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The ‘everything is everywhere’ framework: Holistic network analysis as a marine spatial management tool

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ABSTRACT

The North Sea hosts numerous man-made structures, some recently installed and others nearing end-of-life, with decisions about their decommissioning at the centre of current debate. Further there are plans for significant expansion of structures relating in particular to offshore wind energy. Here, using a combination of hydrodynamic modelling, particle tracking, and graph network analysis, we evaluate connectivity under two scenarios: existing structures – releasing particles from cells where structures are currently present – and “everything is everywhere” – releasing particles from every cell in the domain. Additionally, we introduce a Connectivity Importance Index (CII) to assess both current and potential future connectivity within the region. The CII under the ‘everything is everywhere’ scenario revealed cells with high potential connectivity that align with, but also extend beyond, those identified under the existing structures scenario, pointing to potentially valuable regions for future structure placement. The relocatable methodology described in this paper allows for the quantification of potential networks, applicable with or without existing habitat data, offering valuable insights for ecologically coherent marine spatial management strategies.

1. Introduction

Larval dispersal and connectivity play crucial roles in the structure & functioning of marine communities (Boulanger et al., 2020; Gilg and Hilbish, 2003; Weersing and Toonen, 2009). Consequently, they are central to conservation policy undertaking on-going efforts to maintain healthy and biodiverse ecosystems and promote the sustainable management of resources (e.g. the Marine Strategy Framework Directive (DEFRA, 2019), the UK Marine Policy Statement (UK Government, 2011), the Blue Belt Programme (UK Government, 2023a), Natura 2000 (European Commission, 2023), and the Convention on Biological Diversity (United Nations, 1992)).

Globally, coastal waters are home to a plethora of man-made structures such as artificial reefs, harbours, offshore wind turbines, oil and gas platforms, and large stretches of concrete sea defences (Firth et al., 2016). While these structures provide valuable services, they can also have a profound impact on connectivity by modifying dispersal pathways (Mayorga-Adame et al., 2022; McLean et al., 2022). The presence of these structures can function as ‘stepping stones’ (Adams et al., 2014; Airoldi et al., 2015; Bishop et al., 2017; Coolen et al., 2020), creating bridges between patches of habitat that were previously unconnected (Degraer et al., 2020; Gates et al., 2019). While this enhanced connectivity may be considered valuable in efforts to counteract the negative effects of habitat fragmentation on ecological network functioning (Baguette et al., 2012), it can result in negative or unintended consequences, such as facilitating range expansion of invasive species (McLean et al., 2022; Page et al., 2006; Reigel, 2015).

Oil and gas infrastructure, and increasingly, offshore renewable energy installations are now prolific features of the marine environment. Worldwide, there is an estimated 12,000 offshore oil and gas platforms

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in the sea, many of which are approaching end-of-life. There is, however, considerable debate over how to decommission these structures, including what is the best option for the environment and society (Knights et al., 2024a), for meeting environmental targets (Knights et al., 2024b), and the existing legal barriers (see Knights et al., 2024c for a review). In the northeast Atlantic, structures must be entirely removed (with exceptions for some parts of structures under specific permits) under regional legislation (OSPAR Decision 98/3), whereas elsewhere, structures can be repurposed from “rigs to reefs” - leaving structures in place at the end of their operational life to serve as artificial reef habitat (Bull and Love, 2019; Pereira et al., 2023). In addition, there are plans to significantly expand the number of platforms related to renewable energy to meet the challenges of decarbonisation and energy security.

There are costs and benefits of removing structures at end-of-life for both biodiversity and society depending on the decommissioning option chosen (Knights et al., 2024b). Removal (complete or partial), relocation and repurposing each have distinct implications for both marine ecosystems and stakeholders. The OSPAR Decision 98/3 mandating the complete removal of disused offshore installations (with certain exceptions) is grounded in the precautionary principle, aiming to prevent potential adverse effects on the marine environment such as long-term pollution risks (Shams et al., 2023), and the facilitation of invasive species leading to long term ecosystem instability (Schulze et al., 2020). However, removal can also disturb established marine communities that have adapted to these artificial habitats, potentially leading to localized biodiversity loss, and that complete removal may not always be the most beneficial option (Ounanian et al., 2020; Sommer et al., 2019). Some suggest that leaving structures in-situ or repurposing them elsewhere can create artificial habitats that benefit biodiversity (Fowler et al., 2018), In some countries, such alternatives have been implemented with considerable success (e.g. the ‘Rigs-to-Reefs’ programme in the USA: Bull and Love, 2019). While options other than complete removal often present obvious financial benefits, there is a lack of clear evidence that supports a particular option for its benefits to biodiversity (Lemasson et al., 2023, 2024).

Connectivity plays a crucial role in maintaining ecosystem resilience, supporting species dispersal, and preserving genetic diversity. Fragmentation or disruption of connectivity caused by decommissioning decisions can have profound implications for marine ecosystem health. For example, removing structures without considering their role as ‘stepping-stone’ habitats may hinder recovery of species with limited dispersal abilities, such as sessile invertebrates or reef-associated fish (Adams et al., 2014; Bishop et al., 2017). Understanding marine connectivity patterns may help to shed light on this decommissioning dilemma, providing insight into how the placement of existing, new (i.e. offshore wind turbines), or repurposed (oil and gas) infrastructure might affect ecological processes (Bailey et al., 2014; Foley et al., 2010), and how commissioning and decommissioning could be strategically undertaken to minimise disruption to the functioning of natural ecological systems, while contributing to environmental, economic and societal sustainability.

Connectivity assessment has not been routinely applied to offshore construction (Bergström et al., 2014). In the North Sea, structures have been in place since the mid-20th century. Yet, of the 1500 platforms in the region with an average age of 25 years (Scotland’s Marine Assessment, 2020; UK Government, 2023b), decommissioning is a rapidly looming and costly challenge for the region (Knights et al., 2024c). In two recent studies, particle tracking and network analysis approaches were used to assess dispersal among existing offshore oil and gas structures in the North Sea (Mayorga-Adame et al., 2022), and assess how five different decommissioning options might affect regional connectivity (Tidbury et al., 2020). Both studies provide valuable insights into spatio-temporal patterns of generalised species dispersal and connectivity in the region and highlight the value of network analysis as a tool for visualising connectivity. However, they adopt a “one-size-fits-all” approach to infrastructure rather than a case-by-case assessment as advocated by Knights et al. (2024c), which may not deliver the best outcomes for the environment or society. Further, if the aim is to determine if structures should be left in place, moved (repurposed elsewhere), or removed entirely, with a view to enhance, maintain, or constrain connectivity, then a regional analysis of connectivity that extends beyond existing infrastructure locations is required.

Connectivity modelling in marine ecosystems employs various approaches to quantify the exchange of larvae across spatial scales. These methods often integrate biological, physical, and environmental data to assess ecological processes. Hydrodynamic models simulate water movement and circulation patterns driven by physical forces, such as tides, winds, and currents. These models provide the foundational data for understanding larval transport in marine systems. Particle tracking is a complementary technique that models the dispersal of particles (representing larvae) within hydrodynamic flows. These models can incorporate biological traits such as planktonic larval duration to improve predictions of dispersal patterns. Building on this, graph network analysis uses the release and final destination points from the particle tracking model to conceptualise connectivity as a network of nodes (habitats) and edges (dispersal links). This approach allows for the identification of the relative importance of specific regions to overall connectivity, and pinpoints critical stepping stones or corridors within the environment. Biogeochemical models can further extend the analysis by linking connectivity with ecological and chemical processes, such as primary production. This integration provides a broader perspective of ecosystem functionality and highlights locations where connectivity may be particularly beneficial for sustaining populations.

Here, using a combination of these techniques, we assess the potential connectivity of the North Sea, and present a generic (i.e. community level not species-specific) prediction of ‘connectivity hotspots’ (or lack of) within the region. In this study, we use the term ‘community-level’ to refer to the combined connectivity patterns of multiple taxa with similar dispersal characteristics, rather than to an ecological community defined by species interactions. Unlike previous studies, our aim is to compare and contrast two scenarios: (1) connectivity among current offshore man-made structures and the relative importance of individual ‘patches’ (structures) to network functioning, and (2) connectivity among patches across the entire North Sea where ‘everything is everywhere’ to identify areas of high and low connectivity, with a view to identify locations where connectivity may be critical to marine ecosystem health.

