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SEE
A North Sea Perspective on Shipping,
Energy and Environmental Aspects
in Maritime Spatial Planning

# Connectivity among marine protected areas, particularly valuable and vulnerable areas in the greater North Sea and Celtic Seas regions

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# Introduction to the connectivity study

The NorthSEE project is focusing on transnational coordination between plans and planning processes in the North Sea Region on three main topics: Energy, Shipping and Environment. For the environmental strand the partners have been researching the designation of Marine Protected Areas (MPAs) and other marine conservation measures, as well as the application of the Ecosystem Based Approach (EBA) in the planning processes.

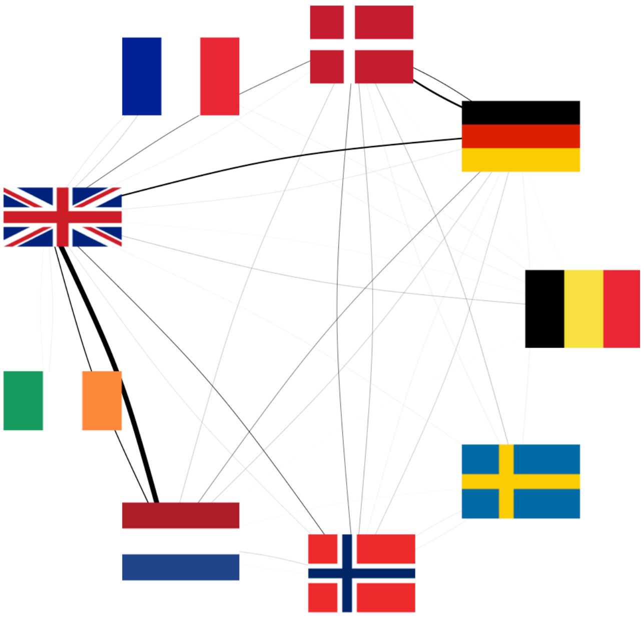
This report is part of WP3 environment and deals with the connectivity of MPAs in the North Sea. The reasons for this is that the North Sea ecosystem is interlinked and does not respect land borders. In MSP, it is important to understand the way in which a marine conservation site is relevant to areas elsewhere, and what significance different sites may have for the ecosystem as a whole.

Another incentive for analyzing the ecological coherence, is that the OSPAR Recommendation 2003/31, amended by OSPAR Recommendation 2010/2, on a network of Marine Protected Areas (MPAs) sets out the goal of OSPAR Contracting Parties (CPs) to continue the establishment of the OSPAR Network of MPAs in the North-East Atlantic. In the status report of 2016, OSPAR identified the need to using case-studies of connectivity to illustrate how the use of life-history traits information in combination with oceanographic modelling products can improve confidence in MPA network connectivity assessments.

This study meets the need described by OSPAR. In order to have a better understanding of ecological relationships and conditions, the connectivity between all marine protected areas (MPAs) and particularly valuable and vulnerable areas (as part of the Norwegian Management Plans), have been analyzed. This was done by applying a state-of-the-art biophysical model that represents the pelagic dispersal stage of a range of marine organisms approximated by passive drift. The larvae of lesser sand eel (Ammodytes marinus) were used as model species.

The study was initiated and financed through the NorthSEE project on request of the Norwegian Environmental Agency (NEA/Miljødirektoratet) and was carried out by the Norwegian Institute for Marine Research.

# Connectivity among marine protected areas / particularly valuable and vulnerable areas in the greater North Sea and Celtic Seas regions



Mats Huserbråten, Even Moland, Per Erik Jorde, Esben Moland Olsen, and Jon Albretsen

*Institute of Marine Research, Flødevigen*

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## 1. Preface

The Norwegian Institute of Marine Research (IMR) was requested by the Norwegian Environment Agency (NEA) to perform a study to elucidate on the topic of ecological coherence of marine protected areas (MPAs) in the greater North Sea region. A natural point of departure was to analyse the connectivity of the already established network of MPAs ratified by the Oslo-Paris (OSPAR) agreement. The project group at IMR identified the shelf seas within the greater North Sea and Celtic Seas regions as the proper scale of such a study, encompassing all the smaller maritime areas of (from west to east): Celtic Sea, Irish Sea, English Channel, North Sea, Skagerrak, Kattegat, as well as the Irish and Scottish continental shelf from south of Ireland, past Scotland, and all the way to the Norwegian west coast. NEA also wanted their management areas for lesser sand eel (*Ammodytes marinus*) in the North Sea to be included in the analyses. The management areas for lesser sand eel are identified as particularly valuable and vulnerable areas in the Norwegian management plans, and are areas of national importance for biological production. For the sake of this study, the particularly valuable and vulnerable areas were given equal weight in the analyses as the OSPAR MPAs. IMR here present a report on such a study that aimed to validate the connectivity of the OSPAR MPA network by biophysical modelling.

**Cover figure** reflects the relative contribution of the participating countries towards the connectivity of the OSPAR network of MPAs, where thickness of arcs represents export from one nation’s MPAs to another nation’s MPAs in a clockwise direction. Dominating the exchange within the network is the high connectivity found between MPAs located on the Dogger Bank in the central North Sea.

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## 2. Executive summary

The aim of this report was to elucidate on the potential connectivity within the already established OSPAR network of marine protected areas (MPAs) in the greater North Sea and Celtic Seas regions and the particularly valuable and vulnerable areas (PVVAs) in the Norwegian part of the North Sea (together hereby referred to as ‘the network’). This was done by applying a state of the art biophysical model that represents the pelagic dispersal stage of a range of marine organisms approximated by passive drift.

The network analyzed here can at first glance be perceived largely as an empty network, as reflected in either a lack of management plans or lack of reporting of such plans for the majority of MPAs that constitutes the network. For complementarity to this study we thus recommend a follow-up study that summarizes the management actions taken within the network along with any expected effects of actions taken and communicate this clearly–as this presents itself as a knowledge gap at the time of this study. We do want to convey that this knowledge gap entails some limitation to this study, as a central assumption is that all MPAs reported to OSPAR has some form of protection, ensuring viable populations of marine organisms within the MPAs.

Yet, should the participating countries decide to fulfill the OSPAR objective of a well managed network of MPAs and consequently give some level of protection within the MPAs, our *ad-hoc* analyses revealed a well-designed and highly connected network, where dispersal of pelagic larvae from the network may potentially supply almost the entire greater North Sea and Celtic Seas region with larvae.

At the same time there were some areas along the edge of the European continental shelf that did not receive larvae from MPAs–however, it is debatable whether MPAs as management tools would be effective within the open and highly advective environment found along the edge of the continental shelf, as the mobility of species spawning there is high (e.g. blue whiting, mackerel, saithe, hake, and cod), and their long egg and larval stage duration results in a vast dispersal potential; in which case effects from MPAs are not readily discernable from environmental variability.

Based on our comprehensive analyses on connectivity, and the synthesis between our connectivity results with the physical, biological and environmental data analyzed in the study, we present recommendations for conservation priorities in the event that conflicting interests might arise where the integrity of the network could be questioned or further conservation measures (e.g. fishery closures) considered (see Figure 1 for overview, and section *5.5 Conservation priorities* for further details).

Should one nominate areas where placement of further MPAs should be considered, we would recommend striving to create redundant dispersal pathways between the Celtic Seas and greater North Sea regions. This would mainly involve establishing new MPAs along the Irish western coast within the Irish Coastal Current, and along the edges of the Fladen Ground in the path of the Fair Isle Current.

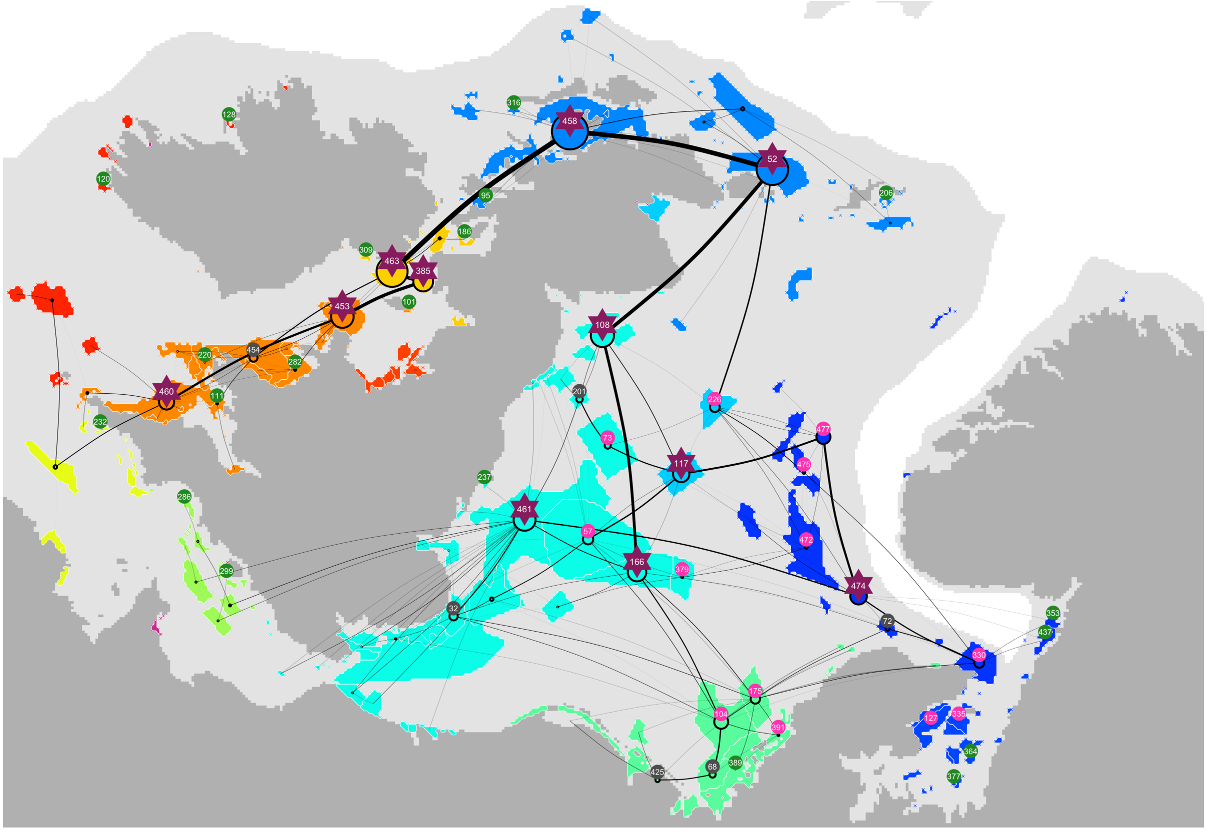

**Figure 1** Connectivity and conservation priorities in the greater North Sea and Celtic Seas regions. Here purple stars represent MPAs/PVVAs with highest priority for conservation, while pink, green, and grey circles are of second priority (with numbers as they appear in Table 1, section *5.5 Conservation priorities*). Size of coloured circles (without numbers) reflects how central the MPA/PVVA is for the overall connectivity of the network, while thickness of black lines reflects how important a given connection is in exchange of larvae (in a clockwise direction). Colour of MPA/PVVAs represents clusters of well-connected MPAs as identified in section *5.1 Topology of the network*. Note that the map is rotated ≈45° relative to true north due to the projection of the ocean model.

## 3. Introduction

The biological effects of MPAs are thoroughly described in the scientific literature, where MPAs typically contain higher densities and biomass of species affected by human activities (mainly fishing) outside the protected areas, and in addition have higher biodiversity than in surrounding areas (Fenberg et al. 2012, Baskett & Barnett 2015). Moreover, in order to maximise the viability of the protected populations, MPAs should be connected by the dispersal of pelagic offspring within the network (Palumbi 2004, Gaines et al. 2010). At the core of this notion of connectedness lays the theory of the dynamics of metapopulations, a bedrock in population ecology that names high connectivity among–and decreased mortality within–sub-populations as two of the most important processes that increases the resilience of the metapopulation as a whole (Hanski 1991). At the same time, ecological studies where connectivity among MPAs has been quantified in the wild are rare due to the expensive and labour-intensive methods currently available to document it (Sale et al. 2005, but see Harrison et al. 2012 and Almany et al. 2013, 2017 for examples). A substitute for such labour-intensive field studies is the use of hydrodynamic models coupled with particle tracking algorithms (e.g., Cowen et al. 2006). A few such biophysical modelling studies have previously been carried out to address connectivity among MPAs in the OSPAR area, such as the dispersal of several priority species between the Scottish areas (Gallego et al. 2016), in the Irish Sea (Gormley et al. 2015), and for deep-sea species north of the European Continental Shelf (Fox et al. 2016)–yet to date no study has looked at connectivity across the North Sea, Skagerrak, Kattegat, Celtic Sea, and Irish Sea as a whole (hereinafter referred to as the greater North Sea and Celtic Seas regions). It is worth mentioning that Roberts et al. (2010) looked at dispersal around the British Isles, but their ocean model was only based on tidal motion, and the precision of these results is low due to the high impact of prevailing winds on the currents in the area (Holt & Proctor 2008).

A short summary of the stated goals of the OSPAR MPA network is to (OSPAR 2006): (1) protect, conserve, and restore species, habitats and ecological processes that are adversely affected as results of human activity; (2) prevent degradation of and damage to species, habitats and ecological processes according to the precautionary principle; and (3) protect and conserve areas that best represent the range of species, habitats and ecological processes present in the OSPAR area. Furthermore, the OSPAR Commission has presented a set of guidelines on how to best develop an ecologically coherent network of MPAs within the OSPAR region. Roughly speaking, these guidelines can be divided into four design criteria (OSPAR 2006): (1) MPAs should contain one or more priority elements (termed *features*, can be individual species, habitats or biological processes) listed in OSPAR (2008a); (2) MPAs should contain a representative range of features across bio-geographical boundaries (as defined by Dinter 2001); (3) in order for features protected within the MPAs to be resilient/viable, the areas should be large enough to maintain/contain the features and preferably they should be replicated within each bio-geographical region; and (4) to maximise the network's viability and resilience to external effects the areas should also be connected through the dispersal of offspring/individuals.

In the absence of empirical data on the dispersal of for example eggs, larvae, fragments, or spores among the candidate areas, OSPAR developed a rule of thumb (the so-called "Madrid criteria" for ecological coherence) as a proxy for how the MPAs should be distributed geographically (OSPAR 2008b). The Madrid criteria suggest a maximum distance between MPAs of 250 km in coastal waters (within the territorial waters of the participating countries), 500 km offshore (within exclusive economic zone), and 1000 km in areas outside of national jurisdiction. The criteria were developed by review of the scientific literature and have most likely facilitated a faster creation process than would otherwise be possible in anticipation of empirical data. This is also explicitly stated in the OSPAR guidelines for MPA establishment (OSPAR 2006, Principle 10, page 7): "Lack of knowledge with regard to connectivity in the marine environment should not prevent the development of the OSPAR MPA network." Moreover, in the latest status report from the OSPAR biodiversity committee, the Intersessional Correspondence Group on Marine Protected Areas (ICG-MPA) provided recommendations for further work to measure the effectiveness of the already established OSPAR MPA network. As one of a total of seven points for improvements it was stated that (OSPAR 2016, page 32): “[Case studies of connectivity should be used] to illustrate how … life-history traits information in combination with oceanographic modelling products can improve confidence in MPA network connectivity assessments"; thus, the ICG-MPA wished a direct validation of the network by oceanographic-biological dispersal modelling (i.e. biophysical modelling).

