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Connectivity of Benthic Priority Marine Species within the Scottish MPA Network

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Summary

- A biophysical modelling approach that accounts for regional oceanographic variation and some degree of biological realism was used to estimate larval transport of 18 benthic invertebrates identified as priority marine features for possible nature conservation MPAs.

- Mean transport distance was mostly related to the duration of the pelagic larval phase (PLD), although season of spawning and distance to shore were also important factors.

- Larvae of species with a PLD ≥ 30 days that were not solely associated with sea lochs or near-shore regions could be advected from the Celtic Sea to the Greater North Sea OSPAR sub-region. These species include tall sea pen, burrowing anemone, spiny lobster and most bivalve molluscs.

- Due to the limited distance between possible MPAs, connectivity among protected regions should be possible for many species with PLD ≤ 10 d within OSPAR sub-regions.

- Those species at risk of local impacts due to low connectivity were species with a short PLD (burrowing amphipod, northern feather star, pink soft coral and northern sea fan) and/or present only in a small number of MPAs (heart cockle and horse mussel). Possible MPAs that were too close to shore to resolve in this analysis are also likely to be less dispersive environments than open water possible MPA sites.

- The model estimates of larval transport could be significantly influenced by larval behaviour and hatching times, highlighting the need for better information on these parameters. Information on habitat suitability is also needed to resolve suitable settlement areas. Future high resolution hydrodynamic models should allow us to improve our estimation of connectivity.

Introduction

The establishment of networks of Marine Protected Areas (MPAs) is becoming a widely used approach to protect vulnerable habitats and species and promote resilience in marine ecosystems. European countries are currently working towards a network of marine protected areas under the auspices of the Oslo-Paris Commission (OSPAR). The components of the OSPAR MPA network are intended to help protect, conserve and restore relevant habitats and species which are, or may be, adversely affected as a result of human activities. While there are various definitions for characterising a network, in the OSPAR context it is characterised by coherence in purpose and by the connectivity between its constituent parts. Connectivity is defined in the present study as the extent to which animal aggregations in different parts of a species range are linked by the exchange of larvae, juveniles or adults (Palumbi, 2003) although in the OSPAR context it also includes dependence of one habitat type on another for structural integrity (Roberts *et al.,* 2003).

Scotland is currently developing its contribution to the OSPAR network of MPAs implemented through the Marine (Scotland) Bill 2010. Under this Bill, 33 Nature Conservation MPA proposals have been identified and proposed to Parliament, whilst a further four potential sites for MPAs remain to be fully assessed. If approved, these Nature Conservation MPAs will help complete an evolving MPA network in Scotland's seas that already includes 46 (with the potential for one more) Special Areas of Conservation, 45 seabird colony Special Protected Areas, 61 Sites of Specific Scientific Interest, and eight fisheries management areas. The Nature Conservation MPAs have been identified for features (the collective term for species, habitats and geology) that currently do not have sufficient protection or are of functional importance to the ecosystem. The Scottish MPA project follows OSPAR advice in considering sub-regions when addressing replication and connectivity. Scottish waters fall into four OSPAR sub-regions: Region I (Arctic waters), Region II (Greater North Sea), Region III (Celtic Seas), and Region V (Wider Atlantic).

Replication of features within and among sub-regions is necessary to spread risk against damaging events and long term change affecting individual MPAs. Risk of local extinction is generally higher in isolated aggregations with low connectivity (Hanski, 2004) and so the number of MPAs within a sub-region needs to reflect the scale of connectivity of species and life stages that are deemed to be priority marine features (PMFs). MPAs also have the potential to offer a wider ecosystem benefit through the build-up of reproductive mass and spill over of individuals and/or export of offspring. This potential for spill over and export of larvae is, therefore, an important consideration in the location and replication of MPA sites designed to protect PMFs (Palumbi, 2003).

OSPAR accepts that information on connectivity between sites will emerge over time and suggests that in the absence of dispersal data, connectivity may be approximated by ensuring the MPA network is well distributed in space, reflecting the scale of its location. For example, the near-shore is generally dominated by finer scale processes than the offshore, and so MPAs in offshore regions should be larger and further apart than those in near-shore areas. Further, given the variety of PMF species and habitats that are being considered for protection by MPAs, it will never be possible to account for all scales of connectivity among PMF species in siting and replication. Ecological guidance for the Marine Conservation Zones (MCZ) in England and Wales has largely followed OSPAR guidance in proposing that similar protected habitat should be separated, where possible, by no more than 40-80 km between MPA boundaries. This scale was derived from a simple model of PMF larval transport that focussed on residual tidal flow (Roberts *et al.*, 2010). However, in Scottish waters, evenly distributing MPAs across sub-regions makes little sense because of the diversity of habitats from the deep sea in the far west to inshore fjordic sea lochs, as well as the largely unidirectional large scale circulation patterns in Scottish waters (Turrell, 1992; Figure 1). Therefore, it is important to account for the known patterns and regional variation in current flow regimes in recommending the level of replication within and among sub-regions.

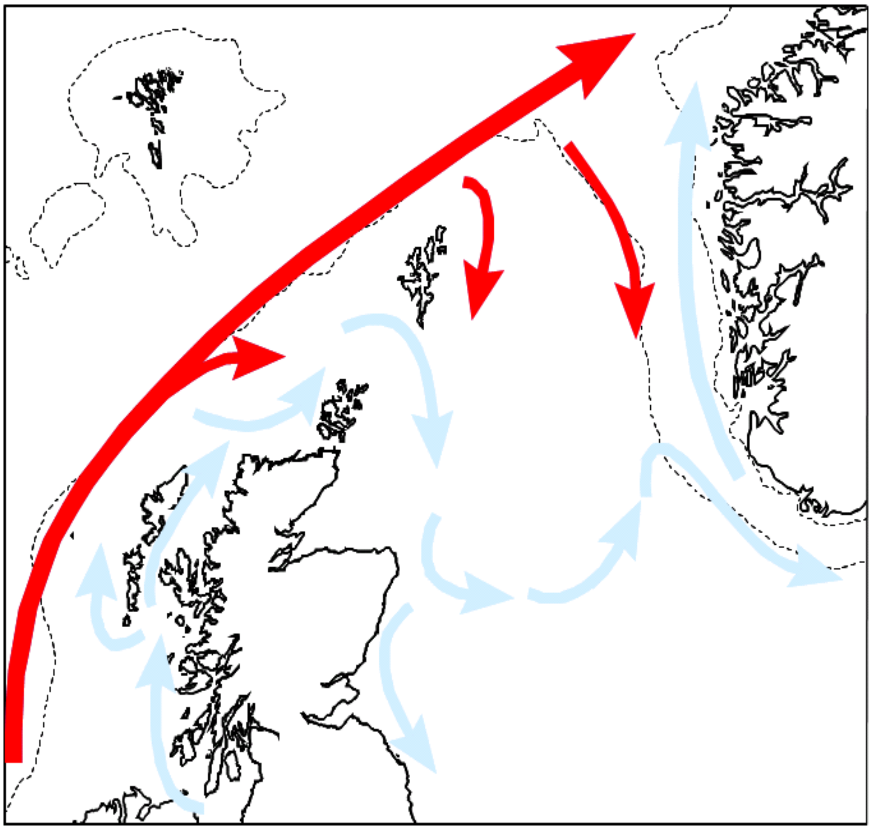

Figure 1: General surface circulation pattern around Scotland. Red arrows are water of Atlantic origin and blue arrows are coastal currents.

Many PMF species are epi-benthic animals that have a planktonic larval phase, but are sessile or have limited mobility following settlement. Hence, an understanding of dispersal of PMF larvae is essential for considering export and connectivity. Hydrographic conditions, interacting with the potential movement (vertical or horizontal) of PMF larvae, determine larval transport, so a biophysical modelling approach can be used to estimate transport from spawning to settlement sites. Such an approach requires output from a hydrodynamic model, as observational data necessary to quantify spatially and temporally resolved three-dimensional currents are virtually impossible to acquire at the relevant broad range of scales, in addition to ecological information such as spawning time, mortality, larval behaviour, planktonic larval duration (PLD) and settlement time window. Unfortunately, too little is known about the life cycle of PMF species to derive accurate species-specific transport estimates, particularly for the fireworks anemone, white cluster anemone, small brackish water snail and gravel sea cucumber, which were not included in this modelling exercise due to lack of sufficient biological information. Heart sea urchin was not modelled either, as it was only associated with a number of inshore MPAs not resolved by the hydrodynamic model (see below). Nevertheless, in general it was possible to generalize on the probable extent of PMF species transport from available evidence. In the following sections, evidence relevant to connectivity is given for those PMF species that have had the largest influence on the choice of MPAs (Table 1).

Table 1

Identified invertebrate Priority Marine Features in Scottish territorial waters.

Phylum	Priority Marine Feature (PMF)	Species name
Cnidaria	Burrowing sea anemone	*Arachnanthus sarsi*
	Fireworks anemone	*Pachycerianthus multiplicatus*
	Northern sea fan	*Swiftia pallida*
	Pink soft coral/sea fingers	*Alcyonium hibernicum*
	Tall sea pen	*Funiculina quadrangularis*
	White cluster anemone	*Parazoanthus anguicomus*
Mollusca	Fan mussel	*Atrina pectinata/fragilis*
	flame shell	*Limaria hians*
	Heart cockle	*Glossus humanus*
	Horse mussel	*Modiolus modiolus*
	Iceland cyprine/Ocean quahog	*Arctica islandica*
	Native oyster	*Ostrea edulis*
	Small brackish water snail	*Hydrobia acuta neglecta*
Arthropoda	Amphipod	*Maera loveni*
	Crayfish/spiny lobster	*Palinurus elephas*
Echinodermata	Gravel sea cucumber	*Neopentadactyla mixta*
	Heart sea urchin	*Brissopsis lyrifera*
	Northern feather star	*Leptometra celtica*

Cnidaria

A number of cnidarians, vulnerable to towed bottom gears, are important PMF species. The tall sea pen (*Funiculina quadrangularis*) is predominantly sessile, although attachment to soft sediments is temporary and so, if disturbed, they can drift into the currents and move location. This species spawns between October and January but the PLD of the plannular larvae is not known. The PLD and settlement competency period of a similar species, *Dendronephytha hemprichi*, is relatively long (65 days) and the larvae can actively swim (Dahan and Benayahu, 1997). In contrast, the plannular larvae of the northern sea fan, *Swiftia pallida* are thought to be lecithotrophic with a short pelagic larval duration, suggesting limited potential for larval dispersal (Hiscock *et al*., 2001). Sea fans are also sessile once settled, with a permanent attachment to the substrate.

Mollusca

The bivalve, *Modiolus modiolus* is adapted to live partially buried, attaching itself to both soft and hard substratums by byssal threads. Individuals are reported to release gametes throughout the year (Brown and Seed, 1977) with peaks of spawning in spring and early summer (Comely, 1978; Jasim and Brand; 1989), but localised environmental factors, particularly temperature, are exceedingly important in controlling the annual reproductive cycle of this species (Brown, 1984; Seed and Brown, 2004). There are various estimates of PLD for the planktonic veliger stage. For example, under ambient summer water temperatures in Strangford Lough (Northern Ireland), larval duration was found to take approximately 38 days, although a settlement experiment showed that swimming veligers were present in the water column almost two months after initial settling commenced (Roberts *et al*., 2011). The Ocean Quahog (*Arctica islandica*) is a long-lived bivalve often living for more than a 100 years (Witbaard, 1997). Spawning is protracted, and varies with location. The settlement of larvae may occur over several months and is believed to occur throughout the adult distribution ranges. Duration of the larval phase is approximately 55 days post fertilisation for temperatures of 8.5-10°C and 32 days at 13°C (Lutz *et al.,* 1982). Fan mussels (*Atrina fragilis*) are burrowing bivalves which have a temporary attachment to the substrate, so dispersal of settled individuals is likely to be very limited (<1m). They have been reported to spawn in the summer although there are no verifiable records regarding spawning times or PLD in the primary literature. The native oyster (*Ostrea edulis*) has been found to spawn during the summer months (mid-May to September), coincident with spring tides and the new or full moon (Yonge, 1960; Wilson and Simons, 1985). Reproductive development and spawning is dependent on temperature (Wilson and Simons, 1985), although the exact temperature that illicits spawning is likely to fluctuate with area and local adaptation (Korringa, 1952). After internal fertilization, eggs are incubated for seven to ten days before release into the plankton (Tyler-Walters, 2008a). The larvae are pelagic for 11-30 days (Bierne *et al*., 1998; Tyler-Walters, 2008a). Flame shell (*Limaria hians*) can occur in large aggregations and can swim actively if disturbed, but dispersal by this means is unlikely to be significant compared to the larval stage. Spawning times vary with latitude but in Scottish waters they have been recorded from May-June with peak settlement from July-August (Trigg, 2009).

Arthropoda

Maera loveni, is a mud-dwelling infaunal amphipod, which lives in depths of 20-400 m. It is a northern cold water species that has reached its southern limit in Scotland where it is sparsely distributed around the coast. They deposit their eggs within a brood pouch on the underside of the adult female's body. Amphipods have no larval stages; the eggs hatch within a few weeks directly into a juvenile form. Dispersion is limited to crawling, swimming, and “rafting" on algae. The adults are potentially capable of swimming in currents, apparently only doing so if disturbed (Highsmith, 1985), but their dispersal potential is not known. Spiny lobster, *Palinurus elephas*, spawn one clutch per year from around July to October (Ansell and Robb, 1977; Hunter, 1999). Females incubate the eggs for around nine months with the larvae (phyllosoma) hatching in early summer (Hunter, 1999). The PLD may be very long, one to six months (Mercer, 1973; Marin, 1985). After mating and egg-laying, individuals may undertake migrations to deeper water in Atlantic waters (Ansell and Robb, 1977; Hunter, 1999), although tagging studies in the Mediterranean also indicate that they can remain quite site attached (Follesca *et al*., 2008).

Echinodermata

The northern feather star, *Leptometra celtica*, is a crinoid echinoderm. Reproduction is via the pinnules, which rupture and release sperm and eggs into the surrounding sea water (Barnes, 1982). The fertilised eggs hatch to release a free-swimming vitellaria larva, which does not feed and only lasts a few days before settlement and metamorphosis into the adult. In another feather star species, larvae settled between two and twelve days after hatching (Kohtsuka and Nakano, 2005). Adult feather stars are usually sedentary, attaching themselves to the substratum (such as sponges or corals) with flexible cirri, but they can crawl and swim by undulating their arms.

Aims

It is clear from available accounts that the larval phase will account for nearly all of the dispersal potential of the PMF benthic species and that uncertainties regarding PLD and spawning times will not allow accurate predictions of larval transport to be made. Therefore, in the present study, a relatively simple biophysical modelling approach that accounts for regional oceanographic variation and some degree of biological realism was used, as described below.

