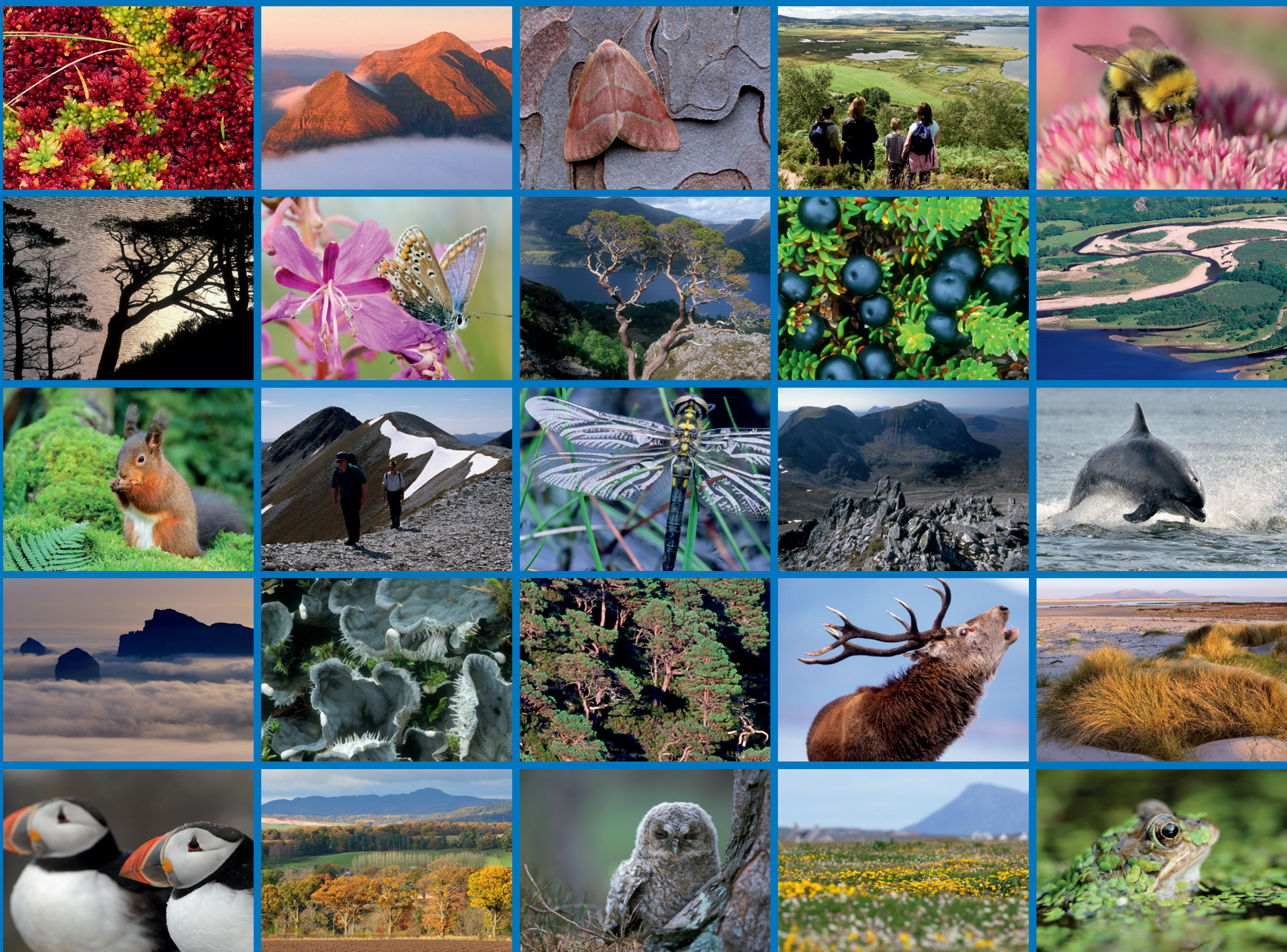
Scottish Natural Heritage
Research Report No. 1048

Connectivity of selected Priority Marine Features within and outwith the Scottish MPA network



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RESEARCH REPORT

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RESEARCH REPORT

Summary

Connectivity of selected Priority Marine Features within and outwith the Scottish MPA network

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Project No: 116881
Contractor: Hannah Millar, Rory O'Hara Murray, Alejandro Gallego, Kate Gormley and Flora Kent
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Keywords

connectivity; Priority Marine Features (PMFs); horse mussel beds; flame shell beds; Marine Protected Areas (MPAs); particle tracking; habitat suitability modelling

Background

Marine Protected Areas (MPAs) are designated for the protection and conservation of a range of species and habitats found in Scottish seas. Effective conservation action relies on understanding the linkages between protected features within MPAs and the relationship that they have with species and habitats outwith the network. Two Priority Marine Features (PMFs), horse mussel beds and flame shell beds are currently protected features in a number of MPAs. Both of the characterising species are benthic and sessile as adults and rely on the pelagic larval phase for transport to other areas. Due to the difficulty in obtaining measurements of the spawning behaviour of benthic species, there is little information available on their connectivity around Scotland. Coupled particle tracking and hydrodynamic models are an excellent method for investigating the connectivity of benthic species populations, where the larvae are transported by oceanic currents. It is also important to consider the habitat suitability of the areas where the particles travel to.

Main findings

- There is a predominately clockwise transport of larvae around the Scottish coastline. This is more apparent for the larvae originating from horse mussel beds than flame shell beds, due to their greater occurrence and because horse mussels have a longer pelagic larval duration than flame shells.
- A distinction can be made between horse mussel beds in the south-west and north-west, with connectivity within each region. The Small Isles NCMPA appears to act as a link between the two regions, as it receives larvae from horse mussel populations in the south-west and exports larvae to the north-west.
- Orkney horse mussel beds receive larvae from west coast of Scotland populations. Model simulations show that within the Orkney populations, the beds self-recruit and are weakly connected to each other.
- Horse mussel beds in Shetland are mainly isolated from other Scottish populations. All the Shetland population self-recruit to some degree, and all the populations within Shetland are well connected.

- The horse mussel bed in the Berwickshire and North Northumberland Coast SAC has low self-recruitment and this area receives no larvae from other known Scottish horse mussel beds. There may be horse mussel beds in the Firth of Forth supplying larvae to areas in south east Scotland, but this requires further investigation.
- All the flame shell bed release areas self-recruit and are weakly connected to at least one other area.
- There is some level of regional separation between flame shell beds, with the Mull of Kintyre acting as a regional divide.
- The flame shell beds around Loch Linnhe and Mull appear to be weakly connected
- The flame shell beds east of Skye (in Loch Carron and Loch Alsh) appear to be connected
- Habitat suitability modelling found a high number of potentially suitable habitat areas for both PMFs investigated.
- The release areas were found to export larvae to many of these new suitable habitat areas. If PMFs are found to occur in these areas, they could be important links between known beds and potential candidates for protection.
- Some modelling results were found to be sensitive to the spatial resolution of the hydrodynamic model used, highlighting the potential importance of reproducing relevant fine-scale circulation features.
- This study has highlighted the need for future work, particularly on the larval behaviour of PMF species and the impact of climate change on the connectivity of protected species and habitats.

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1. INTRODUCTION

Currently, the Marine Protected Areas (MPA) network covers approximately 20% of Scottish waters. This network includes, amongst others, Nature Conservation Marine Protected Areas (NCMPAs) designated under the Marine (Scotland) Act 2010 and Special Areas of Conservation (SAC) which come under the EU Habitats Directive (Scottish Government, 2018). For the purposes of this report all designations shall be called MPAs, unless explicitly named. The aim of MPAs is to contribute to the conservation of marine habitats, species, geology and landforms, and to the overall health of Scotland's marine environment. Effective conservation action relies on understanding the linkages between protected features both within and outside protected sites.

Priority Marine Features (PMF) are species and habitats which have been identified as being of conservation importance in Scotland's seas. Examples of a number of these features are currently afforded some protection by MPAs. The National Marine Plan states that development and use of the marine environment must not result in significant impact on the national status of PMFs. This study investigates connectivity between both protected and unprotected areas of two PMFs, flame shell (*Limaria hians*) beds and horse mussel (*Modiolus modiolus*) beds. Both flame shells and horse mussels are benthic and sessile as adults, relying solely on the pelagic larval phase for transport to other areas. Their distribution is also relatively restricted in Scotland's seas, making it more important to improve our understanding of connectivity. Modelling is used in this study to estimate the probability of individual horse mussel and flame shell beds being connected to other beds. The results are combined with habitat suitability modelling to identify other potentially suitable areas for horse mussels and flame shells to survive and form beds.

Most marine invertebrate populations are connected by the movement of genetic material via larval dispersal (Palumbi, 1994). Therefore, life history factors such as the timing of spawning, pelagic larval duration and larval behaviour have considerable implications for the extent to which such populations may be connected (Carson *et al.,* 2010). Mackenzie *et al*. (2018) carried out genetic analysis of selected horse mussel bed populations in Scotland and found that distance was not a key driver in the level of genetic similarity, suggesting that hydrodynamic forces and coastal geography play a greater role in determining genetic connectivity of horse mussels. However, only a small number of sites were sampled in that study.

Cowen *et al*. (2007) define population connectivity as the exchange of individuals among geographically separated sub-populations. Co-consideration of both genetics and larval dispersal modelling can act as a means of validating either approach and therefore strengthen conclusions regarding actual levels of population connectivity between sites (Coscia *et al*., 2013). Results from genetic analysis can validate larval dispersal model predictions and larval dispersal modelling can help to explain the mechanism behind population genetic connectivity. Gormley *et al.* (2015), for example, combined genetic analyses and hydrodynamic modelling of larval dispersal from the same populations within the Irish Sea to assess horse mussel bed connectivity. However, no such study has been carried out in Scotland and neither aspect of connectivity has so far been investigated for flame shell beds.

Gallego *et al*. (2013) used a biophysical model to estimate larval transport of 18 benthic features to determine connectivity between proposed MPAs in Scotland. However, this study did not include populations outside MPAs and did not incorporate habitat suitability to determine settlement areas. Further research in this area will help us to define ecological connectivity of protected features and identify wider scale management needs both within MPAs and beyond MPA boundaries.

1.1 Larval spawning and behaviour

Hydrodynamic and particle tracking models are increasingly being used to characterise patterns and quantify spatial and temporal variability in larval dispersal from potential 'source' areas of recruitment to their likely settlement or 'sink' locations (e.g. Elsäßer *et al.,* 2013). However, the validation of such predictions depends on the availability of information on larval dispersal distances, which are inherently difficult to measure directly (Cowen and Sponaugle, 2009).

The success of bivalve reproduction and timing of spawning can vary dramatically between different regions (e.g. see Brown, 1984), and is dependent on environmental variables (e.g. food availability; Starr *et al.*, 1990). The number of larvae surviving to the point of settlement is often unknown (Cowen and Sponaugle, 2009). Furthermore, suitable habitat must also be available at sites identified as larval sinks (as well as the source locations) if the larvae are to successfully settle, grow and survive (Elsäßer *et al.*, 2013). Information on the timing and location of spawning, the survivorship of the pelagic larvae and the distribution of suitable settlement habitat is required to effectively model larval dispersal.

The incorporation of larval behaviour can have significant consequences for biophysical modelling (also known as particle tracking) simulations. For example, North *et al.* (2008) found that including oyster larvae swimming behaviour in larval dispersal modelling experiments had an impact on distances travelled, transport success and the degree of connectivity between sub-populations.

The main transport mechanism of larval dispersal is residual currents, particularly in the open ocean. Figure 1 shows the average residual currents pattern around Scotland with the mean current strength for September from a hydrodynamic model, the Scottish Shelf Model (SSM) shown by the shading. The most persistent circulation features are indicated with the arrows. The most westerly current shown here is the northward (and here north easterly) flowing European Slope Current (ESC), which is confined by the continental slope (Inall *et al*., 2009). The Scottish Coastal Current (SCC) flows northward up the west coast from the Irish and Clyde Seas (Knight and Howarth, 1999) and is further freshened by the outflow from the Scottish sea lochs. North of Orkney the SCC combines with oceanic water to form the Fair Isle current, an important inflow to the North Sea. The East Shetland Atlantic Inflow is a southerly wind and density driven residual current (Turrell *et al*., 1996). Both the East Shetland and Fair Isle currents turn east (following the bathymetry) to form the Dooley Current (Turrell *et al.,* 1996). The SCC continues down the Scottish east coast, following the same direction as the main anti-clockwise (cyclonic) residual circulation within the North Sea.

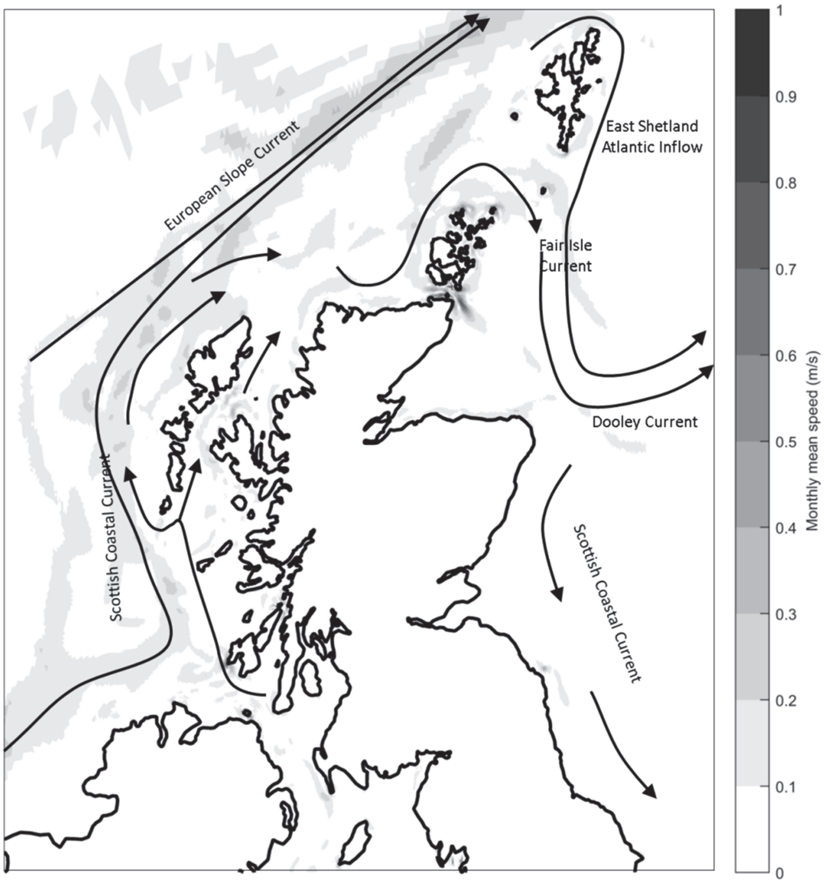

Figure 1. Average monthly residual currents around Scotland, for September from the Scottish Shelf Model. Arrows show key features of surface circulation (taken from Turrell et al., 1996), and the shading indicates the strength of the residual currents from the SSM.

1.1.1 Horse mussels

Horse mussel (*Modiolus modiolus*) recruitment is highly variable, not only seasonally but between years (Holt *et al.,* 1998). Early studies suggest that *M. modiolus* are trickle spawners (Brown, 1984; Seed and Brown, 1977), however, experiments carried out during the *Modiolus* Reef Restoration project suggest that gamete release peaks in the autumn in Strangford Lough (Fariñas-Franco and Roberts, 2018).

Information on *M. modiolus* larval behaviour and mortality rates is limited. According to Roberts *et al*. (2011), fertilisation rates in lab experiments can be as high as 89%, although subsequent survival rates are very low. However, given the difficulties experienced maintaining *M. modiolus* in the aquarium, mortality is likely to be higher than in the wild (although predation should also be considered a factor for wild populations). Efforts to identify *M. modiolus* larvae and seasonal recruitment patterns in the field have also been hampered by the resemblance of *M. modiolus* larvae to *Mytilus edulis* larvae (Schweinitz and Lutz, 1976). Such limitations should be considered when reviewing information on larval behaviour for particle tracking modelling studies.

1.1.2 Flame shells

Information on flame shell (*Limaria hians*) spawning and larval behaviour in Scotland is also limited; attempts to maintain adults in the laboratory have largely been unsuccessful and most of the information available is from field experiments to study recruitment (e.g. Trigg, 2009).

Trigg (2009) explored various aspects of *L. hians* ecology including reproduction and recruitment through field experiments. Observations of sexually ripe gonads indicated that spawning occurs in Loch Creran (west coast of Scotland) from the middle of April to the end of July with the majority occurring in May and June. However, timing of spawning may vary between beds around Scotland.

Recruitment of *L. hians* in Loch Creran was found to begin in June and then peter out in September (Trigg, 2009). The majority of settlement occurred in July and August with many fewer recently settled spat found either side of these months. Lebour (1937) suggests that *L. hians* larvae spend a few weeks as plankton during the pelagic phase before settling as post larvae.

1.2 Habitat preferences

Connectivity can be considered as either genetic connectivity (i.e. genetic similarity between populations which acts at a population level) or ecological connectivity. Ecological connectivity is important on an individual level and determined by the ability of a species to reach an essential habitat (e.g. to lay eggs, meet partners, feed, etc.). Marine bivalves such as *M. modiolus* require specific conditions to survive and grow as a biogenic reef formation (e.g. see Gormley *et al*., 2013). For example, there is evidence that bivalve larvae are attracted to certain substrates based on the presence of biofilms (Hadfield and Paul, 2001), chemical cues and even sound (Lillis *et al*., 2013). Therefore, the incorporation of spatial information on suitable habitat in parallel with larval dispersal modelling can help determine ecological connectivity, which can be applicable for conservation measures such as restoration (Elsäßer *et al.,* 2013).

1.2.1 Horse mussels

Horse mussel beds develop in areas of weak to strong water movement, in depths of 5-220 m, although most known beds are in 20-50 m (SNH, 2018a). Habitat suitability modelling by Elsäßer *et al.* (2013) found that depth and substrate were the key drivers in *M. modiolus* distribution. Depth explained ~49% of the variation in the distribution of *M. modiolus* with a peak in the probability of occurrence around 30 m, but generally high between 20-40 m. *M. modiolus* presence was positively associated with mud and sand substrata, with *M. modiolus* most frequently occurring in fine substrates while occurrence was negatively associated with cobbles, boulders, gravel, bedrock and pebbles.

Gormley *et al.* (2013) also used *M. modiolus* occurrence data to create an environmental envelope analysis to determine suitable habitat for *M. modiolus* beds across the UK. The preferred range of environmental attributes was characterised in terms of the interquartile ranges of the environmental variable values over the known occurrence locations. The selected conditions for the analysis were; depth: 0-20 m; temperature: 9-10°C; current speed: 0.5-1.115 m s^{-1}; slope: 0-0.345%; and salinity: 34-35 PSU. The difference in depth preference compared to Elsäßer *et al.* (2013) may be due to the presence data used. Key environmental landscape characteristics associated with *M. modiolus* beds were sea lochs, assorted shallow and shelf sediment plains comprising differing substrates and tidal conditions, as well as photic rock.

1.2.2 Flame shells

L. hians communities are commonly found on shallow sublittoral ground composed of sand and mixed muddy gravel and in varying tidal currents (0.25-1.5 m/s) (Connor *et al.,* 2004; Hall-Spencer and Moore, 2000). *L. hians* has also been described as living on coarse sandy gravel sediments with individuals occurring from the low water mark down to about 100 m water depth (Hayward and Ryland, 1990). However, *L. hians* beds are most frequent in water depths of 5-25 m, occasionally down to depths of >40 m (SNH, 2018b) in a range of salinity levels

(18-35 PSU) (Lieberknecht *et al.,* 2004). Cook (2016) found that crushed shell provided a successful restoration settlement substrate for *L. hians* at Port Appin (west coast of Scotland), with juvenile *L. hians* abundance 339% higher compared to a reference site. The reference site was historically a flame shell bed, but the species has not been recorded there in recent years. Environmental variables such as depth have been used to map flame shell bed areas. However, further work is required to determine suitable habitat for flame shell beds across Scotland.

1.3 Aims

The aim of the current study was to investigate the degree of connectivity between existing known locations of two PMFs, horse mussel beds and flame shell beds, both within and outwith the currently designated MPA network. Connectivity was investigated using a particle tracking model forced by hydrodynamic model output at two different resolutions, to explore how model resolution might influence the estimated degree of connectivity. Other areas of potentially suitable habitat were investigated using habitat suitability modelling and the connectivity between these areas and the known beds was explored.

2. METHODOLOGY

2.1 Hydrodynamic and particle tracking models

The hydrodynamic model used in this study is the Scottish Shelf Model (SSM), an unstructured-grid, three dimensional Finite-Volume Community Ocean Model (FVCOM) developed by Marine Scotland Science. The SSM consists of a wider domain coarser resolution model covering the whole of the Scottish continental shelf (Wolf *et al.*, 2016a) as well as a number of higher resolution sub-models in some areas within that domain (O'Hara Murray & Gallego, 2017; Price *et al.*, 2016a,b,c,d). The wider SSM model has been run for a single climatological year representing present day (1990 - 2014) climatic conditions (De Dominicis *et al.*, 2018a), and the sub-models are nested within this model. The outputs from the wider domain model and the sub-models have been combined to form an integrated output data set. This integrated output covers the same spatial extent as the wider domain model but in addition has higher resolution in the areas covered by the sub-domain models (Wolf *et al.*, 2016b). For a full description of the SSM and the derivation of the climatological forcing see De Dominicis *et al.* (2017).

Due to the increased complexity and higher horizontal resolution of the integrated grid output the simulations take a considerable time to run in comparison to the coarser grid output. Therefore, the coarser grid output was used in the current study in order for all the simulations to be completed in the time available. Where the coarser grid did not resolve some of the sea lochs adequately for given release areas (see 2.5 below), the integrated grid was used. Details and comparisons of the areas included are provided in Section 3.1.2.

A Lagrangian particle tracking model, FVCOM I-State Configuration Model (FISCM) was used (Liu *et al*., 2015, https://github.com/GeoffCowles/fiscm). This code tracks released virtual particles, representing the larvae of horse mussels and flame shells, that are forced by the SSM outputs. Here, the particles were assumed to be passive (no directed swimming) and were subject to advection by currents and diffusion, with a horizontal diffusivity of 10 $m^2 s^{-1}$ (Okubo, 1971). The particles were tracked on a 10 minute interval, using hourly hydrodynamic model outputs, and the particle locations saved to file every 3 hours. The FISCM settling option was implemented here, where after the pelagic larval duration the particles are forced to settle and are no longer tracked.

2.2 Defining release areas

Information on the known locations of the PMFs was available as point source observational data records. The spatial extent of the beds was not included in these records and therefore release areas needed to be defined to represent the extent of the assumed bed area. This was also beneficial to reduce the number of areas investigated, as records in close geographical proximity were combined (see below). Release areas were defined from point source presence data and release points were created within the areas, as detailed below.

To define the particle release areas, firstly the tidal excursions at the known point source positions were calculated over a spring-neap tide using the SSM output. This provided an estimate of the potential distance the released particles could be displaced during a single M_2 tidal cycle (12.42 hours) alone. The results from the known point source positions formed a distribution of tidal excursions that were positively skewed. The median tidal excursion for each species was therefore chosen. These were 6.4 km for horse mussel beds and 12.66 km for flame shell beds; the difference in the distances was due to the location of the point source data and differences in tidal excursion in those particular areas. In ArcGIS 10.3 a buffer was applied to each known presence point based on the median tidal excursion distance. Any overlapping buffer areas were combined using the dissolve tool in ArcGIS 10.3, making the assumption that two point source data records within a tidal excursion distance would belong to the same bed. These areas were then clipped to the SSM mesh, thus ensuring that the release areas were covered in the model. Where the areas were within a protected area the release areas were clipped to the extent of the protected area to allow for comparisons between beds located inside and outside MPAs. Figures 2 and 3 show the release areas and the presence data points for horse mussel beds and flame shell beds respectively, defined on the coarser SSM grid. Also shown are the currently designated MPAs. At the time of writing, the Loch Carron MPA was under consultation, and the boundary of the urgent MPA designation is shown in Figures 2 and 3. All the release areas have been named and these are listed in Table 1 for the horse mussel bed release areas and Table 2 for the flame shell bed release areas.

Using Matlab 2017b, a regular grid of 0.01º (approximately 1.1 km) was defined over each release area. So as not to introduce numerical bias, the same number of particles were released at each time step at each release location over the spawning window. This was selected to be 10 particles, as a compromise so that the smaller areas released sufficient particles and the larger areas did not release too many particles to be tracked with the available computational resources, whilst achieving numerical stability to account for the random effect of diffusion.

Previous studies of particle tracking of *M. modiolus* spawning released particles from point sources every 5 minutes (Elsäßer *et al.*, 2013). As the current particle tracking was carried out over a longer time period and also over significantly larger release areas, it was not computationally feasible to match this rate of release. Therefore, to simulate the trickle spawning behaviour of *M. modiolus* (Brown, 1984; Seed and Brown, 1974), different release rates were explored and a release rate of 10 particles every 12 hours over the spawning window was ultimately chosen. Over the duration of the simulations, this release rate reflects the changes to current speeds over the full tidal cycle. A higher release rate was therefore not required. There was no information available for *L. hians* spawning behaviour. Therefore, 10 particles were released daily. The total number of release locations and particles for each release area can be found in Annex 1.

A spawning window between June and October was selected for *M. modiolus* based on available literature, with a peak spawning period between mid-July - mid-September (Brown, 1984; Comley, 1978; Elsäßer *et al.*, 2013). The spawning window has been found to differ based on the geographic location of the beds, with individuals in higher latitudes (i.e. Norway and Sweden) found to spawn later than in Northern Ireland (Brown, 1984). Not enough information was available on spawning windows for Scottish horse mussel beds and so the entire known spawning months (June to October) were therefore included (Brown, 1984; Comely, 1978; Elsäßer *et al.*, 2013). The settlement window was selected to be the same as a previous particle tracking study in the Irish Sea, 34-56 days (Elsäßer *et al*., 2013).

For *L. hians* both the settlement and the spawning windows were taken from Trigg (2009). Based on this information, a spawning window between April and July and the settlement window of 20-25 days were chosen. Table 3 summarises the spawning and settlement windows selected for the current study for both horse mussels and flame shells.

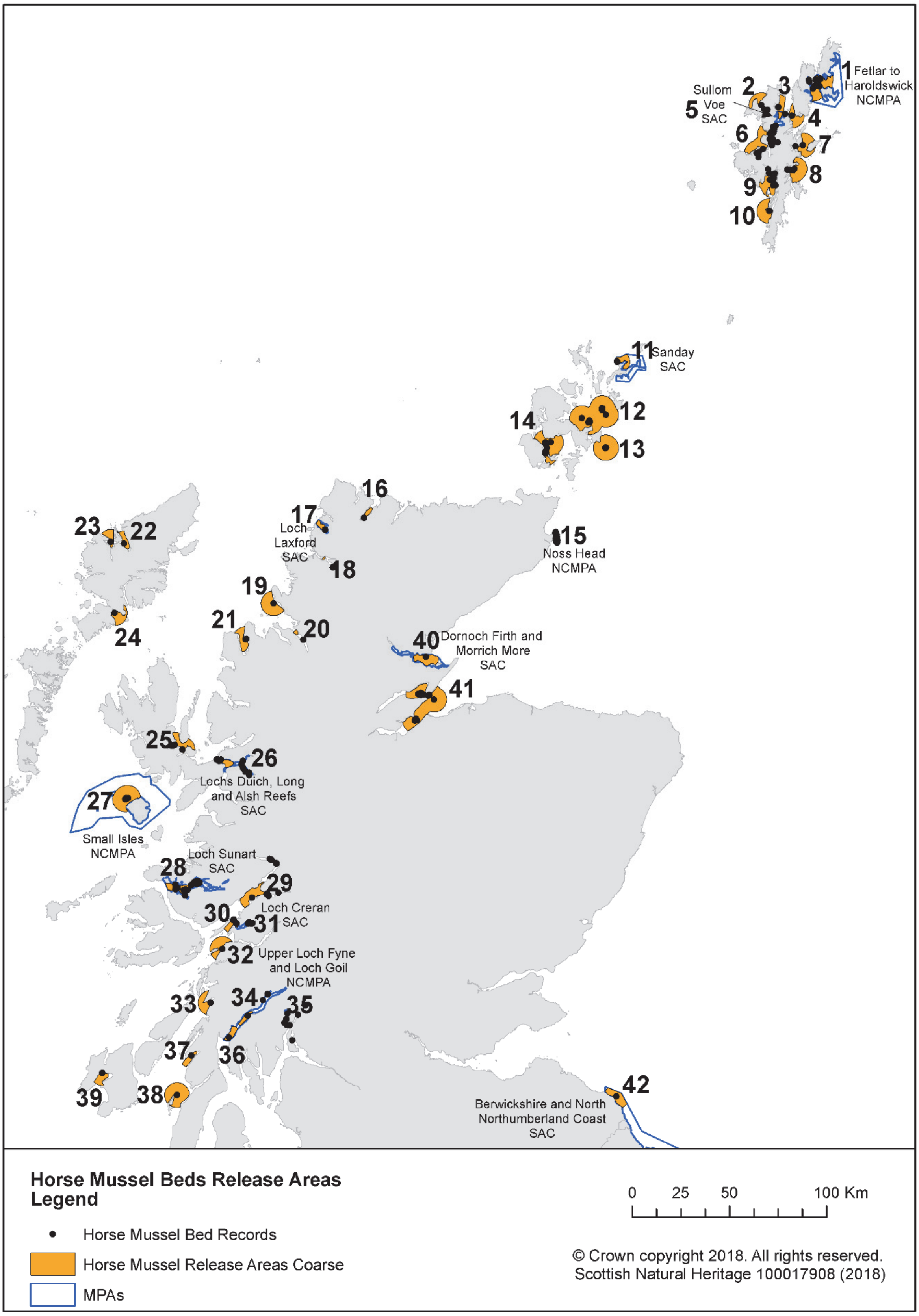

Figure 2. Release areas for horse mussel beds based on the presence points, defined on the coarser SSM grid*. Also shown are designated MPAs (blue outline) for horse mussel beds.*

Table 1. Location names for horse mussel bed release areas. Where the release area is a MPA it has been highlighted in bold.

