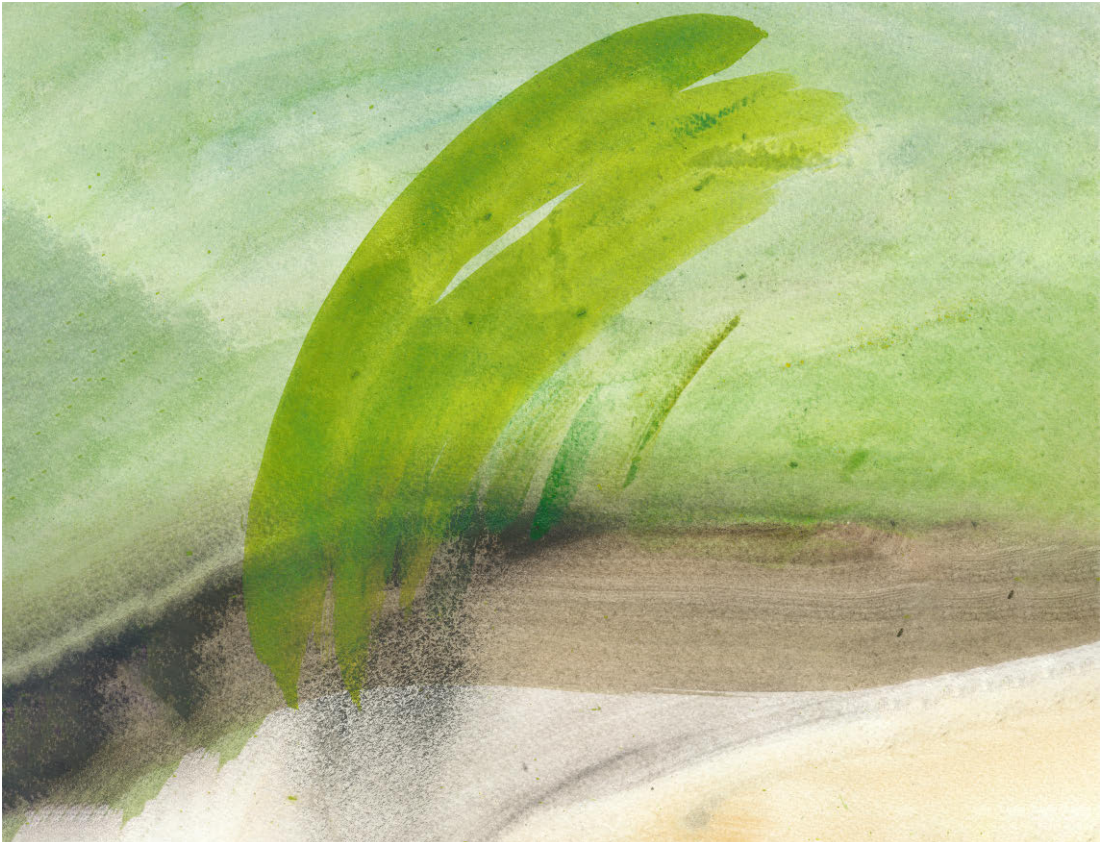


Maria Emilia Röhr

Environmental Drivers Influencing the  
Carbon Sink Capacity of Eelgrass  
(*Zostera marina*)







# Environmental Drivers Influencing the Carbon Sink Capacity of Eelgrass (*Zostera marina*)

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## Abstract

The accelerating increase of atmospheric CO<sub>2</sub> concentrations have caused regime shifts and changes in the net carbon balance of both terrestrial and marine systems worldwide. Blue carbon, the organic carbon sequestered by vegetated coastal ecosystems such as seagrasses, salt marshes, and mangroves, accounts for over half of the carbon captured by plants on Earth. Unfortunately, large areas (>33%) of these habitats have been lost in the past 50 years. Eelgrass, *Zostera marina*, is among the most abundant seagrass species in the world, but until now, the knowledge base on its capacity to sequester and store organic carbon has remained unclear. In this thesis, the magnitude of *Z. marina* blue carbon stocks was quantified at local, regional and global scales. In addition, the abiotic and biotic factors causing variation in *Z. marina* carbon stocks was explored. The results from this thesis revealed that *Z. marina* blue carbon stocks are considerable, although variation was notable at all spatial scales studied. While the *Z. marina* blue carbon stocks in some regions were relatively modest, hot spots for *Z. marina* carbon storage were also identified, especially in the Kattegat-Skagerrak and Mediterranean regions. Furthermore, the results from this thesis revealed that *Z. marina* blue carbon stocks are comparable to that of tropical seagrass species, other blue carbon ecosystems and even terrestrial ecosystems. The majority of the variation in the *Z. marina* blue carbon stocks was explained by sediment-related attributes, i.e. mud content (particle size <63 µm), degree of sorting, and the fraction of *Z. marina* detritus in the sediment carbon pool. Laboratory experiments showed that the decomposition of *Z. marina*, *Stuckenia pectinata*, and *Cladophora glomerata* was higher in mud compared to sand. Finally, the results from this thesis revealed that organic carbon and nitrogen stocks in *Z. marina* sediments along the west coast of Sweden were among the highest reported for *Z. marina* ecosystems. The monetary value of the organic carbon and nitrogen sequestration along the Swedish west coast was one of the highest reported for an ecosystem service by seagrasses. The results of this thesis call for more efficient protection of seagrass meadows and other blue carbon ecosystems, and urge for better integration of these ecosystems into global carbon budgets.

KEYWORDS: *Zostera marina*, Seagrass, Carbon dioxide, Carbon accumulation, Carbon sink capacity, Carbon budgeting, Carbon storage, Blue carbon, Carbon sequestration, Nitrogen stock, Climate change, Ecosystem services, Decomposition, *Cladophora glomerata*, *Stuckenia pectinata*, Sediment quality, Baltic Sea

## Sammanfattning

Den ökande koldioxidhalten i atmosfären har förorsakat regimskiften, och förändringar i koldioxidbalansen i både terrestra och marina ekosystem. Det organiska kol som binds av kustekosystem som t.ex sjögräsängar, marskland och mangrove kallas för blått kol (blue carbon). Dessa kusthabitat står för över hälften av det kol som binds av växter, men över 33% av dessa habitat har förlorats de senaste 50 åren. Ålgräs, *Zostera marina*, är en av de mest utbredda sjögräsarterna globalt, men vår kunskapsbas angående denna arts kapacitet att binda och lagra organiskt kol har hittills varit bristfälligt undersökt. I denna avhandling kvantifierades ålgrässets kollagringskapacitet på olika rumsliga skalor, samt vilka abiotiska och biotiska faktorer som styr variationen i ålgräsängarnas kollagringsförmåga. Resultaten visade att ålgrässets kollagringsförmåga är betydande, men varierar kraftigt mellan olika områden. Medan mängden kol i endel regioner var relativt modest, hittades bl.a. i Kattegat-Skagerrak och Medelhavet ålgräsängar med stor kollagringskapacitet. Specifikt visade studien att ålgräsängarnas kollagringskapacitet är jämförbara med tropiska sjögräsarter, andra kustekosystem och även terrestra ekosystem. Den största delen av variationen i ålgrässets kollagringsförmåga förklarades av sedimentets lerhalt (partiklar <63 µm), sorteringsgrad och andelen ålgräsdetritus i sedimentet kolreservoar. Laboratorieexperiment visade att nedbrytningen av *Z. marina*, *Stuckenia pectinata* och *Cladophora glomerata* var snabbare i lera jämfört med sand. Slutligen visade studier från svenska västkusten att ålgräsängarnas kol- och kvävelager var bland de största som rapporterats för ålgräsängar. Penningvärdet för ålgräsängarnas kol- och kvävebindning längs den svenska västkusten är bland det högsta som rapporterats för en ekosystemtjänst för sjögräsängar. Resultaten från denna avhandling uppmanar till effektivare skydd av sjögräsängar och andra viktiga marina ekosystem som lagrar kol, samt en bättre integrering av marina kolsänkor i den globala kolbudgeten.

NYCKELORD: *Zostera marina*, sjögräs, koldioxid, kolackumulering, kollagringsförmåga, kolsänka, blått kol, kolbudget, kvävelager, klimatförändring, ekosystemtjänster, nedbrytning, *Cladophora glomerata*, *Stuckenia pectinata*, sedimentkvalitet, Östersjön

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## List of original publications

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- I. **Röhr, M. E.**, Boström C., Canal- Vergés P., Holmer, M. (2016). Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences*, 13, 6139-6153.
- II. **Röhr, M. E.**, Holmer, M., Baum J.K., Björk, M., Boyer, K., Chin, D., Chalifour, L., Cimon, S., Cusson M. Dahl, M., Deyanova, D., Duffy, J. E., Eklöf, J. S., Geyer, J. K, Griffin, J. N., Gullström, M., Hereu, C. M., Hori, M., Hovel, K. A., Hughes, R., Jorgensen, P., Kiriakopolos, S., Moksnes, P.-O. Nakaoka, M., O’Connor, M. I., Peterson, B., Reiss, K., Reynolds, P. L., Rossi, F., Ruesink, J., Santos, R., Stachowicz, J. J., Tomas, F., Lee, K.-S., Unsworth, R. K. F., Boström, C. (2018). Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. *Global Biogeochemical Cycles*, doi/abs/10.1029/2018GB005941.
- III. **Röhr, M. E.**, Boström, C., Holmer, M. Role of carbon source and sediment type for blue carbon pools in seagrass sediments. (Manuscript).
- IV. Moksnes, P.-O., **Röhr, M. E.**, Holmer, M., Eklöf, J. S., Eriander, L., Infantes, E., Boström, C. Assessing impact and costs of eelgrass loss on sediment carbon and nitrogen stocks in NW Sweden (Manuscript).



**Table 1.** Author contribution to the individual Papers included in the thesis. CB= Christoffer Boström, MH= Marianne Holmer, ER= Emilia Röhr, PC= Paula Canal, MD= Martin Dahl, MG= Martin Gullström, PM= Per Olav Moksnes, PJ= Pablo Jorgensen, JE= Johan Eklöf, LE= Louise Eriander, EI= Eduardo Infantes.

	<b>Paper I</b>	<b>Paper II</b>	<b>Paper III</b>	<b>Paper IV</b>
<b>Original idea and experimental design</b>	CB, MH	CB, MH, ER	MH, ER	PM
<b>Data collection</b>	CB, ER, PC	All co-authors	CB, ER	PM, CB
<b>Data analysis</b>	ER, CB, MH	ER, CB, MH, MD, MG, PJ	ER	PM, ER
<b>Manuscript preparation</b>	ER, CB, MH, PC	ER, CB, MH	ER, CB, MH	PM, ER, MH, CB, JE, LE, EI

## Carbon terminology

- *Blue carbon*: organic carbon stored, sequestered or released from vegetated coastal marine ecosystems.
- *Brown carbon*: Light-absorbing carbon released from combustion of organic matter.
- *Black carbon*: carbon particles with the morphological and chemical properties typical of soot and dust particles resulting from impure combustion of fossil fuels.
- *Green carbon*: Carbon captured through photosynthesis and stored in terrestrial plant biomass.
- *Carbon stock per unit area*: carbon stored in the living and dead biomass of specific species or ecosystems usually given as:  $\text{g C m}^{-2}$  or  $\text{t C ha}^{-1}$  or  $\text{Pg C km}^{-2}$  ( $1 \text{ Pg} = 1 \text{ Gt} = 10^{15} \text{ g}$ ).
- *Carbon sequestration/accumulation/burial*: the accumulation and storage of carbon into reservoirs other than atmosphere usually given as:  $\text{Mt C yr}^{-1}$  or  $\text{Pg C yr}^{-1}$ .
- *Carbon sink*: ecosystems large enough to absorb substantial amounts of atmospheric carbon in which the rate of carbon sequestered exceeds the rate of carbon lost through respiration and export.
- *Carbon sink capacity*: capacity of specific species to absorb and store carbon in their living and dead biomass.
- *Carbon source*: ecosystems or organisms in which the rate of carbon released through respiration and export exceeds the rate of carbon sequestered.
- *Carbon donor*: carbon binding organisms or ecosystems, which contribute to carbon sequestration of adjacent carbon reservoir.
- *Carbon stock*: carbon stored in living and dead plant biomass and sediments.
- *Carbon budget*: an amount of carbon that a country, company, organization or individual has agreed it will produce within specific time frame.
- *Global carbon budget*: sum of global exchange of carbon between all carbon reservoirs.
- *Carbon cycle*: series of processes, in which carbon exchanges from carbon reservoir to another and back.
- *Carbon flux*: the transfer of carbon between carbon reservoirs.
- *Carbon pool*: the pool of carbon stored in a specific ecosystem or geographical location.

