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Distribution, structure and function of Nordic eelgrass (Zostera marina) ecosystems: implications for coastal management and conservation

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ABSTRACT

1. This paper focuses on the marine foundation eelgrass species, *Zostera marina*, along a gradient from the northern Baltic Sea to the north-east Atlantic. This vast region supports a minimum of $1480\,km^2$ eelgrass (maximum $>2100\,km^2$), which corresponds to more than four times the previously quantified area of eelgrass in Western Europe.

2. Eelgrass meadows in the low salinity Baltic Sea support the highest diversity (4–6 spp.) of angiosperms overall, but eelgrass productivity is low ($<2\,g\ dw\ m^{-2}\ d^{-1}$) and meadows are isolated and genetically impoverished. Higher salinity areas support monospecific meadows, with higher productivity (3–$10\,g\ dw\ m^{-2}\ d^{-1}$) and greater genetic connectivity. The salinity gradient further imposes functional differences in biodiversity and food webs, in particular a decline in number, but increase in biomass of mesograzers in the Baltic.

3. Significant declines in eelgrass depth limits and areal cover are documented, particularly in regions experiencing high human pressure. The failure of eelgrass to re-establish itself in affected areas, despite nutrient reductions and improved water quality, signals complex recovery trajectories and calls for much greater conservation effort to protect existing meadows.

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4. The knowledge base for Nordic eelgrass meadows is broad and sufficient to establish monitoring objectives across nine national borders. Nevertheless, ensuring awareness of their vulnerability remains challenging. Given the areal extent of Nordic eelgrass systems and the ecosystem services they provide, it is crucial to further develop incentives for protecting them.

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INTRODUCTION

Eelgrass meadows (here defined as a discrete continuous or patchy vegetated area ranging in size from approximately 0.0001 to >1 km^2) play a critical structural and functional role in many coastal ecosystems across the globe. Important ecosystem services for society include, for example, provision of nursery and feeding areas with high faunal diversity and production, primary productivity, nutrient recycling and carbon sequestration and storage (Duarte, 2002; Spalding *et al.*, 2003). Eelgrasses are also important indicator species because they are sensitive to eutrophication, and reflect and integrate water quality over longer time periods (Krause-Jensen *et al.*, 2008).

Threats to eelgrass ecosystems are both local and global. To a large extent they are driven by human-mediated factors such as overfishing, eutrophication and habitat destruction. In addition, they are also affected by biological factors such as disease and climate change factors such as heat waves, increased precipitation (with subsequent increases in floods), land run-off, altered turbidity and salinity (Short and Neckles, 1999; Orth *et al.*, 2006). Present worldwide estimates suggest a 30% reduction of areal cover over the past 30 years (Waycott *et al.*, 2009). In Scandinavia, large-scale losses have been recorded in Denmark since the 1900s, and case studies in west Sweden since the mid-1980s and in Poland point to local losses of 60 to 100% (Baden *et al.*, 2003; Boström *et al.*, 2003). The alarming rate of decline illustrates that eelgrass meadows are among the most threatened ecosystems on the planet (Orth *et al.*, 2006; Duarte, 2009; Waycott *et al.*, 2009).

Numerous studies have shown that good water quality is the most important factor needed for eelgrass sustainability as turbidity and high epiphyte loads can rapidly decimate meadows. Despite this knowledge, however, there are few demonstrations of seagrass recovery owing to improved physical and chemical conditions alone (Tomasko *et al.*, 2005). Case studies suggest that the relationship between changes in environmental conditions and ecosystem state is complex and often non-linear, and that the process of recovery is constrained by a combination of several factors (Duarte *et al.*, 2009; Krause-Jensen *et al.*, 2012). For example, the relative abundances of top predators, intermediate predators and mesograzers strongly mediate macroalgal blooms and influence eelgrass ecosystem structure and function (Valentine and Duffy, 2006). Nutrient enrichment, temperature and/or salinity are also factors influencing algal growth. Depending on their combination and strength, the coupling among stressors can lead to unexpected shifts in species interactions and energy flow pathways in seagrass ecosystems (Moksnes *et al.*, 2008; Baden *et al.*, 2010). Another factor with unknown interaction effects is the infection of seagrasses with potentially pathogenic endophytes (e.g. *Labyrinthula* sp., Bockelmann *et al.*, 2011). Thus, understanding the complex interplay between anthropogenic stress, environmental conditions, seagrass dynamics and the associated food webs constitute a major challenge for seagrass ecologists and coastal managers. Moreover, recent evidence for bottom-up and/or top-down control clearly highlights the importance of an ecosystem approach to understand and predict seagrass losses and recovery (Crowder and Norse, 2008).

In both science and management a more integrative understanding of stress responses in seagrasses over a range of geographic scales is needed. In both the narrow and broad contexts, biodiversity, plasticity and adaptive potential must

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be evaluated at hierarchically-linked levels including: individual populations of a species, i.e. the seagrass itself (as the habitat forming species and key primary producer); the community of associated flora and fauna (as players in the food web) and pathogens (as direct stressors); and the ecosystem. At all levels, abiotic stress factors including nutrients, salinity, light and temperature influence vital rates such as recruitment, growth and mortality. Consequently, to address ecosystem structure and functioning of seagrass communities in such a holistic context requires interdisciplinarity.

This review provides a first synthesis of Nordic seagrass ecosystems. Hierarchical and spatial complexity is addressed from the inner Baltic Sea to north-east Atlantic Scandinavia. Broad-scale distribution patterns are identified and analysed, and key features such as seagrass productivity and faunal diversity are compared across regions. The extent of long-term changes is demonstrated and loss-drivers are identified, i.e. environmental stressors causing declines (MEA, 2005). Specifically we provide:

1. a synopsis of published eelgrass work in the Nordic region for the period 1890–2010;
2. a presentation of the current distribution and a total cover estimate of eelgrass including an analysis of changes in plant and ecosystem traits along environmental gradients;
3. case studies that illustrate long-term dynamics and loss drivers of eelgrass;
4. a review and perspectus on the role of genetic biodiversity in the contexts of population connectivity and adaptive potential of eelgrass;
5. a comparison of the structure and function of associated food webs, with emphasis on fish and mesograzers.

The review is concluded with a discussion of the challenges faced in conservation of Nordic eelgrass systems and development recommendations for integrative research that will close identified gaps in our knowledge and provide the foundation for the development of long-term conservation measures.

STUDY AREA

The focus of this work is on eelgrass ecosystems along a >3000 km biogeographic gradient in the Baltic–Atlantic transition zone (Figure 1). The area extends from the brackish (<6 psu) archipelago areas of the northern Baltic Sea to the fully saline (>30 psu) Atlantic Norwegian coastline. The Baltic Sea is connected to the Atlantic via the Danish Straits and covers almost 400 000 km^2. With a catchment area of 1 700 000 km^2 and a population size of 85 million people, this enclosed area is heavily impacted by human pressures (Korpinen *et al.*, 2012). As this area is characterized by a number of physical, chemical, biological, and evolutionary gradients (Boström *et al.*, 2003; Johannesson and André, 2006, and references therein) and most coastlines support eelgrass meadows, it forms a unique arena for comparative studies of drivers of eelgrass growth, distribution and loss. Six subregions are identified and compared (Figure 1): 1. Atlantic (Norway), 2. Skagerrak (Norway, western Sweden), 3. Kattegat/Belt Sea (Denmark, western Sweden, north-eastern Germany), 4. southern Baltic Sea (north-eastern Germany, Poland, Lithuania), 5. Baltic Proper (eastern Sweden, Finland) and 6. north-eastern Baltic Sea (Estonia, Latvia). The division is based on expert opinions about similarities and differences in physical, chemical and biological features in the regions. In addition, a distribution map for Iceland is presented, but this region is not included in any other analysis. The distribution and role of eelgrass meadows in Iceland is poorly understood. The main threats to the meadows are landfill and road construction across fjords, and new initiatives for mapping and protecting Icelandic eelgrass are in preparation (R. Sigurdardottir, pers. comm.).

MATERIALS AND METHODS

Literature review

To obtain a comprehensive picture of the status and scope of Nordic eelgrass research and to identify knowledge gaps, peer-reviewed articles dealing with different aspects of the biology, ecology and distribution of eelgrass in the study region were surveyed and compiled. This was done primarily by utilizing authors' libraries, previous literature compilations (Baden and Boström, 2001; Boström *et al.*, 2003) and ISI Web of Knowledge

Figure 1. Study area and position of the six subregions compared. 1. Atlantic (Norway), 2. Skagerrak (Norway and western Sweden), 3. Kattegat/Belt Sea (Denmark and western Sweden, Germany), 4. southern Baltic Sea (Germany, Poland, Lithuania), 5. Baltic Proper (eastern Sweden and Finland), and 6. north-eastern Baltic Sea (Estonia, Latvia). Dashed lines indicate salinity isohalines. Numbered black circles (1–6) within regions 2, 3 and 5, indicate location of meadows included in the faunal study. A distribution map from Iceland is presented in Figure 4, but this region is not included in comparisons of the subregions.

(keywords; *Zostera marina*, Baltic Sea, Sweden, Denmark, Norway, Finland, Estonia, Germany, Poland). Unpublished information, thesis works and reports were included occasionally if no other information was available. The compiled list of papers is available as supplementary journal material and covers the time period 1890–2010 and seven countries (Denmark, Sweden, Germany, Norway, Finland, Estonia and Poland).

Hydrography

Secchi depths for all study areas originated from a data collection (Aarup, 2002) and was made available by the International Council for the Exploration of the Sea (ICES). The data collection of Aarup was further supplemented with more

recent data submitted to ICES Oceanographic Database and Services (ICES, 2010). Salinity and concentrations of nutrients and chlorophyll *a* for the North Sea (region 1) were extracted from ICES Oceanographic Database and Services (ICES, 2010). For the Baltic Sea (regions 2–6), the data were extracted from the Data Assimilation System (DAS) developed and hosted by the Baltic Nest Institute, Stockholm Resilience Centre, Stockholm University (Sokolov and Wulff, 2011). The oceanographic data were associated with the study areas by combining the positions of the measurements with an ESRI ArcGIS shape file containing the spatial definitions of the study areas, using the software package SAS/GRAF 9.2 (SAS Institute Inc., 2010). The data were limited to contain only measurements taken from the

upper 20 m of the water column. Mean, median, 10th and 90th percentiles of each parameter were then calculated for each of the study areas for the period 2005 to 2010, using the statistical software package SAS/STAT 9.2 (SAS Institute Inc., 2009).