Release Area Number	Location Name
1	**Fetlar to Haroldswick NCMPA**
2	Ronas Voe
3	Yell Sound North
4	Yell Sound East
5	**Sullom Voe SAC**
6	Busta Voe to Brindister Voe
7	Dury Voe and Lunning Sound
8	Wadbister Voe and Gletness
9	Weisdale and Whiteness Voes
10	West and East Burra
11	**Sanday SAC**
12	Stronsay Firth and Shapinsay Sound
13	Copinsay
14	Scapa Flow
15	**Noss Head NCMPA**
16	Loch Eriboll
17	**Loch Laxford SAC**
18	Loch a Chairn Bhain
19	Summer Isles
20	Loch Broom
21	Loch Ewe
22	Loch Ròg An Ear
23	Loch Ròg
24	Loch an Tairbeairt
25	Loch Sligachan and Caol Mòr
26	**Lochs Duich, Long and Alsh Reefs SAC**
27	**Small Isles NCMPA**
28	**Loch Sunart SAC**
29	Lochs Leven and Linnhe
30	Port Appin Narrows, Loch Linnhe
31	**Loch Creran SAC**
32	Firth of Lorn
33	Loch Craignish
34	**Upper Loch Fyne and Loch Goil NCMPA (Upper Loch Fyne)**
35	**Upper Loch Fyne and Loch Goil NCMPA (Loch Goil)**
36	**Upper Loch Fyne and Loch Goil NCMPA (Otter Ferry)**
37	Loch Caolisport
38	Sound of Gigha
39	Loch Indaal
40	**Dornoch Firth and Morrich More SAC**
41	Cromarty Frith and Moray Firth
42	**Berwickshire and North Northumberland Coast SAC**

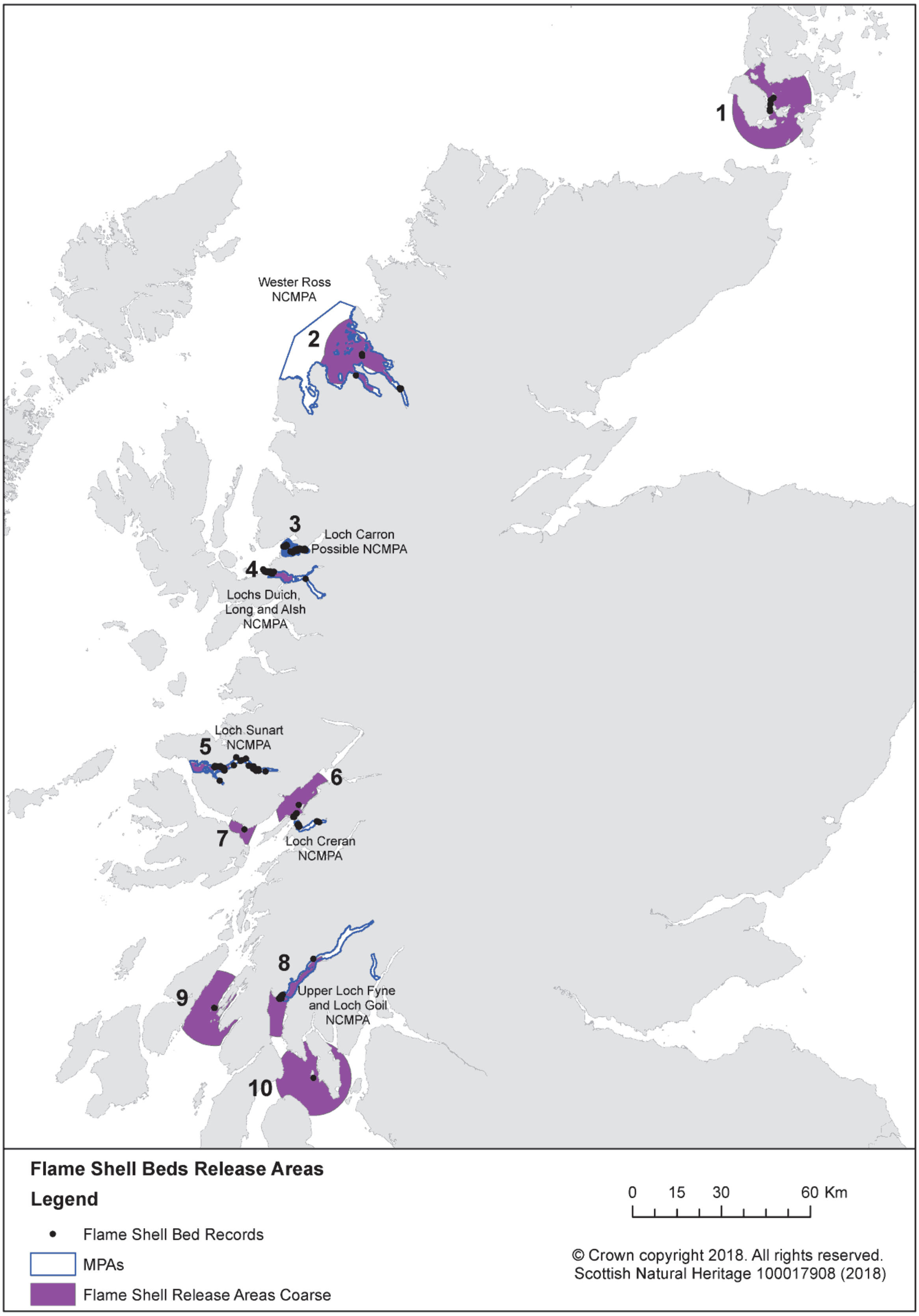

Figure 3. Release areas for flame shell beds based on the presence points, defined on the coarser SSM grid. *Also shown are designated MPAs for flame shell beds (blue outline).*

Table 2. Location names for flame shell bed release areas. Where the release area is a MPA it has been highlighted in bold.

Release Area Number	Location name
1	Scapa Flow and Hoy
2	**Wester Ross NCMPA**
3	**Loch Carron NCMPA**
4	**Lochs Duich, Long and Alsh NCMPA**
5	**Loch Sunart NCMPA**
6	Loch Linnhe
7	Sound of Mull
8	**Upper Loch Fyne and Loch Goil NCMPA**
9	Sound of Jura
10	Sound of Bute

Table 3. Spawning window dates and settlement window details for both species

	Horse mussels (*Modiolus modiolus*)	**Flame shells (*Limaria hians*)**
Spawning window	1st June - 31st October	1st April - 31st July
Settlement window	34 - 56 days	20 - 25 days

2.3 Habitat suitability modelling

A presence-only model, Maxent (Maximum Entropy), which predicts the geographic distribution of a habitat or species based on its optimal environmental niche (Phillips and Dudík, 2008), was used to assess whether the particles were reaching areas of suitable habitat. The algorithm in Maxent minimises the relative entropy between two probability densities, one from the presence data and the other from the input environmental layers, defined in covariate space (Elith *et al*., 2011). The feature records provided by SNH of horse mussel beds and flame shell beds were used as the presence data.

Environmental layers previously used in Gormley *et al.* (2013) for horse mussel beds habitat suitability were used here. The layers had a grid resolution of 0.005^0, covering the UK. Details of all the variables included are listed in Table 4.

Table 4. Environmental variables considered in Maxent habitat suitability modelling.

Environmental variable	Details
Bathymetry	GEBCO_08 30-second arc Bathymetry resolution (GEBCO, 2011). Depth (m).
Slope	Adapted in ArcGIS 10.3 from GEBCO_08 Bathymetry. Percentage gradient of the seafloor (%).
Bottom temperature	NOAA, World Ocean Atlas (Locarnini et al., 2009). Climatological annual mean bottom temperature (°C).
Bottom salinity	NOAA, World Ocean Atlas (Antonov *et al*., 2010). Climatological annual mean sea bottom salinity (PSS).
Current speed	Atlas of UK marine renewable energy resources (DTI, 2004). Supplemented by Current speed data on UKHO Navigation Charts (Digimap Marine, 2012) and BODC oceanographic data (BODC, 1998). Average spring current speed (ms^{-1}).
Landscape	UKSeaMap/MESH webGIS (Connor *et al*., 2006). Seabed landscape features, broad patterns in seabed character.

The outputs of the model runs were validated using the area under the curve (AUC). If the AUC was above 0.9 then it indicated that the result prediction is very good and there was a high probability of the habitat being present. The models were replicated 10 times, with the presence data internally split into 90% training and 10% test points. There were no absence data available for either habitat investigated and so 10,000 pseudo-absence points were included. Please see the Discussion section about assumptions and limitations of the habitat modelling used in this project.

2.4 Analysis of modelled outputs

To analyse the particle tracking outputs from FISCM, Matlab 2017b was used. All the settled tracked particles from each release area were read in, along with the release area polygons. Using the 'in-polygon' function the numbers of particles either remaining in the release area (self-recruitment) or moving to other release areas were then counted. If a particle reached a release area at any point during the settlement window, it was included in the count. As a window of potential settlement was included in the analysis, it was thought best to include other areas the particle could potentially reach during the pelagic duration of the larvae and so the particle could end up in more than one release area. Basically, each particle does not represent a single individual that could only settle once in a given location but a collection of individuals spawned in the same area (release location) within the same spawning event (particle release instance), which could settle in a multitude of locations within their settlement window. Once the particle had reached the settlement window end it was no longer counted. The number of particles that were found in each release area during the settlement window was calculated and expressed as a percentage of the total number of released particles in a connectivity matrix. The stronger connections, where connections were ≥1%, were mapped spatially using ArcGIS. The spatial results are presented as maps showing connections between areas. The connections of <1% were excluded as they were deemed to obscure the more important connections displayed in the figures.

For the habitat suitability analysis the average output raster of the replicated runs of the Maxent model was plotted in ArcGIS as a percentage probability of suitable habitat being found. The raster output of Maxent was then multiplied using raster calculator to convert the output into a percentage. This raster layer was then reclassified into 10% bands and converted into a polygon. Using the threshold of suitable habitat defined by Gormley *et al*. (2013), above 50% being classified as most suitable habitat, these areas were selected and separated. A 500 m buffer was applied around the selected areas in order to merge some of the neighbouring suitable areas and the output was saved as a polygon file. The overlapping release areas were removed from the polygon file leaving only newly identified suitable habitat areas from the Maxent modelling.

2.5 Model assumptions and limitations

As with any modelling study a number of assumptions have been made here and each model will also have its own underlying uncertainties.

The hydrodynamic modelling output used in the study is a climatology representing a 25 year period 1990 - 2014 (De Dominicis *et al*., 2018a). This means that extreme (e.g. storm) events were not included and inter-annual variability cannot be estimated. The results from this study will represent an average year of current conditions. The wider domain SSM output which was primarily used here does not adequately resolve some of the sea lochs, and therefore some of the areas where *L. hians* and *M. modiolus* beds are known to occur. These areas were therefore not included. To overcome this issue, some of the worst affected release areas have been simulated using the integrated grid output version of the SSM, which combines the coarser and finer resolution model outputs, and the results are presented in Section 3.2. It would be advantageous to include all the other release areas using the integrated output in order to track the particles into these areas not currently well resolved by the coarser grid. However, this would be a very computationally expensive exercise that should be performed in the future, when more appropriate computing resources become available and/or changes to the particle tracking code increase the efficiency of the simulations.

For the larval behaviour in the particle tracking simulations, a number of assumptions and simplifications were made, such as the pattern and duration of spawning and length of the pelagic duration and settlement window for each species. There is also no directed swimming behaviour implemented (not even vertical migration) and no mortality was built into the particle tracking model so all particles "survive" the duration of the simulations. To quantify survivorship correctly we would have also needed an estimate of numbers spawned, which was not available. The number of particles released from each area aims to replicate the duration of the spawning season and the spatial extent of spawning only, and is not a measure of offspring production. Therefore it does not reflect a realistic absolute number of larvae and also the rate at which the particles are released does not reflect the quantitative temporal distribution of spawning. To implement a greater degree of biological realism that addresses these aspects would require a much greater biological knowledge and field data than are currently available. The implications of model assumptions and simplifications will be considered in the Discussion section.

3. RESULTS

3.1 Particle tracking modelling

3.1.1 Horse mussel beds

From the feature records of known horse mussel beds around Scotland, 42 release areas were investigated, including 12 designated MPAs. The spawning window selected for this study was over 5 months from June until October, with a settlement window of between 34 - 56 days after spawning.

Figure 4 shows the connectivity matrix for all the horse mussel areas investigated. The percentage of particles from each release area is shown. If the release site is an MPA then the area is highlighted in blue, with the name of the designation shown. The release areas are reordered in the matrix to reflect the predominately clockwise transport of particles around Scotland due to the residual circulation. Based on these results five geographic regions are defined - South-west Scotland (release areas 28 - 39), North-west Scotland (release areas 16 - 27), Orkney Islands (release areas 11 - 14), Shetland Islands (release areas 1 - 10), and Moray Firth (including Noss Head, release areas 15, 40, 41) – and these are indicated in the matrix. Each of the regions is reasonably self-contained with only a limited amount of weak import/export between them. North-west Scotland exports larvae to the Orkney Islands (with a number of connections with ≥1% of particles). South-west Scotland exports particles to North-west Scotland, but all the connections are <1% of the total number of particles. The Shetland Islands export to the Orkney Islands, but all the connections are extremely weak, with <0.03% of the particles reaching Orkney in all cases. The Orkney Islands also export to the Moray Firth, but all the connections are due to <0.8% of the particles. North-west Scotland also exports to the Moray Firth (<0.9% of particles).

The matrix shows that there is some degree of self-recruitment for all of the areas (dashed diagonal line) and these levels are summarised in *Table 5*. Most of the intra-region connections are above the dashed self-recruitment line, indicating that the regions are connected in a clockwise manner around the Scottish coastline.

The results show that all release areas within the Shetland Islands region are connected to one another. This is also the case for the Orkney Islands region. There is also a high degree of inter-connectivity within the other regions. Within the North-west Scotland region the flow of particles is predominantly northward, with the southern release areas exporting to the northern ones.

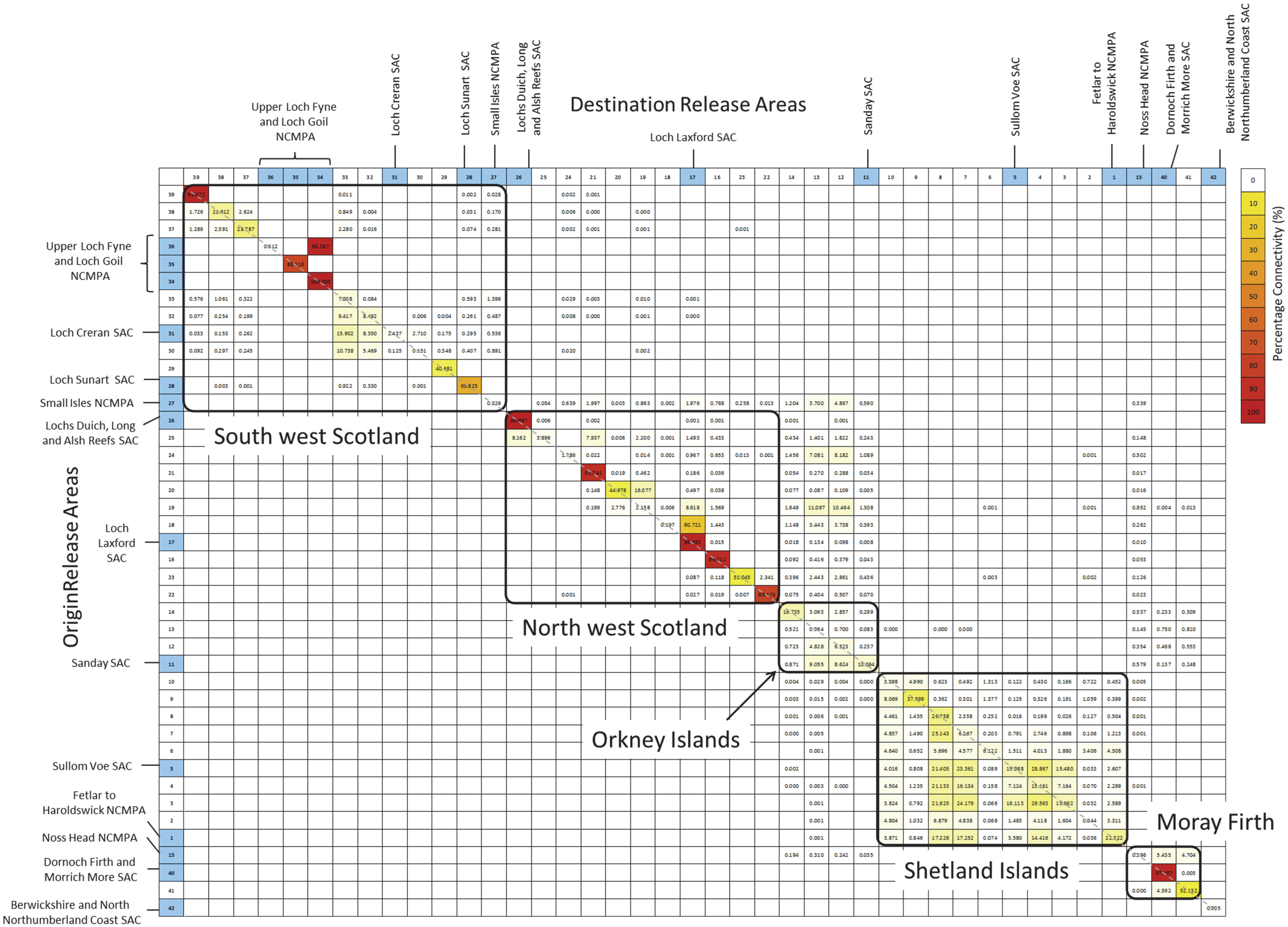

Figure 4. Connectivity matrix which shows the percentage of the particles from the origin release areas reaching the destination release areas for horse mussel beds. The diagonal dashed line indicates where self-recruitment could occur. The order of the release areas has been changed to reflect how the particles were transported around the Scottish coastline.

Table 5. Self-recruitment percentage value for all horse mussel bed release areas. Where the release area is a MPA it has been highlighted in bold.

Release area number	Self-recruitment (%)	Location name
1	**22.3**	**Fetlar to Haroldswick NCMPA**
2	0.0	Ronas Voe
3	15.7	Yell Sound North
4	15.2	Yell Sound East
5	**16.0**	**Sullom Voe SAC**
6	6.1	Busta Voe to Brindister Voe
7	6.3	Dury Voe and Lunning Sound
8	26.8	Wadbister Voe and Gletness
9	37.6	Weisdale and Whiteness Voes
10	3.9	West and East Burra
11	**10.1**	**Sanday SAC**
12	6.5	Stronsay Firth and Shapinsay Sound
13	1.0	Copinsay
14	16.7	Scapa Flow
15	**0.4**	**Noss Head NCMPA**
16	96.2	Loch Eriboll
17	**99.4**	**Loch Laxford SAC**
18	0.2	Loch a Chairn Bhain
19	2.2	Summer Isles
20	45.0	Loch Broom
21	95.7	Loch Ewe
22	89.5	Loch Ròg An Ear
23	51.0	Loch Ròg
24	1.8	Loch an Tairbeairt
25	3.9	Lochs Sligachan and Caol Mòr
26	**99.7**	**Lochs Duich, Long and Alsh Reefs SAC**
27	**0.2**	**Small Isles NCMPA**
28	**65.8**	**Loch Sunart SAC**
29	40.7	Lochs Leven and Linnhe
30	0.2	Port Appin Narrows, Loch Linnhe
31	**2.4**	**Loch Creran SAC**
32	8.5	Firth of Lorn
33	7.0	Loch Craignish
34	**100.0**	**Upper Loch Fyne and Loch Goil NCMPA (Upper Loch Fyne)**
35	**88.4**	**Upper Loch Fyne and Loch Goil NCMPA (Loch Goil)**
36	**0.6**	**Upper Loch Fyne and Loch Goil NCMPA (Otter Ferry)**
37	28.8	Loch Caolisport
38	21.6	Sound of Gigha
39	99.4	Loch Indaal
40	**97.5**	**Dornoch Firth and Morrich More SAC**
41	52.1	Cromarty Frith and Moray Firth
42	**0.9**	**Berwickshire and North Northumberland Coast SAC**

The stronger (≥1%) connectivity results are also plotted spatially in the following figures and for clarity the release areas have been sub-sectioned into four areas, Shetland Islands (Figure 5), Orkney Islands and surrounding release areas (Figure 6), north-west Scotland (Figure 7) and south-west Scotland (Figure 8). The percentage of connectivity between different release areas is shown as varying line thickness and the level of self-recruitment in each area is represented by different sized circles. The percentage of self-recruitment is also shown underneath each release area number. Arrows show direction of connection (from origin to destination). Only connections where ≥1% (when rounded to 1 decimal place) of the particles originating from one area reach another area are shown in these figures. Whilst it is difficult to quantify the potential ecological significance of the weaker connections (< 1%), displaying them in the figures obscures the patterns displayed by the stronger connections (although they are presented in the connectivity matrices).

The Shetland Islands appear to be somewhat isolated from the other areas, although Figure 4 shows there are five extremely weak connections from the North-west and Orkney release areas (<0.003% of particles). However, Figure 5 shows that Shetland is well connected internally with all the release areas showing relatively strong inter-connections. The Shetland release areas do not have a high level of self-recruitment, with the majority of the particles travelling out of the release area and into other release areas around Shetland.

The Orkney Islands release areas are also well connected to each other with low levels of self-recruitment (Figure 6). They do, however, receive particles from release areas on the north-west coast of Scotland (Figures 7 & 8).

Within the north-west coast of Scotland there is a high level of self-recruitment in some of the release areas, particularly within the sea lochs (Figure 7). Some of these areas in the north-west show the greatest travel distance to other areas, in particular release areas 24 and 25 (Loch an Tairbeairt and Lochs Sligachan and Caol Mòr). This is due to the residual current which runs up the west-coast of Scotland and around to Orkney.

Interestingly, the south-west of Scotland release areas are not very well connected to the north-west Scotland release areas, apart from release area 27 (Small Isles NCMPA) which has stronger connections to the north-west region including the Loch Laxford SAC, as well as Orkney (Figure 8). The remaining connections are relatively weak with <0.03% of particles connecting to other north-west release areas. The Small Isles NCMPA lies on the boundary between the south-west and north-west regions, and could well have been incorporated into the north-west region. It was chosen to be in the south-west region as it acts as a sink for particles from a number of the south-west release areas. The south-west areas are quite well connected to each other, with again some high levels of self-recruitment within the sea lochs.

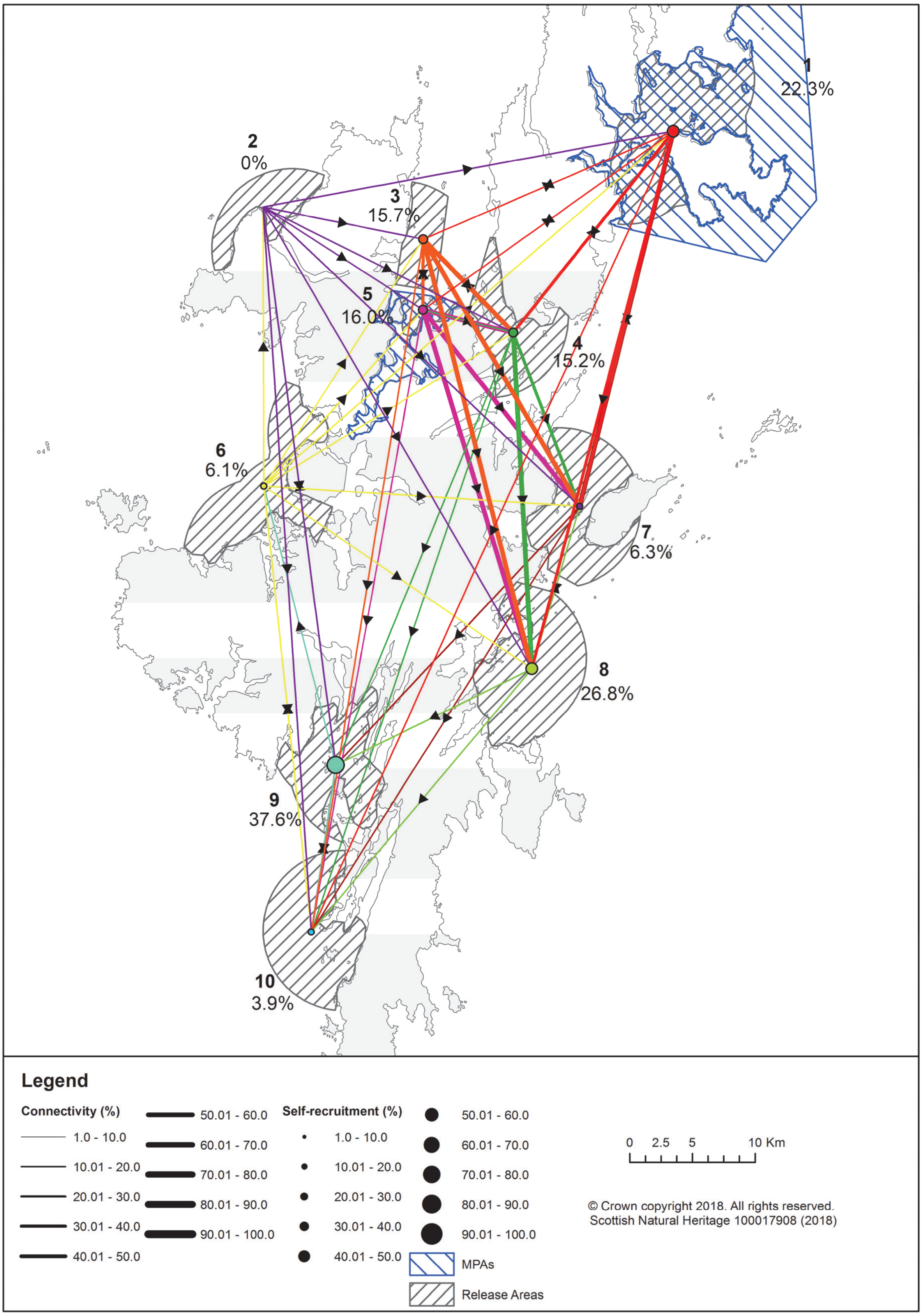

Figure 5. Horse mussel beds self-recruitment (weighted circles, and also shown as percentage value below release area number) and connectivity (weighted lines) in the Shetland release areas. Release areas are differentiated by colour. Only the connections due to >1% of particles are shown.

