



A network analysis of connected biophysical pathways to advice eelgrass (*Zostera marina*) restoration

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ABSTRACT

The North Sea and the Baltic Sea, including Danish coastal waters, have experienced a drastic decline in eelgrass *Zostera marina* coverage during the past century. Around 1900, eelgrass meadows covered about 6700 km² of Danish coastal waters while the current potential distribution area is only about one third of this. In some areas, the potential distribution area is far from realized, and restoration efforts are needed to assist recovery. Such efforts are challenging, and resource-demanding and careful site selection is, therefore, important. In the present study, we aim to identify the connectivity of eelgrass populations as a basis for guiding site selection for restoration. We developed a coupled biophysical model to study eelgrass dispersal in the Kattegat. Partly submerged particles simulated the dispersal of reproductive eelgrass shoots containing seeds during the flowering season July–September. We then used network analysis to identify the potential connectivity between populations. We evaluated connectivity based on In-strength, Betweenness and Eigenvector centrality metrics and identified key areas in the Kattegat such as the central part of Aalborg Bay, to be considered to restore the network of *Z. marina* patches. The study proves the potentials of combining hydrodynamic models and network analysis to support marine conservation and planning, and highlights the importance of collaboration between ecologists, oceanographers, and practitioners in this endeavour.

1. Introduction

A major concern in the current geological era is the human impact on marine and coastal ecosystems (Norström et al., 2016). Seagrass meadows are among the many negatively affected ecosystems due to direct local and regional scale impacts on biodiversity, habitats and their processes, but also through global scale changes, such as climate change. Combined, these processes are pushing seagrass ecosystems towards their resilience limits, compromising their overall functioning and, therefore, the ecosystem services they provide (Short and Neckles, 1999). Among seagrasses, eelgrass (*Zostera marina* L.) is a subtidal marine angiosperm that grows in temperate waters, often forming extensive underwater meadows. Eelgrass is widely distributed across the northern hemisphere, where it occurs in shallow sheltered settings to maximum depths ultimately set by water clarity. Eelgrass and other seagrasses are habitat forming species with an essential role in shaping

the community structure and the ecosystem functioning in marine environments (Hemminga and Duarte, 2000). They provide food resources, habitat or nursery areas for a wide range of aquatic organisms, such as invertebrates, fish and birds, thereby enhancing biodiversity (Duarte et al., 2013a). They also play a role in carbon and nutrient sequestration and coastal protection (Duarte et al., 2013b; Greiner et al., 2013).

Large-scale losses of seagrasses have occurred worldwide, largely driven by human-mediated factors such as eutrophication and habitat destruction by e.g., coastal development and dredging fisheries and with climate warming emerging as additional stressor (Waycott et al., 2009; Orth et al., 2006a; Duarte et al., 2020; Dunic et al., 2021). Once losses of seagrass exceed a tipping point, the vegetated state may transition to an alternative stable state of bare seafloor (McGlathery et al., 2013; Maxwell et al., 2016). This happens as the seagrass meadow loses functionality including its ability to stabilize the sediments and reduce

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resuspension and turbidity. In turn, internal feed-back mechanisms of the bare seafloor state maintain the turbid state and counteract recolonization (McGlathery et al., 2013; Maxwell et al., 2016). Fragmentation of seagrass meadows also reduces meadow connectivity and the supply of propagules to unvegetated sites (Jahnke et al., 2018).

Protection and restoration efforts are undertaken to halt losses and stimulate recovery. There are recent examples of positive trends (de los Santos et al., 2019; Turschwell et al., 2021) but recovery is challenged by the interaction of multiple stressors that caused fragmentation, by loss of connectivity and by feed-back mechanisms counteracting

recovery (Maxwell et al., 2016). Active restoration can catalyse recovery of seagrass meadows and associated ecosystem services (Orth et al., 2020; Tan et al., 2020). The most successful eelgrass restoration project to date restored meadows by seeding areas that fulfilled eelgrass habitat conditions but had lost connectivity to mother populations (Orth et al., 2020). However, restoration efforts are generally costly and have a history of relatively low success rate often due to poor site selection (Bayraktarov et al., 2016; van Katwijk et al., 2016). Careful selection of restoration sites is, therefore, essential and can be guided by knowledge on meadow connectivity in addition to information on where habitat

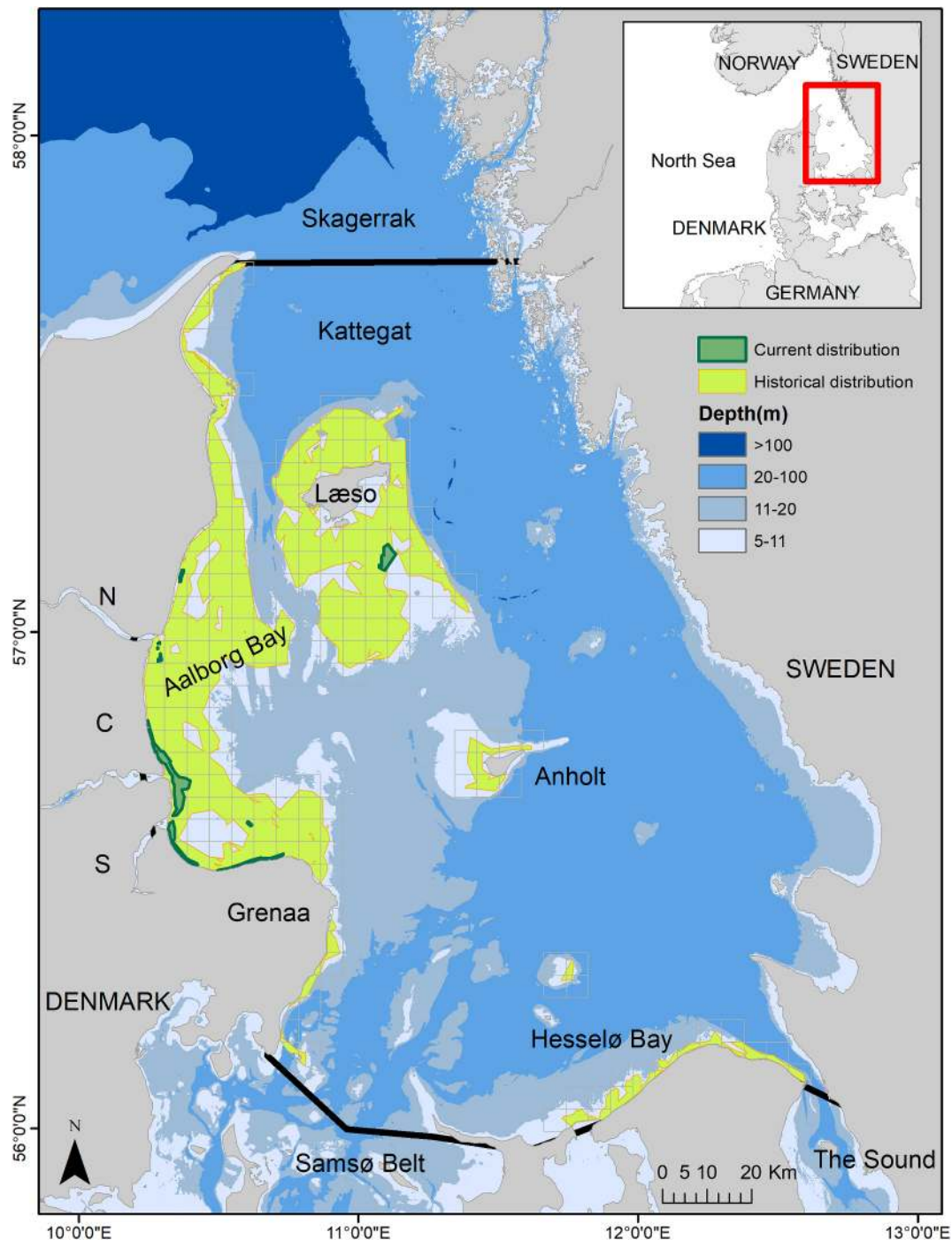


Fig. 1. Study area and bathymetry in the Kattegat (Denmark). Eelgrass historical distribution is shown as light green polygons and is used as release areas of particles in the IBM (defined as >10% probability of eelgrass cover (Stæhr et al., 2019), which resembles the historic distribution in the 1900 (Petersen, 1914)). Eelgrass current distribution is shown as dark green polygons (defined as >50% probability of eelgrass cover (Stæhr et al. 2019)). Model boundaries are shown as black lines, and the 5 km grid used for the graph theory analysis is shown in grey. Aalborg Bay is divided into 3 regions: North (N), centre (C) and South (S).

requirements are fulfilled (e.g. Kuusemäe et al., 2016).

In the North Sea and Baltic Sea region, including Danish coastal waters, eelgrass experienced major losses in the 20th century, and seagrass populations do not yet show recovery trends at the national scale although nutrient loading of estuaries and coastal systems have been reduced over the past three decades (Flindt et al., 2016; Krause-Jensen et al., 2020). Around 1900, Danish *Z. marina* meadows covered approximately 6726 km², equivalent to ca. 15% of all Danish marine waters (Petersen, 1893). In the 1930s, eelgrass coverage declined due to the so-called “wasting disease”, so that in 1941, the distribution area was decimated to only 7% of the reported in 1901 (summarised by Rasmussen 1977). Case studies document partial recovery in the 1950s and 1960s (Rasmussen, 1973; Frederiksen et al., 2004) before the peak of eutrophication around 1980 but the status of eelgrass was not closely followed until nation-wide monitoring started in 1989. A habitat suitability model quantifies the current potential area of eelgrass at 2200 km², i.e., 1/3 of the area in 1900 (Staehr et al., 2019). Combined analysis of all available data highlights that eutrophication and trawling are the key factors limiting recovery (Krause-Jensen et al., 2020). The same study also points at vast areas in NW Kattegat, which supported extended meadows in the past but are currently bare (Fig. 1). This suggests that recovery could be limited by distance to source populations and that restoration may be needed to assist recovery. A first pilot-scale restoration is planned in the area, and there is a need for thorough studies of eelgrass connectivity to guide selection of further restoration sites.

