Restoration and management of eelgrass (*Zostera marina*) on the west coast of Sweden

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Doctoral Thesis

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Faculty of Science
2016

Cover illustration: Louise Eriander

ISBN 978-91-628-9904-2 (PRINT)
ISBN 978-91-628-9905-9 (PDF)
Available at http://hdl.handle.net/2077/47969

Printed in Gothenburg, Sweden 2016
By Ineko AB

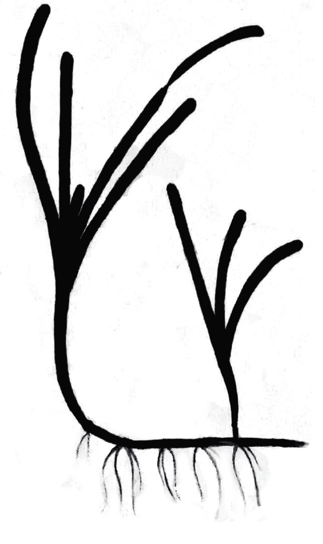
"In the end, we will conserve only what we love,
we will love only what we understand,
and we will understand only what we are taught."

BABA DIOUM

ABSTRACT

Since the 1980s over 60% of eelgrass (*Zostera marina*) habitats have been lost from the Swedish NW coast, resulting in significant losses of the valuable ecosystem services provided by these habitats. The eelgrass loss has largely been attributed to the effects of eutrophication and overfishing, but coastal development could constitute an additional threat, since eelgrass often reside in shallow sheltered areas, where pressure from exploitation is high. In response to the historical losses, restoration of eelgrass ecosystems is being proposed by national agencies to assist recovery, but methods have not been available for high latitude environments, where the short growth season, ice-formation in the winter and muddy, organic-rich sediments present unique challenges for restoration. The overall aim of this thesis was to 1) develop methods suitable for large-scale restoration of eelgrass in high latitude, Scandinavian waters, 2) increase our understanding of environmental conditions that promote or impede eelgrass growth along the NW coast of Sweden and 3) assess the local and large-scale effect of shading by docks and marinas on eelgrass and identify problems with the current management, which allows for continued exploitation along the Swedish coast. The results presented in this thesis demonstrate that shading from docks and marinas constitutes a significant threat to the already decimated coverage of eelgrass along the NW coast of Sweden. In total, 480 ha of eelgrass habitat was estimated to be negatively affected, corresponding to more than 7% of the present areal coverage of eelgrass in the region. Results also show that eelgrass habitats are rarely assessed or considered within decisions for dock construction, and 80% of applications in areas with eelgrass were approved. Furthermore, the presence of protected areas only marginally reduces the number of approved cases. In order to stop this gradual deterioration of eelgrass habitats, and to achieve both national and international goals on environmental status, there is a need to revise management practice and include a large-scale perspective when assessing the effects of small-scale development. Results from field and laboratory studies demonstrate that eelgrass shoots have a strong capacity to acclimatize when transplanted between different depth, light- and hydrodynamic exposure conditions, through adjustments in morphology, pigmentation and growth strategy. They further show that transplants have the ability to store carbohydrates at light levels down to 11% of the surface irradiance (SI), but that light levels above 18-20% of SI are needed to ensure positive growth, and that even greater levels likely are required to ensure high vegetative reproduction and winter survival at sites targeted for restoration. Results from field studies in the southern parts of the NW coast demonstrate that water quality conditions have deteriorated in many areas where large historical meadows have been lost (1-2 m reduction in the maximum depth distribution of eelgrass). Eelgrass recovery and restoration in these areas are presently not possibly due to sediment resuspension and bottom drifting algal mats, suggesting that a local regime shift has occurred after the loss of eelgrass. It is therefore critical that management efforts focus on the protection of the remaining eelgrass beds in these areas, since losses may be irreversible over the foreseeable future and affect the water quality negatively also in neighbouring areas. The results from these studies further demonstrate that careful site selection is imperative for successful eelgrass restoration along the Swedish NW coast, where light attenuation, sediment grain size and the presence of drifting algal mats are key variables to consider. Results from method assessments for eelgrass restoration suggest that both shoot- and seed methods can be successfully used to restore eelgrass at this latitude and that high vegetative reproduction occur in shallow areas, where shoot densities can increase with >500% over 2 growth seasons. In deeper areas slow vegetative reproduction, a shorter growth season and high winter losses make restoration difficult. The high losses of seeds, particularity in shallow areas, as a result of transport by currents, bioturbation and predation, make restoration with seeds inefficient. The recommended method for large-scale restoration of eelgrass along the Swedish NW coast includes transplantation of single unanchored shoots without sediment from the donor meadow.

Keywords: Eelgrass | Restoration | Management | High latitude | Method assessment | Environmental requirements | Acclimatization | Carbohydrate storage | Vegetative reproduction | Seed loss | Coastal development | Legal challenges



POPULÄRVETENSKAPLIG SAMMANFATTNING

Viktiga marina miljöer världen över har gått förlorade eller försämrats som ett resultat av människans ökade nyttjande av haven och dess resurser. Sjögräsängar är ett exempel på en sådan miljö, där ca 29% av den globala utbredningen har försvunnit det senaste århundradet och där de fortsatta årliga förlusterna gör att sjögräsängar idag anses vara ett av de mest hotade ekosystemen i världen. Sjögräs tillhör gruppen gömfröiga växter och utgörs av ca 60 olika arter globalt, och återfinns längs med alla världens kontinenter, utom Antarktis. Denna grupp av växter är relativt ung och till skillnad från alger så härstammar sjögräs från landväxter som anpassat sig till att leva under marina förhållanden för runt 100 miljoner år sedan.

Ålgräs (*Zostera marina*) är en av de mest spridda arterna av sjögräs globalt och den vanligaste sjögräsarten i svenska vatten. På den svenska västkusten återfinns ålgräs vanligtvis växande i grunda vikar (0,5–5 m djup) på sand- eller lerbotten, med låg till måttlig vågexponering. Genom sin förmåga att växa på mjukbottnar tillför ålgräset en fysisk struktur till dessa grunda kustmiljöer, vilket höjer artrikedomen i området. Ålgräsängar utgör unika habitat som bidrar med en lång rad viktiga ekosystemfunktioner, varav vissa är värdefulla för oss människor. De fungerar som en viktig födo- och uppväxtplats för en lång rad organismer, däribland ett stort antal fisk- och kräftdjursarter. Ålgräset bidrar också till att skapa klarare vatten lokalt, genom att plantornas bladverk saktar ner vattenrörelser och gör att partiklar i vattnet lättare sjunker till botten och genom att de med sina rötter och jordstammar (rhizom) stabiliserar botten, vilket hindrar sediment från att virvla upp. Ålgräsängar är också viktiga ur ett globalt perspektiv då de minskar övergödning och växthuseffekten genom att de effektivt tar upp och lagrar in stora mängder näring och kol i sedimentbotten.

Längs den svenska Bohuskusten har mer än 60% av allt ålgräs försvunnit sedan 1980-talet. På grund av dessa växters höga ljuskrav (ca 20% av ljuset vid ytan) så är de känsliga för mänskliga aktiviteter som försämrar vattenkvalitén eller orsakar skuggning av botten och de stora förlusterna som skett längs Bohuskusten anses främst bero på negativa effekter av övergödning och överfiske av stora rovfiskar. En annan orsak till förluster av ålgräs är kustexploatering, där byggnationer i vatten kan orsaka direkta effekter genom att ängar förstörs, eller indirekta effekter genom att de utgör en permanent skuggning av botten. Eftersom ålgräs ofta växer i grunda skyddade miljöer, där trycket från exploatering är högt, befarades kustexploatering kunna utgöra betydande negativa effekter på den redan decimerade utbredningen av ålgräs längs med kusten. När arbetet med denna avhandling påbörjades var effekter av småskalig kustexploatering (bryggor och små marinor) på ålgräs dåligt studerade i svenska vatten.

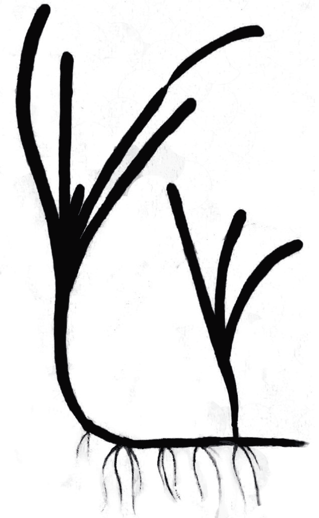
Förutom behovet av att skydda återstående ålgräsängar så har många länder börjat undersöka möjligheterna till att hjälpa återhämtningen av historiska förluster genom att restaurera ålgräsängar. I USA har ålgräsrestaurering en lång historia av att användas både för att återfå historiska förluster men också i kompensationssyfte vid planerade aktiviteter som kan komma att påverka ålgräsängar negativt. Restaurering av ålgräs har på senare år utförts i en rad länder både i förvaltningssyfte och i experimentella studier och börjar idag anses vara ett funktionellt och viktigt verktyg för att återfå förlorade ängar.

I Sverige har myndigheter på senare år visat ett växande intresse för restaurering av ålgräs, vilket skulle fungera som ett viktigt steg för att uppnå de krav som ställs från EU på uppnående av som minst en 'god ekologisk status' i våra kustområden. När studierna i denna avhandling påbörjades var restaurering av ålgräs dåligt studerat vid höga nordliga latituder och utvärderingar av lämpliga metoder samt möjligheterna till att restaurera historiska bestånd saknades. I denna avhandling presenteras resultat från fältstudier där metoder för ålgräsrestaurering undersökts och där möjligheter och svårigheter vid restaurering har utvärderats. Vidare presenteras resultat från laboratorieförsök, där ålgräsets förmåga att anpassa sig till olika ljusnivåer har studerats, liksom ljusets påverkan på tillväxt och inlagring av kolhydrater. Dessutom presenteras resultaten från interdisciplinära studier där de ekologiska effekterna av- och juridiska orsakerna bakom småskalig kustexploatering på ålgräsbottnar har studerats. Det övergripande syftet med denna avhandlingen har varit att förbättra förvaltningen och utveckla metoder lämpade för storskalig restaurering av ålgräs längs den svenska västkusten.

Resultaten från **papper I** visar att småskalig kustexploatering längs Bohuskusten har en negativ påverkan på en betydande areal (480 hektar) av potentiell ålgräsbotten, vilken utgör över 7% av arealen hos den nuvarande ålgräsutbredningen längs kusten. Den lokala påverkan på ålgräset var starkt beroende av designen på bryggan. Flytbryggor orsakade alltid en total förlust av ålgrässkott under bryggan samt 63% lägre täckning av skott generellt, jämfört med pålade bryggor. Studien av beslut avseende byggande av bryggor (strandskyddsdispens och anmälan av vattenverksamhet), visade att flytbryggor var den vanligaste typen av bryggor i ansökningar, samt den vanligaste typen av beviljade nya bryggor. Studien visade även att ålgräs mycket sällan nämns i ansökningar; endast i 12% av alla beslut från områden där ålgräs var bekräftat enligt satellitbildsanalys. Även då ålgräsförekomsten var bekräftad, hade denna mycket liten påverkan på beslutet och totalt sett blev 80% av alla ansökningar i ålgräsområden godkända. Förekomsten inom särskilt legalt skydd av områden (genom naturreservat, naturskyddsområde och Natura 2000-område) minskade antalet godkända ansökningar, men bryggansökningar som låg både inom naturskydd samt hade ålgräs blev fortfarande godkända i 69% av alla fall. Denna studie visar därför att ålgräs i dagsläget har ett mycket svagt faktiskt skydd gentemot det ökade trycket från exploatering längs kusten. Problemet med dagens tillämpning av lagstiftning som rör småskalig exploatering tycks ligga i att varje enskilt ärende anses utgöra ett mycket litet intrång i dessa grunda kustmiljöer. Detta är problematiskt då studien visar att den sammanlagda effekten av bryggors påverkan är betydande, vilket inte överensstämmer med de icke-försämringskrav för marina miljöer som EU satt upp. För att hindra ytterligare förluster av ålgräsbestånden längs med Sveriges västkust finns därför ett behov av restriktioner för bryggbyggnationer som kan komma att påverka ålgräset negativt. Detta skulle kunna åstadkommas genom tydliga krav på att förekomst av ålgräs måste beskrivas i ansökningar om dispens från strandskydd och anmälan om vattenverksamhet, samt genom att ålgräsförekomst får en större betydelse i bedömningsprocessen av ansökningar. Det finns också ett behov av att se dessa enskilda intrång i ålgräsmiljöer utifrån ett större perspektiv, där skadan exempelvis sätts i relation till den lokala förekomsten av ålgräs i området. Vidare bör anläggande av flytbryggor över ålgräsbottnar undvikas. För att kunna föreskriva tydliga riktlinjer för förvaltare som fattar beslut angående byggnationer längs kusten behövs ytterligare studier där det undersöks hur de negativa skuggningseffekterna från bryggor kan minskas.

Resultaten från **papper II**, **III**, **IV** och **V** visar att valet av en lämplig restaureringslokal är avgörande för att ålgräsrestaurering skall lyckas och att detta bör ske genom testplantering samt mätning och övervakning av miljöförhållanden vid lokalen. Generellt tyder resultaten från dessa studier på att ljusförhållanden, sedimentets kornstorlek samt närvaron av drivande algmattor är viktiga variabler som påverkar överlevnaden och tillväxten av ålgräs, medan sedimentets organiska halt och sulfidinnehåll tycks ha en mindre effekt på ålgräsets överlevnad i de miljöer som undersökts. Resultaten visar även att skotten har förmåga att lagra in kolhydrater vid låga ljusnivåer (11% av ljuset vid ytan) men att ljusförhållandena på lokalen bör överstiga 18-20% av ljuset vid ytan för att möjliggöra ålgräsöverlevnad. För att säkerställa hög tillväxt samt flerårig överlevnad kan dock ännu högre ljusnivåer (>30% av ljuset vid ytan) krävas. Detta gör att restaurering på djupa lokaler samt lokaler med försämrad vattenkvalité försvåras, då tillväxthastigheten samt längden på tillväxtsäsongen minskar och stora förluster av skott sker över vintern. Dessutom påvisar studierna att det kan vara mycket svårt att restaurera en förlorad ålgräsäng, då förlusten av de positiva effekter som ålgräset har på vattenkvalitén kan leda till stora förändringar i miljön och ett tillstånd som domineras av lokal uppgrumling av sediment och drivande algmattor, vilket hindrar naturlig återhämtning samt försök till restaurering av ålgräs. Det är därför viktigt att påpeka att restaurering av ålgräs inte alltid är möjligt, vilket understryker vikten av att skydda kvarvarande ängar, särskilt i områden där stora förluster redan har skett.

Resultaten från **papper IV** och **V** visar att både ålgrässkott och frön med framgång kan användas vid restaurering av ålgräs längs den svenska västkusten och att hög tillväxt kan ske i grunda (1-3 m djup) områden. Vidare visar de att ålgrässkott har en stark förmåga att acklimatisera sig när de flyttas mellan olika miljöförhållanden (djup-, ljus- och vågexponeringsförhållanden) genom förändringar i form, tillväxtstrategi och pigmentering. Detta betyder att det växtmaterial som används vid restaurering inte behöver matcha miljöförhållandena på lokalen där planteringen skall ske. Restaurering med frömetoder kan i dagsläget inte rekommenderas för användning vid storskalig restaurering av ålgräs, då förlusterna av frön är stora samt fröskottsöverlevnaden låg i vissa områden. Resultaten av olika metoder för att plantera frön visar att de stora förlusterna sannolikt beror på en kombination av biologiska och fysiska faktorer, där bortförsel av frön med strömmar, nedgrävning eller konsumtion orsakad av djur är de viktigaste orsakerna. Den i dagsläget rekommenderade metoden för storskalig restaurering av ålgräs längs den svenska västkusten innefattar plantering av enskilda vuxna skott med en kort bit rhizom, utan sediment från skördelokalen. Restaureringsförsök enligt denna metod visade på mycket god tillväxt i grunda (1-1.5 m) miljöer med en ökning i skottäthet på >500% under två tillväxtsäsongen.



LIST OF PAPERS

This thesis is based on the following papers, referred to in the text by their roman numerals.

PAPER I: **Eriander L.**, Laas K., Bergström P., Gipperth L., Moksnes P.-O. The effects of small-scale coastal development on the eelgrass (*Zostera marina* L.) distribution along the Swedish west coast – ecological impact and legal challenges. *In manuscript.*

PAPER II: **Eriander L.** Light requirements for successful restoration of eelgrass (*Zostera marina* L.) in a high latitude environment – acclimatization, growth and carbohydrate storage. *Submitted manuscript.*

PAPER III: Moksnes P.-O., **Eriander L.**, Infantes E., Holmer M. Local regime shifts prevent natural recovery and restoration of lost eelgrass beds along the Swedish west coast. *In manuscript.*

PAPER IV: **Eriander L.**, Infantes E., Olofsson M., Olsen J.L., Moksnes P.-O. 2016. Assessing methods for restoration of eelgrass (*Zostera marina* L.) in a cold temperate region. *Journal of Experimental Marine Biology and Ecology*. 479, 76-88.

PAPER V: Infantes E., **Eriander L.**, Moksnes P.-O. 2016. Eelgrass (*Zostera marina*) restoration on the west coast of Sweden using seeds. *Marine Ecology Progress Series*. 546, 31-45.

Related publications not included in this thesis:

Moksnes P.-O., Gipperth L., **Eriander L.**, Laas K., Cole S., Infantes E. 2016a. Förvaltning och restaurering av ålgräs i Sverige – Ekologisk, juridisk and ekonomisk bakgrund. *Havs- och vattenmyndighetens rapport* 2016:8, 148 pp., ISBN 978-91-87967-16-0.

Moksnes P.-O., Gipperth L., **Eriander L.**, Laas K., Cole S., Infantes E. 2016b. Handbok för restaurering av ålgräs I Sverige – Vägledning. *Havs- och vattenmyndighetens rapport* 2016:9, 146 pp., ISBN 978-91-87967-17-7.

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BACKGROUND

Seagrasses

Seagrasses are an ecological group of monocot flowering plants (angiosperms), found within 4 families in the order Alismatales (Les et al. 1997, Larkum et al. 2006). This group of plants are relatively young and colonized the marine environment in the early cretaceous period (around 100 million years ago; Larkum and den Hartog 1989). Seagrasses are the only group of vascular plants that have adapted to fully submerged marine conditions (as oppose to mangrove and salt marshes in the intertidal zone) and have evolved a number of adaptations in order to live and reproduce under these conditions (Arber 1920, Larkum et al. 2006, Olsen et al. 2016). These adaptations include salt tolerance, chloroplasts located within the epidermis, lack of stomata and a thin cuticle layer which allows for the uptake of nutrient and gases through the leaf surface, intercellular air chambers (lacunae), which aid in the diffusion of oxygen from leaves to roots and rhizome located in the anoxic sediment, and hydrophilous pollination (e.g. Pedersen et al. 1998, Fredriksen and Glud 2006, Olsen et al. 2016).

Seagrasses comprise less than 60 species worldwide (Short et al. 2007), and contrary to other important marine ecosystems, which are confined to certain latitudes (e.g. mangroves, coral reefs and kelp forests), seagrasses have adapted to a wide array of environmental conditions and can be found along all continents of the world except Antarctica (Green and Short 2003). The diversity of seagrasses is highest within the Indo-Pacific region, (12-15 species), and lower within the North Atlantic and North eastern Pacific (1-2 species; Green and Short 2003).

The seagrass *Zostera marina* L. (eelgrass) has a wide global distribution with recordings from the Gulf of California at 26°N (Cabello-Pasini et al. 2003) to Greenland, Iceland and Norway at 64-70 °N (Green and Short 2003, Jørgensen and Bekkby 2013, Boström et al. 2014, Olesen et al. 2015), and is the dominating species in the temperate North Atlantic and North Pacific (den Hartog 1970, Short et al. 2007). Eelgrass of the temperate North can be found growing on soft bottom habitats in estuaries and shallow areas along the coast, typically forming dense monospecific meadows, from the intertidal down to depths of 10-15 m, in areas with high water clarity (Borum et al. 2004, Short et al. 2007, Boström et al. 2014). The morphology of these plants (Box 1) varies both depending on geographical location and local environmental conditions, typically with taller shoots at higher latitudes (Short et al. 2007) and within deeper or more sheltered location (Olesen and Sand-Jensen 1993, Krause-Jensen et al. 2000, Vichkovitten et. al. 2007). Furthermore, eelgrass generally exhibits large seasonal variations in shoot density, morphology and biomass production as a result of variations

Box 1: Morphology of eelgrass plants

The shoots of *Zostera marina* plants have between 3-7 leaves, that protrude from a leaf sheath, which protects the newly formed leaves and the growth zone (meristem). The leaf length varies substantially depending on where the plants grow, but is on average between 30-60 cm, with a leaf width between 3-12 mm (Larkum et al. 2006). Below ground tissue consists of rhizomes and roots, which anchors the plant in the sediment and is the major storage organ for non-structural carbohydrates (Burke et al. 1996). As the terminal shoot and the horizontal rhizome grow, new leaves are formed and old leaves are shed, leaving scars (nodes) along the length of the rhizome. Lateral shoots are produced on a branches along the rhizome, and is the means by which eelgrass spread through vegetative clonal growth. During the reproductive season, specialized reproductive shoots are formed, which are taller than the rest of the meadow (*see* Fig. 1C), with male and female flowers inside spathes. Pollen are spread with water currents and after fertilization, seeds develop within the spathes. When seeds are mature they drop from the shoot, and sink to the bottom, completing the eelgrass life cycle. Sometimes reproductive shoots detach and travel with surface currents, which can result in seed dispersal to new locations (Källström et al. 2008).

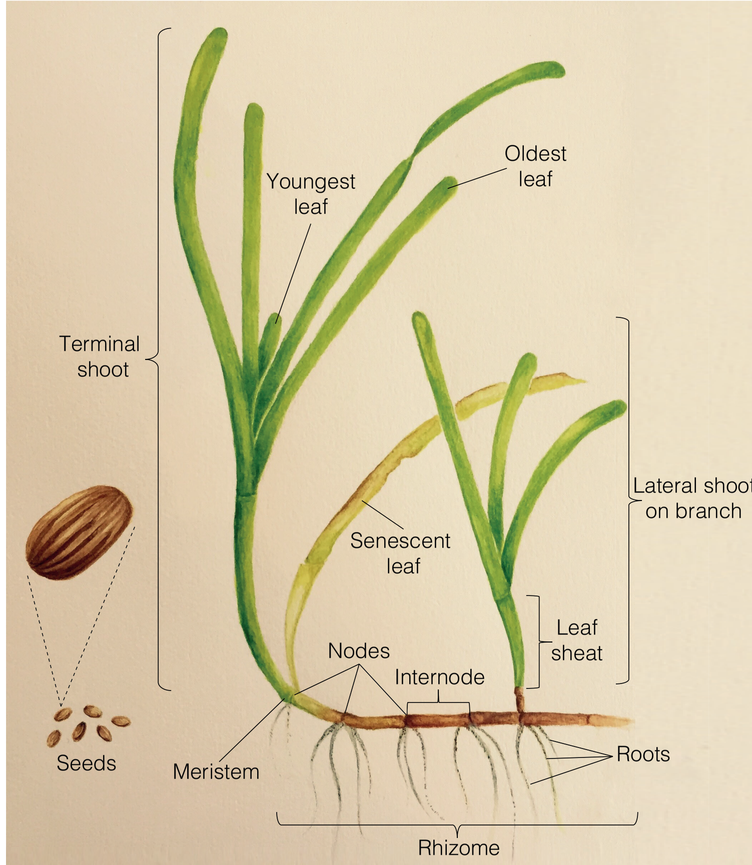


Illustration: *L. Eriander*

in temperature and light (Solana-Arellano et al. 1997, Wong et al. 2013, Clausen et al. 2014). Eelgrass reproduce both sexually through seed development on reproductive shoots and asexually, through vegetative clonal growth (Box 1) and are in most areas perennial, although annual stands can be found e.g. in the Wadden Sea (van Katwijk et al. 2000).

Eelgrass and other species of seagrass are ecosystem engineers and exhibit many structural and functional properties that makes them key ecosystems within shallow coastal areas, and an important source of ecosystem services (e.g. Gotceitas et al. 1997, Costanza et al. 1997, Bos et al. 2007, Hasegawa et al. 2008, Fourqurean et al. 2012, Cole and Moksnes 2016, Fig. 1). Seagrasses provide substrate, shelter, feeding and nursery environments for a large variety of species (e.g. Orth et al. 1984, Gotceitas et al. 1997, Short et al. 2001, Whitlow and Grabowski 2012). They stabilize the sediment with their roots and rhizomes, slow down water movement and facilitate the settlement of particles from the water column with their canopy (Moore 2004, Bos et al. 2007, Hansen and Reidenbach 2012), which decrease resuspension, protect against coastal erosion and lead to increased water clarity (Bos et al. 2007, van der Heide et al. 2007, Hasegawa et al. 2008, Carr et al. 2010, Orth et al. 2012). In a global aspect seagrasses are important for nutrient trapping and cycling (Costanza et al. 1997, Hemminga and Stapel 1999, Moore 2004, McGlathery et al. 2012) and for their capacity to sequester carbon from the atmosphere (Duarte et al. 2005, Fourqurean et al. 2012, Duarte et al. 2013).

