2017-06-16

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Ross, RE

http://hdl.handle.net/10026.1/9494

Author's Accepted Manuscript

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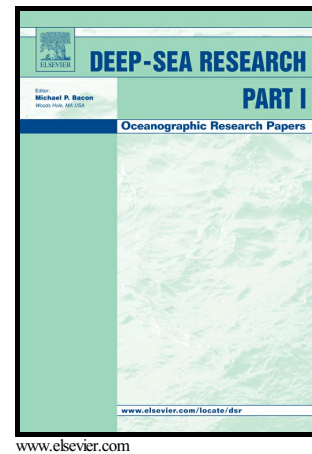
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Cite this article as: Rebecca E. Ross, W. Alex M. Nimmo-Smith and Kerry L. Howell, Towards 'ecological coherence': assessing larval dispersal within a network of existing Marine Protected Areas, *Deep-Sea Research Part I*, http://dx.doi.org/10.1016/j.dsr.2017.06.004

Towards 'ecological coherence': assessing larval dispersal within a network of existing Marine Protected Areas

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Abstract

The Convention on Biological Diversity mandates the establishment of Marine Protected Area (MPA) networks worldwide, with recommendations stating the importance of 'ecological coherence' (a responsibility to support and perpetuate the existing ecosystem) implying the need to sustain population connectivity. While recommendations exist for integrating connectivity data into MPA planning, little advice exists on how to assess the connectivity of existing networks. This study makes use of recently observed larval characteristics and freely available models to demonstrate how such an assessment could be undertaken. The cold water coral (CWC) *Lophelia pertusa* (Linnaeus, 1758) is used as a model species, as much of the NE Atlantic MPA network has been designated for CWC reef protection, but the ecological coherence of the network has yet to be assessed. Simulations are run for different behavioural null models allowing a comparison of 'passive' (current driven) and 'active' (currents + vertical migration) dispersal, while an average prediction is used for MPA assessment. This model suggests that the network may support widespread larval exchange and has good local retention rates but still has room for improvement. The best performing MPAs were large and central to the network facilitating transport across local dispersal barriers. On average, passive and active dispersal simulations gave statistically similar results, providing encouragement to future local dispersal assessments where active characteristics are unknown.

1.0 Introduction

In response to global pressure, networks of MPAs are being established worldwide aiming to put in place management methods for the effective protection of species and ecosystems. Signatories to the Convention on Biological Diversity (CBD) are bound by its recommendations, which state that species and ecosystems must be "conserved through effectively and equitably managed, ecologically representative, and well connected systems of protected areas" (CBD, 2010). The IUCN World Parks Congress (IUCN, 2003) recommended that the international community should "build the best available science on connectivity into marine and coastal protected area network design, in order to create networks that are ecologically coherent". Many other regional regulations cover a similar remit. Although a legal term which is hard to interpret, Ardron (2008) defines "ecological coherence" as an MPA network which:

i.   "Interacts and supports the wider environment"

ii. "Maintains the processes, functions and structures of the intended protected features across their natural range"

iii. "Functions synergistically as a whole such that the individual protected sites benefit from each other to achieve the above two objectives"

iv. "Additionally… may be designed to be resilient to changing conditions"

While there are many other aspects that need to be addressed to fulfil these criteria, implicit within these requirements is a need to understand the interaction between designated MPAs and their wider environment, including the connectivity of the target species. Should MPAs within a network be 'disconnected', the network could not be self-sustaining or 'ecologically coherent'. Likewise should an MPA protect a 'sink' habitat (*sensu* Pulliam, 1988), this area could degrade due to lack of protection for its larval supply sites.

Larval dispersal is an important factor in quantifying connectivity, especially for sessile benthic species reliant on their larval phase as the only means of long distance dispersal. Larval dispersal research has already been integrated into MPA planning, primarily advising on MPA spacing (Botsford *et al.*, 2001; Gaines *et al.*, 2003; Shanks *et al.*, 2003), size (Botsford *et al.*, 2001; Shanks *et al.*, 2003), and persistence (Jessopp *et al.*, 2007). However all advice is currently based on several studies of shallow water taxa, and even then the advice is highly variable (Botsford *et al.*, 2001; Jones *et al.*, 2009; Shanks *et al.*, 2003; Wedding *et al.*, 2013). Even fewer data are available on the larval dispersal of deep sea organisms, leaving offshore MPA planning reliant upon the same limited shallow water advice (Roberts *et al.*, 2010). Due to policy driven time pressures, MPA networks worldwide have suffered from this lack of connectivity data at point of designation. While advice is available on how to incorporate connectivity data into MPA network design, there is little guidance on how to assess an existing designated network and make recommendations for its improvement when new data become available.

Recently Hilario *et al.* (2015) recorded 72 eurybathic and 21 deep sea species worldwide whose planktonic larval duration (PLD) has been estimated. There was a statistically significant difference in the mean PLD for shallow vs deep organisms suggesting that advice based on shallow water species may be inappropriate. Few of these deep sea species have known larval characteristics (in terms of their swimming ability, buoyancy, growth rates, vertical distribution, mortality, etc.). The PLD and larval characteristics of the cold water coral (CWC) *Lophelia pertusa* (Linnaeus, 1758) have recently

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been described (Larsson *et al.*, 2014) supplementing previous reproductive observations about the

species (Brooke & Järnegren, 2013; Rogers, 1999; Waller & Tyler, 2005,). *L. pertusa* is commonplace

as solitary colonies attached to hard substrate (Hovland, 2005; Mortensen & Buhl-Mortensen, 2004,

2005; Wilson, 1979,). However certain conditions promote the aggregation of colonies into

substantial reefs and carbonate mounds (Howell *et al.*, 2011; Roberts & Wheeler, 2006) which

themselves provide a habitat for many other species. These CWC reef features have been a major

target for conservation efforts. In the NE Atlantic, an international network of offshore MPAs has

been established predominantly for the protection of CWC reef habitat. To date there has been no

assessment of the ecological coherence of this network in terms of evidence based larval dispersal

capability beyond the application of standard spacing guidelines derived from the dispersal

capabilities of shallow water organisms.

The main aim of this study is therefore:

- To use *L. pertusa* as a model species to introduce a novel method of MPA network

    assessment in order to interpret their 'ecological coherence'.

In Larsson *et al.*'s (2014) *ex situ* study of *L. pertusa* larvae, observations were suggestive of vertical

migration ability. Larvae with vertical swimming abilities are thought to have the ability to enhance

or reduce the dispersal potential of passive larvae. They may use their swimming ability to reach

depths with differing current speeds and directions (Shanks *et al.*, 2003; Sponaugle *et al.*, 2002;

Young *et al.*, 1996a, 1996b, 2012), along with different temperatures which impact larval

metabolism and therefore rates of development (Young *et al.*, 2012). Cowen *et al.* (2006) propose

that highly mobile fish larvae use vertical swimming abilities to promote area retention rather than

enhancing dispersal distance. By contrast, Young *et al.* (2012) found there could be a modest

enhancement of dispersal ability by modelling the potential dispersal of the cold seep siboglonid

worm *Lamellibrachia luymesi* (Van Der Land & Nørrevang, 1975) should they reach the upper water

column. Indeed basic comparison of differing depth releases across several taxa in the Intra-American seas suggested that there could be different effects of vertical migration dependent only on location and PLD (Young *et al.*, 2012).

This study also has the opportunity to compare potential active and passive larval dispersal strategies and their impact on MPA dispersal assessments. As *ex situ* larval observations may be difficult to extrapolate into reality (Maldonado 2003, 2006; Metaxas & Saunders, 2009), a passive simulation provides an opposite extreme for tempering the range of potential larval strategies and therefore dispersal patterns of a single species. This comparison may also be useful for extrapolations to other species with undescribed larval characteristics; quantifying the potential for variation in dispersal patterns on a network scale, should a passive strategy be assumed until more data is available.

The secondary aim of this study is therefore:

- To compare potential active and passive dispersal scenarios to inform managers of the potential consequences of incomplete species understanding (as this is likely to be the situation for most deep-sea species).

2.0 Methods

2.1 Study area

This study was undertaken in the NE Atlantic in the Extended Economic Zones (EEZs) west of UK and Ireland (Fig. 1a). Twenty-eight offshore MPAs were considered in this example, each having been designated by the UK or Irish Governments, or the North East Atlantic Fisheries Commission (NEAFC).

