Spatial patterns of within-stock connectivity provide novel insights for fisheries management

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While concepts of connectivity are increasingly used in determining locations for marine protected areas, they are much less applied in the management of fish stocks, which are assumed to be well-mixed populations. However, due to seascape structure and often asymmetrical dispersal, the stocks of many species are unlikely to be well-mixed and there is potential to enhance management by utilising emerging ecological modelling approaches that incorporate functional connectivity. Here we apply a new model, MerMADE, that couples biophysical modelling of dispersal with spatial population demography, to predict within-stock patterns of connectivity of sandeels in the North Sea. By deriving origin- and destination-centrality measures we highlight a set of key origin sites within the area occupied by the stock that contribute immigrants to many other sites and also identify patches that are particularly isolated, unlikely to receive immigrants from elsewhere. We show that the connectivity characteristics of the stock has a strong impact on how rapidly it recovers following a major harvesting event that leads to a patch depletion. Furthermore, the recovery of a local population will depend on the demographic status of the sites from which it can obtain immigrants. Thus, sites that provide strong out-centrality (especially if they themselves have weak in-centrality) and sites that are especially isolated should be harvested less heavily. To reduce the potential for local or regional stock collapse, models incorporating both biophysical dispersal and local demography are needed to support spatially-explicit management of commercial marine species.

Keywords: functional connectivity, depletion events, marine dispersal, demography, MerMADE, sandeels

1 INTRODUCTION

Across terrestrial, freshwater and marine environments, work on ecological connectivity has typically focused on what are termed structural (Moilanen & Nieminen 2002, Bender et al. 2003) and functional estimates (Treml et al. 2008, Cowen & Sponaugle 2009, Huret et al. 2010) but on their own these do not indicate how effective connectivity will be for any particular objective. While structural connectivity provides measures and metrics for the spatial pattern of suitable habitat in the environment, functional connectivity considers also how individuals move within the environment, taking into account species-specific traits (Pulliam 1988, Turgeon et al. 2010)

In many marine species where dispersal is largely limited to a pelagic larval phase, the combination of an individual’s dispersal traits, its location and the surrounding hydrodynamics will determine its potential movement trajectories, probability of survival and which habitat patches it might successfully arrive at (Burgess et al. 2014, Bode et al. 2018, Bashevkin et al. 2020). However, patch-level connectivity characteristics also depend on spatial demography, as large high-quality patches generally provide a greater number of emigrants than small poor-quality patches (Cabral et al. 2016). The relative importance of patches to functional connectivity within a patchily structured metapopulation is therefore determined by a combination of dispersal and demography (Hanski 1998, Hastings & Botsford 2006, Botsford et al. 2019).

Management of marine species often targets maintaining biodiversity and sustainable harvest of fisheries (Hastings & Botsford 2003), sometimes with the aim of measuring effects such as spillover from marine protected areas (MPAs) as metrics of success (Burgess et al. 2014). Generally speaking, connectivity (structural or functional) between MPAs is not taken into account when designing management strategies, instead focusing on single populations as closed systems (Hastings & Botsford 2006, Leis 2007). This sometimes leads to management measures being ineffective because the spatial configuration does not support the connectivity dependencies of the network of populations (Sale et al. 2005). The need for more dynamic approaches to management to future-proof for species' range shifts due to climate change means temporal as well as spatial connectivity dynamics need to be incorporated into predictive mechanistic models (Travis et al. 2013, Zurell et al. 2022). In terrestrial studies there has been some recent progress in this direction with the development of models that incorporate connectivity modelling with demographic modelling, thus enabling the population level outcomes of managing the landscape for connectivity to be predicted (Bocedi et al. 2014, 2021).

With the exception of identifying spatial restrictions, such as marine protected areas (MPAs), spatial ecology has played a minor role in the scientific advice underpinning fisheries management. Advice is typically focussed on estimating sustainable levels of catch in a geographically defined stock, that is assumed to be a discrete group with the same vital rates and little mixing with adjacent stocks (Gulland 1983, Stephenson 2002). However, failure to account for spatial structure in fisheries management may lead to unexpected risks of overexploitation (Cadrin & Secor 2009, Ying et al. 2011, Cadrin 2020) and has been linked to the loss of local spawning components (Smedbol & Stephenson 2001, Ames 2004). Site attachment and a low level of intra-stock mixing may affect the vulnerability of patches to local depletion (Wright et al. 2019). Spatial restrictions on fishing have been used to mitigate such a risk (Halliday 1988, Pickett et al. 2004) and conservation management of rare fish species has focussed on how networks of marine protected areas can be used to protect key sources of recruits and promote connectivity to benefit population persistence

(Burgess et al. 2014). We explore the potential benefits of considering spatial ecology and functional connectivity in this context, using a sandeel stock in the North Sea as our case study.

The lesser sandeel, *Ammodytes marinus,* is prey to many piscivorous fish, seabirds and marine mammals and the main sandeel species in one of the largest fisheries in the North Sea (Sparholt 1990, Engelhard et al. 2014, Wanless et al. 2018, Wilson & Hammond 2019, ICES 2022a). It is also a species with a strong site attachment following settlement as a juvenile, linked to the individuals' dependence on coarse sand into which they burrow at night and during periods of low temperature and plankton production (Wright et al. 2000, Henriksen et al. 2021). The main phase of dispersal occurs after the demersal eggs hatch (Régnier et al. 2018) and before the juveniles settle, with the planktonic larvae being dispersed by currents (Proctor et al. 1998, Christensen et al. 2007, Wright et al. 2019). *Ammodytes marinus* (hereafter referred to as sandeels) tend to remain within 10 km of where they settle, while feeding in spring and summer on zooplankton (van der Kooij et al. 2008, Wright et al. 2019).

Concern that a single total allowable catch for the North Sea did not account for important regional differences in sandeel population dynamics led to a review of stock structure in 2010 (ICES 2010). This review used information on the distribution of spawning (Proctor et al. 1998) and fishing grounds (Jensen et al. 2011), hereafter referred to as patches for consistency, together with estimates of larval mixing to divide the North Sea into seven sandeel stocks in distinct geographical areas where average annual exchange across stock boundaries was <5% (Christensen et al. 2008). The geographical boundaries of most stocks were revised slightly in 2016 to account for spatial differences in fishing pressure and data collection among fishing nations (ICES 2017). Regional variation in growth and maturity across the North Sea appeared to be largely consistent with the stock delineations (Bergstad et al. 2001, Boulcott et al. 2007, Rindorf et al. 2016). However, substantial differences in the level of recruitment to patches are known to occur within stock areas (Wright 1996, Rindorf et al. 2019) and differences in the size and age composition of sandeels among patches suggest local variation in mortality within these stocks (Jensen et al. 2011). Consequently, it may be difficult to identify local depletion at the scale of patches from stock level metrics, and this could be relevant to sandeel availability to nearby predators, as well as to local and regional stock level persistence.

Concerns about the risk of local depletion of sandeel patches have been raised previously (Wright 1996, Johannessen & Johnsen 2015), and linked to the concentration of fishing in areas where sandeels regularly aggregate to feed on plankton (Mackinson & Van der Kooij 2006, Jensen et al. 2011). Due to their aggregating behaviour, sandeel schools can be repeatedly targeted and fishing fleets have the capacity to deplete local densities to below detectable levels within weeks (Johannessen & Johnsen 2015). The reliance of some breeding seabirds on nearby sandeel abundance has led to calls for predator requirements to be considered in the management of the sandeel fishery (Monaghan 1992, Hill et al. 2020) . In 2000, the northeast UK sandeel closure (Figure 1A) (STECF 2007) was established following a sandeel fishery that developed off the Scottish east coast in the early 1990s that was linked to poor seabird breeding success at adjacent colonies (Rindorf et al. 2000), together with evidence that their foraging area was part of a separate population from other North Sea areas (Wright et al. 1998). The evidence for a separate population would later result in the definition of the northern and central North Sea stock (SA4; ICES, 2010). Concern over local depletion also led to a Norwegian closed area approach in their stock area, SA3r, where temporary closures are rotated to promote recovery of depleted patches (Johannessen & Johnsen 2015).

In this case study, we explore how functional connectivity and local demography affect the recovery potential of patches and population resilience in sandeels. We focus on the SA4 stock, where fishing is partly restricted by the northeast UK area closure, and investigate the potential effect of patch depletion. We use the individual-based modelling framework MerMADE (R. Allgayer et al. preprint; doi:10.1101/2022.11.15.51661) to produce an estimate of realised connectivity that takes species-specific dispersal traits and decision-making into account as well as the local hydrodynamics which produce asymmetrical connectivity patterns. We then employ network theory methods (Treml et al. 2008, Fox & Bellwood 2014, Jacoby & Freeman 2016, Magris et al. 2018), using patches as nodes and movement of successful dispersers as weighted edges, to calculate the in- and out-degree centrality measures – the number of patches supplying dispersers to and being supplied by a particular patch, respectively – to identify both important and vulnerable patches within the system (Jacoby & Freeman 2016). Such network theory methods are useful in representing dispersal potential to identify areas that act as key sources of immigrants (e.g., Magris et al. 2018) and have been used in the marine context before (Treml et al. 2008, Fox & Bellwood 2014). The fact that MerMADE incorporates both dispersal and population dynamics in its simulations allowed us to determine how well-mixed the stock assessment area is and investigate the effects of local patch depletion events, recovery potential, and overall population viability.

