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The impacts of human-made structures on larval connectivity in the northern North Sea

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North Sea human-made, offshore structures (e.g. oil/gas platforms, offshore wind farms) provide a hard substrate habitat for benthic marine species which can spread between sites during their larval stage. Here, we aim to address how the installation of additional human-made structures, like new wind farms, or decommissioning of existing ones, like oil and gas platforms at the end of service, contribute to changes in larval connectivity. We use particle tracking model simulations to assess the ecological connectivity of benthic species in the northern North Sea during two contrasting years to highlight seasonal to annual variability. The methodology of releasing an extensive set of particles over a wide area produces our Retrospective Particle Tracks dataset. The sets of simulations can be interrogated to understand if additional human-made structures placed in any locations in the northern North Sea could potentially affect the ecological connectivity. Network metrics were used to identify connectivity between sites. Clustering of existing structures identifies a region that acts as an interchange between other structures which may otherwise only be connected during intermittent periods. The addition of new human-made structures located in areas with stronger residual current flow would enhance the connectivity.

The North Sea seafloor sediment is mostly covered by mud, sand and gravel with 100,000 km^2 (15%) of natural hard substrate supplemented by ~27,000 shipwrecks[1,2]. Offshore structures such as oil rigs and wind farms are an additional hard substrate resource for potential epibenthic species settlement. Human-made structures, despite providing only a small proportion of the total area of hard substrate, can provide hard-substrate in locations where natural hard-substrate is not otherwise present[3]. Benthic species can spread between sites during their larval stage. Recruitment of epibenthic flora and fauna (or biofouling) is part of the process where offshore structures function as human-made reefs, attracting mobile fauna[4,5]. Coolen et al. (2020) identified 193 species that inhabit hard substrate environments in the North Sea[5]. Generally, they found little difference in the population of communities present on natural rocks as opposed to steel structures such as wind farms and oil rigs.

How the ecological connectivity of benthic species in the North Sea will be affected by the decommissioning of existing structures or the introduction of additional ones remains understudied. Here, the ecological connectivity of benthic species refers to the movement of individuals and therefore genes between these structures or nodes[6–8]. Structures, acting as nodes, may be places where the individuals come from (source) or go to (destination). If a node performs neither role, its presence may be assumed to have no effect on existing habitat connectivity. If a node performs both roles, it may be considered a stepping stone between sites. If a stepping stone is created between two previously unconnected sites, this may have a fundamental effect on population structure[9]. Stepping stones may act in a uni- or bi-directional manner. Highly connected networks generally improve resilience in marine systems[8] and recovery time from disturbance[10]. For example human-made structures can play a role in species conservation and in enhancing resilience of protected species by acting as stepping stones, because they could facilitate the creation of a system of densely interconnected clusters of species, with both natural and human-made reefs[11]. Human-made structures could also provide the only suitable habitats for some species at far offshore locations for pelagic larvae that would otherwise have been lost offshore[5]. Human-made structures could also serve as habitat for pelagic larvae to spread to areas that are otherwise too distant to reach in a single generation[5]. However, through the same stepping stones mechanism human-made structures can facilitate the introduction of non-native invasive species into previously un-colonised geographic areas[12–15].

At present, the policy for offshore structure decommissioning in the North Sea is provided by the OSPAR Commission and focuses on removal

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of structures, with a few technical exceptions. However, of 40 experts surveyed 95% said a more flexible policy on decommissioning could be a benefit to the North Sea environment[16]. In another question (which was a poorly defined multiple answer question), the same experts were asked about decommissioning options that should be considered for offshore oil and gas installations in the North Sea which showed mixed opinions with 47% in favour of the most popular partial removal technique and 41% in favour of full removal[16]. This is because of the ecological benefit that structures can provide as human-made reefs as well as providing protection from trawling around the structures, but do we have a responsibility to reduced our impact on the ocean environment. With ecological connected structures, a broader view of the network should be regarded if a more flexible policy for decommissioning were implemented, highlighting the need to understand connectivity between structures. The survey shows there are differences in opinions of individuals with regard to removal and leaving structures in place and highlights the need for robust discourse on the topic[16]. Additional evidence is needed to support this discourse and future policy making[17–20].

Empirical evidence shows the benefits of connectivity of marine ecosystem information to marine conservation planning[21,22]. The aim of marine conservation planning is to ensure the persistence of a metapopulation (a population of populations distributed in discrete habitat patches that are linked by occasional dispersal) across a range of species[23] and connectivity is one part of metapopulation dynamics. For marine conservation planning, there is ongoing debate[24] over whether to base conservation on extent and quality of habitat, ignoring connectivity or to prioritize site protection by network structure and connectivity. Kininmonth et al. (2011) found that for network persistence, protection needs to prioritize hubs or clusters with high connectivity[23]. Current generation of computational tools for spatial conservation planning can also incorporate information on connectivity ([24,25] and references therein).

Connectivity can be assessed using several means: species similarity[26,27], genetic similarity[28–30] or physical connectivity simulating the physical movement of individuals in ocean currents[3,31]. Here, we use the latter. Physical connectivity has been previously assessed using particle tracking larval dispersal modelling to identify likely pathways by which invasive species arrive at offshore structures, independent of active transport (e.g. on ships), and could spread to other structures[15]. This has been taken a step further in the North Sea by using the particle tracks between offshore structures in combination with network connectivity metrics[3,31].

The methodological approach that we have taken makes the dataset we have created potentially exploitable for different applications. We firstly create a large, generic particle tracking dataset which we call the Retrospective Particle Tracks dataset. We can then activate additional structure locations during the connectivity metrics analysis, without the need of re-running the particle tracking model for specific locations. The latter differentiates our approach from existing studies, e.g. refs. 11,31 which analyses the ecological connectivity of existing structures only. We also take a broader view of environmental conditions over seasonal and annual timescales and

