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Multi-generational dispersal and dynamic patch occupancy reveals spatial and temporal stability of seascapes

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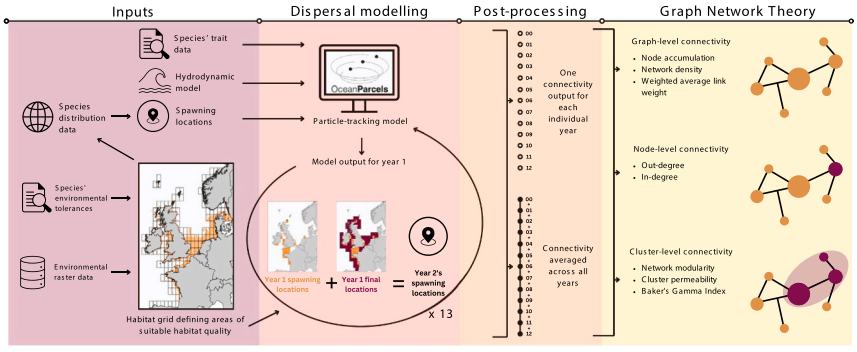
HIGHLIGHTS

- A novel multi-generational framework for assessing ecological network stability
- Yearly change in dispersal hinders invasive spread but is rarely explicitly modelled.
- Multi-generational dispersal quantified using biophysical models and graph theory
- Connectivity of Pacific oysters remained temporally stable, enabling rapid spread.
- Identification of highly connected locations supports management prioritisation.

GRAPHICAL ABSTRACT



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ABSTRACT

The success of non-native species (NNS) invasions depends on patterns of dispersal and connectivity, which underpin genetic diversity, population establishment and growth. In the marine environment, both global environmental change and increasing anthropogenic activity can alter hydrodynamic patterns, leading to significant inter-annual variability in dispersal pathways. Despite this, multi-generational dispersal is rarely explicitly considered in attempts to understand NNS spread or in the design of management interventions. Here, we present a novel approach to quantifying species spread that considers range expansion and network formation across time using the non-native Pacific oyster, *Magallana gigas* (Thunberg 1793), as a model. We combined biophysical modelling, dynamic patch occupancy models, consideration of environmental factors, and graph network theory to model multi-generational dispersal in northwest Europe over 13 generations. Results revealed

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that *M. gigas* has a capacity for rapid range expansion through the creation of an ecological network of dispersal pathways that remains stable through time. Maximum network size was achieved in four generations, after which connectivity patterns remained temporally stable. Multi-generational connectivity could therefore be divided into two periods: network growth (2000−2003) and network stability (2004–2012). Our study is the first to examine how dispersal trajectories affect the temporal stability of ecological networks across biogeographic scales, and provides an approach for the assignment of site-based prioritisation of non-native species management at different stages of the invasion timeline. More broadly, the framework we present can be applied to other fields (e.g. Marine Protected Area design, management of threatened species and species range expansion due to climate change) as a means of characterising and defining ecological network structure, functioning and stability.

1. Introduction

Population connectivity (the movement of individuals between discrete populations) in the marine environment is a key process that structures biodiversity across geographic space (Álvarez-Noriega et al., 2020; Cristiani et al., 2021). For marine benthic organisms, larval dispersal underpins genetic diversity, population development and growth across multiple spatial scales (Hogan et al., 2012; Baguette et al., 2013; Ross et al., 2017) and is vital to understanding the dynamics of metapopulations and metacommunities (Melià et al., 2016). It is of particular importance in the case of non-native species (NNS), for which larval dispersal can be critical to range expansion and invasion success (Pergl et al., 2020). Consequently, over time much attention has been paid to the development and improvement of methods to quantify connectivity, for example by increasing the accuracy of biophysical models (e.g., James et al., 2019; Swearer et al., 2019; Leis, 2021), developing genetic techniques to examine connectivity over time (e.g., Gagnaire, 2020), and integration of these two approaches (Levin, 2006; Bernal-Durán et al., 2024).

Whilst recent methodological developments have greatly advanced our ability to quantify marine connectivity, measuring dispersal empirically remains logistically constrained given the spatial scale of the oceans and the microscopic life-history stages characteristic of many marine species during their dispersal (Knights et al., 2006; James et al., 2019; Álvarez-Noriega et al., 2020). Consequently, two main tools have emerged to indirectly measure dispersal and connectivity within the marine environment. Population genetics are often used to identify connectivity at broad spatial and temporal scales (Hogan et al., 2012, Anglès d'Auriac et al., 2017, Gagnaire, 2020), but has received limited use to elucidate dispersal processes over relatively short (generational) time scales and distances (Hedgecock et al., 2007, White et al., 2010, but see Robitzch et al., 2020, Dubé et al., 2020 for recent advancements using kinship analysis). This is especially true for NNS, which often exhibit founder events resulting in low genetic variability compared to source populations (Meistertzheim et al., 2012). Alternatively, biophysical modelling that combines individual-based models incorporating biological information of individual organisms, oceanographic data and particle-tracking to simulate and estimate dispersal (Treml et al., 2008; Melià et al., 2016) is an approach that can potentially overcome the difficulties associated with estimating small-scale multi-generational dispersal in genetic analyses (Saura et al., 2014).

Implicit measures of multi-generational dispersal consistently demonstrate its importance to the functioning and stability of ecological networks (Boulanger et al., 2020; Legrand et al., 2022). However, multiple dispersal events that account for metapopulation growth over time are rarely explicitly modelled due to the complexity of biological systems (James et al., 2019) and the computational expense of running simulations (but see Boulanger et al., 2020). Developing approaches to overcome these limitations is especially relevant given the fact that seascapes increasingly exhibit relatively rapid, dynamic changes in patch occupancy over space and time; a result of environmental disturbance (Lookingbill et al., 2010; Firth et al., 2021), new marine artificial structures that can act as stepping-stones for dispersal (Henry et al., 2018; van der Molen et al., 2018) and dynamic changes in species distribution under climate change (Rinde et al., 2016; Curd et al., 2023).

As the distribution of marine species continues to change over time as a result of these factors, identifying areas of potential future expansion is of both interest and concern, particularly in the case of NNS, that often come with significant costs to the environment and society (Cuthbert et al., 2022; Diagne et al., 2021). Recently, the spatial extent of the Pacific oyster, *Magallana gigas* (Thunberg 1793), has expanded rapidly in its non-native range, occupying available space at a rate of 23.1 km y^{-1} (Clubley et al., 2023). Despite this, our understanding of the contribution of larval dispersal to the spread of *M. gigas* is limited (but see Robins et al., 2017 and Wood et al., 2021). For range-expanding species like *M. gigas*, where eradication is no longer likely nor feasible (Herbert et al., 2016), knowledge of the relative importance of dispersal to variation in connectivity and growth of populations underpins risk-based surveillance measures and prioritisation of management strategies (Locke and Hanson, 2009; Riera et al., 2021).

When used in conjunction with biophysical modelling, graph theory can be an effective tool for examining spatial variation in connectivity over multiple generations (Peterson et al., 2019). In this approach, a graph represents a network of (meta-)populations connected by dispersal (Baguette et al., 2013). Quantitative descriptions of such a graph, or network metrics, can be used to provide information on the structure and connectedness of the network at different spatial scales of connectivity. Metrics include spatial patterns in connectivity across the whole seascape, the identification of key populations that may act as important sources or sinks of larvae, and grouping of populations into clusters where dense larval exchange takes place (Table 1).