As no scientific studies has looked at the connectivity among the OSPAR MPAs across the greater North Sea and Celtic Seas regions as a whole, we here aim to address this knowledge gap. More specifically, we will: **(1)** evaluate to what degree the already established OSPAR MPA network is ecologically coherent (i.e. assess the validity of the Madrid criteria), as suggested by OSPAR's biodiversity committee and ICG-MPA; **(2)** identify areas that based on connectivity estimates stand out as especially important should the integrity of MPA network be questioned or additional protection measures be afforded;

**(3)** identify knowledge gaps where further investigations are needed; and finally **(4)** we illustrate the functioning of the network with a case study on the connectivity of lesser sand eel (*Ammodytes marinus*) in the North Sea, as this keystone species have a life history that demands special attention to its management due to its population sub-structuring (*viz.* theory of the dynamics of metapopulations, Hanski 1991). To address the connectivity of the already established OSPAR network of MPAs (together with the PVVAs hereby referred to as 'the network') we here apply a state-of-the-art biophysical model that represents the pelagic dispersal stage of a range of marine organisms approximated by passive drift, replicated over 27 years of simulations (1990-2016). In our study we made a set of central *assumptions*, thus entailing the application of our results with a few *limitations*. The assumptions are: (1) our modeling approach is representative for organisms that have a bipartite lifecycle, which means that subsequent to their pelagic dispersal stage, organisms settle out of the pelagic into sedentary life stages where post-settlement movement is negligible; and (2) MPAs that constitutes the network have some form of protection, ensuring viable populations within the MPAs. We do want to emphasize that the assumption of negligible post-settlement movement is met for a diverse range of phyla present in the study area, including most benthic polychaetes, bivalves, and cnidarians, as well as many fish and crustaceans making our results widely applicable. However, we do acknowledge that the first assumption of protection was not possible to verify within the scope of our study. At the same time, if the goal of protection within the network is reached some time in the future, our results should remain valid given the large set of possible dynamical outcomes that our model represents (i.e. high temporal replication).

## 4. Materials and Methods

### *4.1 Synoptic overview of the large scale circulation patterns in the study area*

On the western side of the study domain, from Brittany (France) in the south, past the western coast of Ireland, and to the Fair Isle Passage north of Scotland, there is a coastal current running northwards along the coastline, here termed the Irish Coastal Current (ICC, see Figure 2 for schematic outline of currents). The ICC only separates from the coast to follow the fronts across the English Channel, St. George's Channel and North Channel (Fernand et al. 2006, Holt & Proctor 2008). Upon thermal stratification in summer however, these fronts are situated further offshore than in winter, for example reducing the exchange between the Celtic and Irish Sea (Brown et al. 2003). Within the thermally stratified water column inshore of these fronts, circulation is driven by tidal movement and currents are usually an order of magnitude lower than the residual currents outside the fronts (Holt & Proctor 2008).

Continuing into the Fair Isle Passage, the Fair Isle Current (FIC) transports the coastal water originating from west of the British Isles into the North Sea between Orkney and Shetland. Its path continues south past the Scottish coast, and before reaching 57°N it turns east in an anti-clockwise fashion, while deflecting parts of its mass south along the English coast and onto the shallower central/southern North Sea plateau (i.e. the Fulton Drift, FD) (Turrell 1992).

Also entering the North Sea from the north is the East Shetland Current (ESC), which transports Atlantic water into the North Sea in a southern direction along the eastern side of Shetland. Upon reaching 58°N, the East Shetland current also turns east and aligns with the FIC in a double-entrainment along the 100 m isobath, and together they form an anti-clockwise gyre over the Fladen ground. A branch of this double Fair Isle/East Shetland current (together referred to as the Dooley Current, DC) turns around the Ling bank and into Skagerrak, although with diminished strength (Svendsen et al. 1991, Turrell et al. 1996).

In the Norwegian Trench we find the bulk inflow of Atlantic water (Norwegian Trench Inflow, NTI) to the North Sea (Winther & Johannessen 2006, Hjøllo et al. 2009). However, the majority of this inflowing Atlantic water gets topographically steered along the western slopes of the Norwegian Trench at depth, and gets retroflected and eject underneath the Norwegian Coastal Current (NCC) on the eastern side of the Trench before reaching 59°N (Furnes et al. 1986).

The final (and smallest) source of Atlantic water flowing into the North Sea is through the English Channel (Channel Inflow, CI), yet for the most part of the year the circulation in the shallower southern parts of the North Sea is mainly driven by tidal motion. There is also a coastal current that transports freshwater from the major European rivers (Rhine and Elbe), along the Danish Jutlantic coast (i.e. the Jutlantic Coastal Current, JCC), and into the Skagerrak (Otto et al. 1990). Here in the Skagerrak the less saline water masses originating from the southern North Sea mixes with the brackish water from the Baltic current (BI), and gets transported out of the system via the NCC (Kristiansen & Aas 2015).

Whereas density differences and upstream conditions are the main forcing mechanisms driving the large scale currents in the study area over longer temporal scales, in winter and spring the currents can be highly variable both in direction and strength due to the prevailing winds (Holt & Proctor 2008). For example, in the period 1960-2000 variation in strength and direction of wind represented by the North Atlantic Oscillation (NAO) explains 44% of the total variation in winter/spring surface circulation of the North Sea (Mathis et al. 2015). Generally positive phases (i.e. westerly wind anomalies) yield high Atlantic inflow between Orkney and Shetland as well as an increased eastward and southward flow over the entire North Sea priming the counter-clockwise flow-through of the northern North Sea-Skagerrak circulation cell; whereas in extreme negative phases the circulation in the southern and central North Sea effectively stops, and most of the Orkney and Shetland inflow follows the Dooley current, rather than flowing into the southern North Sea (Furnes 1980, Winther & Johannessen 2006, Hjøllo et al. 2009). There is also a second mode of variation in winter circulation, independent of the NAO, explaining 22% of the variation in the past half-century. This second mode is characterized by episodes of high and low pressure system build up over the British Isles, which results in increased prevalence of north-western wind anomalies, leading to increased inflow of Atlantic water in the Norwegian Trench and over the open northern boundary between Shetland and the Trench, but also significantly decreasing the English channel inflow as well as reducing flow along continental Europe (Mathis et al. 2015).

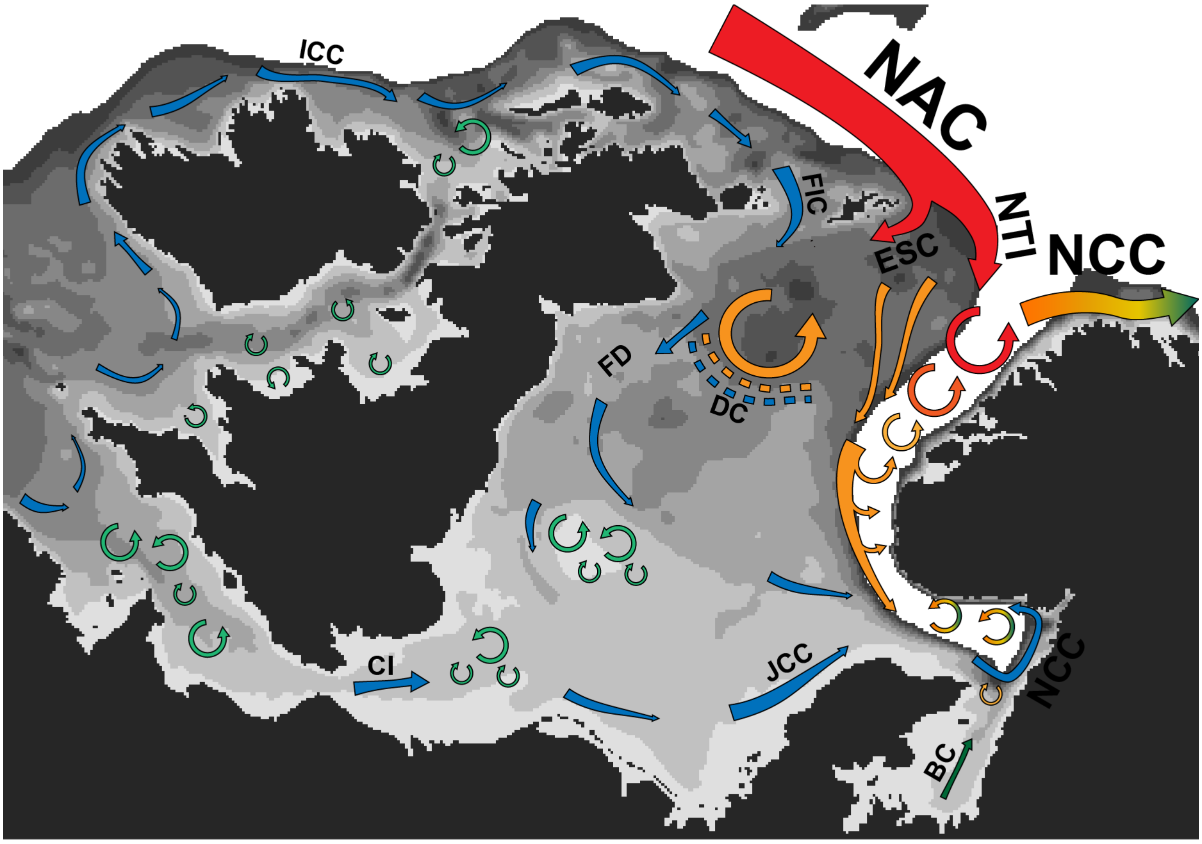

**Figure 2** Schematic outline of the main currents in the study area, where red arrows represents Atlantic water masses, orange arrows transformed Atlantic water (mainly cooled by heat exchange with atmosphere), blue arrows coastal water masses, and green circles/arrows indicates tidally mixed

waters with little residual flow. Here width of arrows and font size roughly scale to water transport. The abbreviated names of currents mentioned in text are (described in a clockwise manner): Irish Coastal Current (ICC), Fair Isle Current (FIC), Fulton Drift (FD), Dooley Current (DC), Channel Inflow (CI), Jutlantic Coastal Current (JCC), Baltic Current (BC), Norwegian Atlantic Current (NAC), East-Shetland Current (ESC), Norwegian Trench Inflow (NTI), and Norwegian Coastal Current (NCC).

### *4.2 Ocean circulation model and particle tracking algorithm*

The hydrodynamic model used to represent the currents and oceanographic conditions in the model area was a Regional Ocean Modeling System model (ROMS, http://myroms.org), a free-surface, hydrostatic, primitive equation ocean model (e.g. Shchepetkin & McWilliams 2005, Haidvogel et al. 2008). The time-varying arrays from the ROMS contained velocity fields and physical variables with a temporal resolution of 24h, a horizontal resolution of 4km x 4km, and a vertical resolution of 32 terrain following depth coordinates covering the North Atlantic and all the Nordic seas. More information about the ocean model and how it was forced (e.g. boundary conditions, atmospheric drivers, and freshwater input) can be found in Lien et al. (2013).

The advection of particles in the horizontal plane was modelled by the Runge-Kutta 4th order method, as implemented in IMR's standard particle tracking algorithm LADIM (Lagrangian Advection and DIfusion Model, Ådlandsvik & Sundby 1994). No vertical movement of particles was implemented. To prevent that bottom topography restrict the drift of particles (e.g. due to "beaching" of particles) they were fixed at depth between 0 and 10 m, which was the minimum depth interval available in the model. Particle trajectory simulations where run from February 1st to September 1st with a new set of particles released from MPAs every day of the simulation period, repeated for every year between 1990 and 2016. Thus 27 years of simulations ensured that most dynamical outcomes of different current regimes were realized, making the results presented here highly representative for both past and future drift scenarios. To make the analyses representative for a range of organisms with different length of their pelagic larval duration (PLD), we analyzed sequential segments of the drift trajectories, with PLD lengths classified into stepwise increments of 10, from 10 to 110 days. Here 1000 particles were every day for 180 days (starting at February 1st), where release location of the particles was chosen randomly among all 4km × 4km grid cells of the ROMS bottom-matrix that was within the extent of the MPAs. To quantify settlement, both within and outside MPAs, we integrated the number of days spent by particles in proximity of each grid cell of the bottom-matrix of the ROMS model that was shallower than 200 m. The same approach was used to quantify connectivity, where if a larva from one MPA was located within another MPA during the larva's "settlement phase" (i.e. during the final ten days of its dispersal phase) for at least one day, a connection was made. Since settlement days were integrated over subsequent ten-day periods, larvae could potentially spend their "settlement window" in several different MPAs.

### *4.3 Physical, biological and environmental data*

The spatial extent of- and information about individual OSPAR MPAs, the occurrence of OSPAR threatened or declining habitats, and bottom abrasion estimates was downloaded from OSPAR data and information management system ODIMS (available at: https://odims.ospar.org/maps). Here only MPAs situated on the European continental shelf at depths less than 200 m were included in the study (i.e. encompassing the entire sublittoral zone). Also included in the analyses were the Norwegian management areas for sand eel, identified as having especially high importance for biological production in the North Sea (available at: https://kartkatalog.miljodirektoratet.no/Dataset/Details/702). Bottom substrate data was extracted from the EUSeaMap project (available at: http://www.emodnet-seabedhabitats.eu/access-data/download-data), a European broad-scale seabed habitat map (Populus et al. 2017). Average summer (June, July, August)- and winter temperature (December, January, February) was extracted directly from the time-varying arrays of the ROMS archive. To be able to make inferences at the smallest comparable spatial scale, of which the ocean model had the coarsest resolution, all variables were extrapolated to each 4km × 4km grid cell of the ROMS bottom-matrix within the study area (see Figure 3 for spatial extent of MPAs, and section *Supplemental materials* maps for the other variables referred to above). This process of extrapolation caused some of the listed MPAs to disappear, owing to their small size and thus falling between grid points. Although the omission of some areas from the analyses was unfortunate, given their modest size they would most likely have had a negligible impact on the results.