Present and historical distribution of eelgrass

The eelgrass distribution data are the most complete data set compiled so far from this region, and is based on the available georeferenced findings of eelgrass in each study region. Sources include individual researcher observations and data available through research projects and national mapping and monitoring programmes. Recent data series on eelgrass depth limits are from the Danish Nationwide Aquatic Monitoring and Assessment Programme (DNAMAP) initiated in 1989 (http:// www.dmu.dk/en/water/marinemonitoring/mads/ macrovegetation/data/). The deepest observation of 10% cover along each depth gradient was computed using linear regression to interpolate this depth from the deepest observations of cover above and below 10%. Means were calculated for open coasts and fjords, which were grouped in exposed fjords and sheltered fjords (Hansen and Petersen, 2011).

Historical eelgrass data represent the period 1880–1930 with the densest representation of data around year 1900. Historical data originate from a wide range of sources which were recently compiled and analysed (Krause-Jensen and Rasmussen, 2009). The most complete historical study was the Danish nationwide survey of eelgrass depth distribution by Ostenfeld (1908). Other historical studies assessed eelgrass distribution in specific areas or focused on benthic fauna or macroalgae and only occasionally included observations of eelgrass. In the historical surveys, eelgrass was typically sampled from a ship using a grab or a dredge, and the surveys provide point observations of eelgrass presence/ absence at specific water depths. Here the deepest observations from a given area is used as an estimate of the depth limit (Krause-Jensen and Rasmussen, 2009, their category 1 data). As the historical methods were unlikely to identify individual eelgrass shoots and very sparse meadows, it was assumed that the deepest observations represent about 10% eelgrass cover. Historical eelgrass data were grouped in

'open coasts' and 'fjords'. The long-term monitoring of eelgrass in Norway consists of a series of beach seine hauls in association with studies of cod recruitment that started in 1919 and are still running. At present, ~130 beach seine stations are included in the sampling programme, 38 of which have been sampled since 1919. From 1933 onwards, observations on bottom flora by an aqua-scope were included (Johannessen *et al.*, 2011). In Germany, both mapping (aerial surveys 1994–1998, GPS surveys in 2003 and ongoing research, University of Kiel) and monitoring (EU-Water Framework Directive, WFD) data are available and the distribution of eelgrass is available both as polygon and point information.

Eelgrass meadow structure and productivity

Estimates of eelgrass above- and below-ground biomass, shoot density, leaf shoot growth and leaf biomass production rates at locations ranging in latitude from 54.08 to 63.35° N and in longitude from 6.58 to 25.28° E were compiled. Samples were collected within frames ranging in size from 0.025 to 0.25 m^2 with 3 to 10 replicates per meadow. The majority of studies only report above-ground biomass and shoot density and was only sampled once during the period of seasonal biomass maxima (July–September). For studies of seasonal biomass changes, the annual maxima were recorded. All data on daily eelgrass production were obtained with leaf marking techniques.

Eelgrass epifauna and fish

In order to describe the diversity and evaluate the role of fauna in Nordic eelgrass ecosystems, in particular the role of mesograzers and their link to higher trophic levels, literature values on the abundance and biomass of eelgrass epifauna and fish was compiled from six areas (Figure 1); Skagerrak: Jephson *et al.* (2008), Baden *et al.* (2012), Öresund North: Baden *et al.* (2012), Öresund South: Lundgren (2004), Jephson *et al.* (2008), Kiel Bight: Gohse-Reimann (2007), Bobsien (2006), Bobsien and Brendelberger (2006), Kalmar Sound: Jephson *et al.* (2008), Gulf of Finland: Boström, unpublished data. The average epifaunal biomass and abundance presented for each region represent

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the average of two separate meadows (n = 5–6 quantitative mesh bag samples per meadow), except for Kiel Bight, where the average represents replicate samples (n = 6) from a single meadow. The mesh size used was 200 μm, except for 250 μm in the Gulf of Finland and 355 μm in the Kiel Bight. However, as focus was on macrofauna, these minor differences are unlikely to influence comparisons of the large-scale abundance, biomass and diversity patterns found. To standardize and compare data sets, conversion of faunal dry weight (DW) to ash-free dry weight (AFDW) was carried out by using conversion factors for benthic invertebrates (Baden and Pihl, 1984; Rumohr *et al.*, 1987). To convert fish wet weight to AFDW, the wet weight was multiplied by a factor of 0.22 (S. Baden, unpublished). As seasonal changes in fish and epifaunal biomass, density and composition are substantial and vary greatly among regions, peak season values, i.e. August for each region are presented. This period represents the faunal post-settlement period with water temperatures of 18–22 °C and the highest eelgrass biomass in all study regions. The average eelgrass shoot density (shoots m^{-2}) and biomass (g DW m^{-2}) from the corresponding faunal survey are also provided. All faunal data are presented as number of individuals and biomass per unit area (m^2). Quantitative sampling of intermediate predatory fish (2–14 cm) in Skagerrak and Gulf of Finland was carried out using a beach seine (mesh size 5–10 mm, Baden *et al.*, 2012), while a diver-operated net bag on a circular frame (diameter: 30 cm, area: 0.07 cm^2) was used in Öresund N. An enclosure trap (6 mm mesh, 2 m^2) was used in S Öresund (Lundgren, 2004) and in the Kiel Bight (Bobsien, 2006).

Eelgrass genetics

Specific findings on eelgrass genetics are reviewed and compared with more global surveys that have been conducted for eelgrass. For readers unfamiliar with genetic data, an in-depth explanation of (1) the types, strengths and limitations of genetic data; (2) the types of questions that can be addressed; and (3) how genetic data are analysed and interpreted for eelgrasses (especially *Z. marina*) can be found in Procaccini *et al.* (2007).

Eelgrass management and conservation

To obtain an up-to-date picture of management and conservation strategies for eelgrass in the study area, the Nordic Seagrass Network (a 4-year research network funded by NordForsk 2010–2013), arranged a workshop for invited experts from each region (>50 academic scientists and managers/ governmental scientists), and the results of this workshop are described in the Discussion.

RESULTS

Present knowledge base: summary of published work

In total, 260 scientific publications of various aspects of the ecology and biology of eelgrass in the Nordic region were identified for the period 1890–2010 (Figure 2; Supplementary Material). In total, 31 papers were published during the first 79 year period (1890–1969), indicating an output of less than one (0.3) paper per year. Since the 1970s (1970–1979; 14 publications), there has been a doubling of seagrass publications each decade, peaking at 128 publications in the last decade (2000–2010, 12.8 papers per year). The analysis indicates a strong geographical bias with the majority of work deriving from Denmark – the country with the longest eelgrass research tradition in Scandinavia (Figure 2 (a)). The number of multi-authored papers resulting from joint projects peaked at 10 in the last decade, highlighting increased Nordic collaboration. The research areas differ markedly among countries analysed, indicating important areas of expertise as well as knowledge gaps (Figure 2(b)). For instance, plant biology has dominated Danish eelgrass research while the proportion of studies of eelgrass fauna is much higher in Sweden, Finland, Norway and Estonia. Eelgrass genetics has been a strong research area in Germany (49% of the published work) and 27% of the international collaborative studies have focused on eelgrass population genetics (Figure 2(b)).

Hydrographical gradients

The hydrographical conditions differ markedly among regions (Figure 3). In the outer regions (1–3, Figure 1), salinity decreases gradually from >30 psu
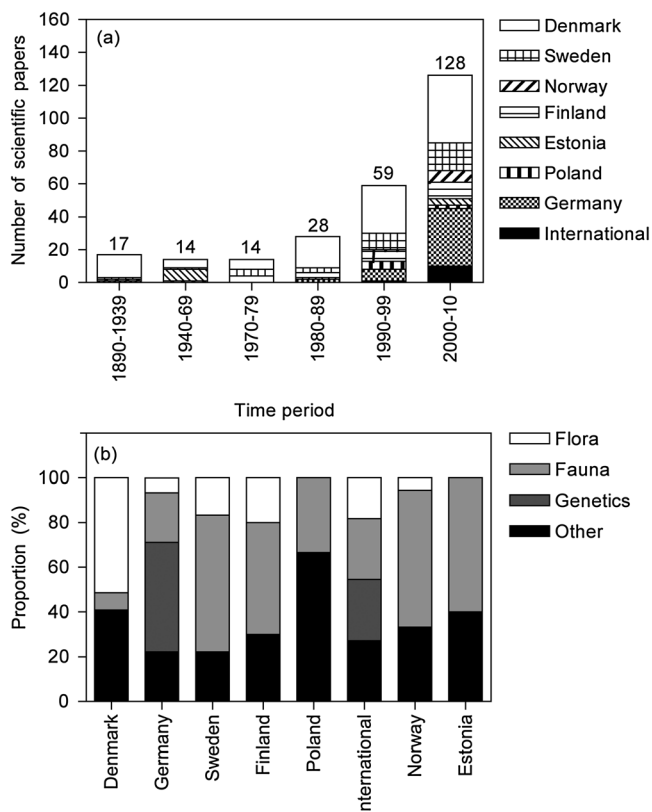
Figure 2. Number of peer reviewed scientific papers dealing with eelgrass ecology for the time period 1890–2010 by country (a) and by topic (b). In (a) international refers to multi-authored papers with contributions from more than a single country. The papers included in the analysis are presented in the Supplementary Material.