For each of the Priority Marine Feature species, we will present maps of the distribution of particles representing individuals at the end of their larval phase (PLD) and maps showing presence of larvae during their settlement window over any proposed MPA visited by those larvae released from those relevant MPAs (see Methods section). In both cases, when spawning takes place over more than one “season”, season-specific maps will be presented. We will also present colour matrices that show the relative connectivity between origin and destination MPAs, based on the percentage of all particles released at each origin MPA. These results have been obtained for all spawning seasons individually, in the case of species that spawn in more than a single season, but only results combined over all seasons will be shown here. Finally, as described in the Methods section below, we will provide Tables with summary statistics (mean and standard deviation) of the dispersion distance from each origin MPA, for each spawning season (distance in km along a direct line between the particle start and end positions). Some additional analysis of general patterns emerging from these results will be presented at the end of the Results section.

Methods

Our modelling approach involved the following components.

1. The output from an existing hydrodynamic model covering Scottish waters and the compilation of a climatological flow-field to represent “average” conditions.

2. Proposed MPA locations as “source” and “target” areas for the dispersal of individual species (at the relevant life stage for dispersal).

3. Species life cycles divided into categories, based on common biological characteristics that may influence dispersal patterns, such as the duration of larval phase/settlement window and season of spawning.

4. Simplistic Individual-Based Models that allow the characterisation at individual level of the origin, destination and trajectory of particles representing PMF larvae, and could also be used to simulate the interplay between physical transport and biological characteristics such as development, mortality and “behaviour”, although such interactions were not taken into account here largely due to lack of reliable relevant biological information.

5. Simulation results processed to quantify connectivity and export/import out of/into proposed MPA locations to assess the most suitably located sites and the replication needed.

With respect to 3, year was split into quarters to consider approximate spawning windows, whilst PLD was split into 11 daily time intervals for the 18 PMF species considered. The lack of information on even the most basic behavioural attributes in most cases, such as vertical distribution in the water column, meant that species behaviour could not be considered. An existing hydrodynamic model covering Scottish waters and the compilation of a climatological flow-field to represent “average” conditions was used to predict larval transport. Proposed MPA locations were considered as “source” and “target” areas for the dispersal of individual species (at the relevant life stage for dispersal).

Input Data for PMF Species

A summary of the spawning times and pelagic larval duration (PLD) of these eighteen benthic species that have been important in the possible Scottish MPA network selection is given in Table 2, together with the key supporting literature. As most of these species spawn over a few months, spawning time was considered by season. Some cnidarian settle within ten days of release, whilst the larvae of spiny lobster may drift in the plankton for up to six months. Many bivalves have a one or two month larval duration. Consequently, PLD categories were derived on the basis of these reported ranges. Spawning locations of PMF species were based on the feature under consideration being identified in site descriptions (http://www.scotland.gov.uk/Topics/marine/marine-environment/mpanetwork/MPAParliamentReport). Due to the choice of species, connectivity among some of the proposed MPAs was not considered. Figure 2 shows the distribution of proposed MPAs and the location of MPAs important in the present study (shaded green).

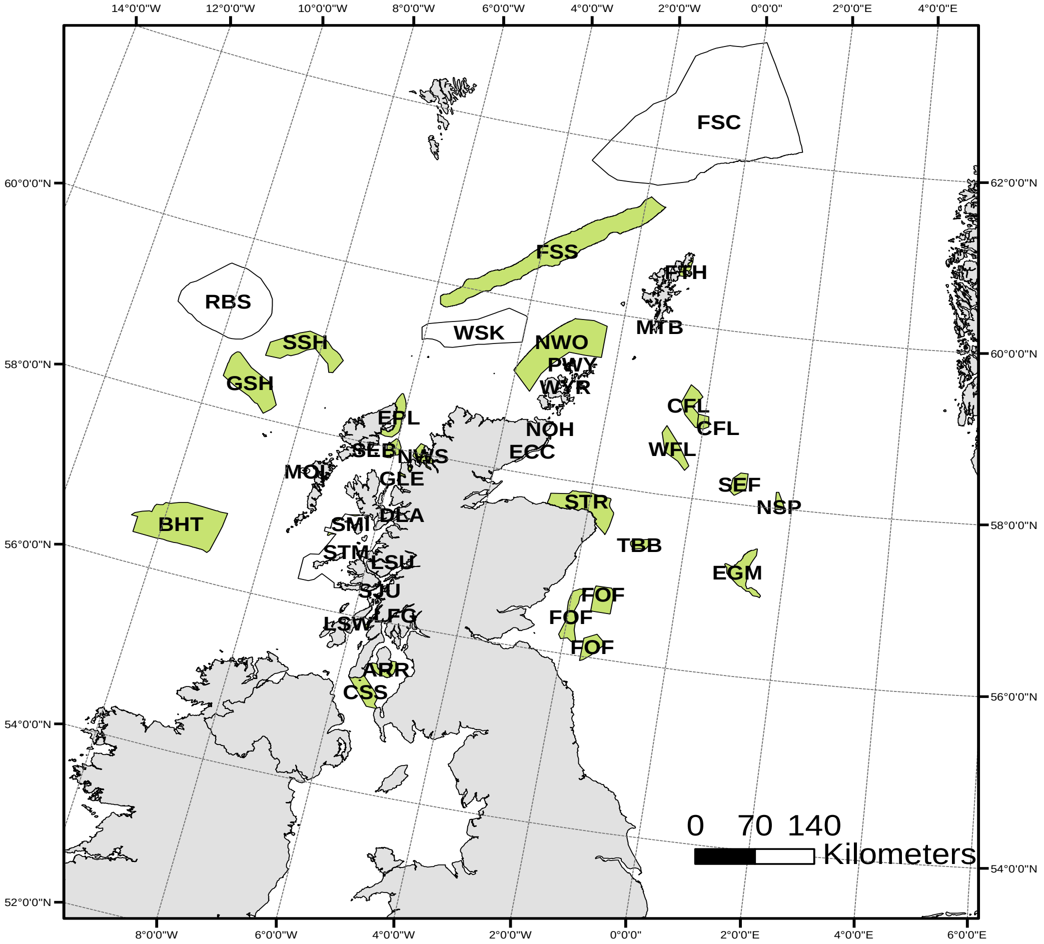

Figure 2: Location of possible Nature Conservation MPAs. Shaded areas refer to MPAs identified as important to benthic invertebrate PMF species, which have been proposed to the Scottish Government. Stipled MPA location refers to a proposed MPA still under review that contains benthic invertebrate PMF species.

Area code descriptions follow overleaf.

Code	MPA	OSPAR
FSC	Faroe-Shetland Channel	I & II
FSS	Faroe-Shetland Sponge Belt	I, II & V
CFL	Central Fladen	II
CFL	Central Fladen (core)	II
ECC	East Caithness Cliffs	II
EGM	East of Gannet and Montrose Fields	II
FOF	Firth of Forth Banks Complex	II
FTH	Fetlar to Haroldswick	II
MTB	Mousa to Boddam	II
NOH	Noss Head	II
NSP	Norwegian boundary sediment plain	II
NWO	North-west Orkney	II
PWY	Papa Westray	II
SEF	SE Fladen	II
STR	Southern Trench	II
TBB	Turbot Bank	II
WFL	Western Fladen	II
WYR	Wyre and Rousay Sounds	II
WSK	Windsock	II & III
ARR	South Arran	III
CSS	Clyde Sea sill	III
DLA	Lochs Duich, Long & Alsh	III
EPL	Eye Peninsula to Butt of Lewis	III
GLE	Gairloch and Wester Loch Ewe	III
LFG	Upper Loch Fyne and Loch Goil	III
LSU	Loch Sunart	III
LSW	Loch Sween	III
MOI	Monach Isles	III
NWS	North-west sea lochs and Summer Isles	III
SEB	Shiant East Bank	III
SJU	Loch Sunart to the Sound of Jura	III
SMI	Small Isles	III
STM	Skye to Mull	III
BHT	The Barra Fan and Hebrides Terrace Seamount	III & V
GSH	Geikie Slide and Hebridean Slope	III & V
SSH	South-west Sula Sgeir Slide and Hebridean Slope	III & V
RBS	Rosemary Bank Seamount	V

Table 2

Spawning times and pelagic larval duration of the benthic PMF. Spawning time key: W=winter, S=spring, Su=summer, A=autumn, NK=not known (all seasons assumed). *reference relates to a similar species, as no other published information is available.

Species	Spawning time	Settlement window (d)		Reference Number	
		min	max	spawning time	'settlement window'
White cluster anemone	AW	1	10	70	70, 71
Fireworks anemone	NK	1	10	-	57
Amphipod	NK	1	10	-	78
Northern feather star	NK	1	10	-	5*, 44*
Pink soft coral/sea fingers	Su	1	10	30, 38	7*, 9*, 13*, 14*, 20*, 28*, 74*
Northern sea fan	SuW	1	10	34	86
Heart cockle	A	1	30	61	64*, 56*, 52*, 68*
Gravel sea cucumber	SSu	1	30	40	36*, 3, 54*
Native oyster	Su	10	30	41, 45, 87, 89	1, 8, 41, 82
Small brackish water snail	SSu	20	30	5, 23	23
Horse mussel	AWSSu	30	40	10, 11, 15, 16, 75	59*, 67, 81
Fan mussel	SSuA	30	50	51*, 60*, 77	60*
Flame shell	Su	20	60	73*, 79	46, 83
Heart sea urchin	SuA	40	60	12, 21, 22,	12, 43*, 50*, 58*
Ocean quahog	SuA	40	60	72	49
Tall sea pen	AW	28	65	18, 19, 37	25*, 35*, 47*, 69*, 84*
Burrowing sea anemone	SSuA	28	90	63	25*, 35*, 47*, 69*, 84*
Crayfish, spiny lobster	Su	60	180	2, 39	2, 39, 55, 76*

Hydrodynamic Model

Year-specific daily 3-dimensional flow-fields for an area between 50-65° N latitude and 15° W - 15° E longitude were obtained by running the SNAC model (Logemann *et al*., 2004) for 16 years, between 1995-2010, forced with air pressure data from the European Centre for Medium-Range Weather Forecasts (ECMWF) Operational Data set. Daily 16-year averages were then calculated for each hydrodynamic model grid node. M_2 tidal velocities were superimposed onto residual currents at each node. The spatial resolution of the model was 0.125° latitude by 0.250° longitude, corresponding approximately to < 15 km in our model domain, with 11 fixed (Z) vertical layers.

Bio-Physical Model

Due to the lack of detailed biological information for most PMF species, further simplifying assumptions were made within the bio-physical model. Particles representing larvae of the invertebrate species of interest were released at 5 km regular spacing, within the MPAs under consideration. Particles were only released from start positions considered “wet” (i.e. water depth > 0m), based on the model bathymetry. As a consequence, five MPAs were excluded from the simulations because they were too close to the coast to be resolved by the model. Rosemary Bank and other deep water locations west of 15° W were also disregarded, but this is unlikely to affect the outcome of our study because PMF species were largely restricted to the European continental shelf. One hundred particles were released from each start location within each MPA, making up a total of just under 290,000 particles per simulation. The simultaneous release of multiple particles from each point was necessary for numerical stability to account for the stochastic effect of horizontal diffusion. Spawning times were assigned to seasons (spring, summer, autumn and winter) and represented by single particle releases at the mid-point of each season (calendar days 80, 172, 264 and 355, respectively). Particles were kept at a constant depth (25 m) throughout the simulations, which were run for a total of 180 days. The tracking time-step was one hour and particle positions were stored at daily intervals. The particle tracking methodology has been described in detail by Gallego and Heath (2003) and Heath and Gallego (1998, 2000).

Analysis of Simulation Results

The simulations described above were common to all PMF species, so the stored model results were queried off-line on the basis of simplified biological information (Table 2), to extract data applicable to individual species. The criteria used were spawning season (one or more seasons, depending on information in the literature; when the timing of spawning was unknown, all seasons were selected), approximate settlement time window (≤PLD) and origin MPA. Origin MPA was identified on the basis of species presence data in the 2011 GEMS database and species identified as an important feature in the selection guidelines for each MPA. We assumed a uniform distribution over the whole MPA area of each species present.

Based on the above criteria, the outcome of the bio-physical simulations was queried for each species, to extract the tracks that originated in the relevant MPA(s) in the appropriate season(s). The final particle positions at the end of the settling period were recorded, as an indication of the export potential of that species to other (protected and non-protected) areas. The presence of particles on any MPA (including their origin MPA) during the settlement period was also recorded, as an indication of connectivity between MPAs. These results were displayed as maps. In addition, the relative connectivity between source and sink MPAs, as percentage of all particles released at each source MPA was shown as colour matrices for each species (where multiple spawning seasons occurred, we only present cumulative connectivity plots over all relevant seasons). We also produced Tables for each species with summary statistics (mean and standard deviation) of the dispersion distance from each origin MPA, assuming a straight line between the origin and destination at the end of the PLD. Note that several MPAs could be visited by the same particle during the settlement period (we measured *potential* contact and made no assumptions about how a pelagic larva would decide to settle and finalise its pelagic stage sometime within its settlement window). Also, we quantified contacts with all MPAs along the drift track, regardless of whether a species had been recorded on a given MPA, as a nil record does not necessarily preclude the presence or potential presence of the species on that area (MPA suitability for any given species was not examined here). Finally, as particle positions were only stored daily for post-processing, it is possible that we missed particles over MPAs between position recording intervals. Note that, as the focus of the study was to investigate connectivity between and export potential from MPAs, we did not consider the potential export of larvae from non-protected areas.

Analysis of General Patterns

A Generalised Additive Model (GAM) was fitted to mean transport distance estimates (response variable) derived for each species by MPA and quarter (season) combination. Maximum pelagic larval duration and distance to shore were considered as continuous explanatory variables and OSPAR region and quarter were treated as factors. As the effect of explanatory variables may not have been linear, these terms were treated as splines within the GAM. A gamma response distribution coupled with a log-link function was chosen due to the increasing variance in the response variable with the explanatory covariates. A minimum adequate model was derived by removing terms from the full models successively, comparing successive models with an ANOVA with an F statistic.

Results

Cnidaria

Tall Sea Pen (*Funiculina quadrangularis*)

As tall sea pen spawn between October and January and the PLD and settlement competency period of a similar species is 65 days, in our connectivity simulations tall sea pens were assumed to spawn in autumn and winter, with a settlement window of 28-65 days. Based on presence data, particles were released from the following MPAs: SMI, NWS, CFL, CFL, SSH, GSH and BHT.

Figure 3a shows the distribution of particles at the end of the settlement window (right panels) and identifies the MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top: autumn; bottom: winter). The potential widespread distribution of offspring and the significant connectivity potential is the result of its relatively long pelagic larval duration (PLD) period. An index of the distance covered by the larvae in their PLD is presented in Table 3.