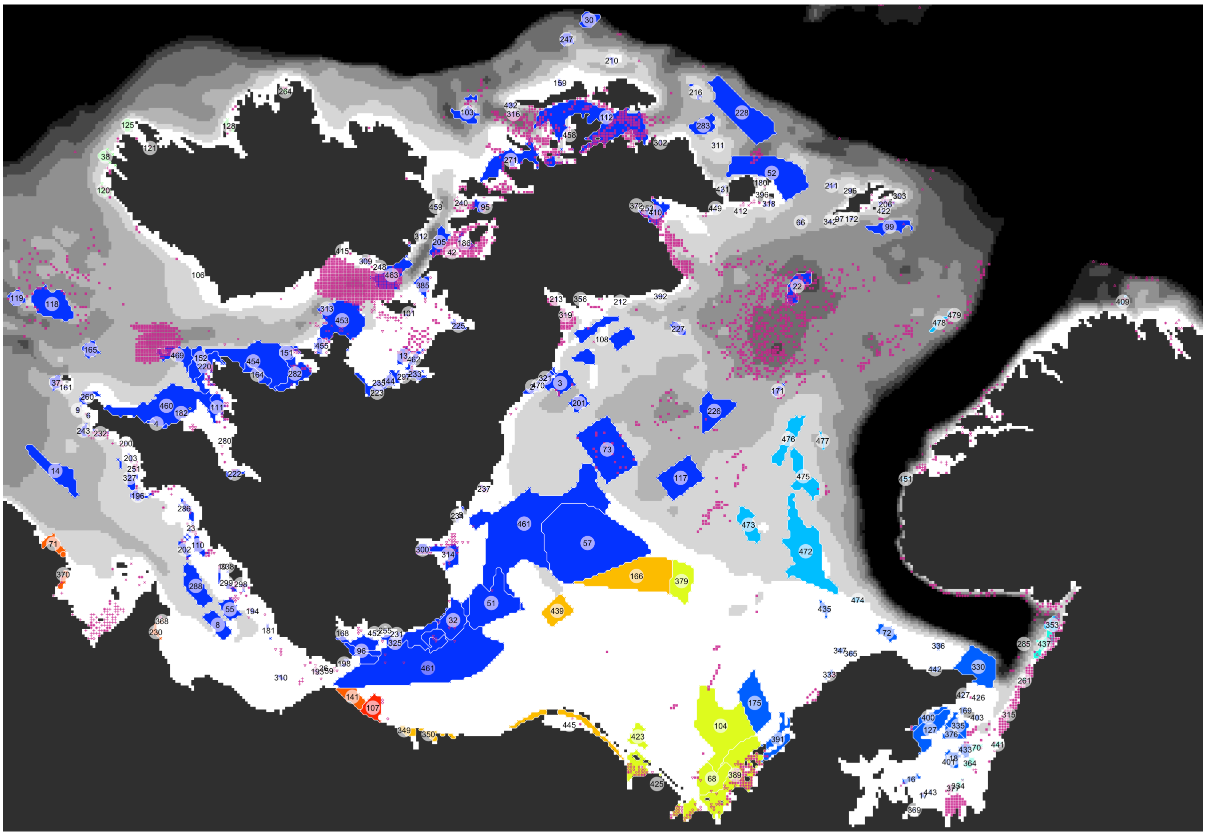

**Figure 3** Spatial extent of MPA/PVVAs established by the nine participating countries bordering the study area (where each colour represent the MPAs of a participating country), projected into the coordinate system of the ocean model (i.e. the ROMS bottom-matrix). Also plotted is the presence of features of conservation priority identified by OSPAR (purple symbols) and bathymetry of the study area, where areas of shaded grey represents depth range from 25 to 200 metres by increments of 25 metres.

For the case study on connectivity of sand eel among greater North Sea MPAs we estimated a “sand eel index” for each MPA based on the abundance of sand eel caught in the ICES international bottom trawl survey, North Sea (IBTS-N, available at: https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx) in the time period between 2010 and 2016. To estimate the spatial abundances of sand eel we fitted a generalised additive model (GAM) to the data with a log-link, using geographic coordinates of trawl hauls and the abundance of sand eel caught in the hauls (i.e., a 3-d poisson GAM). The estimated sand eel spatial abundance was subsequently extrapolated to each 4km × 4km grid point in the model area that was covered by the IBTS-N. For each MPA the sand eel index was calculated as the sum of abundances estimated at each 4km × 4km grid point within a MPA, log-transformed and scaled between 0 and 1. The sand eel index was later used in weighting of the connectivity matrix (see section: *Weighting of transport matrices*).

### *4.4 Weighting of transport matrices and network analyses*

Pineda et al. (2007) distinguishes between the three important concepts of propagule advection; namely larval transport, dispersal, and connectivity, where: (1) larval transport is defined as the physical process of advection of propagules (eggs, larvae, spores etc.) with ocean currents or similar processes; (2) where dispersal also includes the processes of settlement; and finally, (3) connectivity additionally encompass post-settlement mortality. Whereas the physical transport process was well modelled by our particle trajectory model, empirical data on settlement and post-settlement mortality rates were not available for this study. Thus, here we implemented a simplification of the settlement and post-settlement process by weighting the number of imported particles settling into a MPA with the similarity in substrate composition (as proxy for settlement probability), and bottom temperature (as proxy for post-settlement survival) of where the particle was coming from to where it settled. As a metric of similarity in substrate composition we calculated the Euclidean distance between pairs of MPAs, computed using Pythagora's formula among site-points positioned in a $p$-dimensional Euclidean space (Legendre & Legendre 2012), represented by the proportion of grid cell covered by the seven bottom substrate types in the study area (see *Supplemental materials*). As a temperature similarity metric we used the average difference in bottom temperature between two MPAs, divided by the standard deviation of bottom temperature in the whole continental shelf in the study area (i.e., standardised difference in temperature), scaled between 0 and 1, where similarity of 0 represented a difference of three standard deviations (or more). Each element (i.e. from $i^{th}$ MPA to $j^{th}$ MPA) in the transport matrix was thus subsequently multiplied by its corresponding element in the similarity matrices representing the difference in bottom substrate and summer and winter temperature (see *Supplemental materials* and for representation of connectivity matrix, both as a matrix, and visualised as a network).

Identifying barriers to connectivity in the highly advective and structurally homogenous habitat that is found in the greater North Sea and Celtic Seas regions is in itself a challenging task. Thus, here we applied the information theoretic clustering algorithm INFOMAP, specifically designed to identify clusters of well connected areas within a weighted and directed network (Rosvall & Bergstrom 2008). In practical terms the method identifies areas of the surface flow that is well connected, represented by a random walker stepping across the weighted and directional/asymmetric connectivity matrix. If/when the walker spends a proportionally longer time in certain areas of the connectivity matrix, that particular sub-space of the graph is deemed a cluster (see Rossi et al. 2014 and Ser-Giacomi et al. 2015 for applications of this algorithm, or Jacobi et al. 2012 for a similar application but using optimisation theory). These spatially delimited units we henceforth refer to as 'clusters of well connected MPAs', or just 'clusters'. Moreover, to quantify the overall connectivity of the network we calculated the betweenness centrality both between MPAs and their connections constituting the network. Betweenness centrality is the number of times a particular node (i.e., MPA) serves as a stepping-stone in the shortest paths between all other pairs of nodes in the network. This measure can be used to identify important connections/areas that facilitate connectivity across the network as a whole.

In the case study on sand eel we used a subset of the transport matrix made for the main study, where only connections made by eggs and larvae hatched between 1st of February and 1st of May and with a PLD between 60 and 90 days was used. Subsequently, the sand eel transport matrix was weighted by the sand eel index described in previous section as proxy both for spawning stock biomass (i.e., egg production) and settlement and post-settlement survival probability within MPAs. Here the rationale was that the spatial abundance of sand eel estimated by the Poission-GAM gave a rough estimate of both spawning stock biomass within each MPA, as well as suitability of habitat for settlement/post-settlement survival within each MPA. The scaling of the sand eel transport matrix was a two-step process: firstly, to scale production within MPAs (and thus to scale exports) we multiplied each row of the matrix with the eel index of each MPA, and subsequently to scale imports (i.e. settlement and post-settlement survival probability) we multiplied each column of the matrix with the eel index.

## 5. Results and discussion

### *5.1 Topology of the network*

Based on the simulated dispersal of 4 860 000 "larvae" released from 209 MPAs, replicated over 27 years of simulation, and averaged over ten different PLDs ranging from 10 to 110 days, around 27% of larvae settled within MPAs making a total of ≈113 000 000 connections. Moreover, a total of 12 clusters of well-connected MPAs were detected in the surface flow (0-10 m) within the greater North Sea and Celtic Seas regions (Figure 4). Here we describe the identified clusters roughly in a clockwise sequence around the British Isles, as this was generally how they were related to each other (*viz.* the large scale circulation patterns, Holt & Proctor 2008). As the Western Approaches (WAP) and Western English Channel (CHW) clusters were located at the starting point of the coastal current running along the western and northern margin of the study area, they naturally acted as sources to the Celtic Sea (CEL) cluster. In a stepping stone fashion with a net northwards flow, CEL was connected to the Irish Sea (IRS) and Scottish North (SCN); but was also weakly connected in a two-way manner to Liverpool Bay (LIV). There was also a weak two-way connection between CHW and Channel East (CHE), but where CHE was more connected to the Dogger Bank (DOG) cluster than the western areas. However, contrary to what would be expected given the residual northwestward flow of the Irish Coastal Current (Fernand et al. 2006), there was very limited connectivity between the WAP and SCN clusters.

Continuing along the northern margin of the study area, the SCN was connected to the Devil’s Hole (DVH) and DOG clusters, mainly acting as a net source to these areas, as particles were flowing with the Fair Isle Current flowing into the North Sea through the Fair Isle Passage and the East Shetland Current entering the North Sea east of Shetland (Svendsen et al. 1991, Turrell et al. 1996). The DVH, DOG, and German Bight (GRB) clusters all supplied the Northern North Sea and Skagerrak (NSS) cluster with recruits, as is highly parsimonious given that the vast majority of the water masses that enters the North Sea, exits via the Norwegian Coastal Current (Winther & Johannessen 2006).

Also manifesting itself in the network topology was a net eastward flow from the CHE cluster, and into DOG, from DOG to GRB, and from GRB into the NSS. A small portion of particles also connected the GRB to Skagen-Kattegat (SKA) cluster.

Do note that the ecological effect of the connectivity among clusters are expected to be low, as only 0.5% of all settlement-days accrued within MPAs outside the native cluster–that is, a larvae originating from a MPA within a particular cluster spent on average 0.5% of its “settlement window” of ten days within a MPA within a cluster other than where it was released. At the same time, up to 34% of settlement-days was retained within MPAs constituting the cluster, making some of the clusters highly coherent and self-sufficient (e.g. DOG, GRB, and CEL, all having around 30% retention), while some areas had a high leakage (i.e. low coherence) with a retention of around 6% of total settlement days within the cluster (e.g. NSS, WAP, and SKA).

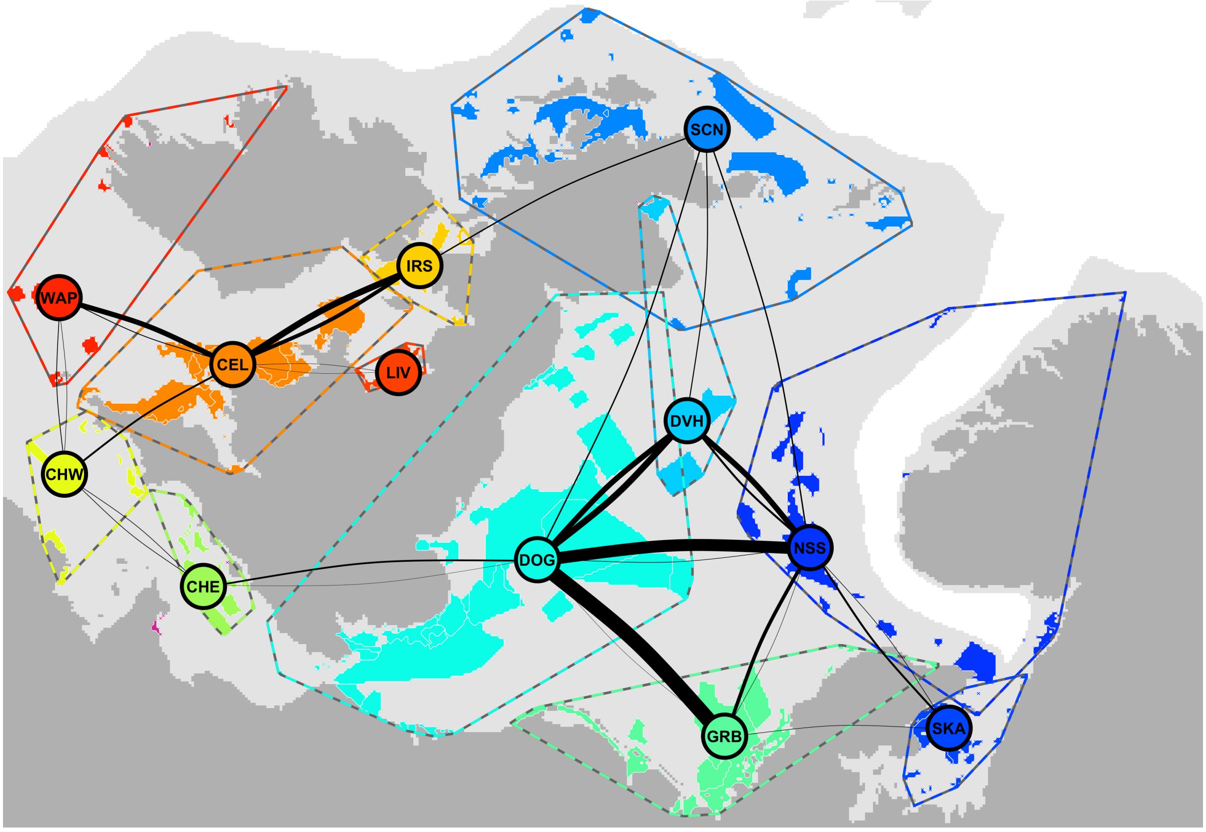

**Figure 4** Large scale topology of the network within the greater North Sea and Celtic Seas regions. Here coloured MPAs represents clusters of well-connected areas identified by INFOMAP algorithm, while thickness of arcs represents the number of particles exported from a given cluster in the clockwise direction.

Looking at the estimated betweenness centrality of the MPAs and their connections, some areas were more important in linking the network than others. A major feature of the network was the series of "stepping-stones" of shortest paths starting at the Bristol Channel Approaches (no. 460), and continuing along the path connecting the areas West Wales Marine (no. 454), North Anglesey Marine (no. 453), Luce Bay and Sands (no. 385), North Channel (no. 463), Inner Hebrides and the Minches (no. 458), North-West Orkney (no. 52), Firth Of Forth Banks Complex (no. 108) and Doggerbank (no. 166) (Figure 5). In practical terms, if for example leaving out the Inner Hebrides and the Minches or the North-West Orkney MPAs (no. 458 and 52), the overall export of propagules from the Celtic Seas to the greater North Sea regions would be greatly reduced. Although the most important paths in connecting the network, as indicated by the high betweenness centrality, had a slightly below the median absolute exchange in settlers compared to all the other connections in the network, and thus probably have a minor direct demographic effect; the connections may play an important role in exchange of genes, or as a path for re-colonization should for example a rare species go locally extinct within the North Sea. For example, in absolute numbers, the estimated exchange of larvae per year from MPA no. 463 to 458, from 458 to 52, and from 52 to 108 (i.e. the three most important connections in the network) was 3, 25, and 6; this out of ca. 1670, 9030, and 4700 larvae released in the three MPAs per year, respectively; which makes up on average 0.1% of total production within the three MPAs ending up in one of the other MPAs.

A total of 25 MPAs received less than 5% of the median number of larvae (import and self-recruitment combined), indicating low connectivity. Additionally, a total of seven MPAs received no particles from either itself or from other MPAs (Figure 5). The vast majority of these loosely connected areas where located close to, or immediately adjacent to land. We do note that a known weakness of the biophysical model is its poor ability to represent realistic flow of water masses and particles close to complex coastlines. Thus, whether the low connectivity observed for these coastal MPAs is an emergent property, or if it is an artifact of the method can only be speculated. At the same time some of these areas of low connectivity may have a genuinely low connectivity with the network. For example, MPA no. 479 that has been identified as of being high importance for the management of sand eel in the North Sea is situated within a current (the NAC) that only briefly enters the North Sea. Due to the position of the Viking Bank PVVAs within the NAC they may be more important as sources to areas along the Norwegian western/northwestern areas as opposed to the North Sea (for further discussion on the Viking Bank PVVAs see section *5.4 Case study on lesser sand eel in the North Sea*).