(Sources: <http://thesciencedictionary.org>,  
<https://dictionary.cambridge.org/dictionary/english>,  
<https://www.merriam-webster.com/dictionary>, <https://www.climate-change-guide.com>)

# 1. Introduction

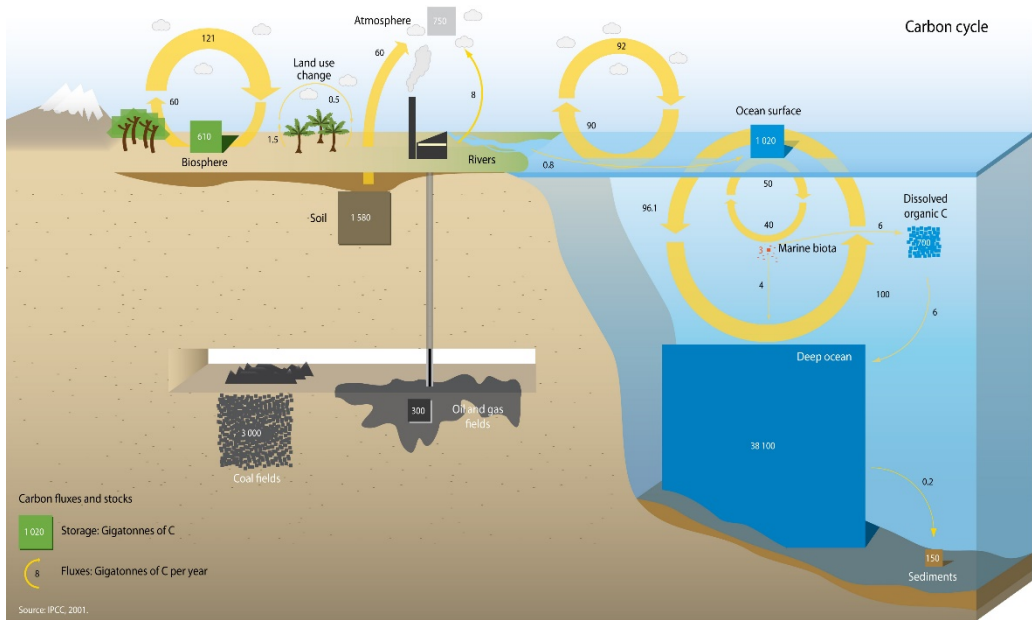
The atmospheric CO<sub>2</sub> concentration is higher than in the past 800 000 years (405 ppm) and has increased ~40% from the preindustrial value of 280 ppm (IPCC, 2018). The climate change induced accelerating environmental changes have led to increases in occurrence of extreme weather events, ocean warming, sea-level rise, deoxygenation and ocean acidification (IPCC, 2018, Gattuso et al., 2018; Magnan et al., 2018), causing regime shifts in e.g. productivity and carbon balance of both marine and terrestrial ecosystems (Maxwell et al., 2016; Ciais et al., 2013; Magnan et al., 2018). The increased CO<sub>2</sub> emissions are primarily consequences of anthropogenic pressures, such as use of fossil fuels, coastal development, changes in land use and eutrophication (Ciais et al., 2013; IPCC, 2018). In 2015, 195 countries signed the Paris Climate Change Agreement to limit global warming to 2 °C, to reduce greenhouse gas emissions substantially by 2050 and to provide economic support for 3<sup>rd</sup> world countries, which would enable them to participate in alleviation of these emissions. The agreement allowed individual countries to set their own national targets, but regrettably, recent studies have shown strong evidence that with the current level of national pledges, the goal of limiting global warming to 2°C is likely to fall short (Barbier et al., 2018; Magnan et al., 2018). Coastal vegetated ecosystems are among the most productive ecosystems in the biosphere, supporting multiple ecosystem services and biodiversity, including significant CO<sub>2</sub> uptake and long-term carbon storage and sequestration (e.g. Smith 1981; Costanza et al., 1997; Nelleman et al., 2009; Duarte et al., 2005, 2013a, 2013b, 2017). With the current pace of the climate change, both marine and terrestrial ecosystems face various challenges to adapt to the changing environment. Regrettably, in the past 50 years coastal vegetated ecosystems have suffered severe (1/3) losses of their habitat area (Duarte, 2017). In the past decades, scientists have urged the global leaders to include coastal vegetated ecosystems as part of climate change mitigation and carbon trading programs (Duarte & Cebrian, 1996; Nelleman et al., 2009; Duarte et al., 2005, 2013b; Luisetti et al., 2013; Howard et al., 2017a; Gattuso et al., 2018, **Paper I and II**). In the absence of financial incentives for protection of coastal carbon, the losses of these ecosystems will inevitably continue (Murray et al., 2011; Locatelli et al., 2014; Barbier et al., 2018).

## 1.1. Carbon cycling in the oceans

The atmospheric CO<sub>2</sub> enters the ocean at ocean-air interface via gas exchange processes driven by the partial CO<sub>2</sub> pressure difference between air and ocean, also known as the solubility pump (Ciais et al., 2013). In addition to solubility pump, the carbon in the oceans is transported via (1) biological pump, in which dissolved CO<sub>2</sub> is fixed through photosynthesis in to plant biomass and respired back as CO<sub>2</sub>, (2) physical pump, which transports dissolved inorganic carbon (hereafter DIC) and dissolved and particulate organic carbon (hereafter DOC and POC) by hydrodynamic forces vertically and horizontally between water layers and (3) marine carbonate pump, in which two bicarbonate (HCO<sub>3</sub><sup>-</sup>) ions are divided into one carbonate (CO<sub>3</sub><sup>2-</sup>) and one dissolved CO<sub>2</sub> molecule in formation of calcareous oceanic organisms. This process is also known as biogenic carbonate precipitation and in contrast to the solubility and biological pump the CO<sub>2</sub> produced in the calcification of these marine organisms is actively released back to the atmosphere, especially as the process occurs in the surface waters (Ciais et al., 2013, Emerson, 2014).

Around 95 % percent of all the carbon actively circulating (for durations < 10 000 years) on earth lies in the oceans, from which majority is in the deep sea as DIC in the form of bicarbonates, carbonates, dissolved CO<sub>2</sub> and carbonic acid (H<sub>2</sub>CO<sub>3</sub>). The pools of carbon in the surface and deep sea are enormous (1020 and 38 000 Pg C, respectively), the inorganic carbon within these pools has a residence time of up to 110 000 years, while the turnover of organic carbon within these pools is relatively fast (up to a few decades) (Garrison, 2009; Nelleman et al., 2009; Ciais et al., 2013) (Fig. 1). In general, these carbon pools are usually not considered as a long-term organic carbon sinks (here defined as ecosystems, in which rate of primary production, organic carbon accumulation and storage is higher than rates of respiration and export) due to their susceptibility for decomposition within few years to decades (Nelleman et al., 2009; Ciais et al., 2013). Living marine biota, such as phytoplankton and other marine micro-organisms, store ~3 Pg of organic carbon (hereafter C<sub>org</sub>) in their biomass, this fraction being relatively small compared to that stored in terrestrial biota (~610 Pg C), although in terms of carbon fluxes, their magnitude is almost equivalent (~50 Pg C y<sup>-1</sup>) (Schlesinger & Bernhardt, 2013) (Fig. 1). Part (~700 Pg C) of the carbon in the oceans is in the form of DOC and POC in the water column, while a relatively small fraction (150 Pg C) is DOC and POC buried in the sediments, where it accumulates by ~0.2 Pg C annually and can persist for time scales of millennia or longer and thus, can be

considered to be stored in long term (Denman et al., 2007; Hansell et al., 2009) (Fig. 1).



**Figure 1.** Generalization of carbon cycling on earth and the magnitude of carbon stocks within each major carbon pool. 1 Gigatonne=1000000000 tons. Graph: Riccardo Pravettoni, UNEP/GRID-Arendal, <http://www.grida.no/resources/7559>

## 1.2. Coastal blue carbon

The studies on blue carbon started already in the early 1980's when Smith (1981) published an article focusing attention on the role of marine macrophytes, macroalgae in particular, as carbon sinks. The work by Smith was not truly recognized until Duarte and Cebrian (1996) calculated vegetated coastal habitats as generally net autotrophic communities, responsible of large fraction of production and burial of  $C_{org}$  in the marine realm. In their early studies, they highlighted the particular importance of marine angiosperms for the oceanic carbon burial. In 2005, Duarte et al. provided first estimates on the magnitude of  $C_{org}$  burial by seagrass ( $83 \text{ g C m}^{-2} \text{ y}^{-1}$ ), mangroves ( $139 \text{ g C m}^{-2} \text{ y}^{-1}$ ) and salt-marsh ecosystems ( $151 \text{ g C m}^{-2} \text{ y}^{-1}$ ) equivalent to  $\sim 40\%$  of their net primary production, and identified the role of these ecosystems as globally important carbon sinks (Duarte et al., 2013a, 2017). In 2009, the term blue carbon was coined by Nelleman et al., to describe the carbon sequestered and stored by these three ecosystems, in particular. The work by Smith (1981) has got some recent updates, which have

highlighted the importance of other phyla, such as macroalgae and other marine angiosperms, for oceanic carbon cycling and  $C_{org}$  sequestration (Trevathan-Tackett et al., 2015; Hill et al., 2015; Krause-Jensen & Duarte, 2016; Krause-Jensen et al., 2018). In 2018, Krause-Jensen et al. estimated, that macroalgae contributes  $\sim 0.2 \text{ Pg C y}^{-1}$ , equivalent to about 11% of their net primary production, as a donor of  $C_{org}$ , which is further exported and potentially buried in the sediments of adjacent blue carbon ecosystems, or alternatively, to the sediments and waters of pelagic and deep sea. As in the case of macroalgae, carbon produced in any marine ecosystems may contribute significantly to the carbon pool elsewhere through seascape connectivity, even at distance of up to thousands of kilometres, thereby biasing the ecosystem specific carbon budgets (Huxham et al., 2018).

The three major blue carbon ecosystems i.e. mangroves, salt marshes and seagrasses (Herr et al., 2012) cover only  $\sim 0.2\%$  of the ocean floor, yet they are estimated to account for up to 33% of the total oceanic carbon uptake, equivalent to total of  $\sim 0.4\text{-}6.5$ ,  $9.4\text{-}10.4$  and  $4.2\text{-}8.4 \text{ Pg C}$  stored for long-term in the sediments of salt marshes, mangroves and seagrasses, respectively (Duarte et al., 2013a, 2017). In addition to the high primary production by these ecosystems, their efficient carbon storage capacity is promoted by the generally anoxic conditions in their submerged sediments and consequently, majority of the carbon stored by Blue Carbon ecosystems is stored in their sediment compartment and only small fraction ( $<3\%$  for seagrasses) of the  $C_{org}$  stocks is in the living biomass (Kennedy & Björk, 2009; Nelleman et al., 2009; Kennedy et al., 2010; Fourqurean et al., 2012, **Paper I and II**). Furthermore, a large, but yet unknown fraction, of their net primary production is being exported, the current estimates for export being  $\sim 25$ ,  $30$  and  $19\%$  of the net primary production of seagrass, mangrove and saltmarsh ecosystems, respectively (Duarte & Cebrian, 1996).

The carbon stored in blue carbon ecosystems is usually stored for thousands of years, i.e. the oldest seagrass  $C_{org}$  stocks being dated back some to 12500 years (Mateo et al., 1997). One of the major factors affecting the longevity of carbon stocks stored by blue carbon ecosystems is the rate of decomposition of the sequestered plant material (e.g. Wakeham & Canuel, 2006, **Paper III**). In decomposition, bacteria gain energy from the breakdown of decaying material and release substrate-bound carbon in respiration as  $\text{CO}_2$  (e.g. Wakeham & Canuel, 2006, Arndt et al., 2013). Decomposition, in turn, is primarily dependent on the chemical quality of the decaying plant material, the composition of the decomposing microbial community, temperature, and the biogeochemical conditions within the sediments in which the decomposition is taking place (Enriquez et al., 1993; Aller, 1994; Wakeham & Canuel, 2006, Arndt et al., 2013

**Paper III).** The progression of decomposition is usually fastest during the first months when the more labile tissues are being utilized, while the remaining refractory compounds decompose with considerably slower rates (Romero et al., 1992; Enriquez et al., 1993). In addition, decomposition is also affected by the fauna residing in the sediments, which alter the lability of organic matter and carbon in the sediments via e.g. bioturbation (Aller, 1994). In bioturbation, fauna modify both physical structure and biogeochemistry of sediments by providing oxygen to the anoxic sediment layers by their bioturbating activity, thus promoting faster decomposition and potentially causing microbial priming, re-activation of the previously dormant bacteria to re-start the breakdown of refractory material and the carbon within, in the sediments (Trevathan-Tackett et al. 2018).

### 1.3. Seagrasses and blue carbon

Seagrasses are marine foundation species comprising of 76 species of marine angiosperms covering 300 000–1 647000 km<sup>2</sup> of the world's ocean floor (Duarte et al., 2005; Jayathilake & Costello, 2018). For general overviews of their biology and ecology, see e.g. Hemminga & Duarte, (2000) and Green & Short, (2003). In terms of blue carbon, the role of seagrasses is particularly emphasized due to their large areal extent and distribution over almost the entire biosphere (Hemminga & Duarte, 2000; Duarte et al., 2005). Seagrasses grow under a wide range of different environmental settings covering gradients in e.g. light, temperature, salinity, depth, nutrient status and exposure (Hemminga & Duarte, 2000). In general, the primary factor controlling seagrass production, morphology and distribution is irradiance, in which seagrasses have some of the highest demands of any aquatic plant group (> 11% of incident radiation) (Duarte, 1991; Hemminga & Duarte, 2000; Gattuso et al., 2006). Seagrasses modify their surrounding environments by e.g. reducing sediment resuspension and water flow and enhancing organic and inorganic particle trapping via their canopy structure, leading to changes in sediment composition (muddification), carbon balance and nutrient dynamics (Fonseca & Cahalan, 1992; Gacia & Duarte 2001, Gacia et al., 2002; Agawin & Duarte, 2002; Koch et al., 2006; Hendriks et al., 2008). Due to these traits and multiple other functions and ecosystem services they provide (see e.g. Cole & Moksnes, 2012; Luisetti et al., 2013; Unsworth & Cullen-Unsworth 2013; Hejnowich et al., 2015; Nordlund et al., 2017; Moksnes et al., 2018) seagrasses are considered as important ecosystem engineers (Jones et al., 1994).