Here, we present a novel approach using graph network theory to quantify the potential multi-generational, multi-scale connectivity of *M. gigas* – an important marine NNS in north-west Europe. Our aims were two-fold: (1) to describe emergent patterns in connectivity over a multi-generational time scale, and (2) to assess the degree of temporal variation and/or stability in connectivity of a dynamic network through time as *M. gigas* undergoes range expansion. We used a combination of biophysical modelling, consideration of suitable habitat areas and graph theory at three biologically relevant spatial scales of connectivity to answer the following questions: (i) to what degree are populations across the seascape connected in space and time?; (ii) which populations contribute most strongly to network connectivity?; and (iii) do dispersal patterns create distinct clusters of highly connected populations? This multi-generational, integrative approach provides a means for the assessment of patterns in, and the temporal stability of, connectivity resulting from larval dispersal at broad spatial scales that can be used as a tool towards NNS management and horizon-scanning, as well as being extended to other systems.

2. Methods

2.1. Hydrodynamic model

Hydrodynamic fields to force the biophysical models were obtained from the 7 km Atlantic Margin Model (AMM7, O'Dea et al., 2012), which uses the Nucleus for European Modelling of the Ocean (NEMO) ocean circulation model (Madec et al., 2019) and has been extensively

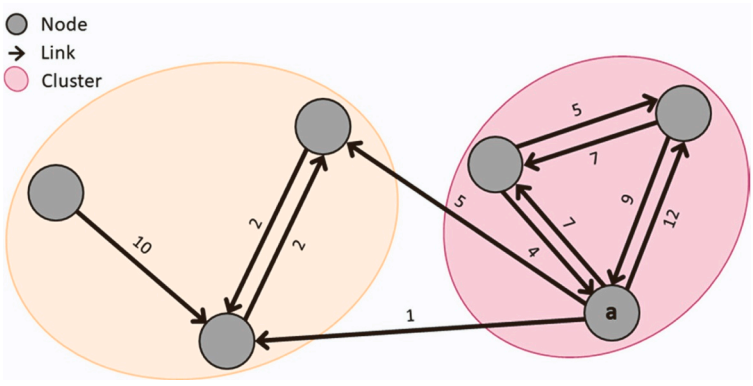
described and validated (see O'Dea et al., 2017 for details). Hourly 3D velocity fields were provided by the Met Office, covering a domain of 43°N - 65°N, 13°W - 13°E (Fig. 1) for the period 2000–2012; a period during which rapid expansion of *M. gigas* has been observed across multiple countries (Clubley et al., 2023).

2.2. Identifying suitable habitat for spawning and settlement

To ensure that spawning and settlement locations of particles in the biophysical models were environmentally relevant, a deterministic spatial grid method of location selection like that used by Wood et al. (2021) was implemented. Environmental raster data at 0.08° resolution covering the study domain were obtained for four key parameters

Table 1
The graph network metrics used in the present study, and their calculation for an arbitrary network (Urban and Keitt, 2001; Treml et al., 2008).

Network metric	Description	Example for an arbitrary network
Number of nodes	The total number of points, each representing a theoretical population of Pacific oysters, in the network.	
Network density	The ratio between the number of links present in the network and the total number of possible links the network could contain (present / possible).	
Link weight	The number of particles that travelled from one node (n_i) to another (n_j).	
Out-degree	The number of outgoing links from a node.	
In-degree	The number of incoming links to a node.	
Cluster	A group of densely connected nodes identified using a fast-greedy community detection algorithm that seeks to directly optimise the modularity of the network.	**Number of nodes:** 6 **Network density:** 0.37 (11 present links / 30 possible links) **Link weight:** represented by the numbers on each link **Out-degree of node 'a':** 4 **In-degree of node 'a':** 2 **Number of clusters:** 2 **Network modularity:** 0.3 – relatively poor division into clusters **Cluster permeability:** 9.4% (6 particles exchanged between two clusters / 64 particles exchanged in total)
Network modularity	A measure of how separated each node is from all other nodes, bound between 0 (poor division into clusters – links are even across the entire network) and 1 (dense connections within clusters and sparse connections across clusters).	
Cluster permeability	The percentage of all particle exchange within the network that occurred between two different clusters.	



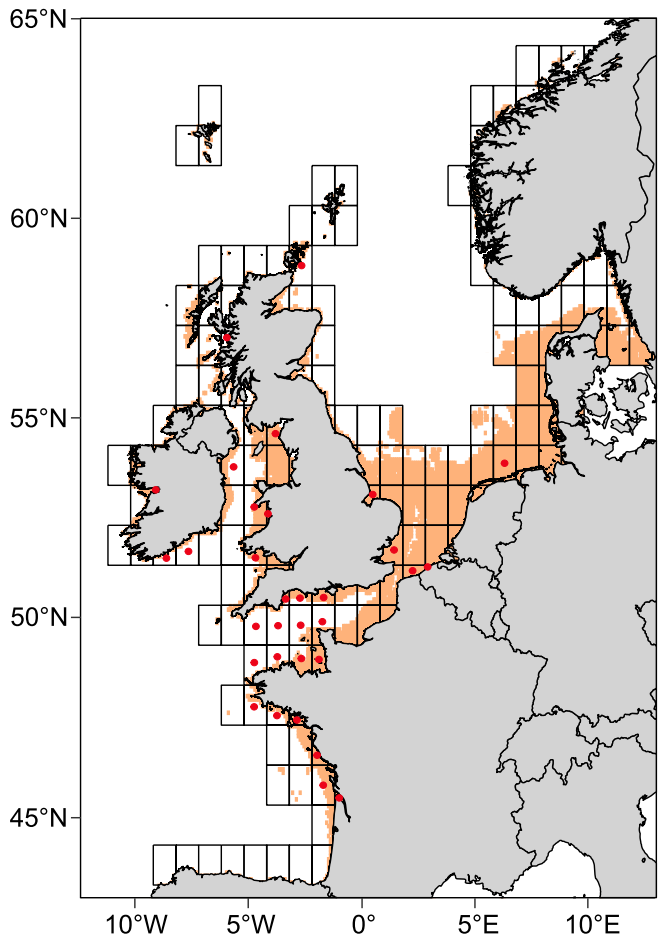


Fig. 1. A map of the study domain (43°N - 65°N, 13°W - 13°E). Coloured squares show environmental (depth, temperature, salinity and substrate type) raster data (0.08° resolution) representing suitable habitat for Magallana gigas settlement, with the overlaid grid cropped to only those grid cells in which raster data are present to create a 'habitat grid' (1° resolution). Points in red show the initial spawning locations of *M. gigas* used for the biophysical model for the year 2000 ($n = 32$), which were derived from distribution data for the species up to this time point.

determining suitable habitat for *M. gigas* settlement, growth, and survival: depth (MARSPEC, Sbrocco and Barber, 2013), temperature (SST; MARSPEC), salinity (Bio-ORACLE, Assis et al., 2018) and substrate type (EUSeaMap; Vasquez et al., 2023). These data were combined and cropped to include only those cells containing suitable conditions for *M. gigas* larvae across all parameters, as determined by the published scientific and grey literature (Fig. 1; Table S1). A spatial polygon grid with 1° resolution (~111 km latitudinally × 47–81 km longitudinally) was superimposed over the extent of the resulting data and cropped to retain only grid polygons where data were present (hereafter 'habitat grid'), resulting in a grid of 180 spatial polygons (Fig. 1).

2.3. Particle tracking model

Potential dispersal patterns of *M. gigas* larvae were modelled using OceanParcels (version 2.3.0) – a Lagrangian particle tracking model (Delandmeter and van Sebille, 2019). Using the NEMO AMM7 hydrodynamic data, particles were advected using a fourth-order Runge-Kutta solver, spatially centred using an Arakawa C-grid, at a time step of 5 min (sufficient to accurately capture dispersal predictions; Fig. S1). The 7 km grid of the AMM7 domain resolves the majority of energy in mesoscale eddies (Chelton et al., 1998), but a horizontal random walk is often added to the advective solution to represent missing eddy dispersion (Reijnders et al., 2022). Here, a relatively low value of horizontal diffusivity of Kh = 1 $m^2 s^{-1}$ was selected to add variability and produce an ensemble capable of representing uncertainty in the knowledge of the state of the system. Using a similar grid resolution (1/16°), Kaandorp et al. (2020) found a best fit to observed statistics using a Kh = 10 $m^2 s^{-1}$ but saw very similar results for Kh = 1 $m^2 s^{-1}$. For higher resolution models such as IFREMER's 4 km MARS3D + ICHIOPS, often only advection is used (Bedington et al., 2022).