2 MATERIALS & METHODS

2.1 Software

This study used the individual-based, coupled biophysical modelling framework MerMADE (R. Allgayer et al. preprint; doi:10.1101/2022.11.15.51661) which incorporates hydrodynamic data with population dynamics, demography and evolutionary functionality to predict dispersal in marine environments. This makes our model uniquely suited to asking how dispersal and population dynamics are linked for marine species. Contemporary models for aquatic environments tend to focus solely on the dispersal phase and do not track impacts over generations (i.e. CMS (Paris et al. 2013), Icthyop (Lett et al. 2008)). Terrestrial counterparts, on the other hand, though more inclusive where population dynamics and evolution are concerned (i.e. RangeShifter (Bocedi et al. 2021)), lack the 3D, hydrodynamically forced environment.

MerMADE operates in a spatially explicit 3D environment, factoring bathymetry and the external forcing of hydrodynamics into the movement potential of individuals. The flexibility this tool offers in terms of modelling changes in behaviour during dispersal as well as regulating life history parameters before and after the dispersal phase, makes it especially applicable to a species as complex as sandeel. MerMADE provides a dynamic tool which allows patterns of realised connectivity to emerge from the interaction between a species and the seascape it inhabits, making it highly suitable for investigating questions of population persistence and disturbance response. In this section, we present parameter values taken from the literature for MerMADE simulations. We do not go into detail about calculations or functionality. Further model details are given in Allgayer et al 2022 and in its user manual, which is available along with the software here: https://github.com/MerMADEsoftware.

2.2 Seascape

For this paper we treat the wider North Sea stock of sandeels as a metapopulation, made up of populations–represented by the stock assessment areas– which are in turn made up of subpopulations, here illustrated as patches. We assume that reproduction takes place on the scale of a patch, consistent with observations of newly hatched larvae (Proctor et al. 1998) and dispersal is between patches within a stock assessment area, but exchange of dispersers between stock assessment areas is limited. This assumption has been made as the fishery is managed as discrete stocks, contained within delineated assessment areas. This approach suits definitions in the field of metapopulation theory (Hanski 2001, Sale & Kritzer 2006, Carson et al. 2011, Burgess et al. 2014). Hereafter, the ‘population’ refers to the cumulative number of individuals within SA4, and a ‘subpopulation’ refers to the numbers in a single patch.

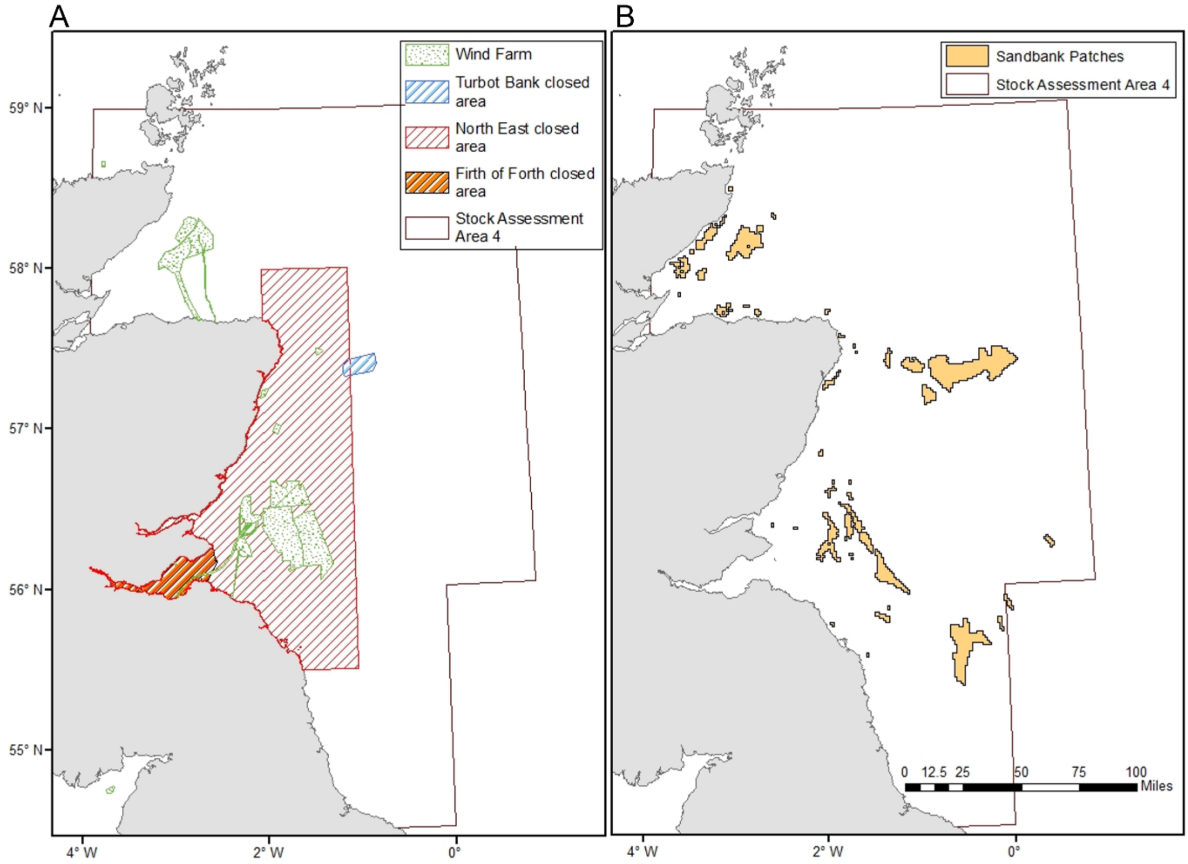

Figure 1: A) Closed areas where sandeels are not commercially fished and locations of operational or recently approved offshore windfarms within Stock Assessment Area 4 (SA4) of the North Sea. B) Sandbank patches within SA4, signifying sandeel sites used in this study.

Sandeels, as the name suggests, depend on sandy areas, so we ran MerMADE as a patch-based model, using sandbanks to represent distinct patches. Base habitat type maps were produced from a combination of fishing data-derived patches (Jensen et al. 2011) and the resulting output from a sandeel-specific species distribution model by Langton et al. (2021). This resulted in 43 patches within SA4 (Figure 1B). The resolution of the structured spatial grid was 1.5 km in the horizontal directions and 10 m in the vertical direction.

All sandbank patches identified in these datasets were considered to be suitable and to have the same carrying capacity of 48 individuals m^{-2} (Langton et al. 2021). In reality, carrying capacity is spatially heterogeneous, with higher densities located on sandbanks made up of coarse sand with low silt content. However, MerMADE does not have the functionality to integrate this information at present and the resolution of habitat data we acquired would not have allowed us to specify habitat quality to that degree, therefore we had to assume homogeneous habitat quality and assign the same carrying capacity for all patches (48 individuals m^{-2}, taken from the predicted density given presence with no silt and high sand content in Langton et al. 2021).

Sandeels are incredibly numerous, with the latest population estimate in SA4 being between 16.9 billion and 127.8 billion individuals (ICES 2022b). In order to maximise computational efficiency, we utilised “super-individuals”, where one modelled super-individual represented 21 million individuals in situ. This number is biologically arbitrary but simply represented the ratio that made these simulations computationally feasible. This scaling of individuals required adapting the carrying capacity of suitable habitat to .022 super-individuals ha^{-1}. With the resolution of 1.5 km, this produced a starting population of approximately 3000 super-individuals in SA4. We acknowledge that this is a significant simplification and may invite demographic stochasticity when demographic probabilities are applied to a super-individual (i.e., mortality, reproduction, etc). We return to this important consideration in the discussion. Henceforth, we use ‘individual’ to refer to one of the super-individuals. The difficulty that the ratio of settled individuals to dispersing offspring poses is a computational one and further development of the use of super-individuals is needed to create a better balance between computational efficiency and biological realism. This discrepancy is no doubt the underlying issue that leads to very few coupled biophysical models representing both demography and dispersal.

Hydrodynamic data in the form of *u*, *v* and *w* velocity vectors (eastward, northward and upward, respectively, measured in ms^{-1}) were sourced from the Scottish Shelf Waters Reanalysis Service (SSW-RS) (Barton et al. 2021), based on the Scottish Shelf Model developed by Marine Scotland Science. Every other year of the 50-year simulation, MerMADE read in new hydrodynamic data taken from the time period 2004-2014. Though not every year was included, because the differences in hydrodynamics in the space of a single year are minimal, we still captured larger-scale changes over a decade, which we then cycled for the remainder of the 50-year simulation. We acknowledge that this makes assumptions about the predictability and variability of hydrodynamics in this area, but as interannual differences in the connectivity matrix were small, we deemed this a reasonable compromise for increased computational efficiency in not reading in new data every yearly timestep of the model. The month of March was chosen as sandeel eggs in SA4 hatch between February and May, usually with a peak in March (Régnier et al. 2017), and therefore the hydrodynamics would largely match what the larvae experience in their first few weeks of dispersal.

2.3 Parameterising the model

We ran the MerMADE model treating sandeels as a sexually reproducing, stage-structured species that undergoes dispersal in the larval phase and then settles permanently, consistent with field data (Wright et al. 2019). As sandeels are single batch spawners (Boulcott & Wright 2008), we allowed one reproductive event per year. Reproduction was modelled similarly to broadcast spawning in that allocation of mates was randomly sampled with replacement. This means each male was equally likely to be paired with each female and a male could mate more than once.