While existing connectivity indices, such as those proposed by Opsahl et al. (2010) and Pascual-Hortal and Saura (2006), have proven effective in terrestrial and social network systems, they have limitations in dynamic marine environments. Opsahl et al.’s framework uses a tunable parameter (α) to adjust the balance between how well-connected an area is and how strong those connections are. While this flexibility in valuable in certain contexts, it does not incorporate ecological factors like food availability, which are critical for larval survival. Similarly, the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006), emphasised habitat connectivity in static systems, such as forests, but does not capture dynamic processes like larval dispersal, driven by hydrodynamics.

In the North Sea, where understanding both structural connectivity and ecological functionality is critical, a tailored approach is required. To address these gaps, we introduce the Connectivity Importance Index (CII), which integrates graph network metrics and primary productivity to provide a holistic, community-level assessment of connectivity, ensuring the index is tailored to the dynamic and ecological complexities of the North Sea.

2. Methods

2.1. The study area

A uniform 30 × 30 km grid extending between 49.7°N to 65.3°N and 6.05°W to 9.77°E was created to overlay the North Sea and explore connectivity (Fig. 1). The size of the cell was chosen to balance connectivity resolution against computational demands when exploring connectivity over the entire study domain. Grid cells including land were cropped using a land mask (GEBCO Compilation Group, 2020) to ensure that just the sea was included in the grid. Grid cells beyond the limits of the North Sea, as defined by the International Hydrographic Organisation (International Hydrographic Organization, 1953), were removed. The total number of cells was 582. Data for the locations of artificial marine structures in the North Sea were obtained from the OSPAR Inventory of Offshore Installations (OSPAR Commission, 2019) (oil and gas rigs) and the European Marine Observation and Data Network (EMODnet, 2014) (wind farms).

Two connectivity scenarios were performed and compared: (1) connectivity among grid cells containing man-made structures, and (2) connectivity among all grid cells in the domain i.e. ‘everything is everywhere’ (Fig. 1).

2.2. The hydrodynamic model

The unstructured mesh finite-volume model FVCOM (Chen et al., 2003) was run from 2011 to 2015 in the North Sea domain and used to drive the offline particle-tracking model PyLag (version 0.6.1: Uncles et al., 2020). FVCOM is a prognostic unstructured-grid finite volume free-surface 3D primitive equation coastal ocean circulation model. Vertical turbulent mixing was modelled with the General Ocean Turbulence Model (GOTM) using a κ-ω formulation (Umlauf and Burchard, 2005), whilst horizontal mixing was parameterised using the Smagorinsky scheme (Smagorinsky, 1963) with a coefficient of 0.04. The unstructured horizontal grid allows variable resolution across the domain to reflect the complexity of the flow and scale of bathymetric features. The resolution of the model varies between ~1 km and 20 km across the domain with the areas of high resolution concentrated on those with structures in the North Sea. The vertical grid consists of 25 layers of terrain-following (sigma) coordinates, these are hybrid in form, being regularly spaced in water less than 120 m depth and telescoping to have higher resolution in the surface and bottom boundaries for deeper water. Bathymetry is interpolated onto the model grid from the European Marine Observation and Data Network (EMODnet) Digital Terrain Model (DTM) (http://www.emodnet-hydrography.eu). Lateral boundary conditions were taken from the Atlantic Margin Model retrieved via the CMEMS service (Copernicus Marine Service, 2020), and adjusted to the internal tidal solution. Atmospheric boundary data, including heat fluxes and surface stresses, were generated by downscaling the National Oceanic and Atmospheric Administration’s (NOAA) Global Forecast System model using a configuration of the Weather Research and Forecasting model (WRF; Skamarock et al., 2008) for the UK shelf. The WRF outputs were saved every 3 h and converted to FVCOM surface forcing using the COARE3.0 bulk air-sea flux parameterisations (Fairall et al., 2003). The river input is an annual climatology based on gauge data from EMODnet.

2.3. The particle tracking model

The Lagrangian trajectory model PyLag (Uncles et al., 2020) was forced by the hourly output of the FVCOM hydrodynamic model to generate particle trajectories for a range of planktonic larval durations within the North Sea domain (*see 2.5*). PyLag utilises a fourth order Runge-Kutta scheme for particle advection, with numerical integration conducted over a 100-s timestep. Horizontal turbulence statistics from the hydrodynamic model were used to parameterise the diffusion term, which introduces stochastic displacement to the particle position following an incremental Weiner process.

Virtual larvae were constrained to the surface waters in the simulations – i.e. vertical advection and diffusion were omitted from the model and a restorative property was applied to return particles to the surface after each time step. This was deemed appropriate for three reasons. One, the aim of this study is to identify connectivity hotspots for a range of planktonic taxa rather than a single species, thus the inclusion of larval vertical movement behaviour (i.e. swimming: Knights et al., 2006; James et al., 2019) cannot be included. Second, as the inclusion of larval behaviour has been shown to reduce predicted dispersal distances through exposure to depth-differentiated current speeds and directions (James et al., 2023; Sundelöf and Jonsson, 2012), consideration of passive surface-advected particles provides a ‘maximal dispersal’ scenario. Third, the omission of vertical advective and diffusive terms within the model reduces computational resource requirements for in-model calculations thereby reducing simulation run-length, allowing a greater number of scenarios to be modelled. The model was parameterised to have reflective boundaries, so that if a particle reached a boundary it was returned to its last known location, however, as the domain of the underlying hydrodynamic model was much larger than that of the 30 × 30 km grid, this was only relevant when a particle reached land, with particles travelling beyond the boundaries of the grid and not returning by the end of their simulation time being omitted from the analysis. A full description of the equations used within the PyLag model can be found in de Vries et al. (2023).

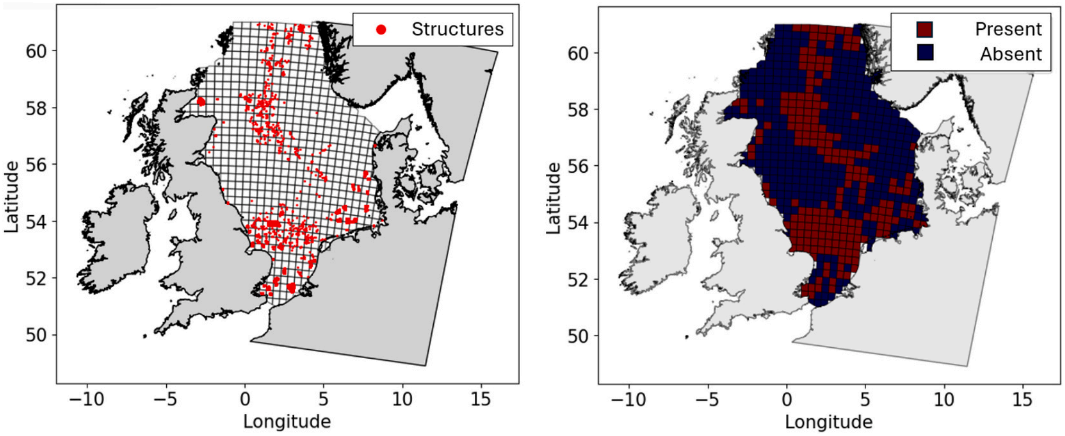

Fig. 1. The 30 × 30 km gridded North Sea study domain. Showing *(left)* the locations of existing oil/gas rigs (OSPAR Commission, 2019) and wind farms (EMODnet, 2014) within the region, and *(right)* the presence/absence of these structures within each cell in the grid.

2.4. Quantifying primary productivity

FVCOM was coupled to the European Regional Seas Ecosystem Model (ERSEM): a generic and well established lower-trophic level marine food web and biogeochemical cycling model (Butenschön et al., 2016). ERSEM resolves the ecosystem dynamics with nutrients and carbon cycles in the low trophic levels and was used here to provide estimates of phytoplankton carbon biomass to function as a proxy for primary productivity, providing a food availability metric for meroplanktonic species. A comprehensive review of the biogeochemical representation and mathematical formulations in ERSEM are described in detail in Butenschön et al. (2016). Phytoplankton is a primary food source for many marine larvae. By including phytoplankton biomass in our model, we can better assess the availability of food resources along potential dispersal routes, thus identifying areas where larvae are more likely to survive and thrive. This allows us to undertake an ecosystem-based management approach by providing insights into the ecological linkages between primary producers and higher trophic levels (Pfeiffer-Herbert et al., 2007; Thomas et al., 2016). Simulations for February and July of 2011–2014 were averaged and surface values for diatom, picophytoplankton, nanophytoplankton and microphytoplankton carbon biomass were re-gridded from the unstructured FVCOM grid to the 30 × 30 km study grid using a nearest neighbour interpolation method in python using the package ‘nctoolkit’ (Wilson and Artioli, 2023).

