Title

Scenario-dependent functional connectivity in a crowded seascape: habitat suitability, shipping pressure and marine infrastructure in the North Sea

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Abstract

Context

Marine spatial planning increasingly needs seascape connectivity evidence to balance biodiversity conservation, offshore energy development and shipping. However, predicted functional connectivity depends strongly on how habitat suitability and human-use pressures are translated into resistance surfaces.

Objectives

This study tested how shipping and marine infrastructure alter HSM-derived connectivity metrics for four North Sea species: Atlantic cod, European plaice, harbour porpoise and grey seal.

Methods

Species-specific habitat suitability models were developed using broad oceanographic predictors and local habitat/productivity predictors. Core habitat was then overlapped with shipping density, offshore wind infrastructure and oil/gas infrastructure. Functional connectivity was compared between habitat-only and infrastructure-weighted resistance scenarios using Circuitscape. Movement-threshold analyses tested whether connectivity conclusions were robust to literature-informed species movement limits. Cumulative current, core habitat and pressure layers were then combined into connectivity-pressure priority categories.

Results

Combined environmental models performed best for Atlantic cod, harbour porpoise and grey seal, while local habitat/productivity predictors performed best for European plaice. Core habitats were substantially exposed to human use: 31.2–65.8% occurred in high-shipping areas, 62.0–81.8% occurred within 25 km of offshore wind infrastructure, and 58.9–76.0% occurred within 25 km of oil/gas infrastructure. The infrastructure-weighted scenario produced lower median effective resistance and higher conductance across all species, with resistance decreases of 9.4–18.2% and conductance increases of 10.3–22.2%. Movement-threshold analyses showed that demersal fish had

stronger changes in resistance magnitude, while harbour porpoise showed greater sensitivity in the identity of strongest links. High-connectivity/high-pressure areas were spatially restricted.

Conclusions

These results show that suitable habitat in the North Sea is embedded within shipping and infrastructure pressure, and that including these pressure metrics can provide sensitivity metrics for predicted connectivity. Scenario-based connectivity modelling can support marine spatial planning by making resistance assumptions transparent and identifying where empirical validation is needed.

Keywords: Marine spatial planning; seascape connectivity; habitat suitability models; resistance surfaces; offshore infrastructure; North Sea

Introduction

With increasing pressure from offshore infrastructure, shipping and energy development, marine spatial planning has become crucial for reconciling biodiversity conservation with expanding human use of marine seascapes (Douvere 2008; Halpern et al. 2008; Martins et al. 2023). Marine spatial planning supports ecosystem-based management by organising competing uses of marine space while maintaining ecological function (Douvere 2008). Shelf seas are particularly important because they concentrate a range of productive habitats with fisheries, shipping routes, human infrastructure (offshore renewable energy and oil and gas infrastructure) and conservation designations within relatively constrained areas (Halpern et al. 2008; Börger et al. 2015; Martins et al. 2023).

Planning biodiversity conservation in these areas is challenging as habitat suitability is not spatial or temporally static. Species distributions respond to environmental gradients, but infrastructure can restructure the seascape by modifying habitat and altering how species move (Bishop et al. 2017; McLean et al. 2022; Lemasson et al. 2024). As a result, movement and seascape connectivity are relevant metrics for conservation planning, particularly where management aims to maintain ecological networks (Taylor et al. 1993; Keeley et al. 2019; Cameron et al. 2022).

Ecological connectivity describes the degree to which a seascapes or landscapes facilitate or impede the movement of organisms, materials and energy among habitat units (Taylor et al. 1993). Structural connectivity refers to the physical arrangement of habitat patches or seascape elements, independent of the movement behaviour of a particular species. Functional connectivity refers to how organisms respond to that spatial structure, and is therefore species-specific and dependent on movement capacity, behaviour and the resistance or permeability of the seascape (Tischendorf & Fahrig 2000; Calabrese & Fagan 2004). Resistance describes the relative cost of moving through different seascape conditions, while permeability describes the ease with which movement can occur. Low-resistance or high-permeability areas are expected to facilitate movement, whereas high-resistance areas may restrict or redirect movement pathways (Taylor et al. 1993; McRae et al. 2008; Zeller et al. 2012). In marine systems, functional connectivity can influence dispersal, migration, recolonisation, population recovery, genetic exchange and access to key resources (Cowen et al. 2006; Treml et al. 2008). Connectivity-aware planning can help identify where potential movement pathways exist and pinpoint conservation priorities (Pittman 2018).

Seascape connectivity can be measured and inferred depending on chosen methodology, species and data available (Selkoe et al. 2008; Cowen & Sponaugle 2009; Treml et al. 2008; Wilcox et al. 2023). Most direct field approaches are often expensive and spatially restricted with limited extension. Telemetry, acoustic tracking, mark–recapture, genetic analyses, larval dispersal models usually provide the most accurate demographic connectivity estimates (Cowen et al. 2006; Treml et al. 2008; Russell et al. 2014; Staveley et al. 2019). If this data is not available, the most common approach are broad-scale multi-species assessments that rely on model-based predictions. One common approach is to use habitat suitability models or species distribution models to infer on potential habitat use and then translate these surfaces into resistance or permeability layers (Elith & Leathwick 2009; Stuart et al. 2021). Connectivity can then be estimated using a variety of methods such as least-cost paths, graph theory or circuit theory (Treml et al. 2008; Thomas et al. 2014; Weeks 2017; Virtanen et al. 2020). Circuit theory can be the most accurate for seascape connectivity analysis as it represents movement across multiple possible pathways rather than assuming a single optimal route.

Additionally, it produces metrics that account for all possible connections and it uses a random walk framework where animal movement mirrors animals randomly exploring complex landscapes (McRae et al. 2008; Anantharaman et al. 2020).

Compared with terrestrial landscapes, marine connectivity is harder to represent because movement pathways are shaped by dynamic oceanographic processes, three-dimensional habitat structure and species-specific use of the water column, rather than by horizontal habitat configuration alone (Cowen et al. 2006; Treml et al. 2008; Boschetti et al. 2020). Boschetti et al. (2020) showed that connectivity patterns can vary with shelf circulation, and that mean connectivity may poorly represent interannual variation. This is relevant for scenario-based seascape modelling as hydrodynamic factors and habitat gradients may provide a baseline against which pressure or infrastructure influence are interpreted.

Another major uncertainty in seascape connectivity modelling is how to define the resistance surface. Resistance surfaces translate environmental or anthropogenic gradients into relative movement cost, but this translation is rarely directly validated. Zeller et al. (2012) showed that resistance surfaces are widely used to infer movement where direct data are limited but also highlighted strong uncertainty in how resistance values are assigned. Habitat suitability is often transformed into resistance by assuming that high suitability represents low movement cost and low suitability represents high movement cost (Zeller et al. 2012; Keeley et al. 2016; Dutta et al. 2022). This assumes that habitat use is a reliable proxy for movement, which may be weak for mobile species that can cross areas they do not regularly occupy (Keeley et al. 2017).

This uncertainty increases when human-use layers are incorporated. Artificial marine structures can perform multiple ecological functions: they may create hard substrate, concentrate prey, modify local hydrodynamics, act as stepping stones, redirect movement, or generate disturbance and risk. Bishop et al. (2017) discussed how ocean sprawl can modify ecological connectivity by changing the movement of organisms and resources across seascapes, while McLean et al. (2022) reviewed how offshore oil and gas structures may conserve, enhance or disrupt connectivity depending on species, scale and mechanism. Infrastructure therefore should not be considered as either uniformly negative or uniformly beneficial in resistance models.

Empirical studies support this interpretation. Russell et al. (2014) showed that grey and harbour seals can use anthropogenic structures, including wind turbines and pipelines, in ways consistent with foraging. Arnould et al. (2015) found similar use of seafloor structures by Australian fur seals, including pipelines, cable routes, wells and shipwrecks. Also, recent metapopulation modelling suggests that oil and gas infrastructure may play only a minor role in connectivity in some systems (Galaiduk et al. 2024). Nevertheless, resistance surfaces are increasingly used in marine spatial conservation planning because they provide a practical way to translate limited ecological data into planning-relevant connectivity metrics, therefore understanding how to include infrastructure as resistance is key for further analyse connectivity metrics.

