fjord, the nutrient loads are 740 t-N year⁻¹ and 23 t-P year⁻¹ (Fig. 1C).

A pilot mussel mitigation farm was operating from 2012 to 2014 and reopened from 2017 to 2018 in As Vig as part of the BONUS OPTIMUS project (<https://www.bonus-optimus.eu/>) (Fig. 1A, B). The area of the mussel farm was 11.3 ha and the farm consisted of 40 tube-net cultivation units (SmartUnit, www.smartfarm.no) moored at a 10–20 m distance (Hylén et al., 2021a). Blue mussel larvae (*Mytilus edulis*) were collected on the tube-nets by natural settling during May–June in 2017 and 2018. Unfortunately, most of the mussel biomass was lost during the summer of 2017 due to a storm event. In 2018, mussels were sampled four times on 12 July, 23 August, 27 September, and 27 October for estimations of individual biomass and shell length as described by Taylor et al. (2019). Harvested mussel biomass in early November 2018 was 729 ± 25 t fresh weight (FW) (Taylor et al., 2021).

During field campaigns, sediment fluxes of NH₄, NO₃, DIN, and PO₄, oxygen consumption, sedimentation of particulate organic nitrogen (PON), denitrification, and DNRA were measured below the mussel farm and upstream at a reference station with similar depth (Fig. 1C) on 26–30 June 2017 (no mussel farm), 9–12 July 2018 (post-settlement) and 22–27 October 2018 (pre-harvest) (Hylén et al., 2021a; Hylén et al., 2021b). In addition, current speed was measured on 10–11 July and 22–24 October in 2018 outside the mussel farm in As Vig and converted to daily means for comparison with model results. The reported in situ observations from the reference station and the mussel farm were used for validation of the mussel growth model and the sediment model in the present study.

2.2. Model set-up

We applied the FlexSem model framework for setting up a coupled hydrodynamic-biogeochemical-sediment model for the area (Larsen et al., 2020; Maar et al., 2023a). The model framework was previously applied to study the impacts of mussel farming (Maar et al., 2020; Maar et al., 2023b), mussel transplantation (Maar et al., 2021), mussel dredging (Pastor et al., 2020), and dispersal of mussel larvae (Pastor et al., 2021) in coastal areas. The hydrodynamic model solves the Navier-Stokes equations for velocities and the advection-diffusion equations for the transport of tracers (e.g., heat, salinity, nutrients). The turbulent part of the

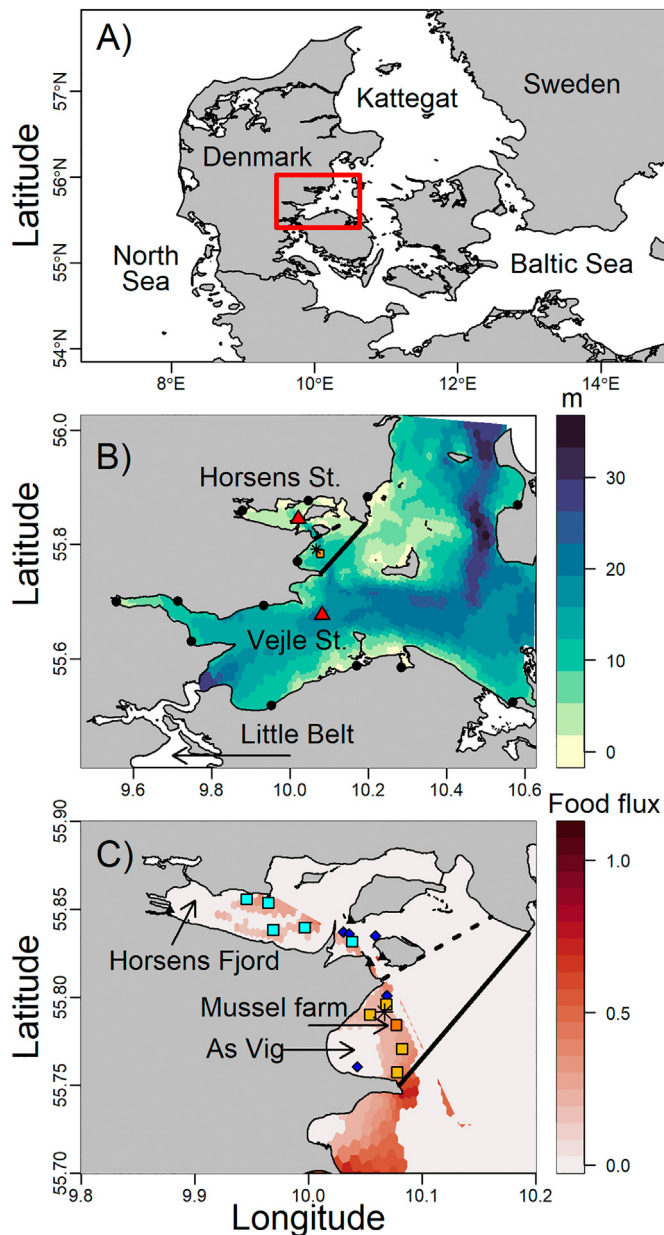


Fig. 1. A) Map of the study area (red square) in the SW Kattegat, B) model domain showing bathymetry (m depth), the monitoring stations, Horsens St. and Vejle St. (red triangles), and freshwater sources (black circles), C) local map with the pilot mussel farm (dark orange square), and the reference station (asterisk) in As Vig. Model locations of mussel farms in scenario “BAY” (orange squares) and scenario “FJORD” (cyan squares). Black triangles are harbors, and the blue diamonds are fish farms. The background color is the food flux ($\text{mg-Chl } a \text{ m}^{-2} \text{ s}^{-1}$). The ‘zero’ values include the area exclusion due to Natura 2000 areas, depth restrictions, and shipping routes. The dashed black line is the separation between Horsens Fjord and As Vig, and the solid line is the transect used to calculate nutrient transports between As Vig and the Kattegat.

hydrodynamic solution was modeled by a k-epsilon model in the vertical (Burchard et al., 1998; Warner et al., 2005) and a Smagorinsky model in the horizontal (Smagorinsky, 1963). The model uses an unstructured mesh with 3497 elements with a total area of 1798 km^2 (Fig. A1A). The square root length of each element varies from 133 m around the mussel farm to 1791 m at the open boundaries with an average of 717 m. Maximum water depth was 36 m and the vertical resolution was 1 m in the four top layers including a flexible surface layer followed by three 2 m

thick layers, one 4 m layer, two 6 m layers, and a 10 m bottom layer. A surface heat budget model was forced by atmospheric model data (wind speed, cloud cover, dewpoint temperature, and precipitation) obtained from Aarhus University (Skamarock et al., 2008). Run-off and nutrient (nitrogen and phosphorous) loads were obtained from the SWAT catchment model with 11 sources with daily resolution (Molina-Navarro et al., 2017). Furthermore, nutrient input from the fish farms in the fjord was included. The model runs in the present study was conducted from 2017 (no mussel farm) to 2018 (with mussel farm).