2.5. Experiment setup

Multiple simulations were undertaken to encompass potential seasonal and interannual variation in larval dispersal. Simulations were run in winter (February) under mixed water column conditions, and in summer (July) under stratified conditions, over a 4-year period (2011–2014). Passive particles were released from the centroid of every cell in the grid. Each cell in the grid functioned as both a source (i.e. particles were released from it) and sink (i.e. particles could settle in it) location. To capture variation in dispersal due to tides, 100 particles were released from each cell each day at the surface at midnight over a 14-day period, starting on the first day of February/July. This number was deemed appropriate as a trade-off between model complexity and computation efficiency and followed a similar precedent set by previous connectivity modelling studies within this region (Mayorga-Adame et al., 2022). A total of 814,800 particles were tracked from the start of each simulation for a maximum of 28 days. Planktonic larval duration can be highly variable across taxa, ranging from a few minutes to several months (Shanks, 2009), and so our study chose a maximum PLD of 28 days with the aim to provide computationally feasible baseline information applicable to organisms with a variety of dispersal periods that could serve as a starting point for more complex multispecies larval connectivity studies. This maximum PLD has also been previously used in generic species connectivity studies in this region (Mayorga-Adame et al., 2022). Particle locations (xy) were extracted from simulation results representing 7-, 14-, 21-, and 28-day model planktonic larval durations (PLD herein). While we acknowledge that environmental factors such as temperature and food availability can influence PLD length, our approach provides a representative snapshot of larvae that develop within this timeframe. This range encompasses a variety of regionally common invertebrate taxa, including commercially important species such as decapod crustaceans (*Homarus gammarus* (Schmalenbach and Franke, 2010), *Palaemon serratus* (Baudet et al., 2024)), bivalves (*Mytilus edulis* (Widdows, 1991), *Cerastoderma edule* (André and Rosenberg, 1991), *Ostrea edulis* (Robert et al., 2017)), and echinoderms (*Echinus esculentus* (Tyler-Walters, 2008)). Rather than focusing on a single species, this approach captures broad-scale connectivity patterns for taxa with PLDs that fall within this modelled range. As a single particle was assumed to represent multiple individual larvae, particles were not removed from the system at any timepoint, allowing onward connections from the same ‘larval cohort’. Consequently, particles could potentially settle at every timestep they were extracted. To examine connectivity between existing artificial structures only, a two-step filter was applied to the particle tracking results. The first step filtered particles released from cells containing structures, and the second filtering for particles reaching cells containing structures by the end of their PLD. This filter was applied for particles at 7-day, 14-day, 21-day and 28-day intervals.

All PLD/month/year simulation outputs for both scenarios were grouped prior to connectivity analysis to provide a holistic view of connectivity that captures PLD, season and inter-annual variation.

2.6. Evaluating particle dispersal distance

Analysis of the Euclidian (or ‘straight-line’) distance travelled by the simulated particles was undertaken in R (v.4.3.2). Distance (km) was calculated for each particle and a new grouping variable ‘group’ was created by concatenating PLD, month, and year to form a unique identifier for each simulation. To assess the differences in Euclidean distances travelled across different groups, we first evaluated the normality of the data using Anderson-Darling tests. Given the non-normality of the data, non-parametric methods were utilised. To manage the size of the dataset and ensure computational feasibility, a randomised 10 % subsample of the original data was used. The Kruskal-Wallis test was used to determine if there were statistically significant differences in distances across groups and to further analyse the differences between pairs of groups, pairwise Wilcoxon rank-sum tests were performed, adjusted for multiple testing using the Bonferroni correction. Significant pairwise comparisons were identified based on adjusted p-values ($p < 0.05$). The rank-biserial correlation coefficient was calculated to provide effect size metrics for each pairwise comparison to quantify the magnitude of differences (small < 0.3, moderate ≥ 0.3 - <0.5, large > 0.5: Cohen, 1988; Wilcox, 2012). Summary statistics, including median and interquartile range (IQR), were also calculated for each group.

2.7. Network analysis

Graph network theory was implemented using the “igraph” package (Csárdi and Nepusz, 2010) in R (version 3.4.2). Connectivity matrices generated from the particle tracking simulations quantified connectivity of the seascape between all cells (‘everything is everywhere’) and cells with man-made structures. Each cell within the 30 × 30 km grid cell is denoted as a ‘node’ and connections between pairs of nodes based on particle tracking simulations were denoted as ‘edges’ i.e. links between nodes (Urban and Keitt, 2001). The importance of each node to connectivity was described using metrics: in-degree, out-degree, node betweenness, and modularity (community detection). In-degree provides a count of the number of in-links reaching the node from other nodes, and out-degree a count of the number of out-links from a given node to other nodes, aiding in the identification of source-sink dynamics in the study region. Node betweenness is calculated as the sum of the fraction of node-pairs shortest paths that pass through a given node. Nodes with high betweenness are likely to significantly influence the flow of particles within the network and be critical to maintaining connectivity.

Network graphs were created using the ‘graph from adjacency matrix’ function in ‘igraph’, considering the direction of movement of the particles and including a weighing factor that considered the number of particles travelling along each edge between nodes. A fast-greedy community detection algorithm (Clauset et al., 2004) was used to identify clusters of densely connected nodes where intra-particle exchange was high and inter-particle exchange was low. In the context of graph theory and network analysis, a ‘community’ refers to groups of nodes within the graph that are more densely connected to each other than to the rest of the graph. The modularity of the overall network, ranging from 1 to -1, was also calculated to quantify the quality of the community structure. Positive modularity scores suggest that the graph has more edges within communities than would be expected in a random network, with the strength of the community structure (i.e. the density of the connections between the nodes with communities) indicated by the proximity of the modularity score to 1. The size, strength, and density of each community was calculated by the number of nodes within each identified community, the sum of the edge weights within each community, and how many edges are present in each community graph relative to the total number of possible edges, respectively.

Community strength and community density are related but distinct concepts in graph theory. Community strength measures the overall strength of connections within a community using the weights of edges. Higher values indicate stronger internal connections. Community density, on the other hand, measures the proportion of existing edges relative to the total possible edges, ignoring edge weights. Higher density means a greater proportion of possible connections are present within the community (Lancichinetti and Fortunato, 2009).

2.8. Connectivity importance index (CII)

The Connectivity Importance Index (CII) was calculated to quantify the contribution of each node (i.e. grid cells containing offshore structures in scenario 1 and grid cells in the entire domain in scenario 2) to overall connectivity in the network integrating graph network metrics - out degree, in degree, node betweenness - with primary productivity data derived from the FVCOM-ERSEM output. The formulation of the CII is designed to identify nodes that are critical for connectivity and ecological relevance, particularly for larval dispersal and survival.

The novel connectivity method was developed over the use of existing methods, such as Opsahl et al. (2010) and the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006), as these methods have limitations in dynamic marine systems. Osphal et al.'s framework relies on a tunable parameter (α) to balance the importance of edge weights and node degree, which requires prior knowledge or assumptions about the relative importance of these factors. In marine environments, such as the North Sea, this relative importance is often unknown and varies across species, spatial scales, and temporal contexts. Additionally, Opsahl et al.'s method does not incorporate ecological variables, such as food availability, which are critical for larval survival. Similarly, the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006), while effective in static terrestrial system does not account for dynamic processes such as larval dispersal driven by hydrodynamics. By integrating both structural and ecological data, the CII overcomes these limitations and is particularly suited for assessing connectivity in the dynamic, multi-species context of this study.

2.8.1. Mathematical formulation

For each node i in the network, the following metrics were calculated:

- **Out-degree** ($D_{out,i}$): The number of connections from node i to other nodes, representing dispersal potential from i.
- **In-degree** ($D_{in,i}$): The number of connections to node i from other nodes, representing its importance as a settlement site.
- **Node Betweenness** (B_i): A measure of how often node i acts as a bridge along the shortest paths between other nodes, capturing its role a stepping stone in maintaining connectivity across the network.
- **Primary Productivity** (P_i): The productivity value at node i, taken directly from the FVCOM-ERSEM biogeochemical model.

Each metric was normalised to between 0 and 1 using min-max normalisation:

$$M_i' = \frac{M_i - min(M)}{max(M) - min(M)}$$

Where M_i represemts the value of the metric for node i, and $min(M)$ and $max(M)$ are the minimum and maximum values of the metrics across all nodes.

Subsequently, a z-score was calculated for each normalised metric:

$$Z_{M,i} = \frac{M_i' - \mu_M}{\sigma_M}$$

Where μ_M and σ_M are the mean and standard deviation of the normalised metric M respectively.

