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

2   Maria Emilia Röhr[1,2*], Christoffer Boström[1], Paula Canal- Vergés[3], Marianne Holmer[2]

4   [1]Åbo Akademi University, Faculty of Science and Engineering, Environmental and Marine

5   Biology, Artillerigatan 6, 20520 Åbo, Finland

6   [2]University of Southern Denmark, Department of Biology, Campusvej 55, 5230 Odense M,

7   Denmark

8   [3]Danish Shellfish Centre, DTU Aqua, Technical University of Denmark, Øroddevej 80, 7900
9   Nykøbing Mors, Denmark

11   * Corresponding author;

13   Emilia Röhr (mrohr@abo.fi)

14   Abstract

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

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

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

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

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

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

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

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

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

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

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

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

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

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

30 12 % and contribution of *Z. marina* detritus to the sediment surface Corg pool explain > 10 % of

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

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

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

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

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

36 and the hydrodynamic regime.

37 Keywords: Blue Carbon, eelgrass, seagrass, carbon stock, carbon accumulation, sequestration,

38 carbon sink

40 Introduction

41

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

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

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

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

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

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

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

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

50 respiration and export.

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

52 (Orth et al. 2006). Although seagrass meadows only cover globally about 300 000 - 600 000 km^2

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

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

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

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

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

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

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

60 000 t C km^2 (Fourqurean et al. 2012). More importantly, carbon in submerged sediments is

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

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

63

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

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

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

67 region is estimated to support >6 000 individual meadows covering at least 1 500 – 2 000 km^2,

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

69 2003, Boström et al. 2014). Consequently, this region plays a key role in the coastal carbon

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

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

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

73 2009). This decline could have severe consequences on the total capacity of marine ecosystems

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

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

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

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

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

79

80

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

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

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

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

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

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

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

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

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

90 capacity and carbon dynamics in coastal seagrass areas.

91

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

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

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

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

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

97 to be enriched in $\delta^{13}C$ compared to other potentially sources of Corg in the seagrass sediments,

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

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

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

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

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

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

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

105 scales.

106

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

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

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

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

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

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

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

114 eelgrass meadows at local and regional scales?

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

116 meadows, respectively.

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

118

119 Materials and methods

120 Study area

121

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

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

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

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

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

127 10 sites per region) and therefore carbonates were not removed from the sediment samples

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

129 2014). The study sites in each region spanned a gradient from sheltered to exposed areas. The

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

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

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

eutrophication, and exhibits naturally steep environmental gradients, as well as, strong seasonality in temperature and productivity (Boström et al. 2014).

Limfjorden is a brackish water area in the Jutland peninsula connected to both North Sea and Kattegat with salinity ranging from 17 to 35. The Fjord has a surface area of ~1500 km^2 and a mean depth of 4.7 m (Olesen and Sandjensen 1994, Wiles et al. 2006, Petersen et al. 2013). Funen is located between the Belt Seas in the transition zone where waters from Baltic Sea and Kattegat meet. The salinity of the area ranges between 10 and 25 and the annual mean water temperature ranges from 10-15° C (Rask et al. 1999). This study was conducted in shallow (< 10 m) fjords around Funen. Also the Danish areas are heavily influenced by human pressures, especially eutrophication from intense agricultural farming. (DMU; Danmarks Miljøundersøgelser, 2003).

Field sampling

All samples were collected from depths of 2.5-3 m by scuba diving. At all sites, three replicate sediment cores (corer: length: 50 cm, diameter: 50 mm) were taken randomly at a minimum distance of 15 m from each other. The corer was manually forced to a depth of 30-40 cm and the sediment between 0-25 cm was used for the analysis. The cores were capped in both ends under water, and kept in a vertical position during transport to the laboratory. Eelgrass production and biomass were measured at all sites from four randomly chosen locations within the eelgrass meadow. In the vicinity of each sediment core, shoot density was counted using a 0.25 m^2 frame, and above- and belowground biomass samples were collected with a corer (diameter 19.7 cm) and bagged underwater. Additionally, when present, samples of plants and algae (drift algae, other angiosperms, phytoplankton and epiphytes) considered likely carbon sources in the eelgrass meadows were collected from each site for identification and analysis of stable isotope composition. Approximately 10 g wet material was collected for each species. Annual eelgrass

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

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

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

163   transported to the laboratory for further analysis.

164

165   Seagrass variables

166

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

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

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

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

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

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

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

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

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

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

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

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

179   as reference material.

180

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

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

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

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

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

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

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

188 of the Finnish and Danish Meteorological Institutes, respectively.

189

190 Sediment variables

191

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

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

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

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

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

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

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

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

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

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

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

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

204 (< 5 %) and considered insignificant compared to the organic fraction (1-2 order of magnitude

205 higher).

206

207 Corg stock and Corg accumulation calculations

208

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

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

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

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

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

214   2014) and given as Corg in g C m^{-2}. In Finland the estimated areal extent was 30 km^2, while in

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

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

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

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

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

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

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

222

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

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

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

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

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

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

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

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

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

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

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

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

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

236

237   Sediment carbon sources

238

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

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

241   Isosource model using the δ13C obtained from stable isotope analysis of *Z. marina* leaves, living

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

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

244   the sediment surface carbon pool.

245

246   Data analysis

247

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

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

250   used as fixed factors for the biological response variable (sediment organic carbon stock, g C m-

251   ^{2}). In addition we ran reduced, countrywise DistLm models in order to better address the

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

270

271 Results

272

273 Seagrass meadow and sediment characteristics
274

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

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

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

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

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

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

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

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

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

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

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

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

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

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

289 0.94±0.014 t C ha^{-1} in Finland and Denmark, respectively. The root:shoot-ratio was slightly

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

291 0.15 to 6.45 in Finland and Denmark, respectively. The annual production of eelgrass for Finland

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

293 ^{2} y^{-1}) being lowest at Jänisholm and highest at Ryssholmen. In Denmark, the mean annual

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

295 2172 g DW m^{-2} y^{-1}). Production was lowest and highest at Dalby and Visby, respectively (Table

296 1).