Release locations were derived from a high-resolution habitat distribution model as published by Ross *et al.* (2015; which in turn was based on 222 observational transects). The 250m multibeam-

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based Scleractinian reef model was thresholded to ≤1100m to ensure reefs were dominated by *L. pertusa*. The model output was then re-gridded to the horizontal sensitivity threshold defined by model sensitivity testing (0.005°) (Ross *et al.*, 2016). Grid centroids of high reef probability located within offshore MPAs were used as release locations (Fig. 1b). Additional locations in the Darwin Mounds and NW Rockall Bank MPAs were added based on observational data (where reefs are

(b) Release points based on reef model predictions inside MPAs

Point spacing after Ross et al. (2016)

Release points <1100m

Ross et al. (2015) Scleractinian reef model

(a)

1 Wyville Thompson Ridge
2 Darwin Mounds
3 Rosemary Bank
4 Geikie Slide & Heb Slope
5 E Rockall Bank
6 NW Rockall Bank
7 Anton Dohrn
8 Barra Fan & Heb Terr.
9 Haddock Box
10 SW Rockall Emp o' Brit
11 SW Rockall Bank k2
12 SW Rockall Bank g3
13 SW Rockall Bank g2
14 SW Rockall Bank k1
15 Logachev Mounds
16 Porcupine Bank
17 S Porcupine Bank
18 Hovland Mounds
19 Belgica Mounds
20 Canyons
21 Hatton Bank
22 Hatton Rockall Basin
23 HRB I1
24 HRB I2
25 Hatton Bank m1
26 Hatton Bank m2
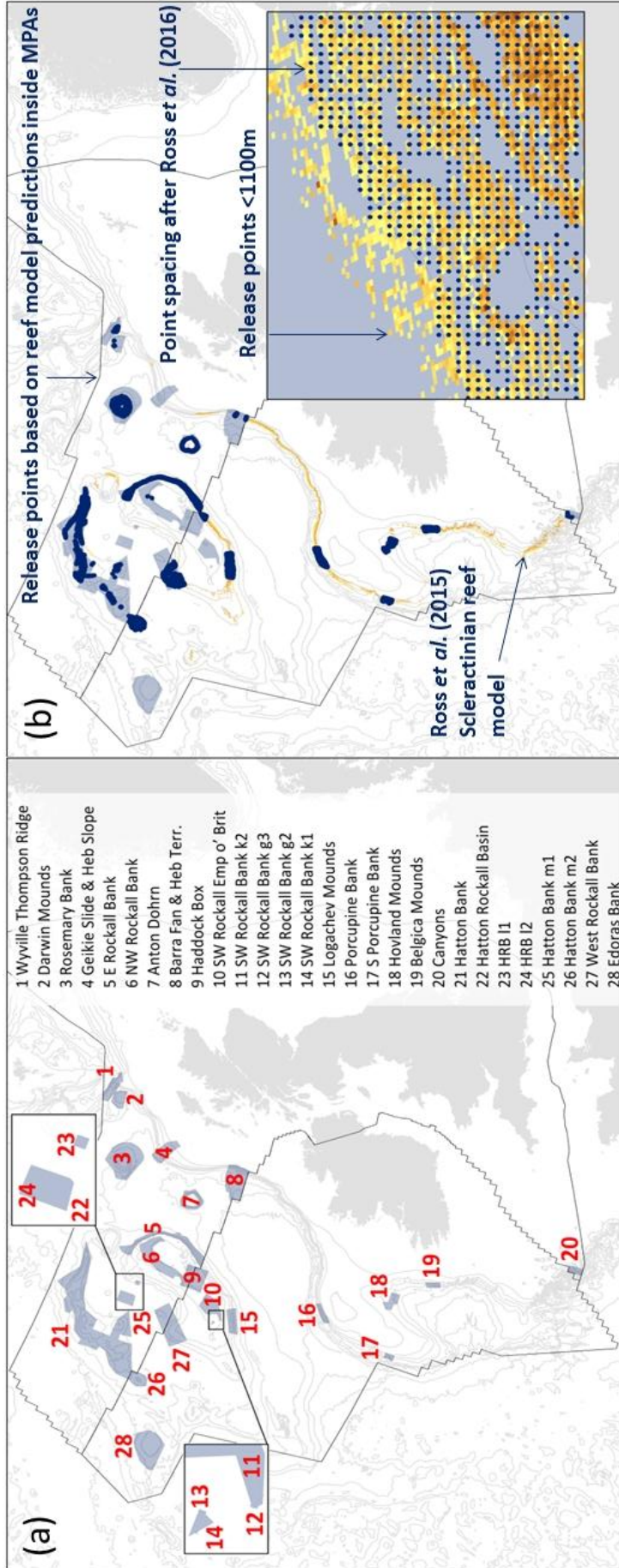27 West Rockall Bank
28 Edoras Bank

Figure1 The Location of the study area, the wider MPA network, and larval release sites. **(a)** All the offshore MPAs considered and named in this study, and their relation to the UK and Irish Extended Economic Zones. Abbreviations other than compass directions are "Heb"- "Hebridean", "Emp o' Brit" – "Empress of Britain", "HRB"- "Hatton Rockall Basin". Alphanumeric references (e.g. k2, g3, l1, m2) are North East Atlantic Fisheries Commision designations. **(b)** The location of modelled Scleractinian Reef Predicted Presence (RPP; orange/pale squares) from Ross *et al.* (2015), and the interpreted release locations (dark dots) which are sited within MPAs and shallower than 1100m to ensure that reefs are dominated by *Lophelia pertusa* (Linnaeus, 1758). Inset shows an example of how release locations were interpreted based on the RPP and spacing sensitivity tests (Ross *et al.*, 2016). Maps were plotted in ArcGIS (v.10.3, http://desktop.arcgis.com/en/arcmap/) using GEBCO 30-arc-second bathymetry (http://www.gebco.net/) and projected in Albers Equal Area Conic with modified standard parallels (parallel 1 = 50.2°, parallel 2 = 58.5°). MPA shapefiles are available from JNCC (UK) http://jncc.defra.gov.uk/protectedsites/SACselection/gis_data/terms_conditions.asp, NPWS (Ireland) https://www.npws.ie/maps-and-data/designated-site-data/download-boundary-data, and NEAFC (International) http://www.neafc.org/closures/coordinates.

associated with smaller topographic features than the Ross *et al.* (2015) model can resolve).

Releases were depth stratified to every 50m spanning 150m-1000m. Vertical sensitivity of the model pairing at shallower depths is much higher than this, but the high computational load from so many release locations prohibited greater stratification in this example study.

MPAs with no reef habitat suitability were still considered potentially suitable for solitary colonies or smaller aggregations of *L. pertusa*. These MPAs were allowed to capture larvae, but did not act as larval sources.

2.2 Model set up

2.2.1 Hydrodynamic model

The HYbrid Coordinate Ocean Model (HYCOM) is a global hydrodynamic model gridded at 1/12° horizontal resolution (approx. 8km). Although this is a relatively coarse spatial resolution, a preliminary test of two potential models deemed HYCOM as the better representative of local circulation when compared against observational data (Ross *et al.*, In Review). The native hybrid vertical coordinate system, characteristic of HYCOM, for the purposes of deep water studies is predominantly sigma (terrain-following), compressing to greater resolution in areas of steep topography. Outputs from the model are freely available online, reformatted from the hybrid

coordinates to a 40 depth layer z-level vertical grid making it compatible with many particle simulator models. Daily snapshots provide reasonable temporal resolution (Putman & He, 2013), but inherently excludes tides likely resulting in higher velocities than in nature (Müller *et al.,* 2010). Unfortunately a tidal model at this scale is both hard to get ahold of and requires much greater computational power to utilise. The hydrodynamic model supplies the velocity vectors, which inform the advection protocols within the particle simulator. This study uses data from HYCOM+NCODA global reanalysis experiment 19.1, using data from 2003, 2007 and 2010. These years represent a range of North Atlantic Oscillation (NAO) indices (positive, negative, and neutral), as the NAO has been linked to the variability in the hydrodynamics of the Rockall Trough region (Holiday *et al.*, 2000, Ullgren & White, 2010). A model sensitivity study found this approach to be more representative of a larger time series of simulations than using fewer years of simulation or three non-NAO linked years (Ross *et al.* 2016).

2.2.2 Particle simulator

The Connectivity Modeling System (CMS; Paris *et al.*, 2013) is a freely available offline particle simulator specifically designed for the simulation of larval dispersal with multiple modules allowing easy integration of biological data. The core model uses a fourth order Runge-Kutta method to differentiate particle positions through space and time. The CMS also allows the integration of a random walk impulse to simulate additional diffusion of particles beyond the instruction of the hydrodynamic model. This study used CMS v.1.1 with a diffusivity of $7m^2 s^{-1}$ every 4 hours in line with Wood *et al.* (2014, after Okubo, 1971).