The CII for each node was then calculated by summing the z-scores of the four metrics:

$$\mathrm{CII}_i = Z_{D_{\mathrm{out},i}} + Z_{D_{\mathrm{in},i}} + Z_{B_i} + Z_{P_i}$$

Finally, the combined CII values were standardised to between 0 and 1 using min-max normalisation:

$$CII_i' = \frac{CII_i - min(CII)}{max(CII) - min(CII)}$$

2.8.2. Rationale

The chosen metrics reflect complementary aspects of node importance – directional connectivity provides insights into dispersal potential and settlement significance, betweenness emphasises the roles of nodes in maintaining overall network connectivity, and primary productivity integrates ecological function, identifying nodes where larvae are likely to have sufficient food resources for survival and development.

The CII assigns equal weightings to these metrics, reflecting the current lack of definitive knowledge about the relative importance of each variable to connectivity. While some metrics, such as primary productivity, may have a more direct influence on larval survival in certain contexts, other metrics, like node betweenness, are crucial for understanding the structural cohesion of the network. Equal weightings ensure that all metrics are considered impartially, avoiding introducing biases introduced by subjective assumptions. By integrating both structral and ecological metrics in equal measure, the CII provides a balanced framework for assessing the contributions of individual nodes to connectivity.

3. Results

3.1. Analysis of euclidean distance travelled by particles

The Kruskall-Wallis analysis revealed statistically significant differences ($x^2 = 1{,}016{,}296$, degrees of freedom = 31, $p < 0.001$) between all groupings of planktonic larval duration (PLD), month and year on the Euclidian (straight-line) distance travelled by the particles (Fig. 2). Median distances travelled increased with PLD duration (45.63 km at 7-days PLD, 75.4 km at 14-days PLD, 100.7 km at 21-days PLD, and 124.32 km at 28-days PLD; Fig. 2; Appendix 2), though there was considerable variation in distances between individual particles. Seasonal and interannual differences were also observed, with particles travelling a median distance of 32.4 km further during February simulations than July simulations, and 2014 being the year where particles, on average, travelled the furthest (86.04 km in 2011, 86.93 km in 2012, 59.12 km in 2013, and 110.71 km in 2014; Appendix 2).

A Wilcoxon rank-sum test results demonstrated significant differences between most PLD/month/year groupings ($n = 496$), with only 4 groupings (0.8 % of all pairings) not statistically significant. These were:

- *14-day PLD in February 2011 and 21-day PLD in July 2012* (*p-adj* = 0.154),
- *14-day PLD in February 2012and 21-day PLD in February 2013* (*p-adj* = 0.297),
- *14-day PLD in February 2013 and 7-day PLD in February 2011* (*p-adj* = 0.321), and
- *14-day PLD in July 2012 and 28-day PLD in July 2013* (p-adj = 0.346). ().

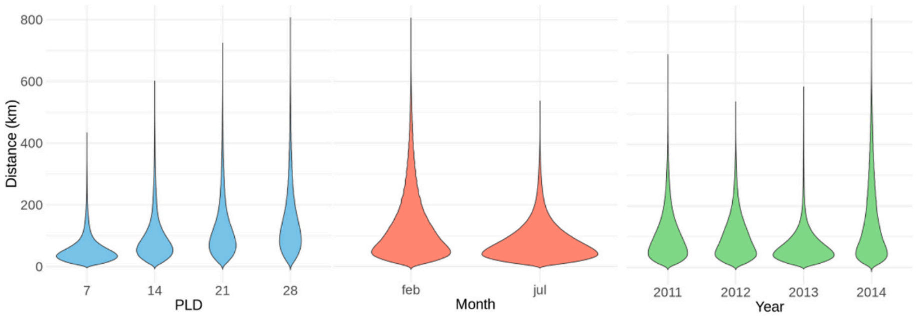

Fig. 2. Distribution of the Euclidian ('as the crow flies') distance travelled (in kilometres) by particles across various levels of PLD (7, 14, 21, and 28 days), Month (February and July), and Year (2011–2014).

Effect sizes (rank-biserial correlations) varied among significantly different groupings. Small effect sizes (<0.3) were found in 38.51 % of pairwise comparisons, moderate effect sizes ($0.3 <$ effect size ≤ 0.5) in 26.61 %, and large effect sizes (<0.5) in 34.07 %. The average effect sizes across all PLDs, month and year groupings was moderate (Appendix 2).

3.2. *Connectivity between existing structures (oil/gas rigs and wind farms)*

The analysis of connectivity among cells containing existing locations of artificial marine structures (oil/gas rigs and wind farms) in the North Sea reveals insightful patterns in how these structures form communities and how these communities are interconnected. In total, 36 % of the grid cells in the domain (212 out of 582) contained artificial structures. Approximately 51 % of all particles released from cells containing one or more structures reached another cell containing a structure by the end of their PLD. The likelihood of the particle reaching a cell containing a structure, however, decreased over time (Appendix 3). Through network analysis of locations of particles both released from and settling within these cells (collated simulation outputs for all PLD's (7, 14–21- and 28 days), months (February and July) and years (2011–2014)), five distinct communities were identified, each varying in size, strength, and density – with an overall modularity score for the network of 0.59 (Fig. 3).

Located off the east coast of Scotland, the smallest community (community 1: yellow) has only eight nodes. Despite its small size, it has relatively high density (i.e. the ratio of actual connections (edges) to all possible connections between nodes in the community) (0.77), though the overall strength (i.e. the weight of connections (edges) within the community) is low (32,877), suggesting that while the nodes are tightly knit, the total number of connections or interactions is limited. The north North Sea region (community 3: green) contains a slightly larger community with 28 nodes and the highest density (0.95). This indicates a very compact and interconnected group of nodes. However, despite its higher density, the community's strength is moderate (339,896), reflecting a greater but not disproportionately large number of connections when compared to the larger networks. The three larger networks that were identified were in the central North Sea (Community 4: blue) and in the southern North Sea (Community 1: red, and Community 5: purple), containing 63, 58, and 55 nodes, respectively (Fig. 2). Community 1 (red) exhibited relatively high density, with a score of 0.83. The strength of this community was 1,285,856, indicating a substantial total weight of connections, suggesting that the nodes are highly interconnected and that the network is well-integrated. Community 4 (blue), which is the largest community with 63 nodes, showed a strength of 1,158,390. Despite its large size, its density was relatively lower at 0.54, suggesting that although this community has a significant amount of connectivity, the proportion of realized connections is lower compared to Communities 1 and 3, indicating a more sparsely connected structure. Community 5 (purple) had 55 nodes and a strength of 983,005. The density of this community was 0.73. Although its strength was lower compared to Communities 1 and 4, this Community's density was relatively high, indicating a moderately interconnected network with frequent interactions among its nodes.

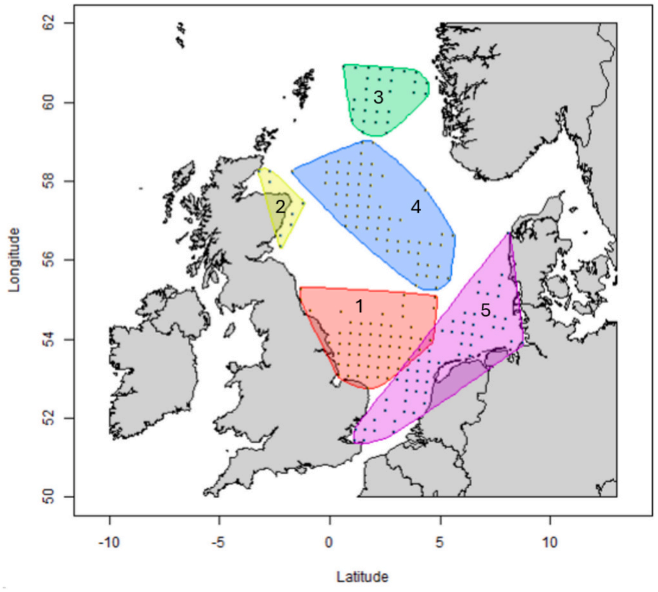

Fig. 3. Identified connected communities of artificial structures within the North Sea domain as calculated by 'igraph. Simulation results for multiple planktonic larval durations (PLDs: 7,14,21, and 28 days), opposing seasonalities (well-mixed/stratified: February/July), and multiple years (2011-2014) were collated to give an overview of that could be generically applied to the region over a range of temporal scales and considers connectivity at a multi-species level. Dots denote the centroid of each release cell, which functioned as 'release nodes' in the particle tracking model.