297

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

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

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

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

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

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

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

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

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

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

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

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

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

311 76 %) (Table 1). Sediment porosity was similar in both regions, and ranged from 0.25 to 0.30 in

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

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

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

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

316 2).

317

318 Organic carbon stocks

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

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

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

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

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

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

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

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

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

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

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

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

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

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

333

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

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

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

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

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

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

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

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

342 (2100 km^2: Boström et al. 2014), we estimate a total monetary value of the present

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

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

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

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

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

348   minimum and maximum areal loss estimates, respectively.

349

350   Corg accumulation

351

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

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

354   4.20 mm y^{-1}, respectively. The low Corg accumulation in Finnish meadows was a result of low

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

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

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

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

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

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

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

362   3.636 and 0.75, 4.741 and 9.859 Mt C y^{-1}) than the estimated total Corg accumulation in Finnish

363   eelgrass meadows.

364

365   Carbon sources

366

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

368   22.8 to -18.9 ‰ and -17.6 to 13.5 ‰, in Finland and Denmark respectively. The analytical error

369   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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

384

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

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

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

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

389   1.5-32 %, being lowest and highest in Tvärminne and Lyddaren, respectively (Fig. 5).

390

391   Environmental factors explaining carbon pools

392

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

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

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

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

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

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

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

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

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

402 each).

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

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

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

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

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

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

409

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

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

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

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

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

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

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

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

418 variability.

419

420 Discussion

421

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

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

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

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

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

427   on seagrass carbon stocks and accumulation.

428

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

445   overlooked.

446

447   Extrinsic drivers of carbon sequestration in seagrass meadows

448

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

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

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

452 2015), and may thus be a useful proxy for the sink capacity. In addition, it is well known, that

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

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

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

456 Corg (Kennedy et al. 2010).

457

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

refractory organic compounds in the seagrass belowground parts and high C:N:P-ratios of seagrass tissue in general make seagrasses less biodegradable than most marine plants and algae (Fourqurean and Schrlau 2003, Vichkovitten and Holmer 2004, Kennedy and Björk 2009, Holmer et al. 2011, Röhr et al in prep.). The slow decomposition rates are also a result of reduced sediment conditions commonly encountered in Danish seagrass meadows (Kristensen and Holmer 2001, Holmer et al. 2009, Pedersen et al. 2011). Despite the extensive distribution (2-29 ha), high biomasses (300-800 g DW m^{-2}) and major impact of drifting algal mats on coastal ecosystem functioning (Norkko and Bonsdorff 1996, Salovius and Bonsdorff 2004, Rasmussen et al. 2013, Gustafsson and Boström 2014), the stable isotope composition of the sediments suggests that drift algae had a surprisingly minor influence on the sediment surface Corg pool in both regions. Thus, despite present on several sampling sites, drift algae is likely exported and mineralized in deeper sedimentation basins. Furthermore, we found that at all study sites in both regions, there were several other potential sources influencing the sediment surface Corg pool. Similarly, Bouillon et al. (2007) showed that in seagrass sediments adjacent to mangrove forests in Kenya, none of their sites had seagrass material as the sole source of Corg, and instead mangrove-derived detritus contributed significantly to the seagrass sediment Corg pool.

Similarly to the contribution of *Z. marina* to the sediment surface carbon pool, the root:shoot-ratio explained 12.7 % of the variation in the Corg stocks when both regions were included in the model, but in the reduced countrywise models it was important driver for Corg stocks in only Denmark. Accordingly, the highest Corg stocks, belowground biomass and root: shoot-ratio was found in Thurøbund (Denmark). In Finland, the highest root: shoot-ratio (2.07) was found at Kolaviken, with a relatively low Corg stock (397 g C m^{-2}). Due to higher degree of exposure at the site (degree of sorting 0.7 φ) compared to Thurøbund (1.4 φ) it is likely that large portion of the eelgrass production was exported away from the meadow and not stored in the sediment. The mean shoot densities were almost identical between regions, and shoot density did not contribute to the model explaining Corg.

506

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

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

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

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

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

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

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

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

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

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

517 namely Visby and Nyborg (DK).

518

519 Geographical comparisons of carbon stocks and accumulation

520

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

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

523 2009, Mcleod et al. 2011, Fourqurean et al. 2012). In Duarte et al. (2005) the data set used for

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

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

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

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

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

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

530 (14270 t C km^{-2}). In contrast, our estimate for the carbon stock in the top 25 cm for Danish and

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

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

533

534   Consequences of seagrass loss for carbon pools

535

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

537   1879 primarily due to anthropogenic pressures (Waycott et al. 2009), thus weakening the

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

539   1970s, the Baltic Sea has been subject to strong anthropogenic pressures (Conley et al. 2009)

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

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

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

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

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

545   (17.45 mg C cm^{-3}) measured at the Danish sites, the lost Corg stock is estimated to 23-27 Mt C

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

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

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

549   significant loss of Corg stocks.

550

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

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

553   281 and 1809 € ha^{-1}, respectively. Pendleton et al. (2014) calculated a global estimated

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

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

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

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

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

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

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

561

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

582   (Duarte et al. 2013a).

583

584   Copyright statement

585

593

594   Acknowledgements

595

596   This work is part of a double degree program between Åbo Akademi University (ÅAU) and

597   University of Southern Denmark (SDU). The study was funded by The Maj and Tor Nesslings

598   Foundation and University of Southern Denmark. We are grateful for Archipelago Centre

599   Korpoström and University of Southern Denmark for excellent working facilities. Tiina Salo and

600   Karine Gagnon are acknowledged for field assistance and Katrine Kierkegaard and Birthe

601   Christensen for their assistance in the laboratory work.

602

603

604

605

606

607

608

609

610

611

612

613

614

615

616

617

618

619

620

621

622

623

624

625

626

627

628

629

630

631

632

633

634

635

636

637   References

638

Alongi, D. M.: Carbon Cycling and Storage in Mangrove Forests. Ann. Rev. Mar. Sci. 6:195–219, 2014.