As offshore renewable energy expands in the North Sea, the spatial footprint of infrastructure is increasing (Bugnot et al. 2021; Martins et al. 2023). Offshore wind farms can affect marine species across planning, construction, operation and decommissioning phases. Potential effects include noise, displacement, habitat modification, changes in benthic communities, electromagnetic fields from subsea cables and altered predator–prey interactions (Bray et al. 2016; Taormina et al. 2018; Causon & Gill 2018). Operational wind farms may also function as artificial reefs by adding hard substrate and modifying local ecosystem structure (Degraer et al. 2020; Lemasson et al. 2024). These effects are not uniform across species because responses depend on mobility, habitat association, sensitivity to disturbance and whether species avoid, tolerate or use artificial structures. Shipping and oil and gas infrastructure add additional pressure. Shipping can contribute to chronic noise, disturbance, collision risk and spatial pressure, while oil and gas platforms, pipelines and subsea structures can create physical habitat, influence movement and alter local hydrodynamics, but also introduce contamination and disturbance (Bakke et al. 2013; McLean et al. 2022; Burdon et al. 2018). From a marine planning perspective, there’s clear uncertainty on how to include human-use layers with environmentally suitable habitat and whether their inclusion in connectivity models change predicted effective resistance and conductance. This is especially relevant in the North Sea, where offshore infrastructure is spatially extensive and likely to influence species-specific habitat and movement pathways.

Habitat suitability models and seascape connectivity models are increasingly used in marine conservation planning (Weeks 2017; Virtanen et al. 2020; Stuart et al. 2021; Kang et al. 2024). However, fewer studies have tested how infrastructure pressure change HSM-derived resistance surfaces and identified its influence in connectivity metrics across multiple species. The main gap is whether pressure metrics can be isolated and incorporated into resistance models in a way that predicted effective resistance can inform rather than define connectivity metrics. This may be relevant to clearly identify the role of infrastructure in connectivity analysis for different species as well as improve the use of resistance surfaces in marine planning. Human structures can act as habitat, disturbance source, pressure layer, stepping stone, movement modifier or hydrodynamic feature, depending on species, life stage and spatial context. Translating these roles into simplified resistance or conductance metrics remains difficult, especially when direct movement data are unavailable. However, treating infrastructure as uniformly positive or negative risks over-simplifying it.

Additionally, a scenario approach is therefore more appropriate to assess if habitat-only or infrastructure resistances can provide information on how pressure metrics alter predicted connectivity. Connectivity models can estimate different metrics that may change with pressure. For example, information on the number of links among habitat nodes and if overall networks may include connections (or links) that are unlikely to be retained for species with limited movement capacity. Resistance-based connectivity outputs are known to be sensitive to scale, methodology and species movement (Treml et al. 2008; Dertien & Baldwin 2023). Therefore, a clear understanding of species movement patterns and potential use of habitat is necessary to test these outputs.

For this, this study uses four ecologically contrasting North Sea species—Atlantic cod (*Gadus morhua*), European plaice (*Pleuronectes platessa*), harbour porpoise (*Phocoena phocoena*) and grey seal (*Halichoerus grypus*), and it aims to model habitat suitability, quantify overlap between core habitat and human-use pressure, and test whether infrastructure-weighted resistance surfaces change predicted effective resistance and conductance relative to habitat-only resistance models. Specifically, the study aims to (1) quantify if broad oceanographic and local habitat/productivity gradients influence species habitat suitability across the North Sea; (2) identify how shipping pressure and

marine infrastructure overlap with core suitable habitat across species; (3) determine if adding infrastructure pressure metrics to resistance surfaces change predicted effective resistance and conductance compared with habitat-only resistance models; and (4) define if high habitat suitability, predicted connectivity and human-use pressure can be used for seascape planning. This study aims to understand the role of pressure in connectivity analysis and inform potential frameworks for including connectivity in marine spatial planning.

Methods

2.1 Study area and species occurrence data

The study focused on the North Sea (51.0–62.5°N and 2.8°W–10.5°E), a heavily used temperate shelf sea characterised by intensive shipping, offshore energy development, oil and gas infrastructure, fisheries and overlapping biodiversity conservation areas. The study covered the southern, central and northern North Sea, including adjacent coastal and shelf waters around the United Kingdom, Norway, Denmark, Germany, the Netherlands and Belgium (Fig.1). The Greater North Sea covers approximately 750 000 km² and reaches depths of up to about 700 m, although most of the basin is shallow shelf habitat. Much of the seabed is composed of mud, sandy mud, sand and gravel, with shallow southern and coastal areas contrasting with deeper northern waters and the Norwegian Trench. It has a temperate climate and supports a mosaic of benthic, pelagic, coastal and offshore habitats, including productive shelf waters, soft-sediment benthic habitats, sandbanks, estuaries, tidal flats and coastal transition zones (Ducrotoy et al. 2000).

Four focal species were selected to represent contrasting ecological niches and movement capacities: Atlantic cod (*Gadus morhua*), European plaice (*Pleuronectes platessa*), Harbour porpoise (*Phocoena phocoena*) and Grey seal (*Halichoerus grypus*). These species represent demersal fish, benthic-associated flatfish, cetaceans and foraging marine mammals. Species occurrence records were obtained between 2000-2024 from GBIF – Global Biodiversity Information Facility (Derived dataset GBIF.org 2026) using *rgbif* (Chamberlain & Boettiger 2017; Chamberlain et al. 2025). Records were

cleaned before modelling, duplicates and spatially uncertain records were removed. Spatial thinning (of 10km) was applied to reduce spatial bias. Final datasets contained 804 Atlantic cod records, 757 European plaice records, 8740 harbour porpoise records and 6906 grey seal records. Analyses were conducted in R 4.3.1 (R Core Team 2023) using *dplyr* and *spThin* (Aiello-Lammens et al. 2015; Wickham eta al. 2026).

2.2 Environmental and human-pressure predictors

Environmental predictors represented gradients influencing habitat suitability and human-use pressures relevant to marine spatial planning (Table 1). Predictors were checked to assess collinearity using Pearson correlation coefficients (Fig. S1). Variables were grouped into three model blocks: broad oceanographic predictors, local habitat/productivity predictors and a combined block. The broad oceanographic block included: sea surface temperature, salinity and current speed. The local habitat/productivity block included: bathymetry and chlorophyll-a. The combined block included all five environmental predictors (GEBCO Compilation Group 2023; Tyberghein et al. 2012, Assis et al. 2018).

Human-pressure predictors included shipping density, distance to offshore wind infrastructure and distance to oil/gas infrastructure (EMODnet Human Activities 2024). Shipping density was used as a direct pressure layer. Distance-to-infrastructure were converted into proximity pressure layers, with higher values assigned closer to offshore wind and oil/gas infrastructure.

2.3 Species distribution models (SDM's) and habitat suitability

Species distribution models (SDM's) were fitted separately for each species using cleaned occurrence records and randomly sampled background points. Occurrence and background points were intersected with the environmental raster stack. SDM's were fitted for the three predictor blocks. Occurrences were coded as presences and background points as background records. Background

points were randomly sampled across the North Sea modelling domain to represent available environmental conditions. They were not treated as true absences; rather, they provided the environmental background against which GBIF occurrence records were contrasted in the presence-background models (Phillips et al. 2006; Phillips et al. 2009; Elith et al. 2011). Data were split into training and testing subsets using a 70:30 split. SDM's were fitted using *maxnet*, an R implementation of Maxent presence–background modelling based on regularised regression (Phillips et al. 2006; Elith et al. 2011; Phillips et al. 2017). Maxent and related correlative SDMs are widely used in marine habitat suitability modelling, particularly where survey coverage is uneven and spatial predictions are needed for conservation, fisheries and marine planning (Reiss et al. 2011; Pittman & Brown 2011; Melo-Merino et al. 2020; Karp et al. 2025). Linear and quadratic classes were used to allow for simple monotonic and unimodal responses while limiting model complexity and fitting. Maxent and related correlative SDM's are widely used in marine habitat suitability modelling, particularly where survey coverage is uneven and spatial predictions are needed for conservation, fisheries and marine planning (Reiss et al. 2011; Melo-Merino et al. 2020; Karp et al. 2025).

