Support letter

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Associate Editor
Mr. Gerhard Herndl
Biogeoscienes
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Dear Editor

Please find attached the second thorough revision of our manuscript (bg-2016-131) entitled "Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows " by Maria Emilia Röhr, Christoffer Boström, Paula Canal- Vergés and Marianne Holmer to be considered for publication in Biogeosciences. Firstly, we would like to thank both of the reviewers as well as the Editor for their contribution and valuable input to the revision process of this manuscript. We found the comments most useful in further focusing and clarifying the manuscript text and tables.

We have now focused on re-analyzing our samples so, that in addition to the model that included both regions, we have ran a reduced, country wise DistLm analysis in which environmental drivers for Corg stocks were studied separately for Finland and Denmark. We have as well worked on harmonizing the terminology regarding the Blue Carbon calculations and results.
In addition, we have improved the style and data presented in tables 1 and 2 and figures and figure legends 1, 3 and 4.

We are including the detailed responses to the comments by Referee 2 in the section below together with revised manuscript with visible track changes. We have also attached a revised manuscript with no visible track changes to file manager. Our reply and answers to Referee 1 and the first version of the revised manuscript has been posted on the interactive discussion site earlier in summer 2016.

Looking forward to your response,

Thank you for your consideration!

Sincerely,

Emilia Röhr, MSc

Åbo Akademi University and University of Southern Denmark

Comments and answers to referee 2:

Received and published: 14 July 2016

This study has collected a range of relevant data with which to provide estimates of organic carbon storage in Finland and Denmark. The data set would certainly be a useful addition to the growing literature of carbon storage in seagrass meadows and uniquely provides an indication of the range of carbon stocks observed for a single species of seagrass in different regions. The manuscript would require a major revision before being suitable for publication. The description of methods and presentation of results are confusing in terms of context values and units. Many are small points but collectively it becomes very frustrating to try and discern what has been done. The discussion needs to be kept focussed and relevant.

Specific comments:

1. Study area: Line 126 the reference of Kristensen and Andersen 1987 seems at odds to the proceeding sentences as it is a methodological paper that uses different mixtures of sand/eelgrass and shell to examine methods of analysis. A better reference would be Leipe T et al., 2011 Geo-Mar Lett 31, 175-188 who have analysed and obtained low PIC The inorganic content analysis on the samples could then be used to test that this is a common observation.

Answer: Reference corrected (new line 125).

2. In testing carbonate content, 10 samples were taken from each region, so was this from each station i.e. full coverage of sites?

Answer: Yes, samples were from each of the 10 study sites in both regions. Info added in text line 126-127.

3. What are the units, wt%C or CaCO3? A line stating that that TC was therefore taken to represent OC is needed.

Answer: The value is given as percent based on the weight percent of IC and TC in the sample; e.g. the IC content was 0.01%DW and the TC content was 0.20%DW, accordingly the proportion of IC is 5% of TC (lines 125-129).

4. Can the study sites be identified that made up the gradients of sheltered to exposed (see that on line 317 sorting is used to identify).

Answer: For a comprehensive picture, sites were chosen to represent the full range of environmental conditions in each region (see Fig. 1). The sites were chosen on previous (>20 yrs) mapping projects of environmental settings of eelgrass beds in respective regions. To quantify the exposure regime in a standardized way, the organic content, degree of sorting and silt fraction gives an integrated measure of the type of setting eelgrass grows in (see Table 1, Fig. 2).

Field sampling:

5. If cores taken to 40cm, why were C stocks only estimated to 25cm?

Answer: We couldn't force the corer down to 40 cm depth at all of the sites therefor 0-25 cm was chosen to be the undisturbed depth section to be analyzed. In addition, 25 cm sediment cores have been widely used in similar studies and for normalization to the top 1 m of the sediments (eg. Fourqurean et al. 2012, Lavery et al. 2013). Comment added in lines 150-151.

6. Replicate cores taken at 5m for sediment but 15m apart for biomass? Clarify.

Answer: Corrected, 15 meters for both samplings, line 150.

7. Seagrass and sediment variables: In determining the stable isotopic composition of above and below ground biomass and sediments it seems odd to use the term particulate organic carbon, just OC would be a better description.

Answer: Corrected OC instead of POC for entire ms, tables and figures.

8. The method of d13C analysis is given but an estimation of sample analytical error for biomass and sediment is needed. It is unclear whether all OC data is derived from the mass spectrometric determination of d13C. Again error on sample analysis should be provided. It is confusing to know that the sediment has been analyzed for OM and OC content and yet the OM content is not discussed only presented in Table 1. OC instead of OM should be presented in table 1.

Answer: The analytical error (2.8 %) from the analysis has been added to the ms in line 369. The OC data is derived from the mass spectrometric determination of d13C. We have added a column including OC values to Table 1.

9. C stocks and accumulation: line 220 →C stocks "obtained by depth integration of the POC mg C cm-3 of 0-25cm sediment layers would give units of mg C cm-2. which if multiplied by the areal extent of seagrass would give units of mg C, not g Corg m-2 as reported. Suddenly the notation has changed to Corg, need to be consistent.

Answer: We have clarified this part in the ms line 210-214→ New text: "The Corg (obtained by depth integration of the carbon density (mg C cm^{-3}) of 0-25 cm sediment layers (mg C cm^{-2}) of the sampled region was multiplied with estimated seagrass area of the region based on the most recent areal estimates (in km^2) of seagrass distribution available in the literature (Boström et al. 2014) and given as Corg in g C m^{-2}."

10. The areal extent of Danish seagrass is given but not the Finnish (30km2?).

Answer: We have added a line stating the areal estimate for Finland (30 km^2) also to this section of the ms (line 214) the areal extent of Finnish meadows can also be seen in text line 330 and Table 2.

11. Economic loss would be better presented as loss in stock (pool) and rate of addition as separate values.

Answer: Unfortunately we do not understand this comment. Clarification is needed in order to potentially address something. In line 528 we have defined the magnitude of loss in Corg stock.

12. Is the economic loss in the last 100 years based on change areal extent times change in sequestration rate and biomass, but presumably no change in sediment C pool?

Answer: Yes, we have measured the OC from existing eelgrass meadows and as there is no data available on the OC content of lost eelgrass meadows, we have assumed that if the lost meadows would have been present, the measured OC content would have been maintained.

13. Results: If the C content of the biomass is known then why is the DW data used to determine the Corg pool in the living seagrass?

Answer: We have already corrected this part of the ms in connection with the Referee #1 comments. We use g DW OC m^{-2} for determining the Corg pool, not the whole biomass (line:227)

14. It would be informative to have the dry bulk density data in Table 1 (rather than silt content) as it is not presented elsewhere.

Answer: Good point; sediment dry density has been added to Table 1, in addition to silt content.

15. Given that OC data for the sediments is available, why are the OM results presented in the text? Especially as the OC stock section now presents the data as g C cm^{-3}.

Answer: The OM results are presented only as single sentence stating the average value of OM at each region (line 305 and 306). The average OC results for each region has been added to text in to lines 308-309 and OC values for each site have been added to Table 1.

16. Need to rationalize terms as it is confusing to use the same term Corg stocks (g C cm-3) in line 324 and (g C m-2) in line 329 and Table 2. g C cm-3 (carbon density).

Answer: Corg stock (mg C cm-3) has been re-named to "carbon density".

17. The Corg accumulation section includes the sediment trap data. It is presented as gDW, not in OC and the relevance or significance of the measurements are not obvious. They would be better omitted.

Answer: Sediment trap results have been omitted from the entire ms.

18. The areas represented by Finland, Limfjorden and Funen seagrass should be provided.

Answer: We have added the areal extent of Finnish meadows to line 214, the numbers are also given on l.330 (Finland) and 332(Denmark minimum and maximum) and in Table 2 (Finland, Funen, Limfjorden, Denmark minimum and maiximum areal extent).

19. In the isotope section the sediment and source data should be presented before the results of the mixing model.

Answer: The ms structure is now changed so that the sources are presented before the mixing model results.

20. Allochthanous carbon is said to be a major contributor to the sediment (line 394-395), but no isotope value is given for its source term and it is not included as a component of Fig 5. It is not clear what it represents and is an input of terrestrial organic matter included or are there no significant riverine inputs to the area?

Answer: "Allochtonous material" has been deleted from the ms. We have used phytoplankton values from plankton sieves or literature as source in Fig. 5 and text. Input of terrestrial organic matter was not included as a source. The Finnish sampling sites are in the archipelago, where riverine inputs are not significant sources of OM. Similarly, the study sites in Denmark are not in close proximity of rivers, therefor terrestrial input was not included as a source.

21. Given the range of values for the sources it is difficult to understand how *P. pectinatus* and *R. maritima* can be isotopically distinguished from Z. marina in the mixing model for Finland

Answer: R. maritima was not included in any models as it was not present at our study sites. R. cirrhosa contributed less than 5% to the sediment surface 13C signal at four Finnish sites and one Danish site and was included in the mixing model analysis when present. Lines 372-380 describe which species where present at the individual study sites. The values overlapping represent the range of the 13C signal in replicate samples for these species. When the 13C signals for each species were checked for individual sites, the signals for

different species differed significantly enough and running isotope mixing model analysis was thus possible to be made (eg.site Ängsö: Z. marina -10.12 to-10.50‰, R. cirrhosa -11.04‰, P. pectinatus -9.21‰).

22. Discussion: Suggest discussion of sed trap data is removed as it adds little to the discussion.

Answer: Sediment trap data has been removed.

23. Analysis would be improved if it would highlight the differences in stock/accumulation, sources and particular influences (table 4) between Finland and Denmark given the difference in environmental factors

Answer: We have re-analyzed our samples so, that in addition to the model that included both regions, we have ran a reduced, countrywise DistLm analysis in which environmental drivers for Corg stocks were studied separately for Finland and Denmark. We have added text explaining the results of these new analysis in to results section (lines 393-417) and to discussion section (lines 460-468).Our main finding in the new analysis was that biological variables (root to shoot- ratio, fraction of Z. marina from the sediment surface Corg pool) were important environmental drivers for Corg stocks in Denmark, while in Finland the sedimentary variables were better predictors for magnitude of Corg stocks.

24. Overall the discussion could be shortened as there is a lot of extraneous text (more focussed) and consistent. One example is from the C accumulation and stock. Why not just compare with latest and most complete C stock assessment of Fourqurean et al., 2012 that has superceded all the other estimates.

Answer: We have modified the discussion section so that it is more focused and consistent and the length has been reduced with 17 lines (10%).

25. Are data for *Z. marina* included in the Fourqurean data set, if so, a comparison with this data would be more relevant.

Answer: Fourqurean et al. 2012 does not report separate values for Z. marina.

26. Table 3 C stock 627 g m-2, line 520its 6900 t km-2, maths is wrong here?

Answer: The numbers have been corrected (line 521).

27. I do not see the relevance of comparing with tropical mangroves and marshes.

Answer: Comparison with mangroves and salt marsh has been removed from the ms.

28. In the comparison with stocks from Australia and Asia this would only be appropriate if the stocks were all calculated in the top 25cms.