3.3. *Potential connectivity of the North Sea under the 'everything is everywhere' approach*

The network analysis of the North Sea under the 'everything is everywhere' scenario revealed three distinct communities, each with distinct characteristics: the western side of the northern North Sea (WNNS: community 1: red), the eastern side of the northern North Sea (ENNS: community 2: green), and the southern North Sea (SNS: community 3: blue) (Fig. 4). The overall modularity score for the network was 0.5. The WNNS was the smallest community, comprised of 92 nodes (15.8 % of all nodes), and exhibited the weakest community strength at 2,533,503. However, it boasted the highest density of 0.64, indicating a highly interconnected and cohesive structure despite its smaller size. In

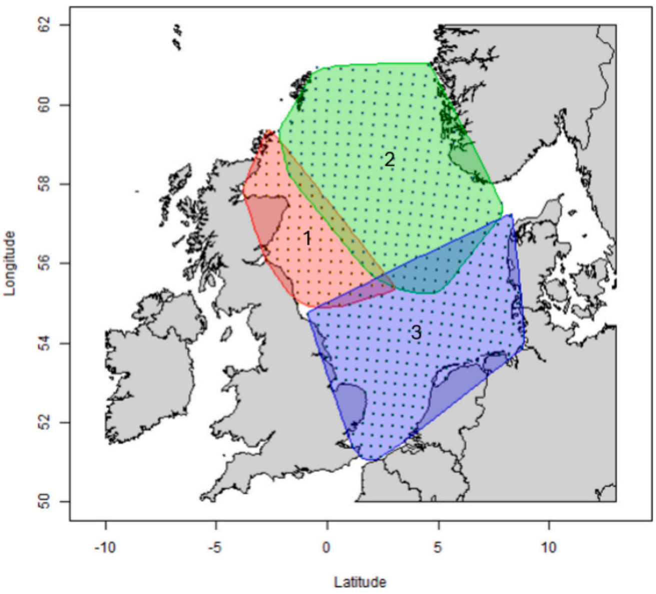

Fig. 4. Community analysis based on connectivity under the 'everything is everywhere' framework within the North Sea domain. Simulation results for multiple planktonic larval durations (PLDs: 7,14,21, and 28 days), opposing seasonalities (well-mixed/stratified: February/July), and multiple years (2011–2014) were collated to give an overview that could be generically applied to the region over a range of temporal scales and considers connectivity at a multi-species level. Dots denote the centroid of each release cell, which functioned as 'release nodes' in the particle tracking model.

contrast, the ENNS was the largest community with 266 nodes (45.7 % of all nodes) and the greatest community strength of 8,789,453. Despite its extensive size and strong interactions, the ENNS had the lowest edge density of 0.5, suggesting a less cohesive internal network. The Southern North Sea community, with 224 nodes (38.5 % of all nodes), demonstrates intermediate characteristics with a community strength of 7,877,883 and an edge density of 0.53, reflecting a robust yet moderately interconnected community.

In total, 17 % of particles were lost outside the model boundaries, increasing over time from 6.8 % after 7 days, to 10.5 %, 13.8 % and 17.0 % after 14, 21 and 28 days, respectively.

3.4. Identifying 'hotspots' of connectivity

Using all particle track data to rank cells based on their importance to connectivity across the North Sea region, four metrics were quantified namely: 'out degree' - indicating importance as source'; 'in degree' – indicating importance as a sink'; 'node betweenness' – indicating importance as a stepping stone'; and 'food availability' – indicating the productivity of the cell' (see Appendix 4 for definitions and formulations of the graph theory metrics). These metrics were also integrated into a Connectivity Importance Index (CIIs: Fig. 7).

Under the existing structures scenario, there were spatial differences between the locations with the greatest importance as sources and sinks. Cells with highest source and sink values were more southerly, occurring in the southwestern (~53°N, 2°E) and central southern North Sea, respectively (Fig. 5a and b). Both areas fell within community 1 of the network analysis between structures (Fig. 3: red).

Under the 'everything is everywhere' scenario, cells throughout the middle of the North Sea were important sources, whereas highest value

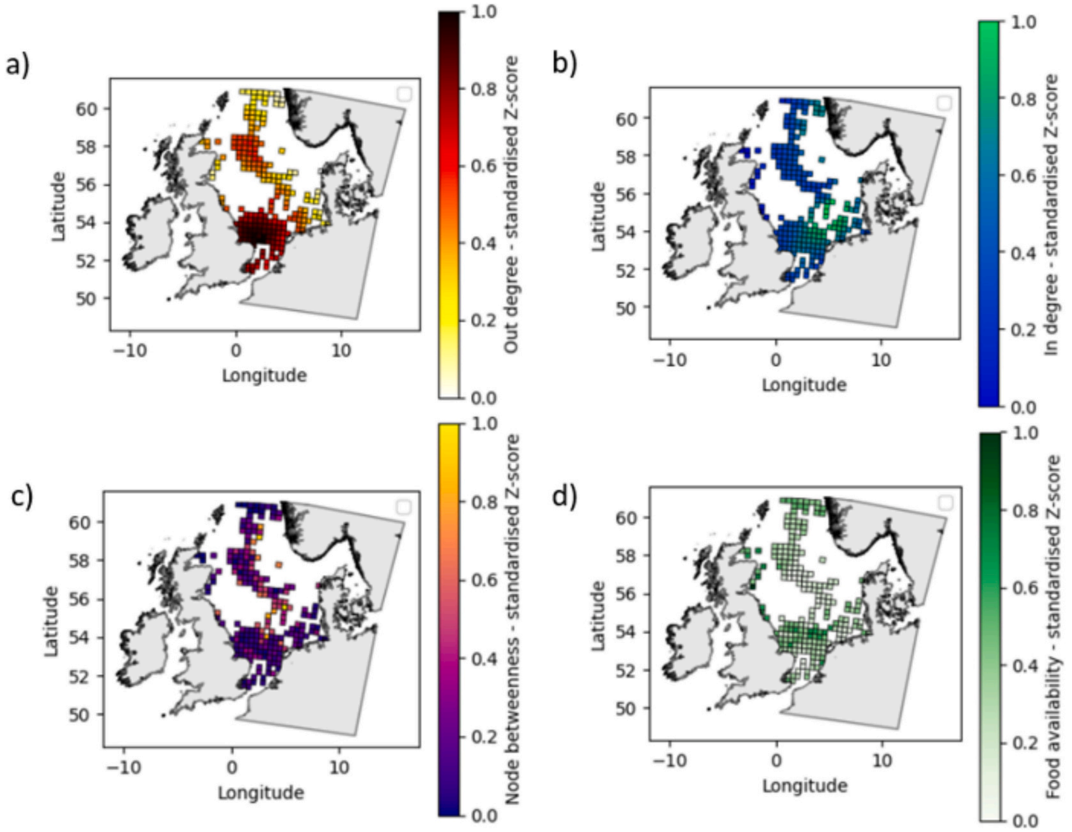

Fig. 5. Standardised importance (standardised *Z*-scores) of each cell containing existing artificial structures as a source (a), sink (b), stepping stone (c) and to primary productivity (d). a, b, and c were calculated using graph traversal algorithms in 'igraph', and food availability (d) was taken from average surface values for diatom, picophytoplankton, nanophytoplankton and microphytoplankton carbon biomass from FVCOM-ERSEM simulations for February and July 2011 and 2012, re-gridded to the 30 × 30 km study grid using a nearest neighbour interpolation.

sink cells were aggregated in the northeastern North Sea along the coasts of Denmark and Norway (Fig. 6a and b). A small number of cells were particularly important as stepping stone locations (node betweenness values >0.8), which occurred in the centre of the North Sea extending between 54° and 60° latitudes (Fig. 6c). Higher productivity was more strongly associated with coastal areas and intersecting the Southern North Sea between Southeast England and Northeast Denmark (Fig. 6d).

The CII showed spatial variation in the relative importance of cells under the two tested scenarios (Fig. 7: a and b). The CII indicated cells in the southern North Sea (spanning communities 1 and 5 of the existing structure scenario) as important under both scenarios, with a cell of very high CII value (>0.7) identified under the existing structures scenario at 55°N, 4°E (Fig. 7a). The integrated CII generated under the 'everything is everywhere' scenario indicated a small number of cells with very high CII values (>0.7: Figs. 7b and 8)). Many of these fell in similar locations to high connectivity cells under the existing structures scenario (i.e. the Southern North Sea), and in similar locations to cells with high node betweenness values under the 'everything is everywhere' scenario (Fig. 6c).

Crucially, a significant hotspot in the northwestern North Sea (Fig. 7b: 59°N, 4°E) (falling in community 2 of the 'everything is everywhere' network analysis (*see 3.2:* Fig. 3*; green*)) was not detected when looking solely at connectivity between structures (Fig. 7).

