

The Pan-Baltic environmental optimization strategies of mussel farming

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About

Baltic Blue Growth is a three-year project financed by the European Regional Development Fund. The objective of the project is to remove nutrients from the Baltic Sea by farming and harvesting blue mussels. The farmed mussels will be used for the production of mussel meal, to be used in the feed industry. 18 partners from 7 countries are participating, with representatives from regional and national authorities, research institutions and private companies. The project is coordinated by Region Östergötland (Sweden) and has a total budget of 4,7 M€.

Partners

- Region Östergötland (SE)
- County Administrative Board of Kalmar County (SE)
- East regional Aquaculture Centre VCO (SE)
- Kalmar municipality (SE)
- Kurzeme Planning Region (LV)
- Latvian Institute of Aquatic Ecology (LV)
- Maritime Institute in Gdańsk (PL)
- Ministry of Energy, Agriculture, Environment, Nature and Digitalization of Schleswig-Holstein (DE)
- Municipality of Borgholm (DK)
- SUBMARINER Network for Blue Growth EEIG (DE)
- Swedish University of Agricultural Sciences (SE)
- County Administrative Board of Östergötland (SE)
- University of Tartu Tartu (EE)
- Coastal Research and Management (DE)
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Summary

In the coming years blue growth initiatives including sustainable harvest of farmed mussels will be increasingly in the political focus. Maritime spatial planning can support such initiatives by offering greater confidence and certainty for investors. In order to allocate marine space for the mussel farming, spatial planners have to be informed about areas having environmental conditions conducive to mussel production. Prior to the BBG project, such information did not exist for the entire Baltic Sea area. Under this task we assembled spatially extensive datasets of key drivers of mussel production and then used spatial modelling tools to spatially quantify the potential production of blue mussels at the Baltic Sea scale. This task produced a Pan-Baltic map showing mussel production potential and potential environmental sensitivity to farming activities. The resulting map is very important for Maritime Spatial Planning in the Baltic Sea because it supplements and contextualizes the detailed information collected from focus farms. This unique combination of highly detailed, spatially intensive information and regionally extensive Pan-Baltic data sets allowed us to constrain and contextualize estimates of benefits and possible risks of these single farm locations and to prepare evidence-based guidance for future farm locations.

Introduction

"Blue growth" is an umbrella term applied to various aspects of ocean sustainability (Eikeset et al. 2018). The term arose from the sustainable development discussions of the 1970s and has been articulated by the FAO as a series of approaches to support more productive and sustainable use of aquatic resources. These approaches focus on economic, environmental and social goals so as to build resilience of coastal communities, restore the productive potential of fisheries and aquaculture, support food security, alleviate poverty and sustainably manage living aquatic resources. Pinto et al. (2015) note that Blue growth policy in Europe has been driven by demands to implement new innovative ocean activities (e.g., biotechnology and renewable energy) and revitalize existing sectors (e.g., fisheries and tourism). It has also recently been highlighted that ocean activities are a smaller proportion of GDP in more developed economies compared to other regions such as southeast Asia, where Blue economy initiatives are being increasingly developed, although the extent that these initiatives align with the sustainability aspects of Blue growth is uncertain (McIlgorm 2016). Overall, a stronger reliance on factual data concerning environmental changes, as well as economic benefits, will increase the uptake and application of Blue growth concepts in developed and developing economies.

Burgess et al. (2018) have articulated five rules for pragmatic Blue growth. They suggest that it is necessary to define objectives and quantify tradeoffs; use existing data in a more clever way; engage stakeholders; measure impacts and focus on institutions, not behaviors. The FAO concept of blue growth can be operationalized through maritime spatial planning (MSP), a fundamental tool that promotes the sustainable development of marine environments in a way that accommodates the needs of competing economic sectors and minimizes conflict (Directive 2014/89/EU).