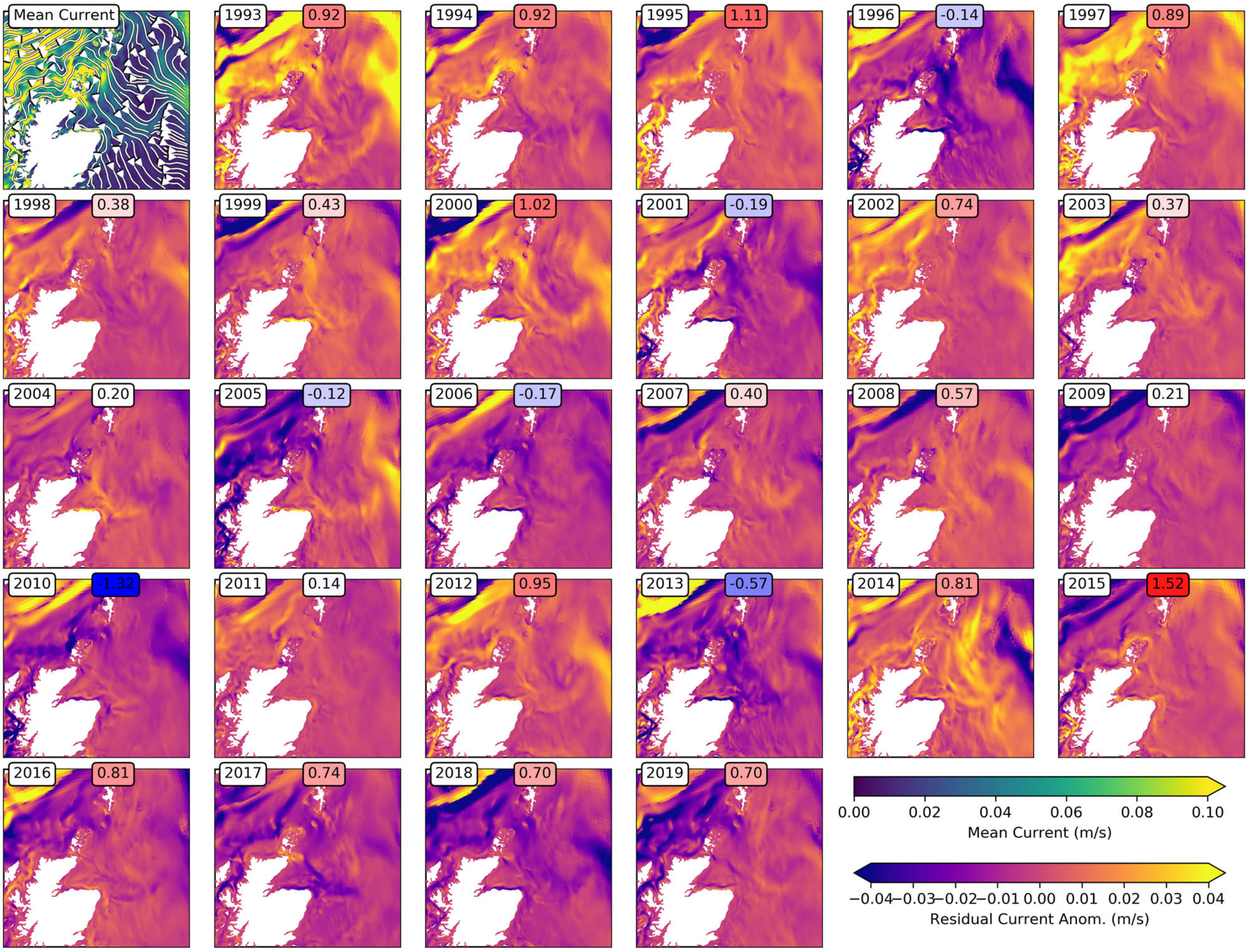


Fig. 1 | Winter mean and anomaly residual current speed. Mean residual current speed of the Scottish Shelf Water—Reanalysis Service during winter (January–March) and the residual current speed anomaly from the mean for each year 1993 to 2019. The coloured box in the top right of each panel shows the mean North Atlantic Oscillation (NAO) index for the winter (January–March) of the year. Observational NAO index is consistent with ERA5 NAO index.

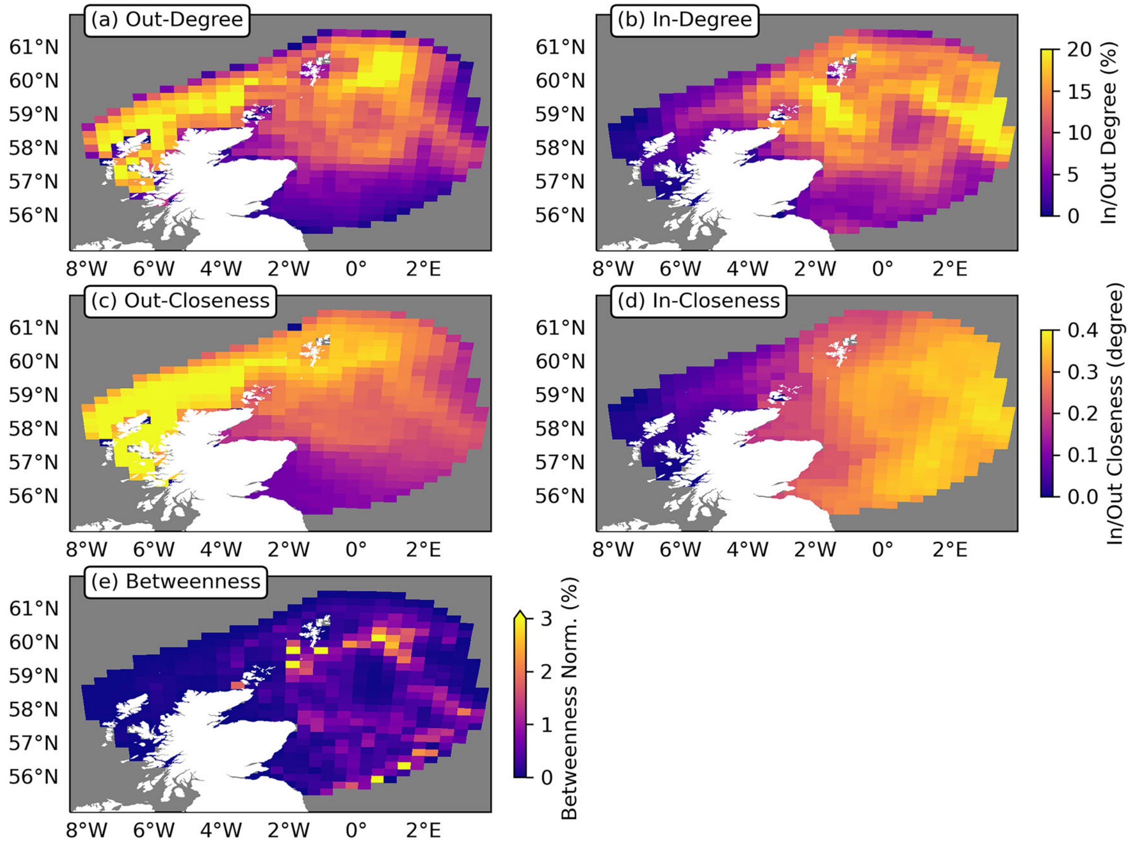


Fig. 2 | Winter 2014 connectivity. Connectivity metrics based between all possible source and destination nodes (locations) for winter (JFM) 2014 for particle stracked for 90 days. **a** Out-degree; **b** In-degree; **c** Out-closeness centrality; **d** In-closeness centrality; **e** Betweenness centrality. For all connectivity metrics a minimum of 100 particles connecting two locations must be met for a valid connection. The same figure but for summer (JAS) 2014 can be found in Supplementary Fig. 2.

we achieve more robust statistics by releasing particles over longer time periods than existing studies[3,11,24,31].

In the Results section (Section "Results"), we assess the connectivity from two perspectives: (1) exploring the connectivity metrics of the dataset; (2) a case study on the connectivity of existing infrastructure, where we assess how the removal of structures (i.e. oil and gas platforms) would affect the connectivity. Section "Discussion" is the 'Discussion' of our findings. In Section " Methods ", we present the "Methods"; we suggest reading the Methods before the results. Model validation and the sensitivity to number of particles are in the Supplementary Methods.

Results

The approach to particle tracking we take in this paper allows us to retrospectively identify sources and sinks of particles that have been forward advected by currents with the addition of turbulent diffusion. Without restricting the release locations of particles to existing structures, instead we release particles over the whole northern North Sea and select the source and destination locations a posteriori, during the connectivity metrics analysis. This means that we have created a dataset of potential trajectories that can be easily interrogated to assess the changes in ecological connectivity for different applications. Our results are subsectioned into: (1) exploring the connectivity metrics of the dataset; (2) a case study on the connectivity of existing offshore structures e.g. for decommissioning.

For the particle trajectories simulations of larvae, we picked two years: 2014 and 2017. These years were selected because they represent different residual current conditions in the North Sea. 2014 has above average strength residual winter currents and 2017 has below average strength residual currents (Fig. 1). It has been reported that the first mode of variability in residual currents is influenced by wind driven variability associated with the North Atlantic Oscillation (NAO)[32–34]. Residual currents tend to be stronger with positive NAO index but the mode only accounts for 44% of variability[32]. This makes NAO unreliable as the sole metric for deciding which years to use to represent the range of residual current, as exemplified by 2015–2019 (Fig. 1). 2014 has a winter NAO index 0.81 and 2017 has an NAO index 0.74 so should have similar residual current anomalies but they do not. It is because the currents do not follow the NAO index that we select our larvae analysis years based on the residual currents.

Connectivity metrics of the dataset

Figure 2 presents network connectivity metrics calculated from the particle tracking data in 2014. In comparison to 2017, we can differentiate the effect of strong from weak residual current forcing. The out-degree and out-closeness centrality show similar spatial patterns with >20% out-degree and >0.4° out-closeness centrality west of Orkney (Fig. 2a, c). East of Orkney the out-degree and out-closeness decline to <2% and <0.15° respectively in the south-east. The out-degree shows also a ring feature centred at 59°N, 1°E. In 2017, the out-degree and out-closeness centrality show spatial patterns similar to 2014 but with less strength, 15% out-degree and 0.30° out-closeness (Fig. 3a, c). Overall, the intensity of out-degree and out-closeness is lower in 2017 than 2014. We can also make a comparison between the amount of time particles are advected for as an analogy for the pelagic larval duration. Figure 4a, c shows the out-degree and out-closeness for particles tracked for 20 days (instead of 90 days) in 2017 the year with weak currents. This provides a lower boundary with very limited connectivity as the out-degree peaks ~3% and the out-closeness peaks around 0.15° (Fig. 4a, c).