Eelgrass in global decline

Seagrasses are today considered one of the most threatened ecosystems of earth, and have suffered a widespread global decline with a loss of more than 29% of the areal extent over the last 140 years and an annual loss of around 7% yr^{-1} since the 1990s (Waycott et al. 2009). Large losses of eelgrass have been reported from many countries, including USA (Fonseca et al. 1998), Poland (Kruk-Dowgiallo 1991), Holland (Giesen et al. 1990), Germany (Munkes 2005), Denmark (Fredriksen et al. 2004), Norway (Jørgensen and Bekkby 2013) and Sweden (Baden et al. 2003), and anthropogenic impacts are believed to be the major cause behind this decline (Short and Wyllie-Echeverria 1996, Borum et al. 2004, Waycott et al. 2009). Coastal and estuarine habitats are particularly susceptible to environmental degradation as a result of an increasing human population inhabiting the coastal zone and the concomitant anthropogenic pressure it infers (Lotze et al. 2006). Due to an exceptionally high light requirement (on average 20% of surface irradiance; Dennison et al. 1993), eelgrasses are exceedingly vulnerable to activities that affect the water clarity and light attenuation.

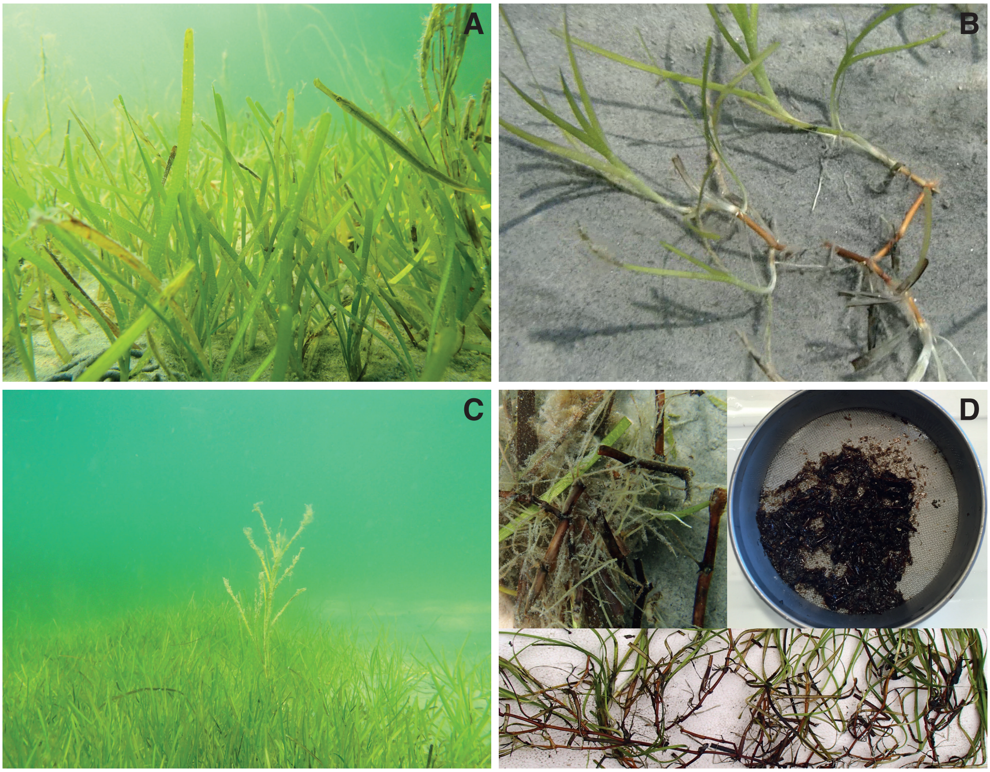


Fig. 1. Illustrations of some of the ecosystem services provided by eelgrass. A) Eelgrass constitute an important habitat for many organisms, including the pipefish (*Syngnathus typhle*) seen in the picture. Some of the species that depend on these habitats are of high commercial importance, e.g. cod. B) Eelgrass reduce resuspension and stabilize the sediment through their rhizomes and roots, which can form complex mats below the sediment surface. In the picture the sediment has been removed to expose the below ground tissue. C) The eelgrass canopies reduce current velocities and facilitate trapping of particles, which together with the stabilization of sediments, increase water clarity in areas around eelgrass meadows. In the picture a reproductive shoot protrudes above the rest of the vegetative shoots in the meadow. D) Much of the biomass produced by these plants ends up buried in the sediment, where it can be stored for centuries. This makes eelgrass an important carbon sink. The organic material captured by the 1 mm sieve in the picture was collected from 15-40 cm depth in the sediment below an eelgrass meadow in a sheltered bay on the NW coast of Sweden and consists of partly degraded leaf and rhizome tissue. Photos taken by: L. Eriander.

Eutrophication and costal development are generally considered two of the most detrimental stressors affecting seagrasses (Short and Wyllie-Echeverria 1996, Waycott et al. 2009). Nutrient loads increase the phytoplankton production and growth of filamentous algae, both of which affect the light available for these plants (Duarte 1995, Cloern 2001). Coastal development affects seagrass both directly by removal of meadows through activities such as dredging and indirectly by activities and structures that shade or create turbid conditions, unfavourable for seagrass growth (Burdick and Short 1996, Schoellhamer 1996, Ruiz and Romero 2003, Erftemeijer and Lewis 2006).

Furthermore, increasing evidence suggests that overfishing of organisms on high trophic levels (e.g. large predatory fish or marine mammals) can have a negative impact on eelgrass through cascading top-down effects within food webs, which favours fast growing algae (Heck et al. 2000, Moksnes et al. 2008, Baden et al. 2012, Hughes et al. 2014, Östman et al. 2016). Seagrasses are ecosystem engineers and their ability to stabilize sediments and increase water clarity functions as an important self-generating positive feedback mechanism that improves the growing conditions for the plant and help systems recover after disturbances. However, when seagrasses are lost, these self-generating mechanisms also diminish, which can result in environmental changes, which reduce water quality conditions and limit seagrasses ability to recolonize the area (Box 2; Troell et al. 2005, van der Heide et al. 2007, Maxwell et al. 2016).

Means to protect and help eelgrass recovery

In order stop the degradation and loss of eelgrass, measures are needed which improve management and mediates recovery of lost eelgrass ecosystems. Because of their importance in providing ecosystem services, many countries have realized the need to include eelgrass and other seagrass species in their marine management plans (Borum et al. 2004, Orth et al. 2006, Waycott et al. 2009, Cole and Moksnes 2016) and as an important indicator of water quality conditions within marine environmental monitoring programs (Bricker et al. 2003, Yamamuro et al. 2003, Orth et al. 2010, Baaner and Stoltenborg 2011, Marba et al. 2013). Furthermore, in Europe, several directives commissioned by the European Union (EU), with the objectives of achieving good environmental status of the marine environment, directly or indirectly aid in the protection of eelgrass. In the Water Framework Directive (WFD; 2000/60/EC), the abundance of marine angiosperms (e.g. eelgrass) is one of the determinants for ecological status of coastal waters, and many countries including Denmark, Norway, Germany and Great Britain today use eelgrass as an environmental indicator for determining ecological status according to this directive (Marba et al. 2013). In the Marine Strategy Framework Directive (MSFD; 2008/56/EC) eelgrass is mentioned as an important environmental indicator for eutrophication, and protection and restoration of eelgrass is also in line with the EU Biodiversity Strategy (European Commission, 2011) and the Directive on the conservation of natural habitats and of wild fauna and flora (Habitat Directive; 92/43/EEC). The latter requires member states to establish Natura 2000 areas, which aim to protect threatened species and habitats.

Box 2: Illustration of a regime shift in an eelgrass meadow

The figure demonstrates what could happen to an eelgrass ecosystem when it is subjected to disturbances and shifts from one stable state to another (Scheffer et al. 2001), in this case illustrated by vegetated and unvegetated soft bottom conditions. In **stable state 1** a large and dense eelgrass bed exists. At minor disturbances the eelgrass meadow can recover to pre-disturbed conditions (illustrated by the black curves). This recilience is driven by self-generating, positive feedback mechanisms (e.g. stabilizing of sediment, trapping of particles which improve water clarity), which gets stronger with the size and density of the meadow (illustrated by the green arrows) and facilitates eelgrass growth. However, if the disturbance is large or prolonged the ecosystem may reach a threshold level (illustrated by the red line crossing the horizontal dashed line). At this size the mechanisms, which previously facilitated growth of the meadow, are now replaced with self-generating mechanisms which are unfavorable for eelgrass growth, which gets stronger with the reduced size of the meadow (illustrated by red arrows). This eventually causes a collapse of the eelgrass meadow which result in a new **stable state 2**, without vegetation. These self-generating mechanisms could for example be increased resuspension of bottom sediment as the stabilizing effect of the eelgrass meadow diminishes, leading to reduce light conditions, or an increased amount of drifting algal mats on the bottom which cause shading or uprooting of eelgrass, as seen in **paper III.** Local studies that determine the feedbacks which influence and control these two states might be an important step to ensure successful restoration and conservation of eelgrass (Maxwell et al. 2016).

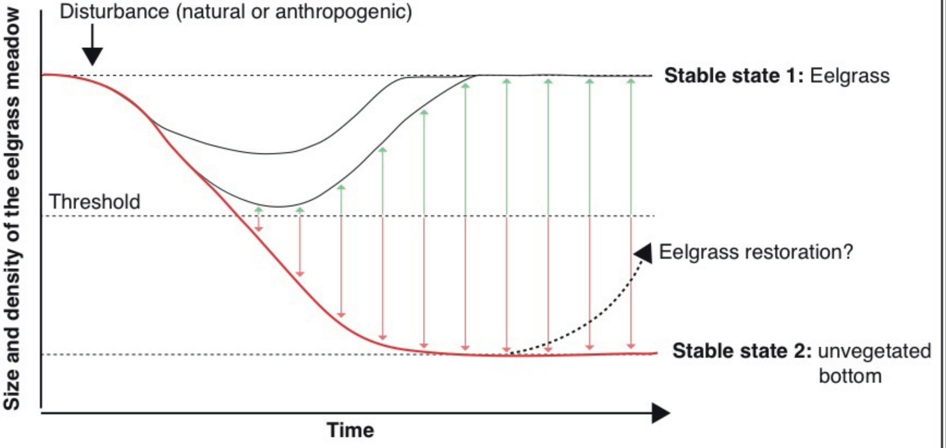


Illustration: *Modified from Van Andel and Aronson 2012*

As a mean to mitigate losses and help the recovery of eelgrass, policies and guideline on how to perform restoration of eelgrass have been developed in the USA (e.g. Fonseca et al. 1998, California; NOAA 2014, Massachusetts; Evans and Leschen 2010) and recently also in northern Europe (e.g. The Netherlands; de Jonge et al. 2000, van Katwijk et al. 2009). In the USA, eelgrass transplantation has been used as a mean to restore damaged or lost eelgrass meadows since the 1940s (Addy 1947), and successful mitigation of losses has since then been performed in several areas (e.g. Boston Harbour, MA; Leschen et al. 2010, Virginia Coast Reserve, VA; Orth and

McGlathery 2012, Southern California; Olsen et al. 2014), with the returning of important ecosystem services as a result (Orth et al. 2012, Cole and McGlathery 2012, Lefcheck et al. 2016). Over the past 20 years, transplantation trials and restoration of eelgrass have been performed in many countries (e.g. the Netherlands; van Katwijk et al. 1998, Bos et al. 2005, Korea; Li et al. 2010, Japan; Tanaka et al. 2011) and is becoming an important and functional management tool for initiating recovery and for mitigating losses of eelgrass (Paling et al. 2009, Leschen et al. 2010, Marion and Orth 2010, Shafer and Bergstrom 2010, De Groot et al. 2013). Despite the increased interest in eelgrass restoration, far from all transplantation trials and restoration efforts have been successful, with a global success rate of 37% for seagrass in general (van Katwijk et al. 2015). This is the case also for trials performed in Northern Europe (Cunha et al. 2012). According to a global meta-analysis of seagrass restoration, the high number of failed efforts are linked to the small scale of many project, where larger efforts generally show higher success (van Katwijk et al. 2015). Furthermore, inadequate selection of sites has been identified as a driver behind failure (Fonseca et al. 1998, van Katwijk et al. 2015), where sites do not have the physical or biological conditions necessary to sustain eelgrass growth (Short et al. 2002, Paling et al. 2009, Fonseca 2011). In many of these cases, poor water quality and insufficient light conditions have been identified as the cause behind failure of transplants (e.g. Moore et al. 1997, Leschen et al. 2010). Additional factors, which can affect survival at a site include sediment quality (Krause-Jensen et al. 2011), exposure (van Katwijk and Hermus 2000), bioturbation (Philippart 1994, Davis et al. 1998, Delefosse and Kristensen 2012, Neckles 2015) drifting macroalgae (Valdemarsen et al. 2010, Rasmussen et al. 2012) and extreme temperature conditions (Moore and Jarvis 2008, Tanner et al. 2010).

Also, the choice of restoration methods can affect the outcome (van Katwijk et al. 2015). The most commonly used methods for restoring eelgrass involves transplantation of vegetative shoots within intact sediment cores or the transplantation of shoots with bare roots and rhizomes, with or without anchoring (Fonseca et al. 1998, van Katwijk et al. 2015). Furthermore, the use of eelgrass seeds is emerging as a cost-effective and efficient method for large-scale restoration (Pickerell et al. 2005, Orth et al. 2012). Guidelines regarding suitable methods and appropriate site characteristics for eelgrass restoration are generally based on local studies (e.g. Fonseca et al. 1998, Short et al. 2002, van Katwijk et al. 2009).

Because of the wide range of factors that could potentially affect the outcome of a restoration effort, it is essential to have a general knowledge of the study system aimed for restoration. Furthermore, a local and regional understanding of suitable methods, environmental requirements and growth characteristics have been identified as vital for successful restoration to occur (Campbell 2002, Ganassin and Gibbs 2008, Cunha et al. 2012, van Katwijk et al. 2015).

Eelgrass in Sweden

In Sweden eelgrass (*Z. marina*) is the largest and most dominant species on seagrass, both along the west and the east coast (Boström et al. 2003). Furthermore, the Swedish Red List includes two threatened *Zostera* species; *Z. noltii* (dwarf eelgrass) and *Z. angustifolia* (narrow leaved eelgrass; ArtDatabanken 2015). The dwarf eelgrass is smaller and predominantly found in intertidal areas in the southern parts of Europe (Borum et al. 2004), with only scattered recordings from locations along the west coast of Sweden. Narrow leaved eelgrass has been recorded along the west coast of Sweden. However, many scientists do not consider this as a valid species but a synonym or variety of *Z. marina* (World Register of Marine Species 2016). Furthermore, two species of widgeon grass (*Ruppia maritima* and *R. cirrhosa*) are common in more brackish waters on both the west and the east coast of Sweden. However, due to their inability to grow under fully marine conditions they are sometimes not considered to be 'true' seagrasses (den Hartog 1970).

Along the NW coast of Sweden, eelgrass is perennial and grows subtidally in monospecific meadows (Boström et al. 2003), commonly found within sheltered areas in soft muddy sediments, high in organic content (10-25%; Baden and Pihl 1984, Jephson et al. 2008) at depths between 0.5-5 m (Boström et al. 2003). The morphology of eelgrass in this area varies substantially depending on depth and exposure (*see* Fig. 3C), with large seasonal variations in biomass and shoot density (Baden and Pihl 1984, Boström et al. 2014). The growth season extends from May to October in shallow areas, reaching a maximum biomass and shoot density between July to September (Baden and Pihl 1984, Boström et al. 2014), after which it decreases as a result of low light and low temperature conditions (Baden and Pihl 1984, Olesen and Sand-Jensen 1994). Eelgrass reproduce sexually over the summer months in this region, with pollination occurring from the end of June to September and mature seeds can be found on reproductive shoots from the end of July to September (Infantes unpubl. data). In Scandinavian waters eelgrass seeds normally lay dormant in the sediment over the extended winter period and germinate in April to May (Olesen 1999, Olesen et al. 2016).

Since the 1980s, extensive losses of eelgrass, in the order of 10 000 ha (Moksnes et al. 2016a) have occurred on the NW coast of Sweden, with a decrease in coverage of more than 60% (Baden et al. 2003, Nyqvist et al. 2009), and an estimated loss of ecosystem services worth >350 million US$ (based on three ecosystem functions; fish habitat, carbon and nitrogen uptake; Cole and Moksnes 2016). These losses have largely been attributed to the effects of coastal eutrophication and overfishing (Moksnes et al. 2008, Baden et al. 2010, 2012). Successful efforts to reduce the nutrient load to coastal waters over the past 20 years has improved water quality in many coastal areas (Moksnes et al. 2015, Anon. 2016) but no recovery of eelgrass meadows have occurred (Nyqvist et al. 2009). The reason behind the lack of natural recovery in these areas is not known and restoration of eelgrass may be an important tool to recover historical losses.

Since eelgrass mainly grow in shallow sheltered bays, commonly targeted for development in water (e.g. building of docks and marinas), coastal exploitation may be an additional factor responsible for eelgrass loss. In Sweden, eelgrass is (potentially) protected from detrimental exploitation through the general shore protection legislation issued in the 1950s, which protects the shore against activities that infringe on the access to the shoreline by the general public and on the living conditions for plants and animals (Swedish Environmental Code; SEC; chapter 7, section 13-18). Also, approximately 50% of the present eelgrass distribution along the NW coast of Sweden is located within some type of area protection (predominantly nature reserves and/or Natura 2000 areas; Moksnes et al. 2016a), which may further protect eelgrass from exploitation, since exemptions from the general shore protection should normally not be granted within these areas (SEPA 2012). Despite this, exploitation by docks and marinas has increased significantly along the coast of Sweden in the last decades (Kindström 2006, Hellström 2007, Petterson 2011, Sundblad and Bergström 2014), which suggests that damage to eelgrass habitats is allowed to continue. However, it is unclear why current Swedish legislation fails to prevent small-scale coastal development from continuing in areas with eelgrass, and what effect this type of development has on the local and large-scale eelgrass coverage along the coast. The substantial losses of eelgrass and the continued exploitation along the coast, indicate that Swedish legislation is insufficient in protecting eelgrass ecosystems, which makes environmental objectives posted by the EU (as described above), hard to meet. Furthermore, regional and national objectives motivate an improved management and restoration of eelgrass. Under regional marine conventions such as OPSAR and HELCOM, eelgrass mapping and monitoring are required and eelgrass protection is urged (OSPAR 2012, HELCOM 2013) and according to national Swedish environmental quality objectives, such as the goal of '*A balanced Marine Environment, Flourishing Coastal Areas and Archipelagos*', the aim is to maintain ecosystem services and a high biodiversity within shallow coastal environments, and to restore degraded habitats (Anon. 2012). The demands and objectives declared in national and international policy documents therefore constitute an important driver for national work concerning eelgrass management. In the last decade the interest has increased from national agencies and managers to use restoration of eelgrass as a mean to reduce historical losses and compensate for losses resulting from exploitation (Moksnes 2009, SwAM 2015). However, when the work included in this thesis was initiated, the knowledge regarding restoration of eelgrass at high latitude environments was limited (Alaska; Philips and Lewis 1983, Denmark; Christensen et al. 1995) where no large-scale restoration efforts had been performed, and it was unclear whether methods developed for lower latitudes would be suitable here.

The short growth season, ice scouring during winter and sediments with high organic content and sulphides (Jephson et al. 2008, Holmer et al. 2009), are factors that could pose challenges for eelgrass restoration on the Swedish west coast. Since eelgrass rely on stored carbohydrates to survive the extended winter period (Vichkovitten et al. 2007), and high losses of shoots naturally occur over the winter (Olesen and Sand-Jensen 1994), transplanted shoots and seeds needs to be able to acclimatize, increase in shoot numbers through vegetative reproduction and store carbohydrates over the limited growth season following transplantation. Furthermore, the morphology of eelgrass plants varies greatly depending on environmental conditions, and general guidelines often suggest a close match between the conditions at the donor site and the area targeted for restoration (Fonseca et al. 1998, van Katwijk et al. 1998). However, as a result of the large losses of eelgrass meadows along the Swedish NW coast, this match criterion might be hard to fulfil, due to scarcity or geographically distant donor populations. It is therefore important to investigate if the morphology and origin of transplants affect their establishment success within new environments and if they have the ability to acclimatize to new environmental conditions. When it comes to restoration with seeds in these areas, possible seed loss mechanisms are important to study, especially since eelgrass seeds lay dormant in the sediment over the winter season, which could potentially create a bottleneck for establishment, with high losses due to erosion and transport of seeds and seedlings away from suitable habitats (Lillebø et al. 2011, van Katwijk and Wijgergangs 2004, Bos and van Katwijk 2007). Furthermore, fauna such as green shore crabs and lugworms, which are abundant on the Swedish west coast, have been associated with seed loss through predation (Infantes et al. *in review*) and extensive burial (Valdemarsen et al. 2011, Delefosse and Kristensen 2012), respectively.

AIMS

Due to the large losses of eelgrass that have occurred along the Swedish NW coast there is an urgent need to improve the management of these ecosystems and apply measures to recover historical losses. To facilitate this, the overall aim of this thesis was to support the development of an improved management of small-scale coastal development, to increase our understanding of environmental conditions that promote or impede eelgrass growth and to develop methods suitable for large-scale restoration of eelgrass on the NW coast of Sweden. The specific aim of each paper was:

Paper I: (1) to assess the local and large-scale effect of shading by docks and marinas on eelgrass habitats along the Swedish northwest coast. (2) to identify problems with the current legislation, which allows for continued exploitation. (3) to determine how the presence of eelgrass and area protection affect the approval of dock construction.

Paper II: (1) to determine the ability of eelgrass transplants to acclimatize to variable low light conditions at different temperatures, and how different light and temperature conditions affect growth characteristics and carbohydrate storage of transplants. (2) to investigate how eelgrass grown under different light conditions cope during severe shading at different temperatures and how shading affects the carbohydrate stock of transplants.

Paper III: (1) to determine if restoration of eelgrass is possible in areas that have experienced large eelgrass losses. (2) to identify processes and possible feedback mechanisms that may prevent recovery of eelgrass at historical eelgrass areas.

Paper IV: (1) to compare and evaluate restoration methods at typical environmental conditions along the NW coast of Sweden and develop cost-effective methods for large-scale restoration. (2) to determine if eelgrass could be successfully transplanted between sites with different depths and exposure.

Paper V: (1) to determine suitable restoration methods with seeds (2) to identify the main causes for seed and seedling losses in different environments and to determine the optimal time for seed planting.

METHODS

The studies included in this thesis extend from assessments of methods for eelgrass restoration in the field and several years of environmental monitoring, to laboratory mesocosm studies aimed at extracting detailed knowledge of processes which are of importance for eelgrass restoration. This thesis also has a strong focus on improving management of eelgrass habitats on the NW coast of Sweden, where results from studies have been evaluated also from a management perspective, for example by identifying methods that are viable for large-scale restoration or by identifying areas where eelgrass restoration is difficult and protection measures are needed. In addition, interdisciplinary studies have been performed, where the goal has been to improve management of coastal exploitation. All studies included in this thesis have been performed on the NW coast of Sweden (Fig. 2).

Interdisciplinary approaches

As part of my PhD project I have worked in close association with researchers from other disciplines, especially with scientists of environmental law, both through affiliation to the interdisciplinary graduate school, organized by the Gothenburg Centre for Marine Research at the University of Gothenburg (with PhD students from natural and social sciences), and through the involvement in the interdisciplinary research program ZORRO (Zostera Restoration; www.gu.se/zorro). In the ZORRO program marine ecologists, environmental lawyers and environmental economists work together with issues related to management and restoration of eelgrass. Through this collaboration the study presented in **paper I** was initiated, which combines the assessment of ecological impacts from small docks and marinas along the coast of Sweden with empirical investigations of the legal process behind decisions to approve dock construction. In this study, satellite data on eelgrass distribution along the coast were overlapped with the position of docks within applications in order to determine if eelgrass presence affected the decision. This combination of legal and ecological data is not common within environmental research, but it provided an opportunity to examine how legal protection of eelgrass in theory is realized in practice. Through this interdisciplinary approach we were able to identify issues with the current management practice, which allows for exploitation of eelgrass habitats to continue, despite their acknowledged importance within national and international environmental policies. Furthermore, by identifying both the causes behind continued exploitation and the ecological impact it imposes on eelgrass habitats, we were able to make more specific recommendations on how management could be improved or revised to prevent net-losses of eelgrass habitats and how to minimize the negative effects from future development.