Anderson, M.J., Gorley, R.N. and Clarke, K.R.: PERMANOVA for PRIMER: guide to software and statistical methods. Plymouth, United Kingdom: PRIMER-E Ltd., 2008.

Atwood, T.B., Connolly, R.M., Euan, G.R., Lovelock, C.E., Heithaus, M.R. and Hays, G.C, Predators help protect carbon stocks in blue carbon ecosystem. Nat. Clim. Change 2015.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. and Silliman, B.R.: The value of estuarine and coastal ecosystem services. Ecol. Monogr.,81(2):169-193, 2011.

Boström C., Baden S., Bockelmann A., Dromph K., Fredriksen S. and Gustafsson C.: Distribution, structure and function of Nordic eelgrass (Zostera marina) ecosystems: implications for coastal management and conservation. Aq. Cons. Mar. Freshwater Ecosyst.,24(3):410-434, 2014

Boström, C,. Törnroos, A. and Bonsdorff, E.: Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape. J. Exp. Mar. Biol. Ecol., 390(2):106-117, 2010.

Boström, C., Bonsdorff, E., Kangas, P. and Norkko, A.: Long-term changes of a brackish-water eelgrass (Zostera marina L.) community indicate effects of coastal eutrophication. Estuar. Coast. and Shelf Sci. 55(5):795-804, 2002.

Boström, C., O'Brien, K., Roos, C. and Ekebom, J.: Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. J. Exp. Mar. Biol. Ecol ,335(1):52-73, 2006

Bouillon S. and Boschker H.TS.: Bacterial carbon sources in coastal sediments: a cross-system analysis based on stable isotope data of biomarkers. Biogeosciences, 3(2):175-185, 2006.

Bouillon, S., Dahdouh-Guebas, F., Rao, A.V.V.S., Koedam, N. and Dehairs, F.: Sources of organic carbon in mangrove sediments: variability and possible ecological implications. Hydrobiologia, 495(1-3):33-39, 2003.

Bouillon, S., Dehairs, F., Velimirov, B., Abril, G. and Borges, A.V.: Dynamics of organic and inorganic carbon across contiguous mangrove and seagrass systems (Gazi Bay, Kenya). J. Geophys. Research-Biogeosciences 112(G2):G02018, 2007.

Burnham, K.P. and Anderson, D.R.: Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach (2nd Edition). Secaucus, NJ, USA: Springer, 2002.

Conley, D.J., Björck, S., Carstensen, J., Bonsdorff, E., Destouni, G. and Gustafsson, B.G.: Hypoxia- related processes in the Baltic Sea. Env. Sci. Tech., 2009.

DMU-report, Ærtebjerg, G., Andersen, J.H. and Hansen, O.S.(Eds.): Nutrients and Eutrophication in Danish Marine Waters . A Challenge for Science and Management, National Environmental Research Institute, Denmark, 2003.

Downie, A., von Numers, M. and Boström, C.: Influence of model selection on the predicted distribution of the seagrass Zostera marina. Estuar. Coast. and Shelf S.,121:8-19, 2013.

Duarte, C.M. and Cebrian, J.: The fate of marine autotrophic production. Limnol. Oceanogr., 41(8):1758-1766, 1996.

Duarte, C.M., Middelburg, J.J. and Caraco, N.: Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences,2(1):1-8, 2005.

Duarte, C.M., Kennedy, H., Marba, N. and Hendriks, I.: Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. Ocean Coast Man., 83:32-38 2013.

Duarte, C.M., Losada, I.J., Hendriks, I.E., Mazarrasa, I. and Marba, N.: The role of coastal plant communities for climate change mitigation and adaptation. Nature Clim. Change,3 (11):961-968, 2013.

Folk, R.L. and Ward, W.C.: Brazos river bar: a study of significance of grain size parameters. J. Sediment Petrol 1957;27:3, 1957

Fonseca and Fisher, J.S.: A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. Marine ecology progress series.Oldendorf,29(1):15-22, 1986

Fonseca, M.S. and Cahalan, J.A.: A preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coast. Shelf Sci. 1992 12; 35(6):565-576, 1992.

Fourqurean, J.W. and Schrlau, J.E. Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. Chem. Ecol. 19:373-390, 2003.

Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marba, N., Holmer, M. and Mateo, A.M.: Seagrass ecosystems as a globally significant carbon stock. Nature Geoscience, 5(7):505-509, 2012.

Fry B. and Sherr E.B. d13C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci., 27:13, 1984.

Fry, B., Scalan, R.S., Parker, P.L.: Stable Carbon Isotope Evidence for 2 Sources of Organic-Matter in Coastal Sediments - Seagrasses and Plankton. Geochim. Cosmochim. Acta 41(12):1875-1877, 1977.

Gacia, E., Granata, T.C. and Duarte, C.M.: An approach to measurement of particle flux and sediment retention within seagrass (Posidonia oceanica) meadows. Aquat. Bot., 65(1-4):255-268, 1999.

Gacia, E. and Duarte, C.M. and Middelburg, J.J.: Carbon and nutrient deposition in a Mediterranean seagrass (Posidonia oceanica) meadow. Limnol. Oceanogr. 47(1):23-32, 2002.

Gattuso. J.P., Frankignoulle, M. and Wollast R. Carbon and carbonate metabolism in coastal aquatic ecosystems. Ann. Rev. Ecol. Syst., 29:405-434, 1998.

Greiner, J.T., McGlathery, K.J., Gunnell, J. and McKee, B.A. Seagrass Restoration Enhances "Blue Carbon" Sequestration in Coastal Waters. Plos One, 8(8):e72469, 2013.

