Thesis for the degree of Doctor of Philosophy

Blue Oceans with Blue Mussels

Management and planning of mussel farming in coastal ecosystems

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Blue Oceans with Blue Mussels – Management and planning of mussel farming in coastal ecosystems

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Experts have no more right than others, but they are wrong in a more advanced way!

Thesis summaries

English abstract

Eutrophication is one of the largest and most serious global threats to the marine environment. The effect of eutrophication has become increasingly clear during recent time, and major economic and political efforts are being made to tackle its causes and consequences in Sweden and its surrounding seas. Mainly, it is the dramatic increase in the supply of nitrogen and phosphorus that has several undesirable effects on marine ecosystems. More and more emphasis is placed on how to utilize the natural processes in restoration measures of eutrophic coastal areas. One such proposition is to use mussel-farms with substantial capacity for filter-feeding to “clean” coastal waters by assimilation of particulate material and removal of potentially large amounts of nutrients from coastal areas at harvest.

In this thesis, several aspects of mussel farming have been studied in a series of experiments as a step in the process to develop and evaluate the concept of mussel farming as restoration measurement in eutrophic coastal areas. The experiments were designed and attempts made to evaluate three major issues 1) effects of mussel farming on water quality, 2) spatial patterns of growth and 3) mitigation of negative effects in sediments beneath mussel farms. The first issue was attempted to evaluate using a before-after control-impact design with two mussel farms and two reference locations. Transplanted mussels were used to investigate spatial and temporal variability and thus the predictability of mussel growth. Predictive models were then developed and evaluated with the best model implemented into GIS, producing a map of predicted growth. In a series of field and laboratory experiments the survival and growth of a bioturbating polychaete on mussel faeces and the impacts on nutrient and oxygen fluxes across sediment-water interface of its activities were evaluated.

Due to loss of mussels, presumably because of predation, the planned evaluation of local effects of mussel farming and its potential as a mitigation tool was not possible. This shows that the use of mussel farming in mitigation efforts is quite unpredictable and development of techniques used are needed. However, the extensive data collected can be used to evaluate spatial and temporal variability of the sampled parameters and provide important information for future attempts to evaluate effects of action programs. The studies show that growth is highly variable both between sites and times, both between and within years. Despite the variability there is some predictability in terms of growth in soft tissue, while for growth in shell length it is more difficult. Prediction of growth indicates that about 15 % of the investigated area belongs to the highest growth class. The highest growth rates were generally observed in the innermost areas, in fjords and other protected areas. These are also the areas that are in most need of restoration activities. This fact, from the perspective of utilizing mussel farming in mitigation efforts, is positive. The studies also point on the importance of understanding the complex systems in coastal areas. One environmental variable does not always influence the growth in the same manner. The influence may vary between both levels of growth and levels of the variable itself but also depends on other environmental factors within the system. Further improvement of growth prediction requires refinements of predictors with regard to both the nature and quality. As perhaps the greatest negative impact of mussel farming, it is important to minimize the effect of biodeposition on the sediment. The results indicate that the use of natural processes such as bioturbation may be a possibility. The polychaete *Hediste diversicolor* showed improved growth while a positive effect on the decomposition of organic matter was obtained with an improved sediment environment as a result. The effect was mainly indirect presumably through increased microbial activity due to the mechanical impact on the sediment by the polychaetes.

In summary, this thesis provides important insights into several aspects of the potential and sustainability of mussel farming as a mitigation tool and the results provide a base for scientifically based planning of aquaculture. Under the right conditions, mussel farming has the potential to be a useful and sustainable mitigation method but due to the complexity of the system it can be quite unpredictable and further studies are needed. The use of bioturbation by polychaetes, and possibly other organisms, has the potential to mitigate sediments negatively impacted by mussel farms and thus has the potential to be an important component in future mitigation measure using mussel farming. However, technical developments are needed before the approach can be used in practice.

Keywords: Coastal management, Growth, Modelling, *Mytilus edulis*, Planning, Predict, Restoration, Mitigation, Aquaculture, Bioturbation

Populärvetenskaplig sammanfattning

Ett av de största och mest allvarliga globala hoten mot den marina miljön är övergödning (eutrofiering). Övergödningseffekterna har blivit allt tydligare de senaste årtiondena och stora ekonomiska och politiska insatser genomförs för att komma till bukt med dess orsaker och konsekvenser i Sverige och omgivande hav. Främst är det den dramatiska ökningen i tillförseln av kväve och fosfor som har medfört flera tydliga och oönskade effekter på de marina ekosystemen. Allt större fokus läggs på hur man ska kunna använda naturliga processer i restaureringsåtgärder av övergödda kustområden. Ett förslag är att använda musselodling och musslornas filtrering av partiklar från vattnet för att ”rena” kustvattnen. Skörd av musslor kan potentiellt ta bort stora mängder kväve och fosfor från kustområderna.

I den här avhandlingen, som bygger på resultat från flera experiment, har viktiga aspekter av musselodling studerats som ett steg i processen att förverkliga konceptet med musselodling som restaureringsåtgärd i övergödda områden. Försöken utformades för att utvärdera tre viktiga aspekter av musselodling som restaureringsåtgärd: 1) effekter av odling på vattenkvaliteten, 2) rumsliga mönster av tillväxt och 3) lindrande av negativa effekter på underliggande sediment. Den första av dessa frågor försöktes utväderas genom ett storskaligt experiment med två musselodlingar och tillhörande referenslokaliteter och en ”before-after control-impact” design. Transplaneterade musslor användes för att undersöka rumslig och tidsmässig variation och därmed förutsägbarheten i tillväxt. Prediktiva modeller utvecklades och utvärderades och en karta över predikterad tillväxt togs fram genom att den bästa modellen implementerades i GIS. Förmågan hos en havsborstmask att överleva och tillväxta på musselfekalier och dess aktiviteters påverkan på flöden av näringsämnen och syre över sediment-vatten ytan utvärderades genom en serie av fält- och laboratorieförsök.

På grund av en kraftig nedgång i mängden musslor på odlingarna, förmodligen orsakad av predation, kunde den planerade utvärderingen av musselodlingars lokala effekter och dess potential som en restaureringsåtgärd inte genomföras som planerat. Detta visar på att musselodling som restaureringsåtgärd kan vara ganska oförutsägbart och teknisk utveckling krävs. Den omfattande mängden data som samlats in kan dock användas för att utvärdera rumslig och tidsmässig variation hos det provtagna variablerna. Detta kan bidra med viktig information för framtida utvärderingar av åtgärdsprogram. Studierna visar på att tillväxten är mycket variabel både mellan platser och tillfällen, såväl mellan år som tidpunkter inom året. Trots den stora variationen så finns det en viss förutsägbarhet i köttillväxt medan för tillväxt i skallängd så är det svårare. Prediktion av tillväxt visar på att ungefär 15 % av det undersökta området uppvisar tillväxt motsvarande den bästa tillväxtklassen. Den snabbaste tillväxten återfinns generellt sett i det inre kustområdet inne i fjordar och andra skyddade miljöer. Det är också dessa områden som är i störst behov av mijlöförbättrande åtgärder vilket är positivt ur aspekten att utnyttja musselodling som en restaureringsåtgärd. Studierna visar också på vikten av att förstå hur de komplexa system som kustområderna utgör fungerar och att en och samma ekologiska variabel inte alltid har samma inverkan på tillväxten utan påverkan kan variera både mellan nivåer av tillväxt och nivåer av variablen själv men också beroende på interaktioner med andra faktorer i systemet. För att förbättra prediktioner om musseltillväxt ytterligare är viktigt att förfina prediktor variablerna med avseende på kvalitet och mekanistiska karaktär. Som den kanske största negativa inverkan av musselodlingar är det viktigt att minimera effekten av biodeposition på sedimentmiljön. Resultaten visar på att nyttjande av naturliga processer som bioturbation kan vara en möjlighet. Havsborstmasken *Hediste diversicolor* visade på en förbättrad tillväxt samtidigt som en positiv effekt på nedbrytningen av organiskt material erhölls med en förbättrad sedimentmiljö som följd. Effekt var till största del indirekt med ökad mikrobiell aktivitet som följd av havsborstmaskarnas mekaniska påverkan på sedimentet. Dock behövs vidare studier av de specifika effekterna för att klarlägga den fullständiga potentialen av detta.

Sammanfattningsvis, så även om den här avhandlingen inte kunnat ge svar på alla frågor rörande musselodling som restaureringsåtgärd så bidrar den med ny kunskap och nya insikter som kan utgöra grunden för vidare studier och fortsatt utveckling av såväl mussel industrin som åtgärdsprogram för övergödda områden samt för skötsel och planering av kustnära områden. Under rätt förhållanden finns det en viss potential för musselodling som en hållbar restaureringsåtgärd men med ett komplext system så kan effekten vara svårförutsägbar och vidare studier behövs. Nyttjande av havsborstmaskars, och troligen även andra organismers, bioturation har potentialen att lindra de negativa effekter på sedimentet som musselodlingar har och kan därmed vara en viktig komponent i framtida restaureringsåtgärder där musselodlingar utnyttjas. Emellertid så behövs teknisk utveckling inom området innan ett sådant tillvägagångsätt kan utnyttjas i praktiken.

List of papers

This thesis is a summary of the following papers:

I

Bergström, P., Lindegarth, S. and Lindegarth, M. 2013. Temporal consistency of spatial pattern in growth of the mussel, *Mytilus edulis*: implications for predictive modelling. *Estuarine, Coastal and Shelf Science* 131, 93-102

Including: Bergström, P. et al 2013. Corrigendum to "Temporal consistency of spatial pattern in growth of the mussel, *Mytilus edulis*: implications for predictive modelling, *Estuarine, Coastal and Shelf Science* 133, 308

II

Bergström, P., Lindegarth, S. and Lindegarth, M. Modelling and predicting the growth of the mussel, *Mytilus edulis*: implications for planning of aquaculture and eutrophication mitigation. *Manuscript*

Including: A priori selection of predictor variables. Supplementary material to Bergström et al 2014. Modelling and predicting the growth of the mussel, *Mytilus edulis*: implications for planning of aquaculture and eutrophication mitigation.

III

Bergström, P., Environmental influence on mussel (*Mytilus edulis*) growth – a quantile regression approach. *Manuscript*

IV

Bergström, P., Hällmark, N., Larsson, K.-J. and Lindegarth M. Faeces from the mussel *Mytilus edulis* provides a better food source for the polychaete, *Hediste diversicolor*, compared to natural organic material. *Manuscript*

V

Bergström, P., Carlsson, M. S., Lindegarth, M., Petersen, J. K., Lindegarth, S. and Holmer, M. 2014. Testing the potential for improving quality of sediments impacted by mussel farms using bioturbating polychaete worms. *Submitted manuscript*

Other related work

Dunér Holthuis, T., **Bergström, P.**, Lindegarth, M., and Lindegarth, S. 2014. Developing and testing procedures for monitoring recruitment of mussels and fouling tunicates in mariculture. *Submitted manuscript*

Bergström, P., Lindegarth, M. and Lindegarth, S. 2013. Restaurering av övergödda havsvikar med hjälp av miljömusselodling. En rapport från projekt Hav möter Land. Rapport nr 21

Holmer, M., Carlsson, M., **Bergström, P**. And Kjerulf Petersen, J. 2013. Digging worms for remediation of sediments impacted by mussel farms. A report from project Hav möter Land. Report nr 34

Introduction to the Blue mussel's ocean

The importance and value of coastal ecosystems

Coastal areas, a scene of complex interactions between atmospheric, terrestrial and oceanic factors (Cloern and Jassby 2008), cover approximately 7 % of the earth's surface and comprise some of the most productive and valued ecosystems of the world (Holligan and de Boois 1993, Costanza et al. 1997, GESAMP 2001). Throughout history, coastal habitats have been important to humans for fishing and in providing other resources (Jackson et al. 2001, Lotze and Milewski 2004) and today the estimated value of coastal ecosystem services exceeds $12.6*10^{12}$ US$ (Costanza et al. 1997). Still, we are just beginning to recognize just how important the contribution of these ecosystems is to human well-being and how much we really affect them (Doughty et al. 2010, Marris 2011). In that context recent emphasis on ecosystem based management and important goods and services offers a systematic way to reveal values and benefits of coastal system (Table 1, de Groot et al. 2002, Millennium Ecosystem Assessment 2005). Ensuring the delivery of marine goods and services require the maintenance of ecological processes that underpin the functioning of the ecosystem (Agardy 1994, Daily 1997, Roberts et al. 2003).