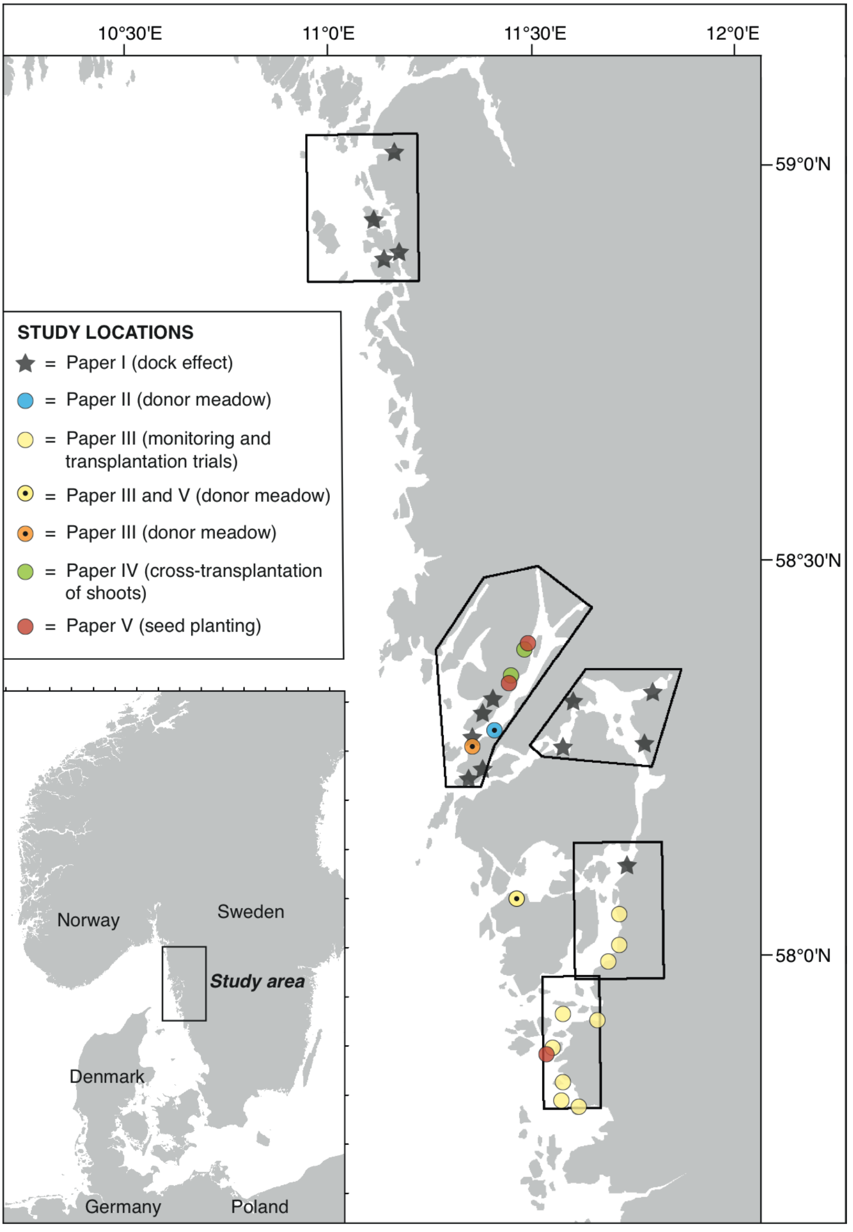


Fig. 2. Map showing the location of studies performed in the thesis and the donor meadow used for transplant material. The areas inside boxes along the coast demonstrate the 5 study regions used in **paper I**, where field surveys of eelgrass coverage have been performed in 1980, 2000, 2003 and 2004 (Baden et al. 2003, Nyqvist et al. 2009).

In restoration ecology the need for scientific studies of methods and processes that can affect the outcome of a restoration effort is eminent. However, in order to convey these findings into management actions there is also a need to work interdisciplinary with people from governmental agencies and other science disciplines (e.g. environmental law, environmental economics). And albeit **paper II**, **III**, **IV** and **V** do not include an obvious interdisciplinary involvement, the motivation behind these studies was not solely based on a scientific curiosity but had an overarching purpose of improving eelgrass management in Sweden. The results from these studies have since been incorporated into guiding documents on the management and restoration of eelgrass in Sweden, produced by the ZORRO program for the Swedish Agency for Marine and Water Management, which also incorporates the legal and economic aspects of eelgrass restoration (*see* **related publications**; Moksnes et al. 2016a,b).

Use of historical monitoring- and survey data

Historical surveys of eelgrass coverage and environmental conditions can be of great importance during several aspects of eelgrass management and restoration. In **paper III**, new losses of eelgrass were determined by mapping the present distribution of eelgrass and comparing it with the distribution in the 1980s and 2004. Furthermore, the historical distribution of eelgrass was compared with the present maximum depth distribution (calculated from light measurements and survival of eelgrass transplants), which gave an indication of changes in water quality conditions in areas where losses of eelgrass have occurred. Information on historical eelgrass coverage can also be important when selecting sites for restoration, since these might have a higher likelihood of sustaining eelgrass growth (Fonseca et al. 1998, Short et al. 2002). In **paper III**, historical eelgrass data were used to find the sites where the possibility of eelgrass restoration was evaluated. Comparisons between historical and present eelgrass coverage could further be used to define reference conditions for eelgrass coverage in a specific region or along the Swedish coast, which could be important for preventing the risk of shifting baselines (McHarg and Mumford 1969, Papworth et al. 2009). The importance of historical data for defining reference conditions is further supported by the EU MSFD (2008/56/EEC) and have been used to set goals in terms of recovery and restoration of eelgrass along the Swedish NW coast (Moksnes et al. 2016a).

In **paper I**, the estimate of large-scale impacts from docks and marinas on eelgrass along the NW coast of Sweden was possible through available data on development along the coast (SEPA 2010) and on eelgrass coverage within 5 areas of the coast (Fig. 2), from 1980-2014 (Baden et al. 2003, Nyqvist et al. 2009, Lawett et al. 2013, Envall and Lawett 2016). These 5 areas were treated as representative for the entire NW coast of Sweden, and the proportion of docks and marinas overlapping with the historical and present eelgrass distribution in these areas was extrapolated to estimate the total number of docks and marinas on eelgrass bottoms along the whole NW coast.

Laboratory study of light and temperature effects

When performing eelgrass planting in in the field, the cause behind success or failure can sometimes be hard to determine because of the number of interacting environmental variables (e.g. temperature, sediment characteristics, nutrient concentration and light) that could affect the outcome. Furthermore, since many of these variables can experience large and unpredictable fluctuations, their effect on a specific response variable can be hard to distinguish. By studying light and temperature effects on eelgrass under laboratory conditions in **paper II**, I was able to control the exact amount of light received by each treatment and keep the temperature treatments constant. The 3 light treatments chosen in this study were based on previous literature describing the minimum light requirement (MLR) for eelgrass growth, which varies between 11-34% of the surface irradiance (SI; e.g. Olesen and Sand-Jensen 1993, Ochieng et al. 2010), and on the light conditions measured at the maximum depth distribution of eelgrass in **paper IV** (18% of SI). To determine what light levels these relative proportions of the SI correspond to in the study region (58°2"N), the mean integrated daily photosynthetic photon flux density (PPFD) was calculated over the growth season (May-October) from measurements of surface irradiance recorded by the Swedish Meteorological and Hydrological institute (SMHI; average 2010-2014). The mean integrated PPFD at the surface was 28.3 mol photons m^{-2} day^{-1} and the treatment light levels corresponding to approximately 11, 18 and 34% of SI were 3, 5 and 10 mol photons m^{-2} day^{-1}. The different light levels were achieved through shading with meshed screening material between the light source and the water surface. Light intensities were controlled throughout the experiment with light loggers (Lux; HOBO, UA-002-64, Onset) calibrated against a PAR-meter (apogee MQ-200).

When mesocosms experiments are performed with flow-through seawater, fouling can become a problem. Since epiphytes on eelgrass can reduce the amount of light reaching the leaf with as much as 70-90% (Brush and Nixon 2002), measures were taken to reduce the growth of epiphytes. Loggers were cleaned and epiphytes and filamentous algae were removed by hand twice weekly from the mesocosms. Furthermore, grazers (*Littorina littorea* and *Gammarus locusta*) were added to each mesocosm to control growth of diatoms and epiphytes. Shoots were also photographed on each sampling occasion, to determine any differences in the epiphyte coverage, as this could possibly affect the response variables (e.g. eelgrass morphology and leaf pigments).

By collecting the shoot transplants used in this study from the same depth at the donor meadow (Fig. 2) and by measuring the morphology at the start of the experiment, I was able to avoid large initial variations in response variables (i.e. morphology, pigmentation and carbohydrate concentration), which could have masked the response to treatment conditions. During the simulated severe shading event, the effects of previous light condition and temperature were studied through measurements of mortality, shoot morphology and carbohydrate concentration in the rhizome. Shoots were considered dead when leaves were shed, completely brown or wilted or when the texture of the rhizome was soft (Mills and Fonseca 2003).

Monitoring of environmental variables and site selection

During site selection for restoration it is of great importance to monitor environmental variables (e.g. light, sediment characteristics, temperature, turbidity, chlorophyll in the water and sulphide in the sediment) to determine the suitability of a site for eelgrass growth and survival (e.g. Short et al. 2002, Leschen et al. 2010). Monitoring of environmental variables is further important during restoration, since it could help explaining the cause behind failure or success of a restoration effort. Some of these variables e.g. sediment characteristics and organic content vary less over the season and might be sufficiently measured at one specific time point. However, other variables, e.g. light, temperature, turbidity and chlorophyll a in the water, might change more rapidly (within days or hours) and unpredictably within shallow coastal areas, making point measurements unsuitable when monitoring these environmental conditions, especially if they are to be used to evaluate the suitability of a site for eelgrass restoration. Therefore, continuous monitoring with instruments that can log data might be required in order to get a good estimate to base evaluations on.

Light is often considered one of the most important environmental factors for determining habitat suitability for eelgrass growth (e.g. Dennison 1993, Fonseca et al. 1998). National monitoring of water clarity or light attenuation along the Swedish coast is commonly performed using Secchi discs, once per month. However, in shallow areas relevant for eelgrass restoration, this method has several serious limitations. For example, water clarity cannot be estimated if the depth is shallower than the Secchi-depth (which is often the case). Furthermore, since these measurements can only be collected through field visits during relatively calm conditions they may overestimate the mean light conditions at a site. To avoid bias estimates of light conditions, light levels were monitored continuously over the growth season, both in the method assessment papers (**paper IV** and **V**) and in the study of key processes affecting eelgrass growth and survival (**paper III**). Light loggers were placed at two different depths at each site and light conditions were logged simultaneously at 15-min intervals over the growth season (May-October). The measurement of light at two depths allowed us to calculate the water column light attenuation coefficient (K_d; m^{-1}), which can be used to estimate light conditions at any specific depth (Box 3). A good estimate of K_d is therefore invaluable when determining suitable depths for eelgrass restoration at a specific site, or for explaining the outcome of restoration efforts.

In **paper III**, key processes, which could influence the restoration success and be of importance during site selection were determined through extensive monitoring and sampling of environmental variables and test-planting of eelgrass. The sites included in this study were located in the southern parts of the Swedish NW coast (Fig. 2), where extensive eelgrass losses have occurred. The study included both sites that have experiences historical losses and sites where small eelgrass meadows remain today. The growth and survival of eelgrass in these sites were related to environmental conditions such as light, sediment characteristics (gran size, organic-, water and sulphide content) and drifting algal mats. Furthermore, the cause behind water column turbidity and low light conditions in historical eelgrass areas was investigated through point measurements of total suspended solids (TSS) and chlorophyll a and through simultaneous monitoring of light, chlorophyll a and turbidity (NTU).

Total sulphur (TS; %) and the fraction of sulphur in the plants originating from the sediment sulphide ($F_{sulphide}$; %) were measured in leaves, rhizomes and roots of transplanted eelgrass shoots after 1 and 2 months following transplantation. This was done to determine if sediment sulphide and sulphide intrusion in plant tissues could explain difference in eelgrass survival and growth between sites. Furthermore, at two sites where eelgrass beds have been lost, shoots were planted at different depths (with different light and wave exposure conditions) and the effect of protection against drifting algal mats and anchoring of shoots on eelgrass survival and growth was assessed.

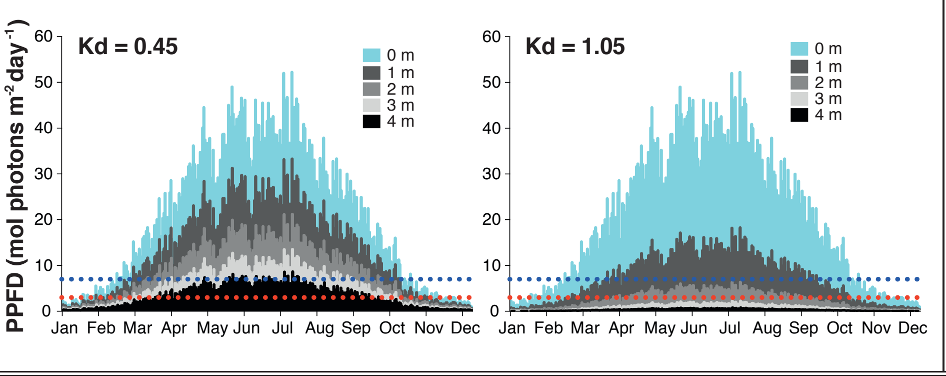
Box 3: Measurements of light and the effect of Kd

Light is one of the most important environmental factors for eelgrass growth and survival, which makes it an essential variable to measure when selecting suitable sites for restoration. By monitoring light conditions at two depths over the growth season a representative mean value for the light attenuation coefficient (K_d) can be calculated according to the Beer-Lambert equitation (e.g. Dennison et al. 1993). This equation can further be used to estimate the light conditions at any specific depth given that the mean K_d value is known and that light recordings exist from one depth. This was done to create the figure below, where light measurements of the integrated daily photosynthetic photon flux density (PPFD) recorded in air by the Swedish Meteorological and Hydrological Institute (SMHI) was used to estimate the daily PPFD reaching 1-4 m depth at two sites with different mean K_d-values (0.45 and 1.05), over a year. Although these light levels are likely an overestimation, since they disregard the reflection and refraction of light taking place at the water surface, they serve as an example on how light changes depending on K_d and depth. In the figure, the red and blue dotted lines indicate light levels of 3 and 7 mol photons $m^{-1}day^{-2}$, which here represent the levels needed for eelgrass survival and non-light limited growth, respectively (Thom et al. 2008). The figure demonstrates that higher water column light attentuation (higher K_d) and greater depth result in lower light conditions and a reduced length of the growth season.

At a K_d of 0.45 at 4 m depth the light levels are >3 mol photons $m^{-2}day^{-1}$ from April to the end of September, but >7 mol photons $m^{-2}day^{-1}$only on a few days between May to July. At 1 m depth at the same site, light levels are >3 mol photons $m^{-2}day^{-1}$ from February to the end of October, and >7 mol photons $m^{-2}day^{-1}$ from March to the end of September. This means that eelgrass planted at 1 m will have a longer time to grow each season compared to shoots planted at 4 m, and recieve light levels needed for non-light limited growth on >200 days, compared to ~20 days at 4 m depth. This will likely result in much faster vegetative reproduction and less winter losses during eelgrass restoration at 1 compared to 4 m depth (*see* **paper II**, **IV** and **V**).

The length of the growth season also depends strongly on the light attenuation at the site. At 2 m depth and K_d of 0.45 and 1.05 light levels are >3 mol photons $m^{-2}day^{-1}$ from mid February to mid October and from April to the end of August, respectively. This means that the growth season can vary substantially (in this example with 3 months) at the same depth, depending on the water quality conditions at a site (*see* **paper III**).

These type of calculations could be useful when determining appropriate depths for eelgrass restoration at a specific site. However, since water quality conditions can change rapidly due to e.g. weather conditions or primary productivity in the water colum, the use of monthly estimates of K_d might be more accurate when determining site suitability or appropriate depths for restoration.



Assessment of methods for eelgrass restoration

When determining suitable methods for eelgrass restoration and when evaluating factors that may influence the success of these methods, time consuming long-term studies in the field are often required. In **paper IV** and **V**, we evaluated restoration methods with shoots and seeds over a 14-month period (2 growth seasons) from transplantation (**paper IV**) and germination (**paper V**). In **paper IV**, sites were also revisited after 27 months to estimate areal coverage and shoot density. These studies were performed primarily within the Gullmars fjord (Fig. 2), where only minor losses of eelgrass have occurred and the conditions for eelgrass growth were considered good. The goal of these studies was not only to establish scientific methods for eelgrass restoration, but also to develop methods which are suitable and cost-effective to use for large-scale restoration of eelgrass. Therefore, the time required to perform harvesting and planting according to the different methods was an important aspect taken into account. Furthermore, since restoration of eelgrass involves collection of transplant material (shoot or seeds) from a donor meadow, the impact on these environments were evaluated after harvesting according to the different methods. The success of the different methods was evaluated through sampling of shoot numbers in plots over the experimental period. This allowed us to closely monitor how well shoots and seedlings were doing, depending on the restoration method, and how growth was affected by different environmental conditions.

In **paper IV**, 3 methods of transplanting shoots (Fig. 3A1-3) and 1 method for planting seeds (Fig. 3A4) were evaluated in a cross-transplantation experiment between 4 sites; deep and shallow areas within a two bays (Fig. 2) with contrasting exposure regimes (sheltered and exposed). This was done to assess if eelgrass could be successfully transplanted between sites with different environmental conditions, where the morphology of shoots differed significantly (Fig. 3C). Furthermore, a baseline genetic survey was conducted to assess whether the morphology of shoots in the 4 sites could be a result of a phenotypically plastic response to local conditions or a result of specifically adapted genotypes. In **paper V**, 3 methods for planting seeds were evaluated (Fig. 3B1-3) within 4 sites with different depth and exposure conditions, and within 1 site in the southern part of the NW coast (Fig. 2), where eelgrass have been lost. The methods included in this study were designed to reduce the negative effects of different possible seed loss mechanisms (Fig. 3B1-3; i.e. hydrodynamics, predation and bioturbation). The results from these studies were used to draw conclusions regarding the major causes behind seed and seedling losses in different environments typical for the NW coast of Sweden. Furthermore, this study was performed both during the fall when mature seeds naturally drop from reproductive shoots in the area, and during the spring before natural germination occurs in the field to determine if winter storage of seeds (Fig. 3B4), would reduce the loss of seeds and increase establishment of seedling.

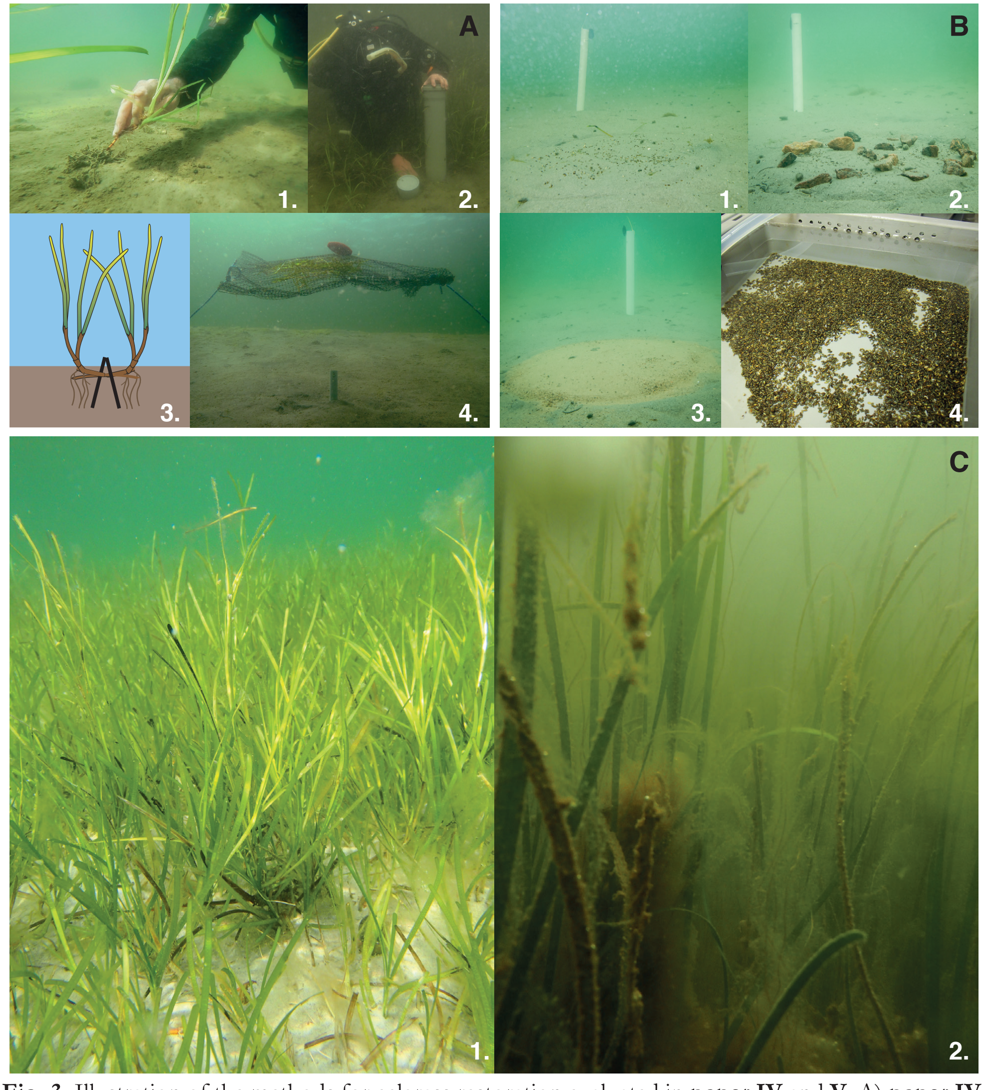


Fig. 3. Illustration of the methods for eelgrass restoration evaluated in **paper IV** and **V**. A) **paper IV**; 1. The single-shoot method (Orth et al. 1999), where single transplants are planted without sediment, 2. The plug method (Fonseca et al. 1998), where transplants remain inside intact sediment cores from the donor meadow 3. The anchoring method (Davis and Short 1997), where two single transplants are anchored in the sediment using bamboo skewers and 4. The method of distributing seeds from reproductive shoots within mesh-bags (Pickerell et al. 2005). B) **paper V**; 1. The control treatment with seeds distributed on top of the sediment to mimic natural seed dispersal, 2. The rock treatment, which aims at producing vortices in the flow, that could help trap and bury seeds, 3. The sand treatment, which aims at protecting against predation and transport by currents and 4. Showing seeds under storage conditions in the lab for planting in the spring. C) **paper IV** showing the morphology of shoots in the most divergent environments within the cross-transplantation experiment; 1. Shoots from the exposed-shallow site (1.0-1.3 m depth) with a mean leaf length of 23 cm and 2. Shoots from the sheltered-deep site (4.0-4.5 m depth) with a mean leaf length of 87 cm. Photos in A and B taken by E. Infantes and photos in C taken by L. Eriander.

PRESSURES FROM SMALL-SCALE EXPLOITATION

When the study performed in **paper I** was initiated the effects of shading by docks on eelgrass coverage had never been investigated in Scandinavian waters. Furthermore, the large-scale cumulative effects on eelgrass habitats from small-scale coastal development (i.e. docks and marinas) along the NW coast of Sweden were unknown. In **paper I** the local and large-scale impact on eelgrass from small-scale coastal development was determined and the effect of eelgrass presence and areal protection on the approval of dock construction was investigated in order to gain an understanding of the legal challenges that allow for exploitation of eelgrass habitats to continue along the Swedish NW coast.

The results from **paper I** reveal large negative effects from shading on the coverage of eelgrass underneath and adjacent to docks and marinas. The dock design (floating or elevated on poles) had a great influence on the extent of this negative impact. Floating docks always displayed zero coverage of eelgrass underneath and a significantly lower eelgrass coverage at all sampling distances from the dock (on average 64% reduction in coverage), compared with docks elevated on poles (on average 42% reduction in coverage; Fig. 4A). The correlation between eelgrass coverage and light observed in the study suggests that the negative impacts on eelgrass was driven by shading from docks (and boats) and possible by reduced water quality around floating docks. Floating docks generally had a stronger shading effect on the bottom compared to elevated docks, and a significant positive correlation was seen between dock height above the water surface and eelgrass coverage below docks. Furthermore, the difference could be explained by additional shading from boats, which were >5 times more numerous around floating docks. This was supported by the observation of a distinct boarder between low eelgrass coverage and 100% coverage at a distance of 7-8 m from the edge of floating docks, which coincides with the length of many boats (Fig. 4B). Also, the water column light attenuation coefficient (K_d) was generally higher in the waters surrounding floating docks. The reason behind this is not clear, but could potentially be a result of higher boating activity or movement of floating docks which could create increased resuspension (Yousef 1974, Abul-Azm and Gesraha 2000, Kelty and Bliven 2003). Although these effects were not studied, the results suggest that floating docks or docks with many boats could have considerable greater negative effects on bottom vegetation, than those caused by dock-shading. Previous studies from the USA have demonstrated similar negative effects from docks, where floating docks substantially decreased the eelgrass coverage or caused a complete loss of eelgrass on the bottom below (Fresh et al. 1995, Burdick and Short 1999, Fresh et al. 2006). Due to these detrimental effects, several guidelines regarding dock construction have been issued in the USA, which states that floating docks should be avoided if possible and that docks should be located a minimum of 1.5 m above the mean high water level to minimize the negative impacts from shading on seagrass (Shafer and Lundin 1999, NOAA 2014). In Sweden, no official guidelines exist regarding dock construction. Furthermore, the analyses of applications for dock construction performed in **paper I** demonstrate that there is lack of consistent requirements issued by the authorities regarding dock design, with no requirements or restrictions relating to floating docks. The study also reveal that floating docks were the most common design within applications to build new docks and amongst new constructions. Also, 23% of all modifications of docks consisted of a change from elevated to floating docks, indicating a preference and increasing trend for this type of dock design. This is worrying and the results from **paper I** indicate a need to develop guidelines for construction of docks that minimize the negative effects from shading and where floating docks should be avoided over eelgrass bottoms.