The generally net autotrophic seagrasses play a primary role in C<sub>org</sub> production and nutrient cycling in many coastal regions (Duarte & Cebrian, 1996; Duarte et

al., 2005, 2010; Tokoro et al., 2014, **Paper I, II and IV**). Current estimates suggest that seagrasses may store annually  $\sim 0.5\text{--}1.1$  Pg C, averaging at  $83\,000$  t C km<sup>-2</sup> (Duarte et al., 2010; Mcleod et al, 2011; Fourqurean et al., 2012; Macreadie et al., 2013). In general, their capacity for efficient carbon storage can be attributed to six core factors: (1) high rate of primary production (Duarte & Cebrian, 1996; Duarte et al., 2005, 2010), (2) high root: shoot ratio (Hemminga, 1998), (3) high C:N:P ratio, (4) high proportion of refractory compounds in seagrass tissues (Fourqurean & Scharlau, 2003; Vichkovitten & Holmer, 2004), (5) the generally anoxic conditions in seagrass sediments (Kristensen & Holmer, 2001) and (6) high rate of sedimentation (Gacia et al., 2002; Koch et al., 2006; Hendriks et al., 2008). Thus, seagrass meadows, in which production and accumulation of autochthonous, seagrass derived detritus and allochthonous organic materials is high, while rate of decomposition is slow, are likely to have the highest carbon sink capacity per area (Kennedy et al., 2010; Mazarassa et al., 2018, **Paper I and II**).

Unfortunately, despite the important role seagrasses play for multiple ecosystem services,  $\sim 51\,000$  km<sup>2</sup> of global seagrass coverage has been lost over the past 130 years, making them one of the most threatened ecosystems on the planet (Orth et al., 2006; Duarte et al., 2010; Waycott et al., 2009). In 2009, Waycott et al. estimated an annual loss rate of 5-7%, equivalent to  $110$  km<sup>2</sup> of lost seagrass area each year. As seagrass habitats are located near shore, they have been especially sensitive to anthropogenic-induced pressures, such as eutrophication, overfishing, habitat fragmentation and destruction, forestry and commercial developments (Orth et al, 2006; Waycott et al, 2009; McLeod et al. 2011; Dahl, 2017; Ricart et al., 2017). These stressors may have led to unexpected changes in energy flow pathways and trophic cascades further influencing the net carbon balance of these ecosystems (Baden et al. 2010; Moksnes et al., 2018, **Paper IV**). Consequently, the loss of seagrasses has led to negative feedback mechanisms in many locations i.e. the increased water turbidity resulting in poorer light conditions hindering the potential recovery of these ecosystems (Macreadie et al., 2015; Marba et al., 2015, Moksnes et al., 2018).

#### **1.4. Knowledge gaps in seagrass blue carbon studies**

Global seagrass distribution has long been uncertain due to insufficient mapping and data gaps from certain geographical regions (e.g. South-Pacific Ocean). In addition, it is extrapolations rather than direct measurements, that the distribution data of many regions has been based on, when it has been available in the first place (Duarte et al. 2010; Fourqurean et al., 2012). This uncertainty in the global seagrass distribution data has challenged the adequate estimation on the



magnitude of the global seagrass blue carbon stocks. Recent studies have offered some much needed improvements to these estimates as in 2018, Jayahilake and Costello modelled seagrass distribution using ~43 000 occurrence records and 13 environmental variables, resulting in predicted seagrass biome that was over two-folds higher than the earlier upper estimates (change from upper range of 600 000 to 1646788 km<sup>2</sup>). However, even if the model makes it possible to establish where seagrasses has historically existed, their current status and existence still needs to be verified through field surveys.

Furthermore, the current estimates on the magnitude of global seagrass carbon storage are largely based on values derived from studies on *Posidonia oceanica*, which is a species particularly capable of storing C<sub>org</sub> in their extensive (up to several meters thick) rhizome mats, while the estimates for most other seagrass species are still insufficient or lacking entirely (Kennedy et al., 2010; Greiner et al., 2013; Fourqurean et al., 2012; Macreadie et al., 2013; Duarte et al., 2013a; Lavery et al., 2013; Serrano et al., 2014, 2015; **Paper II**). In addition, when data for other species has been applied, the estimates has often been biased by large number of sites from tropical regions while region-specific values are still missing for many parts of the world (Duarte et al., 2013; Lavery et al., 2013; Fourqurean et al., 2012; Mazarassa et al., 2015, 2018). The robust extrapolation of values measured from the sediments of a single species (*P. oceanica*) or only one or few latitudinal regions has led to considerable amplifications on the magnitude of global seagrass C<sub>org</sub> stocks and created a demand for more adequate estimates taking into account both the local environmental drivers as well as regional and species-specific differences in seagrass C<sub>org</sub> sequestration (Duarte et al., 2013b; Mazarassa et al., 2018; **Paper II**).

Moreover, recent studies (Mazarrasa et al., 2015; Howard et al., 2017a, Saderne et al., 2019) have drawn focus on the magnitude of carbonate stocks within the seagrass meadows. Mazarrasa et al. (2015) provided an estimate on the global average carbonate stocks in the top 1 m of seagrass sediments of 654 t C ha<sup>-1</sup>. The median from their study (~643 t C ha<sup>-1</sup>) for carbonate reserves was almost five-fold higher than the median by Fourqurean et al. (2012) for global seagrass C<sub>org</sub> stocks (~140 t C ha<sup>-1</sup>), suggesting a potential offset of a significant proportion of seagrass carbon sink capacity, especially in the tropical regions, in which the calcifying epiphytes are more abundant compared to seagrasses growing on higher latitudes (Mazarassa et al., 2015; Duarte, 2017; Mazarassa et al., 2018; Howard et al., 2017b, Saderne et al., 2019). Similarly, in 2019, Saderne et al., estimated the annual inorganic carbon burial in seagrass ecosystems to 0.015-0.062Pg of inorganic carbon, however, their study also identified that the inorganic carbon

was mainly derived from allochthonous sources rather than local calcification, and that the seagrass ecosystems acted as sites of net  $\text{CaCO}_3$  dissolution and thus, the inorganic carbon within the studied seagrass ecosystems would not hinder their capacity to act as carbon sinks. However, the comparison of  $\text{CaCO}_3$  burial and calcification by Saderne et al. (2019) was based on three geographical locations (Florida Bay; USA, Balearic Islands; Spain and West Shark Bay; Australia) while the proportion of both blue carbon and carbonate reserves in seagrass meadows and knowledge on their sources of origin remains to be quantified for many parts of the world.

Finally, the knowledge on the fate of carbon from lost seagrass meadows is still scarce and limited to results from samples gathered from certain restricted geographical areas, despite the fact that the global loss rates of the seagrass areas are accelerating (e.g. Macreadie et al., 2013; Marba et al., 2015; Moksnes et al., 2018). In addition, the rate, sources and fate of exported carbon remains unclear for many species and geographical regions, although carbon produced in any blue carbon ecosystem may also contribute significantly to the  $\text{C}_{\text{org}}$  stocks of other adjacent ecosystems (Duarte & Krause-Jensen, 2017; Krause-Jensen et al., 2018; Huxham et al., 2018). Furthermore, to date, the role of fauna in sediment carbon sequestration and release is poorly understood, although recent studies suggest, that bioturbation may multiply the release of  $\text{C}_{\text{org}}$  up to several folds, potentially turning the role of these ecosystems from carbon sinks into hot spots of carbon loss (Thomson, 2017; Trevathan-Tackett et al., 2018).

## 2. Aims and scope of thesis

The main aim of this thesis was to explore the magnitude and variation in  $C_{org}$  stocks and accumulation in the sediments of eelgrass, *Zostera marina*. *Z. marina* is among the most abundant seagrass species in the world, dominating all marine areas in the temperate Northern Hemisphere, except Mediterranean, thus potentially playing an important role in the coastal carbon sequestration and accumulation (Duarte & Sand-Jensen, 1990; Spalding et al., 2003; Moore & Short, 2006; Boström et al., 2014).

Specific aims were to

- (1) clarify the role of *Z. marina* meadows, as potential carbon sinks or sources in both in the Baltic Sea (**Paper I**) as well as in the temperate Northern hemisphere (**Paper II**) and to investigate the abiotic and biotic factors explaining the variability in *Z. marina*  $C_{org}$  stocks at local, regional and global scales (**Papers I-II**),
- (2) examine the magnitude of *Z. marina*  $C_{org}$  stocks compared to other seagrass species, other blue carbon ecosystems and terrestrial ecosystems (**Paper II**),
- (3) determine the decomposition of two angiosperms (*Z. marina*, *Stuckenia pectinata*) and one algal species (*Cladophora glomerata*) abundant in the Baltic Sea and to explore their importance for the formation of sediment blue carbon stocks in the region (**Paper III**), and
- (4) quantify and compare the magnitude of *Z. marina*  $C_{org}$  and nitrogen stocks between historic and existing *Z. marina* sites along west coast of Sweden, and to explore the monetary value of these stocks (**Paper IV**).

### 3. Study areas

The field sampling for **Paper I** was carried out in two regions of the Baltic Sea, i.e. the Archipelago Sea in Southwest coast of Finland and Funen and in Limfjorden areas in Denmark, which notably differ in salinity, temperature and annual production rates. The sampling took place in the summer 2014 (Fig. 1 in **Paper I**). The study sites in both regions spanned a gradient from sheltered to exposed areas (Fig. 1 in **Paper I**). Baltic Sea is a temporally and spatially diverse marine area of 400 000 km<sup>2</sup> characterized with permanent halocline, salinity gradient, strong seasonal peaks in temperature and productivity and riverine runoff from an area four times larger than the actual sea itself, with an estimated average annual riverine input of carbon of ~ 0.11 Pg C (Conley et al., 2009; Kulinski & Pempowiak, 2011). Baltic Sea sediments are typically low carbonate, mineral sediments consisting of glaciofluvial deposits and majority of the carbon in the sediments is in organic form (Leipe et al., 2011). Riverine input is the single most important source of allochthonous organic matter and C<sub>org</sub> to the Baltic Sea followed by transport from North Sea to the Baltic Sea (Kulinski & Pempowiak, 2011). Other sources of allochthonous carbon include atmospheric deposition, point sources and fisheries (Kulinski & Pempowiak, 2011). The shores of Baltic Sea offer home for ~85 million people, making the region heavily impacted by anthropogenic-induced pressures (Conley et al., 2009; Andersen et al., 2017). Especially since the 1950s, eutrophication has caused strong environmental changes in the Baltic Sea, including increases in the production of autochthonous carbon leading to increases in the extent of hypoxic water column and sediments due to increased input of organic matter and elevated rates of microbial degradation following it (Conley et al., 2009; Andersen et al., 2017). In the Baltic Sea, *Z. marina*, is the most abundant seagrass species covering 1500-2100 km<sup>2</sup> of the seafloor with over 6 000 individual meadows, although large scale losses of *Z. marina* coverage area have occurred during the last century (Boström et al. 2002; Spalding et al. 2003; Boström et al., 2014). The meadows extend from saline (>25) waters in the South to the brackish (5-6) Archipelago Sea in the Northern parts of the Baltic Sea.

The data for **Paper II** was collected through a collaboration of scientists within the *Zostera Experimental Network* (ZEN; [www.zenscience.org](http://www.zenscience.org); e.g. Duffy et al., 2015, **Paper II**) in 2015 (n= 54). The network covered 13 countries (Bulgaria, Canada, Denmark, Finland, France, Japan, Korea, Mexico, Norway, Portugal, Sweden, United Kingdom, USA) and 36 latitudes across 8 ocean margins and seas; Eastern and Western Atlantic, Eastern and Western Pacific, Baltic Sea, Black Sea, Mediterranean Sea, and Kattegat-Skagerrak (Fig. 1 in **Paper II**).

The study for **Paper III** was conducted as a long-term (12 months) laboratory experiment in 2015-2016. Sediment samples for the experiment were collected from the Finnish Archipelago Sea, at two sites, one with high silt content sediment (~14 % of <63  $\mu\text{m}$  grain size), namely Eriksvalla, and one with low silt content (~1 % of < 63  $\mu\text{m}$  grain size), namely Likholmen. Plant samples for the laboratory experiment were collected from Fårö at the outer Archipelago Sea, in June 2015.