With about 40 % of the world's human population living within 100 km from the coastline (Agardy and Alder 2005), the potential impact on the coastal environment is tremendous. For a long time, humans have used, changed and polluted the ocean without considering the impact on ecosystems and their ability to provide goods and services (Jackson et al. 2001, Townend 2002, Lotze and Milewski 2004, Lotze et al. 2006, Worm et al. 2006, Halpern et al. 2008b, Gill et al. 2009). This fact has resulted in the now visible, heavily degraded coastal environment. Although not new, the severity of pressures and impacts are continuing or accelerating despite various national efforts to halt degradation of the marine environment (Millennium Ecosystem Assessment 2005, Defeo et al. 2009). Restoring and protecting our precious coastal ecosystems requires change in our approach to the ocean and a range of strategies for successful planning, management and conservation of marine areas.

Table 1. Some examples of goods and services provided by the marine environment. (Modified from UNEP-WCMC, 2006)

Ecosystem goods and services	
Regulating	*Coastline protection from natural hazards*
	Soil and beach erosion regulation
	Climate regulation
	Water quality maintenance
Provisioning	*Subsistence and commercial fisheries*
	Aquaculture
	Medicinal products
	Ornaments e.g. jewelry, decoration
Cultural	*Tourism*
	Recreation
Supporting	*Nutrient cycling*
	Nursery habitats
	Biodiversity

Threats to coastal ecosystems

Increasing and changing human threats

The development of human civilizations has historically often been concentrated to rivers and coastal areas where access to water facilitated transportation and trade (e.g. Van Andel 1981, Vitousek et al. 1997). Thereby, these waters have been affected by anthropogenic activities under long time. For most part of history, it was unthinkable that human could directly influence the marine environment other than in local and insignificant ways. With the industrial revolution, this changed. Coastal systems experience growing population and increasing exploitation pressures with rapid changes of the heterogeneous ecosystems as a result. The balanced state of marine environments is disrupted by our activities and today no marine area is unaffected by human activities (Halpern et al. 2008b). The changes to coastal systems are driven by a range of factors including coastal development, overexploitation of resources and pollution (Agardy and Alder 2005). Our understanding of how abiotic and biotic factors interacts and drive the functioning of ecosystems has rapidly advanced during the last decades and there is a growing awareness of how ecosystems respond to global environmental changes (Sutherland et al. 2013). In 2001, the United Nations presented a list of 20 global issues concerning the deterioration of the marine environment; one of the points listed were eutrophication and the associated anoxia (GESAMP 2001).

Eutrophication

One of the major threats to coastal systems is the continuing supply of nutrients (e.g. Rosenberg 1985, Diaz and Rosenberg 2008). The link between nutrients and productivity has been known since the pioneering work by Weber (1907) and Johnstone (1908). In the oceans, the major limiting nutrients are nitrogen and phosphorus (Ryther and Dunstan 1971, Nixon et al. 1996, Howarth 1988, Tyrell 1999, Howarth and Marino 2006). Together with hydrogen, carbon, oxygen and sulphur these elements constitutes the major building blocks for all biological macromolecules (Schlesinger 1997). Nitrogen is a vital substance for all living organisms with an average cell containing roughly 5 % nitrogen. As a result of this, biological life dominates the regulation of the global nitrogen cycle. Among the primary nutrients, phosphorus is the scarcest in the natural environment. Phosphorous also has a key role in a number of essential biochemical functions (Westheimer 1987) and is almost exclusively present as phosphate in marine environments. The marine cycles of phosphorus, nitrogen and carbon are closely linked through the photosynthetic fixation of these elements by phytoplankton, which forms the base of most marine food webs.

Human activities have increased both the amount of and the rate by which nutrients, particularly forms of nitrogen and phosphorus, reach the oceans, creating conditions with excess nutrients in many areas of the world (Cloern 2001). The term "eutrophic" was first introduced by Weber in 1907 to describe plant growth induced by nutrient supply. Due to the complexity of causes, effects and processes concerning eutrophication, a number of different definitions have been proposed both by researchers and international organizations (Steele 1974, Gray 1992, Vollenweider 1992, Heip 1995, Nixon 1995, OSPAR 2003, UNEP(DEC)/MED WG. 231/14 2003). Today, the most used definition is the European Environmental Agency's (EEA):

> "Enhanced primary production due to excess supply of nutrient from human activities, independent of the natural productivity level for the area in question".

Although anthropogenic increases in loadings of organic matter and nutrients began centuries ago with cultural development and land conversion, the effects on coastal environments did not accelerate until the middle of the 20's century, coinciding with the dramatic growth in consumption of chemical fertilizers. Today eutrophication is a global and widespread problem (Vollenweider 1981, Carpenter et al. 1998, Cloern 2001, Diaz and Rosenberg 2008) and considered as one of the major threats to the function and services supported by coastal ecosystem (GESAMP 1990, Nixon 1990, Gray 1992, National Research Council 1994, Paerl 1995, Edebo et al. 2000, Cloern 2001, Schindler 2006, Smith and Schindler 2009) and not a single coastal system remains unaffected by human activities (Richardson and Poloczanska 2008).

In summary, humans are compromising the marine ecosystems services and functions which are essential to the well-being of both the ecosystem itself and the human communities across the world (Agardy and Alder 2005). So, there are many reasons to care. But there are also other more aesthetical and ethical reasons (Harris et al. 2006). For example, humans are the main reason to many ecosystems malfunctions so it falls to us to help these. We should not forget that the ecosystems can easily survive without us but that our existence heavily depends on them.

Managing and planning coastal ecosystems

Policies for protection and measures

Protecting marine waters from harmful consequences of anthropogenic nutrient enrichment is a challenge for resource managers worldwide because sources and routes to the ocean are so diverse. Since the effects of anthropogenic eutrophication became evident, numerous governmental and intergovernmental commitments have been made to reduce the loading of nutrients. In Europe, the European Union (EU), OSPAR and others have put forward several directives and programs in an attempt to reduce the amount of nutrients reaching the aquatic environment and to help protect it. Some of the most important directive and programs are summarized in Table 2.

Table 2. Summary of the most important governmental directives and programs in the battle against eutrophication.

Directive/Program	Year	Objectives
The Nitrates Directive "91/676/EEC"	1991	Deal with protection of waters against pollution caused by nitrates from agricultural sources
The Habitat Directive "92/43/EEC"	1992	Per se does no assessments of eutrophication but sets requirements that contribute to it by aiming to protect biodiversity though conservation of natural habitats and relevant measures to maintain or restore favorable status of natural habitats
The Water Framework Directive "2000/60/EC"	2000	Establishing a framework for community action in the field of water policy with the ultimate goal of achieving "good ecological and chemical status" for all community waters by 2015 and plans for long-term sustainable management of all water basins should be put forward
The OSPAR Eutrophication Strategy	2003	To combat eutrophication in the OSPAR maritime area, in order to achieve and maintain by 2010 a healthy marine environment where eutrophication does not occur
HELCOM Monitoring and Assessment Strategy "26/2005"	2005	Sets out the basis for how the HELCOM contracting states commit themselves to carry out their national monitoring programs and work together to produce joint assessments aiming to reveal how visions, goals and objectives set for the Baltic Sea marine environment are met and to link the quality of the environment to management
Baltic Sea Action Plan (HELCOM)	2008	To restore the good ecological status of the Baltic marine environment by 2021
Marine Strategy Framework Directive "2008/56/EC"	2008	To protect more effectively the marine environment across Europe. It aims to achieve good environmental status of the EU's marine waters by 2020 and to protect the resource base upon which marine-related economic and social activities depend
Framework for Maritime Spatial Planning "2014/89/EU"	2014	Aims to promote the sustainable growth of maritime economies, the sustainable development of marine areas and the sustainable use of marine resources

Measures to protect and mitigate effects of eutrophication

There are many ways of mitigating the impact of anthropogenic activities on the marine environment, for example, management and strategies for protection of ecosystems, building public awareness and initiatives that encourage conservation (Salafsky et al. 2002, Leslie 2005, Lundquist and Granek 2005). But, some of the most important considerations are those that handle the restoration of already affected systems. Restoration ecology is a relatively young research field within the aquatic environment (Buijse et al. 2002, Omerod 2004, Goreau and Hilbertz 2005, Young et al. 2005), and include various activities, ranging from habitats restoration, restoration of ecosystem processes and functions to protection and management strategies. In general, mitigation efforts can be divided into two different approaches; reducing or halting the impacts or dealing with the causes of the problems. As a result of the complexity of marine ecosystems and the vast amount of different human activities affecting the environment, restoration efforts often fail or fall short of their objectives. Among the most common reasons for failure are inappropriate use of techniques, inconsistent approach, poor project design and failure to address the root cause. Other important factors are inadequate monitoring and failing in public awareness and support.

To reduce the eutrophication and the effects that follow of it, the emissions of, among other nitrogen and phosphorous needs to be controlled (Howarth 1988, Smith et al. 1999, Conley et al. 2009b). This is relatively easy to do with well-defined point sources, such as sewage plants, whereas for nonpoint sources it is more difficult (Smith et al. 1999). All approaches in combating eutrophication follows one of two general ideas. To attack the symptoms or the root of the problem, i.e. excess inputs of nutrients and organic matter. During the past decades different multidimensional ways to manage the emissions of nutrients have been discussed, including 1) restoring wetlands and creating riparian buffer zones between farms and surface waters (Frostman 1996, Boesch and Brinsfield 2000, Boesch et al. 2001, Mitsch et al. 2001), 2) improving the efficiencies of fertilizer applications and reduction of the amount used and 3) improvement of N and P removal from wastewater. During the last decades, the idea of using filter-feeding organisms in mitigation efforts to control and remove excess nutrients from marine areas have been brought forward (Kuenzler 1961, Officer et al. 1982, Takeda and Kurihara 1994, Haamer 1996, Ferreira et al. 2009, Gren et al. 2009).

Maritime spatial planning

Spatial planning has for long time been used as an essential tool for managing land-use but in the marine environment this approach is still young and emergent. Only during recent years that maritime spatial planning (MSP) has become crucial part of ecosystem-based management in marine environments (Douvere 2008). MSP can broadly be described as (Ehler and Douvere 2007):

> "A process of analysing and allocating parts of three-dimensional marine spaces to specific uses or non-use, to achieve ecological, economic, and social objectives that are usually specified through a political process"

Although similarly to spatial planning on land, the context and outcomes of MSP differs from land planning due to the three-dimensional and dynamic nature of marine environments (Gilliland and Laffoley 2008). As a consequence of the decreased status of our oceans various countries, including Sweden (through a newly adopted law), now use MSP to achieve a more sustainable use of their marine resources. On top of these national initiatives, the European Union are developing common frameworks and policies in the area of MSP (e.g. the EU "Roadmap for maritime spatial planning", COM 2008), the latest being the "Framework for maritime spatial planning" established in July 2914 (European Commission 2014). One important component in MSP and other similar processes is reliable spatial information on structural and functional components of the ecosystem (e.g. COM 2012). Condensed into comprehensive maps, such information provides powerful tools for planning and negotiation among conflicting interest.

