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Investigating the role of larval dispersal models in the development of an 'ecologically coherent' network of deep sea marine protected areas

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INVESTIGATING THE ROLE OF LARVAL DISPERSAL MODELS IN THE DEVELOPMENT OF AN 'ECOLOGICALLY COHERENT' NETWORK OF DEEP SEA MARINE PROTECTED AREAS

By

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Author's declaration

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Publications:

- Work from Chapter 1 was included in the publication: Hilário *et al.* 2015 Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. Frontiers in Marine Science 2, 6. doi:10.3399/fmars.2015.00006
- Chapter 2 has been submitted to the Public Library of Science (PLoS ONE) journal and has recently been resubmitted after revision. Ross, Nimmo-Smith and Howell. Increasing the depth of current understanding: Sensitivity testing of deep sea larval dispersal models for ecologists.

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- Chapter 4 will be ground truthed then prepared for submission to a conservation journal compliant with NERC open access requirements.

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- 14th International Deep sea Biology Symposium, Aveiro, Portugal, August 2015. Keynote oral presentation. "Lagrangian model wars: comparing predictions of deep sea larval dispersal".
- International Marine Conservation Congress, St John’s, Newfoundland, Canada. July/August 2016. Oral presentation. “Using larval dispersal models to answer questions about offshore MPA network connectivity”.
- Many internal MBERC and MPRG seminars given and attended.

Research Cruises during PhD:

- MRV Scotia, Wyville Thomson Ridge and Faroe Shetland Channel, October 2012, cruise ref 1512S, 2 weeks.
- RV Celtic Explorer, Hatton Rockall Basin, Porcupine Bank and Porcupine Seabight, July 2015, cruise ref CE15011, 3 weeks.
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Abstract

INVESTIGATING THE ROLE OF LARVAL DISPERSAL MODELS IN THE DEVELOPMENT OF AN 'ECOLOGICALLY COHERENT' NETWORK OF DEEP SEA MARINE PROTECTED AREAS

Rebecca Eleanor Ross

There is currently worldwide pressure to establish Marine Protected Area (MPA) networks which are self-sustaining and will persistently protect habitats and species. In order for MPA networks to be effective, the species targeted for conservation must be able to disperse between protected areas and maintain a gene-flow necessary for population sustainability and persistence. This warrants new research on how to quantify and map faunal dispersal to ensure that protection will be effective and sustainable.

Population genetic methods have merit, with the ability to track parentage and gene flow between areas directly. However the costs, quantity of samples, and time required to genetically quantify dispersal for multiple species make these approaches prohibitive as the only method of assessment, especially in relatively inaccessible offshore waters. Dispersal modelling is now becoming more accessible and may fulfil immediate needs in this field (although ground truthing will be necessary in the future).

There have been very few dispersal modelling studies focussed on deep sea or offshore areas, predominantly due to the lack of high resolution hydrodynamic models with sufficient

geographic extent away from shore. Current conclusions have been drawn based on shallow water coastal studies, informing offshore MPA network size and spacing. However the differences between these two environments may mean that dispersal abilities are not comparable. Deep water receives less influence from wind and weather, and the scales are vastly different in terms of a) the depth ranges covered, b) the planktonic larval durations (PLDs) of animals, and c) the geographic areas concerned as a consequence.

Global hydrodynamic models with reasonable resolution are now becoming more accessible. With the outputs from these models, and freely available particle simulators, it is becoming more practical to undertake offshore deep water dispersal studies.

This thesis aims to undertake an analysis of these accessible modelling tools within a deep sea context. The guidelines which are currently available to dispersal modellers are yet to encompass the needs of deep water modellers which may require some additional considerations given the extended depth range covered and the different hydrodynamic drivers away from the air/sea interface.

Chapter 1 reviews the larval dispersal process, the factors which may affect dispersal success, and those which should be incorporated into future predictions of dispersal. The current methods for assessing larval dispersal are explored covering genetics, elemental tagging and modelling approaches with an extended look at modelling considerations. Existing marine conservation policy is also touched on in the context of connectivity and larval dispersal.

Chapter 2 is designed to inform future deep sea modellers on how to parameterise and understand a dispersal model. As models appear as a ‘black box’ to the majority of users, sensitivity tests can offer a way of scaling model inputs and tempering expectations from model outputs. A commonly used model pairing (the HYCOM hydrodynamic model and the Connectivity Modeling System) is assessed, using parameters which link to the temporal and spatial scales of mixing in the modelled system: timestep of particle tracer, horizontal and vertical positioning of release points, release frequency of larvae, and temporal range of simulation. All parameters were shown to have a decreased sensitivity with depth, with patterns reflecting local watermass structure. Future studies observing similar hydrodynamic conditions seeking to optimise their model set up would be advised to stratify their model release locations with depth. A means to incorporate all sensitivity test results into optimal input parameters for future studies is demonstrated.

Chapter 3 investigates whether dispersal models provide any advantage over a “sphere of influence” estimate based on average current speeds and PLDs: there is no use pursuing dispersal modelling if the outputs are too erroneous to provide any advantage over a back-of-the-envelope calculation. This chapter examines the outputs of two dispersal models driven by two different hydrodynamic models in order to observe the variability in prediction between models. This model comparison revealed a greater disparity between hydrodynamic model predictions than has been previously understood by ecologists. The two models compared (POLCOMS and HYCOM) may equally be considered as suitable to promote realism in the study region, but slight differences in resolution and numerical error handling resulted in dispersal predictions from which opposing conclusions can be drawn. This chapter therefore emphasises the necessity for model ground truthing before predictions can be trusted.

Chapter 4 assimilates the findings of the previous chapters and applies their advice to a study of MPA network dispersal connectivity. Using the hydrodynamic model which performed best in chapter 3 (HYCOM), a simulation was undertaken for cold water coral (*Lophelia pertusa* (Linnaeus 1758)) larval dispersal between already established MPAs in the NE Atlantic. As larval characters have only been observed *ex situ*, dispersal was simulated using two null models (passive and active vertical migration) and averaged to provide an intermediate prediction. A method for assessing dispersal within MPAs and MPA networks is offered based on the intermediate prediction, as well as a network wide assessment of the difference in dispersal patterns for passive and active larvae. It was found that the existing network performs well at supplying larvae to non-networked sites, but performs poorly at supplying other MPAs. The ‘best’ MPAs were central to the network and facilitated the traverse of regional gaps in

suitable habitat. The ‘worst’ MPAs were peripheral to the network and small in size. Network-wide passive and active dispersal matrices had no significant difference between them. However site specific variability in the effect of vertical migration was detected subject to variability in local topographic barriers to dispersal, only some of which could be surmounted with vertical migration.

All chapters aim to inform future deep sea dispersal modellers, and encourage exploration of this tool in other contexts, as well as marine conservation. The thesis cautions against the transplantation of shallow water assumptions to deep water environments, and advocates region specific studies and mandatory ground truthing of predictions. An upcoming study will ground truth the findings of this thesis with both genetic and oceanographic data, allowing the accuracy of study results to be quantified.

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1. Introduction

The deep sea remains the least known ecosystem on earth and yet it is facing increased anthropogenic pressures (Ramirez-Llodra *et al.* 2011) both through direct exploitation (e.g. bottom trawl fisheries (Roberts 2002, Gianni 2004, Norse *et al.* 2012, Pusceddu *et al.* 2014, Clark *et al.* 2016), and deep sea mining (Collins *et al.* 2013, Moskvitch 2014, Wedding *et al.* 2015)) and through indirect impacts (e.g. pollution (Ramirez-Llodra *et al.* 2011, Mestre *et al.* 2014, Pham *et al.* 2014, Woodall *et al.* 2015) and climate change (Glover and Smith 2003, Maier *et al.* 2009, Jones *et al.* 2014)).

As a result deep sea animals are facing rapidly changing environmental conditions and fragmentation or degradation of habitats on top of natural biotic and abiotic pressures but we are as yet unaware of their resilience to these changes (Ramirez-Llodra *et al.* 2011). It is therefore imperative that we increase our knowledge and understanding of this environment in order that appropriate management decisions can be made to balance our inevitable exploitation and minimise our impact on biodiversity.

A major gap in our understanding of deep sea ecosystems is in population ecology and the ability of deep sea species to disperse. There are many functions of dispersal: to increase genetic diversity and avoid interaction with kin, to increase the chance of offspring reaching favourable conditions, or to escape unfavourable conditions including overcrowding and habitat quality (Matthysen 2012), but the result is an expansive structured population with consequences for species survival and evolution.

Knowledge of dispersal is imperative for current efforts in marine conservation (Gaines *et al.* 2003). Conservation policy, in many guises (e.g. locally the Convention on Biological Diversity (CBD 2010), the OSlo-PARis Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR 2003), the Marine Strategy Framework Directive (MSFD 2008) and the European Commission Habitats Directive (1992)), all stipulate (using different terminology) the need to ensure that Marine Protected Areas (MPAs) are established in networks which promote self-sustaining conservation of multiple species. This necessitates knowledge of dispersal to ensure that MPAs are designated in a network with appropriate siting and spacing to allow the target species to travel between protected areas and maintain genetic diversity sufficient to ensure the survival of the species without relying on unprotected sub-populations.

This thesis aims to contribute to our understanding of the dispersal ecology of non-vent/seep deep sea benthic invertebrates, especially with a view to aiding marine conservation. Adult life stages are relatively immobile so these animals rely upon a microscopic larval phase for dispersal (and to a lesser extent gametes and post-larvae). The decision to omit vent and seep biota is based on this already being a well explored specialism (see e.g. Mullineaux and France 1995, Vrijenhoek 1997, Tyler and Young 1999, 2003, Mullineaux *et al.* 2005, Adams *et al.* 2010, Vrijenhoek 2010, Adams *et al.* 2012, Yorisue *et al.* 2013, Beedessee *et al.* 2013, Arellano *et al.* 2014, Roterman *et al.* 2016), with “average” deep sea biota being largely ignored in this field. This introductory chapter will investigate our current knowledge of the dispersal process in non-vent deep sea benthic invertebrates and the methods which can be used to investigate it.

1.1 Larval dispersal

Classically populations in the marine environment were thought to be panmictic: there were no geographic barriers to dispersal as there is on land, and the existence of planktonic dispersal phases could allow currents to carry organisms around the globe (Cowen *et al.* 2000). There is still evidence of some well mixed populations in both shallow (Mora *et al.* 2011) and deep water (Clague *et al.* 2011, Etter *et al.* 2011, Wieman *et al.* 2014), but we now know this is far from a rule – there are frequent barriers to dispersal in the form of changing environmental conditions and retentive oceanographic processes (Treml *et al.* 2015, Kleypas 2015), and populations are less dispersive than originally perceived, even in the case of highly motile species (Cowen *et al.* 2006, Gallindo *et al.* 2006, Ayata *et al.* 2010, Foster *et al.* 2012).

Tracking dispersal pathways of mobile species may be complex, but tracking microscopic larvae poses obvious scale related barriers to in situ observation (Havenhand 1995, Levin 2006, Cowen *et al.* 2007, Kool *et al.* 2013). Current knowledge of marine larval dispersal can be broken down into three stages: release, transport, and settlement. Each stage is discussed here to gain an overview of the factors for consideration when investigating dispersal, and the scales of complexity which can potentially be encountered.

1.1.1 Release

At the most basic level dispersal ability is defined by a species' larval mode: brooders are restricted to an entirely benthic life cycle and are considered the least capable of distant dispersal (Gage and Tyler 1991). Planktonic larval forms have a much larger capacity for dispersal, due to their potential for hydrographic transport (Thorson 1950, Vance 1973). Contrary to Thorson's Rule that energetic and reproductive requirements would make non-planktonic forms dominate (Thorson 1950), all shallow water larval modes have been found to exist in the deep sea (Young 1994). It is still under debate whether some species may have more than one larval mode, known as 'poecilogony'. O'Hara *et al.* (2014) found that a species of ophiuroid known to be a brooder is able to disperse to seemingly isolated habitat fragments, suggesting planktonic larvae may occasionally occur, enhancing dispersal ability. Ellingson and Krug (2015) discovered that a species of nudibranch known to have both planktonic and aplanktonic larvae were related across sites and larval types, although mitochondrial lineages are appearing to diverge suggesting that poecilogony may be driving reproductive isolation and speciation in this species. The apparent rarity of this state may indicate that its occurrence is usually a sign of species divergence.

Planktonic larval forms are traditionally classified into two different nutritional modes: planktotrophic larvae are reliant upon an exogenous food supply and are small with the capacity to grow at various rates dependent upon food supply (Thorson 1950); lecithotrophic larvae carry their own energy supply, often in the form of a yolk mass, making them larger and unable to feed on external food sources, with a more predictable rate of growth (Thorson 1950). Although treated as a dichotomy there is evidence of a continuum of maternal provisioning and quantity of exogenous food requirements, such as the existence of facultative feeders that can eat during their pelagic phase but do not need to (see Allen and Pernet (2007) for a review of the potential intermediate nutritional modes).

Nutritional mode may have an influence on the fecundity of the species. Due to maternal energy costs it is broadly thought that planktotrophs can release large numbers of eggs to counteract mortality, while lecithotrophs invest more energy per egg to the detriment of fecundity (Gage and Tyler 1991, Young 2003). However two species of galatheid crustaceans from the genus *Munidopsis,* with similar egg size and therefore probably the same nutritional mode, were found to have fecundities of 13eggs and 294eggs respectively suggesting high variability is possible (Van Dover *et al.* 1985, Young 2003). Fecundity amongst planktonic developers in the deep sea can range from tens to hundreds of thousands of eggs, although evidence is limited as to how many mature and are released into a larval cohort (Young 2003).

The bottom boundary layer (BBL) represents the initial interaction with the water column, and the area with frictional influence from the topography (Jumars *et al.* 2001). As a result the immediate interface (on a scale of centimetres) with the seafloor presents as a viscous sub-layer where horizontal velocity is proportional to the Coriolis parameter, giving it the capacity to trap larvae and other particulate matter (Gage and Tyler 1991). Quinn and Ackerman (2015) showed the capacity for bottom roughness at this distance to have additional retentive properties relevant to gametes and larvae. However gametes and larvae are often released from a raised position, and anything with a grain size greater than one third the thickness of the sub-layer can likely induce a turbulence sufficient to induce mixing (Gage and Tyler 1991). Beyond the viscous sub-layer the BBL logarithmically increases in horizontal velocity, resulting in a layer of intense vertical mixing, strong shear currents and varying velocities (Pepper *et al.* 2015), with turbulence increasing with rough topography (Gage and Tyler 1991, Rahm and Svensson 1989). Although horizontal current velocities may be sufficient to overpower the limited swimming capacity of a larva, turbulent fluctuations in flow velocity have been found to be of a comparable magnitude to larval swimming capacity allowing swimming larvae to vertically adjust their position in the BBL and potentially reach the free-flowing currents above (Jumars *et al.* 2001).

Larval buoyancy will also affect the ability to escape the BBL. Negatively buoyant relatively passive larvae will likely be entrained within the benthic boundary layer which may reduce their dispersal potential (Jumars *et al.* 2001). However this may be advantageous to some species, especially those restricted to ephemeral habitats such as the bone-eating worm *Osedax* spp.: entrainment in the BBL can maximise contact with the seabed, minimise dilution away from other members of the species, and ensure retention within an area of the water column where chemo-kinetic responses may be possible, although increased encounters with suspension feeding predators is also likely (Jonsson *et al.* 1991). Some shallow water species are known to utilise the flow in the BBL using “sails” such as mucous or byssal threads (Jumars *et al.* 2001).

Buoyancy is thought to be governed by maternal provisioning. Villinski *et al.* (2002) found high concentrations of wax esters only in buoyant pelagic lecithotrophic gastropod larvae, with equivalent planktotrophs found to have reduced levels of wax ester and negative buoyancy. Relatively few deep sea species have been investigated in terms of their buoyancy and the universality of buoyancy versus larval mode has not been tested (Young *et al.* 2012).

Seasonality of reproduction may also affect dispersal ability insofar as there being the potential to profit from seasonal hydrographic conditions or food availability. Seasonality was never expected of deep sea organisms, but expectations changed with the discovery that particulate matter from the surface can reach the seafloor and therefore periodicity in organic flux can occur (Rowe and Staresinic, 1979, Deuser and Ross, 1980, Scheltema, 1994, Tyler *et al.* 1994), while benthic storms and turbidity currents can periodically alter seafloor conditions (Hollister and McCave, 1984, Tyler *et al.* 1994, Harris 2014). Now many deep sea species are known to have seasonal reproductive cycles, often attributed to seasonality in phytodetritus fall from the surface (Gage and Tyler, 1991, Tyler, 1988, Tyler *et al.* 1994). However only opportunistic species with rapid reproductive cycles have been found to be able to synchronise with food availability (Brooke and Järnegren 2013). For species-specific information Young (2003) provides a summary of known life history traits among deep sea invertebrates including egg size, fecundity and seasonality of reproduction.

1.1.2 Transport

While size and swimming ability of larvae may vary, ocean currents are the dominant driver of dispersal. Hydrodynamic parameters affecting dispersal operate on a number of scales, in space, time and complexity, the importance of which needs to be determined in the context of the location, depth and disperser being studied.

At a simplified level, hydrodynamics can be considered in terms of stratification and currents. The deep ocean is stably stratified, with slower currents driven by horizontal density/pressure differences, while currents in shallow waters are driven by wind stress and tidal forcing. Water masses comprise the strata of the deep sea, harbouring different densities, temperatures and chemistries dependent upon when and where they were formed or modified. These differing conditions can affect the environmental tolerances of a larva limiting its distribution to within water mass boundaries (Copley *et al.* 1994, Young *et al.* 1996a, 1996b, Arantes *et al.* 2009, Miller *et al.* 2011). Between water masses the pycnocline (density gradient) can create a physical barrier, or retentive mechanism, to larvae who are small enough (<10mm) to be affected by differing viscosity/buoyancy force ratios (Richardson Numbers) (Yick *et al.* 2009, Ardekani and Stocker, 2010, Doostmohammadi *et al.* 2012). Neighbouring water mass currents may differ in both velocity and direction (Fiksen *et al.* 2007).

The scale of relevance to the larva is much finer though, and the complex mesoscale, sub-mesoscale, and small scale oceanographic phenomena are likely to perturb any estimates based on synoptic scale phenomena. Ocean fronts create barriers to horizontal transport equivalent to a pycnoclines, although flow-based physical barriers can also form here (Possingham and Roughgarden, 1990, Gaylord and Gaines, 2000, Sponaugle *et al.* 2002). Eddies can be formed at ocean fronts or where geostrophy is destabilised (baroclinicity) aiding vertical transport or filamentation resulting in aggregations of larvae between eddies with heightened densities and velocities (Bécognée *et al.* 2009, Harrison *et al.* 2013). Areas of upwelling where surface waters are blown aside may aid vertical transport of larvae found within a deeper water mass, although changes in pressure may be adverse to survival (Young *et al.* 1996b, Harrison *et al.* 2013).

Topography may also have a substantial effect on oceanographic phenomena. Flow modification varies with height, shape, location, and water properties (White *et al.* 2007, Lavelle and Mohn 2010), but topography will always impact upon local oceanography (White *et al.* 2005). At a mid-ocean ridge strong along ridge currents may make passive transport faster at depth (McGillicuddy Jr. *et al.* 2010). Seamounts and banks have been found to cause tidal amplification, internal tide generation, trapped waves, current deflection, isopycnal doming, eddy dissipation and collision, or enhanced vertical mixing (White *et al.* 2007, Lavelle and Mohn 2010). Fieberling seamount was found to display tidal rectification and doming of isopycnals characterised by down welling at the seamount centre, outwelling at the level of the rim, and inward return flows above the level of the rim (Kunze and Toole, 1997, Mullineaux and Mills 1997). The result was a vertical compression of larval distribution near the seamount and in the outwelled regions, with hydroid settlement restricted to within the same 40km of the seamount centre (Mullineaux and Mills 1997); similar phenomena have been observed at many other raised topographic features (Lavelle *et al.* 2003, Hanel *et al.* 2010, González-Pola *et al.* 2012). Enclosed circulation cells have previously been attributed to Taylor-Proudman dynamics (the Taylor column or cap), although the persistent forcing required to generate these phenomena mean that in reality the phenomena are ephemeral and are the result of periodic forcing, such as tidal rectification (White and Mohn, 2002, Lavelle and Mohn, 2010, White *et al.*

2007). Of particular impact to larvae are retention phenomena, both for nutritional benefit (Boehlert 1987) and self-recruitment (Lavelle and Mohn 2010); although periodicity may result in episodic eddy shedding, advecting high densities of larvae and potentially causing mass recruitment events downstream (Mullineaux 1994). Amplified seabed currents may also be of advective benefit, but they are also an attractor to high standing stocks of filter feeding biota which can increase predation potential (Boehlert 1987). Whatever the physical phenomena, flow patterns are likely to be altered for significant distances downstream of topography (Royer 1978, Boehlert 1987).

At the scale of individual larvae water viscosity, turbulence and diffusion must be considered. Water viscosity has a larger influence on smaller particles, particularly where their swimming ability is limited (they have a low Reynolds number) (Podolsky and Emlet 1993). As viscosity varies with temperature there is potential for temperature induced changes on larval swimming and sinking ability (Podolsky and Emlet, 1993, Bolton and Havenhand 1997). Diffusion acts as the main dispersion parameter, altering larval concentration with impact on predation and advective trajectories within a cohort (Largier 2003). Causes are traditionally related to eddy diffusion and turbulence, but any small scale and therefore non-advective process may result in diffuse dispersion (Largier 2003).

Interaction with physical processes may change substantially if swimming behaviour is sufficient to alter the position of the larvae in the water column. Directed swimming of larvae may respond to external cues resulting in geotaxis, chemotaxis, rheotaxis, and phototaxis amongst others (Metaxas, 2001, Sponaugle *et al.* 2002). Generally ontogenetic migrators are positively buoyant, negatively geotactic and positively phototactic during ascent (Metaxas 2001). Swimming speeds of invertebrate larvae do not usually exceed a few millimetres per second but there are instances where propulsion however small could be advantageous (Jumars *et al.* 2001). Hetland *et al.* (2002) suggest that periodic cross-frontal transport may be possible for larvae with persistent upward swimming behaviours through entrainment in buoyant plumes . While Doostmohammadi *et al.* (2012) investigated the effect of swimming morphology on overcoming viscosity finding that pullers (organisms which generate forward thrust in front of their bodies) could enhance their vertical swimming velocity in higher viscosities.

Although evolutionarily centred on food supply and predator avoidance, vertical swimming and buoyancy may provide a larvae with means of reaching varying current speeds potentially enhancing or subverting dispersal ability (Young *et al.* 1996a, Sponaugle *et al.* 2002, Shanks *et al.* 2003, Young *et al.* 2012). Young *et al.* (2012) did find a modest enhancement of dispersal ability for simulations of siboglinid worm *Lamellibrachia luymesi* (van der Land and Nørrevang 1975) dispersal as buoyant or vertically migrating swimming simulators, compared with passive simulators released in the northern Gulf of Mexico. However Shanks *et al.* (2003) argued that passive models could also overestimate dispersal distance, e.g. by enhancing larval metabolism at warmer temperatures (Young *et al.* 2012), thereby reaching settlement competency earlier. Laboratory experiments have found larvae of some deep sea species which can tolerate the varying environmental conditions which would be encountered, and a few reports of deep sea invertebrate larvae being collected from the surface waters suggest vertical migration may be exhibited (Young *et al.* 2012). However Maldonado *et al.* (2003, 2006) discovered that the active horizontal swimming observed in sponge larvae reared in the lab was rarely seen in field observations, recommending caution in assuming effects on dispersal ability when such behaviours are recorded ex-situ.