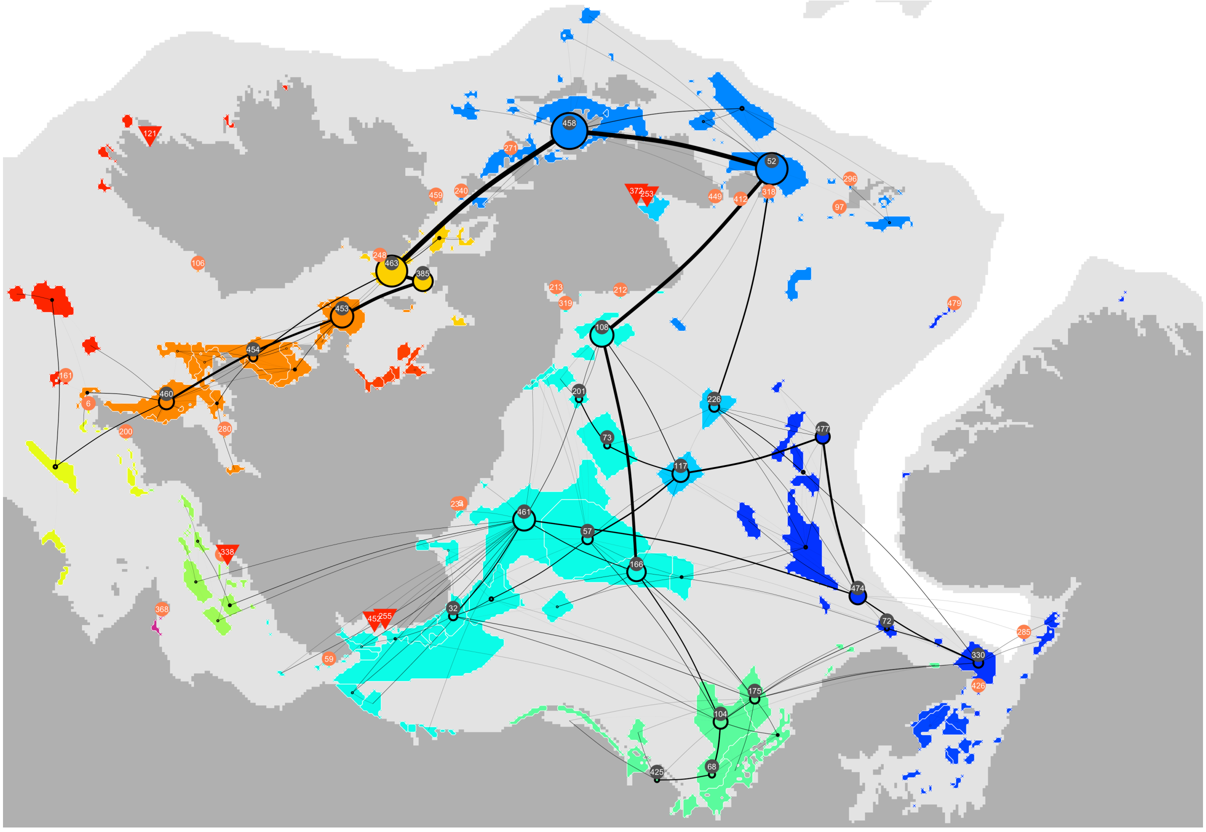

**Figure 5** Connectivity among MPA/PVVAs in the greater North Sea and Celtic Seas regions. Here sizes of coloured circles represent the calculated betweenness centrality of each MPA (i.e. how important the areas area in connecting the network), and thickness of arcs represents the betweenness centrality of their respective connections in the clockwise direction. Grey circles indicate the MPAs that had the 20 highest betweenness centrality-value, with numbers corresponding to their index in Table 1 (see section on *Conservation priorities*). Orange circles represents areas that have low connectivity, while red triangles are areas with no connectivity. Colour of MPAs represents clusters of well-connected areas identified by the INFOMAP algorithm.

### *5.2 Retention within-, and transport among MPAs*

The proportion of settlement days that was retained within native MPAs; that is, the same area that the particle was released from (i.e. self-recruitment within an MPA); was up to 0.4 for larvae with the shortest PLD, and steadily declining to below 0.1 at the longest PLD (Figure 6A). In contrast, the relationship between the proportion of settlement days spent within another MPA than the native area the particle was coming from and PLD followed a dome-like shape. Here the highest amount of settlement days accrued within other MPAs was ascertained when PLD was in the range 40-50 days at ≈0.17, and steadily declining towards a median of ≈0.12 at the longest PLD duration (Figure 6B). The remainder of settlement days, i.e. 1-($p_{\text{retained}}$+$p_{\text{connected}}$), was thus dispersed throughout the unprotected areas surrounding the

MPAs, as will be described in the next section. The cumulative distance at which 50% of connections were made was 88 km for the shortest PLD, and out to 176 km for the longest PLD (Figure 6C). The distance out to which 95% of the connections had been made (i.e., close to the maximum distance of any connection) was 206 km and 421 km for the shortest and longest PLD (Figure 6D).

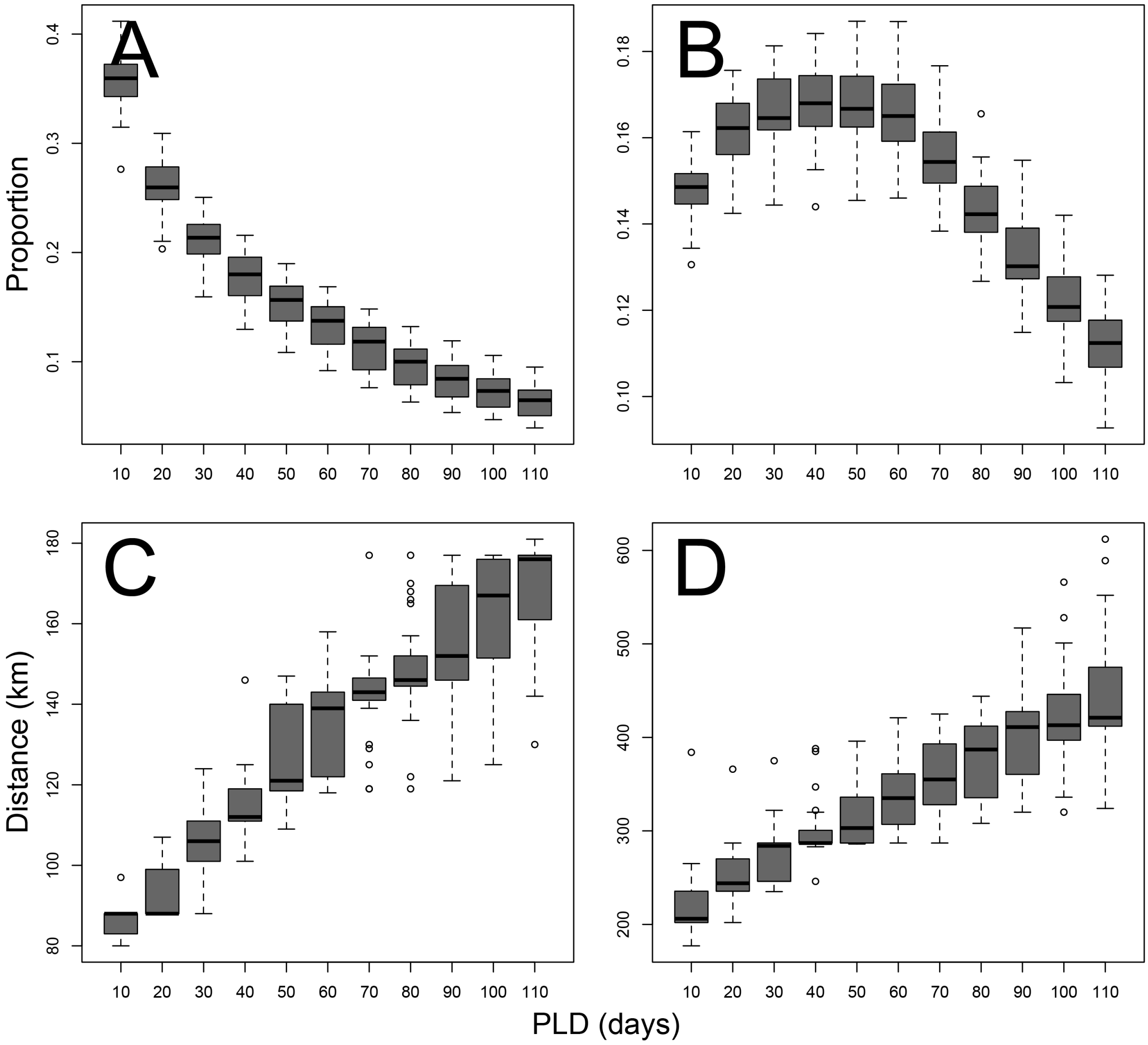

**Figure 6** Boxplots of: **(A)** of proportion of settlement days accrued within native MPAs (i.e. self-recruitment) plotted against pelagic larvae duration (PLD); **(B)** proportion of settlement days accrued within MPAs other that the native MPA (i.e. estimated connectivity) vs. PLD; **(C)** cumulative distance between source and sink MPA where 50% of settlement days had accrued vs. PLD, where the proportion that was retained within the native MPAs was subtracted; and **(D)** distance between source and sink MPA within which 95% of settlement days had accrued vs. PLD. Here the grey boxes represents the 1st and 3rd quartiles of the distributions, black bars within boxes the overall median of the distributions, stapled lines (i.e. the "whiskers") the interquartile range, and circles the outliers.

### *5.3 Dispersal from MPAs into unprotected[*] areas*

Overall, the ability of the network to supply larvae/benthic recruits outside MPAs was high. Especially satisfactory was the continuum of high coverage in the southern parts of the North Sea, stretching from the eastern parts of the English Channel, along a wide swath across the entire southern part of the North Sea and into the Skagerrak. There was also a high coverage in parts of the Celtic Sea, Irish Sea, and Liverpool Bay, as well as within the Scottish areas of Argyll, Minches, Marlin, and Fair Isle Passage. The lowest coverage was found along the continental shelf edge, stretching from south of Ireland and all the way into the Norwegian Trench, as well as along the coastlines of most countries (Figure 7). Do note that the superlatives used to describe the coverage has to be interpreted relative to each other, and not taken literally, as no validations have been done in field studies.

A major factor influencing this measure of relative coverage is the amount of water transported through the area (i.e. the level of “thinning”, or dilution of particles). For example on the Dogger Bank where retention of particles is high due to low residual flow, there will naturally be many settlement days accumulating due to the particles lingering on the bank. Whereas for example along the continental slope from east of Shetland and into the Norwegian Trench where the rate of transport of water is highest in the study area (Winther & Johannessen 2006), which leads to a low retention time of particles in the area, drastically reducing the amount of settlement days accumulating there. At the same time, it is debatable whether MPAs as management tools would be effective within the highly advective environment found along the edge of the continental shelf, as the mobility of species spawning there (e.g. blue whiting, mackerel, saithe, hake, and cod) is high and their long PLD results in a huge dispersal potential, in which case effects from MPAs are not readily discernable from environmental variability (Pelc et al. 2010). Also note the low coverage directly adjacent the coastline of most countries (i.e. red dots primarily occurring south and east along the coast), which is an artifact of the particle tracking model and calculation method of the settlement coverage, and can safely be ignored. This in contrast to wider areas along the coast that indicated low coverage, for example within semi-enclosed bays, which most likely are real phenomena arising from not having MPAs within the bay or along that particular coastal segment.

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[*] Note that although most of the MPAs listed in OSPAR’s database either completely lack or have not reported a management plan, and thus has an unknown protection status, we here refer to areas outside MPAs as unprotected, see final paragraph in *Introduction* and section *5.5 Conservation priorities*.

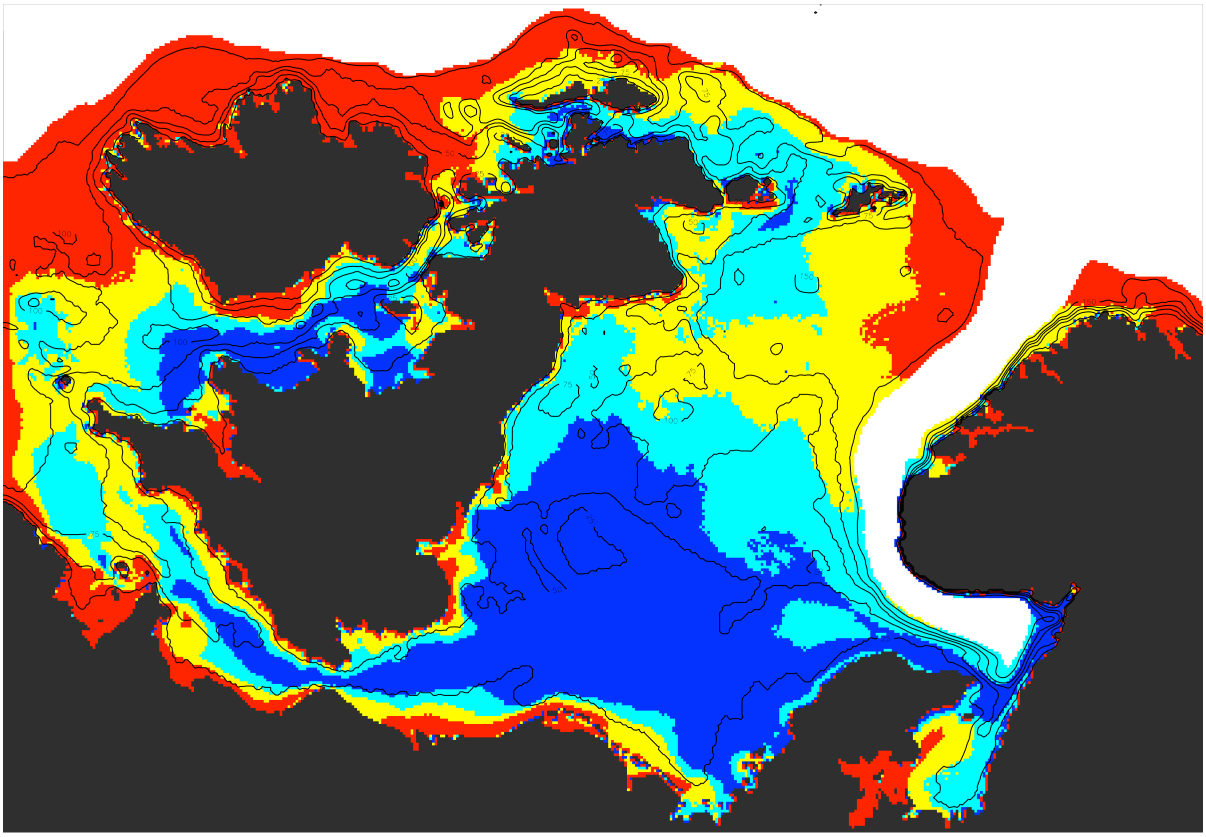

**Figure 7** Density of potential settlement of larvae originating from MPAs, which can be interpreted as "very good" (blue), "good" (light blue), "acceptable" (yellow), or "low" (red) coverage, as classified by the 1st, 2nd, and 3rd quartiles of the integrated settlement distribution. Note that these categories have to be compared relative to each other, rather than taken literally.

The inter-annual variability in settlement patterns was inversely related to the coverage, with high variability of settlement where coverage was low, for example along the continental shelf edge, and low variability almost everywhere else where the integrated settlement was at least at an acceptable level (Figure 8). The high variability of coverage that was found along the continental shelf edge is mainly due the highly advective pelagic habitat found there (as discussed in previous paragraph), as well as the high variability in strength and direction of prevalent winds (especially in spring), which directly influences the flow of particles into/along the shelf edge (Heath et al. 1999, Fox et al. 2016). The high variability in settlement patterns found along the coastline mainly follows the same causation as the low coverage found there (as discussed in previous paragraph).