Answer: Lavery et al. 2013 has indeed calculated the Corg stocks in the top 25 cm normalized to top 1 meter. Miyayima et al. 2015 has calculated the Corg stocks directly from 1 meter cores. Similarly to Lavery et al. 2013, we have calculated the Corg stocks we measured in the top 25 cm and extrapolated to 1m.

29. Why are different units used for comparisons km2, m2 and ha-1.

Answer: Different units have been used depending on the context, so that our numbers are comparable with numbers from other published papers that we are referring to.

30. The discussion of cost of seagrass loss contains a lot of speculation and should be reduced. How viable is it to compare Danish stocks with those in Sweden and Germany? Line549 onwards

Answer: We have focused and shortened this section in the ms and deleted comparison between our study regions and Swedish and German meadows (line 534-> of the old version of the ms).However, the comparison

was included in the first place because Danish meadows are generally very similar to those in Sweden and Germany while the Finnish meadows are perhaps outliers in this geographical context, and we found this interesting information to compare.

31. Does this mean that it was assumed that all the carbon was lost from 25 cm of sediment in the calculation?

Answer: Yes.

32. What was the basis for this assumption?

Answer: We have based this assumption on the fact that the erosion should be enhanced when the protection from the leaf-canopy and the rhizome-root mat is lost, and that the organic rich sediment should be easily transported away. Currently, we are aware of two studies (Serrano et al. 2016, Marba et al. 2014) regarding how much of the sediment in seagrass beds are eroded when beds are lost, both studies are conducted in the Australian Oyster harbor in Posidonia oceanica meadows. In addition, in the well-cited paper by Fourqurean et al. 2012 they assume that the top meter of the sediment is eroded and oxidized when a seagrass bed is lost, so in comparison with that study, 25 cm could be considered conservative estimate.

33. Why is the loss being discussed now 50 years when it was 100 years in the results.

Answer: We do not understand this comment as we find no such section in the discussion in which the losses would be discussed for 50 years.

34. Further minor comments Line 290- 291 state "proportion" but have reported %.

Answer: Has been corrected in to "fraction" (line 284).

35. When reporting mean values the error associated with the mean should also be reported. Line 291, 292: give mean %OC of biomass (that is used to determine C content ha-1)

Answer: We have added the mean % OC of biomass (lines 285 and 286). SEM values have been added to referred sentence (line 288-289).

36. Line 293: change to C units.

Answer: The units have been changed (line 231).

37. Line 306: the silt data is presented in Figure 2 and Table 1 (sorting data in Figure 2 but not referenced in the text).

Answer: Reference to fig. 2 has been added to line 315.

38. Line 326: In Figure 3 the max scale for Finland OC density is 20 and, but text reports value of 22 mg C cm-3, which must represent individual sediment values, it would be better if means for the site were reported in the text.

Answer: Values from individual replicates have been replaced with mean values (line 320 and 322).

39. Line 333: Finland stock ranged from – but only a single value given.

Answer: We think there is a misunderstanding here, since we found no such error in the ms. A single value is discussed and represented for Finland as there was only one eelgrass area estimate for Finland (line 330).

40. Line 335: the min C stock for Denmark is different in the text to that given in Table 2.

Answer: The values have been corrected to the ms lines 331-332.

41. Line 356: should be annual areal Corg

Answer: This part has been clarified in the text line 352.

42. Line 373: allochthanous

Answer: "Allochtanous" has been deleted from the ms.

43. Line 383: were not where

Answer: "Where" has been corrected to "were" (line 367).

44. Line 473: does this data relate to drifting algal mats?

Answer: This sentence (currently lines 485-488) is not actually relating to drifting algal mats, but rather describing the importance of understanding that the sediment OM pool is almost always a mix of different sources and it is very unlikely that the OM pool would consist only of a sole source of OM.

45. Figure 1: label a, b and c, which sites are shown?

Answer: Labelling has been added to the figure.

46.   Figure 3: axis and legend is wrongly labelled as sediment profiles of particulate organic carbon content. This would have units of wt% or gC g-1.

Answer: The axis and legend has been changed in to C mg C cm-3 in Fig. 3.

47. Figure 4: the legend "organic carbon stocks (Corg, g C m-2) "is confusing.

Answer: The legend for Fig. 4 has been changed to Corg stocks (g C m^{-2}).

48. Fig 5: It would be easier to discern the different source if patterns rather than shading were used.

Answer: We find shading is visually easier to interpret, since many of the sections are small and using patterns for these sections makes the figure more "messy" and harder to interpret. Since the fig. legend is organized exactly in the same order as the bars, it makes it very difficult to mix the different sources.

49. Table 2: column 5 should be Mt.

Answer: This has been corrected to the table 2.

Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows

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1   Abstract

2

3   Although seagrasses cover only a minor fraction of the ocean seafloor, their carbon sink capacity

4   accounts for nearly one-fifth of the total oceanic carbon burial and thus play a critical structural

5   and functional role in many coastal ecosystems. We sampled 10 eelgrass (*Zostera marina*)

6   meadows in Finland and 10 in Denmark to explore seagrass carbon stocks (Corg stock) and

7   carbon accumulation rates (Corg accumulation) in the Baltic Sea area. The study sites represent

8   a gradient from sheltered to exposed locations in both regions to reflect expected minimum and

9   maximum stocks and accumulation. The Corg stock integrated over the top 25 cm of the

10 sediment averaged 627g C m^{-2} in Finland, while in Denmark the average Corg stock was over six

11 times higher (4324 g C m^{-2}). A conservative estimate of the total organic carbon pool in the

12   regions ranged between 6.98-44.9 t C ha^{-1}. Our results suggest that the Finnish eelgrass

13   meadows are minor carbon sinks compared to the Danish meadows, and that majority of the

14   Corg produced in the Finnish meadows is exported. Our analysis further showed that > 40 % of

15   the variation in the Corg stocks was explained by sediment characteristics i.e. density, porosity

16   and silt content. In addition, our analysis show, that the root:shoot-ratio of *Z. marina* explained >

17   12 % and contribution of *Z. marina* detritus to the sediment surface Corg pool explain > 10 % of

18   the variation in the Corg stocks. The mean monetary value for the present carbon storage and

19   carbon sink capacity of eelgrass meadows in Finland and Denmark, were 281 and 1809 € ha^{-1},

20   respectively. For a more comprehensive picture of seagrass carbon storage capacity, we

21   conclude that future Blue Carbon studies should in a more integrative way, investigate the

22   interactions between sediment biogeochemistry, seascape structure, plant species architecture

23   and the hydrodynamic regime.

26

27   Introduction

28

29   The atmospheric carbon dioxide (CO_2) enters the ocean via gas-exchange processes at the ocean-

30   atmosphere interface. In the ocean dissolved inorganic carbon is fixed in photosynthesis by

31   primary producers, and released again through respiration. A large percentage of this fixed

32   carbon is stored and sequestered in the sediments of vegetated coastal ecosystems of which the

33   three globally most significant are saltmarshes, mangrove forests and seagrass meadows (Herr

34   et al. 2012). The carbon stored by these ecosystems is known as Blue Carbon (Duarte et al. 2005

35   Duarte et al. 2013a, Nellemann et al. 2009). Blue Carbon ecosystems function as carbon sinks, in

36   which the rate of carbon sequestered by the ecosystem exceeds the rate of carbon lost through

37   respiration and export.

38 Seagrass meadows play a critical structural and functional role in many coastal ecosystems

39 (Orth et al. 2006). Although seagrass meadows only cover globally about 300 000 - 600 000 km²

40 of the ocean sea floor, corresponding to 0.1 to 0.2 % of the total area, their carbon sink capacity

41 (capacity of seagrasses to absorb and store carbon in living and dead biomass and in the

42 sediments) may account for up to 18 % of the total oceanic carbon burial (Gattuso et al. 1998,

43 Duarte et al. 2005, Kennedy et al. 2010, Fourqurean et al. 2012). A large portion of the carbon

44 sequestered (captured and stored) by seagrasses is stored in sediments with a conservative

45 value of 10 Pg C in the top 1 meter of seagrass sediments (Fourqurean et al. 2012).

46 Consequently, recent global estimates imply that seagrass sediments store almost 25 200 to 84

47 000 t C km² (Fourqurean et al. 2012). More importantly, carbon in submerged sediments is

48 stored for timescales of millennia while terrestrial soils are usually less stable and only

49 sequester carbon up to decades (Hendriks et al. 2008).

50

51 The coasts of Scandinavia and the Baltic Sea are key distribution areas for eelgrass (*Zostera*

52 *marina* L.) meadows (Boström et al. 2002, Boström et al. 2014). The meadows extend from fully

53 saline (>30) along the Norwegian coast to brackish (5-6) archipelago areas of Finland. This

54 region is estimated to support >6 000 individual meadows covering at least 1 500 – 2 000 km²,

55 which is four times more than the combined eelgrass area of Western Europe (Spalding et al.

56 2003, Boström et al. 2014). Consequently, this region plays a key role in the coastal carbon

57 dynamics, but we presently lack estimates of the role of eelgrass for carbon storage in temperate

58 sediments. Seagrasses are lost at accelerating rates and it has been estimated that 29 % of global

59 seagrass area has disappeared since the initial recording of seagrasses in 1879 (Waycott et al.

60 2009). This decline could have severe consequences on the total capacity of marine ecosystems

61 to store and sequester carbon in addition to the other ecosystem services seagrass meadows

62 provide. Little is known about the magnitude of carbon emissions from degraded seagrasses

63 ecosystems, not to mention its economic implications. A recent study points out, that despite the

64 importance of these ecosystems in the global carbon budget, none of the three Blue Carbon

65 ecosystems have been included in global carbon market protocols (Pendleton et al. 2012).

66

67

68 Seagrasses exhibit marked differences in shoot architecture and grow under variable

69 environmental settings, making direct extrapolations between species and locations difficult.

70 Consequently, there is a pressing need to better understand which factors are causing variability

71 in carbon storage (Corg stocks, carbon stored in living and dead seagrass biomass and

72 sediments) and the capacity of seagrass meadows to sequester carbon (Corg accumulation) in

73 seagrass sediments. Indeed, recent studies show considerable influence of seagrass habitat

74 setting, sediment characteristics and species-specific traits on the variability in carbon storage

75 capacity in seagrass meadows (Duarte et al. 2013a, Lavery et al. 2013, Miyajima et al. 2015).

76 Such differences contribute to uncertainty in local and global estimates of the carbon storage

77 capacity and carbon dynamics in coastal seagrass areas.

78

79 In order to determine seagrass Corg stocks and Corg accumulation, knowledge on the sources of

80 the carbon stored in the sediments is also crucial. The different Corg sources vary in their

81 turnover compared to seagrasses (sources other than seagrasses being typically faster) and

82 volumes of standing stock (typically less) and thus affect the dynamics of the Corg stocks and

83 accumulation (Fry et al. 1977, Kennedy et al. 2004, Kennedy et al. 2010). Seagrasses are known

84 to be enriched in δ^{13}C compared to other potentially sources of Corg in the seagrass sediments,

85 such as plankton, macroalgae, allochtonous carbon material, seagrass epiphytes, and benthic

86 microalgae (Kennedy et al. 2004, Kennedy et al. 2010, Fry and Sherr 1984, Moncreiff and

87 Sullivan 2001, Bouillon et al. 2002, Bouillon and Boschker 2006, Macreadie et al. 2014). Thus,

88 the stable isotope signals of seagrasses and other potential Corg sources can be relatively easily

89 and reliably used as a proxy for identification of the origin of Corg in seagrass sediment carbon

90 pool (Kennedy et al. 2010). Unfortunately, the current knowledge base on how these factors

91   interact and influence carbon fluxes and storage is, at best, limited at both local and global

92   scales.