Eelgrass populations spread vegetatively from the edge of existing meadows and colonize new areas by seed dispersal mediated by marine currents. In most regions, including Danish coastal waters, eelgrass populations maintain vegetative shoots throughout the year with only a fraction of the population flowering each year (Blok et al., 2018). Seeds are negatively buoyant (Delefosse et al., 2016) and dispersal distances are, therefore, often short (Orth et al., 2006b; Kuusemäe et al., 2018). However, eelgrass seeds can be dispersed along the bottom by bedload transport (Koch et al., 2010) and long-distance seed dispersal is mediated by rafting of detached flowering shoots with seeds (Harwell and Orth, 2002; Erftemeijer et al., 2008; Hosokawa et al., 2015; Källström et al., 2008; Triest et al., 2018; Pereda-Briones et al., 2018). Flowering shoots are buoyant and can float from 2 weeks to several months depending on the condition of the flowering shoot at the time of detachment (Harwell and Orth, 2002; Kuusemäe et al., 2018).

Individual-based models (IBM) of Danish eelgrass populations in Odense Fjord and the Skagerrak-Kattegat region (Kuusemäe et al., 2018; Jahnke et al., 2020) have indicated highly connected meadows and areas where connectivity has become limited over the last century. However, rather than just highlighting source and destination areas in a connectivity matrix (Magris et al., 2016), it is necessary to move towards an understanding of the marine metapopulation dynamics, identifying for example those key locations that act as bridges linking populations together, or central populations connected to other important ones. In this context, methodologies for analysing complex networks have the potential to analyse a system of biophysical connections, revealing new topological and dynamic features of a network of marine areas connected by passive transport and dispersion of elements between them (Ospina-Alvarez et al., 2020a). In network analysis, a system of connected elements, a graph, can be defined as a network. A graph data structure consists of a set of vertices or nodes (e.g., habitat patches, islands and populations) (Romero-torres et al., 2018), and the edges of the graph are the connections or links in the network (e.g., adjacency, dispersal probability) (Fig. 2) (Essam and Fisher 1970). Network analysis provides insight into system properties and identifies nodes that promote connectivity by their central position in the network, i.e., habitat patches connected to many other patches, or groups of well-connected nodes with a high potential flow of individuals or propagules and that act as bridges between distant areas. The study of network connectivity through the identification of central nodes and

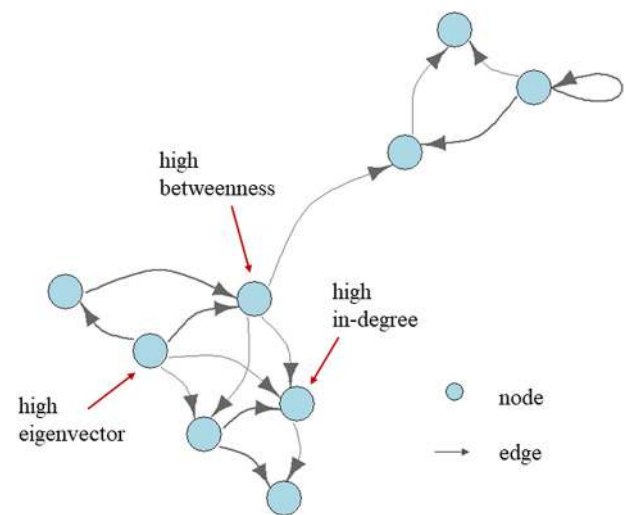


Fig. 2. Example of a graph represented by nodes and edges. Direction of the edge is represented with an arrow and the thickness of the arrow reflects the weight or strength of the connection. The addressed centrality measures are shown in the figure: Weighted in-degree (in this paper referred to as in-strength centrality), Betweenness centrality and Eigenvector centrality.

edges has given rise to a myriad of centrality measures, each of which highlights important aspects that describe the cohesion, or lack thereof, in a set of connected elements, traditionally referred to as a graph (Freeman 1979). Network analysis and the use of graph theory tools has allowed a better understanding of marine ecosystems (Trembl et al., 2008; Andreello et al., 2017; Pérez-Matus et al., 2017) and their associated services (Saunders et al., 2016; de Juan et al., 2021; Ruiz-Frau et al., 2020; Ospina-Alvarez et al., 2021), generating valuable insights into the structure and functioning of connected populations, communities, habitats or management areas, but also into how these are connected to the production and delivery of services that people value and demand (e.g., Halpern et al., 2010; Ospina-Alvarez et al., 2020b).

The aim of this study is to identify the potential connectivity of the eelgrass populations in the Kattegat with a focus on guiding the selection of sites for restoration. To accomplish this objective, we 1) develop a transport and dispersal model of the eelgrass *Z. marina* by coupling a hydrodynamic and an individual-based model using the FlexSem framework 2) analyse the dispersal potential and connectivity of a system of biophysically interconnected seagrass patches over time and 3) use network analysis and calculate centrality measures to identify eelgrass patches that act as key areas promoting system connectivity. Our approach identifies key sinks and keystone areas that prevent network fragmentation, pointing to where restoration efforts should be directed. This approach sets the basis for a wider adoption of coupled biophysical models, network analysis and the use graph theory tools to inform and advise marine conservation and planning.

2. Materials and methods

2.1. Study area

The study area is in Aalborg Bay and the Kattegat, a transition zone between the North Sea and the Eastern Baltic Sea (Fig. 1). The hydrography of the Baltic Sea is determined by strong inputs of river water, the topographic succession of sills and basins, and the narrow entrance to the North Sea via the inner Danish straits. Normally, salty Atlantic water penetrates the Baltic Sea through the bottom layer of the North Sea, Skagerrak and the Kattegat. The Baltic Sea water flows as the Baltic Current in the surface layer through the Kattegat to the Skagerrak (Leppäranta and Myrberg, 2009). The surface velocity is dominated by currents generated by local westerly winds influenced by the North

Atlantic Oscillation (Hurrell and Deser, 2010). Most of Kattegat has a water depth of 10–50 m with deeper parts to the northeast facing the northern boundary to Skagerrak (Fig. 1).

2.2. Hydrodynamic model

To model the physical environment in the Kattegat, a 3D hydrodynamic model was developed in the FlexSem framework (Larsen et al., 2020) using an orthogonal computational mesh (Fig. A1). The unstructured computational mesh has open boundaries in the north towards Skagerrak and the North Sea (Fig. 1), in the southeast at the Sound - the strait between Denmark and Sweden, and in the southwest with the Samsø Belt, connection to the Baltic Sea. The mesh consists of 2840 polygons with a high resolution of 200 m in the Aalborg Bay and a lower resolution of 4.5 km towards Sweden. The model implements 20 vertical z-layers ranging in thickness from 2 m in the top 10 layers to 10 m in the bottom layers, yielding a total of 21368 computational cells. The model's computational mesh is shown in Appendix A Fig. A1. Open boundary forcing of water level, temperature, salinity and velocities were interpolated from Copernicus Marine Environment Monitoring Service (CMEMS <https://marine.copernicus.eu>). Because the Copernicus data generally underestimates the salinity in the deep water, salinity and temperature data was adjusted using measured data from the Danish National Monitoring Database (ODA <https://odaforalle.au.dk>). Profiles of salinity and temperature were interpolated to the model layer depths and the model-measurement difference calculated for each profile. The difference was interpolated in time between the profiles and this difference was added to the open boundary conditions. Meteorological forcing data of wind velocities, temperature, cloud cover and precipitation were downloaded from the Copernicus ERA5 hourly data (<https://cds.climate.copernicus.eu>). River discharges of freshwater from 14 sources were obtained from the High-resolution pan-European water model (E-HYPE) (Hackett et al., 2013). The model was run for the years 2017, 2018 and 2019, each year initialized with temperature and salinity values from the Copernicus data. These years represent a range of North Atlantic Oscillation (NAO) index values (Hurrell and Deser, 2010) to take the interannual variability into account. The NAO index values were obtained from <https://www.cpc.ncep.noaa.gov>. For more information on the hydrodynamic model validation see Appendix A.

2.3. Individual-based model of drifting shoots

The dispersal of seed-bearing eelgrass shoots was simulated with a Lagrangian IBM implemented in the FlexSem framework (Larsen et al., 2017). Particles represented suspended seeds with a short dispersal phase (1 and 5 days) (Källström et al., 2008; Erftemeijer et al., 2008) and reproductive shoots containing seeds with a longer dispersal phase (10, 20 and 30 days) (Erftemeijer et al., 2008; Hosokawa et al., 2015; Jahnke et al., 2018). Shoots are positively buoyant and particles in the model drifted in the surface, whereas the seeds sink fast and disperse only a few meters around the shoots from where they are released (Ruiz-Montoya et al., 2012; Meysick et al., 2019). Particles were therefore given different dispersal days (1, 5, 10, 20 and 30) (Jahnke et al., 2018), to account for the different sinking times of the seeds alone and the seeds in the shoots (for practical reasons we will refer as seed dispersal despite the two different dispersal methods). The flowering season was set to range from July to September (Blok et al., 2018) with a peak occurring in August. A total number of 200,000 particles were released in each simulation. The release was made at the beginning of each month, 20% in July, 50% in August and 30% in September. The proportion of particles was also set for the different dispersal days, resulting in five classes, and assuming that most seeds were released from shoots with long dispersal (Jahnke et al., 2018): I) 2% of the particles with one day of dispersal to account for the seeds released and settled in the nearby areas due to processes such as bedload transport, II) 3% with five dispersal days, III) 10% with 10 dispersal days, IV) 20% with 20

dispersal days and finally V) 65% with 30 dispersal days to account for the shoots with a long dispersal. The process was applied for three consecutive years 2017, 2018 and 2019.