The CII for cells containing structures (Fig. 7a) shows that community 4 (*see 3.2:* Fig. 3*; red*) and community 5 (*see 3.2:* Fig. 3*; purple*) have the greatest impact on network connectivity within the region, and community 1 (*see 3.2:* Fig. 3*; yellow*) has the smallest impact. Cells with high levels of connectivity were identified in all communities of the 'everything is everywhere' framework (*see 3.3:* Fig. 4*;* Fig. 7b). To demonstrate the theoretical practical applications of the 'everything is everywhere' CII, in Fig. 9 we demonstrate the optimal positions of the 212 cells currently containing existing structures within the domain under the view of enhancing (left) and diminishing (right) connectivity.

4. Discussion

The North Sea hosts numerous man-made structures, with many more planned and many nearing end-of-life, with decisions about their decommissioning at the centre of current debate. Here, using a combination of hydrodynamic modelling, particle tracking, and graph network analysis, we evaluate connectivity under two scenarios: existing structures and "everything is everywhere". Additionally, we introduce a Connectivity Importance Index (CII) to assess both current and potential future connectivity within the region. This dual approach supports informed decision-making, allowing for both targeted enhancements to existing networks and strategic planning for future expansions to maximize connectivity and ecosystem health (Botsford et al., 2009; Mumby and Hastings, 2008). We also present a theoretical practical application of the CII, highlighting the optimal locations for the existing man-made structures in the North Sea under the viewpoints of enhancing and diminishing connectivity, respectively.

The Connectivity Importance Index (CII) under the 'everything is everywhere' scenario reveals cells with high potential connectivity that align with, but also extend beyond, those identified under the existing structures scenario. This suggests that while some critical areas are highlighted in both scenarios (i.e. the Southeastern North Sea), others gain importance when considering a hypothetical network expansion. Notably, the presence of high CII values in areas like the Northwestern North Sea, which were not flagged by the existing structure analysis, points to potentially valuable regions for future structure placement.

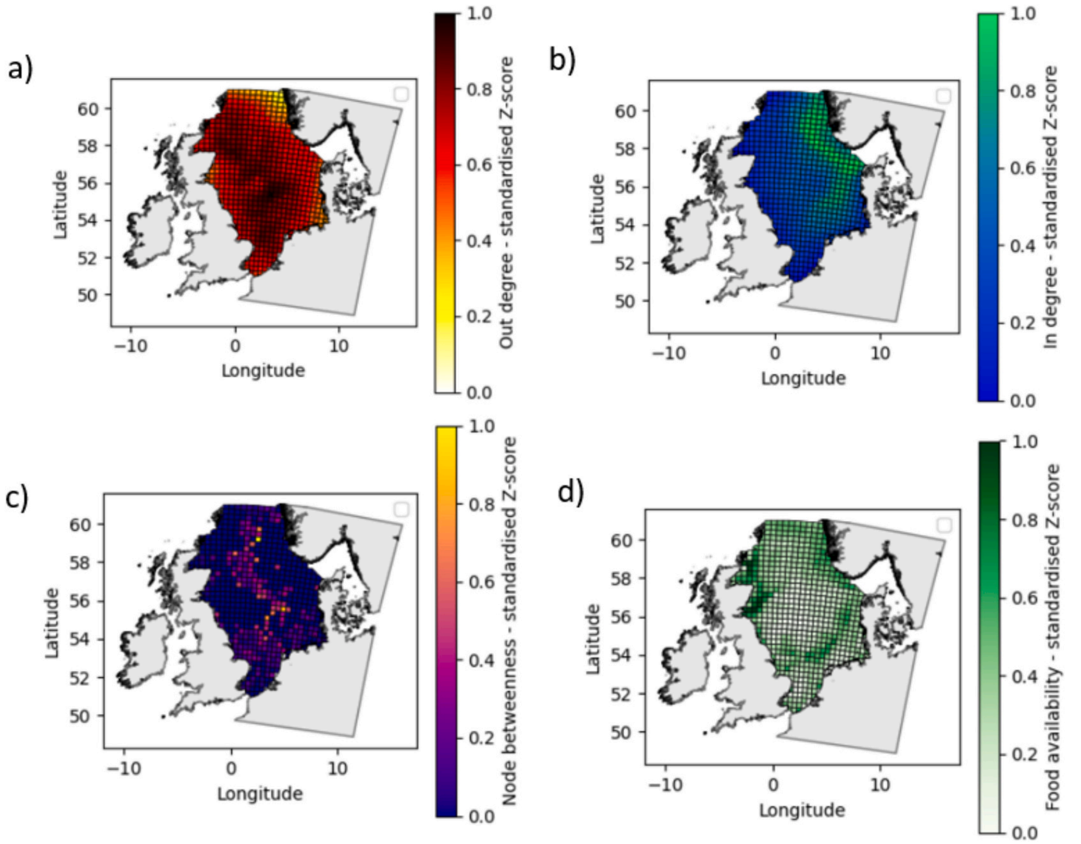

Fig. 6. Standardised importance (standardised *Z*-scores) of each cell within the North Sea study domain as a source (a), sink (b), stepping stone (c) and primary productivity (d). a, b, and c were calculated using graph traversal algorithms in 'igraph', and food availability (d) was taken from average surface values for diatom, picophytoplankton, nanophytoplankton and microphytoplankton carbon biomass from FVCOM-ERSEM simulations for February and July 2011 and 2012, re-gridded to the 30 × 30 km study grid using a nearest neighbour interpolation.

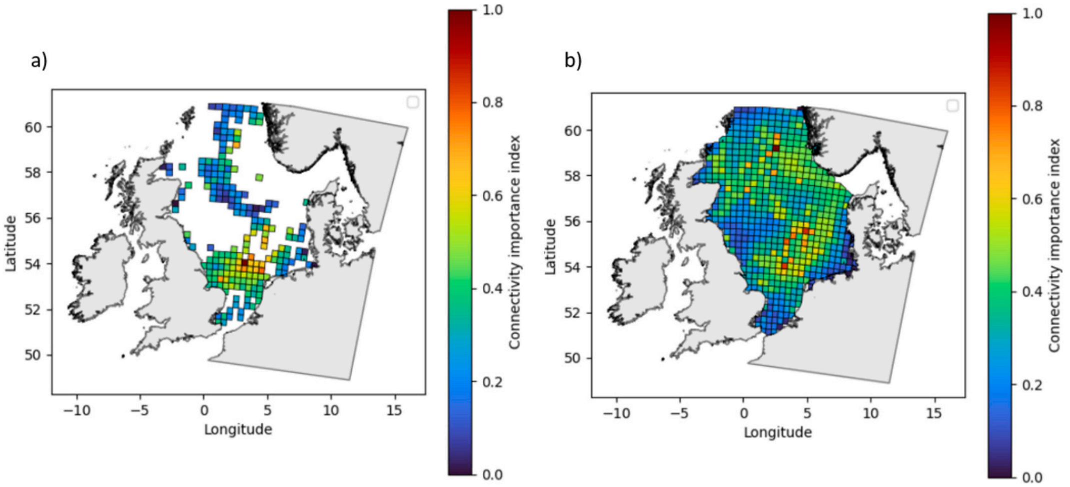

Fig. 7. The Connectivity Importance Index (CII) of each 30 × 30 km cell (calculated from the standardised sum of the Z-scores of the out degree, in degree, node betweenness and food availability of each cell) under two scenarios: existing locations of oil, gas and wind structures in the North Sea (a) and ‘everything is everywhere’ (b).

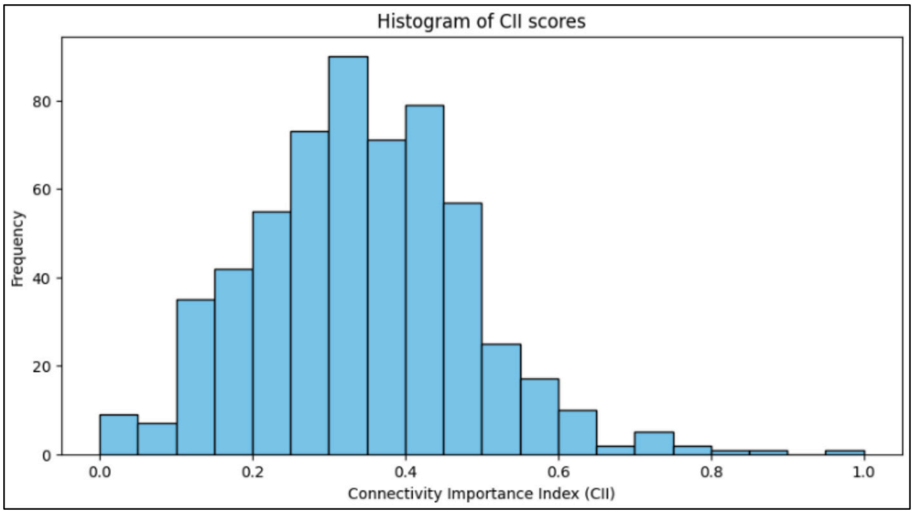

Fig. 8. Frequency distribution of the CII under the ‘everything is everywhere’ scenario.