The field sampling for **Paper IV** was carried out in Marstrand area along the west coast of Sweden in the summer 2015 and 2016 (Fig. 1 in **Paper IV**). Marstrand area expands from river Nordre in the South to the city of Stenungsund in the North. Since the 1980's, 20-90% of *Z. marina* coverage in the area has been lost, the highest loss rates found in the southern parts, while at the northern parts, the losses have been less severe (Moksnes et al., 2018). For the study, four meadows with existing *Z. marina* coverage and four areas that have lost *Z. marina* coverage in the past 40 years in Marstrand were sampled. As the meadows still persisting in Marstrand are fragmented and significantly reduced in size, four sites were also sampled in a more pristine nearby area, Gullmarsfjord, where losses of *Z. marina* coverage has been < 5% (Baden et al. 2003; Nyqvist et al. 2009) (Fig. 1 in **Paper IV**). The four sites within each of the areas (Marstrand, Marstrand lost eelgrass, Gullmarsfjord) were chosen to represent four types of exposure (sheltered, semi-sheltered, semi-exposed, and exposed).

## 4. Material and methods

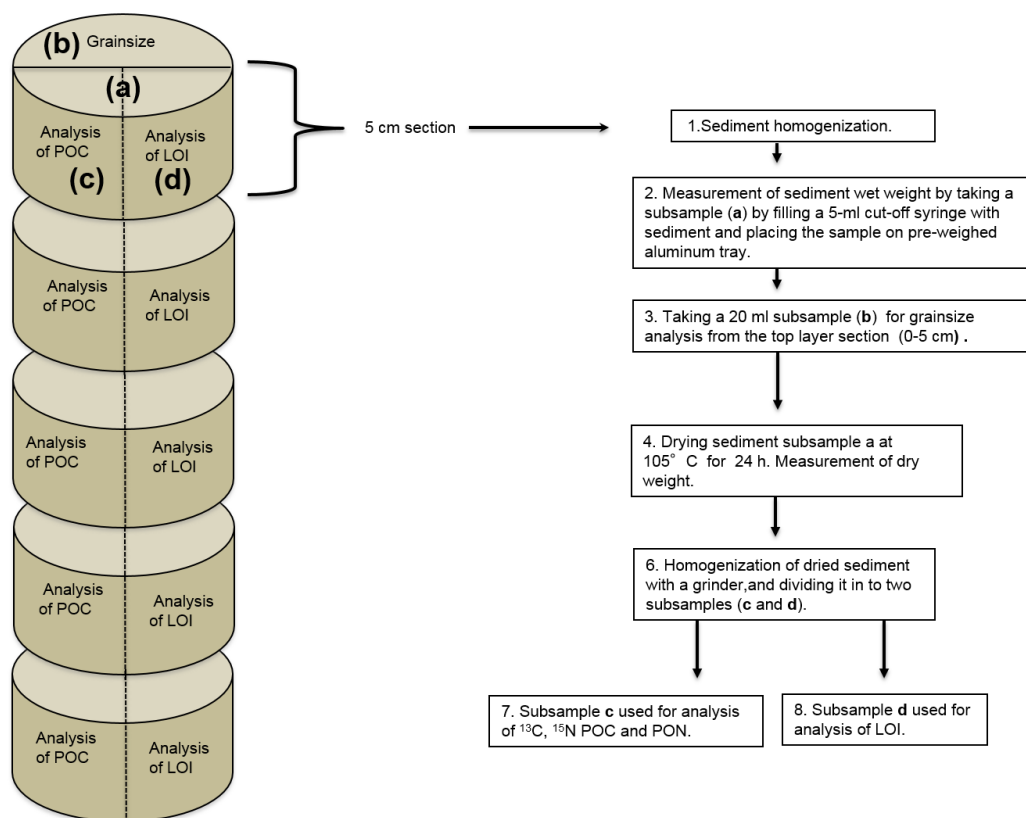
### 4.1. Field sampling and laboratory work

#### 4.1.1. Plant sampling and processing

The plant samples for **Papers I, II and IV**, were collected from depths of 0.2 to 3.8 m by SCUBA diving (see materials and methods sections in **Papers I, II and IV** for site-specific sampling depths). The aboveground *Z. marina* biomass and living and dead rhizomes were dried separately to a constant weight (48 h in 60° C). Only the living rhizomes were used for the belowground biomass measurements. The root: shoot ratio was calculated as the ratio between below- and aboveground biomasses. *Z. marina* shoot density was counted using a 0.25 m<sup>2</sup> frame. For **Paper I**, annual *Z. marina* production was determined from estimates of previous growth by applying the horizontal rhizome elongation technique (Short & Duarte, 2001). To evaluate the potential contribution of different carbon sources to the sediment surface carbon pool also other carbon sources (drift algae, other marine angiosperm species, phytoplankton and epiphytes) considered to be the most potential alternative carbon sources in the studied *Z. marina* meadows were collected and dried to constant weight as described above.

#### 4.1.2. Sediment sampling and processing

Sediment samples were randomly collected by inserting three replicate sediment cores (length: 50 cm, diameter: 50 mm) at a minimum distance of 15 m from each other to a depth of 30-40 cm. The 0-25 cm section of the sediment core was used for analysis in **Papers I and II** while 0-35 cm section was used for **Paper IV**. The sediment samples were analysed for sediment water content (%), dry density (g cm<sup>-3</sup>) and porosity ( $\phi$ ) by weighing a 5 mL subsample before and after drying at 105 °C for 6 h (Fig. 2). The sediment grain size ( $\phi$ ) was determined from the upper layer (0-5 cm) of the sediment cores using a Malvern Mastersizer 3000 particle size analyser for **Papers I, II and IV**, while for **Paper III**, the grain size was analysed by use of sieve series (63, 125, 250, 500, 1000 and 2000  $\mu$ m). The sediment silt content (%) was calculated based in the 0-63  $\mu$ m grain size fraction. Degree of sorting, used as a proxy for exposure in **Papers I, II and IV**, was calculated from the different sediment grain size fractions, following calculations described in detail by Folk & Ward (1957). The dried sediment samples were homogenized and sediment organic matter content (%) was analysed as loss of ignition, 4 h in 520 °C (Fig. 2).



**Figure 2.** Example of sediment core processing and subsamples taken from each core.

#### 4.1.3. Analysis of organic carbon (POC) and nitrogen (PON)

The plant POC, PON and stable isotope composition of carbon and nitrogen (hereafter  $^{13}\text{C}$  and  $^{15}\text{N}$ ) were measured from the living *Z. marina* aboveground biomass and from both living and dead rhizomes by use of Thermo Scientific, delta V advantage, isotope ratio mass spectrometer connected to C:H:N elemental analyser. For the analysis of these variables in the aboveground biomass, a pooled sample of two youngest leaves from 10 randomly selected shoots were collected and dried separately. The plant C: N ratio was calculated as a ratio between POC and PON in the samples. The POC, PON,  $^{13}\text{C}$  and  $^{15}\text{N}$  content in sediment samples and samples for other potential carbon sources were analysed with mass spectrometer as described above for plant materials. The contribution of different carbon sources to the sediment surface (0-5 cm)  $\text{C}_{\text{org}}$  pool was analysed by use of mixing model software Isosource 1.3 (Phillips & Gregg, 2003) (**Paper I**) and R-function “mixSIR.unknownGroups” (Ward et al., 2011) (**Paper II**).

#### 4.1.4. Plant decomposition experiment

In **Paper III**, the aim was to contrast the decomposition rates from three different species of plant and algae material (*Z. marina* rhizomes and leaves, *S. pectinata* rhizomes and *C. glomerata*) abundant in the Baltic Sea. *S. pectinata* is a fresh- and brackish water macrophyte, often competing with *Z. marina* for suitable habitat. *C. glomerata* is among the most abundant drifting algae found in the Baltic Sea, in where it forms extensive annual blooms (Wallentius, 1984; Vahteri et al., 2000). In the experiment, the different plant materials were incubated in anoxic closed sediment incubations (Kristensen and Hansen, 1995) in two different sediment types, low (>63  $\mu\text{m}$ ) and high silt (0-63  $\mu\text{m}$ ) content, namely sand and mud, to explore the importance of sediment composition and plant species on decomposition and formation of sediment blue carbon stocks. The experiment lasted for 363 days and included eight terminations (after 7, 21, 49, 92, 148, 222, 293, 363 days from the start of the experiment). The pore water analysed for **Paper III** was extracted by placing sediment from the incubation vial into centrifuge vial and centrifuged at 3000 rcf for 10 min. Concentrations of sulphate ( $\text{SO}_4^{2-}$ ) and total carbon dioxide ( $\text{TCO}_2$ ) were measured from the pore water. The samples for measurement of  $\text{SO}_4^{2-}$ , and  $\text{TCO}_2$  concentration were preserved and frozen prior to analysis. The  $\text{SO}_4^{2-}$  concentration in the extracted porewater was analysed with Dionex ICS 2000 Ion Chromatography System and flow injection and diffusion cell principle (Hall & Aller, 1992) was used for determination of  $\text{TCO}_2$  concentration. The decomposition rate ( $\text{nmol cm}^{-3} \text{d}^{-1}$ ) of the different plant materials was calculated as accumulation of decomposition product ( $\text{TCO}_2$ ) over time, using linear regressions, and multiplying the slope from the linear regression with the corresponding sediment porosity. Due to lack of regressions with  $p < 0.05$ , only 0-92 days period was used for the decomposition calculations.

## 4.2. Data analysis

### 4.2.1. Carbon stock calculations

The calculations used for estimation of *Z. marina*  $\text{C}_{\text{org}}$  stocks and accumulation used in **Papers I–IV** are described below:

**Carbon density ( $\text{mg C cm}^{-3}$ ):** *section-specific sediment POC ( $\text{mg C gDW}^{-1}$ )*  
*\*corresponding sediment dry density ( $\text{g cm}^{-3}$ ).*



**Depth-integrated  $C_{org}$  stock ( $g\ C\ m^{-2}$ ):** Sum of section-specific carbon density \* depth of the corresponding sediment section, in each sediment section (2-5 cm) of the entire 25 cm sediment core.

**Total  $C_{org}$  stocks:** the average depth-integrated  $C_{org}$  stock\* the estimated seagrass area of the corresponding region.

**$C_{org}$  stock projected to 100 cm ( $t\ C\ ha^{-1}$ ):** the depth-integrated (0-25 cm)  $C_{org}$  stock \*4

**The carbon accumulation ( $Mt\ C\ y^{-1}$ ):** the average depth-integrated  $C_{org}$  stock \* corresponding regional seagrass area\* regional sediment accumulation rate (from literature).

**Annual areal eelgrass carbon accumulation ( $t\ C\ ha^{-1}\ y^{-1}$ ):** the average depth-integrated  $C_{org}$  stocks / time that it takes to accumulate this stock with a specific sedimentation rate.

**Total carbon content in the average living above-and belowground *Z. marina* tissue ( $t\ C\ ha^{-1}$ ):** Above- or belowground *Z. marina* biomass per unit of area \* the average POC content (%) measured from the corresponding plant tissue.

**The total carbon pool ( $t\ C\ ha^{-1}$ ):** Sum of (1) annual areal eelgrass carbon accumulation (2) total carbon content in the average living above-and belowground *Z. marina* tissue and (3) the average depth-integrated  $C_{org}$  stocks ( $t\ C\ ha^{-1}$ ) in *Z. marina* sediments in the corresponding region.

#### 4.2.2. Monetary value of carbon stocks

To calculate the monetary value for present and lost *Z. marina*  $C_{org}$  stocks in Finland and Denmark (**Paper I**), the regional  $C_{org}$  stocks ( $t\ C\ km^{-2}$ ) were multiplied with social cost of carbon (SCC) based on emission year 2010 ( $40.3\ \text{€}\ t\ C^{-1}$ , United States Government, 2010). For the monetary evaluation of lost *Z. marina*  $C_{org}$  stocks for the same study, the magnitude of lost *Z. marina* area over the past 100 years was estimated (only for Denmark, as no data was available for Finland) and multiplied with the current average  $C_{org}$  stocks for the region and SCC. To calculate the monetary value for present and lost *Z. marina*  $C_{org}$  stocks for **Paper IV** a valuation framework by Keeler et al. (2012) and developed by Cole & Moksnes (2016) was used. This valuation does not take into account lost carbon sequestration capacity, but assesses one-time loss of carbon and nitrogen associated with their release from sediments and plant tissue, after loss of *Z.*

*marina* coverage. The valuation was done based on two scenarios: (1) a conservative approach assuming no sediment has been eroded due to lost seagrass coverage and based on simply subtracting the difference in carbon and nitrogen stocks between areas with and without *Z. marina* coverage, and (2) a less conservative approach, in which 35 cm of eroded sediment following loss of seagrass coverage was assumed, based on changes in sediment POC, PON and  $^{13}\text{C}$  composition. For the monetary valuation of carbon release in **Paper IV** literature estimates of SCC based on emission year 2015 and discount rate of 3% (132 US\$ t  $\text{C}^{-1}$ ; United States Government, 2016) was used, while for monetary valuation of nitrogen release, the actual costs of nitrogen reduction from measures taken by local authorities in the Marstrand area (193 SEK per kg nitrogen; 22 US\$ kg  $\text{N}^{-1}$  in 2018) was used.

#### 4.2.3. Statistical analysis

In **Paper I**, the relative importance of environmental, biological and sediment variables for the variation in *Z. marina* sediment  $\text{C}_{\text{org}}$  stocks ( $\text{g C m}^{-2}$ ) was explored using Distance based linear model (DistLm) in PRIMER 6 PERMANOVA+ package (Anderson et al., 2008). This method first tests the correlations between individual explanatory variables and the response variable following a model construction, to enable finding a model with best predictive power. Stepwise procedure for model construction was chosen, as it allows both addition and removal of variables during model construction. AICc (Akaike Information Criterion with a correction for finite sample sizes) was chosen for information criterion, as it is suitable for data sets, in which number of response variables is small compared to the number of predictor variables.