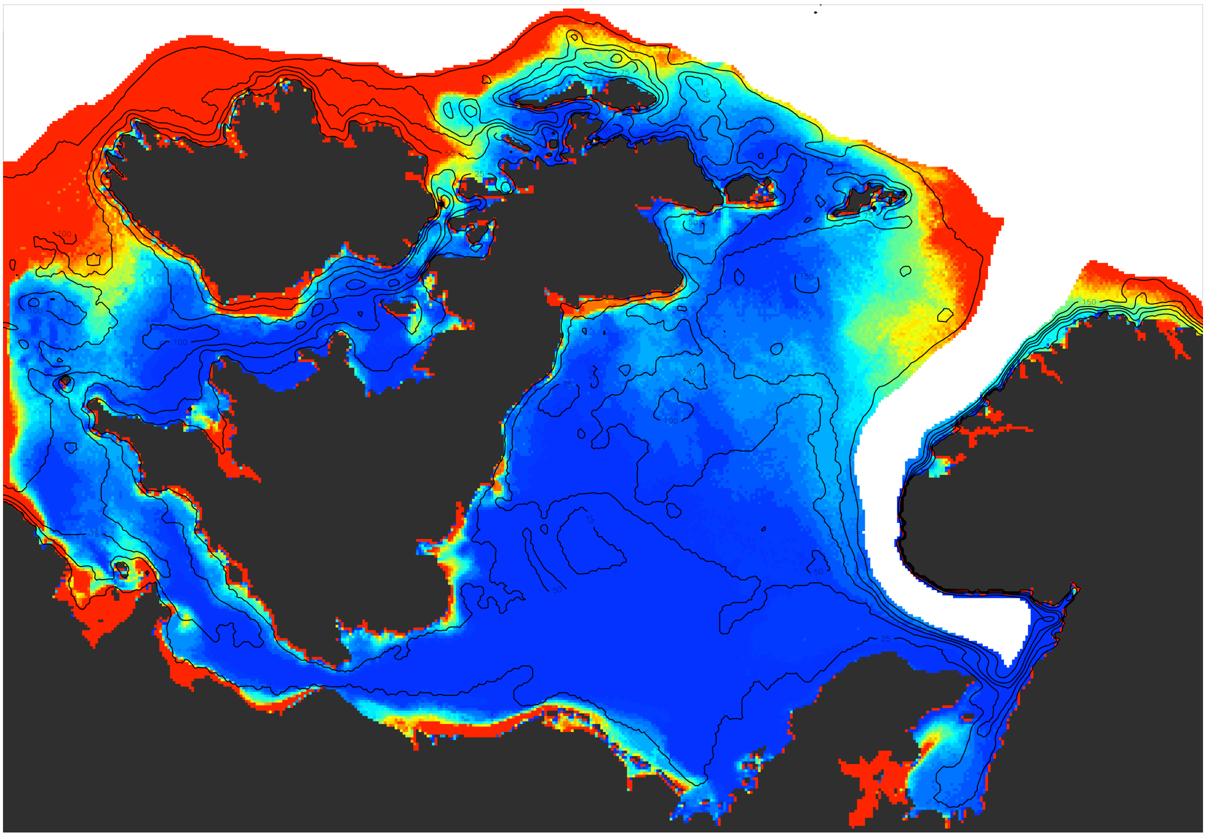

**Figure 8** Inter-annual variation in settlement patterns. Here the color scale represents the number of years (out of 27) where the given grid cell received a certain level of settlement days, i.e. areas where settled larvae are located every year (blue), half of the years (green), and only a few years (red).

Looking at the area of influence of the 12 clusters of well-connected areas; that is, the area where settlement from one particular cluster represents the majority of settlement days; there was a clear alignment with the large-scale circulation patterns (Figure 9). Here the MPAs constituting the WAP cluster supplied larvae to the Celtic and Irish shelf, while CEL dominated in the more inshore areas of the Celtic Sea and the Saint George's Channel, only to be replaced by the IRS cluster within the Northern Channel. Although the area of influence of the WAP cluster covered a fair stretch along the Irish western coast, there was a distinct break in coverage between the WAP and SCN just north of Ulster and Donegal Bay. SCN covered a wide swath across the entire northern part of the study area, while NSS covered the area along the Norwegian Trench all the way into the Skagerrak, only interrupted by the SCN along the eastern slopes of the Ling Bank and down towards the Eigersunds Bank. At the same time, the DOG cluster dominated almost the entire southern part of the North Sea, stretching all the way from the English Channel in the west, into the coastal waters of southern Skagerrak together with the GRB cluster.

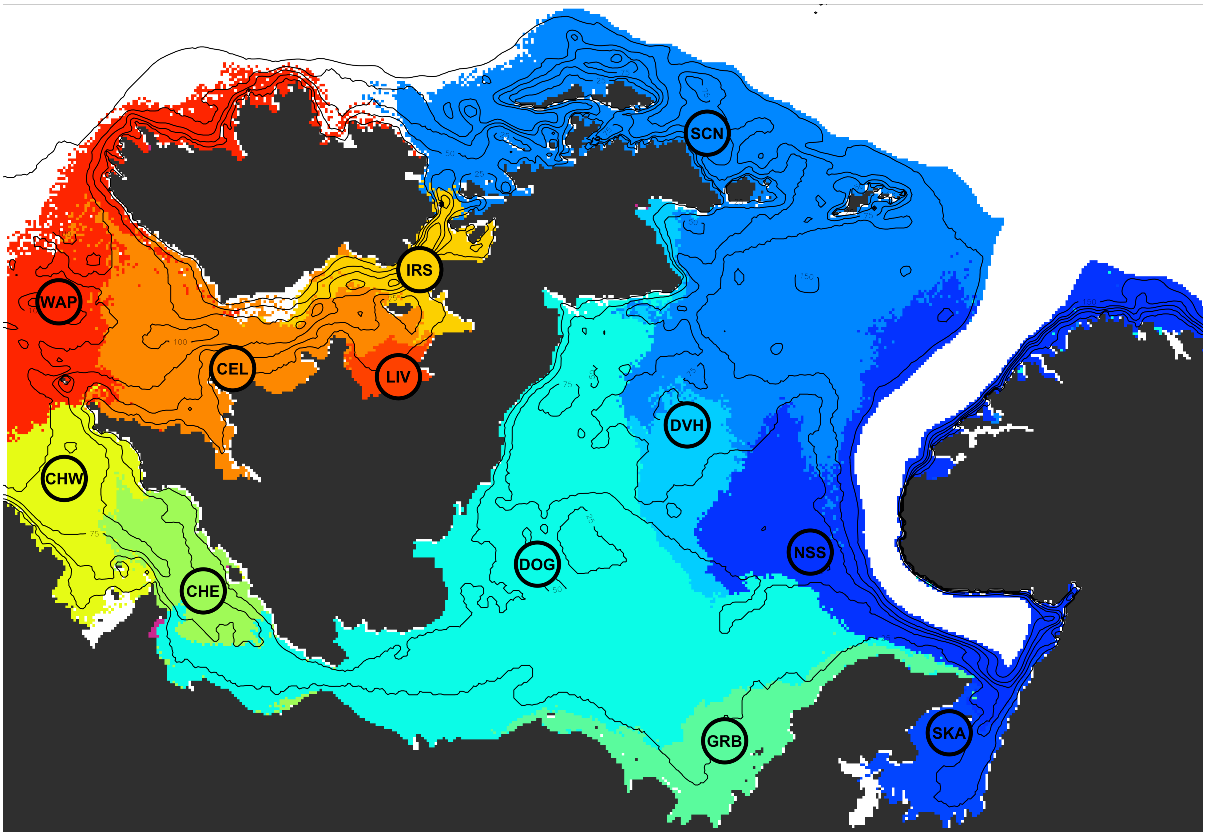

**Figure 9** Area of influence of the identified clusters of well-connected MPAs, i.e. the coloured areas represents the area where settled larvae originating from one particular cluster represents the majority of settled larvae.

### *5.4 Filling the network with purpose: protection of a keystone species in the North Sea, the lesser sand eel*

Over-exploitation characterise many marine populations in the world where more than 60% of the world's fished stocks should be fished less to reverse or avoid previous or on-going collapses (Worm et al. 2009). A proposed solution to safeguard against unsustainable harvesting, while at the same time replenish fished populations, is the use of no-take marine reserves as management tools (Gell & Roberts 2003, Harrison et al. 2012). Of all the fished species in the North Sea, there are few species more suitable for an area-based protection scheme than the lesser sand eel (*Ammodytes marinus*), where the four major criteria taken into consideration here are: (1) the stock has been shown to be prone to overfishing reflecting the inadequacy of traditional management tools (ICES 2017); (2) their high specificity in bottom substrate requirements leads to high site fidelity of juveniles and adults (Wright et al. 2000, Holland et al. 2005), making the process of identifying suitable sites for protection relatively easy; (3) the sand eel holds a key position in the marine food web of the North Sea, being a crucial link between lower levels (i.e., zooplankton) and higher levels such as seabirds

(Frederiksen et al. 2007), where a large, viable population of lesser sand eel is a prerequisite for a healthy food web in the North Sea (Wanless et al. 2005); and finally (4), the fragmented nature of sand eel habitat across the North Sea seascape leads to sub-structuring of the stock (Gibb et al. 2017), which call for extraordinary management actions–*viz.* reducing patch mortality and ensuring connectivity among patches, two of the most important processes that increases the resilience of a fragmented population (Hanski 1991). However, do note that even though striving for protection will most likely benefit the North Sea sand eel population in the long run, changes in environmental conditions can confound the effect of protection (Greenstreet et al. 2006). This sensitivity to environmental conditions is largely because the recruitment strength of sand eel is highly dependent on certain species of zooplankton (Arnott & Ruxton 2002, Van Deur et al. 2009), of which abundance in turn is highly dependent on climate (Beaugrand et al. 2008, Beaugrand & Kirby 2010).

To the results of the case study focused on sand eel in the North Sea; the modelled spatial abundance of sand eel was mainly concentrated across the central North Sea, from the north-western tip of the Dogger Bank and into the Skagerrak. There were also elevated estimated abundances from over the Utsira high and north towards the Viking Bank, as well as south towards the German Bight and north of Orkney. The modelled distribution compared well with the distribution of commercial catches of sand eel in the North Sea (ICES 2017). Moreover, there was a high connectivity between the areas located on the Dogger Bank, with relatively less connectivity among the other areas that had a sand eel index (Figure 10). Besides this strong connection between Southern North Sea (no. 461) and Doggerbank (no. 57), and to some extent among Southern North Sea, Doggerbank, and Swallow Sand (no. 73), the average levels of exchange indicate low demographic impact of the connectivity. We thus suggest an even finer network of no-take marine reserves to augment the existing network, matching the small patch sizes of sand eel preferred habitat. A point of departure would be to perform a similar analysis to our large scale connectivity study, but on a much smaller scale, based on the fishing areas defined by ICES (2017) and bottom substrate–at the time of this study, the data of the spatial extent of the sand eel fishing areas were not publicly available, and the resolution of the ROMS ocean model applied here we consider too crude to represent these small-scale processes adequately.

Worth mentioning is also the low connectivity observed for the Viking bank PVVAs, which have been identified as specially important in the management of the North Sea sand eel populations. While it is indeed true that the Viking Bank had a low connectivity with the network in the North Sea, this is mainly because most of the water masses that flows through this particular area only briefly visits the Norwegian Trench en-route to the Norwegian Sea. The Viking Bank may thus play an important part in the population dynamics of downstream populations, for example along the Norwegian western coast, as have been hypothesised to be the case for North Sea cod also spawning on the Viking Bank (Huserbråten et al. 2018).

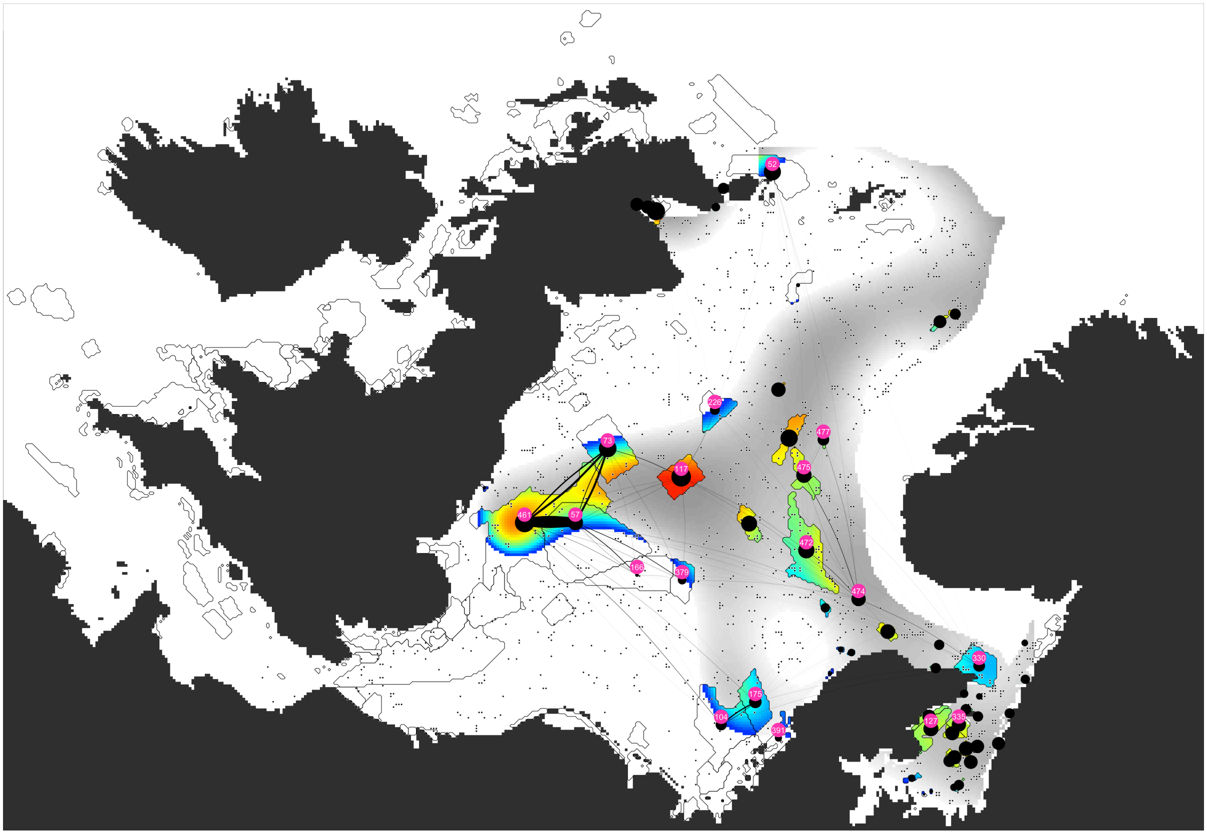

**Figure 10** Connectivity of sand eel between MPAs in North Sea. Here pink circles represents areas that contains sand eel and also exports larvae to other areas containing sand eel. Black arcs represents export of sand eel from one MPA to another in a clockwise direction, and circles represent the sand eel index estimated for the MPA (note that the sand eel index is approximately the logarithm of the modelled sand eel abundance). Rainbow colours represent the modelled spatial abundance of sand eel within MPAs (based on ICES IBTS-N), from low abundance (blue) to high (red); while Grey shade in background represents the modelled abundance outside the MPAs. Small black dots represent the sampling locations for the IBTS-N.