Habitat suitability was predicted for each species and predictor block. Models were evaluated using AUC on withheld testing data, and AUC was used to compare predictor-block performance within each species (Fielding and Bell 1997; Pearce and Ferrier 2000). The best-performing block was retained as the species-specific habitat suitability model and for the exposure and connectivity analyses.

Selected predictions were treated as relative habitat suitability surfaces. Core habitat was defined as cells in the 75th quartile of predicted suitability for each species. Continuous suitability surfaces were also converted into habitat-based resistance layers by rescaling suitability to 0–1 and reversing it so that high suitability represented low resistance:

$$R\_HSM = 1 + 99 \times (1 - HSM\_scaled)$$

Where HSM_scaled is the rescaled habitat suitability value. This produced resistance values from 1 to 100, with 1 representing lowest resistance and 100 highest resistance. This transformation treats

habitat suitability as an inverse proxy for movement cost, but resistance surfaces remain scenario-based assumptions unless independently validated (Zeller et al. 2012; Keeley et al. 2016). *Terra* was used for data processing, *dplyr* for data manipulation and plots were produced using *ggplot2* (Hijmans 2024; Phillips et al. 2017; Wickham 2016; Wickham et al. 2023).

2.4 Pressure exposure of predicted core habitat

Pressure exposure was quantified by overlaying species-specific core-habitat with the human-pressure layers. Shipping exposure was calculated by extracting shipping-density values from core-habitat cells and summarising mean and median shipping density. High-shipping areas were defined as cells in the 75th quartile of shipping density, and the percentage of core habitat in high-shipping areas was calculated for each species. Infrastructure exposure was quantified using distance-to-infrastructure. For offshore wind and oil/gas infrastructure, the mean, median and interquartile distances from core-habitat cells to infrastructure were calculated, and the percentage of core habitat within 25 km. The 25 km radius is consistent with the outer range of disturbance distances reported for marine mammals during offshore wind construction, including harbour porpoise responses around 20–25 km and seal displacement up to 25 km during pile-driving activity (Dähne et al. 2013; Russell et al. 2016).

2.5 Resistance surfaces and connectivity scenarios

Connectivity analyses compared two resistance scenarios: habitat-only and infrastructure-weighted. The habitat-only scenario used the reversed suitability surfaces. The infrastructure-weighted scenario combined reversed suitability with shipping density and proximity to offshore wind and oil/gas infrastructure. Shipping density was rescaled from 0 to 1 and distance-to-infrastructure were rescaled and reversed so that cells closer to infrastructure had higher pressure values.

Infrastructure-weighted resistance was calculated as:

$$Rinfra = 1 + 99 \times [(0.60 \times R\_HSM) + (0.20 \times S) + (0.10 \times W) + (0.10 \times O)]$$

Where *R_HSM* is reversed habitat suitability, *S* is scaled shipping density, *W* is offshore wind proximity and *O* is oil/gas proximity. The 0.60 habitat, 0.20 shipping, 0.10 wind farm proximity and 0.10 oil/gas proximity weighting was specified to test how adding human-use structure altered predicted connectivity in relation to the habitat-only model. This considered shipping and infrastructure proximity as components of the functional seascape rather than as an additive resistance and was used to assess scenario sensitivity to species responses. Habitat suitability was given the highest weight (0.60) as HSM-derived resistance provide the environmental baseline, following practice in connectivity studies where suitability is translated into resistance or permeability when direct movement data are unavailable (Zeller et al. 2012; Keeley et al. 2016; Stuart et al. 2021). Human-use pressure layers were assigned the remaining weight (0.40) to test whether anthropogenic seascape structure altered predicted connectivity. Shipping received a higher weight (0.20) because it is a continuous activity-pressure layer, while offshore wind and oil/gas infrastructure were each assigned lower weights (0.10) as they represent as proximity-based variables (Bishop et al. 2017; McLean et al. 2022; Wilcox et al. 2023; Lemasson et al. 2024).

Connectivity was estimated using circuit-theory modelling in Circuitscape (Anantharaman et al. 2020), which represents the seascape as a conductive surface and estimates potential connectivity across multiple pathways rather than a single least-cost route (McRae et al. 2008; Dickson et al. 2019). For each species and scenario, resistance surfaces were used to calculate pairwise effective resistance and conductance among habitat nodes.

Effective resistance between nodes (*i*) and (*j*) was calculated as:

$$R\_eff_{ij} = V_{ij} / I$$

where R_eff_{ij} is pairwise effective resistance, V_{ij} is the voltage difference between nodes and *I* is the injected current. Lower R_eff_{ij} values indicate lower cumulative movement cost across the resistance surface (McRae et al. 2008; Dickson et al. 2019).

Pairwise conductance was calculated as:

$$C_{ij} = 1 / R\_eff_{ij}$$

Where C_{ij} is pairwise conductance. Higher C_{ij} values indicate stronger relative connectivity between habitat nodes (McRae et al. 2008; Dickson et al. 2019).

Effective resistance was interpreted as relative movement cost, and conductance as relative connectivity strength (McRae et al. 2008). Habitat nodes were derived from species-specific core habitat. A limited number per species was defined to a maximum of 40 nodes to keep pairwise analyses comparable (Anantharaman et al. 2020). Pairwise connectivity was first estimated under an unrestricted all-pair network, where all possible node pairs were evaluated.

2.6 Movement-threshold connectivity sensitivity

The unrestricted all-pair network assumes that all habitat nodes are potentially connected. To assess the influence of this assumption, connectivity comparisons were repeated using species-specific movement thresholds. Thresholds retained only node pairs separated by distances considered plausible under movement assumptions for each species.

Thresholds were derived from published movement studies (Table S3). These movements were classified in three categories, according to distance used in the models: conservative, central and dispersal. Atlantic cod thresholds (50km/177km/578km) were based on short-range movement, mean migration distance and maximum recorded migration distance around the British Isles (Neat et al. 2014). European plaice thresholds (50km/241km/314km) were based on North Sea seasonal migration and spawning-area fidelity (Hunter et al. 2003). Harbour porpoise thresholds (20km/100km/380km) represented daily movement, broader displacement and larger-scale offshore movement from telemetry studies (Sveegaard 2011; Nielsen et al. 2013; van Beest et al. 2018). Grey seal thresholds (40km/230km/2100km) represented haul-out sites associated movement, offshore foraging and long-distance travel in the North Sea (McConnell et al. 1999; Russell and McConnell 2014).

For each species and threshold, node pairs exceeding the threshold distance were removed before comparing habitat-only and infrastructure-weighted resistance. The number and percentage of retained links were calculated alongside median percentage change in effective resistance R_eff_{ij} and

conductance C_{ij} rank correlation between scenarios, and similarity in the strongest link. Strongest-link similarity was assessed using the Jaccard index between the top 25% strongest links in each scenario and the percentage of habitat-only strongest links retained under infrastructure weighting.

2.7 Cumulative current and connectivity-pressure priority categories

For each species, cumulative current maps were generated from the infrastructure-weighted scenario using Circuitscape (Anantharaman et al. 2020). Cumulative current represents the relative concentration of potential movement flow across the resistance surface when habitat-node pairs are connected. Higher values indicate areas expected to carry a greater potential connectivity under a specified scenario.