Mussel farming: opportunities, problems and suggested solutions

Aquaculture is an ancient tradition, stretching back more than 2500 years. The first written note on aquaculture is from about 475 B.C. and a work on fish breeding ("*Yang Yu Ching")* by Fan Lee (synonymous; Fan Li and Fan Lai) describing commercial fish pond cultures (Borgese 1980, Landau 1992). Bivalve culture (oysters) was first mentioned about 350 B.C. While aquaculture has its roots in ancient Asia, it was not until 1970's that aquaculture started to increase the ecosystem service of food provisioning worldwide and today more than 220 different species are farmed and the total production exceeds 63 million tons (FAO 2012). Advances in technology and production methods have increased aquaculture and led to it becoming a significant source of food and income for a large part of the world population. With increasing population, the world will need 50-100 % more food by the end of our generation (Hazell and Wood 2007, Godfray et al. 2010) and aquaculture in coastal waters will be an important component of this expansion (see review by Bostock et al. 2010).

In many ecosystems, filter feeding bivalve species function as ecosystem engineers (sensu Jones et al. 1994) and foundation species (*sensu* Dayton 1972), providing structural habitat complexity and enhanced habitats by connecting the substrate with the water column (Thompson and Bayne 1974, Crooks 2002, Gutiérrez et al. 2003, Koivisto and Westerbom 2010, Markert et al. 2010). By filtering suspended particulate nutrients (Dame et al. 1991, Prins and Smaal 1994, Dame 1996, Prins et al. 1998) and regenerating inorganic nutrients (Wotton and Malmqvist 2001, Richard et al. 2006, Richard et al. 2007a, Richard et al. 2007b, Carlsson et al. 2009, Jansen et al. 2011, Carlsson et al. 2012) to the environment, mussels play an important role in the benthic-pelagic coupling of nutrient cycles (Figure 1).

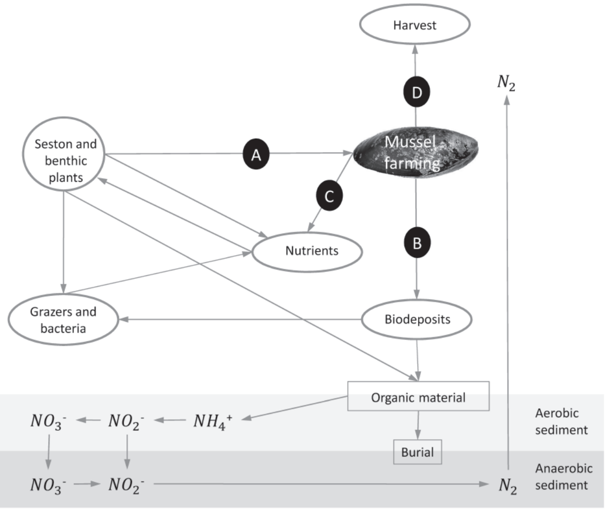

Figure 1. Conceptual diagram of bivalve aquaculture interactions in coastal ecosystems related to: (A) the removal of suspended particulate matter (seston) during filter feeding; (B) the biodeposition of undigested organic matter in faeces and pseudofaeces; (C) the excretion of ammonia nitrogen; and (D) the removal of materials (nutrients) in the bivalve harvest (modified from Cranford et al. 2006)

By their sheer numbers, mussels filter enormous amounts of water every day and are generally known to have a positive impact on the environment with reduced seston concentrations (Asmus and Asmus 1991, Newell 2004), increased water transparency (Schröder et al. 2014) lower nutrient concentrations (Nakamura and Kerciku 2000, Newell 2004) and improved water quality (Ostroumov 2005, Zhou et al. 2006) thus providing a sustainable production of seafood (Smaal 2002). This important role should be possible to utilize in restoration efforts in shallow eutrophicated areas. Since the mussels capture nutrition at an early stage in the food web it would make an ecological advantage if this "filtering capacity" could be used as a measure to remove excess nutrients from the oceans by the means of farming and harvesting mussels (Figure 2).

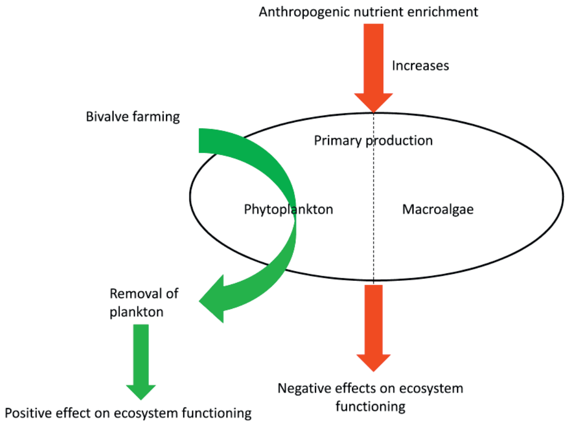

Figure 2. Conceptual idea of using mussel farming as a mitigation tool in eutrophied coastal areas

Due to the fact that bivalve aquaculture production is growing worldwide and that the development is almost exclusively established in near-shore or estuarine habitats (Perez Camacho et al. 1991, Penney et al. 2002, Myrand et al. 2009), the concern about its impact on the environment is increasing (Heasman et al. 1998, Mirto et al. 2000, Black 2001, Giles et al. 2006, Duarte et al. 2008) and much work has been focused on understanding these processes (e.g. Davenport et al. 2003, Holmer et al. 2008). The negative effects on benthic environments are relatively well known (See reviews by Cranford et al. 2008, McKindsey et al. 2011, Shumway 2011) while the pelagic effects are less known mainly because of its high temporal and spatial variability. Mussels do not just incorporate nutrients into their tissue, they also produce faeces and pseudofaeces (hereafter collectively referred to as biodeposits) that are excreted and that nurture their food source (Hawkins and Bayne 1985, Navarro and Thompson 1997, Ward and Shumway 2004). Biodeposits run the risk of increase the deposition of organic matters on the sediment surface (Haamer et al. 1999, Hartstein and Rowden 2004, Callier et al. 2006, Callier et al. 2009, Carlsson et al. 2009, Robert et al. 2013), resulting in an increased eutrophication effect including changes in sediment chemistry (Cranford et al. 2009, Carlsson et al. 2010, Nizzoli et al. 2011, Carlsson et al. 2012, Wilding 2012) and increased sediment oxygen consumption (Christensen et al. 2003, Nizzoli et al. 2005, Giles and Pilditch 2006, Richard et al. 2006, Robert et al. 2013). However, these effects are generally very local and only exceeds roughly 50 m from the farm area (Mattsson and Lindén 1983, Chamberlain et al. 2001, Hartstein and Rowden 2004, Callier et al. 2006, Giles et al. 2009). In total, biodeposits from aquaculture increase the sedimentation by a factor of 2 to 4 depending on environmental conditions (Grenz 1989, Gontier et al. 1992) although it might be argued that even with a local increase in sedimentation the total sedimentation on the basin scale is reduced (Petersen et al. 2012, Rose et al. 2012).

Addressing the problems associated with organic enrichment of sediment is important for a successful use of farming in restoration measurement and for sustainable growth of the aquaculture industry. The biogeochemical cycling and mineralization processes are controlled by a complex matrix of interactive processes and variables, including biological activities and physical conditions (Middelburg and Levin 2009, Valdemarsen et al. 2010, Laverock et al. 2011, Voss et al. 2013). Microbial organisms drive the degradation of organic matter, nutrient and carbon cycling in the sediment through a sequence of oxidative reductions (Carpenter and Capone 1983, Blackburn and Nedwell 1988, Herbert 1999, Figure 3).

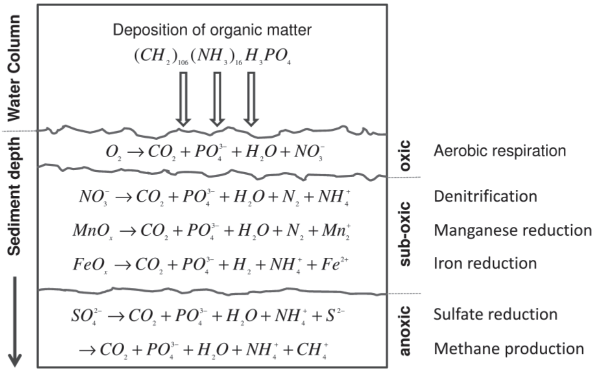

Figure 3. Schematic illustration of the general metabolic processes in different layers of the sediment in coastal marine environments.

However, the microbial processes are strongly facilitated by movement, feeding and burrowing by fauna which influence the architecture and functional complexity of the seafloor (Aller 1982, Mermillod-Blondin et al. 2004, Meysman et al. 2006, Laverock et al. 2011), creating a three-dimensional mosaic of oxic/anoxic interfaces (Figure 4). These activities, referred to as bioturbation (*sensu* Richter 1952), significantly influence the nature and rate of the biogeochemical processes (Lee and Swartz 1980, Jørgensen and Revsbech 1985, Andersen and Kristensen 1991, Aller and Aller 1998, Bird et al. 1999, Christensen et al. 2000, Heilskov et al. 2006, Waldbusser and Marinelli 2006) favouring aerobic processes (Kostka et al. 2002, Nielsen et al. 2003b, Nielsen et al. 2003a). Oxygen is the most favourable electron acceptor (Fenchel et al. 1998), hence the presence or absence of oxygen is an important determinant for many redox sensitive processes such as the decomposition rates of organic matter (Froelich et al. 1979, Thamdrup 2000, Conley et al. 2009a). Thus bioturbation and bioirrigation by organisms has the potential to increase the assimilative capacity of the sediment, by increasing the sediment-water interface and sediment oxygen levels. The first to realize that this type of small-scale reworking activities by tiny organisms can dramatically change the system at far larger scales was Charles Darwin in his work in earthworms and soil formation (Darwin 1881). The concept was then introduced to the marine environment by Davidson (1891).

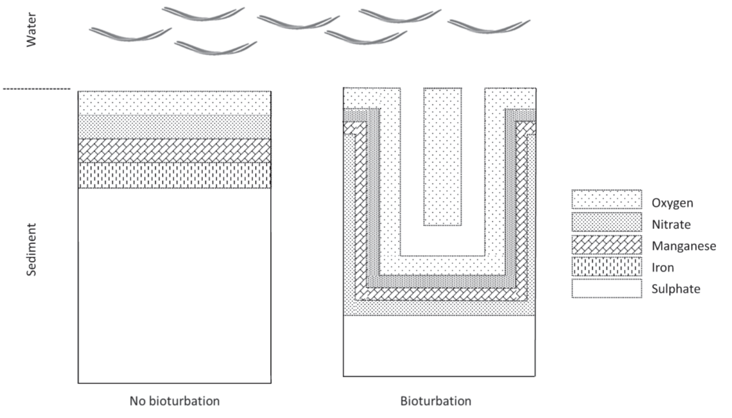

Figure 4. One-dimensional schematic illustration of the vertical succession of major oxidants associated with organic matter decomposition in marine sediments. Comparison between non-bioturbated and bioturbated sediments. Modified from Aller (1982)

A major component of coastal sediment environments are different species of polychaetes, which dig into the sediment creating tubes and burrows as well as flushing their burrows with overlying water. Being known as "ecosystem engineers", their activities strongly influence the sediment conditions (Hutchings 1998, Giangrande et al. 2005, Quintana et al. 2007, Meadows et al. 2012, Norkko et al. 2011). Being able to utilize burrowing organisms, tolerant to high degrees of organic matter and relatively low oxygen levels would provide a stable method in the remediation of organically enriched sediments (Lindqvist et al. 2009).