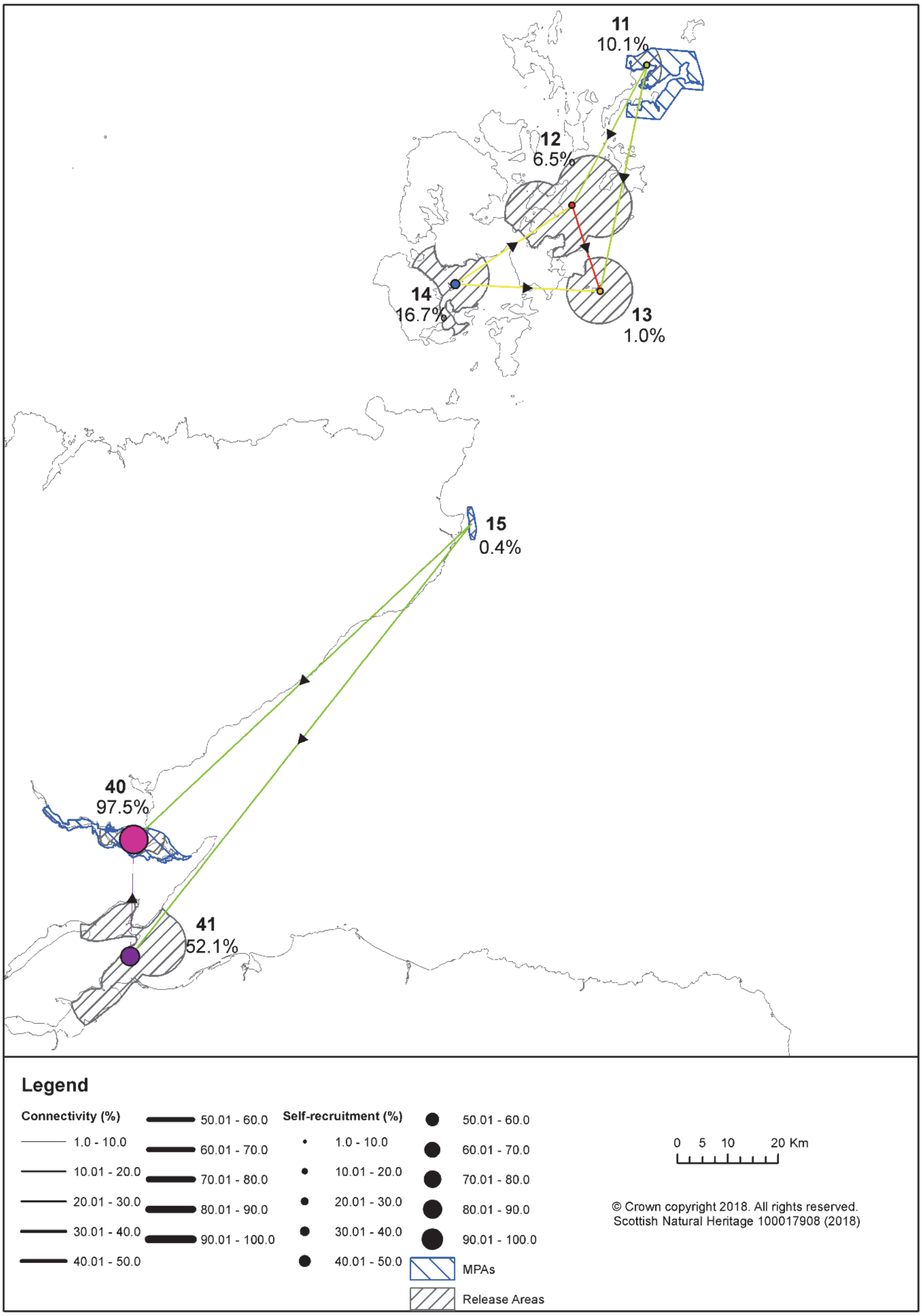

Figure 6. Horse mussel beds self-recruitment and connectivity in the Orkney and north-east Scotland release areas. Only the connections due to >1% of particles are shown.

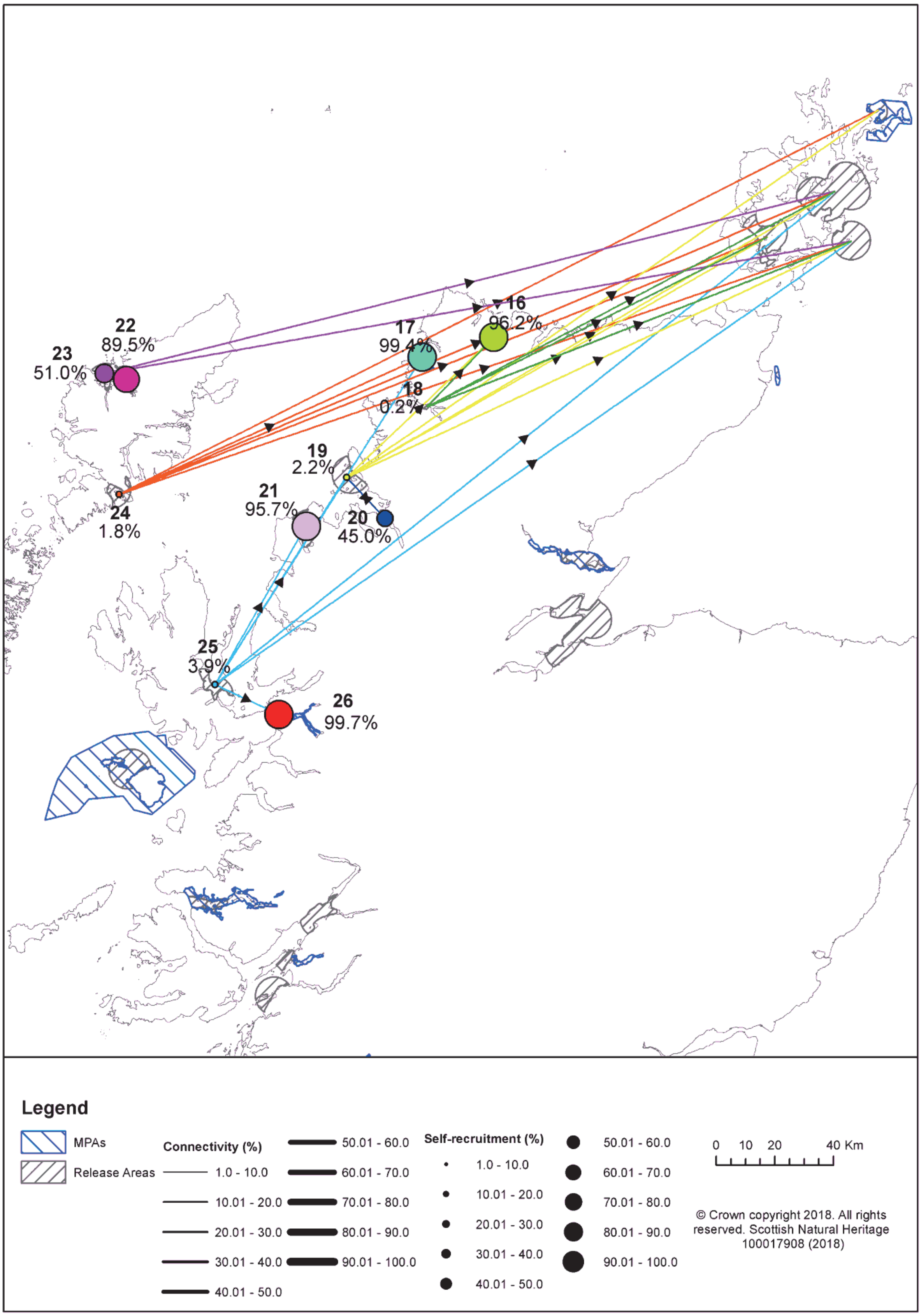

Figure 7. Horse mussel beds self-recruitment and connectivity from north-west Scotland release areas. Only the connections due to >1% of particles are shown.

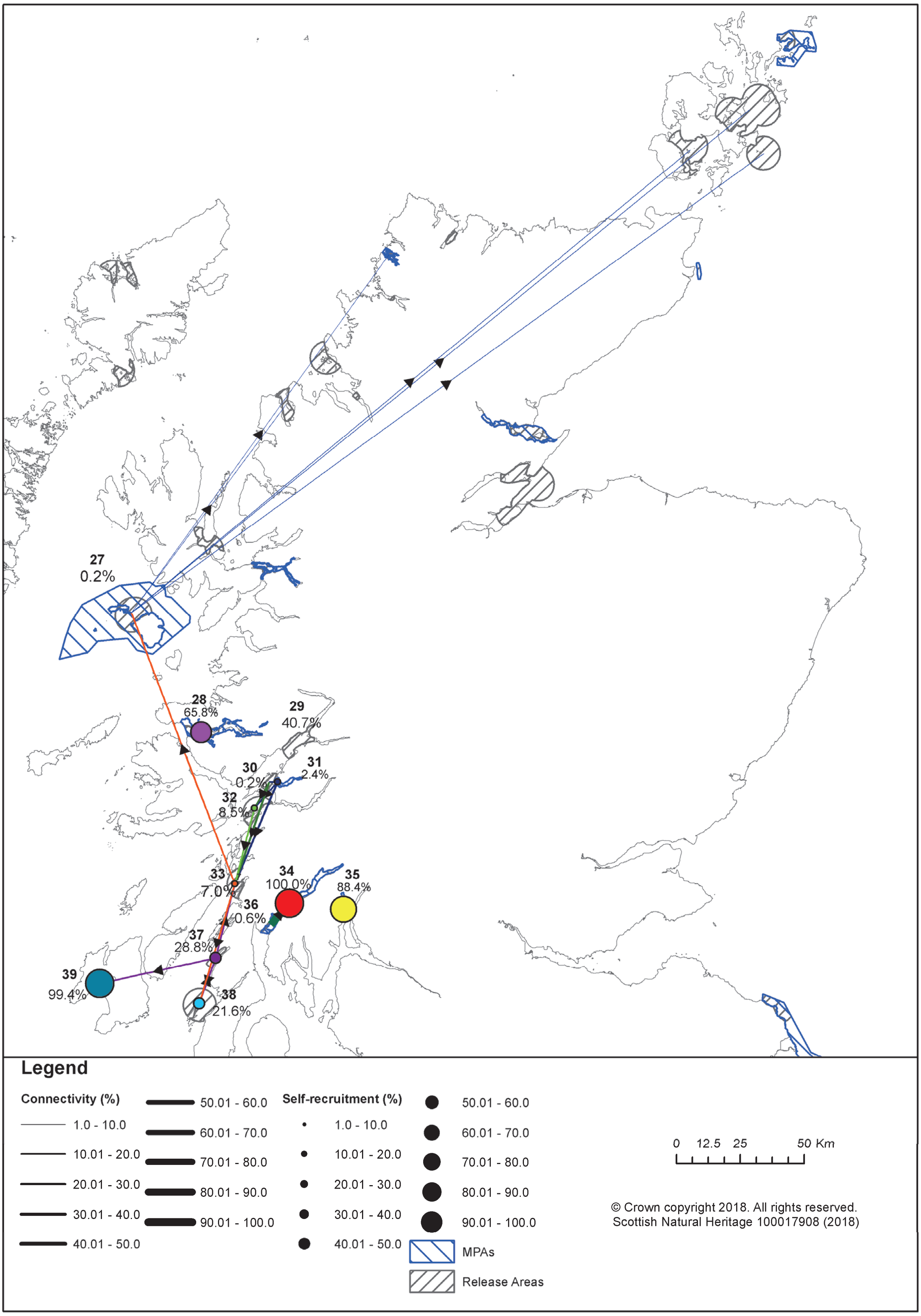

Figure 8. Horse mussel beds self-recruitment and connectivity from south-west Scotland release areas. Only the connections due to >1% of particles are shown.

Release area 42 (Berwickshire and North Northumberland Coast SAC) did not have any connections to other areas in Scottish waters, and the self-recruitment level was low at 0.9% (Figure 4), and so the results for this release area have been presented differently. Figure 9 shows the particle densities at the end of the tracking simulation, 56 days after the last particles were released. This is the percentage of the total number of particles released during the simulation in each 0.05° x 0.05° regular grid square. Each grid square has an area of approximately 30 km^2. A logarithmic scale is used to show the difference between patches of low particle density. Due to the residual circulation, the particles leave the release area and generally move south, and could be connected to horse mussel beds in England. It is not clear from the current investigation whether Release area 42 (Berwickshire and North Northumberland Coast SAC) receives particles from other areas to populate the bed, given the low level (<1%) of self-recruitment in the current simulations. The densities of particles at the end of each of the horse mussel bed simulations are presented in Annex 2.

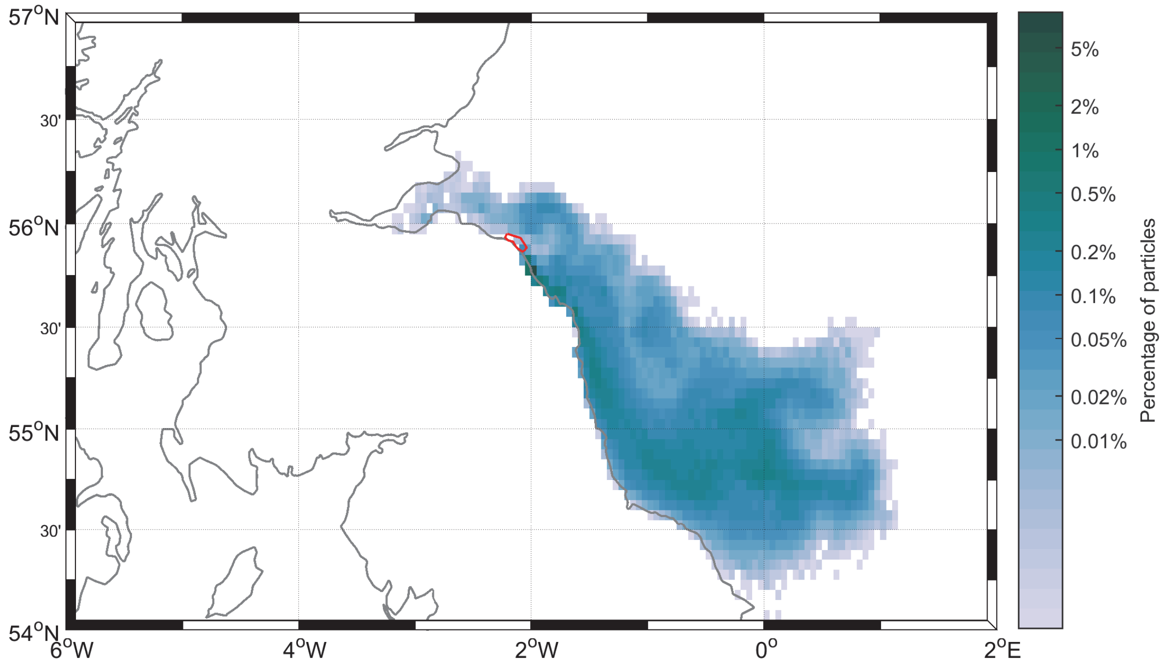

Figure 9. Particle densities 74 days into the particle tracking simulation for release area 42 (Berwickshire and North Northumberland Coast SAC).

3.1.2 *Flame shell beds*

From the feature records of known flame shell beds around Scotland, ten release areas were investigated. Flame shell beds are found on the west coast of Scotland and also Orkney. There are currently six designated MPAs for flame shell beds, including the recently designated Loch Carron MPA.

Figure 10 shows the connectivity matrix for all the flame shell release areas investigated. The percentage of particles from each release area settling in each of the other release areas is shown. The release areas are reordered in the matrix to reflect the predominantly clockwise transport of particles around Scotland, and the release areas that are designated as MPAs are indicated. All the release areas show some degree of self-recruitment, although this is very low for Loch Linnhe (release area 7, 0.5%). Loch Linnhe is, however, weakly connected to release areas 7 and 9, the Sound of Mull and Sound of Jura, respectively. All the release areas are connected to at least one other area, although this connection is weak in some cases, e.g. Loch Sunart NCMPA only acts as a sink for 0.001% of particles from the sound of Jura (area 9).

Table 6 summarises the percentage of self-recruitment for all flame shell bed release areas investigated. These results, and the stronger connections in Figure10 (≥1% of particles when rounded to 1 decimal place), are shown spatially in Figure 11.

Origin Release Area \ Destination Release Area	10	8 (Upper Loch Fyne and Loch Goil NCMPA)	9	6	7	5 (Loch Sunart NCMPA)	4 (Lochs Duich, Long and Alsh NCMPA)	3 (Loch Carron Possible NCMPA)	2 (Wester Ross NCMPA)	1
10	13.677	1.519								
8 (Upper Loch Fyne and Loch Goil NCMPA)	0.777	98.575								
9			28.212			0.001				
6			2.741	0.546	1.694					
7			18.868	0.017	4.332					
5 (Loch Sunart NCMPA)			0.007		5.608	61.414				
4 (Lochs Duich, Long and Alsh NCMPA)							99.116	0.468		
3 (Loch Carron Possible NCMPA)							0.098	36.710		
2 (Wester Ross NCMPA)									50.215	1.619
1										30.652

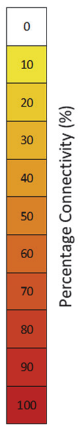

Figure 10. Percentage connectivity matrix for flame shell bed release areas. The diagonal dashed line indicates where self-recruitment could occur. The order of the release areas has been changed to reflect how the particles were transported around the Scottish coastline.

Table 6. Self-recruitment percentage value for all flame shell bed release areas. Where the release area is an MPA it has been highlighted in bold.

Release area number	Self-recruitment (%)	Location name
1	30.7	Scapa Flow and Hoy
2	**50.2**	**Wester Ross NCMPA**
3	**36.7**	**Loch Carron possible NCMPA**
4	**99.1**	**Lochs Duich, Long and Alsh NCMPA**
5	**61.4**	**Loch Sunart NCMPA**
6	0.5	Loch Linnhe
7	4.3	Sound of Mull
8	**98.6**	**Upper Loch Fyne and Loch Goil NCMPA**
9	28.2	Sound of Jura
10	14.8	Sound of Bute

The simulations for the flame shell bed release areas indicate that all areas investigated show some level of self-recruitment. The connectivity to other areas is generally weak, however, especially compared to the *M. modiolus* results. This is most likely because the settlement window and pelagic larval duration for *L. hians* is not as long in duration as that of *M. modiolus,* and therefore the particles may not travel as far. There are also fewer, and more spread out, *L. hians* release areas modelled. The ten release areas investigated show some degree of regional isolation. The Sound of Bute and Upper Loch Fyne and Loch Goil NCMPA (release areas 10 and 8, respectively) are connected to one another, with more particles moving from Bute to Upper Loch Fyne. These two areas are separated from the Sound of Jura (release area 9) by the Mull of Kintyre. The Sound of Jura is connected to release areas 5 - 7 (Loch Sunart NCMPA, Loch Linnhe and the Sound of Mull, respectively), with particles predominantly moving south to the Sound of Jura but also a very weak connection (0.001%) moving north to Loch Sunart (Figure 10). Loch Carron (release area 3) and Lochs Duich, Long and Alsh are weakly connected to one another (Figure 10; <0.5% of particles). These areas are likely to be more strongly connected to one another in reality, as the narrow channel of Kyle Rhea is not resolved in the coarser grid hydrodynamic model. Finally, the Wester Ross NCMPA exports particles to Scapa Flow and Hoy.

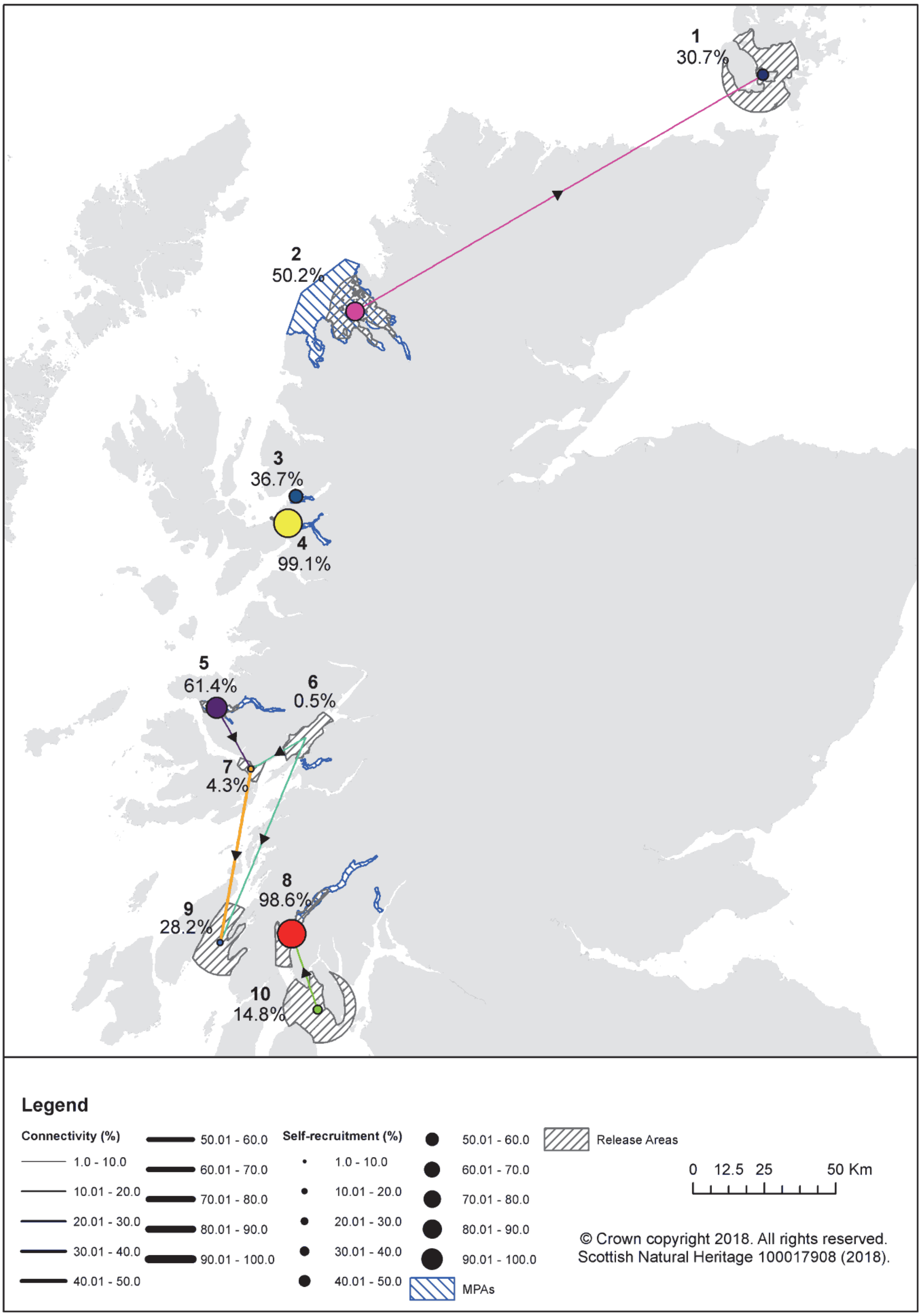

Figure 11. Flame shell beds self-recruitment and connectivity for all release areas. Only the connections due to >1% of particles are shown.

3.2 Comparison between coarser and integrated output results

As some of the release areas, in particular the sea lochs, were not fully resolved by the coarser SSM grid, the integrated output version was used for five selected horse mussel bed release areas; Release area 2 (Ronas Voe), 17 (Loch Laxford SAC), 18 (Loch a Chairn Bhain), 33 (Loch Craignish) and 26 (Lochs Duich, Long and Alsh Reefs SAC). The results from these simulations were compared with the coarser grid results for these areas. The integrated output could not be used for all the areas within the lifetime of the project, due to computational constraints.

Figure 12 shows the particle densities at the end of the simulation for Release area 17 (Loch Laxford SAC) on the north-west coast, as simulated using the coarser and integrated grids output, respectively. The coarser grid particles mainly stay within the release area and the small number which do travel out of the area pass through the Pentland Firth and around Orkney, and extremely low densities were in the Moray Firth at the end of the simulation. The integrated grid results show a much greater density of particles travelling out of the release area, although they show broadly the same qualitative pattern of dispersal as the coarser grid particles, with low densities of particles also reaching Shetland and reasonably high densities going down the east coast and into the northern North Sea. These results suggest that both simulations are similarly representing the coarser scale residual currents, but differ in their representation of the detailed hydrodynamics in/around Loch Laxford. This local difference in the export from Loch Laxford leads to seemingly quite different results in terms of the long distance export of particles. The differences between the coarser and integrated output simulations may change the degree of connectivity between some areas, and could introduce new connections between regions or remove reported connections. One potential connection predicted by the integrated grid, but not the coarser grid, is between the mainland west coast and Shetland. However, this connection appears to be extremely weak, with only a small number of particles reaching Shetland.

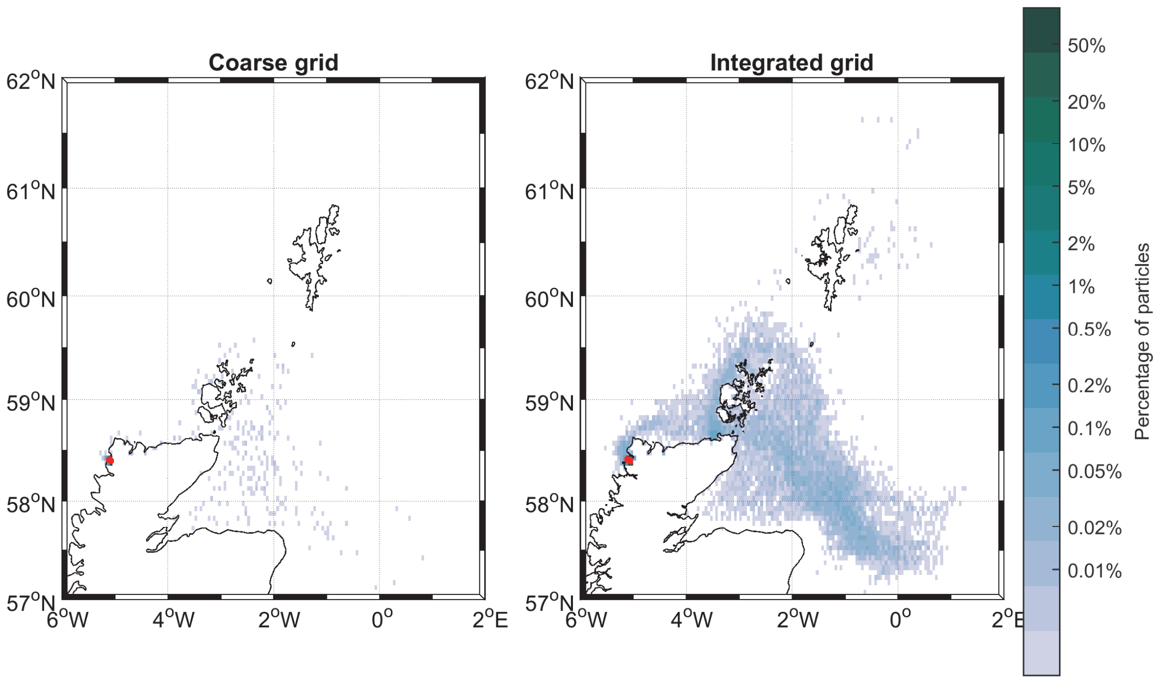

Figure 12. Particle densities at the end of the simulation for Release area 17 (Loch Laxford SAC). Results from the coarser grid (left) and integrated grid (right).

Figure 133 shows the end particle densities for Release area 18 (Loch a Chairn Bhain) on the north-west coast. The coarser grid results show more dispersal of the particles than the integrated grid for this release area. Whilst Figures 12 and 13 show that there is broad agreement between the coarse and integrated grid results, there are clear discrepancies in these examples in terms of the densities of particles that exit the sea lochs and enter the residual circulation around Scotland. These differences are due to the differing hydrodynamic forcing within the north-west coast sea lochs between both simulations, resulting in fewer particles being exported from the inner sea lochs in the integrated grid simulations. This is not surprising, as the coarser grid does not resolve the circulation in these areas to the same detail. Figure 144 shows monthly mean (September) flow vectors from the coarser and integrated grids for this region of north-west Scotland. The enhanced resolution of the integrated grid clearly resolves the coastline and local flow features much better, including local eddies. The sea lochs are also much more highly resolved. These differences lead to Loch Laxford and Loch Chairn Bhain exporting and retaining, respectively, considerably more particles in the integrated grid simulations than in the case of the coarser grid simulations.

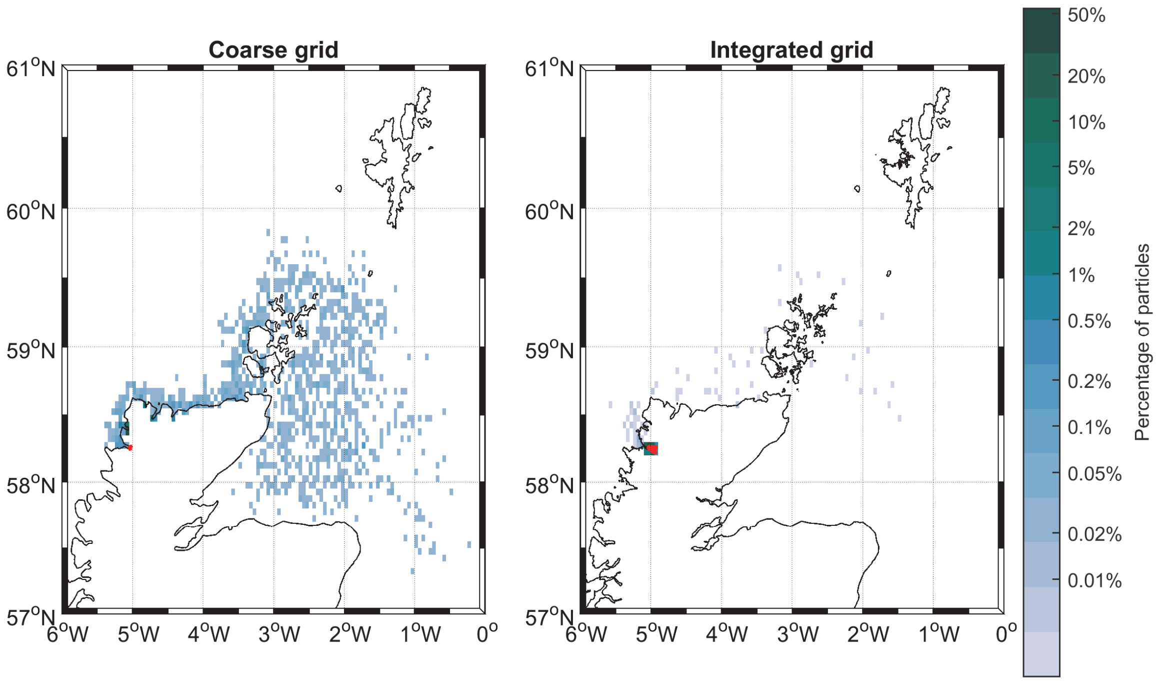

Figure 13. Particle densities at the end of the simulation for Release area 18 (Loch a Chairn Bhain). Results from the coarser grid (left) and integrated grid (right).