to around 20 psu when moving from the Atlantic Norwegian coast to Skagerrak and Kattegat. When entering the Baltic, salinity drops rapidly and values typically drop from 10 psu in region 4 (eastern Germany, Poland) to <7 psu along the Swedish east coast and the northern Baltic Sea (Figure 3(a)). In contrast, nutrient concentrations increase along the gradient, with Tot-N and Tot-P showing similar geographical trends (Figure 3(b), (c)). The most nutrient-rich areas are regions 3 (Kattegat, Kiel Bight, Öresund) and 6 (Estonia, Latvia). However, a large part of the nutrients in inner basins of the Baltic Sea represent riverine inputs of dissolved organic matter that are not bioavailable (Nausch and Nausch, 2011; Voss *et al.*, 2011). The degree of nutrient pollution is clearly reflected in higher pelagic productivity (Chl-*a*) and reduced water clarity (Secchi depth), the latter especially in the easternmost parts (region 6) of the Baltic Sea (Figure 3(d), (e)). In

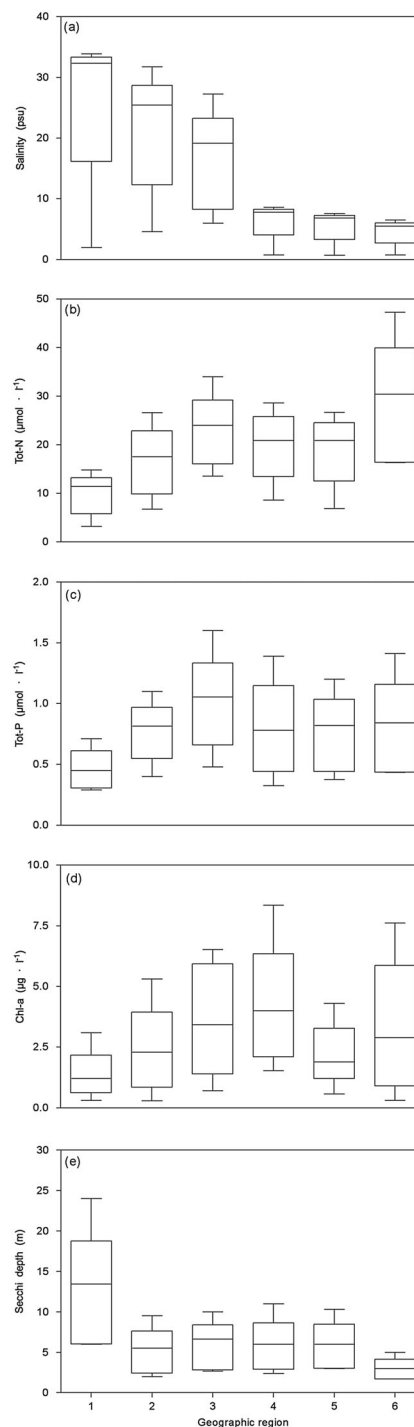
Figure 3. Box plots (median and 25th and 75th percentile) with whiskers (maximum and minimum) representing the hydrographical gradients in six subregions of the study area: (a) salinity, (b) total nitrogen, (c) total phosphorus, (d) chlorophyll-a, and (e) Secchi depth.

addition, hypoxia significantly increases inorganic phosphate concentrations in the Baltic Sea basin (Conley *et al.*, 2002).

Table 1. Number of eelgrass, *Zostera marina* records in the Baltic Sea region, the number of georeferenced, quantitatively mapped areas (polygons) and the estimated minimum total areal cover (km^2) in each geographic region. The analysis does not take into account differences in percentage cover and shoot density. For location of regions see Figure 1. For data sources and references, see Results

Region	Points	Polygons	Min. area (km^2)
1. Atlantic (W NOR)	299	299	18
2. Skagerrak (S NOR, W SWE)	3451	-	237
3. Kattegat, Belt Sea (W SWE, DEN, GER)	1665	566	920
4. Southern Baltic Sea (GER, POL)	19	23	57
5. Baltic Proper (E SWE, SW FIN)	1149	-	90
6. North Eastern Baltic Sea (EST)	273	-	155
7. Iceland	93		5?
Total	6949	888	1482

Eelgrass geographical distribution and coverage estimates

The total number of georeferenced records in Scandinavia, including Iceland, is 6949 (Table 1, Figure 4). Based on published data, information from national mapping programmes and expert opinions, the estimated minimum total coverage of eelgrass is at least 1460 km^2. This number is largely influenced by eelgrass area estimates from Denmark, which range from 673 to 1345 km^2, assuming they constitute 10 to 20% of the historical distribution, respectively. Thus, using the more optimistic estimate for Denmark (20% of the historical distribution), the total eelgrass area in Scandinavia exceeds 2100 km^2.

Region 1 – Atlantic

Eelgrass is found in all mapped counties along the Norwegian Atlantic coast i.e. Rogaland, Hordaland, northern and southern Trøndelag, Sogn og Fjordane, Nordland and Troms (Bekkby *et al.*, 2011, unpublished data from the national mapping programme, http://www.dirnat.no/kart/naturbase/). Eelgrass is also observed in the northernmost county, Finnmark (70.2°N, Knut Sivertsen pers. comm.). In Troms county (70°N), eelgrass meadows are found both within the subtidal and the intertidal zones (3 m tidal amplitude). The largest eelgrass meadow was found in Trøndelag (64°N, 0.8 km^2), with a total

of 90 mapped meadows covering an area >15 km^2. Meadow size in the counties in mid- and northern Norway varies on average between 0.018 and 0.23 km^2 (Bekkby *et al.*, 2008). Further south around Bergen, 96 eelgrass meadows have been mapped (size range 0.03–0.04 km^2). The deepest record of *Z. marina* is 13 m in Rogaland (national mapping programme in 2011, unpublished data).

Region 2 – Skagerrak

The total number of mapped eelgrass meadows in southern Norway exceeds 3300 meadows, with a total cover of 50.3 km^2 (http://www.dirnat.no/kart/naturbase/). The average meadow size is 0.0152 km^2 (range 0.000085–1.1 km^2). *Zostera noltii* has been recorded at three localities in the Oslofjord (Lundberg, 2009). Along the Norwegian and the Swedish Skagerrak eelgrass is found in exposed sandy areas as well as in sheltered bays with high sediment organic content (Naturbase, http://dnweb12.dirnat.no/nbinnsyn/, Baden and Boström, 2001). The total area of eelgrass in this region is estimated at 134 km^2 (Stål and Pihl, 2007).

Region 3 – Kattegat, Belt Sea

This region comprises the coastal areas of south-western Sweden, Denmark and Germany. Most of the Swedish records (358) are from the Malmö/Öresund (the Sound) region and are included in the eelgrass area estimate for the combined Danish and Swedish Öresund region (below).

In Denmark, eelgrass is found in both inner fjords and along moderately exposed coasts as documented by observations from 1189 monitoring sites, but is lacking from the exposed North Sea coast (Figure 4, data from the Danish national marine database MADS). The total eelgrass area in Denmark has not been measured. However, estimates from a subset of 20 coastal water bodies, including those with the largest eelgrass meadows of the country, add up to 496–573 km^2 over the period 1994 and 2005, so this is a minimum estimate of the distribution. These surveys were conducted by local environmental authorities based on aerial photography and/or diver observations. The most extensive eelgrass areas were found in the Archipelago of southern Funen (179.3 km^2),

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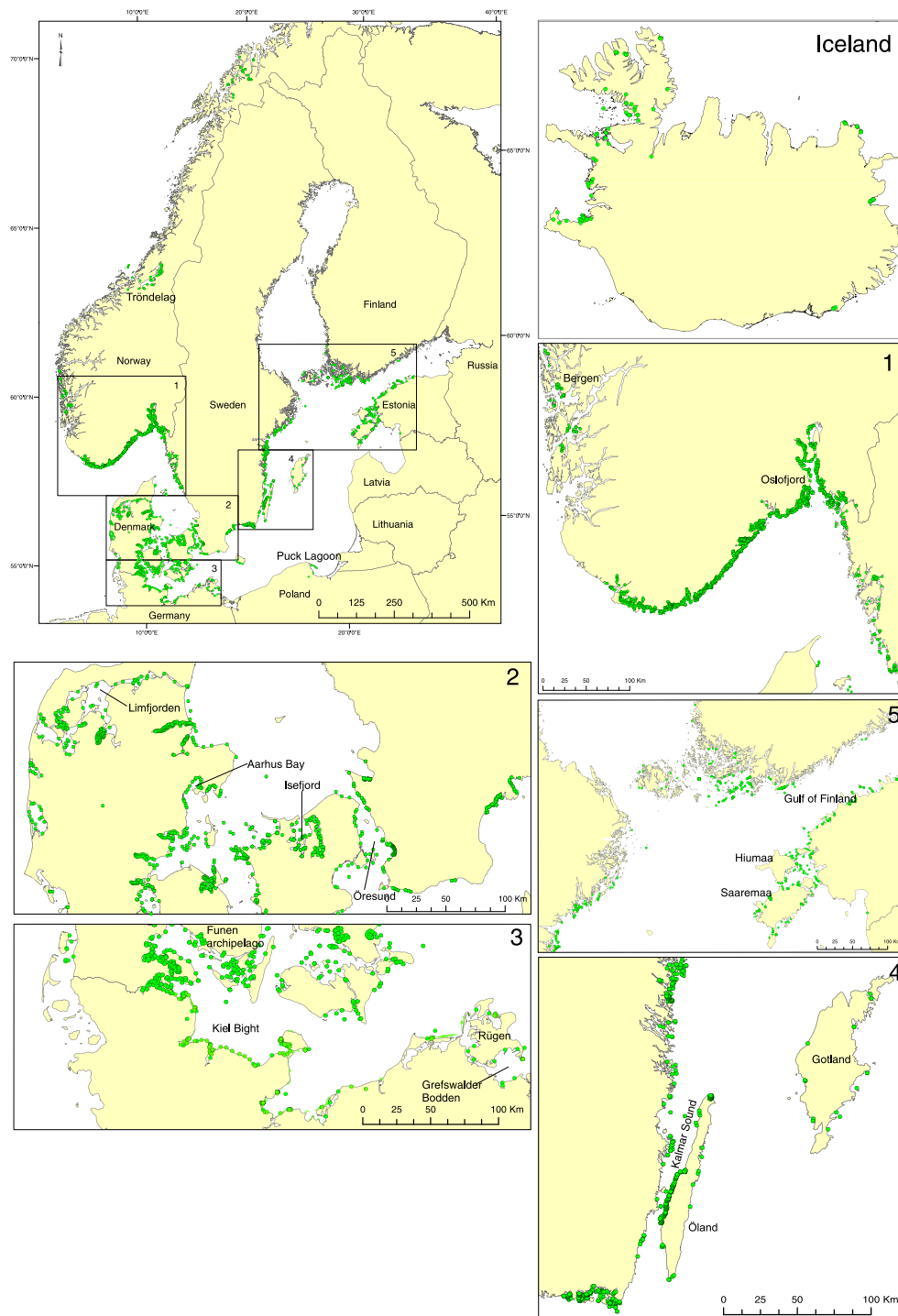
Figure 4. Distribution of *Z. marina* in Scandinavia with enlargements (1–5) of the main distribution areas including Iceland.