Gustafsson, C. and Boström, C.: Algal mats reduce eelgrass (Zostera marina L.) growth in mixed and monospecific meadows. Journal of Experimental Marine Biology and Ecology.461:85-92, 2014.

Hendriks, I.E., Sintes, T., Bouma, T.J. and Duarte, C.M.: Experimental assessment and modeling evaluation of the effects of the seagrass Posidonia oceanica on flow and particle trapping. Mar. Ecol. Prog. Ser. 356:163-173, 2008.

Herr, D., Pidgeon, E., Laffoley, D. (Eds.).:Blue Carbon. Policy Framework: Based on the Discussion of the International Blue.Carbon PolicyWorking Group, IUCN and Arlington, Gland, Switzerland, USA: CI. viþ39pp, 2012.

Holmer, M., Duarte, C.M., Boschker, H.T.S. and Barron, C.: Carbon cycling and bacterial carbon sources in pristine and impacted Mediterranean seagrass sediments. Aquat. Microb. Ecol., 36(3):227-237, 2004.

Holmer, M., Baden, S., Bostrom C and Moksnes P.: Regional variation in eelgrass (Zostera marina) morphology, production and stable sulfur isotopic composition along the Baltic Sea and Skagerrak coasts. Aquat. Bot., 91(4):303-310, 2009.

Holmer, M. 2009. Productivity and biogeochemical cycling in seagrass ecosystems. In Coastal Wetlands: An Integrated Ecosystem Approach, ed. G.M.E. Perillo, E. Wolanski, D.R. Cahoon and M.M. Brinson, 377-401. Amsterdam, The Netherlands.

Holmer, M., Wirachwong, P. and Thomsen, M.S.: Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species. Mar. Biol.,158(2):297-309, 2011.

Kennedy, H., Gacia, E., Kennedy, D.P., Papadimitriou, S. and Duarte, C.M.: Organic carbon sources to SE Asian coastal sediments. Estuar. Coast. and Shelf S. ,60(1):59-68, 2004.

Kennedy, H. and Björk, M.: Seagrasses, in The Management of Natural Coastal Carbon Sinks in Coastal Ecosystems: Investigating and Realising the Potential. 2009.

Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M. and Marba, N.: Seagrass sediments as a global carbon sink: Isotopic constraints. Glob. Biogeochem. Cycles, 24:GB4026, 2010.

Kristensen, E. and Holmer, M.: Decomposition of plant materials in marine sediment exposed to different electron accepters (O-2, NO3-, and SO42-), with emphasis on substrate origin, degradation kinetics, and the role of bioturbation. Geochim. Cosmochim. Acta, 65(3):419-433, 2001.

Lavery, P.S., Mateo, M., Serrano, O. and Rozaimi. M.: Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service. Plos One ,8 (9):e73748, 2013.

Legendre, P. and Anderson, M.J.: Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments (vol 69, pg 1). Ecol. Monogr. , 69 (4):512-512, 1999.

Leipe, T., Tauber, F.,Vallius, H., Virtasalo, J., Uścinowicz, S.,Kowalski, N.,Hille, S., Lindgren, S.,and Myllyvirta, T.:Particulate organic carbon (POC) in surface sediments of the Baltic Sea. Geo-Mar. Lett. 31:175-188,2011.

Macreadie, P.I., Baird, M.E., Trevathan-Tackett, S.M., Larkum, A.W.D. and Ralph, P.J.: Quantifying and modelling the carbon sequestration capacity of seagrass meadows - A critical assessment. Mar. Pollut. Bull., 83(2):430-439, 2014.

Marba, N., Arias-Ortiz, A., Masque, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., Garcia-Orellana, J. and Duarte, C. M.: Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. J.of Ecology 103:296-302, 2015

Mcleod,E., Chmura, G.L., Bouillon, S., Salm, R., Bjork, M. and Duarte, C.M.: A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front. Ecol. Env., 9(10):552-560, 2011.

Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., Adachi, H. and Yamano, H.: Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. Glob. Biogeochem. Cycles, 29(4):397-415, 2015.

Moksnes, P.-E. and Cole, S. G.: Valuing multiple eelgrass ecosystem services in Sweden: Fish production and uptake of carbon and nitrogen. Front. Mar. Sci. 2(121):1-18, 2015.

Moncreiff, C.A. and Sullivan M.J.: Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. Mar. Ecol. Prog. Ser., 215:93-106, 2001.

Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., De Young, C. and Fonseca, L.: Blue Carbon. A Rapid Response Assessment, 2009.

Norkko, A. and Bonsdorff, E.: Rapid zoobenthic community responses to accumulations of drifting algae. Mar. Ecol. Prog. Ser., 131:143-157, 1996.

Olesen, B. and Sandjensen, K.: Patch Dynamics of Eelgrass Zostera marina. Mar. Ecol. Prog. Ser. 106(1-2):147-156, 1994.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W. and Heck, K .L.Jr. : A global crisis for seagrass ecosystems. Bioscience, 56(12):987-996, 2006.

Pedersen, M. Ø., Serrano, O., Mateo, M.A, Holmer, M.: Temperature effects on decomposition of a Posidonia oceanica mat. Aquat. Microb. Ecol. 65: 169-182, 2011.

Pendleton, L., Donato, D.C., Murray, B.C., Crooks, S., Jenkins, W.A. and Sifleet, S: Estimating Global "Blue Carbon" Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. Plos One, 7(9):e43542, 2012.

Petersen, J.K., Maar, M., Ysebaert, T. and Herman, P.M.J.: Near-bed gradients in particles and nutrients above a mussel bed in the Limfjorden: influence of physical mixing and mussel filtration. Mar. Ecol. Prog. Ser., 490:137-146, 2013.

Phillips, D.L. and Gregg, J.W.: Source partitioning using stable isotopes: coping with too many sources. Oecologia, 136(2):261-269, 2003.