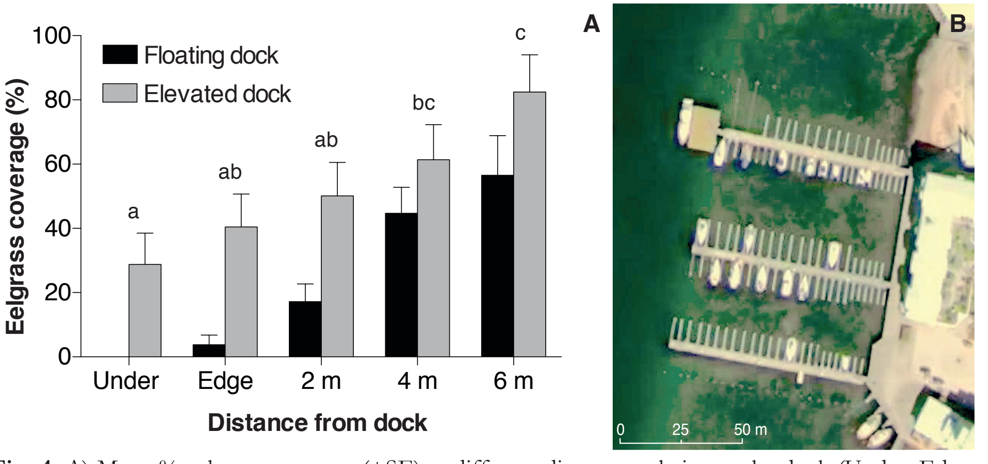


Fig. 4. A) Mean % eelgrass coverage (+SE) at different distances relative to the dock (Under, Edge, 2, 4 and 6 m from dock edge) from **paper I**. Different letters above bars indicate significant differences in coverage between the different sampling distances (Tukeys HSD P <0.05). The difference between dock designs (floating and elevated) was significant independent of distance from the dock (**paper I**; Table 2). B) Eelgrass coverage (seen as green patches at 0-75 m from the shoreline) from aerial photography around three floating docks on the NW coast of Sweden, demonstrating the reduced coverage adjacent to docks in areas occupied by boats, and the sharp border between low and high density in between docks.

Few studies have gone beyond the local scale and investigated the cumulative large-scale impacts from docks and marinas on eelgrass. The results from **paper I** demonstrate that approximately 58 ha of eelgrass have been lost and that an additional area of 422 ha of eelgrass habitat have been negatively affected by docks and marinas on the Swedish NW coast. This area may appear small compared to historical eelgrass losses (Baden et al. 2003, Nyqvist et al. 2009, Moksnes et al. 2016a), but corresponds to over 7% of the present eelgrass distribution of approximately 6300 ha on the NW coast of Sweden (E. Lawett unpubl. data). Furthermore, in areas that have suffered particularly high losses of eelgrass, the proportional impact may be even greater, which is true for the southern parts of the NW coast. Here only around 13 ha of eelgrass remain today (>98% loss since the 1980s; **Paper III**), which is approximately the same size as the area negatively affected by docks and marinas in the same region today. Extensive monitoring of light conditions performed in this region and comparisons with the historical depth distribution of eelgrass indicate that the potential maximum depth distribution has decreased locally with 1-2 m (**Paper III**), which could leave the remaining eelgrass even more susceptible to additional shading from docks.

The assessment of dock applications presented in **paper I**, regarding exemptions from shore protection and notifications of water operations, showed a general absence of eelgrass assessment in the applications and the decision processes for dock construction, where eelgrass was explicitly mentioned only in 12% of the cases where satellite inventories indicate a high likelihood of eelgrass presence. Furthermore, the confirmed presence of eelgrass had little influence on the decision, as 75% of applications were still approved. The explanation to this lack of assessment and consideration for eelgrass could be that applications are evaluated individually. On these terms, the lost value of ecosystem services is only related to the individual case, which means that the impact from a single dock could be considered relatively innocent. However, the mean size of docks accepted for construction was on average 80 m^2, and as demonstrated, the negative effects reach beyond 6 m from the dock edge.

The result from **paper I** also demonstrate that the presence of eelgrass (indicated by satellite image analysis) and direct legal protection of the area (i.e. nature reserves, EU Natura 2000 areas and national parks) had little positive effect on the protection of eelgrass habitats against exploitation (Fig. 5). The overall approval rate inside and outside of protected areas was 59% and 90%, respectively. In protected areas, the approval rate was higher in areas with eelgrass compared to areas without eelgrass (69 and 49%, respectively; Fig. 5). These results indicate that area protection rather than eelgrass is the governing factor that decrease the number of approved applications. However, the high approval within protected areas is surprising since the protection was clearly acknowledged within the decisions, meaning that no information gap exists regarding protected areas, as could be stated for the presence of eelgrass. That area protection has little impact on reducing coastal development is supported also by a previous study from one of the municipalities investigated in the study presented in **paper I**, where no difference was seen in the increase of docks built inside and outside protected areas between 1988-2008 (Hellström 2007).

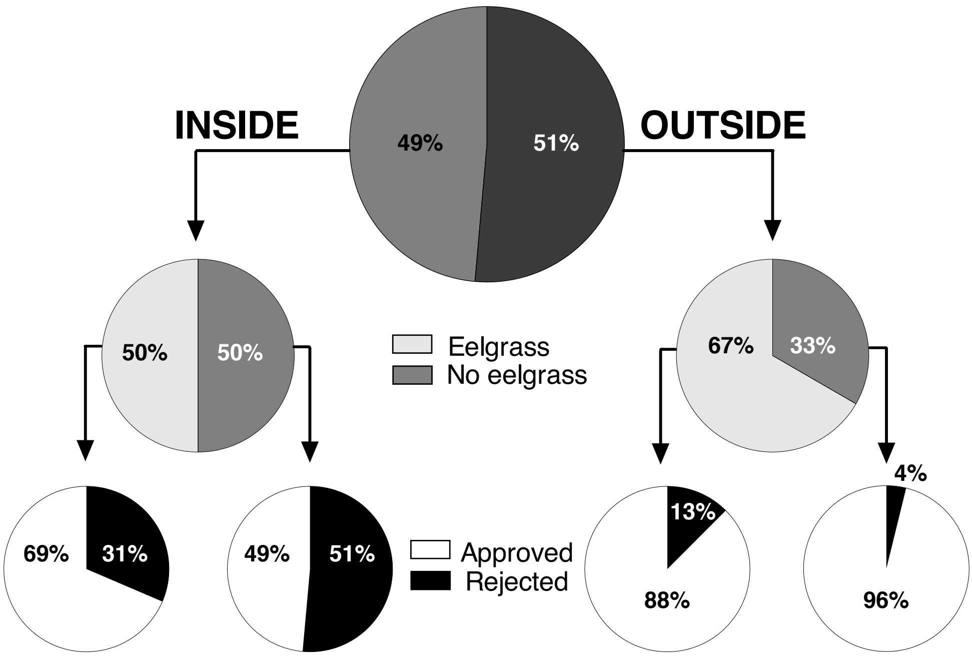


Fig. 5. Descriptive presentation of the applications for dock construction from **paper I** showing the proportion of applications inside and outside of protected areas (i.e. nature reserves, EU Natura 2000 areas and national parks) in the top pie, the percentage with and without eelgrass inside and outside of protected areas in the middle pies and the proportion of approved and rejected applications within each category in the bottom pies.

These results are in conflict with national guidelines issued by the Swedish Environmental Protection Agency, which state that exemptions from the shore protection should generally not be granted inside protected areas or areas with eelgrass (SEPA, 2012). The in-depth analysis of decisions for approving dock construction in protected areas, indicates that previous development in an area can influence the decision. Approval of construction in such areas are sometimes justified by the argument that the area is already exploited in such a way that it is of no value to the purpose of the shore protection. However, based on the results from the ecological impact study presented in **paper I**, it could be strongly questioned if a habitat adjacent to an existing dock or marina has no value to the purpose of the shore protection, which is also to preserve the living conditions for plants and animals (SEC; chapter 7, section 13), since eelgrass can still exist at high densities between docks (Fig. 4B). If previous exploitation in an area is considered a valid reason to grant an exemption from the shore protection, this is alarming since it would allow coastal exploitation to spread unimpeded. Moreover, the results presented in **paper III** demonstrate that water transparency can decrease with over 1 m when an eelgrass meadow is lost, due to increased sediment resuspension. Such changes likely occur at a threshold size of the meadow, when it becomes too small to stabilize the sediment, after which the remaining eelgrass is quickly lost by the decreasing water quality (Duffy et al. 2014, Maxwell et al. 2016). Thus, in areas where eelgrass has already suffered large losses and is presently fragmented, a relative small-scale exploitation of eelgrass may push the system over the tipping-point, causing an accelerating loss of eelgrass.

Overall the results presented in **paper I** indicate that small-scale coastal development is allowed to continue despite the presence of national and international environmental objectives which promote: eelgrass protection (OPSAR 2012, HELCOM 2013), avoidance of further degradation of coastal waters, including the loss of marine flowering plants (angiosperms; WFD; 2000/60/EC) and maintenance of ecosystem services and high biodiversity within shallow coastal environments (Anon. 2012). The results also show that the cumulative number of docks along the coast has a significant effect on eelgrass coverage. Despite this, the current Swedish management of coastal exploitation does not hinder further degradation, although there are tools within the present Swedish legislation to be used and, at least regarding shore protection, clear guiding documents issued by the Swedish EPA, on how to apply the legislation (SEPA 2012). The issues with the current management therefore appear to result from problems in applying the legislation, where small impacts on eelgrass from docks do not mediate a sufficient consideration. The recommendations for improving management of eelgrass, based on the results in **paper I** include a stronger compliance to national guidelines, which clearly identify eelgrass habitats and protected areas as environments where exemptions from the shore protection should generally not be granted (SEPA, 2012). To fulfil these recommendations and make defensible decisions regarding dock construction, there is a need for authorities to increase the demand for information provided by the applicants, e.g. regarding bottom conditions, where all negative impacts on eelgrass should be reported. Here, available satellite data could work as an effective tool for applicants and managers. Furthermore, an increased restrictiveness is needed for approving dock constructions when eelgrass habitats are present, also in areas with previous development. For protected areas, it may be important to revise regulations and goals of the nature reserve to ensure it provides eelgrass and other important marine habitats with protection from destructive human activities.

There is also a need for managers on a local and regional level to consider large-scale cumulative effects and apply a landscape perspective to coastal development. To facilitate this, each small-scale project should be related to the spatial distribution of important habitats and other human activities along the coast. This type of *marine spatial planning* has started to emerge as an important tool to achieve sustainable use of marine resources (Douvre 2008) and is also a requirement by the EU Marine Spatial Planning

Directive (MSPD; 2014/89/EU). For eelgrass this would entail mapping of the eelgrass distribution and all coastal exploitation in the affected region, and assessing the relative impact of the construction on both the local and regional eelgrass populations.

Furthermore, in cases where construction has been approved, compensatory restoration of eelgrass could function as a measure to prevent net-losses of eelgrass habitats along the coasts. This is also in line with requirements to achieve national and international goals of protection and no-net-loss of eelgrass habitats (Anon. 2012, OSPAR 2012, HELCOM 2013). In the USA, the U.S. Clean Water Act has acknowledged that small damages to important marine habitats can lead to large-scale effects, through a no-net-loss policy. With reference to this policy, the California eelgrass mitigation policy (NOAA 2014) requires compensation through restoration of eelgrass for all impacts larger than 10 m^2. Based on this policy a guideline for compensatory restoration of eelgrass in Sweden was recently developed, which recommend to use compensation for all exploitation cases where more than 100 m^2 of eelgrass is negatively affected (Moksnes et al. 2016a).

Finally, if we are to meet the increasing demand for boat space along the coast without further degrading coastal habitats, there is a need to move away from the perception that everyone has the right to a private dock or keeping the boat in the water when it is not in use. This could possibly be accomplished through information campaigns about the benefits of renting boats, or keeping boats out of the water when not in use (which also decrease the problems with fouling) and through the installation of more commonly accessed boat ramps with parking space for trailers, or marinas with boat storage on land and launching assistance.

REQUIREMENTS AND CHALLENGES FOR EELGRASS RESTORATION

Proper site selection is the key for performing successful restoration of eelgrass, where environmental conditions need to be evaluated to ensure that the site can sustain eelgrass growth (Fonseca et al. 1998, van Katwijk et al. 2015). Literature regarding environmental requirements for eelgrass growth and site selection have identified several key parameters that needs to be considered, including water quality conditions, sediment characteristics, wave exposure and biological disturbances (e.g. Dennison et al. 1993, Fonseca et al. 1998, Koch 2001, Short et al. 2002, van Katwijk et al. 2009, Fonseca 2011). However, recommendations of threshold conditions for these variables are not consistent in the literature, which suggest that requirements for eelgrass growth may vary depending on the region. Furthermore, challenges for eelgrass restoration often depend on the local conditions in the area (Fonseca 2011, Cunha et al. 2012, van

Katwijk 2015), which is why a local and regional understanding of environmental requirements and threats to eelgrass growth is eminent for successful restoration. Some of the potential challenges for eelgrass restoration along the NW coast of Sweden include a short growth season, ice cover and scouring in shallow areas during the winter and sediments with high clay- and organic content. Through the studies performed in **paper II**-**V** the environmental requirements and challenges for eelgrass restoration along the NW coast of Sweden were investigated. These studies included sampling of physical and biological site characteristics and monitoring of environmental variables and eelgrass transplant survival and growth. Studies were performed both in potential restoration sites, where historical losses of eelgrass have occurred, and in areas which today sustain healthy meadows. Furthermore, a laboratory study was performed to study the effects of light and temperature on eelgrass acclimatization and growth.

Light

Insufficient light conditions are one of the major drivers behind eelgrass loss and failure of restoration efforts (Moore et al. 1997, Fonseca et al. 1998, Waycott et al. 2009, van Katwijk et al. 2015) and this variable was monitored in several of the studies included in this thesis. In **paper II**, a laboratory study was designed to test how different light levels affected growth and survival of single adult eelgrass transplants. The results from this study demonstrate that although transplants were able to survive and grow at light levels down to 3 mol photons m^{-2} day^{-1}, the vegetative reproduction through lateral branching was significantly reduced below 5 mol photons m^{-2} day^{-1} (Fig. 6A). These results suggest that 3 mol photons m^{-2} day^{-1}, which corresponds to approximately 11% of the surface irradiance (SI) over the growth season (May-October) in the study region is within the minimum light requirement (MLR) for growth of eelgrass transplants, which is consistent with previous laboratory studies (Olesen and Sand-Jensen 1993). However, levels above 5 mol photons m^{-2} day^{-1} or 18% of SI is required for a high rate of lateral shoot production. The production of new shoots through vegetative reproduction is essential in any restoration project since the goal is to increase the density of sparsely planted shoots to densities equivalent to natural meadows, which in Scandinavian waters is mainly accomplished through vegetative reproduction rather than sexual (Olesen and Sand-Jensen 1994, Källström et al. 2008, Olesen et al. 2016). Furthermore, since winter mortality in this region can result in 59-76% shoot loss (**paper IV**), lateral shoot production (and storage of carbohydrates, *see below*) during the first season may be essential for reducing the risk of complete transplant mortality over the winter. Similar to the general difference in morphology between eelgrass growing in shallow and deep areas, reduced production of lateral branches under low light conditions is likely an acclimatization response by the plant to available light, where more energy is allocated towards vertical growth rather than vegetative reproduction, which has also been demonstrated in natural eelgrass meadows (Olesen et al. 2016). However, this is the first study which investigates how the branching frequency of adult eelgrass transplant changes in response to light (seedlings; Bintz and Nixon 2001, Ochieng et al. 2010).

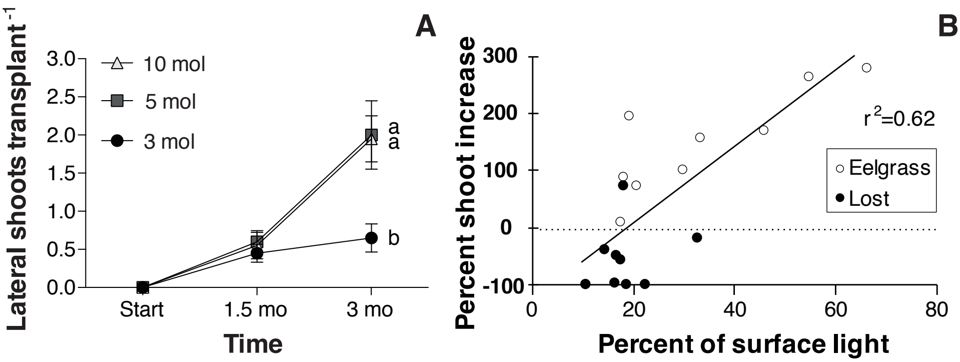


Fig 6. A) Results from **paper II** showing the mean number of lateral shoots per transplant (±SE) at the start at 1.5 months and at 3 months in to the experiment for the 3 light treatment (n=10). Different letters next to the mean value indicate significant differences between treatments at the specific sampling time ($p<0.05$; Tukey's HSD). B) results from **paper III** showing the relationship between the average percent of surface light reaching the bottom (May-September) and the average percent shoot increase of transplanted eelgrass shoots between July-September. The sites are separated into areas where eelgrass was present or lost at the time of planting. The trend-line show a significant linear relationship.

The eelgrass transplantation trials performed under *in situ* conditions in **paper III** and **IV** confirm this correlation between light levels and the rate of shoot increase, with positive growth generally occurring at light levels above 20% of SI (Fig. 6B). Furthermore, the results from **paper IV** demonstrate that long-term survival (over 2 growth season) and a large positive shoot increase (50-550%) requires light levels between 30-66% of SI, while light levels of 18% SI resulted in a (40%) loss of shoots. These results indicate that the MLR for positive growth is higher under field conditions compared to laboratory conditions. One explanation to this could be the shorter growth season within areas that experience low light conditions, as demonstrated in **paper IV**. In this study, the site receiving 18% of SI was located at a depth of 4.0-4.5 m and had a growth season which was ~2 months shorter compare to shallow (1.0-1.5 m depth) sites. Therefore, a combination of light limited growth, less time to grow and high winter losses could explain why long-term survival under field conditions requires higher light levels. Furthermore, since light levels fluctuate in the field, variation around the mean values, could result in periods with light levels below optimal conditions for eelgrass growth and thereby explain the estimated higher light requirement. Such fluctuations in light could be caused by pulses of turbid water, as observed in **paper III** or variations in phytoplankton production (Greve and Krause-Jensen 2005). The importance of variations in light for eelgrass growth is supported by previous studies which suggest that pulses of increased light attenuation, rather than the mean light condition over the season are important for determining the maximum depth distribution of eelgrass (Zimmerman et al. 1991, Moore et al. 1997). Furthermore, high turbidity and fine sediments, particularly within sites investigated in **paper III**, may also have resulted in a higher light requirement by eelgrass transplants, as sedimentation on leaves can significantly reduce the amount of light available to the plant (Tamaki et al. 2002). Also, light requirement has been seen to increase in more turbid waters for seagrass in general (Duarte et al. 2007) and for eelgrass in areas where sediments have a high content of clay and organic compounds (Kenworthy et al. 2014).

Unlike vegetative shoot transplants, seed shoots displayed a positive growth at light levels between 13-18% of SI, at 4-5 m depths (**paper IV** and **V**). However, a reduced number of leaves (on average 3 leaves shoot^{-1}) were seen on shoots growing at 13% of SI (**paper V**), which could indicate light stress (Carr et al. 2012, **paper II**, **paper III**). Furthermore, great losses of seed shoots occurred over the winter, with a 50% loss of shoots measured after the second growth season, suggesting that these light conditions were not sufficient to allow long-term survival. Similar results have been seen during natural seed establishment in Denmark, where seedlings managed to germinate and established at depths >6.2 m, but with only 8% survival the first year (Olesen et al. 2016).

The estimated light requirement by eelgrass varies substantially in the literature between approximately 11-34% of SI and 1.2-12.6 mol photons m^{-2} day^{-1} (Olesen and Sand-Jensen 1993, Dennison et al. 1993, Bintz and Nixon 2001, Gattuso et al. 2006, Thom et al. 2008, Ochieng et al. 2010), which demonstrates the importance of performing local studies of eelgrass response to light and of light requirements for successful restoration. In summary, the results from **paper II**, **III**, **IV** and **V** suggests that restoration of eelgrass is generally not recommended in areas with average light levels below 18-20% of SI over the growth season and that light levels above 30% of SI might be required to ensure high rates of lateral branching and long-term survival. Furthermore, careful and continuous monitoring of light (*see* Box 3) should be performed before determining if a location is suitable for large-scale restoration of eelgrass.

Severe shading, carbohydrate storage and temperature

Apart from constant low light conditions as a possible cause behind transplant failure, transplanted or natural meadows are likely to experience periods with severe shading conditions lasting for days to months, for example due to shading by algae (Hauxwell et al. 2003), high turbidity (Moore et al. 1997, Cabello-Pasini et al. 2002) or low seasonal light conditions (Staehr and Borum 2011). Eelgrass survival during such events can be accomplished through the mobilization of carbohydrates stored in rhizomes, roots and leaves during favourable light conditions (Zimmerman et al. 1995, Alcoverro et al. 1999). In **paper II**, the ability of eelgrass transplants to store carbohydrates in the rhizomes under variable low light conditions was investigated. Furthermore, the carbohydrate concentration and survival of transplants was examined during severe shading conditions. The results from this study demonstrated that transplants were able to store carbohydrate equally well at light levels from 10 down to 3 mol photons m^{-2} day^{-1} (possibly achieved through the ability of shoots to acclimatize to variable light, *see below*). The survival during 3 weeks of severe shading was surprisingly high and the overall 50% drop in rhizome sucrose concentration over the same period, suggest that this was enabled through the use of stored carbohydrates. However, temperature conditions significantly affected the shoots ability to survive during severe shading, with 16% and 0.57% mortality at 20°C and 12°C, respectively over the same period. These results indicate that shading might be worse if it occurs during the peak growth season (July-August), when water temperatures are high, or if it co-occurs with periods when carbohydrate concentrations are naturally depleted (i.e. during early spring; Zimmerman et al. 1995, Vichkovitten et al. 2007 or following transplantation as demonstrated in **paper II**). The continuous flow-through of seawater from the Gullmars fjord ensured oxygenated conditions within mesocosms in **paper II**, which could explain the prolonged survival of shoots under severe shading. However, this might not be the case during sever shading in the field, where low oxygen conditions, e.g. due to high organic matter mineralization or high temperatures, can lead to rapid mortality and an increased problem with toxic sulphide intrusion in plant tissues (Holmer and Bondgaard 2001, Plus et al. 2003, Greve et al. 2005, Holmer et al. 2005, Pulido and Borum 2010).

At low light (3 mol photons m^{-2} day^{-1}) and high temperature (20°C) no negative effects were seen on survival of eelgrass transplants in **paper II**, suggesting that plants were still able to maintain a positive carbon balance, despite the faster increase in respiration rate relative to photosynthesis accompanied by higher temperature (e.g. Short and Neckles 1999, Lee et al. 2007, Staehr and Borum 2011). However, as demonstrated in **paper V**, the temperature within shallow bays on the NW coast of Sweden can reach 25°C over the summer months and several studies have reported negative effects on eelgrass morphology and survival at temperatures ranging from 25-30°C (Orth and Moore 1986, Touchette et al. 2003, Echavarria-Heras et al. 2006, Moore and Jarvis 2008, Moore et al. 2014). Furthermore, high temperature conditions can increase the risk of tissue anoxia in eelgrass (Greve et al. 2003) and increase the negative impacts on eelgrass from anoxic events (Pulido and Borum 2010). High temperature could therefore potentially become a problem for transplanted eelgrass in the field, especially if they coincide with periods of severe shading, as was shown in **paper II**.

The low winter survival of transplants observed in **paper IV** and **V**, particularly in deep sites (64-76% shoot loss), is likely a result of depleted carbohydrate reserves, where the shorter growth season in combination with low light conditions might have led to an inability of shoots to store sufficient amount of carbohydrates to survive the winter. Because of the shorter growth season in deep areas, plants likely need to utilize stored carbohydrates earlier in the season compared with shoots growing shallow. Furthermore, since temperature is still relatively high (15-20°C) towards the end of the growth season, this could increase the mortality rate of shoots under unsaturated light conditions (**paper II**). This suggestion is supported by the observed loss of shoots at the end of the growth season (between August and October) in the deepest site in **paper IV**, while shoots in the shallower areas continued to increase in numbers over the same period. The length of the growth season might therefore have important consequences for the carbohydrate stock of transplants and thereby affect their ability to survive the winter. Carbohydrate content in the rhizome at the end of the growth season could therefore be a good indicator of the ability of transplanted eelgrass to survive winter conditions, as have been demonstrated for the dwarf eelgrass, *Z. noltii* (Govers et al. 2014).