Cumulative current was used as the connectivity layer for the priority analysis. Cumulative current values were log-transformed using $log(1+x)$ for mapping. A pressure index was calculated as the mean of scaled shipping density, offshore wind proximity and oil/gas proximity. Within each species' core habitat, cells in the 75th quartile of cumulative current were classified as high connectivity, and cells in the 75th quartile of the pressure index were classified as high pressure. These binary layers were crossed to produce four categories for spatial prioritisation: high connectivity/high pressure, high connectivity/low pressure, low connectivity/high pressure and low connectivity/low pressure.

3. Results

3.1 Species-specific habitat suitability

Habitat suitability models showed species responses to local habitat/productivity predictors and broader oceanographic gradients (Fig. 2; Table 2; Table S1). The broad oceanographic block included sea surface temperature, salinity and current speed, while the local habitat/productivity block included bathymetry and chlorophyll-a. Model performance was generally high, but the best-performing predictor block differed among taxa.

Atlantic cod suitability was highest across shallower shelf areas of the southern and western North Sea and was best predicted by the combined environmental model (AUC = 0.893). European plaice showed a similar shelf-associated pattern but was best predicted by the local habitat/productivity model (AUC = 0.893), contrasting with cod. Harbour porpoise had the broadest area of high suitability across the central and southern North Sea; the combined model performed best, but with lower performance compared with fish species (AUC = 0.791). Grey seal suitability was concentrated across shelf and coastal areas, especially in the southern and western North Sea, and was also best predicted by the combined model (AUC = 0.870).

Overall, plaice showed the clearest local habitat/productivity response, whereas cod, harbour porpoise and grey seal distribution were better explained by models integrating local and broad oceanographic predictors.

3.2 Core habitat exposure to shipping and infrastructure

Core habitats showed substantial overlap with human-use pressure across the North Sea (Fig. 3; Table S2). Between 31.2% and 65.8% of species-specific core habitat occurred in high-shipping areas, with mean shipping density within core habitat ranging from 3.77 to 9.38. This indicates that predicted core habitat was consistently exposed to shipping pressure, although the magnitude of exposure varied among species.

Core habitats were also located close to offshore infrastructure. Median distance to offshore wind infrastructure ranged from 10.0 to 17.0 km, and 62.0–81.8% of core-habitat cells occurred within 25 km of offshore wind infrastructure. Proximity to oil/gas infrastructure was similarly high, with median distances ranging from 9.9 to 18.1 km and 58.9–76.0% of core habitat occurring within 25 km of oil/gas infrastructure.

3.3 Scenario-dependent connectivity

Under the unrestricted all-pair network, infrastructure reduced median effective resistance and increased conductance for all species (Fig. 4; Table S4). The strongest response occurred in the demersal fish. European plaice showed the largest change, with median resistance decreasing by 18.2% and conductance increasing by 22.2%, followed by Atlantic cod (-13.8%; +16.0%). Same pattern for grey seal (-11.7%; +13.2%) and harbour porpoise (-9.4%; +10.3%), however, lower values suggesting lower sensitivity among mobile marine mammals.

3.4 Movement-threshold connectivity sensitivity

Movement-threshold analyses showed that infrastructure affected potential connectivity links at different scales (Fig. 5; Table 3; Table S5). Under central movement thresholds, median resistance still decreased for all species, with the strongest changes in demersal fish: European plaice (-16.5%) and Atlantic cod (-14.6%). Grey seal showed an intermediate response (-12.8%), while harbour porpoise showed the weakest resistance change (-8.0%).

Strong-link stability showed a different pattern. Under central thresholds, cod and plaice retained all strongest habitat-only links (Jaccard = 1.00; 100% top links retained), and grey seal remained highly stable (Jaccard = 0.95; 97.3%). Harbour porpoise showed link reorganisation, with lower similarity (Jaccard = 0.81) and reduced top-link retention (89.5%). Infrastructure weighting mainly changed resistance for demersal fish, while harbour porpoise showed higher sensitivity of retention of strongest links.

3.5 Connectivity-pressure prioritisation

Across species, high connectivity/high-pressure areas represented a small proportion of core habitat, ranging from 1.0% for Atlantic cod to 2.8% for European plaice and grey seal (Fig. 6; Fig. S4; Table S6). Most core habitat was classified as low-connectivity/low-pressure, representing approximately 51–53% of core-habitat cells across species. The remaining area was mainly separated between high-

connectivity/low-pressure and low-connectivity/high-pressure categories, each accounting for approximately 22–24% of core habitat.

4. Discussion

4.1 Integrating habitat suitability, pressure exposure and connectivity

This study tested how species habitat suitability, pressure exposure and infrastructure-weighted resistance can be integrated in predicting seascape connectivity across a heavily used shelf sea. This study adds to existing seascape connectivity studies by focusing on the translation of pressure layers into resistance-based connectivity metrics. Previous work has shown that habitat suitability can inform marine connectivity and spatial prioritisation as a resistance surface and through graph theory, circuit theory and other conservation planning approaches (Weeks 2017; Virtanen et al. 2020; Stuart et al. 2021; Kang et al. 2024). While others have tested how seascape connectivity can improve marine species distribution modelling or conservation prioritisation (Cecino et al. 2021; Wilcox et al. 2023). However, this study contributes by isolating infrastructure pressure metrics and test whether adding them to HSM-derived resistance surfaces changes predicted effective resistance and conductance across multiple species.

The results also support treating infrastructure as a functional component of the seascape. Marine built structures are expanding globally (Bugnot et al. 2021), and offshore energy infrastructure can produce dynamic changes in the North Sea (Martins et al. 2023). Is described that offshore structures can provide hard substrate and alter benthic communities by modifying local habitat conditions, with additionally influencing movement or act as stepping stones. They can also introduce disturbance, contamination, collision risk and ecological traps (McLean et al. 2022; Lemasson et al. 2024). This mixed evidence shows that infrastructure should not be an option when deciding if to include in connectivity analysis but also should not be imposed into a single permeability interpretation, such as beneficial or detrimental.

This showed that infrastructure-weighted scenarios reduced median effective resistance and increased conductance across species. By including infrastructure pressure metrics, the spatial structure of the resistance surface influenced differently predicted connectivity metrics. This is consistent with empirical evidence that some species use anthropogenic structures, such as seals using wind turbines and pipelines (Russell et al. 2014), but also evidence showing that oil and gas infrastructure may play only a minor role in metapopulation dynamics in some systems (Galaiduk et al. 2024). As a scenario, infrastructure will change predicted connectivity metrics, but the direction may remain species- and context-dependent.

This framework may help define how connectivity models are sensitive to decisions regarding resistance surface's purpose, scale and movement assumptions when movement data is unavailable (Cameron et al. 2022; Dertien & Baldwin 2023). By comparing habitat-only and infrastructure-weighted resistance, this study tests whether predicted connectivity is robust to the representation of infrastructure pressure. By adding movement thresholds latter on in the connectivity analysis, it tests whether pressure results persist when links are constrained by species-specific movement assumptions. This may be useful for marine planning interpretation as functional connectivity may be introduced as a sensitive measure to compare before-after impacts of infrastructure.

4.2 Species-specific habitat suitability, exposed core habitats and connectivity metrics

The habitat suitability models showed that the four species were structured by different combinations of local habitat/productivity and broader oceanographic gradients. Atlantic cod, harbour porpoise and grey seal were best explained by combined environmental models, whereas European plaice was best explained by the local habitat/productivity block. This supports the use of species-specific HSMs and how combining environmental scales in shelf-sea modelling may reflect both local seabed-associated conditions and broader oceanographic gradients.

Plaice distributions are linked to shelf structure, depth, seabed-associated conditions and productivity. In this study, bathymetry and chlorophyll-a likely captured part of that local habitat/productivity

459 structure, although sediment and finer-scale benthic habitat variables were not included. Previous
460 work on plaice connectivity in the North Sea shows that spatial structure is essential for managing
461 these populations (Ulrich et al. 2013). Nevertheless, plaice and cod HSM's show that demersal fish
462 can differ in the environmental scale at which suitability is best predicted.