The time a larva spends in transit is dependent upon their Planktonic Larval Duration (PLD) – an ontogenetic measure of time spent in planktonic larval form, ending with the point at which the larva has developed a competency to settle. There are repeated reports of a proportional relationship between PLD and dispersal distance (Shanks, 2009, Shanks *et al.* 2003, Kinlan and Gaines, 2003, Siegel *et al.* 2003, Young *et al.* 2012). However there are also contrasting reports (Shanks, 2009, Mercier *et al.* 2012) suggesting that oceanographic processes and larval behaviour complicating matters (Levin 2006), for example Largier (2003) attributes diffusion as a major contributor to the non-linear observations of PLD/dispersal distance. For the purposes of this study it is important to note that PLD has been estimated for only 21 true deep sea species over a variety of taxa, 93 if you include eurybathic species (mostly echinoderms) (Hilário *et al.* 2015), so however important the metric, a lot of data is lacking in this field.

1.1.3 Settlement

The ability to settle requires that larvae sink in order to find and select an appropriate benthic habitat. Downward transport may be through advection, swimming or passive sinking (Jumars *et al.* 2001). At this stage of development larval swimming ability is usually improved, individuals may be larger post-feeding and pre-metamorphosis, and the larvae generally become negatively buoyant, positively geotactic and negatively phototactic (Butman, 1987, Metaxas 2001). Larvae are then reintroduced to the turbulent boundary layer where rate of settlement success will be determined by rate of contact flux and probability of encountering suitable habitat (Jumars *et al.* 2001). It is widely accepted that most larvae have the ability to choose their settlement site prompted by a suite of chemical, sedimentolological or textural cues in order to detect habitat or conspecifics (Jumars *et al.* 2001, Short and Metaxas 2011): for the echinoid *Strongylocentrotus purpuratus* (Stimpson 1857) for example, a combination of turbulence and potassium cues have been found to stimulate settling competency (Gaylord *et al.* 2013). Koehl and Hadfield (2010) found, at the scale of the larvae, olfactory prompts create filamentous clouds meaning it is more likely the frequency of encounters rather than sensitivity to concentration of chemical cues that prompts settlement behaviour. Lillis *et al.* (2014) also suggest that sound could be a factor in larval settlement cues, particularly where reefs are a target habitat. Furthermore the larvae will experience fluctuating hydrodynamic forces dependent upon the fine scale topography of the habitat with changes over a spatial scale of millimetres both pre-settlement and upon landing (Koehl and Hadfield 2010). Limited species specific settlement information is available however, due to the difficulties of monitoring the process. Mass colonisation of similarly aged siboglinid worms (*Lamellibrachia sp.*) suggested to Short and Metaxas (2011) that gregarious settlement must have occurred potentially due to conspecific detection. They were also able to estimate 5% post-settlement mortality due to empty tubeworm case counts, but this is not possible for any species without a detectable remnant or indicator of death (Short and Metaxas 2011). Laboratory experiments require well behaved larvae and replication of adequate flows and cues which can be complex (Koehl and Hadfield 2010). Sun *et al.* (2010) were able to detect a settlement preference for rough natural surfaces with biofilm amongst soft coral (*Drifa spp*.) larvae, but Brooke and Young (2003) were unable to tempt the scleractinian coral *Oculina varicosa* (LeSueur 1821) larvae with substrate cues. Instead they found the few larvae that settled (c. 23 days) did so on the sides of the container, and subsequently all died of bio-fouling, with remaining larvae still swimming by the time of experiment termination at 42 days. This may be a case of delayed settlement which is a known capability of some species, including some corals, molluscs and asteroids, when no appropriate settlement cues have been encountered (Arellano and Young 2009, Metaxas and Saunders 2009). However delayed settlement increases chances of larval or post-settlement mortality, which can offset any benefits of increasing chance of contact with an appropriate settlement habitat (Metaxas and Saunders 2009).

The chances of finding a suitable habitat diminish with selectivity, PLD, and habitat patchiness (Sponaugle *et al.* 2002). Cowen *et al.* (2000) showed that diffusion and mortality may result in very low recruitment at distant habitats, and if habitat is scarce it can often be down to fecundity and self-recruitment to ensure persistence of the population (Sponaugle *et al.* 2002).

Successful dispersal requires that the larvae settle in appropriate habitat and survive to reproduce; it is their offspring that can continue the stepping stone action. This requires post-settlement survival which in part will be controlled by condition upon arrival to ensure metamorphosis can take place (Cowen and Sponaugle, 2009, Clark *et al.* 2010) along with the availability of conspecifics which have also survived to adulthood in order to facilitate sexual reproduction and continue the flow of genes.

1.1.4 All stages

At any point during the dispersal process larval mortality is likely to be great (Metaxas and Saunders 2009). Estimates vary up to >90%, but in reality figures are likely to vary with location, species, larval size/age, predator/prey distribution, cohort density, as well as abiotic factors such as temperature, pressure, dissolved mineral concentrations and photo-damage (Rumrill 1990, Young *et al.* 1996b, Morgan and Christy 1996, Aquino-Souza *et al.* 2008, Cowen and Sponaugle 2009, Metaxas and Saunders 2009). Therefore direct measurement is rarely possible with estimates generated by theoretical modelling, predator-prey laboratory experiments, or analysis of gamete release and dispersion versus post-larval settlement; a combination of methods is recommended to ensure figures are meaningful (Rumrill 1990). Predation is likely to be the greatest cause of mortality to larvae, although the relative contribution of factors contributing to mortality is unknown, and mortality is likely to vary with developmental stage or size (Metaxas and Saunders 2009). Much of larval swimming ability is therefore likely directed towards avoiding predation, although this probably results in trade-offs with regard to nutrient availability and other factors (Cowen and Sponaugle 2009).

Pressure and temperature tolerances are also likely to be a strong factor in deep sea larval survival. Young (1996a, 1996b) has undertaken many studies with deep sea fauna finding some with strict temperature pressure tolerances, potentially restricting adult bathymetric distributions also (e.g. echinoid *Echinus affinis* (Mortensen 1903), asteroid *Plutonaster bifrons* (Wyville Thomson 1873)), while others seem less restricted and have even been found in surface collections (e.g. ophiuroid *Ophiocten gracialis* (Sars 1871)), (Tyler and Gage 1982, Young 1994). Temperature is considered one of the most important factors to larval growth, with suboptimal temperatures resulting in slower growth (via changes in metabolism) and longer development times which can increase mortality (Metaxas and Saunders 2009).

While many of these factors may affect larvae on an individual level, climate change studies also look into the long term variation of abiotic factors which may potentially affect connectivity on an evolutionary scale. Temperature and nutrient availability can affect the PLD of some species (Cowen and Sponaugle 2009); while the availability of aragonite, necessary to fauna with shells or calcareous skeletons, is also likely to change with ocean acidification (Orr *et al.* 2005, Guinotte and Fabry 2008).

Seasonality must also be considered for any study. Temporal oceanographic patterns may be interannual (e.g. El Nino), seasonal (e.g. seasonal thermoclines) or diurnal (e.g. diurnal thermoclines), with impact across all scales of transport. Drivers may originate at the surface but deep convective mixing, upwelling regimes and internal wave propagation can penetrate deeper waters, along with the vertical flux of organic matter to the ocean floor. Benthic storms are known to occur due to deep penetrating vorticity: a meander of the gulf stream was recently found to propagate a benthic storm 4km below when it broke off to form a ring (Gardener *et al.* 2014), altering bottom current velocities to speeds capable of suspending sediment and dispersing larvae (Klein 1987). In temperate latitudes deep convective mixing in winter months can result in the depth of the surface mixed layer reaching 1000m potentially actively promoting vertical migration (New and Smythe-Wright 2001). Effects on nutrients and other fauna can also impact larval feeding, predator numbers, and seasonal reproduction, so time and location of a study must be considered within this context.

1.2 Marine dispersal research

Both at depth and in shallow water there remains little coherency in observed patterns of dispersal (Cowen *et al.* 2007). Initially it was thought that populations would be relatively "open" – mobile species having few boundaries to dispersal and those reliant on natal dispersal having currents able to carry larvae long distances and maintain a well-mixed gene pool (Cowen *et al.* 2000). However Cowen *et al.* (2006) found that even in reef fishes with high potential mobility, larval dispersal distances were only at a magnitude of 10-100km; their mobility used to promote retention rather than enhance dispersal. Passive dispersers too have been found to have disjointed distributions with oceanographic barriers to dispersal resulting in distinct genetic structuring in populations of corals (Gallindo *et al.* 2006, Foster *et al.* 2012) and other invertebrates (Ayata *et al.* 2010).

In deep water, seamounts have provided an ideal test-bed for these studies – providing islands of inherently fragmented habitat where investigation of endemism, species turnover and genetic studies can highlight whether dispersal and therefore gene flow is occurring between seamounts and/or continental slopes (see McClain (2007), Pitcher *et al.* (2007), Clark *et al.* (2010), Rowden *et al.* (2010), Schlacher *et al.* (2010), and Shank (2010) for reviews on seamount science). Howell *et al.* (2010) compared seamount, bank and slope benthic fauna within the Rockall Trough region of the NE Atlantic and found they were faunally indistinct with little or no endemism suggestive of high dispersal potential in the region. However chemosynthetic mussels in New Zealand (Smith *et al.* 2004), and a coral species in Hawaii (Baco and Shank 2005) showed significant population genetic structuring between proximate seamounts. Clark and Bowden (2015) assessed community similarity on Antarctic seamounts and found the least similar seamount was not the most geographically isolated of those studied, but one found in a cluster with several others. Dispersal patterns can also vary between species at the same location: Cho and Shank (2010) identified different directions of historic migration and different levels of population genetic structure between four ophiuroid species in the New England Seamounts which were found instead to be correlated with dispersal mode and coral host species (e.g. the gorgonians of genus *Paramuricea ,* Thoma *et al.* 2009).

These findings contribute to the debunking of seamount-specific paradigms suggesting high endemism due to their island-like quality (*sensu* MacArthur and Wilson (1967)) as a result of “geographic isolation”. Many seamounts have been observed with apparent endemic fauna (Richer de Forges *et al.* 2000, Samadi *et al.* 2006, Stocks and Hart 2007, Miller *et al.* 2010, Miller *et al.* 2011), but there are plenty of incidences to the contrary (Parker and Tunnicliffe 1994, Hall-Spencer *et al.* 2007, O'Hara 2007, von der Hayden *et al.* 2007, Lundsten *et al.* 2009, Miller *et al.* 2010), with “isolation” increasingly being evidenced as independent of geographic distance (Shank 2010, Clark and Bowden 2015).

Furthermore there is a question as to whether “seamounts” should be considered a habitat in and of themselves (McClain 2007, Howell *et al.* 2010, Rowden 2010). There are a huge variety of shapes, sizes, and ages of seamount, all of which affect the hydrography, environmental conditions and substrates encountered, making it hard to separate seamounts from banks, shoals, slopes or any other arbitrarily defined topographic feature as being of any special significance as marine habitats; it would be more appropriate to consider like-for-like depths, substrates and environmental conditions as the habitats representing the (sub-) population "islands" of significance (McClain 2007, Howell *et al.* 2010). Other deep water island-like habitats considered in the literature include whale falls (Glover *et al.* 2005), sunken wood (Yearsley and Sigwart 2011), vents (Mullineaux *et al.* 2005) and nodules (Miljutin *et al.* 2011) all of which have obligate species making the comparison far more appropriate.

One pattern which does appear to be emerging concerns gene flow on a vertical cline. The depth differentiation hypothesis (DDH) observes that there is a peak in diversity at bathyal depths (approximately 200-2000m) when compared to deeper or shallower waters (Rex and Etter 2010). Bathymetric structuring of genotypes has been observed on multiple occasions (Etter *et al.* 2005, Howell *et al.* 2004, Zardus *et al.* 2006, Cho and Shank 2010, Miller *et al.* 2011, Baco and Cairns 2012, Clague *et al.* 2012, Quattrini *et al.* 2015). This may be due to a number of factors – Howell *et al.* (In Prep) suggest a potential link between broad scale habitat fragmentation at shallow and bathyal depths and slowing current speed with depth potentially resulting in the least potential for connection in the bathyal. This relies upon there being limited dispersal in the vertical which may be the case for multiple species where environmental tolerance of both larvae and adults may restrict the bathymetric range of survivors (Young and Tyler 1993, Young *et al.* 1996a,b, 1998, Brooke and Young 2009, Bennet 2012, Brown and Thatje 2014), or water mass boundaries may create physical barriers to dispersal in the vertical (Yick *et al.* 2009, Ardekani and Stocker 2010, Doostmohammadi *et al.* 2012), but there have also been instances of deep sea larvae being caught in surface waters (Bouchet and Waren 1994, Sumida *et al.* 2000, Arellano *et al.* 2014) and isotopic evidence of some species natal migration into warmer waters (Bouchet and Fontes 1981, Killingley and Rex 1985, Dittel *et al.* 2005), therefore this alone could not explain the DDH.

1.2.1 Dispersal study methods

Investigations of dispersal ecology require a number of decisions on scale: the physical scale at which the habitat is considered fragmented, and the temporal scale at which populations may be considered disconnected. It is here that the aim of the study and the method used are important to define. **Figure 1 Error! Reference source not found.** reproduced from Levin (2006) provides an overview of the scales of study possible with different larval dispersal investigative methods.

Genetics

Genetic methods are potentially the most definitive – successful connectivity requires dispersal, survival and continued gene flow (Shank 2010, *sensu* Hedgecock *et al.* 2007) the effect of which can be tested using genetic markers (information about suitable genetic markers can be found in Hedgecock *et al.* (2007)). However necessarily you will be looking at evolutionary timescales and historic population dynamics which is useful in discovering migration patterns and population persistence and stability, but less useful in assessing modern day population dynamics, and cannot identify mechanisms of isolation (Kool *et al.* 2013).

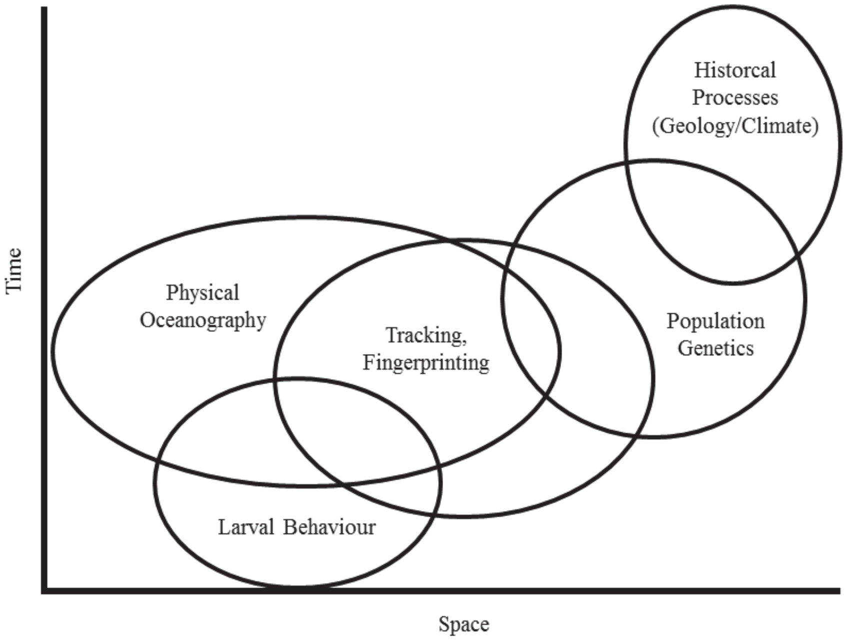

Figure 1 Temporal and spatial scales relevant to different approaches to the study of larval dispersal (reproduced after Levin (2006)).

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Isolation-by-distance (IBD) measurements can be used to estimate average dispersal distance; Palumbi (2003) found that IBD is apparent when populations are separated by 2-5 times the mean larval dispersal distance, resulting in an estimate of average dispersal distance of 25-150km for several fish and invertebrate species. There are weaknesses in this method however. Establishing which genetic markers are appropriate for the purpose at hand is species specific and time consuming, and will not always give desired results. Baco and Cairns (2012) used six mitochondrial markers to investigate species overlap in the deep sea coral genus *Narella*, finding that two of these are not even sufficient to resolve genera, none could resolve all the species, and all six considered together resolved only 83% of morphological species. It is therefore recommended that inferences made from genetic data should be made in tandem with ancillary sources of connectivity information (Hedgecock *et al.* 2007). Potentially some of the genetic studies which suggest panmixia are suffering from similar issues where different markers may have told a different story (e.g. similar to recent findings in North Atlantic copepods (Blankco-Bercial and Bucklin 2016), now elucidated by next generation sequencing techniques). Recent genomic parentage and barcoding methods do allow better contemporary quantification of connectivity over just a couple of generations and sequences hundreds of thousands of markers compared to the tens of markers targeted by older techniques (Luikart *et al.* 2003, Hedgecock *et al.* 2007, Kool *et al.* 2013). Such genomic techniques may be the future of population genetics in the deep sea, especially given the lack of well-developed primers for the vast majority of species (Baco and Cairns 2012, Boschen *et al.* 2016). Regardless of technique, genetic metrics of dispersal necessitate large quantities of samples, with associated costs for attaining these as well as high processing costs.

Elemental tagging

Elemental tagging techniques are emerging as a method of identifying the natal source of an individual on a contemporary timescale and to some extent the trajectory (Levin 2006). Artificial tagging is usually not advised given the dilution rates, but a few success stories have emerged from fluorescently tagging vast numbers of (fish) larvae, mostly elucidating retention patterns (Levin 2006). Natural tagging in the form of stable isotope and trace element analysis is still emerging as a technique, and could go hand in hand with genetic studies given the requirement for samples. The aim is to identify signatures of water masses and diet shifts which can be used to piece together life history information such as PLD (Herzka *et al.* 2002), and position of natal sources and transit based on the water chemistry they have passed through (Swearer *et al.* 1999). Chang *et al.* (2015) were able to detect a shallow water pelagic larval phase in deep water cusk eels through otolith microstructure and stable isotope composition. However this geochemical technique requires the organism to retain aspects of the larval structure post-settlement (e.g. molluscs, fish otoliths). Furthermore the chemical properties of the water masses they pass though must be well documented and distinguishable from each other, making this approach better suited to coastal and estuarine studies until technology catches up to allow more subtle detections (Levin 2006, Thorrold *et al.* 2007). Further information on this technique can be found in reviews by Levin (2006) and Thorrold *et al.* (2007)

Modelling

Lagrangian particle tracing methods (hereafter termed "biophysical models"), traditionally employed by atmospheric scientists and oceanographers, can be used to simulate the release of passive particles in an ocean general circulation model (GCM) (or another source of velocity fields) to track the fate of drifters as carried by the currents (Lavelle and Mohn 2010). These passive drifters, which can be released either forwards or backwards in time and space, can represent larvae and identify likely dispersal pathways, highlighting mechanisms of dispersal and oceanographic barriers to dispersal (Werner *et al.* 2007). Particles can also be given "behaviour", simulating swimming abilities such as diel vertical migration, or ontogenetic buoyancy properties to adjust predictions where dispersal is likely not passive (Levin 2006, Werner *et al.* 2007). These methods are well established in general connectivity research, with reviews by Levin (2006), Miller (2007), and Werner *et al.* (2007) highlighting some of the previous research in this field. The benefit of this technique is that it can be used on a variety of time scales (Levin 2006).

Such biophysical models have been used to address minimal/maximal estimates of dispersal (Blanke *et al.* 2012, Bonhommeau *et al.* 2009, Young *et al.* 2012, Howell *et al.* In Prep) with maximal dispersal distances aiding in the identification of the rare events which contribute to evolutionary scale population expansion and persistence (Cowen and Sponaugle 2009, Nathan *et al.* 2012, Kool *et al.* 2013). There are also advanced modelling methods capable of simulating evolution: Individual (or agent) Based Models (IBMs) allow each simulated individual to independently move through its lifecycle (Kool *et al.* 2013) allowing emergent properties to arise from selective forces. These models require input of accurate biotic, abiotic and life history parameters (e.g. mortality rates, metabolic rates, feeding, distribution through the water column, etc) in order to simulate dispersal inclusive of recruitment estimates (Fiksen *et al.* 2007, Miller 2007, Aiken *et al.* 2011). Where this has been possible models have also been used to trace, for example, the site of habitual spawning grounds (Pous *et al.* 2010, Garavelli *et al.* 2012, Catalán *et al.* 2013). Werner *et al.* (2001) considers IBMs as the de facto standard tool for studies of fish recruitment, but in the context of the current study the majority of the tuning abiotic, biotic and life history parameters are rarely known for deep sea species (Young *et al.* 2012), so advanced biophysical modelling in the deep sea remains at the mercy of future research.

Studies based on contemporary time scales offer a different insight into population management and demography (Cowen and Sponaugle 2009). While geochemical tagging occurs within this time frame, it is rare that you can acquire enough samples to infer demography. Modelling methods can provide a quantitative measure of dispersal, defining the average route and distance of dispersal paths from a release site (Cowen *et al.* 2007, Cowen and Sponaugle 2009, Kool *et al.* 2013). On this scale modelling studies can be used to inform marine protected area (MPA) networks (Fogarty and Botsford 2007, Basterretxea *et al.* 2012, Soria *et al.* 2012, Treml and Halpin 2012) as well as providing retention estimates and an idea of regularity of connection through sexual reproduction (Cowen *et al.* 2000, James *et al.* 2002, Sponaugle *et al.* 2002, Paris and Cowen 2004, Levin 2006, Almany *et al.* 2007, Cowen and Sponaugle 2009). But the most common application of modelling studies is to explore and quantify the effect of physical drivers on dispersal and isolation (Bonhommeau *et al.* 2009, Martins *et al.* 2010, Blanke *et al.* 2012, Soria *et al.* 2012, Young *et al.* 2012, Berline *et al.* 2013, Li *et al.* 2014). This is beneficial to any study where life history traits are lacking, allowing null models to be built for the effects of behaviour on dispersal (Paris *et al.* 2007, Carr *et al.* 2008, Paris *et al.* 2009, Sundelöf and Jonsson 2011), the relationship between PLD and dispersal ability (Siegel *et al.* 2003, Young *et al.* 2012), and exploration of other abiotic/biotic factors (Ayata *et al.* 2010, Martins *et al.* 2010, Treml and Halpin 2012). These can then be compared with empirical observations at a later date, whilst establishing basic dispersal limits within an ecological timeframe. Due to the nature of some oceanographic models, studies with confirmed physical drivers can also be forecasted under different conditions with applications in climate change research (Aiken *et al.* 2011).