Planning and management of coastal environment

Fundamental for healthy coastal ecosystems are a sound systematic approach to planning, management and monitoring of the environment. Even if it means slightly different to different people, the underlying concept dates back to the beginning of the human society. Maintaining ecological processes that underpin the functioning of marine ecosystems requires the management of marine resources to occur at an appropriate spatial scale. Planning at the broad spatial scale of ecosystems alleviates the impact of human activities on the delivery of ecosystem services as activities would be managed at a scale similar to that of the associated ecological processes (Halpern et al. 2008a). Combining MSP with ecosystem-based management (EBM), generally called ecosystem-based marine spatial management (EB-MSM), and an ecosystem service framework (ESF) is a good way to ensure the sustainability of marine systems and the services they provide (Guerry et al. 2012). However, without effective monitoring, evaluation and adaptation; a successful outcome of marine management approaches is unattainable (Day 2008). With data on ecosystem structure and functions with few exceptions being collected using small scale sampling methods, decisions about planning and resource-use are often based on incomplete information (Toner and Keddy 1997, Joy and Death 2004). The ability of geographic information systems (GIS) to integrate spatial data and visualize results have proved essential for landscape-scale analyses (Frohn 1998, Johnston 1998) and become an important tool for managers of environments at ecosystem-scale (Remillard and Welch 1993, Ferguson and Korfmacher 1997, Kelly 2001).

Aim of thesis

The overall aim of this thesis was to experimentally and analytically evaluate the potential for farming of blue mussels as a tool in remediation efforts in nutrient enriched coastal areas. This was investigated in a series of experiments along the Swedish west coast. Three major issues and approaches were attempted: (1) a large-scale experiment on effects on water quality using a before-after control-impact design; (2) a large-scale experiment and analysis of spatial patterns of growth using transplanted mussels (Papers **I**, **II** and **III**) and; (3) field and laboratory experiments on the potential for mitigation of negative effects in sediments beneath mussel farms (Papers **IV** and **V**).

The results of these analyses are presented in the thesis summary and in five papers. While the two latter of these issues resulted in conclusive and successful experiments, the large-scale experiment on effects on water quality were largely inconclusive. This was due to massive mortality of mussels, removing the experimental treatment of the experiments. Despite the fact that this means that the results do not warrant a scientific publication on its own, the lessons learnt from this experiment has potentially important implications for the usefulness of mussel-farming as a tool for restoring coastal ecosystems. Therefore, the aims and conclusions of this experiment are briefly discussed in the thesis. The specific aims of the individual papers are described below.

This thesis consists of five separate studies with specific objectives (Figure 5), which are briefly presented here.

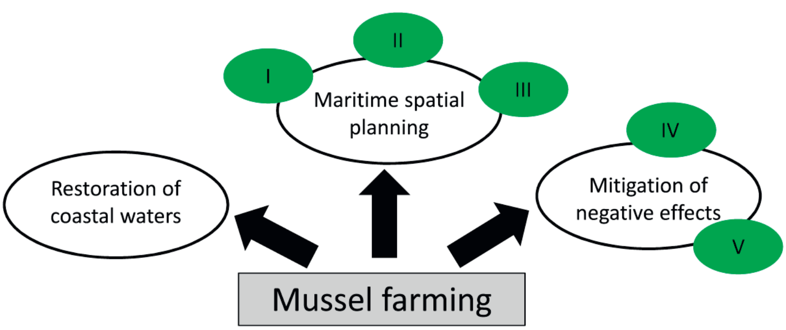

Figure 5. Overview of the different studies in this thesis and their respective point of attack on the question of mussel farming in mitigation efforts of eutrophied coastal environments. I-V is the paper involved

Water quality effects of mussel farms

The aim of this experiment was to experimentally investigate effects of mussel farming on the water quality. The purpose was to evaluate the effect on two different spatial scales; small (10^2m) and a larger (10^3m) scale. This was attempted by establishing mussel farms in May 2011 at two previously unfarmed areas with corresponding reference locations and sampling of several water quality parameters during a two-year period. An extensive design was implemented involving sampling of water quality parameters (e.g. nutrients, Secchi depth, chlorophyll *a* and phaeopigment) and ecological conditions at the bottom (e.g. epibenthic macrofauna and oxygen conditions using video) before the recruitment of mussels. Samples were taken at 8 occasions until September 2012. However, because there was a huge loss of mussels from both farms during the course of the experiment, the experiment did not provide a useful test of the effects of the mussel farms, which were suitable for scientific reporting. Nevertheless, the insights and data collected during this experiment can provide valuable information about challenges associated with mussel-farming as a method for restoring eutrophicated coastal waters.

Spatial patterns of mussel growth

Paper I:

In this paper we examined the temporal consistency of spatial patterns in growth of *Mytilus edulis*[1]. The data were used to empirically assess the limits to spatial prediction due to uncertainties in estimation of growth patterns at different spatial scales. This was evaluated by screening for suitable growth variables, determination of measurement error and individual variability followed by quantification of spatial variability and temporal consistency of growth and determination of predictability. Knowledge of growth rates patterns and consistency is essential for understanding the function of the ecosystem as well as for successful conservation, planning, (including empirical modelling) and management of coastal environments. With the purpose of the study being to assess the empirical limits for future predictive models, we did not evaluate the causal mechanisms behind observed patterns.

Paper II:

Temporal consistency observed in paper I indicated that there was potential for predictive modelling of blue mussel growth. In developing and evaluating predictive models of bivalve growth we studied the influence of different modelling techniques, classifications and explanatory variables in the performance of the models with the overall aim of evaluating and testing the predictability of spatial growth-patterns of *Mytilus edulis*. We also evaluated the possibility to use modelled data of predictor variables in predicting mussel growth as full covering data is rarely available for large areas. For the purpose of this modelling, growth data were collected from more than 100 sites on the Swedish west coast over a three year period. Maps on spatial distribution of mussel growth based on the models developed in this study provide useful insights for planning and management of the Swedish west coast.

[1] Linnaeus, C. 1758, Systema Naturae per regna tria naturae, secundum classus, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius: Holmiae. ii. pp 824

Paper III:

Even though predictive models of classification type such as the models developed in paper **II** provide a more stable prediction and are more easily applied in management and planning strategies it is also of interest to evaluate the absolute growth potential. The third paper aimed at investigating the relationship between absolute growth of *M. edulis* and environmental parameters using the less commonly used quantile regression technique. The paper also aimed at evaluating how these relationships vary within the span of several commonly measured environmental variables.

Mitigation of negative effects of mussel farms

Paper IV:

For the successful outcome of any attempts of restoration using mussel farms it is important to control for these potential negative impacts through sedimentation of biodeposits. A first step towards developing methods for utilizing the effect of bioturbation/bioirrigation in mitigation efforts of sediments influenced by mussel farms is to investigate the potential of various infauna to survive and utilize this excess of organic matter. The aim of this paper (**IV**) was to evaluate the potential of faeces and pseudofaeces from *Mytilus edulis* as food source for the polychaete *Hediste diversicolor* (O. F. Müller 1776[2]). Here we test hypothesis that the survival of *H. diversicolor* is not negatively influence by mussel faeces but instead can utilize and grow on mussel faeces. A secondary aim was to investigate whether the burrowing activities by *H. diversicolor* influence the fluxes of nutrients and oxygen in a different way in mussel farm influenced sediments compared to unaffected sediments.

Paper V:

After demonstrating that *Hediste diversicolor* can both survive in farm sediments and utilize mussel faeces as the only food source in paper **IV**, we investigated if these burrowing "ecosystem engineers" can be used to relieve the sediment from some of the potential burden of mussel farm biodeposits by stimulating degradation and thus increase the assimilative capacity of the sediment. We used two, common and relative pollution tolerant species of polychaetes; *H. diversicolor* and *Capitella capitata* (Fabricius 1780[3]) in a series of laboratory and field experiments where the effect on sediment-water fluxes, degradation of organic matter and the general properties of the sediment was analysed.

[2] Müller, O.F. 1776. Zoologica Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characters, nomine, et synonyma imprimis popularium. Havniae. XXXII, 274 pp.

[3] Fabricius, O. 1780. Fauna Groenlandica, systematice sistens, Animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli prout detegendi occasio fuit, maximaque parte secundum proprias observationes: Hafniae [Copenhagen] et Lipsiae

Methods

This chapter describes the study area, the main organisms and the general methodological approaches and techniques used in the studies of this thesis. For more detailed description of methods used please turn to the methodological section of the individual papers.

Study area and field sampling

The studies in this thesis were based on three main experiments; 1) effects on water quality were investigated using a large-scale experiment with mussel farms and corresponding reference locations in previously unfarmed areas; 2) growth patterns were studied using transplanted mussels and 3) mitigation of negative effect in sediments were evaluated in a series of field and laboratory experiments. These experiments were performed in two general areas, 1) the Swedish west coast and 2) Limfjorden, Denmark (Figure 6). The west coast of Sweden is open to Skagerrak and Kattegat, influenced by Atlantic water masses and harbouring the highest marine biodiversity in Sweden. Furthermore, it is characterised by a small tidal range (0.2-0.3 m), rocky shores and a salinity ranging from 20 to 30 depending on place, time of the year and river runoff. Limfjorden is a shallow, brackish sound with mainly soft and sandy sediments forming a natural channel intersecting the northern part of Jutland, from the North Sea in the west to Kattegat in the east, with tidal range of about 10 cm and is heavily influenced by nutrient enrichment.

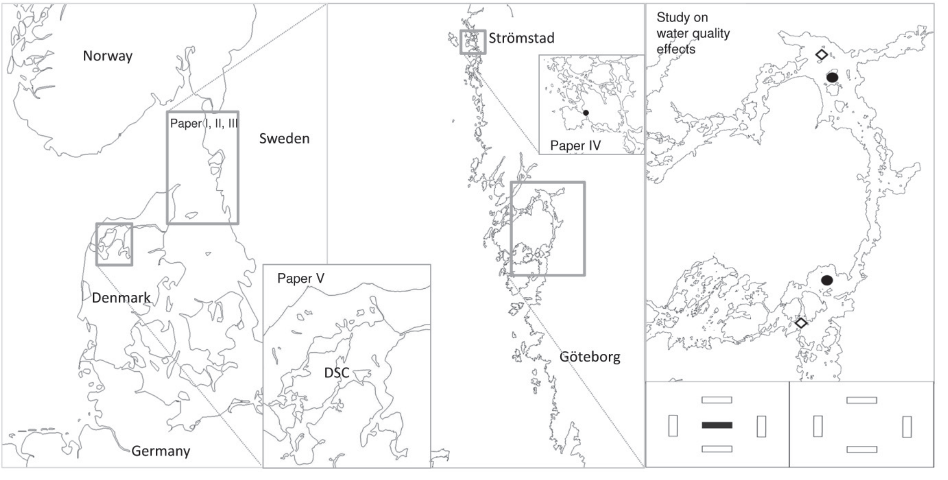

Figure 6. Geographic location of sampling and experimental areas used. Areas marked Paper I-V and "Study on water quality effects" represent the areas for the respective studies. Filled circles represent bays where mussel-farms were established and diamonds represent reference sites (see text for further description of sampling design for the latter.

Water quality effects of mussel farms

An experiment was designed to detect effects of mussel farming on water quality at small and large spatial scales (10^2m and 10^3m). Data on water quality parameters (e.g. nutrients (N, P & Si), Secchi depth, chlorophyll *a* and phaeopigment) were collected before and after the establishment of mussel farms in previously unfarmed areas. In total 18 sites distributed in two farms and two reference locations were sampled during a two-year period (Figure 6). All four stations had similar environmental conditions at the start of the experiment. The experiment was designed using a "beyond BACI" approach (e.g. Underwood 1992, Underwood 1994) to allow detection of short- and long-term effects within experimental bays ($\approx 10^2$ m), and among bays with mussel farms and those without ($\approx 10^3$ m). On the smaller scale samples from within the farm were compared to samples taken in sites around the farm while at the larger scale comparisons were performed at the level of bays.