The winter survival of eelgrass transplants could further be affected by ice formation in shallow areas. Ice was present over the winter in both bays assessed in **paper IV**. The sampling of shoot density in plots after the winter suggests that some losses could be related to ice-scouring, since marking poles had moved and several plots, particularly in the shallow site of the sheltered bay, had suffered a complete loss of shoots. Thus, restoration should be avoided at depths <1 m, in order to minimize disturbance from ice.

Acclimatization

The ability of shoots to acclimatize to the environmental conditions at the restoration site is another important process during eelgrass restoration, which could possibly also affect the transplants ability to store sufficient amount of carbohydrates. Eelgrass plasticity has previously been demonstrated both within established meadows over the season (e.g. Olesen and Sand-Jensen 1994, Wong et al. 2013) and after transplantation between different environments (Schanz and Asmus 2003, Li et al. 2010). However, knowledge of the extent of and time required for this plastic response to occur is not well studied and could be essential when selecting donor material or the optimal time for planting, especially since close matching of donor material is not always possible. The acclimatization potential was studied both under laboratory conditions in **paper II**, where morphometrics and pigment content of leaves were measured over a period of 3 months under variable low light conditions and in **paper IV** where cross-transplantations were performed between environments which displayed large differences in the morphology of shoots (Fig. 3C). The results from **paper IV** demonstrate that eelgrass transplants have a strong capacity to adjust their morphology in order to acclimatize to new environmental conditions. At 14 months after transplantation, significant differences were seen in the morphology of shoots depending on the planting site. However, despite the dramatic differences in morphology at the time of transplantation, all shoots within a planting site had the same morphology independent of origin (Fig. 7A). As an example, shoots originating from the sheltered-deep site (at 4-4.5 m depth), displayed a mean maximum leaf length of 120 cm and 3 lateral branches along the rhizome when planted within its original site, but displayed a mean maximum length of 40 cm, with 19 lateral branches when planted in the shallow-exposed site (1.0-1.3 m depth) (Fig. 7A). This demonstrates that besides morphological changes, the growth strategy also changes during acclimatization to new environmental conditions, as was also shown by the significant difference in branching frequency in response to light in **paper II**. The baseline genetic survey performed in **paper IV**, further supports that the observed change in morphology of transplants was due to a plastic response, suggesting that donor plants do not have to exactly match the morphology of plants targeted for restoration.

The results from **paper II**, confirm the acclimatization capacity of these plants and further demonstrate that a response in morphology and pigmentation occur rapidly after transplantation to a new light environment. Within 1.5 months, significant differences were seen between transplants grown under 10 compared to under 3 mol photons m^{-2} day^{-1}. Plants in the lowest light treatment had significantly taller leaves, larger leaf area per weight and a higher concentration of pigments in the leaves (Fig. 7B). This is consistent with a photo-acclimatory response by plants to increase the light harvesting capacity relative to biomass, and thereby respiratory demand (Dennison and Alberte 1982, Olesen and Sand-Jensen 1993, Short et al. 1995, Bintz and Nixon 2001). The fast acclimatization response by these plants could further explain why no difference was seen in the capacity of transplants to store carbohydrates under different light conditions (**paper II**). The method assessment study with seeds in **paper V**, where reproductive shoots were harvested from a distant donor population at a depth of between 1.0-1.5 m, further supports the ability of eelgrass to acclimatize, since seedlings were able to grow from depths of 1-5 m, with significantly different morphology as a result of depth, 4 months after germination.

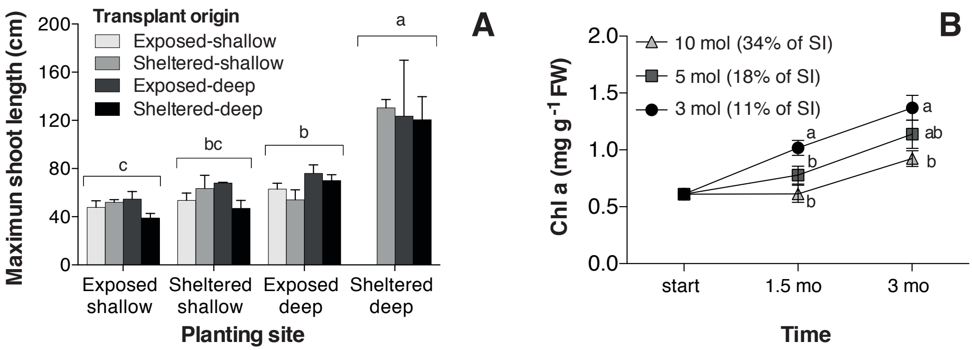


Fig. 7. A) Results from the cross-transplantation study with shoots in **paper IV** showing the mean maximum shoot length (+SE) of shoots collected from the 4 planting sites (exposed; shallow and deep, sheltered; shallow and deep), separated by transplant origin, at the final sampling 14 months after transplantation. Different letters above grids indicate significant different means depending on planting environment (SNK-test at $P < 0.05$; $n = 6$). B) Results from **paper II** showing the mean chlorophyll a concentration in leaves (±SE) at the start, at 1.5 months and at 3 months into the experiment for the 3 light treatment ($n=10$). Different letters next to the mean value indicate significant differences between treatments at the specific sampling time ($p<0.05$; Tukey's HSD).

Despite the strong ability of these plants to acclimatize to new conditions, the results from **paper IV** also suggest that cross-transplantation between highly divergent environments, in terms of light level should be avoided. This was evident from the complete mortality when shoots originating from the exposed-shallow site were planted in the sheltered-deep environment, where shoots naturally are >150% taller (Fig. 3C). This mortality however, did not occur until the winter, which suggests that plants were not able to fully acclimatize and store enough carbohydrates over the first season. This further emphasise the importance of monitoring test-planting until after the first winter, before evaluating the suitability of a site for restoration.

Sediment characteristics and hydrodynamics

Other factors which may influence the survival of transplants and the success of restoration efforts involves those relating to sediment characteristics. Previous studies have indicated that sediments with a high clay and silt content are unsuitable for eelgrass growth, but recommended threshold conditions vary between 20-70% clay and silt (Koch 2001, Short et al. 2002, Leschen et al. 2010). Furthermore, sediment with high organic content and reduced pore water exchange due to fine grain size can have high concentrations of sulphide (Holmer and Nielsen 1997, Koch 2001), which can be detrimental to the plants if they coincide with reduced light conditions (Holmer et al. 2005). This variability and possible site dependent effects indicate that local studies are needed to make assumptions regarding suitable sediment characteristics for eelgrass growth.

Sediment characteristics (i.e. grain size, organic content and water content) were measured in all studies performed under *in situ* conditions (**paper III**, **IV** and **V**) and in **paper III** sediment sulphides were measured together with intrusion of sulphide into transplanted eelgrass shoots to determine its effect on survival and growth. The results from **paper III** indicate a strong correlation between clay and silt content in the sediment and percent shoot increase of eelgrass transplants after 3 months (Fig. 8A). Similar to the study by Leschen et al. (2010), high growth generally occurred at silt and clay content below 30 to 35%, while no survival of shoots was found at levels exceeding 60%. The major reason for this correlation appears to be that light generally decrease (higher K_d) as the percentage of silt and clay increase (Fig. 8B), indicating that higher resuspension occurs with finer sediments, causing the observed negative effect on eelgrass growth (*see* the discussion on regime shift *below*). The study further demonstrates that organic content and sulphide content in the sediment porewater had little effect on growth and survival of eelgrass transplants, at the levels measured in **paper III**. Organic content did not correlate with the growth of eelgrass transplants and $F_{sulphide}$ and TS was lower (significantly so for $F_{sulphide}$) at sites which displayed low growth. Furthermore, the $F_{sulphide}$ in leaves in July displayed a significant positive correlation with the growth recorded in September (TS showed a positive trend). Healthy meadows are found at the study region in sediments with an organic content >25% (Jephson et al. 2008, Moksnes et al. 2016b), suggesting that high organic content by itself is not preventing eelgrass growth on the NW coast of Sweden. That eelgrass can grow in sediments with high organic content was also supported in **paper IV** and **V**, where both natural and planted eelgrass grew at 4-5 m depth in sediments with an organic content of 11.3%, and a water content of 74%. To our knowledge, eelgrass restoration has never previously been assessed in this type of environment, which are common within sheltered bays on the NW coast of Sweden. The results from **paper IV** and **V** demonstrate that both eelgrass shoots and seeds (shoots produced from planted seeds) can survive for several years in these type of sediments, despite the low light conditions (13-18% of SI; **paper IV** and **V**). Moreover, seedling establishment was higher here compared to shallower sites, suggesting lower seed loss and/or higher germination within deep organic rich sediments, which is consistent with results demonstrating a positive effect of anoxia, organic content and fine sediments on the germination of eelgrass seeds (Moore et al. 1993, Tanner and Parham 2010, Jarvis and Moore 2015). However, these type of sediments could potentially pose other challenges for restoration, including a reduced capacity of seedlings to anchor in the sediment (Lillebø et al., 2011). Furthermore, large-scale restoration using hand-planted shoots might be difficult, since the high water- and organic content make the sediment sensitive to resuspension, which reduce the visibility during planting (**paper IV**).

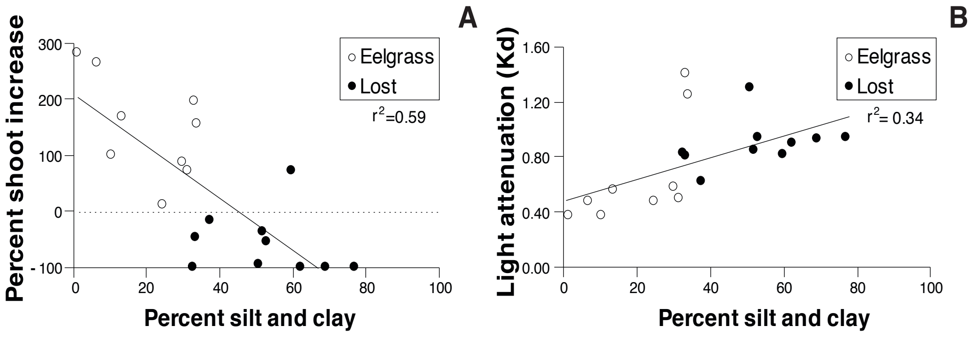
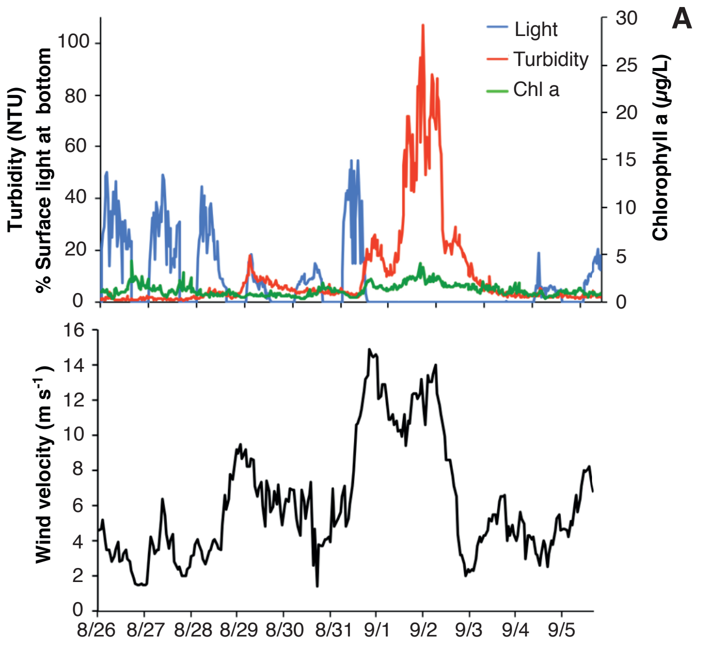


Fig. 8. Results from **paper III** showing the linear correlation between percent silt and clay and A) the shoot increase between July-September and B) the average seasonal light attenuation coefficient (K_d) in the water between May-September. The sites are separated into areas where eelgrass was present or lost at the time of planting. The trend-lines show significant linear relationships.

Sediment characteristics are highly driven by hydrodynamic exposure (i.e. waves and currents), where coarse sediments, low in organic content indicates high exposure and fine sediments, high in organic content, indicates low exposure, sheltered environments (Fonseca et al. 1983). The results from the method assessments performed in **paper IV** and **V**, show that hydrodynamic exposure could potentially affect the outcome of restoration efforts with shoots and seeds. In the cross-transplantation study, where shoots were transplanted between environments with different depth and exposure (**paper IV)**, high losses of transplants occurred when shoots from the sheltered-deep site were planted within the exposed-shallow site. This was likely a result of the taller shoots generating more drag, which would increase the risk of being up-rooted during strong wind events, in the shallow more hydrodynamic environment. Similar results have also been shown in the Wadden Sea, for *Z. marina* and *Z. noltii* transplanted from a sheltered to an exposed location (van Katwijk and Hermus 2000, Schanz and Asmus 2003). However, shoots generally performed well in the exposed-shallow site, which had a sediment consisting of 98.7% sand and an organic content of 0.4%, and anchoring trials performed in this environment did not increase the survival or growth of transplants. This is further supported by the results in **paper III**, where shoot anchoring did not increase survival and growth of transplants at depths between 1-2 m. This suggests that hydrodynamic exposure does not pose a problem for shoot transplants (of intermediate size; 30-50 cm leaf length) in environments with similar sediment composition. In contrast, seeds appeared to be more adversely affected by hydrodynamic exposure as indicated by the results in **paper V**, where >99% of seeds were lost in the same exposed-shallow site, and establishment increased with increasing depth and reduced exposure.

Regime shift

As the nutrient levels have decreased and the water clarity increased along the NW coast of Sweden since 1992 (Moksnes et al. 2015, Anon. 2016) recovery of eelgrass would be expected in areas where losses have occurred due to light limitation. However, the monitoring of eelgrass coverage performed in **paper III** demonstrates a continued loss within the southern parts of the NW coast, where the largest historical losses of eelgrass have occurred (Baden et al. 2003, Nyqvist et al. 2009). The results from **paper III** suggest that since 2004, an additional 290 ha of eelgrass have been lost from this area, and only an estimated 2% of historical meadows remain today in the most affected areas. Furthermore, despite the general increase in water clarity along the coast, results from continuous light monitoring in these areas reveal that the theoretical maximum depth distribution (based on the requirement of 20% surface irradiance) has decreased locally with 1-2 m in areas which have lost large meadows, and that light levels at historical eelgrass areas are generally below 20% also in the shallower areas (Fig. 6B). Furthermore, the results from test-planting of eelgrass shoots (**paper III)** and seeds (**paper V)** in these areas suggest that eelgrass can no longer survive at depths where it grew historically. Measurements of chlorophyll a at multiple sites in this region and monitoring of turbidity, chlorophyll a and light during one month at one historical eelgrass area indicates that wind- and wave driven local resuspension of sediment, rather than eutrophication driven phytoplankton production is the main cause behind the high turbidity and low light conditions in areas where eelgrass have been lost (Fig. 9A). The unusually high content of silt and clay (including glacial clay) in these sediments (33-77%) appears to makes them sensitive for resuspension, allowing moderate wind events to create plumes of turbid water that decrease the light conditions locally for days, as supported by the correlation between silt and clay content, attenuation of light and the growth and survival of eelgrass (Fig. 8). Test-planting of eelgrass shoots and seeds in these areas (**paper III** and **paper V**) further suggest that disturbance from bottom drifting algal mats prevent eelgrass survival. These algal mats consist primarily of perennial fucoid species, which today cover large areas of the shallow bays in the southern parts of the NW coast (Fig. 9B). Through their movement over the bottom these mats can cause up-rooting of transplanted shoots or seedlings, as have also been demonstrated from studies in Denmark (Valdemarsen et al. 2010).



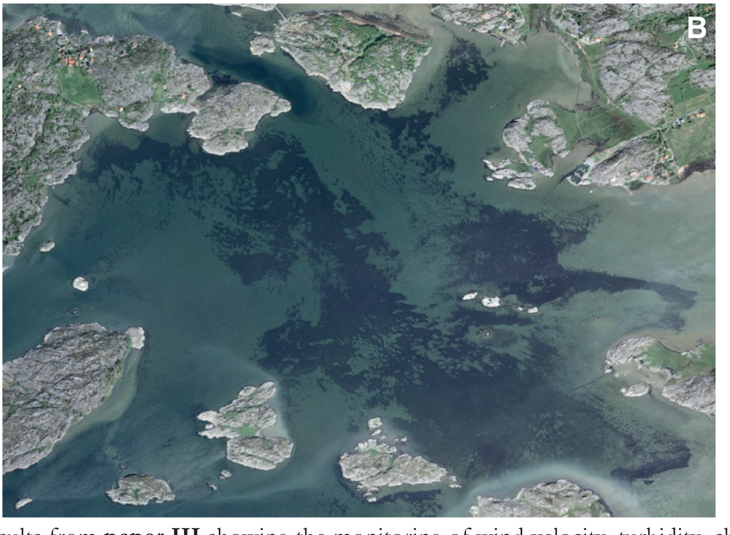


Fig. 9. A) Results from **paper III** showing the monitoring of wind velocity, turbidity, chl a and light during a wind event at a site which has experienced loss of eelgrass meadows. During a strong wind event on September 1, with westerly winds at around 14 m s^{-1}, turbidity peaked to around 80 NTU and light intensity at the bottom decreased to close to zero for 3 days. Levels of Chl-a remained relatively stable around 2-4 mg l^{-1} during the whole period, suggesting that sediment resuspension is the cause behind the low light conditions. B) Showing a shallow (<2.5 m) bay in the southern parts of the Swedish NW coast, where losses of a >200 ha eelgrass meadow have occurred since the 1980s. The dark areas on the bottom are drifting algal mats consisting primarily of perennial fucoid species. Orthophoto from: Lantmäteriet/metria 2014.

Overall, the results from **paper III** suggest that a local regime shift has occurred after eelgrass beds have been lost in the study area (see Box 2), where sediment resuspension and drifting algal mats prevent natural recovery of eelgrass and make restoration very difficult. A similar type of regime shift has occurred within the Dutch Wadden Sea (van Katwijk et al. 2000, van der Heide et al. 2007), which has experienced large losses of eelgrass, and where the light conditions remain deteriorated, despite efforts to reduce the nutrient load, and eelgrass beds have failed to recover despite restoration efforts. Furthermore, these drifting algal mats may also strengthen the turbid regime under which eelgrass growth is prohibited, since they can increase sediment resuspension through physical abrasion (Canal-Vergés et al. 2010). Therefore, it might be important to, not only study the co-occurrence of feedback mechanisms that keep an environment locked in an undesirable state, but also the interaction between these mechanisms. The ongoing loss of eelgrass shown in **paper III**, despite of the decreasing nutrients loads, indicates that this regime shift is self-generating and spreading. It is therefore critical that management efforts focus on the protection of the remaining eelgrass beds, since further losses may be irreversible over the foreseeable future and affect the water quality negatively, also in neighbouring areas. Furthermore, there is a need to incorporate feedback mechanisms within conservation and restoration of eelgrass, as suggested in the review by Maxwell et al. (2016).

RESTORATION METHODS

Another important aspect of eelgrass restoration includes the selection of appropriate techniques for planting. Historically, the most common methods have included transplantation of vegetative shoots (Fonseca et al. 1998, 2011, van Katwijk et al. 2015), but in the last 20 years, restoration methods with seeds have been developed and successfully used in some areas (Granger et al. 2002, Pickerell et al. 2005, Golden et al. 2010, Orth et al. 2012). However, suitable and efficient methods for large-scale restoration of eelgrass may vary depending on site-specific characteristics of the area targeted for restoration, e.g. due to differences in wave exposure, water quality conditions, sediment conditions or associated fauna (e.g. Fonseca et al. 1998, van Katwijk and Wijgergangs 2004, Golden et al. 2010, Leschen et al. 2010). Local studies and method assessments could therefore increase the chances of performing successful restoration. So far little information has been available regarding different methods for eelgrass restoration in high-latitude areas (*see* Christensen et al. 1995 for small-scale transplantation trials with eelgrass shoots in Denmark). In the studies performed in **paper IV** and **V**, different methods for planting eelgrass shoots and seeds were assessed with the overall goal of finding suitable and efficient methods for large-scale restoration of eelgrass along the NW coast of Sweden.

Shoot methods

In **paper IV**, different methods for planting vegetative eelgrass shoots were assessed. These methods involved transplantation of shoots within intact sediment cores according to the plug method (Fonseca et al. 1998; at a shoot density of 52 shoots m^{-2}) and without sediment according to the single-shoot method (Orth et al. 1999; at a shoot density of 16 shoots m^{-2}; Fig. 3A). Shoots were cross-transplanted between 4 sites with different depth and exposure conditions according to the two methods. Furthermore, a shoot anchoring method (Davis and Short 1997; with a shoot density of 32 shoots m^{-2}; Fig. 3A) was assessed in the exposed site, to test whether anchoring would increase the initial shoot survival. The results from **paper IV** demonstrate that transplanted eelgrass shoots have the potential to grow and spread rapidly when environmental conditions are suitable, with an increase from 7.5 m^2 of sparsely planted eelgrass (at a shoot density of 16-52 shoots m^{-2}) to between 26-46 m^2, at a shoot density similar to natural beds 27 months after transplantation in the shallow sites. Significant differences were seen in the shoot increase between the two unanchored methods, where single transplants without sediment grew faster at all sites compared with shoots transplanted in sediment plugs. The average increase in shoot numbers were 424 and 120%, for the single-shoot and plug method, respectively, from start to the final shoot-count, 14 months after transplantation (Fig. 10). These results are in contrast to most studies, which suggest that transplantation within sediment is less stressful for the plant, since shoots are left in an undisturbed rhizosphere (Phillips 1990, Fonseca et al. 1998). The reason behind these results are not clear, but could be associated with competition for space and resources before rhizomes and roots have expanded outside of the plug. This could explain the lag-period in growth observed amongst shoots planted according to the plug method, which did not experience a positive growth until >2 months following transplantations (Fig. 10). This initial lag-period could also explain differences between the two methods the second growth season, since lower shoot increase during the first season would result in fewer shoots in plots after winter losses, and could possibly also have affected the ability of shoots to store carbohydrates over the first growth season. The results therefore indicate the importance of growth during the first season following transplantation. In addition to the lower growth rate, the plug method was also more labour intensive, requiring 2.5 x more time for harvest and planting compared to the single-shoot method, and resulted in larger impacts on the donor meadows, with holes left in the sediment. The single-shoot method did not result in any visible negative effects on donor meadows, and additional studies have demonstrated that 40% of the shoots in a meadow can be harvested according to this method without negative effects on shoot density 4 months after harvest (Moksnes et al. 2016b).

The shoot anchoring-method tested in the exposed site demonstrated that transplantation of twice as many shoots (as the single-shoot method) and anchoring of rhizomes did not increase the survival or proportional growth of transplants. These results suggest that transplantation of twice as many shoots may have led to competition between transplants, which resulted in the lower proportional growth. Previous studies assessing anchoring of shoots according to different methods further reveal that shoots planted according to the single-shoot method have an anchoring strength equivalent to natural meadows ten days after transplantation (Moksnes et al. 2016b), suggesting that additional anchoring may be excessive under the range of physical conditions assessed in **paper IV** and **III**, as long as planting is performed under calm weather conditions.

The results from **paper IV**, further demonstrate large differences in growth between shallow and deep sites (Fig. 10). Although this difference was depending on the origin of shoots (*see* Fig. 4 in **Paper IV**), the overall average shoot increase from start to the final sampling, 14 months after transplantation was 528% and 550% in the shallow sites (Fig. 10A,B) and 51% and -40% in the deep sites (Fig. 10C,D). The results therefore suggest that restoration of eelgrass might be difficult within deep areas (>3 m with light levels <30% of SI), where the rate of vegetative reproduction is light limited. However, shoots transplanted according to the single-shoot method within shallow sites, produced on average 4.5 new lateral shoots from June to October the first growth season, based on the average increase of shoots in plots. A similar rate was also seen in the laboratory study in **paper II**, where 2.0 new lateral shoots were produced under the high and mean light treatment over a period of 3 months. These rates are high compared to those described for established meadows in the high latitude north (annual rates of 0.6-1.5 branches shoot^{-1}; Olesen and Sand-Jensen 1994, 0.009 branches shoot^{-1} day^{-1}; Olesen et al. 2016). The high growth rates during transplantation likely result from a lack of conspecific competition for nutrient and light, when shoots are sparsely planted within an environment not previously occupied by vegetation. This is supported by previous studies which have demonstrated that the highest production of branches within natural meadows occur early in the growth season, when light levels are high and the density of the meadow is low, and decline later in the summer as a result of self-shading, when the density of the meadow increases (Olesen and Sand-Jensen 1994).