### *5.5 Conservation priorities*

Synthesising the knowledge gathered during the study, we made a short-list of 50 prioritised MPAs from the initial long list of 209 areas, based on four well-defined criteria (as will be described below). We assigned the highest priority to 11 areas, based on their integral role as stepping-stones connecting the Celtic Seas and greater North Sea domains of the network. Here the criterion used was that the highly prioritised areas all had a betweenness centrality more than 40% of the highest value of any area in the network, a threshold which ensured that the shortest path between the Celtic Seas and greater North Sea domains of the network would remain intact. Thereafter we identified 39 areas of secondary conservation priority, based three specific set of rules. The three different categories of second priority either: (1) contained a feature for conservation priority as identified by OSPAR (2006); (2) were shown to both contain a high number of sand eel and served as sources of sand eel larvae to other PVVAs/MPAs; or (3) had a central position in the network as indicated by their above zero betweenness centrality, although not having as important position as the 1st priority MPAs (Table 1). Do note that of the 50 short-listed areas, only 14 had a management plan associated with them–and only one of the MPAs in the highest priority category had a management plan associated with it. However, this particular area was related to the Norwegian management of sand eel in the North Sea, and not for biodiversity conservation *per se*.

Managers should also consider giving added protection to the 32 MPAs that had low or no connectivity with the network (Figure 5); this because of the low amount of larvae received from other MPAs, at least theoretically decreasing their resilience (cf. discussion in the *Introduction*). However, given the uncertainty in the ability of the model in representing a realistic flow along the coastline, this advice has to be evaluated from a case-to-case basis where detailed local knowledge of currents and topography has to weigh in.

Furthermore, of all the 50 short-listed MPAs, 18 had a higher than average bottom abrasion than the average in the study area (either on surface of substrate or sub-surface) indicative of higher than average bottom trawl activity; but only two of these areas were fished significantly more than the average (i.e., more than two standard deviations above the mean). On the other hand, none of the areas where trawled significantly less than the average of the study area. It is important to note that the vast majority of studies where positive effects of MPAs have been documented are indeed areas that have some restriction on fishing activity applied within their borders (as summarised by Fenberg et al. 2012 and Baskett & Barnett 2015). This important requirement (i.e. less or no fishing) must not be under-communicated when designing management plans for these areas (as discussed in Agardy et al. 2011). Apart from a few of the Danish MPAs and the Norwegian PVVAs, none of the registered areas where management goals had been supplied indicated a restriction to fishing. Thus, it appears to be a mismatch between the understanding of the mechanisms behind the biological functioning of MPAs, management actions, and observed fishing activity. On the other hand, since we have no further information on the management plans of most of the MPAs, we can make no inference on whether this is in line with management goals or not. In any case, we stress that the conservation benefits expected from MPAs mainly arises from regulating the fishing activity within the area, and the 50 areas short-listed here would be good candidates for such fishing closures (at least on the basis of this connectivity study), should such management actions be prioritised.

**Table 1** Summary table with conservation priorities identified in the study. Listed here is the number associated with the individual MPA in OSPARs database, the cluster it was assigned to, the country within which exclusive economic zone the MPA was located, and priority class it was assigned to. Further information includes: average substrate abrasion (i.e., trawling, both surface of substrate and subsurface), size of MPA in number of grid cells in ROMS bottom-matrix, year of designation, name of MPA in native language, median depth within ROMS bottom-matrix, average summer (JJA) and winter (DJF) temperatures (estimated from ROMS archive), the modelled sand eel index and export level of sand eel larvae to other areas, betweenness centrality within the network, and Shannon's diversity index for both diversity of OSPAR features within the area and the substrate diversity.

| Index | Cluster | Country | Priority | Managment plan | Abrasion surface | Abrasion subsurface | Size | Designated | Name | Depth | Winter | Summer | Sand eel index | Sand eel export | Betweenness centrality | Diversity feature | Diveristy substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 474 | NSS | NOR | 1 | yes | 3.0 | 1.2 | 7 | 2009 | TOBISFELT | 50 | 6.6 | 11.0 | 0.7 | 0.1 | 0.5 | 0.0 | 0.7 |
| 472 | NSS | NOR | 2 | yes | -0.2 | -0.3 | 326 | 2009 | TOBISFELT | 50 | 6.6 | 10.2 | 0.8 | 0.0 | 0.1 | 0.0 | 0.2 |
| 330 | NSS | DNK | 2 | yes | 2.3 | 2.2 | 150 | 2009 | SKAGENS GREN OG SKAGERRAK | 41 | 6.4 | 11.6 | 0.6 | 0.0 | 0.3 | 0.0 | 1.0 |
| 475 | NSS | NOR | 2 | yes | -0.1 | -0.3 | 87 | 2009 | TOBISFELT | 66 | 7.0 | 8.5 | 0.8 | 0.0 | 0.1 | 0.0 | 0.1 |
| 477 | NSS | NOR | 2 | yes | 0.0 | -0.3 | 7 | 2009 | TOBISFELT | 78 | 7.2 | 7.5 | 0.6 | 0.0 | 0.4 | 0.0 | 0.0 |
| 72 | NSS | DNK | 3 | yes | -0.2 | 0.2 | 30 | 2009 | GULE REV | 25 | 6.0 | 13.6 | 0.7 | 0.0 | 0.1 | 0.0 | 0.6 |
| 437 | NSS | SWE | 4 | yes | 0.3 | 0.7 | 34 | 2006 | KOSTERFJORDEN-VÄDERÖFJORDEN | 44 | 6.4 | 11.7 | 0.0 | 0.0 | 0.0 | 1.1 | 1.0 |
| 353 | NSS | NOR | 4 | non transfered | -0.3 | -0.1 | 22 | 2010 | YTRE HVALER | 59 | 6.9 | 10.0 | 0.0 | 0.0 | 0.0 | 1.1 | 1.3 |
| 127 | SKA | DNK | 2 | yes | NA | NA | 93 | 2009 | ÅLBORG BUGT, ØSTLIGE DEL | 10 | 3.2 | 16.9 | 0.8 | 0.0 | 0.0 | 0.0 | 0.9 |
| 335 | SKA | DNK | 2 | non transfered | -0.6 | -0.6 | 40 | 2007 | STRANDENGE PÅ LÆSØ OG HAVET SYD HERFOR | 10 | 3.7 | 17.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.4 |
| 364 | SKA | SWE | 4 | yes | 0.1 | 0.1 | 11 | 2006 | LILLA MIDDELGRUND | 34 | 6.3 | 13.2 | 0.7 | 0.0 | 0.0 | 0.7 | 1.0 |
| 377 | SKA | DNK | 4 | yes | -0.6 | -0.6 | 2 | 2009 | STORE MIDDELGRUND | 31 | 6.0 | 13.6 | 0.3 | 0.0 | 0.0 | 0.7 | 0.7 |
| 458 | SCN | GBR | 1 | non reported | -0.1 | 0.1 | 519 | 2017 | INNER HEBRIDES AND THE MINCHES | 37 | 7.7 | 12.4 | 0.0 | 0.0 | 1.0 | 1.4 | 1.8 |
| 52 | SCN | GBR | 1 | non reported | -0.5 | -0.6 | 270 | 2014 | NORTH-WEST ORKNEY | 68 | 8.0 | 10.6 | 0.9 | 0.1 | 0.9 | 0.0 | 0.9 |
| 206 | SCN | GBR | 4 | non reported | -0.4 | -0.5 | 11 | 2014 | FETLAR TO HAROLDSWICK | 56 | 7.4 | 10.3 | 0.0 | 0.0 | 0.0 | 0.7 | 1.0 |
| 316 | SCN | GBR | 4 | non transfered | -0.5 | -0.5 | 9 | 2012 | EAST MINGULAY | 131 | 8.7 | 9.5 | 0.0 | 0.0 | 0.0 | 0.7 | 0.6 |
| 95 | SCN | GBR | 4 | non reported | -0.5 | -0.1 | 2 | 2014 | LOCH SWEEN | 22 | 6.8 | 13.4 | 0.0 | 0.0 | 0.0 | 0.7 | 0.0 |
| 117 | DVH | GBR | 1 | non reported | -0.6 | -0.6 | 157 | 2016 | FULMAR | 75 | 7.4 | 7.7 | 1.0 | 0.1 | 0.5 | 0.0 | 0.1 |
| 226 | DVH | GBR | 2 | non reported | -0.5 | -0.6 | 116 | 2014 | EAST OF GANNET; MONTROSE FIELDS | 81 | 7.7 | 8.0 | 0.5 | 0.0 | 0.3 | 0.0 | 0.3 |
| 461 | DOG | GBR | 1 | non reported | 0.1 | 0.4 | 1643 | 2017 | SOUTHERN NORTH SEA | 30 | 7.0 | 14.6 | 1.0 | 1.0 | 0.6 | 0.7 | 0.6 |
| 166 | DOG | NLD | 1 | non reported | -0.1 | 0.3 | 306 | 2009 | DOGGERBANK | 29 | 6.3 | 14.3 | 0.1 | 0.0 | 0.5 | 0.0 | 0.6 |
| 108 | DOG | GBR | 1 | non reported | -0.5 | -0.3 | 139 | 2014 | FIRTH OF FORTH BANKS COMPLEX | 51 | 7.0 | 11.1 | 0.0 | 0.0 | 0.6 | 0.0 | 0.6 |
| 57 | DOG | GBR | 2 | non existent | -0.2 | -0.2 | 806 | 2011 | DOGGER BANK | 22 | 6.4 | 14.8 | 0.8 | 0.7 | 0.3 | 0.0 | 0.6 |
| 73 | DOG | GBR | 2 | non reported | 0.0 | -0.4 | 309 | 2014 | SWALLOW SAND | 63 | 7.4 | 8.8 | 0.9 | 0.3 | 0.2 | 0.0 | 0.2 |
| 379 | DOG | DEU | 2 | non existent | -0.3 | 0.4 | 109 | 2008 | DOGGERBANK | 30 | 6.4 | 14.0 | 0.4 | 0.0 | 0.1 | 0.0 | 0.1 |
| 32 | DOG | GBR | 3 | non transfered | -0.4 | 0.4 | 99 | 2011 | HAISBOROUGH, HAMMOND AND WINTERTON | 19 | 5.8 | 16.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.7 |
| 201 | DOG | GBR | 3 | non reported | -0.6 | -0.6 | 32 | 2014 | NORTH EAST OF FARNES DEEP | 67 | 7.5 | 9.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.6 |
| 237 | DOG | GBR | 4 | non transfered | 0.0 | -0.4 | 4 | 2005 | FLAMBOROUGH HEAD | 16 | 6.1 | 14.3 | 0.1 | 0.0 | 0.0 | 0.7 | 1.0 |
| 104 | GRB | DEU | 2 | non existent | -0.4 | -0.2 | 368 | 2008 | SYLT.AUSSENR.-OESTL.DT.BUCHT | 21 | 5.3 | 16.0 | 0.5 | 0.1 | 0.4 | 0.0 | 0.5 |
| 175 | GRB | DNK | 2 | yes | -0.4 | -0.4 | 162 | 2007 | SYDLIGE NORDSØ | 20 | 5.0 | 16.0 | 0.6 | 0.1 | 0.3 | 0.0 | 0.7 |
| 391 | GRB | DNK | 2 | non transfered | 0.1 | 1.0 | 70 | 2009 | VADEHAVET MED RIBE Å, TVED Å OG VARDE Å VEST FOR VARDE | 10 | 2.6 | 18.3 | 0.3 | 0.0 | 0.1 | 0.0 | 0.5 |
| 68 | GRB | DEU | 3 | non reported | 0.0 | 1.0 | 105 | 2005 | S-H SEABIRD PROTECTION AREA | 13 | 4.0 | 17.5 | 0.0 | 0.0 | 0.2 | 0.7 | 0.9 |
| 425 | GRB | DEU | 3 | yes | 0.0 | 1.0 | 103 | 2006 | LOWER SAXONY WADDEN SEA | 10 | 3.7 | 18.2 | 0.0 | 0.0 | 0.1 | 1.1 | 0.3 |
| 389 | GRB | DEU | 4 | yes | 0.1 | 1.3 | 248 | 2005 | S-H WADDEN SEA NATIONAL PARK | 10 | 3.1 | 18.3 | 0.0 | 0.0 | 0.0 | 1.1 | 0.4 |
| 286 | CHE | GBR | 4 | non transfered | -0.6 | -0.5 | 21 | 2011 | LYME BAY AND TORBAY | 31 | 8.8 | 15.6 | 0.0 | 0.0 | 0.0 | 1.4 | 1.4 |
| 299 | CHE | GBR | 4 | non transfered | NA | NA | 14 | 2005 | SOUTH WIGHT MARITIME | 24 | 7.7 | 17.3 | 0.0 | 0.0 | 0.0 | 1.1 | 1.0 |
| 232 | CHW | GBR | 4 | non transfered | NA | NA | 5 | 2005 | FAL AND HELFORD | 29 | 9.9 | 14.1 | 0.0 | 0.0 | 0.0 | 0.7 | 0.7 |
| 463 | IRS | GBR | 1 | non reported | 0.4 | 0.9 | 95 | 2017 | NORTH CHANNEL | 58 | 8.2 | 11.4 | 0.0 | 0.0 | 0.9 | 0.7 | 1.7 |
| 385 | IRS | GBR | 1 | non transfered | -0.6 | -0.6 | 29 | 2005 | LUCE BAY AND SANDS | 21 | 7.3 | 14.1 | 0.0 | 0.0 | 0.6 | 0.0 | 0.9 |
| 186 | IRS | GBR | 4 | non reported | 0.4 | 0.9 | 18 | 2014 | SOUTH ARRAN | 38 | 7.1 | 12.6 | 0.0 | 0.0 | 0.0 | 1.1 | 1.5 |
| 309 | IRS | GBR | 4 | non transfered | -0.6 | -0.5 | 7 | 2005 | MURLOUGH | 20 | 7.2 | 12.9 | 0.0 | 0.0 | 0.0 | 0.7 | 1.0 |
| 460 | CEL | GBR | 1 | non reported | -0.4 | 0.0 | 293 | 2017 | BRISTOL CHANNEL APPROACHES / DYNESFEYDD MOR HAFREN | 34 | 9.1 | 15.6 | 0.0 | 0.0 | 0.4 | 0.0 | 0.9 |
| 453 | CEL | GBR | 1 | non reported | -0.4 | -0.1 | 192 | 2017 | NORTH ANGLESEY MARINE / GOGLEDD MON FOROL | 43 | 8.4 | 13.6 | 0.0 | 0.0 | 0.6 | 1.1 | 1.2 |
| 454 | CEL | GBR | 3 | non reported | -0.4 | -0.2 | 270 | 2017 | WEST WALES MARINE / GORLLEWIN CYMRU FOROL | 26 | 8.4 | 15.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.6 |
| 220 | CEL | GBR | 4 | non transfered | -0.2 | -0.1 | 86 | 2005 | PEMBROKESHIRE MARINE / SIR BENFRO FOROL | 39 | 9.0 | 14.9 | 0.0 | 0.0 | 0.0 | 1.4 | 1.1 |
| 282 | CEL | GBR | 4 | yes | -0.6 | -0.6 | 76 | 2005 | PEN LLYN A`R SARNAU / LLEYN PENINSULA AND THE SARNAU | 10 | 6.7 | 17.1 | 0.0 | 0.0 | 0.1 | 1.8 | 1.1 |
| 111 | CEL | GBR | 4 | non transfered | -0.6 | -0.6 | 40 | 2005 | CARMARTHEN BAY AND ESTUARIES / BAE CAERFYRDDIN AC ABEROEDD | 23 | 7.2 | 17.0 | 0.0 | 0.0 | 0.1 | 0.7 | 0.7 |
| 101 | CEL | GBR | 4 | non transfered | -0.6 | -0.5 | 5 | 2012 | RAMSEY, ISLE OF MAN | 12 | 7.3 | 14.6 | 0.0 | 0.0 | 0.0 | 0.7 | 0.7 |
| 120 | WAP | IRL | 4 | non transfered | -0.2 | -0.5 | 11 | 2009 | ROARINGWATER BAY AND ISLANDS | 58 | 9.6 | 12.0 | 0.0 | 0.0 | 0.0 | 0.7 | 1.5 |
| 128 | WAP | IRL | 4 | non transfered | -0.6 | -0.6 | 8 | 2010 | KILKIERAN BAY AND ISLANDS | 23 | 8.3 | 15.1 | 0.0 | 0.0 | 0.0 | 0.7 | 0.4 |

## 6. Conclusions, advice and future research needs

Our *ad-hoc* analyses revealed a well-designed and potentially highly connected network, where dispersal of pelagic larvae from MPAs and PVVAs may potentially supply almost the entire greater North Sea and Celtic Seas region with benthic recruits–given that the species assemblage is present and maintained with viable spawning biomass, or even enhanced spawning biomass if closed to fishing, within MPAs. However there were some uncovered areas along the edge of the European continental shelf, but it is debatable whether MPAs as management tools would be effective within the highly advective environment found along the edge of the continental slope. Should one nominate areas where placement of further MPAs should be considered, we would recommend striving to create redundant dispersal pathways between the Celtic Seas and greater North Sea regions. This would mainly involve new areas along the Irish western coast within the Irish Coastal Current, and along the edges of the Fladen Ground within the path of the Fair Isle Current.