Since sandeel eggs hatch in the same year that they are spawned, we combined the egg stage and the dispersing larval stage into a single Stage 0 for the Leslie matrix governing population dynamics in MerMADE (Table 1). The remaining stages we assigned based on fecundity and age: a settled juvenile stage that is not yet reproductively mature, and Adult 1, Adult 2 and Adult 3 stages with fecundities of 2477, 3036, and 8065 eggs, respectively (Boulcott & Wright 2011).

Table 1: Transition matrix for sandeels with reduced fecundity to reflect mortality at egg-stage. Note that the 97% dispersal mortality is not included in this matrix as it is applied per-step during dispersal.

	Stage 0	Settled juvenile	Adult Stage 1	Adult Stage 2	Adult Stage 3
Stage 0	0	0	74.31	91.08	241.95
Settled juvenile	1	0.1323	0	0	0
Adult Stage 1	0	0.4977	0.0126	0	0
Adult Stage 2	0	0	0.6174	0	0
Adult Stage 3	0	0	0	0.63	0.63

However, since the egg stage is included in Stage 0, we applied an estimated survival rate of 3% to the eggs before hatching, reducing the fecundities to 74.31, 91.08 and 241.95, respectively. This 3% value was the value needed to explain the decrease between total stock fecundity and stock numbers of a year-class, given the estimate of larval mortality, using fecundity at length from Boulcott and Wright (2011), maturity at length and age from (Boulcott et al. 2007) and numbers at age from the ICES stock assessment. At the time of hatching, larvae are 5.3mm in length (Régnier et al. 2018). Natural annual survival probability was assumed to be equal for all settled stages at 0.63 (ICES 2017) until a maximum age of 10 years was reached and individuals automatically died.

MerMADE introduces stochasticity into the model by sampling individual fecundity from a Poisson distribution using these calculated fecundities as means. Also, negative density-dependence in at least one vital rate has to be incorporated such that subpopulations stabilise in size (i.e. don't grow exponentially and overshoot their carrying capacity), though they may still decrease in density to the point of extinction. There is evidence from the North Sea for density-dependence in both recruitment(Arnott & Ruxton 2002) and in survival (Rindorf et al. 2019) and this may be context dependent as well as vary temporally from year to year. Here, we incorporate negative density-dependence in fecundity and settlement probability of dispersers, which is sufficient to enable us to investigate the effect of local patch depletions and the potential for local recovery following those events. Allgayer et al. 2022 provide further details on density dependence. Survival rates are also treated as probabilities to mimic the stochastic nature of these parameters.

The planktonic Stage 0 is the only stage allowed to undergo dispersal. During dispersal, individuals employ a hybrid dispersal technique: a pre-competent, passive larval stage before reaching 10mm in length, after which they undergo diel vertical migration (DVM) until they develop to be 26mm in size (Jensen et al. 2003). At this point, they are considered competent pelagic juveniles and they are able to actively seek out suitable habitat for settlement, which they are able to detect from a distance of 4.5km away (see Table A.1 for DVM details). For simplicity's sake, we continue referring to individuals as larvae even after competency is reached. Individuals grow according to a modified Gompertz growth model (T. Régnier unpubl. data, see Appendix Table 1 for parameter details). When the larvae have reached the required size at the end of the passive stage, they cease migrating vertically and begin to respond to their environment with a swimming speed proportional to their body size (in this case 1 body length s^{-1}), which allows more depth and spatial control over their dispersal. Their caudal, dorsal and anal fins are, by this point, fully developed (Jensen et al. 2003). The influence of the current on larval behaviour reduces as they continue to grow, and their swimming ability increases. Orientation may therefore vary from the direction of the current, allowing more freedom to explore the seabed for suitable sandbanks for settlement. If suitable habitat is detected, travel becomes biased towards that direction, though the force of the current continues to act on them.

Survival rates for pelagically dispersing larvae are commonly accepted to be quite low, and we assumed a dispersal-related mortality of 0.042 day^{-1} (Régnier et al. 2017), which, over the course of a 70-day Pelagic Larval Duration (PLD) would equate to 97% mortality. This is applied as a per-step mortality rate during the transfer phase of dispersal as it by proxy captures factors such as predation in transit. For a full list of parameter values, refer to Table A.1 in the Appendix.

2.4 Local Patch Depletion

Using these input parameters, we ran the first set of simulations with the purpose of establishing a connectivity matrix of all the patches present within our study area. This simulation ran for 50 years, and we constructed a connectivity matrix of the cumulative transport of juveniles across that timeframe. We ran 20 replicates in order to establish a mean value, accounting for the stochasticity inherent in the MerMADE framework.

Network analyses identified critical vertices with a high out-degree centrality, which measures how many patches each patch supplies with *outgoing* successfully settling juveniles, and high in-degree centrality, measuring the number of patches that each patch is receiving juveniles from. We used these to identify important origin and destination patches, respectively. Therefore, for the remainder of this paper, we will refer to these centralities as origin- and destination-centrality measures to avoid confusion. These patches were then used in the next stage to assess the potential impact of local patch depletion events. We investigate the relationship between patch size, origin- and destination-centrality, and effect on overall population stability.

In this initial control simulation, we allowed the patch depletion simulations to have a 20-year burn-in period to let dynamics settle before introducing disturbance. This allowed us to identify the effects of depletion more easily at various patches and across the system.

In patch depletion simulations, the subpopulation at the chosen patch effectively experienced 95% mortality, leaving the patch at only 5% of its previous density before the next reproductive event. This difference corresponded to the range in density found in dredge-based estimates for a range of grounds within SA4 (ICES 2022b), and so was assumed to reflect the potential change possible in a heavily harvested patch. This patch was then allowed to be replenished by incoming juveniles during the next dispersal event and did not experience local depletion again for the rest of the 50-year model run. This method was repeated for each patch identified in the baseline simulation and we compared the time needed to recover, impact on overall population size, as well as patch-level subpopulation sizes. With these simulations, we wanted to investigate the required time for targeted patch recovery and stabilisation of larval connectivity patterns and overall population size.

To investigate the effect of repeated local depletion, we introduced depletion events once every other year for the duration of the 50-year simulation. Again, we looked at patch viability and successful disperser percentages, comparing the extent of the knock-on effects of eliminating various key patches.

3 RESULTS

Individual movement tracks (Figure 2) demonstrated the effects that local hydrodynamics will have on connectivity patterns. The currents in the northwest corner of the study area often seem to transport individuals cyclically, keeping dispersers settling in patches that are relatively close-by geographically. This most likely ensures high connectivity between those patches and high settlement success for dispersers originating from those patches. Individuals dispersing from the most eastern of these patches are also transported southwards along the coast, connecting this otherwise fairly isolated cluster with the rest of the system within SA4.

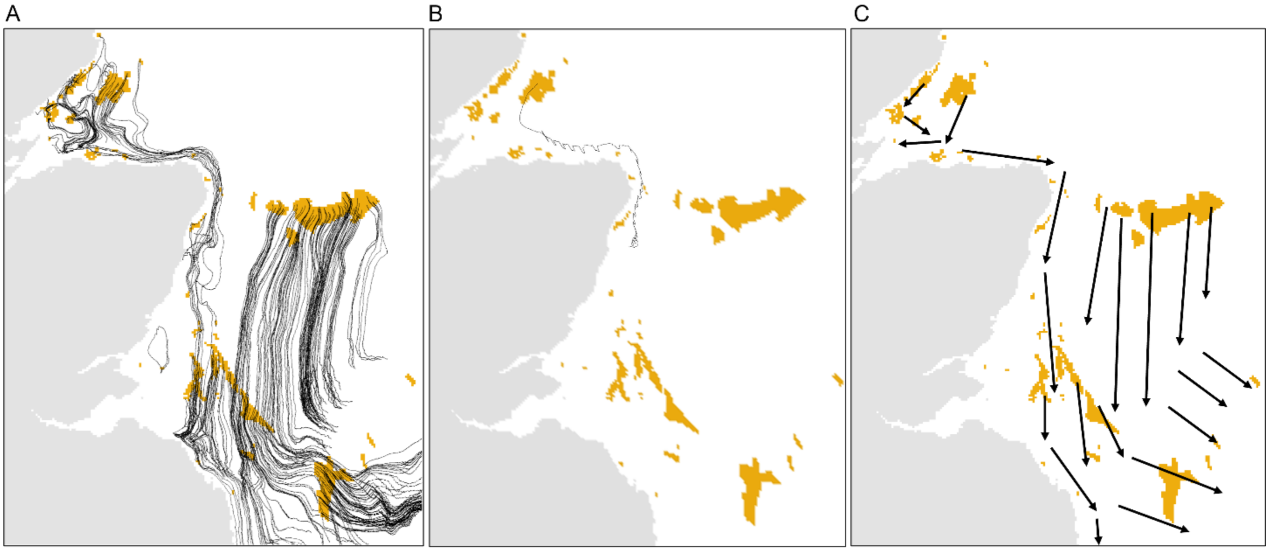

Figure 2: Individual movement tracks indicate where individuals are likely to end up after undergoing a single dispersal event, depending on their natal patch. A) Tracks of 10% of dispersers (so as not to obscure patterns with sheer volume of tracks). B) Example of a single track for detailed visualisation of behavioural changes during dispersal (passive to diel vertical migration to active). C) General directionality of dispersers with arrows indicating direction of movement.