The Baltic Sea drainage basin is densely populated, with more than 80 million inhabitants, and all water from the drainage basin runs into the Baltic Sea. Human activities result in large quantities of nutrients (phosphorous and nitrogen) being released from various sources, such as sewage treatment plants, industrial activities and runoff from agricultural land. These excess nutrients end up in the Baltic Sea, leading to intensified eutrophication, one of the main global threats to marine ecosystem health. The symptoms of eutrophication include shifts in species composition from perennial to ephemeral species, excessive growth of opportunistic benthic and pelagic algae, bluegreen algal blooms, increased turbidity, oxygen depletion and disappearance of sensitive biota. Forty years of land-based eutrophication control measures have failed to solve the problems of algal blooms, oxygen free dead zones and biodiversity loss in the Baltic Sea caused by excessive levels of nitrogen and phosphorus. Legacy nutrient accumulation in the Baltic Sea makes land-based measures ineffective and costly. Thus, sea-based (*in situ*) solutions are needed to effectively remove legacy nutrients from the marine environment and contribute to solving eutrophication problems in the Baltic Sea.

Worldwide, aquaculture (including mussel production) has been fastest growing sector of the food industry since 1970s. Moreover, mussel farming is widely perceived as a tool for mitigating eutrophication effects. The blue mussel (*Mytilus trossulus/edulis*) is a keystone species in the Baltic Sea that grows abundantly in many areas despite the low salinity. This is species is commercially

farmed at multiple locations on the more saline European Atlantic coast (e.g., Denmark, Netherlands, Swedish West coast). However, mussels grow more slowly and to a smaller size in the Baltic Sea, compared to mussels growing in the Atlantic. Prior to the BBG project, there were no large scale maps documenting production potential of mussel farming and possible environmental consequences. As part of the Baltic Blue Growth project, six mussel farms in different locations were investigated regarding their growth potential. In order to provide the knowledge base needed to assess the eutrophication control potential of mussel farming at the Pan Baltic Sea scale, we did the following. First, we compiled all available data on the growth of mussels in the Baltic Sea region (the BBG farm data, earlier similar initiatives, published scientific papers). We then assembled a spatially extensive dataset of key drivers of mussel production. Finally, we used state of the art spatial modelling tools to quantify the production of blue mussels at the Baltic Sea scale. This task produced a Pan-Baltic map showing mussel production potential and sensitivity of the environment to mussel farming.

When MSP gives unconditional support to sustainable Blue growth activities including mussel farming then the sector will expand production and deliver greater benefits to society. In order to allocate marine space for mussel farming, however, policymakers and spatial planners must have access to information about which areas have environmental conditions conducive to mussel production and at what rates nutrient removal can be expected. Prior to the BBG project, mussel farming was considered to have a remarkable, but still largely unexplored blue growth potential to extract nutrients from the marine environment and reduce internal nutrient storage in the Baltic Sea. The map of mussel production potential produced under this task is a very important milestone because it allows stakeholders and other actors to analyze the benefits/risks of mussels farming over the whole Baltic Sea area.

Methodology

Distribution and productivity patterns of species depend on their ecological niche, which consists of a multi-dimensional environmental space. In general, non-independent effects are common in nature (Hoffman et al. 2003; Raynaud et al. 2003) and, therefore, neither the species niche nor the resulting distribution range can be predicted from separate effects of individual environmental variables. A suitable habitat is often defined by complex interrelationships among a multitude of environmental variables that can be largely divided into three broad categories: direct environmental gradients, indirect environmental gradients, and resource gradients. Direct environmental gradients include factors such as salinity, which ranges from near freshwater levels in the Inner (northern) Baltic Sea to near marine at Outer Baltic Sea near the outlet. Indirect environmental gradients can often be easily measured, but represent only proxies for a set of underlying gradients, which affect organisms directly while it may be difficult to measure or disentangle the effects of these underlying gradients (Austin et al. 1980ab; Austin & Smith 1989). Water depth is a typical indirect environmental gradient in the marine realm. Resource gradients are substances consumed by organisms and direct environmental gradients represent features that have direct physiological impact on growth but are not consumed. The picture gets more complicated as the same factor may have an impact simultaneously via different pathways. For example, the currents which control water movement can indirectly affect the habitat of suspension feeding Mytilus trossulus/edulis by modifying sedimentation rates or affect sessile mussels directly by physically disturbing or detaching animals (Westerborn et al. 2008; Sandman et al. 2013). Furthermore, the filter feeding mode and sedentary lifestyle of mussels prescribe an intrinsic need for a vector of food delivery. Thereby, water movement can also impact benthic suspension feeders through a third pathway, by modifying the resource supply while limiting the amount of food reaching mussels (Dahloff & Menge 1996; Saurel et al. 2007; Kotta et al. 2015).