2.2.2.1 *Passive simulations*

Larval release was simulated daily from 4th January – 4th March in each year, capturing the seasonal reproduction period observed in Norway (Brooke & Järnegren, 2013) and in the NE Atlantic (Waller & Tyler, 2005). Although it is likely there would only be one or two spawning events per season

(Brooke & Järnegren, 2013; Wallet & Tyler, 2005), daily releases were performed to capture the full range of potential larval trajectories possible within this period (Ross *et al.*, 2016). In each release event from each release location, 100 larvae were released. This is substantially lower than reality (Waller and Tyler (2005) observed an average fecundity of 3300 oocytes per cm^2 per colony), but within the model this number represents a proportional rather than complete representation of larval fates. Scaling up larval release numbers could potentially improve statistical robustness of rare connections, but the greater computational power required for simulation and analysis seemed unnecessary when this study is focussed on dominant pathways of dispersal.

The CMS's seascape module allocated release locations to MPA polygons and tracked which MPA polygons the larvae settle in. Planktonic larval duration (PLD) was assumed to be 57days with larvae considered competent to settle in MPA polygons from day 30, in line with the laboratory observations of Larsson *et al.* (2014).

2.2.2.2 *Active simulations*

Larsson *et al.*'s (2014) observations suggested that *L. pertusa* may undertake a vertical migration. Supplementary Fig. S1 shows the maximal active vertical swimming speeds, heights, and timings (after Larsson *et al.,* 2014). Simulated larvae below 550m depth (the conservative approximate depth of the permanent thermocline in February (White & Dorschel, 2010)) were assumed to adhere to 8-9°C swimming speeds, while those that transitioned into, or originated in, shallower waters adopted the speeds observed at 11-12°C. All larvae were instructed to follow the vertical migration maximum as defined by Larsson *et al.* (2014). Apart from this vertical migration modification, all other parameters echoed passive simulations.

2.2.2.3 *Comparison and combination of simulations*

Passive and active simulations were compared, both to examine the variability in potential dispersal patterns for *L.pertusa*, and to consider the impact of incomplete knowledge in future larval dispersal simulations for species where larval characteristics may be unknown. As real dispersal patterns are likely to be neither entirely passive nor entirely active, the main MPA assessment is based on an average of both active and passive strategies.

Across 3 years of simulation, 51 712 release locations, 90 days of releases, 100 larvae per release, and 2 larval strategies, a total of 2 792 448 000 larval trajectories were simulated. Due to the large number of releases, all models were run using Plymouth University's High Performance Computing (HPC) facility.

2.3 Analysis

An MPA dispersal matrix, based on MPA start and end polygons per trajectory, was produced per year, per depth, and per larval mode (passive/active) in the statistical software environment R (R Core Team, 2014). Depth matrices were then summed, and averaged across years to give a matrix per larval mode for the passive vs active comparison. A combined matrix was then produced, averaging across larval modes, for use in the main MPA assessment.

2.3.1 Passive versus active larvae

Passive versus active larval modes were compared qualitatively and quantitatively across all MPAs. The quantitative comparison used a Kolmogorgov-Smirnov test with bootstrapping (n=1000) performed in R (Sekhon, 2011) to compare whole matrices.

CMS trajectory outputs logging individual larval positions per day of tracking were utilised to produce maps of dispersal from the Darwin Mounds as an example MPA. Trajectory files, logging particle positions over time, were processed using a custom script in R to produce a Geographic Information System compatible line shapefile of all trajectories (across all depths and larval modes) simulated from the Darwin Mounds. Line files were then transferred to ArcGIS 10.1 and spatially

joined, per larval mode, to a grid of half HYCOM resolution (0.0416665°) to produce spatial 'heat-maps' of track density. Heat maps show larval trajectories as a spatial grid, colour coded with 'hot' colours where there is a high density of larval trajectories.

Dispersal kernels (frequencies of dispersal distance) for passive and active dispersal from the Darwin Mounds were created in Matlab, using the Haversine formula to convert start and end coordinates of particles into curved earth distances.

2.3.2 MPA assessment

A suite of metrics was developed based on two qualities deemed of importance to MPA and network performance:

a) Supplier performance: the ability to act as a supplier of larvae to itself (local retention) the rest of the network, and outside of the network

b) Retainer performance: the ability to retain settling larvae from other network suppliers (note that survival is not quantified by these models – only the potential arrival of larvae)

Both of these qualities are necessary for an MPA to be self-sustaining and to contribute to the sustainability and 'ecological coherence' of the network.

Individual MPAs

Within the greater network, each individual MPA was assessed based on these qualities, using a ranking system. Individual MPA supplier performance was quantified as an average ranking of several sub-criteria.

- The proportions of supplied larvae which are locally retained, retained by another MPA, or are retained outside of the network

- The number of larvae supplied

- The number of MPAs supplied with larvae

- The evenness of strong supply across MPAs in the network

As all larval fates are important, in this example it was assumed that an ideal MPA, or network, would have a 3-way balanced split between larval fates, i.e.:

33.3% of larvae should be supplied outside of network

33.3% of larvae should be locally retained

33.3% of larvae should be supplied to other MPAs within the network.

Other target proportions could be allocated by policymakers if a particular quality should be deemed especially desirable.

The number of larvae supplied is important to recognise when considering the potential for the MPA to perform well. The number of MPAs supplied is a function of its importance within the network and contributes to network resilience. Supplying larvae to multiple MPAs means that protection can be maintained should any one MPA be adversely impacted.

However, a count of MPAs supplied alone is insufficient without an additional evenness measure, as weak links should not be considered on an equal footing to strong links. The supplier evenness metric was adapted from Simpson's Diversity Index (D) (Simpson, 1949).

$$D = \sum \left(\frac{n}{N}\right)^2$$

As with its traditional usage, this application of Simpson's D is heavily weighted towards the MPAs with the most larvae (akin to species dominance) but is not sensitive to the number of MPAs (akin to species richness (Magurran, 2004)). In this case n = the number of supplied larvae retained per MPA

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along a row of the dispersal matrix, and N = the total number of larvae supplied to any MPA (i.e. row totals from the dispersal matrix), the summation providing a row/MPA-source-specific index. Simpson's index is expressed here as 1/D in order that more even dominance gives a higher index.

Individual MPA retainer performance was assessed under the following criteria:

- Number of larvae captured/retained

- Number of MPAs supplying larvae

- Evenness of retainer's suppliers (this time using column-wise totals and summations in 1/D)

For MPAs that were both retainer and supplier, two final assessment metrics were calculated:

- A rating as a net source or sink based on the proportion of supplied larvae replaced by retention (inclusive of local retention).

- An average of supplier and retainer rankings providing a final performance ranking.

MPA networks

An overall MPA network assessment was calculated for each of the sub-networks (Irish, NEAFC, UK) and the combined regional network. This was based on the assumed ideal larval fates (i.e. proportions of MPA released larvae which were lost to outside the network, stayed within supplier MPAs, and were retained within the network) again using a 3-way balance split as an example target.