Prevailing currents move southwards along the coast before turning east at the bottom of our study seascape, transporting individuals outside of our domain of SA4. The largest patch on our map, Patch 26, contributes many dispersers to this south- and eastwards movement, but is not well situated for receiving many individuals from elsewhere within SA4. The south-western patches, in contrast, conveniently catch dispersing individuals, making them important destination patches. These highways of movement to the south and east indicate where a large proportion of individuals may be lost from SA4, contributing instead to SA1r (central and southern North Sea, Dogger Bank), which is where most of the fishery is located. The tracks show that where individuals start their journey from within even a single patch matters. It is also important to note that clusters of patches which might be predicted to have high connectivity due to geographical proximity, such as those in the south-western corner of our seascape, would not be available to individuals dispersing from those patches due to the prolonged passive stage of dispersal before competency. Individuals are not physiologically capable of taking advantage of that suitable habitat.

The movements of all successful dispersers were captured in a connectivity matrix, a convenient format to perform network theory analyses on the system. Each cell within the connectivity matrix contains the mean number of individuals transported from one patch to another per year, across the 20 replicates. Before performing any analysis, however, we can already observe spatial patterns in connectivity by visualising the connectivity matrix directly (Figure 3). It is clear that areas such as the Moray Firth cluster of patches (Figure 1B) are not only well connected among themselves, but also contribute greatly to downstream patches, as many arrows originate there and connect the Moray Firth cluster with the Forth of Firth cluster, for example. Using this representation, it is immediately clear that certain patches neither gain dispersers from other patches within SA4 nor significantly contribute recruits to the population, such as patches 0, 2,6,10, 13, 25, 27 and 41. The more isolated patches such as Turbot Bank (26) and its neighbours also don’t receive any input from upstream patches (see Table A.2 for full list of names corresponding to patches). This figure clearly shows that while some areas are well connected, a large portion of SA4 is not well connected, inferring that the stock assessment area can’t be considered to be broadly well-mixed.

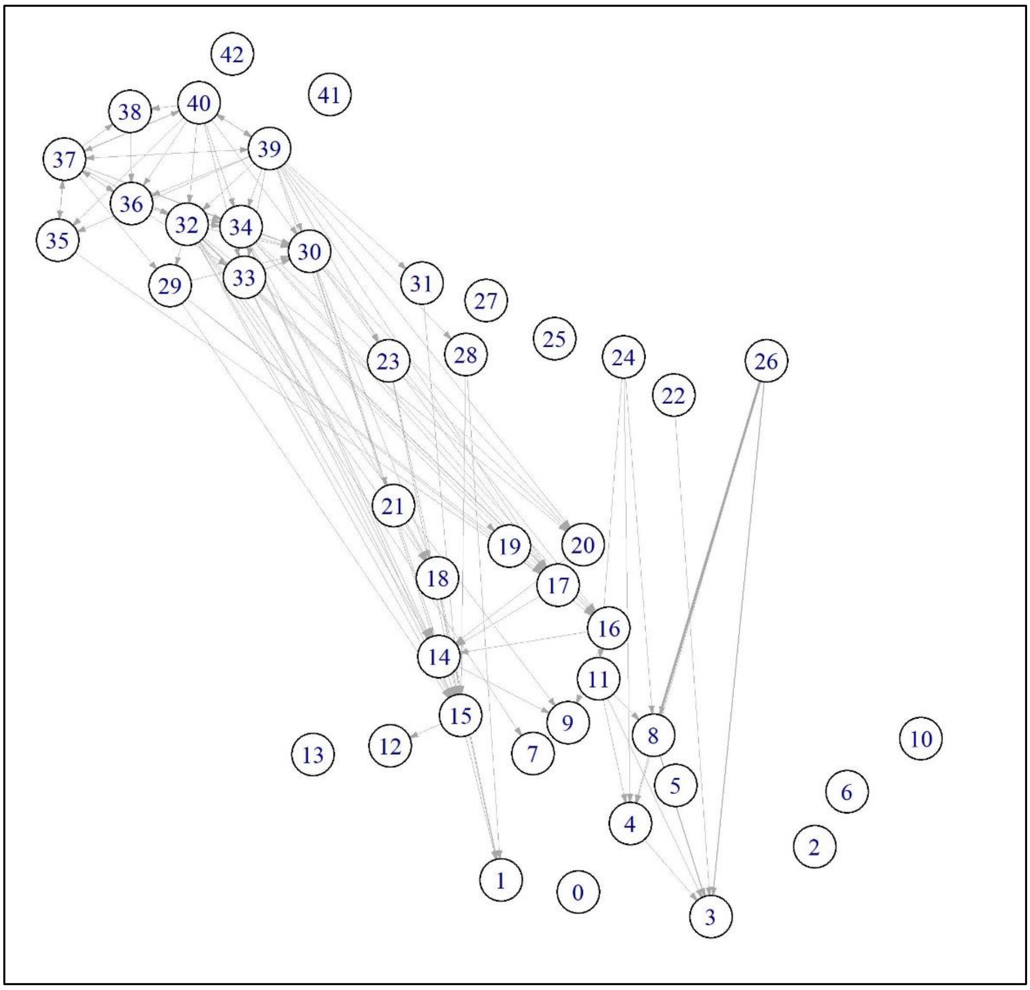

Figure 3: Graphic representation of network connectivity in SA4. Circles represent patches, which are arranged in a geographically accurate configuration. Arrows indicate movement of individuals from one patch to another, with thicker arrows representing higher volume of dispersers. This figure highlights areas that are well connected (e.g. around patches 30 and 14) as well as areas that lack incoming dispersers (e.g. patches 0, 2, 6,10, 13, 25, 27 and 41). The arrows represent the means of the connectivity matrices compiled from 20 replicates, however only connections with an average value >0.75 are shown for visual clarity. Omitted cases were rare connections and did not represent the connectivity most likely to be present in the system. For more detail, see Figure 8.

The values in the connectivity matrix also allow us to measure self-recruitment of a particular patch, which is the proportion of settling individuals that originated in that patch

(Botsford et al. 2009). This metric gives us insight into the isolation of a patch, as low levels of self-recruitment would indicate a greater input from other patches and therefore a less isolated destination, while high levels of self-recruitment would mean the majority of new recruits originate in that patch and therefore recolonisation opportunities might be limited. In Figure 4, we show the self-recruitment values for the patches in SA4. The northwest Moray Firth cluster of patches, in general, have low to mid proportions of self-recruitment, indicating a high level of connectivity, which corresponds with Figure 3. The exceptions here are patches 39-42, which have moderate to high values. This is most likely due to the same cyclical hydrodynamics that ensure the high connectivity of that area keeping individuals local and due to the size of Patch 39, this results in high local retention of individuals. Again referring to Figure 3, there are few patches north of patches 39 and 40, therefore opportunities for input from upstream are limited. Given the apparent importance of Smith’s Bank (39) in feeding the rest of SA4 (Figure 3), this higher level of isolation is a valuable insight. Moving south, the cluster of patches around Turbot Bank (26) have very high proportions of self-recruitment, which is unsurprising given the lack of incoming dispersers from anywhere in SA4 (Figure 3). Similarly, the isolation of patches 2, 6 and 10 is reflected in their self-recruitment measures. The Firth of Forth patches (7-20, except 10) as well as Eventyre Bank (3) have reasonably low levels with a few exceptions, which corresponds to the southward movement of individuals from the north and northwest patches within SA4, leaving those patches less isolated. Where Figure 3 is a graphical representation of connectivity, measures of self-recruitment provide a more quantitative measure of isolation within this stock assessment area.

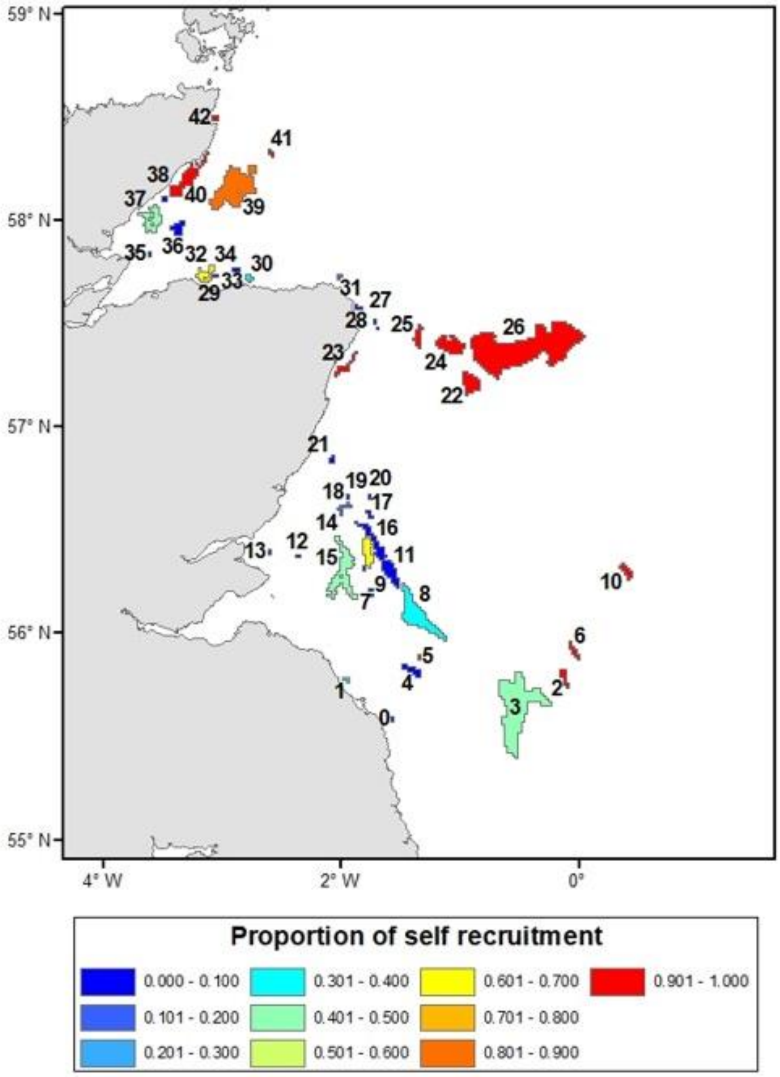

Figure 4: Measures of self-recruitment indicate degree of isolation of patches within SA4.