Machine learning provides a theoretical framework that moves beyond traditional paradigm boundaries. Considering "complex realism" and our weak theoretical foundations, modelling is seen here as a sophisticated tool to improve our understanding on the relationship between environment and biota. In contrast to traditional methods, machine learning avoids starting with a data model but rather uses an algorithm to learn the relationship between the response and its predictors (Hastie et al. 2009). Even here, however, some ecological understanding is a prerequisite when it comes to selecting environmental variables for the model. Specifically, in order to succeed in identifying and quantifying relationships between the environment and biota, the model should incorporate at least the most important direct and resource gradients as well as capture the multitude of interactions between these environmental gradients and biota. The novel predictive modelling technique called Boosted Regression Trees (BRT) combines the strengths of machine learning and statistical modelling. BRT has no need for prior data transformation or elimination of outliers and can fit complex nonlinear relationships. The BRT also avoids overfitting the data, thereby providing robust estimates. What is most important from an ecological perspective is that BRTs automatically detect and model interactive effects between predictors. The method copes with different non-linear relationships including thresholds and unimodal responses which are common in ecological data but difficult to analyze using more traditional methods. Due to its strong predictive performance, BRT is increasingly used in ecology (Elith et al. 2008; Kotta et al. 2013, 2015).

Here, we used BRT modelling to quantify the relative contribution of resource, abiotic environmental and biotic interaction gradients on the potential of production and nutrient removal of blue mussels in the Baltic Sea region. A total of 9478, 1516 and 4912 mussel samples were harvested and measured from farms in the Outer, Central and Inner Baltic Sea. In total, 121 composite samples of whole mussels (shell and soft tissue) were available for dry matter and nutrient analysis (Figure 1).

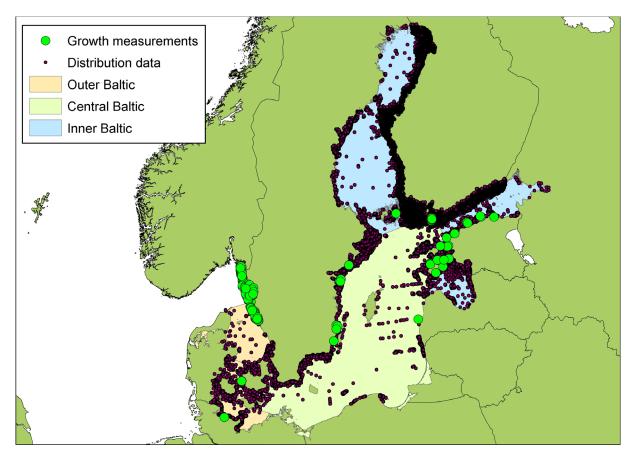


Figure 1. Location of sampling points for the distribution and growth of Blue mussels. Colours depict different sub-regions of the Baltic Sea.