3.0 Results

3.1 MPA assessment

The combined matrix of all simulations across all years, depths, and larval modes is shown in Fig.2a. Larval flow appeared to be predominantly northwards, both in the Rockall Trough (white rows) and the Hatton Rockall Basin (HRB, grey rows) (i.e. high larval counts were generally to the left of the local retention diagonal boxes). Flow between the HRB and the Rockall Trough mainly came from Hatton Bank (MPA number 21, in Fig. 1a and 2b) and West Rockall Bank (MPA 27) flowing east, and East Rockall Bank (MPA 5) and the Logachev Mounds (MPA 15) flowing west. The majority of MPAs in the wider network performed well, with released larvae spreading to an average of seven other MPAs, including an average of three strong (upper quartile) connections.
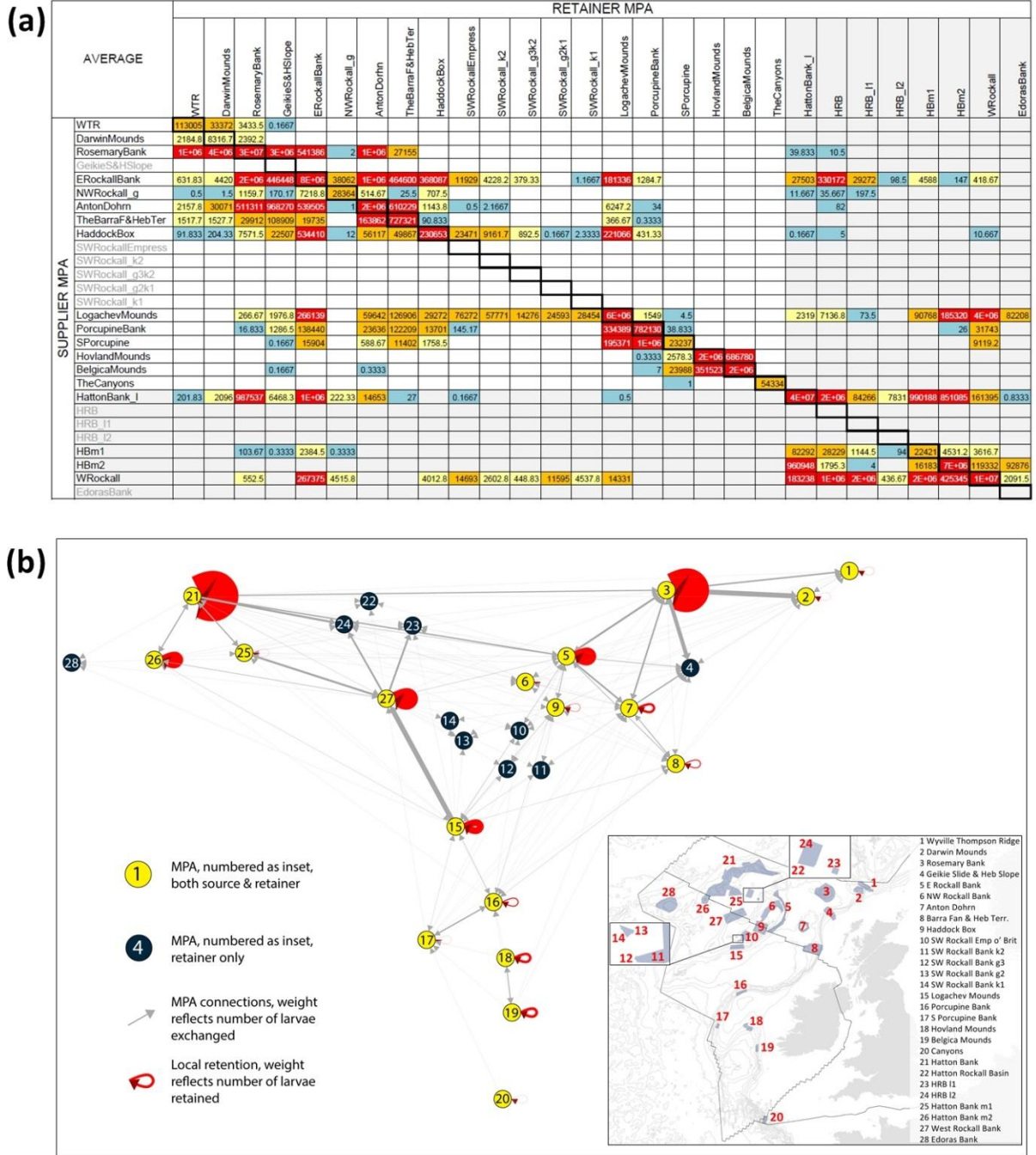
(a) AVERAGE — RETAINER MPA / SUPPLIER MPA

SUPPLIER MPA \ RETAINER MPA	WTR	DarwinMounds	RosemaryBank	GeikieS&HSlope	ERockallBank	NWRockall_g	AntonDohrn	TheBarraF&HebTer	HaddockBox	SWRockallEmpress	SWRockall_k2	SWRockall_g3k2	SWRockall_g2k1	SWRockall_k1	LogachevMounds	PorcupineBank	SPorcupine	HovlandMounds	BelgicaMounds	TheCanyons	HattonBank_I	HRB	HRB_I1	HRB_I2	HBm1	HBm2	WRockall	EdorasBank
WTR	113005	33372	3433.5	0.1667																								
DarwinMounds	2184.8	8316.7	2392.2																									
RosemaryBank	1E+06	4E+06	3E+07	3E+06	541386		2	1E+06	27155												39.833	10.5						
GeikieS&HSlope																												
ERockallBank	631.83	4420	2E+06	446448	8E+06	38062	1E+06	464600	368087	11929	4228.2	379.33		1.1667	181336	1284.7					27503	330172	29272	98.5	4588	147	418.67	
NWRockall_g	0.5	1.5	1159.7	170.17	7218.8	28364	514.67	25.5	707.5												11.667	35.667	197.5					
AntonDohrn	2157.8	30071	511311	968270	539505	1	2E+06	610229	1143.8	0.5	2.1667				6247.2	34							82					
TheBarraF&HebTer	1517.7	1527.7	29912	108909	19735		163862	727321	90.833						366.67	0.3333												
HaddockBox	91.833	204.33	7571.5	22507	534410	12	56117	49867	230653	23471	9161.7	892.5	0.1667	2.3333	221066	431.33					0.1667	5					10.667	
SWRockallEmpress																												
SWRockall_k2																												
SWRockall_g3k2																												
SWRockall_g2k1																												
SWRockall_k1																												
LogachevMounds		266.67	1976.8	266139			59642	126906	29272	76272	57771	14276	24593	28454	6E+06	1549	4.5				2319	7136.8	73.5		90768	185320	4E+06	82208
PorcupineBank		16.833	1286.5	138440			23636	122209	13701	145.17					334389	782130	38.833									26	31743	
SPorcupine			0.1667	15904			588.67	11402	1758.5						195371	1E+06	23237										9119.2	
HovlandMounds																0.3333	2578.3	2E+06	686780									
BelgicaMounds			0.1667				0.3333										7	23968	351523	2E+06								
TheCanyons																				54334								
HattonBank_I	201.83	2096	987537	6468.3	1E+06	222.33	14653	27	0.1667						0.5						4E+07	2E+06	84266	7831	990188	851085	161395	0.8333
HRB																												
HRB_I1																												
HRB_I2																												
HBm1			103.67	0.3333	2384.5	0.3333															82292	28229	1144.5	94	22421	4531.2	3616.7	
HBm2																					960948	1795.3	4		16183	7E+06	119332	92876
WRockall		552.5			267375	4515.8		4012.8	14693	2602.8	448.83	11595	4537.8	14331							183258	1E+06	2E+06	436.67	2E+06	425345	1E+07	2091.5
EdorasBank																												

(b) Visualisation of MPA network connections (legend):

- 1 = MPA, numbered as inset, both source & retainer
- 4 = MPA, numbered as inset, retainer only
- arrow = MPA connections, weight reflects number of larvae exchanged
- loop = Local retention, weight reflects number of larvae retained

Inset list:

1 Wyville Thompson Ridge
2 Darwin Mounds
3 Rosemary Bank
4 Geikie Slide & Heb Slope
5 E Rockall Bank
6 NW Rockall Bank
7 Anton Dohrn
8 Barra Fan & Heb Terr.
9 Haddock Box
10 SW Rockall Emp o' Brit
11 SW Rockall Bank k2
12 SW Rockall Bank g3
13 SW Rockall Bank g2
14 SW Rockall Bank k1
15 Logachev Mounds
16 Porcupine Bank
17 S Porcupine Bank
18 Hovland Mounds
19 Belgica Mounds
20 Canyons
21 Hatton Bank
22 Hatton Rockall Basin
23 HRB l1
24 HRB l2
25 Hatton Bank m1
26 Hatton Bank m2
27 West Rockall Bank
28 Edoras Bank

Figure 2 (a) Average MPA dispersal matrix and **(b)** Visualisation of MPA network connections. **(a)** Numbers recorded within the matrix are the number of larvae supplied from the supplier MPA (left-hand axis) to the retaining MPA (top axis) averaged across years and larval modes. Read the matrix left to right to judge an MPA as a supplier, or top to bottom to judge an MPA as a retainer. Diagonal boxes represent local retention (larvae supplied from and retained in the same MPA). Colours are based on the matrix's larval count quartiles for ease of scaling whether a count is high or low relative to others in the matrix (Q): blue (or grey numbers <300) <Q1, yellow (or light) =Q1-Q2(median), orange (or grey numbers >8000) = Q2-Q3, red (or dark with white text) >Q3. MPAs are roughly ordered North to South, with grey shaded MPAs ordered N to S in the Hatton Rockall Basin (HRB) west of those in white. Supplier MPAs in grey text did not host any release locations based on the Ross *et al.* (2015) habitat suitability model but these MPAs are still eligible as larval retainers. **(b)** MPAs are numbered and configured as shown in Figure 4 (inset here for ease of comparison).