Spatial patterns of mussel growth

All mussel growth data used in these studies (Paper **I**, **II** and **III**) were based on a transplantation method where blue mussels, from a single area, were transplanted into randomly selected sites within randomly selected areas with a total water depth between 6 and 20 m. The transplanted mussels were kept in semi-soft cages (25*10*10 cm), tied to concrete blocks and buoyed to float submerged at 2 m below surface at all times. From each cage, 15 mussels were randomly selected for measurements after two months' growth. For Paper **II** and **III**, data on a wide range of water parameters available from national and regional sampling programs were used.

Mitigation of negative effects of mussel farms

The potential for survival and growth (Paper **IV**) of *Hediste diversicolor* under different sediment and food regimes was evaluated in a study at Tjärnö while studies on the effect of polychaetes on nutrient and oxygen fluxes (Paper **V**) were performed in the vicinity of Danish Shellfish Centre in Nykøbing Mors. The field experiments were performed at an existing mussel farm and a reference site in Lysen Bredning, Limfjorden were polychaetes were added to the sediment in different densities (including controls without polychaetes) and kept in place by specially designed frames. After 5 weeks sediment samples were collected and analysed. Sediment cores used in the laboratory study on bioturbation and bioirrigation effects (Paper **V**) were all collected by scuba-divers. Mussel faeces were produced by keeping blue mussels in large aerated tanks with continuous water flow and salinity and faeces collected from the bottom of the tank using siphon-tube (Paper **IV** & **V**).

Main study organism - *Mytilus edulis*

In Europe, one of the most common bivalve species is the blue mussel (*Mytilus edulis*), which occurs, often in dense masses, from Spain in south (Sanjuan et al. 1994) to Svalbard in north (Berge et al. 2005) and from high intertidal to shallow subtidal areas attached to the substrate by byssus threads (Seed and Suchanek 1992, Gosling 2003, Figure 7, Figure 8). The scientific name *Mytilus* stems from the ancient Greek word "Mutilos" used by Aristotle (384-332 BC) to describe an edible bivalve, a fact that is confirmed by the specific epithet "edulis" meaning edible. Being a common and edible species it has been heavily utilized by humans for centuries.

Apart from being economically important in farming and fishing, blue mussels are also very important components in many shallow marine communities in temperate regions (Alpine and Cloern 1992, Dame 1993, Dame 1996). In these communities, blue mussels often form extensive beds of living mussels and dead shells. These beds are important for food webs and the structural matrix of the environment. For example, mussels create microhabitats which provide shelter and refuge from predation for other organisms (e.g. Seed 1976, Suchanek 1985, Seed and Suchanek 1992). These habitats increase species richness and biodiversity (Seed and Suchanek 1992, Borthagaray and Carranza 2007, Norling and Kautsky 2007, Buschbaum et al. 2009) and affect biogeochemical processes in adjacent sediments (Ragnarsson and Raffaelli 1999).

Figure 8. Distribution of *Mytilus edulis* in European waters. Image from www.FAO.org

The mussels also contribute directly to the food web as a food source for many predators, such as crabs, starfishes, fishes, whelks and birds (see Seed and Suchanek 1992, Nagarajan et al. 2006 for references). Extending the concept of food webs to include humans, qualities such as high nutritious value, accessibility and cultural value have led to extensive exploitation of mussels as food source around the globe (Shpigel 2005, Lovatelli 2006, FAO 2011). In recent decades, technological developments have also enabled the growth of an industry based on farming of a range of invertebrates, including bivalves, on artificial structures deployed in the water column (Muir and Young 1998, Gosling 2003, Lindahl et al. 2005). Of an approximate total annual bivalve production, by farming, of 14 500 000 ton, about 15 % belong to the family of Mytilidae which compromises 376 species divided over 44 genera (WoRMS Editorial Board 2014). Their strong attachment, by byssal threads, to the substrate make blue mussels ideal for farming on artificial substrates. In the northern part of Europe the most commonly cultured bivalve species is the *M. edulis,* which together with five other species (*M. planulatus*[4], *M. coruscus*[5], *M. californianus*[6], *M. trossulus*[7] *an M. galloprovincialis*[8]) constitutes the genus Mytilus.

Mussels do not only affect the biodiversity and functioning of the benthos, as suspension feeder's but also remove large amounts of suspended particles and plankton from the water column (Prins et al. 1998, Cranford et al. 2011). Although a single individual of the species *M. edulis* is small, it can typically "process" around 3-5 litres of seawater per hour (Mohlenberg and Riisgard 1979, Riisgård et al. 2003). Thus the filtering activity affects plankton communities and often regulates the abundance, distribution and species composition of plankton communities (Asmus and Asmus 1991, Newell 2004, Maar et al. 2007). A total world harvest of about 200000 ton (FAO 2013), blue mussels transfer 1200-2600 ton N and 120-260 ton P from the sea to land every year. In Sweden the figure is more modest, with roughly 1500 ton blue mussels produced every year, removing 9-19 ton N and 0.9-1.9 ton P (SCB 2011).

Furthermore, by filtering particulate nutrients and regenerating inorganic nutrients to the system the mussels play an important role in the benthic-pelagic coupling of the nutrient cycling (Kaspar et al. 1985, Kautsky and Evans 1987, Baudinet et al. 1990, Christensen et al. 2003, Richard et al. 2006). Growth rates in *M. edulis* and other mytilid bivalves are highly variable in both space and time (Richards 1928, Coulthard 1929, Coe and Fox 1942, Bayne 1965, Seed 1969). This is partly explained by genotype and multilocus heterozygosity (Mallet et al. 1986, Gosling 1992). The majority of variation, in growth however, is environmentally determined by factors such as

[4],[8] Lamarck, J. B. 1819: Histoire naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leurs distribution, leurs classes, leurs families, leurs genres, et la citation des principales éspèces qui s'y rapportent; précédée d'une introduction. Vol. 6. Paris, "chez l'auteur, au Jardin du Roi". vi + 343 + 232 p.

[5] Gould, A. 1861 Descriptions of shells of the North Pacific Exploring Expedition. *Proceedings of the Boston Society of Natural History 7*: 400-409

[6] Conrad, T. A. 1837. Description of new marine shells, from Upper California. Collected by Thomas Nuttall, Esq. Journal of the Academy of Natural Sciences, Philadelphia 7: 227-268

[7] Gould, A. 1850 Shells from the United States Exploring Expedition. Boston Society of Natural History 3:343-345

temperature, food availability and intraspecific competition (Field 1909, Seed 1969, Incze et al. 1980, Dame 1996).

Secondary study organisms

Hediste diversicolor (Common Ragworm)

Inhabiting muddy substrata in brackish water environments throughout Europe, the polychaete *Hediste diversicolor* is a common and ecologically tolerant species in coastal and estuarine ecosystems (Smith 1977, Heip and Herman 1979, Mason 1986, Britton and Johnson 1987, Nicolaidou et al. 1988, Andersen and Kristensen 1991, Arias and Drake 1994). The species is easily collected and maintained in the laboratory and it has therefore been used extensively in experiments. The common ragworm is omnivorous and exhibits a diversity of feeding methods among other carnivory and filter feeding using an eversible pharynx and sensory appendages (Harley 1950, Wells and Dales 1951, Goerke 1966, Evans 1971, Fauchald and Jumars 1979, Rönn et al. 1988, Esselink and Zwarts 1989). It is unknown to what extent *H. diversicolor* utilizes the potential of filter feeding in nature but it has been shown that it can be considered a suspension feeder in laboratory experiments (Riisgård 1991). The construction of burrows by the ragworm increases the sediment-water interface and its ventilation of their burrows extend oxic zones into the sediment, promoting microbial and meiofaunal growth and affecting water and solute transport. This makes *H. diversicolor* an important determinant for sediment biogeochemistry and element cycling, enhancing the release of carbon dioxide and ammonium from the sediment (Kristensen and Hansen 1999, Papaspyrou et al. 2010).

Capitella capitata (Gallery worm)

Being a cosmopolitan small deposit-feeding species in marine benthic environments, *Capitella capitata* can be extremely abundant, normally ranging between several hundred and several thousand individuals per square meter but have been found in abundances of up to 22000 m^{-2}. Many *Capitella* species exhibit a high tolerance to hypoxia, hydrogen sulphide and other sediment conditions avoided by other infauna species (Henriksson 1969, Rosenberg 1976, Tsutsumi 1990, Gamenick et al. 1998). The highest abundances of *C. capitata* are often found in areas with greatly elevated organic content (Tenore 1977, Warren 1977, Tenore and Chesney 1985, Bridges et al. 1994). Like many other benthic polychaetes, *C. capitata* lives within burrows (Hill and Savage 2009) frequently reworking the sediment through their bioturbation. It is this effect of polychaete bioturbation and bioirrigation on sediment-water fluxes of nutrients and other solutes that I was interested in my studies.

Statistical analyses

A range of statistical and numerical techniques have been used to address the variety of experimental approaches used in this thesis. First, the large-scale study on effects of mussel farming on water quality was designed as an asymmetrical analysis of variance (ANOVA), with measurements before and after the establishment of farming units (e.g. "Beyond-BACI" designs, Underwood 1992, Underwood 1994). The aim was to test whether temporal changes in selected water quality variables differed in locations with and without farming units. The experiment was designed to detect small-scale effects within bays and large-scale effects among bays, using planned replication at a range of spatial and temporal scales.

Second, the experiment on growth using transplanted mussels was initially designed to estimate spatial and temporal variability in growth using a hierarchical ANOVA with water bodies, sites and times as factors in a mixed model (Paper **I**). Following analyses of variance components using restricted maximum likelihood estimations, the latter part of the experiment focussed on estimating growth in a large number of water bodies in order to empirically model and predict spatial patterns of growth (Papers **II** and **III**).

Classified, relative growth rates where modelled using classification type modelling (Paper **II**) using four different methods, GAM, Random forest, MARS and Conditional inference (e.g. Guisan and Zimmermann 2000, Elith and Leathwick 2009, for more details, see Paper **II**). These methods are all commonly used in species and habitat distribution modelling. In paper **III**, Local regression (LOESS) (e.g. Jacoby 2000) and quantile regression (e.g. Cade et al. 1999, Cade and Noon 2003) were used to evaluate relationships between environmental parameters and absolute growth rate in blue mussel. In contrast to the most frequently used modelling techniques for predicting a biological response as a function of environmental conditions, quantile regression models provide a possibility to provide forecasts of growth potential (i.e. maximum growth rather than mean) in cases when not all environmental factors are measured. By modelling the upper range of species-environmental relationships it enables the detection of limiting factors effect on species response (Cade et al. 1999, Cade and Noon 2003). Performance of predictive models (Paper **II**) was evaluated using a combination of the confusion matrix, in which the number of predicted and observed presences and absences is summarized (Fielding and Bell 1997), Accuracy (number of correctly classified presences and absences divided by the total number of observations), Sensitivity (number of correct classified presences over all observed presences), Specificity (number of correct classified absences out of all absences) and Area under curve (AUC), which is a measure of how well a parameter can distinguish between two diagnostic groups.

Third, experimental analyses of polychaete survival, growth and bioturbation in sediments affected by mussel deposits (Papers **IV** and **V**) were designed and analysed using multifactorial

ANOVA and appropriate contrasts and *a posteriori* tests according to standard procedures described in for example Underwood (1997). Prior to all analyses, assumptions related to normal homogeneity of variances and normality of residuals were explored using graphical exploratory techniques (e.g. Underwood 1997, Zuur et al. 2010). If deemed necessary, the data were transformed to fulfil these assumptions.

All statistical analyses were done using purpose-built scripts and routines in the statistical software R (R Development Core Team 2014). All GIS analyses, i.e. extraction of predictor data, geographic visualisation of predicted growth rates and summarising analyses in paper **II**, were done using ArcGIS 10.1 (ESRI 2012).