Results

Local patterns

Mussel farming is widely perceived as a tool for mitigating eutrophication effects. However, potentially detrimental impacts including bio-deposits of particulate organic matter can cause adverse effects to the environment (Stadmark and Conley 2011). On the other hand, direct positive effects such as increased transparency and higher biodiversity around the farms have been observed in the BBG project. The monitoring of the BBG mussel farms concluded (results of GoA 2.3 which data were then used in the GoA 2.1. modelling) that the biota under and in the vicinity of the BBG farms

exhibited natural patterns and there were no statistically significant differences in oxygen condition, nutrient concentrations, composition and abundance of phytoplankton and benthic invertebrates. Prior to the BBG project it was speculated that mussel farming could potentially be associated with detrimental impacts of bio-deposits in the sediments underneath the farm. Such deposits could theoretically lead to low oxygen levels in the bottom and anoxic conditions, "dead bottoms", mostly in deep areas with limited water exchange. The BBG monitoring clearly demonstrated that regardless of exposure level and water depth, sufficient water exchange and dissolved oxygen existed in the near-bottom water of most of the studied farms. Similarly, no systematic difference in total sediment carbon existed between farms and reference areas. The sedimentation was somewhat higher under mussel farms compared to reference areas. However, the increased sedimentation did not cause adverse changes in benthic biota. On the contrary, the improved feeding conditions in sediments under the farm unit resulted in more diverse benthic assemblages and thus better bioturbation regime and oxygenation of the sediment. To conclude, the systematic monitoring of six Baltic Sea mussel farms in 2017 and 2018 did not show any pronounced negative environmental impacts. This finding demonstrates that in those sites where environmental conditions support a high production potential, mussel farming can be a sustainable and circular way of removing excess nutrients from the Baltic Sea and recycling them on land.

The mussel production cycle in the Baltic is roughly twice as long as in the western part of Europe. Typically, production units are put into water in spring and harvested before summer 1.5–2 years after. The experimental observations of mussel production potential in the BBG farm areas showed that the largest mussels occurred in the most saline regions of the Baltic Sea. As expected, the highest productivity occurred in the outer region of the Baltic Sea (Kiel and Musholm farms). In most of the farms, productivity was considerably higher at depths of 2 m compared to 5 m with an exception only in the St. Anna farm. Very high losses of mussels occurred in the outer region of the Baltic Sea (Kiel and Musholm farms) but not at those farms located in the central and marginal parts of the Baltic Sea. Thus, the production potential in different areas of the Baltic Sea did not only follow variation in salinity and food availability. It very much depended on the site-specific growth environment where e.g. exposure to waves and predation by round goby and eider ducks can be an obstacle for mussel growth. A thorough screening of a potential mussel farming area with respect to hydrodynamic regime, food availability, predation and weather conditions is therefore highly recommended before a new mussel farm is started.

Interestingly, the Pan Baltic production of mussels was only weakly connected to the types of farming substrates used, suggesting that locally optimal farming solutions may exist. The BBG showed that a focus on farming substrate and gear type allows farmers to focus on cost price and how well the substrate performs with respect to weather and handling. It should be noted that the local potential for mussel productivity is defined by complex relationships between different physical, chemical and biological variables and needs further studies. However, the map presented in this task identifies the most promising areas of the Baltic Sea where these further investigations, including pilot scale farms, are appropriate.

Pan Baltic patterns

The generic results of the Pan Baltic modelling are that the effects of environmental gradients on biota are complex with a plethora of abiotic and biotic factors acting simultaneously. More specifically, direct environmental gradients seem to define the distribution pattern of blue mussels and within the favourable distribution range, resource gradients are likely to have an important role in shaping the production potential of mussels.

Salinity defines the regional patterns of mussels in the Baltic Sea range. Predicted biomass yield increases in a non-linear manner with increasing salinity. In marginal regions, where salinity may be as low as 3 psu, mussels live at the edge of their salinity tolerance. Below this threshold, mainly due to high costs of osmoregulation, blue mussel growth and reproduction become impossible. Our model also shows that above this salinity threshold, the production potential of mussels increased sharply, and levelled off at salinities over 6 psu. A link between salinity and production potential may be also attributed to osmotic stress, as the size of mussels depends on salinity.