Coupling models with genetic studies provides a powerful method of examining the drivers of population structure addressing the disjunction between timescales of connectivity study methods (Werner *et al.* 2007, Kool *et al.* 2013). Foster *et al.* (2012) found that the genetic structuring of the reef building coral *Montastraea annularis* (Ellis and Solander, 1786) in the

Caribbean could largely be explained by larval dispersal; although in one region the physical drivers could not explain the structuring suggesting that there are additional pressures on survival at that location. Kininmonth *et al.* (2010) used biophysical modelling to predict the genetic structure in areas yet to be sampled in order to complete connections in a partially known network, although care must be given here as historical events may be responsible for genetic structure, while biophysical models can only represent the dispersal path of the time period being simulated. Dawson *et al.* (2005) also used this technique to evidence the likely anthropogenic dispersal of a cosmopolitan species of *Aurelia* jellyfish, as physical drivers could not have permitted the panmictic population that exists worldwide.

In the deep sea there have been relatively few modelling studies to date. The few biophysical models built around seamounts have been based solely on passive simulators (Beckmann and Mohn 2002, Chapman and Haidvogel 1992, Goldner and Chapman 1997, Lavelle and Mohn 2010, Howell *et al.* In Prep) undertaken to study retention of particles over particular seamounts, representing larvae or any other passive particle (e.g. pollutant, phytoplankton, nutrients). Beyond these there have only been 3 deep sea studies to date simulating the dispersal of non-vent species with species specific parameters: Yearsly and Sigwart (2011) modelled the dispersal of deep sea wood obligate polyplacophorans, and Young *et al.* (2012) along with some vent species modelled the dispersal potential for two sedimented slope echinoids (*Cidaris blakei* (Agassiz 1878) and *Stylocidaris lineata* (Mortensen 1910)), and Etter and Bower (2015) recently modelled the dispersal of protobranch bivalves in an area of the NW Atlantic with known genetic structuring amongst depths. The lack of studies in this field in part reflects the lack of useful biological characters (e.g. PLD, vertical migration, swimming ability, buoyancy, mortality) necessary to hone a model to approaching reality. However we continue to gain knowledge in these fields, and where knowledge is lacking null models can be built to inform marine managers until observations can be made.

For all the flexibility offered by the modelling method, there are still plenty of weaknesses which should be considered. It should be remembered that this is a model, i.e. “A simplified or idealized description or conception of a particular system, situation, or process, often in mathematical terms, that is put forward as a basis for theoretical or empirical understanding, or for calculations, predictions, etc." (OED Online 2014). All aspects of complexity will not be accounted for by definition, and should not be sought after (Evans *et al.* 2012). All parties who are to make use of the model outputs should be made aware of this. The GCM inputs also suffer from this caveat with the added issue that hydrodynamic models are likely to be designed with a specific alternative purpose in mind (e.g. optimised to research heat flux or geostrophy). Most fundamentally the output from any model is a prediction which means nothing without validation – and while the modelling process does not require physical samples to undertake, it is still necessary to perform some form of sampling in order to ground truth predictions.

1.2.2 Modelling methods

Many of the considerations of the modelling process are reviewed in a report edited by North *et al.* (2009), with recommendations made for each of the parameters. However further clarification of the ecological implications of technical oceanographic parameters may be beneficial, with the context of this study requiring adjustment of North *et al.* 's (2009) recommendations which are currently designed for modelling the dynamics of fish early life. While the processes are equivalent for fish and benthic invertebrate larvae, the scales of effects are necessarily different due to differences in swimming ability and growth potential (Metaxas and Saunders 2009). The greatest challenge lies in the multiple scales of physical processes relevant to the larvae.

Biophysical modelling requires a pairing of hydrodynamic velocity field data with a particle simulator which will track the theoretical larvae over time and space according to the input velocity, directional, and behavioural data. The first step is therefore to select an appropriate source of velocity fields. Fossette *et al.* (2012) review the pros and cons of using empirical data (both Eulerian and Lagrangian) or inferred data such as satellite observations or general circulation models (GCMs). Considerations must be based on data availability and scales of relevance to the study and oceanographic processes to be resolved.

With the depth and spatial range implicit in deep sea studies, GCMs or other hydrographic models must be used to supply velocity vectors, but an expectation that all processes can be captured in one model is ill-informed (Cowen *et al.* 2007). In an ideal situation you would have a hydrographic model tailored to your purpose and trained on your area with high resolution bathymetry and accurate weather forcing, but this is very unlikely to be the set up offered to the average biologist who will require a suitably qualified oceanographer dedicated to the project to make this happen. Instead biologists are often directed to GCMs which are published models, primarily used by oceanographers, with parameters tailored to reproducing particular conditions relevant to the study of various aspects of ocean physics, albeit often with customisable elements. At this point the biologist must either find an oceanographer to tailor the model, must learn to run these models themselves, or must accept the outputs of an existing model and therefore assess whether its parameters are adequate to capture the processes required for the biophysical simulation. Table 1 lists a number of GCM parameters with translations for

Table 1 GCM parameters translated for ecologists.

These details may be of use when trying to interpret or choose between GCMs. For more detail see (Lacroix *et al.* 2009).

Parameter	Options	Meaning	Consideration for ecological studies	Example GCMs and ecological references
Equations	Primitive	Basic rule set (comprising Navier-Stokes equations and associated classical assumptions) for defining fluid velocities and other properties as presented on a sphere whilst prioritising horizontal motion over vertical – i.e. probably what you want	Adequate for most applications	ROMS - Aiken *et al.* 2011 - Young *et al.* 2012b MITgcm (with more complex options too - no ecological applications as yet) SPEM (stretched) - Mohn and White 2007 HAMSOM - Soria *et al.* 2012
	Quasi-Geostrophic	Assumes a near-balance between Coriolis and pressure gradients allowing vertical vorticity, reduced resolution of gravity waves, and bigger time steps	Less stable, more suited to advanced simulations of specific oceanographic phenomena	Q-GCM (specialist, no ecological refs)
Scale	Temporal, spatial	Models are designed to resolve specific time-steps and spatial scales- generally of 1day to 1000s of years, and 10km to 10000km. Spectral models are non-spatial and relates to waveforms for ocean atmosphere interactions.	There are implications for the type of oceanographic phenomena captured - thermohaline circulation at the coarsest extent, wind-driven circulation at the mean extent, and mesoscale eddies at the finest extent (Figure 2). If resolving an eddy you will need 6-10 nodes across the eddy this helps determine the spatial scale desired (and necessarily shortens the time-step - see time-step) (Lacroix *et al.* 2009). Ignore spectral scale models. Watch for temporal resolution being high when the model is run, but averaged when stored in an output (usually daily, 5-day or monthly – if so try and stick with daily).	HYCOM (global)- Foster *et al.* 2012 - Young *et al.* 2012b MITgcm (global to regional - no ecological applications as yet) ROMS (regional) - Aiken *et al.* 2011 - Young *et al.* 2012b MARS (regional) - Ayata *et al.* 2010
	Speciality	Models may be designed for specialist purposes, e.g. shelf, sea-ice, ocean-atmosphere interactions	The physics involved in these models are more specialist than more generalised models, e.g. shallow waters are necessarily more affected by wind-forcing (shelf model), with geostrophy more dominant at depth (deep basin model), so care should be given to using specialist models only where appropriate. Models based in spectral space are based on wave forms for ocean-atmosphere interactions and are unsuitable for ecological modelling.	ORCA025-LIM2 (coupled ice-ocean for polar models) - Renner *et al.* 2012 SEOM (spectral, ignore)
Vertical grids N.B. These refer to the native grids the model is run in, watch out for output files being averaged into different grids for compatibility with other software – e.g. the available HYCOM outputs are z level but the model itself is run as a hybrid.	Z (geopotential)	Vertical layers are at regular bathymetric intervals, i.e. corresponds with depths	Simplified models, which resolve vertical pressure gradients, mixed layers, and equation of state well, but cannot resolve terrain, horizontal diffusion or stratification with implications for tracer (e.g. larvae, nutrient) advection/diffusion. Possible to restrict vertical transport (proxy for stratification), and modern stretched grid models better resolve shallow depths. Better for shallow water/surface layer studies.	HAMSOM - Soria *et al.* 2012
	σ (sigma)	Terrain following – a set number of vertical layers is equally spread through water column, thus layering is denser in shallows and disparate in the deeps	Corrects z-grid issues of terrain resolution, still no stratification or horizontal diffusion. Can also have highly resolved surface layers and vertical restrictions may simulate stratification but depth values cannot assume to be maintained. Best for simple topographic effects in shallow waters.	NEMO/OPA- Bonhommeau *et al.* 2009 - Blanke *et al.* 2012 - Howell *et al.* In Prep POM - Basterretxea *et al.* 2012) MARS - Ayata *et al.* 2010 ROMS (regional) - Aiken *et al.* 2011 -Young *et al.* 2012b MITgcm (no ecological applications as yet) SPEM (stretched) - Mohn and White 2007
	Isopycnal	Vertical layers follow immiscible density layers simulating stratification	Good representation of ocean interior stratification, improved horizontal diffusion, but equation of state not simplified results may vary with choice of reference pressure, and layers are only potential density surfaces and therefore do not account for pressure effects on density resulting in inaccuracy and instability in tracer accumulations at depth or in polar regions (Gnanadesikan 1999).	MICOM - Galindo *et al.* 2006
	Hybrid	Either generalised sigma-grid models hybridising the z and sigma grids or HYCOM hybridising all three	Generalised sigma- improves bottom boundary layer processes, maintains simplified equation of state, continued issues with isopycnals and horizontal diffusion. HYCOM is isopycnal in the stratified ocean interior, terrain following in shallow waters and z-gridded in the mixed layer or where no stratification is present	NEMO - Bonhommeau *et al.* 2009 - Howell *et al.* In Prep HYCOM - Foster *et al.* 2012 - Young *et al.* 2012b
Horizontal Grids (Arakawa and Lamb 1977)	A	SSH, T, S data and velocity vectors all recorded at same location on a horizontal plane (e.g. cell centre)	Concurrent physical data has better accuracy but has low model stability	DieCAST - Ordines *et al.* 2011
	B	SSH, T, S data staggered from velocity vectors on a horizontal plane (e.g. cell centre then cell corners)	Improved model stability, density solved by differential equations to give average values where velocity vectors are situated	MOM (climate studies)
	C	SSH, T, S data, north-south velocity vectors, and east-west velocity vectors all staggered on a horizontal plane (e.g. all at different locations on a grid)	Highest model stability, but all data are staggered so values are averaged by solving differential equations at any given point. Pre-requisite for many particle tracer models (e.g. ARIANE)	ROMS -Aiken *et al.* 2011 -Young *et al.* 2012b HYCOM - Foster *et al.* 2012 - Young *et al.* 2012b MITgcm (no ecological applications as yet) SPEM (stretched) - Mohn and White 2007 HAMSOM - Soria *et al.* 2012
Discretization (solution of equations within a finite and discrete environment)	Finite Difference	Solves equations using discrete grid of nodes (cuboid grid)	All of domain with equal precision (or lack of)	POLCOMS, DieCAST - Ordines *et al.* 2011 ROMS - Aiken *et al.* 2011 - Young *et al.* 2012b HYCOM - Foster *et al.* 2012 -Young *et al.* 2012b
	Finite Element	Custom grid of nodes (of triangles/pyramids) allows better solution of equations in complex domains, precision can vary where needed	Some areas of domain with high precision and some with low - best used where there are both complex oceanographic phenomena requiring better resolution and other areas which can be assumed less complex warranting less precision.	DNML models (e.g. Quoddy) - Brickman and Smith 2002 - Lough and Manning 2001
	Finite Volume	Solves equations for a small volume/packet of water interpreted as fluctuations through its surfaces	Allows for unstructured meshes with mass conserved	MITgcm (no ecological applications as yet)
Assumptions	Hydrostatic, Non-hydrostatic, Quasi-Hydrostatic	H - Flow considered at equilibrium with velocity at each point constant over time. NH - equilibrium not assumed. QH- near-equilibrium assumed	H- Ignores horizontal Coriolis effects, not representative at small scales .NH- used for resolving mesoscale processes but is computationally intensive. QH- includes horizontal component of Coriolis effect. All relate to assumptions of baroclinicity.	ROMS(H/NH) - Aiken *et al.* 2011 - Young *et al.* 2012b MITgcm(H/QH/NH) (no ecological applications as yet) SPEM (stretched)(H) - Mohn and White 2007 HYCOM (H) - Foster *et al.* 2012 - Young *et al.* 2012b
Other parameters for consideration (also applies to tracer model which can sometimes manipulate these further)	Time-step	Model stability is often hinged on ensuring that the time-step (the time interval between new calculations) is restricted by grid size to avoid the propagation of disturbance/error beyond one grid cell.	There are computational implications of shorter time-steps which are required for high spatial resolutions. This can be addressed by using unstructured grids (see discretization) or models with mode splitting which computes fast processes on a short time-step and slow processes on a long time-step	option within models
	Boundary conditions	The model does not know whether it is a part of a larger system or is isolated, so this is instructed to the model to either allow processes to permeate the edges of the model (open) or provide a reflective surface simulating e.g. land (closed) however boundary effects usually remain	Select a domain that exceeds the area you require to minimise the boundary effects being suffered within the relevant domain to your model	option within models
	Sub-grid-scale processes	Processes that occur at a smaller spatial scale than the model grid may still be parameterised in the form of eddy diffusivity	Alterations in eddy diffusivity may help resolve sub-grid-scale processes, although some equations account for this more than others. Increased diffusivity may improve model stability but care must be given to the specifics (Lacroix *et al.* 2009)	option within models
	Coordinate system	As with any spatial domain the horizontal grid is representative of a spherical earth and there are multiple ways to interpret this into a regular grid	Curvilinear orthogonal grids are appropriate for large domains, while local domains (e.g. an estuary) may use more simple Cartesian grids. Sometimes tri-polar grids are used which can prove more problematic when mapping/measuring distances	option within models
	Initial conditions	The state of the ocean at start of model - requires temperature, salinity, weather, and movement conditions	Use to represent your area as faithfully as required. Climate models can provide appropriate data to "force" the model. Models may require time to "spin up" sometimes in the order of months, making well established continually running models more desirable for biological processes. Models forced by local weather data may me more accurate in your area than more generalised models.)	option within models

TABLE 1

biologists, along with example models and example biological references to aid model selection (although availability is often a deciding factor). It is important to note that the format of the model outputs may negate some of the advantages of the live model, so both must be checked if it is model outputs which will be used. Werner *et al.* (2007) review the scales of capability from basin to reef scales, highlighting the multi-scale overlap and interaction of physical and biological processes which make a (preferably two-way) nested model design the most realistic to larval transport pathways. GCMs with unstructured horizontal grids can also address this issue, focussing high resolution grids over areas of complex physics and sacrificing resolution where processes can be justifiably simplified (Werner *et al.* 2007). Coastal studies may find both of these options available but the deep sea will likely require new custom models.

Accepting the need for GCMs, there are several inadequacies which should be heeded and assessed in the context of a biophysical study. The biggest inadequacies of GCMs may lie in the lack of local and fine scale processes which could be of great relevance to a larva (Metaxas and Saunders 2009). Figure 2 shows the temporal and spatial range of GCMs relative to oceanographic phenomena (from Tsujino *et al.* (2010) after von Storch and Zwiers (2004)) which draws attention to the kind of processes not directly resolved. Lacroix *et al.* (2009) give the example of a 20km eddy requiring a 3km grid to resolve it (6-10 grid points of coverage are required), which is suggestive of what would be required to resolve sub-mesoscale and small scale processes. Sub-grid-scale parameterisation only captures diffusive effects on resolved phenomena and should not be presumed to have captured all the intricacies (Lacroix *et al.*, 2009). Indeed sub-mesoscale and small scale processes are still not fully understood, so models can still only be considered approximately adequate at the scale of a larva (Werner *et al.*, 2007).

Issues of resolution should also extend to temporal choices. The outputs of highly spatially resolved GCMs are often temporally averaged to account for seasonal effects or reduce computational requirements, but Putman and He (2013) show that this reduces the scale of hydrographic phenomena captured and can result in erroneous trajectory predictions when groundtruthed with observational data. Even a relatively fine temporal averaging, e.g. daily outputs, will have cut out tides and any sub-diurnal phenomena (see Figure 2 for examples) the implications of which should be carefully considered. This can be counteracted by using an ‘online’ particle simulator (a simulator run live within the hydrodynamic model), again likely requiring the skills of a collaborative oceanographer. Also of concern to this study are issues of resolving stratified flow over topography (Werner *et al.* 2007). In areas of steep topography the complex dynamics are not easily resolved in a single model due to numerical complications of dealing with an artificially stepped bathymetric grid: cross-referencing with high resolution observations where possible is advised to inform model choice and validate predictions prior to pairing with a simulator (Werner *et al.* 2007). This is further exacerbated by the lack of high resolution bathymetry over large spatial scales which would be required to establish more accurate models, to the extent that seamounts 1-2km high have only recently been able to be detected using satellite altimetry (Sandwell *et al.* 2014), and even this resolution of data is not yet incorporated into GCMs.

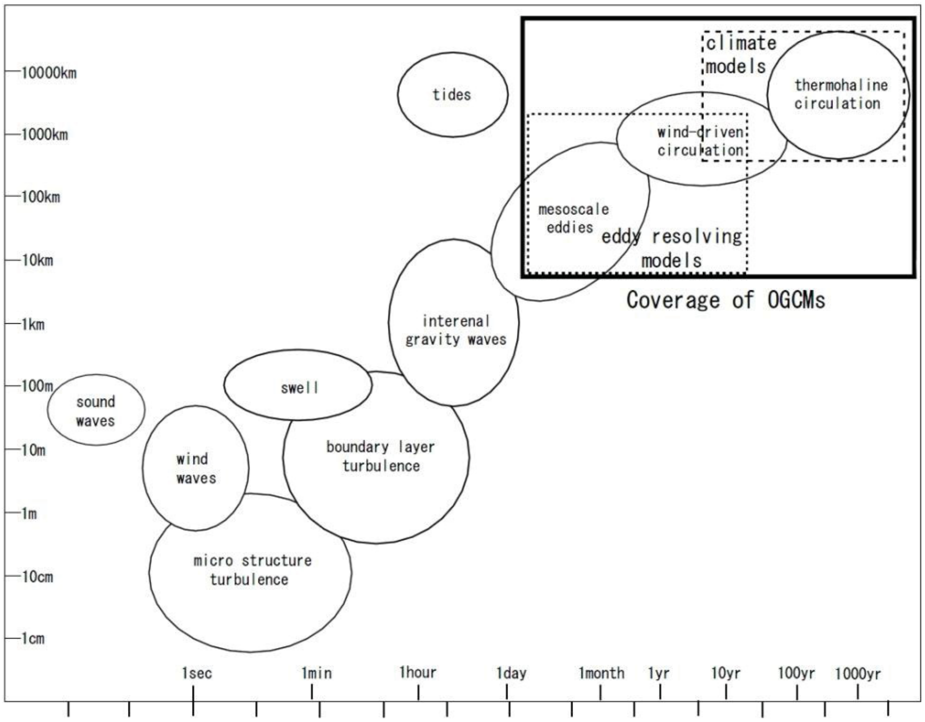

Figure 2 The temporal and spatial restrictions of general GCMs as related to oceanographic phenomena (Tsujino *et al.* (2010) after von Storch and Zwiers (2004);

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The choice of GCM to some extent will limit which particle simulator you can choose: hydrodynamic models can be set up with completely different output data structures, so an offline particle simulator compatible with the chosen GCM output and structure must be used. Factors such as horizontal and vertical grid of the GCM outputs need to be checked for compatibility. North *et al.* (2009) gives an overview of particle simulator best practices and recommendations, however this is placed in an analytical setting, without covering any specific software which represent the most accessible methods for non-physicists.

Table 2 is intended to fill this gap, translating some of North *et al.'*s recommendations into the capabilities of existing, customisable, offline particle simulator models, along with their compatibilities and usability. Critical recommendations include the use of random displacement (or walk) models (RDM) discretized with high order Runge-Kutta routines for higher numerical accuracy (North *et al.* 2009).

Metaxas and Saunders (2009) review the "bio" components of biophysical models in the context of marine benthic invertebrates, stressing the importance of including parameters only when they are known or can be reasonably estimated. Not all simulators have the capability to easily include these so thought must be given to the necessity of such parameters for the study at hand, as well as their availability for specific taxa. Where these data are available inclusion is advised as they can vastly alter connectivity parameters (Young *et al.* 1996a, Sponaugle *et al.* 2002, Shanks *et al.* 2003, Young *et al.* 2012). Cowen *et al.* (2000) found inclusion of both mortality (0.2 day^{-1}) and diffusion (100m^{2} s^{-1}) with patchy settlement habitat parameters produced a model of Caribbean reef connectivity up to nine orders of magnitude less connective than passive transport estimates which exclude these parameters. This highlights the need to target the purpose of the model, and ensure the benefits of the parameters outweigh their uncertainty. A major benefit of simulator models is the ability to both simulate forward and backward dispersal, identifying both the fate and source of a larva (North *et al.* 2009, Howell *et al.* In Prep) but it should be noted that parameters such as mortality and diffusion cannot be reversed (Batchelder 2006).