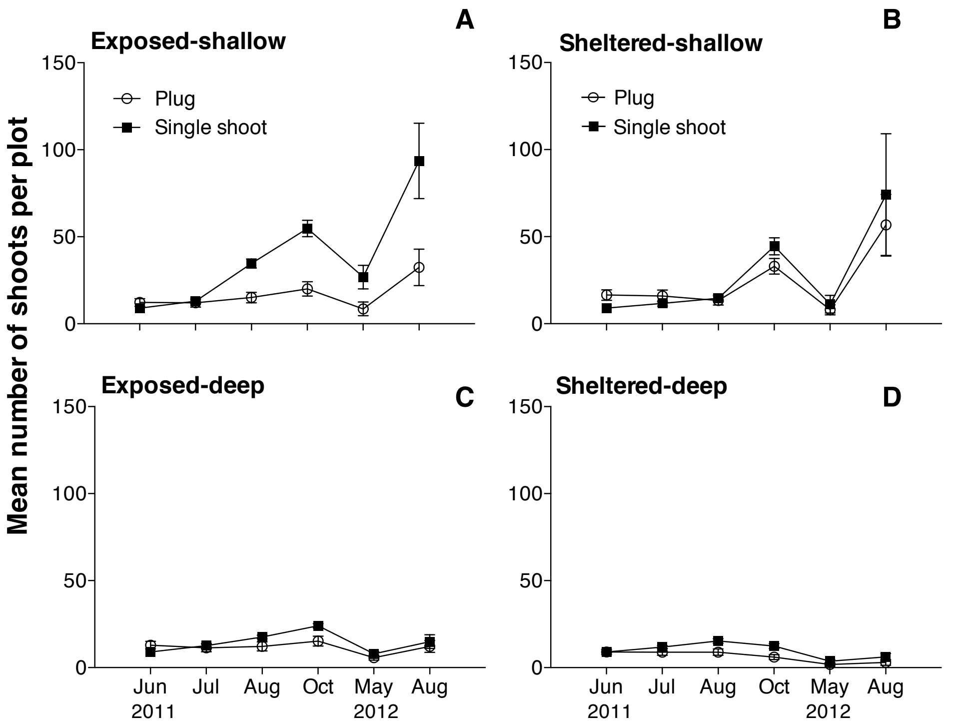


Fig. 10. Result from the cross-transplantation study in **paper IV**, showing the mean number of shoots per plot (±SE) at the start of the experiment (June-2011) and 1, 2, 4, 12 and 14 months after transplantation, at the 4 planting sites, A) Exposed-shallow, B) Sheltered-shallow, C) Exposed-deep and D) Sheltered-deep and according to the two planting methods (independent of origin; n=12; Fig. 3A). The graph is modified from Fig. 3 in **paper IV**.

Furthermore, growth may also benefit from the long summer days at this latitude, together with relatively high temperature within shallow areas (15-25°C; **Paper V**). During the peak growth season (July-August) the two shallow sites in **paper IV**, experienced light levels >100 µmol photons m^{-2} s^{-1} for 10-13 hour each day. These results suggest that lateral branching during transplantation within shallow areas are likely to have a more direct relationship to light at the surface during the first season, when density of transplants is still low, allowing for a rapid increase in shoot numbers. It could therefore be an advantage to plant shoots according to the single-shoot method (Orth et al. 1999), one by one, with relatively large distances (25 cm) between plants, since shoots are able to grow to high densities before the first autumn following transplantation. These recommendations differ from other studies which suggest transplantation of shoots in groups or bundles (Merkel 1988, Davis and Short 1997, Fonseca et al. 1998).

Overall, the results from **paper IV**, demonstrate that adult eelgrass shoots have the potential to be used for large-scale restoration of eelgrass on the NW coast of Sweden. They further suggest that transplantation of shoots at a density 16 shoots m^{-2} is recommended for restoration in shallow habitats (1-3 m) with the range of physical conditions assessed in the paper.

Seed methods

Restoration with seeds has the potential to become a cost-effective method for large-scale restoration of eelgrass (Marion and Orth 2010), since large quantities of seeds can be collected relatively easy, and spread over large areas, with less effort compared to hand-planting of shoots. The results from **paper IV** and **V** demonstrate that it is possible to use seeds for eelgrass restoration along the Swedish NW coast. However, great losses of seeds constitute a problem for the use of this method for large-scale restoration. In **paper IV** seeds distributed from mesh-bags (Pickerell et al. 2005; Fig. 3A) was assessed within the 4 sites. In **paper V**, 3 methods for seed planting were assessed (Fig. 3B), to determine suitable methods and to identify the main causes for seed and seedling losses.

The results from **paper V**, demonstrate that high losses of seeds occur over the winter, where only 0-1.5% of seeds remained within the sediment during spring (8 months after planting), at depth between 1-3 m (Fig. 11A). However, significantly more seeds remained within the sediment at 5 m depth, on average 9-41% (Fig. 11A). The establishment of seedlings, sampled in June, was generally low, but also increased with depth, from on average 0.5% at 1-2 m depth to 4.3% at 5 m depth (Fig. 11B). At the depths recommended for restoration along the NW coast of Sweden (1-3 m depth), these results demonstrate establishment rates, which are low compared to earlier studies (<4%; Golden et al. 2010, 5-7%; Orth et al. 2003, Pickerell et al. 2005, Marion and Orth 2012). The increased establishment with depth is likely explained by the higher seed retention at the deeper sites, and this in turn could be explained by hydrodynamics (as mentioned in the discussion *above*), where transport of seeds by waves and currents could be a major cause behind the high loss within shallow sites. This is supported also by previous studies from Denmark where high losses (98%) of seed mimics was demonstrated during a wind event in a similar shallow habitat (Delefosse and Kristensen 2012). Bioturbation may further explain the high losses of seeds from shallow site in **paper V**, as lugworm (*Arenicola marina*) abundance was high (18 individuals m^{-2}) and densities of >10 individuals m^{-2} have the ability to bury seeds deeper than 6 cm over a period of 10 months (Valdemarsen et al. 2011, Delefosse and Kristensen 2012), which is below the limit for successful germination (Greve et al. 2005, Jarvis and Moore 2015).

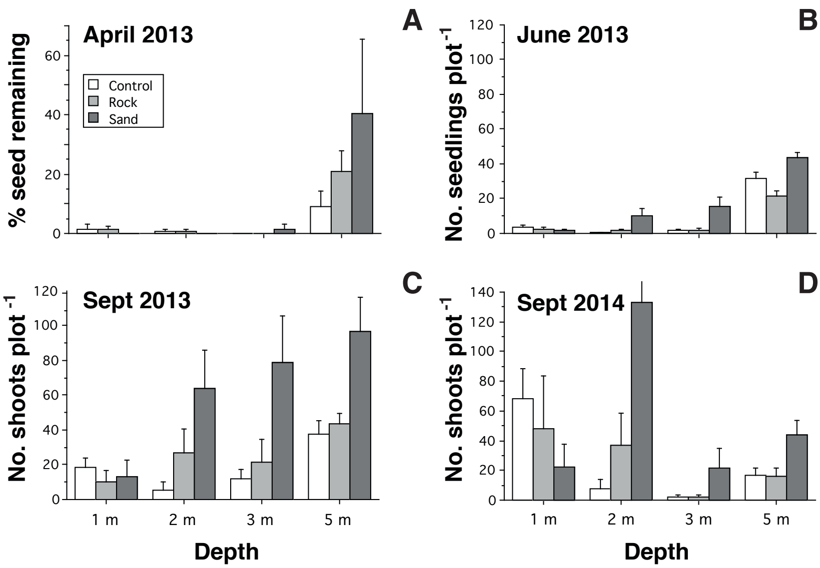


Fig. 11. Result from the seed planting study in **paper V**, showing mean (+SE) A) percent of seeds remaining in the sediment after the winter B) number of seedlings within plots in June C) number of shoots in plots in September at the end of the first growth season and D) number of shoots in plots in September at the end of the second growth season at 4 depths assessed in the study and according to the three planting methods (Fig. 3B). The graph is modified from Fig. 4 in **paper V**.

Significantly higher establishment of seedlings was found when seeds were covered with a layer of sand at 2 to 5 m depth (Fig 11B); on average 85% higher establishment compared to the control treatment. However, no consistent positive effect was seen from adding rocks to restoration plots, which were believed to increase trapping and burrowing of seeds (E. Infantes *unpubl. data*). The layer of sand may function as a protection against hydrodynamic exposure. However, the significant positive effect of sand also at 5 m depth (where hydrodynamic forces are low) indicate that the sand further protects the seeds against predation. Likely from the green shore crab (*Carcinus maenas*), which was abundant at all depths assessed, and which have been shown to consume large quantities of seeds unless seeds are covered with sediment (E. Infantes et al. *in review*). That burial of seeds can reduce seed loss and increase establishment is consistent with previous studies (Marion and Orth 2012). Furthermore, the results from **paper V** demonstrate that seed planting may be difficult in regions where drifting algal mats cover large areas of the bottom (*see* the discussion on regime shift *above*), as poor survival of seedlings was seen in the site located in the southern parts of the NW coast, where large losses of eelgrass have occurred (**paper III**). Overall, these results suggest that high seed and seedling loss rather than low germination is the bottleneck for establishment along the NW coast of Sweden.

The result from **paper V** further show that a positive shoot growth occurred within all sites during the first summer, and that the significant positive effect of the sand treatment remained, possibly by increasing the anchoring capacity of seedlings or by increasing the permeability of the deep sediment with high clay- and organic content (Fig. 11C). Although the number of shoots was higher in the deep sites at the end of the first growth season, the growth rates were higher within the shallow sites, with an 8-fold increase in shoot numbers from June to September (Fig. 11B,C). At the end of the second growth season, the difference in establishment between shallow and deep sites was no longer visible (Fig. 11D), as a result of the >10 x higher growth rate of shoots in shallow areas, seen both within **paper IV** and **V**. These results suggest that seedlings behave similar to adult transplants, in that vegetative reproduction limits the shoot increase within deeper areas. And although seedling establishment within deeper areas might be an important natural process, which helps to maintain shoot densities in areas where vegetative growth is limited by light, as suggested by Olesen et al. (2016), the slow growth and high winter losses make restoration in these areas difficult also with seeds.

Since eelgrass seeds in the study region lay dormant in the sediment during the winter and germinate the following spring, the study in **paper V** further assessed if storage of seeds over the winter and planting in the spring, would increase the seedling establishment, which have been shown during shorter periods of seed storage in other areas (Marion and Orth 2010b). This would minimize the exposure time to factors that could lead to seed loss, e.g. predation, bioturbation and winter storms. Surprisingly, no increase in the seedling establishment was seen in comparison to plantings performed in the fall. Furthermore, since 36% of seeds were lost during the 8 months of storage (i.e. due to premature germination or loss of viability), this suggest that it is more cost-effective to plant seeds in the fall. Overall, the results from **paper V and IV**, demonstrates that seeds have the potential to be used for restoration of eelgrass on the Swedish NW coast, as patches formed by the growing seedlings survived in all environments. However, the high losses of seeds and low establishment pose a challenge, particularly in shallow areas, which needs to be addressed before large-scale restoration with seeds can be recommended in this region. Furthermore, the cost of restoring eelgrass according to the seed methods available today is more than 3x higher, and takes 2 years longer compared to shoot methods, from site selection to an established meadow (Moksnes et al. 2016b).

CONCLUSIONS AND FUTURE PROSPECTS

The results presented in this thesis provide an important foundation of knowledge for performing eelgrass restoration in high latitude environments. They demonstrate differences in shoot survival and growth between methods and environments, and highlight potential challenges, which can help increase the chances of performing successful eelgrass restoration. They further display the great potential of eelgrass transplants to grow when environmental conditions are favourable. In addition, the vulnerability of these habitats is demonstrated, both to the effects of coastal exploitation, but also to self-generating effects that can prevent recolonization and restoration in certain areas. The studies have further resulted in the development of national guidelines, which will hopefully aid in the improvement of management and restoration of eelgrass in Sweden (Moksnes et al. 2016a,b).

The study of small-scale exploitation in **paper I** demonstrates significant negative effects on eelgrass from the cumulative number of docks and small marinas along the NW coast of Sweden. It further reveals that eelgrass presence is rarely assessed or considered in applications or decisions for dock construction and that protected areas, only marginally reduces the number of approved constructions in eelgrass habitats. This situation is not in line with Swedish national guidelines for management of threatened habitats and protected areas, which makes it difficult for Sweden to reach national and international environmental objectives regarding coastal water status. To improve management of eelgrass in relation to dock construction, Swedish management authorities need to demand better information regarding bottom conditions in areas targeted for exploitation and be more restrictive in granting exemption from the shore protection and approving docks in areas with eelgrass. There is also a need for authorities to make decisions that take into account the cumulative, large-scale impacts on eelgrass from all human development in the affected area, and how a continued net-loss of eelgrass would affect the achievement of national and international goals and commitments. In cases where the construction has been approved, compensatory restoration of eelgrass could be used to mitigate the loss of important ecosystem services. Also, future studies are needed on how to minimize shading and reduce additional negative effects from docks, which could be used for developing guidelines regarding dock construction over valuable shallow coastal habitats along the Swedish coast.

The results from **paper II**, **III**, **IV** and **V** demonstrate that careful site selection through test-planting, monitoring and measurements of environmental conditions is imperative for successful restoration of eelgrass on the NW coast of Sweden. The results from these studies suggest that degraded water quality conditions, due to sediment resuspension and drifting algal mats, are the major factors preventing natural recovery and restoration of eelgrass in areas where meadows have been lost. Such problems could be indicated through measurements of clay and silt proportions (grain size) in the sediment or through direct measurements of water quality conditions. The studies further indicate that a minimum of 20% surface irradiance is required for eelgrass survival, but that higher light levels (>30%) might be required to ensure long term survival and fast lateral growth. Therefore, restoration is generally recommended at depth between 1-3 m (in areas with high water clarity) to ensure high growth and sufficient storage of carbohydrates over the first growth season. Sites with a clay and silt content of more than 40% should generally be avoided as they are often associated with more frequent resuspension and high turbidity conditions. Furthermore, the results demonstrate that it might be very difficult to restore historical meadows at some parts of the coast, as the loss of the engineering properties provided by these ecosystems can lead to a regime shift into an alternative stable state, dominated by local resuspension and drifting algal mats that prevent eelgrass growth. Therefore, it is essential to acknowledge that restoration is not always possible, which emphasise the importance of protecting remaining meadows, especially in areas where large losses have already occurred. Since these local regime shifts appear to have affected large parts of the southern NW coast of Sweden, they constitute a major challenge for restoration and conservation of eelgrass. Future studies are needed to increase our understanding of the thresholds for positive feedbacks, which promote eelgrass growth and how to break the feedback mechanisms that keep an environment locked in an unvegetated state (e.g. engineering of the environment or efforts to reduce specific disturbances). Furthermore, since eelgrass transplants were able to survive under complete darkness for an extended period of time (>1 month) under laboratory conditions (in **paper II**), the rapid mortality of shoots at historical eelgrass sites (within 1-3 months; **paper III**) suggests that additional factors other than light (and algae) may be responsible for the mortality. There is therefore a need for further studies that increase our understanding of factors or processes that might impede eelgrass survival at historically vegetated sites. The effects of sedimentation on leaves is one such factor that might be worth studying in these environments, since deposits of sediment were constantly found on the leaves of transplanted eelgrass within deep or more sheltered areas in **paper III**. Sedimentation on leaves may reduce the amount of light available to the plants, but could possibly also have further implications, e.g. by weighing leaves down or causing burial of shoots. The dumping up dredged material in the coastal zone is a process which may increase the amount of suspended material in the water column and thereby the sedimentation on leaves. Normally it is forbidden to dispose of dredged material inside the Swedish archipelago, but exemptions are regularly granted even in the southern parts of the Swedish NW coast, where <2% of the historical eelgrass meadows remain. The impact on water quality (e.g. turbidity and duration of negative effects) and eelgrass health by such dumping events is poorly studied along the Swedish coast, and could therefore constitute an important research project, studied both from an ecological and a legal perspective.

The results from **paper IV** and **V** suggest that transplantation of single unanchored shoots is the most cost-effective method to use for large-scale restoration of eelgrass on the NW coast of Sweden. Additionally, the high acclimatization potential by these plants indicates that donor environments do not have to exactly match the depth and exposure conditions at the restoration site. Test-plantings indicate that 4 divers can restore 1 ha of eelgrass (at a shoot density of 16 shoots m^{-2}) in 40 days according to this method (Moksnes et al. 2016b). In contrast, a cost-estimate performed by Moksnes et al. (2016b), based on the results from **paper IV** and **V**, demonstrates that the cost of restoring 1 ha of eelgrass would be almost 3 times higher using seeds compared with single unanchored shoots, due to the high loss of seeds and the low establishment, particularly in high-energy environments. Therefore, restoration using eelgrass seeds cannot be recommended for large-scale restoration, with the methods available today. Further studies are needed to develop cost-effective methods that reduce these high losses, e.g. focusing on effective ways of burrowing seeds, as this was shown to significantly increase the establishment rate (**paper V**). Furthermore, the seasonal losses of shoots revealed in these studies demonstrate that winter survival constitutes a challenge for eelgrass restoration in high latitude environments and show that long-term monitoring is critical for the evaluation of restoration success.

While the results from this thesis provide functional methods and guidelines for eelgrass restoration along the Swedish NW coast, it is important to emphasise that restoration of eelgrass is very labour intensive, costly and not always possible. Furthermore, since hand-planting is required during restoration according to the recommended methods, the scale of possible restoration projects is likely limited to areas of less than 10 ha per year. It is therefore, not realistic that restoration alone will be able to re-establish the 1000s ha of eelgrass lost along the NW coast. Instead restoration must be seen as a way of initiating natural recovery by performing restoration efforts in strategically chosen locations, in combination with large-scale measures to improve environmental conditions for eelgrass growth. In addition, the presence of functional methods for eelgrass restoration also allows for demands to be made regarding compensatory restoration of eelgrass. This could constitute an important tool to mitigate losses caused by coastal exploitation, which would be one way to prevent the slow degradation of remaining eelgrass meadows along the NW coast of Sweden. The studies performed within the ZORRO program have resulted in the development of a 'national eelgrass mitigation policy for Sweden' (HaV 2016, Moksnes et al. 2016a), which describes how compensation for eelgrass loss should be evaluated and performed.

MY CONTRIBUTIONS TO THE PAPERS

PAPER I: The effects of small-scale coastal development on the eelgrass (*Zostera marina* L.) distribution along the Swedish west coast – ecological impact and legal challenges.

L.E., P-O. M., L.G., and K.L. designed the study. L.E. and K.L. carried out the field work. K.L. identified and revised the dock applications. L.E. analysed the ecological and legal data with contribution from K.L. and P.B. L.E. wrote the manuscript with contribution from K.L. and comments from P-O. M., L.G. and P.B.

PAPER II: Light requirements for successful restoration of eelgrass (*Zostera marina* L.) in a high latitude environment – acclimatization, growth and carbohydrate storage.

L.E. designed the study, carried out the experiment and performed the sample and data analysis with contribution on the carbohydrate analysis by Somnath Dana. L.E. wrote the manuscript with comments from P-O. M.

PAPER III: Local regime shifts prevent natural recovery and restoration of lost eelgrass beds along the Swedish west coast.

P-O. M., L.E., and E.I. designed the study. P-O. M., L.E. and E.I. carried out the fieldwork. L.E., P-O. M., M.H. and E.I. carried out sample and data analysis. P-O. M wrote the manuscript with comments from L.E., E.I. and M.H.

PAPER IV: Assessing methods for restoration of eelgrass (Zostera marina L.) in a cold temperate region.

L.E. and P-O. M. designed the study. L.E., P-O. M., E.I. and M.O. carried out the fieldwork. L.E., M.O. and J.L.O. performed sample and data analysis. L.E. wrote the manuscript with comments from P-O. M., E.I. and J.L.O.

PAPER V: Eelgrass (Zostera marina) restoration on the west coast of Sweden using seeds.

E.I., P-O. M. and L.E. designed the study. E.I., P-O. M. and L.E. carried out the fieldwork. E.I. wrote the manuscript with comments from P-O. M. and L.E.

THANK YOU!

These past five years have been such an amazing experience. Probably the most challenging and exhausting experience I will ever face but also the most rewarding and fulfilling. My fascination with seagrasses started during my bachelor thesis, when I got to map and sample seagrasses on a remote Island off the coast of Tanzania. After a short (and fun!) detour into the world of ocean acidification, I once again found myself amongst the angiosperms and *Zostera marina*. Throughout the course of this PhD project (and the hours spent on boats, in the water, in the lab, in front of the computer or dry-snorkelling in one of my mesocosms) my fascination for seagrasses has grown, and so has the sentiment of doing something important and meaningful. This has really been an intense learning experience, both scientifically and on a personal level. Hopefully I will get to continue working with these amazing plants in one way or another and spread the word of the existence, importance and vulnerability of these lush meadows that hide beneath the water surface along our coasts.

I would like to thank all the fantastic people that I have met along the course of this project and none of this would have been possible without the support from you; my family, my friends and my colleagues. First of all, I would like to give my supervisor **Per-Olav Moksnes** an eelgrass-meadow-full of gratitude. This is not the first academic achievement that you have supervised me through, and I am forever grateful that you gave me this opportunity. We have had so many great discussions, mostly about science, but also about literature, music and the (un)importance of social media and you have taught me plenty of useful things, e.g. how to glue strings to crabs in the most optimal way, the knots that every sensible marine biologist should know and the joy of cage-studies (which I will probably avoid as much as possible in my future scientific career…). Thank you for being so supportive and encouraging during these years and for always being engaged in the work that we have performed and for all the fun field days and emergency cheeseburgers at 11 o'clock at night. Your drive is envious, and your studies are always HUGE! I hope that we will continue to collaborate in the future, in one way or another, in our quest to save the seagrass! A big thank you also to my co-supervisor **Lena Gipperth** for showing me that environmental law is actually quite interesting ☺. Thank you for all your insightful comments and ideas during our work together and for the delicious seafood dinners at your beautiful home in Marstrand. I hope that we will collaborate in the future on this important path of interdisciplinarity. I would also like to thank the rest of the co-founders of our epic ZORRO group. **Kristjan Laas** – thank you for a nice collaboration and for our weird but productive road trip along the Bohus coast; swimming back and forth underneath docks in random locations, getting yelled at by angry boat owners and eating lots of ice cream. **Eduardo Infantes** – thank you for all the hours we have spent together on the blue waters around Gullmarn (and the brown waters in Kungälv). Thanks for the many good discussions. It has been great getting to know and work with you. Sometimes however, our MacGyvering skills have back fired…I remember an incident with floating rocks ☺. **Scott Cole** – it has been very nice getting to know you and to get a glimpse into the world of environmental economy. It was such a luxury being guided by you and your wonderful mum during our visit in San Diego. I would also like to thank everyone in the **Graduate school** for all the nice meetings, discussions and fascinating glimpses into the social science discipline and **Kerstin Johannesson** for many interesting seminars and insightful advice and perspectives on science. Thank you also to my co-authors **Marianne Holmer**, **Jeanine Olsen** and **Per Bergström** for sharing your expertise and contributing to the work included in this thesis.

Thank you to all my amazing friends and colleagues on the 5th floor. **Josefin Sefbom** – jag är så glad att jag lärt känna dig. Vi har haft så mycket roligt under dessa år (speciellt under våra upptåg i NYC!) och den senaste tiden har du varit ett enormt stöd. Tack för alla G&Ts på 'ballen' (alltså ni stockholmare…) och alla pratstunder om allt mellan himmel och jord. Längtar tills vi får hem dig till goa Göteborg igen! **Sussie Gross** – du är en så himla härlig person som alltid gör det roligt att komma in till jobbet. Tack för alla skratt, trevliga besök hos oss på vischan, pysselkvällar och för att du alltid har något roligt att berätta som man inte visste (det kanske vi skall tacka apan för?!). **Maria Karlberg** – bättre roomie får man leta efter! Tack för alla trevliga pysselkvällar, AWs och knäppa katt-klipp och för att du alltid har insiktsfulla (och likt din handledare) skarpa råd att komma med i jobbsituationer. Marren och Sussie, snart drar vi och gör Ghent osäkert tillsammans med Josse! **Lisa Sundqvist** – det har varit så trevligt att dela kontor med dig dessa år. Tack för alla samtal och blöta AWs, all dans till grym synthmusik och för att du alltid haft koll på det administrativa när man i panik undrat vem man skall vända sig till med diverse blanketter. **Malin Olofsson** – min tredje superba skrivbordsgranne. Tack för alla trevliga samtal, medförfattarskap och alla fältdagar vi haft ihop i Gullmarn och Kungälv. **Jenny Egardt** – tack för trevliga AWs och en sjukt trevlig konferens i Portland, där vi åt som kungar och drack som sjömän! **Daniela De Abreu** – it's been really great getting to know you. Thank you for a lovely conference stay in Portland, for nice chats and for your wonderfully strong Mozambican flue medicine that helped me through the conference ☺. **Monica Appelgren** – du är så fantastisk! Tack för alla trevliga pratstunder i lunchrummet och framförallt, stort tack för att du alltid har varit så otroligt hjälpsam och glad när jag kommit med förvirrade frågor och funderingar. **Inger Wallentinus** – tack för alla värdefulla kommentarer på min kappa och för att du alltid är så hjälpsam och vill dela med dig av din kunskap om vårt älskade ålgräs. **Angela Wulff** – allt sedan jag började studera på universitetet för en sisådär 14 år sedan (!) har du varit någon jag sett upp till. Du är en fantastisk pedagog och har alltid bra och konkreta råd att komma med. **Kristina Sundbäck** – som var min examinator under nästan hela min doktorandtid. Stort tack för ditt engagemang och ditt alltid lika glada humör. Tack vare dig kommer jag alltid att uttala MFB med finlandssvensk brytning ☺. Tack också till min examinator **Helle Ploug** för att du med intresse och engagemang tog dig an mig i sista minuten. **Sven Toresson** – Botans egen handy-man. Stort tack för att du alltid är så hjälpsam med stort som smått. Stort tack också till **Fabian Roger**, **Christian Alsterberg**, **Anders Torstensson**, **Anna Godhe**, **Lars Gamfeldt**, **Erik Selander**, **Pelle Åberg, Mikael Hedblom**, **Gurpreet Kahlon**, **Justin Pearce** och alla andra medarbetare på botan som gjort det trevligt att komma in till jobbet!