Öresund (162 km^2), Limfjorden (95 km^2 in 1994 and 18 km^2 in 1998/99), Isefjord (31 km^2), Kalundborg Fjord/Sejerø Bay (24.9 km^2), Flensborg Fjord (16.2 km^2) and Aarhus Bay (13.9 km^2). The Danish

eelgrass area around year 1900 was roughly estimated at 6726 km^2 (Petersen, 1914) and comparisons between historical and recent maps from two key eelgrass areas, Öresund and

Limfjorden, suggest that the present meadows constitute only 20–25% (Boström *et al.*, 2003), and as little as 5% if based on the 1998/1999 eelgrass estimate for Limfjorden. Methodological differences imply considerable inaccuracy in the estimates, but if such changes are general for Danish eelgrass meadows then the actual distribution area represents only 10–20% of the historical area and the present eelgrass area could be in the range of 673 km^2 (10% of 1900 area) to 1345 km^2 (20% of 1900 area).

In Germany, eelgrass is common on sandy bottoms along the entire coast. In addition, *Z. noltii* has been recorded at 20 sites. At sheltered locations, i.e. lagoons, fjords, and bays with salinities >12 psu, *Z. marina* and *Z. noltii* co-occur, but inhabit different depths with *Z. noltii* usually inhabiting the shallow (<1 m) littoral zone. Multispecies meadows of *Z. marina* and *Zannichellia palustris*, *Potamogeton pectinatus* and *Ruppia* spp. are common between 8–10 and 18 psu (Jegzentis, 2005; K. Fürhaupter, pers. comm.). The total number of eelgrass polygons is 589 with a total area of 146.5 km^2. The data set is further divided into five classes based on percentage eelgrass cover with most meadows (n = 337, total area 102.5 km^2) within the 25–50% cover class. The most dense meadows (75–100% cover) comprise 130 meadows with a total area of 7.4 km^2. Additional eelgrass records include EU-WFD monitoring stations of eelgrass depth limits (n = 72), and the whole coastline of Schleswig-Holstein (400 km of coast surveyed systematically) with a total minimum cover of 80 km^2 (P. Schubert, in prep.).

Region 4 – southern Baltic

This region comprises the eastern, brackish water areas of Germany around the Island of Rügen and the Greifswalder Bodden estuary, and the Polish coast including Puck Lagoon. Here and particularly further north (regions 4–6), eelgrass meadows typically contain 1–5 plant species of freshwater origin, e.g. *Potamogeton* spp., *Zannichellia* spp., *Ruppia* spp. (Kautsky, 1991; Selig *et al.*, 2007; Salo *et al.*, 2009). The total area of mapped eelgrass around Rügen is about 9 km^2 (T. Meyer, T. Berg, K. Fürhaupter and H. Wilken unpubl. data). The Baltic coast of Poland is devoid of eelgrass owing to exposure but the sheltered Puck Lagoon supports today about 48 km^2 of eelgrass (J-M Weslawski, pers.comm.).

Region 5 – Baltic proper

Eelgrass is common along the east coast of Sweden, including the islands of Öland and Gotland (919 records). Eelgrass meadows are also found in the archipelago areas of Åland Islands and SW Finland (232 records). The northernmost record of eelgrass in the Baltic is in the Rauma archipelago, Finland (61°3.1'N, 21°19.1'E, 5.6 psu, H. Rinne pers. comm.). The estimated area of eelgrass along the Swedish east coast is 60–130 km^2 (S. Tobiasson, pers. comm., Boström *et al.*, 2003) and 30 km^2 in Finland (C. Boström, unpublished data).

Region 6 – north-eastern Baltic

Eelgrass has been recorded on 273 stations along the Estonian coast and around the islands of Hiiumaa and Saaremaa. This region is characterized by vast areas of shallow (<10 m), sandy habitats with moderate wave exposure, which appears to be optimal for eelgrass. Eelgrass grows in patchy mixed meadows often together with *Potamogeton* spp. and *Zannichellia palustris* with the deepest records at 9 m depth (Möller and Martin, 2007 and references therein). Based on presence data and predictive modelling using 13 environmental variables, the total estimated minimum cover of eelgrass in Estonian waters is 155 km^2 (T. Möller, unpublished data, Estonian Marine Institute database).

Iceland

The present distribution map of eelgrass around Iceland contains 95 records, but is mostly based on historical records, with about half of the observations dated from the period 1820–1940. Thus, many positions may have a large error (500–5000 m) and a more detailed mapping programme is under preparation (R. Sigurdardottir, pers. comm.).

Eelgrass plant variables

Meadow structure; shoot density and biomass

Shoot density at the time of maximum above-ground biomass is highly variable (72–3948 shoots m^{-2}),

but does not show significant differences between regions (Kruskal–Wallis test, $P = 0.0896$) (Figure 5(a)). Part of the large variability in shoot density is explained by differences in water depth (0.7–4.0 m) among sampled meadows. Hence, shoot density is generally highest in shallow water and decreases exponentially with depth: shoot density = 1788 * exp(-0.627 m) ($r^2 = 0.3777$, n = 50). An additional large data set from Öresund further highlights that eelgrass meadows from this area are very dense, reaching 2000 shoots m^{-2} in the shallow water and declining towards deeper waters (Krause-Jensen *et al.*, 2000). There is no significant relationship ($r^2 = 0.001$, n = 37) between salinity (5.2–26 psu) and shoot density. Shoot density and above-ground biomass are significantly correlated ($r^2 = 0.4179$, n = 58), as described by the equation: above-ground biomass = 1.06* shoot density$^{0.72}$, suggesting biomass increases with shoot density. The relation between shoot density and biomass is, however, variable and for a given shoot density there is a wide range of biomass values. Accordingly, shoot weight is highly variable (range 0.024–0.834 g dw shoot^{-1}) and differs significantly between regions (Kruskal–Wallis test, $P \ll 0,001$, Figure 5(c)). Meadows in the inner Baltic region, characterized by sparse above-ground biomass, tend to develop small shoots compared with those in the Skagerrak and the Kattegat/Belt Sea region, where shoots are generally larger. The density of flowering eelgrass shoots has only been recorded from populations along the coastal areas of Denmark and Germany. The flowering frequencies range from 0 to 48.8% of total shoot density (n = 17). In the northern Baltic Sea (region 5), flowering shoots are rare and seeds do not ripen during the season (Boström *et al.*, 2004).
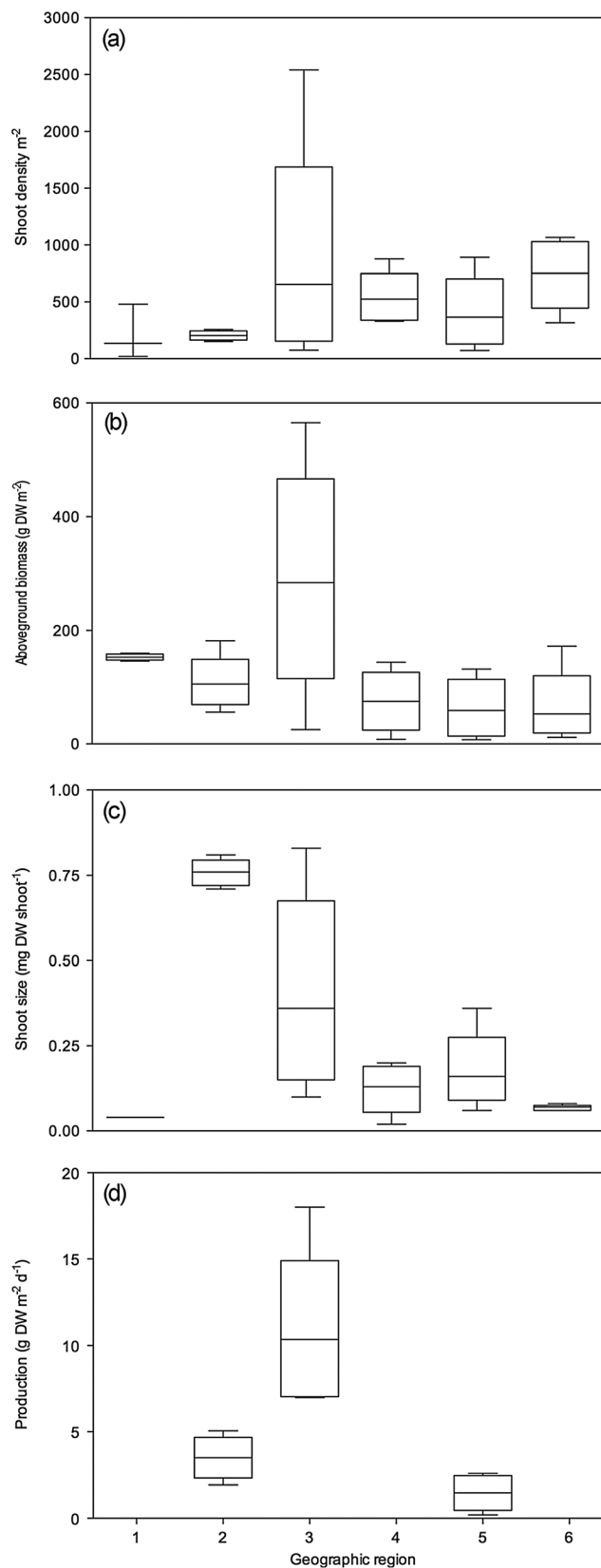

Figure 5. Box plots (median and 25th and 75th percentile) with whiskers (maximum and minimum) representing eelgrass characteristics in the study area. Eelgrass characteristics under different environmental settings in the six subregions of the study area. (a) shoot density, (b) above-ground biomass, (c) shoot size, and (d) production. Data sources: Region 1: Duarte *et al.*, 2002; Sivertsen, 2004, Region 2: Sivertsen, 2004; Holmer *et al.*, 2009, Region 3: Olesen and Sand-Jensen, 1994 and references therein; Reusch and Chapman, 1995; Dist_Stat Data Maasholm, 2001; Jegzentis, 2005; Reusch *et al.*, 2005; National Monitoring Programme, Limfjorden, Denmark 1989–2005; Toxicon, 2009; Gohse-Reimann, 2007, Region 4: Jegzentis, 2005; Bobsien, 2006, Region 5: Boström *et al.*, 2004, 2006; Holmer *et al.*, 2009, Region 6: Möller, 2007; Möller and Martin, 2007, University of Tartu, Estonian Marine Institute database (unpubl.).