Such visualisations go a long way in indicating which patches might be important origin and destination patches within the system. Origin- and destination-centrality measures quantify these relationships. In Figure 5A, we can see that patches with the highest origin centrality are located in the northwest corner where the hydrodynamics ensure a large proportion of individuals remain in the local area, matching what we observed in Figure 3. In contrast, the patches at the southern edge of the seascape have very low origin-centrality since local hydrodynamics transport individuals eastward and out of SA4. This is consistent with the network connectivity (Figure 3).

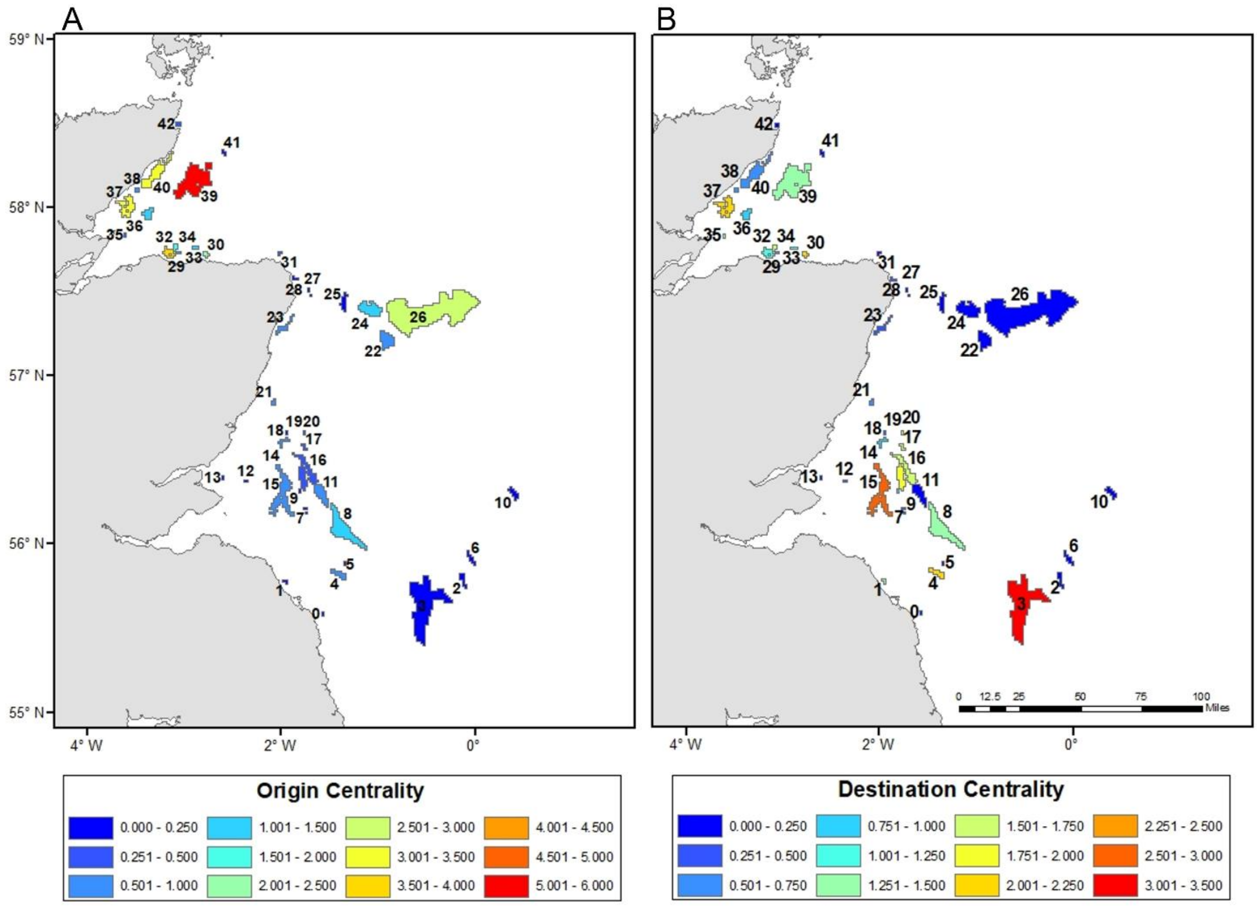

Figure 5: Origin- and destination-centrality measures indicate which patches contribute successfully dispersing individuals to other patches (A) and which patches receive settling juveniles from other patches as important destinations (B).

In Figure 5B, the pattern of patches with high destination-centrality exhibits less of a spatial gradient. As expected, the patches within the northwest cluster receive individuals from several patches. The cyclical hydrodynamics make them good destinations as well as origins. As the individual movement tracks suggest, the southern patches play an important role in receiving many dispersers within the system and have accordingly high destination-centrality values. The largest patch in the system, Patch 26, located in the middle of the domain, is a very poor destination patch, with hydrodynamics sending individuals from the north and bypassing this patch to the west of it, during their passive phase. This would indicate that this patch would be very vulnerable to patch depletion events as it would be difficult to recolonise. It is important to remember that in reality, it is possible that larval input from outside SA4 is possible, since this is by no means a closed system. However, looking at SA4 in isolation, larval transport to Patch 26 is rare. The top origin- and destination- centrality values for this system are presented in Table 2, along with patch size (in cells).

Table 2: Top 10 origin and destination patches in the SA4 seascape, based on their origin- and destination-centrality measures. Sizes are presented in numbers of cells in the seascape MerMADE input as well as total km^2 (cells are 2.25 km^2). Location of these patches can be found in Figure 1B.

Origin					Destination			
Patch	Centrality	Size			Patch	Centrality	Size	
		Cells	Km^2				Cells	Km^2
39	5.46	149	335.25		3	3.17	223	501.75
32	3.55	17	38.25		15	2.79	86	193.5
37	3.20	44	99		37	2.22	44	99
40	3.06	56	126		4	2.21	17	38.25
26	2.66	405	911.25		30	2.07	6	13.5
30	2.01	6	13.5		14	1.94	32	72
34	1.89	5	11.25		16	1.663	38	85.5
36	3.53	16	36		17	1.58	5	11.25
8	1.315	96	216		20	1.53	2	4.5
24	1.232	51	114.75		34	1.51	5	11.25

In order to investigate the effects of patch-level depletion events, we chose a selection of patches with a range of origin-destination characteristics (Table 3). We wanted to compare the responses of both large and small examples of important origin and destination patches.

Table 3: Connectivity metrics and patch characteristics of patches chosen for local depletion simulations. Sizes are presented in numbers of cells in the seascape MerMADE input as well as total km^2 (cells are 2.25 km^2).

Patch	Origin centrality	Destination centrality	Size	
			Cells	Km^2
3	0	3.17	223	501.75
14	0.35	1.94	32	72
26	2.66	0	405	911.25
32	3.55	1.10	17	38.25
39	5.46	1.32	149	335.25

Figure 6 shows the responses in overall, system-wide population size (as opposed to patch-level subpopulation size) when each of these patches is individually depleted either once (Figure 6A, B) or repeatedly (Figure 6C,D). From the drop in overall population size, we can gauge the relative impact of depletion events at each patch. Patch 26 and Patch 3 have the most impact, judging by the sharp drop in population size at the time of first depletion event, 20 years after the start of the simulation. When the depletion event occurs only once and Patch 3 was targeted, system-wide population size recovers fairly quickly.