The model has three open boundaries towards the Little Belt (south) and the Kattegat (east and north) (Fig. 1A). Initial fields and open boundary conditions of temperature, salinity, water level, and velocities were obtained from the Copernicus Marine Environment Monitoring Service (CMEMS, <https://doi.org/10.48670/moi-00010>). Initial fields of nutrients, Chlorophyll *a* (Chl *a*), and oxygen were obtained from CMEMS (<https://doi.org/10.48670/moi-00012>), detritus and zooplankton were set to a low winter value and used after 3 years of spin-up. Open boundary data of ecological variables were obtained from a previous ecological model of the southwestern Kattegat (Maar et al., 2018b) supported by monitoring data of nutrients and Chl *a* at the southern boundary. Benthic suspension feeder biomass was obtained after a spin-up period of three years. For the sediment, organic matter concentrations (C, N, P) and metal-bound P were spatially interpolated from five monitoring stations, initial inorganic nutrient and oxygen concentrations were set to the same value as for bottom water, and deposit feeder biomass was set to a constant value based on monitoring data (Maar and Hansen, 2011), all sediment variable settings were spatially refined after a spin-up period of 9 years.

2.3. Biogeochemical model

The biogeochemical model in FlexSem simulates the cycling of nitrogen (N) and phosphorous (P) using Redfield ratios (Maar et al., 2011; Maar et al., 2016). The 10 state variables describe concentrations of inorganic nutrients (NO_3 , NH_4 , PO_4), three functional groups of phytoplankton (diatoms, flagellates, picoplankton), micro- and mesozooplankton, detritus, and oxygen (Fig. A2). The model considers the processes of nutrient uptake, growth, grazing, respiration, recycling, mortality, and settling of detritus and diatoms (Maar et al., 2018b). The pelagic model is two-way coupled to a sediment biogeochemical model through sedimentation and resuspension of organic matter and diffusive fluxes of nutrients and oxygen (Petersen et al., 2017). Pelagic detritus and diatoms settle into an organic detritus pool and a dead diatom pool, respectively, in the unconsolidated top layer of the sediment. Organic matter in the unconsolidated sediment can be resuspended above a bottom stress threshold, respired, recycled, or gradually transferred to the consolidated sediment layer. The mean sediment organic carbon content was 3–4 % of dry-weight (DW) measured at As Vig (Hylén et al., 2021a) corresponding to an organic matter content of 11–15 % of DW (Carlsson et al., 2009). Resuspension of sediment particles was set to occur above a critical shear stress of 0.04 N m^{-2} that corresponds to sediment with a high organic matter content (Adams et al., 2020). The consolidated sediment has variable C:N:P-ratios and a higher recycling rate of nutrients than the respiration of carbon. Recycled nutrients in the sediment porewater are exchanged with the bottom water through diffusion. A fraction of the recycled NO_3 is lost in the denitrification process (Rysgaard et al., 1999). Nitrification and denitrification are inhibited during hypoxia and instead dissimilatory nitrate reduction to ammonia (DNRA) is dominating (Hylén et al., 2021a). Under oxidized conditions, PO_4 is retained in the sediment by adsorption to Fe or Mn and released, when the sediment becomes reduced. Benthic suspension feeders ingest phytoplankton (diatoms and flagellates), detritus, and microzooplankton, whereas deposit feeders ingest freshly deposited diatoms, detritus, and mussel pellets in the sediment.

Environmental in situ observations at two monitoring stations (Fig. 1B) were extracted from the national database (<https://odaforalle.au.dk>) for model calibration (Vejle Station) and validation (Horsens Station) for 2017–2018. During calibration, phytoplankton growth was adjusted to give

a better fit with Chl *a* concentrations and timing of the spring bloom. The number of sampling occasions was approximately once per week (except for bottom oxygen with 11–13 sampling events per year) at both monitoring Stations (Tables A1 and A2). We compared model data with measured surface (1 m depth) temperature, salinity, DIN (= NH₄ + NO₃), PO₄, Chl *a* concentration, Secchi depth, and bottom oxygen (19 m depth at Vejle station and 17 m depth at Horsens Station). For Vejle Station, monthly observational data of primary production was available based on one to two samplings per month. Photosynthetic carbon assimilation was estimated based on the carbon-14 method (Nielsen, 1952) modified to resolve different photosynthetic parameters in the surface layer and the pycnocline (Lyngsgaard et al., 2014). The uncertainty is 10–25 % based on the variation of input parameters (irradiance, Chl *a* measurements, light attenuation) (pers. comm. S. Markager). Measurements of water level at Hov Habor (Fig. A1) were extracted from DMI (retrieved November 2020). We used the correlation coefficient (R), the relative difference between model and observations (Obs.) (MD = (Model – Obs.) / Obs. * 100 %) and normalized standard deviations (nSD) for the assessment of agreement between model and observations. However, we bear in mind that both observational data and model results include uncertainties and that they operate on different temporal-spatial scales, making a direct comparison challenging (Skogen et al., 2021).

2.4. Mussel farm model

Each mussel farm was placed within one model element (13–18 ha) in three surface layers (0–3 m depth). The growth of the individual mussels in the suspended farm was described using a dynamic energy budget (DEB) model (Kooijman, 2010) previously parameterized and validated for several Danish and German coastal areas (Buer et al., 2020; Taylor et al., 2021). Modeled mussel growth is dependent on temperature, salinity, and food levels (diatoms, flagellates, picophytoplankton, microzooplankton, and detritus) provided by the biogeochemical model (Maar et al., 2015; Buer et al., 2020; Maar et al., 2020). The mussel size-selective retention was 20 % for picophytoplankton (Sonier et al., 2016) and microzooplankton was retained with 20 % efficiency due to escape behavior (Nielsen and Maar, 2007; Jonsson et al., 2009). The preference for detritus and assimilation efficiency of detritus were 20 % lower compared to planktonic food sources (Navarro et al., 1996). Mussel ingestion follows a Holling type II saturation function versus Chl *a* concentrations and ceases at Chl *a* concentrations <0.5 mg m⁻³ due to valve closure (Dolmer, 2000; Maar et al., 2018b). The ingested food is assimilated by a constant assimilation efficiency of up to 17 mg-Chl *a* m⁻³, whereupon it decreases exponentially due to oversaturation of the digestive system (Buer et al., 2020). The DEB model estimates mussel shell length, and individual dry-weight (DW) biomass (divided into structural tissue, reserves, and gonads). Mussel DW-biomass was converted to wet-weight (WW) including shell using a factor of 0.1 (Nielsen et al., 2016). The incorporated nutrients through ingestion follow the Redfield ratio in mussel tissue. In addition, around 40 % and 4 % of the total bounded N and P, respectively, are found in shell and byssus (Petersen et al., 2014). Hence, we assume that a fraction of the metabolized N is built into the shell and byssus instead of being excreted (P in the shell is ignored) and that there is no loss of N from the shell (Maar et al., 2020).