Rask, N., Pedersen, S.E. and Jensen, M.H.: Response to lowered nutrient discharges in the coastal waters around the island of Funen, Denmark. Hydrobiologia, 393:69, 1999.

Rasmussen, E.: The wasting disease of eelgrass Zostera marina and its effects on environmental factors and fauna. Seagrass ecosystems. A scientific perspective. New York: Marcel Dekker Inc., 1977.

Rasmussen, J.R., Pedersen, M.F., Olesen, B., Nielsen, S.L. and Pedersen, T. M .: Temporal and spatial dynamics of ephemeral drift-algae in eelgrass Zostera marina, beds. Estuar. Coast. and Shelf S.

119:167-175, 2013.

Salovius, S. and Bonsdorff , E.: Effects of depth, sediment and grazers on the degradation of drifting filamentous algae (*Cladophora glomerata* and *Pilayella littoralis*).Journal of Experimental Marine Biology and Ecology.298:93-109,2004.

Schlacher,T.A and Conolly, R.M.: Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. Methods in Ecology and Evolution 5(6):541-550,2014.

Serrano, O., Lavery, P.S., Rozaimi, M. and Mateo, A. M.: Influence of water depth on the carbon sequestration capacity of seagrasses. Global Biogeochem. Cycles 28(9):950-961, 2014.

Short, F. and Duarte, C.M.: Methods for the measurement of seagrass growth and production. In: Short and Cole, editors. Global seagrass research methods Amsterdam: Elsevier; p. 155-182, 2001.

Spalding, M., Taylor, M., Ravilious, C., Short, F., Green, E.: Global overview: The distribution and status of seagrasses. In: Green, E.P. and Short F.T.: editors. World Atlas of Seagrasses: Present Status and Future Conservation. Berkeley California: University of California Press, p. 5-26, 2003.

United States Government. Technical Support Document: Social Cost of Carbon for Regulatory Impact Analysis Under Executive Order 12866 (United States Government Interagency Working Group on Social Cost of Carbon, Washington, DC), 2010.

Vichkovitten, T. and Holmer, M. Contribution of plant carbohydrates to sedimentary carbon mineralization. Org. Geochem., 35(9):1053-1066, 2004.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C. and Olyarnik, S.: Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. USA, 106(30):12377-12381, 2009.

Wiles, P.J., van Duren, L.A., Hase, C., Larsen, J. and Simpson, J.H.: Stratification and mixing in the Limfjorden in relation to mussel culture. J. Mar. Syst., 60(1-2):129-143, 2006.