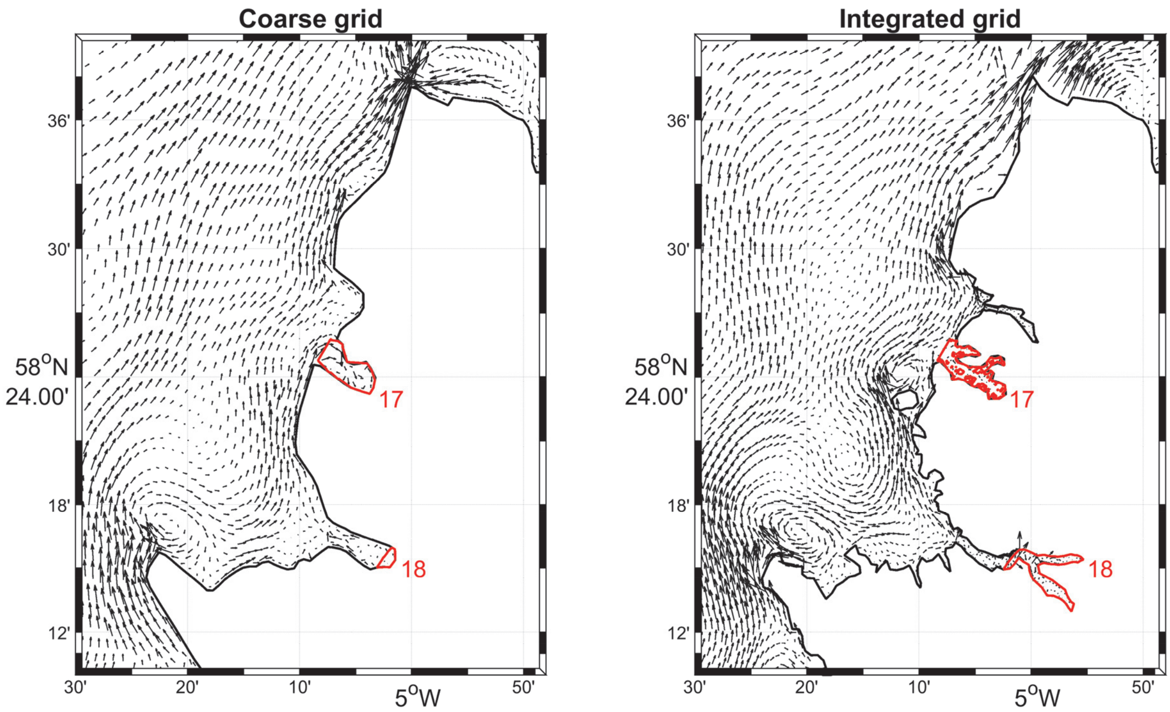

Figure 144. Residual currents taken from the coarser grid (left) and integrated grid (right) SSM version in the area surrounding Release areas 17 and 18 (Loch Laxford SAC and Loch a Chairn Bhain). Red polygons illustrate how the release areas are resolved by the respective grids.

Figure 15 shows the end particle densities for the coarser grid and the integrated grid SSM versions for Release area 33 (Loch Craignish). The overall trend of a predominant northerly movement of particles is simulated in both model runs. However, more of the particles forced by the integrated grid output travel further both southerly and northerly compared to the coarser grid. This is because the circulation in this region is likely to be much better represented, and more highly resolved, in the integrated model output. It is most likely that the strength of the residual circulation is similar in both models, but the integrated grid appears to force the particles out of the inner sea lochs and into the main residual flows more quickly than the coarser model.

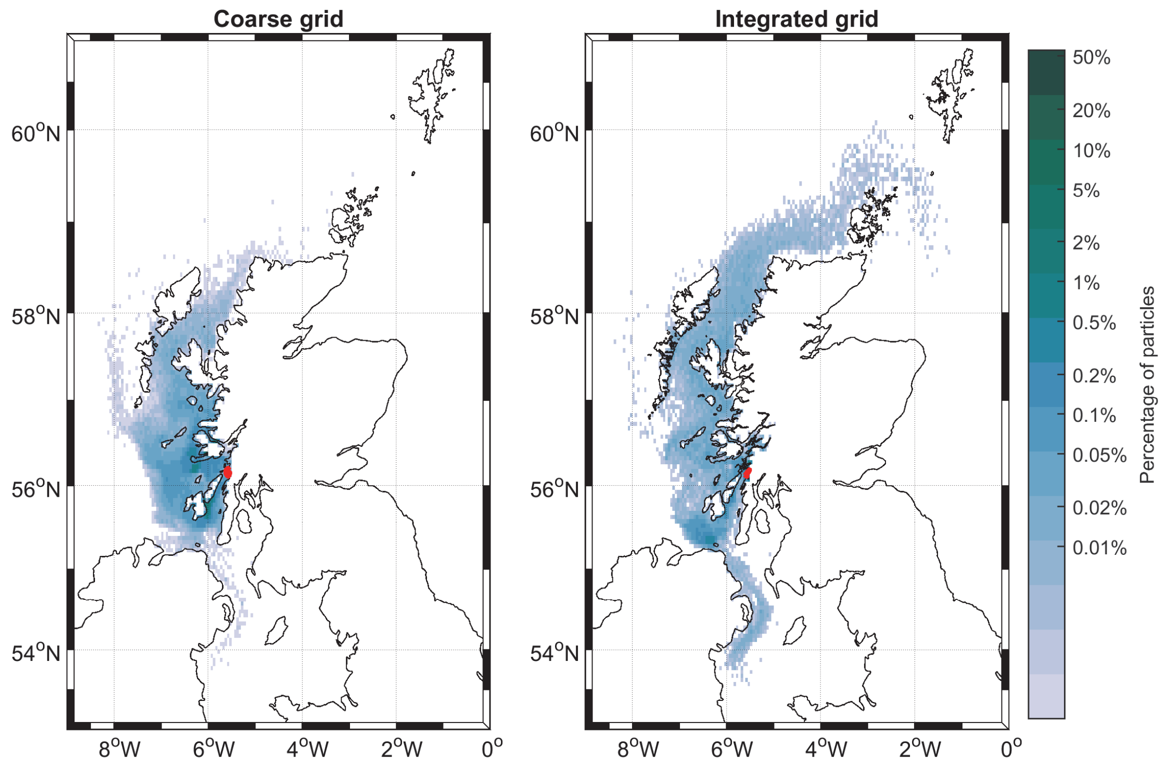

Figure 15. Particle densities at the end of the simulation for Release area 33 (Loch Craignish). Results from the coarser grid (left) and integrated grid (right).

The end position particle densities from Release area 26 (Lochs Duich, Long and Alsh Reefs SAC) are shown in Figure 16. The particles forced by the coarser grid output are retained in the release area and very few travel out of the area. In comparison, the particles forced by the integrated grid output do leave the release area and travel up and round to Orkney and Shetland, and potentially the NE coast of Scotland. The residual currents in the area (Figure 17) may explain the distinct differences: the coarser grid does not resolve Kyle Rhea (the strait between the Isle of Skye and the mainland) and the hydrodynamics in the surrounding bodies of water, some of which are known to be of high amplitude, are not well represented in the coarser grid simulations. These high amplitude flows force the particles out of the Loch Alsh region and into the North Minch, where they are then transported north.

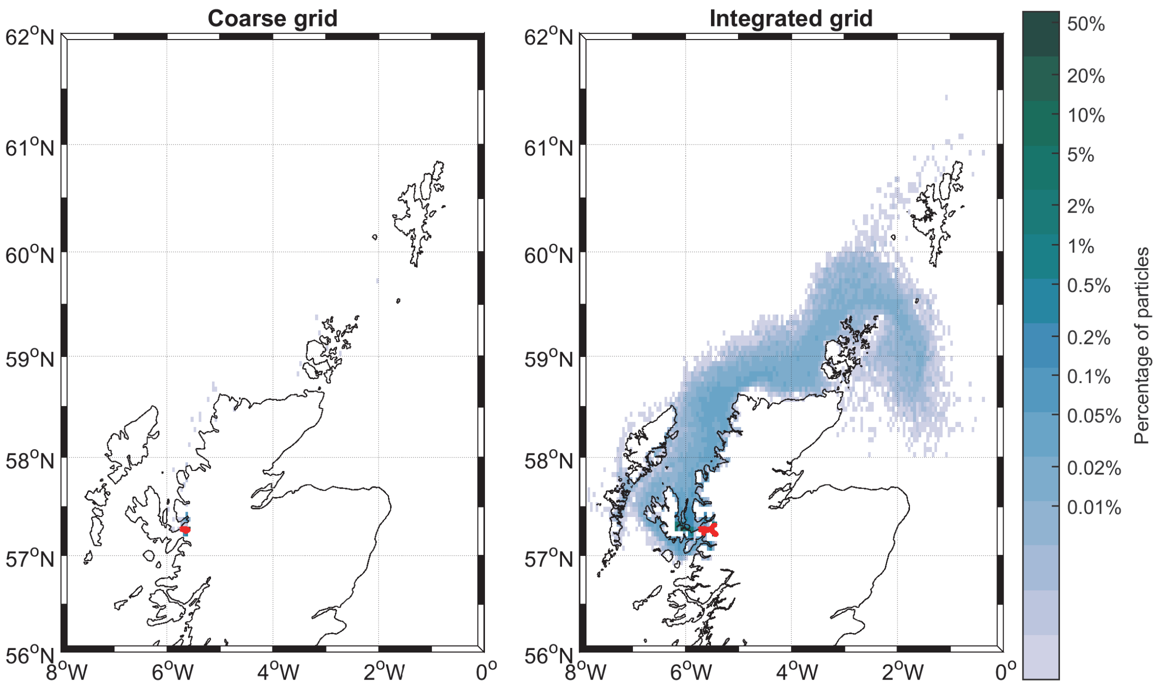

Figure 16. Particle densities at the end of the simulation for Release area 26 (Lochs Duich, Long and Alsh Reefs SAC). Results from the coarser grid (left) and integrated grid (right).

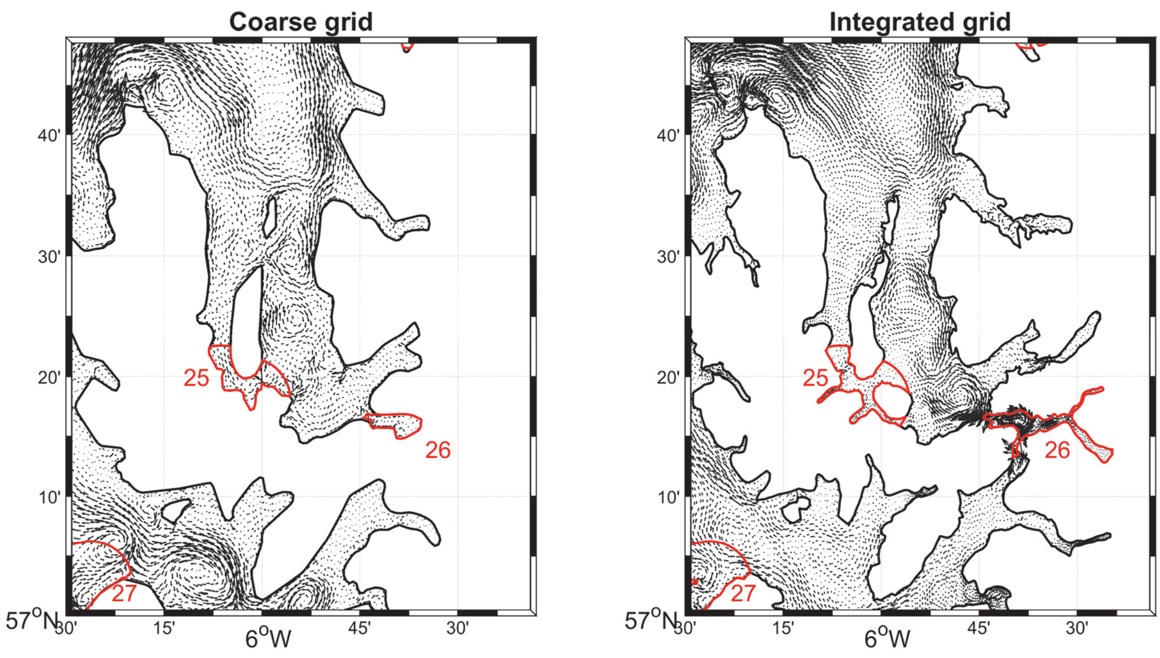

Figure 17. Residual currents taken from the coarser grid (left) and integrated grid (right) SSM version for the area surrounding Release area 26 (Lochs Duich, Long and Alsh Reefs SAC). Red polygons illustrate how the release areas are resolved by the respective grids.

3.3 Maxent modelling

3.3.1 Horse mussel beds

The result of the Maxent habitat suitability model for horse mussel beds is shown in Figure 18. The average probability of all the replicate runs as a percentage of suitable habitat is plotted, with red and orange representing higher probabilities of suitable habitat. The area under the curve (AUC) for all the replicated runs was 0.992, indicating an excellent prediction. Areas of predicted suitable habitat are mainly found close to the coast. The Shetland and Orkney Islands have a high number of predicted areas of suitable habitat, which corresponds to the high number of feature records found in these areas. The Firth of Tay and the Firth of Forth also have new predicted areas.

The percentage contribution to each environmental variable is presented in Table 7. The bathymetry layer has the greatest contribution (63.4%) to the prediction followed by the landscape layer (22.9%) which represents the type of habitat and the maximum bottom temperature had a small contribution (7.9%). The average current speed, mean bottom salinity and slope did not have a significant contribution to the prediction of suitable habitat. The response curves for all the variables are presented in Annex 4.

Table 7. Environmental layer percentage contribution to Maxent output for horse mussel beds

Variable	Percentage contribution (%)
Bathymetry	63.4
Landscape	22.9
Bottom temperature	7.9
Current speed	3.1
Slope	2.4
Bottom salinity	0.3

Figure 19 shows the areas of most suitable horse mussel habitat, as predicted by the Maxent modelling. These areas were defined using the threshold of suitable habitat (greater than 50% probability of occurrence) described by Gormley *et al*. (2013). Overlapping release areas have been removed, so that only new areas of predicted suitable habitat are shown.

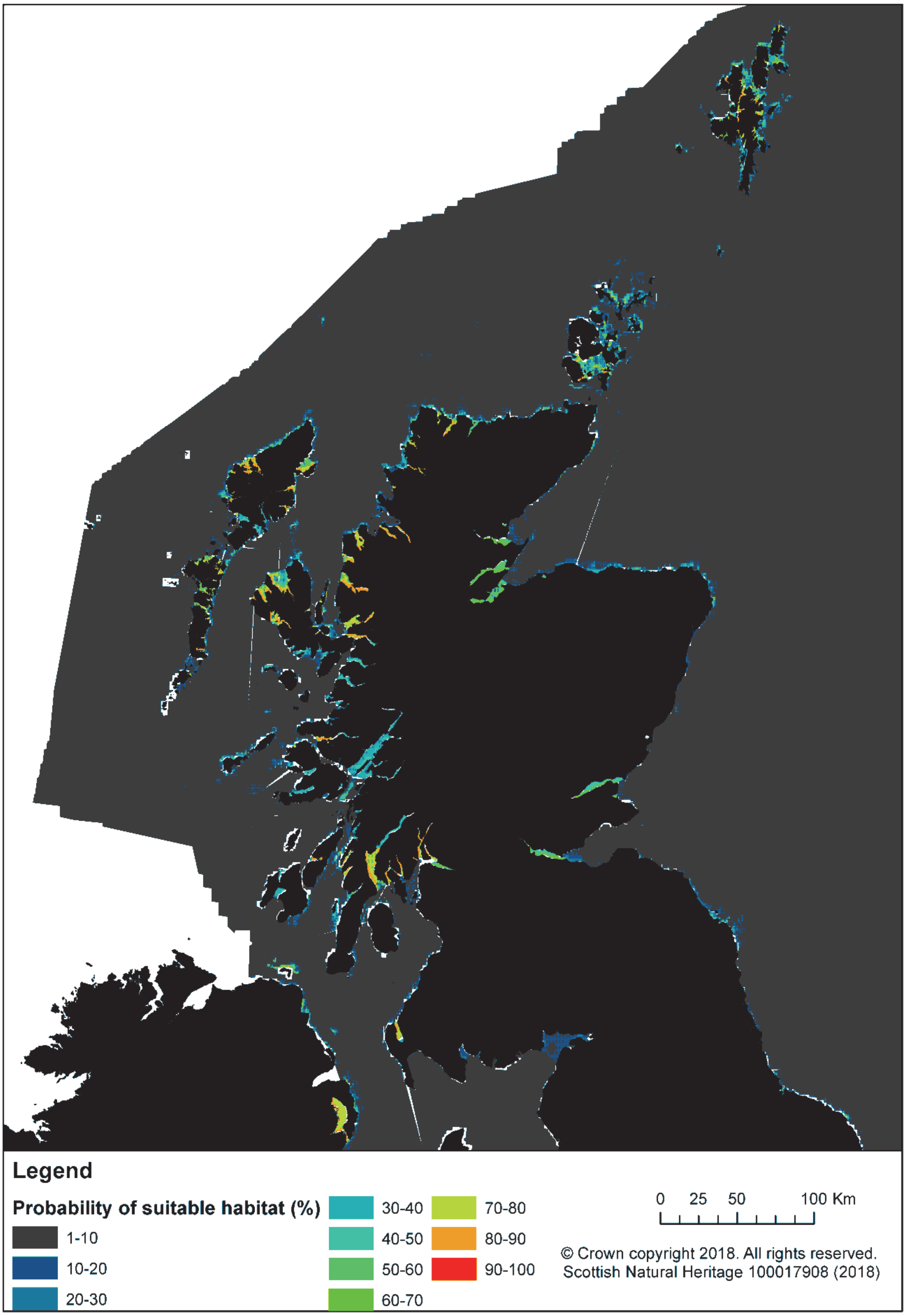

Figure 18. Maxent output predictions of habitat suitability for horse mussel beds, red and orange colours indicate a high probability of suitable habitat.

Figure 19. Predicted most suitable habitat areas for horse mussel beds outside the release areas considered. Orange polygons are predicted areas with >50% probability of suitable habitat, with locations of known horse mussel beds removed. These areas are numbered and shown in more detail in Annex 5.

3.3.2 Flame shell beds

Figure 20 shows the Maxent predictions of suitable habitat for flame shell beds around Scotland. The percentage contributions to the prediction for all the environmental layers included in the model are shown in Table 8. The main contribution to the prediction is the landscape (57.5%), followed by the bathymetry (36.4%). The other environmental variables did not have a significant contribution to the habitat suitability prediction. The response curves for all the variables are presented in Annex 4. The AUC for all the replicated runs was 0.997, indicating excellent prediction.

The predicted areas are mainly located on the west coast of Scotland. There are no very high (90-100%) areas of probability predicted by the model.

Table 8.Environmental layer percentage contribution to Maxent output for flame shell beds.

Variable	Percentage contribution (%)
Landscape	57.5
Bathymetry	36.4
Slope	4.8
Bottom salinity	0.9
Bottom temperature	0.2
Current speed	0.2

Figure 21 shows the areas of most suitable habitat for flame shells, using the threshold of suitable habitat defined by Gormley *et al.* (2013). Overlapping release areas have been removed, so that only new areas of predicted suitable habitat are shown.

Figure 20. Maxent output predictions of habitat suitability for flame shell beds, red and orange colours indicate higher probability of suitable habitat.

Figure 21. Predicted most suitable habitat areas for flame shell beds outside the release areas considered. Purple polygons are predicted areas with >50% probability of suitable habitat, with locations of known flame shell beds removed. Numbers identify suitable habitat areas used in the connectivity analysis.

3.4 Connectivity to predicted suitable habitat areas

From the Maxent results the most suitable habitat areas, defined as being above 50% probability, were selected using ArcGIS. These areas were then combined with the particle release areas for a particle connectivity analysis. For the cases where the predicted suitable area fell within one of the predefined particle release areas, the predicted area was not considered in addition to the release area. Using Matlab, the larval export from the release areas to these suitable habitat areas was calculated and the results are presented graphically in the sub-sections below. It was only possible to calculate the larval export from the original release areas to the newly defined suitable habitat areas. This is because the particle tracking simulations only released particles from the original release areas. Performing equivalent simulations with particles released from the predicted suitable habitat areas was beyond the scope of the current project, which focused on the export of particles from, and connectivity between, areas of known habitat, based on presence data.

Both horse mussel bed and flame shell bed release areas were found to have new additional connections to other areas defined by the Maxent modelling.

3.4.1 Horse mussel beds

The percentage of larval export from horse mussel release areas to the Maxent predicted suitable habitat areas is shown in Table 9 (west coast) and Table 10 (north/east coasts). The connections due to >1% of particles are presented graphically in Figures 22 – 25. These figures indicate which release areas export larvae to the suitable habitat areas. Only the larval export from the release areas to the suitable habitat areas is shown, i.e. connections between the release areas (shown in Figures 5 – 8) are not shown.

Figure 22 shows how the ten Shetland release areas connect (≥1%) to the areas of suitable habitat identified from the Maxent modelling. Table 10 confirms these connections, and shows that nine of the ten Shetland release areas export to all the Shetland suitable habitat areas. These suitable habitat areas were mainly predicted to be around the north of the Shetland Islands, but there were also some smaller areas in the south of the islands, and on Foula (to the west of Shetland) and Fair Isle (Annex 5).

Table 10 also shows that the Shetland release areas export a low percentage (consistently <0.1%) of larvae to Orkney and the east coast suitable habitat areas. The larval export from the release areas to the predicted suitable habitat areas found that Shetland was again well connected internally and is somewhat isolated from the rest of the horse mussel beds investigated, due to the very low levels of export out of Shetland. Within Shetland, beds in the Sullom Voe SAC were predicted to be connected to suitable habitat areas off Lunna Holm (28%) and north of Whalsay (26%).

Figure 23 shows the larval export from the release areas in Orkney and north-east Scotland to the predicted suitable habitat areas, due to connections >1% of larvae. Whilst most of the suitable habitat areas in the Islands of Orkney receive >1% of larvae from the release areas in the region, there are some which do not. However, Table 10 shows that many of the suitable habitat areas receive <1% of the larvae from the Orkney release areas. Table 10 also shows how the suitable habitat areas around Orkney also receive larvae from the north-west Scotland region (Figure 24 shows the >1% connections), and the Small Isles NCMPA (Figure 25 shows the >1% connections). The Copinsay and Stronsay Firth and Shapinsay Sound release areas (release areas 12 and 13) export >1% of larvae south to predicted habitat areas in the outer Moray Firth (Figure 23). This is a region where there are no MPAs or release areas, so these predicted habitat areas make potentially important connections to a region otherwise not represented in the results (Section 3.1.1).

It is interesting to note that whilst there is only a weak connection from the Orkney release areas to the Noss Head NCMPA release area (area 15, <1% of particles) there are stronger connections to two predicted suitable habitat areas on the east coast (Figure 23), one on the north coast of the Moray Firth and one on the south coast. This could be because the particles reach the Noss Head NCMPA before the start of the settlement window. The particle density figures presented in Annex 2 show that at the end of the particle tracking simulation the particle densities are an order of magnitude higher along the Moray Firth coastlines (~1%) than at Noss Head (~0.01%). These predicted suitable habitat areas in the Moray Firth, could be important areas to maintain connectivity along the east coast if horse mussel populations are found to be present.

Figure 24 shows the (>1%) larval export from the release areas in the north-west of Scotland to the suitable habitat areas. The overall pattern is one of northerly and north-easterly export of larvae from the release areas, leaving the suitable habitat areas on the west of Lewis and Harris, and the west of Skye, seemingly unconnected. However, note that we have not investigated here the potential connectivity between non-protected areas of predicted suitable habitat Table 9 shows that these west coast Lewis areas do receive a low percentage (<<1%) of larvae from the release areas.

Figure 25 shows the >1% of larval export form the south-west Scotland release areas to the predicted suitable habitat areas. The Mull of Kintyre appears to act as a boundary dividing the Loch Fyne MPAs and suitable habitat areas and the areas to the west. The Small Isles NCMPA (area 27) exports to the habitat areas further north, and there are connections (~2%) from release area 38 (Sound of Gigha) to suitable habitat areas in Northern Ireland. Table 9 shows that in addition to these stronger connections, there are weaker (<1%) connections, both with the south-west region (including export to Northern Ireland) and form the south-west to the north-west region.

Table 9: Percentage larval export matrix for horse mussel bed release areas exporting to the Maxent areas of suitable habitat in the west of Scotland. The order of the release areas has been changed to reflect how the particles were transported around the Scottish coastline. The numbers of destination suitable habitat areas are indicated in Annex 5. Stronger connections are shaded.

Release areas

South west Scotland (destination areas 1–40, release areas 39–27); North west Scotland (destination areas 41–100, release areas 26–22)

Destination predicted suitable habitat areas	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	21	20	19	18	17	16	23	22
1		0.009	0.002				0.001																	
2		0.009	0.001																					
3		0.004																						
4		0.010																						
5		0.008	0.006				0.001																	
6		0.011	0.007				0.001																	
7		0.164	0.074				0.029	0.001		0.003														
8		0.019	0.015				0.002	0.000																
9		0.026	0.020				0.004	0.000		0.002														
10		0.000																						
11		0.081	0.052				0.012			0.002														
12		0.087	0.055				0.019	0.000		0.002														
13		0.000																						
14		1.893	0.810				0.265	0.016		0.009														
15		1.963	0.774				0.261	0.018		0.011														
16		0.011																						
17		10.885	11.000				7.721	2.461	1.628	2.646		0.012												
18		0.001																						
19	0.001	16.139	18.040				13.967	5.501	4.197	5.859		0.029												
20		0.001																						
21																								
22																								
23	0.003	0.200	0.129				0.036	0.000	0.011	0.002														
24	0.001	1.963	4.888				2.038	2.138	2.557	2.429		0.080												
25	0.011	3.321	7.946				9.044	10.279	13.967	11.799		0.518												
26		0.000		1.894																				
27					1.561																			
28					5.463																			
29	0.007	0.991	2.546				6.260	7.747	11.770	8.965		0.493												
30					10.639																			
31					99.439																			
32					81.607																			
33	0.011	0.528	1.555				5.678	9.084	21.005	10.664		2.670												
34	0.051	1.479	0.878				0.169	0.010		0.014														
35	0.028	0.633	1.037				4.366	2.370	3.279	3.444		0.014												
36	0.052	1.479	0.778				0.118	0.006		0.003														
37	0.075	1.726	0.879				0.232	0.055	0.055	0.080														
38	0.029	0.488	0.190				0.207	0.099	0.098	0.130														
39	0.005	0.084	0.260				1.631	0.724	0.732	1.158		0.987												
40	0.014	0.250	0.590				3.039	1.459	1.880	2.230		0.005												
41	0.001	0.010	0.002				0.002						0.197											
42	0.002	0.007	0.004				0.001	0.001					0.167											
43	0.002	0.009	0.006				0.001	0.001		0.002			0.232											
44														0.084	1.410									
45														0.010	1.013									
46													0.000	0.017	1.300									
47		0.000	0.008				0.088	0.025	0.022	0.036			5.291											
48													0.000	0.286	2.491									
49													0.000	0.017	0.775									
50							0.001						0.659		37.841	0.001								
51													0.108	0.008	2.939	0.001								
52							0.001	0.000					0.307	0.002	16.351	0.002								
53	0.001	0.009	0.005				0.059	0.014		0.030			0.048											
54	0.006	0.060	0.033				0.044	0.011		0.012			0.584											
55	0.006	0.028	0.037				0.219	0.051	0.066	0.125			0.109											
56	0.001	0.006	0.005				0.008	0.001		0.002			0.093											
57	0.002	0.001					0.003	0.002					0.801	0.007	15.615	0.008								
58	0.005	0.013	0.020				0.090	0.018	0.011	0.039			2.109	0.003	5.006	0.027								
59	0.009	0.021	0.020				0.146	0.037	0.022	0.073		0.001	0.232											
60	0.010	0.054	0.032				0.049	0.007		0.019			0.833			0.001								
61	0.001									0.002			0.218	0.005	5.379	0.001								
62	0.011	0.053	0.021				0.060	0.012		0.031			0.472			0.012								
63	0.007	0.029	0.009				0.027	0.006		0.019			0.719			0.039								
64	0.005	0.036	0.028				0.058	0.009	0.011	0.020			0.231			0.062								
65		0.003	0.001				0.003	0.002		0.006			0.378			0.017								
66	0.003	0.032	0.020				0.054	0.013	0.022	0.027			0.525			0.235								
67	0.001	0.005	0.004				0.022	0.002	0.011	0.019			1.591		0.568	0.004								
68	0.001	0.001					0.003	0.002		0.003			0.638	0.004	7.506	0.006								
69		0.004					0.008	0.002		0.006			0.241			0.149								
70		0.001	0.004				0.006	0.000		0.002			0.249			0.043								
71	0.007	0.024	0.023				0.074	0.018	0.044	0.052			0.467		0.001	0.506			0.000				0.004	0.002
72													0.309		0.685	0.005	0.479	3.027	0.736					
73							0.001						0.602			0.089								
74		0.002					0.008	0.001		0.005			0.335		0.000	0.804			0.001				0.272	0.065
75			0.001				0.003	0.000		0.003			0.187		0.000	0.445			0.002				0.262	0.055
76							0.001						0.472			0.079								
77													0.117		0.136	0.006	0.028	0.322	0.434				0.001	
78													0.283			0.057								
79							0.002						0.873		1.305	0.053	0.226	4.344	1.595				0.003	0.003
80		0.001					0.005			0.003			0.921		0.005	3.364	0.001		0.013				1.882	0.459
81							0.001						0.351		0.463	0.038	0.089	0.628	5.122				0.002	
82		0.000					0.001						0.256		0.001	0.680	0.002		0.007				1.105	0.282
83													0.485			0.075								
84													0.163		0.130	0.042	0.011	0.066	0.219	2.885			0.005	0.001
85		0.000	0.001										0.443			0.040							2.198	0.203
86							0.001			0.002			0.567		0.034	1.330			0.006				3.036	0.918
87								0.000					0.213		0.163	0.106	0.023	0.033	0.730	6.131	9.329		0.011	0.002
88													0.118		0.080	0.044	0.010	0.049	0.202	1.574	1.470		0.005	
89													0.010		0.007	0.004	0.001		0.062	0.426	0.789			
90													0.894		0.648	0.521	0.088	0.197	5.685	39.607	69.972		0.034	0.006
91							0.001	0.001					1.406	0.001	1.108	0.443	0.110	0.568	1.298	11.705	0.729		0.058	0.013
92													0.110		0.077	0.061	0.016	0.011	0.578	4.328	7.516		0.002	
93													0.007		0.008	0.001	0.002		0.006					
94		0.000											0.575			0.030							3.012	0.494
95													0.345			0.013							1.718	0.329
96							0.001	0.000					1.640	0.001	1.213	0.565	0.112	0.563	1.506	11.902	2.217		0.065	0.019
97													0.841		0.065	1.604	0.001		0.007				4.262	1.280
98													0.405			0.015							2.048	0.441
99													1.366		0.070	1.723	0.001		0.006				5.976	1.606
100							0.003	0.000					1.764		1.274	0.748	0.097	0.536	0.920	2.492	0.023		0.090	0.012
101		0.001	0.001										0.000											

Table 10: Percentage larval export matrix for horse mussel bed release areas exporting to the Maxent areas of suitable habitat, along the north and east coasts and in the Northern Isles. The order of the release areas has been changed to reflect how the particles were transported around the Scottish coastline. The numbers of destination Maxent areas are indicated in Annex 5. Stronger connections are shaded.