93

94   In this study, we contrast storage, accumulation rates and sources of the accumulated carbon in

95   eelgrass (*Zostera marina*) meadows in two regions differing in salinity, temperature and

96   seagrass productivity, namely Finland and Denmark. Specifically we asked;

97   (1) How large is the carbon storage capacity (Corg stocks) of Baltic Sea eelgrass meadows?

98   (2) Which are the environmental factors determining the variability of carbon storage (Corg

99   stocks) and accumulation (Corg accumulation) at local and regional scales?

100   (3) How do the sediment characteristics influence the carbon storage (Corg stocks) of

101   eelgrass meadows at local and regional scales?

102   (4) How much carbon (Corg stocks) is presently stored in Finnish and Danish eelgrass

103   meadows, respectively.

104   (5) What is the present and historically lost (only in Denmark) monetary carbon value?

105

106 Materials and methods

107 Study area

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109 Plant and sediment samples were collected in June-September 2014 from 10 sites in Finland

110 (The Archipelago Sea) and 10 sites in Denmark (Funen and Limfjorden) (Fig. 1). The Baltic Sea

111 sediments are typically mineral sediments consisting of glaciofluvial deposits and only a small

112 fraction of the sediment carbon content consists of carbonates (Leipe et al. 2011). The inorganic

113 carbon content in our samples was low and contributed with 0.5-5 % of total carbon content (n=

114 10 sites per region) and therefore carbonates were not removed from the sediment samples

115 prior to the analysis to avoid analytical errors in low organic samples (Schlacher and Connolly

116 2014). The study sites in each region spanned a gradient from sheltered to exposed areas. The

117 Archipelago Sea of southwestern Finland is a shallow (mean depth 23 m), brackish (salinity 5-6)

118 coastal area characterized by a complex mosaic of some 30.000 islands and skerries (Boström et

119 al. 2006, Downie et al. 2013). The region is heavily influenced by human pressures, especially

120 eutrophication, and exhibits naturally steep environmental gradients, as well as, strong

121 seasonality in temperature and productivity (Boström et al. 2014).

122
123 Limfjorden is a brackish water area in the Jutland peninsula connected to both North Sea and

124 Kattegat with salinity ranging from 17 to 35. The Fjord has a surface area of ~1500 km^2 and a

125 mean depth of 4.7 m (Olesen and Sandjensen 1994, Wiles et al. 2006, Petersen et al. 2013).

126 Funen is located between the Belt Seas in the transition zone where waters from Baltic Sea and

127 Kattegat meet. The salinity of the area ranges between 10 and 25 and the annual mean water

128 temperature ranges from 10-15° C (Rask et al. 1999). This study was conducted in shallow (< 10

129 m) fjords around Funen. Also the Danish areas are heavily influenced by human pressures,

130 especially eutrophication from intense agricultural farming. (DMU; Danmarks

131 Miljøundersøgelser, 2003).

132

133 Field sampling

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135 All samples were collected from depths of 2.5-3 m by scuba diving. At all sites, three replicate

136 sediment cores (corer: length: 50 cm, diameter: 50 mm) were taken randomly at a minimum

137 distance of 15 m from each other. The corer was manually forced to a depth of 30-40 cm and the

138 sediment between 0-25 cm was used for the analysis. The cores were capped in both ends under

139 water, and kept in a vertical position during transport to the laboratory. Eelgrass production and

140 biomass were measured at all sites from four randomly chosen locations within the eelgrass

141 meadow. In the vicinity of each sediment core, shoot density was counted using a 0.25 m^2 frame,

142 and above- and belowground biomass samples were collected with a corer (diameter 19.7 cm)

143 and bagged underwater. Additionally, when present, samples of plants and algae (drift algae,

144   other angiosperms, phytoplankton and epiphytes) considered likely carbon sources in the

145   eelgrass meadows were collected from each site for identification and analysis of stable isotope

146   composition. Approximately 10 g wet material was collected for each species. Annual eelgrass

147   production was determined from estimates of previous growth by applying the horizontal

148   rhizome elongation technique (Short and Duarte 2001). From each site, five replicate rhizome

149   samples with the longest possible intact rhizome carefully removed, were collected and

150   transported to the laboratory for further analysis.

151

152   Seagrass variables

153

154   In the laboratory, the above- and belowground biomass was separated and eelgrass leaves and

155   rhizomes were cleaned from epiphytes, detritus and fauna with freshwater and gently scrubbed

156   with a scalpel. All plant material was dried to constant weight (48 h in 60° C). The belowground

157   biomass was separated into living and dead rhizomes and dried separately. Only the living

158   rhizomes were used for the belowground biomass measurements while samples of both living

159   and dead rhizomes were used for analysis of organic carbon (OC) and stable isotopic

160   composition of the organic carbon (δ^{13}C). The root: shoot-ratio was calculated as the ratio

161   between below- and aboveground biomasses of *Z. marina* samples. A pooled sample of 2

162   youngest leaves from 10 randomly selected shoots were collected prior to drying from the

163   aboveground biomass samples and dried separately for analysis of OC and δ^{13}C. All samples

164   were analyzed by Thermo Scientific, delta V advantage, isotope ratio mass spectrometer. The

165   measured isotope ratios were represented using the δ- notation with Vienna Peedee belemnite

166   as reference material.

167

168   Determination of annual eelgrass production was done by measuring length of each individual

169   internode of the rhizomes to the nearest millimeters. To obtain an estimate of the mean annual

170   production per site, internode length measurements of individual replicates (n= 5) were pooled.

171 Due to lack of two annual production peaks in both regions the annual production was estimated

172 based on the distance between shortest and longest measured internodes, assuming that they

173 represent the time point when the water temperature was at its minimum and maximum

174 average, respectively. The time points for the water temperatures were obtained from databases

175 of the Finnish and Danish Meteorological Institutes, respectively.

176

177 Sediment variables

178

179 In the laboratory, sediment samples were sliced into sections of 2-5 cm, where the upper 10 cm

180 layer was divided into 2 cm layers and the remaining part in 5 cm layers. From each subsample

181 visible plant parts and fauna were removed before the sediment was homogenized. From the 0-2

182 cm section a subsample of 20 ml was taken for grain size analysis by a Malvern Mastersizer 3000

183 particle size analyzer. The sediment silt content was calculated as the fraction with particle size

184 of 2-63 μm from the range of all particle sizes (Folk and Ward 1957). Sediment water content,

185 dry bulk density and porosity were determined from a subsample of 5 ml that was taken using a

186 cut-off 5 ml syringe and weighed before and after drying at 105°C for 6 h from all sediment

187 layers. The dried sediment samples were homogenized in a mortar and divided into two

188 subsamples from which one was used for analysis of sediment organic matter content (OM, as

189 loss of ignition: 4 h in 520°C), and the other for analysis of sediment δ^{13} C and OC as described

190 above for the plant materials. Inorganic carbon content was low in sediments from both regions

191 (< 5 %) and considered insignificant compared to the organic fraction (1-2 order of magnitude

192 higher).

193

194 Corg stock and Corg accumulation calculations

195

196 To estimate sediment Corg stock and Corg accumulation of Finnish and Danish eelgrass area we

197 used averages from 10 sites from each region in our calculations. The Corg (obtained by depth

198 integration of the carbon density (mg C cm^{-3}) of 0-25 cm sediment layers (mg C cm^{-2}) of the

199 sampled region was multiplied with estimated seagrass area of the region based on the most

200 recent areal estimates (in km^2) of seagrass distribution available in the literature (Boström et al.

201 2014) and given as Corg in g C m^{-2}. In Finland the estimated areal extent was 30 km^2, while in

202 Denmark the extrapolations were based on the minimum and maximum estimates of the areal

203 extent, respectively (673 and 1345 km^2; Boström et al. 2014). Results for carbon burial (applied

204 by multiplying the Corg stock, regional seagrass area and sediment accumulation rate estimate

205 from literature) in each area are given as Corg accumulation (t y^{-1}). Due to lack of long term

206 monitoring of sediment accumulation in eelgrass meadows, we used available minimum,

207 average and maximum sediment accumulation rates in seagrass meadows obtained from

208 literature (Duarte et al. 2013b, Serrano et al. 2014, Miyajima et al. 2015).

209

210 To calculate the total Corg pool in Danish and Finnish eelgrass sediments, we summed the

211 following three components: (1) the annual eelgrass carbon accumulation rate (Corg

212 accumulation in t C ha^{-1}y^{-1}, calculated by dividing the measured Corg stocks (C g DW m^{-2}) in each

213 region with time that it takes to accumulate this stock with a sedimentation rate of 2.02 mm y^{-1}),

214 (2) the total C in the average living aboveground and belowground *Z. marina* tissue (t C ha^{-1}),

215 and (3) the mean Corg stocks (t C ha^{-1}) in eelgrass sediments in Denmark and Finland,

216 respectively. To calculate the present and lost economic value of eelgrass carbon stocks, we used

217 the social cost of carbon of 40.3 € t C^{-1} (United States Government 2010) and multiplied this

218 value with the Corg stocks (t C km^{-2}). To estimate the Danish eelgrass losses over the past 100

219 years in economic terms, we used the calculations above, but accounted for the annually lost

220 sequestration value by multiplying the rate by 100. We used the most recent loss estimates for

221 Denmark for the period 1900-2000, assuming that the present coverage constitutes 10 % or 20

222 % of the historical area, respectively (Boström et al. 2014).

223

224   Sediment carbon sources

225

226   The Isosource 1.3 isotope mixing model software (Phillips and Gregg 2003) was used to estimate

227   the contribution of different carbon sources to the sediment surface Corg stock. We ran the

228   Isosource model using the $\delta^{13}C$ obtained from stable isotope analysis of *Z. marina* leaves, living

229   and dead rhizomes and for samples of other abundant Corg sources within the meadow (n=1-5)

230   with increments of 1 % and tolerance of 0.1. Numbers are given as percentage contribution to

231   the sediment surface carbon pool.

232

233   Data analysis

234

235   All statistical analyses were performed using the PRIMER 6 PERMANOVA+ package (Anderson

236   et al. 2008). A 2-factor mixed model was used, where sampling sites and region (FIN, DEN) were

237   used as fixed factors for the biological response variable (sediment organic carbon stock, g C m^{-2}

238   ^{2}). In addition we ran reduced, countrywise DistLm models in order to better address the

239   possible differences in regional environmental drivers for Corg stock. Prior to analysis, the

240   environmental predictor variables (degree of sorting, sediment dry density, sediment water

241   content, sediment porosity, sediment silt content, sediment organic content, annual production,

242   root: shoot-ratio, shoot density and percentage of *Z. marina* detritus contribution to Corg) were

243   visually inspected for collinearity using Draftsman plots of residuals. Due to autocorrelation

244   between sediment variables (water content, porosity and dry density) sediment water content

245   was removed from the environmental variables. To achieve normality in the retained

246   environmental variables, data was log-transformed (log(X+1) and Euclidean distance was used

247   to calculate the resemblance matrix. The biological response variable (Corg stock in g C m^{-2}) was

248   square-root transformed and Bray-Curtis similarity was used to calculate the abundance matrix.