The network analyzed here can at first glance be perceived as an empty network, as reflected in either a lack of management plans or lack of reporting of such plans for the majority of MPAs that constitute the network. It is not our intention here to relegate the network to mere “paper parks”, because it is our expressive belief that the network can act more like a scaffolding ready to be filled with purpose, as long as managers and Contracting Parties to OSPAR communicate the content of the network in an honest way and commit to future action. For complementarity to this study we thus recommend to OSPAR a follow-up study that summarizes the management actions taken within the network and communicate this clearly, along with any expected effects of actions taken. OSPAR databases should be updated accordingly. Subsequently, studies that quantify the biological state within MPAs and their conservation effect should be commissioned.

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## 8. Supplemental materials

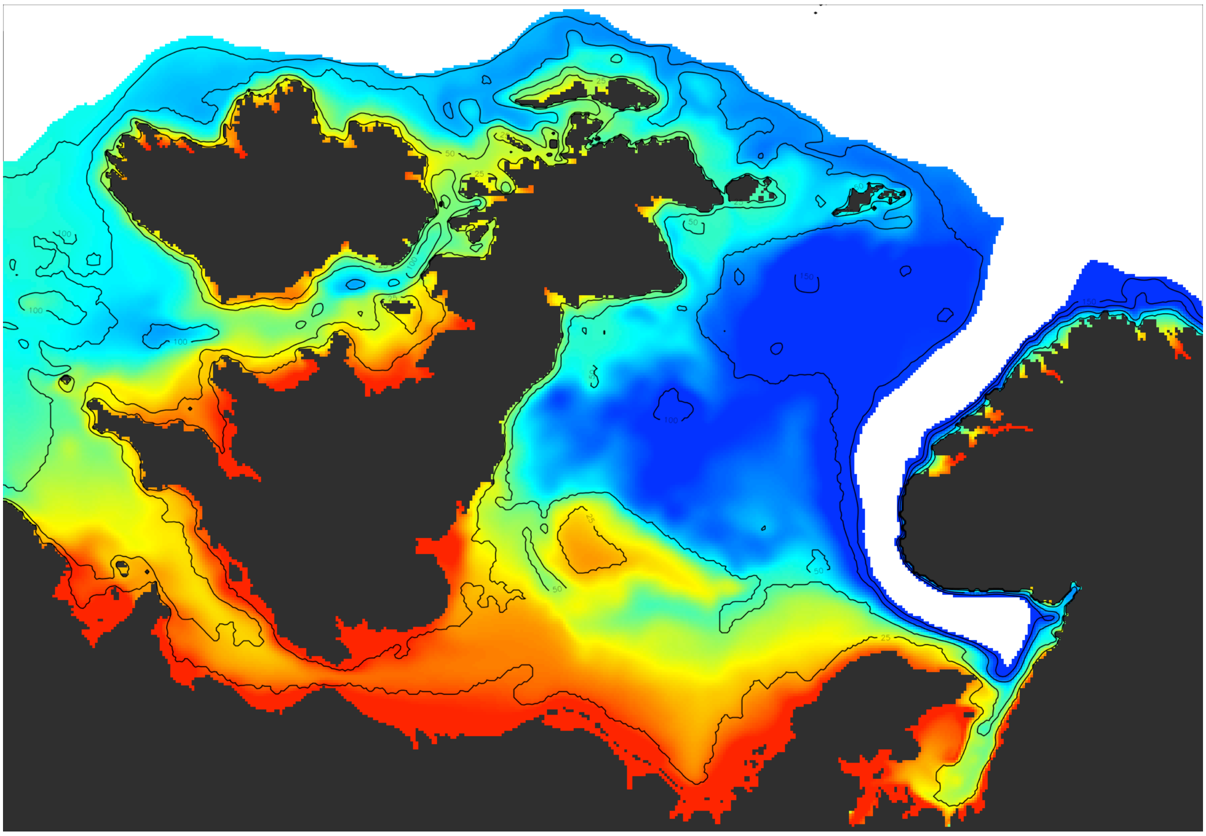

**Figure S1** Average bottom temperature in summer (June, July, August), between 1990 and 2016 calculated from the ROMS ocean model, from warm (red), temperate (green), and cold (blue) areas.

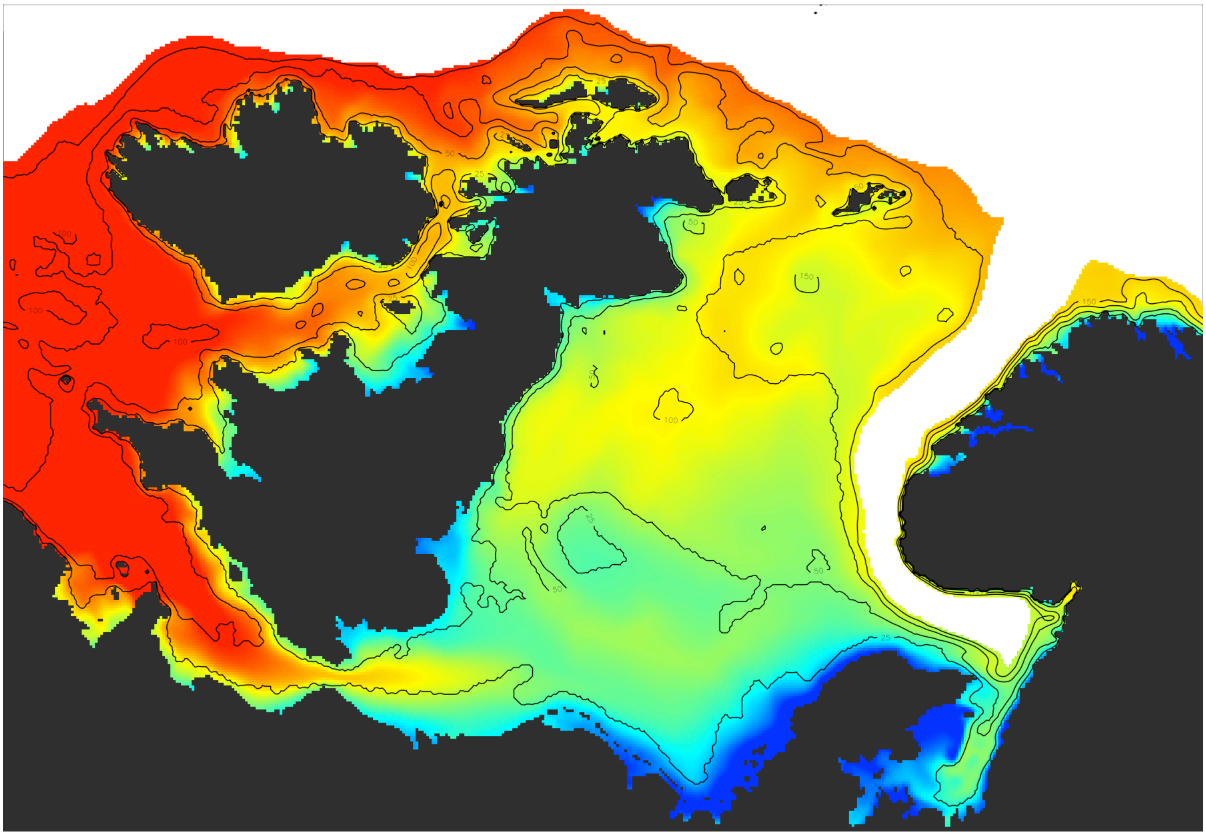

**Figure S2** Average bottom temperature in winter (December, January, February), between 1990 and 2016 calculated from the ROMS ocean model, from warm (red), temperate (green), and cold (blue) areas.

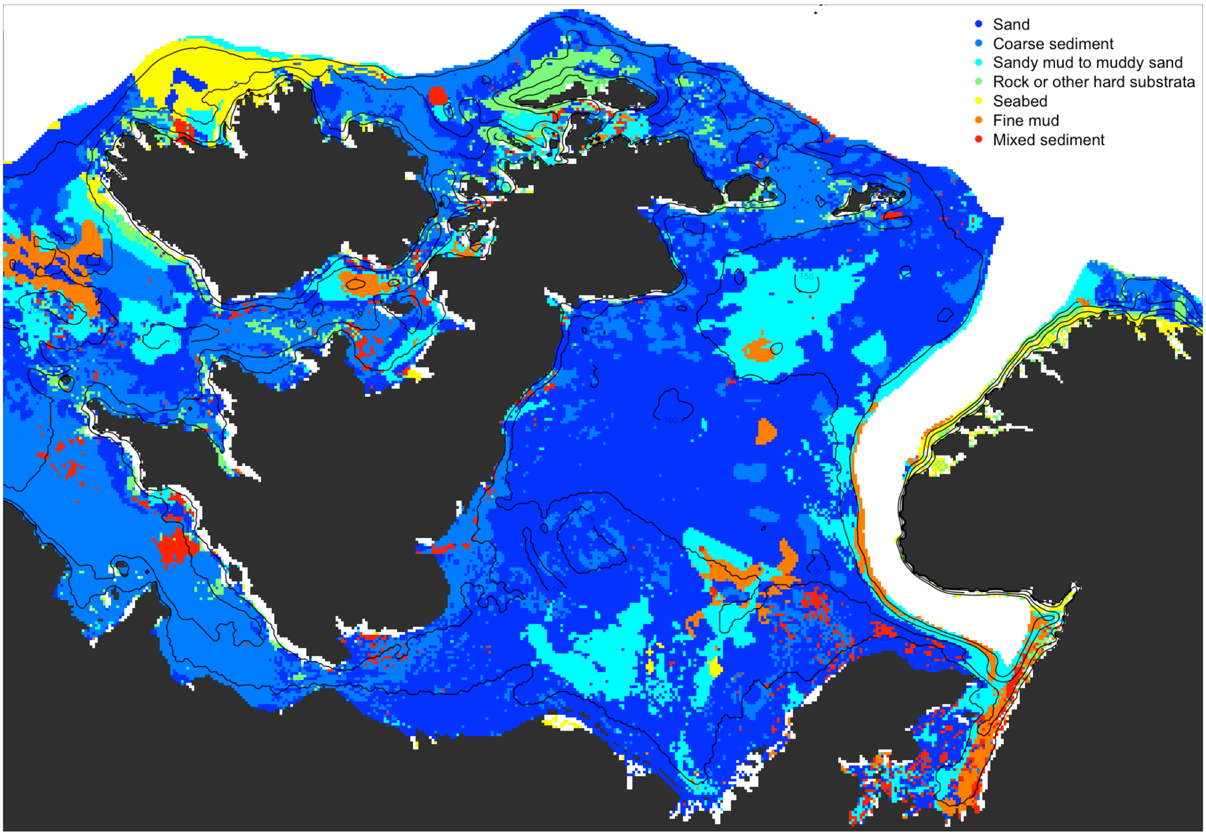

**Figure S3** Bottom substrate in the study area extrapolated from the EUSeaMap project, projected into the ROMS bottom-matrix.

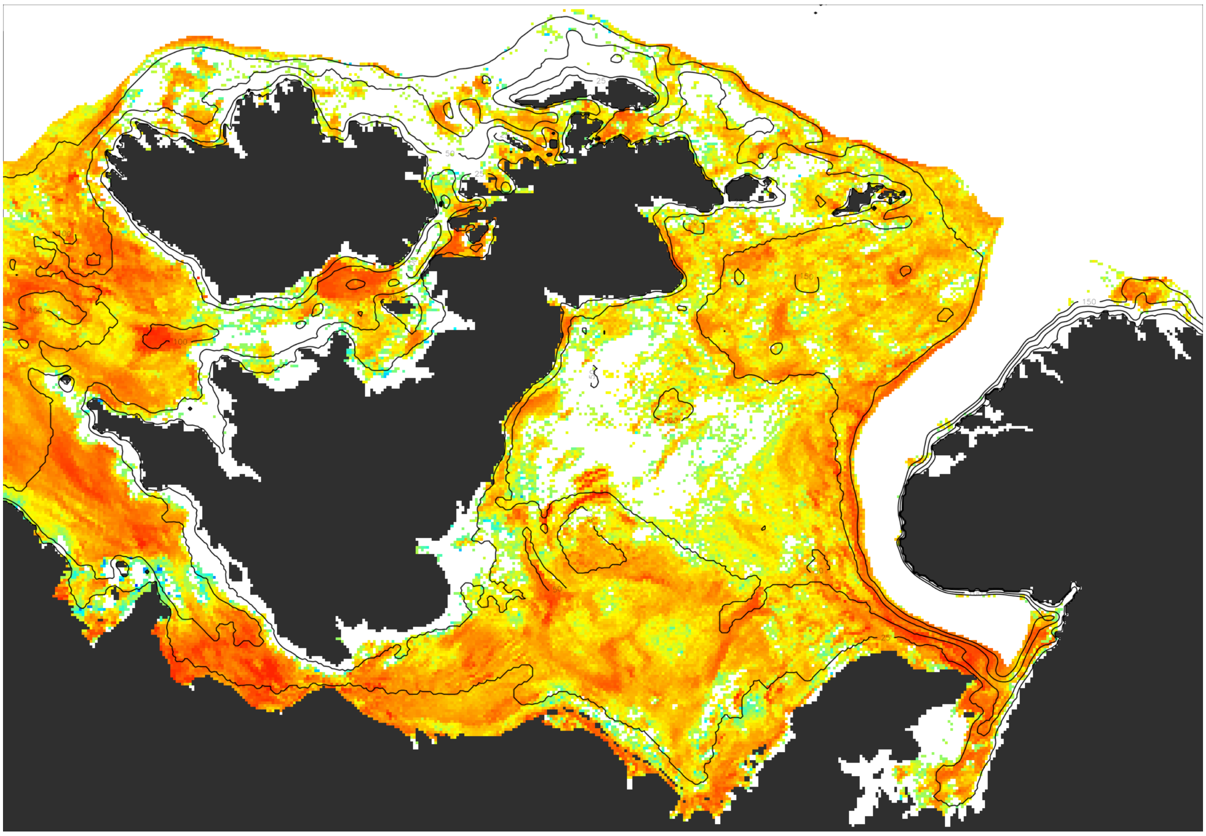

**Figure S4** Abrasion from trawling in 2015, on and below substrate surface summed together, projected into the ROMS bottom-matrix. Here high trawling activity is represented in red, medium in green, and low activity in blue.