In **Paper II**, the relative importance of environmental, biological and sediment variables for explaining the variation in *Z. marina* sediment  $\text{C}_{\text{org}}$  stocks ( $\text{g C m}^{-2}$ ) was explored by use of *partial least squares* (PLS) regression in SIMCA 13.0.3 software (UMETRICS, Malmö, Sweden, Wold et al., 2001). PLS technique was chosen as the technique can handle multi-collinearity and large numbers of predictor variables (Carrascal et al., 2009). To visualize the relationships between  $\text{C}_{\text{org}}$  the different ocean margins or seas with the different predictor variables, a *principal component analysis* (PCA) was used.

In **Paper III**, changes over time in the measured variables were determined from linear regressions. The influence of fixed factors, plant material (5 levels) and sediment types (2 levels) on decomposition rates were tested by a two-way factorial analysis of variance (ANOVA,  $n=6-8$ ) in SPSS 2.1. Tukey's test was used for *post hoc* comparisons.

In **Paper IV**, the impact of lost *Z. marina* coverage on sediment composition and  $C_{org}$  stocks and their interactions with explanatory variables were analysed with a series of two-way ANOVA, in which the different area types (3 levels) and exposure types (4 levels) were used as fixed factors. To analyse the changes in sediment composition over depth, the same explanatory variables were analysed in a series of two-way factorial ANOVA, in which sediment depth (7 levels) and exposure type (4 levels) were used as fixed factors, and each area type was tested in separate analyses. Changes in sediment composition down to 1.2 m sediment depth inside and outside Gullmarsfjord were tested separately using sediment depth (5 levels) and habitat (2 levels) as fixed factors (for details, see **Paper IV**). The relationship between the average sediment organic and water content with sediment carbon and nitrogen concentration were analysed with linear regression analyses. Multiple comparison *post hoc* tests were performed using the Student–Newman-Keuls (SNK) procedure.

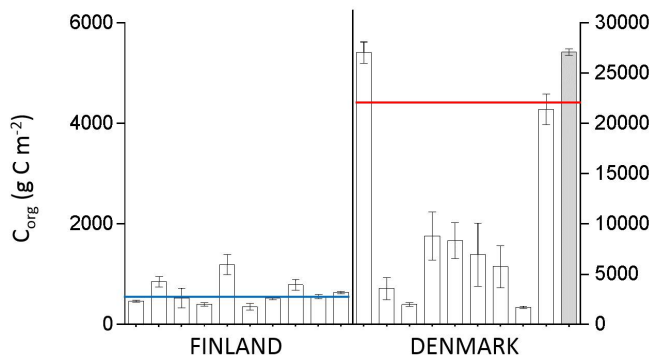
**Table 2.** Summary of methods, areas, sites, variables and statistical methods applied in **Papers I-IV.**

Paper	Country/ Sampling area	Number of sites	Sediment variables	Biological variables	Environmental variables	Response variable	Statistical methods
I	Finland Denmark	20	Dry density, water content, porosity, OM & POC content, <sup>13</sup> C, grain size, mud content, carbon sources	Above- and belowground biomass, shoot density, root:shoot ratio, annual plant production, plant POC & <sup>13</sup> C	Degree of sorting	Sediment C <sub>org</sub> stocks, source contribution to sediment	Distance based linear model (DistLm)
II	Finland Denmark Sweden Norway France Bulgaria Portugal UK USA Canada Mexico Korea Japan	54	Dry density, water content, porosity, OM, POC and PON content, <sup>13</sup> C & <sup>15</sup> N, grain size, mud content, carbon sources	Above- and belowground biomass, shoot density, root:shoot ratio, annual plant production, plant POC & PON content, <sup>13</sup> C & <sup>15</sup> N, C:N ratio	Salinity, water depth, water temperature, degree of sorting	Sediment C <sub>org</sub> stocks, source contribution to sediment	Linear regression analysis, Partial least squares regression (PLS)
III	Eriksvalla Fårö Likholmen		Dry density, water content, porosity, OM, POC & PON content <sup>13</sup> C & <sup>15</sup> N, grain size, mud content, carbon sources, pore water SO <sub>4</sub> <sup>2-</sup> & TCO <sub>2</sub>	Plant POC, PON, <sup>13</sup> C & <sup>15</sup> N, C:N ratio	Plant species, sediment composition	Decomposition rate	Linear regression analysis, Two-way factorial ANOVA
IV	Swedish west coast	12	Dry density, OM, POC & PON content, <sup>13</sup> C & <sup>15</sup> N, grain size, mud content, carbon sources	Above- and belowground biomass, shoot density, root:shoot ratio, plant POC & PON content, <sup>13</sup> C & <sup>15</sup> N, C:N ratio	Fetch	Sediment C <sub>org</sub> stocks source contribution to sediment	Linear regression analysis, Two-way factorial ANOVA

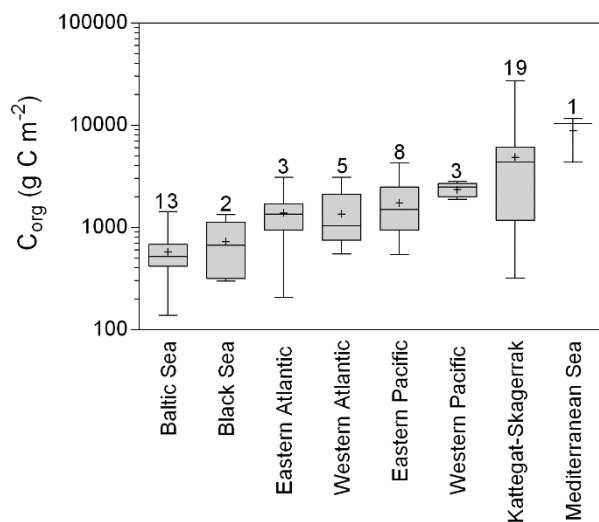
## 5. Results and discussion

### 5.1. Variation in *Z. marina* sediment $C_{org}$ stocks at local and regional scales

In **Papers I and II**, a high spatial variability in site- and region-specific *Z. marina* sediment  $C_{org}$  stocks was shown (Fig. 3 and 4). In **Paper I**, the average  $C_{org}$  stocks were almost 7-fold higher in the Danish *Z. marina* meadows compared to the Finnish meadows ( $4324 \pm 1188$  and  $627 \pm 25$  g C m<sup>-2</sup>, respectively), although variation particularly within the Danish sites was substantial (Fig. 3). Similarly, in **Paper II**, the average regional  $C_{org}$  stocks ranged from  $578 \pm 43$  and  $725 \pm 159$  g C m<sup>-2</sup> in the Baltic and Black Seas to over 15-folds higher  $C_{org}$  stock ( $8793 \pm 2248$  g C m<sup>-2</sup>) at the Mediterranean site, while the variation within regions was substantial (Fig. 4). Moreover, in **Paper II**, sites at Kattegat-Skagerrak region had two to eight fold higher average  $C_{org}$  stocks ( $4862 \pm 741$  g C m<sup>-2</sup>) compared to rest of the studied regions. Furthermore, 9 out of 10 of sites exhibiting the highest  $C_{org}$  stocks were found in Kattegat-Skagerrak, further supporting the role of this region as a hot spot for carbon sequestration (Fig. 4). In addition, the results from **Paper IV** also showed considerably high organic nitrogen stocks found at the *Z. marina* meadows within Kattegat- Skagerrak region.



**Figure 3.**  $C_{org}$  stocks (g C m<sup>-2</sup>) 0-25 cm of sediment in Finnish and Danish eelgrass (*Zostera marina*) meadows. Note that the value of Thurøbund (grey bar) corresponds to right y-axis. The red line represent the average  $C_{org}$  stocks for Denmark ( $4324$  g C m<sup>-2</sup>), while the blue line represents the average  $C_{org}$  stocks for Finland ( $627$  g C m<sup>-2</sup>) (**Paper I**).

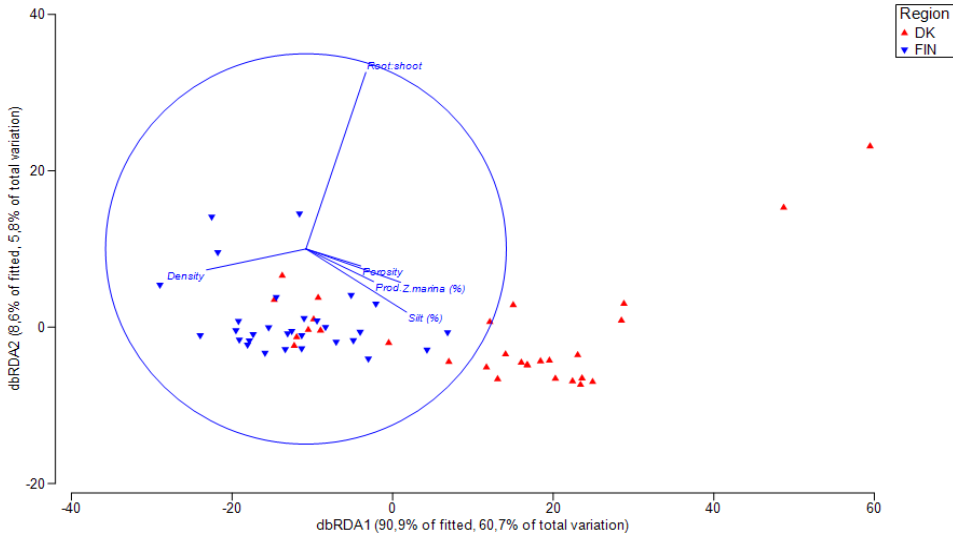


**Figure 4.** Seagrass (*Z. marina*) sediment organic carbon stocks ( $C_{org}$  g C m<sup>-2</sup>) across the ocean margins and seas in the top 25 cm of the sediment. Box plots represent first and third quartiles and are shown with medians (horizontal line), means (+). Whiskers represent the 2.5-97.5 percentiles. Number of sites per ocean margin/sea is given above the whiskers (Röhr et al., 2018).

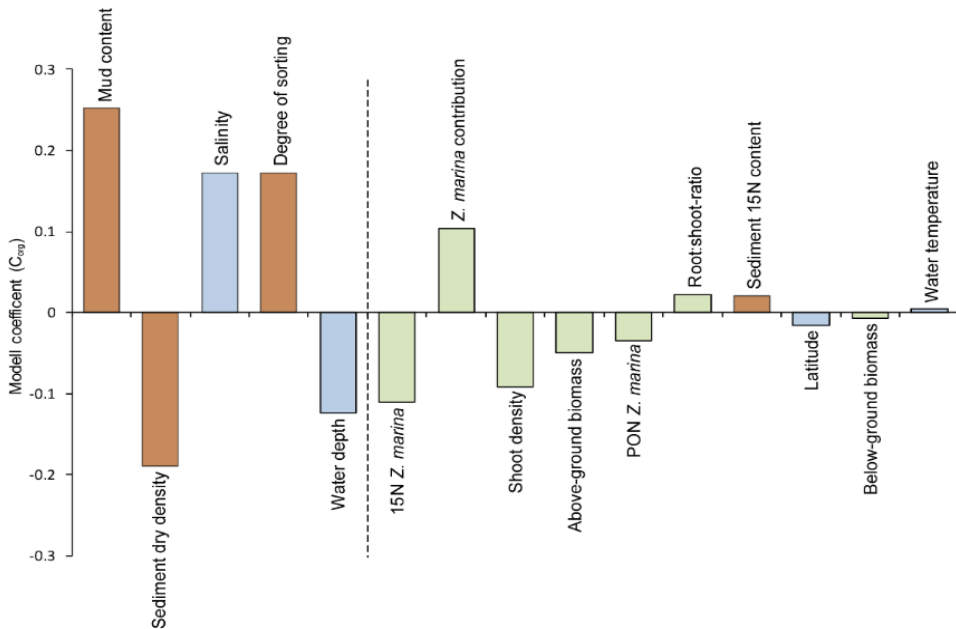
Similarly, recent estimates have shown considerable variation in the global estimates for seagrass  $C_{org}$  stocks both within and between species (e.g. Lavery et al., 2013; Miyajima et al., 2015; Dahl et al., 2016; Serrano et al., 2014, 2016; Eriander, 2017; Ricart et al., 2015, 2017; Gullström et al., 2018; Mazarassa et al., 2018; **Paper I and II**). These studies have linked the within-species variation to differences in environmental conditions and habitat setting, such as sediment characteristics, geomorphology, sediment oxygenation, temperature, water depth, light availability, seascape configuration, inorganic carbon concentration in the water column, turbidity and exposure. In contrast, the between-species variation has been shown to primarily depend on species-specific traits in plant morphology, canopy complexity, root: shoot ratio, chemical composition, structural characteristics of refractory material, plant growth patterns and turnover rates (Duarte & Chiscano, 1999; Mateo et al., 2006; Mazarassa et al., 2018). In general, larger seagrass species (e.g. *Posidonia* spp. and *Thalassia* spp.) tend to have higher biomass production, root: shoot ratio, fraction of refractory material and capacity for particle trapping and thus, hold larger sediment  $C_{org}$  stocks (Duarte & Chiscano, 1999; Hemminga & Duarte, 2000; Fourqurean & Schlau, 2003; Duarte et al., 2010; Lavery et al., 2013; Rozaimi et al., 2016; Serrano et al., 2016; Mazarassa et al., 2018). However, in contrast, some studies have shown, that also small seagrass species (e.g. *Halophila* spp. and *Halodule*

spp.) may hold considerably high sediment  $C_{org}$  stocks due to location in depositional areas with high input of allochthonous material, although these stocks usually consist of a higher proportion of labile forms of carbon and therefore do not promote long-term carbon sequestration (Lavery et al. 2013; Mazarassa et al., 2018).