249   The relative importance of different environmental variables was determined by use of DistLm,

250   a distance-based linear model procedure (Legendre and Anderson 1999). DistLm model was

251 constructed using a step-wise procedure that allows addition and removal of terms after each

252 step of the model construction. AICc (Akaike Information Criterion with a correction for finite

253 sample sizes) was chosen as information criterion as it enables to fit the best explanatory

254 environmental variables from of relatively small biological dataset compared to number of

255 environmental variables (Burnham and Anderson 2002). An alpha level of significance of 95 %

256 (p<0.05) was used for all the analysis. All means are reported as mean ± SE (SEM).

257

258 Results

259

260 Seagrass meadow and sediment characteristics
261

262 In general, the Finnish meadows were found on exposed sandy bottoms while the environmental

263 settings of the eelgrass meadows in Denmark were more variable (Fig. 2). Shoot density was

264 nearly equal in both regions, averaging at 417± 75 (shoots m^{-2}) in Finland and 418±32 (shoots

265 m^{-2}) in Denmark. In Finland variation between sites (112-773 shoots m^{-2}) was greater than in

266 Denmark (300-652 shoots m^{-2}). In Denmark the highest shoot density was found at the most

267 exposed site (Nyborg), while in Finland the highest shoot density was found at Sackholm, a fairly

268 sheltered site. The lowest shoot densities in Finland and Denmark were found in Tvärminne and

269 Løgstør, respectively. The mean aboveground biomasses were 101±3 and 145±5 (g DW m^{-2}) and

270 the mean belowground biomasses 79±5 and 148±13 g (DW m^{-2}) at Finnish and Danish sites,

271 respectively. In Denmark, the mean fraction of OC in aboveground and belowground *Z. marina*

272 tissue was 35±0.32 % DW and 29±1.10 % DW, respectively, while the corresponding numbers

273 for Finland were 38±0.24 % DW and 36±0.27 % DW, respectively. Given an average total *Z.*

274 *marina* biomass (above- and belowground) of 293± 22.31 (Denmark) and 180±9.60 g DW m^{-2}

275 (Finland), we estimate the Corg pool in bound in living seagrass biomass to 0.66±0.005 and

276 0.94±0.014 t C ha^{-1} in Finland and Denmark, respectively. The root:shoot-ratio was slightly

277 lower in Finland (0.87±0.05) than in Denmark (1.14±0.12), and varied between 0.29 to 3.29 and

278 0.15 to 6.45 in Finland and Denmark, respectively. The annual production of eelgrass for Finland

279 (average 524 ± 62 g DW m^{-2} y^{-1}) showed relatively low variation between sites (270-803 g DW m^{-2} y^{-1})

280 being lowest at Jänisholm and highest at Ryssholmen. In Denmark, the mean annual

281 eelgrass production was almost twice as high (928 ± 159 g DW m^{-2} y^{-1}) with large variation (470-

282 2172 g DW m^{-2} y^{-1}). Production was lowest and highest at Dalby and Visby, respectively (Table

283 1).

284

285 The sediment characteristics varied significantly between Finland and Denmark. There was a

286 significant difference ($F_{1, 9} = 14.7$, $p<0.003$) between regions in terms of silt content, which was

287 generally lower at Finnish (6.3 ± 1 %) sites than at Danish sites (20.2 ± 3.9 %), although in

288 Denmark the variation between sites ranged from 0.8 % at Nyborg to 31.6 % at Thurøbund

289 (Table 1, Fig. 2). In Finland, the variation between sites was lower and ranged from 1.6%

290 (Kolaviken) to 15.5 % (Sackholm). At the Finnish sites the mean sediment dry density was

291 higher (1.35 ± 0.01 g cm^{-3}) compared to the Danish sites (1.25 ± 0.02 g cm^{-3}), and the Finnish sites

292 exhibited lower within-region variability ranging from 1.1 g cm^{-3} at Lyddaren to 1.5 cm^{-3} at

293 Långören, while the Danish sites varied from 0.3 g cm^{-3} at Thurøbund to 1.5 g cm^{-3} at Visby. The

294 Finnish sites showed consistently lower pools of organic matter (LOI: 1.4 ± 0.3 %DW) compared

295 to the average of Danish sites (LOI: 3.9 ± 1.5 % DW). Similarly, the mean OC content was lower in

296 Finland (0.24 ± 0.033) than in Denmark (1.75 ± 0.563). Consequently, the mean water content was

297 similarly lower in Finland (20.9 ± 0.4 %: range 16-29 %) than in Denmark (37.4 ± 1.8 %: range 17-

298 76 %) (Table 1). Sediment porosity was similar in both regions, and ranged from 0.25 to 0.30 in

299 Finland, and from 0.20 to 0.40 in Denmark. At the Finnish sites, the proxy (degree of sorting)

300 that was used to estimate exposure, varied from 0.8 to 1.5 (φ), with Kolaviken being the most

301 exposed and Ängsö being the most sheltered site. In Denmark degree of sorting varied from 0.6

302 to 2.1 (φ,) with Nyborg and Visby being the most exposed and sheltered sites, respectively (Fig.

303 2).

304

305   Organic carbon stocks

306   The profiles of carbon densities (g C cm^{-3}) in the upper 25 cm of the sediment showed marked

307   differences both between and within the sampled regions. At the Finnish sites, where eelgrass

308   typically grows at exposed locations, the sediment carbon densities were low (mean 2.6±0.09

309   mg C cm^{-3}) and declined with depth at most of the 10 study sites (Fig. 3). At the Danish sites,

310   however, the sediment carbon density were more variable (mean 17.45±9.42 mg C cm^{-3}) both

311   within and between the sites (Fig. 3). Depth integrated Corg stocks (0-25 cm, g C m^{-2}, Fig. 4)

312   were particularly high at one sheltered site in Funen, namely Thurøbund. This site is

313   characterized by soft sediments with high organic content, high annual eelgrass production and

314   high belowground biomass (Table 1). The lowest eelgrass Corg stocks in Denmark were found at

315   two relatively exposed and sandy sites, namely Nyborg and Dalby (Fig. 4). The estimate of

316   average total Corg stock in Finland was 0.019±0.001 Mt C taking the total area of eelgrass into

317   account (30 km^2; Table 2). Using minimum and maximum estimates of the eelgrass area in

318   Denmark the estimates for mean total sediment Corg stock in Denmark were 2.164±0.005 Mt C

319   or 5.868±0.014 Mt C, respectively (673 and 1345 km^2; Table 2).

320

321   Using an annual carbon accumulation value of 0.05 and 0.35 t C ha^{-1} y^{-1} for Finland and

322   Denmark, respectively, and assuming sediment accumulation of 2.02 mm y^{-1} on average (Table

323   2), the total pool of Corg in the *Z. marina* meadows (Corg bound in living biomass, sediment Corg

324   stock and Corg accumulation) corresponds to 6.98 t C ha^{-1} (698t km^{-2}) and 44.9 t C ha^{-1} (4490 t

325   km^{-2}) for Finland and Denmark, respectively. Using the social cost of carbon of 40.3 € t C^{-1}

326   (United States Government 2010), the present economic value of eelgrass carbon in Finnish and

327   Danish eelgrass meadows is estimated at 281 and 1809 € ha^{-1}, respectively. Using an average of

328   these values (1045 € ha^{-1}) and a conservative estimate of the eelgrass acreage in the Baltic Sea

329   (2100 km^2: Boström et al. 2014), we estimate a total monetary value of the present

330   sequestration by eelgrass meadows to be 219.4 million euro. Given the total eelgrass loss in

331   Denmark for the time period 1900-2000 is between 5381 km^2 (present area 20 % of historical

332 distribution) and 6053 km^2 (present area 10 % of historical distribution), this equals to a Corg

333 loss of 0.042 and 0.048 Gt C, respectively. Using the acerage value (1045 € ha^{-1}) these areal loss

334 estimates corresponds to a lost economic value between 562 and 632 million euro, for the

335 minimum and maximum areal loss estimates, respectively.

336

337 Corg accumulation

338

339 The estimates for annual Corg accumulation in the Finnish seagrass meadows (30 km^2) were

340 low (0.002, 0.016, 0.033 Mt C y^{-1}), when applying sediment accumulation rates of 0.32, 2.02 and

341 4.20 mm y^{-1}, respectively. The low Corg accumulation in Finnish meadows was a result of low

342 mean Corg stocks and relatively small size of seagrass area compared to Denmark (Table 2). The

343 estimates for annual Corg accumulation for the Danish sites differed between the two sub-

344 regions Limfjorden (18 km^2) and Funen (179 km^2). At the sampling sites around Funen, the Corg

345 accumulation was 0.139, 0.881 and 1.832 Mt C y^{-1}, while in Limfjorden the Corg accumulation

346 was lower (0.006, 0.038 and 0.079 Mt C y^{-1}) and similar to Corg accumulation for Finland. Using

347 upper and lower eelgrass areal estimates, total Corg accumulation based on 3 sediment

348 accumulation rates in Denmark were more than four orders of magnitude higher (0.376, 2.373,

349 3.636 and 0.75, 4.741 and 9.859 Mt C y^{-1}) than the estimated total Corg accumulation in Finnish

350 eelgrass meadows.

351

352 Carbon sources

353

354 The δ^{13}C values of the surface sediment within regions where quite homogenous ranging from -

355 22.8 to -18.9 ‰ and -17.6 to 13.5 ‰, in Finland and Denmark respectively. The analytical error

356 for the sediment δ^{13}C values was 2.8 %. The δ^{13}C in *Z. marina* tissues ranged from -11.4 to -8.5

357 ‰ and from -12.5 to -8.2‰, in Finland and Denmark, respectively. There was no significant

358 difference between living above- and belowground tissue and decomposed belowground tissue

359 and samples were pooled in the isotope mixing model. Although *Z. marina* was the dominant

360 seagrass species in Finland, the study sites included both monospecific and mixed seagrass

361 meadows. Mixed meadows typically contained pondweeds, e.g. *Potamogeton pectinatus* and

362 *Potamogeton perfoliatus*. In particular, *P. pectinatus* (δ^{13}C -11.3 to -7.6 ‰) and *P. perfoliatus*

363 (δ^{13}C -15.6 to -12.6 ‰) were both present at five of the Finnish study sites (Jänisholm,

364 Sackholm, Hummelskär, Tvärminne and Fårö) and *P. pectinatus* was present at Kolaviken,

365 Ryssholmen and Lyddaren. *Ruppia cirrhosa* (-11.5 to -8.8 ‰) was less abundant and found at

366 three of the Finnish sites (Sackholm, Ängsö, Kolaviken) and at one study site in Denmark

367 (Kertinge). The δ^{13}C for phytoplankton ranged from -24.6 to -22.6 ‰ and -18.6 to 16.4 ‰, in

368 Finland and Denmark, respectively. Drift algae was present at all Danish study sites, except

369 Thurøbund, and had δ^{13}C values from -17.9 to -13.5 ‰, but only at five Finnish sites (Ängsö,

370 Ryssholmen, Fårö, Långören and Hummelskär) with δ^{13}C values ranging from -20.0 to -16.3‰.

371

372 The isotope mixing model indicated that at all Finnish sites, phytoplanktonic material was the

373 major contributor (43-86 %) to the sediment surface Corg pool. In Denmark *Z. marina*

374 contributed with 13-81 % to the sediment surface Corg pool, contribution being lowest at the

375 most exposed site in Nyborg and highest in Visby. The corresponding numbers for Finland were

376 1.5-32 %, being lowest and highest in Tvärminne and Lyddaren, respectively (Fig. 5).