The release area was determined from the habitat model by Staehr et al. (2019), with the assumption that the historical distribution of eelgrass corresponds to the areas with a probability >10% of encountering eelgrass (light green polygons in Fig. 1). This mapped release area compares well with the early records of eelgrass (Petersen, 1893, 1914; Ostenfeld, 1908). The historic occurrence data of eelgrass were digitised as polygons in a GIS software (ESRI GIS and Mapping Software), where each polygon was considered an eelgrass meadow (Fig. 1). We consider areas of historical distribution as potential habitats for future restoration and reestablishment. This approach fits with the study conducted by Jahnke et al. (2018) where the historical distribution of eelgrass in the 1900s was considered. The current distribution of eelgrass was also mapped (dark green polygons in Fig. 1). This time the >50% probability of presence was extracted from the potential eelgrass distribution model (Staehr et al., 2019). This assumption also fits with a habitat map for submerged marine vegetation based on satellite data from 2018 (DHI GRAS, <https://marine-vegetation.satlas.dk/>), and with bottom features visible in aerial images from Krak Nordic technological company.

Particles were released randomly within the historical area as a surface release and drifted according to their assigned number of drift days. Particles were forced to stay in the surface (Kuusemäe et al., 2018) for the entire simulation time, but by stopping them at contrasting times we simulated seeds dropping from the shoots at various locations. Particles were influenced by advection from ocean currents. The movement of the shoots directly influenced by wind (hereafter, windage) was set to 0. Contrary to other studies including windage, it is known that reproductive shoots of *Zostera marina* move at nearly the same velocity as the surface current (Pereda-Briones et al., 2018). In addition, a diffusivity coefficient of $0.01 \text{ m}^2 \text{ s}^{-1}$ was applied to describe the diffusion of particles affected by turbulence (Huret et al., 2010; Tremblé et al., 2015). Once the number of drift days was reached for the specific class, the particles stopped moving in the domain and the end location was recorded. A sensitivity analysis was conducted to test the response of number of particles and area division (not shown).

2.4. Network analysis and graph theory

To obtain the connectivity network, the initial and end positions of particles were extracted from the model output. In order to assess connectivity at a regional scale, the study area was divided into a 5 km grid. At first, a non-parametric Lagrangian Kernel Density Estimation (KDE, Scott, 1992) was used to estimate point density of the dispersed eelgrass seeds around each output raster cell (Xie and Yan 2008; Mitarai et al., 2009). The useful output of the KDE in this analysis is the determination of a series of polygons representing the probability of finding dispersed seeds after a transport process mediated by marine currents and hydrodynamic processes. KDEs were calculated for the whole area and the different years in order to identify the main areas of accumulation of seeds. For the graph theory metrics, the potential connectivity matrices were calculated, and only the grid cells with historic occurrence of eelgrass were used in the assessment (Fig. 1). Potential connectivity is defined as the probability of seed transport from a release area j to a destination area i (Watson et al., 2010). In the potential connectivity matrices, the quantity does not mean actual dispersal, but the probability that it will occur given seed production (Watson et al., 2010). To identify the areas that contribute most to the distinct levels of potential connectivity, three centrality measures were calculated for the nodes and two for the edges.

In-strength, Betweenness and Eigenvector centrality were calculated for each node in the network. In-strength centrality in directed networks (also called weighted in-degree) can be defined as the sum of inward link weights (Squartini et al., 2013; Ospina-Alvarez et al., 2021). In dispersal ecology, nodes with high in-strength scores can act as important

settlement areas for eelgrass seeds. Betweenness centrality captures the degree of interrelation of a given node u with others. This metric is measured by the number of shortest paths (between any pair of nodes in the graph) that pass through the target node u . Hence, this score is moderated by the total number of shortest paths between any pair of nodes in the graph (Freeman et al., 1991; Brandes 2001). A target node would have high Betweenness centrality if it appears in many shortest paths (Freeman, 1979). In an ecological context, nodes with the highest betweenness scores represent fragile nodes that would otherwise fragment or disconnected parts of the network (Fig. 2), acting as key stepping stone patches for movement (Friesen et al., 2019; Kininmonth et al., 2019; Squartini et al., 2013). Eigenvector centrality attempts to capture the qualitative aspect of a node's connections. That is, connections to the most influential nodes (higher number of weighted incoming and outgoing connections) are more important than connections to the least influential nodes, the measure also considers the centrality of neighbours (Bonacich, 1987). In an ecological context, eigenvector centrality can assist to identify the most resilient patches with strong and quality links to other patches (Ospina-Alvarez et al., 2020a); or guide the selection of optimal protected networks with respect to population growth and persistence (Jacobi and Jonsson, 2011). Finally, the edges of the network were evaluated using edge Strength centrality and edge Betweenness centrality identifying strong and fragile links respectively. The more interactions that a node has with another, the higher the weight of the edge.

2.5. Cluster detection

Detecting communities or clusters is of great importance in biology and ecology where systems of connected elements are often represented as graphs (Fortunato and Castellano 2012; Pérez-Matus et al., 2017). In networks where the distribution of links is globally and locally inhomogeneous, some nodes have higher concentrations of links within special groups of nodes and low concentrations between these groups (Newman and Girvan, 2004; Radicchi et al., 2004). This can be important to represent ecologically separated communities based on the likelihood of seed and shoot dispersal, which can then be used to create management and conservation strategies (Frys et al., 2020; Pata and Yñiguez, 2021). Here, we considered the approach to cluster detection using the *Infomap* algorithm (Rosvall and Bergstrom, 2008). According to this method, particles (i.e., eelgrass seeds and shoots) are considered to move in a network system matching the statistical description of connectivity probabilities contained in the connectivity matrix. Using information theory concepts, *Infomap* decomposes the network into a number of clusters that can define oceanic provinces (i.e. clusters of areas) well connected internally, but with minimal exchanges of particles between them (Fortunato and Castellano 2012; Rossi et al., 2014). This algorithm retains the information of the directions and weights of the edges in the network, which we believe is important in this system. The clusters were generated considering the connectivity results for all three years.

All analyses were performed using R v.4.1.0 (R Core Team, 2021). Centrality measures and cluster detection analyses were performed using the R package 'igraph' v.1.2.7 (Csardi and Nepusz, 2006). Betweenness centrality was correctly adjusted to comply with the issues raised by Costa et al., (2017). Network visualisations were made with R packages 'ggplot2' v.3.3.5, 'mapdata' v.2.3.0, 'ggmap' v.3.0.0 and 'ggraph' v.2.0.5 (Wickham, 2021; Becker and Wilks, 2021; Khale et al., 2019; Pedersen, 2021).

3. Results

3.1. Circulation in the Kattegat

The surface circulation in the Kattegat for the modelled months (July–September) presented some inter-annual differences. The

modelled surface current was averaged for each month and the eddy kinetic energy was also calculated to highlight areas with intensified flow. The currents in July were similar in all studied years and presented a northward direction whereas in August, the three years showed southward-oriented surface currents (See Appendix B, Fig. B1, Fig. B2). Despite the similarities across years for currents in July and August, September had a higher inter-annual variability. In September 2017 (Fig. 3a) northward oriented currents were observed in Aalborg Bay and very weak currents in the rest of the modelled area. In 2018 (Fig. 3b), north-directed currents were still observed in Aalborg Bay but contrary to 2017 there was a strong south-directed surface current originating in the boundary with the Skagerrak and continuing all the way down along the Swedish coast and towards Samsø Belt. Finally, in September 2019 (Fig. 3c), contrary to the other two years, the surface current in Aalborg Bay was south-directed, and this pattern characterizes the whole Bay to the southern boundary of the model.

3.2. Shoot dispersal potential

Our primary aim was to identify the connectivity and dispersal potential of eelgrass populations in the Kattegat area. The final positions of the simulated seeds released in the Kattegat within the historical eelgrass distribution area (Fig. 1) were extracted from the model output and used to obtain the Lagrangian KDE (Fig. 4). The seed densities were significantly different between the simulated years. In 2017, the simulated seeds tended to form a main aggregation in Aalborg Bay within a shallow area up to 11 m depth (Fig. 4a), which matches the depth range of historic eelgrass populations in the area (Ostenfeld 1908). In addition, there were two smaller aggregations towards the centre of the Kattegat at the south and north-west side of the island of Læsø, corresponding to deeper areas >20 m depth, i.e., deeper than both current and historical eelgrass occurrence. In 2018, the seed density shifted to the eastern side of the Kattegat, but still showed some main aggregations in Aalborg Bay, this time spread along the north and central coast (Fig. 4b). Finally, in 2019, contrary to the other two years, the main aggregation of simulated seeds was formed in the southern areas near Grenaa (Fig. 4c). There were no seeds released in this area since it is deeper than the lower historical eelgrass depth limit of 11 m. The circulation patterns showed in the previous section, seem to explain the differences in the KDEs for the different years.

3.3. Network analysis through graph theory

The purpose of the network analysis through graph theory was to identify sink areas (high In-strength centrality) important to eelgrass, as well as keystone areas (Betweenness and Eigenvector centrality) that prevent the fragmentation of the network and where restoration efforts should ideally be directed.

3.3.1. Historical distribution

At first, the historical distribution of eelgrass was used for the release of *Z. marina* shoots (light green areas in Fig. 1). Figs. 5 and 6 show the centrality measures calculated from the connectivity matrices. Betweenness centrality was obtained for each year and In-strength and Eigenvector centrality, as a sum of all years respectively.