I would also like to thank the many people I've met during my stays at our beautiful marine stations (Tjärnö and Kristineberg). **Jon Havenhand** – you're such an inspiring person and you always fill my head with enthusiasm for science and with new ideas. **Sussi Baden** – tack för alla trevliga pratstunder, undervisningstillfällen och ålgräsprovtagningar i Norge. **Daniel Johansson** – Du är så jäkla skön och en av de personer som gjorde att jag överlevde 'on the Island'. Ikväll skall vi dansa tills golvet glöder! **Johan Rolandsson** – tack för alla trevliga stunder vi haft på havet, på Tjärnö och i ditt fina hus på Flatön. **Elin Persson** – jag är så glad att vi möttes på Tjärnö, du är en så fin vän! **Bengt Lundve** – du var en klippa under tiden jag satte upp mitt experiment på Kristineberg, tack för all hjälp! Stort tack också till **Emma Johansson**, **Angelica Ardehed**, **Marie M Jensen**, **Stina Jakobsson, Mårten Duvetorp**, **Anna-Lisa Wrange**, **Elin Renborg, Linda Svanberg** och **Anna Wåhlin** för alla trevliga stunder på fältstationer och/eller AWs med ölglas i handen.

Jag skulle också vilja tacka **Ragnar Eide** – min marinbiologilärare under gymnasietiden i Lysekil. Dina fantastiska berättelser och din uppsjö av fakta var det som fick mig att vilja bli marinbiolog. And also a big thank you to all the eelgrass enthusiasts from **Stockholm**, **Finland**, **Denmark** and **Norway**, that I've met along the course of my PhD studies. Stort tack också till mina närmaste vänner I den verkliga världen; **Lisa Korsár** och **Malin Lind**. Ni har varit en fast punkt och en trygghet. Jag älskar er ♥! Lastly, some honourable mentions, utan er skulle jag aldrig klarat av att 'dygna' framför datorn eller sätta upp ett endaste av mina försök: **Swedish Match**, **Arvid Nordquist**, **Ziploc**, **Ty-Rap**, **Sharpie**, **Gardena** and **Osram**.

Till sist vill jag tacka min fina familj och min älskade man, denna avhandling är till er, tack för all er kärlek ♥. **Mamma** och **Pappa** – utan er hade jag aldrig varit här. Tack för ert otroliga stöd och engagemang under de här åren. Tack för allt peppande och tröstande, all uppmuntran och alla uppmaningar (mamma), alla nätter på ert förstklassiga bed and breakfast och för alla hund-, katt- och hönspassningar. Jag älskar er! Världens bästa **bröder**, **svägerskor och brorsdöttrar** – tack för alla pep talks och mysiga stunder under jular, midsomrar, och påsker – det har verkligen fungerat som ett energipiller. Förhoppningsvis kommer vi se mer av varandra framöver, och kanske tillochmed få någon vecka semester ihop nästa sommar ☺. **Bosse** och **Bell** – mina extraföräldrar, tack för att ni ställt upp med otaliga hundpassningar, middagar och uppmuntrande ord. Jag är också evigt tacksam för att ni lyckats producera fram en så fantastisk son ☺. **Familjen Elfström** – tack för allt ert stöd och alla trevliga middagar med diskussioner om statistik, botanik, genus och björnbajs. Det har varit så skönt att ha er att prata med, som kan relatera till båda sidorna av doktorerandet. Jag vill också tacka min lilla tofsvipa, **Stella** – du har dragit upp mig ur kontorsstolen och skingrat mina bekymmer vid otaliga tillfällen. Slutligen, den person som betyder allt, min älskade **Magnus**! Du har funnits vid min sida under mitt kandidatarbete (då jag stack till Tanzania i 3 månader), under mitt mastersarbete (då jag bosatte mig på Tjärnö under 1 år) och nu under mina doktorandstudier (då du fått semestra själv när jag har suttit på en båt eller klistrad vid datorn). Jag är så otroligt tacksam för detta och jag lovar att nästa år slipper du tälta själv i Älvdalen! Jag hade aldrig klarat det här utan dig. Du har varit ett sånt otroligt stöd från början till slut och speciellt dessa sista månader, när du hållit mig på rätt sida galenskapen. Jag älskar dig och längtar efter de kommande kapitlen i vårt liv, du och jag mot världen! ♥

REFERENCES

Abul-Azm, A. G., Gesraha, M. R. (2000). Approximation to the hydrodynamics of floating pontoons under oblique waves. *Ocean Engineering*, *27*(4), 365-384.

Addy, C. E. (1947). Eelgrass planting guide. *Maryland Conservationist*, *24*, 16-17.

Alcoverro, T., Zimmerman, R. C., Kohrs, D. G., Alberte, R. S. (1999). Resource allocation and sucrose mobilization in light-limited eelgrass *Zostera marina*. *Marine Ecology Progress Series*, *187*, 121-131.

Anonymous (2012) Svenska miljömål: preciseringar av miljökvalitetsmålen och en första uppsättning etappmål, Ds 2012:23 (Stockholm: Miljödepartementet, Regeringskansliet). ISBN 978-91-38-23762-5. *In Swedish*.

Anonymous (2016) Havet 2015–2016: Om miljötillståndet i svenska havsområden. Havsmiljöinstitutet, Havs-och vattenmyndigheten, Naturvårdsverket. *In Swedish*.

Arber, A. (1920). Water plants. A Study of Aquatic Angiosperms. Cambridge University Press, Cambridge.

ArtDatabanken (2015) Rödlistade arter I Sverige 2015. ArtDatabanken SLU, Uppsala.

Baaner, L., Stoltenborg, T. B. (2011). Ålegræs på dybt vand? Et biologisk og juridisk omdrejningspunkt for vandplanerne. *Tidsskrift for Miljoe*, 2, 54-59.

Baden, S. P., Pihl, L. (1984). Abundance, biomass and production of mobile epibenthic fauna in *Zostera marina* (L.) meadows, western Sweden. *Ophelia*, *23*(1), 65-90.

Baden, S., Gullström, M., Lundén, B., Pihl, L., Rosenberg, R. (2003). Vanishing seagrass (*Zostera marina*, L.) in Swedish coastal waters. *AMBIO: A Journal of the Human Environment*, *32*(5), 374-377.

Baden, S., Boström, C., Tobiasson, S., Arponen, H., Moksnes, P. O. (2010). Relative importance of trophic interactions and nutrient enrichment in seagrass ecosystems: A broad-scale field experiment in the Baltic-Skagerrak area. *Limnology and Oceanography*, *55*(3), 1435.

Baden, S., Emanuelsson, A., Pihl, L., Svensson, C. J., Åberg, P. (2012). Shift in seagrass food web structure over decades is linked to overfishing. *Marine Ecology Progress Series*, *451*, 61-73.

Bintz, J. C., Nixon, S. W. (2001). Responses of eelgrass *Zostera marina* seedlings to reduced light. *Marine Ecology Progress Series*, *223*, 133-141.

Borum, J., Duarte, C. M., Greve, T. M., Krause-Jensen, D. (Eds.). (2004). *European seagrasses: an introduction to monitoring and management*. M&MS project.

Bos, A. R., Dankers, N., Groeneweg, A. H., Hermus, D. C. R., Jager, Z., de Jong, D. J., Smith, T., de Vlas, J., van Wieringen, M. van Katwijk, M. M. (2005). Eelgrass (*Zostera marina* L.) in the western Wadden Sea: monitoring, habitat suitability model, transplantations and communication. *International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde,* p. 955-109.

Bos, A. R., Van Katwijk, M. M. (2007). Planting density, hydrodynamic exposure and mussel beds affect survival of transplanted intertidal eelgrass. *Marine Ecology Progress Series*, *336*, 121-129.

Bos, A. R., Bouma, T. J., de Kort, G. L., van Katwijk, M. M. (2007). Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuarine, Coastal and Shelf Science*, *74*(1), 344-348.

Boström, C., Baden, S., Krause-Jensen, D. (2003) The seagrasses of Scandinavia and the Baltic Sea. In *World atlas of seagrasses*: *Present Status and Future Conservation* (eds. Green, E. P., Short, F. T.) University of California Press, Berkley.

Boström, C., Baden, S., Bockelmann, A. C., Dromph, K., Fredriksen, S., Gustafsson, C., Krause-Jensen, D., Möller, T., Nielsen, S.L., Olsen, B., Olsen, J., Pihl, L., Rinde, E., 2014. Distribution, structure and function of Nordic eelgrass (*Zostera marina*) ecosystems: implications for coastal management and conservation. *Aquatic conservation: marine and freshwater ecosystems*, 24(3), 410-434.

Bricker, S. B., Ferreira, J. G., Simas, T. (2003). An integrated methodology for assessment of estuarine trophic status. *Ecological modelling*, *169*(1), 39-60.

Brush, M. J., Nixon, S. W. (2002). Direct measurements of light attenuation by epiphytes on eelgrass

Zostera marina. *Marine Ecology Progress Series*, *238*, 73-79.
Burdick, D. M., Short, F. T. (1999). The effects of boat docks on eelgrass beds in coastal waters of Massachusetts. *Environmental Management*, *23*(2), 231-240.
Burke, M. K., Dennison, W. C., Moore, K. A. (1996). Non-structural carbohydrate reserves of eelgrass *Zostera marina*. *Marine Ecology Progress Series*, *137*, 195-201.
Cabello-Pasini, A., Lara-Turrent, C., Zimmerman, R. C. (2002). Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. *Aquatic botany*, *74*(2), 149-164.
Cabello-Pasini, A., Muñiz-Salazar, R., Ward, D. H. (2003). Annual variations of biomass and photosynthesis in *Zostera marina* at its southern end of distribution in the North Pacific. *Aquatic botany*, *76*(1), 31-47.
Campbell, M. L. (2002). Getting the foundation right: a scientifically based management framework to aid in the planning and implementation of seagrass transplant efforts. *Bulletin of Marine Science*, *71*(3), 1405-1414.
Canal-Vergés, P., Vedel, M., Valdemarsen, T., Kristensen, E., Flindt, M. R. (2010). Resuspension created by bedload transport of macroalgae: implications for ecosystem functioning. *Hydrobiologia*, *649*(1), 69-76.
Carr, J., D'Odorico, P., McGlathery, K., Wiberg, P. L. (2010). Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. *Journal of Geophysical Research: Biogeosciences*, *115*(G3).
Carr, J. A., D'Odorico, P., McGlathery, K. J., Wiberg, P. L. (2012). Modeling the effects of climate change on eelgrass stability and resilience: future scenarios and leading indicators of collapse. *Marine Ecology Progress Series*, *448*, 289-301.
Christensen, O., Sortkjær, K.J., McGlathery, P.B. (1995) Tranplantation of Eelgrass. National Environmental Research Institute, Silkesborg Bogtryck, Denmark.
Clausen, K. K., Krause-Jensen, D., Olesen, B., Marbà, N. (2014). Seasonality of eelgrass biomass across gradients in temperature and latitude. *Marine Ecology Progress Series*, *506*, 71-85.
Cloern, J. E. (2001). Our evolving conceptual model of the coastal eutrophication problem. *Marine ecology progress series*, *210*, 223-253.
Cole, L. W., McGlathery, K. J. (2012). Nitrogen fixation in restored eelgrass meadows. *Marine Ecology Progress Series*, *448*, 235-246.
Cole, S. G., Moksnes, P. O. (2016). Valuing Multiple Eelgrass Ecosystem Services in Sweden: Fish Production and Uptake of Carbon and Nitrogen. *Frontiers in Marine Science*, *2*, 121.
Costanza, R., d'Arge, R., De Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neil, R.V., Paruelo, J., Raskin, R.G. Sutton, P., van den Belt, M., (1997). The value of the world's ecosystem services and natural capital. Nature 387: 253-260.
Cunha, A. H., Marbá, N. N., van Katwijk, M. M., Pickerell, C., Henriques, M., Bernard, G., Ferreira, M.A., Garcia, S., Garmendia, J.M., Manent, P. (2012). Changing paradigms in seagrass restoration. *Restoration Ecology*, *20*(4), 427-430.
Davis, R. C., Short, F. T. (1997). Restoring eelgrass, *Zostera marina* L., habitat using a new transplanting technique: the horizontal rhizome method. *Aquatic Botany*, *59*(1), 1-15.
Davis, R. C., Short, F. T., Burdick, D. M. (1998). Quantifying the effects of green crab damage to eelgrass transplants. *Restoration Ecology*, *6*(3), 297-302.
De Groot, R. S., Blignaut, J., van der Ploeg, S., Aronson, J., Elmqvist, T., Farley, J. (2013). Benefits of investing in ecosystem restoration. *Conservation Biology*, *27*(6), 1286-1293.
De Jonge, V. N., de Jong, D. J., van Katwijk, M. M. (2000). Policy plans and management measures to restore eelgrass (*Zostera marina* L.) in the Dutch Wadden Sea. *Helgoland Marine Research*, *54*(2), 151.
Delefosse, M., Kristensen, E. (2012). Burial of *Zostera marina* seeds in sediment inhabited by three polychaetes: laboratory and field studies. *Journal of sea research*, *71*, 41-49.
Den Hartog, C. (1970). The sea-grasses of the world. *North Holland Publ., Amsterdam.*
Dennison, W. C., Alberte, R. S. (1982). Photosynthetic responses of *Zostera marina* L.(eelgrass) to in

situ manipulations of light intensity. *Oecologia*, *55*(2), 137-144.
Dennison, W. C., Orth, R. J., Moore, K. A., Stevenson, J. C., Carter, V., Kollar, S., Bergstrom, P.W., Batiuk, R. A. (1993). Assessing water quality with submersed aquatic vegetation. *BioScience*, *43*(2), 86-94.
Douvre, F. (2008). The engagement of stakeholders in the marine spatial planning process. *Marine Policy*, *32*, 762-771.
Duarte, C. M. (1995). Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*, *41*(1), 87-112.
Duarte, C. M., Middelburg, J. J., Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, *2*(1), 1-8.
Duarte, C. M., Marbà, N., Krause-Jensen, D., Sánchez-Camacho, M. (2007). Testing the predictive power of seagrass depth limit models. *Estuaries and Coasts*, *30*(4), 652-656.
Duarte, C. M., Kennedy, H., Marbà, N., Hendriks, I. (2013). Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. *Ocean & coastal management*, *83*, 32-38.
Duffy, J.E., Hughes, A.R., Moksnes, P.-O. (2014) Ecology of seagrass communities. In: Bertness M.D., Bruno J.F., Silliman B.R., Stachowicz J.J. (Eds.), Marine community Ecology and Conservation. Sinauer Associates, Inc. pp. 271-297.
Echavarria-Heras, H. A., Solana-Arellano, E., Franco-Vizcaíno, E. (2006). The role of increased sea surface temperature on eelgrass leaf dynamics: onset of El Nino as a proxy for global climate change in San Quintin Bay, Baja California. *Bulletin, Southern California Academy of Sciences*, *105*(3), 113-127.
Envall, M., Lawett, E. (2016) Satelitbildsanalys för uppföljning gav vegetation på grund marin botten. Metodtest med fältverifikation för uppskattning av utbredning av ålgräs och annan långskottsvegetation men satelitbildsanalys – jämförelse Sveriges västkust och ostkust. In Swedish. Havs och Vattenmyndighetens rapport 2015:6. *In Swedish.*
Erftemeijer, P. L., Lewis, R. R. R. (2006). Environmental impacts of dredging on seagrasses: a review. *Marine pollution bulletin*, *52*(12), 1553-1572.
European Commission (2011) Our life insurance, our natural capital: An EU Biodiversity Strategy to 2020, *European Commission, Brussels (2011).*
Evans, N. T., Leschen, A. S. (2010). Technical guidelines for the delineation, restoration, and monitoring of eelgrass (*Zostera marina*) in Massachusetts coastal waters. *Massachusetts Division of Marine Fisheries Technical Report TR-43, New Bedford, MA.*
Fonseca, M. S., Zieman, J. C., Thayer, G. W., Fisher, J. S. (1983). The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science*, *17*(4), 367-380.
Fonseca, M. S., Kenworthy, W. J., Thayer, G. W. (1998). Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. *NOAA Coastal Ocean Program, Decision Analysis Series No. 12.*
Fonseca, M. S. (2011). Addy revisited: what has changed with seagrass restoration in 64 years? *Ecological Restoration*, *29*(1-2), 73-81.
Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E.T., Kendrick, G.A., Krause-Jensen, D., McGlathery, K.J., Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, *5*(7), 505-509.
Frederiksen, M., Krause-Jensen, D., Holmer, M., Laursen, J. S. (2004). Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. *Aquatic Botany*, *78*(2), 167-181.
Fredriksen, M.S., Glud, R.N. (2006) Oxygen dynamics in the rhizosphere of *Zostera marina*: a two-dimensional planar optode study. *Limnology and Oceanography*, 51, 1072-1083.
Fresh, K.L., Williams, B.W., Penttila, D. (1995) Overwater structures and impacts on eelgrass (*Zostera marina*) in Puget Sound, Washington. In: Proceedings of Puget Sound Research '95. Puget Sound Water Quality Authority, Olympia, WA, pp. 537–543.
Fresh, K.L., Wyllie-Echeverria, T., Wyllie-Echeverria, S., Williams, B.W. (2006) Using lightpermeable

grating to mitigate impacts of residential floats on eelgrass *Zostera marina* L. in Puget Sound, Washington. *Ecological Engineering* 28, 354-362.
Ganassin, C., Gibbs, P. J. (2008). A review of seagrass planting as a means of habitat compensation following loss of seagrass meadow. NSW Department of Primary Industries, No. 96, pp. 43.
Gattuso, J. P., Gentili, B., Duarte, C. M., Kleypas, J. A., Middelburg, J. J., Antoine, D. (2006). Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and contribution to primary production. *Biogeosciences Discussions*, *3*(4), 895-959.
Giesen, W. B. J. T., Van Katwijk, M. M., Den Hartog, C. (1990). Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquatic Botany*, *37*(1), 71-85.
Golden, R. R., Busch, K. E., Karrh, L. P., Parham, T. A., Lewandowski, M. J., Naylor, M. D. (2010). Large-Scale *Zostera marina* (eelgrass) Restoration in Chesapeake Bay, Maryland, USA. Part II: A Comparison of Restoration Methods in the Patuxent and Potomac Rivers. *Restoration Ecology*, *18*(4), 501-513.
Gotceitas, V., Fraser, S., Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (Gadus morhua). *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(6), 1306-1319.
Govers, L. L., Suykerbuyk, W., Hoppenreijs, J. H., Giesen, K., Bouma, T. J., van Katwijk, M. M. (2014). Rhizome starch as indicator for temperate seagrass winter survival. *Ecological Indicators*, *49*, 53-60.
Granger, S., Traber, M., Nixon, S. W., Keyes, R. (2002) Part 1. Collection, processing and storage. Pages 1–20 in M. Schwartz, editor. A practical guide for the use of seeds in eelgrass (*Zostera marina* L.) restoration. Rhode Island Sea Grant, Narragansett, Rhode Island.
Green, E. P., Short, F. T. (2003). *World atlas of seagrasses*: *Present Status and Future Conservation*. University of California Press, Berkley.
Greve, T. M., Borum, J., Pedersen, O. (2003). Meristematic oxygen variability in eelgrass (*Zostera marina*). *Limnology and Oceanography*, *48*(1), 210-216.
Greve, T. M., Krause-Jensen, D. (2005). Predictive modelling of eelgrass (*Zostera marina*) depth limits. *Marine Biology*, *146*(5), 849-858.
Greve, T. M., Krause-Jensen, D., Rasmussen, M. B., Christensen, P. B. (2005). Means of rapid eelgrass (*Zostera marina* L.) recolonisation in former dieback areas. *Aquatic Botany*, *82*(2), 143-156.
Hansen, J. C., Reidenbach, M. A. (2012). Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. *Marine Ecology Progress Series*, *448*, 271-287.
Hasegawa, N., Hori, M., Mukai, H. (2008). Seasonal changes in eelgrass functions: current velocity reduction, prevention of sediment resuspension, and control of sediment–water column nutrient flux in relation to eelgrass dynamics. *Hydrobiologia*, *596*(1), 387-399.
Hauxwell, J., Cebrián, J., Valiela, I. (2003). Eelgrass *Zostera marina* loss in temperate estuaries: relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series*, *247*, 59-73.
HaV (2016) Kompensationsrestaurering av ålgräs i Sverige – en vägledning. *In Swedish*. Download at: https://www.havochvatten.se/hav/vagledning--lagar/vagledningar/ovriga-vagledningar/algras.html
Heck, K. L., Pennock, J. R., Valentine, J. F., Coen, L. D., Sklenar, S. A. (2000). Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. *Limnology and oceanography*, *45*(5), 1041-1057.
HELCOM (2013) Red List of Baltic Sea underwater biotopes, habitats and biotope complexes. *Baltic Sea Environmental Proceedings* No. 138.
Hellström, H. (2007) Strandexploatering I Strömstad kommuns södra skärgård. Länsstyrelsen I Västra Götalands län. *In Swedish*.
Hemminga, M. A., Marba, N., Stapel, J. (1999). Leaf nutrient resorption, leaf lifespan and the retention of nutrients in seagrass systems. *Aquatic Botany*, *65*(1), 141-158.
Holmer, M., Nielsen, S. L. (1997). Sediment sulfur dynamics related to biomass-density patterns in *Zostera marina* (eelgrass) beds. *Marine Ecology Progress Series*, *146*, 163-171.
Holmer, M., Bondgaard, E. J. (2001). Photosynthetic and growth response of eelgrass to low oxygen

and high sulphide concentrations during hypoxic events. *Aquatic Botany*, *70*(1), 29-38.

Holmer, M., Frederiksen, M. S., Møllegaard, H. (2005). Sulfur accumulation in eelgrass (*Zostera marina*) and effect of sulfur on eelgrass growth. *Aquatic Botany*, *81*(4), 367-379.

Holmer, M., Baden S., Moksnes P-O., Boström, C. (2009) Regional variation in stable sulfur isotopic composition of eelgrass (*Zostera marina*) along a salinity gradient from the Baltic Sea to Skagerrak. Aquatic Botany 91:303-310.

Hughes, B. B., Eby, R., Van Dyke, E., Tinker, M. T., Marks, C. I., Johnson, K. S., Wasson, K. (2014). Recovery of a top predator mediates negative eutrophic effects on seagrass (vol 110, pg 15313, 2013). *Proceedings of the NationalL Academy of Science of the United States of America*, *111*(9), 3644-3644.

Infantes, E., Crouzy, C., Moksnes, P.-O. (*in review)* Seed predation by the shore crab *Carcinus maenas*: a positive feedback preventing recovery of eelgrass *Zostera marina*? PLOS ONE.

Jarvis, J. C., Moore, K. A. (2015). Effects of seed source, sediment type, and burial depth on mixed-annual and perennial *Zostera marina* L. seed germination and seedling establishment. *Estuaries and Coasts*, *38*(3), 964-978.

Jephson, T., Nyström, P., Moksnes, P. O., Baden, S. P. (2008). Trophic interactions in *Zostera marina* beds along the Swedish coast. *Marine Ecology Progress Series*, *369*, 63-76.

Jørgensen, N. M., Bekkby, T. (2013). Historical and present distribution of Zostera marina in the high north (Troms County, northern Norway)–a decline over the last century. *Botanica Marina*, *56*(5-6), 425-430.

Kelty, R.A., Bliven, S. (2003) Environmental and Aesthetic Impacts of Small Docks and Docks, Workshop Report: Developing a Science-Based Decision Support Tool for Small Dock Management, Phase 1: Status of the Science. NOAA Coastal Ocean Program Decision Analysis Series No. 22. National Centers for Coastal Ocean Science, Silver Spring, MD. 69 pp.