In 2014, in-degree shows the values > 20% around Orkney and Shetland, but also east of 2°E. This is because the Orkney-Shetland area is a link between east and west of the domain with strong currents enabling a wide range of source locations to these destinations. The in-closeness centrality shows values >0.35° in the east and south of the domain, where

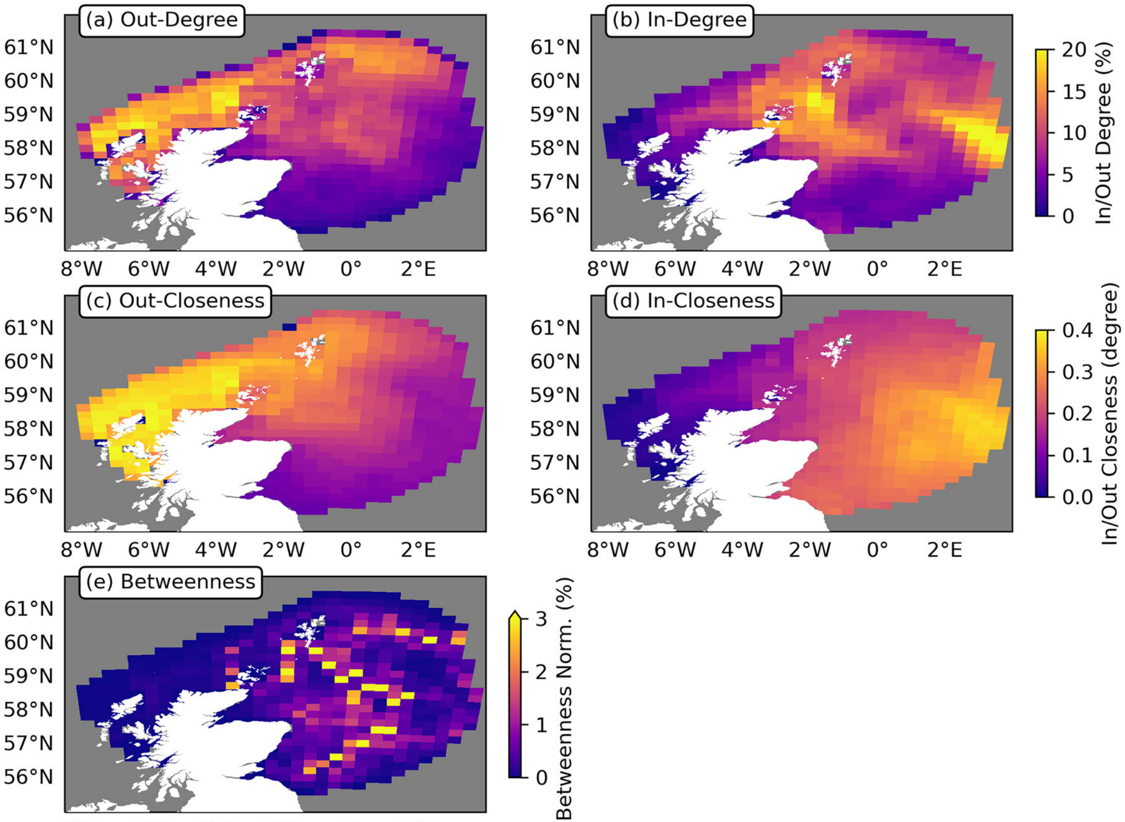


Fig. 3 | Winter 2017 connectivity. Same as Fig. 2 but for winter (JFM) 2017. **a** Out-degree; **b** In-degree; **c** Out-closeness centrality; **d** In-closeness centrality; **e** Betweenness centrality. The same figure but for summer (JAS) 2017 can be found in Supplementary Fig. 3.

residual currents tend to be directed. Given the in-closeness accounts for connections via other locations, it is to be expected that the largest values are in the south and east where residual currents lead. This is complementary to the pattern in the out-closeness centrality. In-degree shows a ring structure at 59°N, 1°E, like the out-degree. In 2017, in-degree shows maximum values > 15% around Orkney and the ring structure is not present (Fig. 3b, d). In-degree values south of 57.5°N are 5%, half what is found in 2014. In 2017, in-closeness had the same spatial pattern as 2014 but with a 0.1° reduction. In general, the pattern of in/out-closeness reflect the path of residual currents which flow from west to east. These are the Scottish Coastal Current and the Atlantic Inflow Current[35,36]. For comparison with 20 days of particle tracking in 2017, the in-degree peaks at ~3% and the in-closeness peaks at 0.15° (Fig. 4b, d). Given that the in/out-closeness is less affected than in/out-degree by tracking particles for 20 days instead of 90 days, suggests the greater requirement for intermediate locations.

The betweenness quantifies locations that are on the shortest route between all other locations as a percentage (Fig. 2e). This has been normalised by the number of pairs of nodes. The betweenness highlights locations that are both a strong destination and a source that can act as a bridge between other locations. This means that additional structures located where the betweenness is high act as stepping stones. In 2014, the locations with betweenness >2% are east of Orkney in one main arc of elevated betweenness at 59°N from 2°W to 2°E (Fig. 2e). The other locations with elevated betweenness roughly align with the horizontal gradients in out-degree, enabling a west-east transfer of connectivity. In 2017, the betweenness is larger than 2014, with three main arcing lines >2% across the northern North Sea (Fig. 3e). There are many more locations with betweenness >2% in 2017 than 2014. This suggests 2017 has more limited direct connectivity and is more reliant on the bridged connectivity to sustain the same network. Given the large differences in betweenness between the two years, only two years are not fully sufficient to perform a well-converged statistic of Betweenness estimations at high resolution. For comparison with 20 days of particle tracking in 2017, as expected, the betweenness is much greater than tracking for 90 days with most of the locations east of Orkney having betweenness > 1.5% and ~ 30 locations with betweenness >3% (Fig. 4e). Some of the arcing patterns found in the 2017, 90 days tracking are present but there are additional features at 3°E and 58°N, 0°E showing the shorter steps particles have to make in the northeastern North Sea.

Connectivity metrics of existing offshore structures

In this part of the paper we consider a case study where the full particle trajectories dataset is filtered to consider source and destinations only from existing offshore structures for decommissioning purposes. The locations of existing offshore structures were compiled from both oil/gas rigs and wind farm structures[37]. We used the locations of offshore structures within our domain to produce a Boolean mask on the regular grid used to assemble the particle trajectories (Fig. 5). We then used this Boolean mask for filtering both the sources (release locations) and the destinations (locations passed through after a 10 days maturity period and up to 90 days larvae lifetime, see Section 'Methods' for details) to only include locations with a structure, before calculating the connectivity metrics and timeseries (any coloured cells in Fig. 5 contain a structure). This filtering means particles must start their trajectory at a grid cell with a structure and settle on a location with another structure.

The out-degree (sources to destinations) is the strongest around 58°N, 0°E where out-degree reaches 8% but there is a second source around 60°N, 2°E with 6% out-degree (Fig. 6a). The out-closeness centrality (including connections via other locations i.e. bridges) has maximum of around 0.08° in the same area as the out-degree around 58°N, 0°E but unlike the out-degree there is not a second peak (Supplementary Fig. 4a). The out-closeness centrality has low values (<0.02°) towards the extremities of the domain. The in-degree (destinations from sources) is