Nodes with high Betweenness centrality represent areas that act as bridges linking groups of nodes in a network. These varied across years. In 2017, nodes located in the northern and central part of Aalborg Bay (#102, 148 and 61 Fig. 5a) showed the highest Betweenness (>0.7 probability), indicating their importance as 'bridge-building' nodes between locations to the north, central and south of their geographical location. These nodes are at the limit of the seed release area shallower than 11 m depth. The connections (edges) between the pairs of nodes linking the populations in the northern part of Aalborg Bay with the ones in the central and southern parts (#102 → 61 and 148 → 102) exhibited the highest edge Betweenness within the network (Fig. 5a). In 2018, the

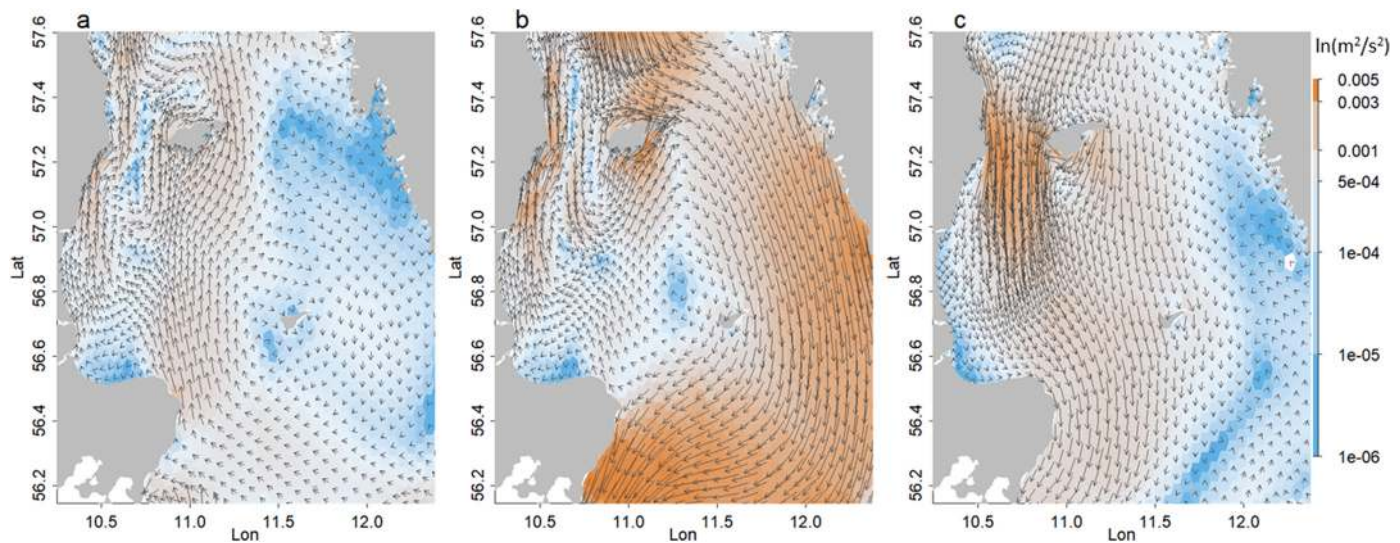


Fig. 3. Surface current maps in September a) 2017, b) 2018 and c) 2019 in the Kattegat. The modelled surface current was averaged for each month. Background colour indicates the horizontal eddy kinetic energy in $\ln(\text{m}^2/\text{s}^2)$. The eddy kinetic energy highlights areas with intensified flow.

nodes with highest Betweenness centrality were in south of Grenaa and Anholt (#25 and 78, Fig. 5b). The connection between the nodes linking Anholt with Grenaa (#78 → 25) exhibited the highest edge Betweenness within the network (Fig. 5b). In 2019, the nodes with highest Betweenness centrality were located along Aalborg Bay and Læsø (#160, 76, 148, 50, 92 and 60, Fig. 5c). The connections between the pairs of nodes linking the eelgrass populations from the south of Aalborg Bay, through the central, northern part and with Læsø (#76 → 50, 60 → 76, and 148 → 160) exhibited the highest edge Betweenness (Fig. 5c).

Unlike Betweenness, In-Strength centrality is a measure of centrality that is calculated based on weighted incoming links and not on distance or connection cost. The nodes highlighted as important for this centrality measure were those with the highest seed recruitment (Fig. 6a). The nodes with high In-strength centrality were similar across years and node (#98) located in the central Aalborg Bay is the one with the highest value. The strongest connections were those linking central part of Aalborg Bay with the northern part (#98 → 205 and #98 → 199, Fig. 6a). These routes concentrated the largest flow of eelgrass seeds between the different nodes of the potential network. The nodes with the highest Eigenvector (>0.7 probability), revealing the influence of a node in the network, were located in the central part of Aalborg Bay (#98, 86 and 82, Fig. 6b). In all three years we do not find connections between Aalborg Bay and Hesselø Bay and Aalborg Bay with Anholt. Some weak connections exist from Anholt and Grenaa, from Anholt to Hesselø island (above Hesselø Bay) and from Hesselø to Hesselø Island. These routes seem to have clear directionalities.

3.3.2. Current distribution

The current distribution of eelgrass was used for the release of *Z. marina* shoots (dark green areas in Fig. 1) and the same centrality measures were calculated as a mean of all three years. Similarly, the nodes with the highest Betweenness centrality (>0.7 probability) were located mainly in the southern part of Aalborg Bay (#58, 41 and 82, Fig. 7a). The nodes with high In-strength centrality were located in the central part of Aalborg Bay (#82, 98 and 86, Fig. 7b), and the nodes with high Eigenvector centrality were located in the southern part of the bay (#57 Fig. 7c). Node 82 in the central part of Aalborg Bay was highlighted in all three measures analysed. Using the current distribution and yearly average, there were no connections between Aalborg Bay and Læsø, between Anholt and Hesselø/Hesselø Bay and between Anholt and Grenaa. Very few connexions still exist between Læsø and Anholt.

3.4. Cluster detection

A total of 6 clusters were detected with the *Infomap* algorithm for the studied years (Fig. 8). Three clusters were located along the Danish coast, one in the central and Northern coastal area of Aalborg Bay, another one in the southern part of Aalborg Bay, and the last one in Grenaa. Two other clusters were detected around the islands of Læsø and Anholt and the last one was detected in Hesselø Bay. The clusters varied among years especially around Læsø and Grenaa (Data not shown).

4. Discussion

4.1. Connectivity and graph theory

We simulated the dispersal and connectivity of eelgrass *Z. marina* in the inner Danish waters through an individual-based model to identify potential areas important for restoration by a graph theory approach. Network analysis through graph theory provides a useful foundation for analysing connectivity because it efficiently handles very large and complex network topologies (Treml et al., 2008). Graph theory provides insights into the system's properties and identifies important or critical nodes with high in-degree (i.e., connected to many other areas) or clusters of well-connected nodes acting as bridges between distant populations (Ospina-Alvarez et al., 2020a). Using the historical distribution of eelgrass as a release area, we were able to identify keystone areas in the network (Betweenness centrality) as well as the potential pathways for shoot transportation (edge-Betweenness) (Fig. 5). These pathways differ across years but were mainly located in the southern parts of the study area close to Aalborg Bay (Fig. 5). Inter-annual differences are expected, since the current patterns differ among years (Fig. 2). Regarding the important settlement areas (nodes with high In-strength centrality), the results pointed at the central and northern part of Aalborg Bay (Fig. 6a), and the most well-connected nodes, connected to other well-connected nodes (nodes with high Eigenvector centrality), were also located in the central part of Aalborg Bay (Fig. 6b). All these highlighted areas are currently devoid of eelgrass (with exception of the area with high eigenvector centrality) and therefore could be valuable to prioritize in future restoration plans. When looking at the same metrics generated using the current distribution of eelgrass as seed release area, the map looks different (Fig. 7a, b, c). We can observe the fragmentation of the system and the loss of connections that were present in the maps with the historical distribution. The

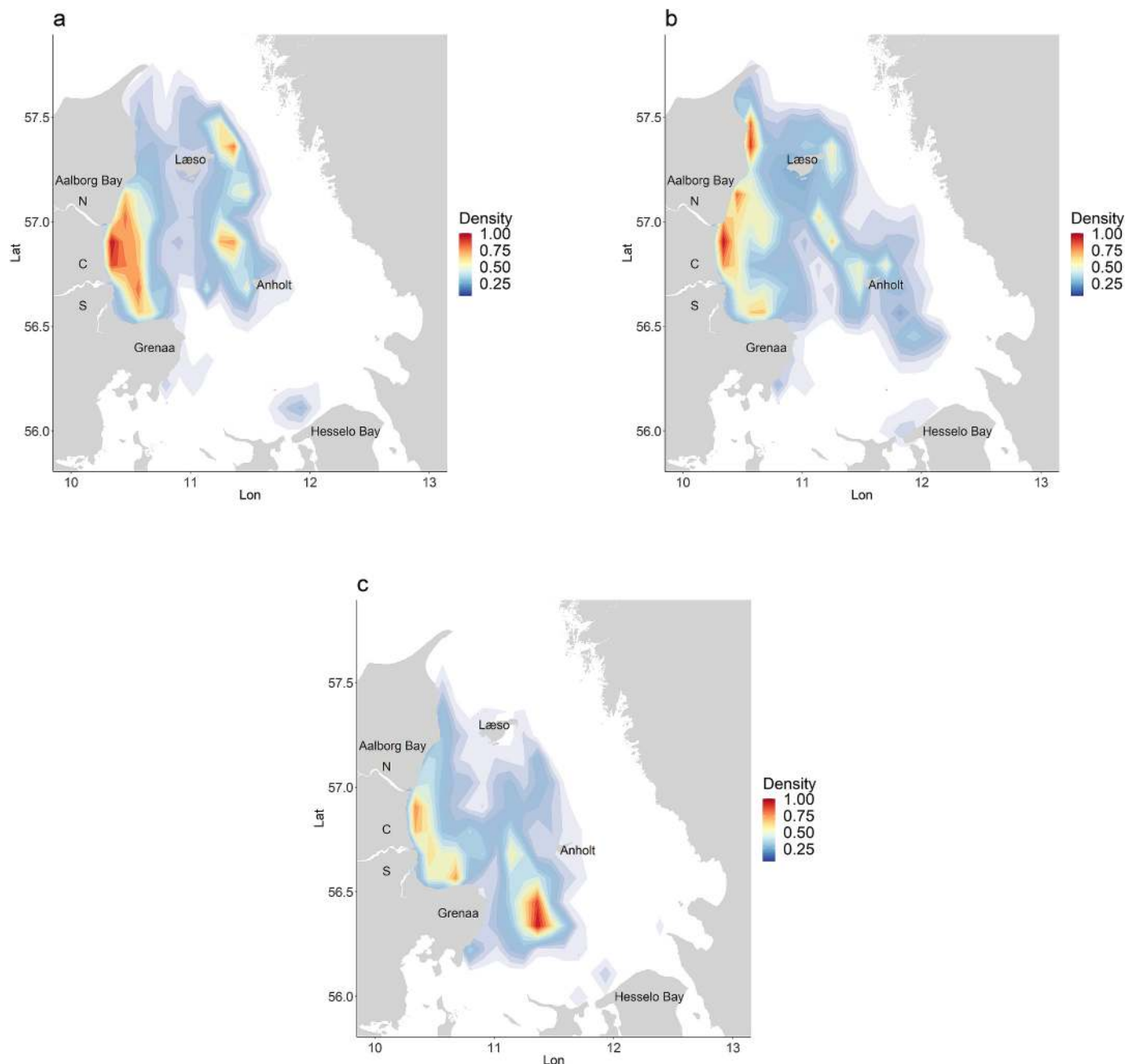


Fig. 4. Lagrangian kernel density estimations (KDEs) in the modelled area for the years (a) 2017, (b) 2018, and (c) 2019. The KDEs were computed given all Lagrangian particle trajectories. Colours indicate the normalised probability density of a particle end location for a given advection time.