Several earlier studies have highlighted the importance of sediment characteristics on the formation of seagrass sediment  $C_{org}$  stocks (Greiner et al., 2013, 2016; Miyayima et al., 2015; Dahl et al., 2016; Jankowska et al., 2016; Serrano et al., 2016; Dahl, 2017). In both **Paper I and II**, sediment characteristics explained a major part (>40 %) of the variation in *Z. marina* sediment  $C_{org}$  stocks (Fig. 5 and 6). In **Paper I**, the major sediment variables predicting the sediment  $C_{org}$  stocks were mud content (sediment grain size <63 $\mu$ m) (titled as silt content in **Paper I**), dry density and porosity, while in **Paper II** the most important explanatory variables were mud content, dry density and degree of sorting (Fig. 5 and 6). Sediments with high proportion of fine particle sizes have been shown to promote decreased permeability of oxygen leading to anoxia, which inhibits decomposition (Mayer, 1994; Burdige, 2007). In addition, due to higher surface to volume ratio on the fine particles, increases in the accumulation of organic matter occur, making the sequestration and persistence of  $C_{org}$  in fine sediments more likely (Mayer, 1994; Burdige, 2007; Wilson et al., 2008; Dahl et al., 2016; Serrano et al., 2016; Miyajima et al., 2017; Mazarassa et al., 2018). The appearance of sediment mud content as the most important predictor variable for the sediment  $C_{org}$  stocks in both **Papers I and II**, as well as the other previous studies, strongly suggests the potential use of this variable as a proxy for seagrass sediment  $C_{org}$  stocks (Fig. 5 and 6).



**Figure 5.** Distance-based Redundancy Analysis (DbrDA) plot showing the environmental parameters (percentage of *Z. marina* in sediment carbon pool, above: belowground ratio, annual eelgrass production, sediment silt (mud) content (%), sediment dry density and sediment porosity) fitted to the variation in the  $C_{org}$  stock ( $g\ C\ m^{-2}$ ) at the Finnish (blue symbols) and Danish eelgrass (*Z. marina*) sites (red symbols), respectively (modified from **Paper I**).



**Figure 6.** Partial Least Square (PLS) regression model coefficient plot showing the relative importance of different predictor variables. Predictor variables are ranked in order of importance (from the left to the right), in which the five variables left of the dashed line have VIP (variable influence on the projection) values above 1 (and hence an above average influence on  $C_{org}$  stocks). Brown bars represent sediment characteristics, green bars represent seagrass-associated variables and blue bars are environmental variables.



Although degree of sorting, which was used as a proxy for exposure, appeared to be among the most important predictor variables for the observed variation in *Z. marina* sediment  $C_{org}$  stocks only in **Paper II and IV**, it is likely, that also part of the variation in *Z. marina* sediment  $C_{org}$  stocks in **Paper I** might have been explained by differences in exposure between the sites. In the northern Baltic Sea, *Z. marina* is usually found growing in relatively exposed locations (Baden & Boström, 2001), and potentially a considerable fraction of their primary production is being exported to deeper locations. Increased hydrodynamic forces also increase sediment resuspension and turbidity, reducing permeability of light into the water column and thus, inhibiting seagrass growth thus undermining the accumulation of seagrass derived, refractory detritus into the sediment  $C_{org}$  pool (Bos et al., 2007; Peralta et al., 2008). Exposure might also partly explain the low proportion of mud ( $< 63\mu\text{m}$ ) in the Baltic Sea sites, as the fine-grain sized sediments usually accumulate in sheltered locations and are more cohesive and erosive under exposure to hydrodynamic forces compared to coarse-grained, sandy sediments (e.g. Joensuu et al., 2018).

The *Z. marina* root: shoot ratio explained  $>12\%$  of the variation in  $C_{org}$  stocks in **Paper I** (Fig. 5). In addition, *Z. marina* contribution to the sediment surface  $C_{org}$  pool explained 10.9% of the variation in sediment  $C_{org}$  stocks in **Paper I**, and the highest  $C_{org}$  stocks were found at the Danish sites, in which *Z. marina* was the main carbon source accumulating in the sediments (Fig. 5 in **Paper I**). At the low  $C_{org}$  stocks sites in Finland, the proportion of allochthonous carbon sources, such as phytoplankton, to the sediment  $C_{org}$  pool was high (Fig. 5 in **Paper I**). These results were supported by recent studies, which have shown that large meadows accumulate higher proportion of autochthonous carbon sources coupled with higher capacity for sequestering sediment  $C_{org}$  compared to small and patchy meadows. In general, in large and continuous meadows also the accumulation of fine sediments is higher, while small and patchy meadows have higher sediment resuspension, coarser sediment and higher input of allochthonous carbon sources (Miyayima et al., 2017; Oreska et al., 2017; Ricart et al., 2017). Indeed, the moderately exposed Finnish *Z. marina* meadows are typically patchy and fragmented, while the Danish meadows may extend up to several kilometres (Baden & Boström, 2001; Boström et al., 2014). Although meadow size was not among the quantitatively measured variables in **Papers I or II**, low mud content and high proportion of allochthonous carbon sources found in the northern Baltic Sea sites compared to high  $C_{org}$  stocks and mud content found in the generally large and continuous meadows at the Kattegat-Skagerrak region suggests for potential influence of seascape configuration and meadow size on the formation

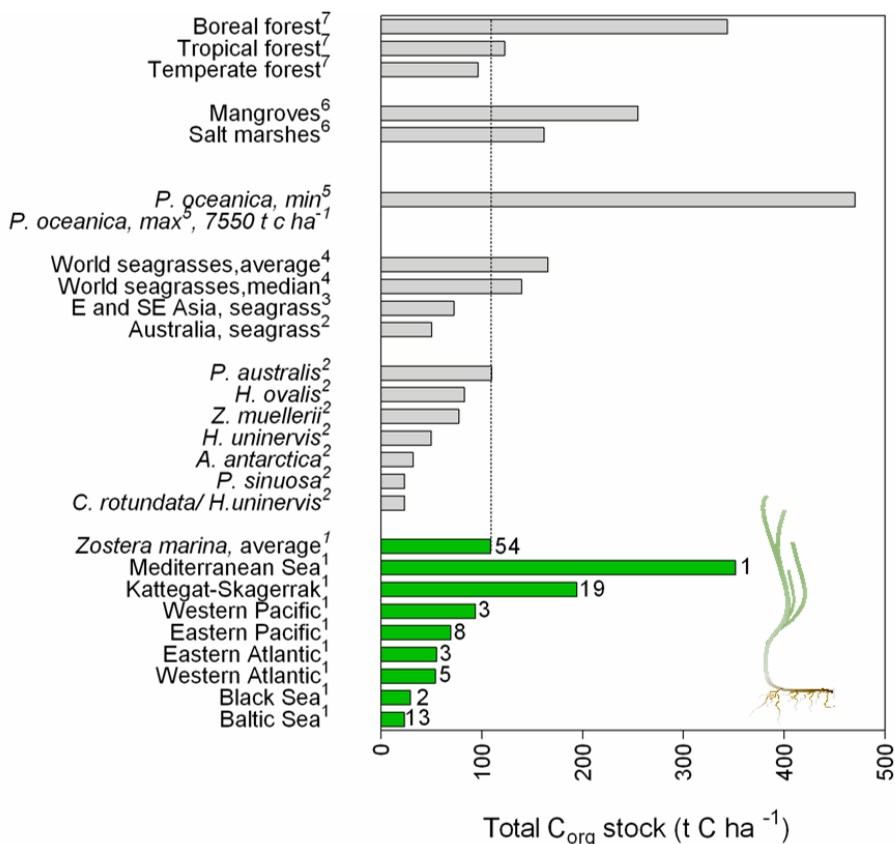
of sediment  $C_{org}$  stocks in these regions. In addition, the seagrass sediment  $C_{org}$  stocks tend to increase with increasing distance from the seagrass-sand edge, making  $C_{org}$  accumulation in continuous meadows more likely than in patchy and fragmented meadows as found at the Finnish sites (Ricart et al. 2015; Oreska et al., 2017; Mazarassa et al., 2018).

In contrast, in **Paper II**, all studied plant related attributes were generally of minor importance (Fig. 6). In **Paper II**, the explanatory power of *Z. marina* contribution to the sediment surface  $C_{org}$  pool was low and *Z. marina* was the main carbon source at only 8 out of 54 sites, contributing on average only  $30.5 \pm 3.1\%$  to the sediment surface  $C_{org}$  pool, which was considerably lower than the global average  $\sim 50\%$  contribution of autochthonous sources estimated for seagrass sediments (Gacia et al., 2002; Kennedy et al., 2010; Samper-Villareal et al., 2016) (Fig. 2c in **Paper II**). The results from **Paper II** also revealed, that regions with high area of seagrass coverage had still relatively modest  $C_{org}$  stocks (e.g. over 4-fold higher areal extent in *Z. marina* coverage at Eastern Pacific compared to Western Atlantic region, yet almost equal magnitude of  $C_{org}$  stocks), suggesting that factors not related to plant attributes were more important in controlling the variation in the local *Z. marina*  $C_{org}$  stocks and further emphasizing the role of sediment variables for the formation of *Z. marina* sediment blue carbon stocks.

## 5.2. Comparison of *Z. marina* sediment $C_{org}$ stocks with other seagrass species and ecosystems

The average projected  $C_{org}$  stocks between regions extrapolated to 100 cm depth in **Paper II** ranged between 23.1- 351.7 t C ha<sup>-1</sup> and averaged at 108.9 t C ha<sup>-1</sup>. The results from **Paper II** revealed, that  $C_{org}$  stocks in *Z. marina* sediments at the temperate Northern hemisphere are higher or of the same size as  $C_{org}$  stocks estimated for many other seagrass species, salt marshes, mangroves and terrestrial ecosystems (Fig. 7). The average projected *Z. marina*  $C_{org}$  stock was higher than that reported for Australian and East and Southeast Asian seagrasses (50.5 t C ha<sup>-1</sup>, Lavery et al. 2013; 72.4 t C ha<sup>-1</sup>, Miyayima et al., 2015) and even higher than the global average (70 t C ha<sup>-1</sup>) by Kennedy and Björk (2009) (Fig. 7). In contrast, the average projected  $C_{org}$  stocks were considerably lower than the average  $C_{org}$  stocks estimated for tropical seagrass meadows (142.2 t C ha<sup>-1</sup>; Alongi et al., 2014), and the median projected  $C_{org}$  stock from **Paper II** (48.6 t C ha<sup>-1</sup>) was almost three-fold lower than the median for global seagrass  $C_{org}$  stocks (139.7 t C ha<sup>-1</sup>) by Fourqurean et al. (2012). Moreover, the  $C_{org}$  stocks used for *P. oceanica* in **Paper II** (Serrano et al., 2014) were 60 to 70 fold higher, than the average projected *Z.*

*marina* C<sub>org</sub> stock in **Paper II**, supporting the extreme capacity of this species in blue carbon sequestration (Fig. 7).



**Figure 7.** The total C<sub>org</sub> stock (t C ha<sup>-1</sup>) in top 100 cm of soil in terrestrial and Blue Carbon ecosystems (boreal forest, mangroves, salt marshes, tropical forest and temperate forest), other seagrass species (*Posidonia sinuosa*, *Posidonia australis*, *Halophila ovalis*, *Zostera muellerii*, *Halodule uninervis*, *Amphibolis antarctica*, *Cymodocea rotundata*/*Halodule uninervis*, *Posidonia oceanica*, Australian seagrass meadows; average, East and Southeast Asia; average, world seagrasses; median) and C<sub>org</sub> projected for *Z. marina* at the different ocean margins and seas in the study area (Baltic Sea, Black Sea, Eastern and Western Atlantic, Eastern and Western Pacific, Kattegat-Skagerrak, and Mediterranean Sea). The green coloured bars indicate the regions sampled for this study. Number of sites per ocean margin/sea is given next to the bars.<sup>1</sup>= this study, <sup>2</sup>=Lavery et al., 2013, <sup>3</sup>= Miyajima et al., 2015, <sup>4</sup>= Fourqurean et al., 2012, <sup>5</sup>= Serrano et al., 2014, <sup>6</sup>= Duarte et al., 2013a <sup>7</sup>= Kennedy & Björk, 2009 (modified from **Paper II**).