Table 2 Offline particle tracer software descriptions and compatibilities with considerations for ecological studies

Tracer	Description	Compatibility	Consideration for ecological studies	Example supporting ecological references
ARIANE	FORTRAN based software able to be used on regional or global scales.	Any volume conserving model e.g. OPA, NEMO, ROMS), C grid required Linux system with FORTRAN library	Has been used with limited behavioural options fixed depth and diel vertical migration through differing fixed depths at 12hr intervals). May be able to integrate more biotic/abiotic data given appropriate reprogramming. No random walk component instead relies upon turbulent sub-grid-scale parameterization in GCM.	Bonhommeau *et al*. (2009a, 2009b), Pous *et al.* (2010), Berline *et al.* (2013)
Connectivity modelling system (CMS)	Stochastic lagrangian model with biotic and abiotic optional modules and multi-nesting capabilities, with accompanying Matlab routines for visualisation. Can download GCM data via OPeNDAP.	A,B,C grid GCMs uses routine to transform to B grid) Requires z level vertical grid Linux system with FORTRAN & NetCDF libraries	Designed for easy use with ecological application, can be used for passive particles with all modules off) or with biotic/abiotic components factored in. Random walk solved by 4th order Runge-Kutta discretization. New, not much published testing yet.	Paris *et al.* (2013), Kough *et al.* (2013), Holstein *et al.* (2014), Wood *et al*. (2014)
Ichthyop	Java based IBM designed for ichthyoplankton dynamics, which can incorporate biotic and abiotic factors.	MARS, ROMS, NEMO, HYCOM	Useful where many factors are known e.g. growth, movement, mortality), may require some simple recoding for species specifics requires a sufficiently limited spatial scale to warrant use of a regional GCM. Tested by comparison to ARIANE and ROFF. Random walk elements integrated into movement sub-model can be solved by either Euler or 4th order Runge-Kutta discretization.	Lett *et al.* (2008), Brochier *et al.* (2009), Martins *et al.* (2010), Yannicelli *et al*. (2012), Garavelli *et al.* (2012), Putman *et al.* (2012), Putman and He (2013), Catalán *et al*. (2014)
LTRANS	Larval transport lagrangian model.	ROMS	Can simulate behaviours or passive, only couples with ROMS, random walk solved by 4th order Runge-Kutta.	Schlag and North (2012), Young *et al.* (2012b), Li *et al.* (2014)
MGET	ArcGIS related toolbox which can download GCM data via OPeNDAP and run a connectivity analysis designed for coral reef connectivity. (Uses method developed by Treml *et al.* (2008)).	Aviso satellite/surface), HYCOM non-polar global or gulf of Mexico), NOAA OSCAR surface), ROMS-CoSiNE pacific) data downloadable. ArcGIS, MGET, Python, PyWIN32, Matlab	Various restrictions of compatible GCMs explained in help e.g. HYCOM depth restricted to 5500m, and area south of 42°N. Probably one of the more user friendly methods. Requires input polygons and rasters which may make this more suited to the reef connectivity modelling it was designed for.	Treml *et al*. (2008), Mora *et al.* (2011), Treml and Halpin (2012)
ROMS OFfline lagrangian Floats ROFF)	A subroutine code for ROMS for tracing drifters, with accompanying matlab routines for visualisation.	ROMS	Has been used with limited behavioural options fixed depth and diel vertical migration through differing fixed depths at 12hr intervals), only suitable for used with ROMS therefore with limited spatial scale.	Carr *et al*. (2008)

As with any modelling process, models should be evaluated and validated where possible. While GCMs are validated before they are published, the thousands of data points they may be validated against in a global context, may translate to only one or two data points located in your relatively small area of interest (Fossette *et al.* 2012). Modelled trajectories can be compared with Eulerian or Lagrangian empirical data, such as global drifter datasets (e.g. Argo) (Fossette *et al.* 2012) and used to tune or assess a GCM prior to coupling with a simulator.

Simulator parameters require tuning too, with basic parameters such as number of particles released, particle release depth, and particle tracking time all found to be sensitive to adjustments in shallow water (Simons *et al.* 2013). While biologists may wish simulate numbers of particles comparable to animal fecundity, thought must be given to statistical reasons for limiting particle release, and any computational restrictions on maximising it, as a rule-of-thumb it is worth flooding the system to ensure that you are accounting for the entire distribution of probable connections. North *et al.* (2009) recommend trialling different numbers of particle release with an aim to finding the asymptote where variability becomes stability. Currently no sensitivity advice is tailored to the range of depths covered in deep sea studies.

Model validation is an iterative process, comparing predictions with observations, adjusting the model accordingly and repeating the process (Cowen and Sponaugle 2009). As with any model this process is advised though problematic: the reason for developing models, especially in the deep sea, is partially in response to the difficulty of obtaining empirical data (Metaxas and Saunders 2009). As a result many theoretical evaluations can remain unvalidated, providing only null models for future validation (Metaxas and Saunders 2009). Connectivity measures may require use of alternative techniques for validation, although historic records and literature can begin to address this (Werner *et al.* 2007). Metaxas and Saunders (2009) provide an overview of challenges to biotic validation, with a reminder that there may be a disparity in sampling, e.g. between evaluating models of dispersal which exclude recruitment estimates with observation of adults that have survived post settlement, which can leave many factors unaccounted for (Sponaugle *et al.* 2002, Warner and Cowen 2002, Metaxas and Saunders 2009).

Model output analysis

Once a model has been created there are a number of methods of output interpretation and visualisation available. Kool *et al.* (2013) provide a review of current analysis methods of population connectivity, considered as a synthesis of both marine and terrestrial knowledge. The most commonly encountered methods in the marine environment are the dispersal kernel, the connectivity matrix and graph theory (Paris *et al.* 2009).

The dispersal kernel is probability density function which scales the distance of dispersal relative to a source population (distance can be quantified either as distance travelled (Lagrangian approach) – the “dispersal distance kernel”; or distance of post-settlement location “as the crow flies” (Eulerian approach) – the “dispersal location kernel”, *sensu* Nathan *et al.* (2012)). The hump of the distribution can be used to define average dispersal mode for ecologically time scaled studies: steep distributions proximate to the y-axis represent closed/retentive populations, while more diffuse Gaussian distributions represent open/dispersive populations (Cowen *et al.* 2007). The tails of dispersal kernels highlight rare dispersal events, which are important in evolutionary studies of range spread, maximal dispersal ability, population persistence and structure, and potential cohort colonisation events of evolutionary significance (Paris *et al.* 2009, Nathan *et al.* 2012). However Kool *et al.* (2013) draw attention to the assumption of radially symmetric dispersal processes inherent in a 2D dispersal kernel, making kernels less suited to the asymmetries of marine dispersal patterns and habitat structure, at least when considered alone.

The connectivity matrix represents a matrix of probability density functions, describing the frequency of dispersal success between source populations (y-axis) and destination populations (x-axis). The result overcomes the 2D dispersal kernel’s assumption of habitat homogeneity (Nathan *et al.* 2012). Connectivity matrices provide a clear visualisation of quantified recruitment and self-recruitment (in the diagonal line); current drift can be seen where only one side of the matrix displays high probabilities; connections of greatest influence can easily be identified; and various sorting methods can be used to highlight source clusters (Cowen *et al.*

2000, Cowen and Sponaugle 2009, Paris *et al.* 2009, Foster *et al.* 2012, Kool *et al.* 2013, Jones *et al.* 2015).

Graph theory presents an alternative visualisation technique, stemming from the study of computer networks it works on a basis of nodes and connections providing methods for analysis of node centrality and influence, while number of connections can imply resilience and communicability (Treml and Halpin 2012, Kininmonth *et al.* 2010, Kool *et al.* 2013, Holstein *et al.* 2014, Jones *et al.* 2015). This approach has found increasing popularity in ecological applications, although care must be given to understanding the limitations of the technique (Urban and Keitt 2001). Many other approaches are available for the visualisation and interpretation of biophysical models; choice of analysis method naturally depends on the study in question (Werner *et al.* 2007, Kool *et al.* 2013).

1.3 Marine conservation

With increasing awareness of human impacts upon the marine environment , there is a worldwide push towards marine conservation and management. International edicts from the IUCN in 1993, the World Summit on Sustainable Development (WSSD) in 2002, the IUCN World Parks Congress in 2003, the Conference of Parties to the CBD in 2004, and the United Nations General Assembly Oceans and Law of the Sea Resolutions in 2003/4, addressed the need for global MPA networks incorporating both national waters and areas beyond national jurisdiction (ABNJs). These political targets, and their subsequent revisions, have now been adopted into both regional and national policy and governance.

Variously through these agreements there is reference to the need for dispersal knowledge. The latest CBD targets say that marine protected area networks should be “ecologically representative and well-connected systems” (Aichi Target 11). The IUCN WPC (2003) explicitly mentions that MPA networks should be “designed to be resilient…[and provide] protection of refugia that can serve as reliable sources of seed for replenishment, and connectivity to link these refugia with vulnerable areas within the network”; and 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” (IUCN WPC recommendation V.22 (IUCN 2003)).

The concept of ‘ecological coherence’ was also integrated into the European commission Habitats Directive (1992) which, prior to the worldwide agreements, was the first international legal framework which committed nations to the protection of species and habitats under their jurisdiction. Article 3 of the EC Habitats Directive stated that: “A coherent European ecological network of special areas of conservation shall be set up… Where they consider it necessary, Member States shall endeavour to improve the ecological coherence”. Although a legal term which is hard to interpret, Ardron (2007) provides a definition of ‘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”

Although this holistic concept incorporates multiple sub-criteria (e.g. the supply of non-living organic carbon, the maintenance of environmental conditions, awareness of the effects of destructive processes outside of the MPA upon the protected ecosystem, etc. (Roberts *et al.* 2003)) an understanding of connectivity and its constituent processes are vital to its achievement (Gaines *et al.* 2003).

From a larval dispersal point of view these criteria reflect the need for an MPA network to: supply larvae to unprotected areas (supporting the wider environment); encourage the persistence of protected populations and communities across their full natural geographic range (maintaining process, functions and structures); mutually exchange larvae between protected areas, promoting persistence and protecting refugia (functioning synergistically as a whole).

Part ii may be the most challenging to satisfy, this necessitates the protection of whole ecosystems, which from a dispersal point of view would require knowledge of many species' reproductive strategies, PLDs, larval behaviours, etc. This is highly impractical for shallow water MPAs, let alone deep sea MPAs where even less is known about the species being protected. One potential approach in the meantime, is to focus on threatened or declining species (an approach adopted by the CBD (2004) and OSPAR (2006)), or species which form a habitat for others (bioherms *sensu* Howell (2010) acting as umbrella species (Roberge and Angelstam 2004)). In the case of offshore MPAs this advice is extended by OSPAR (2006) to say that "the network should have regard to the different aspects of connectivity but not be focussed on one element or one species to the detriment of others. Habitat linkages and species movements can inform decision-making for the location of sites where information is available but, it should be accepted that in most cases our understanding of the connections between sites would emerge over time, especially for species whose ecology is poorly understood."

Existing MPA networks have been informed by larval dispersal research on the whole, with literature providing advice on MPA spacing (Botsford *et al.* 2001, Shanks *et al.* 2003, Gaines *et al.* 2003) , size (Botsford *et al.* 2001, Shanks *et al.* 2003), and persistence (Jessop and McAllen 2007, Burgess *et al.* 2014).

Size and spacing advice has been variable (Jones and Carpenter 2009). Shanks (2003) review of PLDs (n=35 shallow water taxa) suggested there may be a bimodal evolutionary strategy in marine larval dispersers (held up with the addition of more species (total n=67species) in Shanks (2009) study), with species either dispersing <1km, or >20km, so he suggests that MPAs 4-6km in diameter would capture several subpopulations of short dispersers, and networks of MPAs spaced 10-20km apart would capture the subpopulations of the longer dispersers. Botsford *et al.* (2001) caution against the used of average dispersal only as a spacing metric as this could select for shorter dispersing species and change the community composition over time. MPAs sized at least 2x the mean faunal dispersal distance would provide some offset to this effect. Halpern and Warner (2003) suggest variable size and spacing of reserves would be a better approach.

Persistence advice recommends that source and sink information may be useful to MPA design (Jessop and McAllen 2007), and local retention data (fraction of those released retained) can inform the self-sustainability of a MPA (and is more useful than self-recruitment data (fraction of those recruited, usually obtained from genetic data)) (Burgess *et al.* 2014).

More integrated approaches have also been posited, with (usually an average) dispersal distance included in MPA network design, coupled with habitat area targets, and socio-economic impacts to optimise networks before they have been designated (Walters *et al.* 2000, Gaines *et al.* 2003, Treml and Halpin 2012, White *et al.* 2014, Jonsson *et al.* 2016).

The majority of advice for existing network assessment focusses on whether average size and spacing targets were achieved (Wood *et al.* 2008), along with habitat coverage targets (Ross and Howell 2013, O'Leary *et al.* 2016), and socio-economic impacts (Claudet and Guidetti 2010).

Deep sea and offshore MPA networks are being established at the same rate as shallow water and coastal MPA networks, but suffer from a much greater lack of data, largely attributable to the relative inaccessibility of these areas to researchers. There are a relatively small number of offshore 'listed' habitats and species in conservation legislation (De Santo and Jones 2007), due to our lack of knowledge in this area. Deep sea and offshore MPA network establishment advice still largely focusses on the discovery of highly diverse or unique communities (Clark *et al.* 2014), or Vulnerable Marine Ecosystems (VMEs) and species facing imminent human impact (De Santo and Jones 2007, Wedding *et al.* 2013, Schlacher *et al.* 2014, Boschen *et al.* 2016). Currently all offshore connectivity advice is derived from shallow water species data (Wedding *et al.* 2013) although Hilario *et al.* (2016) have begun compiling deep sea PLD data which may in future inform more relevant advice.

With OSPAR promoting the "wait and see" approach to dispersal data integration for offshore networks, no method is currently suggested to assess the larval dispersal connections of exiting MPA networks.

1.4 Conclusions and aims of this thesis

Understanding dispersal and population spatial structures provides many ecological and evolutionary insights as well as having direct applications in the fields of conservation and management (Grimm *et al.* 2003). While traditional Ecology searches for broad scale patterns, it is becoming increasingly apparent that a more case-by-case approach sympathetic to the dynamic complexity of the real world environment may be necessary in order to predict the effects of environmental change on marine populations (Benton and Bowler 2012, Evans *et al.* 2012). At the very least, shallow water and coastal observations taken from the top 2% of the earth's oceans, should not be trusted as being representative of deep water and offshore ecological patterns where factors such as weather , topography and water masses may differently impact the ecosystems in question.

While there are many methods available to investigate dispersal, in the deep sea where sampling can be problematic but exploitation and environmental change continues unabated, biophysical models may provide an important tool for marine managers and conservationists with the proviso that these must be validated before they can be trusted. Given the resources currently available, deep sea biophysical models are possible to construct, but with a lack of species-specific data we may often be restricted to the creation of null models until more data becomes available.

This thesis will aim to investigate the role of larval dispersal models (Lagrangian particle simulations) in future deep sea research, with particular focus on applications within marine conservation. With only three existing deep sea benthic invertebrate (non-vent) dispersal modelling studies (Yearsley and Sigwart 2011, Young *et al.* 2012, Etter and Bower 2015), this remains a field in its infancy.

There are existing studies exploring best practices and sensitivity testing of biophysical models (North *et al.* 2009, Simmons *et al.* 2013), but to date these have all been in shallow waters, where smaller vertical distances and greater effect of weather drivers may alter the patterns observed. The first chapter of this thesis will therefore explore model sensitivity from a deep water perspective. The findings of these tests will then be applied throughout the thesis to ensure a robust approach is taken to all biophysical modelling parameters.

A logical next step is to explore the usefulness of the modelling approach. Many studies have previously estimated dispersal using average geographic distance and PLD (Shanks *et al.* 2003, McClain and Hardy 2010). This is a non-directional spreading approach which permeates into MPA design and is unsympathetic to the directional nature of currents (Gaines *et al.* 2003). A study comparing such metrics with dispersal potential inferred from passive advective biophysical models will highlight whether the disparity in estimates is significant.

This chapter will also compare the passive dispersal trajectories driven by two different hydrodynamic models. The range of hydrodynamic models available is large for a reason, each being tailored to different research avenues and applications. Existing ecological models of larval dispersal have been based on many different hydrodynamic models, the output of which has been implicitly trusted by the authors with varying levels of validation. To date the outputs of different hydrodynamic models, each with features which may recommend it above others, have not been compared. Should outputs agree on the whole, there could be potential for model cross-validation to improve trust in outputs, but should they differ, greater caution would be advised, and the burden of trust solely placed on empirical validation.

The final chapter of this thesis will integrate the advice of the previous two chapters into an assessment of larval dispersal connectivity of an existing MPA network. Currently there is no method for assessing MPA connectivity performance for an existing network. Applied to the greater network of offshore MPAs to the west of the UK and Ireland, this study will fill a gap in the knowledge currently available to regional marine conservationists and managers.

This chapter will also examine the difference between passive and active larval dispersal connectivity patterns. Young *et al.* (2012) observed only a modest difference in dispersal potential during one release month when applying ‘active’ vertical migrating parameters to model the dispersal of the Siboglinid worm *Lamellibrachia luymesi*, which is contrary to studies in shallow water showing active strategies can significantly change dispersal patterns, often in favour of higher local retention rather than dispersal capabilities (Cowen *et al.* 2006). The case study MPA network used in this chapter has been established largely for the protection of reefs formed by the cold-water coral *Lophelia pertusa* (Linnaeus 1758); a species for which larval characteristics have recently been observed. However these active dispersal characteristics are based on laboratory observations, and may not be representative of *in situ* behaviour. This chapter therefore will create two null models of dispersal (one passive and one maximally active informed by *ex situ* observations). The differences between the connectivity patterns of each null model will be examined and compared to the previous literature, before being averaged to form an ‘intermediately active’ prediction for the MPA assessment.

Although many of these studies may seem primitive in comparison to the capabilities of shallow water biophysical models, the deep sea is an area in urgent need of attention in the face of rising exploitation such as deep sea mining. By exploring the possibilities of what can be achieved using existing knowledge this thesis aims to inspire more use of this technology in deep sea studies worldwide, and while species specific data may be considerably lacking for deep sea fauna, there is still opportunity to begin building hypotheses using this technology with existing data.

2. Increasing the depth of current understanding: Sensitivity testing of deep sea larval dispersal models for ecologists

Larval dispersal is an important ecological process of great interest to conservation and the establishment of marine protected areas. Increasing numbers of studies are turning to biophysical models to simulate dispersal patterns, including in the deep sea, but for many ecologists unassisted by a physical oceanographer, a model can present as a black box. Sensitivity testing offers a means to test the models' abilities and limitations and is a starting point for all modelling efforts. The aim of this study is to illustrate a sensitivity testing process for the unassisted ecologist, through a deep sea case study example, and demonstrate how sensitivity testing can be used to determine optimal model settings, assess model adequacy, and inform ecological interpretation of model outputs. Five input parameters are tested (timestep of particle simulator, horizontal and vertical separation of release points, release frequency, and temporal range of simulations) using a commonly employed pairing of models. Procedures are relevant to all marine larval dispersal models. It is shown how results can inform the future set up and interpretation of an ecological study in this area. For example, an optimal arrangement of release locations spanning a release area could be deduced; the increased depth range spanned in deep sea studies may necessitate the stratification of dispersal simulations with different numbers of release locations at different depths; no fewer than 52 releases per year should be used unless biologically informed; 3 years of simulations chosen based on climatic extremes may provide a result with 90% similarity to 5 years of simulation; and this model

setup is not appropriate for simulating rare dispersal events. A step-by-step process, summarising our advice on the sensitivity testing procedure, is provided to inform all future unassisted ecologists looking to run a larval dispersal simulation.

2.1 Introduction

Dispersal has many important ecological functions in regulating the structure of a population. These have consequences for species survival and evolution. Dispersal therefore has an impact upon conservation and management decisions and is a pivotal factor in the establishment of self-sustaining marine protected area networks worldwide.

Biophysical modelling (the use of hydrodynamic data (e.g. in situ ADCP data or the outputs of hydrodynamic models) combined with biological parameters to advect theoretical particles representing animals in order to predict dispersal patterns) is a well-established technique in shallow water dispersal studies. This technique has been applied to studies of e.g. jellyfish (Dawson *et al.* 2005), juvenile turtles (Putman *et al.* 2014), larval fish (Bonhommeau *et al.* 2009), and larval invertebrates (Foster *et al.* 2012) in order to discern the influence of ocean currents on faunal dispersal abilities. A number of review articles are available in this field to familiarise any ecologist with suitable methods and their requirements (e.g. Levin *et al.* 2006, Werner *et al.* 2007, Metaxas and Saunders 2009, North *et al.* 2009, with Metaxas and Saunders (2009) specifically addressing the bio- components such as mortality and larval behaviour - factors which are not addressed in this paper).

In the deep sea however biophysical modelling is still in its infancy due to the paucity of well resolved biological (e.g. larval behavioural data, mortality estimates, swimming speeds, buoyancy, etc.) and oceanographic data required to drive dispersal simulations. To date, deep sea studies are mostly focussed on vent and seep fauna (e.g. Marsh *et al.* 2001, Mullineaux *et al.* 2002, Bailly-Bechet *et al.* 2008, Young *et al.* 2012), with a few more recent studies beginning to apply biophysical models in other settings (e.g. polyplacophoran wood-fall specialists (Yearsley and Sigwart 2011), sedimented slope echinoids (Young *et al.* 2012), protobranch bivalves (Etter and Bower 2015), source-sink hypothesis (Hardy *et al.* 2015)). Most of these studies required the assistance of a physical oceanographer to build and run the models.

Now, with the availability of reasonably resolved hydrodynamic model outputs and custom particle tracking software designed specifically to simulate larval dispersal, the number of deep sea studies is likely to increase. Fossette *et al.* (2012) provide an overview of potential sources of hydrodynamic data, and the supplementary data associated with Hilario *et al.* (2015) reviews some of the offline particle tracking software suited to larval dispersal simulations. These tools could be used without the additional assistance of a physical oceanographer, but there is the risk that ecologists may be faced with a black box: a model which appears to work but whose inner workings are unknown, potentially resulting in misuse and misunderstanding of the models capabilities. This study hopes to offer some guidance to those ecologists who, by design or necessity, choose to fly solo.

While user manuals and literature written on model builds may elucidate many of the model's inner workings, sensitivity testing – the permutation of model input parameters to observe the result in model outputs – can provide practical insight into the workings of the model, define limits on input parameter values, and temper expectations of what conclusions can be drawn from simulations (Stow *et al.* 2009). Existing publications provide some insight into shallow water sensitivity tests (Simons *et al.* 2013) and cautionary tales regarding model temporal and spatial resolution (Putman and He 2013) but to date there is little advice catering to deep sea model users who may encounter additional challenges.

There are three critical caveats of biophysical modelling that need to be understood before undertaking a modelling study: 1) by definition a model is a simplification of reality and therefore cannot be expected to represent every process adequately, 2) hydrodynamic models are usually built by and for physical oceanographers and therefore are not tailored to the needs of larval dispersal modelling and will require some compromise on the part of the ecologist, 3) there is usually a trade-off between model quality and computational power (and this applies to both the hydrodynamic model and the particle simulator). These issues are compounded when working in the deep sea. The potential for longer planktonic larval durations due to metabolic constraints in cold deep sea waters (Bradbury *et al.* 2008, Brown *et al.* 2004, McClain and Hardy 2010) requires that models span large areas, over greater depth ranges than shallow water/coastal studies, usually in locations which are offshore and therefore lacking in high resolution data. Models which best fulfil this requirement are currently based on topographic maps derived from altimetry readings: a method with poorest topographic accuracy over areas of deep water and thick sediment seafloor. New topographic maps (not used in existing models) were produced in 2014 improving existing maps by 2-4times resolution, yet still these are only able to detect seamounts 1-2km tall (Sandwell *et al.* 2014). As topography induces many hydrodynamic features, if the topography is inaccurate or coarsely resolved the hydrodynamics will also suffer. The need to cover large areas of ocean demands coarsened resolution due to computational restrictions involving temporal and spatial averaging which further reduces the accuracy of the hydrodynamics (Putman and He 2013) especially when considering the scales of relevance to a microscopic larva (Metaxas and Saunders 2009).

The environment at depth is often considered more stable than in surface waters but there are still many turbulent events such as benthic storms, caused by turbidity currents and deep penetrating eddies, which may occur 8-10 times a year (Harris 2014) and which are unlikely to be represented within dispersal simulations using most existing large scale hydrodynamic models. This simplified view of deep water is perpetuated in standard model output structures such as the Levitus convention of data structuring where the deeper you go the coarser the output resolution (in Levitus one data point is output every 50m at 150m-300m depth, then every 100m at 300m-1500m, every 250m at 1500m-2000m, and every 500m from 2000m-5500m depth). Therefore biophysical models run from model outputs may result in decreasing sensitivity of parameters with depth due to the coarsening resolution of output data points between which the simulator interpolates.