463 For Atlantic cod, harbour porpoise and grey seal there was a stronger performance of combined
464 environmental models. Cod movement and habitat connectivity can respond to temperature and
465 seasonal environmental structure, as shown in coastal systems by Staveley et al. (2019), while cod
466 dispersal and population connectivity may also be shaped by oceanographic processes, such as
467 circulation and eddy activity (Myksvoll et al. 2014). For harbour porpoise and grey seal, suitability is
468 likely to be harder to capture with static environmental layers as habitat use may trace prey fields and
469 seasonal movement with dynamic oceanographic processes (van Beest et al. 2025). This may also
470 explain why the harbour porpoise model had lower predictive performance than the fish models.

471 Between 31.2% and 65.8% of species core habitat occurred in high-shipping areas, and 62.0–81.8%
472 occurred within 25 km of offshore wind infrastructure. Core habitat was also close to oil/gas
473 infrastructure, with 58.9–76.0% occurring within 25 km of oil/gas structures. Similar overlap between
474 predicted suitable habitat and connectivity-relevant habitats have been reported in marine planning
475 studies (Weeks 2017; Jonsson et al. 2021; Stuart et al. 2021). A limit of understanding pressure
476 metrics is how the overlap is extended over time. The cumulative effect of pressure on core habitats
477 may be translated as disturbance, noise and contamination and show how conservation priorities can
478 be adjusted within the seascape (Weeks 2017). This study uses infrastructure position and potential
479 exposure considering that infrastructure is already established and active. By considering exposure
480 during the planning phase, we can prioritize extensive areas of core habitat cells that can be monitored
481 for cumulative effects and species responses.

482 Another general limitation in applying infrastructure-relevant pressure metrics to seascape
483 connectivity is the availability of data at sufficient resolution. Infrastructure layers are often available
484 as locations, polygons or distance surfaces, but these proxies do not capture the mechanisms by which
485 structures may affect movement. These may include operational status, structure age, foundation type,

depth, local hydrodynamics, noise, electromagnetic fields, contamination risk or prey aggregation (McLean et al. 2022). Similarly, shipping density can represent broad vessel-use intensity, but may not capture vessel type, speed, noise propagation or behavioural response.

As resistance and conductance are scale-dependent: a pressure layer that is useful for mapping regional exposure may be too coarse to represent movement cost for species responding to fine-scale habitat, prey or disturbance gradients. A recent review identified data needs and technical limitations as barriers to translating connectivity into policy and restoration practice (Preston et al. 2025).

Demersal fish showed stronger changes in resistance (18.2% for plaice and 13.8% for cod in the unrestricted network) under the infrastructure scenario, whereas harbour porpoise showed sensitivity in the strongest links (porpoise: Jaccard = 0.81; 89.5% top-link retention). Shipping pressure and infrastructure can alter planning interpretation through different connectivity metrics.

Connectivity outputs are known to change with modelling method, scale and movement assumptions; Dertien and Baldwin (2023) showed that directional and omnidirectional connectivity approaches can produce different spatial priorities, indicating that no single connectivity metric fully captures planning-relevant movement. Wilcox et al. (2023) also showed that different seascape resistance components can be integrated with gene-flow data to produce area-based functional connectivity metrics, reinforcing that resistance and connectivity summaries capture different aspects of movement processes. Therefore, resistance-based marine planning studies emphasise the need to integrate resistance estimates with empirical movement, dispersal or gene-flow data (Wilcox et al. 2023; Preston et al. 2025).

4.3 From resistance surfaces to connectivity priority categories

Connectivity-pressure categories may provide a practical way to translate complex spatial outputs into planning-relevant information. High connectivity and high-pressure areas represented only a small proportion of core habitat, ranging from 1.0% for Atlantic cod to 2.8% for European plaice and grey seal. Most core habitat was classified as low-connectivity/low-pressure, representing approximately

51–53% of core-habitat cells across species. In contrast, high-connectivity/low-pressure areas may represent connectivity space that is worth maintaining, while low-connectivity/high-pressure areas identify exposed habitat. This classification could help inform other models at the local level and support the use of exposure and pressure in resistance surfaces. An example would be to isolate low connectivity/high-pressure areas and calculate the reverse assumption of exposure – this way, we could identify if low connectivity is a byproduct of high pressure.

Additionally, prioritisation can help distinguish areas of potential conflict. For this study, prioritization focused on areas of high-pressure/high connectivity and areas where exposure is high but predicted connectivity is lower. This type of classification can make connectivity outputs more policy-relevant because connectivity metrics are often difficult to translate into planning and management actions. Beger et al. (2022) describe connectivity as an abstract concept that is difficult to operationalise in spatial planning, while Balbar and Metaxas (2019) emphasise the need to make connectivity information more accessible to practitioners. Translating connectivity-pressure categories can provide a planning interpretation of otherwise complex resistance and cumulative-current outputs. Nevertheless, we always need to consider categories as planning hypotheses based on model assumptions and they may always indicate where further evidence should be focused. Finally, a potential an associated uncertainty needs to be included, particularly in systems where direct movement data are limited (Weeks 2017; Virtanen et al. 2020; Cameron et al. 2022).

4.4 Limitations and future research

Habitat suitability models are correlative and depend on the quality, spatial distribution and taxonomic coverage of occurrence records. Species distribution models follow a series of assumptions that need to be meet. For example, occurrence records adequately represent the realised distribution or environmental associations of the species and that selected predictors capture the main ecological gradients shaping habitat suitability (Elith & Leathwick 2009; Phillips et al. 2009). Nevertheless, citizen-science records may account for sampling bias, and modelled relationships may need to be

transferable across the temporal extent of predictions (Elith & Leathwick 2009; Buckley et al. 2010; Troudet et al. 2017).

For this study, resistance surfaces were not calibrated with telemetry, genetic, acoustic or demographic movement data. The resulting corridors, conductance values and current maps should therefore be interpreted as hypotheses of potential functional connectivity (Zeller et al. 2012; Keeley et al. 2016; Wilcox et al. 2023). Additionally, infrastructure was represented using simplified spatial pressure metrics. Distance to offshore wind and oil/gas infrastructure, and shipping density, capture broad spatial patterns of human use, but they do not represent all relevant ecological mechanisms. Future work should test whether different pressure metrics produce similar connectivity conclusions.

This analysis used static or averaged spatial layers as it can be appropriate for a broad seascape-scale comparison. Nevertheless, marine systems are dynamic and species distributions, prey availability, shipping intensity, seasonal movements, temperature, productivity and current structure vary through time (Cowen et al. 2006; Treml et al. 2008; Boschetti et al. 2020). Dynamic connectivity models could test whether priority areas remain stable across seasons, years or future development scenarios. This would be especially relevant for species such as harbour porpoise or highly seasonal species, where static environmental models had lower discrimination and threshold-link identity was more sensitive.

Finally, literature-informed thresholds are useful for sensitivity testing, but they simplify complex movement behaviour into fixed distance limits (Treml et al. 2008; Thomas et al. 2014; Dertien & Baldwin 2023). Future research should compare the predicted conductance and links with telemetry, acoustic detections, genetic connectivity, larval dispersal models or demographic data. Acoustic telemetry studies have shown how observed fish movements can reveal connectivity among MPAs and expose mismatches between protected-area boundaries and species movement scales, reinforcing the need to validate modelled connectivity where possible (Pittman et al. 2014).

Future work should also test the framework under alternative infrastructure futures. Offshore wind expansion, oil and gas decommissioning, changing shipping routes and marine protected area design

will continue to reshape the North Sea (Burdon et al. 2018; Martins et al., 2023). Scenario-based connectivity modelling can help compare these futures, but only if resistance assumptions are tested transparently.

5. Conclusions

This study tested how habitat suitability, pressure exposure and infrastructure-weighted resistance affect predicted functional connectivity across four North Sea species. Habitat suitability was structured by species-specific combinations of local habitat/productivity and broader oceanographic gradients, while core suitable habitats overlapped substantially with shipping and offshore infrastructure.

Infrastructure-weighted resistance changed connectivity metrics across species, reducing median effective resistance and increasing conductance relative to habitat-only models. These results show that suitable habitat is not necessarily low-pressure habitat and that lower connectivity areas can be used in prioritization to test exposure.