377

378 Environmental factors explaining carbon pools

379

380 The combined (FIN + DK) DistLm analysis showed, that three sediment variables (dry density,

381 silt content, porosity) and three plant variables (annual eelgrass production, the root:shoot-ratio

382 and *Z. marina* contribution to the sediment carbon pool) explained 67 % of the variation in the

383 sediment Corg stock (g C m^{-2}) (Table 3 and 4, Fig. 6). Specifically, sediment silt content alone

384 explained > 36 % of the variation in Corg stocks (Table 3). In both regions, exposed sites

385 characterized by sandy, low organic sediments and low silt content, had low Corg stocks. In

386 contrast, at sheltered sites like Thurøbund in Denmark, we measured the highest sediment Corg

387 stock along with highest silt and water content among all sites. Although sediment porosity and

388 sediment dry density also contributed to the model, they were of minor importance (~2 %

389 each).

390 The combined (FIN+ DK) DistLm analysis also showed that the *Z. marina* contribution to the

391 sediment surface carbon pool explained 10.9 % of the variation in the measured Corg stocks

392 (Fig. 6, Table 3 and Table 4). Drift algae was a significant contributor (72 %) to the sediment

393 surface Corg pool at the Danish sites, while it appeared to play only a minor role (0-21 %) in

394 Finland. The carbon sources were generally more mixed at the Danish study sites compared to

395 the Finnish sites where phytoplankton dominated (Fig. 5).

396

397 While the overall model including all sites explained almost 70 % of the variation in carbon

398 stocks (Table 3, 4), and indicated that the most relevant environmental variables were included

399 in this Baltic scale analysis, reduced, countrywise DistLM models revealed different results. In

400 particular, variability in Finnish carbon stocks were explained up to 50 % by geological variables

401 (porosity, sorting and sediment density), while the best sequential model for carbon stock

402 variability at Danish sites explained 75 % of the total variance. In contrast to Finland, the role of

403 eelgrass related variables (relative proportion of *Z. marina* in the sediment and the root:shoot

404 ratio) where most important and explained 40 % and 25 %, respectively of the carbon stock

405 variability.

406

407 Discussion

408

409 Recent studies have shown considerable variation in the global estimates of carbon stocks (Corg

410 stocks) and carbon accumulation rates (Corg accumulation) in seagrass meadows, indicating an

411 incomplete understanding of factors influencing this variability (Fourqurean et al. 2012, Duarte

412   et al. 2013a, Lavery et al. 2013, Miyayima et al. 2015). The Baltic Sea forms a key distribution

413   area for eelgrass in Europe, but similarly to the global data sets, we have so far lacked estimates

414   on seagrass carbon stocks and accumulation.

415

416   In our study, the Finnish eelgrass meadows showed consistently very low Corg stocks and Corg

417   accumulation, and the meadows were minor carbon sinks compared to the Danish meadows.

418   The Danish sites showed more variation in the sediment Corg stock and accumulation and Corg

419   stock was particularly high at one site, Thurøbund (26138 ±385 g C m^{-2}), which is a relatively

420   sheltered site with high organic sediments. Expectedly, due to both larger overall eelgrass

421   acreage and larger Corg stocks in the Danish meadows, the total Corg accumulation (0.38-9.86 t

422   C y^{-1}) was three to four orders of magnitude higher than in the Finnish meadows (0.002-0.033 t

423   C y^{-1}). As eelgrass in Finland generally grow in more exposed locations potentially due to

424   increased interspecific competition with freshwater plants such as common reed (*Phragmites*

425   *australis*) in sheltered locations (Boström et al. 2006), it is probable that most of the Corg

426   produced in the Finnish meadows is exported, and thus incorporated in detrital food webs in

427   deeper bottoms. This argument is supported when applying sediment accumulation rates from

428   literature, as only 0.15 – 2.0 % of the annual production accumulated in Finnish meadows, while

429   the corresponding numbers for Denmark were 0.6 -7.8 %. Duarte and Cebrian (1996) estimated

430   that on average 25 % of the global seagrass primary production is exported, and seagrass

431   detritus may thus contribute significantly to Corg stocks in other locations, a fact that is often

432   overlooked.

433

434   Extrinsic drivers of carbon sequestration in seagrass meadows

435

436   As proposed in previous work accumulation of fine grained size fractions in seagrass sediments,

437   relative to those accumulated in bare sediments, appears to be one of the major factors

438 influencing the carbon sink capacity of seagrass meadows (Kennedy et al. 2010, Miyajima et al.

439 2015), and may thus be a useful proxy for the sink capacity. In addition, it is well known, that

440 seagrasses modify sediments by reducing water flow and consequently increasing particle

441 trapping and sedimentation and reducing resuspension (Fonseca and Fisher 1986, Fonseca and

442 Cahalan 1992, Gacia et al. 2002, Hendriks et al. 2008, Boström et al. 2010) and also increasing

443 Corg (Kennedy et al. 2010).

444

445 In this study, the DistLm analysis showed, that contribution of *Z. marina* to the sediment surface

446 carbon pool was an important driver (> 10.9 %) of the variation in the sediment Corg stock

447 (Table 3 and 4, Fig. 6) when the model included both regions. Surprisingly, the reduced

448 countrywise analysis revealed different results and showed that *Z. marina* contribution to the

449 sediment surface carbon pool was an important driver for Corg stocks only in Denmark. We

450 believe that the countrywise differences in explanatory variables might relate to the more

451 pronounced influence of eelgrass for carbon stocks at Danish sites. Indeed, these sites exhibited

452 on average 30 % higher aboveground biomasses, 45 % higher belowground biomasses, 24 %

453 higher root:shoot- ratios and 44 % higher productivity compared to the Finnish sites. In Finland

454 and the northern Baltic Sea, eelgrass meadows appears to be primarily physically controlled,

455 and thus sediment variables play a relatively more pronounced role. The results from the model

456 were also supported by our data in which we found increasing Corg stocks at the Danish sites,

457 where *Z. marina* was the major source of organic carbon, contributing with 13-81% to the

458 surface sediment Corg, while in contrast, at the Finnish sites where only a minor fraction of

459 carbon buried in sediments derive from eelgrass detritus (1.5-39.6 %) the Corg stocks were low.

460 Correspondingly, the average δ^{13}C value (-16.2 ‰) in the Danish sediment samples was similar

461 to the global median value (−16.3±0.2 ‰) reported by Kennedy et al. (2010) in which on

462 average 51 % of the carbon was derived from seagrass detritus, whereas it was -20±0.6 ‰ in

463 Finland indicative of higher contribution from other more negative carbon sources., such as

464 phytoplankton. The importance of the *Z. marina* contribution to the Corg stocks may be

465 explained by slow decomposition rates of seagrass tissue. Especially, the high proportion of

466 refractory organic compounds in the seagrass belowground parts and high C:N:P-ratios of

467 seagrass tissue in general make seagrasses less biodegradable than most marine plants and

468 algae (Fourqurean and Schrlau 2003, Vichkovitten and Holmer 2004, Kennedy and Björk 2009,

469 Holmer et al. 2011, Röhr et al in prep.). The slow decomposition rates are also a result of

470 reduced sediment conditions commonly encountered in Danish seagrass meadows (Kristensen

471 and Holmer 2001, Holmer et al. 2009, Pedersen et al. 2011). Despite the extensive distribution

472 (2-29 ha), high biomasses (300-800 g DW m^{-2}) and major impact of drifting algal mats on coastal

473 ecosystem functioning (Norkko and Bonsdorff 1996, Salovius and Bonsdorff 2004, Rasmussen et

474 al. 2013, Gustafsson and Boström 2014), the stable isotope composition of the sediments

475 suggests that drift algae had a surprisingly minor influence on the sediment surface Corg pool in

476 both regions. Thus, despite present on several sampling sites, drift algae is likely exported and

477 mineralized in deeper sedimentation basins. Furthermore, we found that at all study sites in

478 both regions, there were several other potential sources influencing the sediment surface Corg

479 pool. Similarly, Bouillon et al. (2007) showed that in seagrass sediments adjacent to mangrove

480 forests in Kenya, none of their sites had seagrass material as the sole source of Corg, and instead

481 mangrove-derived detritus contributed significantly to the seagrass sediment Corg pool.

482

483   Similarly to the contribution of *Z. marina* to the sediment surface carbon pool, the root:shoot-

484 ratio explained 12.7 % of the variation in the Corg stocks when both regions were included in

485 the model, but in the reduced countrywise models it was important driver for Corg stocks in

486 only Denmark. Accordingly, the highest Corg stocks, belowground biomass and root: shoot-ratio

487 was found in Thurøbund (Denmark). In Finland, the highest root: shoot-ratio (2.07) was found at

488 Kolaviken, with a relatively low Corg stock (397 g C m^{-2}). Due to higher degree of exposure at the

489 site (degree of sorting 0.7 φ) compared to Thurøbund (1.4 φ) it is likely that large portion of the

490 eelgrass production was exported away from the meadow and not stored in the sediment. The

491   mean shoot densities were almost identical between regions, and shoot density did not

492   contribute to the model explaining Corg.

493

494   The annual eelgrass production explained only 2.3 % of the variation in the Corg stocks in the

495   combined model. The annual production rates were almost twice as high at Danish sites

496   compared to the Finnish sites. Regional differences in seagrass productivity may be caused by

497   differences in e.g. the inorganic carbon concentration in water column and light availability

498   between the regions (with higher values in Denmark), which both affect the photosynthetic

499   capacity of the plant (Hellblom and Björk 1999, Holmer et al. 2009, Boström et al. 2014).

500   Eelgrass production tend to be higher in physically exposed areas compared to more sheltered

501   areas, which can be due to improved sediment oxygen conditions and hydrodynamical effects

502   (Hemminga and Duarte 2000). This finding was not supported by our study, in which we found

503   the highest annual eelgrass production rates at both the most sheltered and exposed sites,

504   namely Visby and Nyborg (DK).

505

506   Geographical comparisons of carbon stocks and accumulation

507

508   Our estimated Corg stocks for the study sites were generally lower (627-4324 t C km^{-2}) than

509   estimates (25200-84000 t C km^{-2}) found in the literature (Duarte et al. 2005, Nellemann et al.