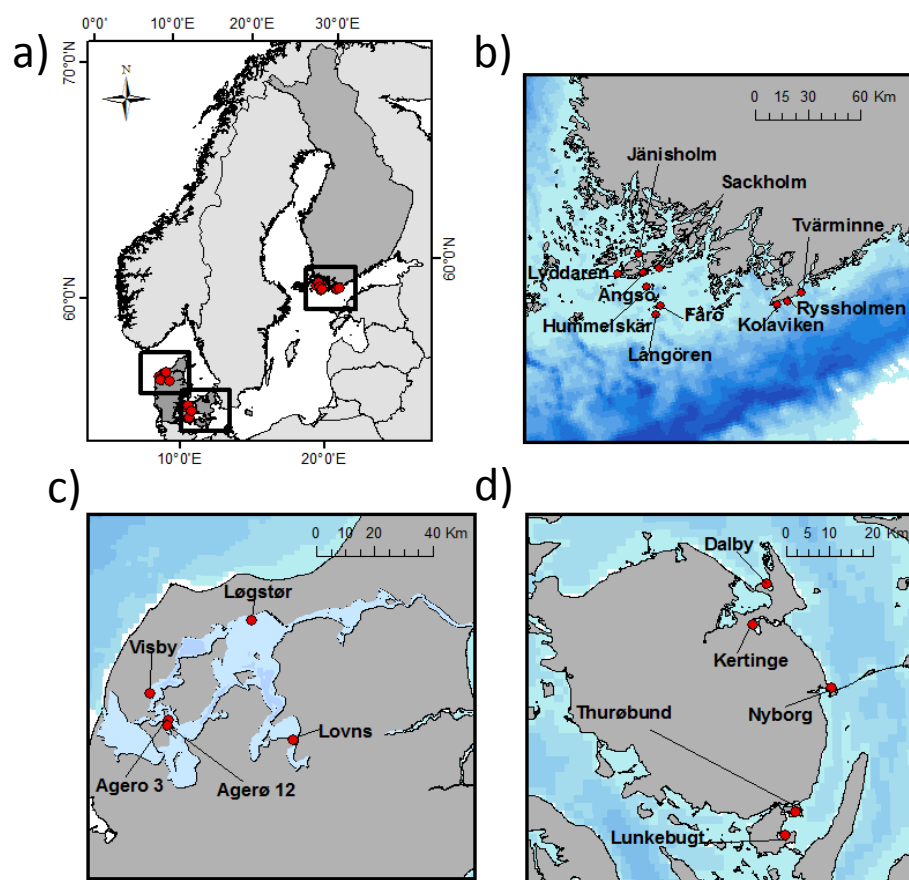
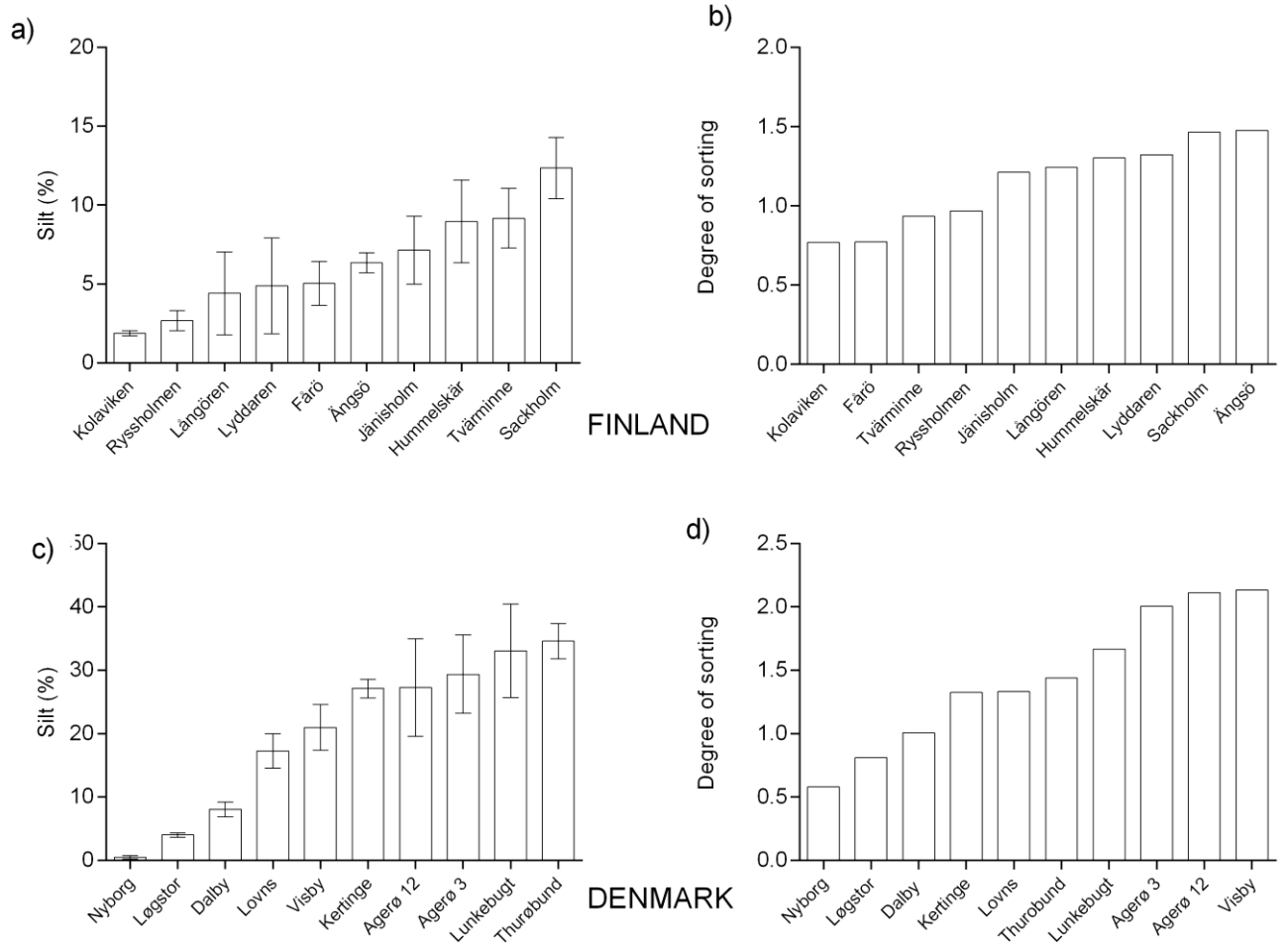