Beyond the trade-offs already built into the construction of the hydrodynamic model, the running of a particle simulator can place heavy demands on computational effort and analysis time (North *et al.* 2009): a problem that would usually be the job of the physical oceanographer to solve, but which would fall to the ecologist if working alone. All of the parameters tested in this study affect the two most computationally intensive aspects of the simulation – the total number of particles being simulated, and the number of velocity fields being loaded into the simulator. It should therefore be a high priority to optimise these parameters: the modeller's aim being to find a balance between obtaining a saturated state within the model where you have fulfilled the full potential of the model's predictive power, whilst not including redundant autocorrelated simulations which are wasteful of computational power and analysis effort.

Knowing these caveats exist (and more besides, see Levin (2006), Werner *et al.* (2007), Metaxas and Saunders (2009), North *et al.* (2009), Hilário *et al.* (2015)), it is important that deep sea ecologists explore the capabilities and limitations of their model setup before undertaking an ecological study: tailoring the inputs to the structure of the model and tempering expectations as to what model outputs may realistically represent. Complementing the work of Simons *et al.* (2013), this study explores the sensitivity of several parameters, all of which may be affected more severely than in shallow-water studies (additional parameters are covered by Simons *et al.* (2013), and neither list is exhaustive of what could or should be tested). While other literature touches on the sensitivity testing of model parameters (e.g. Siegel *et al.* 2003, Tian *et al.* 2009, Blank *et al.* 2012, Peck *et al.* 2012), the purpose of this study is to provide a more step-by-step approach for those ecologists faced with setting up their first larval dispersal model:

The aims of this study are:

a) To describe methods suited to detecting spatial autocorrelation due to model structure and assessing model saturation (similar to undertaking a power analysis)
b) To show how these methods can be used to optimise model inputs and assess model adequacy
c) To highlight the ecological consequences of parameter settings and identify deep sea specific issues to benefit all future larval dispersal research

d) To provide a clear step-by-step procedure for other ecologists to follow when setting up their first larval dispersal model

2.2 Methods

2.2.1 Study area

This study, as an example, is focussed on the Northeast Atlantic in offshore waters west of the UK and Ireland. The region (Figure 3), centred on the Rockall Trough (RT), has been a hotbed for deep sea research for over a century and therefore offers a range of historic datasets which can be used for preliminary ground truthing. The region's currents (e.g. Holliday *et al.* (2000)) and water mass structures (e.g. McGrath *et al.* (2012)) are well documented.

Situated in the centre of the RT, Anton Dohrn Seamount (ADS) was selected as the focal point for the study providing a site for amphi-directional releases across a wide depth range in order to best capture the currents in the area. ADS is a guyot (table mount) with a summit at 521m, and a maximal depth in the South at approximately 2100m, although within the coarse bathymetry of the hydrodynamic model it extends between 600m and 2000m. ADS is also a focal point in Holliday *et al.*'s (2000) observational data for the region which spans 23 years of recordings at 22 full-depth standard location stations.

2.2.2 Hydrodynamic model

Freely available outputs from HYCOM+NCODA GLBa0.08 numerical model were used to provide the velocity fields which drive the particle simulator (hycom.org , (Chassignet *et al.* 2007)). Daily averaged data from 2008-2013 were used in the TR tests with focus on 2012-2013 for all other tests. HYCOM may lend itself well to deep sea studies due to its unique hybrid vertical grid structure within the native model (data are aligned with isopycnals in the open ocean, transforming to terrain-compressing layers over topography ("sigma grid")). The

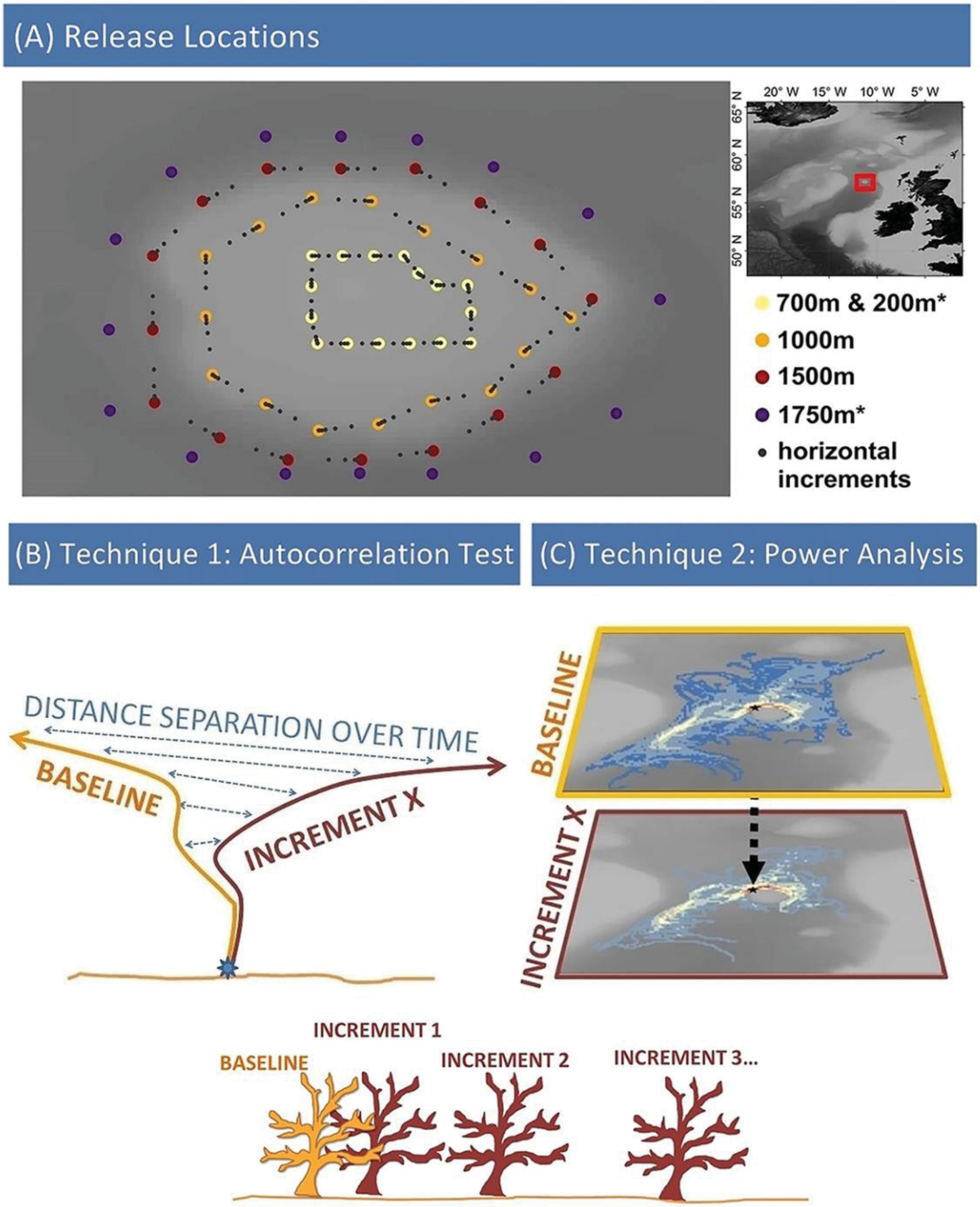


Figure 3 Study area and methods used in this study.

The study area (A) focused on Anton Dohrn Seamount (ADS) in the Rockall Trough region East of UK and Ireland. Release locations were defined based on model topography and equally spaced around the circumference of ADS at three standard depths (700m, 1000m, 1500m) with modified depths for the vertical separation test (200m and 1750m) and increment locations shown for the horizontal separation test (coordinates given in Appendix A1.1 p155). Two analysis techniques were used in this study: (B) The *Autocorrelation tests* are a comparison of each increment track with its corresponding baseline in terms of distance separation over time. (C) *Power Analysis tests* derive a linear correlation between rasters of track density, converting this into the fraction of unexplained variance metric (after Simons *et al.* (2013)). Bathymetry and topography data were obtained online from the GEBCO Digital Atlas published by the British Oceanographic Data Centre on behalf of IOC and IHO, 2003 (GEBCO 30 arc-second grid, www.gebco.net).

accessible outputs however average the native data into the Levitus depth structure. This study does not run a comparison between the native and output particle simulation methods, but does explore the capabilities and limitations of this common output structure which offers the most accessible velocity data to deep sea ecologists.

Vertical velocity is not output as standard from HYCOM and is not available in the HYCOM outputs used by this study. It can be calculated separately based on the continuity equation, but this parameter is known to be noisy, problematic, and would be based on an interpolated grid (output z-level grid) different from the native model (hybrid grid). Therefore vertical velocity was consciously excluded from this study. This is further justified in this case due to average background vertical velocity in the deep ocean being estimated at 10^{-5} cm s^{-1} (i.e. <1m in 100 days) (von Storch 2010), but should this variable be available we would advise its inclusion, especially when conducting simulations in shallower water. Note that test results are likely to be affected by the inclusion of vertical velocity vectors.

The HYCOM Global analysis outputs project their data onto a Mercator horizontal grid for the majority of the world, but north of 47°N they adopt an atypical bi-polar grid. While the study area falls within this potentially problematic region, the particle simulator model used in this study has a facility to translate the hydrodynamic data into a Mercator grid prior to simulations and was tuned for use with HYCOM specifically (but can be used with other model outputs). This facility was used during this study. Note that the more recently available HYCOM Global reanalysis data is already projected onto a Mercator grid north of 47°N.

Some velocity fields from Jan 4th 2012 were plotted using Matlab (v2013a) as an example in order to provide further context to test results.

2.2.3 Particle simulator

The freely available Connectivity Modeling System (CMS) is a recently-developed offline Lagrangian particle simulator (https://github.com/beatrixparis/connectivity-modeling-system (Paris *et al.* 2013)). It was especially developed for larval dispersal modelling with multiple modules available for the integration of biotic and abiotic data and is under continual development with additional modules becoming available for specialist uses. CMS has the facility to interface with the HYCOM servers and download hydrodynamic data directly. It can also utilise z-level stored hydrodynamic data in a variety of formats, whilst also providing a re-gridding routine to adapt any data in problematic formats (e.g. uncommon non-orthogonal projections as mentioned above).

CMS and HYCOM together have already been used as the basis of multiple studies within different fields (including non-biological) and have been employed in studies of coral reef connectivity (e.g. Kough *et al.* 2013, Holstein *et al.* 2014, Wood *et al.* 2014). This study uses the CMS in its simplest configuration; as a passive particle simulator. It uses a 4th order Runge-Kutta method of advection, and prioritises a tricubic interpolation method through space, although will alter this to tri-linear in the vicinity of land, or bicubic if run on a 2D basis (as is used here). A linear interpolation is also run between time snapshots to advect the particle through changing velocity fields.

It should be noted that this study does not test the number of larvae released per spawning event as the model set up used here does not parameterise diffusivity. Without diffusivity all larvae released in one spawning event would follow identical tracks. It is possible to add diffusivity, but in the CMS it would be an arbitrary nest-wide value which itself requires sensitivity testing and careful study-specific consideration. Diffusivity should be tested and used in studies seeking to simulate multiple larvae per spawning event.

2.2.4 Parameters

The following parameters were selected for testing in this study:

- Timestep (TS) of particle simulator
- Horizontal separation (HS) of release points
- Vertical separation (VS) of release points
- Release frequency (RF)

- Temporal range (TR) of hydrodynamic data

The first three parameter tests (TS, HS and VS) aim to **detect spatial autocorrelation as a product of model structure**. In dispersal models, every particle run is expected to provide useful data, but particles released too close together may show related outcomes entirely due to their spatial proximity. This is because model data are gridded (the model resolution defines the distance between data points) essentially causing data to act as if it is categorical rather than continuous. This is true for fine or coarse resolutions and for any interpolations applied; there will always come a point where a release location will be positioned within the same effective grid cell/category as another, thereby acting as a duplicate whose outcome is both unnecessary

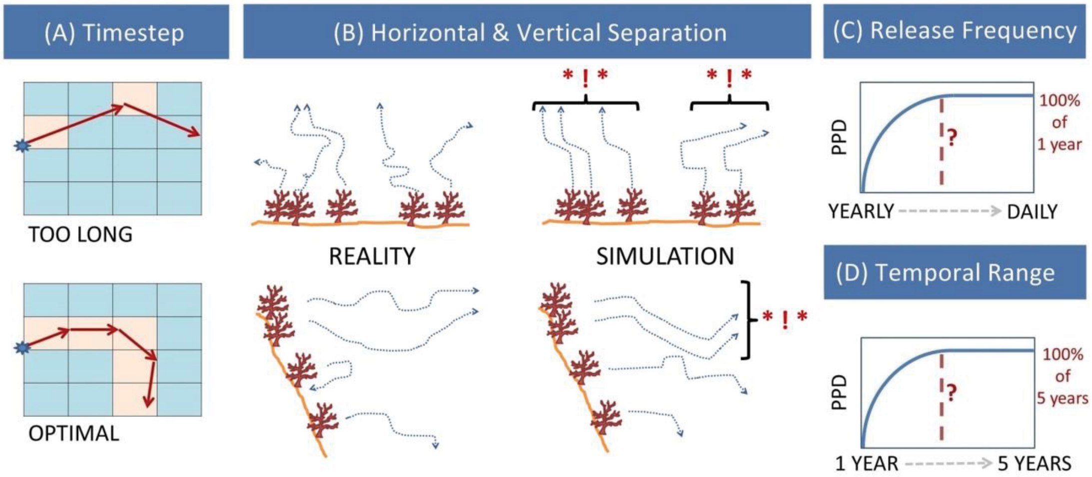


Figure 4 Descriptions of parameters tested in this study.

(A) Timestep of the particle simulator governs how often the simulator asks for instruction. In this heavily simplified diagram, highlighted squares within the model grid have been asked for instruction – if the timestep is too long the resulting pathway may be very different from a timestep which is short enough to interrogate each grid square it encounters. (B) Horizontal and vertical separation of release points (spawning animals) in reality may be very small and yet result in different pathways of dispersal, but in a model simulation proximate release points may be spatially autocorrelated (here marked * ! *) resulting in redundant simulations and a waste of computational power and analysis time. Both (C) release frequency and (D) temporal range tests act like a power analysis aiming to fulfil saturation of the models potential pathways of dispersal (PPD) either by simulating enough spawning events within a given period (e.g. 1 year: release frequency), or by running simulations in enough years to be representative of a larger time period (e.g. 5years: temporal range).

and unmeaningful. The aim of these tests is to ensure that all release positions simulated will represent independent samples from which ecological conclusions can be drawn. Therefore we ask: what is highest resolution parameter setting that does not result in spatially autocorrelated outputs?

The TS of the particle simulator governs how often the simulator interrogates the hydrodynamic model for instruction to redirect the particle. The aim here is to ensure the simulator asks for instruction frequently enough so that data is received from every grid cell along the dispersal pathway (as opposed to passing through several cells without "asking" for directions, Figure **4**). As expected from the relationship between time, velocity and distance, TS is affected by the velocity range in the study area, and the resolution of the hydrodynamic model data (equivalent to distance). Indeed the Courant number (C_r) is often used to test appropriate timesteps (ΔT) for a given grid resolution (ΔL) where average velocity ($\overline{V}$) is known:

$$C_r = \frac{\overline{V}\Delta T}{\Delta L}$$

The test we offer here does not require prior knowledge of average velocity but can be used to back compute average velocity, potentially making this more useful to the ecologist with limited awareness of local currents. Ideally the TS test should be run first to ensure that the results of other tests are not affected by using the wrong default TS.

An ecologist may expect to define the HS of release points using realistic positioning of individual animals or by release area, e.g. habitat patches such as reefs. However within a model proximate populations may be spatially autocorrelated even if they would not be considered as such in real life (Figure **4**): e.g. simulating larval release from individual animals, which may access different turbulences and micro currents in real life, could produce identical predicted pathways of dispersal (PPDs) for 500 proximate animals. Existing studies have recognised this and coarsened their HS using repeated simulations of larval release from randomly chosen coordinates within a release area (e.g. Young *et al.* (2012)) or by using centroids of subdivided area polygons with a size defined by the resolution of the hydrodynamic model (Foster *et al.* 2012, Simons *et al.* 2013, Wood *et al.* 2014). While the resolution of the model may provide a reasonable guide as an upper limit in HS, a concern for those using coarser models is the interpolant of the particle simulator which further refines the model resolution and may allow release points with a sub-grid scale separation distance to produce independent PPDs. By defining the HS at which spatial autocorrelation is no longer a concern, decisions about adequately positioning release points can be better informed. HS should be expected to be dependent upon the horizontal resolution of the hydrodynamic model, the interpolative ability of the particle simulator, and the TS of the particle simulator. The planktonic larval duration (PLD/equivalent to the length of time the simulation is run) is also likely to have an effect as the longer you track particles, the more chance they have to deviate from each other.

The same issue applies to VS, whether spawning animals are situated on a slope or a vertical cliff, the model's vertical resolution may affect the spatial autocorrelation of release points dispersed across depth bands (Figure **4**). Simons *et al.* (2013) tested this parameter between 2m and 30m from the surface, but in the deep sea there is much greater scope for varying sensitivity as the reference depth may be anywhere between 200m -11000m (continental slope - trenches), and the vertical resolution of the model may vary with depth (as is run in the native HYCOM or found in a model output structure such as the previously mentioned Levitus convention). Results will likely be affected by the vertical data structure and the interpolative ability of the particle simulator. If vertical velocities and diffusion are included in model simulations, VS will also be affected by particle simulator TS.

For both the RF and TR tests we **assess model saturation and temporal autocorrelation**. Similar to a power analysis (e.g. finding how many quadrats would be required to represent the species composition of an area) we consider the parameter values which maximise the potential of the models predictive power and search for the coarsest resolution parameter setting which is still reflective of this asymptote. For the parameters tested this can be summarised as asking:

how much temporal resolution can we lose while still adequately representing a high resolution baseline?

RF is akin to the number of spawning events in a given period of time (e.g. hourly, daily, etc.). Reality may define the spawning period e.g. seasonal spawning may limit the simulation to a particular month, but the frequency of spawning events within that period is often unknown. Testing this parameter can offer a means to ensure that the maximum potential number of PPDs have been predicted whilst using the coarsest possible (most computationally economic) parameter setting (defining the point of asymptote Figure **4**). Equally if spawning periodicity is known (e.g. 6 deep sea species with lunar periodicity (Mercier *et al.* 2011), or 2 deep sea corals with annual planulation (Mercier and Hamel 2008)), defining the point where RF reaches asymptote can show whether the model is capable of simulating your required setting, and if not what setting gives equivalent results. RF operates as a function of how temporally variable hydrodynamic conditions are within the model. If it is necessary to run a RF test, this should be done prior to HS and VS tests as it will affect whether you have captured the full variability of the modelled currents and therefore could affect the outcome of these tests. An inadequate RF is called an under-sampling/under-seeding problem (Simons *et al.* 2013, Brickman and Smith 2002). Other methods are available which offer similar results e.g. Brickman and Smith (2002).

Ideally any modelling study will be representative of a longer period of time than actually simulated, e.g. Simons *et al.* (2013) used 3 years of different climatic phenomena (El Niño/La Niña/normal) to encompass the extremes of sensitivity in order to account for any chosen period of simulation in the study area. The TR test examines this sort of assumption by running a simulation over a longer period and checking whether any subset of years within this period (e.g. a set of 3 chosen based on climatic phenomena) could be deemed representative of the full simulation. In this test we aim to discover whether selecting years based on their North Atlantic Oscillation index (which would be a similar approach to Simons *et al.* (2013)) could give similar results to running simulations over the whole period.

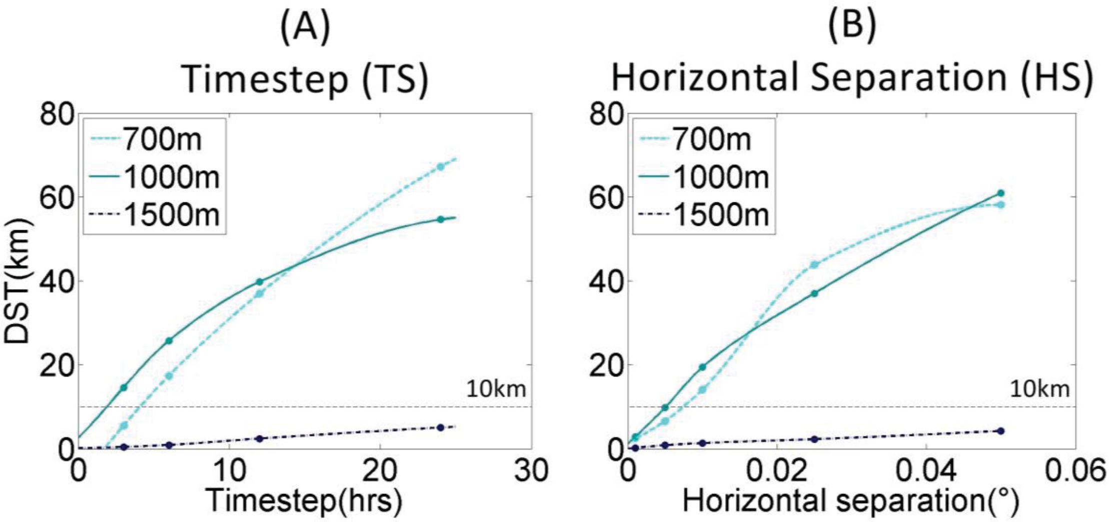
2.2.5 Sensitivity tests

Release locations were defined based on HYCOM output topography, identifying sites which interface with ADS at each depth in order to simulate the release of benthic larvae. Dispersal simulations were run from 16 release locations equally spaced around the circumference of ADS at three different depths (700m, 1000m, 1500m) (Figure 3). The replicate 16 locations and 3 depths were used to control for differing states of hydrodynamic mixing. A planktonic larval duration (PLD) of 100days was used to capture the majority of known PLDs: Hilario *et al.* (2015) includes a study of known PLDs of eurybathic and deep sea species stating that 50% would be accommodated by a PLD of 35d, and 75% by 69d, 100d equating to approximately 90% of species included in that study.