The median above-ground biomass differed significantly among regions (Kruskal–Wallis test, $P < 0.001$, n = 173) with the highest biomasses found in the Kattegat/Belt Sea region (median = 281.6 g dw m^{-2}, n = 86) and the lowest (medians 37.0–72.7 g dw m^{-2}, n = 55) in the central and inner Baltic regions (Figure 5(b)). Estimates of below-ground biomass were only available for three of the six geographic regions. The above-ground biomass was strongly related to below-ground biomass (r^2 = 0.655, n = 26) indicating a rather uniform allocation to rhizome and root biomass relative to leaf biomass among meadows. The ratio of above- to below-ground biomass was highly variable among meadows (range 0.5–7.1) but did not differ significantly among regions (Kruskal–Wallis test, $P = 0.2114$). The total biomass ranged from 16 to 715 g dw m^{-2}, with the densest meadows in the Kattegat/Belt Sea area (Figure 5(b)).

Productivity

The maximum biomass production (measured in June–September) reaches 10.3 g dw m^{-2} d^{-1} (median, n = 5) in the Kattegat/Belt region and is much higher than in the Skagerrak region (3.5 g dw m^{-2} d^{-1}, n = 2) and the Baltic proper (1.5 g dw m^{-2} d^{-1}, n = 6). Leaf plastochrone intervals during summer months, ranging from 5.8 to 11.3 days leaf^{-1}, are independent of geographic region ($P = 0.672$, n = 13). The differences in biomass production among regions are, therefore, independent of leaf formation rates ($R^2 = 0.0227$, n = 13) and linked to higher shoot density and shoot size in the more productive meadows.

Genotypic diversity

Only a few regions in Scandinavia have been genetically surveyed and all of these studies have been based on microsatellite loci. Allelic diversity – a measure of standing genetic variation and potential for adaptation – in the North Atlantic (along the Norwegian coast) and North Sea (Dutch, German, Danish Wadden Sea) is high, followed by a steady decrease from the North Sea into the Skagerrak, Kattegat and central/inner Baltic Sea (Reusch et al., 2000; Olsen et al., 2004). Lower species diversity is typical of the Baltic

Sea as is lower genetic diversity within each species (Johannesson and André, 2006). Allelic diversity is a gauge of genetic adaptive potential and is strongly affected by effective population size. Genotypic diversity (also called clonal diversity) is mixed throughout regions 1–3. The presence of large and old (800–1600 years) clones, increases in region 5, particularly in the Finnish Archipelago (Reusch et al., 1999). Dominance by a few large clones is also characteristic of isolated lagoons and fjords in region 3, (e.g. Limfjorden, Denmark; Ferber et al., 2008). Clonal diversity reflects meadow architecture, its relative longevity and stability as a consequence of vegetative spread vs. recruitment of new individuals. Little is known about regions 4 and 6 although unpublished results suggest low clonal diversity in lagoonal areas, e.g. around Gdansk. Successful dispersal of plants and/or seeds is a prerequisite to gene flow and population connectivity, but this is poorly understood in the study area. Eelgrass populations along the Swedish east coast show moderate isolation by distance, while no isolation by distance has been recorded along the Swedish west coast (B. Källström and C. André, unpubl). The strongest isolation is at the northern limit of distribution in region 5, i.e. Åland Islands and in the Archipelago Sea, SW Finland (Olsen et al., 2004). Eelgrass populations along the Norwegian coast (region 1) show high genotypic diversity but strong isolation by distance (Olsen et al., 2013).

Long-term changes in depth limits and coverage

Regions 1 and 2: Norway and Swedish west coast

In Norway, eelgrass coverage was low in Skagerrak (c. 10%) in the 1930s owing to decimation of eelgrass by the wasting disease, but recovered in the 1950s and 1960s and, except for a temporary decrease in the late 1980s, has remained high (c. 40% cover) until the present (Johannessen et al., 2011). In contrast, the areal extent of eelgrass along the Swedish Skagerrak coast has declined by 60% since the mid-1980s. Although the distribution may vary inter-annually by about 5%, a large-scale long-term decline has been confirmed (Baden et al., 2003; Nyqvist et al., 2009).

Regions 3 and 4: Denmark, Germany and Poland

Eelgrass depth limits in Danish coastal waters have declined markedly from around year 1900 to the recent decades (Figure 6). Along open coasts, the average depth limit was 7 m over the period 1880–1930 as opposed to only 4.3–5.4 m in the period 1989–2010. In the fjords, depth limits averaged 6.5 m over the period 1880–1930 as opposed to 3.1–4.1 in outer fjords, 2.6–3.3 in inner fjords and 1.8–3.3 in Limfjorden in 1989–2010. A major decline in eelgrass distribution occurred in the 1930s caused by the wasting disease (Rasmussen, 1977). Scarce data from the following decades indicated that eelgrass had returned in several areas, particularly through the 1960s and 1970s (Rasmussen, 1977; Frederiksen *et al.*, 2004; Krause-Jensen and Rasmussen, 2009), but no nationwide surveys were available until the national monitoring started in 1989 in response to marked eutrophication effects (Hansen and Petersen, 2011). It is therefore unknown to what extent eelgrass had regained the historical depth distribution before it again declined owing to eutrophication. Over recent decad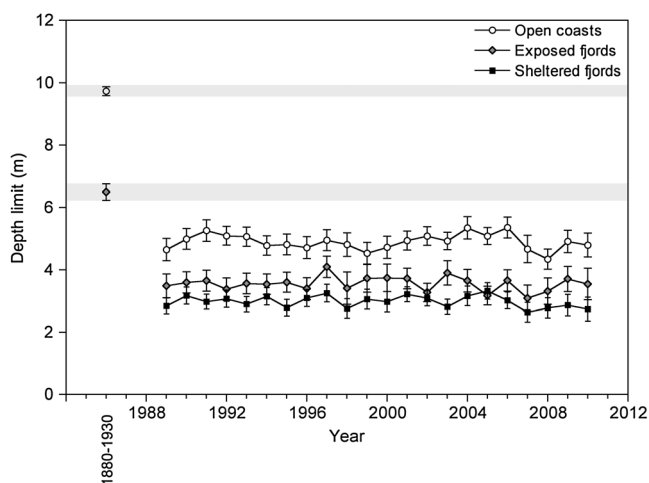es, nutrient loads have been reduced markedly, but neither water clarity nor eelgrass depth limits have yet shown marked positive responses (Hansen and Petersen, 2011).

A decrease in depth limit and thus a reduction in area cover of eelgrass, has occurred along the German Baltic coast. Historical records indicate that dense *Z. marina* meadows commonly occurred down to 8–10 m (maximum 17 m) depth (Reinke, 1889), while the present depth distribution is typically 4–5 m (Meyer and Nehring, 2006; Selig *et al.*, 2007). In the Greifswalder Bodden estuary, dense mixed *P. pectinatus/Z. marina* meadows covered the sea floor in the 1930s and also in the 1950s, but from 1950 to 1980 eutrophication caused a phase shift in terms of increasing phytoplankton biomass followed by a decline in macrophyte cover from 90% to 15% and a decline in depth limits from 14 m to 6 m. In spite of marked reductions in nutrient loadings since 1985, resulting in a 50% decrease in phosphate concentration and a 40% decrease in nitrogen concentration, water quality and macrophyte cover have not improved (Schramm, 1996; Munkes, 2005). Records from the 1930s for the sheltered Schlei fjord also show that *Z. marina* was distributed along at least half of the overall fjord length, whereas since the 1970s eutrophication has constrained the distribution to the outer 10% of the fjord (Meyer *et al.*, 2005). Additional historical records also indicate that *Z. marina* colonized low saline (5–6 psu) estuaries, while the present distribution is restricted to more saline areas which are far less affected by eutrophication (Blümel *et al.*, 2002; K. Führhaupter and H. Schubert, pers. comm.). Further east, along the Polish coast, *Z. marina* is absent owing to exposure and its main distribution in Poland is concentrated to the Puck Bay. Here eelgrass has been increasing since the 1990s, but the present cover (48 km^2) is very patchy and only represents a small fraction of its extensive historical distribution in the Bay (Kruk-Dowgiallo, 1991; Boström *et al.*, 2003).

Figure 6. Temporal development in eelgrass depth limits in Danish coastal waters. Historical data represent means (± s.e.) of all observations along open coasts (n = 232) and fjords (inner, outer and Limfjorden all together, n = 75) for the period 1880–1930 (Krause-Jensen and Rasmussen, 2009). Data from 1989 to 2009 are nationwide means of deepest observations of 10% eelgrass cover in fjords and open coasts as compiled under the Danish national monitoring and assessment programme and modelled by generalized linear models (Hansen and Petersen, 2011).