The DEB model was coupled to an individual-based model (IBM) describing the abundance of mussels over time. The number of spats m⁻¹ of the substrate is known to decrease exponentially over time due to self-thinning and can be described as a function of shell length (Nielsen et al., 2016; Taylor et al., 2019). For mussel abundance m⁻³ farm (N), we used $N = 12,500 \cdot \exp.(-0.099 \cdot SL)$ for shell length (SL) < 25 mm and $N = 1000 \text{ m}^{-3}$ for SL > 25 mm. Hypoxia occurs in bottom waters and will not affect the mortality of suspended mussels in the surface waters. There was feedback from the mussels to the biogeochemical model through filtration of plankton, respiration (O₂), excretion (NH₄, PO₄), and fecal pellet production (Fig. A2). Mussel fecal pellets sink through the water column until settlement on the bottom, from where they could be resuspended, degraded, ingested by deposit feeders, or gradually transferred to the consolidated sediment (Maar et al., 2020). Mussel pellets sink at 0.1 cm s⁻¹ taking

fragmentation in natural waters into account (Carlsson et al., 2010) corresponding to a water residence time of 1.4 h at 5 m depth. The degradation rate of mussel pellets was 0.04 d⁻¹ at 10 °C based on sediment core experiments (Carlsson et al., 2010). The DEB model was initialized on 12 July (day 193) and harvested on 27 October 2018 (day 300) using the first and last farm sampling points, respectively. Model results of mussel biomass and shell length were validated against farm measurements as described for the biogeochemical model.

2.5. Model analysis and scenarios

Model results from 2017 and 2018 were used to estimate monthly means of DIN-, PO₄-, Chl *a*- concentrations, primary production, Secchi depth, mesozooplankton biomass, biodeposition (settling of feces from mussels, detritus, diatoms), bottom oxygen, benthic mussels, and denitrification for each site from July to November (mussel farm period). The monthly means were tested for significant differences between sites using the Welsh *t*-test in R v4.2.2.

All scenarios used forcing data from the year 2018 (Table 1). A baseline scenario ('BASE') without mussel farms and a scenario ('PILOT') describing the pilot mussel mitigation farm in As Vig was conducted. The nutrient extraction potential by mussel aquaculture was up-scaled in two scenarios considering different farm locations (Fig. 1C). In the scenario 'FJORD', five mussel farms were placed inside the Horsens fjord. In the scenario 'BAY', the pilot mussel farm and four extra mussel farms (a total of five farms) were placed in the bay As Vig. In the scenario, 'COMBI', all 10 mussel farms in Horsens Fjord and As Vig were combined.

The simulated mussel farms were placed at water depths between 4.5 and 15.0 m for farm technical reasons, at bottom current speed > 0.02 m s⁻¹ to avoid sediment organic accumulation, a food flux > 0.2 mg-Chl *a* m⁻² s⁻¹ to assure an efficient mussel growth, and outside the main sailing routes (Maar et al., 2020; von Thenen et al., 2020). In addition, mussel farms are not allowed within Natura 2000 area according to the EU Habitat Directive. The distance between mussel farms was 2–4 grid cells (>0.7 km) to avoid severe food competition.

The percentage change for each impact was estimated for the scenarios as an average for the study area (Horsens Fjord and As Vig) relative to the BASE. The results from the scenarios were used to evaluate whether mussel farms located inside the fjord or outside the bay showed the highest nutrient mitigation potential.

2.6. Nutrient extraction and retention estimates

Nutrient extraction was estimated from the harvested mussel biomass and shell in the model. Changes in denitrification (N loss from the system) were estimated as the difference between the scenarios relative to the BASE. Nutrient transport between the study area and the south-western Kattegat was estimated across a transect in As Vig (Fig. 1C). Nitrogen retention due to changes in the ecosystem with mussel farming was estimated as the difference in nutrient transport compared to BASE minus the N-extraction by harvesting in each scenario. The net nitrogen extraction from the system could then be estimated as nutrient extraction by harvesting plus the change in denitrification minus the nutrient retention relative to the BASE. We did not consider phosphorous because only nitrogen reduction is required for this area.

3. Results

3.1. Model calibration and validation

Observations and model results showed clear seasonal cycles at both monitoring stations with warming during summer, depletion of nutrients after the spring bloom, spring- and late-summer peaks of Chl *a* and Secchi depth, and lower bottom oxygen concentrations during summer (Figs. A3-A4). The model calibration for the Vejle Station (Fig. 1B) showed good seasonal agreement with monitoring data of surface temperature,

Table 1

Overview of model scenarios with an abbreviation, number of active farms, farm size, number of years, total FW-harvest, harvest per farm hectare, and short description.

Scenario	No. of mussel farms	Farm area (ha)	Total harvest Kt-FW	Harvest t-FW ha ⁻¹	Description
BASE	0	–	–	–	No farms, baseline
PILOT	1	15.0	1.0	65.7	Pilot farm in As Vig
FJORD	5	73.6	2.5	33.6	Five mussel farms in Horsens Fjord
BAY	5	76.5	3.3	44.6	Pilot farm + four mussel farms in As Vig
COMBI	10	150.1	5.6	37.5	Combined scenario with ten mussels farms in Horsens Fjord and As Vig

surface salinity, surface DIN and PO₄ concentration, Chl *a* concentration, Secchi depth, bottom oxygen, and monthly net primary production (Fig. A3, Table A1). Model validation of the Horsens Station showed likewise a good seasonal agreement with monitoring data (Fig. A4, A7, Table A2). A few Chl *a* peaks in the observations were underestimated by the model (Fig. A4E). Bottom oxygen and current speed showed lower agreement with in situ observations due to fewer sampling events (<13) only during summer (Table A2).