Overall, the study shows that infrastructure pressure metrics can be included before HSM-derived connectivity outputs for planning interpretation. The framework is useful because it separates habitat suitability, pressure exposure and connectivity sensitivity, rather than treating them as the same ecological signal. In data-limited marine systems, this provides a transparent way to generate planning hypotheses, identify where validation is most needed, and compare how infrastructure assumptions shape predicted functional connectivity.

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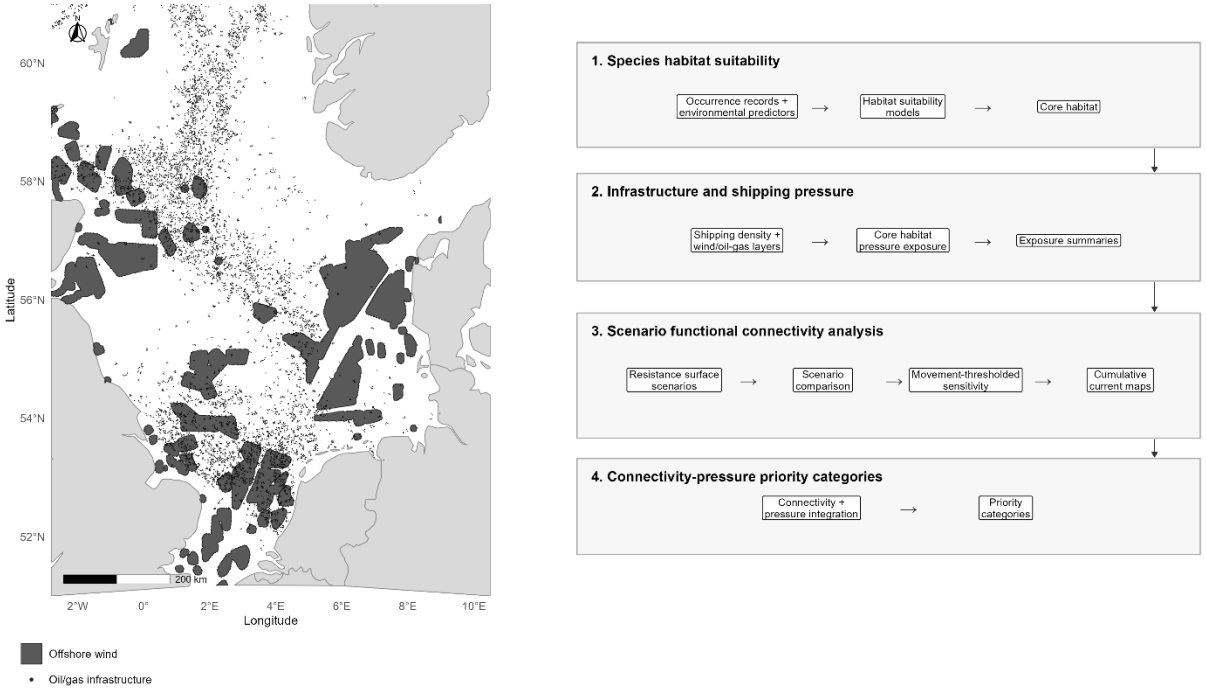
Statements and Declarations

No funding was received to assist with the preparation of this manuscript. The author has no relevant financial or non-financial interests to disclose. **Author contribution:** C.M. conceived and designed the study, acquired and processed the data, conducted the analyses, interpreted the results, and developed the analytical workflow and code used in the work. C.M. drafted and critically revised the manuscript, approved the final version to be published, and agrees to be accountable for all aspects of the work, including the accuracy and integrity of the study. **Data availability:** The data used and generated in this study are available from public repositories and an associated archive. Species occurrence records were obtained from GBIF; GBIF-mediated occurrence attribution is documented through the GBIF derived dataset DOI: https://doi.org/10.15468/dd.gvncsp. The cleaned occurrence dataset and source-dataset attribution table are archived on Zenodo:10.5281/zenodo.22229515. **Ethics approval:** Not applicable. **Consent to participate:** Not applicable. **Consent for publication:** Not applicable.

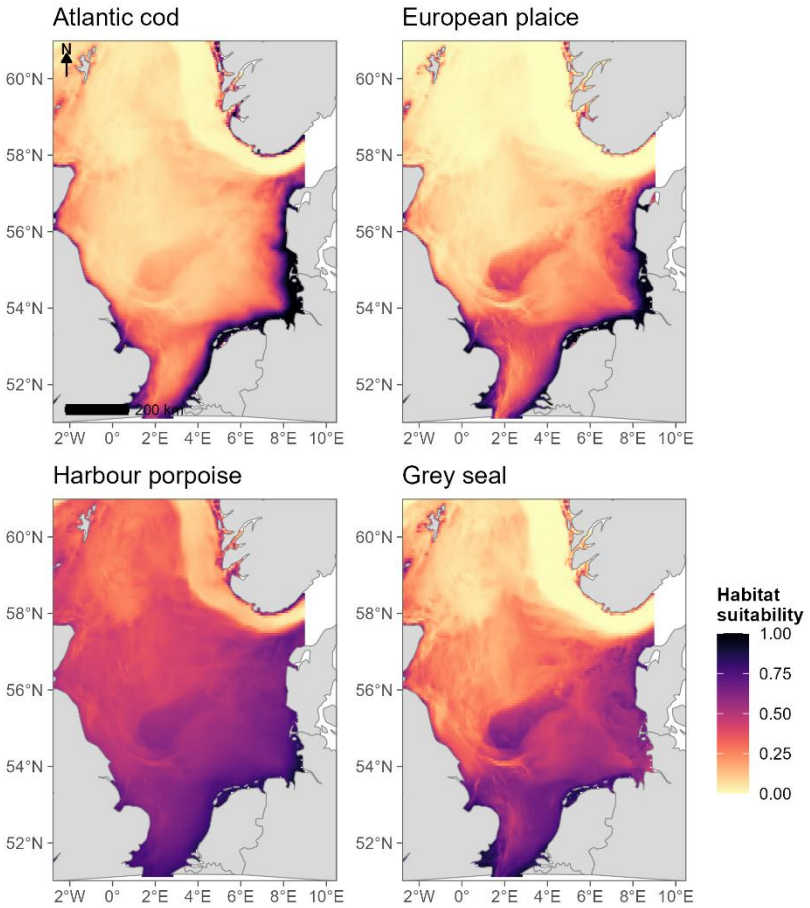
848 **Figures & Tables:**



849

850 **Fig. 1 -** North Sea study area and analytical workflow for scenario-based seascape connectivity

851 modelling



852

853 **Fig. 2 -** Predicted habitat suitability across the North Sea for four marine species. Maps show the best-

854 performing habitat suitability model block for each species based on test AUC