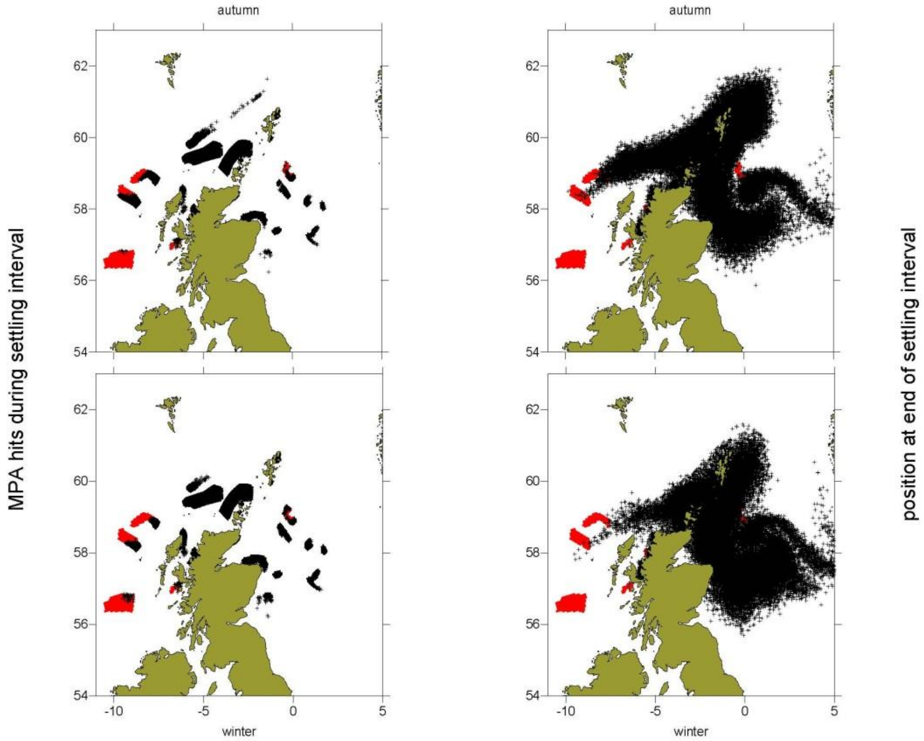

Figure 3a: Black dots show the distribution of particles at the end of the settlement window (right panels) and MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top: autumn; bottom: winter). Red dots show the particle origin positions.

Table 3

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing tall sea pen larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	Autumn		Winter		
MPA	mean	stdev	mean	stdev	n
SMI	398.7342	186.2706	472.1786	245.7127	2400
NWS	541.8706	155.5513	664.4572	138.8007	1200
CFL	161.4177	109.0815	257.1189	209.5545	2900
CFL	247.5095	208.9594	475.5425	265.7354	1000
SSH	842.7279	94.4515	837.1288	97.0671	8300
GSH	905.5469	88.51035	959.7132	111.8897	9100
BHT	735.0193	130.9657	801.8007	101.1855	18700

The results on Table 3 show considerable variability between MPAs (e.g. those from Geikie Slide and Hebridean Slope (GSH) cover considerably longer distance than those from Central Fladen (CFL). Particles released in winter tend to cover longer distances but display greater variability, compared to those in the autumn.

Figure 3b shows a connectivity matrix between origin and (potential) destination MPAs, confirming the pattern that, in the case of tall sea pens, west coast MPAs are considerably more dispersive than North Sea ones.

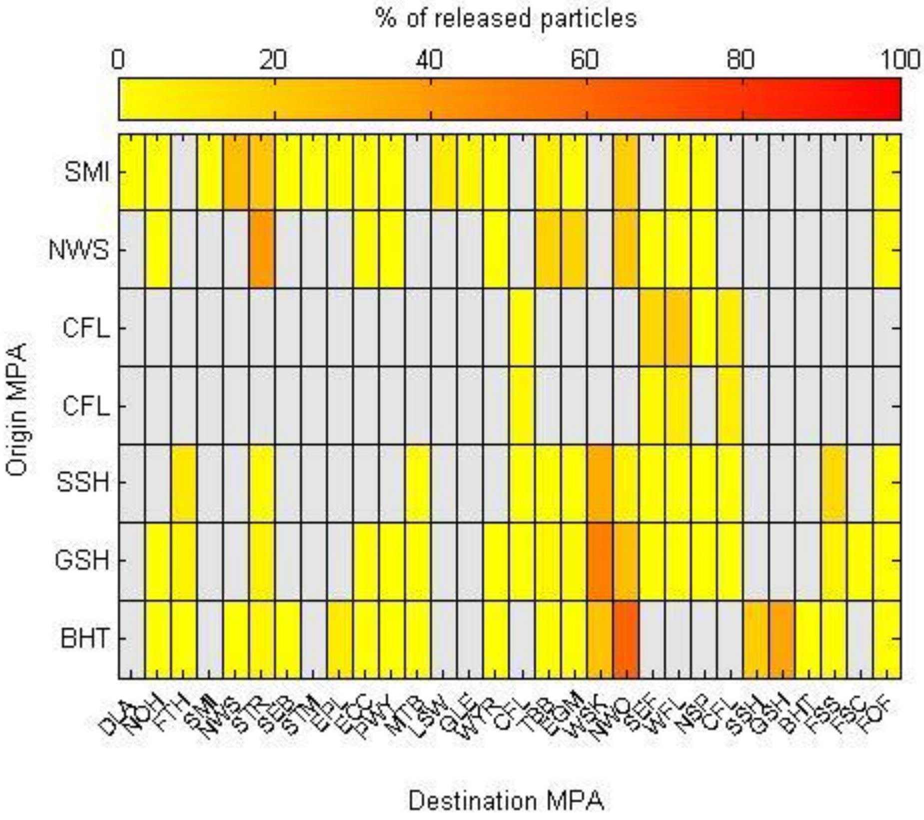

Figure 3b: Matrix showing the percentage of all particles representing tall sea pen released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Northern Sea Fan (*Swiftia pallida*)

As the plannular larvae of the northern sea fan, *Swiftia pallida,* are thought to be have a short pelagic larval duration we assumed a settlement window of one to ten days with spawning in summer and winter. Based on presence data, particles were released from the following MPAs: SMI, SEB, STM, LSW, TBB and FOF.

Figure 4a shows the distribution of particles at the end of the settlement window (right panels) and identifies the MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top: summer; bottom: winter). The potential relatively narrow distribution of offspring and the reduced connectivity potential, including a considerable degree of self-recruitment (see also Figure 4b), is the result of its relatively short PLD period. An index of the distance covered by the larvae in their PLD is presented in Table 4.

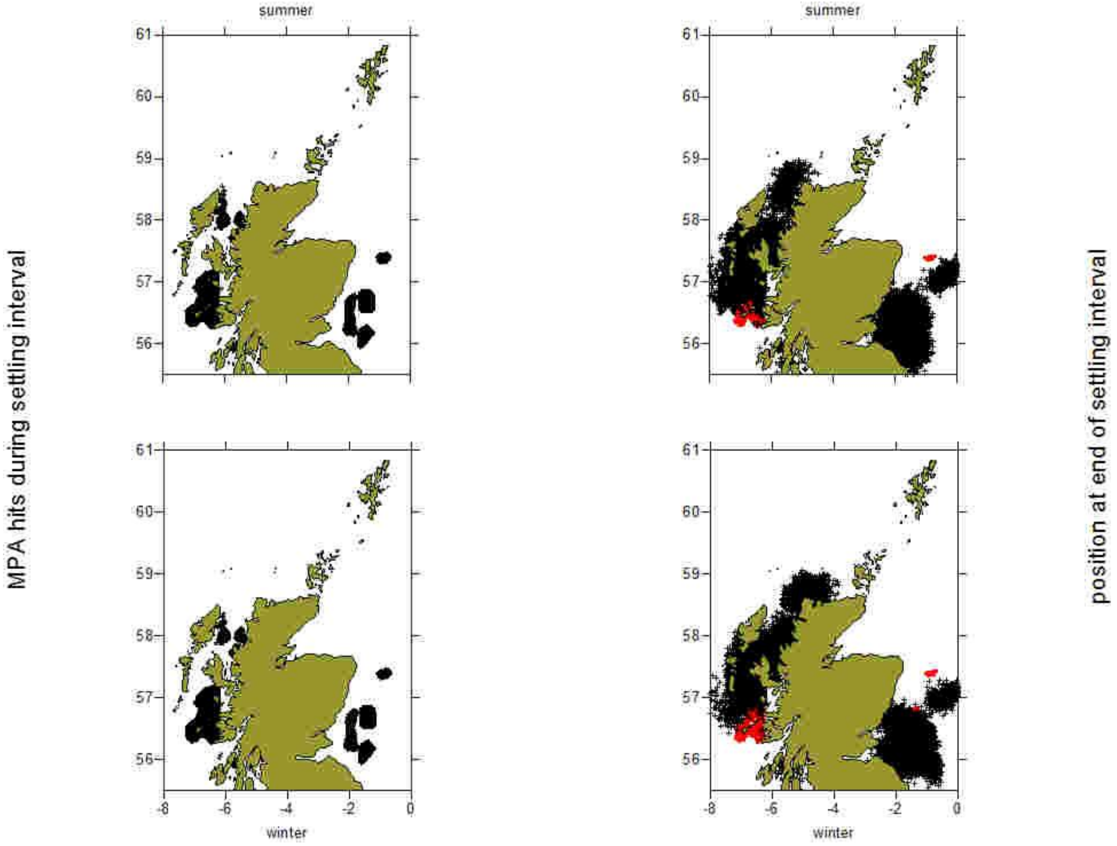

Figure 4a: Black dots show the distribution of particles at the end of the settlement window (right panels) and MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top: summer; bottom: winter). Red dots show the particle origin positions.

Table 4

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing northern sea fan larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	Summer		Winter		
MPA	mean	stdev	mean	stdev	n
SMI	58.93132	33.395	223.0987	136.1454	2400
SEB	83.58833	22.53601	388.1834	63.63042	1200
STM	72.56669	28.09435	237.0058	121.064	14100
LSW	21.96786	22.63312	72.0195	37.45215	100
TBB	64.69743	16.32645	135.9349	28.97287	800
FOF	32.82873	15.25553	112.5105	45.14544	8300

The results on Table 4 show quite a lot of variability between MPAs (e.g. those from Loch Sween (LSW) cover considerably shorter average distances than those from Shiant East Bank (SEB)). Particles released in winter tend to cover considerably longer distances but display greater variability in general, compared to those in the summer.

Figure 4b shows a connectivity matrix between origin and (potential) destination MPAs, confirming the pattern that, in the case of northern sea fans, west coast MPAs are considerably more dispersive than North Sea ones but, overall, the dispersal potential of this species is limited.

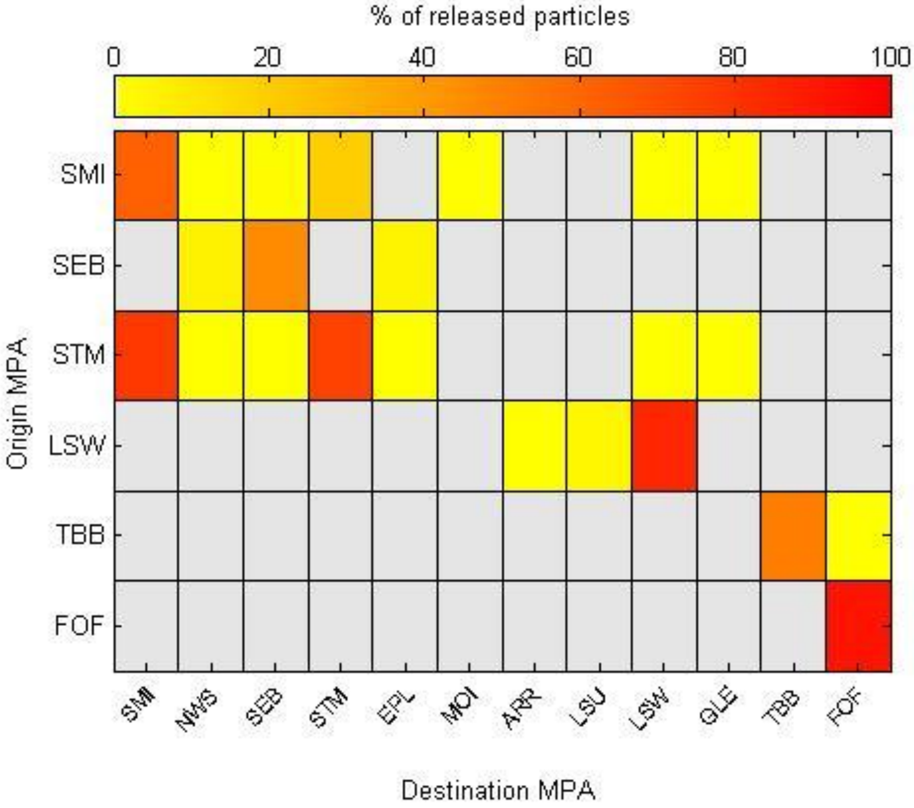

Figure 4b: Matrix showing the percentage of all particles representing northern sea fan released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Pink Soft Coral (*Alcyonium hibernicum*)

Pink soft coral and pink sea fingers spawn in late summer between August and September and the plannular larvae settle shortly after release. So, for the purpose of our connectivity simulations, pink soft corals were assumed to spawn in summer, with a settlement window of one to ten days. Based on presence data, particles were released from the following MPAs: CSS, STM and LSW.

Figure 5a shows the distribution of particles at the end of the settlement window (right panel) and identifies the MPAs locations that these particles drifted over during that period (left panel). The potential distribution of offspring is quite limited, resulting from a short PLD period and limited distribution at origin within the proposed MPAs. An index of the distance covered by the larvae in their PLD is presented in Table 5.

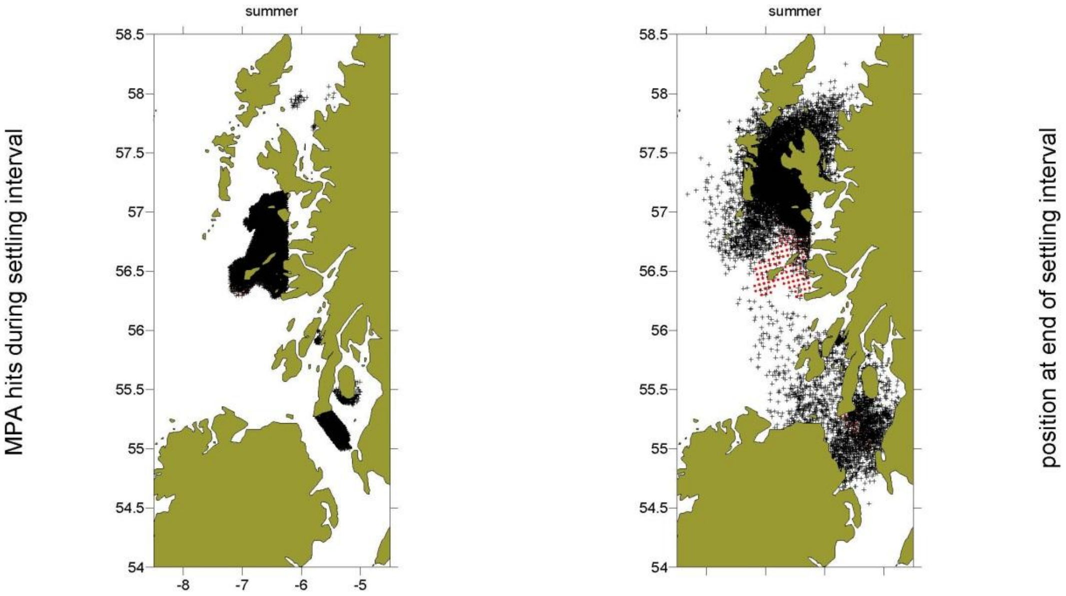

Figure 5a: Black dots show the distribution of particles at the end of the settlement window (right panel) and MPAs locations that these particles drifted over during that period (left panel). Red dots show the particle origin positions.