Model results of the DEB model showed likewise a strong agreement with observations (Table A2) with individual mussel biomass of 0.22 g-DW and shell length of 3.2 cm at harvest time (Fig. 2A, B). Harvest was

higher in the model due to a larger farm area polygon but approximated the estimated harvest value when re-scaled to the actual farm size (Fig. 2C). Secchi depth was improved by around 1 m within the mussel farm compared to the reference station, but this was only significantly different for model results (Welch *t*-test, $p = 0.016$, $n = 8$) and not for observations (Welch *t*-test, $p = 0.056$, $n = 8$) (Fig. A5A). For Chl *a*, there was high variability between days in the observations (Welch *t*-test, $p = 0.70$, $n = 8$), whereas the model showed significantly lower concentrations (Welch *t*-test, $p = 0.012$, $n = 8$) within the mussel farm (Fig. A5B).

Modeled sediment fluxes at the reference station and under the mussel farm showed good seasonal agreement with observations (Fig. A6,

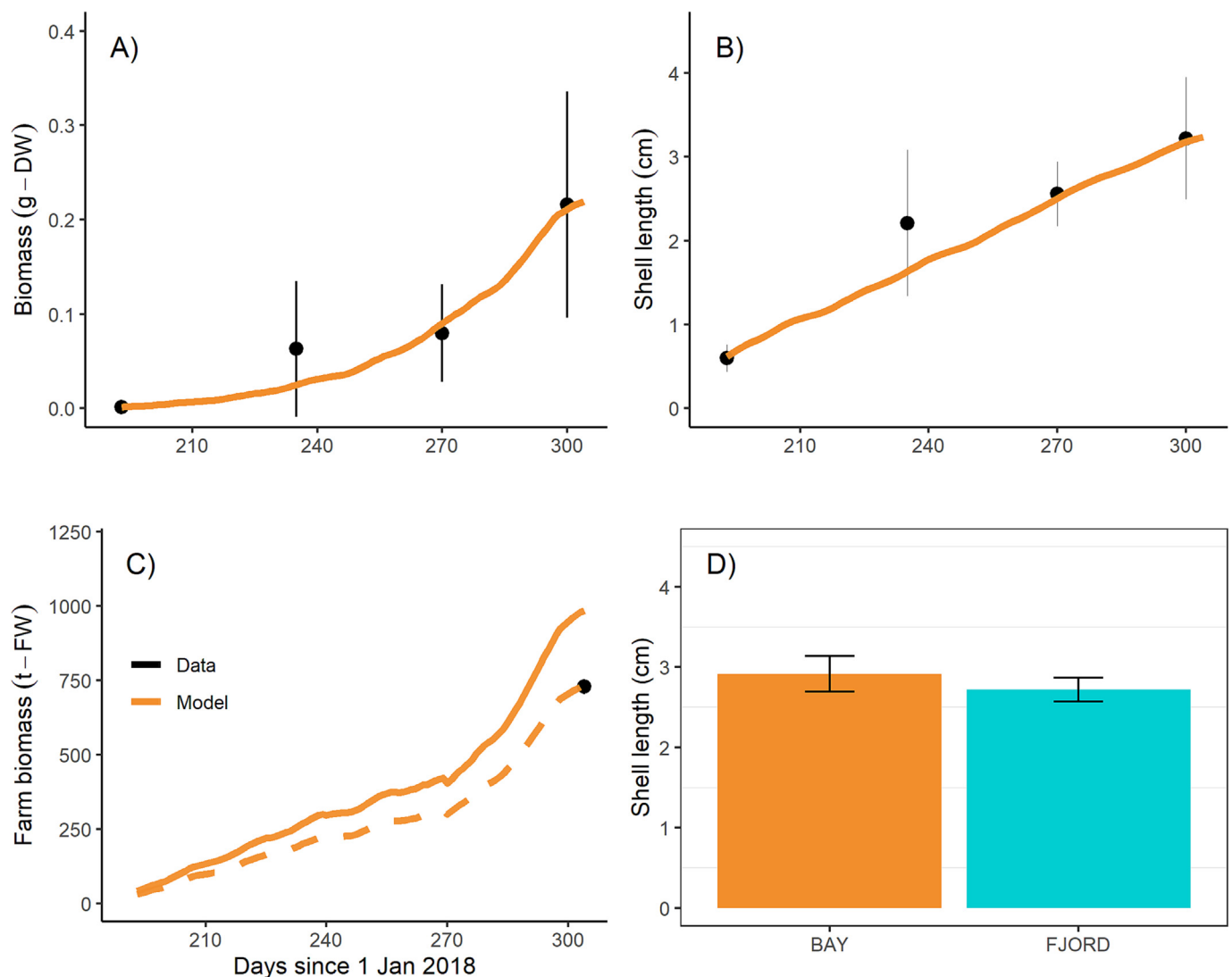


Fig. 2. Results of the mussel DEB model applied to the mussel farm in As Vig. Mean (\pm SD) of measurements and model results of A) mussel individual biomass, B) shell length, C) mussel farm biomass from July to November 2018 (solid line is the model result and dashed line the scaling to actual farm size of 11.3 ha), and D) mean (\pm SD) of shell lengths in BAY and FJORD.

Table A3). PON sedimentation, NH_4 release, DIN release, PO_4 release, and DNRA increased over time with mussel farming relative to the reference site in the model (Fig. A6A, B, D, F, H). Oxygen consumption increased at both sites during summer but was higher below the mussel farm relative to the reference station in October. Denitrification and nitrate uptake were higher below the mussel farm during summer and then decreased to the same level in October as for the reference station in the model (Fig. A6C, G).

3.2. Present conditions at the two sites

The semi-enclosed Horsens Fjord was generally shallower with significantly lower current speeds (Welch *t*-test, $p < 0.05$, $n = 20$) than the more open bay, As Vig (Fig. 3). The main current direction in Horsens Fjord was easterly towards As Vig, whereas the current patterns in As Vig were more complex (Fig. A1B). Benthic mussel biomass was significantly higher and mesozooplankton biomass was significantly lower in Horsens Fjord compared to As Vig (Welch *t*-test, $p < 0.05$, $n = 20$). All other ecosystem variables (temperature, salinity, biodeposition, DIN, PO_4 , Chl *a* concentration, primary production, bottom oxygen, denitrification) were not significantly different between sites although Horsens Fjord generally showed higher values (lower for Secchi depth) and higher variability than for As Vig (Fig. 3).