Food supply is a crucial factor for benthic suspension feeders with sedentary lifestyle. Wave exposure and water chlorophyll a are the environmental parameters most indicative of food supply for mussels. Mussels are able to quickly deplete food from the near-bottom water layer and will starve even with lush phytoplankton in the water column if there is insufficient water movement.

Nonetheless, broad Pan Baltic patterns of mussel productivity were defined by salinity values rather than other environmental variables. The magnitude of the overall effect of salinity on the predicted biomass yield is approximately 13 times the combined magnitude of chlorophyll a concentration and wave exposure. Still, the Pan Baltic modelling of the production potential of mussels showed that the mass of mussels harvested per production unit is much higher than earlier expected. Predicted biomass yield was highest in high-salinity areas of the Outer Baltic estimated at 15 kg m⁻¹ per harvest. With declining salinity, predicted biomass yields varied between 1–3 kg m⁻¹ in the Central Baltic. In marginal (Inner Baltic) regions, predicted biomass yields never exceeded 1 kg m⁻¹ (Figure 2).

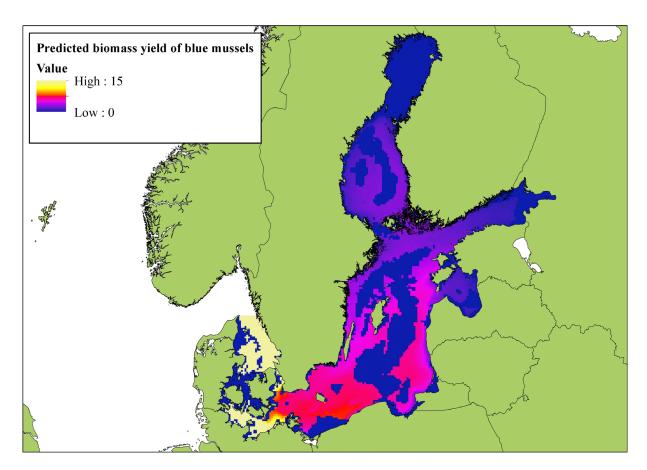


Figure 2. Modelled biomass removal rates (kg m⁻¹) of Blue mussels. Mussels are assumed to have been harvested two years after establishment.

Our measurements also showed that the difference in nutritional content between mussels from the low salinity Baltic Proper (St Anna, Byxelkrok) and the high salinity western Baltic (Musholm and Kiel) is less than what has been previously assumed. In particular, phosphorus content in whole mussels harvested during autumn and winter is similar from high and low salinity sites and nitrogen content was correlated to phosphorus content, as shown in Table 1. More importantly, there was a large seasonal variability in the nutrient content of mussels and such variability patterns varied among the broad Baltic Sea regions.

Table 1. Data from analyses of mussel flesh. Parameters followed by the same letter show no statistically significant difference between regions.

Area	Salinity	Meat Dry Matter %	Percent Soft Tissue	Soft Tissue Fat %	N (% soft tissue dry weight)	P (% soft tissue dry weight)
Western Baltic	High	15.1 a	58 a	9.5 a	9.5 a	1.41 a
Central Baltic	Moderate	14.2 a	52 b	10.3 a	10.3 a	1.48 a
Eastern Baltic	Low	13.7 a	41 c	9.7 a	9.7 a	1.33 a

Thus, it is clear that the high spatio-temporal variability in mussel tissue nutrient concentrations is a main consideration for mussel farming when the primary aim is to remove nutrients from the Baltic Sea basin. Prior to the BBG project, there have been inadequate assessments of such variability, e.g. Hedberg et al. (2018) describes how most estimates of nutrient removal capacity used measurements from only two studies in North America (Lutz 1980) and Denmark (Petersen and Loo, 2004). Peaks in nutrient concentration could be expected (e.g., Dare & Edwards 1975, Ceccherelli & Rossi 1984), and were observed, during high-growth spring and summer months, but this was not the case in the central Baltic Sea region, highlighting the difficulty of generalising patterns and determining underlying causes. Our results have direct application by indicating optimal seasons for harvest in any mussel farming initiative resulting from our modelling (although similar tests of nutrient concentration seasonality will be required in other seas where our case-study results are being applied).