Table 5

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing pink soft coral larvae released from each origin MPA (n is the number of particles released).

	Summer		
MPA	mean	stdev	n
CSS	41.40528	27.13667	2800
STM	68.07873	27.38209	14100
LSW	16.73283	17.34437	100

The results on Table 5 show some differences between MPAs, which reflect their location (the closer inshore, the less dispersive).

Figure 5b shows a connectivity matrix between origin and (potential) destination MPAs. There is a considerable degree of self-recruitment, as a result of relatively inshore MPA locations and short PLD.

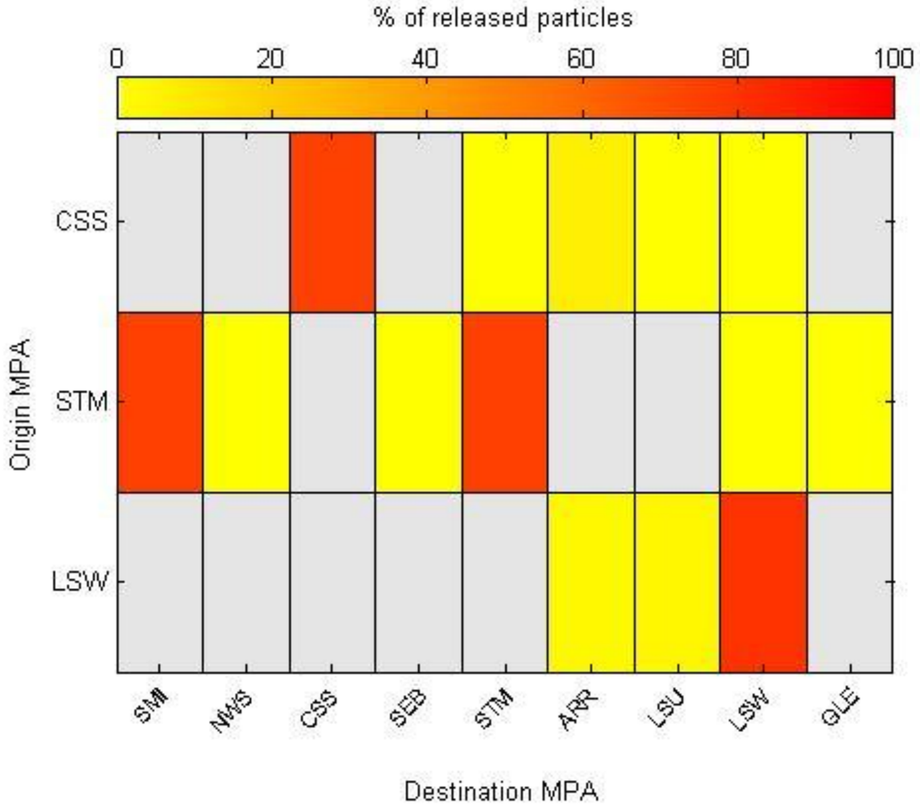

Figure 5b: Matrix showing the percentage of all particles representing pink soft coral released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Burrowing Sea Anemone (*Arachnanthus sars*)

The larvae of the Burrowing anemone (*Arachnanthus sarsi*) are present in the plankton from April to the autumn so we assumed spawning was in spring, summer and autumn. As the PLD of the related *Cerianthus* species range from four weeks to four months we used a settlement window of 28-90 days. Based on presence data, particles were released from the following MPAs: SMI, NWS, STM, EPL, CFL, NWO, SEF, WFL, NSP, CFL, SSH, GSH and BHT.

Figure 6a shows the distribution of particles at the end of the settlement window (three right panels) and identifies the MPA locations that these particles drifted over during that period (three left panels) for each of the three spawning periods (spring to autumn). The potential distribution of offspring and between-MPA connectivity are extremely wide, as a result of a relatively long PLD period and widespread distribution at origin within the proposed MPAs. An index of the distance covered by the larvae in their PLD is presented in Table 6.

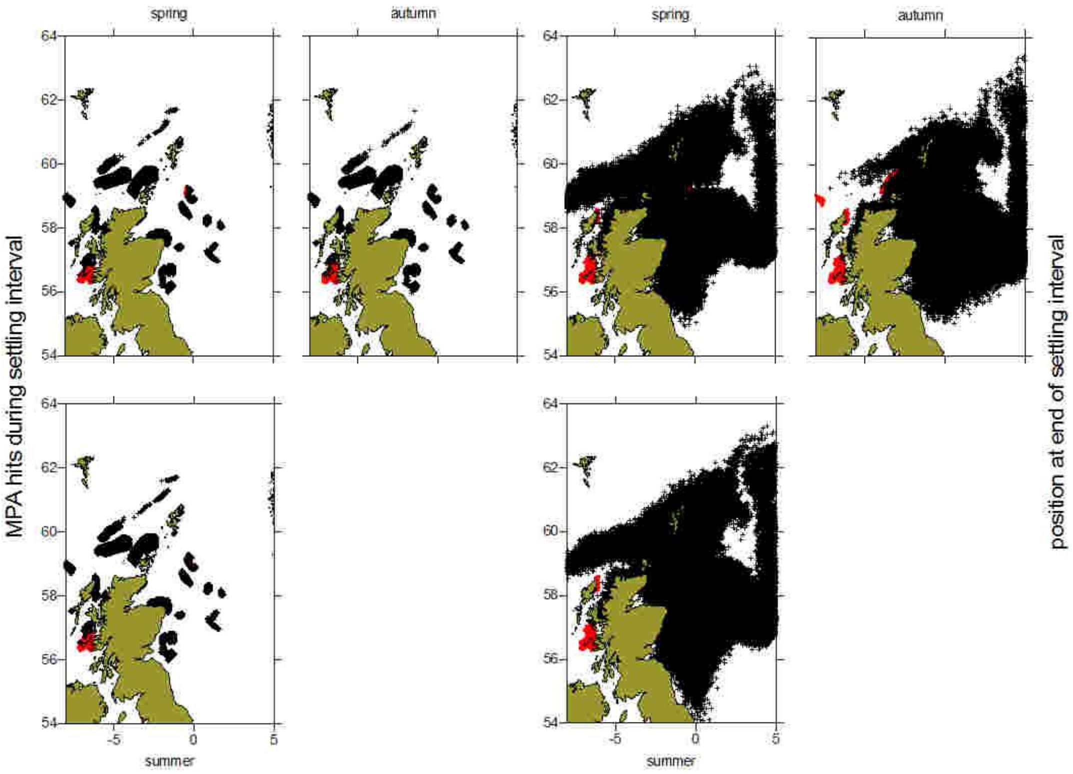

Figure 6a: Black dots show the distribution of particles at the end of the settlement window (three right panels) and MPAs locations that these particles drifted over during that period (three left panels) for each of the spawning periods (top: spring and autumn; bottom: summer). Red dots show the particle origin positions.

Table 6

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing burrowing sea anemone larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	spring		summer		autumn		
MPA	mean	stdev	mean	stdev	mean	stdev	n
SMI	262.7722	99.05911	255.1555	123.6793	376.8256	131.2515	2400
NWS	296.6722	92.02234	330.6136	89.24955	465.8216	111.2949	1200
STM	288.2795	90.58127	284.4247	111.7464	385.4184	120.9899	14100
EPL	431.3364	98.19427	470.2425	91.2673	566.0165	127.0553	2200
CFL	164.8757	128.6385	178.141	133.9859	202.9292	133.3907	2900
NWO	497.0089	122.4901	501.516	106.2314	537.7676	118.4944	17500
SEF	317.3321	86.67873	385.8749	96.25372	390.7663	102.9626	1700
WFL	268.6549	163.4696	273.0761	141.7989	346.1803	118.9167	3000
NSP	360.5706	86.3769	399.9785	109.7099	427.3958	95.44053	800
CFL	175.232	143.4311	184.7308	140.4058	220.932	134.978	1000
SSH	520.0574	76.05066	538.3254	80.94968	543.814	83.85678	8300
GSH	575.8729	73.28264	584.3992	72.81853	599.6261	78.29477	9100
BHT	504.5871	122.0041	544.7715	108.1969	615.5512	69.10734	18700

The results on Table 6 confirm the general patterns observed for other species, i.e. that offshore MPAs tend to be more dispersive than inshore ones, and offspring spawned in west coast MPAs tend to cover greater distances than those in the North Sea. Autumn spawned larvae also tend to travel further than those spawned earlier in the year.

Figure 6b shows a connectivity matrix between origin and (potential) destination MPAs. The results are consistent with the patterns described above (Figure 6a and Table 6).

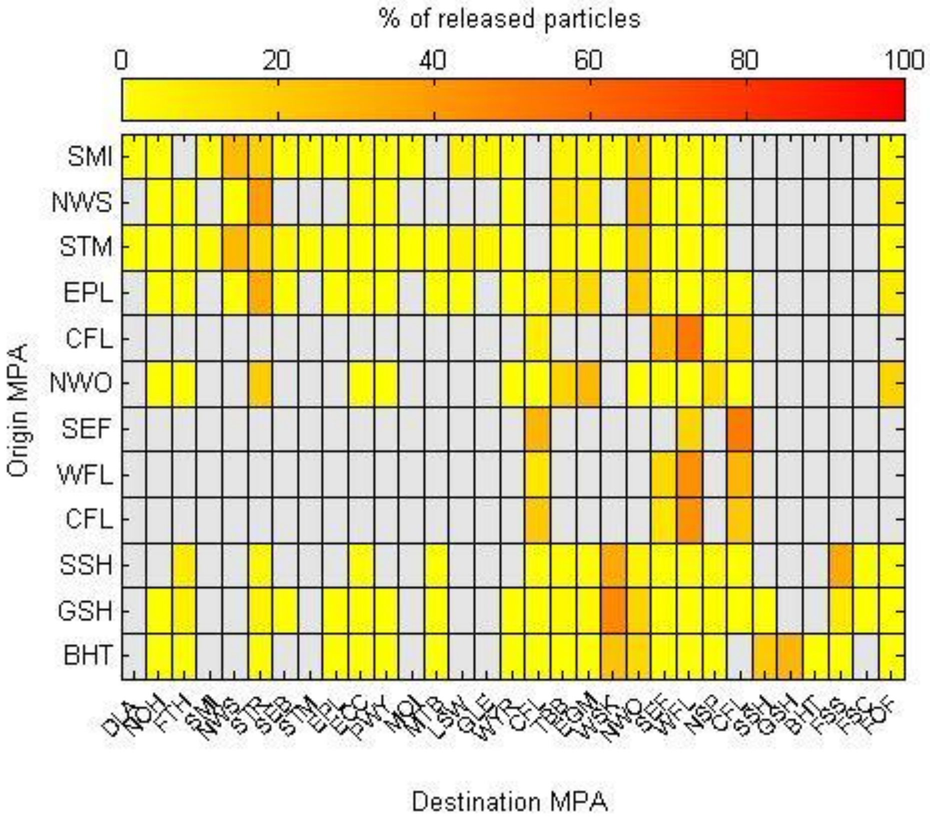

Figure 6b: Matrix showing the percentage of all particles representing burrowing sea anemone released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Mollusca

Horse Mussel (*Modiolus modiolus*)

The bivalve *Modiolus modiolus* has peaks of spawning in spring and early summer and the planktonic veliger stage duration was found to take approximately 38 days. So, for the purpose of our connectivity simulations, horse mussels were assumed to spawn all year-round, with a settlement window of 30-40 days. Based on presence data, particles were released from the following MPAs: NOH, FTH and SMI.

Figure 7a shows the distribution of particles at the end of the settlement window (right panels) and identifies the MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (rows from the top: spring, summer, autumn and winter, respectively). The potential distribution of offspring is relatively wide but connectivity potential is not very strong (see Figure 7b too), resulting from a relatively long PLD period but limited distribution at origin within the proposed MPAs. An index of the distance covered by the larvae in their PLD is presented in Table 7.

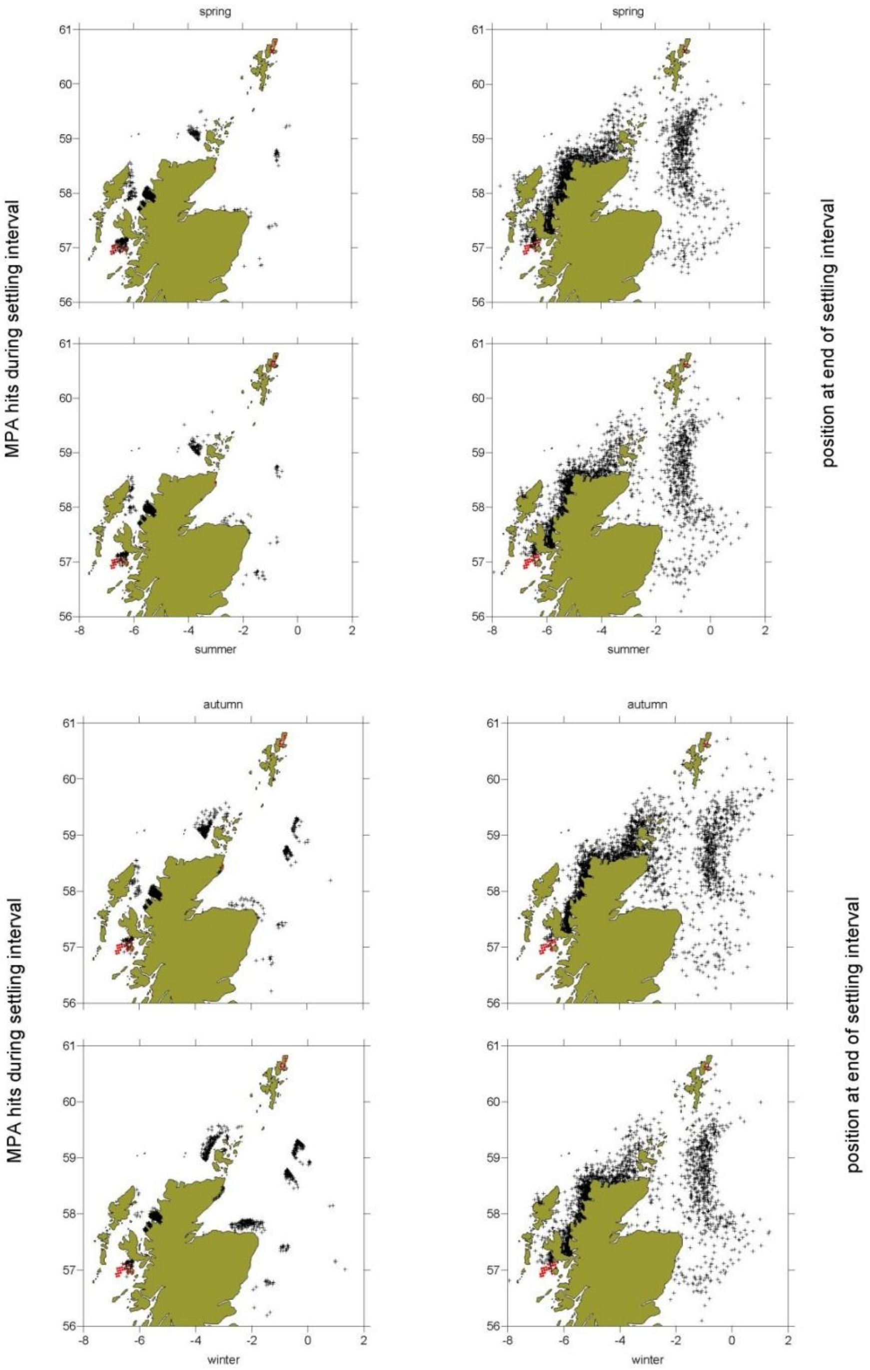

Figure 7a: Black dots show the distribution of particles at the end of the settlement window (right panels) and MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (rows from the top: spring to winter). Red dots show the particle origin positions.