All sensitivity tests were carried out using multiple model runs with all parameters held the same throughout the test except for the parameter being permuted. All tests, unless otherwise stated, use a particle tracking time-step of 1 hour, data from the year 2012 (4th Jan 2012 until 14th March 2013 to be inclusive of 100days tracking from 4th December 2012), the same 16 release positions per depth band at 700m, 1000m, and 1500m (see Appendix A1.1 (p155) for exact release locations of each test), and a monthly RF as standard. Permuted increments for each test and custom setups which differ from the aforementioned standard are shown in Table **3**. HS increment locations were defined in ArcGIS 10.1 using buffers of appropriate radius centred on the baseline release locations, with final increment release locations placed along the seamount contour to maintain the interface with the seamount. All horizontal increments are subgrid-scale compared with the model resolution and are defined in degrees in order to be comparable to the model (projected distance e.g. km would vary with latitude and be different in latitude vs longitude due to the model using grid cells defined in degrees). Standard baseline depths in the VS test were altered to best capture the different Levitus data resolutions. In Levitus, at 200m the next data point is 50m away, at 1000m it is 100m away, and at 1750m it is 250m away whereas at the standard depths used in other tests (700m, 1000m, 1500m) data points are all at the 100m resolution. The TR test was conducted over a five year period and all

Sensitivity Test	Baseline (all increments compared to this)	Increment list	Customisation different from default
Timestep	INDIVIDUAL spawning event at default locations with TS= 1 hour.	3hrs, 6hrs, 12hrs, 24hrs	n/a
Horizontal separation	INDIVIDUAL spawning event at default locations (=0°)	Location modified by +0.001°, +0.005°, +0.01°, +0.025°	n/a
Vertical separation	INDIVIDUAL spawning event at modified standard depths (=0m)	Depth modified by-0.1m,-1m,-10m,-50m	Depths were modified to monitor effect of Levitus structure (200m releases are above summit of seamount)
Release Frequency	MULTIPLE spawning events per individual location from 365 releases (daily through 1 year)	183 releases (2 daily) 104 releases (biweekly) 52releases (weekly), 12 releases (monthly), 4 releases (seasonal)	n/a
Temporal Range	MULTIPLE spawning events per individual location from 5years of releases (12 releases per year)	1yr, 2yr, 3yr, 4yr (multiples are also permuted e.g. 3yr = yr1+yr3+yr5)	n/a

Table 3 Parameters tested in this study



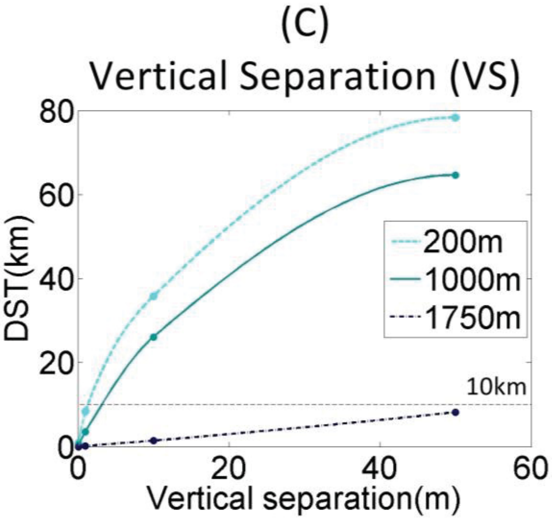


Figure 5 Results of spatial autocorrelation tests.

Parameter increments from tests of (A) Timestep, (B) Horizontal Separation and (C) Vertical Separation, were plotted against median Distance Separation over Time (DST) with a piecewise polynomial interpolant applied between increment values of the same depth. A DST of 10km (based on records of larval habitat detection abilities) was taken as the autocorrelation/independence threshold allowing an optimal increment per depth to be derived from the intersection between the interpolant and the threshold. Optimal values derived from these plots are shown in Table 4.

year combinations within this period compared (5 x 1yr iterations, 10 x 2yr,10 x 3yr, 5 x 4yr, 1 x 5yr), and assessed relative to the North Atlantic Oscillation (NAO) state.

2.2.6 Analysis

There are two analysis techniques used in this study relating to the two methodological aims set out in the introduction (Figure 3).

Detecting spatial autocorrelation due to model structure

Each of the three parameters (HS, VS, and TS) was tested with a track-by-track comparison method in order to detect increment spatial autocorrelation or independence when compared with test baselines. One track is used as a baseline, and the increment track is compared to this over time using the curved earth distance separation between them as a measure of independence/autocorrelation (hereafter termed Distance Separation over Time (DST)). Different release locations (x16), depths (x3) and times (x12) are used as replicates to provide a median averaged result with controls for different current regimes in space and time. There are therefore 576 baseline tracks tested against their corresponding four increment tracks (192 per baseline depth band), totalling 2880 particles simulated per baseline/increment pairing. Analysis was performed in Matlab with DST curved earth distances derived using the haversine equation. All analyses were based on median averaged results as compared to a reference 10km threshold which represents the distance below which tracks would be deemed spatially autocorrelated. This is an arbitrary threshold value which should be defined within the context of the study: in this case 10km was selected as an example due to Foster *et al.* (2012) and Paris *et al.* (2007) agreeing this as a distance where competent larvae are likely to be able to detect and orient towards suitable habitat. Supplementary ANCOVA tests of increment and depth significance were run in the statistical software environment, R.

Assessing model saturation

The two parameters analysed to assess model saturation (RF and TR) could not be compared using a track-by-track comparison as they trial different temporal frequencies and therefore contain multiple tracks per baseline or increment. There are therefore 16 replicates per baseline depth band, or 48 replicates total. This amounts to a minimum and maximum number of particles simulated per test of RF: 192 (seasonal) / 17520 (daily) and TR: 576 (1year)/2880 (5years), with the maxima representing the baselines. The method used for this comparison is similar to that used by Simons *et al.* (2013)). The simulator outputs of particle position per day were converted into track lines in ArcGIS 10.1 and compiled into track density grids, per baseline or increment (i.e. counts of replicate tracks), per 2D spatial cell at half the resolution of the hydrodynamic model (here 0.0416665°). Track density plots differ from particle density distributions as no particle is counted twice per grid cell (representing numbers of tracks rather than repeated particle cell occupancy). The fraction of unexplained variance (FUV) was then found between each baseline/increment pairing:

$FUV = 1 - r^2$, where r is the linear correlation coefficient between track density rasters, as

compared on a cell by cell basis and summarised as a single value per raster pairing. Following Simons *et al.*'s (2013) example, a 0.05 threshold FUV variance was used to define the point where variance was minimal (and therefore the increment gave effectively the same result as the baseline).

2.3 Results

2.3.1 Spatial autocorrelation tests

For all three tests, plots are shown of the median separation distance between each increment/baseline pairing across all replicate locations and all days tracking plotted against increment with a piecewise cubic hermite interpolating polynomial line fitted to the data (Figure 5). These plots can be used in order to identify an increment value below which autocorrelation will occur. These values, hereafter referred to as 'optimal values', are shown in Table 4. Appendix A1.2 (p157) provides boxplots of this data which are provided to give some scale of the variability in the data which may be of use if, for example, rare dispersal events are important to the outcome of the study or if suboptimal parameter values must be used and it is desirable to quantify the error that results. The results of ANCOVA tests of increment and depth significance can be found in Appendix A1.3 (p158). Additional plots of median separation distance between each increment/baseline pairing over time (Figure 6) are shown for the HS test in order to show the effect of PLD on parameter sensitivity.

Horizontal separation

The plot in Figure 5 shows that DST increases with horizontal distance between release points. At 1500m depth, all tested increments were autocorrelated with a median DST well below the example 10km threshold. At 700m and 1000m depth, track deviance increased beyond the threshold at 0.0075° and 0.005° horizontal distance respectively providing a minimum distance for HS at these depths.

Figure 6 shows the effect of PLD (tracking time) upon HS sensitivity, with Hilario *et al.*'s (2015) benchmark PLDs marked as examples. By looking at the median DST per day of tracking, per

Parameter	Test Type	Optimal Value
Timestep (TS)	spatial autocorrelation	2hr (1000m) 4hr (700m) ~48hr (1500m)
Horizontal Separation (HS)	spatial autocorrelation	0.005° (1000m) 0.0075° (700m) ~0.08° (1500m, this model resolution)
Vertical Separation (VS)	spatial autocorrelation	1.5m (200m) 3m (1000m) 60m (1750m)
Release Frequency (RF)	model saturation	150releases per year (700m) 160releases per year (1000m) 75releases per year (1500m)
Temporal Range (TR)	model saturation	4.3yrs monthly releases (700m) 4.3yrs monthly releases (1000m) 4.1yrs monthly releases (1500m)

Table 4 Optimal value results of parameter sensitivity tests.

All tests of spatial autocorrelation result in values less than the optimal value being spatially autocorrelated with the baseline (these tests define a high resolution baseline). All tests of model saturation (akin to a power analysis) result in values greater than the optimal value being temporally autocorrelated with the high resolution baseline. This data is derived from Figure 5 and Figure 7.

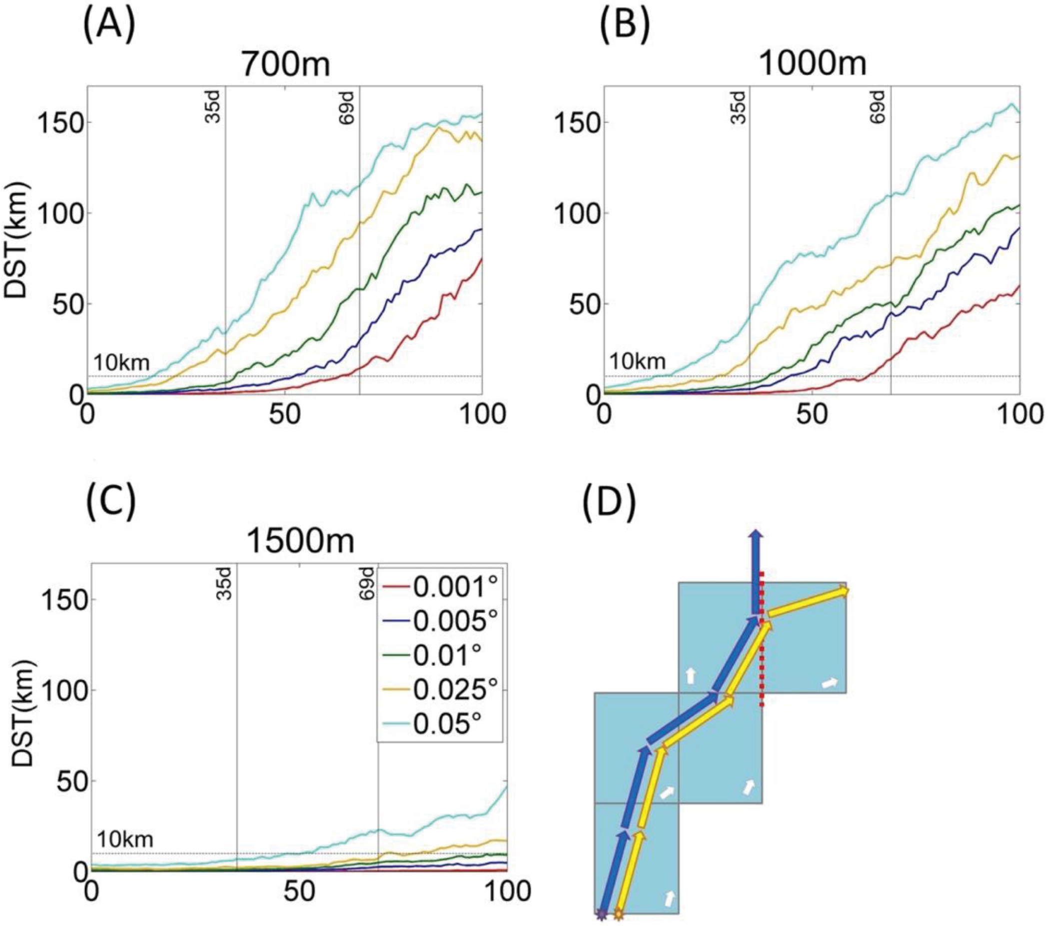


Figure 6 Plots, per depth, of horizontal separation increments Distance Separation over Time (DST) against tracking time (or Planktonic Larval Duration (PLD)).

A 10km autocorrelation/independence threshold is shown and PLDs of 35days and 69days are marked reflecting PLDs which accommodate 50% and 75% of all known PLDs of deep sea and eurybathic species (Hilario *et al.* (2015)). Plots are shown for (A) 700m, (B) 1000m and (C) 1500m simulations. The right-hand diagram (D) demonstrates the possibility of two spatially autocorrelated tracks eventually accessing different instructions (represented by the white arrow in each grid cell) and deviating. This may account for the increased sensitivity over time, and may encourage interpretation as increased likelihood of error over time

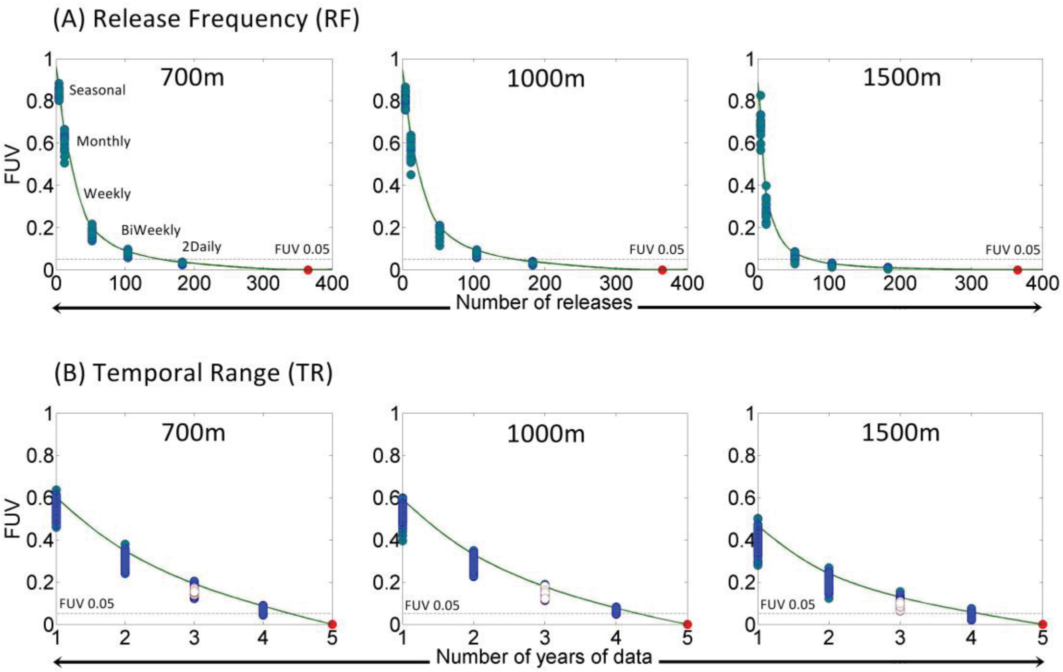
increment, it is clear that in tests with different PLDs the HS sensitivity would be different. In this test all increments of HS would remain autocorrelated (stay within the example 10km independence threshold distance) every day for up to 18 days at all depths. This means that with this model set up you cannot model PLDs of less than 18 days at sub-grid scale spacing without spatial autocorrelation. At 1500m all increments of HS are autocorrelated up to 52 days PLD. In order to model dispersal of species with a PLD of 35 days (Hilario *et al.*'s (2015) 50% of known deep sea species) our results show that at 700m and 1000m depth >0.01° separation between horizontal release locations is required with 0.025° being the first tested increment that fulfils this criteria. At 1500m all increments trialled are spatially autocorrelated and thus a horizontal separation distance of >0.05° (potentially equivalent to model resolution 0.08°) is required. However, to model dispersal of species with a PLD of 69 days (Hilario *et al.*'s (2015) 75% of known deep sea species) horizontal release locations of 0.001° would provide spatially independent larval dispersal pathways at 700m and 1000m. At 1500m >0.025° degrees separation between horizontal release locations is still required with 0.05° being the only tested increment that fulfils this criteria.

Vertical separation

Again all increments tested at the deepest baseline depth (1750m) were considered autocorrelated if using the 10km threshold (Figure 5) although the polynomial interpolation suggests that the threshold for independence may be approached at approximately 60m separation. Therefore it may be advisable to stratify release locations by 60m depth separation when at around 1750m depth. At 200m and 1000m baseline depths, VS is considerably more sensitive, with release locations separated by only 1.5m and 3m vertical distance respectively expected to track independently from each other.

Timestep

All TS tests were compared to a baseline of 1hour. The first (3hr) increment at 1000m depth was already independent from the 1 hour track with the polynomial suggestive of a threshold at approximately 2hrs. It would therefore be advisable to use at least a 2hr timestep at 1000m depth. Interestingly the threshold, and therefore advised timestep, at 700m was closer to 4hr (Figure 5). At 1500m depth the largest increment – 24hrs – still resulted in autocorrelated tracks when using the example 10km threshold. In spite of this it is advisable to stick with at least a daily frequency as the temporal resolution of the hydrodynamic data is also daily.



FUV	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
COR	0.99	0.96	0.91	0.84	0.75	0.64	0.51	0.36	0.19	0

Figure 7 Results of temporal power analysis tests.

Plots, per depth, for (A) Release Frequency and (B) Temporal Range tests, show increment values plotted against FUV scores. An FUV score represents one baseline/increment comparison, with a minimum of 16 replicates per increment (there are more in the temporal range test). A piecewise polynomial interpolant is fitted so that 95% of FUV scores fall below the line. The asymptotic threshold is defined as an FUV of 0.05 after Simons *et al.* (2013). Temporal range tests show FUV scores in white where three year datasets comprise years with optimal NAO indices (2009, 2010, and 2012 – see Figure 8). The table at the bottom shows the relationship between FUV and Pearson correlation values.

2.3.2 Model saturation tests

Each FUV value was plotted per increment and a piecewise cubic hermite interpolating polynomial line fitted to the data in order that 95% of FUV values within each increment fell below it (Figure 7). This ensured that the polynomial was representative of the range of FUV values per increment and means that when the polynomial crosses the threshold 0.05 FUV the

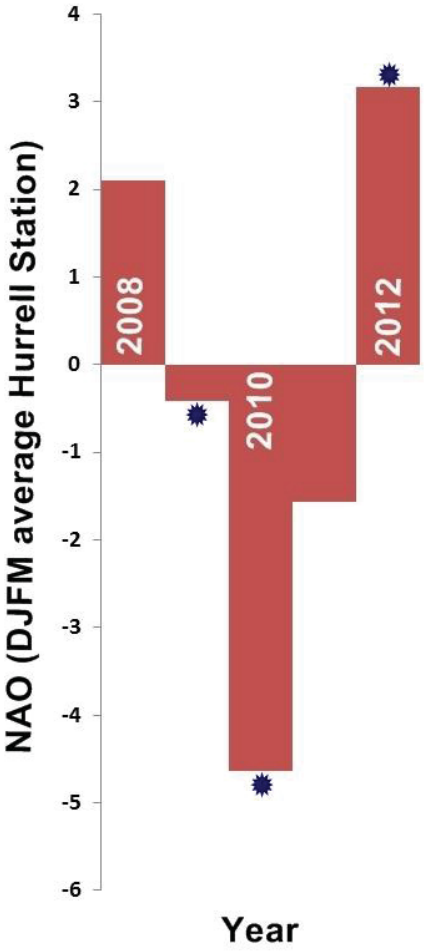


Figure 8 North Atlantic Oscillation (NAO) indices.

Following Simons *et al.*'s (2013) approach to El Niño, data from 2009 (NAO neutral), 2010 (strong negative) and 2012 (strong positive) should provide enough data to represent the full five years of simulations. Indices are plotted as December to March averages as recorded at Hurrell Station. Data sourced from http://climatedataguide.ucar.edu.

variance in FUV values should also have decreased below this value. The increment value where the polynomial crosses the 0.05 FUV threshold, hereafter referred to as the 'optimal value', is shown in Table 4.

Release frequency

The FUV variance (spread of points per increment) decreases steeply with the tested increment resolution (Figure 7) although seasonal releases display little variance at 700m and 1000m, but have large FUV values indicating a correlation between maps of <0.36. The piecewise polynomial suggests that the FUV and 95% of its variance would decrease below the 0.05 threshold at 150-160 releases per year at 700m and 1000m. This result would mean that the track density plots derived from 150-160 releases in 2012 at these depths are effectively the same as track density plots from 365 releases in that year. At 1500m the variance in FUV values per increment is much higher, e.g. seasonal (4 releases in a year) has a spread between 0.55 and

0.85 FUV (equivalent to a range of correlations from 0.70 to 0.28). At 1500m you would need at least 75 releases throughout the year to give an equivalent track dispersal plot to the baseline.

Temporal range

FUV decreases almost linearly with the number of years' data when compared with the full 5 years track density plot (Figure 7). The intersection of the piecewise polynomial with the 0.05 threshold suggests that 4.3 years of data would be required to represent the full 5years at both 700m and 1000m, although approximately 4.1 years of data would be adequate at 1500m. If an approach similar to that of Simons *et al.* (19) was used in this study only the three years starred in Figure 8 would be used, representing the two NAO extremes and a non-NAO event year, with results corresponding to the data points highlighted in white on Figure 7. Only at 1500m do these values approach the threshold FUV value, although they are still >than 0.05. This result suggests that the three NAO states which may be selected as representative of a longer period could not be considered equivalent to the track density plot of a full 5 years of releases.

Hydrodynamic model plots

Matlab plots of the average velocity values for the standard 3 baseline depths are shown in Figure 9.

2.4 Discussion

2.4.1 Optimal values

Using a commonly employed pairing of models (HYCOM Global 1/12° and Connectivity Modeling System), for the Rockall Trough region of the Northeast Atlantic, for a generalised species with PLD of 100 days and monthly spawning events, the optimal model settings for the parameters tested are shown in Table 4. Exceeding optimal value resolution (i.e. reducing distance or timestep, or increasing frequency or number of years of simulation) may result in a waste of computational and analysis effort although all PPDs will be represented; while coarsening resolution (i.e. increasing distance of timestep, or decreasing frequency or number of

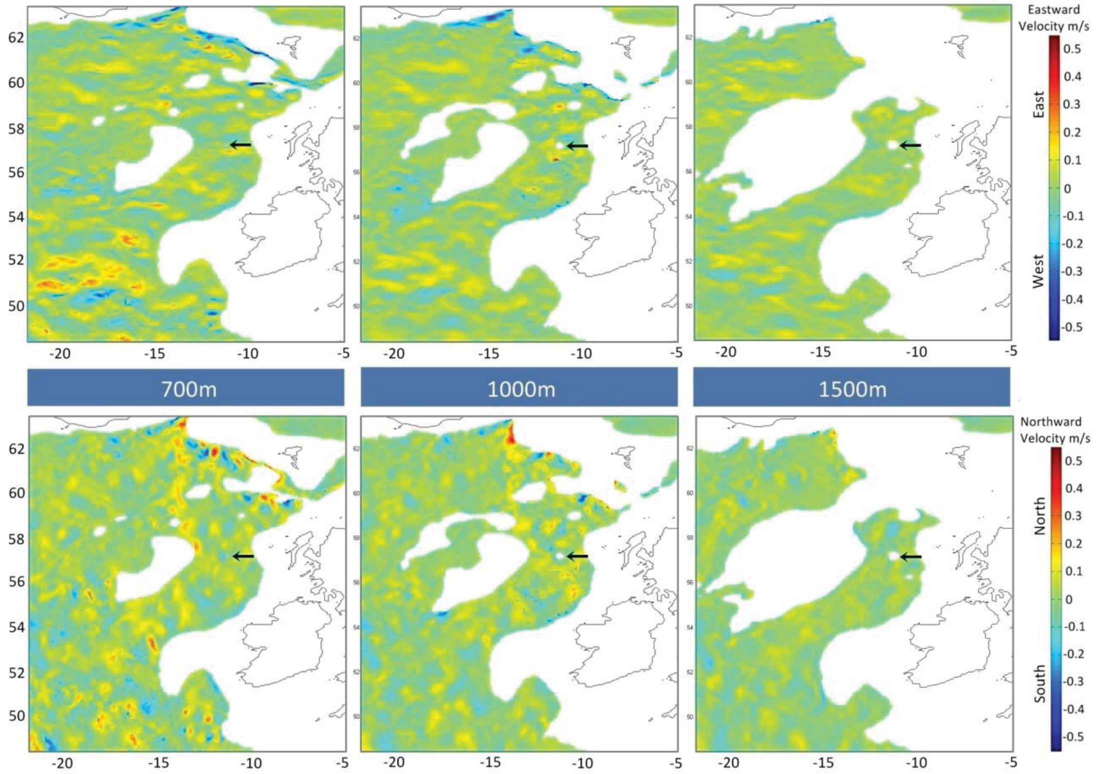


Figure 9 Example horizontal profiles of U and V velocity taken from one day in HYCOM (4th Jan 2012).