Due to a paucity of information on the swimming behaviour and vertical distribution of *M. gigas* larvae, particles dispersed passively using surface-level velocity fields (i.e., at a depth of 0 m). Whilst these decisions can lead to the overestimation of connectivity, such simplifications are commonplace when detailed information on the behaviour of marine larvae are lacking (see, for example, Álvarez-Noriega et al., 2020, Cristiani et al., 2021, and David et al., 2022). Indeed, a sensitivity analysis showed no effect (i.e., ≤2 % difference) of a mortality rate of 0.044 day^{-1} (Galtsoff, 1964; Rumrill, 1990; Wood et al., 2021) on connectivity metrics. Therefore, and as no minimum number of particles was specified for a location to be considered occupied, larval mortality was not included. Sensitivity analysis was conducted to determine the optimal number of particles to be released from each spawning location (Supplementary methods), from which 100,000 particles was chosen (Fig. S2). This number remained consistent in space and time due to a lack of data on *M. gigas* population size and fecundity in each location (Wood et al., 2021; Clubley et al., 2023).

2.3.1. Spawning locations and multi-generational dispersal

Occurrence records of *M. gigas* within the study domain were used to inform spawning locations in the biophysical models. Records were downloaded from four online repositories: Global Biodiversity Information Facility (Derived dataset GBIF.org, 2023), Ocean Biodiversity Information System (OBIS, 2021), NBN Atlas (National Biodiversity Atlas (NBN) Atlas occurrence download, 2021) and the Joint Nature Conservation Committee's (JNCC) Marine Recorder (Marine Recorder, 2021). For a description of compilation and cleaning processes, see Clubley et al. (2023). Records were reduced to only those from the year 2000 or earlier (the first year of the multi-generational model; $n = 714$) and overlaid on the habitat grid. The longitude and latitude of the centroids of grid polygons where at least one occurrence record was present were extracted to form the initial spawning locations of *M. gigas* (Fig. 1, $n = 32$). Using this method, sampling bias resulting from a lack of systematic sampling of *M. gigas* populations in the study domain is minimised.

To incorporate multi-generational dispersal, additional ('new') spawning locations were selected for each year after the year 2000 based on the final locations of particles from the previous year. The final location of each individual particle was overlaid on the habitat grid and particles whose final locations were not contained within a spatial grid polygon were removed from model outputs under the assumption that post-dispersal settlement and establishment would be unsuccessful. The centroids of the spatial polygons within which remaining particles were located were extracted to provide the coordinates of new spawning locations, and added to spawning locations from the previous year such that spawning locations were cumulative through time. Consequently, this creates a high-growth model where rate of spread tends towards maximum dispersal distance.

2.3.2. Parameterising species trait data

Spawning in *M. gigas* is triggered in response to environmental cues such as temperature (Rico-Villa et al., 2009) and lunar phase (Bernard et al., 2016). In this study, the onset of spawning reflected those months for which *M. gigas* is reported to release gametes in the Northern Hemisphere: mid-July–mid-August (Troost, 2010; Anglès d'Auriac et al., 2017). Within the biophysical models, each particle was randomly assigned a spawning date by sampling from a uniform distribution between 16th July and 15th August of each year. All particles were

released at midnight, coinciding with different points in the tidal cycle depending on the date of release, thus accounting for variation in lunar phase and tidal state.

The planktonic larval duration (PLD) of *M. gigas* is unknown but is estimated to be between two and four weeks (Troost, 2010). It is thought that the PLD of individual larvae is variable within this range (Coon et al., 1990; Rico-Villa et al., 2009), and so to capture this variability four different scenarios were modelled (14, 17, 25 and 28 days). Preliminary analysis showed that maximum network size was achieved in the same year (2004) for all PLD scenarios, and there was very little variation in network density each year (average standard error = 0.003; Fig. S3). Consequently, we chose to amalgamate model outputs from each PLD to create one output capturing the full range of dispersal capable by *M. gigas* per year. As a means of restricting dispersal outputs to only those areas likely to provide suitable habitat for *M. gigas* settlement, the coordinates of the final location of each particle were overlaid on the habitat grid, and if the particle did not fall within a spatial grid polygon it was removed from the model output. Across the 13 years modelled, this resulted in the removal of 16.79 % (±0.88) of particles on average from each year.

2.3.3. Model outputs

A biophysical model was run using the methods described above for each year from 2000 to 2012. The geographic coordinates of initial particle positions (source location) and their positions at 14, 17, 25 and 28 days (final positions) were saved as netCDF files, imported into R (Version 4.1.2, R Core Team, 2021) and converted to comma-separated values (.csv) files for post-processing and analysis. Using the habitat grid, the spatial polygon over which the spawning and final positions of each particle lay was determined, and an arbitrary 'spawning ID' and 'final ID' assigned. This information was used to construct a connectivity matrix, C, where C_{ij} represents the number of particles released in grid polygon i whose final location was grid polygon j, and C_{ii} represents the number of particles released in grid polygon i whose final location was also in grid polygon i (particle retention).

2.4. Graph theoretical approach

We applied graph theory to connectivity matrices to characterise and explore temporal variation in the potential connectivity of the seascape network, in which a 'graph' represents a network of nodes connected by links, with each link l_{ij} containing two nodes n_i and n_j (Urban and Keitt, 2001). Here, nodes represent the location of potential populations of *M. gigas* whilst links represent the potential connections between pairs of populations as a result of larval dispersal. Links have a weighting, which corresponds to the number of particles transported from n_i to n_j (Table 1).

All graphs were constructed directionally (i.e., providing 'direction' of particle transport) using the 'igraph' package (Csardi and Nepusz, 2006). A single graph was constructed for each of the 13 years modelled, as well as an 'averaged graph' that incorporated data (and therefore variation) across all years to represent the central tendency (average response) in linkage weight between nodes for the range of years considered. In this graph, averages were weighted by the number of years in which each link was present in the network, such that average link weight ($\overline{x}$) was calculated as follows:

$$\overline{x} = \frac{\sum w_n \times y_n}{\sum y_n}$$

where, for each link between nodes, w_n is the link weight for a given year and y_n is the number of years in which the link was present (the weighting factor).

2.5. Network connectivity metrics

2.5.1. To what degree are populations across the seascape connected in space and time?

We assessed the extent and temporal stability of potential connectivity at the scale of the entire network by examining growth using two metrics for each year: the number of spawning nodes in the network, and network density (concentration of links within the network; Table 1). Additionally, we assessed the strength and temporal stability of links between nodes by mapping link weights from the averaged graph, normalised between 0 (low particle exchange, link is rarely present) and 1 (high particle exchange, link is present in all years). Finally, we used the averaged graph to test the relationship between link weight and the 'seaway distance' (shortest path length when travelling over water, see Clubley et al., 2023) between pairs of nodes using a non-linear least-squares model. Following visual examination of the data, a number of regression fits were compared using R^2 and AIC values, from which an exponential decay curve using the self-starting function 'SSasymp' was chosen and the goodness of fit (pseudo-R^2) tested as follows:

$$y(t) \sim y_f + \left(y_0 - y_f\right)e^{-exp(\alpha)t}$$

where t is the seaway distance, and the measured value y (link weight) starts at y_0 and decays towards y_f at a variable rate of $exp(\alpha)$.