Table 7

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing horse mussel larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	spring		summer		autumn		winter		
MPA	mean	stdev	mean	stdev	mean	stdev	mean	stdev	n
NOH	249.0141	83.19418	232.8721	84.93978	260.3104	78.66676	281.9295	77.72447	100
FTH	213.35	60.20469	221.2325	69.44247	216.3795	54.13975	220.4248	43.37147	600
SMI	178.4879	106.1896	176.5887	109.0172	246.9048	131.9025	292.0999	165.5732	2400

The results on Table 7 show relatively small differences between MPAs and seasons, compared to other species.

Figure 7b shows a connectivity matrix between origin and (potential) destination MPAs. As with other species, the west coast MPA is more dispersive than North Sea ones although this could be partly due to the distribution of MPAs along the west coast, since the dispersal distances were not very different between areas.

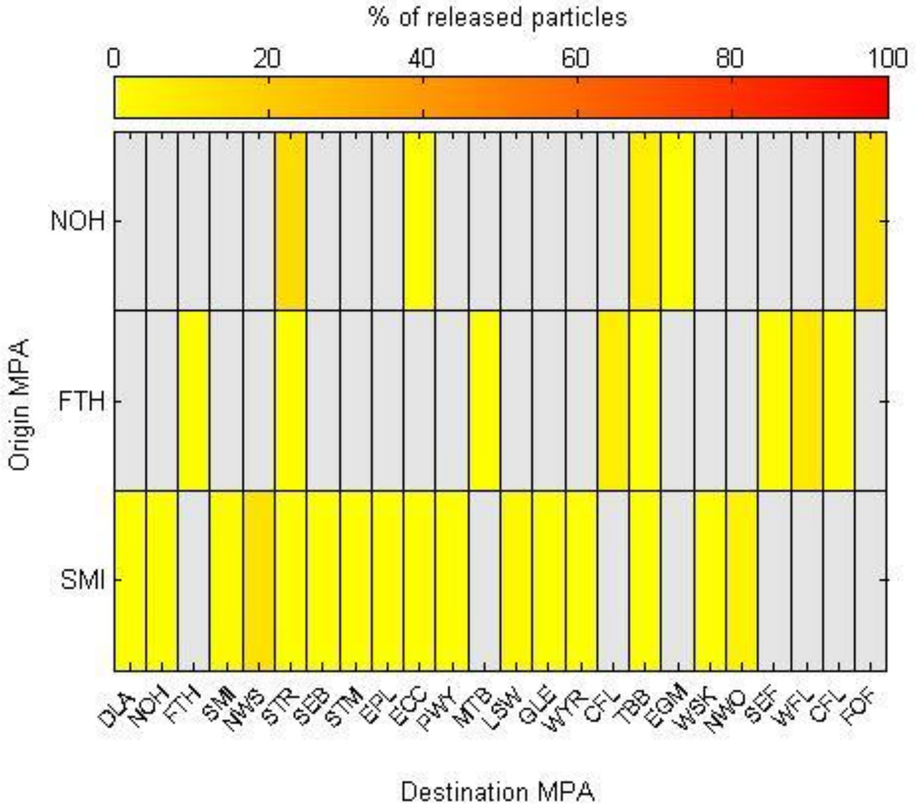

Figure 7b: Matrix showing the percentage of all particles representing horse mussel released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Ocean Quahog (*Arctica islandica*)

As spawning in the ocean quahog is protracted and the duration of the larval phase is approximately 32-55 days we assumed spawning was in summer and autumn, with a settlement window of 40-60 days for the purpose of our connectivity simulations. Based on presence data, particles were released from the following MPAs: NWS, STR, ARR, GLE, EGM, WFL, NSP, BHT, FSS and FOF.

Figure 8a shows the distribution of particles at the end of the settlement window (right panels) and identifies the MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top: spring; bottom: summer). The potential distribution of offspring is very wide and connectivity potential is considerable (see also Figure 8b), as a result of the long PLD period and extensive distribution at origin within the proposed MPAs. An index of the distance covered by the larvae in their PLD is presented in Table 8.

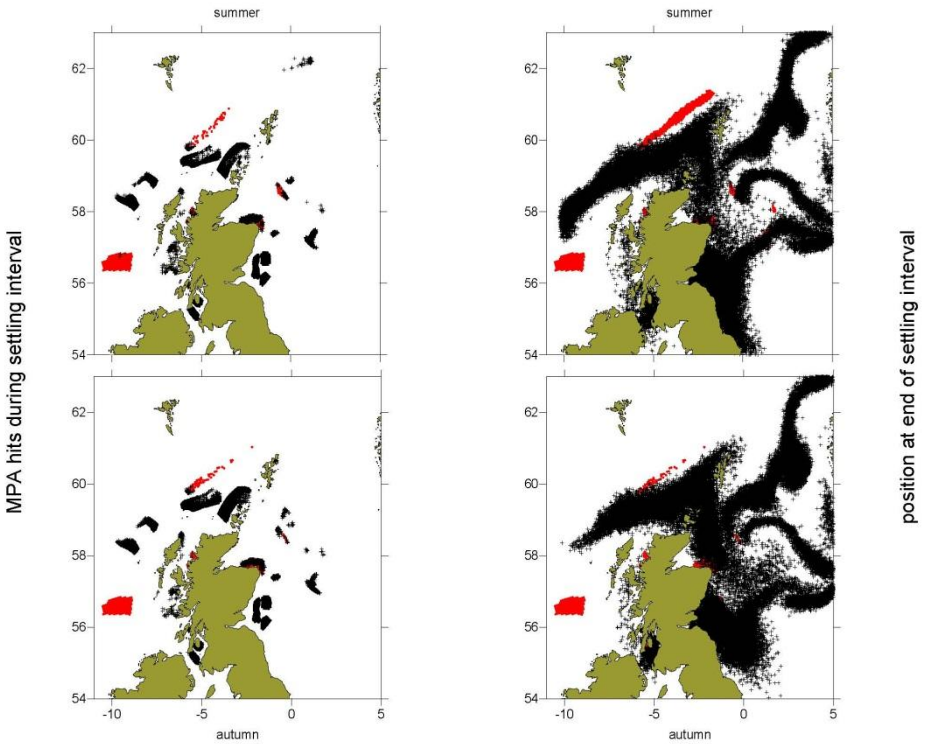

Figure 8a: Black dots show the distribution of particles at the end of the settlement window (right panels) and MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top: summer; bottom: autumn). Red dots show the particle origin positions.

Table 8

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing ocean quahog larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	Summer		Autumn		
MPA	mean	stdev	mean	stdev	n
NWS	210.3894	71.44167	301.467	87.5921	1200
STR	197.8751	71.33853	212.3195	44.46416	7600
ARR	75.12121	62.87876	50.64271	51.43547	1300
GLE	202.6309	55.94869	280.0399	80.62585	300
EGM	304.72	114.9622	221.5995	96.61362	3800
WFL	163.6299	106.9408	254.4092	114.8778	3000
NSP	336.094	139.4325	292.0905	125.6298	800
BHT	349.156	131.5106	471.0206	80.57485	18700
FSS	416.9898	81.69673	397.0485	94.58714	25500
FOF	110.676	53.35329	113.9773	52.88048	8300

The results on Table 8 show wide differences between MPAs (e.g. considerable distances covered by larvae originating from offshore MPAs such as the Faroe-Shetland Sponge Belt (FSS) but smaller in the case of more coastal MPA, with Arran (ARR) as an extreme example. The differences between seasons are not very large, nor are there consistent patterns between MPAs.

Figure 8b shows a connectivity matrix between origin and potential destination MPAs. As with other species, the west coast MPA is more dispersive than North Sea ones although this could be partly due to the distribution of MPAs along the west coast. The patterns observed for dispersal distance were not particularly obvious in the connectivity matrix, probably masked by the east-west coast differences mentioned above.

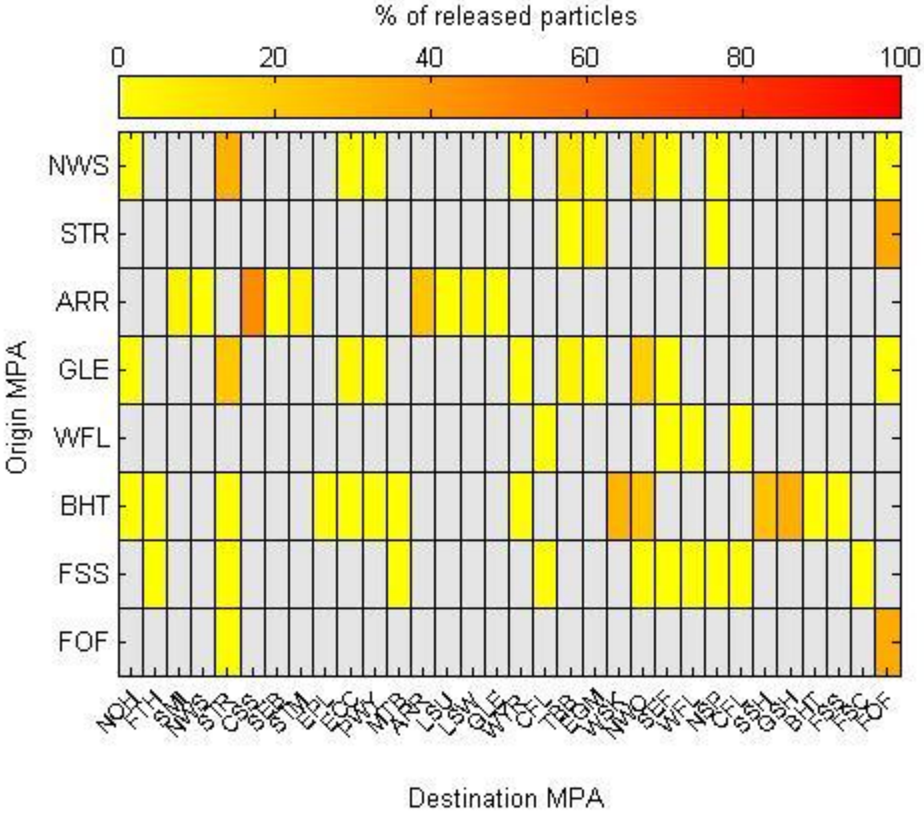

Figure 8b: Matrix showing the percentage of all particles representing ocean quahog released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Fan Mussel (*Atrina fragilis*)

Fan mussels have been reported to spawn in the summer so we assumed spawning was from spring to autumn, with a settlement window of 30-50 days. Based on presence data, particles were released from the following MPAs: SMI, CSS and ARR.

Figure 9a shows the distribution of particles at the end of the settlement window (right three panels) and identifies the MPAs locations that these particles drifted over during that period (left three panels) for each of the three spawning periods (spring, autumn and winter). The potential distribution of offspring is quite wide, with origin MPAs in the west coast potentially being able to contribute offspring to areas in the north and the east, as a result of a relatively long PLD period. An index of the distance covered by the larvae in their PLD is presented in Table 9.

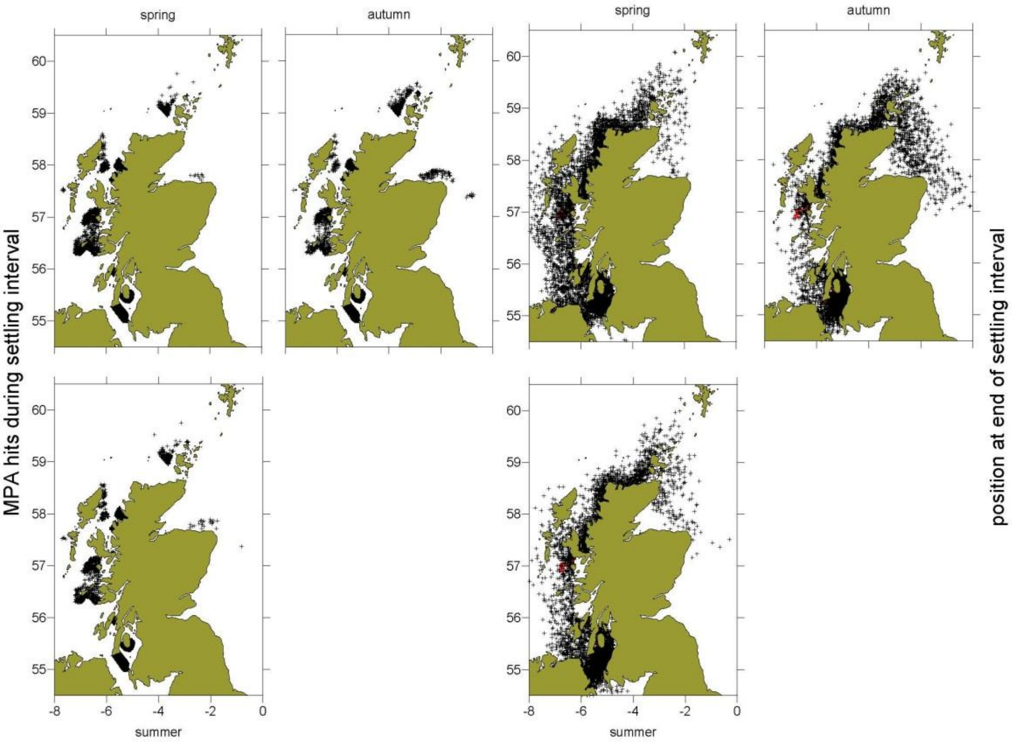

Figure 9a: Black dots show the distribution of particles at the end of the settlement window (three right panels) and MPAs locations that these particles drifted over during that period (three left panels) for each of the spawning periods (top: spring and autumn; bottom: summer). Red dots show the particle origin positions.

Table 9

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing fan mussel larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	spring		summer		autumn		
MPA	mean	stdev	mean	stdev	mean	stdev	n
SMI	215.0326	122.1579	215.8706	132.1664	303.2008	150.6005	2400
CSS	133.2396	100.5229	103.1948	93.99843	89.98832	88.15232	2800
ARR	110.5772	84.0085	82.20794	62.74385	55.20894	50.6603	1300

The results on Table 9 show a range of average distances that reflects the inshore-offshore gradient of origin. The results are quite variable and there are seasonal differences without a clear pattern between MPAs.