Eelgrass epifauna and food web structure

The shoot density of the meadows included in the faunal survey was higher in the Baltic than in the N Öresund, S Öresund and Skagerrak. However, as shoot density is a function of the local (site-specific)

exposure regime (Baden and Pihl, 1984), the meadow structure of the faunal survey sites does not fully reflect the overall pattern found (Figure 7(a)). The mean eelgrass biomass of the sites was 58 g DW m^{-2} (range; 30–120 g DW m^{-2}) while the mean shoot density was 416 shoots m^{-2} (range 200–900 shoots m^{-2}, Table 2). The site in S Öresund represents an extreme in terms of exposure and shoot density (>1000 shoots m^{-2}), while the German site in the Kiel Bight (Falkenstein) exhibited the highest eelgrass biomass (120 g DW m^{-2}).

A marked increase in the number and biomass of crustacean mesograzers >7 mm (mainly Gammarids and Idoteids) was identified when moving from the Swedish Skagerrak coast (0 ind m^{-2}) to the Gulf of Finland (895 ind m^{-2}) whereas the opposite was documented for crustacean grazers <7 mm (mainly small amphipod species <3 mm) with average densities >16 000 ind m^{-2} in the Skagerrak meadows compared with densities of 300 and 3000 ind m^{-2} in Kalmar Sound and Gulf of Finland, respectively (Table 2, Figure 7(b)). The total crustacean biomass was five times higher (2.4 g AFDW m^{-2}) at the low saline Finnish sites compared with the very low biomasses

(0.7 and 0.4 g DW m^{-2}) in Skagerrak and N Öresund, respectively. This contrasting biomass-abundance pattern is explained by a shift in body size in the crustacean grazer assemblage (Figure 7(c)).

Gastropod grazers appeared to be of minor importance in the Skagerrak and Öresund eelgrass meadows, with a contribution to the total abundance and biomass of 15% and 6%, respectively (Figure 7(d)). In contrast, in S Öresund, Kiel Bight and Kalmar Sound, gastropods constituted 50–75% of the total abundance, and in terms of biomass the relative importance of gastropod grazers increased from S Öresund (6%) to Kiel Bight (46%, mainly *Rissoa membranacea* and *Littorina littorea*) and Kalmar Sound (75%, mainly *Theodoxus fluviatilis*, *Hydrobia* spp., and *Rissoa* spp.). With the increasing importance of gastropods, there was a consequent decrease in the proportion of omnivorous crustaceans which constituted 70, 40 and 10% of the total epifaunal biomass in S Öresund, Kiel Bight and Kalmar Sound, respectively, (Figure 7(d)).

Quantitative data on top predatory fish are lacking from most regions, except Skagerrak, while
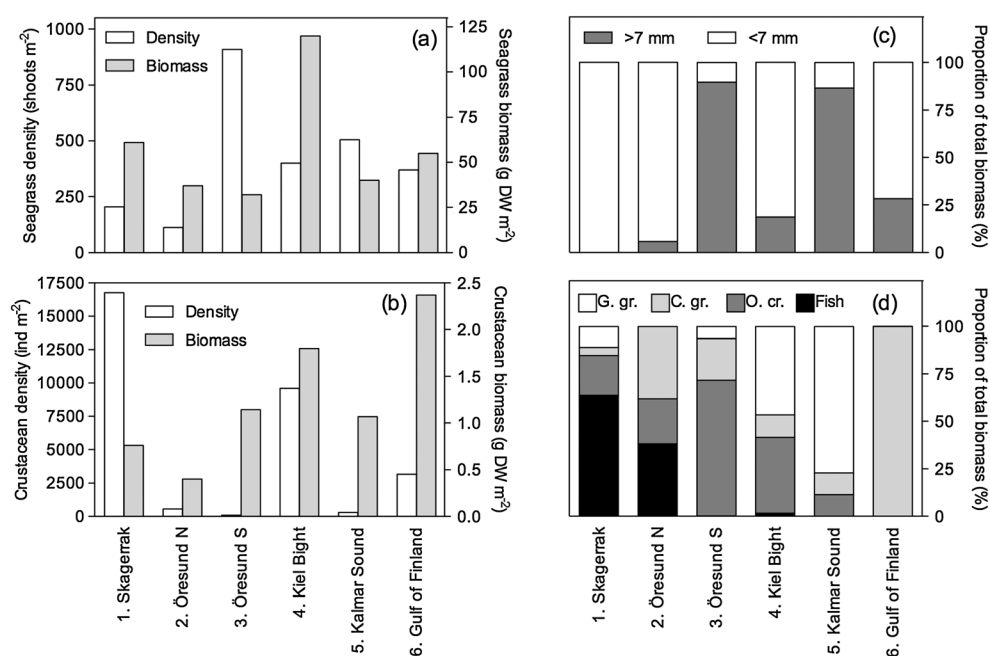
Figure 7. Plant and animal characteristics at selected study sites. For location of sites see Figure 1. (a) Habitat complexity in terms of shoot density and biomass of the faunal survey meadows, (b) crustacean grazers (both mesograzers >7 mm and grazers >7 mm) density and biomass, (c) body size distribution of crustacean mesograzers, and (d) relative biomass contribution (%) of different taxa to total biomass of epifauna and fish; G. gr. = gastropod grazers, C. gr. = crustacean grazers, O. cr. = omnivorous crustaceans.

Table 2. Summary of the trophic structure and main epifaunal groups in eelgrass meadows in the Nordic region. All samples represent late summer (August) values. Abund. = number of individuals m^{-2}, Biom. = biomass g AFDW m^{-2}. Crustacean/gastropod spp. refers to the total number of crustacean and gastropod species, respectively. Seagrass abundance refers to shoot density m^{-2} and biomass to g DW m^{-2} at the faunal survey site. - no data. See Figure 7 for a summary of abundance and biomass data. Data sources are provided in Materials and Methods

	Skagerrak		Öresund N		Öresund S		Kiel Bight		Kalmar Sound		Gulf of Finland	
Trophic group	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.	Abund.	Biom.
Top predatory fish	0.0017	0.022	-	-	-	-	-	-	-	-	-	-
Intermediate predatory fish	32	11.44	1.4	0.4	1.2	0.07	3	0.48	-	-	4	1.3
Omnivore crustaceans	21	3.77	4.24	0.25	42	3.72	13	6	8.5	1.06	-	-
Crustacean grazers (>7 mm)	0	0	33	0.17	88	1.14	1800	1.2	254	1.06	895	1.01
Crustacean grazers (<7 mm)	16759	0.76	532	0.23	10	0.003	7800	0.6	39	0.007	2275	1.36
Crustacean grazers total	16759	0.76	565	0.4	98	1.143	9600	1.8	293	1.067	3170	2.37
Gastropod grazers	1160	1.99	-	-	188	0.33	12000	7	943.5	7.12	250	0.003
Filter feeders	-	-	-	6.94	500	0.70	44350	2.2	-	-	470	0.03
Crustacean/ gastropod spp.	10/4		-		7/5		8/8		7/7		6/4	
Seagrass	204	61	113	37	909	32	400	120	505	40	370	55

intermediate predators are reported from all regions except Kalmar Sound (Table 2). In the Skagerrak, the abundance and biomass of intermediate fish predators (mainly black goby, *Gobius niger*, two-spotted goby *Gobiusculus flavescens* and three-spined stickleback *Gasterosteus aculeatus*) are >14 times higher than in the other regions (Table 2) and linked to the 90% reduction of the cod stock (Svedäng and Bardon, 2003; Baden *et al.*, 2012).

DISCUSSION

This study presents the most complete distribution map of *Z. marina* in the Nordic region to date (Figure 4), along with information on ecosystem structure, diversity, function, long-term dynamics and threats. Clearly, Nordic eelgrass meadows are much more widely distributed than previously reported (Boström *et al.*, 2003), although the present distribution map is mostly qualitative. The total eelgrass coverage of $1480 \, km^2$ should therefore be considered a minimum estimate (maximum $>2100 \, km^2$), highlighting key regions and identifying gaps. In comparison, this minimum coverage estimate is over four times greater than the previously assessed eelgrass coverage of Western Europe ($340 \, km^2$), and of the same order of magnitude as the combined eelgrass area of the

Pacific coast of North America ($1000 \, km^2$), the western North Atlantic ($374 \, km^2$) and Mid-Atlantic coasts of the USA ($292 \, km^2$), i.e. $1666 \, km^2$ (Spalding *et al.*, 2003). Given the important ecosystem services these systems provide, eelgrass meadows should to a much larger extent be incorporated in coastal research, monitoring and resource conservation. To prevent further net loss of eelgrass, region-specific management and monitoring actions are needed that consider the status and special features of different regions and target the most important local loss-drivers.

Below, potential explanations for the large-scale patterns are summarized. Then, pressures in relation to observed losses and factors influencing the resilience of eelgrass in different regions are discussed. Finally, problems and challenges associated with the present conservation of Nordic eelgrass meadows are presented and recommendations for management are provided.

Linking distribution of plants and animals to environmental gradients: complex biotic regulation influenced by salinity

Eelgrass ecosystem structure and productivity are to a large extent governed by light (Dennison, 1987), nutrients (Duarte, 1995; Krause-Jensen *et al.*, 2008; Orth *et al.*, 2010) and salinity (Nejrup and Pedersen, 2008; Baden *et al.*, 2010). Brackish

(5–7 psu) conditions characteristic of the inner Baltic Sea pose significant physiological stress, and may thus influence distribution, growth and reproductive strategy of eelgrass (Nejrup and Pedersen, 2008). However, shoot density and biomass of the compiled shallow eelgrass meadows did not correlate significantly with the large-scale decline in salinity towards the inner Baltic Sea, probably because saturating light in the shallow water allows the plants to cope with the osmotic stress. Shoot density and biomass of the shallow eelgrass populations also showed no clear response to the large-scale differences in water quality across regions. This is probably also because shallow meadows are generally light-saturated and therefore not influenced by negative effects of eutrophication on water clarity, except if algal mats or epiphytes are abundant. In fact, the highest productivities were measured at intermediate salinity at relatively nutrient-rich conditions (~16 psu, region 3, Table 3). However, the important regulating role of light was reflected in significant declines in shoot density with water depth. Also, large-scale and long-term eelgrass declines were generally recorded in the most nutrient-rich areas (region 3) where negative effects of eutrophication are probably most pronounced. Thus, the general picture emerging is a complex response of eelgrass variables to the interacting gradients of water quality, salinity and potential top-down control (see below) with steep clines in both chemical and biological variables particularly at the entrance of the Baltic Sea (Figures 3 and 5, Table 3). A more detailed account of the relative importance of light, nutrients and salinity for the structure of eelgrass meadows in the Baltic Sea would demand a larger combined data set on eelgrass performance at different depths and associated information on the physico-chemical properties of the meadows.