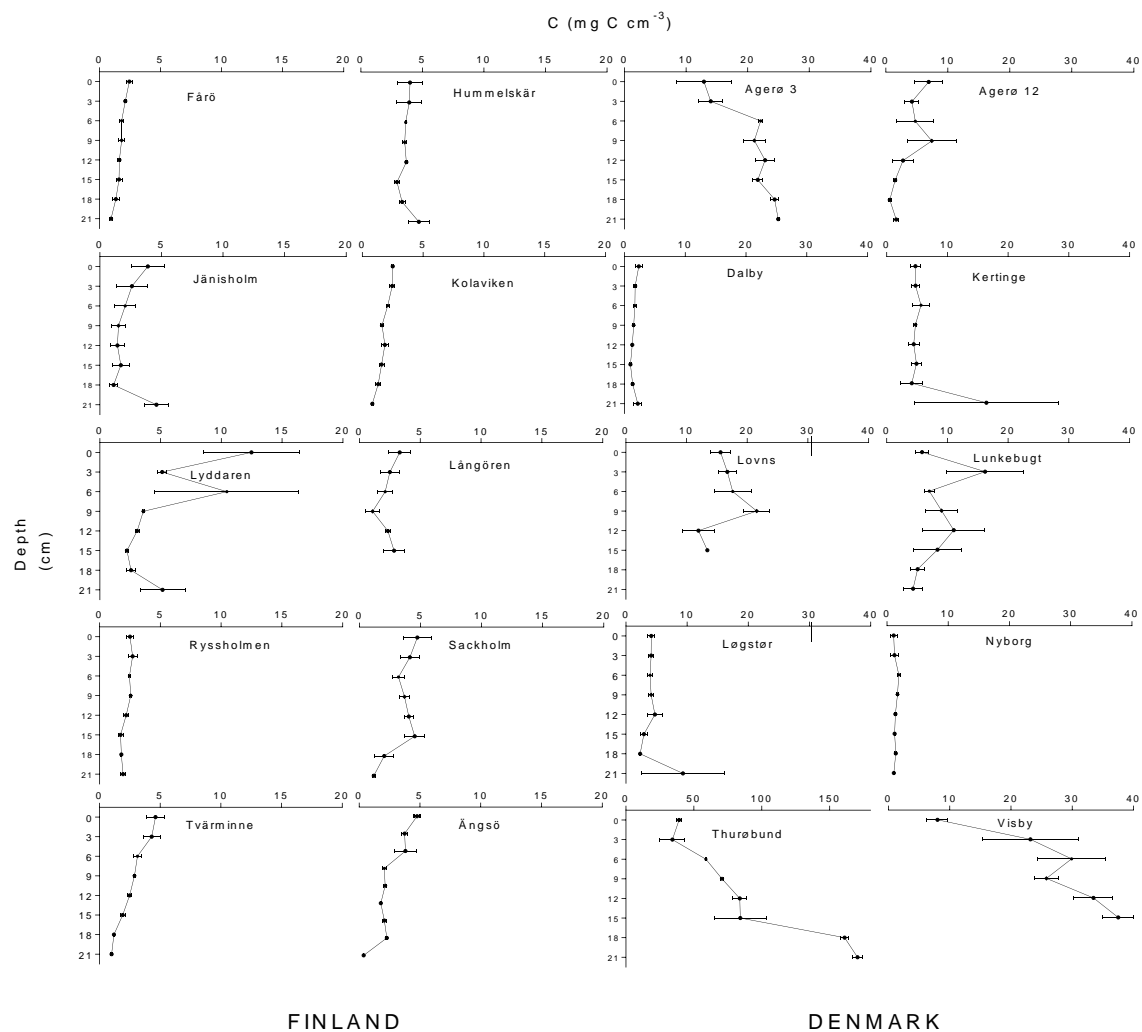
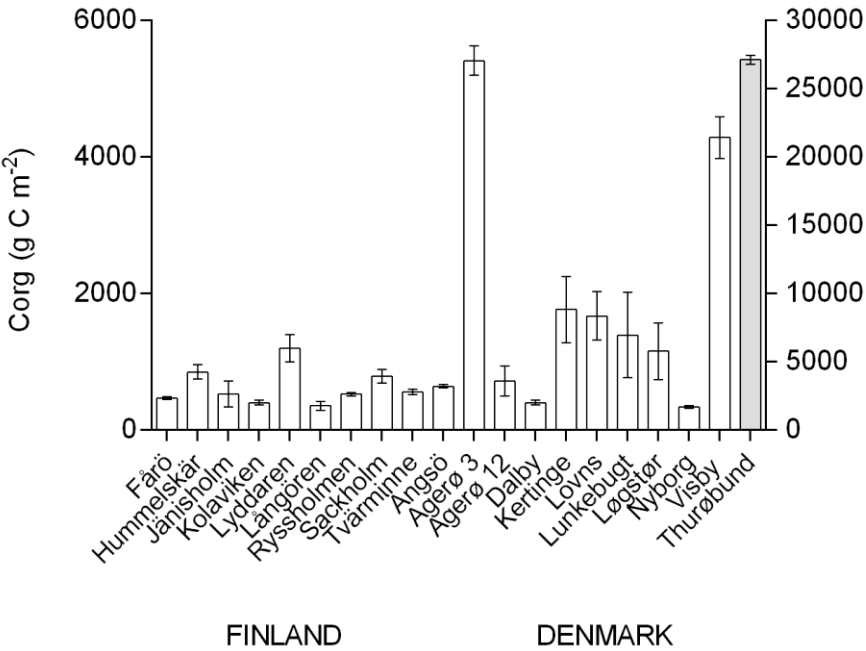