Figure 9b shows a connectivity matrix between origin and (potential) destination MPAs. The results are consistent with the patterns observed in Figure 9a. The matrix also shows, as expected, a greater degree of self-recruitment within Clyde Sea MPAs.

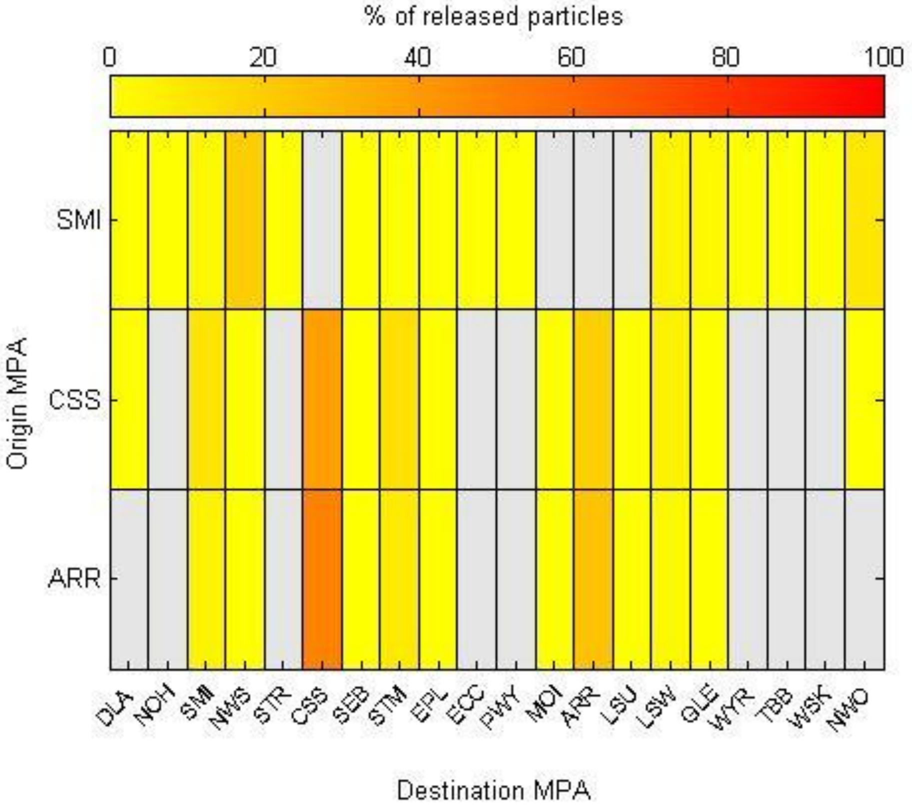

Figure 9b: Matrix showing the percentage of all particles representing fan mussel released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Native Oyster (*Ostrea edulis*)

As the larvae of the native oyster are pelagic for 11-30 days, we used a settlement window of 10-30 days, with spawning in the summer. Based on presence data, particles were released from the following MPAs: NWS, STM, LSW, GLE and WYR.

Figure 10a shows the distribution of particles at the end of the settlement window (right panel) and identifies the MPAs locations that these particles drifted over during that period (left panel). Even though the origin MPAs are all on the west coast, the potential distribution of offspring is relatively wide, resulting from a relatively long PLD period. An index of the distance covered by the larvae in their PLD is presented in Table 10.

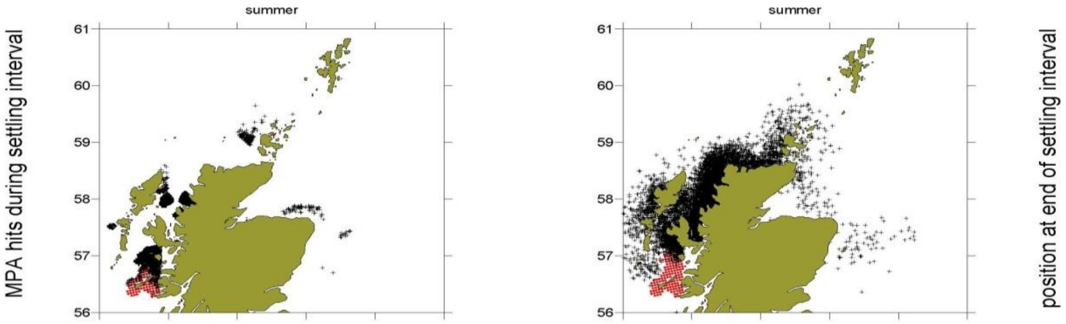

Figure 10a: Black dots show the distribution of particles at the end of the settlement window (right panel) and MPAs locations that these particles drifted over during that period (left panel). Red dots show the particle origin positions.

Table 10

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing native oyster larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	summer		
MPA	mean	stdev	n
NWS	163.35	78.06062	1200
STM	162.339	73.02932	14100
LSW	62.05346	41.44984	100
GLE	151.0637	67.76181	300
WYR	244.9038	89.90069	100

The results on Table 10 show relatively small differences between MPAs, considering that some of these were very small areas, where only small numbers of particles were released (one to three release positions for three of the origin MPAs).

Figure 10b shows a connectivity matrix between origin and (potential) destination MPAs. The results show the potential for relatively long distance transport. Relatively large connectivity values may have been influenced by the small size of some origin MPAs and, consequently, the small number of particles released from those.

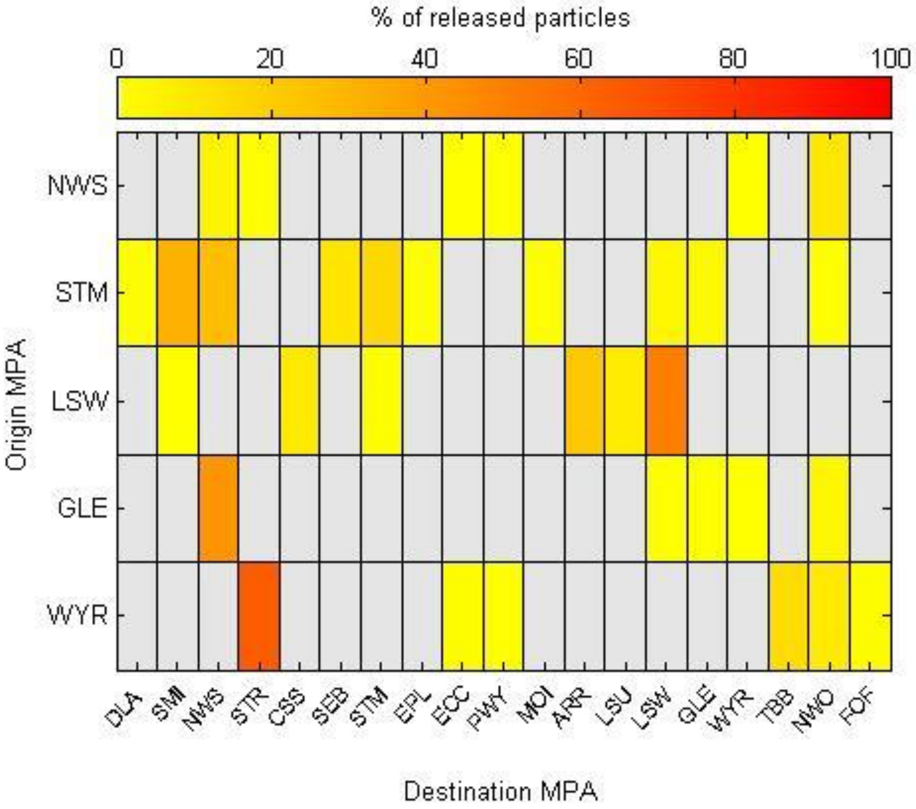

Figure 10b: Matrix showing the percentage of all particles representing native oyster released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Flame Shell (*Limaria hians*)

Flame shell spawn from May-June with peak settlement from July-August in Scottish waters so, for the purpose of our connectivity simulations, flame shell were assumed to spawn in summer, with a settlement window of 20-60 days. Based on presence data, particles were released only from NWS MPA (North-west sea lochs and Summer Isles).

Figure 11 shows the distribution of particles at the end of the settlement window (right) and identifies the MPAs locations that these particles drifted over during that period (left). The potential distribution of offspring is relatively wide, considering the restricted origin, as offspring can potentially reach northern and eastern MPAs. An index of the distance covered by the larvae in their PLD is presented in Table 11a.

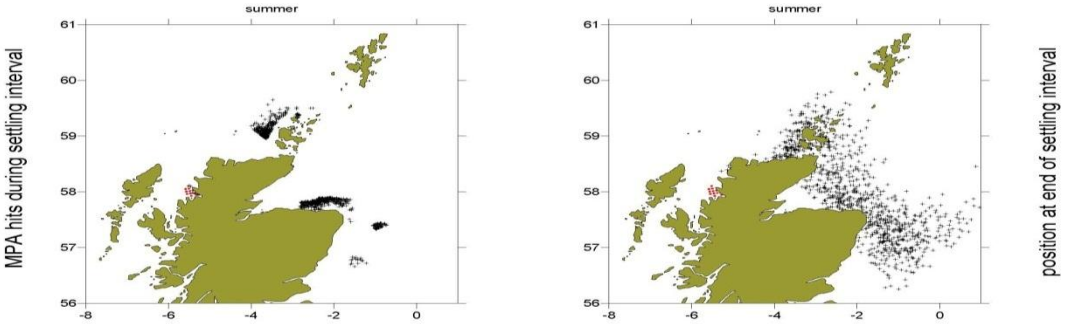

Figure 11: Black dots show the distribution of particles at the end of the settlement window (right panel) and MPAs locations that these particles drifted over during that period (left panel). Red dots show the particle origin positions.

Table 11a

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing flame shell larvae released from the origin MPA (n is the number of particles released).

	summer		
MPA	mean	stdev	n
NWS	210.3894	71.44167	1200

Table 11a is not very informative because only one MPA and season were considered, and the distance between the origin and end-point of the particles ignore the fact that many travelled a considerably longer distance, around the northern coast of Scotland (mainland and northern isles, as it can be inferred from Figure 11).

Instead of a highly one-dimensional connectivity matrix between the single origin MPA and all other (potential) destination MPAs, the percentage of all particles representing flame shell larvae that drift over any MPA during the settlement period of their pelagic phase is presented in Table 11b. The results confirm the patterns observed in Figure 11.

Table 11b

Percentage of all particles representing flame shell larvae released from the origin MPA that drift over any MPA during the settlement period of their pelagic phase.

	Destination								
Origin	NOH	NWS	STR	ECC	PWY	WYR	TBB	NWO	FOF
NWS	1.083	0.667	37.25	2.833	1.75	0.667	5.417	30.58	1.5

Heart Cockle (*Glossus humanus*)

In the Clyde, heart cockle probably spawn at the end of September and their larvae tend to be in the plankton for a few weeks. Therefore, we assumed that heart cockles spawn in autumn, with a settlement window of 1-30 days. Based on presence data, particles were released from a single MPA: GLE.

Figure 12 shows the distribution of particles at the end of the settlement window (right panel) and identifies the MPAs locations that these particles drifted over during that period (left panel). The potential distribution of offspring is relatively wide but disperse, resulting from a moderately long PLD period but very limited distribution at origin within the proposed MPAs (only one small MPA in the simulations, only three distinct particle release positions). An index of the distance covered by the larvae in their PLD is presented in Table 12a.

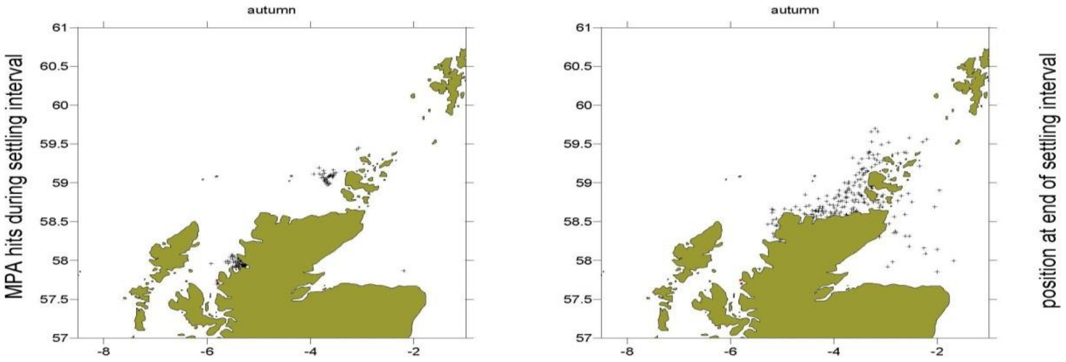

Figure 12: Black dots show the distribution of particles at the end of the settlement window (right panel) and MPAs locations that these particles drifted over during that period (left panel). Red dots show the particle origin positions.

Table 12a

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing heart cockle larvae released from the origin MPA (n is the number of particles released).

	autumn		
MPA	mean	stdev	n
GLE	157.583	47.71967	300

Instead of a highly one-dimensional connectivity matrix between the single origin MPA and all other (potential) destination MPAs, the percentage of all particles representing heart cockle larvae that drift over any MPA during the settlement period of their pelagic phase is presented in Table 12b. The results confirm the patterns observed in Fig. 12.

Table 12b

Percentage of all particles representing heart cockle larvae released from the origin MPA that drift over any MPA during the settlement period of their pelagic phase.

	Destination					
Origin	NWS	STR	SEB	LSW	GLE	NWO
GLE	87.00	0.33	0.67	14.00	15.67	12.00

Most of the heart cockle larvae are transported along the coast to MPA NWS, although other MPAs in the vicinity are also potentially visited and there is some self-recruitment. The offspring can potentially reach MPAs in Orkney and into the northern North Sea.

Arthropoda

Amphipod *(Maera loveni)*

As amphipods have no larval stages and dispersion is limited to crawling, swimming, and “rafting" on algae, we assumed these amphipods spawned all year-round, with a settlement window of one to ten days. Based on presence data, particles were released from the following MPAs: NWS, STR, ARR, GLE, EGM, WFL, NSP, BHT, FSS and FOF.

Figure 13a shows the distribution of particles at the end of the settlement window (right panels) and identifies the MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top to bottom: spring to winter). The potential distribution of offspring is very limited, as a result of the life history characteristics of this animal. An index of the distance covered by the offspring is presented in Table 13.