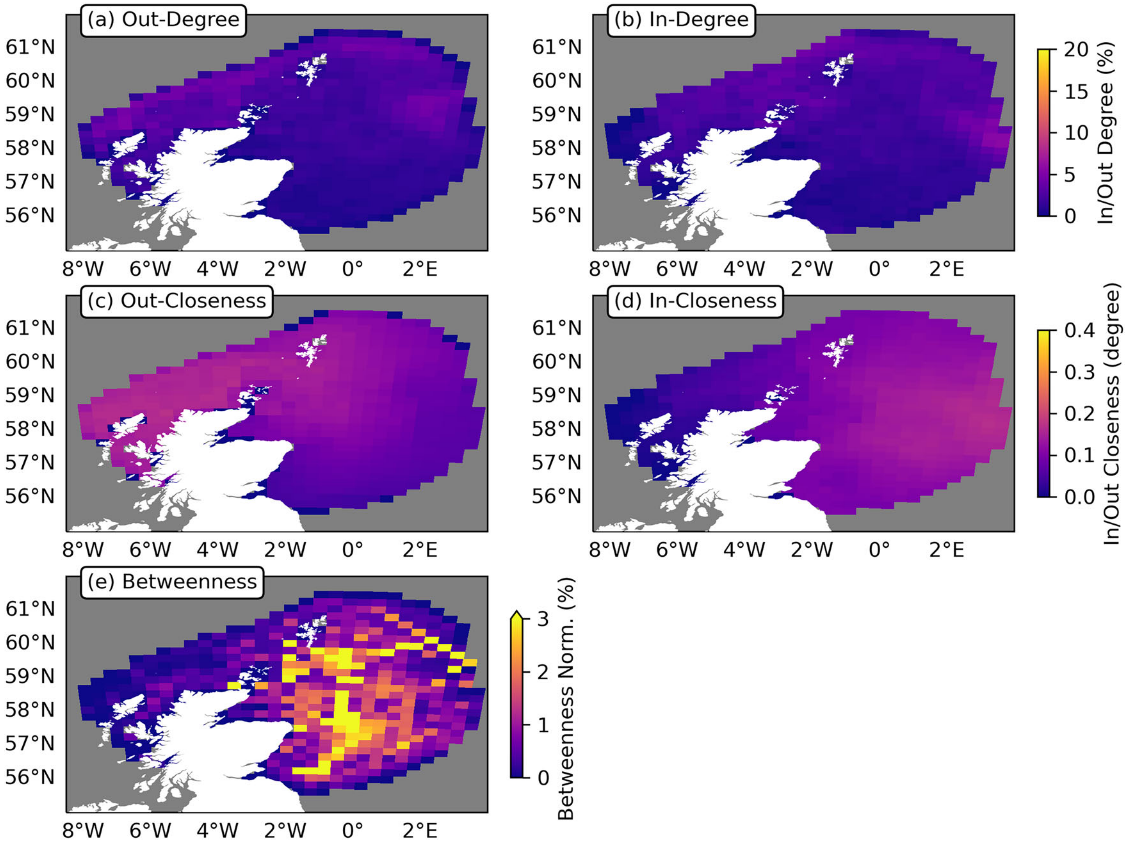


Fig. 4 | 20 Day connectivity. Same as Fig. 2 but for winter (JFM) 2017 and for particles tracked for 20 days instead of 90 days. **a** Out-degree; **b** In-degree; **c** Out-closeness centrality; **d** In-closeness centrality; **e** Betweenness centrality.

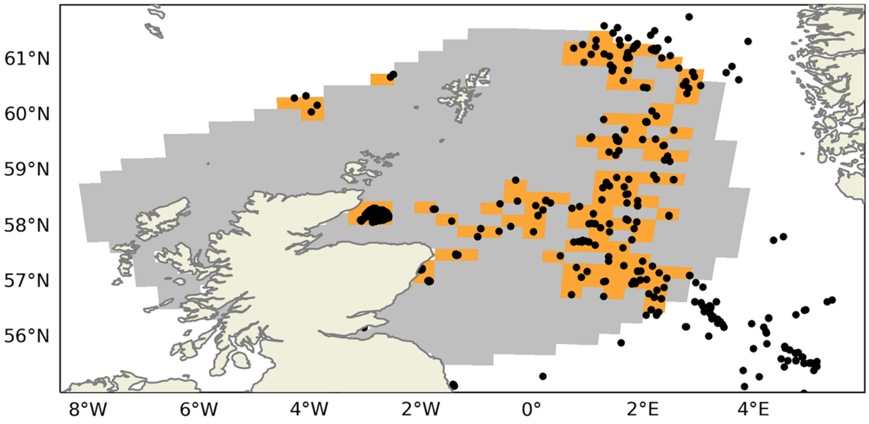


Fig. 5 | Offshore structures map. Offshore structures present in the analysis region. Offshore oil/gas rigs and wind farm structures (black points). The coloured areas will be referred to in more detail in Fig. 6. The colours show the Boolean mask, where each coloured area represents the installation grid cells in each clustering module (see Fig. 6f). Dark grey (module zero) is the particle release zone. Light grey is land.

largest at 8% at 58°N, 2°E, with elevated values east of 1°E (Fig. 6b). This leaves a low region west of 2°W and north of 60°N where very few particles from structures could settle. The in-closeness centrality is similar to the in-degree, only indicating more destinations for the structures to the east of 0°E (Supplementary Fig. 4b).

Here we calculate betweenness where any structure can be a source to structures and a structure can then act as a bridge to other structures. The betweenness in Fig. 6e shows 14 structures have >0.15% of bridges connecting structures to the rest of the particle release locations. These locations could be key in keeping a diverse larval population in the remaining structures, but also in spreading non-native species. The more isolated structures not acting as a source or destination are less important for maintaining the network, and those structures could be removed at the end of their life.

We have calculated clustering in Fig. 6f, an additional connectivity metric. The clustering metric from offshore structures shows discrete modules which we define as peaks greater than 45%. These modules have relatively high internal connectivity between locations within the module and lower external connectivity between modules. The number of modules in the clustering was chosen around the spatial peaks in the clustering coefficient shown. Therefore, our modules identify important barriers to larval dispersal and may be analogous to regions that act as a community with larger genetic similarity within larval populations[38]. The clustering metric highlights regions known as modules that represent communities within the network. The modules have been named 1: Edge, 2: Coast, 3: Central, 4: North, 5: South.

The time-varying connectivity between the modules is shown in Fig. 7. This shows the average number of particles received by any structure within

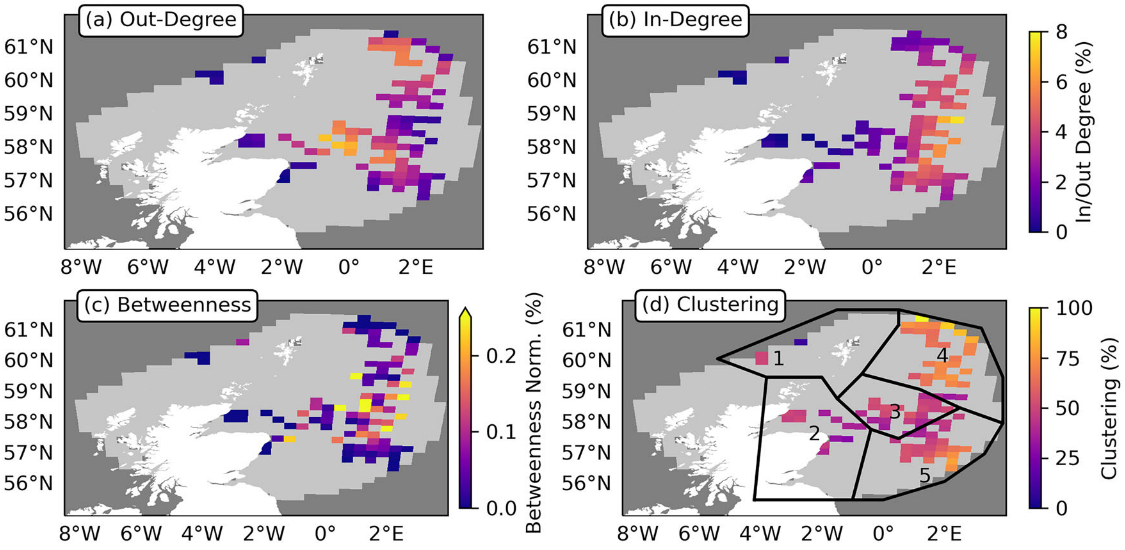


Fig. 6 | Structure connectivity. Average connectivity metrics for 2014 and 2017 for the existing structures. **a** Out-degree; **b** In-degree; **c** Betweenness centrality; **d** shows the clustering metric destination where existing structures are the only source. The main cluster hot spots (known as modules) are identified by regions in black lines in (**d**). The individual structures in each module can be seen in Fig. 5. The modules are named as follows: 1: Edge, 2: Coast, 3: Central, 4: North, 5: South. For all connectivity metrics, a minimum of 100 particles connecting two locations must be met for a valid connection. The out-closeness and in-closeness can be found in Supplementary Fig. 4.