All environmental data from the BBG farms as well as the result of spatial modelling of production potential and nutrient uptake have been stored in a database that can be accessed using the Baltic Blue Growth Operational Decision Support System (ODSS). This GIS-enabled tool functions as an umbrella dissemination tool that dynamically links and geo-references a plethora of information sources. It contains raw environmental data, modelling products, information on mussel farms, pictures and more. Through its analytical capabilities to synthesize and disseminate up-to-date information and knowledge to different end users, the ODSS is designed to facilitate and improve the quality of decision-making of maritime spatial planners, scientists, policy actors and investors. It can be accessed at http://www.sea.ee/bbg-odss

Recommendations

Broad Pan Baltic patterns of mussel productivity were defined by salinity values rather than other environmental variables but across large parts of the Baltic Sea, differences in mussel growth were small. While Blue mussels do grow better in the North Sea than they do in the Baltic, the problem of Baltic Sea eutrophication requires a solution which can be implemented *in-situ*.

The Pan Baltic modelling of production potential showed that the mass of mussels harvested per production unit is much higher than earlier expected. Farms using new technologies which are adapted to growing small mussels have clearly demonstrated that large volumes of mussels can be grown economically at many more locations throughout the Baltic than was previously thought possible. While these new technologies are at the pilot stage, they show a great deal of promise for all aspects of Baltic Sea sustainability.

There was a large seasonal variability in the nutrient content of mussels and patterns varied among the broad Baltic Sea regions. Such high spatio-temporal variability in tissue nutrient concentrations is a main consideration for mussel farming when the primary aim is to remove nutrients from the Baltic Sea basin.

Conclusions

The modelling of mussel production potential has shown that they can be farmed successfully in much of the Baltic Sea when cultivation methods are adapted to the local conditions. Long-line farming of blue mussels is an effective, circular and sustainable method for reducing Baltic Sea eutrophication. The analyses presented here also show that mussel farming can improve the environment by removing nutrients from the sea, resulting in cleaner waters. The environmental effects from mussel farms are largely beneficial, and minimal negative effects were observed in the project mussel farms. On the contrary, project results demonstrate that Baltic Sea blue mussel farms perform important ecosystem services by filtering the water, trapping excess nutrients and contributing to circularity by recycling nutrients from sea to land. Thus, mussel farms in the Baltic Sea can make a significant contribution to controlling eutrophication by taking up nutrients in the water column.

In semi-enclosed water bodies around the world, impacts from eutrophication are increasingly requiring direct (*in situ*) mitigation actions to allow continued provisioning of ecosystem services. By quantitatively integrating all relevant aspects of the filter feeding blue mussel's nutrient extraction potential, our results highlight the feasibility, even in physiologically challenging environments of the Baltic Sea region, of using biofiltration for effectively extending mitigation beyond only controlling nutrient inflow, but also targeting existing internal nutrients.