U velocity measures current speeds in an East (+ve)/West (-ve) direction (top three plots), and V in a North (+ve)/South (-ve) direction (bottom three plots). Anton Dohrn Seamount is marked in each depth slice with an arrow. Areas of different velocity from the background values appear as coloured patches. Profiles from 1000m show the greatest variation in current velocities (more small patches). Profiles from 1500m show the least variation in velocity. Topographic contours are derived directly from HYCOM velocity data.

years of simulation) could omit PPDs which the model was capable of predicting potentially to the detriment of study conclusions.

While it is always preferable to use optimal values (or a higher resolution), sometimes it is not possible to achieve this and coarser values must be used. In this situation the results of sensitivity tests can offer a means to quantify error due to sub-optimal parameter values.

The FUV method offers the best error quantification technique as FUV values are derived from linear correlations (r). The FUV=0.05 threshold and 95% of FUV values variance control used in this study (RF and TS tests) was taken from Simons *et al.* (2013), meaning that 95% of baseline/increment comparison replicates exceeded a correlation of 0.9975. If the threshold was not met, a correlation could be derived from the 95% interpolation line of the highest resolution increment which can be used. For example, the RF test optimal value in this study was 150 releases per year at 1000m, but perhaps a weekly release frequency is the highest resolution setting possible. In the results of this study the weekly (52 releases per year) increment corresponds with an FUV of ~0.2 at 700m and 1000m, and ~0.1 at 1500m. This can be back-computed to a correlation between the weekly and daily PPDs as:

$$FUV = 1 - r^2 \qquad \text{Therefore:} \qquad r = \sqrt{(1 - FUV)}$$

(A table is provided at the bottom of Figure 7 to make estimating this even quicker).

As the FUV is read from the polynomial interpolation this represents the FUV that 95% of replicate FUVs fall below. Therefore at 700m and 1000m the correlation between a weekly and daily release frequency is ~0.96 or greater (FUV 0.2), and at 1500m is ~0.99 or greater. This may help decide or at least report the adequacy of the sub-optimal parameter setting which must be used in place of, and compared to, the optimal setting. As all of these FUV calculations are based on Simons *et al.*'s (2013) criterion 95% variance control value, there is also scope for varying this 0.05 FUV value in line with study aims (something which is also discussed in Simons *et al.* (2013)).

Error/accuracy is not so easily quantified using the described spatial autocorrelation technique, but median DST values of sub-optimal increments could be cited relative to the threshold, and boxplots of all DST values per increment (Figure A1 - 1 available in Appendix A1.2, p157) can provide benchmarks in terms of DST quartiles and outlier ranges. For example, a study undertaken at around 1000m depth would ideally have a VS of ~3m based on a 10km threshold distance according to Figure 5. If the resolution of depth recordings requires VS to be 10m (a sub-optimal value), then the plot in Figure 5 shows that at 1000m a 10m VS should be expected to, on average (median), be separated from a baseline track by ~25km (2.5 times the distance of the optimal value). You can also tell from the box plots (Figure A1 - 1, in Appendix A1.2, p157) that a VS of ~1m (closest to the optimal value of 2m) would have an upper quartile at around 100km, but at 10m VS the upper quartile approaches 250km (also ~2.5 times the optimal value). So perhaps you could estimate the accuracy of a 10m VS to be 2.5 times worse than that of the optimal value.

2.4.2 Model adequacy

As in Simons *et al.* (2013), all tested parameters were affected by the strength of the mixing in the local system as portrayed within the hydrodynamic model. All tests can therefore provide insight into the hydrodynamic conditions within the chosen hydrodynamic model, and offer a means to ground truth the combined hydrodynamic and simulator model's abilities and limitations.

The suite of tests run in this study serve to capture different aspects of the model hydrodynamics with two tests (HS, VS) detecting spatial variance, and two (RF, TR) testing temporal variance, while TS interacts with both. The resolution of the hydrodynamic model may inform some of the combined model limitations, but adjustments need to be made for the interpolation provided by the particle simulator.

Our findings suggest that with increasing depth, fewer sub-grid release positions are required in order to represent the full range of dispersal pathways it is possible to model for this particular pairing of models, and for this region. For this to occur neighbouring data points at shallower depths must produce steep differentials allowing different particle movement instructions to be obtained from interpolated intermediate locations, e.g. neighbouring cells instructing 0.9m s^{-1} Northeast and 0.8m s^{-1} South, may result in an interpolation instructing 0.1m s^{-1} East-Southeast midway between data points. This therefore suggests a high spatial variability in hydrodynamic data.

However our results at depth (1500m, 1750m) were less sensitive. The HS test revealed no independence of tracks until HS approached model resolution, and the VS test recommended separation at ~ ¼ model resolution (our result suggested that release positions should be every 60m at a depth where data points are separated by 250m in the Levitus vertical structure). This lack of sensitivity implies weak differentials between vertically neighbouring cells e.g. neighbouring cells instructing 0.7m s^{-1} Northeast and 0.8m s^{-1} Northeast, may result in an interpolation instructing 0.75m s^{-1} Northeast midway between data points which is very similar to the neighbouring instructions.

Further evidence of this interpretation can be gained by mapping horizontal or vertical slices through the hydrodynamic data. Figure 9 shows an example of three horizontal slices through HYCOM, detailing the current velocities and their variability. It is clear from these plots that current velocities are more variable at 700m and 1000m than at 1500m. Closer inspection of Figure 9 also reveals there to be more patchy instructions at 1000m compared with 700m which accounts for the switch in sensitivity between these depths in HS and TS tests: smaller patches require smaller distances be covered to ensure receipt of every new potential instruction.

Now, with some idea of how the currents behave within the combined model, comparison to empirical data can offer qualitative ground truthing of model predictions offering an assessment of combined model adequacy. HYCOM as a global model has been validated on a global scale but may not adequately represent the study area, so this is worth reviewing.

In this study the literature reveals that all shallower simulations undertaken in this area would occupy the same watermass - the poleward moving Eastern North Atlantic Water (ENAW) which extends down to 1200m and characteristically exhibits mesoscale activity and relatively high current velocities which would result in high variability of instruction through horizontal and vertical space (Holliday *et al.* 2000, Ullgren and White 2010, Sherwin *et al.* 2015). Winter convection in the area should be expected to mix surface waters down to 600m typically, although this may extend to 1000m in severe winters (Holliday *et al.* 2000).

Enhanced variation at 1000m may be due to a combination of factors. Eddies seen at shallower depths will have a smaller footprint at depth although the vorticity remains high and the

Hebrides Terrace Seamount summits at 1000m providing an additional stirring rod Southeast of ADS. There may also potentially be more interaction with intermediate water masses at 1000m: at this depth the core of Wyville Thomson ridge Overflow Water (WTOW) comes down from the north to the west of ADS, while Sub-Arctic Intermediate Water (SAIW) and Mediterranean Overflow Water (MOW) interact with the ENAW in a northward flow to the east of ADS (Ullgren and White 2010).

As a result of this qualitative ground truthing, the combined model in this study may be considered adequate when representing dominant water masses and mesoscale activity, but with no obvious influence of SAIW or MOW, intermediate water masses probably remain un-parameterised (however the WTOW is visible in Figure 9 at both 700m and 1000m depths).

The results of the TS test can also be used to validate the model current speeds as the relationship **velocity=distance/time** can be related to the HS (distance) and TS (time) for each depth e.g. in this study at 700m the recommended TS was 4hrs (equivalent to ~500m/4hr, based on 0.005° sensitivity) suggesting that local current speeds averaged around 0.4 m s^{-1} at this depth; the 1000m test recommends a maximum 2hr TS (750m/2hr, based on 0.0075° sensitivity) equating to current speeds of 0.10m s^{-1}; and the 1500m test may allow a TS >48hrs (8km/48hr, based on 0.08° sensitivity) equivalent to maximum average current speeds of 0.046m s^{-1} (although this result is based on extending the polynomial interpolant far beyond the extent of the graph in Figure 5). The literature does seem to bare out these assumptions with Booth and Meldrum (Booth and Meldrum 1987) recording currents with drifters (drogued between 66m and 166m) around Anton Dohrn as being up to 0.5m s^{-1} especially when caught in eddies, with a background flow of around 0.1m s^{-1}. Although derived from a different isopycnal model initialised from empirical data in the region, New and Smyth-Wright (2001) estimate the Labrador Sea Water in the region (which only starts at 1500m) as ranging in current speeds from 0.004 m s^{-1} to 0.1 m s^{-1}, with some of the weakest of those current speeds recorded in the vicinity of ADS (which was the location of one of their observational transects and is in line with empirical observations reported in Ellet, Edwards and Bowers (1986)).

Both the RF and TR tests are representative of the variability in current velocities over time and can be used to assess this variability within the model. The RF result of 150-160 releases per year as equivalent to a daily release (at 700m and 1000m) suggest currents in this daily averaged model vary on the scale of roughly every 2 days. As tidal cycles are averaged out, this is representative of topographically induced mesoscale activity in the area. The TR result demonstrates high interannual variability in current velocities. This can be assessed against the North Atlantic Oscillation (NAO) data which is often attributed to driving large scale interannual hydrodynamic variability due to its effect on convection regimes (New and Smythe-Wright 2001). The test results show that the NAO dataset would not perform as well as the full test dataset if the 0.05 FUV variance threshold is deemed appropriate. Some literature agrees with this assessment, with NAO being linked to but not fully accounting for the interannual variability in the complex hydrodynamics of the Rockall Trough region (Holliday *et al.* 2000, Ullgren and White 2010).This could have considerable consequence for the amount of data required to build PPDs valid over larger timescales, but at least the FUV and correlation scores can provide some quantitative estimate of how much is, or is not, captured within an NAO based dataset. As it stands using NAO selected years in this study would have a correlation to a 5year baseline of approximately 0.92 (700m), 0.89 (1000m) and 0.95 (1500m) which may be considered adequate depending on the study premise.

This ground truthing processes can inform the scenarios for future studies using this model set up; discerning whether the model set up should be used at all and further putting limits on the interpretations which can be drawn. The results of this study may suggest that HYCOM and CMS broadly agree with the hydrodynamics of the study area, but simulations cannot well represent rare dispersal events. Therefore all future studies using this model set up should be concerned with average PPDs (not rare dispersal events, which would be inadequately simulated) and interpreted within this context. The lack of tides and sub-mesoscale (and even some mesoscale) processes means that any results should be considered overestimates of dispersal abilities as the majority of these un-parameterised processes would have a retentive effect (Mullineaux 1994, Cowen *et al.* 2000). Due to these inadequacies arguably the model would be better served as a statistical representation of dispersal probabilities rather than a deterministic model of larval fates.

The results of the HS over time test confirm that PLD will have an effect on positional sensitivity (Figure 6). These findings demonstrate the fact that autocorrelated tracks over time will eventually become free to deviate by accessing different instructions to the baseline (Figure 6, right-hand diagram) therefore the longer the data is tracked, the more sensitive the parameter value becomes. This effect could be seen either as a need for a smaller separation distance when particles are tracked for longer, or as an increase in error with longer tracking times. Either way the result is informative as to how the model can be run and interpreted.

2.4.3 Ecological and deep sea consequences of these results

Although primarily representative of model performance many of these results can be interpreted within an ecological context and may inform directions of future research.

Kough and Paris (2015) recently undertook a study of spawning periodicity, akin to the RF test, and interpreted the results in terms of the ecological consequences of different spawning strategies. Spawning periodicity was found to control the number and persistence of reef network dispersal connections, with larval behaviour stabilising these connections. They conclude that spawning periodicity should be accurately included within biophysical models of larval dispersal due to the large potential impact on dispersal ability. In the instance where the RF cannot accurately be determined, as is likely especially in deep sea ecology, this study offers a method of statistically predicting PPDs as opposed to the deterministic approach made possible with accurate information. The range of PPDs generated by undertaking sensitivity tests can provide potential maximum and minimum bounds of dispersal or be combined into a single probabilistic PPD. This way a useful prediction can still be made even when species specific data is lacking.

The TR test further supplements conclusions drawn by Kough and Paris (2015), particularly in the event of seasonal spawners (which do also occur in the deep sea, e.g. the asteroid *Henricia* *lisa* (Clark 1949) (Mercier and Hamel 2008) or cold water coral *Lophelia pertusa* (Linnaeus 1758) (Waller and Tyler 2005)). The interannual variation in hydrodynamic conditions exemplified by the TR test shows the potential for change in PPDs over time. In which case the larvae of seasonal spawners may be released asynchronously, accessing different current patterns from previous cohorts. This may impact upon population persistence or potentially even drive speciation events (Carson *et al.* 2010).

Of importance to deep sea ecological research is the effect of depth on parameter sensitivity. As shown previously this sensitivity can be linked to reduced current speeds and variability at depth (at least in this study area). This may mean that organisms accessing deeper currents have reduced potential dispersal abilities, and therefore rely upon stepping-stone like dispersal within larger metapopulations. While there is some evidence in support of this (e.g. abyssal bivalves, (Etter *et al.* 2011)) there is yet to be enough empirical data to ground truth this theory. The effect of depth on parameter sensitivity also means that empirical positional data do not need to be of as high quality/resolution at depth, which may be a relief to deep sea ecologists faced with e.g. the positional data of a trawl's start and end points rather than a modern high resolution ROV location.

2.4.4 Summary and recommendations

This study was undertaken in order to better inform future work in the field of biophysical dispersal models and to enable more deep sea ecologists to perform such modelling studies. To this end we supply the following step-by-step process, to summarise our advice on sensitivity tests, with case study examples shown to demonstrate the thought process.

1. Start Point

You will have:

- Already chosen a model set up (comprising of hydrodynamic model(s) and particle simulator).

- Identified your study area.

- Recognised there are parameters you need where the optimal value is unclear, and/or have recognised you are unaware of the models capabilities and limitations.

- Planned the sort of ecological questions you wish to be asking to ensure that thresholds and parameter choice are suited to future work, including the tracking time/PLDs.

- E.g. this study selected Hycom and CMS both of which are freely available and have previously been used in larval dispersal studies. Tests were performed in the Northeast Atlantic with the aim to pursue future work simulating passive larval release from benthic invertebrates within marine protected areas (MPAs) in the study area.

2. Identify parameters for sensitivity testing

- It is worth performing sensitivity tests for as many parameters as possible, but if you need to prioritise then consider those where the optimal value is unclear, and at least select those which will test the modelled range of mixing strengths through space and time (i.e. representing x/y, depth, time) in your study area.

- If biological individual based model parameters (e.g. behaviour) will be used in the final study, consider performing sensitivity tests on these also, especially where there is any uncertainty as to optimal values.

- E.g. this study considers 5 parameters, including horizontal separation (x/y), vertical separation (depth), and release frequency/temporal range/timestep (time). All parameters affect the two most computationally intensive aspects of the simulation – the total number of particles being simulated, and the number of velocity fields being loaded into the simulator. Additional parameters worth testing in our case may include horizontal and vertical diffusivity values. These will be tested but are excluded here as they are specific to this particle simulator.

3. Identify the methods required for each parameter

- This study offers methods which can be used either where there are individual track baselines, or where there are multitrack baselines. Consider the impact of your research aims upon the methods you use e.g. will you be interested in average dispersal pathways or rare dispersal events?

- In deep sea studies your research may span a large depth range, if so be sure to stratify your testing in order to test for sensitivity differences with depth.

- If multiple PLDs will be used consider retesting for each different tracking time

- Consider what factors may affect each parameter and how they affect each other before designing your tests and order of testing.

- E.g. our research will be interested in average dispersal pathways. Baseline tests were performed at 3 different depths which span the depth range included in future work. Aspects were considered such as the interaction between timestep and horizontal separation, and the impact of hydrodynamic model output structure on vertical separation. Tests against tracking time suggest recommendations will be different for different PLDs.

4. Perform the tests and interpret the results

- We recommend monitoring simulations (e.g. simulation time, record of memory usage) to gauge the parameter's impact upon computational effort.

- The results should help you define input parameter values, gain an understanding of how mixing occurs in your study area within your model, and gauge your capability to fulfil the full predictive power of your model setup.

- At this point some preliminary ground truthing can be performed in order to assess the adequacy of your model in your study area. Comparison to existing literature or datasets (e.g. argo floats) may reveal why your model performs the way it does (e.g. water mass structures) and/or flag your model as inadequate, in which case you must start the process again with a new model setup.

- E.g. results in this case inform the structuring of release grids from specific sites (marine protected areas) – now with optimised values for horizontal and vertical separation of points. Should this result in too many release points (decided by computational power), multiple simulations can be run at shallower depths, using the maximum sub-optimal number of releases still possible, with release location varied at a minimum distance of 0.005° from previous simulations. The effect of depth may recommend a stratification of simulations when performing ecological studies, with deeper MPAs requiring fewer (less separated) release points. Stratification will be informed by the watermass structure within the model. Timestep values did not greatly affect the time taken to run simulations so a timestep of one hour can be used throughout all future simulations. For species where no spawning periodicity is known, a release frequency per year will be set to weekly at a minimum (~90% correlation to a daily output), and will use at least three years spanning max/min/neutral NAO states (90% correlation to 5 years of simulated different NAO states).

5. Proceed to ecological studies using your model setup

- You should now have a more intimate knowledge of the model setup workings and capabilities, allowing you to design your experiments appropriately and interpret your results responsibly.

- E.g. fortunately, as we are interested in average dispersal pathways this model setup should be adequate although this will not be proven until ground truthed. Rare dispersal events will not be well represented especially at depth. Due to the lack of small scale hydrography represented, even in shallower water, results will likely be overestimates as sub-mesoscale and micro-scale hydrography would likely have promoted retention.

6. Repeat the process if the model set up or study area are changed

- New model setups should be retested due to the effect of model resolution, structure, and strength and variability of modelled mixing, on the sensitivity of parameters.
- As the strength of mixing in the study system (within the model) affects parameter sensitivity, different locations including different depths must be retested also.
- E.g. the results of this study are only suited to other dispersal research in the Rockall Trough region of the Northeast Atlantic using HYCOM and CMS ideally between 700m and 1500m (although some guidance is provided between 200m and 1750m due to the vertical separation test).

3. Investigating marine larval dispersal: should I use a model?

Approximations of larval dispersal are useful to address many ecological questions as well as being pivotal in advising the decision making process for conservation and invasive species control. Answers are often sought in time-limited situations precluding the ability to conduct comprehensive sampling efforts. In these situations Lagrangian models may be useful, but the uncertainty of their predictive nature and the interdisciplinary expertise required can give pause to potential users. This study investigates the usefulness of Lagrangian models to inform future users as to their potential and limitations. A deep sea case study is used to compare model predictions to simple estimates of dispersal, extending previous investigations into deep-water. The results of two different hydrodynamic model simulations are also compared to assess the significance of model choice. Lagrangian models were found to be more conservative and spatially-targeted than estimates. The two different hydrodynamic models were found to give contrasting predictions with only broad-scale similarity: a difference that would be substantial to conservation management. This difference emphasizes the need for ground truthing before a model is considered accurate, advocates probabilistic interpretation of predictions in the meantime, and highlights a higher sensitivity to model build and resolution than was previously understood by ecologists.

3.1 Introduction

Larval dispersal is an important ecological process. Many benthic animals rely upon this phase as their only ability to colonise a new area making the process pivotal in survival as well as in population dynamics and persistence (Matthysen 2012).

Existing global efforts to establish networks of Marine Protected Areas would be incomplete without knowledge of larval dispersal: an effective network should be self-sustaining with each MPA supplying larvae to itself and another in order for protected populations to persist (Roberts *et al.* 2003). It is therefore imperative that we gather information on larval dispersal as soon as possible.

Many methods exist that try to tackle this process (see reviews Levin (2006), Cowen and Sponaugle (2009), Kool *et al.* (2013)), however the challenge of tracking microscopic larvae is largely prohibitive to direct assessments (e.g. tracking, elemental tagging and geochemical tracers, see 1) due to the cost and practical limitations of acquiring microscopic samples. Genetic analyses also require a large number of samples and the search for appropriately high resolution genetic markers to enable accurate species identification can remain elusive (Baco and Cairns 2012).

Lagrangian models of larval dispersal arguably provide the most accessible approach. The use of numerical hydrodynamic models to drive simulations of larval dispersal can offer maps predicting which populations may be linked: maps which can be validated and improved over time with the accumulation of physical samples for direct analysis. Simulations may be run using passive particles driven by currents alone or with the addition of biological parameters such as larval behaviour, mortality, or buoyancy, should such biological data be available and relevant (see Levin (2006), Werner *et al.* (2007), North *et al.* (2009), and Hilãrio *et al.* (2015) for further information).

However biological data can be lacking and simulations driven by hydrodynamic models can be coarsely resolved and based on poor bathymetry (Werner *et al.* 2007). With this in mind, is a complex, interdisciplinary, modelled 'simplification' of reality any improvement upon a further simplified quick estimate of larval dispersal derived from time and average current speed?

The crudest estimates of dispersal potential have done just that – using Planktonic Larval Duration (PLD; equivalent to time) and average current speed to estimate potential larval dispersal distances (e.g. Shanks *et al.* (2003), Shanks (2009), McClain and Hardy (2010), based on a distance = speed * time calculation). PLD is often assumed to be proportional to dispersal potential, but this relies upon constant velocities and degrees of spatial separation as the main factors in population isolation (Shanks 2009).There has been some debate over the correlation between PLD and observed dispersal distance (Shanks *et al.* 2003, Shanks 2009, McClain and Hardy 2010) or genetic metrics of dispersal (Siegel *et al.* 2003, Bradbury *et al.* 2008, Weersing and Toonen 2011, Leal and Bouchet 1991). Selkoe and Toonen (2011) conclude that Isolation-By-Distance and PLD are only moderately correlated (R^2=0.34) highlighting that something is still left to be desired in the explanatory power of this metric of dispersal potential. Tests of seamount isolation have already begun to show that while in many circumstances there is a correlation between geographic distance and species population structure (e.g. Leal and Bouchet (1991)), there are cases where populations based on proximate seamounts have been found to be genetically distinct (e.g. Smith *et al.* (2004), Baco and Shank (2005), Cho and Shank (2010)). This highlights the isolatory effects of complex hydrodynamics, such as Taylor-Proudman dynamics on seamounts (White and Mohn 2002, Lavelle and Mohn 2010, White *et al.* 2007), and presents the concept of 'hydrographic isolation' based on the retentive effects of both distance and hydrodynamics. It is the concept of hydrographic isolation that Lagrangian models can factor into predictions of larval dispersal which other more simplified estimates cannot.