2.5.2. Which populations contribute most strongly to network connectivity?

To assess the importance of nodes to network connectivity through time we calculated out-degree and in-degree – proxies for the importance of a node as a source of particles or as a potential settlement location (Table 1). Linear regression was used to test for a relationship between out-degree and in-degree of nodes from the averaged graph, and a density map of spatial grid polygons representing node locations was constructed for both metrics. To test the temporal stability of this relationship, a correlation matrix (Pearson's correlation coefficient, r) was constructed for pairwise combinations of node out-degree and in-degree across all years.

2.5.3. Do dispersal patterns create distinct clusters of highly connected populations?

To identify clusters of nodes between which particle exchange was high and exchange with nodes in other clusters was low, representing potential barriers to dispersal, we used a fast-greedy community detection algorithm (Clauset et al., 2004). This algorithm adopts a hierarchical, bottom-up approach to cluster detection and is deterministic (i.e., will always produce the same output). In brief, each node begins in its own cluster and pairs of clusters within which the nodes share dense connections are merged as the algorithm moves up the hierarchy, producing a group of clusters for which the modularity score is as close to 1 (dense connections within clusters, sparse connections between clusters; Table 1) as possible. The emergent spatial pattern of clusters through time was examined by mapping clusters detected from the averaged graph. To assess the 'strength' of node clusters (i.e., the degree of particle exchange between nodes in different clusters) two metrics were calculated for each year: modularity and cluster permeability (Table 1). Further, to test whether the same node clusters persisted through time, we also calculated Baker's Gamma Index (BGI, also known as Goodman-Kruskal-Gamma Index; Baker, 1974) to test for correlation between two dendrograms (e.g. 2000 vs. 2001); pairwise comparison of all years was undertaken using BGI. BGI values are bounded between −1 and 1. A value of −1 indicates perfect disagreement between node cluster groups (i.e., the node clusters in the two years being compared are exact opposites of one another), a value near 0 suggests no similarity between the node clusters of the two years being compared, and a value of 1 indicates that node clusters in the two years being compared are identical. BGI was calculated using the 'dendextend' package (Galili, 2015).

3. Results

3.1. To what degree are populations across the seascape connected in space and time?

A total of 209,100,000 particles were released from 172 locations over the 13 model runs, of which 156,253,778 (75 %) were 'successful' (i.e., their final location was contained within the habitat grid). The number of spawning nodes within the network increased from 32 nodes in 2000 to a maximum of 164 nodes by 2005, after which an asymptote was reached (Fig. 2a). Similarly, network density was variable between 2000 and 2003, but from 2004 onwards remained relatively stable (Fig. 2b).

When accounting for connectivity across the 13-year period (using the averaged graph), the network appeared densely connected and no isolated patches were identified (Fig. 3). Despite this, and despite temporal stability in network density (Fig. 2b), in most cases normalised average link weight was low (i.e., <0.1; Fig. 3b, d), indicating only a small number of particles typically travelled between the focal pair of nodes. Excluding cases of particle retention to the source node, true link weight values (median = 989, mean ± SE = 17,285 ± 817) generally decreased as the seaway distance between pairs of nodes increased, with 75 % of all links occurring between nodes that were ≤260 km apart (Fig. 4). Despite this, rare 'long-distance dispersal' events among nodes were present, indicating a small but significant number of particles were exchanged between distant nodes in a given year, punctuated by sporadic annual connection failures (Figs. 3c, 4). Although not displayed, particle retention to the source node occurred frequently through time, representing only 0.55 % of existing links but accounting for 31.3 % of all particles released. However, it should be noted that the degree of

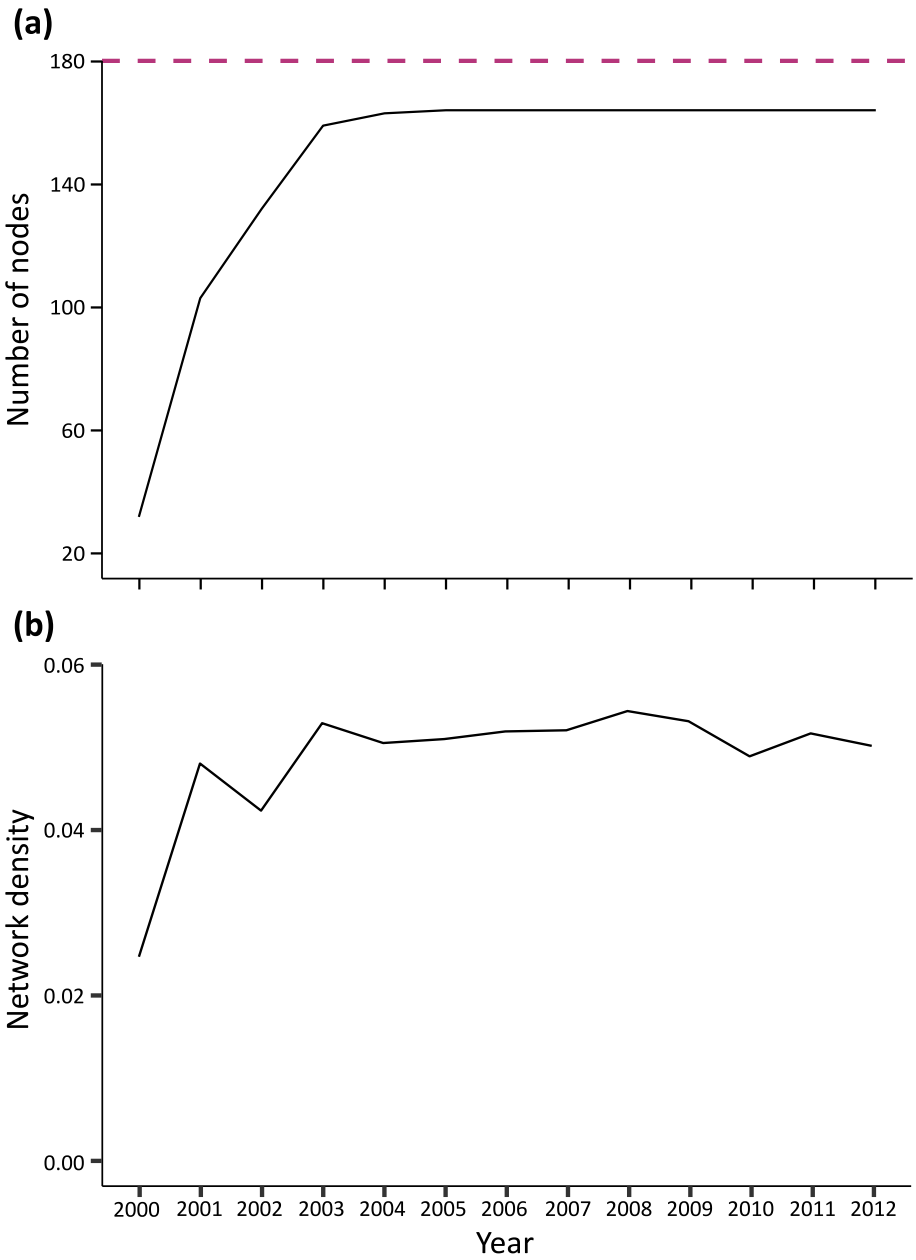


Fig. 2. Measures of network size over time. (a) The number of source (spawning) nodes contained within the network for each of the 13 years modelled. Dashed line indicates the total number of grid polygons in the habitat grid ($n = 180$). (b) Network density for each of the 13 years modelled, representing the ratio between those links present in the network and all possible links within the network. Network density is constrained between 0 (no potential links within the network were realised) and 1 (all potential links within the network were realised).