Although the average projected *Z. marina* C<sub>org</sub> stocks in **Paper II** were ~1/3 lower than the average used for salt marshes (162 t C ha<sup>-1</sup>; Duarte et al., 2013a), the C<sub>org</sub> stocks projected for Kattegat-Skagerrak and Mediterranean regions

(194.5 and 351.7 t C ha<sup>-1</sup>, respectively) were 20% and 117% higher than average C<sub>org</sub> stocks in salt marshes (Fig. 7). As is the case with seagrasses, the conditions in salt marsh sediments (i.e. high primary production, slow rates of decomposition and high accumulation of auto- and allochthonous carbon) are particularly favourable for high C<sub>org</sub> sequestration and their capacity for C<sub>org</sub> burial ranks among the highest of all blue carbon ecosystems (17.2 t C ha<sup>-1</sup> y<sup>-1</sup>) (Nelleman et al., 2009). The similar magnitude of the global average salt marsh C<sub>org</sub> stocks and the *Z. marina* C<sub>org</sub> stocks found in Kattegat-Skagerrak and Mediterranean regions in **Paper II**, could also partly be explained by the similarity in their chemical composition including high proportion of refractory compounds, such as lignin and cellulose, highlighting the importance of plant chemical composition, on the formation and persistence of sediment blue carbon stocks. Similarly, the average projected *Z. marina* C<sub>org</sub> stocks were less than half of the global average C<sub>org</sub> stocks for mangroves (255 t C ha<sup>-1</sup>; Duarte et al., 2013a), while *Z. marina* C<sub>org</sub> stocks in Kattegat-Skagerrak and Mediterranean regions were in line or higher with the global average mangrove C<sub>org</sub> stocks (Fig. 7). As for the latter two blue carbon ecosystems, the high capacity of mangroves to sequester C<sub>org</sub> is largely based on high primary production rates, high rate of sedimentation and high proportion of lignin and other forms of refractory material in their tissues and low oxygen concentration in their submerged sediments resulting in slow decomposition (Donato et al., 2011).

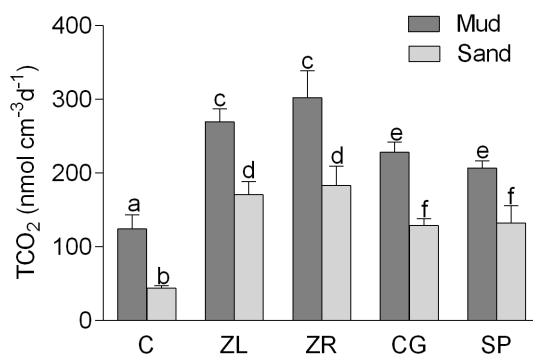
The data from **Paper II** also revealed that the projected *Z. marina* C<sub>org</sub> stocks per unit area were comparable to the average C<sub>org</sub> stocks of temperate forests (122.7 t C ha<sup>-1</sup>, Kennedy & Björk, 2009), but over 3- fold lower than the average C<sub>org</sub> stocks per unit area of boreal forests (343.8 t C ha<sup>-1</sup>) (Fig. 7). The distribution area of boreal and temperate forests and woodlands in the Northern hemisphere is several orders of magnitude higher (2050 billion ha) than that of seagrasses with estimated total C<sub>org</sub> stocks of ~ 260 Pg C (Goodale et al., 2002). However, while the distribution area of the forest land in the Northern hemisphere is wide, the carbon accumulation ranges between ~0.6–0.7 Pg C per year from which only ~ 0.1 Pg C y<sup>-1</sup> is in the soil compartment. In contrast, seagrass carbon accumulation has been estimated to 0.5–1.1 Pg C y<sup>-1</sup>, and in contrast to terrestrial systems, this carbon may be stored for long term, while in general, terrestrial systems are considered as short term carbon sinks (Mateo et al., 1997, 2006). In Finland, the forests bind ~0.7 Pg C in their woody biomass with an annual carbon sequestration rate of 0.035 Pg C. The corresponding numbers for carbon stocks in the Finnish mineral forest soils are ~1.3 Pg C and for soils of peatlands ~5.5 Pg C, while the carbon stock of the Finnish *Z. marina* meadows is only a

small fraction of this (0.000019 Pg C) (Metla, 2015, **Paper I**). The results from **Papers I and II** highlight the importance of exploring the  $C_{org}$  stocks and capacity for  $C_{org}$  sequestration of species within specific water areas in where favourable conditions for  $C_{org}$  sequestration could potentially be found. E.g. in the Baltic Sea, *Phragmites australis* is commonly found growing in estuaries, fladas and glo-lakes, but it is currently unknown how much this plant species contributes to the formation of blue carbon stocks in this region. Moreover, global non-tidal wetlands and tundra store enormous amounts of  $C_{org}$  (1330 - 1580 Pg C and 450Pg C, for tundra and non- tidal wetlands respectively), while the impact of climate change on these stocks is still very poorly understood (Lal, 2008; Schuur et al., 2015; Webb et al., 2017; Finlayson et al., 2018). In discovering suitable areas for  $C_{org}$  sequestration in both marine and terrestrial ecosystems and exploring the potential consequences of climate change on these stocks, use of tools based on geographic information systems (GIS), might prove useful (Flindt et al., 2016; Jayahilake & Costello; 2018).

### 5.3. Differences in decomposition of different plant species

In the Baltic Sea, eutrophication has caused occurrences of massive drift algae and cyanobacterial blooms, which are generally considered more labile than *Z. marina* detritus and thus, more easily decomposed (Holmer & Olesen, 2002; Kristensen & Holmer, 2001; Holmer et al., 2011; Valdemarsen et al., 2014). Although the efforts made in reduction of nutrient emissions have improved the eutrophication status of the Baltic Sea (Anderson et al., 2017; Svendsen et al., 2018) the *Z. marina* meadows in many parts of the region have not recovered with the speed expected (Boström et al., 2014 and references within). Consequently, the loss of *Z. marina* coverage may lead to changes in sediment composition e.g. decrease in accumulation of fine sediments and seagrass derived detritus, which has likely been replaced by increased input of allochthonous carbon sources, such as drift algae species *Cladophora* and *Pilayella* spp. Surprisingly, while the  $C_{org}$  stocks of the *Z. marina* sites studied for **Paper I, II and IV** were higher in seagrass sediments with high mud content, the results from **Paper III** showed significantly higher decomposition, and thus lower potential for the formation of  $C_{org}$  stocks, in muddy (<63 $\mu$ m) sediment incubations compared to incubations conducted in sand (>63  $\mu$ m) (Fig. 8). This result was potentially caused by higher activity and abundance of decomposing bacteria in mud. The results from **Paper III** showed increasing C:N ratio with simultaneous decrease in  $TCO_2$  production for *Z. marina* plant materials, while *C. glomerata* and *S. pectinata* showed the opposite

pattern, further indicating that plant C: N ratio was one of the major variables influencing the rate of decomposition and as has been shown by several earlier studies (Enriquez et al., 1993, Fourqurean & Schrlau, 2003). The  $^{13}\text{C}$  decreased over time in all plant treatments, and the change in carbon isotopic signal was most pronounced in *Z. marina* leaves and *S. pectinata*, highlighting the influence of plant chemical composition during decomposition due to preferential mineralization of the labile POC in these plant materials and suggesting that *C. glomerata* and *Z. marina* rhizomes were more refractory and could potentially contribute more to the formation of sediment blue carbon stocks. Furthermore, the results from **Paper III** revealed that the decomposition of plant detritus was higher for *Z. marina* compared to *C. glomerata* and *S. pectinata* (Fig. 8). This finding was also in line with results from **Paper I** and **II**, in which carbon sources derived from species other than *Z. marina* constituted the major proportion of the sediment  $\text{C}_{\text{org}}$  pool in the northern Baltic Sea. The decomposition pattern of *C. glomerata* and *S. pectinata* was very distinctive from that of *Z. marina* and showed a fast increase in decomposition after initial resistance for decay, suggesting that the sediment biogeochemistry may significantly be affected by the presence of these species. Overall, the results from **Paper III** suggests that studies defining the species-specific decomposition rates and patterns of decomposition under different environmental conditions could enable more reliable estimation of region-specific carbon budgets and contribute significantly to understanding of the formation and persistence of seagrass sediment blue carbon stocks.



**Figure 8.** Decomposition rates in the different plant species and sediment types. C = control, ZL = *Z. marina* leaves, ZR = *Z. marina* rhizomes, CG = *C. glomerata*, SP = *S. pectinata*. Letter above bars denote significantly different values between different plant materials within the same sediment types at  $P < 0.05$  (Tukey's test).

#### 5.4. Comparison of $C_{\text{org}}$ and organic nitrogen stocks in lost and existing *Z. marina* meadows

The results from **Paper IV** revealed significant differences between the historic *Z. marina* sites which had lost *Z. marina* coverage since the 1980's (93 and 5% loss in Marstrand and Gullmarsfjord areas, respectively) and the sites with existing *Z. marina* coverage in the west coast of Sweden. Although anthropogenic pressures in many coastal zones have led to seagrass habitat fragmentation (Montefalcone et al., 2010) and large scale losses worldwide (Waycott et al., 2009), to date, the consequences of seagrass loss on sediment biogeochemistry are poorly known (Moksnes et al., 2018). Furthermore, the global loss rates have accelerated from the median of  $0.9\% \text{ y}^{-1}$  in the 1940's to  $7\% \text{ y}^{-1}$  since 1990's (Waycott et al., 2009), although also opposite patterns have been observed, especially in the higher latitudes, such as the Arctic, in which climate change induced increases in water temperature have led to increased seagrass habitat area (Marba et al., 2018). While to date, the seagrass loss rates have been accelerating, the loss rates for salt marsh have remained relatively unchanged and the loss rates for mangrove forests have slowed from  $1.04\% \text{ y}^{-1}$  in the 1980s to  $0.66\% \text{ y}^{-1}$  at year 2000 (Waycott et al., 2009; Mcleod et al., 2011).

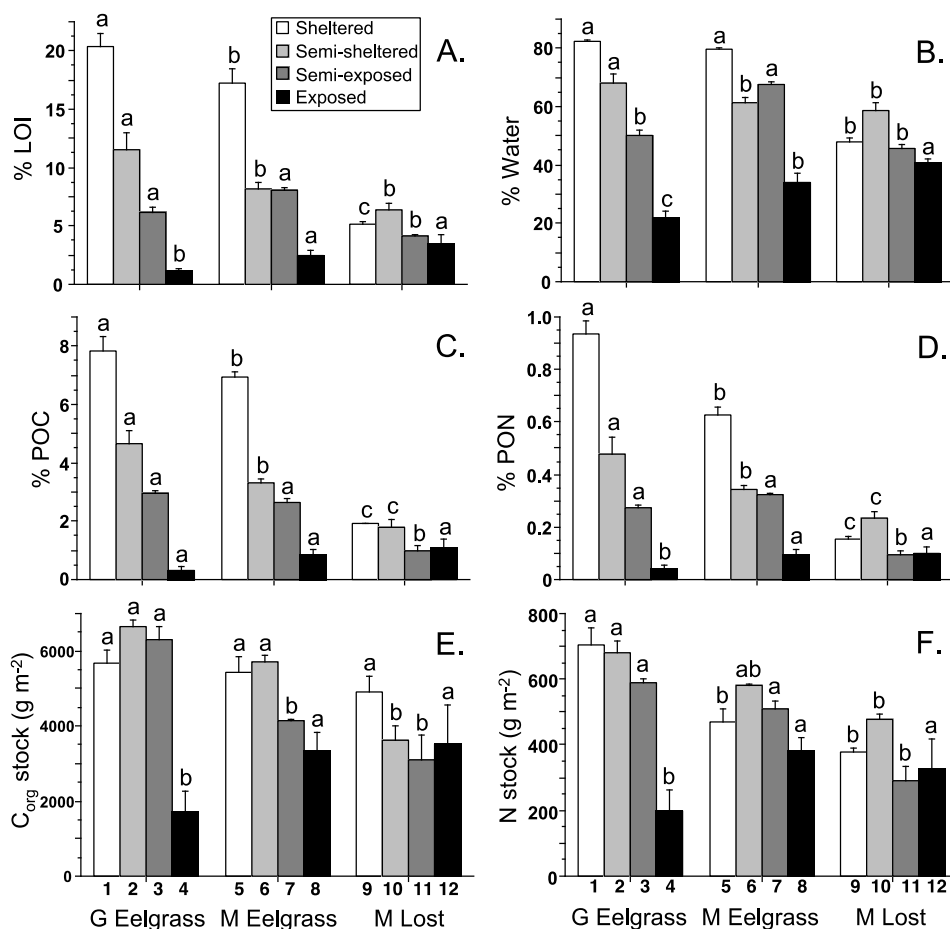
Results from **Paper IV** showed, that the historic sites had on average 2.6 times lower ( $\sim 0.2\%$ ) sediment POC (%) concentration compared to sites with existing *Z. marina* coverage ( $\sim 1.3\%$ ), most likely due to erosion of sediment from the historic *Z. marina* sites (Fig. 9). In addition, the  $C_{\text{org}}$  and organic nitrogen stocks were 28% and 40% higher in the existing *Z. marina* meadows compared to the historic sites. However, although the differences between historic and existing *Z. marina* sites were profound, the differences decreased with increasing exposure at the sites, and were most pronounced at the sheltered and semi-sheltered sites. In particular, at the existing, sheltered *Z. marina* sites, the sediment POC and PON (%) were 11.7 and 10.7 times higher compared to exposed sites, while at the historic *Z. marina* sites, the influence of exposure was weaker (Fig. 9). The differences in the  $C_{\text{org}}$  stocks between existing and lost *Z. marina* meadows in **Paper IV** were lower than results by Macreadie et al. (2015), who showed in their study from lost Australian *Posidonia australis* meadows that sediments from disturbed seagrass meadows had 72% lower  $C_{\text{org}}$  stocks compared to the sediments in the adjacent pristine seagrass meadows. Similarly to results from **Paper I and II**, the results from **Paper IV** showed almost order of magnitude higher average POC concentration and 5 to 13 times higher average nitrogen content, than reported for *Z. marina* sediment in most other regions in the world, further