Results and discussion

Water quality effects of mussel farms

If mussel farms are to be used as a method to improve local water quality conditions in Swedish coastal waters, it is important to evaluate the size and spatial extent of its effects in a realistic setting. Thus the aim of the first experiment was to study the effect on water quality in areas which have been identified as in need of measures by recent WFD assessments. For this purpose an experiment with two farms and corresponding reference locations were set up and run during a two-year period, measuring variables such as nutrient and chlorophyll concentrations and Secchi depth. These are all indicators, which are currently used in the Swedish assessment process (HVMFS 2013:19). The expected production on the farms was 5-10 and 20-25 tons after the first and second year, respectively. After a promising start with steadily increasing amount of mussels, the experiment ran into problems (Figure 9). After reaching a stock of approximately 7 and 8 tons in Havstensfjorden and Halsefjorden respectively in December 2011, practically all mussels disappeared between January and March in both locations, presumably because of predation by eider ducks (*Somateria mollissima* L. 1758[9]). The final production of mussels was 1-1.5 tons on each farm at the end of the experiment in September 2012.

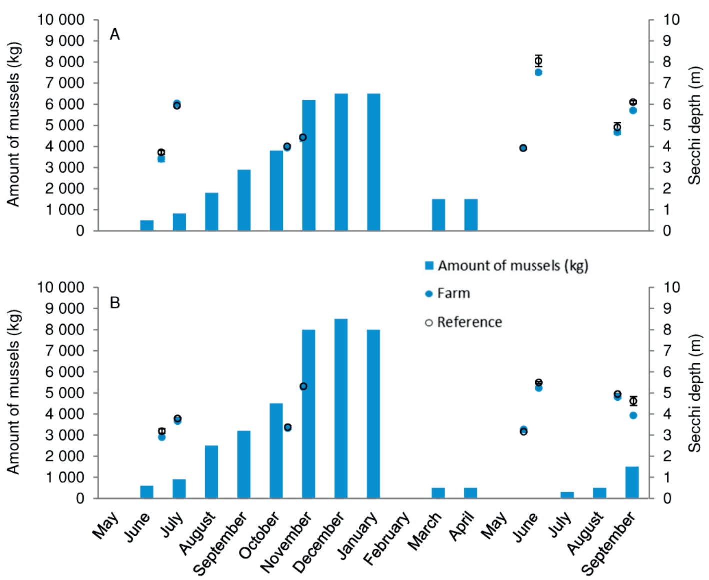

Figure 9. Estimated total amount in kg of *Mytilus edulis* at each mussel farm A) Havstensfjorden and B) Halsefjorden. Average Secchi depth (m) is shown, as circles, for farm (●) and at small-scale (10^2m) reference sites (○).

[9] Linnaeus, C. 1758 Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius: Holmiae. ii, 824 pp.

Thus, due to the reduced amount of mussels, a realistic evaluation of the local effects of mussel-farming in this area and thus its potential as a mitigation tool in eutrophicated coastal areas was not possible. Nevertheless, extensive data on water quality parameters were collected and analysed during the course of the experiment. These analyses can be used to evaluate spatial and temporal variability (Table 3), and thus form valuable information on the future design and dimensioning of experiments to evaluate effects of action programs in areas like these. Some general initial observations from these analyses are that (1) variability among replicates is substantial (15-55 %) for most parameters (except Secchi=1 %), (2) interactive components are important (i.e. differences among locations or sites are not consistent among times) and (3) spatio-temporal patterns of variability differ among water quality parameters.

Table 3. Relative size of variance components ($\frac{100*s_i^2}{\sum s_i^2}$) of selected water quality parameters. Significant components in bold. Estimation of components for a fixed factor (i.e. "Period") is not relevant. Each analysis is based on a total of 384 measurements from two water bodies, two locations per water body, four sites per location, four periods and two times per period (n=3).

Source	Secchi	Chlorophyll *a*	Phaeopigment	Nitrate	Phosphate
Water body, =WB	2.4	0.0	0.0	0.0	0.2
Location, =L(WB)	1.5	5.6	0.0	0.0	**16.9**
Site, S(L(WB))	**1.4**	0.0	0.0	0.0	0.7
Period, P (fixed)	nr	nr	nr	nr	nr
Time, =T(P)	**41.0**	0.0	**12.3**	**65.4**	5.5
WB*P	0.0	0.0	**16.8**	4.3	0.0
L(WB)*P	0.0	0.0	0.0	**8.3**	**19.9**
S(LWB))*P	0.0	0.0	4.1	0.0	0.0
WB*T(P)	9.7	10.0	3.6	**5.5**	**15.8**
L(WB)*T(P)	**34.6**	**47.2**	**3.3**	**2.0**	3.5
S(L(WB))*T(P)	**7.9**	**19.3**	4.8	0.0	**7.5**
Replicates	1.3	17.9	55.1	14.5	30.0

The reduction of mussels also demonstrates the harsh reality facing both the mussel industry and mitigation efforts based on mussel farming. This finding, in accordance with other studies (Dunér Holthuis et al. submitted manuscript), shows that production in mussel farms is not only dependent on initial larval recruitment and growth but that also other non-controllable natural processes such as mortality, due to predation and dislodgement, and repeated recruitment events are important in shaping the dynamic assemblages on mussel farms. These complex processes may limit the potential of utilizing mussels farming in mitigation efforts. As shown in this and other studies (e.g. BalticSea 2020), the amount of harvestable mussels may be quite unpredictable and thus the use of mussel farming as a method for mitigation efforts may not always be straightforward. Furthermore, the observations from this and other experiments, suggest that future mussel farming, whether for mitigation of eutrophication or purely for production of seafood, can benefit greatly from a more pro-active approach to reducing mortality in mussel farms.

Spatial patterns of mussel growth

Although, as indicated by the first study, final production in mussel farms is dependent on several factors interacting the farming process is still highly dependent on the growth of mussels. Thus information on growth rates are important for mussel farming in general and for the successful outcome of mitigation efforts where nutrient removal depends on the amount of nutrient incorporated into bivalves. However, measuring growth at all spatial and temporal levels is impossible and other methods are needed for identifying the most appropriate areas for mussel farming. One commonly used method to deal with the lack of spatial information is empirical, predictive modelling (e.g. Guisan and Zimmermann 2000, Elith and Leathwick 2009). In this approach relationships between a response (in this case growth) and a set of environmental variables are used to predict the response in areas from which no response data are available (e.g. Austin 2002, Legendre et al. 2002, Oksanen and Minchin 2002, Lindegarth et al. 2014). Any modelling effort requires some kind of spatial and temporal consistency in patterns of the response and strong relationships between the response and the environmental factors (Guisan and Zimmermann 2000, Elith and Leathwick 2009). In the first paper (Paper **I**), the potential for predicting mussel growth using an approach based on transplanted mussels was investigated. This approach has previously been successfully used in other monitoring practises (Haynes et al. 1995, Lorini et al. 1998, Odzak et al. 2000, Devier et al. 2005). Here the spatial variability in growth of soft tissue and shell characteristics and the temporally consistency of the observed patterns were successfully investigated. Strong temporal and scale-dependent spatial variability in growth were found (Paper **I, II** and **III**, Figure 10).

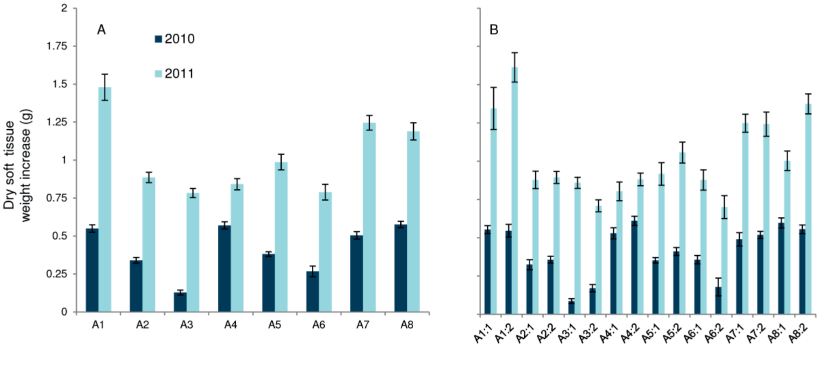

Figure 10. Temporal and spatial variability in soft tissue growth of *Mytilus edulis* in (A) 8 areas and (B) 16 sites; 2 within each area. Error bars represent standard error.

In accordance with the results from several other studies (Hilbish 1986, Mallet and Carver 1993, Handå et al. 2011) our results also suggested that the growth of soft tissue was uncoupled from the growth of the shell. While patterns for growth in shell length, the most commonly used measurement of bivalves size, were complex and largely temporally inconsistent, growth in soft tissue was qualitatively consistent among years at the scale of km (Figure 11, Paper **I**). The findings also suggests that processes affecting the whole coastal area cause substantial differences in growth among years, but that factors varying at the scale of km create strong and persistent spatial patterns of growth, with a potential doubling of productivity by identifying the most suitable locations. Hence there is a potential of doubling the nutrient removal in mitigation effort using mussel farms by selecting these locations. The findings of this paper (**I**) provides a basis for further development of predictive models (Paper **II** & **III**) and mapping (Paper **II**) of soft tissue growth in coastal areas with causes of observed patterns, consequences for mussel farming as a tool for mitigating eutrophication, aspects of precision of modelling and sampling of mussel growth discussed in the papers.

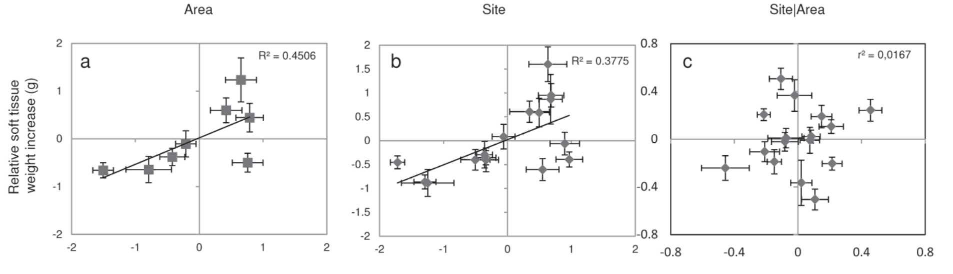

Figure 11. Temporal correlations between spatial patterns of growth in soft tissue of the common bivalve *Mytilus edulis* at two different scales a) area, b) site and c) with the effect of area removed from site effect.

After evaluating the temporal consistency of spatial growth pattern in *M. edulis* and measuring growth at more than 140 sites (Figure 12, Paper **II, III**), predictive capacity of relative mussel growth were further evaluated using four modelling techniques and classification models (Paper **II**). Quantile regression was used for evaluating the potential for modelling continuous growth (Paper **III**). In doing so we not only evaluated the predictive capacity but also how different techniques and classification schemes influence the performance of predictive models and therefore their potential use in planning mussel farming activities (Paper **II**). External validation (i.e. how well the model predicts new data) showed that random forest models performed better than other methods and was the only one of the four techniques evaluated that produced significant models. The same patterns existed independently of classification schemes.

Random forest models based on classification into 3 classes produced the best balance between models with few classes that had higher accuracy and sensitivity with the increase in Accuracy/no information criteria with increased complexity of the models (Paper **II**, Figure 13). Using a classification scheme of equal sized classes, models predicted growth 50-80 % more accurately than randomly assigning growth class (Figure 13, Paper **II**). These models are therefore a better option for the use in planning processes than guessing the growth and thus providing a valuable tool in MSP. The models also provide a possibility for production of comprehensive growth maps for the use in management and planning of the marine environment. Even though the modelling was relatively successful, it is clear that the scope for improving accuracy and resolution is substantial with aspects regarding predictor data are most likely to improve models further.