Yellow/light nodes represent MPAs which were both supplier and retainer, while dark nodes are retainer MPAs only. The strength of dispersal simulated connections are reflected in arrow width (average larval count/1 000 000) Circular arrows in red are local retention indicators also weighted by larval counts. Anton Dohrn Seamount (7) was ranked the best performing (both supplier and retainer) MPA overall, while The Canyons (20) performs the worst. The network diagram was created in R version 3.0.1 using the igraph library. The inset map was plotted in ArcGIS (v.10.3, http://desktop.arcgis.com/en/arcmap/) using GEBCO 30-arc-second bathymetry (http://www.gebco.net/) and projected in Albers Equal Area Conic with modified standard parallels (parallel 1 = 50.2°, parallel 2 = 58.5°). MPA shapefiles available from JNCC http://jncc.defra.gov.uk/protectedsites/SACselection/gis_data/terms_conditions.asp, NPWS https://www.npws.ie/maps-and-data/designated-site-data/download-boundary-data, and NEAFC http://www.neafc.org/closures/coordinates.

Table 1 (next page) MPA performance metrics. Measures of supplier (including local retention), and retainer performance are ranked (in grey columns) from 1 (best) to 18 (supplier performance) or 28 (retainer performance, inclusive of 10 MPAs which did not supply larvae). Best (green/dark grey) and worst (red/black) rankings are highlighted. Supplier performance rankings are: A number of larvae released, B % of larvae supplied Outside of Network (OoN), C % of larvae supplied to other MPAs , D the number of MPAs, E the evenness of supply across MPAs (adapted from Simpson's D), F % of larvae retained locally. Retainer performance rankings are: G average number of larvae retained from any supplier as a percentage of all larvae released, H average number of MPA suppliers, I evenness of MPA suppliers (adapted from Simpson's D). Supplier performance measures in % are ranked with 33.3% as the target (best) proportion. Final MPA metrics use a ratio of larval count retained to supplied to give a rating as average source or sink, with an average of rankings A-I providing the final MPA ranking. MPAs are ordered by the last column from best to worst performing MPA. MPAs which are retainer only are excluded from metrics inclusive of supplier performance data and are ordered by average retainer ranking from best to worst performing MPA.

MPA	Sub-network	MPA size		Supplier Performance												Av Rank	Retainer Performance							Av Rank	MPA Metrics netRating		Av Rank
				Released		OoN		MPAs				Local R					Retained			MPA Sup					Ratio	rating	
		K	Ra	#	A	%	B	%	C	#	D	Simp	E	%	F		Av#	%	G	#	H	Sim	I				
Anton Dohrn	UK	14	15	75690	1	38	2	35	2	16	6	3.7	1	26	3	4.2	51250	3.	7	1	4	3.3	2	4.3	0.7	source	4.25
W Rockall	NEAFC	51	5	36959	5	52	6	15	3	14	4	2.1	7	31	2	4.5	16124	10	3	9	7	1.7	1	8	0.4	source	6.25
The Barra F.	UK	43	6	20340	1	48	4	16	4	11	1	1.9	9	35	4	7.5	21397	1.	1	1	5	4	1	6.7	1.1	sink	7.1
E Rockall	UK	36	8	82791	2	83	1	6.	1	2	1	2.4	6	10	1	8	11888	7.	4	1	3	1.9	1	6.3	0.1	source	7.15
Rosemary	UK	69	2	75376	3	44	5	14	7	1	1	1.8	1	40	5	6.7	33942	22	2	1	1	1.2	2	8.3	0.5	source	7.5
Logachev	NEAFC	16	13	51119	4	78	9	10	8	2	2	2.4	5	11	1	6.5	67723	4.	6	9	7	1.3	1	10.3	0.1	source	8.4
Hatton Bank	UK/NEAFC	15	1	11772	1	63	8	5.	1	1	4	1.4	1	31	1	6.8	37760	25	1	9	7	1.1	2	11.3	0.3	source	9.05
Haddock	NEAFC	34	9	55080	1	79	1	16	5	1	3	3.4	2	4.	1	8	64942	0.	1	9	7	2.2	6	10.3	0.1	source	9.15
Porcupine	Ireland	73	19	28746	6	95		2.	1	1	7	2.8	3	2.	1	10.7	18384	1.	1	9	7	2	1	10.7	0.1	source	10.7
HBm1	NEAFC	14	14	23400	1	38	1	52	1	19		2.6	4	9.	1	8.8	28962	1.	1	6	1	2	9	13	12.4	sink	10.9
HBm2	NEAFC	61	3	15354	8	44	3	7.	9	7	1	1.3	1	48	1	9.8	88654	5.	5	7	1	1.4	1	12.3	0.6	source	11.05
NW Rockall	UK/NEAFC	43	7	45000		14	7	22	1	7	1	1.7	1	63		10.3	71179.	0	2	8	1	2.2	5	13.7	1.6	sink	12
Darwin	UK	13	16	70200	1	81	1	6.	1	3	1	2.1	8	11	9	12	42887	2.	9	9	7	1	2	14.3	61.1	sink	13.15
S Porcupine	Ireland	34	22	95310	1	86	1	13	6	9	1	1.5	1	0.	1	12.3	49848	0	2	6	1	2.2	7	16.3	0	source	14.3
Belgica	Ireland	51	21	15890	7	83	1	2.	1	6	1	1.3	1	14	7	12.2	30045	2	1	2	2	1.5	1	17.7	0.2	source	14.95
WTR	UK	17	12	38388	1	96	1	1	1	4	1	1.6	1	2.	1	14.7	14114	0.	1	9	7	1.2	2	15.7	0.4	source	15.2
Hovland	Ireland	10	18	12186	9	76	1	5.	1	4	1	1.6	1	18	6	11.8	25458	1.	1	2	2	1.3	1	19.3	0.2	source	15.55

Name	Region														
The Canyons	UK	66	20	43200	1 87 1	0	2 1	12 8	54333.8	0	2 1	1		0.1	source
Geikie S. &	UK	22	10						49533.557	3.	8 1	1.9	1	6.7	
HRB	UK	12	17						36893.2	2.	1 1 5	2.4	3	6.0	
Edoras Bank	NEAFC	58	4						17717	0.	1 4 2	2.0	8	16.0	
SW Rockall	NEAFC	20	11						12651	0.	2 7 1	2.4	4	13.0	
HRB l1	NEAFC	12	24	These MPAs do not supply larvae so cannot be assessed as suppliers					17515	1.	1 7 1	1.1	2	18.7	MPAs without supplier performance are not included in these metrics
SW Rockall	NEAFC	12	23						73766.	0.	2 5 2	1.6	1	18.7	
SW Rockall	NEAFC	34	26						32995.	0.	2 4 2	1.3	2	22.3	
SW Rockall	NEAFC	22	27						36188.	0.	2 3 2	1.8	1	21.0	
SW Rockall	NEAFC	14							15997.	0.	2 4 2	1.2	2	23.0	
HRB l2	NEAFC	42	25						8460.2	0.	4 2	1.2	2	24.3	

3.1.1 Individual MPA assessments

Individual MPA metrics, based on rankings of supplier and retainer performance, are shown in Table 1. Rankings B, C and F are based on proximity to 33.3% example proposed optima. A visualisation of MPA network connections is shown in Fig. 2b.

Anton Dohrn Seamount (MPA 7) had the best average ranking of all MPAs, being the joint best performing supplier MPA and best retainer. West Rockall Bank (MPA 27) followed as a close second and acted as the joint best supplier and 2rd best retainer. The Canyons (MPA 20) was the worst performing MPA overall by a wide margin, being both worst supplier and worst retainer.

Hatton Bank (MPA 21) has the best performing rate of both retention from any MPA supplier, and local retention; it is also the largest MPA and releases the most larvae. Larval retention ability (equivalent to rank G in Table 1) was correlated to MPA size (Pearson's r=0.81, n=28, p=<0.01) and MPA size was also correlated to MPA rank (Pearson's r=0.60, n=18, p=<0.01), with larger MPAs performing the best.

Four MPAs acted as net larval sinks (*sensu* Pulliam, 1988): the Barra Fan and Hebrides Terrace Seamount (MPA 8), Hatton Basin m1 (MPA 25), NW Rockall Bank (MPA 6), and the Darwin Mounds (MPA 2). The Darwin Mounds (MPA 2) retained 61 times more larvae than it supplied. The Barra Fan and Hebrides Terrace Seamount (MPA 8) was the closest MPA to having a balanced supply to retention ratio (1.05). Porcupine Bank (MPA 16) and South Porcupine Bank (MPA 17) benefitted the least from MPA network support, replacing <10% of their outgoing larval supply.