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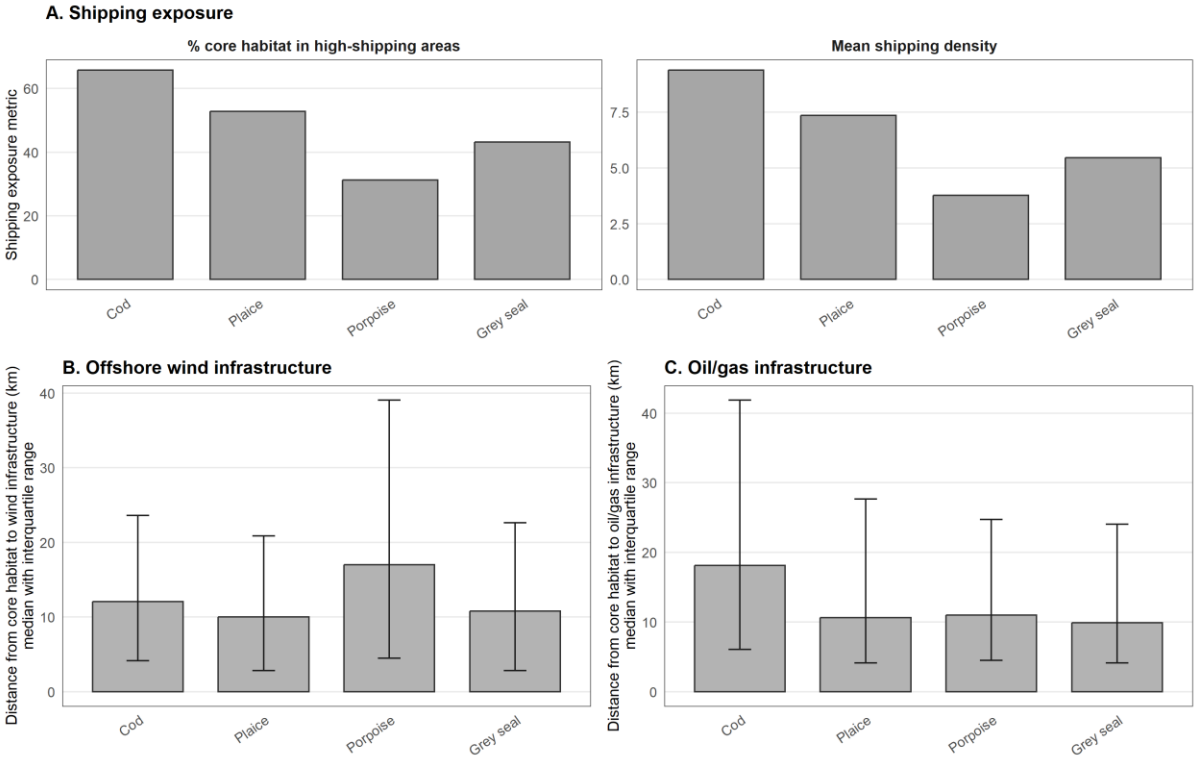

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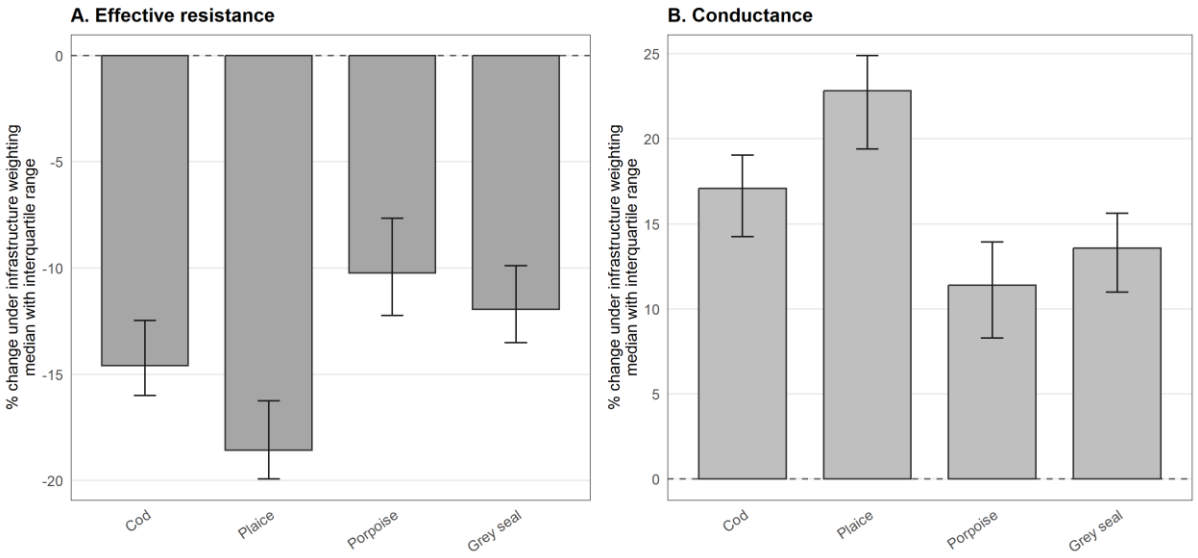
857 **Fig. 3 -** Exposure of core suitable habitat to shipping and marine infrastructure



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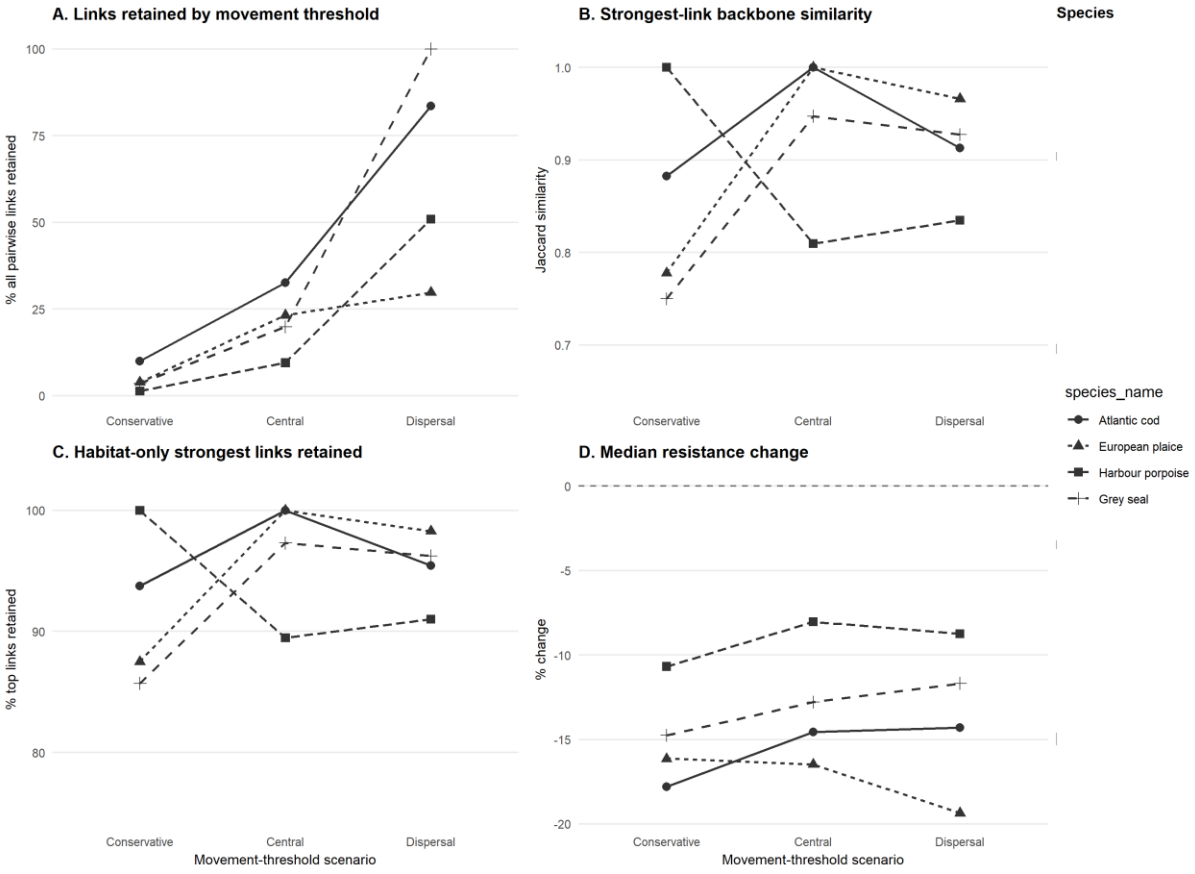
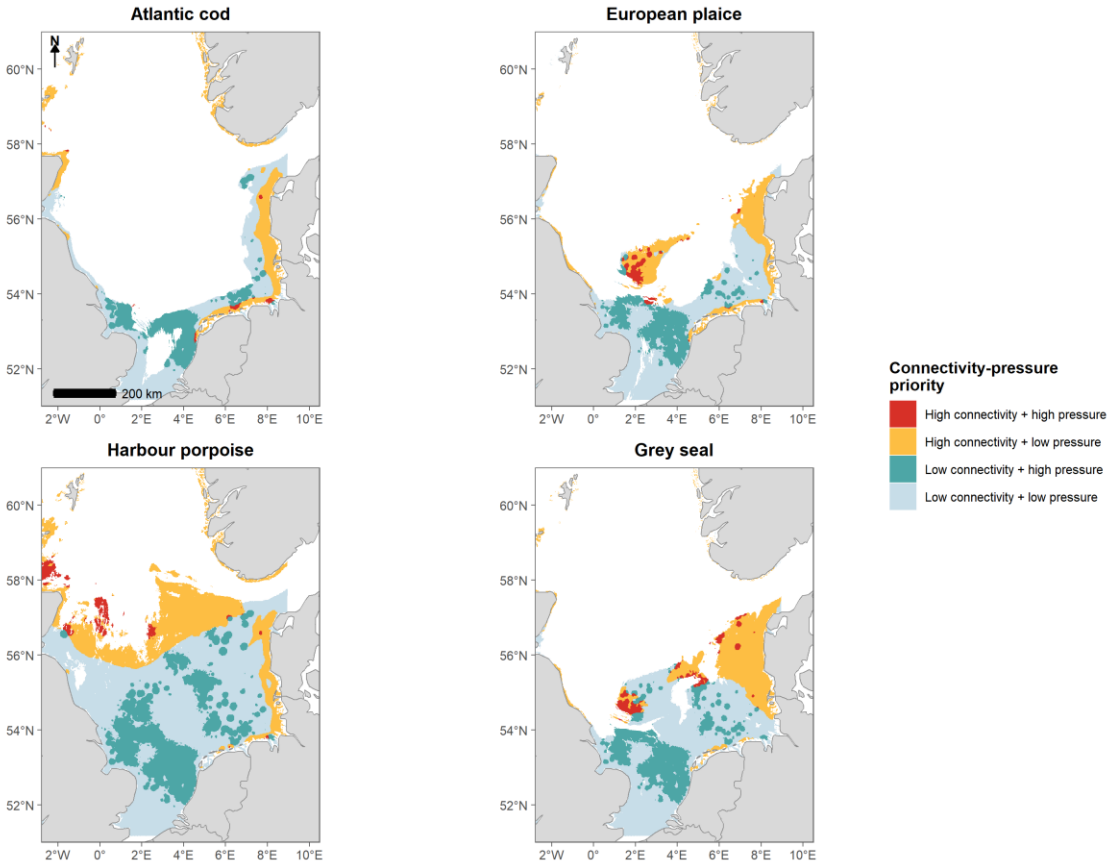
859 **Fig. 4 -** Link-level change in predicted connectivity under infrastructure weighting. Bars show the