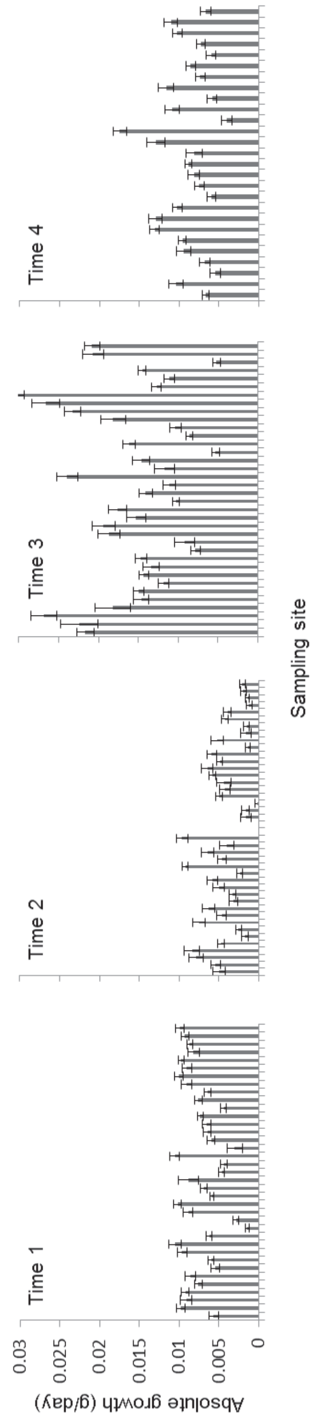

Figure 2. Measured average daily growth of soft tissue (g) of *Mytilus edulis* during the four sampling periods. A total of 144 locations was sampled along the Swedish west coast. Growth values are the average of 15 mussels and the error bars represent standard error.

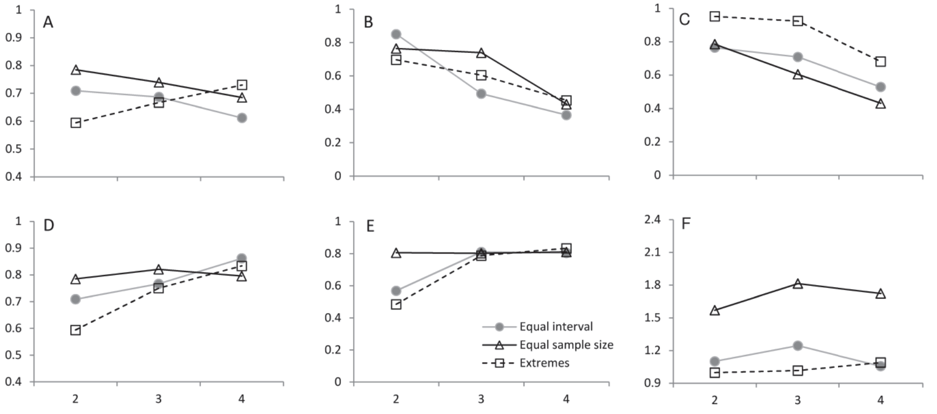

Figure 13. Performance of random forest models of prediction of mussel growth using six criteria A) M-AUC, B) Sensitivity, C) Accuracy, D) AUC between extremes, E) Specificity and F) Accuracy/no information criteria.

Information on the influence of environmental factors on the spatial patterns of organisms is critical in management (Wang et al. 2003). We investigated the importance of selected environmental factors for spatial patterns of soft-tissue growth of mussels. A factor traditionally considered important for growth of marine organisms is salinity (Bayne 1976, Almada-Villela 1984, Hiebenthal et al. 2012). For classification type models (Paper **II**) we found an optimal salinity span between 26 and 29 while when evaluating predictive models of continuous growth (Paper **III**) no such pattern was found. Food supply (Page and Hubbard 1987), for which chlorophyll *a* is considered the best proxy (Rosland et al. 2009, Thomas et al. 2011) is generally considered as an important factor regulating growth of bivalves. However, we were only able to find a weak negative (Paper **II**) or no influence at all (Paper **III**) on mussel growth. Exposure were found to be less important but instead played an important role for generating homogenous nodes in the predictive models (Paper **II**) while in predicting continuous growth, growth seemed to be higher at intermediate exposure (Paper **III**). These results partly contradict other studies which have shown a strong influence of exposure on the growth (Blanchette et al. 2007, Garner and Litvaitis 2013), but also support earlier findings that growth rates decrease when exposure becomes too high (McQuaid and Lindsay 2000, Steffani and Branch 2003). By providing important knowledge on processes governing the growth of bivalves, these papers (**II** & **III**) contribute essential information for planning and management of mussel farming and natural stocks both from the aspect of increasing seafood production but more importantly in a sustainable way and for the use of mussels in mitigation efforts.

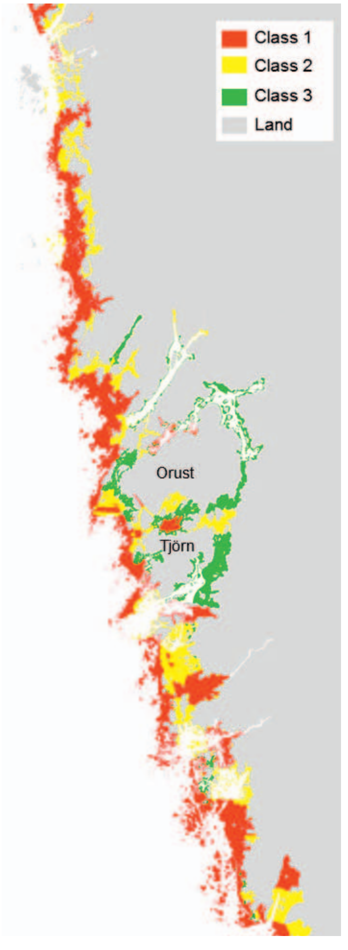

Figure 3. Predicted growth of *Mytilus edulis* along the Swedish west coast based on a 3 class random forest model developed in paper **II**. Using a "traffic light" symbolism the highest growth is found in green areas while read areas are least suitable for growth.

With comprehensive data of environmental factors seldom available for large areas, we also evaluated (in Paper **II**) the possibility of using modelled data, such as salinity and temperature as explanatory variables in predictive models. We investigated how well modelled data reflected the observed data on water quality and the temporal consistency of the spatial pattern of the factors true measurements (Appendix in Paper **II**). These analyses showed that modelled data were correlated to observed data (but variable among levels of spatial and temporal aggregation), and thus there are rational arguments for testing modelled environmental data as proxies for measurements of explanatory factors in predictive models. However, relationships between environmental variables and biological processes (e.g. mussel growth) are rarely straightforward but are often complex and may vary within both environmental variables and response level. By using local regression and quantile regression I was able to evaluate patterns at various levels of response and how these relationships change over the range of different environmental variables. The strongest patterns were found for oxygen concentration, for which increasing concentrations had a negative effect on all growth levels. But the effect increased with higher levels of growth (Paper **III**). In using methods that allow evaluation of such relationships at other scale than mean or median response, this third paper provide important information on the complexity of the environmental control limiting our ability to fully understand and model environmental-growth relationship and thus contribute to the development of tools for planning and management of bivalve farming.

The final part of paper **II** dealt with the utilization of a developed model for prediction and mapping of mussel growth in 3 classes. A map (Figure 14) of predicted growth was created and its concurrence with existing permissions for farm sites of *M. edulis* was evaluated. The prediction revealed a clear pattern with higher growth in bays and estuaries while reduced growth is found in areas with highly variable environment (e.g. close to large river mouths) and in the outer, more exposed, areas (Figure 14). In total, 15.2 % of the area is, according to this prediction, best in terms of high mussel growth and thus most suitable farming of *M. edulis* while in about half (52.9 %) of the area growth is slower and thus these areas should be considered for farming only if the "better" alternatives are unavailable. A comparison with the existing farm site permissions along the west coast showed that half (47 %) of the sites were in fact located inside the area for which models predict the highest growth and only 32 % in areas with the lowest growth (Paper **III**). Thus a predominance of permissions in the areas having a predicted high growth already exists. Using maps of areas identified by Swedish assessments of ecological status (according to WFD) and comparing these with that predicted growth, we can observe a large overlap between areas of predicted highest growth and areas most in need of restoration efforts. This observation suggests that the scope for water quality improvement by mussel farming is favourable in these areas and further demonstrates the potential of results like theses (Paper **II**) as practical tools for the planning authorities and the aquaculture industry.

Mitigation of negative effects of mussel farms

Any successful application of mussel farming for mitigation of eutrophicated coastal areas requires knowledge, not only about growth (Paper **I**-**III**), processes influencing growth (Paper **II**, **III**) and the effect on the water quality, but also about how to deal with the known negative effects of farming practices on sediments. In Paper **IV** and **V** a method using burrowing polychaetes for bioturbation and bioirrigation in organically enriched sediments was evaluated. In Paper **IV**, we investigated the survival and growth of *Hediste diversicolor* in sediments were the organic matter was dominated by mussel faeces compared to a naturally occurring mix of organic matter. We also tested if their burrowing activities had different effects on fluxes of oxygen and nutrient (N and Si) among sediments with different sources of organic matter. This was also done to evaluate how well the polychaetes could utilize mussel faeces as a food-resource. In Paper **V**, we focused on how the nutrient (N and P) and oxygen fluxes varied among species and densities of polychaetes. For utilization of polychaetes or other bioturbating species in mitigation efforts of sediments influenced by mussel farms it is essential that the species used can survive and thrive in these conditions. We showed (Paper **IV**) that the survival of *H. diversicolor* was not significantly influenced by mussel faeces but that, over a period of ten days, the polychaete grew substantially better (17-19 %) in sediments containing mussel faeces than without (3 %), i.e. a six-fold increase in growth (Figure 15).

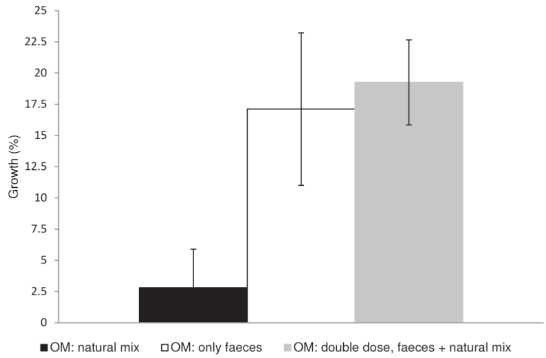

Figure 15. Growth of *Hediste diversicolor* in % of wet weight, under different feeding regimes, over a ten-day period. Error bars = SE

The effect of *H. diversicolor* on chemical fluxes varied among nutrient specimen and type of organic matter. Sediment oxygen consumption (SOC) was highest in sediments with high levels of organic matter but there was also a difference among the type of organic matter with increased SOC in sediments containing mussel faeces. With fluxes within naturally occurring levels and increased growth of *H. diversicolor* the fourth paper suggests that there is a potential use of *H. diversicolor* and its bioturbating activities in mitigation efforts of sediments affected by mussel farms and thus worth further studies.

Biodeposition of organic matter from farms increases sediment oxygen demand and changes the sediments biochemical properties (Grenz et al. 1990, Christensen et al. 2003). The effect of the two species *Capitella capitata* and *H. diversicolor* on the degradation of organic matter from mussel farms and nutrient fluxes across sediment surface were evaluated with a series of field and laboratory experiments (Paper **V**). There was a clear effect of polychaete addition on the degradation of organic matter resulting in increased sediment oxygen consumption (Figure 16, Table 4, and Paper **V**) and this effect was immediate. In accordance with studies that have shown that the effects on bioturbation and degradation rates vary among species (Francois et al. 2002, Mermillod-Blondin et al. 2004, Quintana et al. 2007), we found a stronger influence of *H. diversicolor* than the much smaller *C. capitata* not only on oxygen but also on fluxes of various nutrients across the sediment-water surface (Paper **V**). Both species affected nitrogen fluxes (NH_4^+ and NO_3^-) immediately.