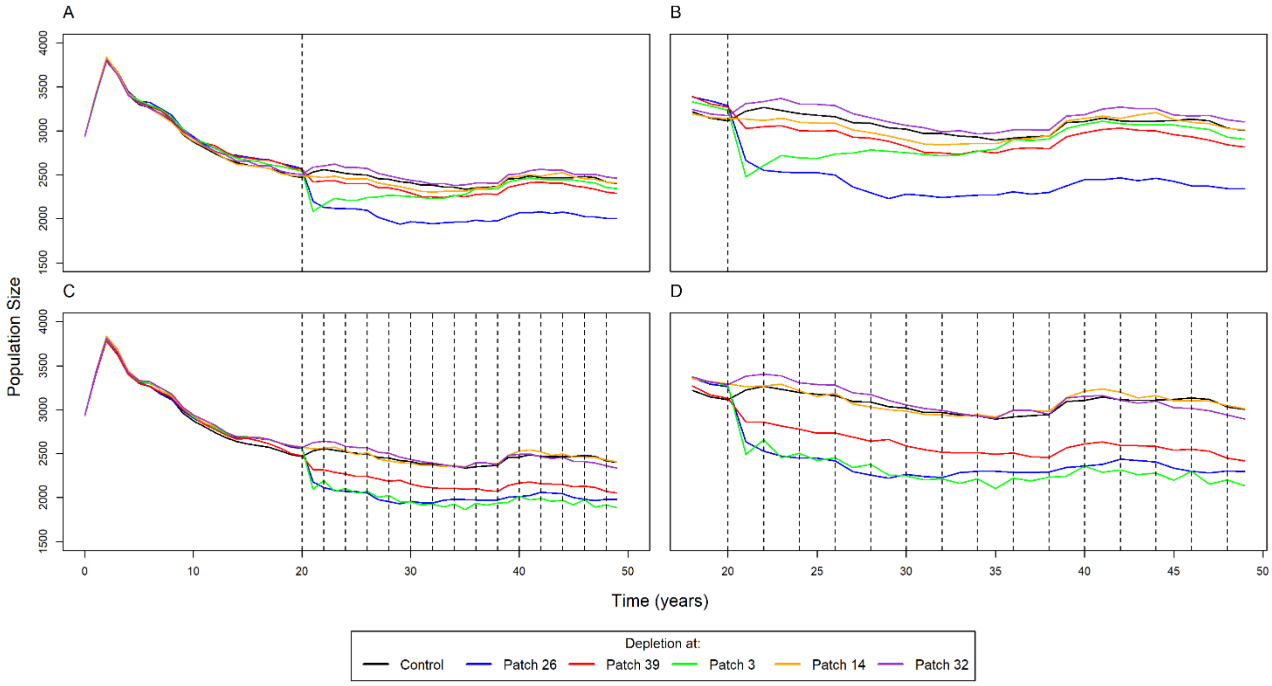

Figure 6: Overall population sizes of the stock across 50 years in MerMADE simulations, comparing effects of singular depletion (A & B) and repeated (C & D) events at five different patches (3,14,26,32,39), both across the whole timespan (A & C) and specifically after the depletion event (B&D, note here that the y-axes are “zoomed in” for clarity). The Control (black line) represents the system with no depletion events. These patches varied in their sizes, locations and their centralities as origins or destinations. The dashed vertical lines indicate the occurrence of depletion events. Note that the initial decrease in population size shows the 20-year burn-in period where the system stabilises after initialisation at half-carrying capacity.

In contrast, population size remained below control-simulation levels when Patch 26 was targeted, mostly likely due to Patch 26 having very little chance of being recolonised and recovery happening very slowly. Depletion at Patch 39 and Patch 14 also caused the overall population size to drop below control-levels but recovered by the end of the simulation. With repeated depletion at Patch 26 or Patch 3, population size remains low, with Patch 39 depletion having slightly less of an effect and repeated depletion at other patches had no discernible significant impact.

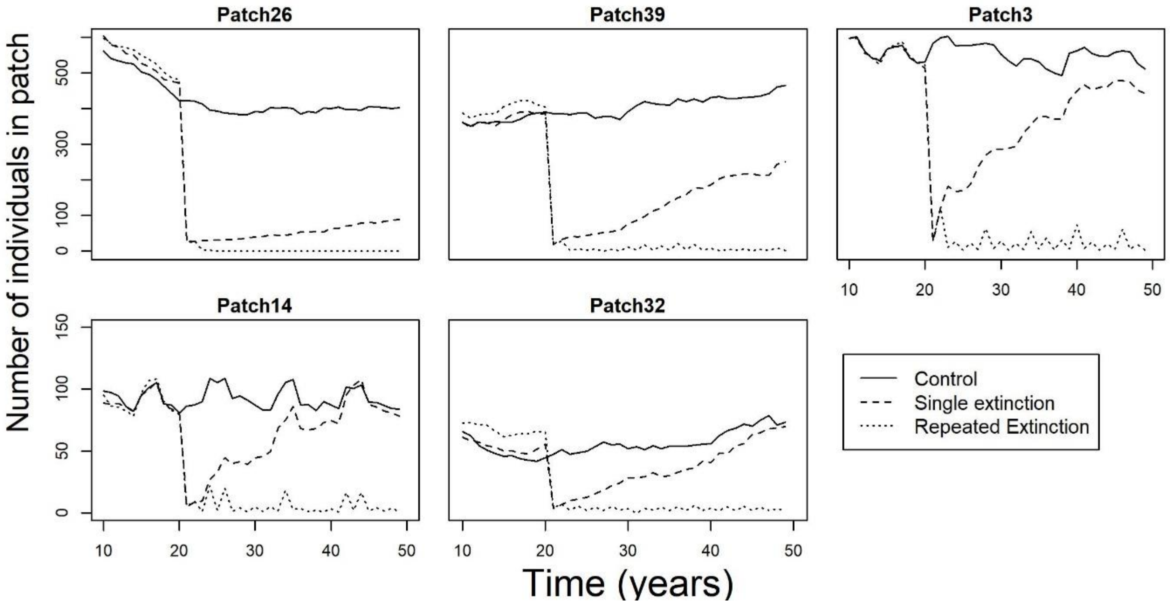

Figure 7: Patch-level subpopulation sizes in MerMADE simulations indicate the effects of single depletion vs repeated depletion events at each patch. Note that y axes are on different scales to better visualise effects across different patch sizes.

From the patch-level subpopulation size outputs (Figure 7) we can observe the depletion-recolonisation cycles (or lack thereof) at each patch. Patch 26 receives no juveniles from upstream patches (Table 3), therefore recolonisation cycles are completely absent. In single-depletion simulations, recovery is a slow process but is present, while in simulations with repeated depletion events, the patch remains at very low densities. This trend is mirrored in patches 39 and 32, though small recolonisation events can be observed and the slope of recovery trend is much steeper. However, the other patches exhibit evidence of being recolonised. All remaining patches except Patch 39 and Patch 3 manage to recover subpopulation sizes comparable to the control simulations when the simulation finished at 50 years after the singular depletion event occurs. The time to recovery does not seem to be affected by size, patches 3 and 14 have very similar recovery speeds, even though Patch 3 is comprised of 223 cells and Patch 14 only has 32. However, all patches remain well below control-level subpopulation sizes when depletion events occur every other year. All patches except Patch 26 exhibit small peaks in subpopulation size as they are recolonised and before the next depletion event. Patch 14 shows the most extreme pulses in subpopulation density, which is unsurprising given that it has the highest destination centrality of the chosen patches (Table 3).

4 DISCUSSION

By developing and applying coupled biophysical dispersal - demographic models we can provide important new tools for assessing how effective seascape connectivity is likely to be for providing key population-level outcomes for fishery managament. Applying this modelling approach, we have illustrated how differences in realised connectivity and habitat size can affect the rate of both patch and population recovery of site attached fish in a hydrodynamic environment using the MerMADE modelling software (R. Allgayer et al. preprint; doi:10.1101/2022.11.15.51661). As has frequently been observed in marine pelagic larval dispersal (Fontoura et al. 2022), the exchange of sandeel larvae among patches in SA4 was asymmetric with some patches only having an important origin role while others were largely destinations. Of the many other patches that were both origin and destination sites, none were directly connected to all other patches within the stock area through annual dispersal. Consequently, the long-term impact of patch depletion on local and stock abundance would be expected to vary within the stock area in relation to local patches' origin-destination characteristics as well as spatial differences in reproductive output among patches. This finding is important as it demonstrates that where fishing occurs within the stock area can impact stock size. The same total stock removal will have different consequences depending on which patches are fished.

Spatial connectivity for fisheries management

Concern over the spatial loss of some marine fish stock components has led to consideration of metapopulation theory. While early reviews suggested it might have limited relevance given the considerable scope for mixing, making patch depletion rare (Smedbol et al. 2002), the patterns of patch recovery evident from the present model simulations confirm the importance of demographic connectivity, which Kritzer and Sale (2004) viewed as the most relevant aspect of metapopulation theory for marine populations (Kritzer & Sale 2004). As the present study shows, sub-population size can be highly dependent on recolonization, especially in patches where there is low self-recruitment. Moreover, contrary to the model of Hastings and Botsford, persistence in sub-populations did not necessarily depend on individuals returning to natal patches as asymmetry in larval transport made some patches far less susceptible to reductions in population size than others (Hastings & Botsford 2006). Our study highlights that considering spatially complex metapopulation dynamics for stage-structured species (here using an individualised Leslie matrix representation) offers considerable potential for improving understanding and management of marine species.

A patch's ability to recover after a depletion event was, predictably, dictated by its importance as a destination patch, providing opportunities for recolonisation. Depletion of large origin patches with low recolonisation potential were found to have substantial long-term consequences to both local and population level recovery rate and therefore resilience to fishing pressure. In contrast, depletion of small patches which regularly receive immigrants from several other patches were found to recover rapidly and seem to have little overall impact on stock size. While specific to a stock of sandeels, these findings do suggest that other species with a strong site attachment may not behave like the well-mixed population assumed in conventional stock assessment models (Cadrin 2020) and associated forecasts. As such this study highlights the need for greater consideration of realised connectivity in developing appropriate spatial stock assessment methodology (Punt 2019).