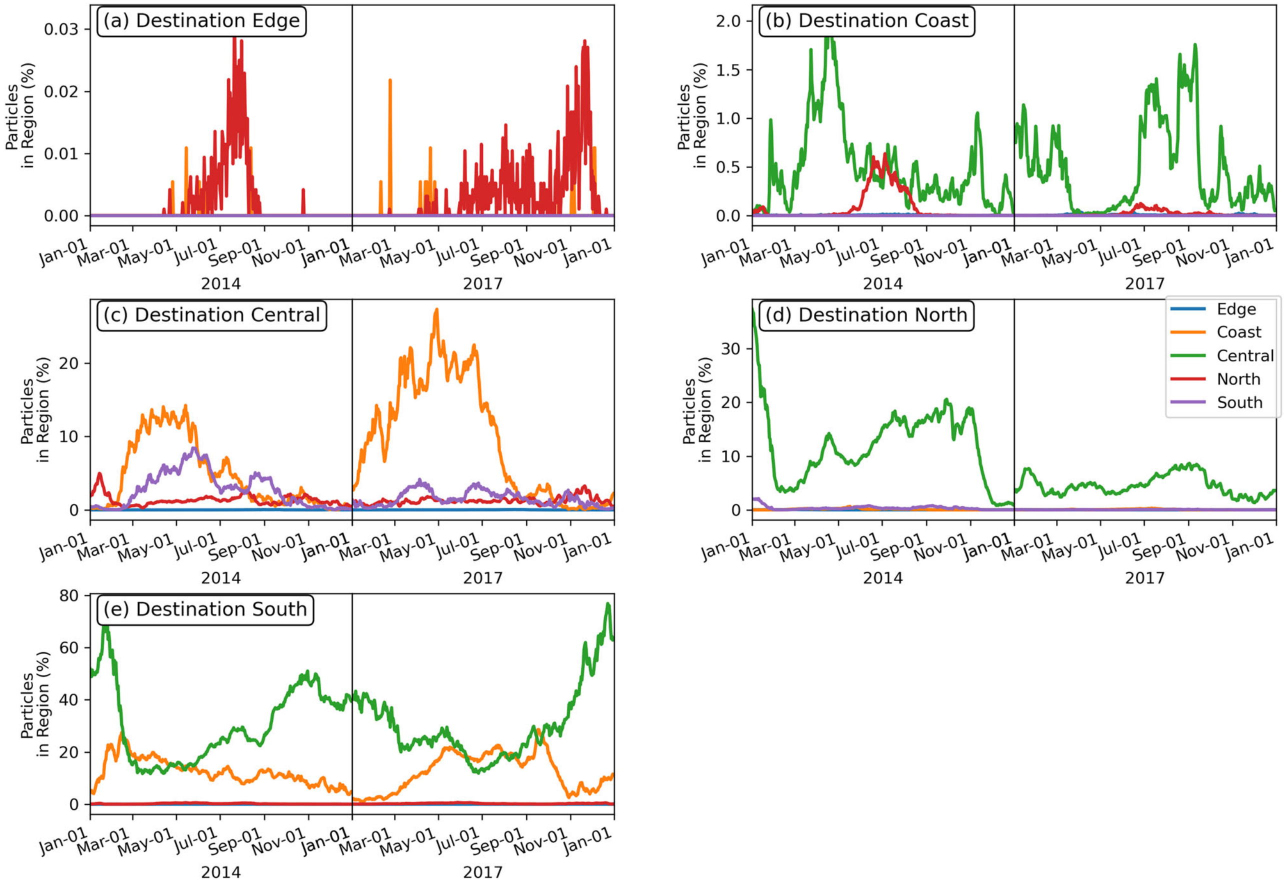


Fig. 7 | Connectivity timeseries of cluster regions. Timeseries for 2014 and 2017 of the percentage of particles per release from a source region connecting to a grid cell in the sink region (see Fig. 6f). In each panel one of the regions is chosen as a destination and all others as possible sources; (**a**) Edge, (**b**) Coast, (**c**) Central, (**d**) North and (**e**) South region. Note the delineation on the x-axis for 2014 and 2017. Each day in the timeseries represents one of the daily releases with the date showing the start of the release, equivalent to larval spawn day (not the date the connection is made). This simulates how many particles from the larval spawn region on given days connect to other sample regions over the particle's lifetime (90 days). Given the particles are aggregated into 10-day bins (maturity period), it is possible for a particle to pass through a site twice if the repeat is outside the 10-day window of the first connection.

the module from any other module. The largest contributor of particles to the Edge module is the North module but this is <0.03% per release of particles from a source region connecting to a grid cell in the sink region at its peak (Fig. 7a). This shows the Edge is very isolated. The Coast module receives the largest number of particles with peaks of >2% per release from the Central module in April 2014 and >1.5% per release in September 2017 (Fig. 7b). This is intermittent, as there are frequently <0.5% per release for most of 2014 and 2017. The North module has a seasonal signal where it contributes >0.5% per release from June to August 2014 and 0.1% per release from June to August 2017.

The Central module has the largest variety of particle sources (Fig. 7d). The Coast module is a seasonal source of particles to the Central Module between February and July in both 2014 and 2017. However, the number of particles in 2014 peaks at 18% per release, while in 2017 the peak is >25% per release. The second contributor to the Central module is the South module with a peak of >8% per release in May 2014. The South module sourced particles show >3% per release from February 2014 to October 2014 and in 2017 March, April, June and July. The North module peaks with a contribution of >4% per release to the Central module in January 2014, but remains at <3% per release in 2014. In 2017 the contribution from the North module to the Central module is <2% per release, except from November when it reaches 3% per release.

The North module primarily receives particles coming from the Central module (>3% per release through most of 2014 and 2017) (Fig. 7d). This has a stronger connection of >15% per release from the Central module in 2014 than the < 8% per release in 2017. The North module also has >2% per release from the South module in January 2014 but this is much reduced for the remainder of 2014 (<1% per release). There are no particles connecting from the South module in the North module in 2017. The South module consistently receives >10% per release from the Central module (Fig. 7e). There may be some seasonality in this, with >40% per release connecting in winter (January, February, October, November and December) in both 2014 and 2017. The South module also receives >10% per release from the Coast module throughout most of 2014 and 2017.

In summary, connections are episodic and vary between 2014 and 2017. In Fig. 7, there are some prolonged periods of numerous connections which underpin high values of connection metrics in Fig. 6. Where connections are rare and weak the average values of metrics in Fig. 6 are implicitly low and uncertain.

Discussion

Our analysis explains the complex networks of connectivity that marine species are able to produce around the northern North Sea. The approach to particle tracking we take allows us to retrospectively identify sources and destinations of particles that have been forward advected by currents with the addition of turbulent diffusion. We combine this with an exhaustive and expansive release of particles to obtain robust connectivity metrics and explore the connectivity from two view points. These two view points improve our understanding of present and future benthic species connectivity networks than could occur:

1. Using the connectivity metrics of the whole dataset, we can consider how adding offshore structures such as wind farms could be a source or sink for larvae assuming they can arrive from, and settle in any location in our study area. This could be plausible if they're using natural hard substrate. For example, if an additional stepping stone is created, it can potentially join two previously poorly connected sites and this might have an effect on the population structure, increasing the resilience of the network, but also potentially introducing non-native invasive species into the network. The 2014 and 2017 networks have expansive areas of the northern North Sea that can be reached within the 80 day larvae maturity window (the particles are able to settle after 10 days of maturity and have a lifetime of 90 days, see Section 'Methods'), as shown by the out-closeness and in-closeness (Fig. 2). If additional structures were deployed, the connectivity would receive the largest increase from deployment at the high betweenness locations in 2014 and 2017 south of Shetland. This is because it would link any additional structures in the west of the domain with the existing structure network in the east of the domain. Describing the number of necessary connections for ecological stability is beyond this study and therefore, the value to larvae of additional redundancy in structures and connectivity cannot be assessed. Placing additional structures towards the northeast edge of the domain or the south of the domain would have a weakest effect on the connectivity because it is both a weak source (out-degree) and a weak destination (in-degree). The weak connectivity in the northwest is because of the weak influence of shelf sourced water (carrying particles) here and export of particles sourced here towards Norway. The weak connectivity of the south of the domain is because particles are carried away from the coast around Peterhead, similar to the coastal freshwater pathway described in Barton et al (2024)[36] (Fig. 1). The particles in the south of the domain could connect with the southern north sea but this is out of scope for this study.
2. For the case study of connectivity of existing offshore structures, the in-degree shows the structures in the Central module are a key source of particles in the network (Fig. 6). The structures in the Central module also acts as an interchange enhancing connectivity between the offshore structures in other modules. Structures in the Central module are more important than structures in other modules for maintaining the present network. Structures in the Coast module do not receive many particles from other module but are an important source to the other modules. Removal of structures in the Edge module would cause the least effect to the overall connectivity of the network. Structures in the South module could be removed since there is also a route for coastal sourced particles through the Central module. Although structures in the North module are a poor source of particles to structures in other modules, they have high internal connectivity (clustering), which suggests this module has more potential for genetic similarity and multi-generational inheritance that could allow benthic species here to adapt and specialise.