3.3. Ecological impacts of mussel farming at the two sites

The BAY scenario with five farms in As Vig showed a higher harvest of 3.3 kt-FW compared to the five farms in Horsens Fjord (2.5 kt-FW, scenario FJORD) (Table 1). In scenario COMBI with 10 farms, harvest roughly corresponded to the sum of FJORD and BAY (5.6 kt-FW). Shell lengths reached 2.7 and 2.9 cm in FJORD and BAY, respectively, and were lower than in the pilot farm scenario PILOT (Fig. 2D).

In the FJORD scenario, mussel farms decreased DIN- and PO_4 concentrations, primary production, and mesozooplankton biomass relative to the baseline scenario without mussel farms (Fig. 4A, D, J, P). Chl *a* concentrations decreased in the areas close to the mussel farms, whereas a slight increase occurred in the inner part of the fjord (Fig. 4G). Secchi depth showed the opposite pattern to Chl *a* with the highest values in the mussel farm area (Fig. 4M). Biodeposition and denitrification decreased (Fig. 5A, J), whereas bottom oxygen increased in most parts of the Horsens Fjord (Fig. 5D). Benthic mussels showed a patchy response with a mixture of increase/decrease (Fig. 5G).

The BAY scenario showed low or no responses of DIN and PO_4 concentrations to intensified mussel farming (Fig. 4B, E). The strongest farming signals were found for Chl *a*, primary production, and mesozooplankton biomass showing a reduction mainly in the farm area (Fig. 4H, K, Q), whereas Secchi depth showed an increase in the same area relative to the BASE (Fig. 4N). Biodeposition and denitrification increased below the mussel farms but showed a slight decrease on the basin scale (Fig. 5B, K). Changes in bottom oxygen and benthic mussel biomass were very low (Fig. 5E, H).

The COMBI scenario showed larger spatial responses with mussel farming at both sites. Especially, DIN and Chl *a* concentration, primary production, and mesozooplankton biomass showed a clear decline and Secchi depth an increase relative to the baseline scenario without mussel farms (Fig. 4C, I, L, R). Biodeposition and denitrification decreased (Fig. 5C, L), bottom oxygen increased (Fig. 5F), whereas changes in benthic mussels were more mixed (Fig. 5I).

3.4. Nutrient extraction and overall performance of the two sites

Nutrient extraction by the pilot farm (scenario PILOT) was 10.7 t-N, and 0.7 t-P (Table 2). The nutrient extraction increased with intensified mussel farming with up to 68.6 t-N in the COMBI scenario. The denitrification decreased relative to BASE in all scenarios (< 2 t-N) due to a lower

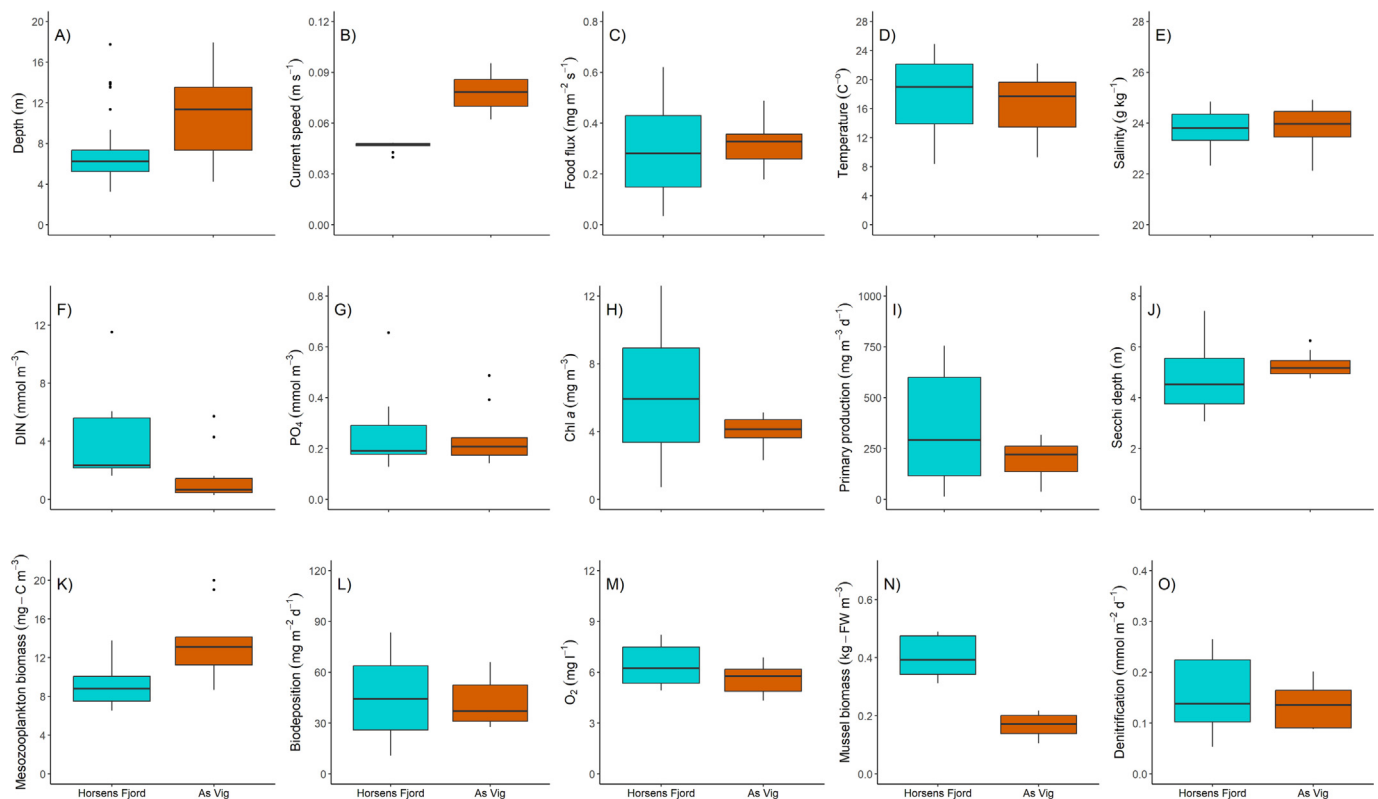


Fig. 3. Modeled water column conditions based on monthly means (July to November) from 2017 to 2018. A) water column depth, B) current speed, C) food flux, D) surface temperature, E) salinity, F) DIN concentration, G) PO_4 concentration, H) Chl *a* concentration, I) primary production, J) Secchi depth, K) mesozooplankton biomass, L) biodeposition, M) bottom oxygen, N) benthic mussels, and O) denitrification for Horsens fjord (cyan) and As Vig (orange). Boxplots show the median, 25th and 75th percentiles (boxes), the full range of (non-outlier) values as whiskers, and outliers as dots.