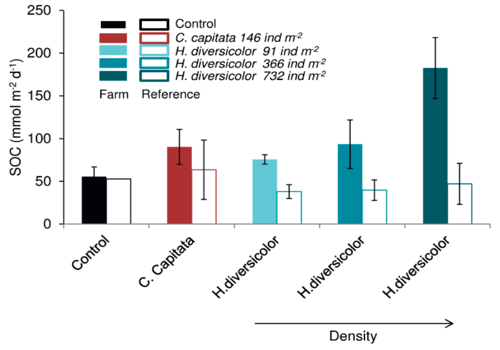

Figure 16. Oxygen consumption in farm- and reference sediments and the influence of *Capitella capitata* and *Hediste diversicolor.*

Investigating the effects of addition of organic matter and *H. diversicolor* on sediment oxygen consumption over time, we concluded that sediments with fauna recovered faster from organic enrichment and that fauna decreased the immediate effect of organic matter addition (Figure 17).

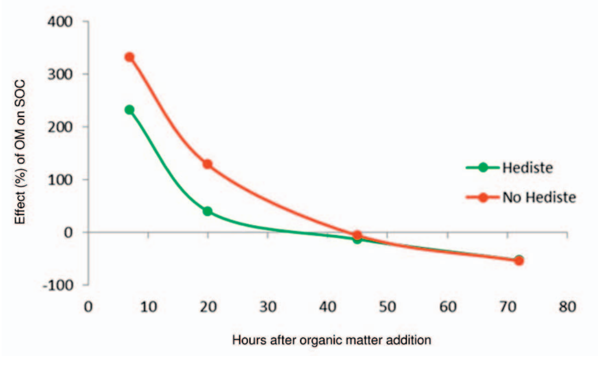

Figure 17. Effect of addition of organic matter on the sediment oxygen consumption in the presence and absence of *Hediste diversicolor*

With both polychaete respiration and polychaete stimulation of microbial processes contributing to the increased oxygen consumption (Banta et al. 1999, Heilskov and Holmer 2003) we used literature values of polychaete respiration to calculate the contribution of each process. From these estimates we found that the increased SOC to a small extent could be explained by polychaete respiration and that the major contribution was through stimulation of microbial processes by polychaete activities (Paper **V**). We also showed that the effect increased with increased density of polychaetes with the highest density having about three times higher stimulation than the intermediate density and six times stronger than the lowest density.

Table 4. Sediment oxygen consumption (SOC), the effect of *Hediste diversicolor* and organic matter on SOC in field experiment.

Station	Density of *H. diversicolor* (m^{-2})	SOC (mmol m^{-2} d^{-1})	Stimulation of SOC by fauna (%)	Effect of organic matter (%)
Reference	0	52.8±n.a.		
	91	38.0±13.9	-28	
	370	39.7±20.8	-25	
	730	47.1±34.0	-16	
Farm	0	55.0±16.4		+5
	91	75.7±9.6	+36	+99
	370	93.4±49.3	+68	+135
	730	182.6±61.8	+229	+314

Overall, our results (Paper **IV** and **V**) support the ideas that polychaetes can be used as a tool for controlling and reducing the negative effects of mussel farming on the biogeochemical processes in the sediment. The larger of the species, *H. diversicolor,* showed most promising. The decomposition of organic matter from mussels was enhanced to a larger extent than have been observed for other types of organic matter (Kinoshita et al. 2008) and at the same time oxidizing the sediment and reducing the accumulation of sulphides. *Hediste diversicolor* is thus a strong candidate for remediation of mussel farm sediments and calculation suggests that the highest density studied could stimulate degradation of up to 80% of the organic matter reaching the sediment surface under a mussel farm (Paper **V**). Increasing polychaete density would probably further enhance degradation. Assuming a linear relationship between polychaete density and stimulation of degradation, calculations suggests that a density of 1000-5000 ind. m^{-2} would be necessary for a complete degradation of the daily biodeposits and hence prevent accumulation of organic matter under farms. These densities are within the same magnitude as naturally occurring densities (Mason 1986, Scaps 2002 and references wherein), However, the accumulation of mussel shells, which is known to occur in high numbers, are not remediated by the polychaetes and still remain a potential problem to solve.

In summary, our results support the idea of using mussel farming as a mitigation effort of eutrophicated areas. By using the appropriate methods for planning, management and site selection, optimal results may be achieved, although the nutrient removal potential, which is correlated to the growth rate of the mussels, varies among places. The potential for nutrient removal is up to twice as high in the most favourable areas compared to less suitable areas.

Conclusions and future perspectives

The research in this thesis spans over a large diversity of issues related to mussel farming and its use for mitigation of eutrophication and seafood production in Swedish coastal waters. In all of the investigated topics, there has been a strong emphasis on conducting large-scale field experiments under conditions that are realistic to a potential farming situation. This general approach has in some instances caused some practical problems, but overall the thesis has successfully given insight into some of the most important questions and challenges for the development of mussel-farming for local reduction of eutrophication effects in coastal areas.

Restoration of coastal waters

The experiment aimed at investigating effects on water quality and benthic conditions based on the establishment of full-scale mussel farms in two eutrophicated water bodies on the west coast of Sweden. This proved more difficult than anticipated. Although ultimately not successful in the attempts to evaluate the effects of mussel farming on water quality the first of the three main experiments still contributed with some important conclusions for the utilisation of mussel farming in mitigation efforts. Mitigation of eutrophicated areas using mussel farming might not be straightforward and processes such as larval recruitment, growth and mortality are important in shaping the dynamic assemblages on mussel farms. Without a clear and simple relationship between growth and final production, the mitigative effect of mussel farming is unpredictable. This potentially limits its use in restoration programs. However, the extensive collection of data on a number of spatial and temporal scales provide a possibility for further evaluation of spatial and temporal variability of indicators used in the current Swedish assessment process thus information for future design and dimensioning of experiments to evaluate effects of restoration measures.

Maritime spatial planning

Maritime spatial planning has been highlighted as a promising tool in the regulation and protection of the marine environment. It offers an integrated approach to manage the multiple and potentially conflicting uses of the environment. This importance if reflected by a number of national and intergovernmental initiatives including “Roadmap for maritime spatial planning” (COM 2008) and in July this year EU adopted the directive 2014/89/EU establishing a framework for maritime spatial planning (European Commission 2014). From an applied perspective, our results show that the approach based on transplanted mussels coupled to empirical modelling is a feasible approach for obtaining scientifically based spatial information on ecological goods and services affected by a complex set of factors. With the existence of consistency in the patterns of soft tissue growth, there is a potential to model and predict mussel growth. This offers opportunities for the use of predictive modelling and mapping of mussel growth in scientifically based planning of aquaculture. The collected data indicate that, by selecting the most favourable areas the productivity of mussel farms can potentially be double compared to least favourable areas and prediction suggest that low, medium and high rates of growth can be expected in 53, 32 and 15 % of the modelled areas respectively. From a research perspective, the results give insights into modelling and processes related to mussel growth. Temporal consistency of spatial patterns is one of the fundamental requirements for predictive modelling, we showed that growth in soft tissue but not in shell length fulfils this. Thus the results provide a basis for further development of predictive modelling of mussel growth in coastal areas. By using different modelling techniques we were able to provide information on the complexity of the environmental control limiting our ability to understand and model environmental relationships, including the growth of mussels, and shown that the key to improving the predictive power of models is the quality of predictors, not the modelling techniques. The studies also demonstrates the potential of quantile regression in marine ecological studies, since this method has the ability to handle cases when a biological response is affected by multiple, limiting and interacting factors, being one of its advantages.

Mitigation of negative effects

With impacts on the sediment environment by biodeposits being the main concern for the sustainability of mussel farming, developing methods that can reduce these potentially negative impacts are sought after. The studies on the potential of bioturbating polychaetes as a mitigation tool in sediments impacted by mussel farms showed that there is a high potential for the use of *Hediste diversicolor* in mitigation efforts. Sediments inhabited by *H. diversicolor* have a higher assimilative capacity of organic matter compared with sediments devoid of benthic fauna. This effect of burrowing polychaetes on the sediment is mainly and indirectly driven by increased microbial activity, likely due to enlarged surface between oxic and anoxic sediments. Not only does *H. diversicolor* increase the assimilatory capacity of the sediment through their burrowing activities, it can also feed directly on the mussel faeces and the result show that the faeces of *Mytilus edulis* provide a better food source for *H. diversicolor* when compared with natural organic material with faster growth recorded in the presence of mussel faeces. From an economical side of non-food mussel farming, this provides a new opportunity with polychaetes like *H. diversicolor* being highly sought after by recreational anglers. Thus the studies support the idea that polychaetes can mitigate negative effects on benthic biogeochemical processes beneath mussel farms. However, technological developments are needed to allow the approach to be used in practice.

The future

This thesis has contributed with important knowledge on 1) temporal consistency of spatial pattern in growth of the blue mussel, 2) the potential to predict growth, 3) the use of predictive models in maritime spatial planning and other planning processes and finally 4) the possibility of using bioturbating organisms to reduce (or fully mitigate) the effects of biodeposition from farms on the sediment communities. Even though this thesis has brought new insight into the possibility of using mussel farming as a tool for mitigation of eutrophicated coastal areas there is still some obstacles to climb before this method becomes a reality. One of the major hinders today is the economical issue – it is too expensive to farm non-food mussels and governmental subsidies are considered necessary to make environmental mussel farming economically sustainable. There is also a need for innovations on the market side on how to utilize the non-food mussels. Mussel meal production as a substitute for fishmeal in animal feed is a promising alternative, which is being developed and tested in Sweden today, although this is not yet cost-effective. Also more studies on the interactions between environmental factors that influence the growth, survival and productivity of *M. edulis,* as well as further investigations into what effects mussel farming really has on the pelagic system and its biological and chemical processes, are needed to establish that mussel farming is a realistic and functioning method for remediation of eutrophicated coastal areas.

Glossary

Aquaculture	Active cultivation of marine and freshwater aquatic organisms such as fish, crustaceans, molluscs and plants under controlled conditions
Biodeposit	Biological produced substances that settles on the bottom, e.g. faeces, pseudofaeces, dead animals etc.
Bioirrigation	The process of benthic organisms flushing their burrows with overlying water. The exchange of dissolved elements between the pore water and the overlying water is an important biogeochemical process in the oceans
Bioturbation	Mixing of sediment by living organisms, especially by burrowing or boring. Aids the penetration of air and water and loosens sediment to promote processes that changes in the texture of the sediment
Ecosystem engineer	An organism that directly or indirectly controls the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials
Ecosystem function	Fundamental processes of natural systems, including nutrient cycling and energy fluxes. Processes that constitutes essential components of ecosystems
Ecosystem goods	Material products that are obtained from natural systems for human use
Ecosystem service	"The conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life"
Eutrophication	"Enhanced primary production due to excess supply of nutrient from human activities, independent of the natural productivity level for the area in question"
Foundation species	Species that has a strong role in structuring a community
Mitigation	Elimination or reduction of human impact on the environment
Remediation	The act or process of correcting a fault or deficiency in the environment
Restoration	Returning an aquatic environment to its original, undisturbed state

Abbreviations

AUC	Area under receiver operating characteristic curve
DSC	Dansk Skaldyrcenter
EB-MSM	Ecosystem-based marine spatial management
EEA	European Environmental Agency
EMB	Ecosystem based management
ESF	Ecosystem service framework
GAM	Generalized additive model
GIS	Geographic information system
LOESS	Local Regression
MARS	Multivariate adaptive regression splines
MSP	Maritime spatial planning
OM	Organic Matter
SOC	Sediment oxygen consumption
WFD	Water framework directive

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