The distribution of particles and variability between the strong and weak forced years is dependent on the residual currents. These transport pathways can be influenced by the current jets of seasonal temperature fronts during the summer[39]. During the winter the currents around Scotland are buoyancy forced with variability from wind driven forcing[34,36,40]. The current speed in winter is weakly correlated with the winter NAO index[32–34]. We have found that NAO index is not a reliable tool for identifying years with strong winter residual current (Fig. 1). The buoyancy forced currents comes from year-round salinity fronts dividing fresher coastal water from more saline Atlantic Water and variability in the freshwater flux can affect variability in the currents[36]. Tidal currents around the northwestern North Sea are strong (~0.4 ms^{-1}) compared to the residual currents (~0.1 ms^{-1})[41,42]. However, the oscillating nature of tidal currents means they mostly move particles in the tidal ellipse and do not contribute as much to moving particles over great distances.

The offshore structure network in the northern North Sea is generally aligned along the residual currents, although the currents can shift depending on variability[35,36]. The Dooley Current in particular flows away from the coast at Peterhead and circulates around the Fladen Ground (a 100–150 m deep area of the North Sea at 58.5°N, 1°E), but can shift north and south depending on the year. In the offshore structure analysis the variability in the currents and fewer number of locations means a larger number of bridges are needed. There are also times when interannual variability causes modules to become disconnected from other modules. This means disconnected modules can be re-connected in other years and the connectivity is only present over longer timescales. This is shown to affect the overall lower number of particles connecting into the North module in 2017 compared to 2014 (Fig. 7). For modules where the disconnection is seasonal, it could be that larvae that spawn out of phase with the seasonal currents i.e. during a disconnect, would never connect directly between the two modules. For example, a connection of particles from the North module to the Coast module could only occur during the summer (Fig. 7).

When planning offshore structures, the variability of residual current will have an effect depending on where and how many additional structures are introduced. For example, the in-degree and betweenness centrality show areas south of Shetland would retain high connectivity in the network regardless of strong or weak residual currents. However, additional structures placed in the west of the domain would have a weaker connectivity during weak residual currents and may even become disconnected from the existing offshore structures in the east of the domain, without also having bridging structures in the high betweenness area in centre of the domain.

In comparison to the work of Tidbury et al. (2020), our approach of using an Eulerian grid is similar but we select locations after running particle tracking[3]. Their use of network metrics provides a quantitative measure of connectivity, however we are unable to make direct comparisons with the results due to the metrics being dependent on the number of nodes used to produce them. Our connectivity metrics maps provide spatial patterns indicating the main source and destination regions for larvae that inhabit the offshore structures. In comparison to Henry et al. (2018) and Mayorga-Adame et al. (2022), we use a larger number of particles, in the full water column, over a longer period time and calculate metrics over the whole northern North Sea in addition to metrics focused on offshore structures[31]. Despite considering different oceanographic conditions (years, season, depth of currents) and different larval characteristics (larval duration and maturity period), the spatial patterns of connectivity they found are similar to our clustering metric, increasing confidence in the robustness of our findings, although without the grid of potential destination locations, the spatial arrangement of the modules is less clear. All presented results treat any connection between 10 and 90 days identically, which we consider fairly representative but not universal. In principle, future work could interrogate the same data with another subset of connections counted as viable for a shorter maturity window or pelagic larval duration.

Our particle tracks have been limited by the constant diffusivity in the horizontal mixing[43]. In reality, diffusivity only plays a minor role in particle movement compared to advective currents. A larger diffusivity could increase the range of pathways and increase the distance that particles could move over their simulation period. Our exhaustive particle placement method (in the Supplementary Methods) shows we have taken reasonable measures to counteract this bias by using more particles that can explore the possible pathways (Supplementary Fig. 1). The currents used to force out particles have not been conditioned with the affects of offshore structures such as wind farms. Chen et al. (2024) show windfarms can affect current speeds by up to 2–3 $\mathrm{cm\,s^{-1}}$ and directional changes up to 100°[44]. Our simulations do not capture that distortion of flow. The omitted effects may be minimal compared to the ~12 km resolution of our output, but that could be investigated in future work.

The node-based connectivity metrics that we used in this work have the advantage of retaining straightforward ecologically relevant information; however are somewhat simplistic if used for conservation planning. In future work, more sophisticated whole-network analysis and multi-objective optimization method[24] can be used to analyse the network. Connectivity needs also to be integrated in spatial conservation planning[25] which is a more systematic and comprehensive planning framework than connectivity alone. The inclusion of connectivity in spatial conservation planning is still challenging[45], especially for remote and poorly known areas or species[25]. However, including connectivity can help to identify areas that do not appear as important at first sight, but play an essential role in ensuring connectivity and network coherence[25].

There are other aspects to the decommissioning process that have not been covered in this study such as the cost to the government if structures left in place later require removal. We recommend an independent cost analysis to address this. There is also the carbon emission cost associated with removing the structures. Again, we suggest analysis to calculate the carbon emissions for various partial and full removal strategies[16].

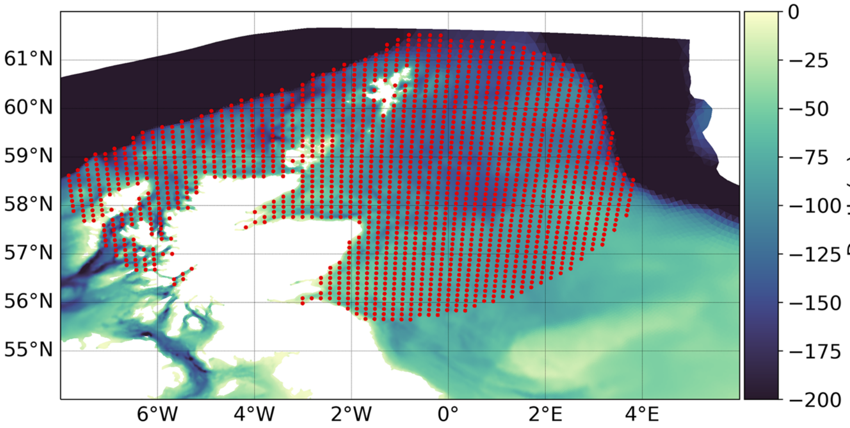
To summarise, this study investigates the connectivity of existing and new additional offshore structures in the North Sea. We explore how removing structures could change connectivity and where adding structures could increase connectivity. Our analysis identified the year 2014 as having strong residual currents and the year 2017 as having weak residual currents, and we make use of this to compare particle dispersal and connectivity under different current regimes. For the planning of additional offshore infrastructure, we find a large network of connectivity that spans from the Western Isles of Scotland past Shetland to the northeastern North Sea. This generally follows the main residual currents of the Scottish Coastal Current and Atlantic Inflow Current. With strong residual currents the connectivity is stronger than with weak currents. The addition of new human-made structures located in areas with stronger residual current flow would enhance the connectivity with a greater probability of larvae directly connecting with another structure. Additional structures placed in areas with high betweenness (bridging areas), e.g. south of Shetland, would increase to connectivity, potentially increase the resilience of the existing network, but also acting as stepping stones for non-native species. Placing additional structures in locations where existing structures are removed/decommissioned could be an approach to maintain the connectivity of the existing network. For the connectivity of existing human-made offshore structures, we find the structures create a network whose connectivity is enhanced by the use of some locations as key bridges to connect extremities to the wider network. Clustering and the temporal analysis of internal/external connectivity have revealed that there is intermittent connectivity between the modules. In combination with seasonal larvae spawning, some modules do not connect annually but interannual variability means connectivity is present over longer timescales. Existing structures are most important (i.e. more connected to rest of the network) in a cluster of structures we call the Central module. Removal of Edge module structures, which are weakly connected to the other modules, would have the least effect on the network. The North module is less connected to the other modules, but has the largest internal connectivity and thus potential for genetic specialization. Our study highlights the need for strategic planning considering environmental factors of residual currents and seasonal to annual effects on species connections.