3.1.2 MPA network assessment

Network assessment metrics were calculated for each individual network and for the combined

wider network (Table 2). Based on an example ideal network criteria with the assumed ideal 33.3%

balance of larval fates, the UK network performs the best (average rank 1), followed by the NEAFC

closures (1.66), the combined network (3), and the Irish network (4). No

Table 2 Network assessment metrics.

Network	Total # larvae released	# supplier MPAs	# retainer MPAs	Network Assessment						
				Local retention %	Rank LR	Supply to other MPAs %	Rank MPA	Supply outside of network %	Rank OoN	**Av Rank**
UK	207090800	9	11	27.13	1	8.59	1	64.28	1	1
NEAFC	321923100	7	15	27.13	1	8.54	2	64.32	2	1.7
Combined Network	583181800	18	28	24.96	3	8.11	3	66.93	3	3
Irish	54167900	4	4	8.01		4.55		87.44		

In this study the ideal network would have a balance of 33.3% each to local retention (LR), supply to other MPAs, and supply outside of network (OoN). In line with Table 1, rankings are shown for each metric, highlighting the best (green) and worst (red) performing networks. Networks are sorted by their average ranking (final column) with the best performing network at the top and worst at the bottom.

network achieves the assumed ideal 33.3% balance, all networks displaying a heavy bias towards

supplying sites exterior to the network. Local retention rates were good for all except the Irish

network, which was comprised of only smaller than average sized MPAs (ranked 18, 19, 21, and 22

out of 28 for size). The proportion of supply to the rest of the network was best in the UK (8.59%),

but was still well below the 33.3% target.

3.2 Passive vs. active

Some qualitative difference was apparent when comparing the active (Fig. 3a) and passive (Fig 3b)

dispersal matrices. The five SW Rockall MPAs received only active larvae, predominantly from

Logachev Mounds and West Rockall Bank; East Rockall Bank made a solid (counts above median)

connection to NW Rockall Bank with active larvae; and West Rockall supplied six further MPAs with active larvae. However, the main differences between the predictions from the two larval modes reflected changes in the movement of small numbers of larvae (counts which are lower quartile or below median). Active dispersal in this study appears to promote higher diffusion of larvae, but local retention was not consistently higher for active larvae than for passive (cf. Cowen *et al.*, 2006), and
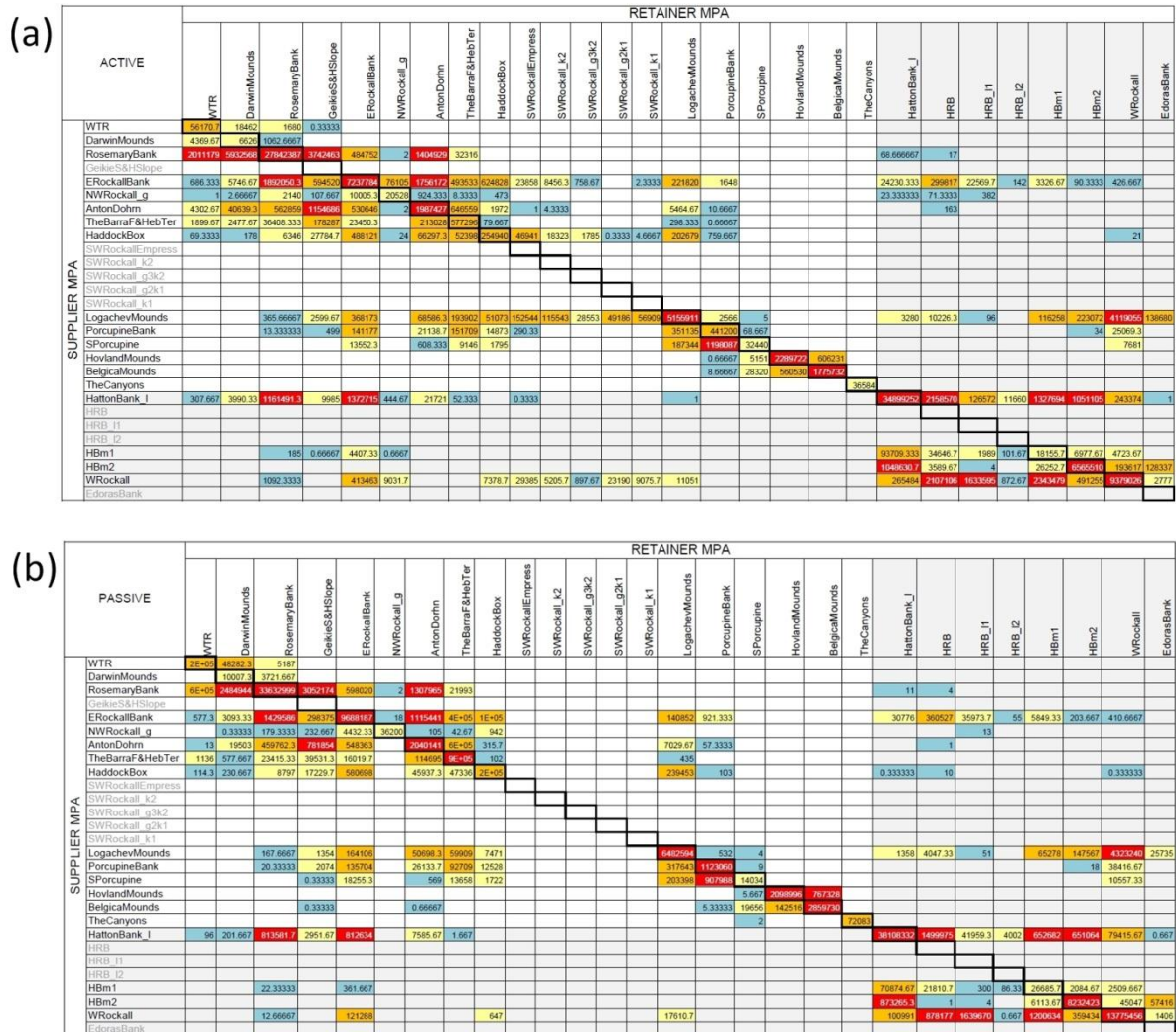
Figure 3 (a) Active and **(b)** Passive dispersal matrices.

Details for interpretation as in **Fig. 1a**, but larval counts are averaged over years only. Note the differences and similarities between these two matrices.
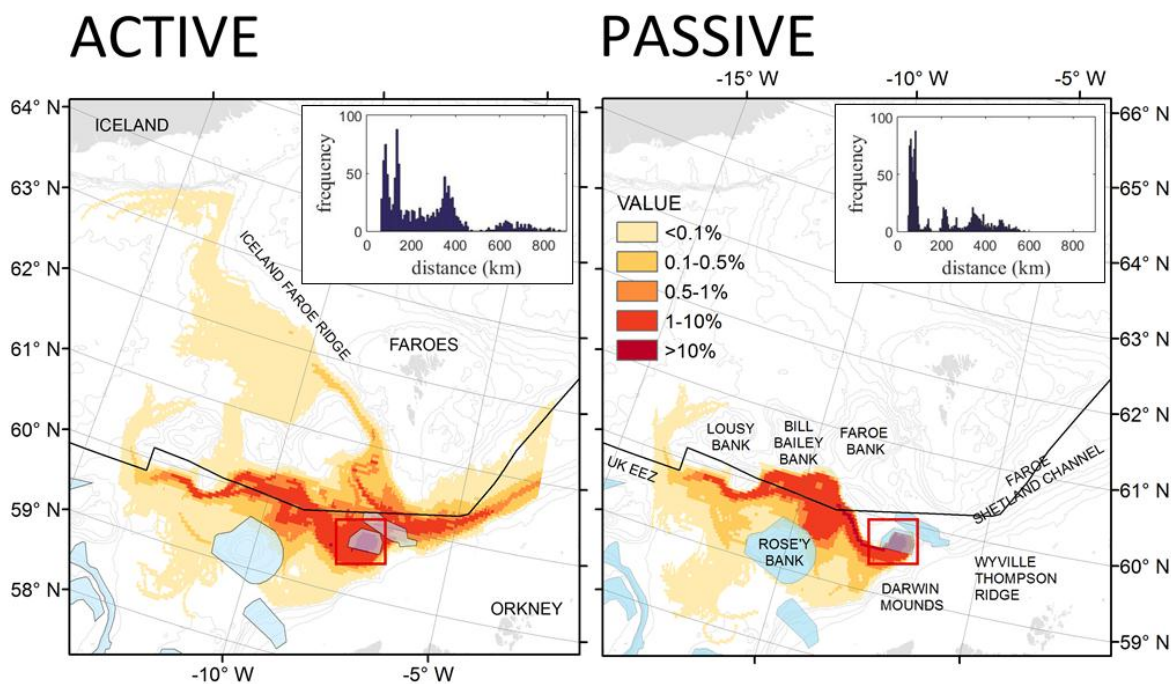
Figure 4 Passive vs Active dispersal from the Darwin Mounds MPA. Trajectory views of larval dispersal from the Darwin Mounds show that passive larvae are exported in high density along the ridge formed by Faroe, Bill Bailey and Lousy Banks. Active larvae are able to cross the Wyville Thomson Ridge allowing a reasonable density of larvae to disperse as far as the Iceland Faroe Ridge with some even reaching the Icelandic shelf. This difference is less detectable when only considering recruitment to MPAs within the study region (i.e. the main difference in the MPA dispersal matrix is that active larvae can also be recruited to Wyville Thomson Ridge MPA). MPA results also show that more passive larvae are retained within the MPA but the trajectory view shows that more active larvae are retained in the greater Darwin Mounds region (red box). This highlights the dependence upon definitions that may vary between studies. n = 70200 larvae released per larval mode. Insets show dispersal kernels created from simulated trajectories at the Darwin Mounds MPA demonstrating the difference in distance travelled by passive and active larvae. Maps were plotted in ArcGIS (v.10.3, http://desktop.arcgis.com/en/arcmap/) using GEBCO 30-arc-second bathymetry (http://www.gebco.net/) and projected in Albers Equal Area Conic with modified standard parallels (parallel 1 = 50.2°, parallel 2 = 58.5°). MPA shapefiles available from JNCC http://jncc.defra.gov.uk/protectedsites/SACselection/gis_data/terms_conditions.asp, NPWS https://www.npws.ie/maps-and-data/designated-site-data/download-boundary-data, and NEAFC http://www.neafc.org/closures/coordinates.