A single local depletion event at the largest patch, east Turbot Bank (26), removed a significant portion of the overall stock and, as there was very little transport of larvae into this patch due to the net residual southerly transport, it was difficult for the stock to reach the original size again. While the simulations assumed no immigrants from outside the stock area, previous larval transport modelling and field observations of young of the year suggest that this patch does occasionally receive sandeels from distant spawning grounds around Orkney, in a different stock area (Proctor et al. 1998). Nevertheless, this limited connectivity does support the view that east Turbot bank has a low potential for recovery. In contrast, the second largest patch, Eventyre Bank (3), was only a destination patch, so although depletion had a short-term effect on stock size, it recovered quickly due to immigrants from an average of ~4 upstream patches. However, repeated depletion hampered population growth in the long run not only due the elimination of local recruits but also those from upstream patches.

Larval retention in the Moray Firth appears important to the origin-destination characteristics of the third largest patch 39, Smith’s Bank, and nearby inshore patches. These patches have both high origin- as well as high destination-centrality scores, meaning they contribute juveniles to their neighbours but also receive individuals from several sources. On average Smith’s Bank supplied 9 downstream patches, mostly in the Moray Firth but also patches off the Firth of Forth. Smaller patches west and north of Smith’s Bank were origin sites for this large patch and most appeared to settle locally. This larval retention is consistent with previous larval transport models and analysis of otolith chemistry variation (Wright et al. 2019). A single depletion event at Smith's bank elicited a dip in stock size but this- was not prolonged.

None of the larger patches mentioned above were within the Northeast UK closed area, where fishing of sandeels is now completely prohibited after several years of the highest ever catches in SA4 from patches off the Firth of Forth (ICES 1999). The importance of these patches as a destination from both adjacent patches as well as larvae dispersed from the Turbot Bank MPA (24) and the north east coastal patches may help explain the maintenance of a targeted fishery prior to the closure. For example, Wee Bankie (14) received juveniles from ~4 other patches, allowing an increase in subpopulation size after a single depletion event. These patches did not contribute to the unprotected patches and so the potential for overspill may be very limited. In contrast, fishing outside the closure may affect immigration to patches within the closed area.

Given the unusual management situation within SA4, with a large closed area, other inshore patches that are not subject to fishing and a Total Allowable Catch (TAC) advised by ICES for the total stock area, the differences in patch vulnerability identified in this study should be of concern. The assessment undertaken is tuned with a survey index whose stations occur within areas that are mostly not fished (ICES 2022b). The advised 2021 TAC resulted in an apparent fishing mortality that well exceeded a locally determined cap (ICES 2022b). Even in the area open to fishing the patches fished vary among years. The Turbot Bank (26) and adjacent patches were targeted in 2021, including the MPA (24), since there are currently no measures prohibiting sandeel fishing (JNCC 2014). Small patch size and isolation linked to inter-patch distance and hydrography may be a greater problem in SA4 than other North Sea sandeel stock areas that are currently fished. A similar study of simulated recovery time for 3 local depletions of 50km areas in stock areas SA1 and SA2 found far more rapid re-colonisation than the present study but the affected sites were closely surrounded by other large extensive patches (Wright et al. 2019).

Although this study focussed on the effects of patch level fishing removals there are other important human pressures on sandeels that could be important to sustainable stocks. Disturbance events that have been shown to negatively affect sandeel populations elsewhere in the world include oil spills. It has been suggested that oil spills could lead to local subpopulation depletion should such an event occur across an area of sandeel spawning habitat (Penttila 2007). Experimental studies have shown that North American *Ammodytes* species (such as *Ammodytes hexapterus*), will reduce their burrowing time or remain completely in the water column and will choose less optimal sediment (ie gravel where fine or coarse sand is preferred) if there is oil contamination in the sediment (Pearson et al. 1984, Pinto et al. 1984). However, when the Braer oil tanker sank in Scottish waters off Shetland, oil contamination had no significant effect on patch density or recruitment despite evidence of hydrocarbon exposure (Wright et al. 1997). Development of offshore marine wind farms in the North Sea are a more permanent pressure, with many now occurring near sandeel habitat, including the Smith's Bank (see Figure 1A), which this study suggests is an important origin patch. Initial evidence on the effects of such developments on changes in habitat quality and sandeel abundance have not suggested a major effect but more research is needed (van Deurs et al. 2012). Dredging and pelagic trawling will be very difficult to conduct safely inside these areas, making them de facto closed areas.

It is worth noting here that the connectivity metrics we present are the *per-year* means of connectivity across 20 replicates. We believe this is a more robust and cautious approach when simulating patch depletion than, say, taking the cumulative movement of individuals across the entire 50-year simulation. We acknowledge that there is sporadic connectivity and that if we had taken the 50-year mean, the system would seem better connected, and origin- and destination-centralities would be higher (Figure 8). However, assuming the connectivity observed across 50 years produces the same recovery opportunities on an annual basis might overestimate the system’s ability to respond to disturbance. This temporal variability in dispersal connectivity does, however, provide some evidence for long-term recovery potential which would be more relevant in the context of other enquiries such as protected area projections.

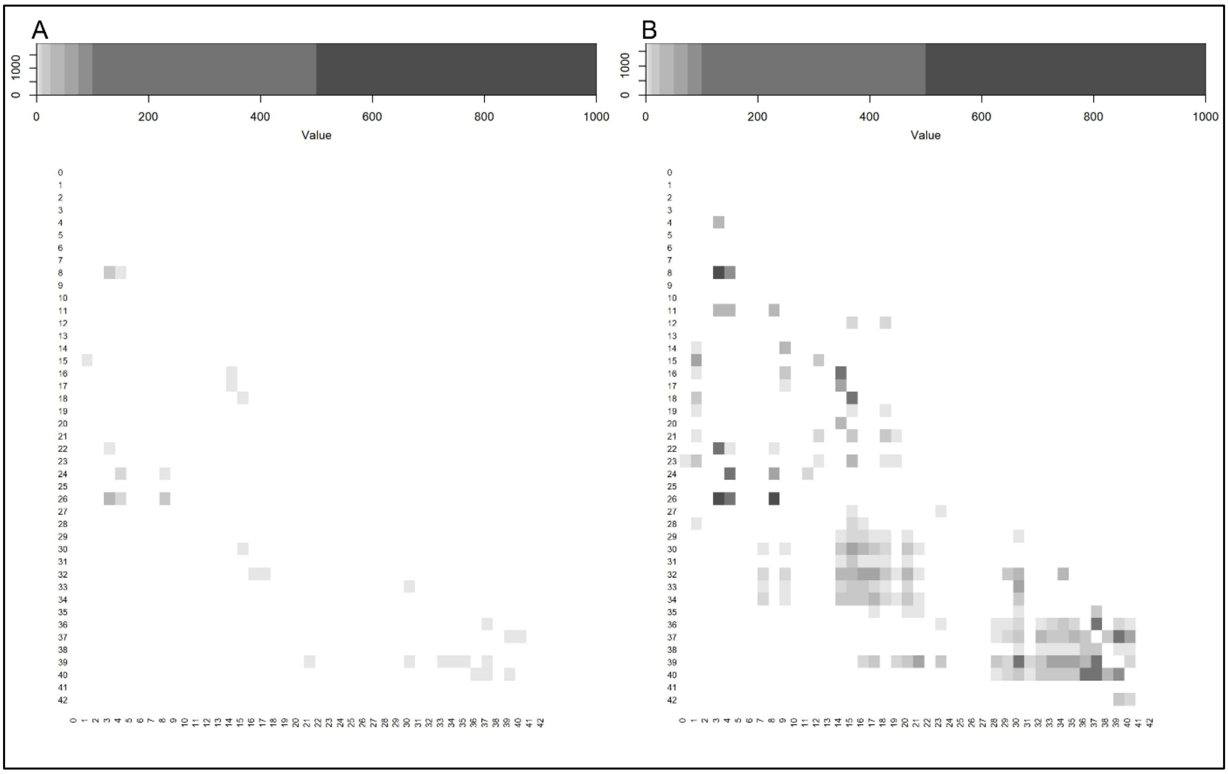

Figure 8: A heatmap representing the movement of individuals from origin patches (y axis) to destination patches (x axis). The greyscale gradient indicates mean volume of individuals for 20 replicates, A) per year and B) cumulatively over the entire 50-year simulation.

In the context of advice provision for fisheries management, particularly where the principal tool is the catch limit (TAC), there are three elements to consider. Most stock assessments, where the current state of the stock is evaluated by estimating population size and fishing mortality, do not explicitly incorporate pre-settlement dispersal, nor other spatial processes, which can lead to biased stock estimates (Cadrin 2020). However, determining local (patch) abundances would be beneficial and necessary for any spatially explicit forecast. Any spatially explicit catch limits, derived from such a forecast, would also need to be at a scale that is likely to be enforceable, which may not be at the individual patch level, but which could be grouped into patch clusters. Forecasts are based on reference points which are calculated using a variety of means, the more effective of which is a management strategy evaluation (MSE, Punt et al. 2016), where simulations over tens of years are conducted on virtual populations to determine the most effective harvest control rule (Punt 2010, Merino et al. 2019, Pérez-Rodríguez et al. 2022). MSE requires an operating model which controls a virtual population and these are usually considered to be steady state over the time frame of the simulation (Punt et al. 2016). Having spatially explicit operating models (Smith et al. 2021) incorporating the dynamics of dispersal as here would be a desirable feature, and essential to determine spatially explicit catch limits.