Release areas

Destination predicted suitable habitat areas	33	27	26	25	24	21	20	19	18	17	16	23	22	14	13	12	11	10	9	8	7	6	5	4	3	2	1	15	40	41	42
102		4.959		2.140	4.548	0.184	0.257	4.227	3.410	0.023	0.412	0.855	0.163	0.176	0.045	0.105	0.179	0.003	0.003									0.018			
103		2.905		1.173	2.958	0.125	0.104	3.038	2.164	0.025	0.223	0.596	0.120	0.238	0.065	0.147	0.246	0.004	0.004	0.000				0.000				0.030			
104	0.001	2.147	0.001	1.194	1.368	0.111	0.257	1.598	2.984	0.013	0.033	0.143	0.027																		
105	0.001	1.768	0.001	1.012	1.127	0.096	0.251	1.348	2.820	0.010	0.025	0.116	0.019																		
106	0.003	4.942	0.002	2.704	3.309	0.235	0.519	4.179	5.443	0.033	14.857	0.467	0.085																		
107	0.002	3.103		1.596	2.218	0.129	0.290	2.101	2.984	0.018	1.193	0.328	0.067																		
108		1.161		0.515	1.039	0.034	0.082	1.057	0.984	0.005	0.148	0.169	0.035																		
109	0.002	2.167		1.087	1.771	0.101	0.180	2.321	2.590	0.028	1.070	0.244	0.053																		
110		1.297		0.475	1.810	0.062	0.033	1.493	0.525	0.018	0.059	0.615	0.096	0.348	0.054	0.175	0.333	0.000										0.015			
111		3.096		1.155	4.286	0.133	0.055	3.575	1.705	0.043	0.133	1.321	0.255	0.821	0.128	0.412	0.843	0.001	0.000									0.068			
112		0.202		0.080	0.317	0.010	0.005	0.333		0.005	0.006	0.112	0.023	0.071	0.015	0.041	0.086											0.005			
113		1.747		0.628	2.836	0.096	0.011	2.841	0.951	0.030	0.115	0.990	0.179	0.608	0.114	0.328	0.758											0.053			
114		1.494		0.550	2.468	0.083	0.011	2.575	1.180	0.018	0.094	0.947	0.164	0.544	0.105	0.301	0.828	0.001	0.000									0.040			
115		0.053		0.020	0.117	0.003	0.005	0.206	0.033		0.014	0.055	0.007	0.050	0.018	0.037	0.845		0.000									0.013			
116		6.030	0.002	2.056	7.832	0.284	0.180	6.303	3.934	0.066	0.309	2.078	0.417	1.796	0.206	0.715	0.907	0.005	0.002	0.000								0.108			
117		0.393		0.170	0.833	0.033	0.016	1.271	0.361	0.013	0.039	0.346	0.051	0.320	0.093	0.220	3.041											0.040			
118		0.573		0.199	0.995	0.028	0.011	1.159	0.361	0.008	0.041	0.379	0.071	0.260	0.057	0.145	0.660											0.030			
119		0.983	0.001	0.359	1.419	0.043	0.027	1.549	0.656	0.013	0.059	0.448	0.088	0.605	0.114	4.371	0.530	0.001										0.055			
120																															
121		0.000			0.001			0.002						0.000	0.000	0.000	0.001														
122		0.003		0.001	0.011	0.001		0.014				0.005		0.005	0.002	0.004	0.047														
123		0.002			0.008			0.014	0.033			0.001		2.068	0.073	0.074	0.063											0.023			
124		1.238	0.001	0.467	1.374	0.054	0.055	1.192	1.082	0.013	0.070	0.362	0.073	4.046	0.137	0.217	0.295	0.003	0.002	0.000								0.050			
125		0.000			0.001									0.000	0.000	0.001	0.002														
126		0.243		0.095	0.290	0.014	0.016	0.288	0.230		0.020	0.075	0.012	2.241	0.059	0.074	0.082	0.001										0.013			
127		0.844		0.318	1.507	0.053	0.016	2.649	0.656	0.040	0.109	0.524	0.086	10.711	0.588	1.409	2.201	0.014	0.008	0.002	0.002		0.002	0.001			0.000	0.194			
128		0.109		0.044	0.213	0.007		0.394	0.066	0.003	0.027	0.063	0.009	0.155	0.146	0.449	0.497	0.000										0.015			
129		0.230		0.088	0.456	0.019	0.005	0.796	0.262	0.013	0.043	0.145	0.025	0.292	0.199	0.696	0.842							0.000				0.030			
130		1.052		0.414	1.724	0.066	0.038	2.899	0.721	0.030	0.127	0.564	0.091	2.765	0.404	1.139	2.114	0.025	0.016	0.004	0.002	0.000		0.002		0.001	0.000	0.184			
131		4.563		1.800	7.143	0.276	0.169	11.794	3.508	0.124	0.473	2.318	0.391	8.966	1.554	4.113	7.634	0.103	0.057	0.012	0.008	0.001		0.004	0.002	0.005	0.002	0.694			
132		0.414		0.152	0.674	0.021	0.005	1.150	0.361	0.010	0.057	0.233	0.043	0.800	0.154	0.538	0.906	0.006	0.003	0.001	0.001	0.000		0.000		0.001	0.000	0.058			
133					0.001			0.000				0.002						0.489	0.746	0.069	0.094	3.263	0.548	0.318	0.564	0.183	0.635				
134					0.001			0.000				0.001						0.390	0.682	0.052	0.082	2.866	0.494	0.278	0.504	0.173	0.651				
135					0.001			0.000				0.002						0.181	0.265	0.023	0.035	1.226	0.180	0.114	0.208	0.075	0.230				
136					0.001													0.054	0.072	0.009	0.009	0.374	0.068	0.042	0.063	0.029	0.079				
137								0.001				0.001						0.525	0.891	0.069	0.143	3.711	0.864	0.522	0.955	0.341	1.540				
138								0.000				0.001						0.136	0.165	0.017	0.027	0.998	0.145	0.104	0.174	0.133	0.583				
139								0.000										0.119	0.128	0.043	0.114	1.119	0.307	0.235	0.280	0.381	2.763				
140																		0.037	0.044	0.018	0.076	0.449	0.141	0.132	0.156	0.241	1.922				
141								0.000										0.277	0.390	0.038	0.104	1.590	1.323	0.656	1.407	0.187	0.294				
142								0.000				0.001						1.008	1.323	0.182	1.468	6.289	21.576	10.256	21.866	2.470	6.833				
143																0.000		0.332	0.314	0.139	0.319	2.589	0.712	0.610	0.723	0.637	4.479				
144																		0.359	0.233	0.326	0.890	2.646	2.721	2.243	2.960	2.040	11.777				
145												0.001						0.187	0.269	0.023	0.021	0.939	0.009	0.012	0.006	0.003	0.007				
146																		0.051	0.062	0.007	0.006	0.245		0.004	0.001	0.001	0.002				
147																		0.383	0.268	0.312	3.441	3.809	28.054	15.884	28.839	4.260	15.244				
148																		0.154	0.096	0.462	0.639	0.848	1.450	1.200	1.531	0.309	0.886				
149																		0.057	0.038	0.220	0.297	0.352	0.731	0.531	0.648	0.132	0.368				
150								0.001				0.001						0.837	0.494	1.231	5.180	6.240	26.190	16.954	27.030	5.413	20.646				
151																		0.010	0.011	0.023	0.119	0.127	0.534	0.380	0.603	0.117	0.439				
152												0.001						0.491	0.468	0.094	0.062	2.276	0.016	0.057	0.018	0.021	0.021				
153																		0.043	0.155	0.030	0.030	0.011	0.035	0.029	0.022	0.028	0.018				
154																		0.119	0.580	0.071	0.096	0.041	0.054	0.086	0.052	0.085	0.060				
155																		0.149	0.093	8.177	7.419	1.804	5.810	5.934	5.569	2.086	4.742				
156																		0.012	0.006	1.640	1.411	0.209	0.674	0.844	0.708	0.333	0.581				
157		0.000			0.001			0.001				0.002						0.041	0.035	0.017	0.014	0.001	0.012	0.010	0.006	0.003	0.004				
158		0.000			0.003			0.002				0.004	0.001					0.074	0.075	0.032	0.030	0.003	0.016	0.020	0.014	0.011	0.014				
159															0.000			0.168	0.096	4.586	4.873	1.913	2.726	3.840	2.740	2.682	2.815				
160		0.001			0.002			0.002				0.009						0.159	0.138	0.063	0.069	0.008	0.052	0.055	0.030	0.019	0.028				
161																		0.294	0.470	0.475	0.512	0.457	0.370	0.454	0.415	0.528	0.423				
162																		0.384	0.214	4.995	5.219	2.923	4.199	4.777	4.150	3.249	4.023				
163															0.000			0.573	0.767	0.955	1.013	1.078	0.913	0.978	0.902	1.171	0.946				
164																		0.534	0.309	6.275	6.556	4.066	5.372	6.108	5.411	4.236	5.320				
165		0.161		0.039	0.460	0.012	0.005	0.336	0.066			0.375	0.064	0.006	0.004	0.005	0.008	0.132	0.118	0.108	0.125	0.055	0.080	0.096	0.075	0.116	0.067				
166		0.167		0.075	0.264	0.009	0.011	0.497	0.295	0.005	0.033	0.067	0.017	0.482	0.478	0.517	0.593	0.003	0.002	0.001	0.000			0.000				7.420	0.001	0.004	
167		0.006		0.004	0.014	0.002		0.076	0.066	0.003	0.006	0.004		0.389	0.916	0.686	0.470		0.000									15.206	0.002	0.011	
168		0.001			0.009	0.001		0.070		0.003	0.004		0.001	0.728	1.884	1.342	0.753											19.677	0.009	0.033	
169						0.001		0.014						0.608	1.288	0.935	0.481											1.649			
170								0.003						0.193	0.515	0.322	0.119											1.183			
171								0.002						0.141	0.340	0.228	0.094											0.494			
172								0.002						0.022	0.042	0.034	0.018											0.172			
173						0.001		0.006						0.304	0.674	0.477	0.223											0.898			
174						0.001		0.004						0.252	0.581	0.394	0.186											0.769			
175								0.002						0.259	0.648	0.422	0.166											0.822			
176														0.000	0.001	0.001												0.005			
177																															
178																															
179																															
180																															
181																															0.002

Orkney and north coast

Shetland Islan

East coast

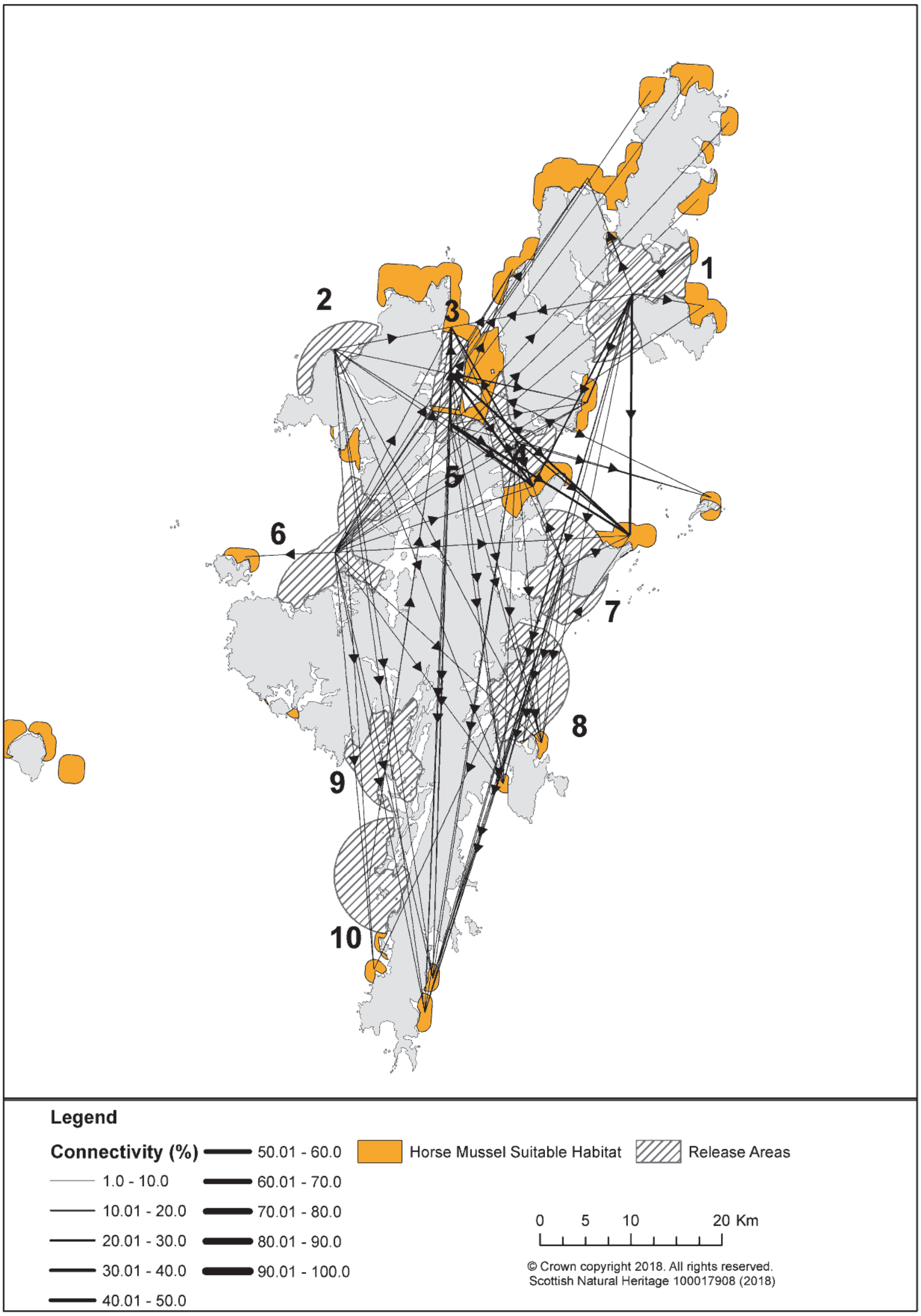

Figure 22. Larval export from horse mussel bed release areas in Shetland to predicted Maxent habitat areas. Only the connections due to >1% of particles are shown.

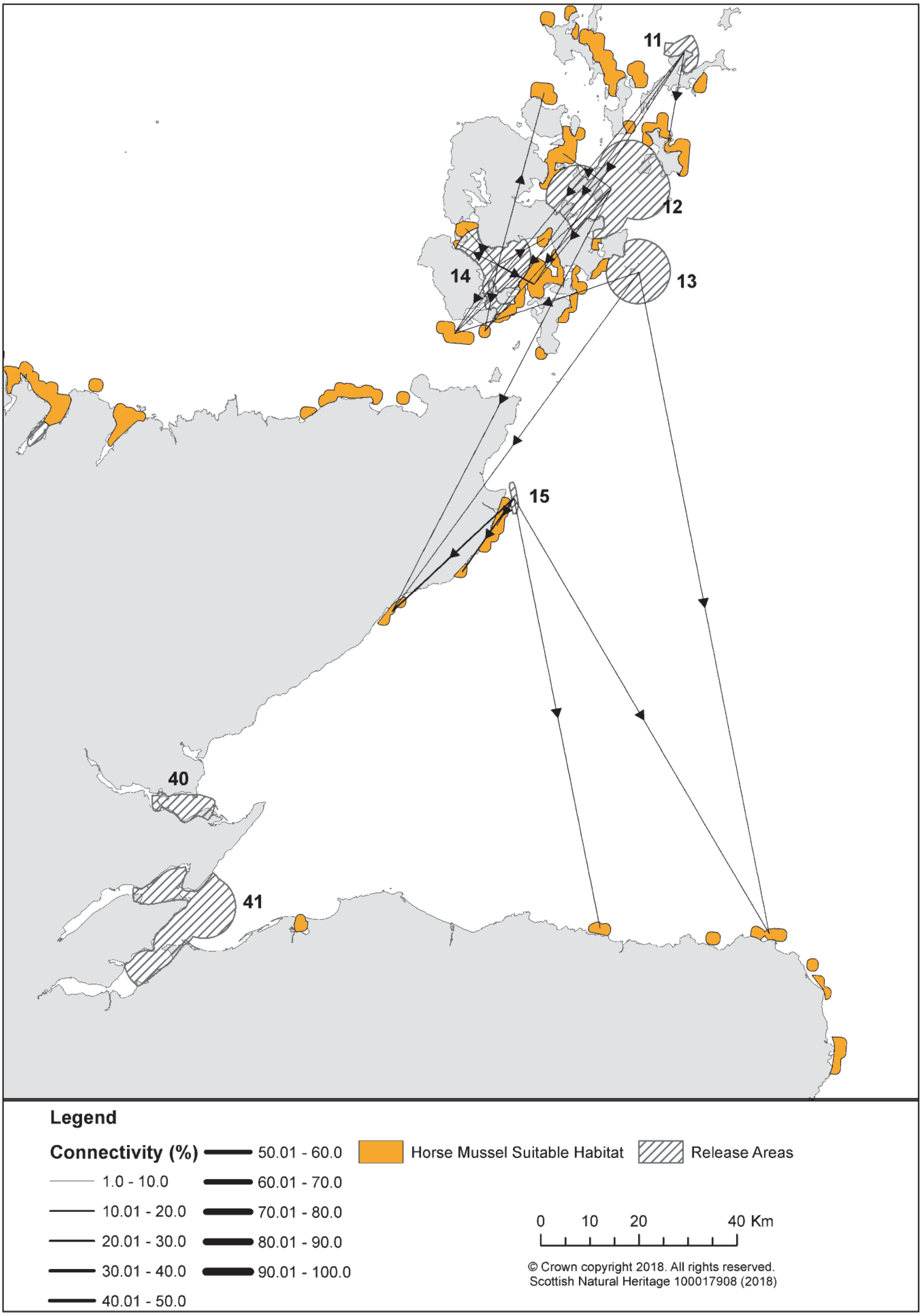

Figure 23. Larval export from horse mussel bed release areas in Orkney to predicted Maxent habitat areas. Only the connections due to >1% of particles are shown.

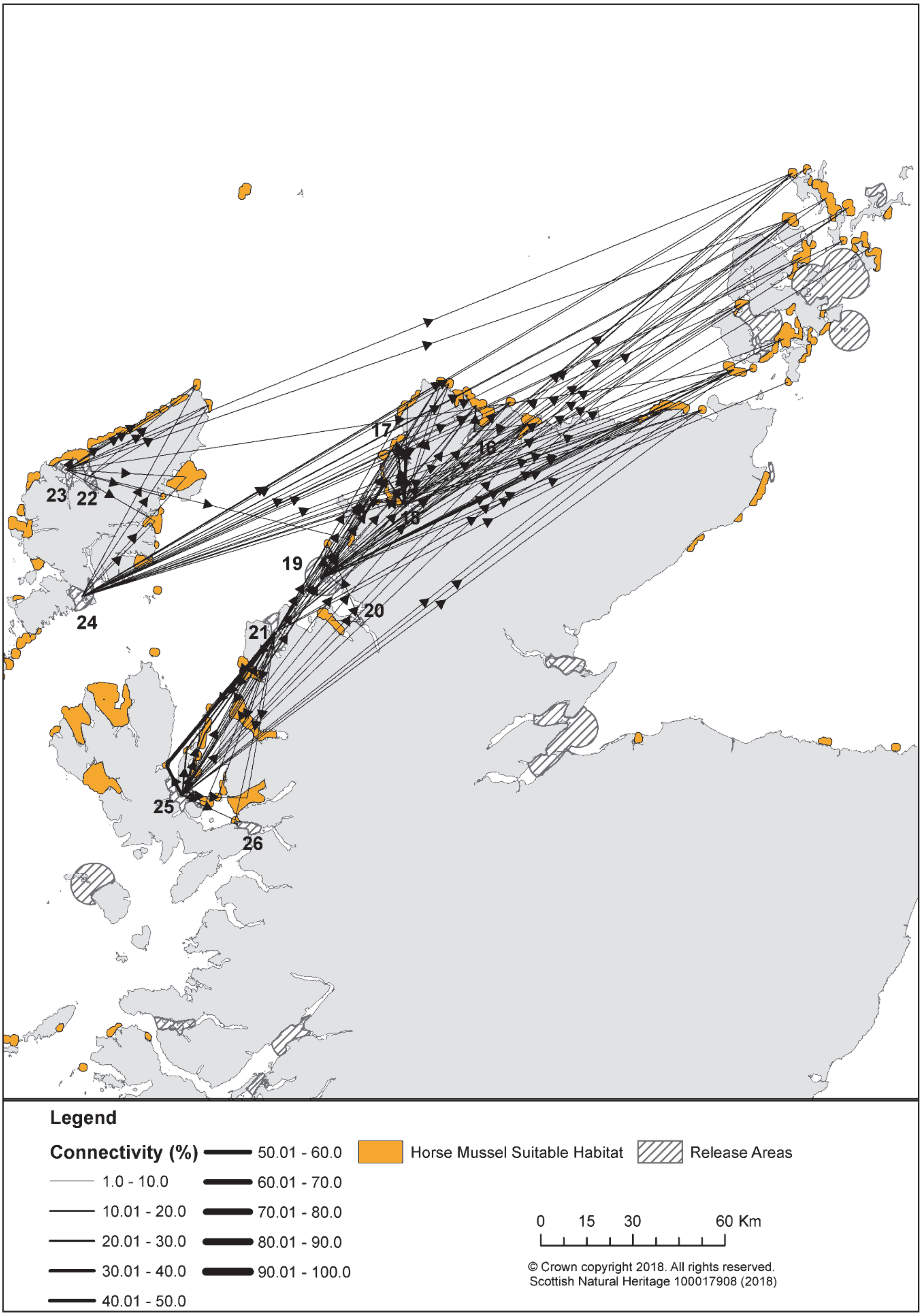

Figure 24. Larval export from horse mussel bed release areas in north-west Scotland to predicted Maxent habitat areas. Only the connections due to >1% of particles are shown.

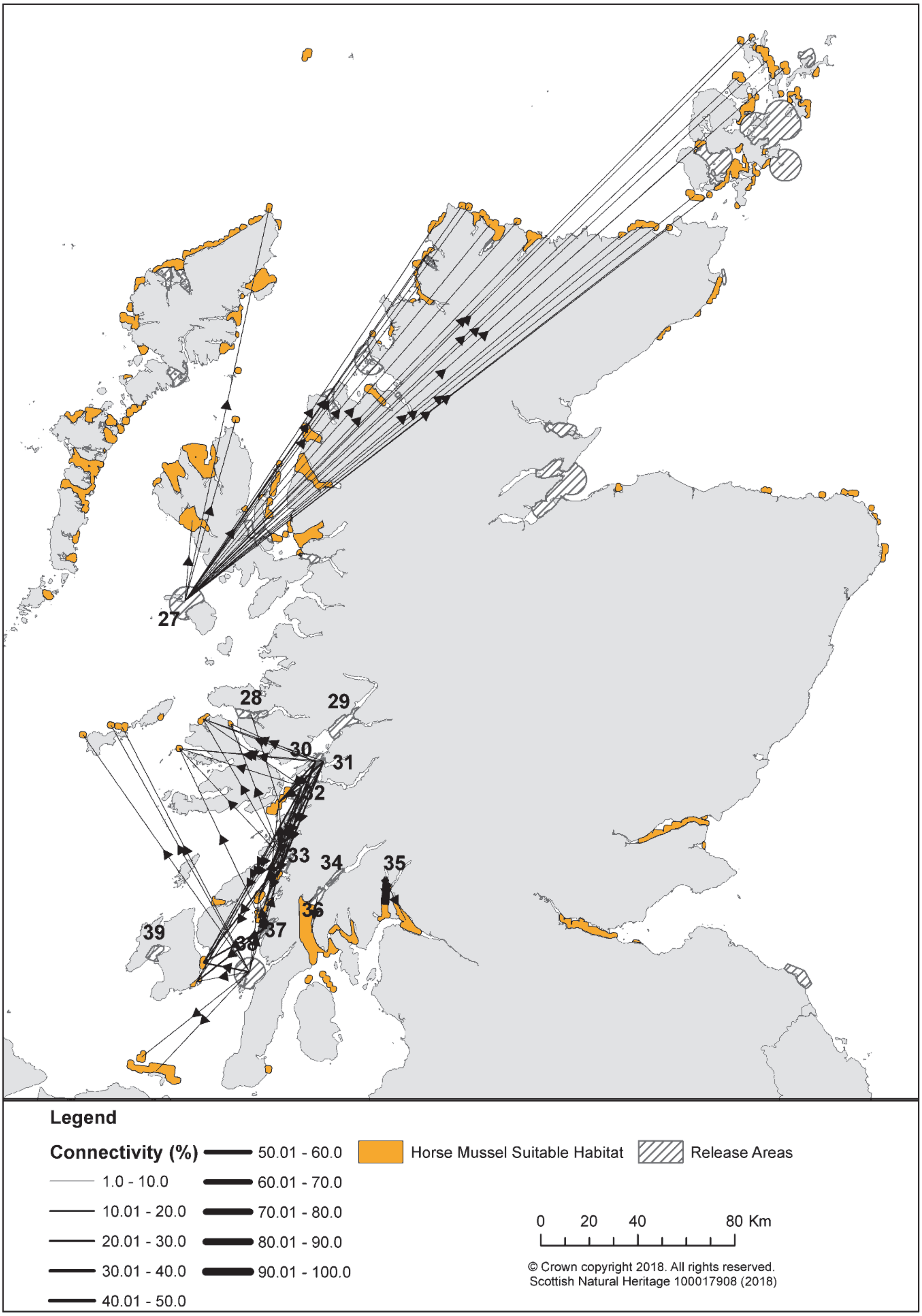

Figure 25. Larval export from horse mussel bed release areas in south-west Scotland to predicted Maxent habitat areas. Only the connections due to >1% of particles are shown.

3.4.2 Flame shell beds

Table 11 shows the percentage of larval export for the flame shell bed release areas to the predicted suitable habitat areas. The connections due to >1% of particles are presented graphically in Figure 26. Only the larval export from the release areas to the predicted suitable habitat areas is shown, i.e. connections between the release areas (Figure 11) are not shown. Release areas 6 and 7 (Loch Linnhe and Sound of Mull, respectively) were found to have the most new connections, in that they exported larvae to the highest number of predicted suitable habitat areas. The Loch Linnhe release area (area 6) exports larvae to predicted suitable habitat areas within Loch Linnhe (e.g. at the entrance to Loch Leven (39% of particle), on the east of Mull and three areas on the mainland north-east of Jura. In addition to the connections shown in Figure 26 there are also weak connections (<1% of particles) from Loch Linnhe to the other predicted suitable habitat areas in Loch Linnhe and on the south of Mull.

The Sound of Mull release area (area 7) exports larvae to three suitable habitat areas on the west and south side of Mull as well as the three suitable habitat areas on the mainland north-east of Jura. In addition to these connections, there are also weak connections (<1% of particles) from the Sound of Mull to the predicted suitable habitat areas in the outer Loch Linnhe, the south-east of Mull and the south of Jura. The three predicted suitable habitat areas north-east of Jura receive larvae from release area 9 (Sound of Jura). The Sound of Jura release area also exports larvae to a nearby habitat area on the south-east coast of Jura (15% of particles).