Methods

In this paper, we used particle-tracking model runs to simulate the dispersal of planktonic larvae from/to locations, first we will outline the datasets used, then the particle tracking implemented and then the analysis carried out.

The advection of particles requires water currents and the diffusion requires diffusion parameters. We used input of currents and vertical diffusion parameters from the existing SSW-RS (https://sites.google.com/view/ssw-rs) which provides a 27-year (1st January 1993 to 31st December 2019) physical reanalysis of the Scottish Shelf Model (SSM) Version 3.02[refs. 36,46, described in more detail in Barton et al. 2024]. To summarise, the SSW-RS uses an unstructured grid hydrodynamic model UK-FVCOM4.0[47]. The domain covers the Scottish continental shelf at relatively high resolution (length of the edge of the unstructured triangle) of 0.5 km close to the coast to 20 km at the Atlantic Ocean boundary, but also covers most of UK waters, the North Sea and the English Channel[48,49]. The model includes the General Ocean Turbulent Model (GOTM) coupled to FVCOM to simulate vertical turbulent mixing[50]. Horizontal mixing was parameterised in FVCOM using the Smagorinsky method with a constant horizontal diffusivity value of 0.2 $\mathrm{m^2s^{-1}}$[51]. The boundaries were forced by regional Nucleus for European Modelling of the Ocean (NEMO) models the Atlantic Margin Model 7 km[52,53], Baltic Sea Physics Reanalysis[54,55] and include tidal forcing from TPXO9-atlas harmonic tides[56]. The atmosphere was forced by the European Centre for Medium-Range Weather Forecasts (ECMWF) dataset ERA5 (ECMWF Reanalysis 5th generation)[57]. SST was assimilated by the Ocean Data Analysis System for Marine Environment and Security for the European Area (ODYSSEA)[58]. The rivers were forced at 912 locations with daily river volume flux and temperature data from the European-Hydrological Predictions for the Environment (E-HYPE)[59]. The river locations came from the Centre for Ecology and Hydrology (CEH)

Fig. 8 | Particle starting locations. Particle starting locations show as red points. The colour scale shows the bathymetry and the lines show the 200 m isobath.



Grid-to-Grid (G2G) model[60] and only covered the coastline of Scotland and Northern Ireland with additional location across the northwest European shelf from the E-HYPE data.

In the Supplementary Methods we make comparisons between particles and drifter tracks. We used drifter data from marine.copernicus.eu(INSITU_GLO_UV_L2_REP_OBSERVATIONS_013_044).

The offshore structure dataset is used from the work of Martins et al. (2023), who have compiled the most accurate representation of present offshore structures in the North Sea from multiple sources (2023)[37].

The particle tracking was carried out using PyLag[61]. Particles are advected using 3D velocities and diffused using 3D Milstein[62], forced by the FVCOM model output (the SSW-RS dataset). Currents and vertical turbulent diffusivity are used as input to the Pylag particle simulations. Sources and destinations of particles that have been forward advected by currents with addition of turbulent diffusion can be retrospectively identified, thus allowing diffusion of particles which would not be physically the same using backwards tracking (although there may be statistical similarly for a large number of particles). Particles contacting the ocean surface, ocean bottom, or a lateral boundary are reflected back into the model domain. Several experiments were carried out using the particle tracking; two experiments for validation purposes against drifters, followed by the main experiments for 2014 and 2017 used for particle simulations of larvae connectivity analysis, referred to as the connectivity experiments.

First, the particle tracking has been tested and validated for two 90-day periods for passive tracers simulating ocean drifters driven by advection and diffusion (see the Supplementary Methods). The drifter particle experiments start 29th January 2019 (Drifter 1) and 13th September 2018 (Drifter 2). These are the dates when the drifters were towards the western side of the domain at a location where their paths crossed. In the following 90 days, these two drifters cross our domain.

Second, 2014 and 2017 are representative of different hydrodynamic conditions: stronger (2014) and weaker (2017) residual currents than average. For these experiments, particles were released over an area covering the northern North Sea (a circle centred at 58.7°N, 2.0°W and with radius 350 km) and only where water depths are shallower than 200 m. Although we do not include all North Sea structures, the boundary of the area where particles were seeded aligns with a region where structures are sparser. Particles were released every 5.83 km (horizontal resolution) and the total number of grid points is 17,920, see Fig. 8. We release 24 particles at each location in order to reach an exhaustive solution for all possible routes a particle could take from the initialisation location, explained in more detail in the Supplementary Methods. Every day of 2014 and 2017 at midnight, 24 virtual larvae (particles) were released in each location uniformly over the water column at 10 m depth intervals from 0 to 190 m inclusive. The 10 m interval represents settled adult species releasing larvae at different depths along hypothetical offshore structures extending from bottom to surface. A total of 484,096 particles were released per day and a total of nearly 177 million particles tracked in a year. Releasing particles every day of the year means they will be released over a full range of the tidal semi-diurnal cycle (with exception of the S2 cycle), a spring neap cycle, and will also sample the non-tidal inter-annual variability of the background flows. This design ensures the particle paths are representative of all likely trajectories.

The locations of the particles are output hourly. The particle-tracking model runs have been designed to be as generic as possible in order to be usable for a range of different larvae species. We have released the particles during the whole year, which would allow to select in a posteriori way a subset of simulations to explore the behaviour of larvae with different spawning months. Furthermore, to capture a wide time range in mobility, but keep computation cost reasonable, each virtual larva is tracked for 90 days. The latter represent an average of the larval duration of the species that can be found in the North Sea[26]. While settling after a longer delay is possible, e.g. *Metridiumdianthus* remains in the water column for longer (180 days[26]), generally settling will occur within 90 days[63], and the runs are restricted to that for computational economy. Particles were assumed to become competent to settle after 10 days (minimum amount of time required for maturity before settling could occur, based on several key epibenthic North Sea species,[26]), and remain suitable for settlement until the end of the simulated pelagic larval duration. In this paper, we present results assuming complete viability to 90 days pelagic larval duration for most of our analysis, but the dataset could be reanalysed for reduced viability at longer delays, i.e. it is possible to cut a posteriori the particle tracks to consider a specific and shorter pelagic larval duration (<90 days). Some species such as Sponges *Porifera* have a short pelagic larval duration of 20 days[26]. We show an example of this with the connectivity for a reduced pelagic larval duration of 20 days to show the minimum range of connectivity. The Retrospective Particle Tracks dataset produced here is made available in Section “Methods”[64].

For the analysis, we have placed the Lagrangian particles on a regular Eulerian sampling grid to provide a dataset that can be used for a broad range of analysis by filtering source and destination locations when calculating the connectivity metrics. The grid cells have a horizontal resolution of 11.67 km (double the resolution of the 5.83 km release grid). The sampling grid covers the same area as the initialisation grid (Fig. 8). By sampling at half the resolution, we ensure most grid cells used as a source have a minimum of 96 particles (4 locations × 24 particles). The particles were integrated vertically assuming larvae have enough control to move vertically to a settling location, and as a result, the calculated depth is not biologically relevant for settling purposes. This means cells can be initialised with up to 1920 vertically integrated particles. Of course, the vertical location is relevant for the currents that displace the particles up to the point of sampling, hence our ubiquitous initialisation in the water column and use of 3D advection and diffusion.