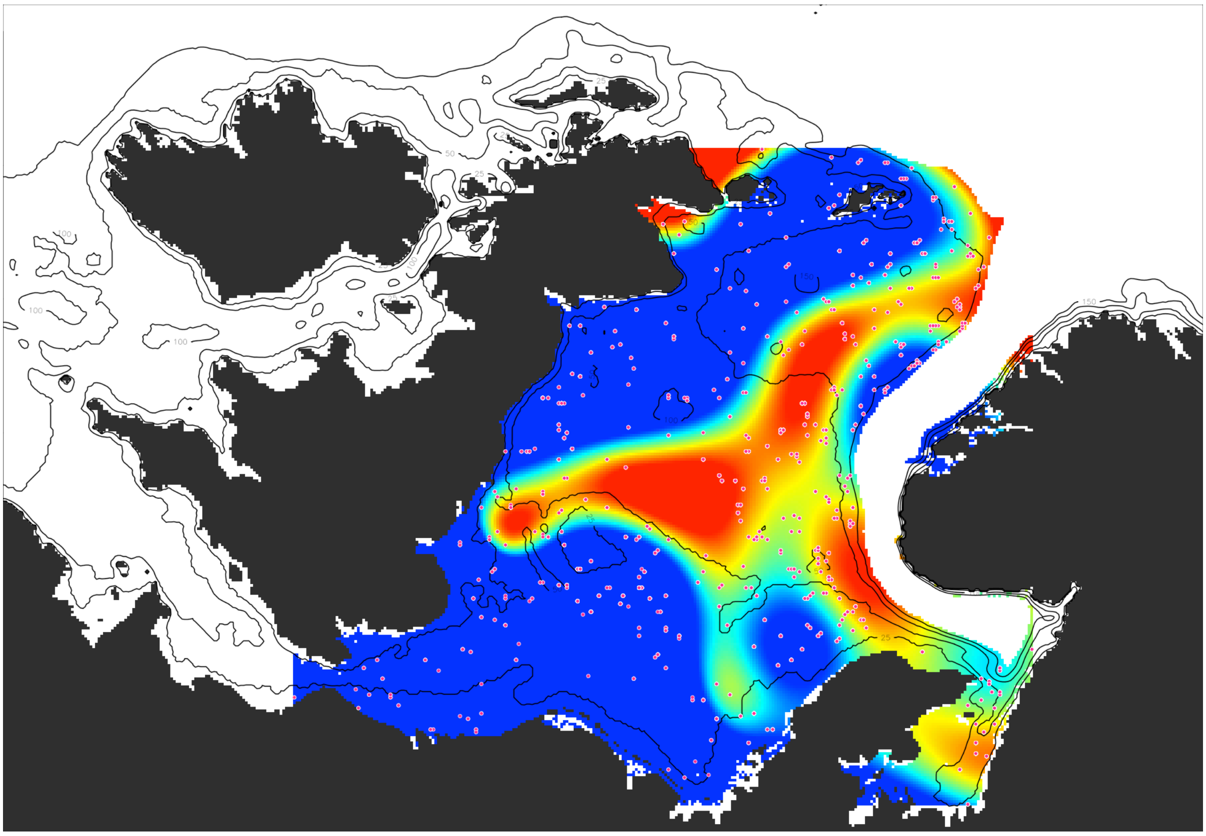

**Figure S5** Estimated spatial abundance of sand eel in the greater North Sea area. Pink circles represent the sampling locations during IBTS-N, while rainbow colours represents the modelled spatial abundance of sand eel (based on ICES IBTS-N), from low abundance (blue) to high (red).

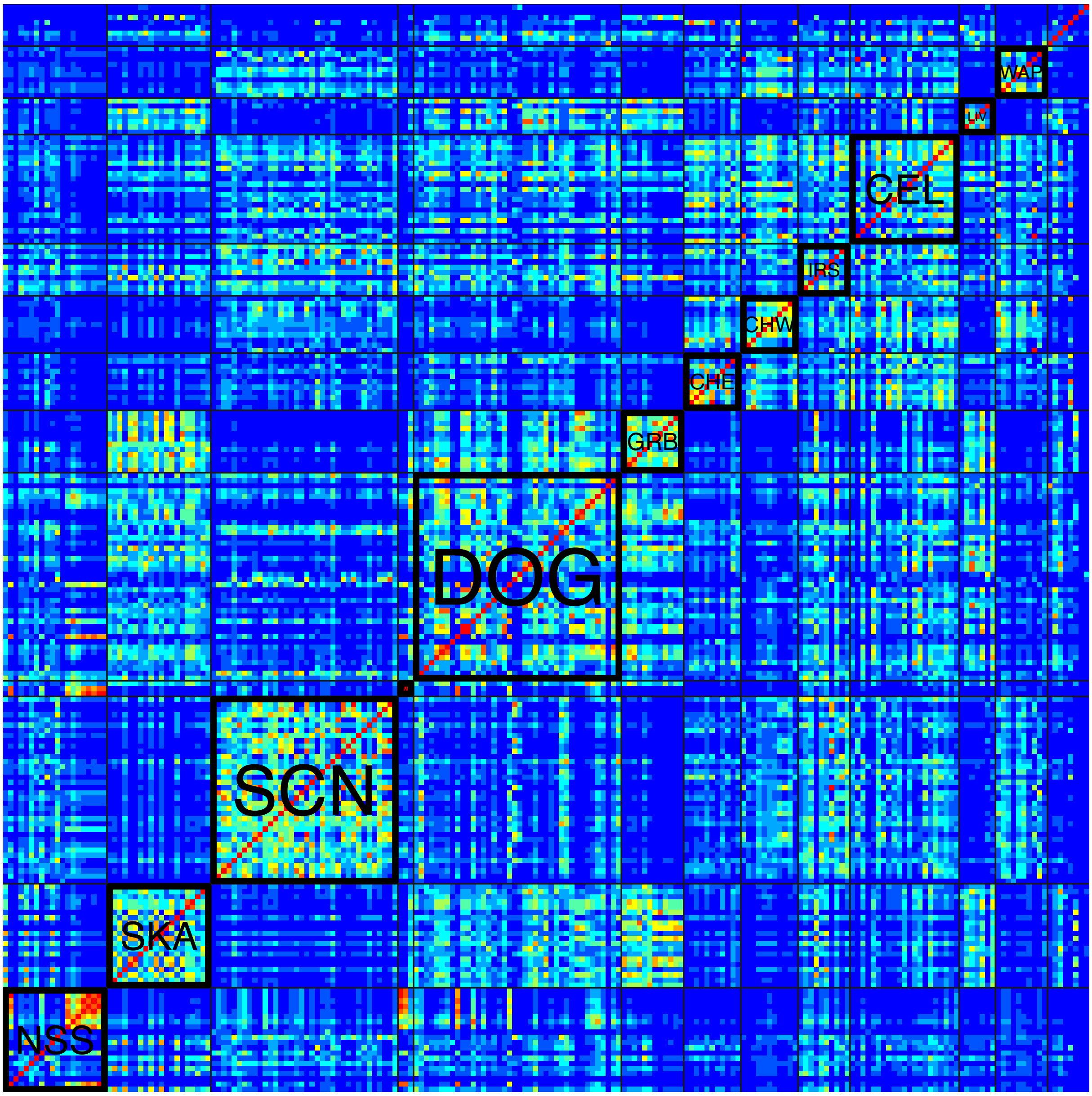

**Figure S6** Habitat similarity matrix used to weigh the transport matrix, where each small point represents the comparted similarity of each pair of MPAs. Here blue points represent dissimilar habitat, while green are half-similar habitat, and red points represents high similararity in habitat and thus a higher likelihood of settlement and/or post-settlement survival.

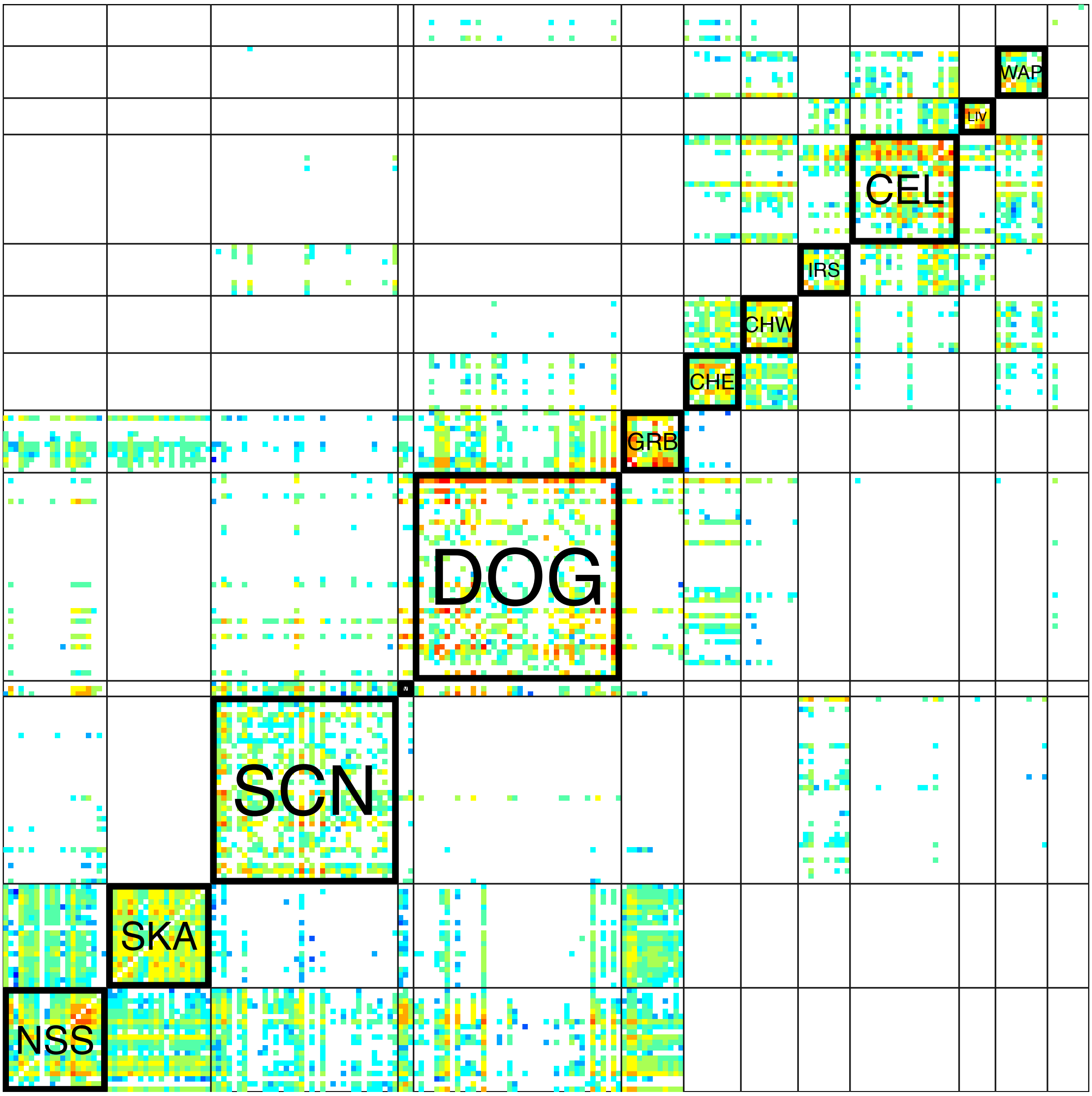

**Figure S7** Visualisation of the connectivity matrix. Squares along the diagonal represent clusters of MPAs with high degree of internal connection, as identified by the INFOMAP algorithm (see materials and methods). Here a comparison along the horizontal axis represents exports and along vertical axis represents imports; where blue points represent weak connections, green are medium strength connections, and red points represents well connected areas. For visualisation purposes the diagonal (i.e. the self-recruitment) is left blank.

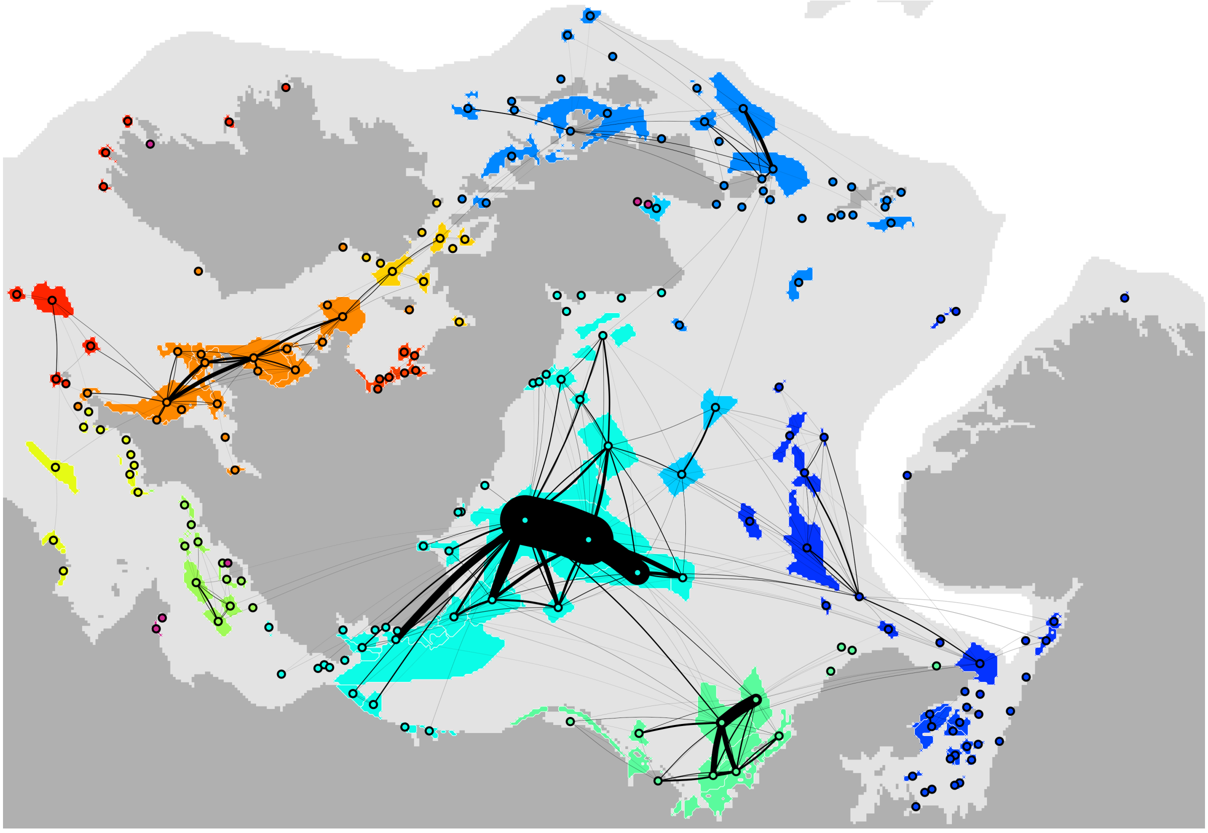

**Figure S8** Visualisation of the connectivity matrix in a network perspective (i.e. the absolute number of larvae exchanged among MPAs), where thickness of arcs represents the strength of connection in a clockwise direction.