Although MerMADE is a very flexible model, there are certain aspects of sandeel life history as well as environmental factors that can’t be fully represented here and detail has been sacrificed in certain areas. Spatial heterogeneity in demographic parameters is not represented in MerMADE at present, with carrying capacities applied per habitat type and therefore, in this case, they are the same across all sandbanks. Similarly, variables such as fecundity and mortality were standardised at a species level. More realistic would be spatially varying demographic rates that correlate with habitat quality, which would potentially influence a patch’s importance within the system as well as that population’s ability to recover after a disturbance event (Figueira 2009, Burgess et al. 2014). Similarly, one of the assumptions made in this study was that fishing pressure is concentrated on one patch only and that the rest of the system experiences no additional fishing mortality on top of natural mortality. In reality, this is not entirely true, although fishing activity at a particular patch can be highly concentrated for a short period of time, sometimes leaving that patch commercially depleted for several years (Johannessen & Johnsen 2015). Future investigations of this nature would need to incorporate distributed fishing pressure across the system. MerMADE does not have the functionality yet to make fishing pressure spatially heterogeneous, therefore we decided to only have one patch targeted per simulation to make resulting patterns clear. This is especially relevant to SA4 because a large portion of it is contained within the northeast UK closed area where no fishing activity is permitted, so applying a blanket fishing mortality would not have been realistic.

Many of our key results are likely to be robust to the simplifications present in the model. The ability of poorly connected patches such as Turbot Bank (26) to recover from repeated depletion-level events such as we are discussing here would likely not be improved by representing variability in demographic rates, since crucial recolonisation events are still rare. The high proportion of self-recruitment at Turbot Bank and surrounding patches (Figure 4) as well as their low destination-centrality values (Figure 5) are indications of their isolation. Similarly, the hydrodynamics affecting that central cluster of patches suggest a low ability for local retention, making self-persistence difficult (Figueira 2009, Burgess et al. 2014). We should acknowledge here that MerMADE represents hydrodynamics in a relatively simple form (3D vectors *u*, *v* and *w*, see Allgayer et al. 2022), which means that it does not include parameters such as density, salinity, turbulence or surface wind stress as other larval dispersal models do (North et al. 2008, Christensen et al. 2008, 2018, Lett et al. 2008, Paris et al. 2013), potentially affecting the fine-scale dynamics such as tidal shifts, local retention and movement along the coastline. However, the broad scale movement of individuals is unlikely to change significantly, therefore we believe the modelling resolution adopted within MerMADE adequately represents the movement of sandeels within this stock assessment area to explore these concepts.

The use of super-individuals in MerMADE, a necessity due to the combination of dispersal and population dynamics in the model as well as the density of sandeels in particular (48 individuals m^{-2}), is an approach increasingly taken by many working in process-based ecological prediction and forecasting (Scheffer et al. 1995, Martens et al. 2021), including in the marine environment (e.g. sea scallops (Chen et al. 2021), harbour porpoises (Gallagher et al. 2022), and European sea bass (Watson et al. 2022)). Greater research is required in developing increasingly effective scaling approaches (including the use of super-individuals) in process-based modelling (Fritsch et al. 2020). High demographic stochasticity is an artefact of using the super-individual methodology and is something we observed, especially with the smaller patches, which are naturally more vulnerable to patch depletion (Engelhard et al. 2008). With these computational restrictions in mind, MerMADE may be unable to capture the full extent of the smaller patches’ contributions and therefore we can’t say with certainty that MerMADE captures the complete connectivity matrix of this network of sandbanks. Nevertheless, we are confident that MerMADE is capable of representing connectivity enough to highlight central as well as vulnerable patches and indicate movement corridors.

Future studies could test annual predictions of connectivity derived from the MerMADE model, at least at a sub-stock scale, using year-specific model runs and corresponding regional variation in natal and settlement otolith chemistry, similar to that used by Wright et al. (2019). Annual indices of sandeel abundance are available from many of the SA4 grounds (Régnier et al. 2017) and these could be used to compare relative inter-annual variability in patch-level subpopulation sizes between the model and observations.

5 CONCLUSION

In this study, we combined the use of MerMADE, an individual-based, biophysical model, with network theory to investigate the effect of commercial depletion of sandeel subpopulations in SA4 of the North Sea. The model's strength lies in the interplay between the environment, dispersal and, notably, demography, which is absent from most contemporary models, but which has been identified as a crucial factor when investigating matters of functional connectivity and management (Figueira 2009). The results presented here are nevertheless a valuable insight into the dynamics and intricacies of patch depletion of sandeel subpopulations. In the future, we would like to take the simulations and results presented here a step further, developing MerMADE's functionality to include spatial heterogeneity in demographic parameters, which will enable a more biologically realistic representation of the pressures and dynamics of the system. Additionally, the role of adaptation and evolution of dispersal parameters in the response of sandeels to repeated depletion-level events remain to be explored. For example, dispersers from upstream origin patches may develop shorter or longer dispersal durations in order to bypass an area of high mortality, given a long enough time period (Baskett et al. 2007). The effect of habitat fragmentation, which this essentially represents, on dispersal traits has been observed previously (Baskett et al. 2007) and MerMADE provides a framework within which to investigate this further. Results from this study further highlight the shortcomings of current area-based fisheries management that fails to take into account subpopulation dynamics.

We provide a clear demonstration of the predicted negative impacts of high intensity fishing on locally fragmented populations.

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Appendix A

Table A.1: Parameter values included in MerMADE simulations for A. marinus and references.

	Parameter	Value	Reference (if applicable)
Emigration	Emigration Probability	0.8	
Transfer	Pelagic Larval Duration (PLD)	70 days	Within range from (Wright & Bailey 1996, Régnier et al. 2017)
	Buoyancy Range	0-80m	
	Diel Vertical Migration range	10m (0-10m at night, 70-80m in the day, unless seafloor is shallower)	(Jensen et al. 2003)
	ρ (slope of size-dependent influence of current)	-0.005	
	Minimum size at diel vertical migration	10mm	(Yamashita et al. 1985, Jensen et al. 2003)
	Minimum size at active dispersal	26mm	T. Régnier unpubl. data
	Step Length when active	1 BL s^{-1}	
	Mortality	0.042 day^{-1}	(Régnier et al. 2017)
Growth (modified Gompertz)	Size at hatching l_0	5.33 mm	T. Régnier unpubl. data
	Maximum size l_{inf}	67.04 mm	T. Régnier unpubl. data
	Growth Parameter K	0.03696889	T. Régnier unpubl. data
	Earliest date of settlement T_i	53 days	T. Régnier unpubl. data
Settlement	Minimum size at active dispersal	26 mm	T. Régnier unpubl. data
	Settlement Probability S_0	1	
	Slope of density dependence function α_s	-6	
	Inflection point of density dependence function β_s	1	
	Settlement buffer	4.5km	

It is worth noting that a few parameters in the above Table A1 have been estimated without evidence from the literature. It is not uncommon that parameter values have no empirical data behind them for a particular species and therefore studies of related species may be used or the parameter value inferred. Here, we have used best judgement for parameters such as emigration probability and settlement parameters.

The emigration phase of dispersal—the "decision to leave"—is represented as a probability. Here, we used 0.8 as emigration probability, ensuring that the majority of hatched larvae undergo dispersal away from their natal site but allowing for a percentage to remain in the natal patch. This was to capture by proxy any mechanisms ensuring retention of dispersers not explicitly included in the model and to compensate for lack of fine detail in the hydrodynamics around the sandbank patches. The slope for the influence of current ρ on movement as an individual grows was estimated using the size at birth, size at competency and associated known swimming speed, under the simplifying assumption that influence of current has a negative linear relationship with size of individual. Density dependent settlement is likewise a probability and we assigned a 100% probability at low densities, there being no evidence in the literature that anything other than suitable habitat was required for settlement. The shape factors α_s and β_s were used as they provided a plausible shape to the density dependence function at the densities we expected in the model. More detail on this calculation can be found in the user manual. The settlement buffer—the distance at which dispersers can sense suitable habitat and adjust orientation—was likewise inferred to be 4.5 as sensory cues often travel many square kilometres (Leis 2007).

Table A.2: Names corresponding to the Patch numbers used to refer to patches within SA4.

0	Farne South	11	Marr Bank south	22	Turbot Bank south	33	Buckie
1	Farne north	12	Bells Rock east	23	Aberdeen Bay	34	Spey Bay offshore
2	Eventyre east	13	Bells Rock	24	Turbot Bank MPA	35	Catbow
3	Eventyre Bank	14	Wee Bankie north	25	Turbot Bank west	36	Himmel
4	Trawlknuser Plads 1	15	Wee Bankie south	26	Turbot Bank east	37	Steeple Ground
5	Trawlknuser Plads 2	16	Marr Bank north	27	Cruden offshore	38	Helmsdale south
6	Eventyre east	17	Scalp Bank SE	28	Rattray Head	39	Smith’s Bank
7	Wee Bankie south	18	Scalp Bank SW	29	Spey Bay inshore	40	Helmsdale north
8	Berwick	19	Scalp Bank NW	30	Cullen	41	Smith’s Bank north
9	Marr Bank west	20	Scalp Bank NE	31	Fraserburgh	42	Noss Head
10	Offshore east	21	Stonehaven	32	Lossiemouth		