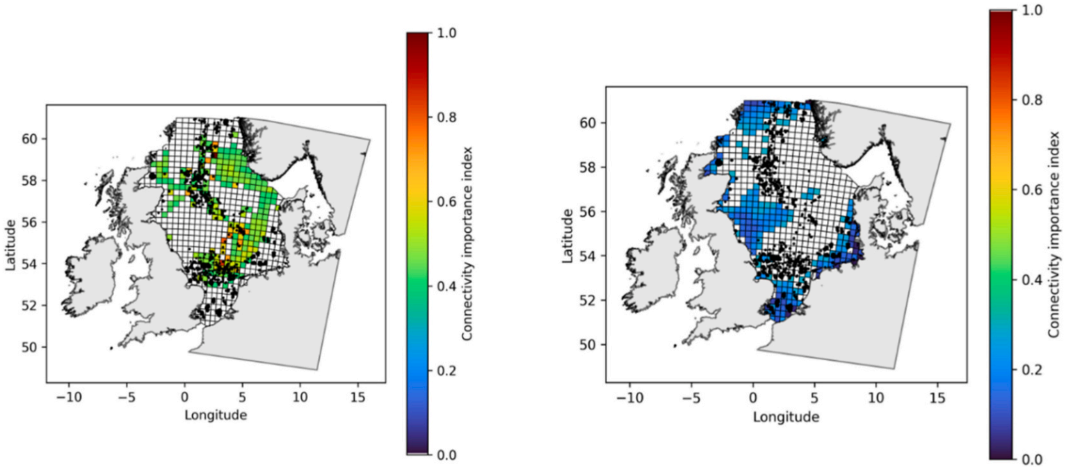

Fig. 9. Visualisation of the optimum locations for the 212 cells containing current structures under the view of enhancing connectivity (left) and reducing connectivity (right).

The CIIs presented in this study show spatial differences throughout the region in the 'importance' of areas to connectivity between the two scenarios, and as such, we argue that integrating both the 'existing structures' and 'everything is everywhere' approaches provides the best possible insight into larval connectivity for a region. The existing structures scenario evaluates the effectiveness of current infrastructure, while the 'everything is everywhere' scenario explores potential for future enhancements. Together, these analyses provide actionable insights for optimizing the placement of marine structures to support and improve larval connectivity across the North Sea.

Our analysis identified significant differences in larval dispersal based on various PLD, month, and year groupings, underscoring the impact of temporal and environmental factors on connectivity, and supporting previous research that these factors influence larval dispersal patterns in biophysical models (Clubley et al., 2024; Gilbert et al., 2010; Hilário et al., 2015; Torrado et al., 2021). By pooling these groups, we capture intra-population differences in PLD, spawning season and inter-annual variation in dispersal, and provide a holistic community-level view of larval connectivity across the North Sea. Future studies utilising this approach to look at specific species, however, should take these identified differences into consideration, as such factors may have substantial implications on larval spread at the species-level.

Understanding the balance between community strength, density, and size is crucial for managing larval dispersal and marine connectivity (Ospina-Alvarez et al., 2020). The network analysis of current structures in the North Sea domain identified five distinct communities, demonstrating a range of network densities, strengths, and sizes (*see 3.2*). Communities with high density (i.e. communities 1, 3, 4 and 5) indicate that the structures within these communities are well-connected. This high internal connectivity might be beneficial for localized interactions but could limit the extent of broader network influence. The relatively weaker connections within the largest community (community 4) in the central North Sea has notable implications: the sparser network structure in comparison to the other communities may offer increased flexibility and resilience, allowing populations to adapt more readily to environmental changes or disturbances (Rossi et al., 2014; Watson et al., 2011). The relatively isolated nature of nodes in this community means that local disruptions may not propagate rapidly throughout the entire network, potentially allowing the community to recover more effectively from localized threats or changes. Conversely, lower density could also imply that Community 4 may be less cohesive, with isolated nodes or subgroups that might struggle to maintain stability in the face of broader disturbances. This may, however, be offset by the high strength of the community, which supports the extensive exchange of nutrients, larvae, and/or genetic material, which is crucial for maintaining ecosystem health and species diversity.

In contrast, the 'everything is everywhere' scenario presents a different picture of connectivity, with three major communities showing varied characteristics (*see 3.3*). The Western North North Sea (WNNS), with its high inter-connectedness and cohesion, may be more resilient to disturbances due to its tight-knit structure but could also be more vulnerable to localized impacts. In the Eastern North North Sea (ENNS), the broad and diverse set of interactions implies this region has the potential to play a critical role in maintaining overall network stability. However, the lower internal cohesion here suggests the resilience of this community is relatively lower. The Southern North Sea, with its balanced characteristics, suggests a well-connected community within the potential to play a significant role in the overall network. Analysis under the 'everything is everywhere' framework also highlighted key geographically clustered bridging regions in the central North Sea, with the potential to function as 'stepping stones' to connectivity. Previous studies have suggested that the decommissioning of structures in this area would result in reduced connectivity (Tidbury et al., 2020), and our findings agree with this. The identification of these areas, irrespective of whether they contain existing structures or not, is beneficial from a spatial management viewpoint. By highlighting these areas over the entire domain, we can provide information that can guide best practices from an ecological perspective for both the commissioning and decommissioning of marine structures (Bishop et al., 2017).

Network analysis using graph theory is becoming an increasingly utilised tool for further understanding seascape connectivity (Treml et al., 2008; Kininmonth et al., 2010; Thomas et al., 2014; Engelhard et al., 2017; Ospina-Alvarez et al., 2020; Tidbury et al., 2020; Mayorga-Adame et al., 2022; Abecasis et al., 2023; Clubley et al., 2024). Graph theory enables the identification of key habitats, corridors, and barriers influencing marine connectivity dynamics, and has been used to evaluate the structure of existing marine reserves (Abecasis et al., 2023; Engelhard et al., 2017), inform the design of Marine Protected Networks (MPAs) (Kininmonth et al., 2010; Ospina-Alvarez et al., 2020), and assess the connectivity of anthropogenic structures in the marine environment (Mayorga-Adame et al., 2022; Tidbury et al., 2020). Despite the range of applications of these studies, they all follow a common scheme: assessing connectivity based on dispersal of propagules from known habitats. While assessing connectivity from known habitats provides valuable insights into population dynamics, it is important to recognize its limitations. Focusing only on known habitats may result in a narrow spatial perspective, overlooking hidden habitats and corridors facilitating dispersal that extend beyond the boundaries of known habitats, and consequently underestimating the true extent of connectivity which may lead to suboptimal conservation and management strategies. Without considering the broader context of connectivity dynamics, conservation efforts may fail to adequately protect critical dispersal pathways, leading to fragmentation, loss of genetic diversity, and diminished resilience of marine populations (Peterson et al., 2020). Our study expands on traditional approaches by incorporating potential habitats, addressing the limitations of focusing solely on known habitats. This broader perspective offers valuable insights for conservation, spatial planning, and sustainable management of marine environments. While the approach undertaken here is a simplified overview of dispersal, omitting factors such as competency settlement window of the larvae, which has been shown to influence connectivity (Cecino and Treml, 2021), and behaviour, shown to influence biogeographic distributions of larvae following dispersal (James et al., 2023), direct comparison between the two scenarios highlights the potential underestimation of connectivity when looking solely at known habitats. This is evidenced by the community structures presented in Figs. 3 and 4, where larger connected communities were identified using the 'everything is everywhere' framework (Fig. 4).

4.1. Limitations and considerations

While this study provides valuable insights into the role of marine infrastructure in shaping connectivity patterns across the North Sea, limitations should be acknowledged to contextualise the findings and guide future research.

While our study provides valuable insights into broad-scale connectivity patterns, we acknowledge its limitations in not explicitly incorporating biological traits such as larval behaviour, vertical migration, and habitat selection, which can significantly influence dispersal trajectories (Sundelöf and Jonsson, 2012). The challenge in accurately parameterising these biological traits and behaviours in biophysical models stems from the limited availability of in situ empirical data, making their inclusion uncertain and potentially leading to highly variable or misleading dispersal predictions (James et al., 2023). In the face of these uncertainties, we argue that our surface-only passive dispersal framework provides a generalised yet robust perspective on connectivity.