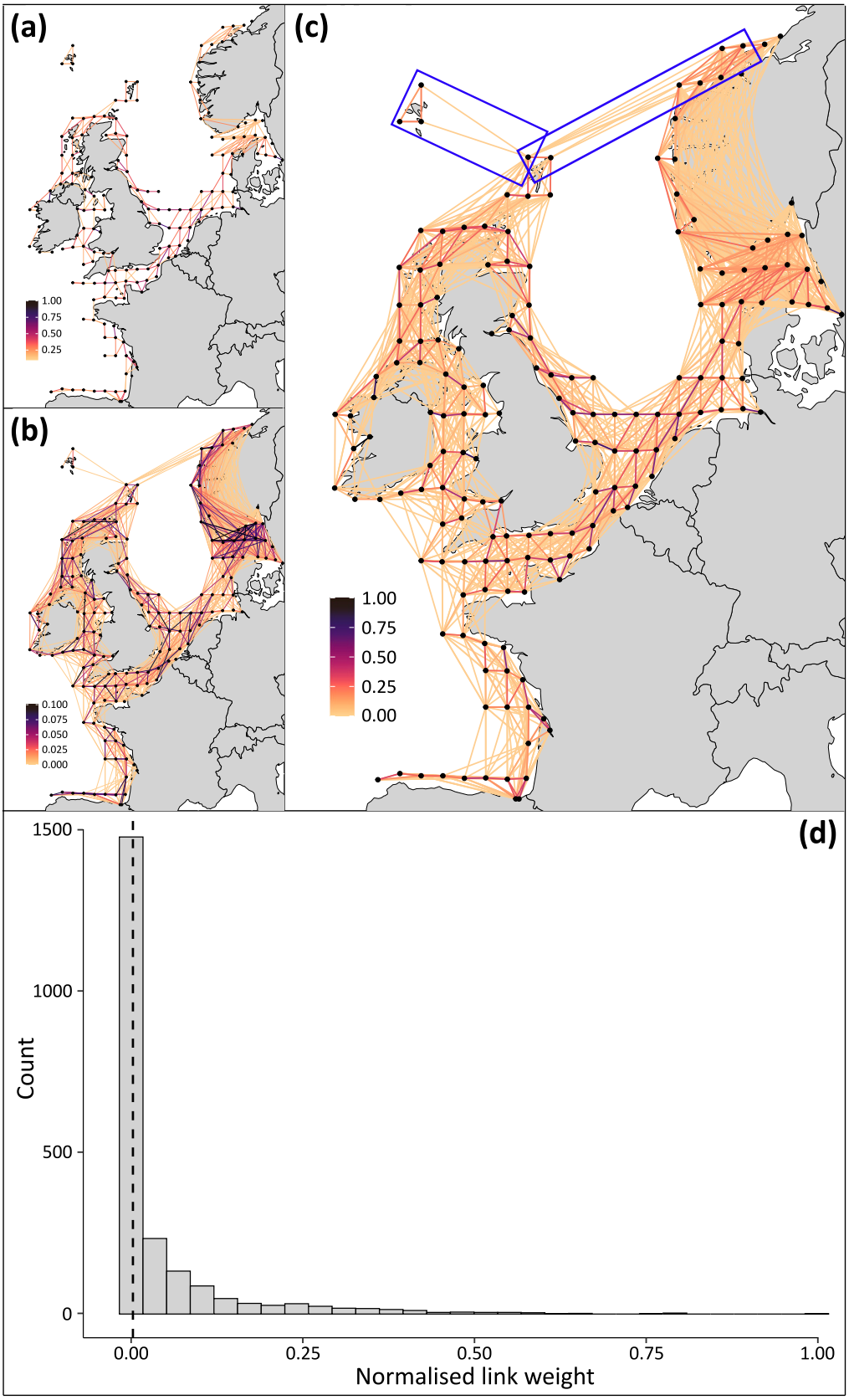


Fig. 3. Link weight of connections between nodes ($n = 172$), not including particle retention, in the averaged graph. In (a), (b) and (c) link weight values have been normalised between 0 and 1 to aid interpretation. Colour represents the strength of the connection. Note the difference in scale between a, b and c. (a) Links with a weight ≥ 0.1. (b) Links with a weight of <0.1. (c) All links present in the averaged graph. Blue boxes in (c) indicate incidences of rare long-distance dispersal. (d) Histogram of normalised link weight from the averaged graph. Line shows the median value of normalised link weight (0.003).

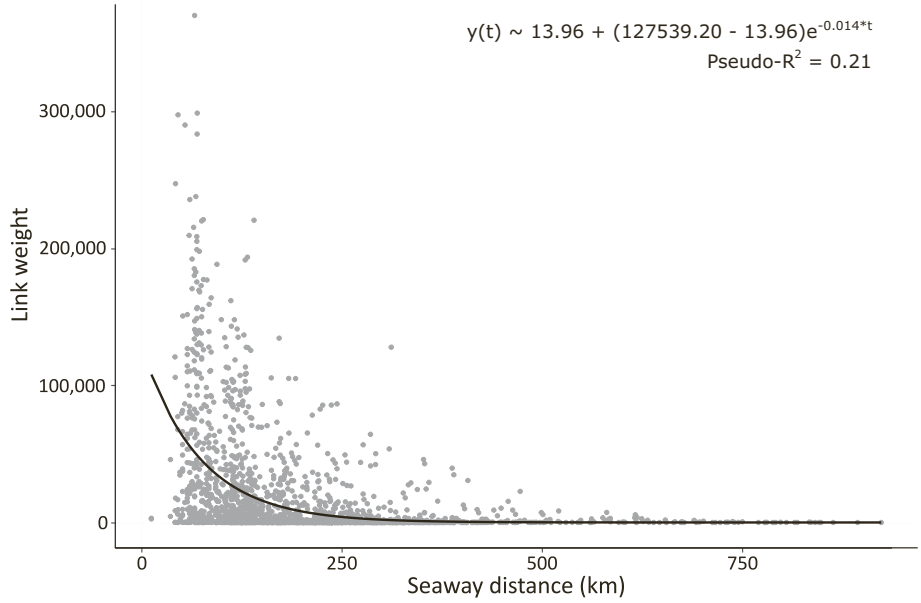


Fig. 4. The relationship between link weight from the averaged graph and seaway distance between nodes (km), excluding particle retention within the source node. Each point in grey represents a link between a pair of nodes. Line shows the result of statistically fitting an exponential decay curve to the data. The equation of the line is shown with model coefficients, where t is the seaway distance and y is link weight, alongside the pseudo-R^2 value.

particle retention is a function of the resolution of the habitat grid (one grid cell = 5217–8991 km^2).

3.2. Which populations contributed most strongly to network connectivity?

Nodes of high out-degree (i.e., that act as a source of particles to numerous locations) tended to also be of high in-degree (i.e., represent the final location of particles from numerous locations), with an increase of around 0.5 in in-degree with every one unit increase in out-degree ($t_{1, 170} = 8.971$, $p < 0.001$, $R^2_{adj} = 0.32$; Fig. 5). Nodes with the greatest numbers of incoming and outgoing links, and therefore likely of high importance to network connectivity, were located off the coasts of southern Norway, Sweden and Denmark in the Skaggerak Strait and Kattegat Sea (Fig. 5b) – a region that also exhibited a high level of particle retention through time (Fig. 3a).

Pairwise comparisons of the out-degree and in-degree of nodes between years demonstrated a period of variation followed by temporal stability in line with the periods of growth and stability in the number of nodes contained within the network (Fig. 2a, Fig. 6). When the network was expanding (i.e., 2000–2002), the relationship between the out-degree of nodes from year pairs displayed interannual switching in correlation between years, suggesting the importance of nodes to connectivity by acting as a source of particles to multiple locations varied by year (Fig. 6, top left). After 2003, when the number of nodes within the domain became relatively stable (Fig. 2a), there were significant positive correlations between all years (i.e., 2003–2012), suggesting a high degree of temporal stability in the role of nodes as a source of particles (out-degree). A similar relationship was also seen for in-degree (Fig. 6, bottom right). Comparing between metrics (Fig. 6, bottom left) indicated that the out-degree and in-degree of nodes was similar between all year pairs after 2003, with generally weaker, but still significant, positive correlations.