supporting the role of Kattegat-Skagerrak region as a global hot spot for *Z. marina* sediment carbon sequestration. The lowest values for all measured variables were consistently found at the exposed sites. The results from **Paper IV** highlighted the importance of exposure and consequently, sediment erosion. The importance of erosion for sediment carbon storage was also demonstrated through scenario analysis applied in **Paper IV**, in which carbon and nitrogen release was 4.3 and 3.5 higher when erosion of the top 35 cm of the sediment following *Z. marina* loss was assumed, compared to the scenario in which no erosion was assumed. Although it was challenging to assess the exact depth of eroded sediment section, several results, such as changes in sediment composition and significantly reduced sediment  $^{13}\text{C}$  signal (-20.7‰ on average), supported that sediment erosion and decomposition had occurred, and that the 35 cm erosion scenario was most likely a conservative estimate (Fig. 10). In addition, the results by Marba et al. (2015), revealed that as a consequence of seagrass loss in seagrass meadow at Oyster Harbour, Australia, 60 years of carbon deposition was also lost through erosion, further supporting the adequacy of the use of the scenario assuming 35 cm of sediment erosion in **Paper IV**. Similarly, in a recent study by Arias-Ortiz et al., (2018) a  $\text{CO}_2$  release of up to 9 billion tons following loss of  $\sim 1000 \text{ km}^2$  of seagrass area since 2002 was reported, due to the heatwave off the coast of Western Australia. The meadow had been accumulating  $\sim 144$  billion tons of carbon over the past 4000 years, and with the lost seagrass area, not only the capacity to sequester carbon, but also the ancient carbon stored within the meadow in the past millenniums was lost. Furthermore, Arias- Ortiz et al., (2018) estimated that the loss of this ancient and one of the most extensive seagrass carbon sink will likely result in additional  $\sim 21$  million of tons of  $\text{CO}_2$  to be released in the next few decades, assuming that the seagrasses in the area will not recover.

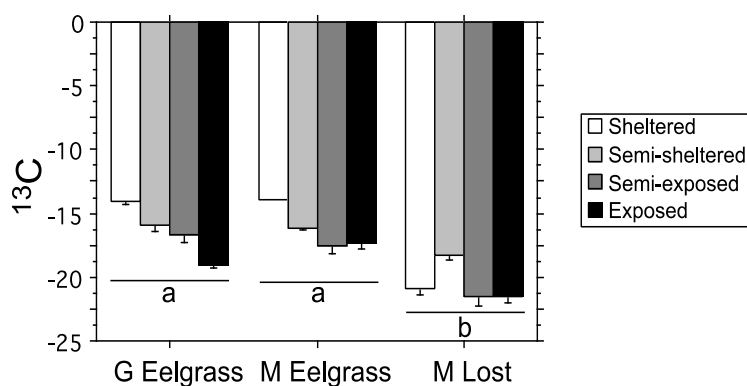
In terms of economy, the results from **Paper IV** showed a substantially higher economic cost resulting from the release of carbon and nitrogen, than that previously estimated for ecosystem service provided by seagrasses. With the conservative approach, assuming no erosion of sediments, the lost carbon and nitrogen stocks in the studied region was estimated to  $\sim 11.5$  and  $1.49 \text{ t ha}^{-1}$ , respectively. These values correspond to economic losses of  $\sim 1489$  and  $32656 \text{ US\$ ha}^{-1}$ , for carbon and nitrogen, respectively. With the less conservative approach, assuming erosion of the top 35 cm of sediment, the lost carbon and nitrogen stocks were estimated to  $\sim 49$  and  $5 \text{ t ha}^{-1}$  equivalent to economic losses of  $\sim 6400$  and  $114\,000 \text{ US\$ ha}^{-1}$ , respectively. Given that the results from **Paper IV** are derived from one country alone, the global loss of near surface carbon from seagrass ecosystems ( $500 \text{ t CO}_2 \text{ ha}^{-1}$ ) estimated by Pendleton et al. (2012) appears to be extremely



conservative. Furthermore, similarly to results from Cole & Moksnes (2016), the results from **Paper IV** suggested, that the organic nitrogen sequestration by *Z. marina* appeared to be 20 folds as valuable as the  $C_{org}$  sequestration. These results indicate, that especially the sheltered *Z. marina* habitats in Kattegat-Skagerrak region appear to act as important carbon and nitrogen sinks and are in particular importance on mitigating eutrophication in the region.



**Figure 9.** Sediment 0-35 cm depth. Concentration % of (A) organic material (LOI), (B) water, (C) particulate organic carbon and (D) nitrogen (%POC and %PON) and (E) the total amount of carbon and (F) nitrogen per square meter ( $C_{org}$ -stock and N-stock), collected at 12 different sites from 3 area types: 4 with eelgrass beds in the Gullmarsfjord area (*G Eelgrass*) 4 with eelgrass beds in the Marstrand area (*M Eelgrass*), and 4 from sites where the eelgrass has been lost in the Marstrand area (*M Lost*). Within each area, the sites were categorized in 4 different exposure types. Letter above bars denote significantly different values between area types within exposure types at  $P < 0.05$  (SNK-test).



**Figure 10.** Stable isotope composition of sediment 0-5 cm depth. Average stable isotope values (-SE) of carbon ( $^{13}\text{C}$ ) in the surface sediment (0-5 cm sediment depth) collected at 12 different sites from 3 area types: 4 with eelgrass beds in the Gullmarsfjord area (*G Eelgrass*), 4 with eelgrass beds in the Marstrand area (*M Eelgrass*), and 4 from sites where the eelgrass has been lost in the Marstrand area (*M Lost*). Within each area, the sites were categorized in 4 different exposure types. Letter above bars denote significant difference values between area types at  $P < 0.05$  (SNK-test).

## 5.5. Implications for climate change mitigation

In 2005, MEA (Millennium Ecosystem Assessments) reported that the national commitments for climate change mitigation set in the Paris Climate Change Agreement have not been fulfilled and the goals set by the agreement are very likely to fail). In 2017, the Union of Concerned scientists released a “Second Warning to Humanity” (Ripple et al., 2017) signed by over 15 000 scientists worldwide, in which humankind was cautioned to reverse the ongoing environmental destruction and its eminent consequences on biodiversity and climate change mitigation. Using the annual loss rates for blue carbon species, Pendleton et al. (2012) calculated a conservative estimate of 0.15-1.02 Pg  $\text{CO}_2$  emissions from the blue carbon habitats annually, equivalent to economic damages of US\$ 6-42 billion and 3-19% of the total global deforestation emissions. Similarly, Luisetti et al. (2013) estimated the coverage area of European blue carbon ecosystems to ~3 billion ha, equivalent to 1.5-4 % of the global blue carbon area and current monetary valuation of US\$ 180 billion. Using scenario based analysis they estimated that if the ongoing trends are not reversed, the losses of European blue carbon ecosystems alone will result in mean economic losses of up to US\$1 billion by 2060.

Unfortunately, to date, the blue carbon ecosystems still remain largely neglected in abatement schemes for atmospheric  $\text{CO}_2$  (Macreadie et al., 2013; Duarte, 2017). While some initiatives for financing mechanisms including

mangroves into their frameworks have been made, the other blue carbon ecosystems (seagrasses, saltmarshes, macroalgae) remain unaccounted (Wylie et al., 2016). Several options for marketization of blue carbon has been suggested, such as financing through the UNFCCC (United Nations Framework Convention on Climate Change), integration of protecting and restoring of blue carbon areas as economic incentives to compensate national targets set in the Paris Climate Change Agreement through e.g. clean developmental mechanisms and involvement of private sectors, such as enterprises, into climate change mitigation agreements and protection of blue carbon ecosystems, as they could potentially gain substantial economic benefits if the ecosystem supporting the goods they require would remain intact (Herr et al., 2017; Howard et al., 2017c; Barbier et al., 2018). The market value of blue carbon could be assessed through use of “damage costs avoided method” in which value of ecosystem is estimated based on the costs that could be avoided through protection of the ecosystem or alternatively, through “replacement cost method” in which the value of the ecosystem is estimated through the cost that would be required if the services provided by the ecosystem would have to be replaced (Campagne et al., 2015; Cole & Moksnes, 2016).

Several attempts have aimed to restore lost seagrass meadows (Leschen et al., 2010; Cunha et al., 2012; Orth et al., 2012; Macreadie et al., 2015; Marba et al., 2015; Infantes et al., 2016, Moksnes et al., 2016, 2018), but unfortunately, the global restoration success has thus far been poor (37% on average) (Katwijk et al., 2015). These studies have shown that regime shifts following seagrass loss make it hard to restore the meadows back to a favourable state, especially when the possible thresholds limiting these shifts have been passed (Maxwell et al., 2016; Flindt et al., 2016; Moksnes et al., 2018). Furthermore, results from these restoration studies have shown, that even if the restoration succeeds, it takes several decades before the carbon sink capacity of the seagrass meadow is restored, and even then, it is often deteriorated from that of the pristine meadow (e.g. Marba et al., 2015; Moksnes et al., 2018). Results from these studies suggest that conservation of marine vegetated ecosystems, rather than restoring them, is potentially the most efficient tool in prevailing their capacity for long term carbon and nitrogen sequestration (Hejnowich et al., 2015; Duarte et al., 2017, Dahl 2017; Moksnes et al., 2018; Mazarassa et al., 2018).

In order to enable policy making that involves these ecosystems as part of climate regulation programmes, a holistic understanding on the factors that control both the  $C_{org}$  sequestration and storage, as well as changes in carbon fluxes that may occur after disturbance and loss of blue carbon area, are urgently

required. By the use of data available for regional *Z. marina* coverage and the  $C_{org}$  stocks within them, the results from **Papers I-IV** could potentially contribute to a more relevant regional policymaking, and offer help in identification of areas with highest potential for carbon sequestration, mitigation of eutrophication and to offset atmospheric  $CO_2$  emissions. In terms of carbon storage capacity, focus should be drawn to initialize restoration and conservation areas especially within the hot spot regions for *Z. marina*  $C_{org}$  sequestration. If no actions are taken, we are in danger of losing this valuable species from vast areas around the globe. Due to its role as a widespread marine foundation species, existence of *Z. marina* is essential, not only to marine carbon sequestration, but also to multiple other marine species and ecosystem services this species sustain.

## 6. Key findings and future perspectives

The results from this thesis revealed that the magnitude of *Z. marina*  $C_{org}$  stocks was considerable, and comparable to  $C_{org}$  stocks reported for other marine and terrestrial ecosystems, but varied significantly both between and within regions (**Papers I–II**). The variability of *Z. marina*  $C_{org}$  stocks was mainly driven by sediment characteristics, most importantly sediment mud content, dry density, degree of sorting and contribution of *Z. marina* to the sediment surface  $C_{org}$  pool (**Paper I–II**). The results from **Paper III** highlighted the importance of both the chemical composition of the decaying plant material and sediment composition for the formation of sediment blue carbon stocks in the Baltic Sea. **Paper IV** confirmed the role of Kattegat-Skagerrak region as a hot spot for *Z. marina*  $C_{org}$  and organic nitrogen sequestration and showed considerable differences between the existing and lost *Z. marina* sediment  $C_{org}$  and organic nitrogen stocks, with a monetary valuation for the carbon and nitrogen sequestration by *Z. marina* in the region being one of the highest ever calculated for an ecosystem service by seagrasses.

The significant variation in *Z. marina*  $C_{org}$  stocks revealed by studies included in this thesis was only partly explained by the measured variables. Lack of deep sediment depth profiles (> 1m) challenged a more precise estimation and dating of the *Z. marina*  $C_{org}$  stocks and accumulation rates. A strong encouragement is given for defining the full sediment depth profiles for the future researchers on the field of blue carbon studies. Deep sediment depth profiles could enable more thorough understanding on the process involved in formation and stability of *Z. marina* sediment  $C_{org}$  stocks over different time scales, as well as blue carbon stocks in general. Furthermore, the importance of water depth and degree of sorting as explanatory variable for the variation in *Z. marina*  $C_{org}$  stocks in **Papers II and IV** indicated, that exposure was arguably an important factor controlling this variation, although it was not quantitatively measured in this thesis. Therefore, future studies exploring the blue carbon stocks of both *Z. marina* and other blue carbon species, should consider including measurements of the export rates from both the studied ecosystem and adjacent locations along with measurements of the fate of carbon exported from historic sites, which has lost the plant coverage. Moreover, as unvegetated sites were not sampled in **Papers I and II**, the importance of sampling of unvegetated sites adjacent to the *Z. marina* meadows is emphasized in order to enable more precise comparison between the *Z. marina*  $C_{org}$  stocks and the reference  $C_{org}$  stocks. For a more integrated understanding of the variation in carbon storage capacity of different marine

species, the future blue carbon studies require investigation of interactions between sediment biogeochemistry, habitat setting, seascape connectivity, species composition and chemical structure as well as the hydrodynamic regime of the studied region.

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