combination of these two model-approaches (i.e., based on historical and current eelgrass distribution as seed release area) thereby help understand the system and identify key areas for eelgrass connectivity in a pristine scenario versus the current scenario. The results suggest that the limited eelgrass distribution in the current scenario still identifies the central part of the Bay as an important area (In-strength and Eigenvector centrality measures), but the current distribution does not have the potential to colonize bare areas in for example Hesselø Bay, Læsø and Anholt.

The use of centrality measures to identify important areas for conservation and management has been applied to other species and locations. In 2008 Trembl et al. modelled the dispersal of coral larvae between reefs throughout the Tropical Pacific. They used Betweenness centrality measure in order to identify critical islands that connect with distant island groups and that should therefore be prioritized for marine

conservation (Trembl et al., 2008). In a more recent study by Andrello et al. (2013), the Mediterranean Marine protected areas (MPAs) were evaluated and the Betweenness centrality was calculated, pointing out crucial nodes to ensure the connectivity between some areas (Andrello et al., 2013). As a last example, Kininmonth et al. (2019) also applied different centrality measures such as degree and betweenness to assess MPAs and target sites with higher larval supply. In our study, In-strength and Eigenvector centrality measures show quite consistent results across years, using both the historical and the current distribution as seed release areas. Betweenness centrality, however, does differ across years and also when using different distributions (historical and current). This variability can be explained by the high intra- and interannual variability in the currents. In order to increase the certainty of the important areas selected by this centrality measure, we would need to run the model for more years and identify possible patterns.

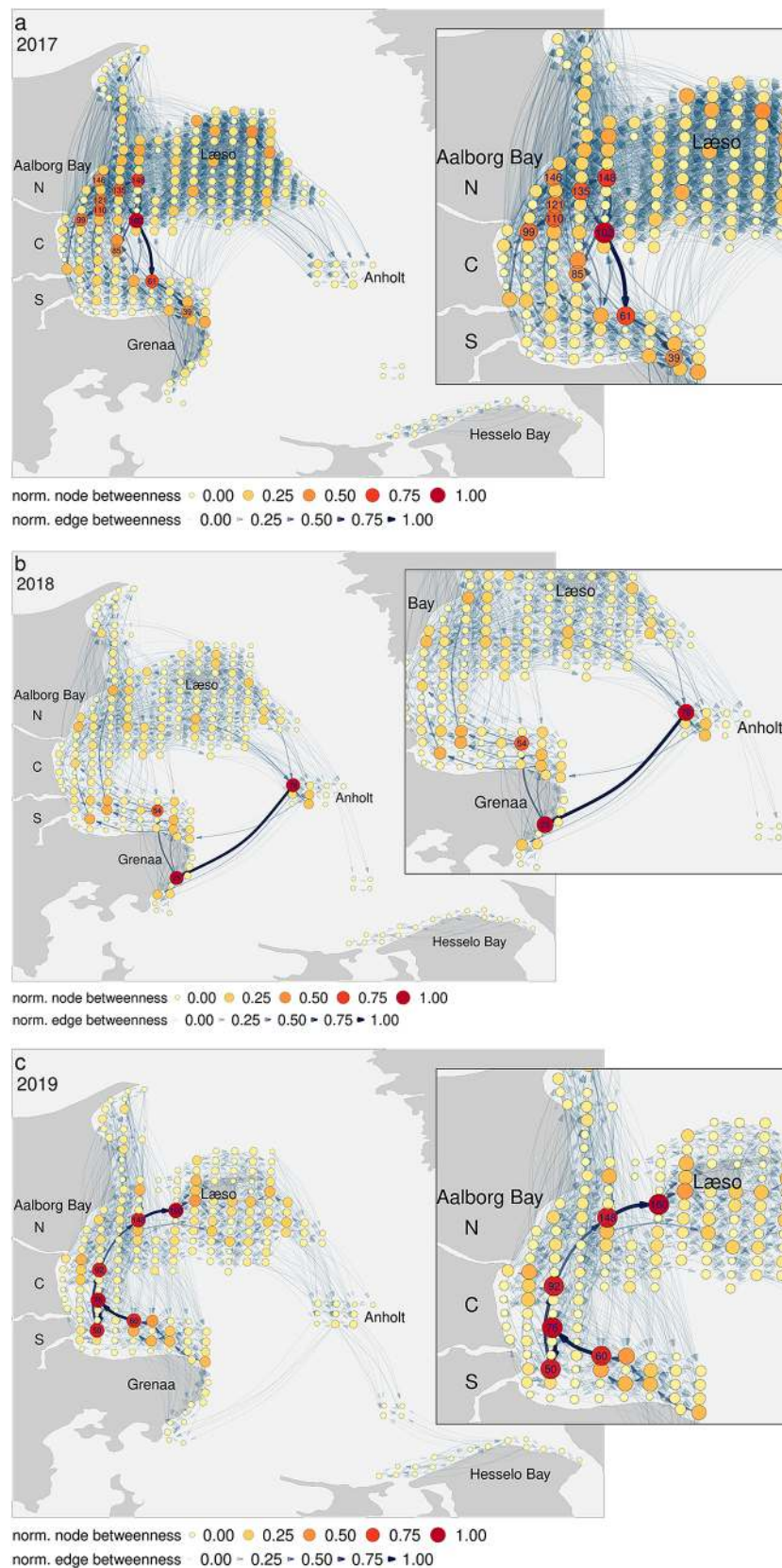


Fig. 5. Connectivity of eelgrass populations described as Betweenness centrality, reflecting fragile nodes, for the simulations conducted in (a) 2017, (b) 2018 and (c) 2019 with a release of shoots from the historical distribution area. Node size and colour symbolise the normalised betweenness, and edge width and colour symbolise normalised edge betweenness. Nodes with a probability >0.5 were labelled in the figures.

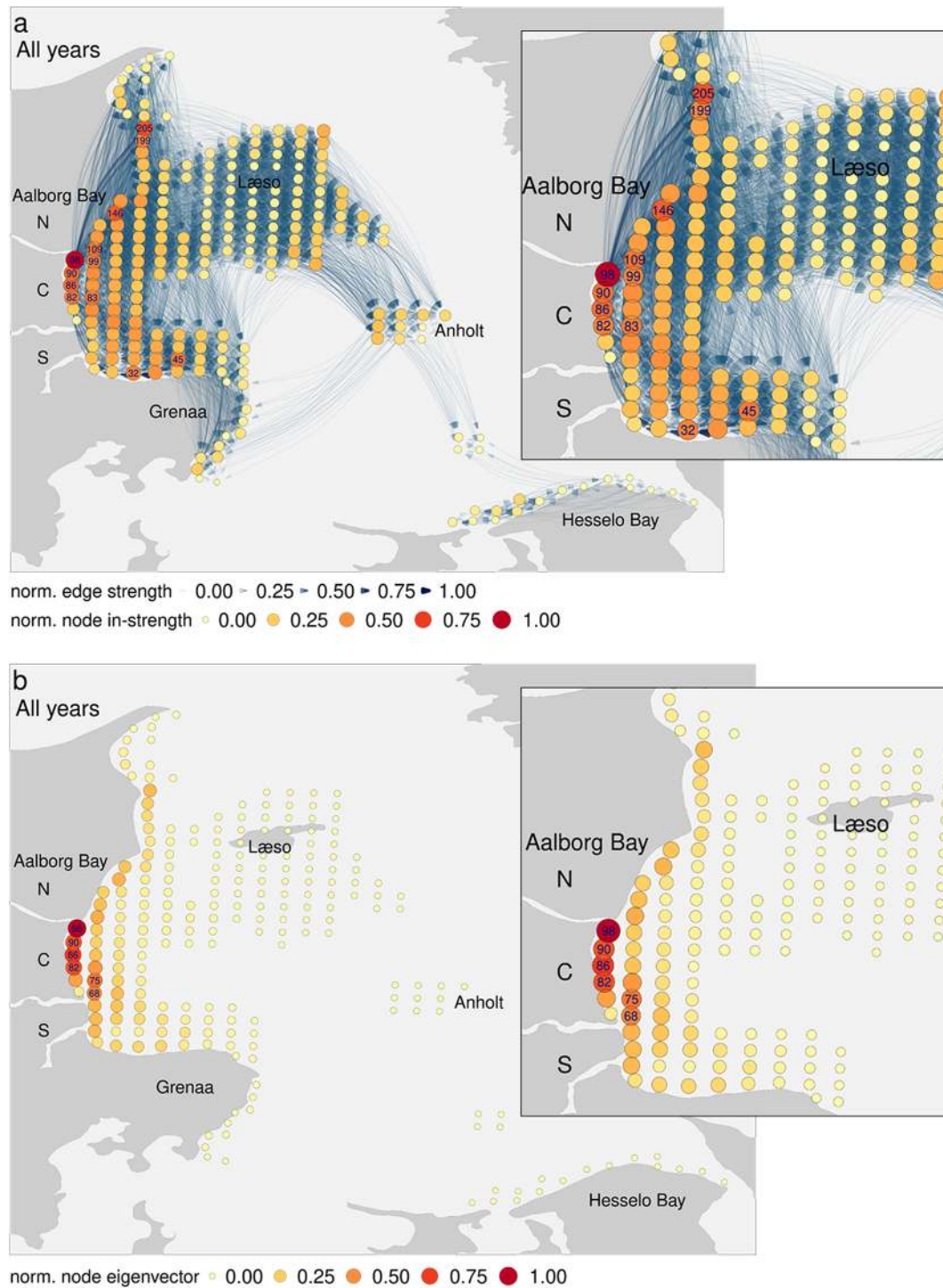


Fig. 6. Connectivity of eelgrass populations described as (a) In-strength, reflecting settlement areas and (b) Eigenvector centrality, reflecting resilient patches, for the simulations conducted in all three years, with a historical release of shoots. Node size and colour symbolise the normalised centrality score and edge width and colour symbolise normalised edge strength. Nodes with a probability >0.5 were labelled in the figures.