The major factor limiting dispersal and establishment of marine (and freshwater) species in the Baltic is salinity (Remane and Schlieper, 1971). Total zoobenthos diversity declines sharply when entering the Baltic Sea (Wallentinus, 1991), but this trend is weak for eelgrass mesograzer diversity. Typically, crustacean and gastropod richness in eelgrass meadows ranges between 6–10 and 4–8 species, respectively, (Table 2). Southern and northern Baltic eelgrass meadows support the highest biomasses of crustacean and gastropod grazers, while intermediate predator abundance peaks in Skagerrak. Differences in the importance of intermediate predators and mesograzers (>7 mm) along the salinity gradient have important implications for both trophic transfer and resilience of eelgrass meadows to present and future stressors. For instance, in Skagerrak and the southern Baltic, crustacean mesograzer reductions and eelgrass loss are linked and partly explained by the overfishing of cod and subsequent dominance of intermediate fish predators and macroalgae (Baden et al., 2003, 2010; Bobsien, 2006; Jephson et al., 2008; Moksnes et al., 2008). In particular, a 10-fold increase in gobids and sticklebacks has been recorded causing an almost total exclusion of idoteids and gammarids (Baden et al., 2012). Similarly, in the Kiel Bight, top predatory fish have declined and eelgrass meadows are dominated by gobiids, pipefish and sticklebacks representing 95% of the total fish assemblage. These intermediate predators prey heavily on eelgrass epifauna with amphipods and isopods representing a significant proportion (51–95%) of the fish community diet (Bobsien, 2006). In comparison, in Öresund where cod populations are not trawled, the epifaunal composition is comparable with the Skagerrak eelgrass fauna in the 1980s (Baden et al., 2012). With lack of buffering mesograzers, especially important during spring time, eelgrass meadows are lost and replaced by filamentous algae (Pihl et al., 2006; Moksnes et al., 2008; Svensson et al., 2012). As eelgrass meadows are key habitats for 0-group cod (Wennhage and Pihl, 2002), such regime shifts translate directly into lost provisioning services in terms of fisheries and coastal tourism (Pihl et al., 2006; Rönnbäck et al., 2007). Contrastingly, in the northern Baltic, abundant mesograzer populations appear to constitute an important buffer against epiphytic overgrowth and even destructive outbreaks of Idotea spp. have been observed in Finnish eelgrass meadows (authors pers. obs. 2011). However, the role of fish predation in controlling Baltic eelgrass mesograzers warrants further study (Baden et al., 2010).

Eelgrass meadows are clearly one of the most diverse coastal ecosystems in Scandinavia. On otherwise species-poor sandy substrates, eelgrass is an important habitat for a rich epifauna and flora

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(Baden and Boström, 2001; Fredriksen *et al.*, 2005; Jephson *et al.*, 2008) which, in turn, support diverse fish communities (Pihl *et al.*, 2006). In addition, the complex root systems facilitate the existence of diverse infaunal communities (Boström *et al.*, 2002; Fredriksen *et al.*, 2010). The mixed Baltic eelgrass meadows support a rich epifauna (Gustafsson and Boström, 2009; Table 2) and co-occurring freshwater angiosperms may also facilitate eelgrass growth and overall ecosystem functioning (Salo *et al.*, 2009; Gustafsson and Boström, 2011). However, in contrast to the low functional redundancy in the eelgrass macrobenthos (Baden and Boström, 2001; Boström *et al.*, 2006), there is high redundancy among the rooted plants in the brackish parts of the gradient. Thus, projected reductions in salinity owing to increased precipitation and runoff will in the future probably cause a gradual recession of the eelgrass and an increase of plants of freshwater origin.

Regime shifts and community resilience – importance of extrinsic stressors and genetic diversity

The Nordic eelgrass ecosystems at the entrance to the Baltic Sea have undergone large-scale losses as a result of the eelgrass wasting disease and eutrophication. Large-scale declines of eelgrass have been reported from areas of the region where water clarity is low, and nutrient concentrations are high, i.e. Danish coastal waters, the Swedish west coast and the Puck Lagoon, Poland. In contrast, an increase in eelgrass distribution was documented from Norway's coast, which has the lowest nutrient

Table 3. Summary of chemical and biological gradients in the study area. Deeper colour intensity refers to a higher number or higher relative importance of response variables. n.d. = no data. The numbering of fauna sites (1–6) is the same as in Figures 1 and 6

	1. Atlantic	2. Skagerrak	3. Kattegat/Belt Sea	4. Baltic Sea, South	5. Baltic Proper	6. Baltic Sea, North
Hydrography						
Salinity						
Chl-a						
Water clarity (Secchi depth)						
Tot-N						
Tot-P						
Eelgrass						
Shoot density						
Biomass						
Shoot size						
Production	n.d.			n.d.		n.d
Allelic diversity						
Genotypic diversity						
Community angiosperm diversity						
Declines (wasting disease, eutrophication)						
Large scale areal increases						
Fauna		1	2, 3	4	5	6
Crustacean mesograzer diversity	n.d.					
Crustacean mesograzer density	n.d.					
Crustacean mesograzer biomass	n.d.					
Omnivorous crustacean biomass	n.d.					
Gastropod grazer biomass	n.d.					
Gastropod grazer diversity	n.d.					

concentrations and highest water clarity in the Nordic region. Eelgrass loss related to food web changes (overfishing and reduction of mesograzers) and subsequent macroalgal blooms also shows a region-specific pattern, with both overfishing and nutrient pollution as equally important stressors in Skagerrak (region 2), while overfishing appears to be of minor importance for the formation of macroalgal stress at both ends of the gradient, i.e. Atlantic Norway and the northern Baltic Sea (Moksnes *et al.*, 2008; Baden *et al.*, 2010).

Phytoplankton blooms, epiphytes, macroalgal mats, dissolved and particulate matter all contribute to light attenuation, but their anthropogenic drivers (i.e. nutrient pollution including internal loading) and overfishing, vary between regions. For instance, increased epiphyte loads owing to reduced grazing pressure caused by overfishing appears to be of low importance in each region, while phytoplankton blooms resulting from anthropogenic nutrient pollution is considered of intermediate or high importance in most regions, except Norway. Accordingly, light levels in terms of Secchi depth are low in all regions except the Atlantic (Norway). However, a relatively large fraction of the nutrients in the inner Baltic Sea are not bioavailable (Nausch and Nausch, 2011; Voss *et al.*, 2011), so the reported coastal nutrient gradient presented here exaggerates the actual difference in nutrient availability between outer and inner parts of the Baltic Sea. Reduced light levels cause reduced depth penetration of eelgrass, and this is most evident in region 3, where long-term data show a reduction in depth penetration in both open and sheltered areas. Surprisingly, no recent large-scale eelgrass losses have been recorded in the low salinity parts of the gradient despite deteriorated conditions (Boström *et al.*, 2002; Möller and Martin, 2007). However, as Secchi depth has decreased throughout the Baltic (Sandén and Håkansson, 1996), it is likely that the historical distribution of eelgrass was much deeper. The general pattern is that in spite of reductions in nutrient load over recent decades, eelgrass distribution and abundance in both Danish, Swedish and German coastal waters do not yet show any general positive trends (Munkes, 2005; Baden *et al.*, 2010; Hansen and Petersen, 2011).

A key question then is: what prevents re-establishment of eelgrass in Nordic waters? There are several indications that coastal ecosystems show complex trajectories of response to nutrient loading and that baselines may shift, thereby hindering the return to a reference situation of the past (Duarte *et al.*, 2009; Kemp *et al.*, 2009; Carstensen *et al.*, 2011), even though recovery within decades may occur (Jones and Schmitz, 2009; Borja *et al.*, 2010). It has been suggested that the loss of eelgrass meadows in Danish fjords caused a regime shift from clear waters with high eelgrass cover to turbid waters with plankton dominance (Krause-Jensen *et al.*, 2012). The latter state apparently counteracts a return to the vegetated state because negative feedback mechanisms such as sediment resuspension maintain the turbid state (Duarte, 1995; Munkes, 2005; Carstensen *et al.*, 2013). Occurrences of anoxia (Pulido and Borum, 2010), unsuitable sediments (Krause-Jensen *et al.*, 2011), physical disturbance by drifting macroalgae and seed burial by polychaetes may also hinder eelgrass recolonization (Valdemarsen *et al.*, 2010, 2011). Moreover, lack of apex predators and thus top-down control on epiphytes and filamentous macroalgae could be an additional burden on eelgrass meadows, as demonstrated along the Swedish west coast (Moksnes *et al.*, 2008). This is supported by the recent results from a mid-Californian estuary where the return of the apex predator sea otter (*Enhydra lutris*) since the mid-1980s increased *Zostera marina* coverage 5 times (Hughes *et al.*, 2013). If the large-scale declines in eelgrass distribution had occurred in the inner part of the Baltic Sea, where eelgrass reproduce primarily vegetatively, the problem would have been even more serious, because the probability of recolonization would be extremely low and recovery would have long perspectives owing to slow clonal growth (Reusch *et al.*, 1999). Recovery of eelgrass in such areas would have to involve transplantation of genetically 'suitable' strains (see below).