strong connections remained consistent with passive simulations. Kolmogorov-Smirnov tests

comparing both whole matrices and just local retention average counts confirmed no significant

difference between passive and active simulations (whole matrices, both naïve & bootstrap adjusted

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K.S test D = 0.0434 p = 0.4523; local retention only, both naïve & bootstrap adjusted K.S test D= 0.0714 p =1). However, if considering only mapped trajectories from the Darwin Mounds (Fig. 4), passive and active dispersal simulations appear to be considerably different. Passive larvae were constrained by the Wyville Thomson Ridge and adjoining banks, with all larvae transiting west and only connecting with Rosemary Bank MPA. Active larvae followed the same westward transit, but were also able to cross the Wyville Thomson Ridge allowing connection to its MPA. This facilitated some spread up the Faroe Shetland Channel to the North East, and to the North West towards Iceland along the Iceland Faroe Ridge. A greater number of larvae were retained within the region of the supplier MPA (marked with a square in Fig. 3), but in practice the average number of larvae retained within the MPA is lower for active larvae (Fig. 3a, 6 626 larvae) than for passive (Fig. 3b, 10 007 larvae).

Dispersal kernels of Darwin Mounds trajectories are shown in Fig. 4(inset). Passive dispersal was right skewed with the majority of settlement occurring near source (<100km dispersal distance) while others travelled up to 550km away likely settling in the region of Lousy Bank (Fig. 4, PASSIVE). Active dispersal was trimodal, with peaks at 100km, 150km and 350km and a maximal dispersal of nearly 900km. Each peak likely reflects the three dominant pathways of dispersal: some follow the passive dispersers westwards, while others cross the Wyville Thomson Ridge and either head NE up the Faroe Shetland channel or NW along the Iceland Faroe Ridge (Fig. 4, ACTIVE).

4.0 Discussion

4.1 MPA dispersal assessment

This study sought to use an example predictive dispersal model to demonstrate how to assess and rank the potential connectivity of an offshore network of existing MPAs. According to this model the MPA network appears to be well interconnected for this species (Fig. 2b). There were very few MPAs

that appeared isolated from the network, and all supplier MPAs were succeeding in locally retaining a proportion of their own larvae, which is positive for future resilience and persistence. However, the vast majority of larvae supplied from protected sites were lost or retained in unprotected areas. This may mean that the network is performing below its full potential, and could benefit from additional or expanded MPAs.

None of the MPAs achieved the suggested 33.3% target for mutual exchange of larvae. It is possible that in this survey area the large regions of unsuitable habitat, in the Rockall Trough and HRB, render this target unachievable due to the inevitable loss of larvae whilst crossing these divides. Larval exchange is already likely to be occurring across these basins between existing MPAs, and it is the best performing MPAs which are providing stepping stones to cross these dispersal barriers: Anton Dohrn (MPA 7; best) in the Rockall Trough, and West Rockall Bank (MPA 27; second best) in the HRB. The Canyons, in UK waters, was the worst performing MPA, as it is the most geographically isolated. Yet improving the connections to this MPA will fall under the jurisdiction of both Ireland and France due to the shape of EEZ boundaries and the underlying topography (Supplementary Fig. S1).

Generally, larger MPAs were found to be better performing, both in terms of their capacity for larval retention and in overall performance ranking. The UK network, which ranked the best of the networks, covers a lot of *L. pertusa*'s suitable habitat (Supplementary Fig. S1) and consists of large MPAs with reasonable area coverage. The Irish network has the greatest room for improvement, with only four relatively small MPAs situated on the continental slope.

The reality for *L.pertusa* is likely to be more complex than is demonstrated in this study. The species exists over a wide range of conditions and depths as solitary colonies, but the habitat is only suitable to form a biogenic reef under more specific conditions (Howell *et al.*, 2011). In order to consider where additional MPAs could be sited to support the network this must be taken into account in this study, but for species with narrower environmental tolerances, this may be done more simply (albeit

remembering that settlement, survival, etc. also remain excluded from predictions). Supplementary Fig. S2 integrates the additional depth range suited to the species but not the reef habitat, and considered in tandem with Fig. 2b, can highlight the areas with the potential to support the existing network. In this case, the huge area of Irish continental shelf that remains unprotected would benefit from further protection, particularly between Porcupine Bank and the Barra Fan and Hebrides Slope (which is in UK waters). This also agrees with recommendations made by Rengstorf *et al.* (2013) derived from their high-resolution *L. pertusa* reef model. The Goban Spur would also be a useful area to explore for future protection in order to better connect The Canyons (under UK jurisdiction) to the Irish network. Rengstorf *et al.* (2013) recommended the Whittard Canyon near this region as an alternative but the complex topography of another canyon feature may promote larval retention rather than larval exchange. The southernmost extent of Rockall Bank may also be a good area for protection in the future, providing support to the Logachev mounds as a stepping-stone for larvae transiting both the Rockall Trough and the southern HRB.

Note that not all MPAs in this study are designated for the protection of *L. pertusa* reef, nor may all release sites based on a habitat suitability model be shown to host a reef in reality. Yet these protected areas may still aid *L. pertusa* protection due to the greater range of conditions suited to solitary colonies, so these MPAs were still included. For those sites designated to protect other species or features, their performance for the protection of L. pertusa is less important but still plays a role in the ecological coherence of the wider network. There are also additional sites that do support *L. pertusa* which were excluded due to lack of access to data or inadequate representation in the model (e.g. The East Mingulay MPA is inshore and not well resolved in the topography of HYCOM).

4.2 Passive vs. active

This study found no statistical difference between passive and active MPA dispersal matrices. This finding is case study area specific and means that in this NE Atlantic region, when considering the

effectiveness of the MPA network, passive dispersal simulations could be adequate to assess dominant connections in the network and individual MPA performance, even when larvae are known to have vertical migrating abilities, or where no larval characters are known.

Many studies have been conducted examining the effect that behaviour may have upon dispersal, and this study's main finding is at odds with the literature that often reports increased local retention in active swimming larvae (Butler *et al.* 2011; Cowen *et al.*, 2006). Paris and Cowen (2004) realised that damselfish larvae used increased swimming ability to descend and stay in the bottom boundary layer if they were near suitable habitat. *L. pertusa* larvae may have this trait as well, with Larsson *et al.* (2014) observing positive geotaxis from day 21 of their PLD (Fig. S1), yet simulations showed no statistical difference between local retention counts in passive and active matrices. This finding is likely attributable to the spatial frame of reference used, and the fact that this study's test is designed to be relevant only to marine managers. The comparison of MPA matrices mean that the effect of larval mode is only being compared on the 8.11% of released larvae which were re-captured within the wider MPA network, thereby excluding the 92.89% of released larvae that settled in non-protected areas. A true ecological comparison would be better based on dispersal kernels or full spatial predictions such as those in Fig. 4.