The identification of connectivity of eelgrass meadows in this study, in terms of centrality measures, can contribute to guide the choice of sites for the restoration of eelgrass meadows in the Kattegat region. Much of the shallow Aalborg Bay is currently devoid of eelgrass, although habitat conditions are suitable across the bay and historical information documents that eelgrass was widely distributed in the area in the past. Using both the historical and the current distribution maps we can identify the important nodes and links that would be essential to connect this network and facilitate the recolonization of eelgrass in the

area.

4.2. Cluster detection and validation

Cluster detection has been used in several marine connectivity studies to identify dispersal barriers and subnetworks (Watson et al., 2011; Frys et al., 2020; Pata and Yñiguez, 2021). These can be very useful tool to help assess management and conservation strategies. Some studies have been conducted in the study area in order to identify

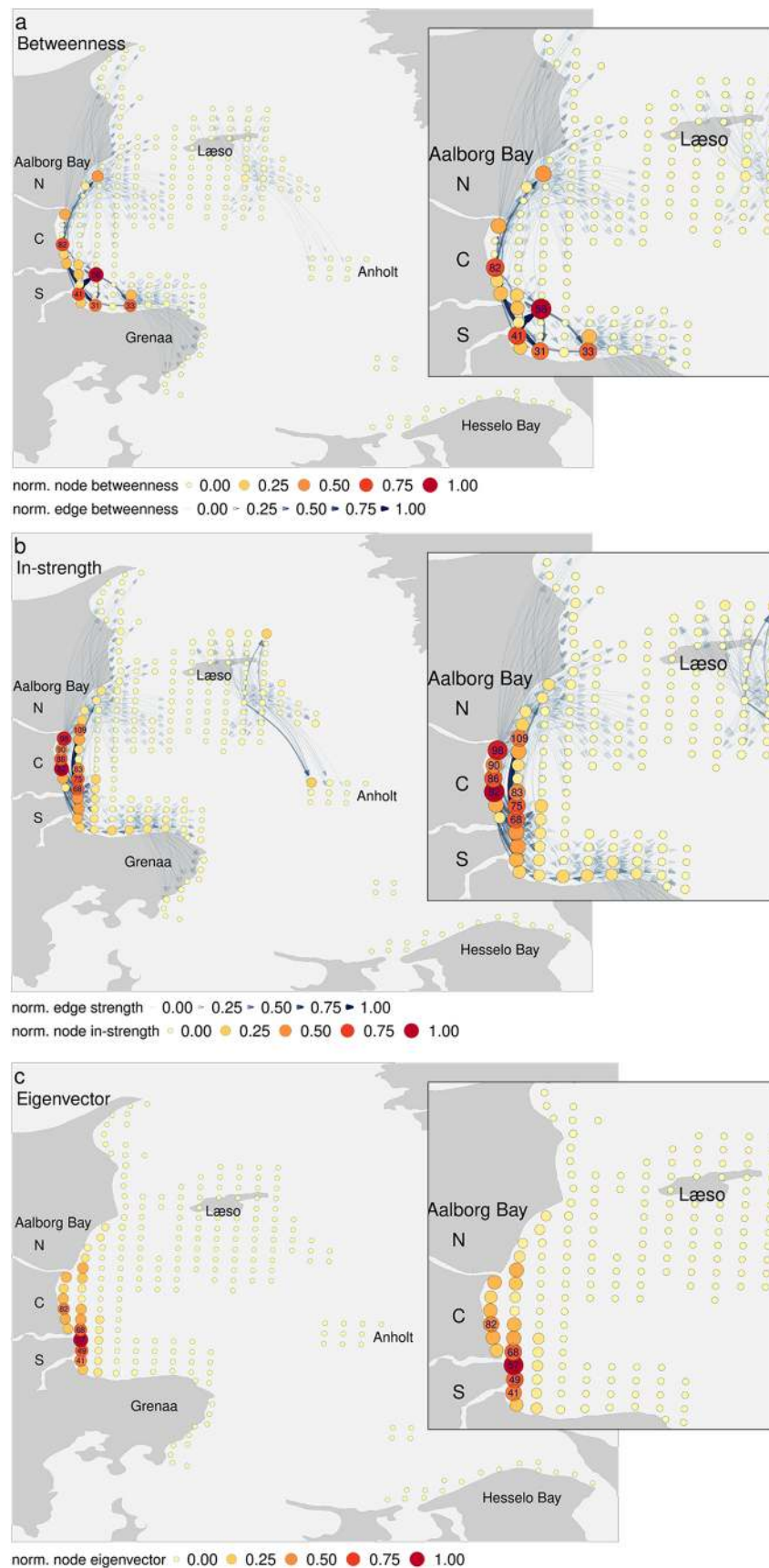


Fig. 7. (a) Betweenness (b) In-strength and (c) Eigenvector centrality for the simulations conducted in all three years, with a release of seeds from the current potential eelgrass distribution area. Node size and colour symbolise the normalised centrality score and edge width and colour symbolise normalised edge betweenness and strength respectively. Nodes with a probability >0.5 were labelled in the figures.

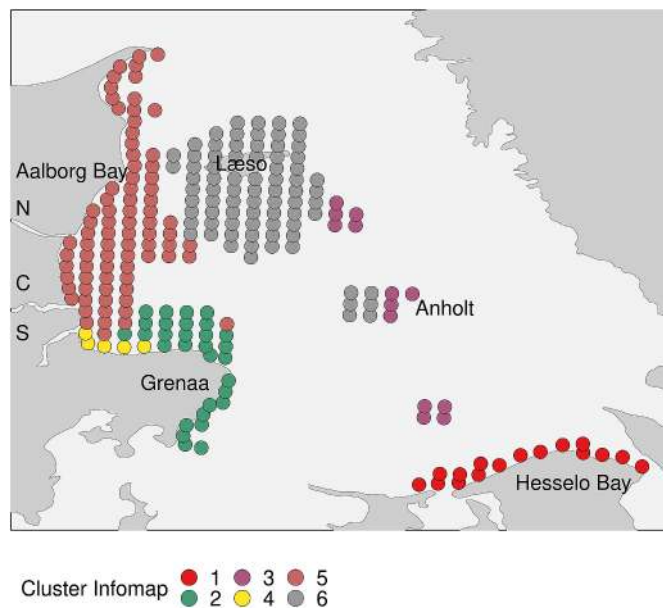


Fig. 8. Oceanographic cluster detection through the *Infomap* algorithm for all years from the historical distribution network. The coloured dots represent the centroids from the release 5 km grid used (Fig. 1). Dots with the same colour indicate areas that have an internal connectivity.

subpopulations or clusters for benthic species with a larval phase (Jacobi et al., 2012; Moksnes et al., 2015) and eelgrass (Jahnke et al., 2018). Moksnes et al. identified dispersal barriers with isolated benthic communities within the study area, which varied between shallow and benthic community types. For the shallow communities which can include seagrasses, the Kattegat was divided into 3 subcommunities. These results fit with our cluster division separating Aalborg Bay into one cluster (our clusters 2, 4 and 5), the area around Læsø in another one (cluster 6) and the third one in the south part of the Kattegat around Hesselø (cluster 1). Jahnke et al. found comparable results to Moksnes et al. studying *Z. marina* and detecting 2 main oceanographic clusters by the same clustering method in the Kattegat. Our study, however, identifies more clusters in this area and this can be due to the model resolution which is up to 200 m in Aalborg Bay compared to the model applied in the other two cases with 3.7 km resolution. The dispersal experiments carried out by Moksnes et al. and Jahnke et al. were repeated for 8 years, whereas our study includes three years, and our study also used a different clustering algorithm. Despite these methodological differences, similar patterns were detected in all these studies, which strengthen the findings.

4.3. Limitations of the study

Existing eelgrass beds are largely maintained by local shoots, whose seeds settle in the meadows and, along with new vegetative shoots, serve as a reservoir for fast natural recolonization in case the canopy is lost, as well as to support depth extension of the meadows (Olesen et al., 2017). However, propagule provision from connected meadows may also add to the genetic variability of established meadows in addition to providing seeds to bare - or poorly vegetated areas. While this study informs on important sites that could be targeted for restoration, there are some limitations that need to be considered. First, we only modelled 3 years with inherent variability in circulation and connectivity results. More years are needed to build confidence in the connectivity predictions and identification of key areas for conservation and restoration. This would require including additional years of ocean current and forcing data for the region. The use of GPS drifters deployed at separate locations could also help us parameterize our model and validate our

IBM. Second, the release area of *Z. marina* shoots and seeds was done from a historical map where eelgrass was present. This approach was chosen in order to analyse the potential connectivity and identify important areas for restoration. Since the current distribution of eelgrass is only a fraction of the historical distribution (dark green areas Fig. 1), the connectivity and graph theory will differ with a change in released area. However, given that the historical area (light green areas in Fig. 1) represents areas where eelgrass either is present or can potentially re-establish, this is a good indication of on where to re-build the lost connections and how the system will evolve in a future scenario. The approach could be further informed by 1) identifying the areas/patches that are repeatedly being highlighted as important according to the different measures, 2) adding those areas as patches to the model, and 3) running the model again with the new “potential” patches recalculating the metrics as we add more release sites. This way we would gain a deeper understanding of the system by testing different combinations before starting restoration plans.