There are also a number of weaker (<1% of particles) connections from the Sound of Jura to Sound of Mull (<0.005%), southern Mull (0.1 - 0.8 %) and Islay (<0.7%). Release area 10 (Sound of Bute) exports larvae to the Loch Long and Gare Loch predicted suitable habitat areas.

Further north, the Loch Carron NCMPA (release area 3) exports larvae to the three surrounding predicted suitable habitat areas. The Lochs Duich, Long and Alsh NCMPA also exports some larvae (0.3 - 0.7%) to these areas.

Table 11. Percentage larval export matrix for flame shell bed release areas exporting to the Maxent areas of suitable habitat. The order of the release areas has been changed to reflect how the particles were transported around the Scottish coastline. The numbers of destination Maxent areas are indicated in Figure 21.

Release Areas

Destination Maxent areas of suitable habitat	10	8	9	6	7	5	4	3	2	1
5									0.9004	
12			0.0002							
14							0.0029	0.0055		
21							0.0029			
23							0.5035	87.5464		
26							0.1756	14.0492		
27							0.1669	3.7596		
38			0.0002							
47				38.7273	0.0031					
49				37.5896	0.0015					
50			0.0013		0.0015	2.3998				
51			0.0006	1.6271	0.3882	0.0205				
53				1.0455	0.0031					
54				0.5178	0.0232					
55				0.0398	0.0031					
56			0.0011		0.0031					
57			0.0021	4.4164	2.6771	0.0046				
58				1.0165	0.9944	0.3575				
59			0.0011	0.3750	0.4191	0.0387				
60			0.8882	0.1271	2.1559					
61			0.6630	0.1688	2.0878					
62			0.2416	0.3308	1.3238	0.0046				
63			0.2605	0.0771	0.8815					
64			1.2310	1.9402	7.8085	0.0159				
65			2.5044	1.3930	7.7018	0.0068				
66	4.2097									
67			2.1590	1.0646	6.0192	0.0068				
68	5.0828									
69	1.1314									
71	0.6729									
73			0.0240							
74			14.7813	0.0393	0.6697					
75			0.6692							

Percentage connectivity (%): 0, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100

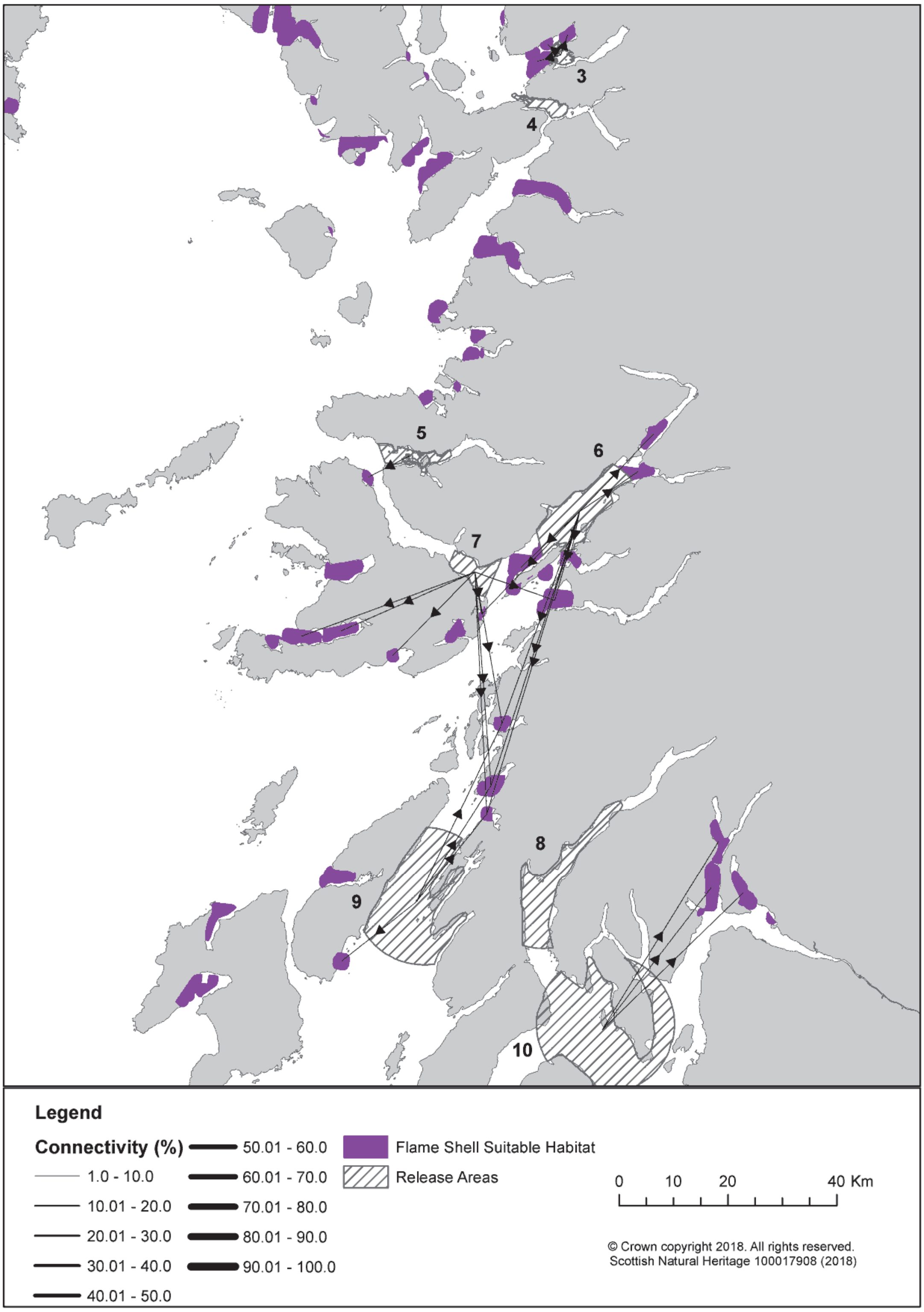

Figure 26. Larval export from flame shell bed release areas to predicted Maxent habitat areas. Only the connections due to >1% of particles are shown.

4. DISCUSSION

As part of the management of Scotland's seas, it is crucial to have an understanding of the potential role served by the existing MPA network, and of the linkages between habitats both within and outwith the MPA network. However, very little is known of the connectivity between benthic features which are protected by MPAs due to the difficulty in obtaining measurements of movement and behaviour of larvae. Modelling the dispersion of particles is a useful tool to investigate potential connectivity between populations of benthic species through dispersal of their pelagic larvae. Connectivity between designated Scottish MPAs has previously been modelled (Gallego *et al*., 2013, 2017), but this is the first study to investigate connectivity between both protected and unprotected areas from known locations.

Horse mussel beds are widespread around the Scottish coast. The results of our modelling found that Shetland populations of horse mussels appear to be isolated from other populations in Scotland, although there are some weak connections (due to <1% of the particles) from the north-west Scotland region. The comparisons made between the integrated and coarser model grid results suggest that the increased resolution provided by the integrated grid may reveal additional connections between horse mussel beds around Scotland, including between the west coast and Shetland. Also, recent analysis carried out by Mackenzie *et al*. (2018) suggested that there are genetic connections between horse mussel beds on the Scottish mainland coast and Shetland. In addition to the possibility of some connectivity between the mainland and Shetland, as discussed above, differences between genetic and particle tracking results could arise, for example, if larval transport between locations is not direct and unknown intermediate horse mussel beds (or horse mussels which are not part of beds) are acting as 'stepping stones'. Within Shetland there are a great number of connections. This is consistent with the results of genetic work; although Mackenzie *et al.* (2018) only sampled three horse mussel beds in Shetland, all of these were found to have high genetic connectivity. The level of self-recruitment is also generally lower in the Shetland areas in comparison to west coast areas investigated.

Currently in Shetland there are two designated MPAs for horse mussel beds, Fetlar to Haroldswick NCMPA and Sullom Voe SAC, which are connected to each other (~3% of particles) and also have reasonably strong self-recruitment (16-22%). The particle tracking results have highlighted that there are strong connections from the designated areas to other beds outside the protected areas. For example, Fetlar to Haroldswick NCMPA has a 17% connection to Release area 7 (Dury Voe and Lunning Sound). As all the Shetland areas are interconnected, if one population was to be damaged this may have impacts on populations in other areas although, conversely, the presence of multiple connections offers some degree of redundancy against local stressors. The Maxent modelling results predict some areas of suitable habitat around Shetland. The release areas and these predicted suitable habitat areas are also well inter-connected within Shetland, so the potential merit of granting protection to some currently unprotected beds for the overall resilience of the network needs to be considered. Overall, our connectivity results suggest that Shetland should be considered isolated in terms of management of horse mussel beds.

Orkney horse mussel beds are weakly connected to each other and there is a low level of self-recruitment (1-16%) within the areas investigated. There is, however, a large influx from west-coast horse mussel beds due to the residual circulation. The Orkney populations have weak (<1%) connections into the Moray Firth. Release area 15 (Noss Head NCMPA) has low self-recruitment (0.4%), and exports larvae to the release areas in the Dornoch and Cromarty Firths (areas 40, 41). The horse mussel bed connectivity results presented here generally agree with the recent genetic analysis by Mackenzie *et al*. (2018). For example, the Noss Head horse mussel bed was found to recruit from external beds with minimal degree of self-recruitment and Mackenzie *et al*. (2018) suggest that both adults and juveniles at Noss Head appear to be genetically connected to individuals sampled from beds in Shetland and, more moderately, to individuals from beds on the west coast. Comparative simulations using the integrated grid in the current study also suggest that larvae from west coast release areas (e.g. Lochs Duich, Long and Alsh SAC and Loch Laxford SAC) may travel as far as Noss Head when fine scale local hydrodynamic features are incorporated in the model.

Particle tracks show that the particles released from Noss Head NCMPA stay within the Moray Firth. However, the investigation into other areas of suitable habitat using Maxent found weak connections to potential areas of suitable habitat in the eastern outer Moray Firth. Feature records are sparse in this area and across the north mainland coast. Therefore, there may be undiscovered horse mussel beds which act as stepping stones between the east and west coast populations. Conversely, a lack of suitable habitat in the Pentland Firth may act as a barrier between the two regions. Further survey work in this region is required to clarify this.

On the north-west coast of Scotland there are varying levels of self-recruitment in the horse mussel bed release areas, with some of the more sheltered sea loch populations such as in release area 16 (Loch Eriboll) having 96% self-recruitment with no connections to or from other areas investigated. It is important to note here the comparisons carried out between the results of simulations using coarser and the integrated grid outputs. Ideally all simulations should be repeated using the integrated grid output. This would likely produce more robust network connectivity results.

The south-west Scotland horse mussel bed areas also have varying self-recruitment with Upper Loch Fyne and Loch Goil NCMPA being fully reliant on self-recruitment. There are connections between populations from Loch Linnhe down to release areas further south. Limited connections between north-west and south-west coast release areas were found. In general, the release areas in the south-west appear to export larvae south and west, while release areas in the north-west appear to transfer larvae northwards. However, the results suggest that the Small Isles NCMPA receives larvae from release area 33 (Loch Craignish) to the south and also acts as a source of larvae for areas on the north-west coast (Loch Laxford SAC) and Orkney (including Copinsay and Scapa Flow). In this way the Small Isles NCMPA appears to provide an important link between the south-west and north-west areas. Simulations run for Loch Craignish suggest potential additional connections with north-west release areas when particle tracking is forced with the integrated SSM grid output, rather than the coarser grid. Again, it will be important to consider how the models capture the detailed hydrodynamics in the area and to further investigate areas in the south-west using the integrated model output. It is possible that more finely resolved flow fields will result in more connections in what is known to be quite a dispersive area in general.

Release area 42 (Berwickshire and North Northumberland Coast SAC) was found to have low self-recruitment (0.9%) and was not connected to the other horse mussel bed release areas considered here. The tracks showed that the particles go southwards and the larvae may therefore be transported to other horse mussel beds in England, which were not included in this study. This raises the question of where the larvae may come from to populate the area. There are tentative records of horse mussel beds in the Firth of Forth (ERT Scotland, 2003; Elliott and Kingston, 1987; Thurstan *et al*., 2013). The current status of these beds has not been confirmed and as such they were not included in this investigation. If these beds were found to be present then this may explain where the Berwickshire and North Northumberland Coast SAC is receiving larvae from, as the circulation would flow south from the Firth of Forth. Further investigation, both in terms of surveying the area and also fine resolution particle tracking modelling would be needed to confirm this. Nevertheless, the lack of suitable habitat for horse mussel beds on the east coast generally suggests that these beds may be more isolated than those on the west coast. The Maxent modelling results predicted additional areas of suitable habitat for horse mussel beds. The connections found between known beds and predicted suitable habitats were consistent with the simulated connectivity patterns between the known beds.

Little is known of flame shell larval behaviour and no known habitat suitability modelling has been carried out, prior to the work completed for this study. Known locations of flame shell beds within Scottish waters are primarily on the west-coast of Scotland, generally in sea lochs or tide-swept narrows. There are also beds in Scapa Flow, Orkney. The more sheltered beds such as Loch Sunart show a higher level of self-recruitment due to retention than others in more coastal locations. Only the Loch Linnhe release area (release area 6) had low (0.5%) self-recruitment, but there were some weak connections found from this area to others nearby. The Orkney release area in Scapa Flow (release area 1) did not act as a source for other known flame shell beds, which is not surprising considering the residual circulation around Scotland. There was a weak connection (1.6%) from Wester Ross NCMPA to the Scapa Flow release area. The particle tracking results predict that the flame shell beds are generally self-recruiting with some weak connections to other areas. Due to the predicted high level of self-recruitment in most release areas investigated, flame shell beds are likely to be vulnerable to localised anthropogenic damage.

The Maxent modelling predicted many new potential areas of suitable habitat for flame shell beds. Connections between the existing release areas and these newly predicted areas of suitable habitat were found, particularly around the south-west coast of Scotland (Loch Linnhe, Mull, Jura, Bute and Loch Fyne). The suitable habitat areas identified in this south-west region require further survey to confirm whether the habitat is present. If flame shell beds are identified the results of this study would provide support for their protection in order to make the flame shell MPA network more resilient to local stressors. The areas at highest risk and requiring greatest protection are the areas largely reliant on self-recruitment and that do not receive larvae from other areas. If these beds are damaged, or adults are lost from the population, then spawning rates and larval numbers would be reduced. Other types of area in need of particular protection are those which act as source populations on which other areas are strongly reliant for recruitment, and any areas which appear to act as key 'stepping stones' e.g. through providing a link between different regions.

Marine Scotland and SNH are working on a project to improve protection of Priority Marine Features outside the MPA network (https://consult.gov.scot/marine-scotland/priority-marine-features/), looking at where some of the most sensitive habitats, including both horse mussel beds and flame shell beds, could benefit from additional management measures. The results presented here help to identify locations where additional protection could improve connectivity between examples of these habitats within the existing network.

The habitat suitability modelling is also useful for suggesting locations for survey. Since this study was carried out further examples of both habitats have been identified through survey work carried out in 2019 (https://www2.gov.scot/Resource/0054/00548608.pdf). Any future hydrodynamic or habitat modelling of horse mussel beds or flame shell beds should take the locations of these new records into account.

The combination of habitat modelling and particle tracking modelling has not been applied comprehensively before in Scottish waters and can be a powerful combined methodology, although both model implementations in the current study suffered from a number of limitations, and opportunities for further work to address these have been identified, as outlined below.

4.1 Future work

This work has raised a number of further questions for future consideration. The recently published horse mussel bed genetics study by Mackenzie *et al*. (2018) and additional ongoing genetics work should be compared in more detail with the outputs of modelling-based connectivity studies such as the present one. Previously, Gormley *et al.* (2015) carried out particle tracking and genetic studies of horse mussel beds in the Irish Sea. The particle tracking results supported the genetic findings that Welsh and Isle of Man populations are not connected to Northern Irish populations. A more detailed analysis of the Scottish horse mussel bed connectivity results (combined genetics, larval dispersal and suitable habitat modelling) may help inform future wider seas management decisions.

It would be useful to establish what percentage of larval connectivity is relevant at an ecological level. This study shows how there are numerous and potentially far reaching weak connections due to extremely low fractions, in many cases <0.001%, of released particles. This study was able to show these weak connections by releasing hundreds of thousands (and in some cases millions) of particles from each of the release areas. Hopefully future genetic and field validation studies will be able to shed some light on this issue.

Larval behaviour is known to be an important aspect to include in bio-physical simulations. For example, studies comparing active and passive particles released from MPAs in the deep Atlantic Ocean found very different connectivity results (Ross *et al*., 2017). However, information on larval behaviour of many benthic species is often lacking, and it is very difficult to quantify. It should be noted that, by necessity, assumptions regarding larval behaviour were made in order to carry out the modelling, and therefore the results should be interpreted with these in mind. In the current model, information from the literature on spawning and larval ecology was used to help define the particle release rate and settlement window. There was no information known about the (e.g. vertical) behavioural movement of the species investigated for it to be included in the model, so passive particles were used. More information on larval behaviour, mortality rates and settling behaviour (e.g. through aquarium and field experiments) is required to improve our ability to predict the movement of larvae and ultimately the successful development of a bed or reef over space and time.

Some of the release areas considered here were poorly resolved in the coarser SSM grid, in that the resolution of the coarser grid was not always sufficient to fully define the release area boundary and/or faithfully replicate the local hydrodynamic features. For example, the coarser grid results for horse mussels characterised the general patterns of connectivity, as the model effectively represents the main circulation patterns around Scotland. However, some of the smaller scale hydrodynamic features within and around sea lochs and headlands are likely to be better represented in the integrated grid. The integrated results show that particles released within sea lochs do not always quickly exit the lochs, allowing them to enter the main residual circulation. This process therefore has an important effect on the eventual destination of the particles - either they stay within the loch, or escape and can be transported widely around Scotland. The time it takes for particles to exit a loch is dependent on the loch's flushing time, which is different for each sea loch and is a complex function of the loch's hydrography. The main discrepancies identified in the simulations, where both model resolution results were available, were release areas 17 (Loch Laxford SAC), 18 (Loch a Chairn Bhain) and 26 (Lochs Duich Long and Alsh Reefs SAC). The integrated grid forced the particles to stay in Loch a Chairn Bhain, but exit Loch Laxford SAC and Lochs Duich Long and Alsh Reefs SAC. This was the opposite result to the coarser grid simulations. Although we carried out a number of integrated grid simulations, these are very computationally expensive and to extend the analysis to all areas would need additional computer resources and/or changes to the model code to reduce the computation time in order for the runs to be completed. One approach may be to focus on a smaller geographic area, such as the south-west Scotland flame shell bed network, and use high resolution hydrodynamic model output but it would be critical to ensure that any reduced domain was big enough to allow all potential dispersal patterns.

It must be pointed out that our simulations were forced by climatological flow fields. These represent “average” conditions and are the most tractable way to study connectivity e.g. for the design of spatial protection measures such as MPAs that would work under general circumstances. However, it is also necessary to investigate the effect of inter-annual variability, including “extreme events”, as these may play a significant role in offspring export and connectivity between areas and populations. This may be particularly important for areas where our simulations have identified low levels of self-recruitment and influx from other areas. Such patterns may also be influenced by other model assumptions, such as lack of biological realism (spawning patterns, spawning intensity, swimming behaviour, larval mortality, settlement preferences, etc.). Sensitivity analyses can be carried out to estimate the importance of such assumptions but, with very limited ecological information available, this can be a very challenging multidimensional exercise beyond the scope of the current project. Therefore, field and laboratory investigations to provide information about these biological processes are necessary and likely to enhance the reliability of our modelling results.

The habitat suitability modelling would benefit from higher resolution data layers than those used in the present study, as this may have influenced the number of significant variables and potentially overestimated the areas identified as suitable, while in some cases suspected suitable areas have not been identified as such in the modelling results. Higher resolution environmental layers are now available, including outputs from the SSM. Although more comprehensive habitat modelling was beyond the scope of the current study, it would be beneficial to investigate using some of these layers to assess if suitable habitat could be better predicted. For example, the salinity layer used in the current results does not have very high resolution. Including a more highly resolved layer, particularly around the coast and freshwater outflows, may alter the predictions. It is also important to validate the habitat suitability outputs from the Maxent model with more field sampling. Also, habitat suitability modelling has currently only provided destination areas for particles and has not considered any potential larval sources from these areas. It would be advantageous to include particle tracking from the predicted areas of suitable habitat for inclusion in the connectivity network, although this would require some field validation to evaluate whether habitat is actually present in the predicted suitable areas. We also recommend that the predicted areas be combined for future analysis in a similar way to how adjacent release locations have been combined in our study. Otherwise the large number of small potentially suitable areas makes the analysis very onerous and difficult to interpret.

Finally, it is also relevant to consider the impact of climate change on connectivity within the network of MPAs for these PMFs, to investigate how future-proof the MPA network may be. The SSM has a future climatology available, based on a 25 year period around the year 2050 (De Dominicis *et al.*, 2018b). The methodology here could be repeated using the future climatological outputs to predict changes in network connectivity due to climate change. However, this climatology is not currently available for the finer resolution models that need to be combined into the integrated grid and, therefore, only coarser-grid simulations could be conducted at present. Further investigation would also be required on the effects of climate change on spawning and larval behaviour in these species, so that relevant biological metrics can be incorporated in modelling. For example, studies on pelagic larval duration and temperature found that in general a temperature increase leads to a reduction in the pelagic larval duration (O’Connor *et al.*, 2007). This would potentially reduce the distance particles can travel, as longer pelagic larval durations allow the particles to travel further distances (Gallego *et al.*, 2013). Climate change could potentially cause connections to be lost due to the reduced pelagic larval duration of species. However, changes in larval behaviour and other ecological effects of climate induced environmental change would also be important to investigate and incorporate in the modelling.

Increased seawater temperatures are also predicted to have an impact on the distribution of protected features such as horse mussel beds (Gormley *et al*. 2013) and, therefore, the management of such habitats should be considered in that context and also across political borders, as the results presented here highlight potential connections between horse mussel populations in Scotland and those that may exist in Northern Ireland and England. Future work should consider the supply and export of larvae to and from areas outside Scottish waters and take into account the overall effects of climate change.

5. CONCLUSIONS

Overall, the current study has described the patterns in connectivity between horse mussel beds and flame shell beds around Scotland both within and outwith the MPA network. This report describes state-of-the-art methodology which can still be refined, on the basis of some of the limitations discussed above, and further developed to investigate connectivity between populations of other benthic species. In particular, some modelling results were found to be sensitive to the spatial resolution of the hydrodynamic model used, highlighting the potential importance of reproducing relevant fine-scale circulation features. The SSM is being continually developed to increase the number of high-resolution areas that can be integrated into the general modelling framework and these results confirm the importance of such an objective.

The connectivity results presented here suggest that some of the investigated horse mussel bed populations have contrasting population connectivity patterns. Some areas were found to be largely reliant on self-recruitment whilst others had much lower self-recruitment but did rely on connections from other areas. This highlights the importance of considering individual beds for protection, and that the management of the PMFs may need to adapt depending on population connectivity. The horse mussel beds could be grouped into distinct regions, with good connectivity within each region. Some of these regions had one way connections to other regions. For example, the north-west of Scotland exports larvae to Orkney and the Moray Firth, and Shetland exports a small percentage of larvae to Orkney.

Flame shell beds were found to be generally more reliant on self-recruitment within individual beds, with fewer connections with other areas, although there is evidence of smaller regional networks which are most likely connected to other regions by additional (unknown) beds not included in the analysis here. The habitat suitability modelling identified areas where additional beds may be present, pending field validation.

In general, the inclusion of habitat suitability modelling to investigate additional potential areas has highlighted that other connections outside the MPA network may also be important to the connectivity and resilience of the population at national level. Further analysis and field investigations are required to validate the presence of PMFs in these locations and therefore refine and authenticate our modelling results.

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ANNEX 1: RELEASE AREAS AND NUMBERS OF PARTICLES RELEASED

Table A1. Horse mussel bed release areas and total number of particles.

Release Area	Number of release locations	Total number of particles released over spawning window
1	119	362,950
2	49	149,940
3	40	122,800
4	69	235,290
5	14	47,880
6	103	317,240
7	100	346,000
8	123	380,070
9	87	269,700
10	104	323,440
11	42	131,040
12	413	1,292,690
13	203	637,420
14	178	560,700
15	13	41,080
16	16	50,720
17	13	41,340
18	1	3,190
19	131	421,820
20	6	19,440
21	58	189,080
22	37	118,400
23	42	134,820
24	62	200,260
25	70	229,600
26	32	110,400
27	163	536,270
28	54	178,740
29	85	280,500
30	21	72,030
31	3	10,320
32	82	272,240
33	65	216,450
34	22	73,480
35	8	26,800
36	30	100,800
37	28	94,640
38	154	522,060
39	40	136,000
40	73	237,250
41	343	1,121,610
42	64	215,680

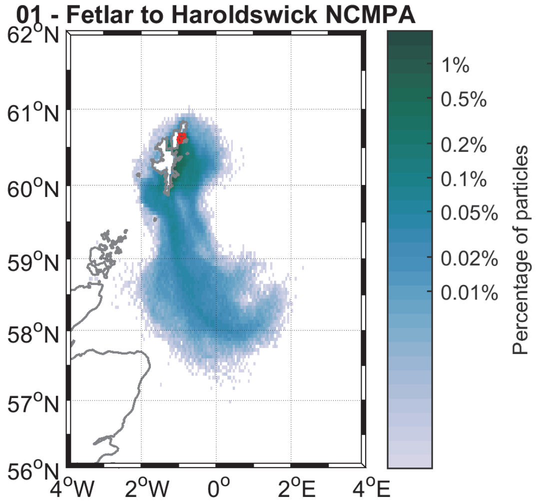
Table A2. Flame shell bed release areas and total number of particles.

Release Area	Number of release locations	Total number of particles released over spawning window
1	589	718,580
2	404	492,880
3	15	18,300
4	28	34,160
5	36	43,920
6	167	203,740
7	53	64,660
8	171	208,620
9	383	467,260
10	502	612,440

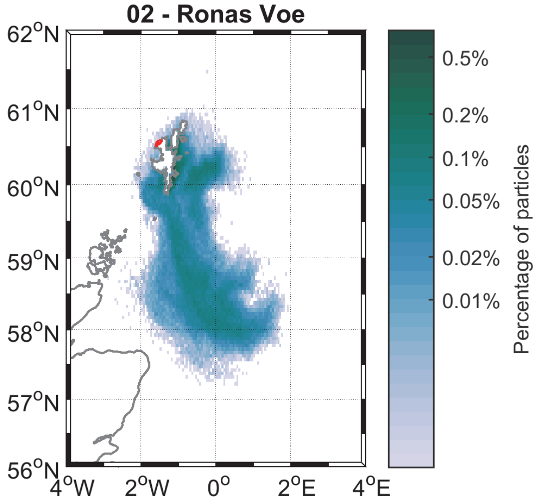
ANNEX 2: PARTICLE DENSITY PLOTS FOR HORSE MUSSEL RELEASE AREAS ON THE COARSER GRID

The following figures show the particle densities at the end of the particle tracking simulations (i.e. 56 days after the last particles were released). The densities shown are the percentage of the total number of particles released during the simulation in each 0.05° x 0.05° regular grid square. Each grid square has an area of approximately 30 km2. A logarithmic scale was used to show the difference between patches of low particle density.