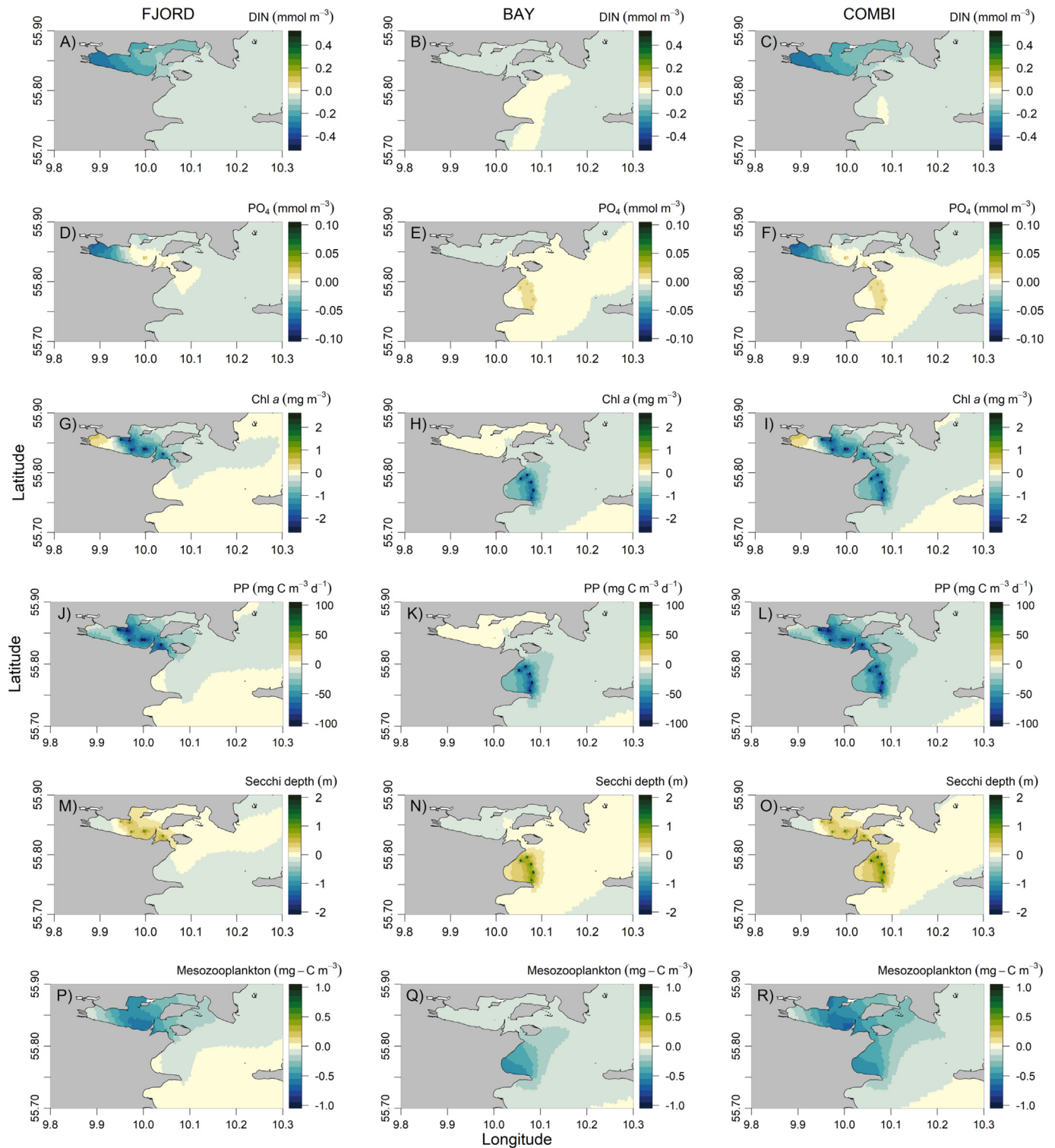


Fig. 4. Spatial differences of surface variables between the scenarios FJORD (first column), BAY (second column), COMBI (third column) relative to the BASE. A-C) DIN, D-F) PO₄, G-I) Chl *a* concentration, J-L) Secchi depth, M-O) Primary production, P-R) mesozooplankton biomass.

biodeposition. Retention of nitrogen was higher in BAY compared to FJORD and highest in the combined scenario COMBI relative to the BASE. The relative net extraction of N was most efficient in FJORD with 88 % of mussel N-harvest (Table 2).

The positive impacts of mussel farming were highest for FJORD showing a highest reduction in nutrient concentrations and biodeposition, and

highest improvement of bottom oxygen compared to BAY (Fig. 6). Changes in Chl *a* concentration, Secchi depth, benthic mussel biomass, and primary production were similar between FJORD and BAY. Mesozooplankton biomass decreased more in FJORD than in BAY which could have implications for higher trophic levels, e.g., fish. The COMBI scenario showed additive effects of FJORD and BAY.