3.3. Do dispersal patterns create distinct clusters of highly connected populations?

Thirteen clusters of highly connected nodes were identified in the averaged graph (Fig. 7), largely formed of groups of nodes proximal to one another, reinforcing the relationship between link weight and short dispersal distances (Fig. 4). In many cases, cluster group location was strongly related to oceanographic features of the domain. For example, nodes in the southern North Sea, the Bay of Biscay, and the western and eastern areas of the English Channel form distinct clusters (Fig. 7), suggesting high levels of particle exchange between nodes within each region but weak exchange between oceanographic areas. Cluster permeability was low and network modularity high (Fig. 7), indicating little particle exchange between clusters despite geographic proximity of nodes in some cases. In fact, particle exchange within clusters represented 93.7 % of all particle exchange, and just 605 links (26 %) occurred between clusters. This result was consistent when metrics were calculated for individual years (Fig. S4).

Baker's Gamma Index (BGI) remained consistently positive over time, albeit with some variation in the strength of correlations aligning with periods of network growth (2000−2002) and stability (2003−2012), indicating that node clusters did not significantly differ across years and therefore the strength of links between the same groups of nodes remained broadly consistent through time (Fig. 7). The greatest BGI value, and therefore the most similar clustering of nodes, was between 2009 and 2010 (Fig. S5), and the weakest BGI, and thus the least similar clustering of nodes, between 2000 and 2008 (Fig. S6). Again, these comparisons reflect periods of network growth and network stability respectively (Fig. 2a).

4. Discussion

Connectivity between populations within the ocean greatly influences the spatiotemporal dynamics of metapopulations and metacommunities (Gawarkiewicz et al., 2007; Baguette et al., 2013). Here, using a dynamic approach we demonstrate how multi-generational biophysical modelling, consideration of suitable habitat areas, and graph theory can be combined to characterise spatial and temporal patterns in the potential connectivity of range-expanding species. Using the non-native *M. gigas* as a model, our results revealed a capacity for rapid spread following introduction and the creation of a stable ecological network of dispersal pathways that underpins persistence should larva establish.

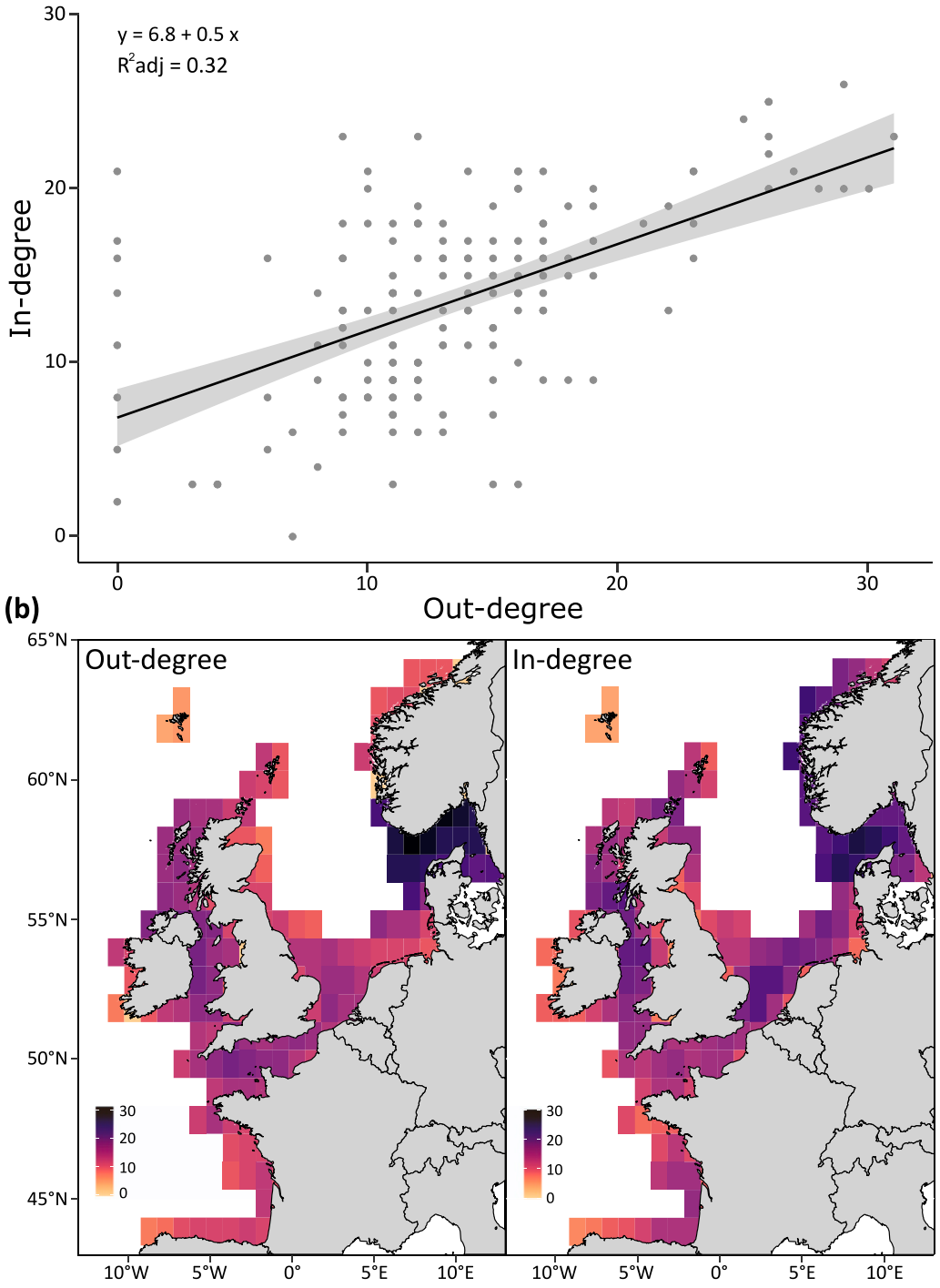


Fig. 5. Node out-degree and in-degree calculated from the averaged graph. (a) The relationship between out-degree and in-degree of nodes. Each point represents an individual node. Line shows the output of a linear model. Shaded area indicates the 95 % confidence interval. (b) Density map of node out-degree (left) and in-degree (right).

4.1. Emergent patterns in multi-generational connectivity

The Pacific oyster is a highly successful invader with far-reaching cascading ecosystem effects (Ruesink et al., 2005; Troost, 2010; Herbert et al., 2016), and the ability to expand rapidly over large spatial scales (Clubley et al., 2023). Indeed, in this study we demonstrated that, independent of larval supply and post-dispersal survivorship, in northwest Europe the seascape network of *M. gigas* populations has the potential to grow to maximum size within just four years. Connectivity within the network was high, indicated by a lack of isolated patches through time, albeit with the formation of distinct clusters of strongly connected populations between which particle exchange was minimal. This suggests that populations within the seascape are likely to be structured, but act as a single regional metapopulation rather than isolated local populations (Swearer et al., 2019; Cristiani et al., 2021). Whilst such a pattern might indicate an 'open system', where locations are connected over large spatial scales (Gawarkiewicz et al., 2007; Ward et al., 2023), the bulk of, and the strongest, connections occurred between locations ≤176.7 km distant from one another. Beyond this distance a significant decline in connectivity was observed.