4.4. Restoration efforts and the way forward

Even if restoration is conducted in carefully selected areas which support future meadow connectivity in the best possible way, the early phase of eelgrass recolonization (both natural and assisted) is critical. The scattered shoots are exposed to high mortality e.g. by uprooting via physical exposure because they do not possess the protective capacity of the larger patches (Frederiksen et al., 2004; Kuusemäe et al., 2016). In addition, bottom shear stress from waves and currents can mobilize the sediment, affecting seagrasses negatively through uprooting and burial (Terrados, 1997; Pereda-Briones et al., 2018). A recent study by Flindt et al. (2022), highlights that Danish estuaries suffer from organic-rich and physically unstable sediments, and that high bed mobility prevents establishment of seedlings through resuspension-driven light limitation and low sediment anchoring capacity (Flindt et al., 2022). The self-protective capacity of eelgrass increases with shoot density and meadow size which can also facilitate trapping and sedimentation (Hendriks et al., 2008), and it is therefore critical to ensure enough scale of restoration plots (in addition to selecting key locations for restoration). The majority of global seagrass restoration trials have been very small in size, which reduces the capacity for self-protection and contribute to explain the low overall survival rate of restored seagrass meadows (van Katwijk et al., 2016). The failure of eelgrass to re-establish itself in Danish coastal waters reflects complex recovery trajectories and calls for assisted restoration at target sites in combination with a great conservation effort to protect and restore the meadows. Such efforts include ensuring clear waters, low nutrient concentrations and protection from dredging and other physical disturbance (Krause-Jensen et al., 2020).

In the era of ongoing global change, the role of ecological restoration has never been as important as now (Aavik and Helm 2018; Duarte et al., 2020). Habitat connectivity is necessary for the vital processes of meta-populations and ecosystems, dispersal of seeds, and the exchange of genetic material between individual habitat patches. Despite the challenges reported in eelgrass restoration, successful cases such as the one by Orth et al. (2020) in the Atlantic coastal lagoons serve as an excellent example of what can be achieved. In addition, Mei et al. (2021) describe several restoration successes in Australia and New Zealand. They point out that many restoration efforts are conducted by researchers in an explicit experimental framework, or by uncontrolled experiments, based on ideas generated from some knowledge of biology and ecology (Vanderklift et al., 2020). A combined understanding of the dispersal mechanisms and reproductive biology of seagrasses is important for making the correct management decisions (Mei et al., 2021). By incorporating graph theory principles, we could increase the success in restoration plans, identifying not only patches with high connectivity and acting as bridges between distant populations, but also the important pathways. We would therefore look at the entire system rather than

looking at individual patches. Thus, identification of sites for seagrass restoration should be carried out collaboratively between managers, scientists and the community (Mei et al., 2021).

In conclusion, the proposed modelling can help guide the selection of priority areas for restoration as an extra tool in the restoration toolbox. Because of their ability to buffer environmental stress and support biodiversity and climate change mitigation and adaptation, the restoration of eelgrass meadows and other seagrasses have gained increasing focus as management actions serving multiple benefits. Therefore, all available tools should be implemented to assist manage and restore these important ecosystems.

Author contributions

APR conceived and designed the analysis, performed the computer simulations, performed the analysis and wrote the paper. AOA developed the network analysis and contributed to the main manuscript (writing, review & editing). JL developed the model and contributed to the main manuscript (methodology and model validation). FTH helped

with the conceptualization and design of the paper and reviewed the main manuscript. DKJ helped with the conceptualization and design of the paper and reviewed the main manuscript. MM helped with the conceptualization and design of the paper, reviewed the main manuscript and supervised the work.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Hydrodynamic model validation

Water level data from 4 harbours in within the model domain (Fig. A1 A) was download from <https://www.dmi.dk/frie-data/>. Corresponding data was extracted from the model output, yielding 4 three-year time series of measured and modelled water levels. Because the reference level of the measured data is not given, the measured data was adjusted to have the same 3 year mean water level as the model data on each station. Given the relatively large open boundaries, the water level is to a large degree determined by the boundary conditions. Fig. A1 (B) show the correlation between measured and modelled water levels at all 4 stations in all three model years (2017–2019). The overall correlation is good with correlation indices between 0.83 and 0.91 for the 4 stations, although errors of up to +0.2 m occur. The model generally underestimates the amplitude of the tidal signal as can be seen in Fig. A1 (C). In Table A.1 quality statistic for the 4 stations for all years (2017–2019) are listed. With an observation error of 3 cm, the Adjusted Relative Mean Absolute Error (ARMAE, Sutherland et al. 2004) falls into the 'good' category (0.2–0.4) for all stations.

Table A.1

Statistics of measured and modelled water level for the 4 stations shown in Fig. A1 A) 2017–2019. Measured and modelled data was matched in time and n is the total number of data point per station.

Station	20002	20101	29002	30017
n	46938	52518	50146	52477
Mean Error	−0.02	0	0	0
Root Mean Square	0.11	0.09	0.1	0.13
Correlation	0.89	0.91	0.87	0.83
ARMAE	0.26	0.21	0.21	0.29
ObsErr	0.03	0.03	0.03	0.03
StdDev measured	0.24	0.22	0.19	0.23
StdDev model	0.22	0.22	0.17	0.17

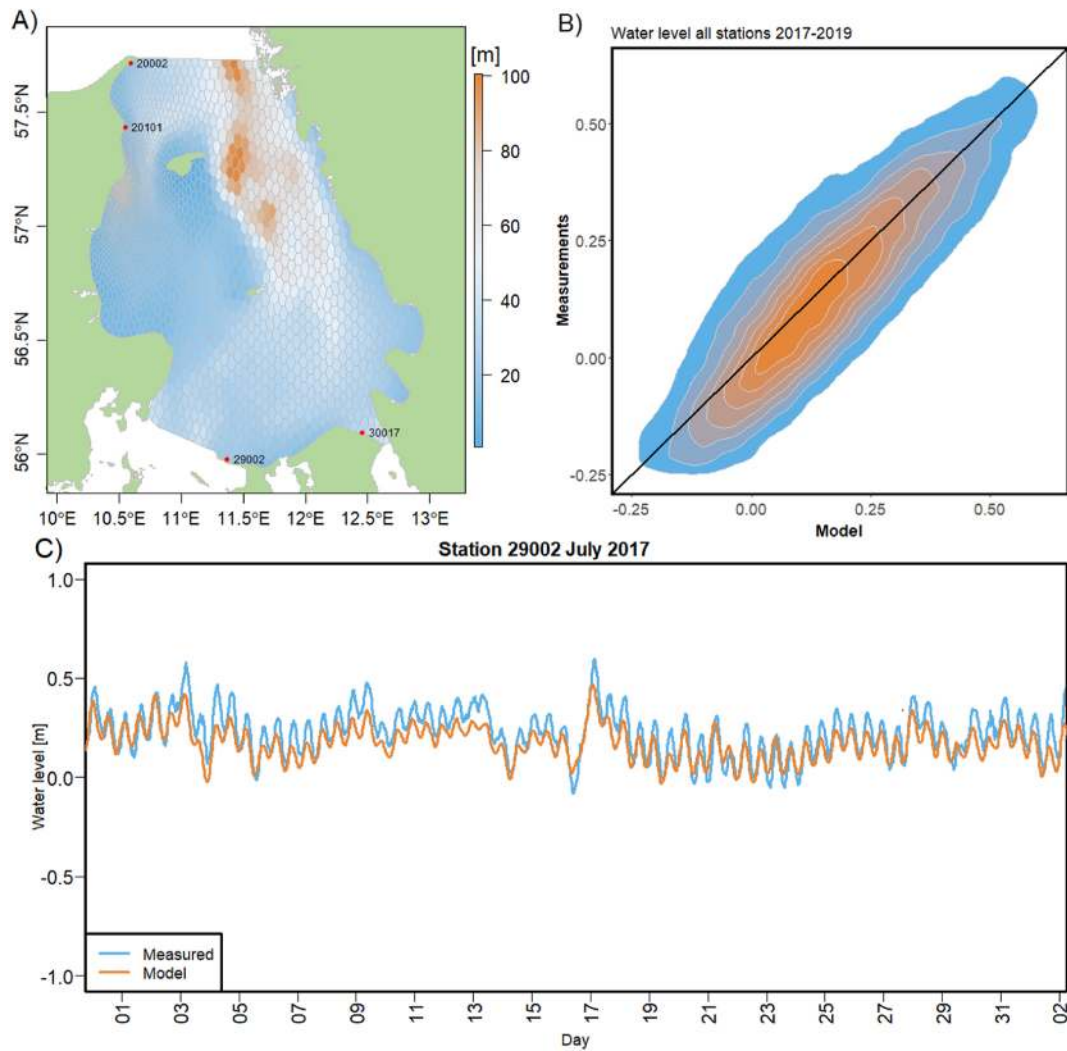


Fig. A.1. A) Computational mesh and bathymetry. Red dots indicate the positions of water level measurements. B) Correlation of model-measured water level for all 4 stations for all years (2017–2019). C) Measured and modelled water level at station 29002 in July 2017.