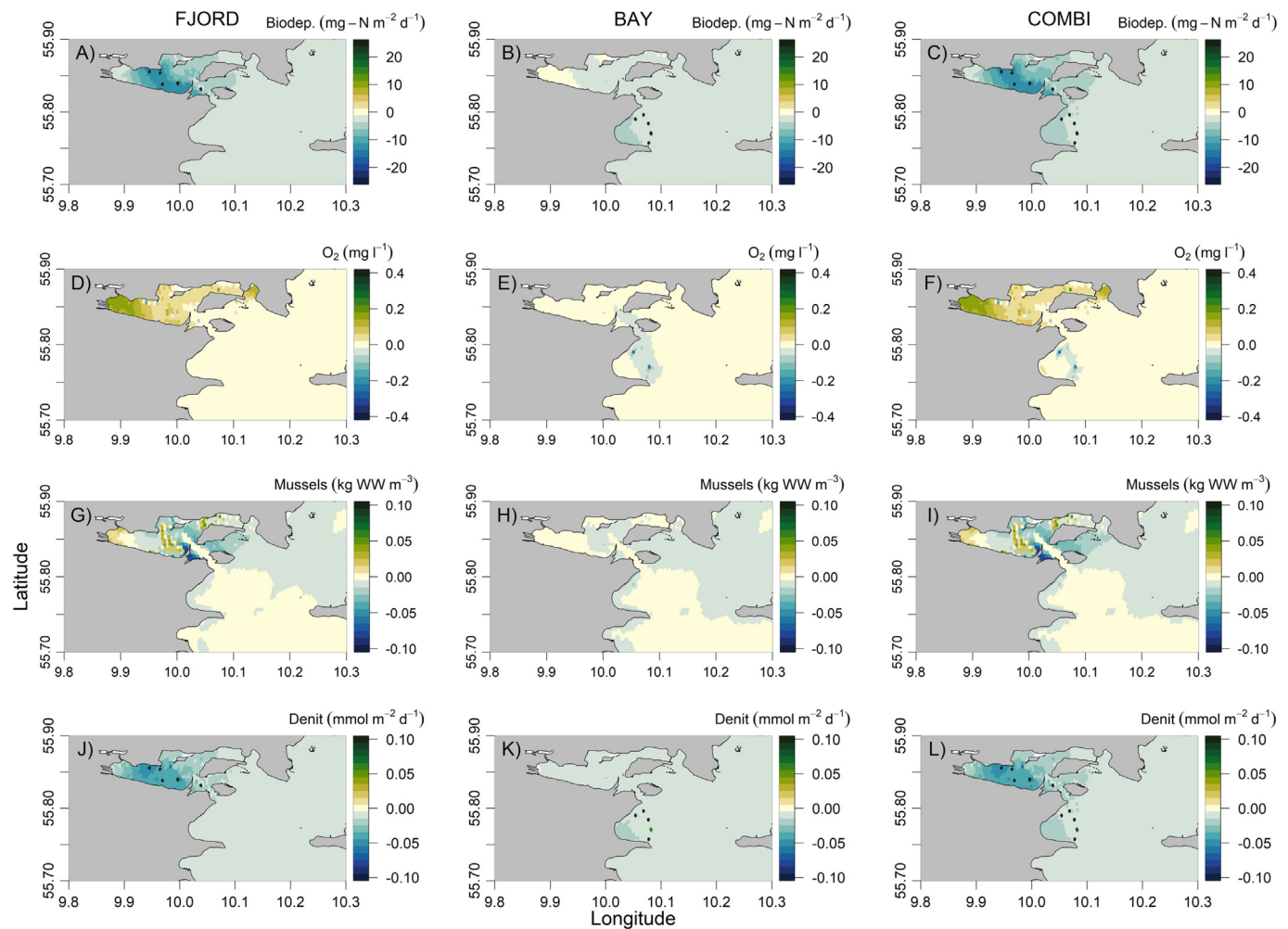


Fig. 5. Spatial differences of bottom- and benthic variables between the scenarios FJORD (first column), BAY (second column), COMBI (third column), relative to the BASE. A-C) Biodeposition, D-F) bottom oxygen concentrations, G-I) benthic mussels, J-L) denitrification.

4. Discussion

4.1. Nutrient extraction at the two sites

Sustainable development of the blue economy requires area-efficient use of marine space and innovative solutions demonstrating net nutrient extraction thereby contributing to the mitigation of eutrophication (Rose et al., 2014; Petersen et al., 2019; Kotta et al., 2020). The present study showed that mussel mitigation culture still has a high net N-extraction when including ecosystem effects, such as changes in biodeposition, nutrient retention, denitrification, and sediment nutrient fluxes in the model (Table 2). Previous field studies measuring nutrient fluxes below mussel farms have questioned the efficacy of the mussel farms to remove nutrients because higher nutrient fluxes were observed in the underlying sediment compared to reference conditions (Nizzoli et al., 2011; Holmer et al., 2015; Murphy et al., 2016; Hylén et al., 2021a). Furthermore, there have

been concerns that retention of nutrients is increased by mussel farming because bio-deposits from mussels sink faster than food particles which could otherwise be advected from the system (Cranford et al., 2007). However, when basin-scale effects such as reduced biodeposition and associated lower nutrient fluxes by mussel farming from the sediment are considered in the model, there was a net N-extraction by mussel culture in all scenarios. Coastal morphology and relatedly, hydraulics, are basic drivers of nutrient dynamics and eutrophication susceptibility (Plew et al., 2020). Tidal range, directional flow, circulation, and stratification can regulate eutrophication effects more than nutrient concentrations in estuaries and coastal water bodies (Hughes et al., 2011). Retention and persistence of eutrophication effects in micro-tidal estuaries is pronounced (Monbet, 1992), as in the case of Danish coastal waters. Net N-extraction (relative to harvested biomass) was highest when the mussel farms were placed within the fjord and closer to the nutrient sources compared to the location in the bay despite the higher harvest potential (Table 2). Hence, the hydrodynamic

Table 2
Results of the model scenarios showing P- and N-extraction by mussel harvesting, changes in N-retention and denitrification relative to BASE, net N-extraction, and % of net extraction relative to N-extraction by harvest.

Scenario	P-harvest extraction (t-P)	N-harvest extraction (t-N)	ΔN-retention (t-N)	ΔDenitrification (t-N)	Net N-extraction (t-N)	%
PILOT	1.2	10.7	0.0	0.0	10.7	100
FJORD	2.9	31.4	1.7	−2.0	27.7	88
BAY	3.9	38.9	10.8	0.0	28.1	72
COMBI	6.6	68.6	12.8	−2.0	53.8	78