The sampling grid means we have an equal number of source and destination (sink) locations. For the source, particles are integrated over their grid cell. For the destination, the particles advecting into grid cells 10 days after release (maturity period) were integrated over the grid. Following the first 10-day immaturity period, subsequent particle locations were integrated on the Eulerian grid into 10-day temporal bins. During any one of these 10-day bins, particles can only connect (settle) within a destination once, however, if a particle connects (settles) a second time in a different 10-day bin it would be counted as a second connection to that destination. The particles are not removed or held stationary in the simulation once they have settled, they are allowed to continue advecting but the location it connected to (and could potentially settle) is recorded. This means it is possible to exceed the theoretical maximum number of particles (4 locations × 24 particles × 20 depths = 1920) connecting one location to another. The Eulerian grid (i.e. connectivity matrix) is not weighted by vertical release interval. This is because a longer structure would provide more surface area for larvae to release from, so it is logical that more particles could be released in deeper water. When we assess whether there is a connection between grid locations, we use a threshold of a minimum of 100 particles required to connect a source and a destination to qualify it as a robust connection. Given that our grid resolution is 11.67 km, 100 particles give an average of 110 m width, wherein a collision with a structure could occur, which is the same order of magnitude as the offshore structures of interest. We also test a 50 particle threshold which increased the magnitude of the number of connections by roughly 25% but did not change the spatial patterns. The post-processed matrices of the retrospective particle tracks dataset produced here is made available in Section 'Methods'[65]. The software used to produce this data and the plots associated with this publication are made available in Section 'Methods'[66].

We are simulating biological larvae particles but we do not add biological particle behaviour such as diel vertical migration, horizontal swimming, substrate selection and settlement, or rates of mortality during dispersal. We see this as a strength in making the simulations adaptable to the maturity window of various species, although additional behaviour cannot be added to the particles themselves. Our technique also avoids introducing errors from adding poorly constrained variables.

The connectivity metrics that we used in this study to describe the network are a measure of the inward and outward connections made to (destination) or from (source) a location/structure. A stronger destination (many inward connections) will increase connectivity by settling larvae from more sites. As an analogy, we can think of the more important destination location similar to a more important website which is likely to receive more links from other websites (which is the underlying assumption of the PageRank Google algorithm). Instead, a stronger source (many outward connections) will increase connectivity by spreading larvae to more sites. For desired species, locations with structures that promote connectivity should be encouraged and preserved. Conversely, for non-native species, such locations might be considered to be undesirable and may require regulation. If a location/offshore structure is isolated, then it has a limited role in the network and that removal or placing of a structure should have little effect on connectivity.

In- and out-degree, in- and out-closeness centrality and betweenness centrality are the main connectivity metrics that we used in this study. In-degree is the sum of the number of inward connections ($v(u, y)$) made to a destination location as a percentage of the total nodes (n): $G(u) = 100((\sum v(u, y))/n)$, where u is a given node and y is other nodes. In-closeness centrality is a measure of the degree of connections required for the whole network to reach a destination; it includes connections that can exist by going via another location, essentially using it as a bridge, i.e. a stepping stone. The in-closeness centrality is calculated as the inverse of the reciprocal of the sum of the length (number of connections) of the shortest paths between the node and all other inward or outward connected nodes. The equation for this is $C(u) = 1/(\sum_y d(u, y))$, where the distance between two nodes $d(u, y)$ is the length of the shortest path between two nodes. If a location/offshore structure acts as a stronger destination (high in-degree and in-closeness) then it will settle larvae from more sites.

Out-degree is the sum of the number of outwards connections made from a source location as a percentage of the total locations (equation is the same as in-degree but for outwards connections). Out-closeness centrality is a measure of the degree of connections required by a source to reach the whole network (equation is the same as in-degree but for outwards connections). This includes connections via other locations in the network (that act as bridges) rather than only those locations directly connected to the location of interest, as for out-degree. In- and out-degree is expresses as a percentage because there is an absolute maximum constant number of connections that are possible, while in- and out- closeness has no absolute minimum or maximum it is the 1/(mean number of connections to all other nodes) i.e. a unit-less degree (°). If a location/offshore structure acts as a stronger source (high out-degree and out-closeness) then it will spread larvae to more sites. If a location/offshore structure is isolated (low in-degree, out-degree, in-closeness and out-closeness), then it has a limited role in the network.

Betweenness centrality is a measure of the total number of shortest paths (σ_{st}) between nodes (s and t) that pass through another node (u). Betweenness centrality is calculated per node ignoring nodes that are neither directly or indirectly attached $B(u) = \sum_{s \neq u \neq t}(\sigma_{st}(u)/\sigma_{st})$. This is then normalised to allow comparison with networks of different sizes with $B(u) = 100(B(u))/(n-1)(n-2)$. Betweenness centrality is important because it indicates locations that are more integral to facilitating connectivity within the network, allowing a larvae to use the location as a bridge to reach a large number of other locations.

We use these metrics for two perspectives: (1) exploring the connectivity metrics of the dataset; (2) a case study on the connectivity of existing infrastructure. For exploring the connectivity metrics of the dataset, any locations of the northern North Sea are considered as a potential source/destination of particles. For the connectivity of existing offshore structures, we use the Martins et al. (2023) dataset[37]. We could have activated the natural hard-substrate location as source and destination of larvae in the connectivity metrics analysis, we have excluded the natural hard substrate from the existing structures scenario of this study because Tidbury et al., (2020) found weak connectivity between the offshore artificial structures and the natural hard-substrate mainly located in coastal areas[3].

In the case of the connectivity of existing offshore structures, used to analyse existing communities, we used a clustering algorithm, similar to algorithms used to create clusters of linked people in social media applications, to partition structures into modules, or communities[67]. Here, we used a graph of directed connections from the source to the destination for calculating the clustering coefficient[68]. This calculated as:

$$K(u) = 100\left(\frac{T(u)}{2\big(deg^{\mathrm{tot}}(u)(deg^{\mathrm{tot}}(u) - 1) - 2deg^{\leftrightarrow}(u)}\right)$$

where $T(u)$ is the number of directed triangles through u. Directed triangles are made of the nodes (locations) where particles are released with edges formed by the directional connections between nodes. $deg^{tot}(u)$ is the sum of in degree and out degree of u and $deg^{\leftrightarrow}(u)$ is the reciprocal degree of node u. This does not require a number of clusters to be specified and instead it is defined as the percentage of all possible directed triangles at each node.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Version 1.0 of the "Post-processed connectivity matrices from PyLag particle tracking model of retrospective particles in the North Sea during two contrasting years (2014 and 2017)" (dataset). This was used to produce the plots in this publication. This is available at https://doi.org/10.5285/2d751fa0-9a38-2aa0-e063-7086abc0c3e0. Version 1.0 of the "PyLag particle tracking model of retrospective particles in the North Sea during two contrasting years (2014 and 2017)" (dataset). This is available at https://doi.org/10.5285/2d751cab-c7a5-2a4a-e063-7086abc0a053. Version 3.02 of the "Scottish Shelf Water—Reanalysis Service (SSW-RS)" (dataset) based on the UK-FVCOM4.0 model which was used as the hydrodynamic model for particle tracking simulation, has all model output preserved at https://doi.org/10.7489/12423-1, available via Open access with registration. Version INSITU_GLO_PHY_UV_DISCRETE_MY_013_044 of the "Global Ocean-Delayed Mode in-situ Observations of surface (drifters and HFR) and sub-surface (vessel-mounted ADCPs) water velocity" (dataset). This is preserved and available https://doi.org/10.17882/86236, available via Open access with registration. Version 1 of "Offshore Energy Structures in the North Sea: Past, Present and Future-March 2023" (dataset). This is preserved and available under Creative Commons License (CC BY 4.0) https://doi.org/10.17630/338d5ba4-5e09-443f-9c08-013d24050c81.

Code availability

Version 0.6.1 of Pylag particle tracking software was used. This is available under GNU General Public License v3.0 and developed openly at GitHub https://github.com/pmlmodelling/pylag. The code used to run the particle tracks and analyse the output. This is available under GNU General Public License v3.0 preserved as Retrospective_Particles_Analysis_v1.0 at https://doi.org/10.5281/zenodo.15309242and available on GitHub https://github.com/b-barton/Retrospective_Particles.

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Author contributions

B.B. wrote the manuscript and performed the experiments and data analysis. M.D. supervised and contributed to the conceptualisation of the project, contributed to drafting the initial manuscript and revised the manuscript during the peer-review process. D.W. supervised and contributed to the conceptualisation of the project, contributed to drafting the manuscript. A.W. provided support to the experiment design, contributed to drafting the manuscript. M.B. provided support to the experiment design.

Competing interests

The authors declare no competing interests.

Additional information

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