510   2009, Mcleod et al. 2011, Fourqurean et al. 2012). In Duarte et al. (2005) the data set used for

511   the calculations was gathered from various studies conducted at different temporal scales and

512   habitat types, as well as different methods for determination of Corg accumulation. Additionally,

513   several of the studies were conducted in the Mediterranean *P. oceanica* meadows - a habitat with

514   superior carbon sequestration and storage capacity (Duarte et al. 2005, Lavery et al. 2013). The

515   average sizes of Corg stocks in Finnish and Danish eelgrass meadows were also considerably

516   lower than the mean values reported by Alongi et al. (2014) for tropical seagrass meadows

517   (14270 t C km^{-2}). In contrast, our estimate for the carbon stock in the top 25 cm for Danish and

518   Finnish meadows (627-6005 g C m^{-2}) are comparable to Australian (262–4833 g C m^{-2}: Lavery et

519   al. 2013) and Asian estimates (3800-12000 g C m^{-2}: Miyajima et al. 2015).

520

521   Consequences of seagrass loss for carbon pools

522

523   Despite the importance of seagrasses, their global distribution has decreased by 29 % since

524   1879 primarily due to anthropogenic pressures (Waycott et al. 2009), thus weakening the

525   carbon sink capacity of marine environments to sequester carbon (Duarte et al. 2005). Since the

526   1970s, the Baltic Sea has been subject to strong anthropogenic pressures (Conley et al. 2009)

527   leading to eelgrass declines in several countries (Boström et al. 2014). In the 1930s, the Danish

528   eelgrass meadows were significantly reduced by the wasting disease (Rasmussen 1977). These

529   regime shifts in Denmark have resulted in a 80-90 % decline corresponding to 6726 km^2 in the

530   beginning of 1900`s to 673-1345 km^2 in 2005, using the minimum and maximum estimates for

531   the current coverage area, respectively (Boström et al. 2014). Using the mean carbon density

532   (17.45 mg C cm^{-3}) measured at the Danish sites, the lost Corg stock is estimated to 23-27 Mt C

533   and these large-scale seagrass declines, which are also found in Sweden and Germany, have

534   eroded the Corg stocks in the Baltic Sea significantly (Table 2). In Finland there is a lack of long-

535   term monitoring, but the meadows appear to be stable and cover at least 30 km^2 with no

536   significant loss of Corg stocks.

537

538   Using a carbon monetary value of 40.3€ C^{-1}, we calculated the monetary value of the present

539   carbon storage and sequestration capacity of eelgrass meadows in Finland and Denmark to be

540   281 and 1809 € ha^{-1}, respectively. Pendleton et al. (2014) calculated a global estimated

541   economic cost of lost seagrass meadows to be 1.9-13.7 billion USD. This value was derived from

542   the cost of lost carbon sink capacity, ignoring other lost ecosystem services including e.g. coastal

543   protection, water quality management, food provision and the role of seagrasses as fisheries and

544   key habitats for marine species (Barbier et al. 2011, Atwood et al. 2015). Our estimate also only

545   considers lost carbon sink capacity and can be compared directly with Pendleton et al. (2014).

546   The present economic value of carbon storage and sequestration capacity of Baltic Sea eelgrass

547   meadows is thus between 1.7 and 12 % out of the global seagrass Blue Carbon value.

548

549   While useful, our and previous work still remain snap shots of complex processes causing local

550   and regional variability in estimates of seagrass Blue Carbon stocks and accumulation. Clearly, in

551   order to produce more reliable estimates of global seagrass carbon sequestration rates and

552   stocks, there is a need for more studies integrating and modeling the individual and joint role of

553   e.g. sediment biogeochemistry, seascape structure, plant species architecture and hydrodynamic

554   regime. Since seagrasses are lost at accelerating rates (Waycott et al. 2009), there is also an

555   urgent need for a better understanding of the fate of lost seagrass carbon (Macreadie et al. 2014)

556   and the development of the carbon sink capacity in restored seagrass ecosystems (Nellemann et

557   al. 2009, Greiner et al. 2013, Marba et al. 2015). Nelleman et al. (2009) proposed the use of

558   carbon trading programs using financial incentives for forest conservation, such as REDD+

559   (Reduced Emissions from Deforestation and Degradation) and NAMAs (Nationally Appropriate

560   Mitigation Actions), to include the blue carbon ecosystems as part of their environmental

561   protection protocol. Both of these carbon mitigation programs require ongoing monitoring of

562   organic carbon storage and emission in the different Blue Carbon ecosystems. In order to

563   manage seagrass meadows, mitigate climate change and produce information required for the

564   carbon trading programs, it is fundamental to understand factors influencing the capacity of

565   seagrass meadows to capture and store carbon. By solving these uncertainties, the conservation

566   and restoration of seagrass meadows can be implemented in the most beneficial manner by e.g.

567   giving priority to protection of the seagrass meadows and species with the highest carbon sink

568   capacity and foundation of restoration projects in areas most suitable for seagrass growth

569   (Duarte et al. 2013a).