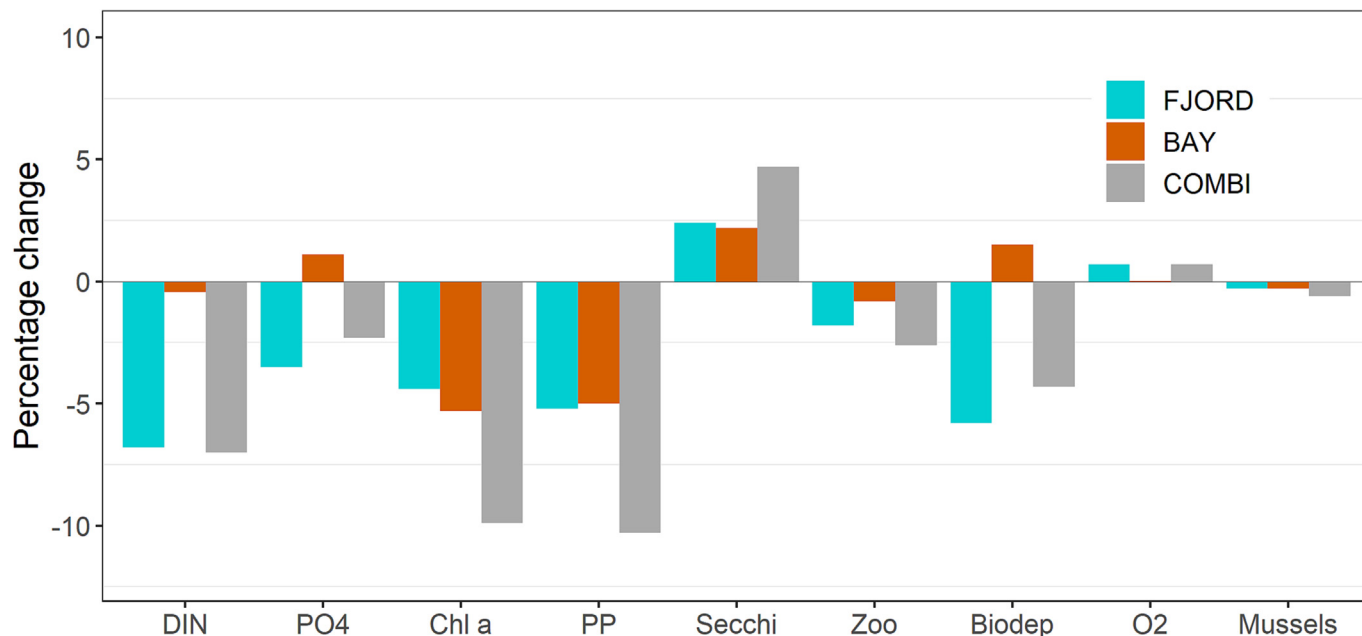


Fig. 6. Changes (%) of DIN, PO₄ (PO4), Chl *a* concentration (Chl *a*), primary production (PP), Secchi depth, mesozooplankton biomass (Zoo), Biodeposition, (Biodep), bottom oxygen (O₂), and benthic mussel biomass (Mussels) in Horsens Fjord and As Vig for the scenarios FJORD, BAY, and COMBI.

regime and geomorphology are important for nutrient retention and transport processes as shown in previous studies (Guyondet et al., 2022; Maar et al., 2023b). In the fjord, the dominant outgoing current direction (Fig. A1B) facilitated an efficient export and low retention of nutrients when combined with a lower biodeposition from mussel farming (Fig. 5A, Table 2). In the bay, current patterns were more complex facilitating higher nutrient retention in general, but higher current speeds diluted the basin-scale effects of mussel farming on biodeposition. Hence, from a eutrophication management perspective, the mussel farms placed within the fjord were more efficient in removing nutrients. When combining mussel farms in both areas, more nutrients were removed from the study area. However, N-extraction cannot be estimated solely from mussel harvesting as ecosystem responses to mussel culture on both farm and basin scales should be included in the nutrient budget (Maar et al., 2023b).

4.2. Ecological impacts of mussel culture

Ecological impacts of mussel culture were more evident in the fjord due to relatively reduced transport and export by water from outside as observed for the bay in the model (Figs. 4, 5, 6). If the aim of mussel mitigation culture is not only to remove nutrients but also to improve water quality, the effects are more evident in semi-enclosed areas with less water exchange than in more open water systems. Similar improvements of ecosystem services such as higher water clarity (Secchi depth), reduced Chl *a* concentrations, lower primary production, lower nutrient concentrations, lower biodeposition, and higher oxygen concentrations were also found in previous model and field studies of bivalve farming at low current speed and/or low flushing regimes (Rose et al., 2015a; Taylor et al., 2021; Maar et al., 2023b). Reduced basin-scale biodeposition in the fjord scenario was associated with a pronounced increase in bottom oxygen concentrations. In conjunction with increased Secchi depths, the fjord scenario may provide favorable benthic habitat conditions for the establishment of other ecosystem engineers, such as seagrasses, stimulating cascading ecosystem services (Beheshti et al., 2022). Model results showed, on the other hand, that mesozooplankton biomass could be reduced by mussel farming due to food competition as found in a model study of a Norwegian fjord (Gatti et al., 2023). A reduction in zooplankton production and biomass could initiate cascade effects in the food web with consequences for higher trophic levels (Nielsen and Maar, 2007; Gallardi, 2014; Maar et al., 2018a).

Furthermore, the spatial redistribution of benthic mussel biomass within the fjord in response to mussel mitigation culture could also affect food web interactions and potentially the mussel fishery. The model results can be used to optimize the balance between farming intensity and ecological impacts in collaboration with stakeholders (e.g., mussel farmers, local community, managers, NGOs, and shipping).

4.3. Management perspectives

Required nutrient reductions to achieve good ecological status according to the WFD are 189 t-N year⁻¹ (27 %, not needed for P) in Horsens Fjord (Miljøministeriet, 2021). However, it may take decades to reach good status due to high internal nutrient loading in the sediment from historical accumulation even though land-based measures are implemented (Timmermann et al., 2019). The scenarios with increased mussel mitigation farms could potentially contribute 15 to 28 % of required nutrient reductions (Table 2). Mussel culture removes nutrients by filtration of phytoplankton within the system, including those released from internal sediment loading, and can accelerate the transition to good ecological status. The difference in efficacy between the FJORD and BAY scenarios demonstrates the importance of location when mitigating eutrophication. While there is a preference for restricting nutrient emissions as close as possible to their source (Bricker et al., 2014) due to historical and existing loads to coastal systems, there is likewise a need to more actively reduce nutrient concentrations in the marine environment (Duarte and Krause-Jensen, 2018). The relative vicinity of the FJORD farms to primary nutrient sources (riparian) and the physical characteristics of the fjord system implies this is a more effective area to directly address excess nutrients.

4.4. Conclusion

The present study is a good example of the use of observations and models in combination, allowing for an improved assessment of both the state of the system and the impact of aquaculture, in this case, mussel culture (Skogen et al., 2021). The applied model allows a full investigation of basin-scale cause–effect relationships and can be used to highlight (dis)advantages by implementing intense mussel mitigation culture (Gatti et al., 2023). The found impacts will be important to consider in other systems about site selection, development of bivalve aquaculture, and

associated sampling strategies for monitoring of the farming impacts (Maar et al., 2023b). Development of bivalve aquaculture without exceeding the ecological and social carrying capacity is important to meet the global sustainable development goals in supporting marine life, food security, and responsible consumption and production (Duarte et al., 2009b; Duarte and Krause-Jensen, 2018; Gephart et al., 2021).

CRedit authorship contribution statement

Marie Maar: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Roles/Writing - original draft, Writing - review & editing. **Janus Larsen:** Software, Visualization, Methodology, Validation, Roles/Writing - original draft, Writing - review & editing. **Vibe Schourup-Kristensen:** Formal analysis, Visualization, Investigation, Writing - review & editing. **Daniel Taylor:** Methodology, Data curation, Formal analysis, Investigation, Writing - review & editing.

Data availability

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 on [Zenodo.org](https://zenodo.org) (Larsen, 2022; Maar et al., 2023a).

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

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.164168>.

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