While our model captures a baseline for dispersal dynamics that is applicable to many pelagic larvae, it is important to recognize its limitations in applicability to species with non-pelagic life histories. Species with direct development or brooded larvae exhibit fundamentally different dispersal mechanisms (Paulay and Meyer, 2006), which are not well represented by our approach. Similarly, species with extended PLDs, due to either innate biology or environmental conditions may experience different dispersal pathways that extend beyond the scope of our simulations. These constraints should be considered when interpreting our results, and future studies may benefit from tailored modelling approaches to account for taxa with alternative dispersal strategies.

We emphasise that our analysis is based on shared dispersal characteristics rather than ecological community interactions. The grouping of taxa in this study is based on similarities in pelagic larval stages and PLD rather than on trophic or ecological dependencies. This approach allows for broader applicability across taxa but does not explicitly capture species interactions that shape ecological communities. Future work incorporating multispecies interactions could provide further insights into how dispersal-driven connectivity influences ecosystem structure and function.

Our decision to focus on winter and summer simulations was based on capturing seasonal extremes in oceanographic conditions, which are primary drivers of larval dispersal pathways (Bashevkin et al., 2020). By selecting these endpoints, we aimed to encompass a broad range of variability in dispersal dynamics, which likely includes transitional periods such as spring. However, we acknowledge that this approach does not fully account for species-specific reproductive timing, and for studies focused on individual taxa, aligning simulations with known spawning periods would enhance biological accuracy.

By acknowledging these limitations, we provide a clear framework for interpreting our results. Future efforts that integrate species-specific biological traits, alternative life history strategies, interspecies interactions, and expanded seasonal simulations will be crucial in refining connectivity assessments and improving the ecological applicability of biophysical dispersal models. Nevertheless, our study serves as a baseline that can be built upon as more empirical data become available, and future research can refine and expand upon our findings to enhance ecological realism and species-specific applicability.

5. Conclusions

The ‘everything is everywhere’ framework in this study offers valuable insights into potential organism distribution in the North Sea, highlighting connectivity across both known and unknown habitats. This broader perspective identifies connectivity hotspots, migration pathways, and areas vulnerable to biodiversity loss, providing a clearer understanding of seascape-scale ecological processes. The methodology described in this paper is relocatable to any marine-based spatial context, and allows for the quantification of potential networks, applicable with or without existing habitat data, and the insights gained from this approach can inform management and conservation strategies, guiding decisions regarding the sustainable management of artificial structures, habitat protection, restoration efforts, and spatial planning of marine protected areas.

CRediT authorship contribution statement

Molly K. James: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gennadi Lessin:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Muchamad Al Azhar:** Writing – review & editing, Software, Methodology. **Michael Bedington:** Software, Methodology. **Charlotte H. Clubley:** Writing – review & editing, Methodology. **Paul Somerfield:** Writing – review & editing, Software, Methodology. **Antony M. Knights:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization.

Declaration of interests

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. Appendix

Appendix 1
Normality tests for distribution of distance_km for all pld/month/year simulations.

PLD	Month	Year	Anderson-Darling statistic	P value
7	feb	2011	30,994.64096	<0.001
7	feb	2012	15,974.9273	<0.002
7	feb	2013	16,597.40913	<0.003
7	feb	2014	12,511.63314	<0.004
7	jul	2011	20,327.98462	<0.005
7	jul	2012	12,362.05041	<0.006
7	jul	2013	6027.499801	<0.007
7	jul	2014	19,915.79057	<0.008
14	feb	2011	17,548.08621	<0.009
14	feb	2012	12,619.36706	<0.010
14	feb	2013	32,757.36984	<0.011
14	feb	2014	7255.113656	<0.012
14	jul	2011	17,921.28186	<0.013
14	jul	2012	15,260.46697	<0.014
14	jul	2013	7240.054447	<0.015
14	jul	2014	21,179.86186	<0.016
21	feb	2011	12,474.04885	<0.017
21	feb	2012	8184.756528	<0.018

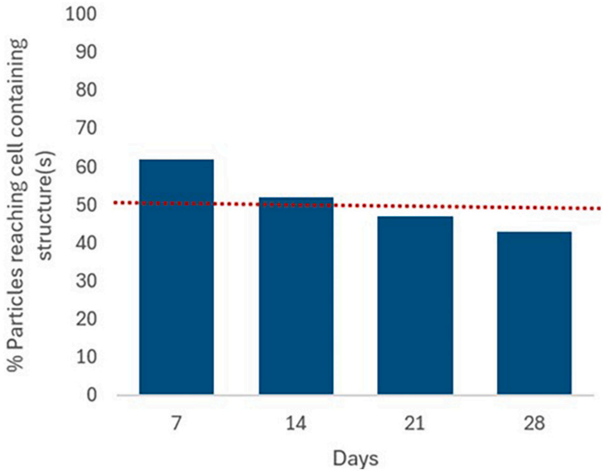
(*continued on next page*)

Appendix 1 (*continued*)

PLD	Month	Year	Anderson-Darling statistic	P value
21	feb	2013	35,155.80785	<0.019
21	feb	2014	4301.514342	<0.020
21	jul	2011	15,017.18821	<0.021
21	jul	2012	14,275.22659	<0.022
21	jul	2013	8429.26373	<0.023
21	jul	2014	19,072.20075	<0.024
28	feb	2011	13,197.10936	<0.025
28	feb	2012	4900.40814	<0.026
28	feb	2013	31,985.93697	<0.027
28	feb	2014	3269.396575	<0.028
28	jul	2011	12,999.93464	<0.029
28	jul	2012	9610.823307	<0.030
28	jul	2013	7127.806065	<0.031
28	jul	2014	15,816.28574	<0.032

Appendix 2
median distance and average effect sizes by group.

	Group	*Median Euclidian Distance (km)*	*Inter Quartile Range (lower bound)*	*Inter Quartile Range (upper bound)*	*Average effect size*
PLD	7	45.63	28.37	70.32	0.432
	14	75.4	46.18	119.5	0.356
	28	100.7	61.03	160.95	0.372
	28	124.32	75.21	197.69	0.415
Month	February	99.86	54.04	117.12	0.422
	July	67.4	39.57	109.12	0.365
Year	2011	86.04	48.85	141.32	0.376
	2012	86.93	47.57	136.71	0.385
	2013	59.12	36.21	91.83	0.362
	2014	110.71	56.11	212.54	0.452



Appendix 3. Likelihood of a simulated particle released from a grid cell containing an artificial structure reaching another grid cell containing an artificial structure by the end of its planktonic larval duration (PLD). Red dotted line denotes the average percent of particles reaching another structure over all explored PLDs.

Appendix 4: Graph theory metrics definitions and formulations

- **Out-degree** ($D_{out,i}$):
  - ***Definition:*** The out-degree of a node i is the total number of outgoing connections (edges) originating from that node to other nodes in the network.
  - ***Formula:***

$$D_{\text{out},i} = \sum_j A_{ij}$$

Where A_{ij} is the adjacency matrix and $A_{ij} = 1$ if there is a connection from node i to node j, otherwise $A_{ij} = 0$.

o **Interpretation:** Indicates the dispersal potential of a node, as it measures how many other nodes can be reached from it

- **In-degree** ($D_{in,i}$):
  - o ***Definition:*** The in-degree of a node i is the total number of incoming connections (edges) directed toward that node from other nodes in the network.
  - o ***Formula:***

$$D_{\text{in},i} = \sum\nolimits_j A_{ji}$$

Where A_{ji} is the adjacency matrix and $A_{ji} = 1$ if there is a connection from node j to node i, otherwise $A_{ji} = 0$.

o **Interpretation:** Represents the importance of a node as a settlement or destination point within the network

- **Node Betweenness** (B_i):
  - o **Definition:** Node betweenness measures how often a node lies on the shortest path between pairs of other nodes in the network.
  - o **Formula:**

$$B_i = \sum\nolimits_{s\neq i\neq t} \frac{\sigma_{st}(i)}{\sigma_{st}}$$

Where σ_{st} is the total number of shortest paths from node s to node t, and $\sigma_{st}(i)$ is the number of those paths that pass through node i.

o **Interpretation:** Captures the role of the node as a connector or stepping stone within the network, facilitating movement between other nodes

Data availability

The code supporting this study are publicly available on Zenodo at https://doi.org/10.5281/zenodo.15001694. This repository includes links to the source code for the FVCOM, ERSEM, and PyLag models, along with scripts for connectivity analysis, community detection, and the calculation of the Connectivity Importance Index (CII), enabling the reproduction of the results presented in this manuscript.

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