860 median percentage change across all pairwise links for each species



861

862 **Fig. 5 -** Movement-threshold sensitivity analysis of predicted connectivity



863

864 **Fig. 6 -** Connectivity-pressure priority categories across the North Sea

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867 **Table 1 –** Environmental and human-pressure predictor variables used in habitat suitability, exposure and resistance modelling

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Variable	Code	Description	Unit	Temporal resolution	Source
Bathymetry	bathymetry	Seafloor elevation raster used as the spatial template and as an environmental predictor. Marine cells have negative elevation values.	m	Static terrain surface	GEBCO_2024 Grid
Water depth	depth_m	Positive water depth derived as the absolute value of marine bathymetry.	m	Static; derived from bathymetry	Derived from GEBCO_2024 Grid
Oceanic depth zone	depth_zone	Categorical depth gradient: shallow coastal (0–20 m), shelf/demersal (20–200 m), deeper offshore (>200 m).	Categorical class	Static; derived from water depth	Derived from GEBCO_2024 Grid
Sea surface temperature	sst	Long-term mean sea surface temperature representing thermal conditions at the ocean surface.	°C	Long-term climatological mean; original Bio-ORACLE layer based on monthly climatologies	Bio-ORACLE, accessed through *sdmpredictors*
Chlorophyll-a concentration	chlorophyll	Long-term mean surface chlorophyll-a concentration, used as a proxy for marine productivity.	mg m^{-3}	Long-term climatological mean; original Bio-ORACLE layer based on monthly climatologies	Bio-ORACLE, accessed through *sdmpredictors*
Salinity	salinity	Long-term mean sea surface salinity representing broad hydrographic conditions.	PSU	Long-term climatological mean derived	Bio-ORACLE,

				from in situ observations	accessed through Copernicus Marine
Current speed	current_speed	Mean horizontal current speed calculated as sqrt(u² + v²) from eastward and northward current components.	m s⁻¹	Long-term mean derived from monthly current layers - usi_* and vsi_*	Service / CMEMS Global Ocean Physics Analysis and Forecast
Shipping density	shipping_density	Mean vessel-density surface representing intensity of vessel activity across the North Sea.	Average vessel presence/density per grid cell; retain native EMODnet units in reporting	Multi-year mean aggregated from annual layers, 2017–2023	EMODnet Human Activities, EU Vessel Density Map
Distance to offshore wind infrastructure	dist_wind_m	Euclidean distance from each marine grid cell to offshore wind-farm infrastructure.	m	Static spatial snapshot corresponding to downloaded infrastructure dataset	Derived from EMODnet Human Activities offshore wind-farm dataset
Transformed distance to offshore wind infrastructure	dist_wind_log1p	Log-transformed distance to offshore wind infrastructure used as a modelling/resistance predictor.	log(1 + m)	Static; derived from dist_wind_m	Derived from EMODnet Human Activities offshore wind-farm dataset
Distance to oil and gas infrastructure	dist_oil_m	Euclidean distance from each marine grid cell to offshore oil and gas wells/infrastructure.	m	Static spatial snapshot corresponding to downloaded	Derived from EMODnet Human Activities oil

				infrastructure dataset	and gas wells dataset
Transformed distance to oil and gas infrastructure	dist_oil_log1p	Log-transformed distance to oil and gas infrastructure used as a modelling/resistance predictor.	log(1 + m)	Static; derived from dist_oil_m	Derived from EMODnet Human Activities oil and gas wells dataset
Shipping-current exposure proxy	shipping_current_proxy.tif	Exploratory proxy combining shipping density and current speed to represent potential exposure to vessel-associated disturbance transported or structured by water movement. This is not a validated acoustic-noise layer.	Compound derived index	Derived from multi-year mean shipping density and long-term mean current speed	Derived from EMODnet vessel-density and CMEMS current-speed layers

Table 2 - Species occurrence records and best-performing habitat suitability model block

Species	Scientific name	Occurrence records retained	Best HSM block	AUC	Core-habitat threshold
Atlantic cod	*Gadus morhua*	638	Combined environmental	0.893	0.266
European plaice	*Pleuronectes platessa*	757	Local habitat/productivity	0.893	0.276
Harbour porpoise	*Phocoena phocoena*	8748	Combined environmental	0.791	0.419
Grey seal	*Halichoerus grypus*	6906	Combined environmental	0.87	0.449

Table 3 - Connectivity scenario sensitivity analysis for unrestricted and movement thresholds

Species	Scenario comparison	Links retained	Δ median resistance (%)	Spearman rank correlation	Jaccard top-25 similarity	Top-25 retained (%)
Porpoise	Central threshold 100 km	74	-8	0.978	0.81	89.5
Cod	Central threshold 177 km	205	-14.6	0.997	1	100
Seal	Central threshold 230 km	147	-12.8	0.995	0.947	97.3
Plaice	Central threshold 241 km	181	-16.5	0.994	1	100
Cod	Unrestricted	630	-13.8	0.993	0.963	98.1
Plaice	Unrestricted	780	-18.2	0.992	0.95	97.4
Porpoise	Unrestricted	780	-9.4	0.99	0.875	93.3
Seal	Unrestricted	741	-11.7	0.993	0.927	96.2

Online Resource 1. Supplementary figures and tables for scenario-dependent functional connectivity in the North Sea.

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