The eelgrass meadows along the biogeographic gradient studied here are all exposed to similar extrinsic stressors, but their intrinsic component of stress tolerance, estimated as the standing genetic variation, varies significantly among regions (Olsen *et al.*, 2004). In the study area, naturally isolated

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meadows usually have low genetic diversity, as has been found in parts of the inner Baltic (Reusch et al., 1999) as well as in lagoons (Olsen et al., 2004) and fjords (Ferber et al., 2008). Thus, at the northern edges of the distribution in region 5, many large meadows consisting of one or a few clones are found. These Baltic populations represent a paradox: long-term (>1000 years) survival under high extrinsic stress (low salinity, ice cover, eutrophication, turbidity) despite very low genotypic diversity. Whether these genotypes represent multi-purpose genotypes with wide reaction norms or specialized, plastic genotypes that have remained largely undisturbed in their current niches over the last millennium is currently unknown. However, given increased maritime transportation and eutrophication in addition to predicted increase in temperature and decrease in salinity, these genetically impoverished low-salinity populations may be at considerable risk. Maintenance of clonal and genotypic diversity can be a 'general insurance' for resilience as communities experience present and future stressors (Reusch et al., 2005; Bergmann et al., 2010). As the protist Labyrinthula zosterae causing the eelgrass wasting disease shows faster growth and cell division at higher temperatures (A.C. Bockelmann, unpubl. data), future climate induced changes may increase eelgrass infections.

Nordic seagrass conservation – priorities, challenges and implications for monitoring

The present work clearly demonstrates that the Nordic and Baltic countries are facing very different management challenges, ranging from development of strategies to compensate for lost eelgrass meadows to protection of pristine meadows and associated species. However, it is evident that additional management measures are needed in order to push the systems to the desired state with higher eelgrass distribution. Moreover, eelgrass landscapes should not be studied and managed in isolation. Rather they should be viewed as one critical link in a functionally-connected mosaic of different coastal habitats (Boström et al., 2011). However, our present understanding of how Nordic eelgrass habitats are linked by means of propagules, geneflow or animal

movements is still very limited, and studies identifying relevant scales and thresholds in habitat connectivity are urgently needed.

European directives constitute the framework for management of the coastal zone within EU member states. The EU-directives that concern coastal areas with eelgrass meadows are the Habitats Directive, the Water Framework Directive (WFD), the Marine Strategy Framework Directive and the Nitrate Directive. In the Baltic Sea and in the north-east Atlantic, the international agreements HELCOM and OSPAR supplement the national and local supervision of eelgrass ecosystems, but have no legislative power. These agreements highlight that eelgrass is under threat and needs further protection, and they encourage coordinated monitoring and management, suggesting for example the compilation of biotope inventories and designation of marine protected areas (http://www.helcom.fi/environment2/biodiv/endangered/Biotopes/en_GB/Seagrass_beds; http://www.ospar.org/documents/dbase/publications/P00426_Zostera_beds.pdf). However, in order to achieve a sustainable coastal zone management that includes the necessary concerns to maintain eelgrass distribution and its ecological function, it is necessary to have updated maps of their distribution. In addition, it is important to have a common knowledge base of proposed actions to ensure eelgrass distribution and functionality.

During a seagrass management workshop arranged by the Nordic Seagrass Network managers, governmental scientists and stakeholders involved in Nordic coastal management discussed needs for efficient eelgrass management. They identified a number of ecological, economic, societal and jurisdictional gaps preventing effective management of Nordic eelgrasses. The main points are summarized in the following:

Legislation and implementation of the EU-WFD. EU member states must ensure good ecological status of coastal ecosystems based on biological indicators of which eelgrasses are one. Member states thus have to monitor the status of the coastal ecosystems including eelgrasses and, in case of non-compliance with the targets, establish the necessary management measures to meet the targets. The EU-WFD does not provide legislation to protect eelgrass, but demands that eelgrasses reflect a good ecological status. The

legislation and actions to ensure this goal vary between countries.

Eelgrass indicators and monitoring. Monitoring programmes are needed in order to document the status and trends of eelgrass meadows and preferably link it to information on physico-chemical conditions, human pressures and possible conservation measures taken in the area. For every region, there is also a need to clearly define what a 'healthy meadow' is, and how to determine it. Standardized quality indices are needed that can be applied to individual meadows as well as to larger spatial scales that cross jurisdictional borders. Once quality indices are in place, strategies for preserving eelgrass meadows can be further developed. As the different Baltic regions face different problems, it is unlikely that a one-size-fits-all plan for eelgrass conservation is realistic. A European-wide survey showed that shoot density, cover and depth extension are the most commonly used indicators, but that even these are not routinely applied across large regions (Marbá *et al*., 2013) and are also lacking from many areas of the Baltic Sea.

Valuation of goods and services. To better argue the value of eelgrass meadows, there is an urgent need for actual numbers (including monetary terms) on eelgrass ecosystems services (e.g. coastal protection, nutrient reduction, carbon sequestration, fisheries production) and how they differ along the Nordic gradient. Presently, Nordic eelgrass meadows are typically overlooked and thus undervalued (or even invisible) in conservation. This review provides a first important estimate of total eelgrass coverage in different regions. However, to provide managers with national and regional estimates of the economic net benefits of healthy eelgrass meadows vs. decreasing meadows, would require more efforts in, for example, combined habitat food web modelling and economic modelling (Rönnbäck *et al*., 2007; Plummer *et al*., 2013).

Restoration. There is also an urgent need for answers as to why eelgrass has not returned to areas where water quality has improved, and the extent to which restoration can mitigate losses. The Nordic area lacks examples of successful case studies on eelgrass restoration, particularly large-scale studies. Moreover, information on suitable donor (genotypes) and recipient (site history) areas is missing. This review will greatly aid in identifying key regions of eelgrass distribution, as well as areas devoid of eelgrass. This is an important starting point for predicitve habitat modelling that will assist coastal managers in identifying both existing and potential eelgrass habitats. However, the main message for management is to prevent loss, as restoration can be difficult and expensive and is not guaranteed to succeed. It is also important to realize, that we lack specific criteria for functional seagrass ecosystems and that the mere presence of eelgrass in restored areas does not necessarily indicate regained ecosystem functions and services in terms of high primary production and species interactions (Simenstad *et al*., 2006; Borja *et al*., 2010).

Biotic interactions. There is an extensive literature on links between nutrients, water quality and eelgrass health. However, with the exception of some areas (e.g. western Sweden and parts of the Baltic Sea), managers are still largely unaware of the importance of top-down control (role of predation and grazing and their interaction) in relation to bottom-up processes (nutrient pollution). As identified in this review, eelgrass food webs differ in structure and function with important implications for eelgrass loss mechanisms. This and previous work (Moksnes *et al*., 2008; Baden *et al*., 2010; Hughes *et al*., 2013) clearly highlights the need for a more holistic and flexible (offshore and coastal) management strategy including stronger links between fisheries management and eelgrass conservation.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Distribution of eelgrass

The quality and completeness of eelgrass distribution maps is variable or lacking in most regions, even though they are a fundamental prerequisite for defining the habitat to be protected and for planning an effective future management and monitoring strategy. Maps should show distribution, abundance and preferably note areas of potential distribution where eelgrass should be able to expand if pressures such as eutrophication are released.

Research bias

This review and analysis reveals the imbalance in focus of eelgrass research across the Nordic region. For example, in Norway, which represents the most diverse and pristine region, a mapping programme was only started in 2007 and only 10 papers dealing with the general ecology of eelgrass have been published between 1998 and 2010. In contrast, Denmark, with one of the longest eelgrass research

traditions in the world, has focused almost exclusively on plant ecology and physiology; and finally, Swedish eelgrass research has been mainly focused on its links to animal and fisheries ecology. Such topical bias complicates comprehensive large-scale comparisons, assessments and monitoring of ecological patterns and processes. On a more positive note, however, this diversity of expertise has tremendous potential for interdisciplinary work and thus a broad scientific basis for management.

Interactions among stressors

Understanding the complex interplay of physical (sediment properties, light, wave exposure), chemical (nutrient pollution, H_2S, anoxia) and biological (top-down forcing, seed mortality, algal mats, pathogen outbreaks) stressors in relation both to human impacts and to climate change scenarios (Korpinen *et al.*, 2012) is central and achievable using meta-analytical and modelling approaches that can be validated with real data. A focus on synthesis is essential to elucidating why re-establishment of eelgrass in disturbed areas often fails, despite improved water quality.

Pathogen outbreaks

Very little is known about what triggers pathogen outbreaks and which regions are at risk (somewhat correlated with salinity). Interestingly, recent studies suggest that *L. zosterae* and two other *Labyrinthula* species are present across the full range of salinities in the study area (Bockelmann *et al.*, 2011). Important knowledge gaps include (a) lack of genetic data on species and strain composition, (b) the role of pathogenic species and strain (physiological) attributes for pathogenicity, (c) the balance between eelgrass growth rate and decline in relation to the survival of a *L. zosterae* infected eelgrass meadow, and (d) potential positive/negative interactions between outbreaks and climate change, in particular increased water temperature and reduced salinity. New molecular techniques for detection of *L. zosterae* are rapid and sensitive but have so far not been applied in conservation surveys (A. Bockelmann, unpubl.).

Monitoring

Monitoring to report on the extent and the ecological status of eelgrass meadows in relation to the EU-WFD's requirements for good ecological status must be based on the established criteria for the coastal water type in the given region. These criteria are developed to deal with specific anthropogenic influences, eutrophication being the most common pressure for eelgrass meadows. A monitoring programme aiming to improve knowledge of the processes involved needs to include a (top-down) delineation of specific questions guided by a conceptual model in which a priori predictions can be tested and management strategies modified accordingly (Lindenmayer and Likens, 2010). In order to be able to analyse their possible influence on the status/trends of the eelgrass meadows, associated information on pressures and physico-chemical variables must be included in the programme. An adequate monitoring programme must also take into account a range of spatial scales and utilize natural gradients (Lepetz *et al.*, 2009). Our biogeographical comparison of these factors may thus serve as a valuable basis for future efforts to improve monitoring of Nordic eelgrass meadows.

Lack of awareness

Among the most pressing tasks today is to increase awareness at all levels and stimulate a dialogue between scientists and the wide variety of stakeholders. Public awareness of their importance is poor as seagrass ecosystems do not hold the status of iconic ecosystems such as coral reefs, despite the fact that they are equally productive. It is therefore critical that communication both in the form of public outreach as well as policy making facilitates cooperative legislation that will ensure sustainable use and preservation of eelgrass systems.

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