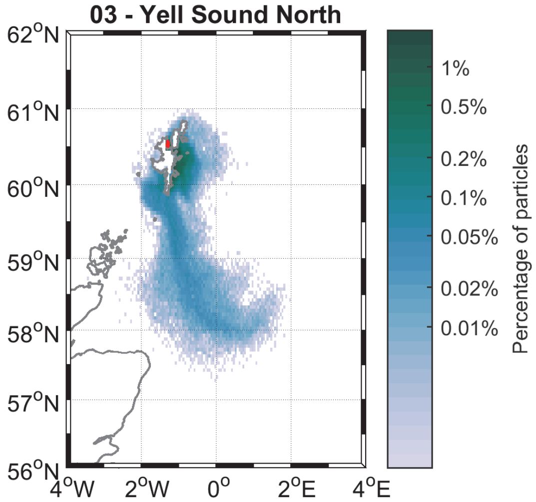
01 - Fetlar to Haroldswick NCMPA



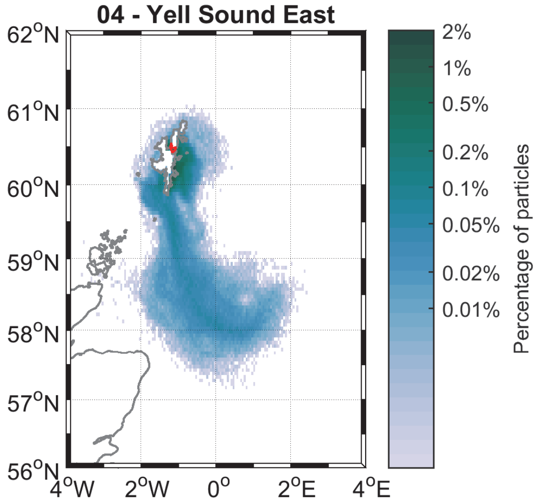
02 - Ronas Voe



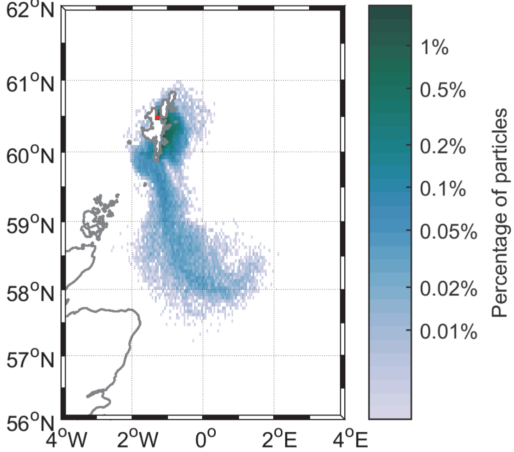
03 - Yell Sound North



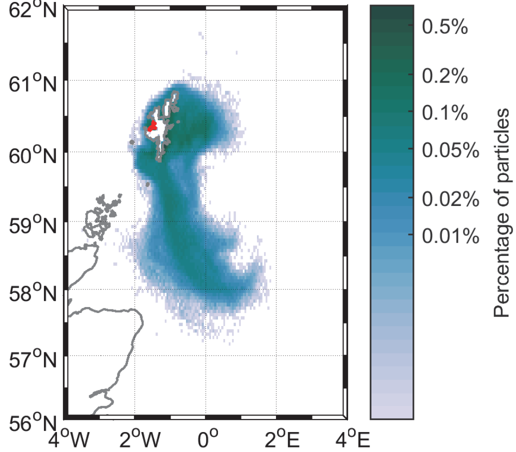
04 - Yell Sound East



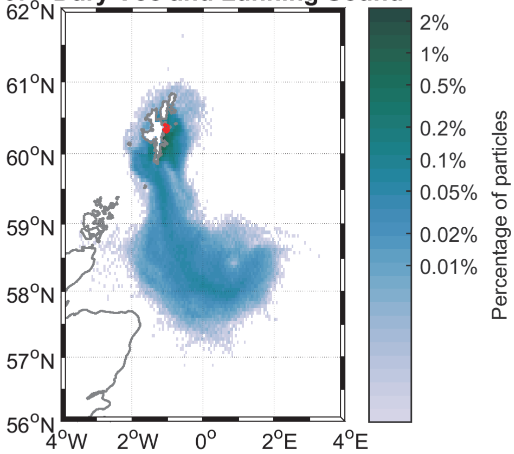
05 - Sullom Voe SAC



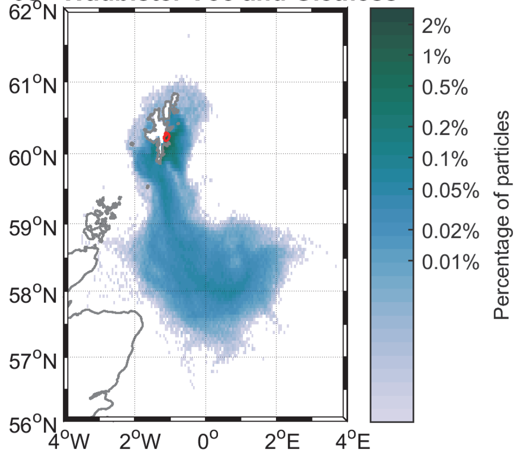
06 - Busta Voe to Brindister Voe



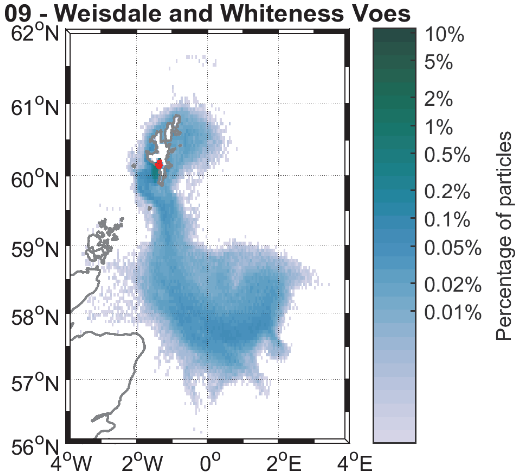
07 - Dury Voe and Lunning Sound



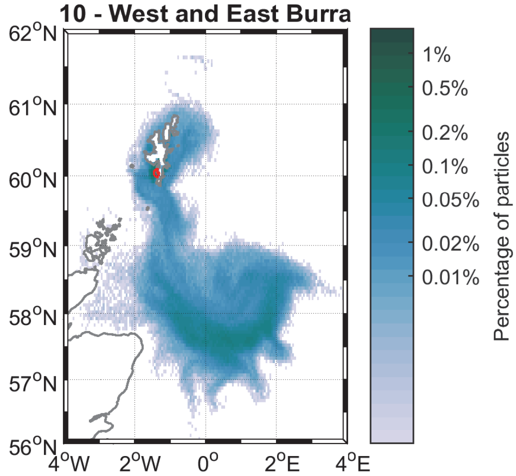
08 - Wadbister Voe and Gletness

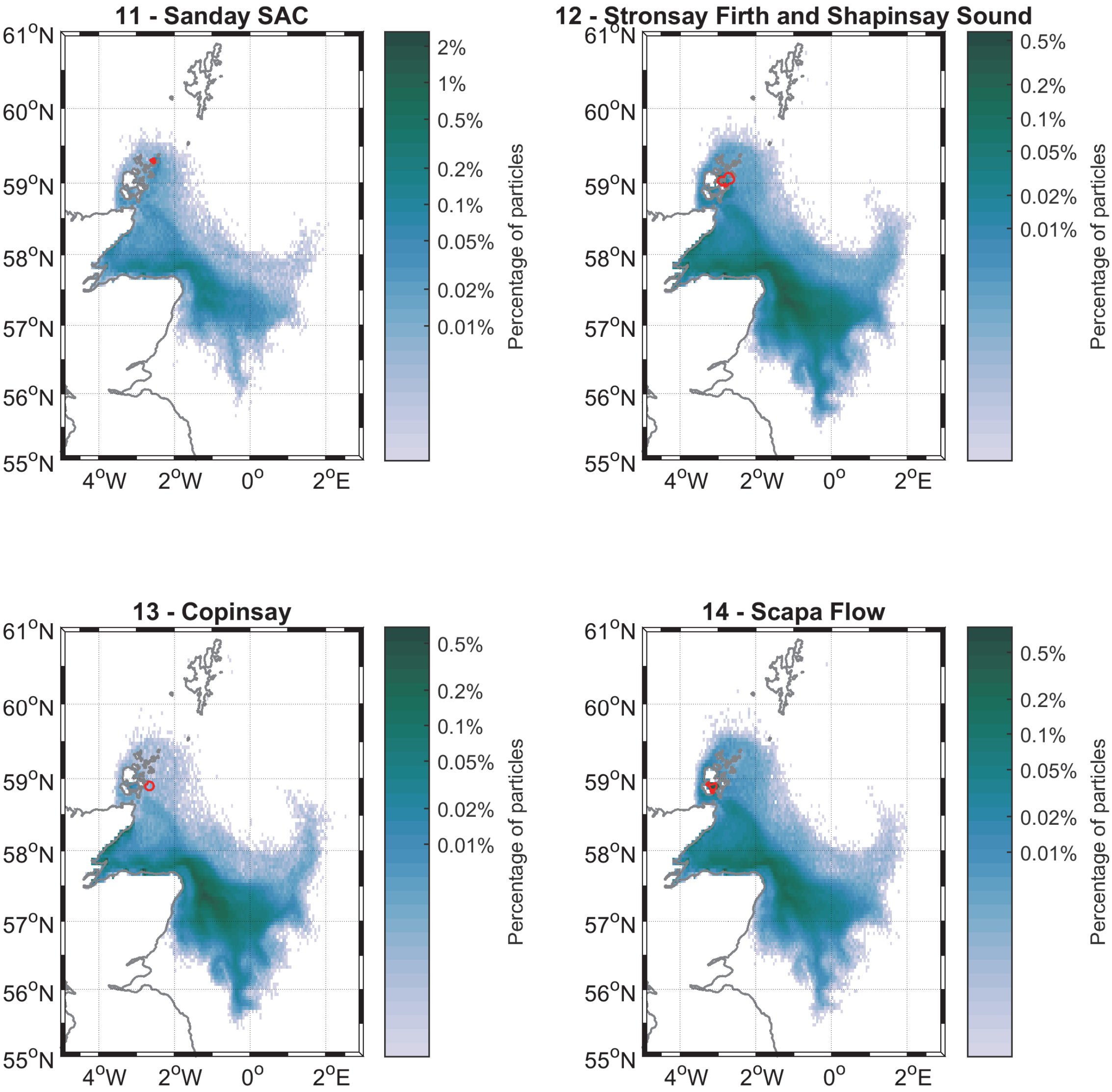


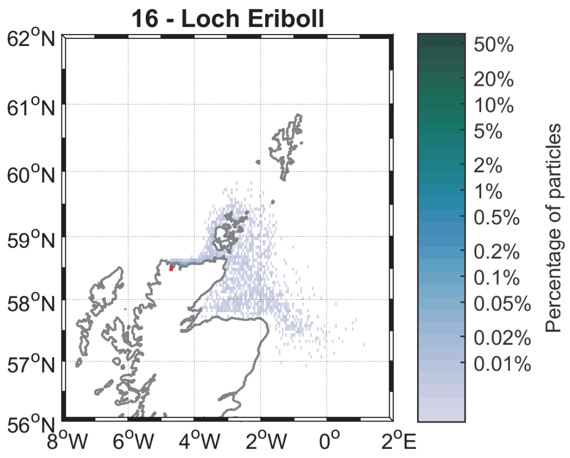
09 - Weisdale and Whiteness Voes

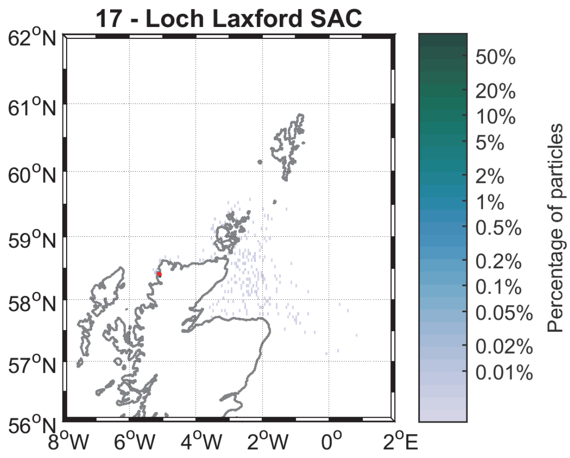


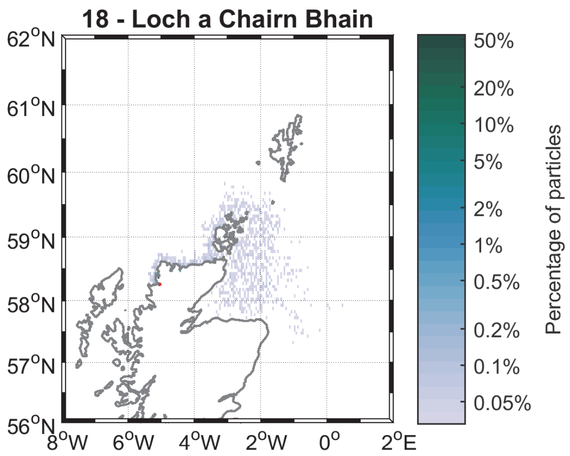
10 - West and East Burra

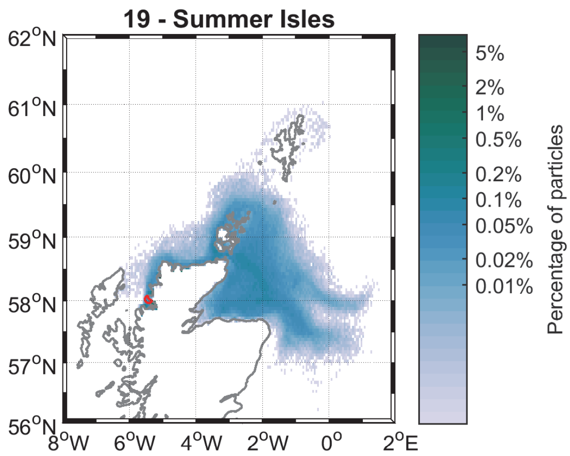


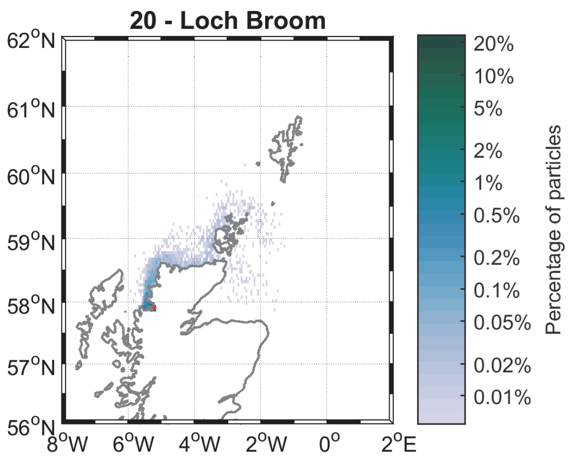

11 - Sanday SAC
12 - Stronsay Firth and Shapinsay Sound
13 - Copinsay
14 - Scapa Flow
61°N
60°N
59°N
58°N
57°N
56°N
55°N
4°W
2°W
0°
2°E
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

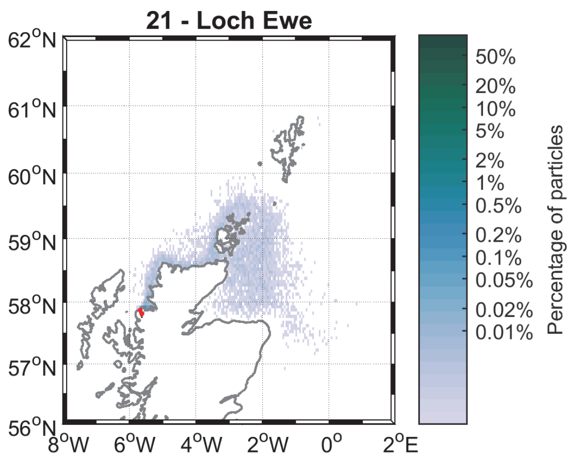

16 - Loch Eriboll
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

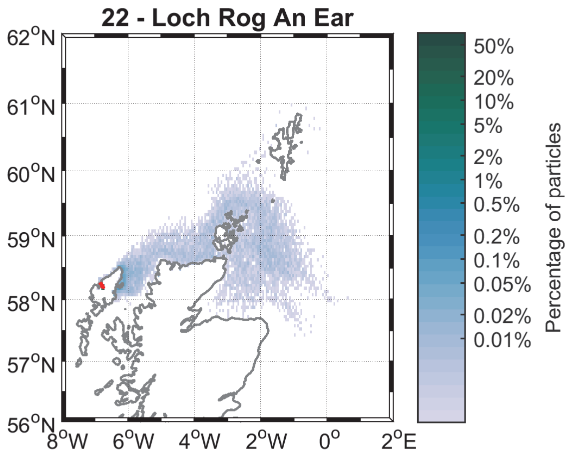

17 - Loch Laxford SAC
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

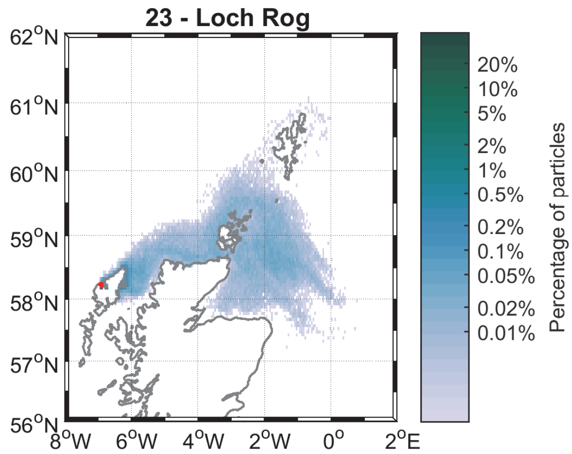

18 - Loch a Chairn Bhain
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
Percentage of particles

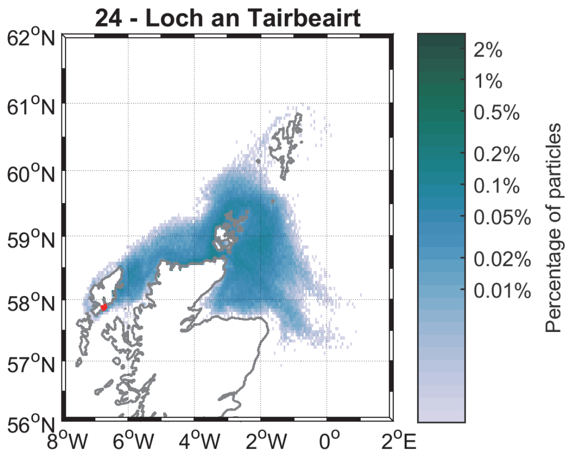

19 - Summer Isles
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

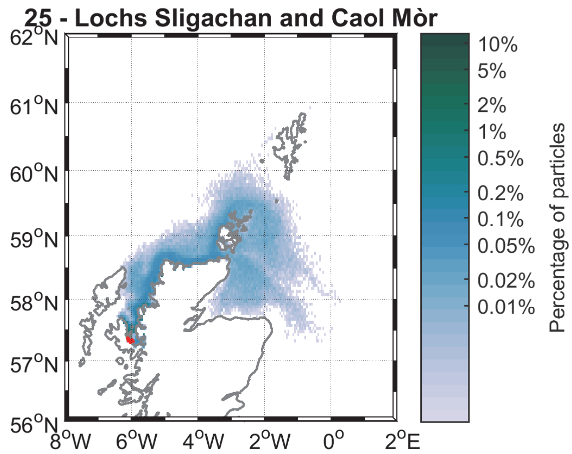

20 - Loch Broom
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

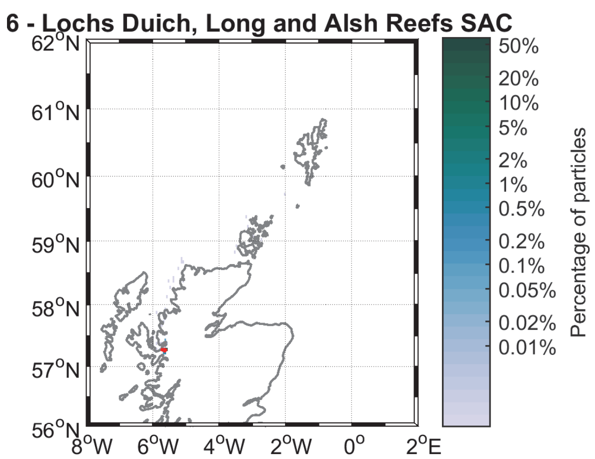

21 - Loch Ewe
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

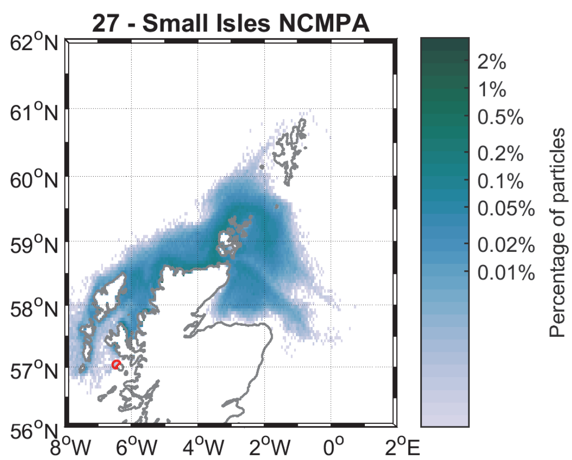

22 - Loch Rog An Ear
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

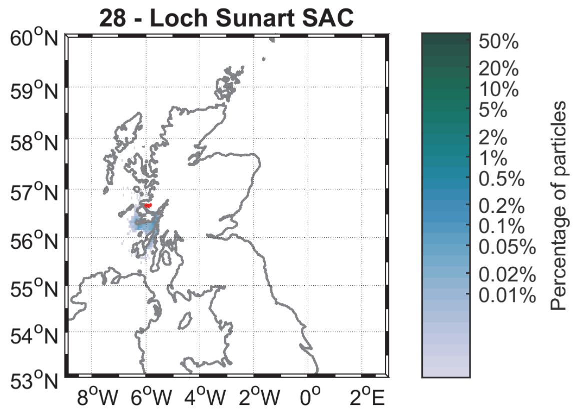

23 - Loch Rog
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

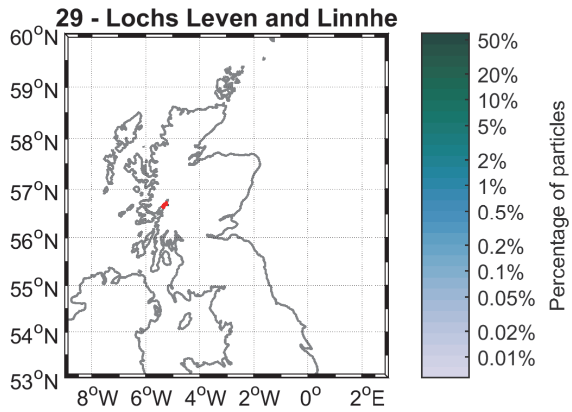

24 - Loch an Tairbeairt
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

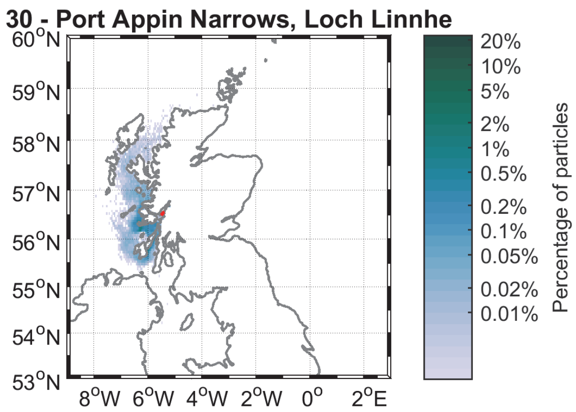

25 - Lochs Sligachan and Caol Mòr
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

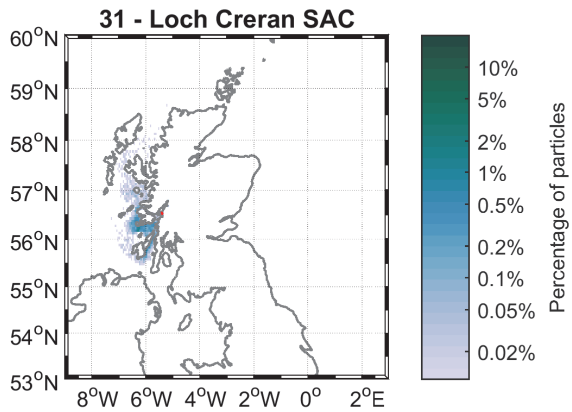

6 - Lochs Duich, Long and Alsh Reefs SAC
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

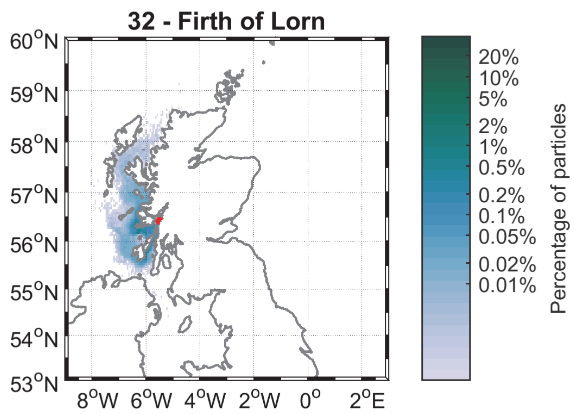

27 - Small Isles NCMPA
62°N
61°N
60°N
59°N
58°N
57°N
56°N
8°W 6°W 4°W 2°W 0° 2°E
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

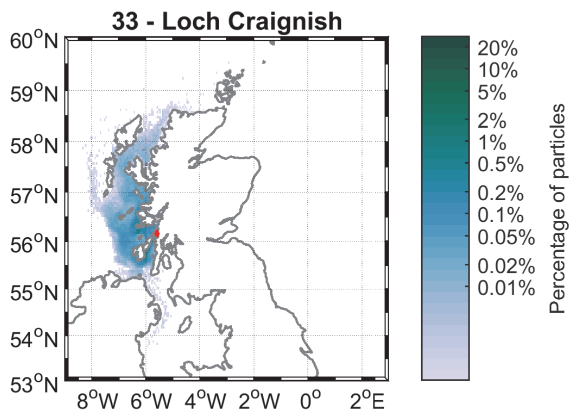

28 - Loch Sunart SAC
60°N 59°N 58°N 57°N 56°N 55°N 54°N 53°N
8°W 6°W 4°W 2°W 0° 2°E
50% 20% 10% 5% 2% 1% 0.5% 0.2% 0.1% 0.05% 0.02% 0.01%
Percentage of particles

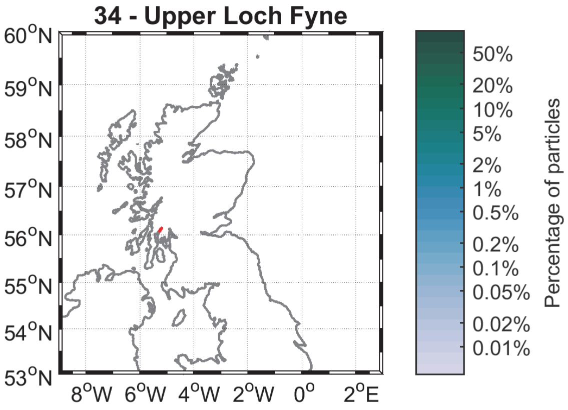

29 - Lochs Leven and Linnhe
60°N 59°N 58°N 57°N 56°N 55°N 54°N 53°N
8°W 6°W 4°W 2°W 0° 2°E
50% 20% 10% 5% 2% 1% 0.5% 0.2% 0.1% 0.05% 0.02% 0.01%
Percentage of particles

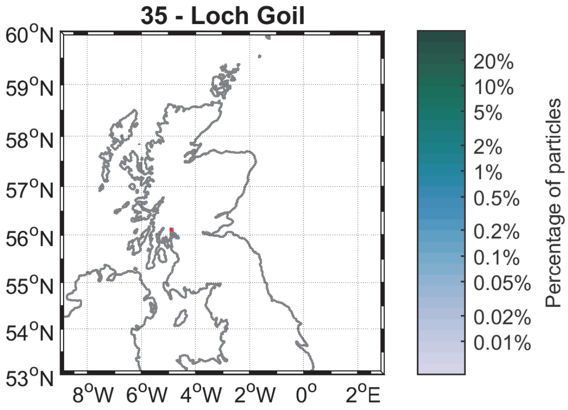

30 - Port Appin Narrows, Loch Linnhe
60°N 59°N 58°N 57°N 56°N 55°N 54°N 53°N
8°W 6°W 4°W 2°W 0° 2°E
20% 10% 5% 2% 1% 0.5% 0.2% 0.1% 0.05% 0.02% 0.01%
Percentage of particles

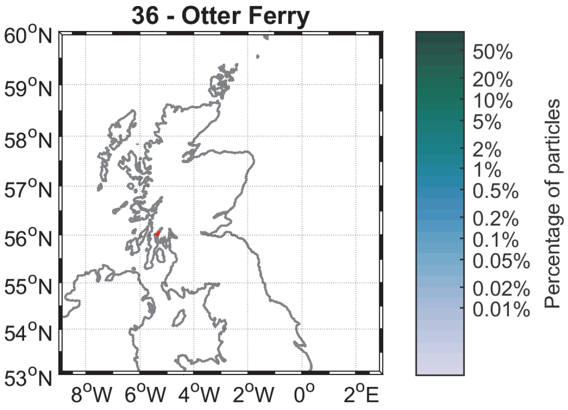

31 - Loch Creran SAC
60°N 59°N 58°N 57°N 56°N 55°N 54°N 53°N
8°W 6°W 4°W 2°W 0° 2°E
10% 5% 2% 1% 0.5% 0.2% 0.1% 0.05% 0.02%
Percentage of particles

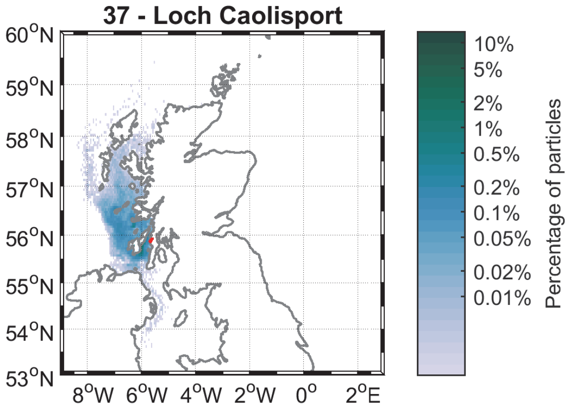

32 - Firth of Lorn
60°N 59°N 58°N 57°N 56°N 55°N 54°N 53°N
8°W 6°W 4°W 2°W 0° 2°E
20% 10% 5% 2% 1% 0.5% 0.2% 0.1% 0.05% 0.02% 0.01%
Percentage of particles