The Darwin Mounds case study shows lower local retention in active simulations based on matrix analysis, but Fig. 3 shows a rectangle around an arbitrary 'local area' inclusive of the Darwin Mounds MPA where a comparison may have drawn the opposite conclusion: that larval retention increased when larvae were active. This highlights the difference between analysis methods that may be appropriate under different scenarios: while a dispersal kernel approach may be the most objective comparison, the dispersal matrix approach used in this study gives a result that is relevant to MPA design and management. It is interesting that such a difference in focus may result in a different conclusion, and cautions that a standard kernel based analysis may be more finely tuned than is necessary for an MPA network assessment.

This varying frame of reference is also an issue in the comparative literature. Young *et al.* (2012) compared larval modes based on median dispersal distances and dispersal kernels with 300km bins. Butler *et al.* (2011) used habitat polygons of varying size reflecting lobster nursery habitats as their areas of local retention (similar to this study's MPA polygon set-up). Edwards *et al.* (2007) considered theoretic multidimensional kernels consisting of location, month, direction, mean/min/max distance, and principle components.

However, the average similarity between passive and active simulation results on a network wide scale does not preclude site-specific variation. The dispersal matrices (Fig. 3) show that in the Haddock Box local retention increased by a third when larvae were active, but at Porcupine Bank retention was two thirds reduced. The results from the Darwin Mounds alone (Fig. 4) also demonstrate a site-specific effect of larval mode, concurrent with the aforementioned studies (Butler *et al.*, 2011; Edwards *et al.*, 2007; Young *et al.*, 2012).

A site-specific response is logical given the location-specific nature of topographic dispersal barriers: only some of those encountered by passive larvae can be overcome by larval vertical swimming ability. This observation is consistent with the variability observed in other studies (Edwards *et al.*, 2007; Young *et al.*, 2012).

While the local retention estimates were similar between larval modes in this study, there was an enhancement in distant dispersal with active larvae in the Darwin Mounds (Fig. 4, not tested at other sites), again paralleling the findings of Butler *et al.* (2011). Young *et al.* (2012) predicted that dispersal of deep sea fauna is more likely to be facilitated by vertical migration due to the potential access to faster currents in surface waters. Although this may not have been the case for the majority of larvae, the tail of the kernel, representing rare connections was extended for active larvae. These rare connections may be important for range extension, especially when there are occasional pulses containing larger cohorts of far ranging larvae which may be enough to sustain

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long range demographic connectivity (in the form of "the storage effect" *sensu* Warner and Chesson (1985)). The number of larvae required to make a demographic connection where the population can be maintained is both unknown and likely to be variable. It is liable to be conditional upon many factors not included in these simulations such as mortality, availability of suitable habitat and conditions, competition with other species (e.g. *Madrepora oculata* (Linnaeus, 1758), or *S. variabilis* below 1000m), survival rates, and settlement density. There is suggestion that the effect of rare connections for *L. pertusa* may be greater than many other species, due to the longevity of the species and of individual clones (Le Goff-Vitry *et al.*, 2004).

Note that the rare dispersal connections are conservative under these modelled scenarios; many oceanographic phenomena are not captured, especially if they are of small spatial or temporal scale, and there is therefore potential for additional larval density diffusive effects in reality. Indeed it is advisable to consider these model predictions as entirely stochastic, with the diffuse tail of the kernel representative of potential error rather than deterministic outcomes of larval fates (Ross *et al.*, 2016, In Review.)

4.3 Ground truthing and hypotheses

At present, all of the local advice offered by this study should be taken as tentative. Modelled results are uncertain until ground truthed to ensure that predictions are reflecting reality and to quantify the margin of predictive error.

Preliminary groundtruthing can be conducted in comparison to local oceanographic (see Ross *et al.* 2016, *In Review*) and biological literature. In this case, HYCOM was selected after comparison to another model (Ross *et al. In Review*), with their performance judged against published oceanographic observational literature (Holliday *et al.* 2015; Holliday & Cunningham, 2013). *L. pertusa* results were compared to Le Goff-Vitry *et al.*'s (2004) genetic connectivity study in the NE Atlantic. Of the sub-populations sampled, they detected some structure between the continental

slope sites relevant to this study, indicating only a moderate flow of genes between sites. They also note a high degree of local retention at the Darwin Mounds and Hovland Mounds, concurrent with local retention rankings in this study. Becheler *et al.* (2015) also conducted a population genetic study on *L. pertusa* in French canyons suggestive of limited structuring but relative panmixia. Both of these studies are in agreement with this study's broader findings suggesting connection between all MPAs but at low levels.

A more comprehensive population genetic study for this case study is forthcoming. Studies integrating marine genetic and dispersal modelling data have proven successful and may be useful to marine managers and ecologists in the future (Foster *et al.*, 2012; Sunday *et al.*, 2014). There is some mismatch in timescales and survival parameters when comparing these types of data (Levin, 2006; Liggins *et al.*, 2013; Metaxas & Saunders, 2009), but advice is available for undertaking and optimising such a cross-comparison (Liggins *et al.*, 2013). Discordance in results can also be informative in diagnosing areas where hydrography is not the only factor driving population structure (Foster *et al.*, 2012; Galindo *et al.*, 2006).

In the meantime, the local results could be used to generate hypotheses for testing with future genetic data. For example, Wyville Thomson Ridge and the Darwin mounds are predicted to receive more than 90% of their larvae from Rosemary Bank, and the Geikie Slide & Hebrides Terrace nearly 70%. Should any of these sites show limited relationship to Rosemary Bank larvae, this could disprove the predictions made by these models. If model predictions are sound then checks can be made of larval modes, e.g. if a large proportion of recruits in NW Rockall Bank originate from E Rockall Bank, larvae may have been vertically migrating.

4.4 Conservation future

This study shows how larval dispersal models could be used to generate a dispersal assessment of an existing MPA network. The results of this case study provide a first assessment of the performance of

the wider NE Atlantic offshore MPA network with regard to its capacity to support dispersal (Foster *et al.*'s (2017) recent study cover other aspects of the region's ecological coherence). As this study is based on a species that is a major constituent of conservation-targeted habitats, the dispersal patterns of this species are critical to the functioning of the example MPA network. A similar approach is advised when first assessing any network, running simulations for a "keystone" species, or several, critical to the conservation objectives of the network. At a later date more predictions can be made for other species, but it is advisable to undertake some form of groundtruthing of initial predictions to ensure that the hydrodynamic model and species characteristics used as inputs to the model have sufficient predictive power to be deemed informative.

While the networks explored in this study are international, it is clear there is still something lacking in the field of international collaboration in marine conservation. Ardron's (2008) 'ecological coherence' criteria explicitly mention that protection should be extended across the protected species/habitat's natural range. This is justification for considering the wider network, but realistically nations will tend toward considering only their own area of jurisdiction. *L. pertusa* occurs and forms reefs throughout the North Atlantic Ocean, so a truly ecologically coherent network would span many nations' EEZs and the high seas from the Caribbean to Norway. International collaboration is taking place in this study area, under the aegis of OSPAR, the EU's Habitats Directive (including the Natura 2000 international network of protected areas), and the NEAFC , but much more collaboration must occur before ecological coherence can be attained, e.g. France is yet to designate offshore MPAs in the Bay of Biscay.

The results of this study demonstrating a similarity between passive and active dispersal in this region may allow these estimates to be suitable to many more species than previously thought, however differing release depths and PLDs will have an effect on how universally these assessments can be applied (Ross *et al.*, 2016). Hilario *et al.* (2015) suggest that 50% of deep water species have a PLD of 35days or less, putting *L. pertusa* in the 3rd Quartile of known deep sea PLDs. Future work in

this region should therefore go towards testing the limits of the existing NE Atlantic network and its ability to support species with shorter PLDs. The predicted low proportion of *L. pertusa* larvae being exchanged between networked sites, is unlikely to improve for species with shorter PLDs. Furthermore, the small MPAs (corresponding with some of the weakest performing MPAs in this study) may be unable to conserve multiple generations of short distance dispersing species – an issue highlighted by Shanks *et al.* (2003) and Botsford *et al.* (2001).

Acknowledgements

Author Contributions

RER conceived of the idea, undertook the analysis, and wrote the manuscript; KLH provided editorial support to manuscript writing; WAMNS and KLH supervised the work offering advice and revisions.

Competing Financial Interest Statement

Conflicts of interest: none.

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Highlights

- A method is proposed for assessing an existing MPA network's dispersal potential
- Passive and active (vertically migrating) larval dispersal is compared
- Large MPAs central to the network performed the best
- <10% larvae were supplied to other MPAs in all three tested networks
- Larval behaviour had a site-specific effect, but was not different at network-scale