References

- Austin MP (1980a) An exploratory analysis of grassland dynamics: An example of a lawn succession. Vegetatio 43: 87–94.
- Austin MP (1980b) Searching for a model for use in vegetation analysis. Vegetatio 42: 11-21.
- Austin MP, Smith TM (1989) A new model for the continuum concept. Vegetatio 83: 35-47.
- Burgess MG, Clemence M, McDermott GR, Costello C, Gaines SD (2018). Five rules for pragmatic blue growth. Marine Policy, 87, 331-339.
- Ceccherelli VU, Rossi R (1984). Settlement, growth and production of the mussel *Mytilus* galloprovincialis. Marine ecology progress series. Oldendorf, 16(1), 173-184.
- Dahlhoff EP, Menge BA (1996) Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. Mar Ecol Prog Ser 144: 97–107.
- Dare PJ, Edwards DB (1975). Seasonal changes in flesh weight and biochemical composition of mussels (Mytilus edulis L.) in the Conwy Estuary, North Wales. Journal of Experimental Marine Biology and Ecology, 18(2), 89-97.
- Eikeset AM, Mazzarella AB, Davíðsdóttir B, Klinger DH, Levin SA, Rovenskaya E and Stenseth NC (2018). What is blue growth? The semantics of "Sustainable Development" of marine environments. Marine Policy, 87, 177-179.
- Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77: 802–813.
- Hastie T, Tibshirani R, Friedman JH (2009) The elements of statistical learning: Data mining, inference, and prediction. New York: Springer-Verlag. 744 p.
- Hedberg N, Kautsky N, Kumblad L, Wikström SA (2018) Limitations of using blue mussel farms as a nutrient reduction measure in the Baltic Sea. Report from Baltic Sea Centre 2/2018. Stockholm: Stockholm University. Available at: https://www.su.se/polopoly_fs/1.406424.1539853328!/menu/standard/file/BSC_Mussels_report_2_2018_lowres.pdf
- Hoffman JR, Hansen LJ, Klinger T (2003) Interactions between UV radiation and temperature limit inferences from single-factor experiments. J Phycol 39: 268–272.
- Kotta J, Kutser T, Teeveer K, Vahtmäe E, Pärnoja M (2013) Predicting species cover of marine macrophyte and invertebrate species combining hyperspectral remote sensing, machine learning and regression techniques. PLoS One 8: e63946.
- Kotta J, Oganjan K, Lauringson V, Pärnoja M, Kaasik A, Rohtla L, Kotta I, Orav-Kotta H (2015) Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. PLoS ONE 10(8): e0136949.
- Lutz RA (Ed.) (1980) Mussel Culture and Harvest: a North American Perspective, Elsevier Scientific Publishing Company, Amsterdam 350 pp.
- McIlgorm A (2016). Ocean economy valuation studies in the Asia-Pacific Region: Lessons for the future international use of national accounts in the Blue Economy. Journal of Ocean and Coastal Economics, 2(2), 6.
- Petersen JK, Loo L-O (2004) Miljøkonsekvenser af dyrking av blåmuslinger. Interregproject III-A "Blåskjellanlegg og nitrogenkvoter". Slutrapport 31.8.2004 (in Danish).
- Pinto H, Cruz AR, Combe C (2015). Cooperation and the emergence of maritime clusters in the Atlantic: Analysis and implications of innovation and human capital for blue growth. Marine Policy, 57, 167-177.
- Reynaud S, Leclercq N, Romaine-Lioud S, Ferrier-Pagès C, Jaubert J, et al. (2003) Interacting effects of CO₂ partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. Glob Chang Biol 9: 1660–1668.

- Sandman AN, Wikström SA, Blomqvist M, Kautsky H, Isaeus M (2013) Scale-dependent influence of environmental variables on species distribution: a case study on five coastal benthic species in the Baltic Sea. Ecography 36: 354–363.
- Saurel C, Gascoigne JC, Palmer MR, Kaiser MJ (2007) *In situ* mussel feeding behavior in relation to multiple environmental factors: Regulation through food concentration and tidal conditions. Limnol Oceanogr 52: 1919–1929.
- Stadmark J, Conley DJ (2011). Mussel farming as a nutrient reduction measure in the Baltic Sea: consideration of nutrient biogeochemical cycles. Marine pollution bulletin, 62(7), 1385-1388.
- Westerbom M, Mustonen O, Kilpi M (2008) Distribution of a marginal population of *Mytilus edulis*: responses to biotic and abiotic processes at different spatial scales. Mar Biol 153: 1153–1164.