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571   Copyright statement

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581   Acknowledgements

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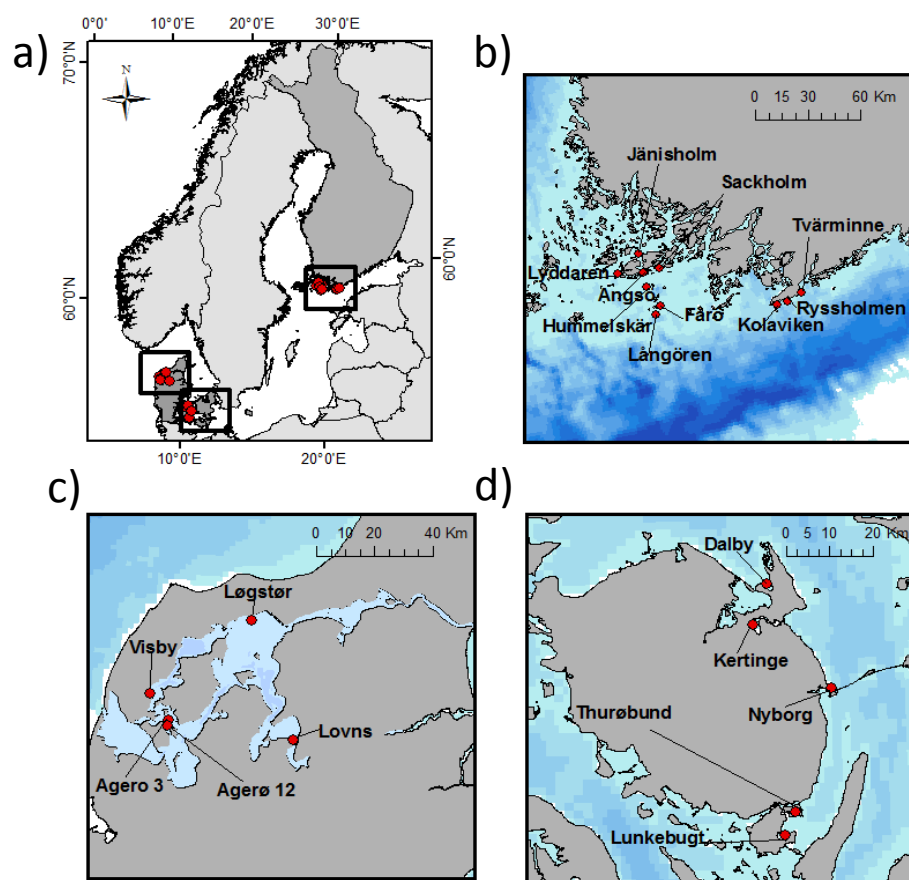
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647 Fig. 1. The study sites in Denmark and Finland. a) study regions, b) Finnish study sites, c)
648 Limfjorden study sites, d) Funen study sites.
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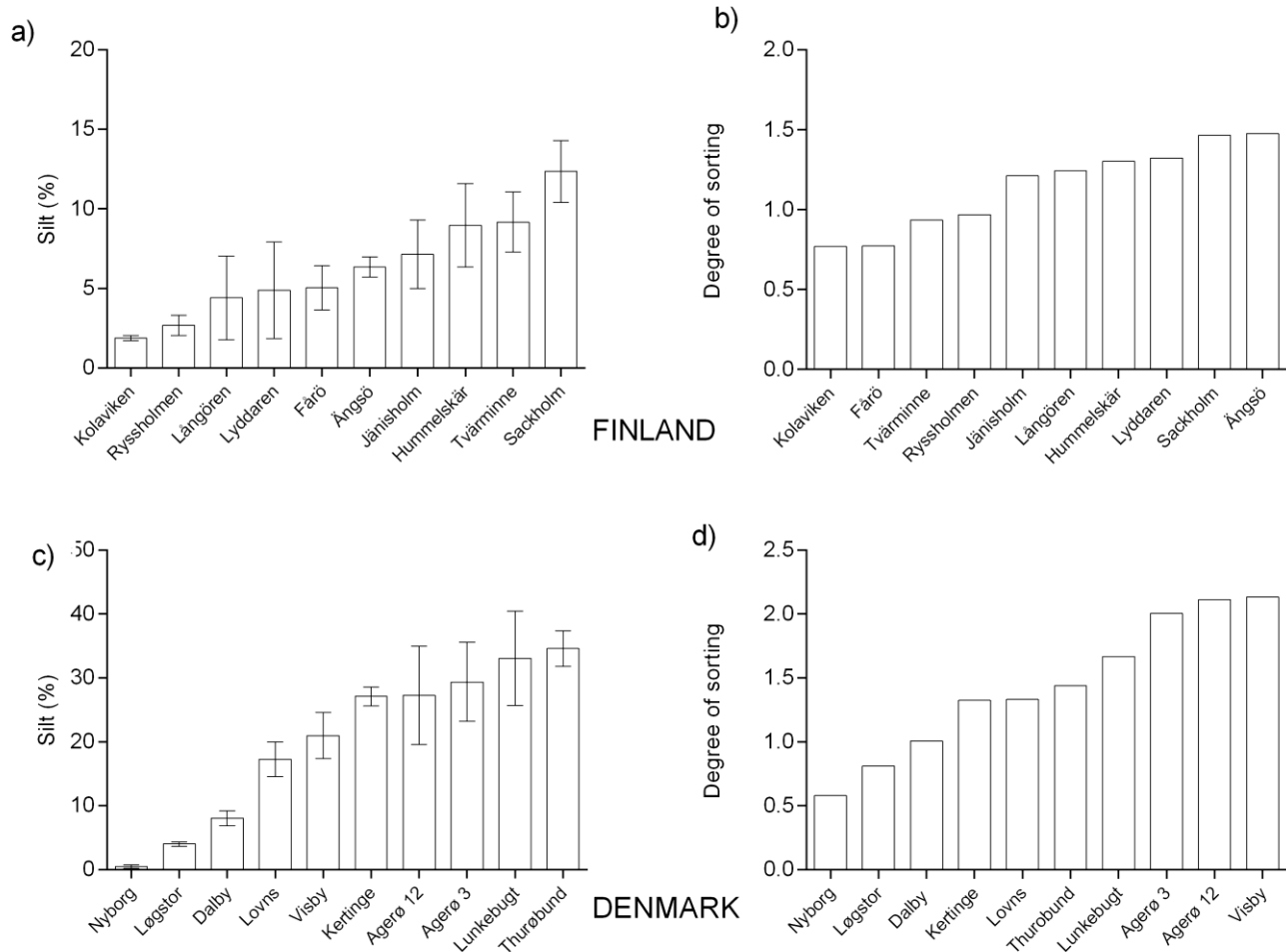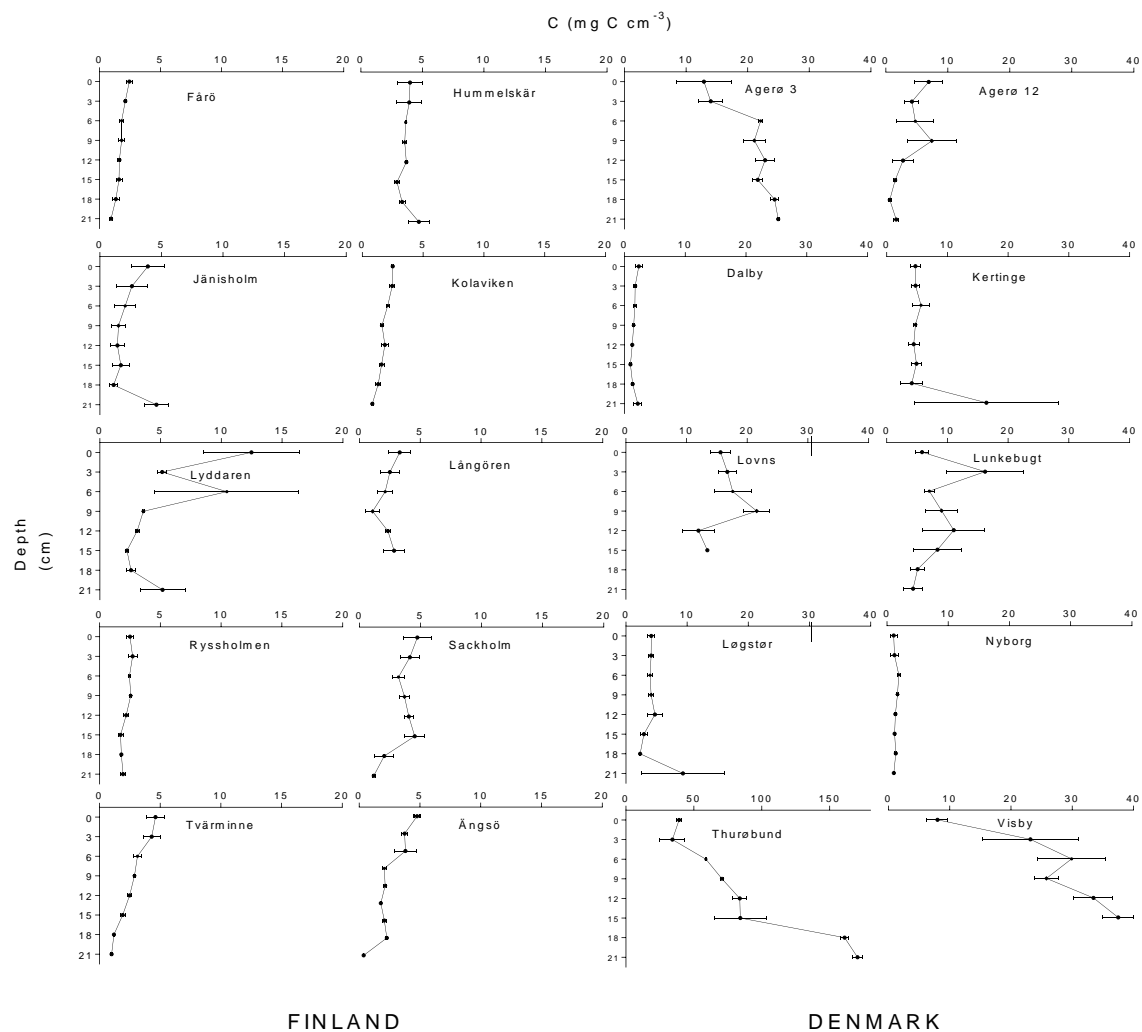653
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Fig. 2. Silt content (%) (a, c) and degree of sediment sorting (b, d) at the study sites in Finland and Denmark, respectively. Lower values in degree of sorting indicate well-sorted sediment types.
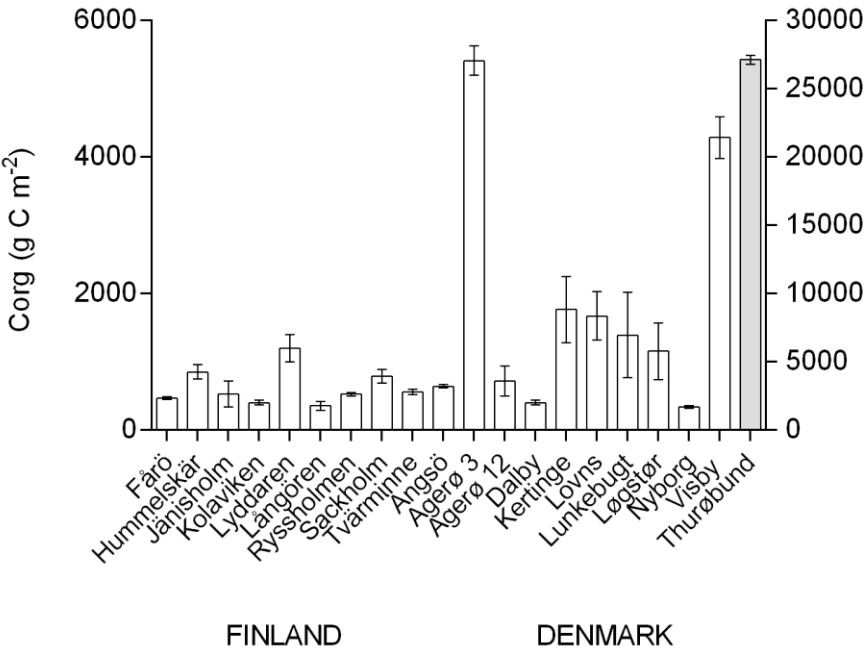
Fig. 3. Sediment profiles of organic carbon density (mg C cm⁻³) in the top 25 cm of the Finnish and Danish eelgrass (*Zostera marina*) meadows. Note the difference in the scale of x-axis between the regions.

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Fig. 4. Corg stocks (g C m^{-2}) in the top 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.

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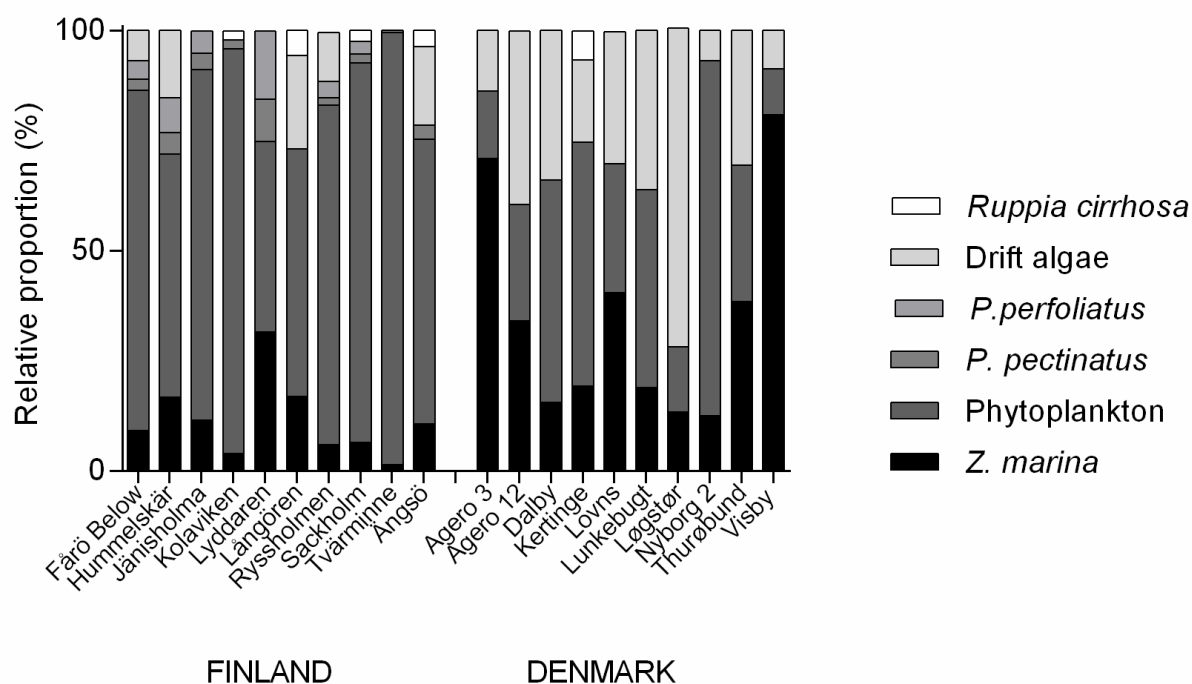
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Fig. 5. Relative contribution of different organic matter sources (*Z. marina, P. perfoliatus, P. pectinatus, Ruppia cirrhosa,* phytoplankton and drift algae) to the ^{13}C signal of the sediment surface layer (0-2 cm) in Finnish and Danish eelgrass (*Z. marina*) meadows.