CTD profiles of temperature and salinity was obtained from the Danish National Monitoring Database (<https://odaforalle.au.dk>) for the 4 stations within in interior model domain that had the best data coverage. Corresponding model data was interpolated to the depths of the measurements. Statistic are shown in Table A.2 and Table A.3 and depicted in Fig. A2 B) and C). The model performance for temperature is good with correlation indices of 0.85–0.95 (Table A.1) and with an observation error of 0.1 deg. C, the ARMAE number of 0.15 or less corresponding to “Excellent”. The overall model performance for salinity is reasonable (Table A.3 and Fig. A2 C)). However, the model consistently underestimates the salinity in the deep water, which can be seen in Fig. A2 C) where the correlation is offset at higher values and in the bottom time series plot in Fig. A2 D) where the stratification generally is underestimated. This is primarily a residual of the initial conditions, which was interpolated from the Copernicus data. The statistical correlation is between 0.45 and 0.88 for the 4 stations (all years) and with an observation error of 0.1 PSU, the ARMAE numbers are 0.1 or less for all stations, corresponding to “Excellent”.

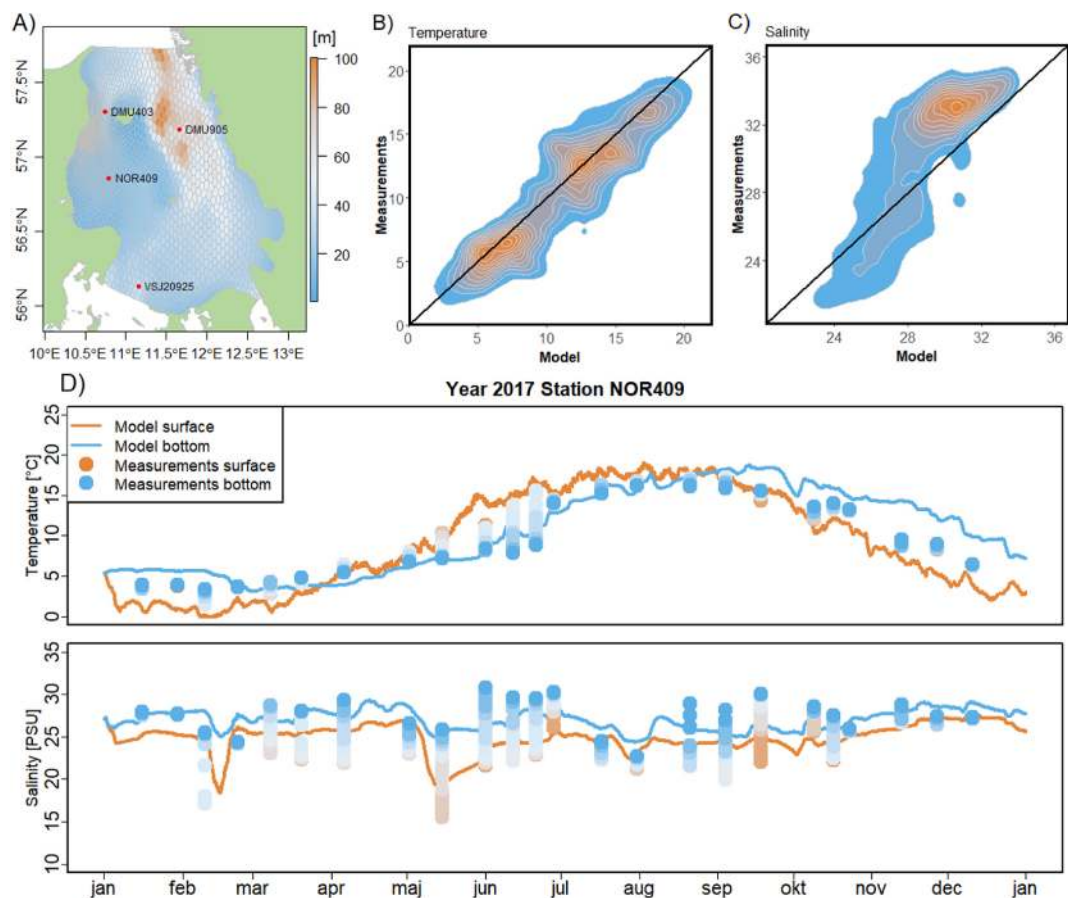


Fig. A.2. A) Computational mesh and bathymetry. Red dots indicate the positions of CTD stations form the Danish National Monitoring Programme. B) and C) Correlation of model-measured Temperature and salinity for all 4 stations for all years (2017–2019). D) Timeseries and modelled and measured temperature (top) and salinity(bottom) at station NOR409 in 2017.

Table A.2

Statistics of measured and modelled temperature for the 4 stations shown in figure A2 for 2017–2019. Modelled data was interpolated to the measurement depths. n is the total number of data points per station.

	DMU403	DMU905	NOR409	VSJ20925
n	5773	3846	4691	14431
Mean Error	−0.93	−0.12	−1.13	−0.41
Root Mean Square	2.09	2.33	2.08	1.62
Correlation	0.91	0.85	0.95	0.93
ARMAE	0.14	0.15	0.15	0.12
ObsErr	0.1	0.1	0.1	0.1
StdDev measured	4.41	4.48	5.26	4.18
StdDev model	4.52	3.8	5.69	3.89

Table A.3

Statistics of measured and modelled salinity for the 4 stations shown in figure A2 for 2017–2019. Modelled data was interpolated to the measurement depths. n is the total number of data points per station.

n	5773	3846	4691	14431
Mean Error	1.97	0.25	−0.72	0.56
Root Mean Square	3.36	2.58	3.41	3.25
Correlation	0.67	0.87	0.45	0.88
ARMAE	0.09	0.06	0.1	0.1
ObsErr	0.1	0.1	0.1	0.1
StdDev measured	3.65	4.39	3.67	5.9
StdDev model	2.14	2.41	2.23	3.67

Appendix B. Hydrodynamic data

The following section provides information on the model hydrodynamic output in the Kattegat for the remaining modelled months. The average currents in July were defined by a northward direction near Grenaa and Aalborg Bay (Fig. B1). In 2017 and 2018 the average currents are very similar. In 2019 we observe a slight difference in the southern part near Grenaa. The currents turned to a south-west direction directing the simulated shoots out of the modelled area towards the Samsø Belt. In August, the three years presented similar current patterns in all areas (Fig. B2), with small differences in speed in the northern part of Aalborg Bay. In this case, the currents in Aalborg Bay as well as the currents near the Swedish coast were all south directed. This behavior would translate in a southward movement of the eelgrass shoots released in Aalborg Bay and Kattegat. In September, the differences between years becomes clearer (Fig. 3, main text).

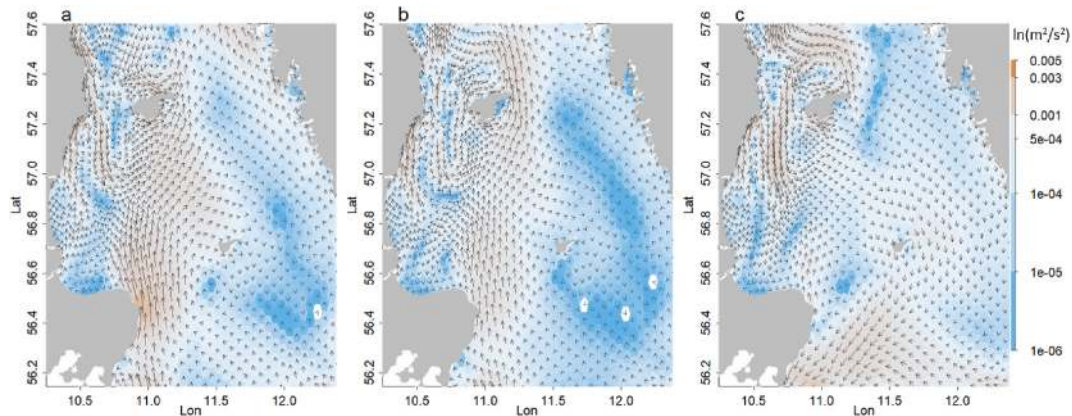


Fig. B.1. Surface current maps in July a) 2017, b) 2018 and c) 2019 in the Kattegat. Background colour indicates the horizontal kinetic energy in $\ln(m^2/s^2)$. The eddy kinetic energy highlights areas with intensified flow. The modelled surface current was averaged for each month.

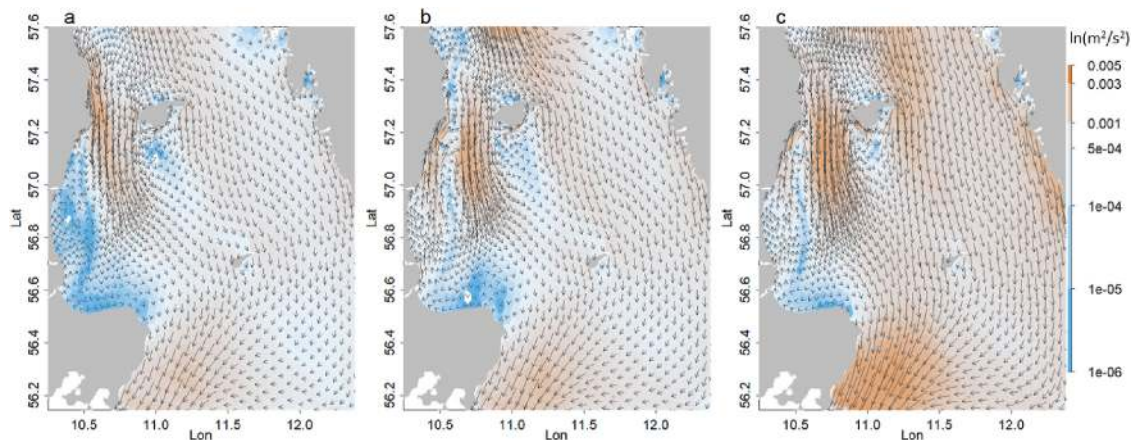


Fig. B.2. Surface current maps in August a) 2017, b) 2018 and c) 2019 in the Kattegat. Background colour indicates the horizontal kinetic energy in $\ln(m^2/s^2)$. The eddy kinetic energy highlights areas with intensified flow. The modelled surface current was averaged for each month.

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