Fig. 1. The study sites in Denmark and Finland. a) study regions, b) Finnish study sites, c) Limfjorden study sites, d) Funen study sites.

675
676
677 Fig. 2. Silt content (%) (a, c) and degree of sediment sorting (b, d) at the study sites in Finland
678 and Denmark, respectively. Lower values in degree of sorting indicate well-sorted sediment
679 types.
680
681
682
683
684
685
686
687
688
689
690
691
692
693
694
695
696
697
698
699

C (mg C cm^{-3})

FINLAND   DENMARK

705 Fig. 3. Sediment profiles of organic carbon density (mg C cm^{-3}) in the top 25 cm of the Finnish
706 and Danish eelgrass (*Zostera marina*) meadows. Note the difference in the scale of x-axis
707 between the regions.

724
725
726

727
728
729
730 Fig. 4. Corg stocks (g C m⁻²) in the top 25 cm of sediment in Finnish and Danish eelgrass (*Zostera*
731 *marina*) meadows. Note that the value of Thurøbund (grey bar) corresponds to right y-axis.
732

733

734

735

736

737

738

739

740

741

742

743

744

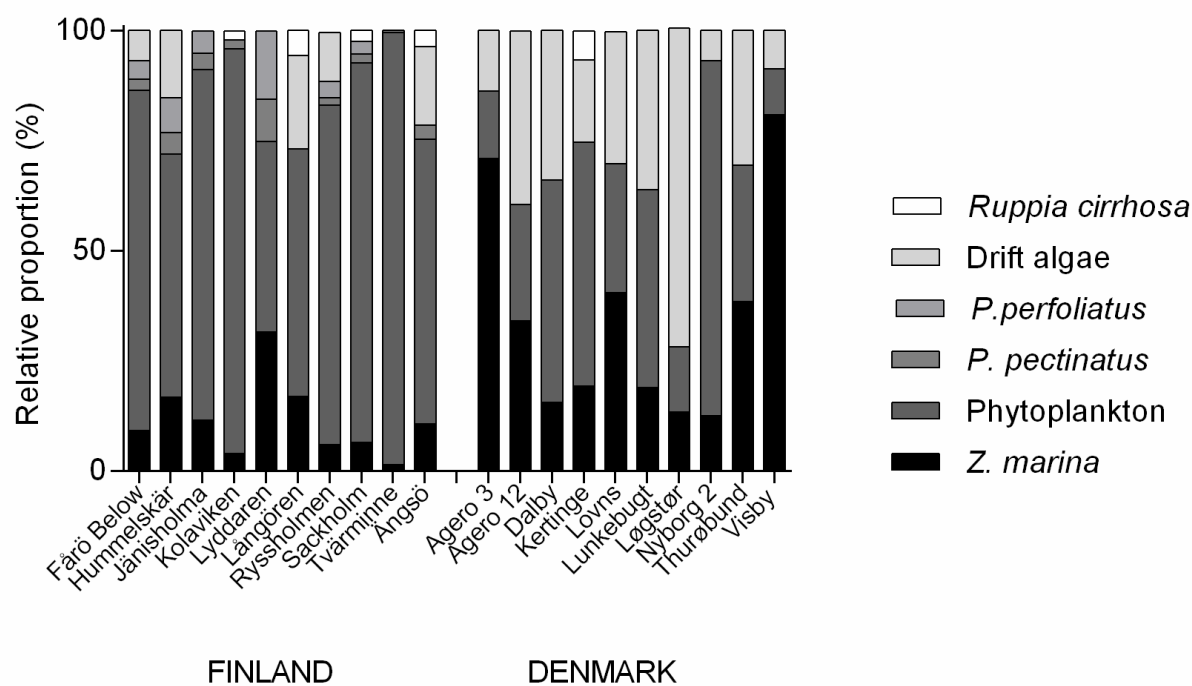
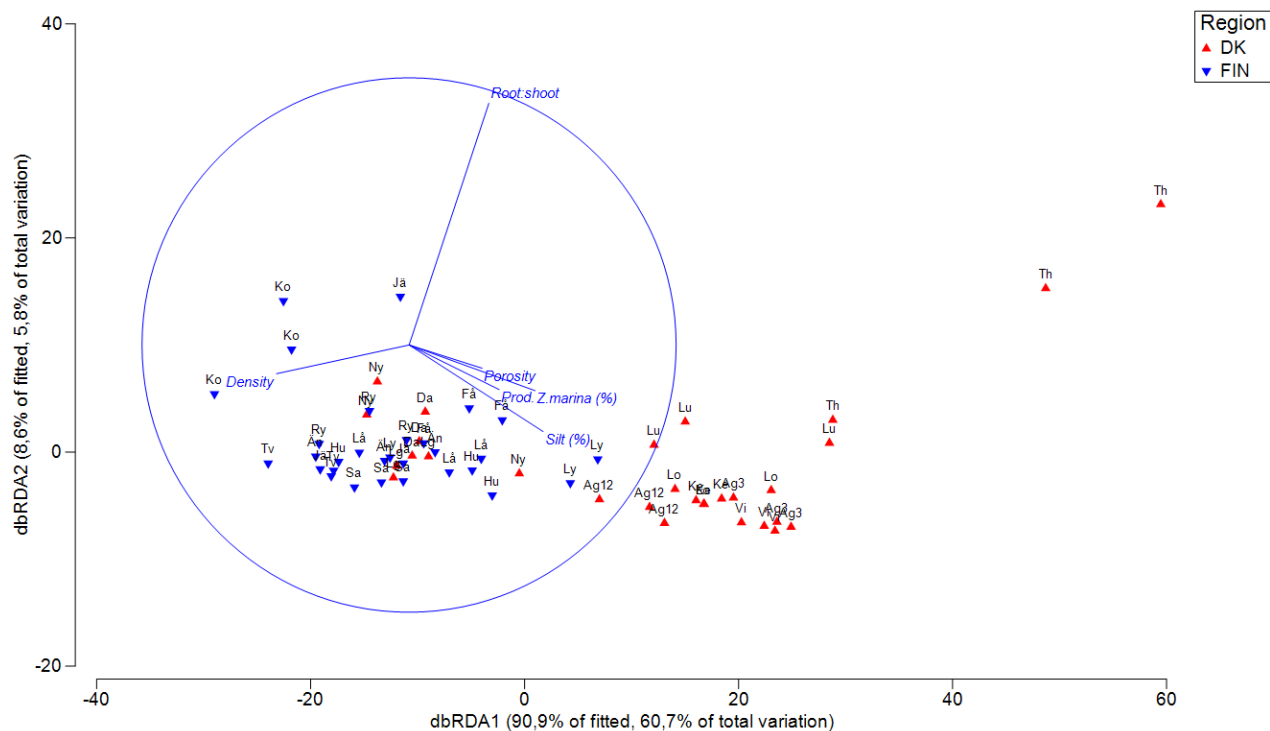
745

746
747 Fig. 5. Relative contribution of different organic matter sources (*Z. marina, P. perfoliatus, P.*
748 *pectinatus, Ruppia cirrhosa,* phytoplankton and drift algae) to the ^{13}C signal of the sediment
749 surface layer (0-2 cm) in Finnish and Danish eelgrass (*Z. marina*) meadows.
750
751
752
753
754
755
756
757
758
759
760
761
762
763
764
765
766
767
768
769
770
771
772
773

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

Table 1. Location, silt content (% silt),sediment dry density (Dry dens. g cm^{-3}), sediment organic carbon content (SedOC, % DW), sediment organic matter content (SedOM, %DW), δ13 C sediment surface, δ13 C *Z. marina* leaves, δ13 C *Z. marina* rhizomes, seagrass shoot density (Shoot dens.,shoots m^{-2}), seagrass above and belowground biomass (AB and BB, gDW m^{-2}), root:shoot-ratio (R:S), and aboveground production (Production, gDW m^{-2} y^{-1}) at the sampling sites. SE (n= 3–4) is given. Annual seagrass production is calculated from pooled values of replicates per site and therefore no SE is shown.

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

799

800 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
801 (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.
802 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
803 is used. n.d= no data. For calculations of annual carbon accumulation three different sediment accumulation rates were applied (0.32 mm y^{-1};
804 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
805 y^{-1} was used.
806

807

808

Region	Seagrass area (km^2)	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

809

810 Table 3. Table from DistLm analysis showing variables in the marginal tests and the results for
811 statistical analysis.
812

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

813

814

815

816

817

818

819

820

821

822

823

824

825

826

827

828

829

830

831

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

834

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		

835

836

837

838

839

840

841

842

843

844

845

846