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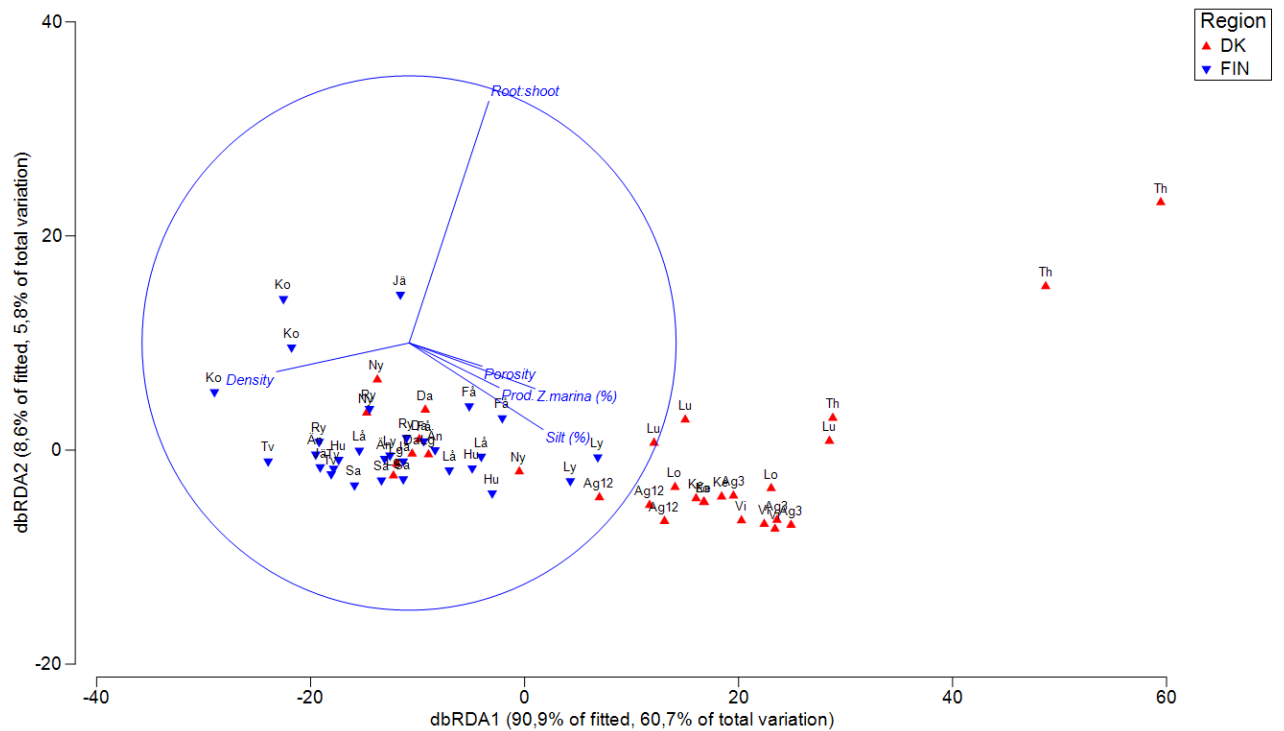752
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Fig. 6. Distance-based redundancy analysis (DbRDA) plot showing the environmental parameters (percentage of *Z. marina* in sediment carbon pool, above:belowground-ratio, annual eelgrass production, sediment silt content [%], sediment dry density and sediment porosity) fitted to the variation in the Corg stock (g C m^{-2}) at the Finnish and Danish eelgrass (*Z. marina*) sites, respectively. Vectors indicate direction of the parameters effect. Site codes: Finland; Ko=Kolaviken, Ry=Ryssholmen, Tv=Tvärminne, Få=Fårö, Ly=Lyddaren, Lå=Långören, Hu=Hummelskär, Jä=Jänisholm, Sa=Sackholm, Än=Ängsö. Site codes: Denmark; Ag12=Agerø12, Ag3=Agerø3, Vi=Visby, Lg=Løgstør, Lo=Lovns, Th=Thurøbund, Lu=Lunkebugt, Da=Dalby, Ke=Kertinge, Ny=Nyborg.

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Country/ Location	Silt content (%)	Dry dens. (g cm^{-3})	SedOM (% DW)	SedOC (% DW)	δ13 C sediment surface	δ13 C *Z. marina* leaves	δ13 C *Z. marina* rhizomes	Shoot density (shoots m^{-2})	AB (gDW m^{-2})	BB (gDW m^{-2})	R:S	Production (gDW m^{-2}y^{-1})
Finland												
Fårö	5.0±1.4	1.32±0.025	0.66±0.07	0.13±0.001	-20.58±0.27	-9.66±0.35	-9,01±0.20	304±32	138±20	167±28	1.27±0.13	773
Hummelskär	9.0±2.6	1.33±0.009	1.06±0.20	0.35±0.019	-19.36±1.22	-9.31±0.28	-9,83±0.25	364±31	70±11	28±2	0.45±0.06	446
Jänisholm	7.1±2.1	1.37±0.076	0.93±0.20	0.33±0.135	-22.05±0.37	-10.84±0.39	-11,01±0.28	128±17	65±16	46±2	1.44±0.53	270
Kolaviken	1.9±0.2	1.34±0.035	0.75±0.02	0.13±0.011	-19.48±0.23	-10.32±0.28	-11,36±0.34	476±96	74±6	149±16	2.07±0.27	324
Lyddaren	4.9±2.5	1.34±0.171	1.75±0.70	0.45±0.094	-13.53±3.52	-8.75±0.35	-9,58±0.29	228±42	86±7	57±12	0.64±0.09	505
Långören	4.4±2.1	1.42±0.046	2.70±2.10	0.19±0.019	-18.88±0.35	-8.51±0.14	-8,87±0.15	436±53	121±46	68±25	0.58±0.06	788
Ryssholmen	2.7±0.6	1.34±0.054	0.89±0.20	0.16±0.004	-20.70±0.34	-11.45±0.13	-11,49±0.29	756±57	160±3	136±16	0.86±0.11	803
Sackholm	12.4±1.9	1.36±0.042	0.95±0.20	0.26±0.027	-21.07±0.78	-10.34±0.68	-9,90±0.34	774±234	110±18	37±9	0.31±0.04	377
Tvärminne	9.2±1.9	1.33±0.034	0.88±0.20	0.20±0.016	-22.73±0.59	-11.61±0.09	-11,50±0.25	112±11	99±16	38±7	0.37±0.01	436
Ängsö	6.3±0.5	1.36±0.052	0.84±0.02	0.20±0.010	-20.05±0.28	-10.28±0.08	-10,27±0.28	604±98	91±6	63±9	0.67±0.05	521
FIN average	6.3±1	1.35±0.014	1.4±0.3	0.24±0.033	-19.85±0.32	-10,11±0.33	10,28±0.32	417±75	101±3	79±5	0.87±0.06	524
Denmark												
Agero 3	29.4±6.2	1.24±0.085	1.94±0.60	2.30±0.082	-12.95±1.67	-9,24±0.47	-11,14±0.22	448±89	181±33	84±8	0.52±0.07	1075
Agero 12	27.3±7.7	1.35±0.173	1.65±0.80	0.29±0.135	-17.35±0.84	-10,68±0.25	-11,94±0.21	404±90	110±2	46±9	0.40±0.08	576
Dalby	8.1±1.2	1.37±0.034	0.67±0.03	0.12±0.009	-17.29±0.69	-9,68±0.27	-10,50±0.56	400±48	76±7	83±10	1.09±0.11	470
Kertinge	27.1±1.5	1.15±0.045	12.59±1.60	3.23±0.236	-16.64±0.20	-9,18±0.10	-9,75±0.08	328±64	90±17	64±14	0.68±0.02	527
Lovns	17.3±2.7	1.22±0.092	2.90±0.50	1.53±0.088	-16.25±2.44	-11,51±0.35	-12,16±0.37	360±27	141±4	100±11	0.70±0.06	848
Lunkebugt	33.0±7.4	1.23±0.227	4.72±2.40	1.71±0.806	-16.93±0.25	-8,86±0.87	-10,60±0.38	347±81	210±10	382±24	1.82±0.08	1056
Løgstør	4.0±0.4	1.23±0.025	0.75±0.03	0.31±0.089	-17.68±0.35	-9,67±0.40	-10,39±0.51	300±14	149±11	63±13	0.42±0.07	755
Nyborg	0.5±0.3	1.17±0.027	0.42±0.02	0.10±0.006	-17.57±1.09	-9,33±0.17	-10,62±0.34	652±30	203±24	214±50	1.00±0.14	1179
Thurøbund	34.6±2.8	1.27±0.030	14.48±0.80	5.78±0.512	-15.54±0.42	-8,17±0.14	-9,03±0.22	420±98	101±16	398±15	4.54±0.70	619
Visby	21.0±3.6	1.25±0.021	1.17±0.06	2.18±0.201	-13.79±1.17	-11,97±0.56	-12,41±0.70	520±21	193±13	49±4	0.25±0.01	2172
DK average	20.2±3.9	1.25±0.022	3.9±1.5	1.75±0.563	-16.20±0.22	-9,82±0.37	-10.85±0.33	418±32	145±5	148±14	1.14±0.13	928

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787 Table 2. Estimated average carbon stocks (g C m^{-2} and Mt C), annual areal carbon accumulation (Corg acc. t C ha^{-1}y^{-1}) and annual carbon accumulation
788 (Annual Corg (Mt C y^{-1}) in Finnish and Danish eelgrass (*Z. marina*) meadows. Denmark$_{lost}$ = eelgrass area of the region lost since the beginning 1900`s.
789 Limfjorden$_{lost}$= eelgrass area of the region lost since the 1900`s. See text for calculations. *) mean carbon density (mg C cm^{-3}) calculated for Denmark
790 is used. n.d= no data. For calculations of annual carbon accumulation three different sediment accumulation rates were applied (0.32 mm y^{-1};
791 Miyayima et al. 2015, 2.02 mm y^{-1}; Duarte et al. 2013b and 4.2 mm y^{-1}; Serrano et al. 2014), for Corg seq the sediment accumulation rate of 2.02 mm
792 y^{-1} was used.
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Region	Seagrass area (km²)	Carbon density (mg C cm^{-3})	Corg stock (g C m^{-2})	Corg stock (Mt C)	Corg acc. (t C ha^{-1}y^{-1})	Annual Corg accumulation (Mt C y^{-1})		
						0.32 mm y^{-1}	2.02 mm y^{-1}	4.2 mm y^{-1}
Finland	30	2.60±0.09	627±25	0.019±< 0.001	0.052	0.002	0.016	0.0328
Limjorden	18	10.57±1.66	2644±207	0.047± 0.007	0.213	0.006	0.038	0.079
Funen	179	24.32±9.15	6005±1127	1.090±0.410	0.491	0.139	0.881	1.832
Denmark$_{min}$	673	17.45±9.42*	4324±1188*	2.164±0.005	0.352	0.376	2.373	3.636
Denmark$_{max}$	1345	17.45±9.42*	4324±1188*	5.868±0.014	0.352	0.75	4.741	9.859
Denmark$_{lost}$	5381-6230	17.45±9.42*	17.45±9.42*	23.478-27.183	n.d	n.d	n.d	n.d

Table 3. Table from DistLm analysis showing variables in the marginal tests and the results for statistical analysis.

MARGINAL TESTS

Variable	SS	Pseudo-F	P-value	Proportion
1. Root:shoot- ratio	5309	10.64	0.002	0.155
2. Sediment dry density	10704	26.37	0.001	0.313
3. Annual eelgrass production	4959	9.82	0.002	0.145
4. Shoot density	48	0.08	0.911	0.001
5. Porosity	3507	6.61	0.01	0.102
6. Silt content (%)	12653	33.99	0.001	0.369
7. C:N-ratio of plant material	464	0.79	0.397	0.014
8. *Z. marina* content (%)	12179	32.02	0.001	0.356
9. Degree of sorting	9725	23.01	0.001	0.284

Table 4. Table from DistLm analysis showing results from the sequential tests and solution given by the analysis.

Variable	AICc	Sum of squares	Pseudo-F	P- value	Proportion	Cumulative proportion	Degrees of freedom
6. Silt content (%)	357.4	12653	33.9	0.001	0.369	0.369	58
1. Root:shoot-ratio	346.0	4375	14.5	0.001	0.127	0.497	57
8. *Z. marina* content (%)	333.6	3745	15.6	0.001	0.109	0.606	56
3. Production	332.2	805	3.5	0.037	0.023	0.630	55
2. Density	331.3	700	3.2	0.049	0.020	0.650	54
5. Porosity	330.8	602	2.8	0.056	0.017	0.668	53
BEST SOLUTION	AICc	R^2	RSS	Variables	Selections		
	330.8	0.668	11363	6	1-3;5;6;8		