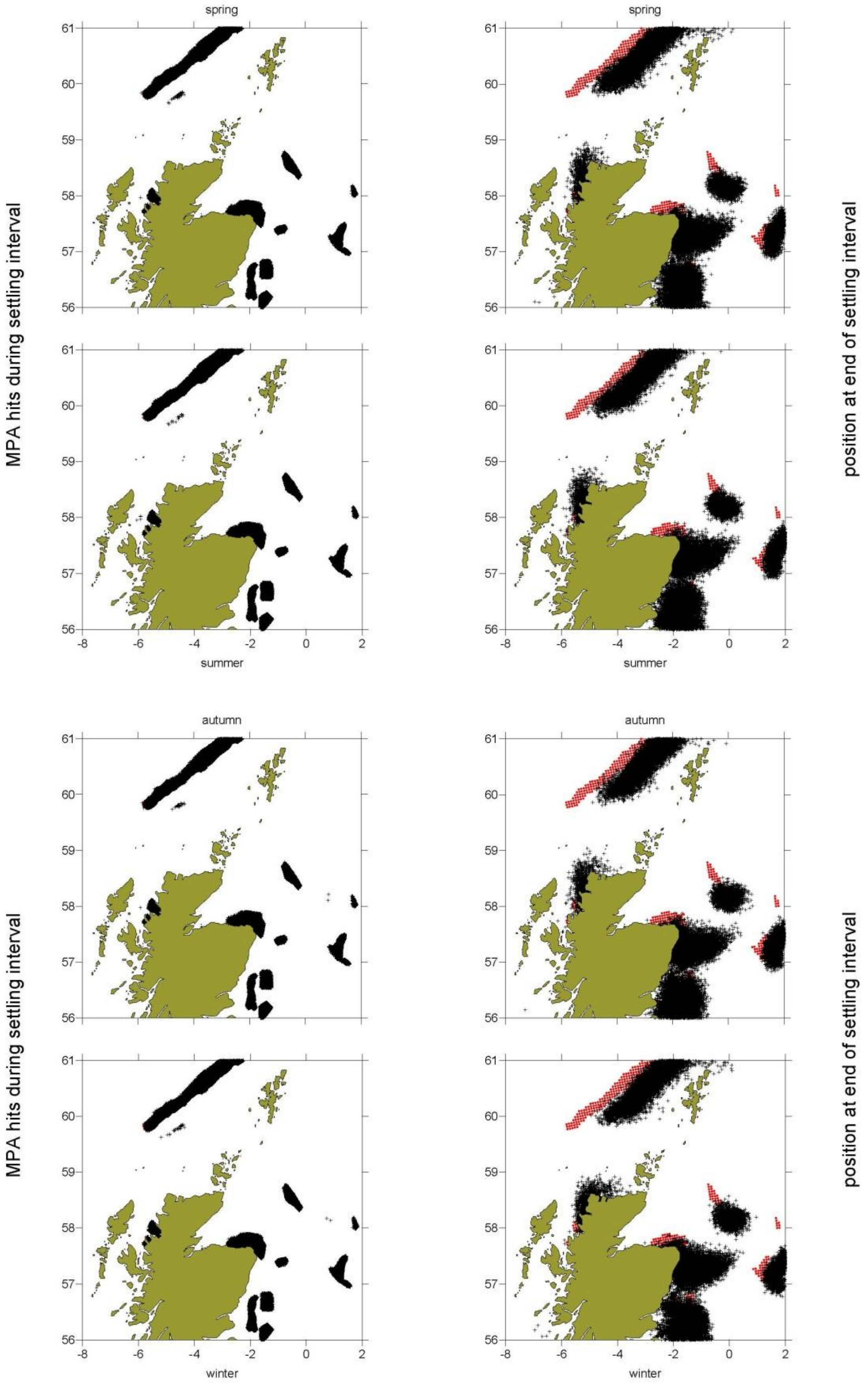

Figure 13a: Black dots show the distribution of particles at the end of the settlement window (right panels) and MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (rows from the top: spring to winter). Red dots show the particle origin positions.

Table 13

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing amphipod offspring released from each origin MPA, for each spawning season (n is the number of particles released).

	spring		summer		autumn		winter		
MPA	mean	stdev	mean	stdev	mean	stdev	mean	stdev	n
NWS	45.71541	19.9395	40.61786	18.85419	49.44458	20.30217	60.3965	23.25147	1200
STR	73.30068	17.13326	72.94866	17.12485	74.44586	18.12632	72.37808	19.24067	7600
ARR	29.70384	16.22294	29.56981	16.26043	28.08696	14.25608	27.70105	14.30954	1300
GLE	50.26104	18.6439	43.82027	16.52504	52.9068	19.21399	64.03978	21.8383	300
EGM	35.99597	11.65453	36.03197	11.9373	32.72312	10.17337	32.60442	9.312925	3800
WFL	52.03145	14.06442	45.3174	13.63996	54.99862	15.19404	55.52642	14.71882	3000
NSP	50.32005	7.560243	48.08747	7.108671	51.16166	7.499674	52.05183	7.24344	800
BHT	33.40955	16.599	34.53022	18.4953	43.34478	19.14527	48.62432	16.13506	18700
FSS	102.975	18.09356	101.692	17.26555	112.0983	17.61639	114.0385	18.46735	25500
FOF	25.78633	11.99884	27.46618	12.67583	29.98636	13.01473	31.95397	13.57806	8302

The results on Table 13 show relatively small differences between MPAs and seasons, compared to other species. The only origin MPA with greater dispersal potential than the rest is the Faroe-Shetland Sponge Belt (FSS), due to its hydrographic characteristics.

Figure 13b shows a connectivity matrix between origin and (potential) destination MPAs. Most origin MPAs are quite retentive, given the biological characteristics of this species, with a small number of relative exceptions.

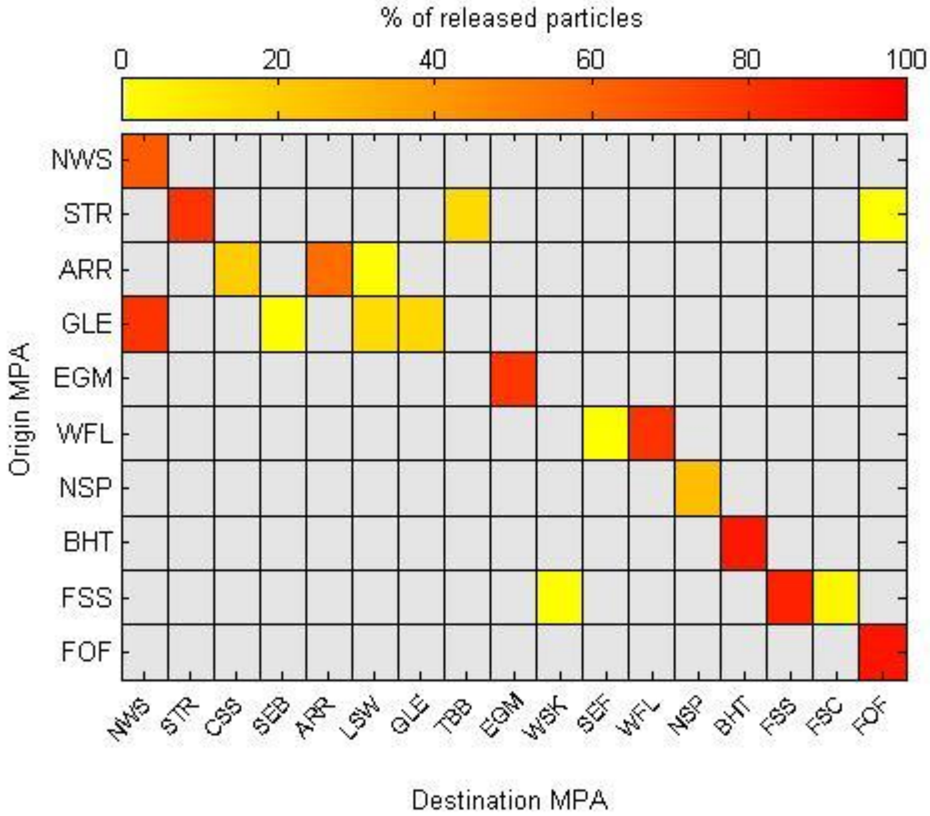

Figure 13b: Matrix showing the percentage of all particles representing amphipods released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Spiny Lobster (*Palinurus elephas*)

For the purpose of our connectivity simulations, spiny lobsters were assumed to spawn in summer as they produce a clutch from around July to October. Larvae may drift for one to six months so a settlement window of 60-180 days was used in the simulation. Based on presence data, particles were released from the following MPAs: SMI, NWS, STR and LSW.

Figure 14a shows the distribution of particles at the end of the settlement window (right panel) and identifies the MPAs locations that these particles drifted over during that period (left panel). The potential distribution of offspring and connectivity potential are extremely wide, given the long PLD period of this species. An index of the distance covered by the larvae in their PLD is presented in Table 14.

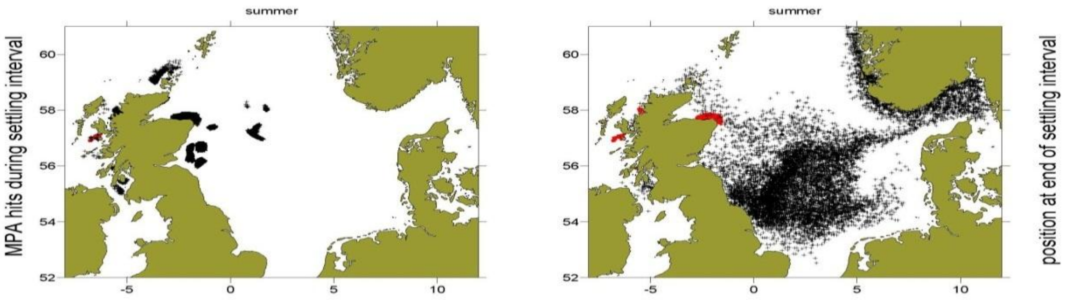

Figure 14a: Black dots show the distribution of particles at the end of the settlement window (right panel) and MPAs locations that these particles drifted over during that period (left panel). Red dots show the particle origin positions.

Table 14

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing spiny lobster larvae released from each origin MPA (n is the number of particles released).

	summer		
MPA	mean	stdev	n
SMI	626.0166	197.1344	2400
NWS	690.7814	118.3799	1200
STR	481.381	202.9256	7600
LSW	139.3821	127.9197	100

The results on Table 14 show some differences between MPAs. The general pattern shows smaller distances closer inshore and more dispersive MPAs in the west, compared to the east coast.

Figure 14b shows a connectivity matrix between origin and (potential) destination MPAs. As with other species, west coast MPAs are more dispersive than North Sea ones. A relatively high proportion of offspring originating from the Loch Sween MPA have the potential to colonise MPAs in the Clyde area (Clyde Sea Sill (CSS) and Arran (ARR)).

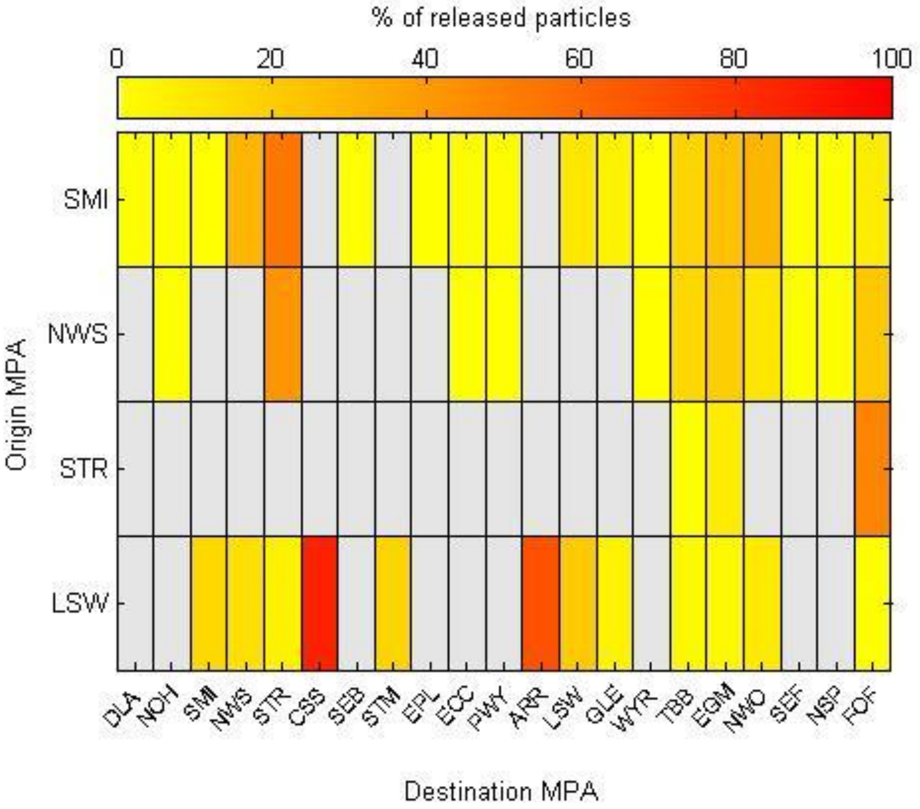

Figure 14b: Matrix showing the percentage of all particles representing spiny lobster released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Echinodermata

Northern Feather Star (*Leptometra celtica*)

The free-swimming vitellaria larvae of northern feather star only last a few days before settlement and so a settlement window of one to ten days was assumed. Due to the limited information on spawning times, we assumed that spawning occurred all year-round. Based on presence data, particles were released from the following possible MPAs; SMI, NWS, MTB and LSW.

Figure 15a shows the distribution of particles at the end of the settlement window (right panels) and identifies the MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (top to bottom: spring to winter). The potential distribution of offspring is low, resulting from the short PLD period, and quite constant between seasons. An index of the distance covered by the larvae in their PLD is presented in Table 15.