Kenworthy, W. J., Gallegos, C. L., Costello, C., Field, D., di Carlo, G. (2014). Dependence of eelgrass (*Zostera marina*) light requirements on sediment organic matter in Massachusetts coastal bays: Implications for remediation and restoration. *Marine pollution bulletin*, *83*(2), 446-457.

Kindström, M. (2006) Vad händer med våra stränder? Rapport 2006:18. Länsstyrelsen I Stockholms län. *In Swedish.*

Koch, E. W. (2001). Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries*, *24*(1), 1-17.

Krause-Jensen, D., Middelboe, A. L., Sand-Jensen, K., Christensen, P. B. (2000). Eelgrass, *Zostera marina*, growth along depth gradients: upper boundaries of the variation as a powerful predictive tool. *Oikos*, 91(2), 233-244.

Krause-Jensen, D., Carstensen, J., Nielsen, S. L., Dalsgaard, T., Christensen, P. B., Fossing, H., Rasmussen, M. B. (2011). Sea bottom characteristics affect depth limits of eelgrass *Zostera marina*. *Marine Ecology Progress Series*, *425*, 91-102.

Kruk-Dowgiallo, L. (1991). Long-term changes in the structure of underwater meadows of the Puck Lagoon. *Acta Ichthyologica et Piscatoria. Supplementum*, (21), 77-84.

Källström B, Nyqvist A, Åberg P, Bodin M, André C (2008) Seed rafting as a dispersal strategy for eelgrass (*Zostera marina*). *Aquatic Botany 88, 148–153.*

Larkum, A. W. D., Den Hartog, C. (1989). Evolution and biogeography of seagrasses. *Biology of seagrasses. Elsevier, Amsterdam*, 112-156.

Larkum, A. W., Orth, R. J., Duarte, C. M. (2006). *Seagrasses*. Springer.

Lawett, E., Olsson, A., Envall, M. (2013) Ålgräs på Västkusten – test av metoder för fjärranalys, kartering, inventering och kvalitetsklassificering. In Swedish. Länsstyrelsen Rapport 2013:84. *In Swedish.*

Lee, K. S., Park, S. R., Kim, Y. K. (2007). Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: a review. *Journal of Experimental Marine Biology and Ecology*, *350*(1), 144-175.

Lefcheck, J., Marion, S. R., Orth, R. J. (2016). Restored eelgrass *(Zostera marina L.)* as a refuge for epifaunal biodiversity in mid-Western Atlantic coastal bays. Estuaries and Coasts, DOI: 10.1007/s12237-016-0141-x.

Les, D. H., Cleland, M. A., Waycott, M. (1997). Phylogenetic studies in Alismatidae, II: evolution of marine angiosperms (seagrasses) and hydrophily. *Systematic Botany*, 443-463.

Leschen, A. S., Ford, K. H., Evans, N. T. (2010). Successful eelgrass (*Zostera marina*) restoration in a formerly eutrophic estuary (Boston Harbor) supports the use of a multifaceted watershed approach to mitigating eelgrass loss. *Estuaries and coasts*, *33*(6), 1340-1354.

Li, W. T., Kim, J. H., Park, J. I., Lee, K. S. (2010). Assessing establishment success of *Zostera marina* transplants through measurements of shoot morphology and growth. *Estuarine, Coastal and Shelf Science*, *88*(3), 377-384.

Lillebø, A. I., Flindt, M. R., Cardoso, P., Leston, S., Dolbeth, M., Pereira, M. E., Duarte, A.C., Pardal, M.A. (2011). Restoration of Seagrass Community to Reverse Eutrophication in Estuaries. In: Wolanski, E., McLusky, D.S. (eds.), *Treatise on Estuarine and Coastal Science, Academic Press, Waltham*, 151-164.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J. B. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, *312*(5781), 1806-1809.

Marbà, N., Krause-Jensen, D., Alcoverro, T., Birk, S., Pedersen, A., Neto, J. M., Orfanidis, S., Garmendia, J.M., Muxika, I., Borja, A., Dencheva, K., Duarte, C.M. (2013). Diversity of European seagrass indicators: patterns within and across regions. *Hydrobiologia*, *704*(1), 265-278.

Marion, S. R., Orth, R. J. (2010). Innovative Techniques for Large-scale Seagrass Restoration Using *Zostera marina* (eelgrass) Seeds. *Restoration Ecology*, *18*(4), 514-526.

Marion, S. R., Orth, R. J. (2010b). Factors influencing seedling establishment rates in *Zostera marina* and their implications for seagrass restoration. *Restoration Ecology*, *18*(4), 549-559.

Marion, S. R., Orth, R. J. (2012). Seedling establishment in eelgrass: seed burial effects on winter losses of developing seedlings. *Marine Ecology Progress Series*, *448*, 197-207.

Maxwell, P., Eklöf, J., van Katwijk, M. M., O'Brien, K., de la Torre-Castro, M., Boström, C., Bouma, T.J., Krause-Jensen, D., Unsworth, R.F.F., van Tussenbroek, B., van der Heide, T. (2016). The fundamental role of ecological feedback mechanisms in seagrass ecosystems-A review. *Biological Reviews*. DOI: 10.1111/brv.12294.

McGlathery, K. J., Reynolds, L. K., Cole, L. W., Orth, R. J., Marion, S. R., Schwarzschild, A. (2012). Recovery trajectories during state change from bare sediment to eelgrass dominance. *Marine Ecology Progress Series*, *448*, 209-221.

McHarg, I. L., Mumford, L. (1969). *Design with nature* (pp. 7-17). New York: American Museum of Natural History.

Merkel, K.W. (1988) Eelgrass transplanting in south San Diego Bay, California. pp. 28– 42. In: Merkel KW and RS Hoffman (eds.). *Proceedings of the California Eelgrass Symposium.* May 27–28, 1988, Chula Vista, California. Sweetwater River Press, National City, CA.

Mills, K. E., Fonseca, M. S. (2003). Mortality and productivity of eelgrass *Zostera marina* under conditions of experimental burial with two sediment types. *Marine Ecology Progress Series*, 255, 127-134.

Moksnes, P.-O., Gullström, M., Tryman, K., Baden, S. (2008). Trophic cascades in a temperate seagrass community. *Oikos*, 117(5), 763-777.

Moksnes, P.-O. (2009) Restaurering av ålgräsängar i Sverige. Länsstyrelsen Västra Götalands län. Rapport 2009. *In Swedish.*

Moksnes, P.-O., Elam, J., Grimvall, A. (2015) Samlad analys av regionala och nationella havsmiljödata. Havsmiljöinstitutet. *Rapport* 2015:2. *In Swedish.*

Moksnes P.-O., Gipperth L., Eriander L., Laas K., Cole S., Infantes E. (2016a) Förvaltning och restaurering av ålgräs i Sverige – Ekologisk, juridisk and ekonomisk bakgrund. *Havs- och vattenmyndighetens rapport* 2016:8, 148 pp., ISBN 978-91-87967-16-0. *In Swedish.*

Moksnes P.-O., Gipperth L., Eriander L., Laas K., Cole S., Infantes E. (2016b) Handbok för restaurering av ålgräs I Sverige – Vägledning. *Havs- och vattenmyndighetens rapport* 2016:9, 146 pp., ISBN 978-91-87967-17-7. *In Swedish.*

Moore, K. A., Orth, R. J., Nowak, J. F. (1993). Environmental regulation of seed germination in *Zostera marina* L.(eelgrass) in Chesapeake Bay: effects of light, oxygen and sediment burial. *Aquatic Botany*, *45*(1), 79-91.

Moore, K. A., Wetzel, R. L., Orth, R. J. (1997). Seasonal pulses of turbidity and their relations to eelgrass (*Zostera marina* L.) survival in an estuary. *Journal of Experimental Marine Biology and Ecology*, *215*(1), 115-134.

Moore, K. A. (2004). Influence of seagrasses on water quality in shallow regions of the lower Chesapeake Bay. *Journal of Coastal Research*, 162-178.

Moore, K. A., Jarvis, J. C. (2008). Environmental factors affecting recent summertime eelgrass diebacks in the lower Chesapeake Bay: implications for long-term persistence. *Journal of Coastal Research*, 135-147.

Moore, K. A., Shields, E. C., Parrish, D. B. (2014). Impacts of varying estuarine temperature and light conditions on *Zostera marina* (eelgrass) and its interactions with Ruppia maritima (widgeongrass). *Estuaries and coasts*, *37*(1), 20-30.

MSFD, Marine Strategy Framework Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy. 2008, L164:19-L164:40. Available online at: http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2008:164:0019:0040:EN:PDF

MSPD, Marine Spatial Planning Directive 2014/89/EU of the European Parliament and of the Council of 23 July 2014 establishing a framework for maritime spatial planning. 2014,L257:135-L257:145. Available online at: http://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri= CELEX:32014L0089&from=EN.

Munkes, B. (2005). Eutrophication, phase shift, the delay and the potential return in the Greifswalder Bodden, Baltic Sea. *Aquatic Sciences*, *67*(3), 372-381.

Neckles, H. A. (2015). Loss of eelgrass in Casco Bay, Maine, linked to green crab disturbance. *Northeastern Naturalist*, *22*(3), 478-500.

NOAA (2014) California Eelgrass Mitigation Policy and implementing guidelines. National Oceanic and Atmospheric Administration (NOAA) West Coast Region October 2014.

Nyqvist, A., André, C., Gullström, M., Baden, S. P., Åberg, P. (2009). Dynamics of seagrass meadows on the Swedish Skagerrak coast. AMBIO: *A Journal of the Human Environment*, *38*(2), 85-88.

Ochieng, C. A., Short, F. T., Walker, D. I. (2010). Photosynthetic and morphological responses of eelgrass (*Zostera marina* L.) to a gradient of light conditions. *Journal of Experimental Marine Biology and Ecology*, *382*(2), 117-124.

Olesen, B., Sand-Jensen, K. (1993). Seasonal acclimatization of eelgrass *Zostera marina* growth to light. *Marine Ecology Progress Ser*ies, 94, 91-99.

Olesen, B., Sand-Jensen, K. A. J. (1994). Demography of shallow eelgrass (*Zostera marina*) populations - shoot dynamics and biomass development. *Journal of Ecology*, 379-390.

Olesen, B. (1999). Reproduction in Danish eelgrass (*Zostera marina* L.) stands: size-dependence and biomass partitioning. *Aquatic Botany*, *65*(1), 209-219.

Olesen, B., Krause-Jensen, D., Marbà, N., Christensen, P. B. (2015). Eelgrass *Zostera marina* in subarctic Greenland: dense meadows with slow biomass turnover in cold waters. *Marine Ecology Progress Series*, *518*, 107-121.

Olesen, B., Krause-Jensen, D., Christensen, P. B. (2016) Depth-related changes in reproductive strategy of a cold-temperate *Zostera marina* meadow. *Estuaries and Coasts*, DOI 10.1007/s12237-016-0155-4.

Olsen, J. L., Coyer, J. A., Chesney, B. (2014). Numerous mitigation transplants of the eelgrass *Zostera marina* in southern California shuffle genetic diversity and may promote hybridization with Zostera pacifica. *Biological Conservation*, *176*, 133-143.

Orth, R. J., Heck, K. L., van Montfrans, J. (1984). Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries*, *7*(4), 339-350.

Orth, R. J., Moore, K. A. (1986). Seasonal and year-to-year variations in the growth of *Zostera marina* L.(eelgrass) in the lower Chesapeake Bay. *Aquatic Botany*, *24*(4), 335-341.

Orth, R. J., Harwell, M. C., Fishman, J. R. (1999). A rapid and simple method for transplanting eelgrass using single, unanchored shoots. *Aquatic Botany*, *64*(1), 77-85.

Orth, R. J., Fishman, J. R., Harwell, M. C., Marion, S. R. (2003). Seed-density effects on germination and initial seedling establishment in eelgrass *Zostera marina* in the Chesapeake Bay region. *Marine Ecology Progress Series*, *250*, 71-79.

Orth, R. J., Carruthers, T. J., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L. (2006). A global crisis for seagrass ecosystems. *Bioscience*, *56*(12), 987-996.

Orth, R. J., Marion, S. R., Moore, K. A., Wilcox, D. J. (2010). Eelgrass (Zostera marina L.) in the Chesapeake Bay region of mid-Atlantic coast of the USA: challenges in conservation and restoration. *Estuaries and Coasts*, *33*(1), 139-150.

Orth, R. J., McGlathery, K. J. (2012). Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. *Marine Ecology Progress Series*, *448*, 173-176.

Orth, R. J., Moore, K. A., Marion, S. R., Wilcox, D. J., Parrish, D. B. (2012). Seed addition facilitates eelgrass recovery in a coastal bay system. *Marine Ecology Progress Series*, *448*, 177-195.

OSPAR (2012) OSPAR Recommendation 2012/4 on furthering the protection and conservation of Zostera beds.

Paling, E. I., Fonseca, M., van Katwijk, M. M., van Keulen, M. (2009). Seagrass restoration. *Coastal wetlands: An integrated ecosystems approach* (eds. Perillo, G., Wolanski, E., Cahoon, D., Brinson, M.) *Elsevier, Amsterdam* pp. 687-713.

Papworth, S. K., Rist, J., Coad, L., Milner-Gulland, E. J. (2009). Evidence for shifting baseline syndrome in conservation. *Conservation Letters*, *2*(2), 93-100.

Pedersen, O., Broum, J., Duarte, C.M., Fortes, M.D., 1998. Oxygen dynamics in the rhizosphere of *Cymodocea rotundata*. *Marine Ecology Progress Series*, 169, 283-288.

Pettersson, K. (2011) Hur mycket tål kusten? Västerhavet 2011, Aktuellt om miljön I Skagerrak, Kattegat och Öresund. *In Swedish*.

Philippart, C. J. M. (1994). Interactions between Arenicola marina and Zostera noltii on a tidal flat in the Wadden Sea. *Marine ecology progress series. Oldendorf*, *111*(3), 251-257.

Phillips, R. C., Lewis III, R. L. (1983). Influence of environmental gradients on variations in leaf widths and transplant success in North American seagrasses. *Marine Technology Society Journal 12, 59-68*.

Phillips, R.C. (1990) Transplant methods. In: Phillips, R.C., McRoy, C.P. (eds.), *Seagrass Research Methods*. UNESCO, Paris, France, PP. 51-54.

Pickerell, C. H., Schott, S., Wyllie-Echeverria, S. (2005). Buoy-deployed seeding: demonstration of a new eelgrass (*Zostera marina* L.) planting method. *Ecological Engineering*, *25*(2), 127-136.

Plus, M., Deslous-Paoli, J.-M., Dagault, F. (2003). Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality. *Aquatic Botany*, *77*(2), 121-134.

Pulido, C., Borum, J. (2010). Eelgrass (*Zostera marina*) tolerance to anoxia. *Journal of Experimental Marine Biology and Ecology*, *385*(1), 8-13.

Rasmussen, J. R., Olesen, B., Krause-Jensen, D. (2012). Effects of filamentous macroalgae mats on growth and survival of eelgrass, *Zostera marina*, seedlings. *Aquatic botany*, *99*, 41-48.

Ruiz, J. M., Romero, J. (2003). Effects of disturbances caused by coastal constructions on spatial structure, growth dynamics and photosynthesis of the seagrass Posidonia oceanica. *Marine Pollution Bulletin*, *46*(12), 1523-1533.

Schanz, A., Asmus, H. (2003). Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea. *Marine Ecology Progress Series*, *261*, 123-134.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591-596.

Schoellhamer, D. H. (1996). Anthropogenic sediment resuspension mechanisms in a shallow microtidal estuary. *Estuarine, Coastal and Shelf Science*, *43*(5), 533-548.

SEC (2000) The Swedish Environmental Code (Miljöbalken). 2000:61. Available online at: http://www.government.se/contentassets/be5e4d4ebdb4499f8d6365720ae68724/the-swedish-environmental-code-ds-200061.

SEPA (2010) Kartering och analys av fysiska påverkansfaktorer i marin miljö. Report no. 6376. ISBN: 978-91-620-6376-4. *In Swedish.*

SEPA (2012) Strandskydd – en vägledning för planering och prövning. Handbok 2009:4, utgåva 2, februari 2012. ISBN 978-91-620-0175-9. *In Swedish.*

Shafer, D., Lundin, J. (1999) Design and construction of docks to minimize seagrass impacts, WRP Technical Notes Collection (TN WRP-VN-RS-3.1), U.S. Army Engineer Research and Development Center, Vicksburg, MS.

Shafer, D., Bergstrom, P. (2010). An Introduction to a Special Issue on Large-Scale Submerged Aquatic Vegetation Restoration Research in the Chesapeake Bay: 2003–2008. *Restoration Ecology*, *18*(4), 481-489.

Short, F. T., Burdick, D. M., Kaldy, J. E. (1995). Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and oceanography*, *40*(4), 740-749.

Short, F. T., Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental conservation*, *23*(01), 17-27.

Short, F. T., Neckles, H. A. (1999). The effects of global climate change on seagrasses. *Aquatic Botany*, *63*(3), 169-196.

Short, F. T., Matso, K., Hoven, H. M., Whitten, J., Burdick, D. M., Short, C. A. (2001). Lobster use of eelgrass habitat in the Piscataqua River on the New Hampshire/Maine border, USA. *Estuaries*, *24*(2), 277-284.

Short, F. T., Davis, R. C., Kopp, B. S., Short, C. A., Burdick, D. M. (2002). Site-selection model for optimal transplantation of eelgrass *Zostera marina* in the northeastern US. *Marine Ecology Progress Series*, *227*, 253-267.

Short, F., Carruthers, T., Dennison, W., Waycott, M. (2007). Global seagrass distribution and diversity: a bioregional model. *Journal of Experimental Marine Biology and Ecology*, *350*(1), 3-20.

Solana-Arellano, M. E., Echavarria-Heras, H. A., Ibarra-Obando, S. E. (1997). Leaf-size Dynamics for*Zostera marina*L. in San Quintin Bay, México: a Theoretical Study. *Estuarine, Coastal and Shelf Science*, *44*(3), 351-359.

Staehr, P. A., Borum, J. (2011). Seasonal acclimation in metabolism reduces light requirements of eelgrass (*Zostera marina*). *Journal of Experimental Marine Biology and Ecology*, *407*(2), 139-146.

Sundblad, G., Bergström, U. (2014) Shoreline development and degradation of coastal fish reproduction habitats. AMBIO: *a Journal of the Human Environment*, 43, 1020-1028.

SwAM, (2015) Swedish Agency for Marine and Water Management. God havsmiljö 2020 Marin strategi för Nordsjön och Östersjön, Del 4: Åtgärdsprogram för havsmiljön. Havs- och vattenmyndighetens rapport 2015:30. *In Swedish.*

Tamaki, H., Tokuoka, M., Nishijima, W., Terawaki, T., Okada, M. (2002). Deterioration of eelgrass, *Zostera marina* L., meadows by water pollution in Seto Inland Sea, Japan. *Marine Pollution Bulletin*, *44*(11), 1253-1258.

Tanaka, N., Demise, T., Ishii, M., Shoji, Y., Nakaoka, M. (2011). Genetic structure and gene flow of eelgrass *Zostera marina* populations in Tokyo Bay, Japan: implications for their restoration. *Marine Biology*, *158*(4), 871-882.

Tanner, C., Hunter, S., Reel, J., Parham, T., Naylor, M., Karrh, L., Busch, K., Golden, R.R., Lewandowski, M., Rybicki, N., Schenk, E. (2010). Evaluating a Large-Scale Eelgrass Restoration Project in the Chesapeake Bay. *Restoration Ecology*, *18*(4), 538-548.

Tanner, C. E., Parham, T. (2010). Growing *Zostera marina* (eelgrass) from Seeds in Land-Based Culture Systems for Use in Restoration Projects. *Restoration Ecology*, *18*(4), 527-537.

Thom, R. M., Southard, S. L., Borde, A. B., Stoltz, P. (2008). Light requirements for growth and survival of eelgrass (*Zostera marina* L.) in Pacific Northwest (USA) estuaries. *Estuaries and Coasts*, *31*(5), 969-980.

Touchette, B. W., Burkholder, J. M., Glasgow, H. B. (2003). Variations in eelgrass (*Zostera marina* L.) morphology and internal nutrient composition as influenced by increased temperature and water column nitrate. *Estuaries*, *26*(1), 142-155.

Troell, M., Pihl, L., Rönnbäck, P., Wennhage, H., Söderqvist, T. S., Kautsky, N. (2005). Regime shifts and ecosystem services in Swedish coastal soft bottom habitats: when resilience is undesirable. *Ecology and Society*. 10, 30.

Valdemarsen, T., Canal-Verges, P., Kristensen, E., Holmer, M., Kristiansen, M. D., Flindt, M. R. (2010). Vulnerability of *Zostera marina* seedlings to physical stress. *Marine Ecology Progress Series*, *418*, 119-130.

Valdemarsen, T., Wendelboe, K., Egelund, J. T., Kristensen, E., Flindt, M. R. (2011). Burial of seeds and seedlings by the lugworm Arenicola marina hampers eelgrass (*Zostera marina*) recovery. *Journal of Experimental Marine Biology and Ecology*, *410*, 45-52.

Van Andel, J., Aronson, J. (2012). *Restoration ecology: the new frontier*. John Wiley & Sons.

Van der Heide, E. H., van Nes, E.H., Geerling, G.W., Smolders, A.J.P., Bouma, T.J., van Katwijk M.M. (2007) Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. *Ecosystems*, 10, 1311-1322.

Van Katwijk, M. M., Schmitz, G. H., Hanssen, L. S., den Hartog, C. (1998). Suitability of *Zostera marina* populations for transplantation to the Wadden Sea as determined by a mesocosm shading experiment. *Aquatic Botany*, *60*(4), 283-305.

Van Katwijk, M. M., Hermus, D. C. R. (2000). Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology Progress Series*, *208*, 107-118.

Van Katwijk, M. M., Wijgergangs, L. J. M. (2004). Effects of locally varying exposure, sediment type and low-tide water cover on *Zostera marina* recruitment from seed. *Aquatic Botany*, *80*(1), 1-12.

Van Katwijk, M. M., Hermus, D. C. R., De Jong, D. J., Asmus, R. M., De Jonge, V. N. (2000). Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. *Helgoland Marine Research*, *54*(2), 117.

Van Katwijk, M. M., Bos, A. R., De Jonge, V. N., Hanssen, L. S. A. M., Hermus, D. C. R., De Jong, D. J. (2009). Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Marine pollution bulletin*, *58*(2), 179-188.

Van Katwijk, M.M., Thorhaug, A., Marbà, N., Orth, R.J., Duarte, C.M., Kendrick, G.A., Althuizen, I.H.J., Balestri, E., Bernard, G., Cambridge, M.L., Cunha, A., Durance, C., Giesen, W., Han, Q., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K.-S., Meinesz, A., Nakaoka, M., O'Brien, K.R., Paling, E.I., Pickerell, C., Ransijn, A.M.A., Verduin, J.J. (2015) Global analysis of seagrass restoration: the importance of largescale planting. *Journal of Applied Ecology* 53, 567-578.

Vichkovitten, T., Holmer, M., Frederiksen, M. S. (2007). Spatial and temporal changes in non-structural carbohydrate reserves in eelgrass (*Zostera marina* L.) in Danish coastal waters. *Botanica Marina*, *50*(2), 75-87.

Waycott, M., Duarte, C. M., Carruthers, T. J., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick G.A., Kenworthy, W.J., Short, F.T., Williams, S.L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, *106*(30), 12377-12381.

WFD, Water Framework Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. 2000,L327:1-L327:72. Available online at: http://ec.europa.eu/health/endocrine_disruptors/docs/wfd_200060ec_directive_en.pdf

Whitlow, W. L., Grabowski, J. H. (2012). Examining how landscapes influence benthic community assemblages in seagrass and mudflat habitats in southern Maine. *Journal of Experimental Marine Biology and Ecology*, *411*, 1-6.

Wong, M. C., Bravo, M. A., Dowd, M. (2013). Ecological dynamics of *Zostera marina* (eelgrass) in three adjacent bays in Atlantic Canada. *Botanica Marina*, *56*(5-6), 413-424.

Yamamuro, M., Kayanne, H., Yamano, H. (2003). δ15N of seagrass leaves for monitoring anthropogenic nutrient increases in coral reef ecosystems. *Marine Pollution Bulletin*, *46*(4), 452-458.

Yousef, Y.A. (1974) Assessing effects on water quality by boating activity. EPA670/2-74-072. U.S. Environmental Protection Agency.

Zimmerman, R. C., Reguzzoni, J. L., Wyllie-Echeverria, S., Josselyn, M., Alberte, R. S. (1991). Assessment of environmental suitability for growth of *Zostera marina* L.(eelgrass) in San Francisco Bay. *Aquatic Botany*, *39*(3-4), 353-366.

Zimmerman, R. C., Reguzzoni, J. L., Alberte, R. S. (1995). Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: role of light availability on metabolism, growth and survival. *Aquatic Botany*, *51*(1), 67-86.

Östman, Ö., Eklöf, J., Eriksson, B. K., Olsson, J., Moksnes, P. O., Bergström, U. (2016). Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems. *Journal of Applied Ecology*. DOI: 10.1111/1365-2664.12654.