Evidence of long-distance dispersal (sensu Kinlan et al., 2005) was present within the network but was typically much weaker and occurred

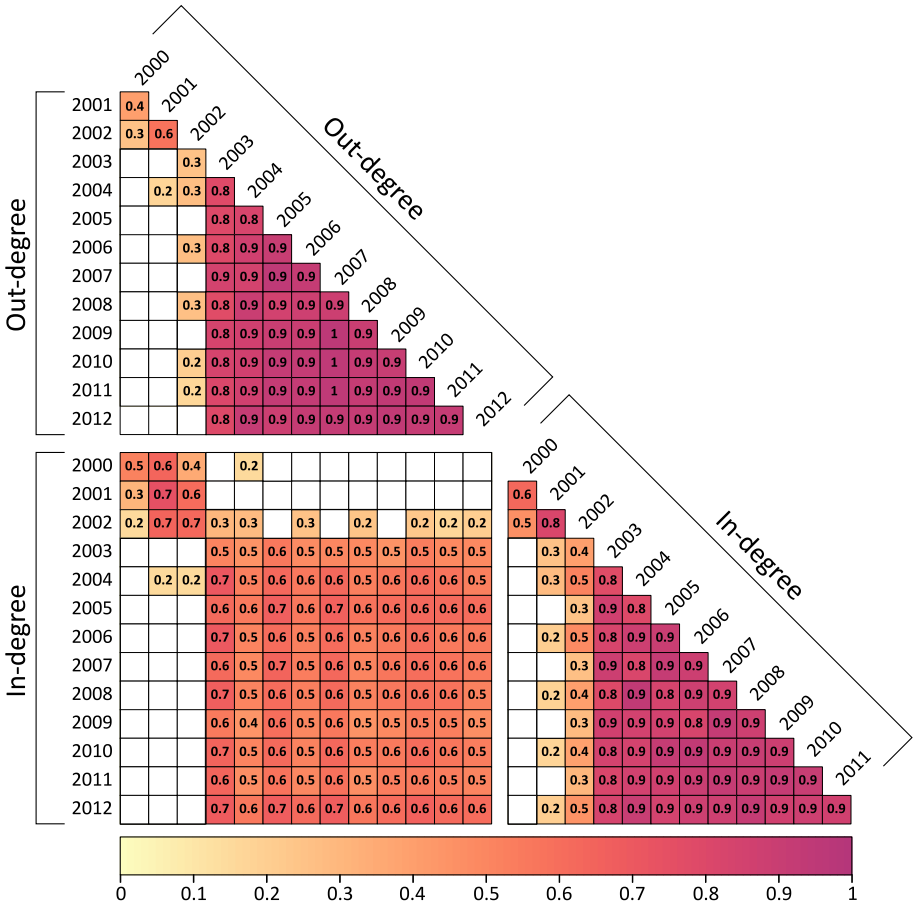


Fig. 6. A correlation matrix showing the temporal relationship between node out-degree and in-degree. Numbers represent Pearson's correlation coefficient, r, for comparisons of out-degree and in-degree between pairs of years. Correlation coefficients are only displayed for significant ($p < 0.05$) relationships. Colour indicates the strength of the correlation. All significant correlations were positive, and as such the scale runs from 0 to 1.

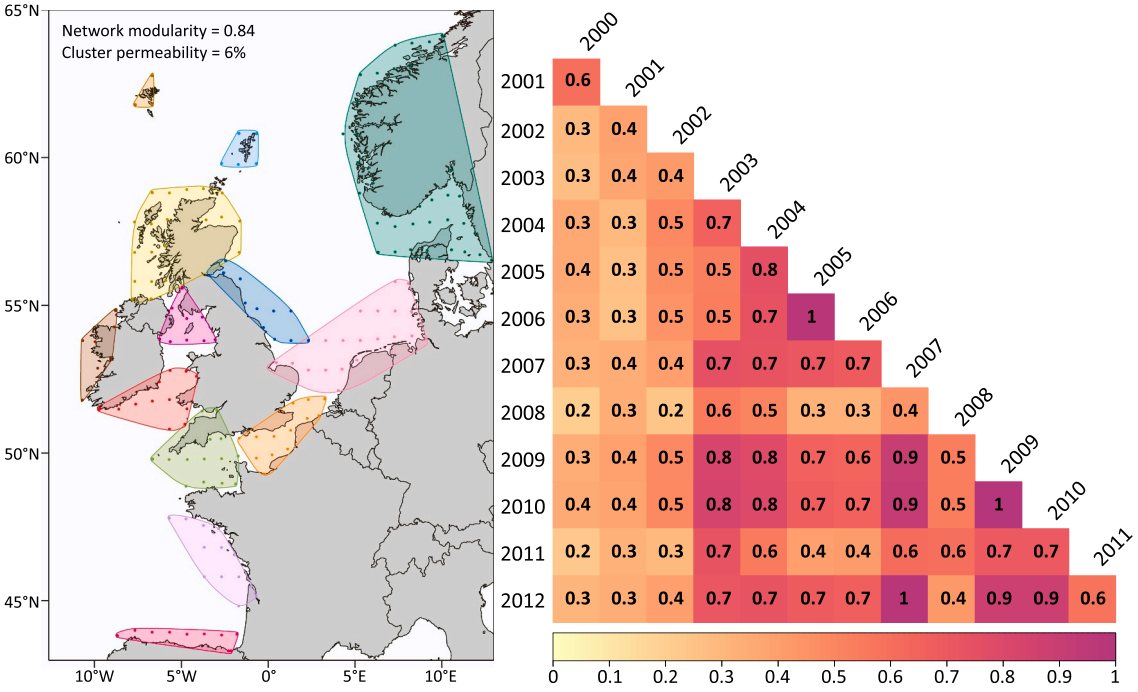


Fig. 7. (Left) Node clusters identified in the averaged graph. Points show node locations and are coloured according to the cluster (coloured polygons) to which they belong. (Right) A correlation matrix showing temporal differences in Baker's Gamma Index (BGI) of the outcome of node clustering for pairs of years. Numbers represent the BGI value. Colour indicates the strength of BGI. All values of BGI were positive, and as such the scale runs from 0 to 1.

more rarely than connections over shorter distances. Nevertheless, long-distance dispersal can be critical in range expansion, promoting genetic diversity and facilitating the spread of adaptations between distant populations (Manel et al., 2019). However, as clearly demonstrated here, the ecological importance of long-distance dispersal events may not be captured by single-generation dispersal models. Hydrological discontinuities or changes in hydrodynamic directionality between years can cause spatial variation in dispersal, and therefore changes in connectivity, within and among years (Ayata et al., 2010; Moritz et al., 2013). Whilst studies are now beginning to incorporate multi-generational dispersal into biophysical models to capture this variation (e.g., the role of populations as stepping-stones for long-distance dispersal; Boulanger et al., 2020), we are the first to examine how changes in patch occupancy associated with range expansion over time and the resultant changes in propagule pressure and dispersal trajectories affect the temporal stability of ecological networks across biogeographic space.

Within the network, we observed a weak positive relationship between the out-degree and in-degree of populations, suggesting several core populations within the network are likely particularly important for the maintenance of connectivity over time by acting as both a source and final location of larvae to and from multiple locations. The Skaggerak and Kattegat Sea areas, where hydrodynamic patterns are well-documented and remain relatively consistent through time (Rinde et al., 2016), were two such areas where locations maintained high out-degree and in-degree values through time. However, locations in these areas were grouped into a single regional cluster in most of the 13 years modelled, suggesting that whilst they are densely connected to one another, they are likely sparsely connected to populations in other clusters. It is therefore possible that whilst such locations appear as high contributors to larval source-sink dynamics, their contribution to broad-scale network connectivity is in fact, limited. It would be illuminating to study the fine-scale population genetics of *M. gigas* with highly variable genetic markers in future, considering our modelling work, to determine whether this is the case.