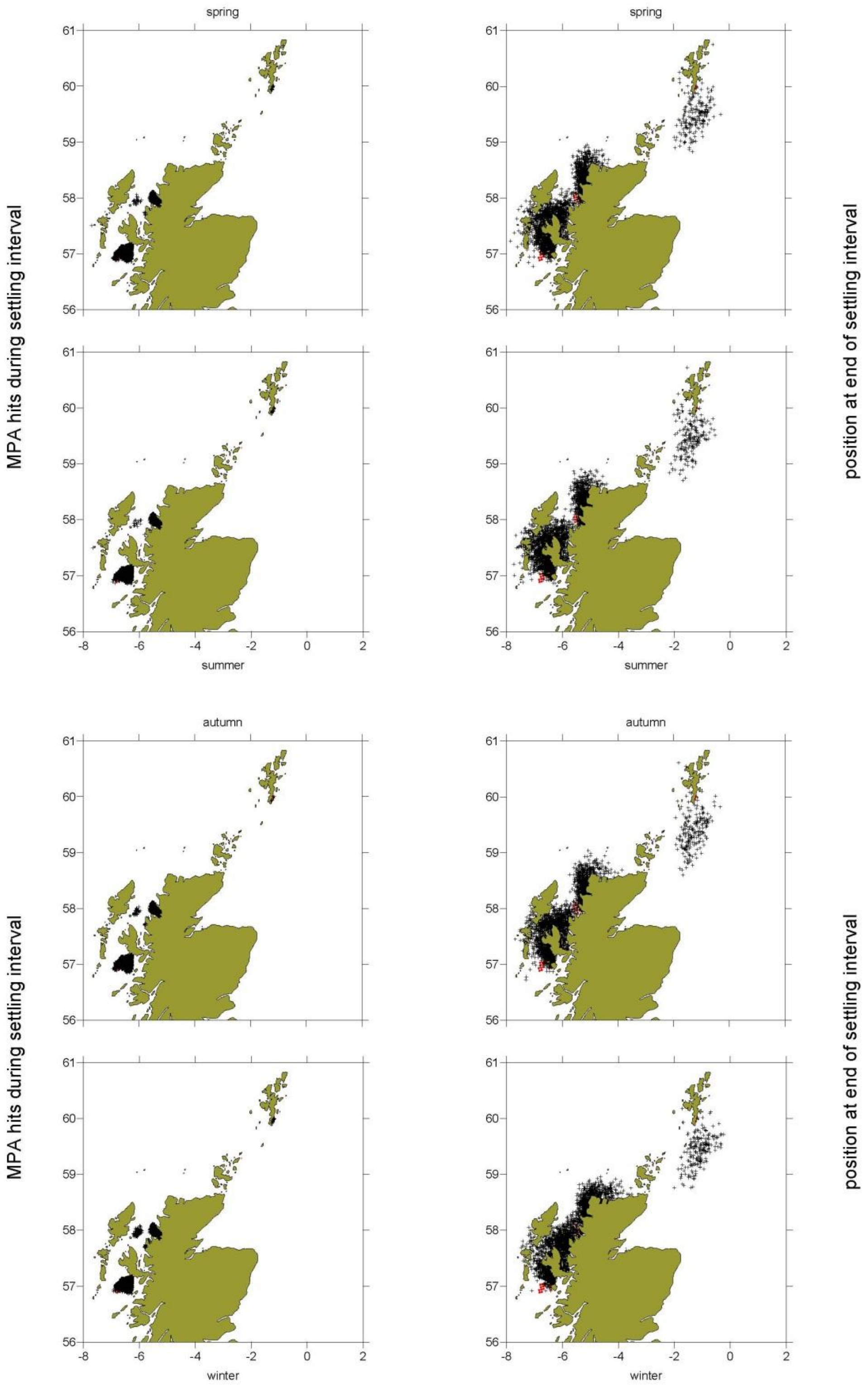

Figure 15a: Black dots show the distribution of particles at the end of the settlement window (right panels) and MPAs locations that these particles drifted over during that period (left panels) for each of the spawning periods (rows from the top: spring to winter). Red dots show the particle origin positions.

Table 15

Mean and standard deviation of the distance (straight line) between start and end position, for each particle representing northern feather star larvae released from each origin MPA, for each spawning season (n is the number of particles released).

	spring		summer		autumn		winter		n
MPA	mean	stdev	mean	stdev	mean	stdev	mean	stdev	
SMI	58.80072	34.80895	58.93132	33.395	63.88066	37.24751	74.00236	45.65417	2400
NWS	52.20294	22.69311	46.40062	20.75867	57.20983	24.6535	72.89097	32.6751	1200
MTB	65.67233	26.93485	68.35814	29.93843	75.50844	29.67039	70.20467	26.56152	200
LSW	24.93985	20.92754	21.96786	22.63312	25.41234	25.30455	25.20322	21.74939	100

The results on Table 15 show relatively small differences between MPAs, with the exception of a very inshore one (Loch Sween (LSW)) and seasons, although winter spawning was generally more dispersive.

Figure 15b shows a connectivity matrix between origin and (potential) destination MPAs. Inshore MPAs like LSW or North-west sea lochs and Summer Isles (NWS) are more retentive (resulting in more self-recruitment) than further offshore MPAs.

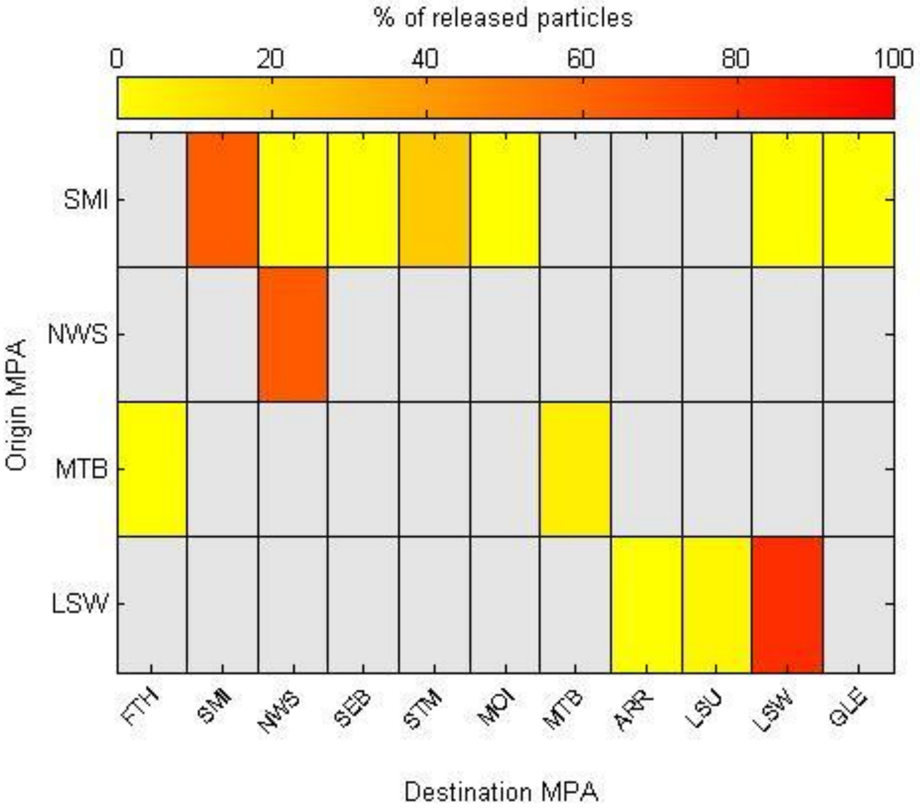

Figure 15b: Matrix showing the percentage of all particles representing northern feather star released from each origin MPA drifting over any MPA during the settlement period of their pelagic phase. Grey boxes indicate zero hits.

Analysis of General Patterns

The GAM fitted to mean transport distance estimates for each species, MPA and season (QUARTER: SPR, SUM, AUT, WIN) combination indicated that maximum pelagic larval duration (PLDMAX; days) and Distance to shore (Distancetoshore; km) had a significant effect on mean transport distance (Table 16). However, only winter had a significantly greater transport rate than other quarters and OSPAR region was not significant when distance from shore was considered.

Table 16

Outcome of fitting successively more complex models up to the minimum adequate model (GAM) to mean particle distance travelled.

Model	d.f.	Deviance explained (%)	F-values	P-values
s(PLDMAX)	1	49	28.49	<0.001
+ fQuarter	3	11.5	8.56	<0.001
+ s(Distance to shore)	1	5.6	4.38	0.017

Discussion

Factors Influencing Larval Transport

As demonstrated by the GAM fitted to mean transport distance for each species and as it would be intuitively expected, the dispersal potential of offspring of any given species was significantly related to the duration of its pelagic larval phase (PLD). Additionally, mean transport varied regionally in relation to distance from the coast and season, although only winter spawning resulted in significantly longer transport patterns, reflecting the influence of generally stronger winds on water circulation. Distance to shore captured most of the geographically-induced variability so OSPAR region did not show a significant effect, although qualitatively it appears as if west coast (part of Region III: Celtic Seas) MPAs are more dispersive than northern North Sea (part of Region II: Greater North Sea) ones. Note that mean straight distance between start and end positions at the end of the PLD is only an approximation of actual transport, for computational expediency. The actual particle trajectories will always be longer due to tidal and random (diffusion) effects, in addition to the circulation around land masses (particularly relevant in the case of larvae of west coast origin transported into the North Sea).

Connectivity between OSPAR Sub-Regions

The model presented here indicates that the larvae of species with a PLD ≥ 30 days that were not solely associated with sea lochs or near-shore regions could be advected from the Celtic Sea to the Greater North Sea OSPAR sub-region, depending on the proximity of the origin MPA to the sub-region boundary in the case of species on shorter PLD. These species include tall sea pen, horse mussel, native oyster, ocean quahog, burrowing sea anemone, spiny lobster and a few other species that had not been identified in Greater North Sea MPAs, such as fan mussel, flame shell and heart cockle. The export potential of these species mean that, if a sufficiently large enough component of the parental population is protected, then these areas may be able to seed unprotected sites of suitable habitat throughout these two sub-regions.

Connectivity within OSPAR Sub-Regions

Connectivity within OSPAR sub-regions was obviously easier to realise in general than between sub-regions. There was some degree of self-recruitment within most MPAs, even in the case of species with later settlement age. In the case of species with shorter PLD (≤ 10 d), the distance between MPAs within OSPAR sub-regions is generally close enough to allow within-sub-region connectivity.

Species at Risk of Local Pressures due to Low Connectivity

The species at greater risk due to low connectivity are generally those with short PLD and/or present only in a small number of MPAs. Species like burrowing amphipod, northern feather star, pink soft coral and northern sea fan are potentially more vulnerable due to their short PLD, while heart cockle or horse mussel have only been identified in a small number of MPAs. Note that a small number of inshore MPAs were not resolved in our analysis but the species those areas seek to protect would be, due to their location, potentially more vulnerable due to their likely less dispersive environment. Further hydrodynamic model developments (see below) should allow us to quantify this and assess or revise the degree of vulnerability of these species.

Model Assumptions and Future Developments

As described in the Methods section, the flow fields used in the current modelling exercise were obtained by averaging a 16-year series of year-specific runs of a statistical model (SNAC; Logemann *et al*., 2004) of a hydrodynamic model (HAMSOM; see Backhaus, 1985), over a geographical domain between 50-65° N latitude and 15° W - 15° E longitude. This approach has a number of limitations that need to be addressed by further research:

- Deep water locations west of 15° W were not included in our analysis. Although, on the basis of prevailing circulation patterns and the PLD of PMF species in those areas, it is unlikely that a significant exchange of organisms between those areas and others within the model domain would take place, a full analysis of Scottish MPA connectivity can only take place when all areas are included. Additional targeted simulations will be carried out to test the need for further analysis.

- Similarly, the relatively coarse spatial resolution of the hydrodynamic model (approximately just 15 km over our domain) prevented us from defining the coastline in sufficient detail to resolve five inshore MPAs. Even though our analysis has shown that dispersal characteristics are inversely related to distance from shore, those inshore MPAs must make some contribution to the wider network, which has not been quantified in our analysis. In the future, a high-resolution (≥ 50 m) hydrodynamic model will resolve these areas and further analysis will be carried out. Likewise, a higher resolution model should also resolve additional oceanographic features that may play a role in the retention or dispersal of organisms.

- The use of climatological (average) flow fields does not allow us to quantify inter-annual transport variability and the potential effect of extreme years on MPA connectivity and species dispersal patterns. However, an effective MPA network can only be designed for prevailing conditions, not rare events. Although the climatological flow fields do not necessarily represent real prevailing conditions (real prevailing conditions may be a succession of highly variable years), a preliminary analysis of year-specific HDM data does not support this hypothesis. However, some further analysis using year-specific flow fields should be carried out to quantify the effect of inter-annual variability, particularly in PMF species with longer PLDs.

Even though spawning time was one of the parameters considered in our simulations, we assumed single one-day spawning events for any given season. First of all, this is biologically unrealistic as species do no spawn synchronously over the whole area of interest, nor are they likely to undertake single spawning events in the middle point of any given season. Sensitivity analysis comparing single egg release events against more realistic Gaussian spawning curves carried out by Gallego (2011) on a similar model system showed an effect that, in our model, would most likely result in offspring dispersion over wider areas, thus resulting in relatively higher connectivity and broader export of larvae. However, given the scarcity of biological information available for most PMF species (in some cases, not even information about spawning season was available), it was not feasible to use more biologically realistic assumptions and we can only note that our simulations can only be a simplified representation of the actual level of biological complexity and that this may have an effect on our results, especially in the case of species where important seasonal differences have been observed in our results (e.g. northern sea fan).

Pelagic larval duration (PLD) was identified in the results of the analysis of individual species and also by our GAM analysis as an important factor for dispersal distance and degree of connectivity. This conclusion is self-evident as larvae that spend a longer time in the pelagic phase will be transported by currents for longer distances and, therefore, have the potential to drift over a greater number of MPAs. However, there is little accurate information about

PLD and settlement windows for many of the PMF species considered here, and in any case we were forced to group PLD and settlement window parameters into a limited number of groups, to keep the post-processing of the original particle tracking simulation data manageable. However, it is important to be aware of the fact that the parameterisation used here was, again, an oversimplification of what happens in nature, although the general patterns derived from our simulations are likely to capture the general transport and connectivity patterns that would take place in reality.

In the absence of detailed biological information, the “behaviour” of particles representing larval PMF species was not accounted for. Particles were kept at a constant depth for the whole duration of their PLD. This is clearly unrealistic, as planktonic larvae are known to display at the very least vertical migration patterns in the water column. The importance of particle behaviour was explored by Gallego (2011) and found to be potentially important. However, once again, there is very little information about larval behaviour for the majority of PMF species, and the environmental data that may act as behavioural cues in nature is absent from the model, so larval behaviour could not be modelled dynamically.

The estimates of connectivity assume that there is suitable habitat for advected larvae to settle in all possible MPAs that are considered. This will of course exaggerate the level of connectivity as, although most possible MPAs contain a range of habitats, they do not include all suitable types. However, too little is currently known about the habitat requirements of most of the PMF species to be able to map the precise areas of suitable habitat.

Overall, we are confident that the current modelling exercise is adequate to provide a general description of the degree of connectivity between proposed MPAs for individual PMF species. Also, it should be noted that no influx from non-protected into protected areas was assumed, while in reality it cannot be expected that PMF species are only present in MPAs. However, this effect may be partially offset by the also unrealistic assumption that PMF species are uniformly present over the whole area of MPAs where they have been identified, an assumption which is likely to result in some degree of overestimation of connectivity and dispersal. Without a comprehensive map of species distribution within and outside MPAs, it is not possible to overcome these potential shortcomings. More detailed biological information would allow us to develop more biologically realistic simulation models but it is not yet clear that a considerably more complex modelling exercise, even if feasible, would result in more realistic results, given the likely uncertainty and variability that would be associated with most biological parameters. However, there are aspects where our analysis could be improved quite feasibly, for example by making use of a more finely resolved hydrodynamic model of Scottish waters when such a model becomes available. In any case, we are confident that the present outcomes are unlikely to change significantly as a result of further developments and, as it stands, the present approach is already considerably more sophisticated than what has been used to define MPA networks in other areas.

The estimation of connectivity suggests that in general there is sufficient replication of PMF species among possible MPAs within and among biogeographic (OSPAR) areas. Tall sea pen, burrowing anemone, spiny lobster and most bivalve molluscs have a sufficiently long PLD to ensure extensive dispersal among MPAs. Even many species with PLD ≤ 10 d that are well represented in the MPA network and inhabit areas away from the coast should have some connectivity within OSPAR regions. This means that any build-up of reproductive capacity of PMF species within protected areas could be expected to have a wider ecological benefit in providing a source of larvae for surrounding regions and adjacent MPAs. However, connectivity is clearly an issue for species that are not well represented in the network such as heart cockle and horse mussel, while burrowing amphipod, northern feather star, pink soft coral and northern sea fan may be more vulnerable to local pressures because of their low potential for dispersal.

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