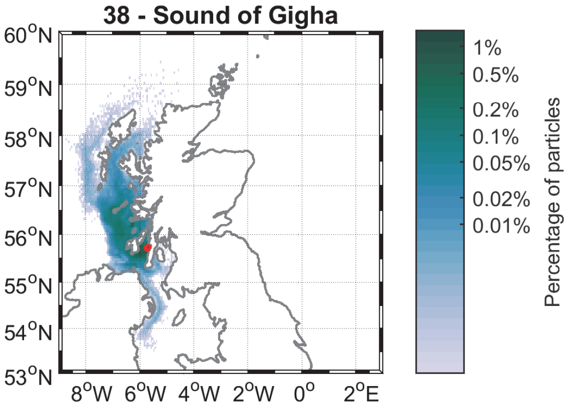

33 - Loch Craignish
60°N 59°N 58°N 57°N 56°N 55°N 54°N 53°N
8°W 6°W 4°W 2°W 0° 2°E
20% 10% 5% 2% 1% 0.5% 0.2% 0.1% 0.05% 0.02% 0.01%
Percentage of particles

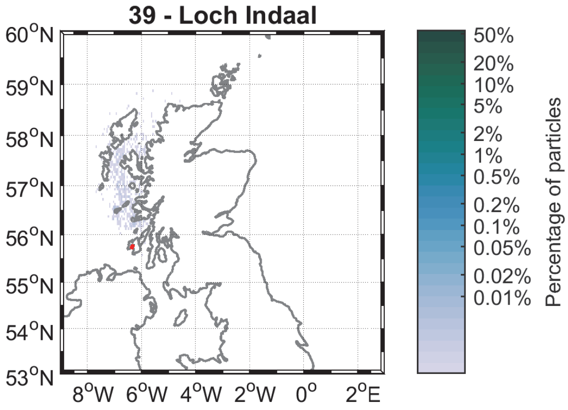

34 - Upper Loch Fyne
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

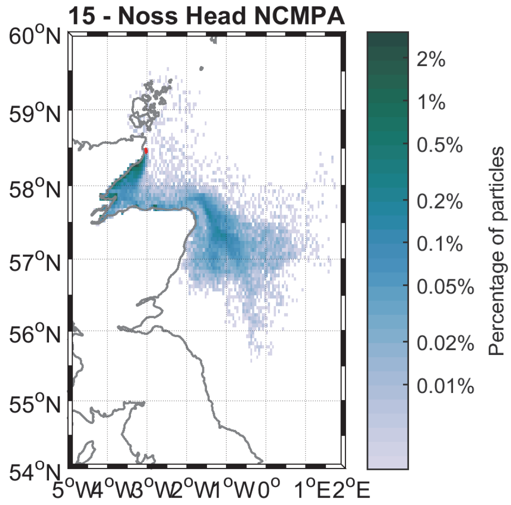

35 - Loch Goil
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
8°W 6°W 4°W 2°W 0° 2°E
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

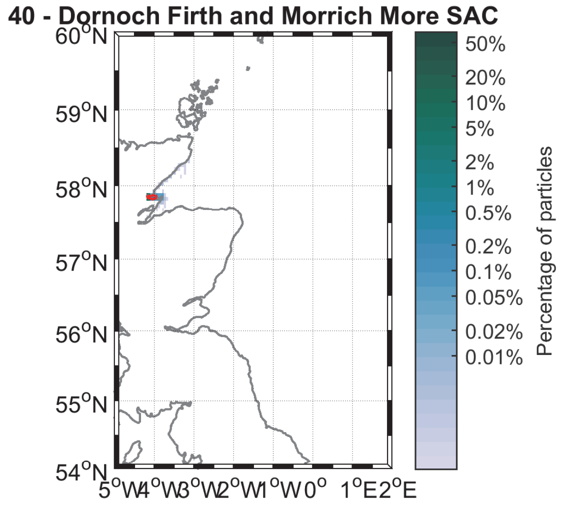

36 - Otter Ferry
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

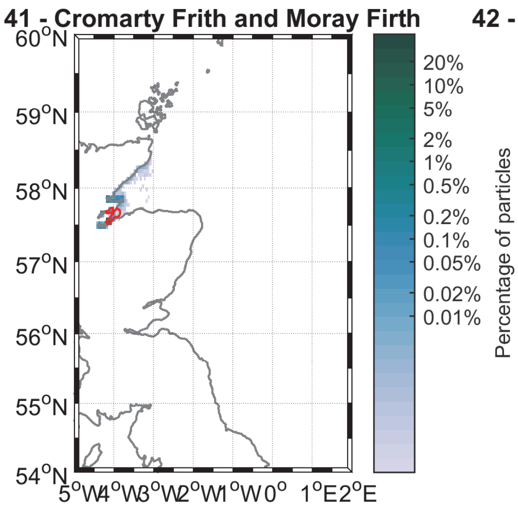

37 - Loch Caolisport
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
8°W 6°W 4°W 2°W 0° 2°E
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

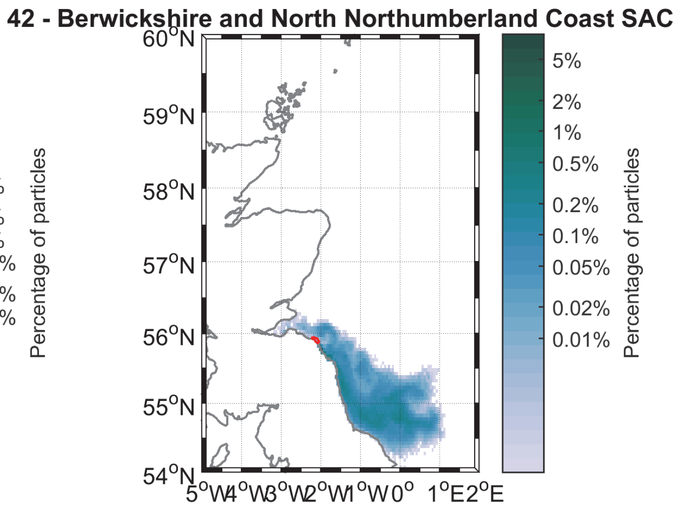

38 - Sound of Gigha
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
8°W 6°W 4°W 2°W 0° 2°E
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


39 - Loch Indaal
60°N
59°N
58°N
57°N
56°N
55°N
54°N
53°N
8°W 6°W 4°W 2°W 0° 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


15 - Noss Head NCMPA
60°N
59°N
58°N
57°N
56°N
55°N
54°N
5°W 4°W 3°W 2°W 1°W 0° 1°E 2°E
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

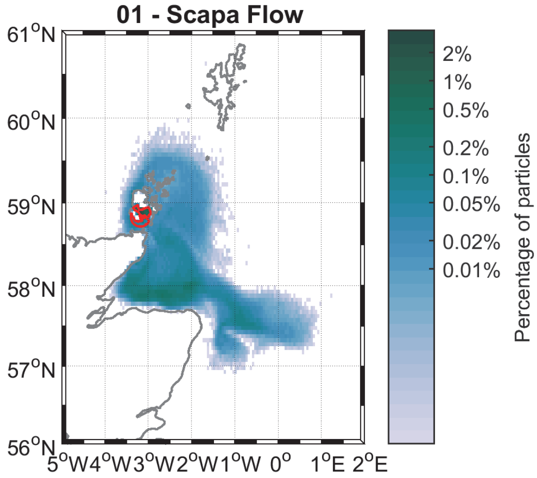

40 - Dornoch Firth and Morrich More SAC
60°N
59°N
58°N
57°N
56°N
55°N
54°N
5°W 4°W 3°W 2°W 1°W 0° 1°E 2°E
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

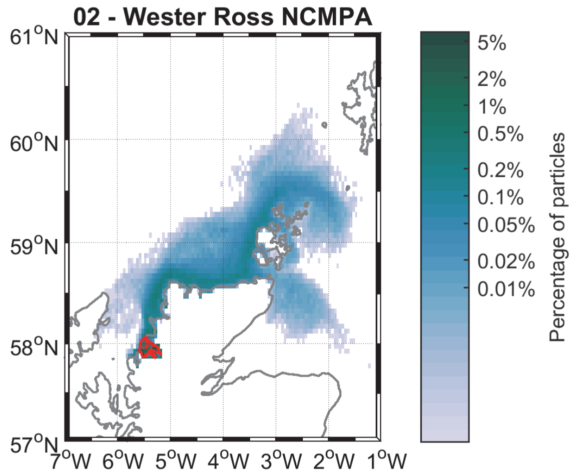

41 - Cromarty Frith and Moray Firth
60°N
59°N
58°N
57°N
56°N
55°N
54°N
5°W 4°W 3°W 2°W 1°W 0° 1°E 2°E
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

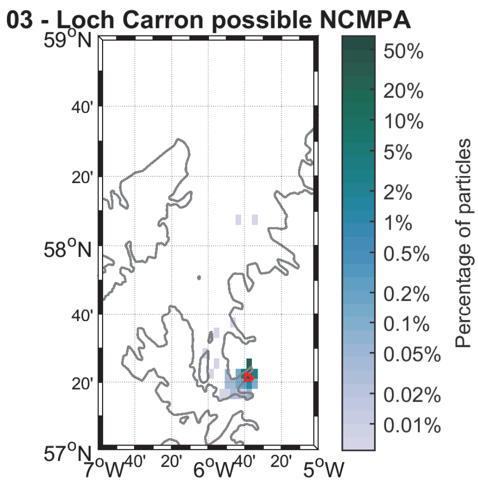

42 - Berwickshire and North Northumberland Coast SAC
60°N
59°N
58°N
57°N
56°N
55°N
54°N
5°W 4°W 3°W 2°W 1°W 0° 1°E 2°E
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

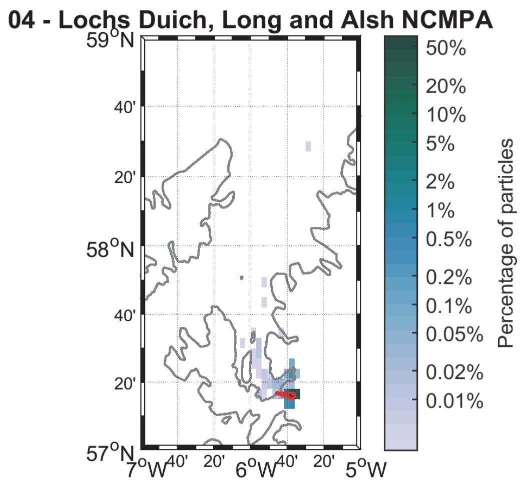
ANNEX 3: PARTICLE DENSITY PLOTS FOR FLAME SHELL RELEASE AREAS ON THE COARSER GRID

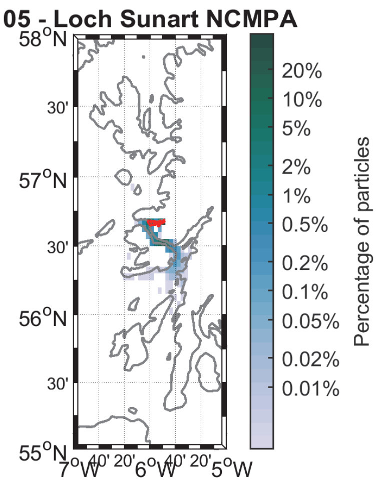
The following figures show the particle densities at the end of the particle tracking simulations (i.e. 25 days after the last particles were released). The densities shown are the percentage of the total number of particles released during the simulation in each 0.05° x 0.05° regular grid square. Each grid square has an area of approximately 30 km2. A logarithmic scale was used to show the difference between patches of low particle density.

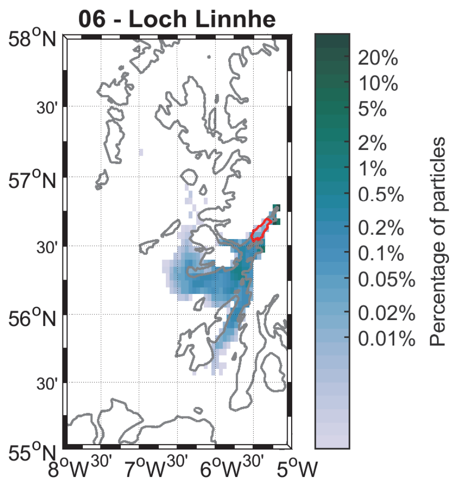

01 - Scapa Flow
61°N
60°N
59°N
58°N
57°N
56°N
5°W 4°W 3°W 2°W 1°W 0° 1°E 2°E
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


02 - Wester Ross NCMPA
61°N
60°N
59°N
58°N
57°N
7°W 6°W 5°W 4°W 3°W 2°W 1°W
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


03 - Loch Carron possible NCMPA
59°N
40'
20'
58°N
40'
20'
57°N
7°W 40' 20' 6°W 40' 20' 5°W
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


04 - Lochs Duich, Long and Alsh NCMPA
59°N
40'
20'
58°N
40'
20'
57°N
7°W 40' 20' 6°W 40' 20' 5°W
50%
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


05 - Loch Sunart NCMPA
58°N
30'
57°N
30'
56°N
30'
55°N
7°W 40' 20' 6°W 40' 20' 5°W
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles


06 - Loch Linnhe
58°N
30'
57°N
30'
56°N
30'
55°N
8°W 30' 7°W 30' 6°W 30' 5°W
20%
10%
5%
2%
1%
0.5%
0.2%
0.1%
0.05%
0.02%
0.01%
Percentage of particles

ANNEX 4: MAXENT ENVIRONMENTAL VARIABLES

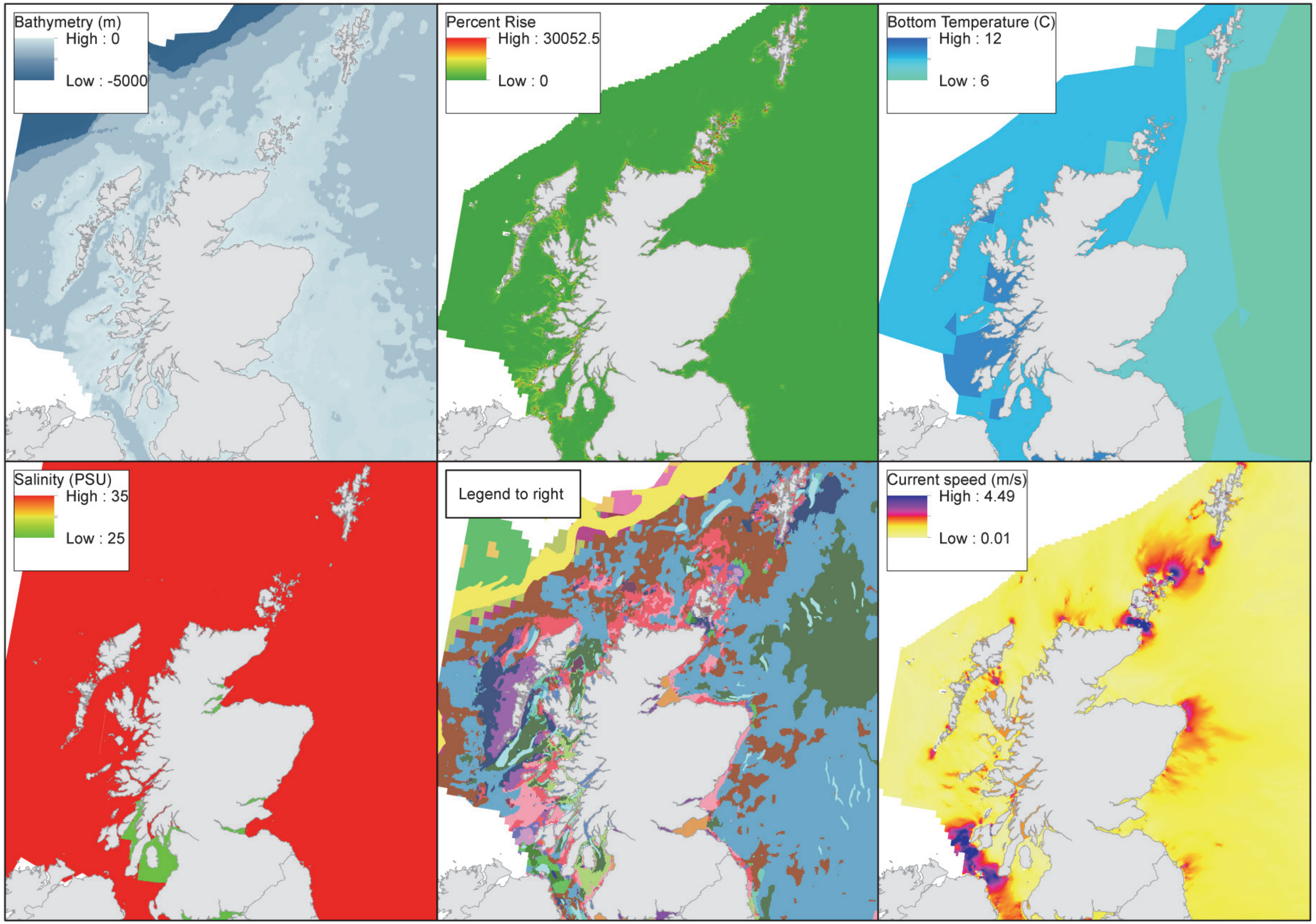
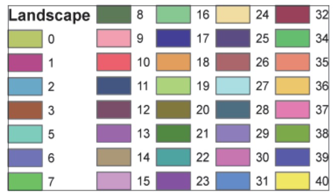


Figure A1. Maxent environmental layers

Colours represent seabed landscape features and broad patterns in seabed character, following Connor *et al*. (2006).



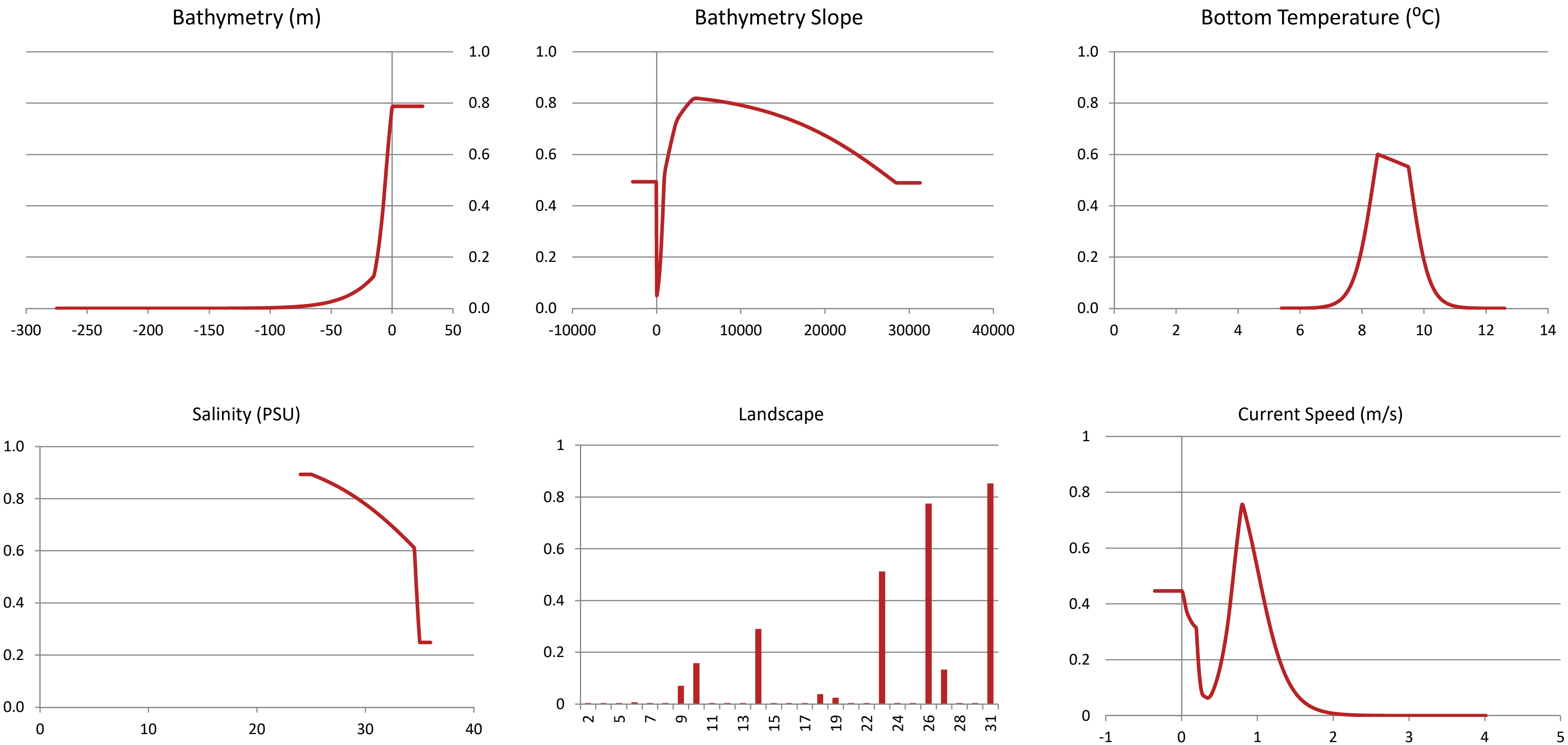


Figure A2. Horse mussel beds Maxent response curves for the environmental variables

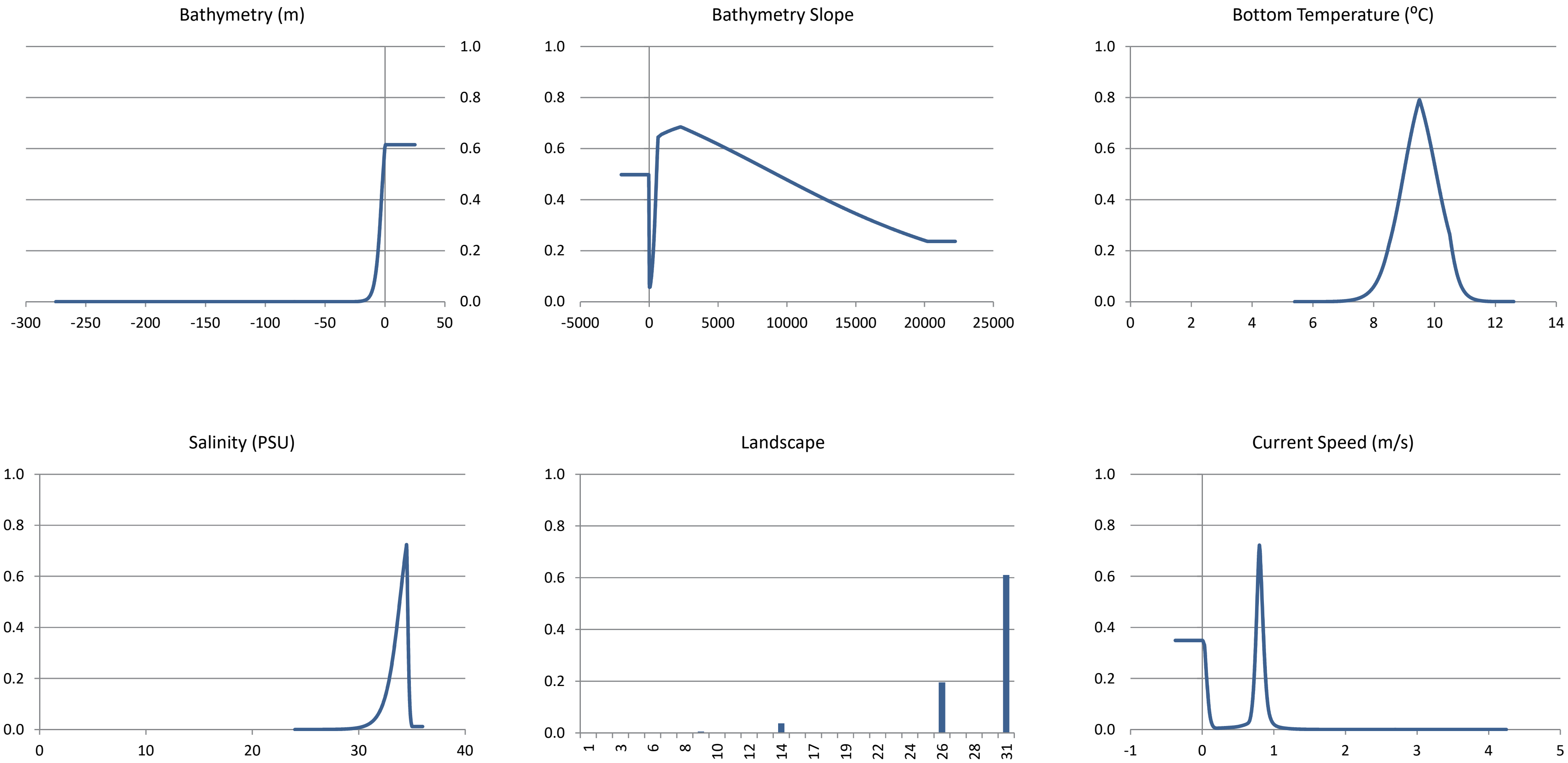


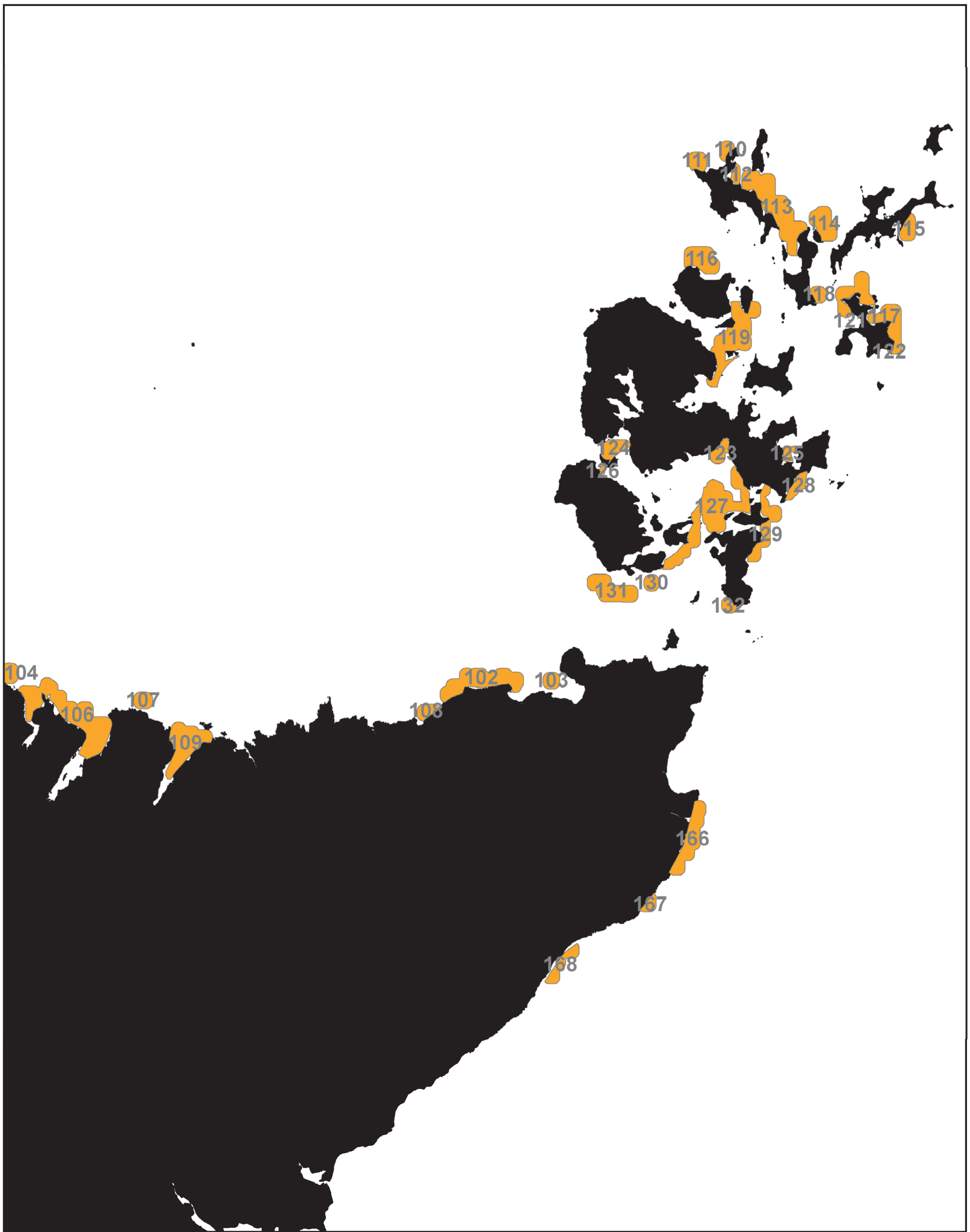
Figure A3. Flame shell beds Maxent response curves for the environmental variables

ANNEX 5: AREAS OF SUITABLE HORSE MUSSEL HABITAT IDENTIFIED USING MAXENT

Legend

Horse Mussel Beds - most suitable habitat areas

0 5 10 20 Km



Legend

Horse Mussel Beds - most suitable habitat areas

0 5 10 20 Km

Legend

Horse Mussel Beds - most suitable habitat areas

0 5 10 20 Km

170
171
169
172
173
174
175
176
177
178
179
180
181
Legend
Horse Mussel Beds - most suitable habitat areas
0 5 10 20 Km

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