There was clear evidence of spatial structure across the network, with 13 discrete clusters of highly connected populations (nodes) identified. This, coupled with consistently high network modularity and low cluster permeability over time, would suggest strong larval exchange, and therefore likely rapid spread of *M. gigas* given successful establishment, between locations within the same cluster. Conversely, limited exchange between locations in different clusters is indicative of potential oceanographic dispersal barriers (Cristiani et al., 2021), particularly in those areas where adjacent nodes were consistently grouped into different clusters and therefore biogeographic separation is not attributable to distance at the scales we examined. Such boundaries may be a result of high levels of larval retention to the source node or environmentally-mediated gradients in relative competition with other species (Pringle et al., 2017). One example is on the south coast of England, where there was a clear divide in the clustering of locations between the eastern and western areas, possibly resulting from the numerous ocean gyres in these areas of the English Channel (Ménesguen and Gohin, 2006). Interestingly, the southern coast of England has also long been recognised as the range edge for many gastropods (Hawkins et al., 2013; Mieszkowska et al., 2005) and is intersected by Forbes' Line (sensu Firth et al., 2021); a biogeographic boundary denoting the 'general limit of southern type species' (Forbes, 1858). Furthermore, it is the location of a genetic discontinuity between northern and southern populations of *M. gigas* (Anglès d'Auriac et al., 2017). This would further suggest that whilst the prevalence of connections between locations in the network is suggestive of an 'open system', barriers to dispersal limit the degree of spread between some populations.

4.2. Applications to NNS management

Variance in connectivity has been shown to slow the spread of NNS (Morel-Journel et al., 2018), and therefore NNS management should always be conducted with multi-generational spread in mind. In our study, potential connectivity varied between years during the network growth phase (2000–2003), but once the number of nodes within the network became stable (2004), it remained temporally stable at all spatial scales considered. Such a transition from growth to stability in a network may represent a 'choke point' in time, after which management becomes much less effective and problematic (Essl et al., 2015). When applied to actively expanding NNS, the method of examining multi-generational connectivity presented here could be used as a forecasting tool to determine time frames for the implementation of effective NNS management (Locke and Hanson, 2009; Sandvik et al., 2022), or better understanding of the likely distributional changes in range-expanding species.

It is of course often the case that NNS are not discovered until rapid spread has already taken place, as was true for *M. gigas* (Troost, 2010; Humphreys et al., 2014). In such cases, the prioritisation of management and surveillance efforts to specific areas ('site-based prioritisation'; Riera et al., 2021) has been suggested as an effective tool, and network metrics have been utilised to this end (Ashander et al., 2022). In our network, the importance of populations to potential connectivity and the grouping of locations into highly connected clusters varied during growth but remained consistent once network size became stable. It follows, therefore, that those sites or groups of sites most important in management would appear to depend on the stage of invasion, and thus it is important that the use of network metrics in NNS management consider the temporal dynamics of location 'behaviour'.

The method of quantifying multi-generational connectivity presented here outlines a framework that can be employed to scale spatial resource allocation, both over broad spatial areas and timescales, to design optimal management solutions for NNS – especially opportune given the ever-increasing cost of NNS management (Jones et al., 2013). Application of this method to areas outside of NNS science, such as for the design of Marine Protected Areas (MPA, Jonsson et al., 2020; Ross et al., 2017), management of species expanding due to climate change (Firth et al., 2009), habitat restoration (Lipcius et al., 2008), greening-of-grey infrastructure (Dafforn, 2017; Firth et al., 2024), decommissioning of offshore oil and gas installations (Lemasson et al., 2022), or the management of threated species (García-Gómez et al., 2015), has high potential and we encourage evaluations of its use in these fields.

4.3. Modelling considerations

Quantifying the complex process of larval dispersal and the connections which it forms inevitably requires some degree of simplification due to the spatial and temporal scales of the dispersal process and the multiple biological and physical factors it involves (Treml et al., 2008; James et al., 2019). Whilst we aimed to characterise potential patterns in connectivity over broad spatial and temporal scales using *M. gigas* as a model species rather than species-specific connectivity patterns, outputs are nevertheless impacted by limited information on the larval development and behaviours of the species (Robins et al., 2017; Wood et al., 2021). Here, a paucity of information on the vertical distribution and behaviours of *M. gigas* larvae necessitated a passive approach to larval dispersal to maximise model output (as adopted by Álvarez-Noriega et al., 2020, Cristiani et al., 2021, David et al., 2022). We considered this to be in line with the precautionary principle of the Convention on Biological Diversity (2016), where in the case of NNS management overestimation of dispersal and spread is more desirable than underestimation, and justified given the likely error that would occur from the parameterisation of one or more inaccurate behaviours (Bode et al., 2019; Leis, 2020; James et al., 2023). However, to improve the realism of future use of these methods we recommend that 3D hydrodynamics are used, and that species' larval behaviours are incorporated where the accurate information exists in order to do so.

In any modelling study, practical constraints of computational

feasibility dictate a trade-off between hydrodynamic model resolution, which can affect how well coastal dynamics are resolved and consequently connectivity measures (e.g., particle retention Ward et al., 2023), and model extent. Here, we used AMM7 (7 km resolution), which provides sufficient resolution to resolve regional scale oceanographic dynamics. Eight suitable polygons within the habitat grid remained 'uncolonised' at the end of the 13-year period modelled (Fig. S7). This was likely due to both their locations in fjord and estuary areas, where hydrodynamic patterns are finely resolved, and to the surface-level transport of particles, as in these areas inflow typically occurs in deep water (Arneborg et al., 2004; Morgan et al., 2014). Regardless, overall patterns in broad-scale connectivity of the network are unlikely to be affected by their omission.

Finally, the habitat grid used to define connectivity between populations was anisotropic, with grid cells measuring ~111 km latitudinally and between 47 and 81 km longitudinally (dependent on latitude). Consequently, connectivity between nodes (measured from grid centroid to grid centroid) was non-mechanistically constrained to incremental increases in distance matching the resolution of the habitat grid, potentially resulting in quantization error. However, preliminary analysis revealed that when connectivity was calculated using an isotropic grid (where longitudinal and latitudinal distance for each grid cell is equal), the degree of error between the number of particles classed as retained using the original anisotropic grid and the isotropic grid across the 13 years modelled is just 0.8 % (Table S2). As such, the anisotropic nature of the habitat grid is unlikely to have affected broad-scale patterns in connectivity.

Using the framework we present here, measures of connectivity (e.g. node degree, cluster size) are naturally dependent on the resolution of the grid used. Future use of this framework for characterising multi-generational patterns in connectivity of populations should base the resolution of grid cells on the aims of the study, the size of the study domain and the management priorities of the focal species/area.

4.4. Conclusions

Population connectivity is inherently biophysical and fundamental to metapopulation and metacommunity dynamics and structure, genetic diversity and the resilience of populations to disturbance and global change (Cowen et al., 2007; Ewers-Saucedo et al., 2016). Given rates of environmental change in the Anthropocene (Wolkovich et al., 2014; He and Silliman, 2019), improved understanding of the role of larval dispersal in connectivity across biogeographic scales has become critical to our efforts to manage invasions, mitigate biodiversity loss and predict change in global species diversity and distribution. Whilst the importance of considering multi-generational dispersal to overall patterns of connectivity has long been recognised (Hogan et al., 2012; Boulanger et al., 2020), to our knowledge, no previous study has developed a dynamic approach for predicting species spread that considers range expansion across time. Our approach uses three key tools: biophysical modelling, consideration of environmental variables and graph network theory to characterise and define ecological network structure, functioning and stability. Utilising each tool in an overarching framework to examine multi-generational dispersal provides an opportunity to quantify connectivity over broad temporal scales and has promising applications not only to the management of non-native species, but in a wide variety of research fields.

CRediT authorship contribution statement

Charlotte H. Clubley: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tiago A.M. Silva:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Louisa E. Wood:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Louise B. Firth:** Writing – review & editing, Supervision, Methodology, Conceptualization. **David T. Bilton:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Enda O'Dea:** Writing – review & editing, Resources. **Antony M. Knights:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

Authors declare no known competing interests.

Data availability

The code used to generate the data and carry out the analysis used in the manuscript are available at https://github.com/cclubley/Multi-generational-dispersal.

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Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175762.

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