To date one study has looked into the power of Lagrangian models over an average current speed based dispersal distance calculation (hereafter referred to as "an estimate"). Shanks examined dispersal distances of marine species with the benefit of additional genetic measures of dispersal distances for 67 species to further ground truth predictions (Shanks 2009). He found the estimate calculation to be the least conservative prediction of dispersal distance (an overestimate), with a Lagrangian model providing more conservative predictions while also overestimating when compared with predictions derived from genetic data.

This study has two aims:

1) To extend Shanks's (2009) comparison into the deep sea and ask: are deep sea dispersal predictions obtained from Lagrangian models different to simple estimates?

2) To explore the variability in model output and the importance of model choice. On this basis we ask: Do two different hydrodynamic models, each selected as potentially suited to larval dispersal simulations in a study area, give similar predictions of dispersal potential?

Shanks's (2009) study focused on shallow-water and coastal species which are concentrated in areas of arguably more complex hydrodynamics and faster current speeds than the deep sea. There is therefore potential for a greater similarity between estimated and modelled dispersal predictions if a similar study is focussed in deep-water.

The deep sea remains both the largest biome on earth and the most unexplored. By definition, the deep sea extends from the continental slope into the deepest trenches spanning a depth range of thousands of metres (200m-11 000m). Larval dispersal models are not routinely applied in deep sea research: previously prohibited by a lack of highly resolved hydrographic models, biological character information and ground truthing data (Hilãrio *et al.* 2015). Now with freely available simulators and hydrodynamic models, and worldwide increased management efforts focussed on conservation in the face of deep-water fisheries (Roberts 2002, Norse *et al.* 2012) and soon mining (Colman Collins *et al.* 2013, Boschen *et al.* 2013), there is likely to be a considerable increase in the popularity of this method.

The cost benefits of using models in deep sea research are much more considerable than in shallow-water due to the disproportionate costs of sampling offshore in deep-water. Yet setting up, running and analysing a model takes a relatively large amount of time, effort, expertise, and therefore money; whereas an estimate prediction could be undertaken in minutes. If models provide refined predictions compared to an estimated prediction in deep-water also, there is greater justification for utilising Lagrangian models in future deep-water research.

The second aim of this study, still framed in the context of a deep sea study but applicable in all larval dispersal simulations, is to assess the consistency in modelled predictions. There is plenty of advice given on how to choose a suitable model (e.g. Werner *et al.* (2007), North *et al.* (2009)) but realistically there will always be limitation of choice due to access. Hydrodynamic models can appear as a black box to ecologists. They are usually made by (and for) physical oceanographers, and are therefore not usually tailored to satisfy larval dispersal modelling. For deep sea studies this is especially true given the distance from shore and large spatial scales, limiting the choice of velocity instructions to global circulation models (GCMs) and occasional custom built models from local observations (which carry their own limitations: see Fossette *et al.* (2012)).

The variety of hydrodynamic models available is testimony to the variation in how they are set up: with different spatial and temporal averaging and grid structures, promoting realism in particular geographic locations or processes while only performing adequately in others. Furthermore each named model is often supplied as source code and customised by the user so any one model name (e.g. POLCOMS, NEMO, MITgcm, ROMS) may represent a family of models where each individual iteration has been tailored to a different purpose (e.g. one focussed on accurately representing heat flux, and another focussed on simulating internal waves).

Logically we would expect some difference if any two models are set up differently, but the question is whether this difference is negligible and therefore cross-validating, or substantial and requiring very careful model selection. The need to source additional data to confirm or reject model predictive ability should be considered mandatory regardless of our result, but if models are found to agree they would provide a first level of validation for each other and therefore allow meaningful research output before additional (in the deep sea, potentially considerable) ground truthing costs are outlaid. Disagreement between models would highlight the importance of hydrodynamic model choice and would emphasise the lack of value in modelled outcomes before ground truthing data can be obtained.

The results of this study should be beneficial to both ecologists and marine managers in all marine settings. By reflexively exploring the usefulness of Lagrangian models as a technique for investigating larval dispersal, we hope to better inform those looking to use this tool in the future.

3.2 Methods

3.2.1 Study area

This study was conducted in the NE Atlantic in the offshore deep sea west of the UK and Ireland (Figure 10). The Rockall Trough is one of the best studied areas of deep sea in the world, providing historic datasets for at least a basic preliminary ground truthing of predictions (e.g. Ellett *et al.* 1986, Holliday *et al.* 2000, New and Smythe-Wright 2001, Ullgren and White 2010, McGrath *et al.* 2012, Sherwin *et al.* 2015).

Arguably this area is not typical of the deep sea due to the rapid changing bathymetry in the presence of banks and seamounts; something which can cause greater uncertainty in hydrodynamic model predictions than a flat abyssal plain (Werner *et al.* 2007) and may result in erroneously diffusive currents causing lagrangian particles (here larvae) to spread more (this is known as ‘the horizontal pressure gradient error’). This could however make for a fairer comparison to complex shallow water and coastal hydrodynamics and also promotes greater similarity to estimate predictions which represent a null model of maximal uncertainty and spreading of larvae.

Particles were released from three locations in the Rockall Trough in order to access different current regimes in the area: Rosemary Bank in the north, Anton Dohrn Seamount in the centre, and Porcupine Bank in the south.

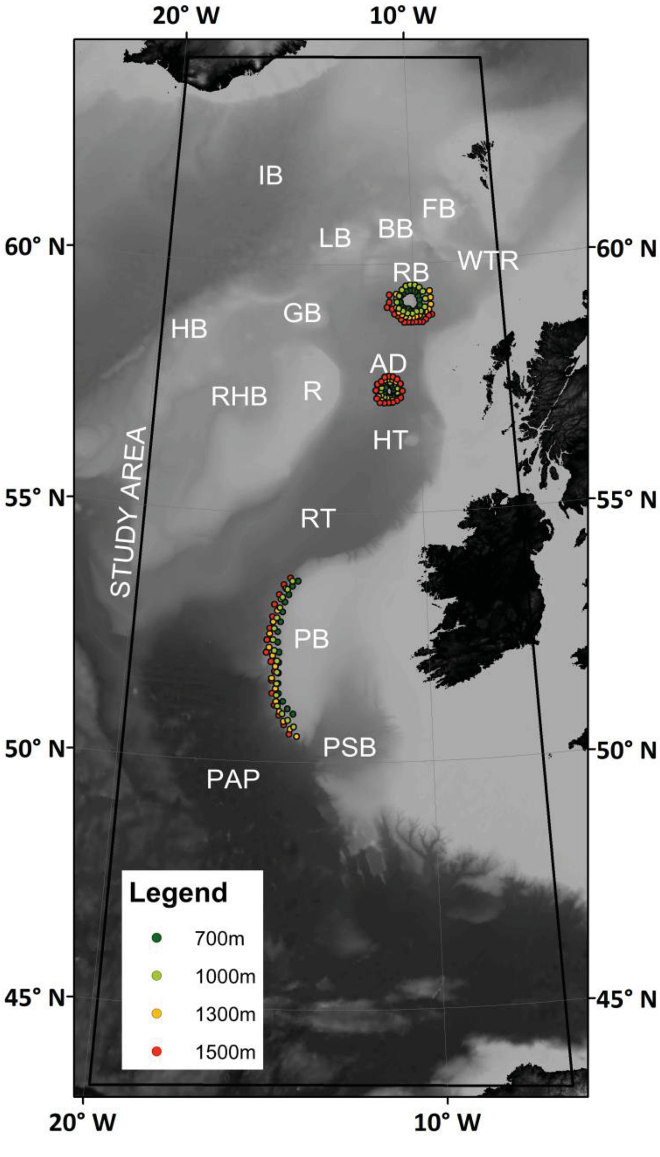


Figure 10 The study area is centred on the Rockall Trough region of the NE Atlantic in the waters west of the UK and Ireland.

The study area bounding box is equivalent to the domain of the POLCOMS model. Larvae were released from 16 release positions in four depth bands (700, 1000, 1300, 1500m) at Rosemary Bank (RB), Anton Dohrn Seamount (AD) and Porcupine Bank (PB). Features of topography mentioned in the text are labelled as follows: Iceland Basin (IB), Hatton Bank (HB), Darwin Mounds (DM), Hatton Rockall Basin (HRB), Rockall Bank (RB), Whittard Canyon (WC), Bay of Biscay (BB). All maps are shown in Albers Equal Area Conic projection with modified standard parallels and meridian (sp1=46°N, sp2=61°N, m=13°W).

3.2.2 Estimate calculation

This deep sea case study relates findings to a plot published in McClain and Hardy (2010, Figure 11). The plot, notably with a caption full of caveats, displays potential larval dispersal distances of deep sea fauna based on two different potential deep sea average current speeds derived from Havenhand *et al.* (2005). This study will use the lower estimated current speed (0.1m s^{-1}) as the estimate, after Ellett, Edwards and Bower (1986) who cite a vector-averaged current speed (over 15 day periods between 1975-1982) of $0.1\text{-}0.2\text{m s}^{-1}$ in the Rockall Trough region, as recorded in the vicinity of Anton Dohrn Seamount.

3.2.3 Lagrangian models

Particle simulators can either be run 'online' or 'offline'. Online simulations are run natively within the hydrodynamic model and benefit from every aspect of the physics parameterised within the model. Offline simulators take time (and potentially space) averaged outputs from hydrodynamic models and use those to drive an independent simulator model. While an online particle simulator is likely to be the most highly resolved, any ecologist looking to perform larval dispersal simulations without considerable assistance from a hydrographic modeller will be limited to obtaining hydrodynamic model outputs and pairing them with an offline particle simulator. The connectivity modeling system (CMS) is a recently developed and freely available offline particle simulator designed especially with larval dispersal modelling in mind (Paris *et al.* 2013, available at https://github.com/beatrixparis/connectivity-modeling-system). Multiple modules allow easy integration of biological data, but this study uses it in its simplest configuration as a passive particle simulator. The core model uses a fourth order Runge-Kutta method to differentiate positions through space and time, and employs a flexible interpolation algorithm allowing hydrodynamic parameters to drive particles closer to land than a fixed algorithm. This model has shown success in recent estimates of coral reef connectivity (Holstein *et al.* 2014, Wood *et al.* 2014, Kough and Paris 2015, Foster *et al.* 2012) as well as driving investigations of abyssal hydrodynamic transport (Van Sebille and Spence 2013) among other

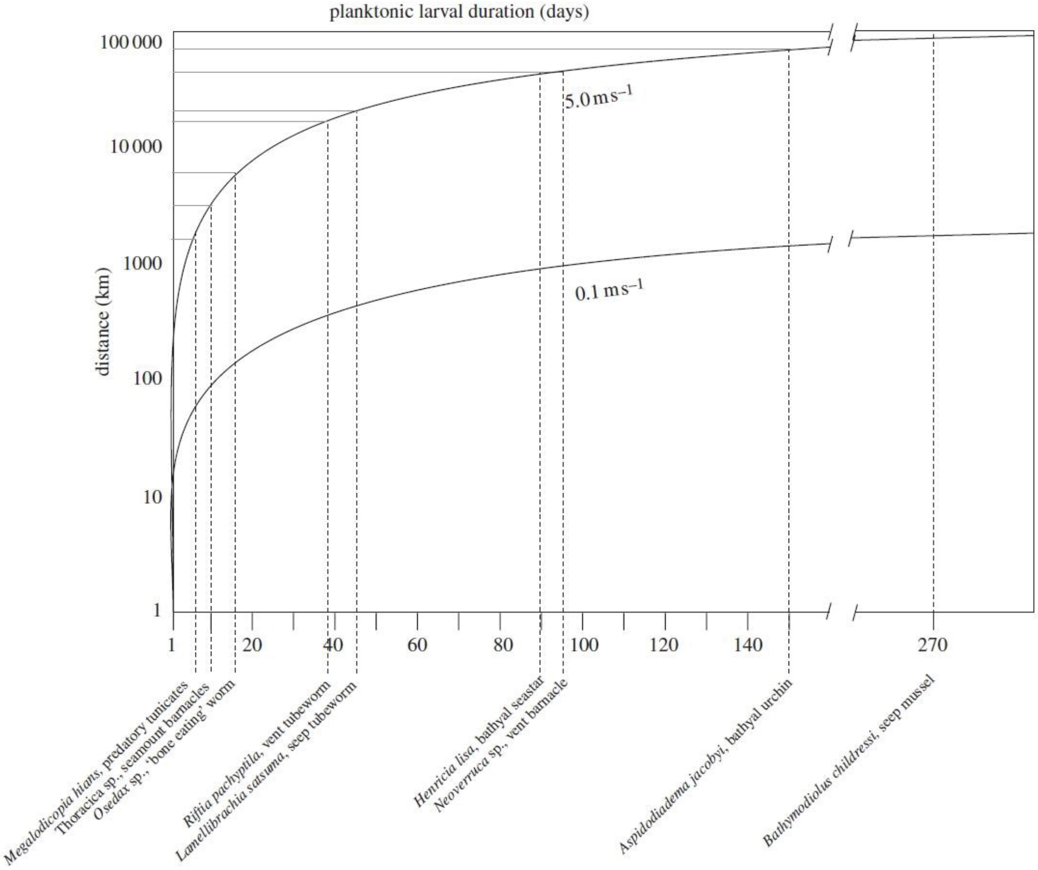


Figure 11 Plot reproduced from McClain and Hardy (2010).

This shows estimated dispersal distances (y axis) based on 0.5ms^{-1} and 0.1ms^{-1} average current speeds against different planktonic larval durations (PLD, days, x-axis). Several published PLDs of specific deep sea fauna are marked for reference. The authors acknowledged that, should current speeds vary in speed and direction (as is likely in reality), dispersal would be much more limited. (Permission to reproduce this figure was granted by The Royal Society.)

studies. An hourly particle tracing timestep was used after a model sensitivity test (Chapter 2), although positional outputs were recorded daily.

Hydrodynamic model 1:POLCOMS

POLCOMS is a shelf and coastal s-coordinate and sigma-level hydrodynamic model (meaning that the vertical grid consists of terrain following depth bands rather than set depth levels) primarily used in UK and Irish waters and previously used by the UK Met Office in weather forecasting – a fact which might recommend it above other models in this area (Holt *et al.* 2001, Wakelin *et al.* 2009). It has been extensively validated over the UK surrounding waters (Holt *et al.* 2005, Holt and James 2006, Holt and Proctor 2008). The 1/6°x1/9° (c. 12km^2) resolution offers an eddy resolving solution, however it will only capture major eddies (c. 64km+ in size based on needing 6 or more data points to adequately resolve an eddy (Lacroix *et al.* 2009)) making this the coarser of the two models being trialled here. It uses a sophisticated advection scheme (the Piecewise Parabolic Method (James 1996)), the Laplacian diffusion with the Smagorinsky (1963) algorithm for horizontal diffusion, and the k-ε turbulence closure scheme; a combination that effectively minimizes numerical diffusion and ensures the preservation of hydrodynamic features such as the north-west European slope current. One major drawback of s and sigma coordinate models is the generation of these spurious currents as a result of errors in horizontal pressure gradient calculations over steep topography. POLCOMS handles the calculation of horizontal pressure gradients by interpolating the pressure onto horizontal planes to reduce the associated errors. The model was run with 40 terrain following depth layers (s-coordinates) although outputs were interpolated to a Levitus standard z-level format (a list of set depths) using Matlab (v.R2013a) in order to make them compatible with the CMS. POLCOMS has been used in several dispersal studies to date (e.g. Lee *et al.* (2013), Phelps *et al.* (2015)).

Hydrodynamic model 2: HYCOM

HYCOM is a freely available global hydrodynamic model developed by the US Navy (www.hycom.org). Its unique hybrid vertical grid system makes it well suited to deep sea studies due to the isopycnal layering in the open ocean and the transition to sigma levels when encountering terrain where the hydrography may become more complex; while shallow-water studies may also benefit from a transition to a z-level (fixed depth) grid in the surface mixed layer. This study used data from HYCOM+NCODA global reanalysis experiment 19.1. The freely available daily averaged model outputs (http://hycom.org/dataserver/) are reformatted to a 40 layer z-level only grid making them comparable to the POLCOMS outputs and compatible with a wide range of particle simulators (see Table 2 in Chapter 1 for a list of offline simulators and their compatibilities). However this averaging will also result in some of the hybrid grid detail being lost. The 1/12° resolution (c. 8km x 4km at study latitude), allows smaller eddies (c. 48km wide) to be captured than in POLCOMS, although this is still coarse relative to reality. The advection and diffusion algorithms are similar to POLCOMS, but HYCOM uses the Mellor-Yamada (1982) Level 2.5 turbulence closure scheme and a massless solution to deep water pressure gradients (Bleck 2006), so there may be a difference in how the two hydrodynamic models handle numerical diffusion and the aforementioned horizontal pressure gradient error. The global nature of HYCOM may be seen as an upside for wide-ranging studies, but is also a downside as the validation of the model was performed on a global scale and therefore may not validate well on a local scale (Fossette *et al.* 2012). HYCOM has already been used in multiple dispersal studies (e.g. Wood *et al.* (2014), Kough and Paris (2015) Foster *et al.* (2012), Christie *et al.* (2010), Mora *et al.* (2011)), including in the deep sea (Adams *et al.* 2011, Young *et al.* 2012).

3.2.4 Model parameters

In both models, particles were released from 16 release positions per depth band from 4 depths (700m, 1000m, 1300m, 1500m). Although not extending to full ocean depth, this study does extend the depth range of Shanks's (2009) study by >1000m. Releases were made daily for 366 days from 4th January 2003-4th January 2004. All particles were tracked for 270 days in line with McClain and Hardy (2010), although daily positional outputs allow sub-setting of this PLD. Both models were run without additional diffusivity parameters as this would be a different setting for each model and subjectively chosen as a nest-wide parameter – this is in line with the study undertaken by Shanks (2009) in comparison to the study of Siegel *et al.* (2003) which did not include additional diffusive parameters. As a result of excluding diffusivity only one particle is released per day as simultaneous releases will follow identical tracks. Neither of this study's hydrodynamic models supply vertical velocity fields (w) so simulations are effectively 2-dimensional. To include w a secondary derivative calculation could be performed, but with background deep ocean w estimated at approximately 10-5 cm s^{-1} (<1m per 100 days) (Von Storch 2010) this is arguably an ineffective parameter to include (except in the vicinity of complex topography and hydrodynamics, neither of which are well represented in large scale hydrodynamic models based on coarse bathymetry (Werner *et al.* 2007)).

3.2.5 Analysis

In order to perform a comparison meaningful to ecologists and marine managers, both distance and spatial predictions were analysed (ecologists often examine dispersal kernels and the potential distance of larval dispersal (e.g. terrestrial (Hovestadt *et al.* 2001, Baguette 2003, Nathan 2006); and marine (McClain and Hardy 2010, Siegel *et al.* 2003, Cowen *et al.* 2007, Nickols *et al.* 2015)), while marine managers may require spatially explicit data examining whether Location X is connected to Location Y (e.g. Treml and Halpin (2012), Anadón *et al.* (2013), Puckett *et al.* (2014)).

Distance comparisons

CMS outputs consisting of daily positions of each simulated particle were converted into Straight Line Distance (SLD) from source, per day, in Matlab (version R2013a) using the Haversine formula to account for earth curvature. A median SLD per day was then calculated for each model as a whole, as well as per depth, per model, and associated quartiles (based on the variability in predicted dispersal distance with different release locations and days) per model. The result was plotted against the average speed 0.1m s^{-1} line in the same format as McClain and Hardy (2010) (Figure 11) for ease of comparison. The difference between the median SLD per day per model was tested using a negative binomial GLM accounting for depth and location. An analysis is given for the full 270 day time frame, with noted reference points at 35 days and 69 days tracking which were discerned by Hilario *et al.* (2015) as the median and 75% quartile PLDs of all deep sea and eurybathic species where PLD is known (n=92 species).

Spatial comparisons

The major limitation of an estimate prediction is that it cannot easily be extrapolated into a spatial prediction without a method to quantify the error caused by assuming a constant current direction. As a consequence this method should be considered non-directional and can only provide a “sphere of influence” type prediction with radius equal to the average predicted dispersal distance. The window of comparison was restricted to the domain of the POLCOMS model as prediction simulated with POLCOMS could not extend outside of this area. As a result, the “sphere of influence” prediction in all cases occupies the entire domain (and beyond); however the 2D simulation method results in different topographic restrictions per depth resulting in topographic cut-outs that differ in size.

A quantitative area of influence comparison was conducted in ArcGIS (version 10.1) using an Albers Equal Area Conic Projection with modified standard parallels (46°N, 61°N). A grid was applied across the POLCOMS domain of constant $4km^2$ cell size (approximately half the HYCOM model resolution). For each depth band, grid cells occupied by topography were removed resulting in the 2D maximal possible area of occupancy. This grid area was considered equivalent to the estimate spatial prediction “sphere of influence” result which would, in all cases, extend beyond this domain.

The prediction of each model was interpreted as a percentage track density per grid cell occupancy in order to provide a spatial “heat map” of dispersal, identifying the “highways of dispersal” according to each model. Track densities were used for the model versus model comparison, while the estimate versus model comparison required a binary (presence only) comparison of occupied cells as track density is not available for the estimate prediction.

A cumulative cell by cell linear correlation coefficient computed in R offers a single correlation value as representative of the comparison between models. This was performed per location per depth and summarised as an average correlation between models.

Additional qualitative assessments, answering questions which may be asked by a marine manger, offer real world interpretations of potential connectivity between sites. These are relevant to scaling the assessment of similarity between predictions to ensure they are useful to a marine manager, e.g. a pair of predictions with 80% similarity may only be considered usefully similar if both predict that site X is connected to site Y.

3.3 Results

3.3.1 Are deep sea dispersal predictions obtained from Lagrangian models different to simple estimates?

Plots of median dispersal distance over time show a difference between deep sea models and estimate predictions (Figure 12 a). Estimate predictions offered the least conservative dispersal distances, being almost double the model predictions from day one, scaling to an average five-fold increase at 35 days, almost seven-fold at 69 days, and twelve-fold at the full 270 days tracking.

An ANOVA confirmed the difference in predictor method median values per day ($p<0.0001$, $F(2,809)=641.5$), with a post-hoc Tukey HSD test confirming both models as statistically different from the estimate ($p<0.0001$).

Spatial comparisons between estimate and model predictions further emphasise this difference, with neither model suggesting connections to the Spanish continental shelf as the estimate would predict, for example (Figure 13). The difference between the estimate and the POLCOMS model is the most pronounced: even though the POLCOMS simulations would not be able to extend beyond the model's domain, there is a large area within the domain that remains untouched by dispersal pathways e.g. none of the simulations suggest connections to the western slope of Rockall Bank within the Hatton Rockall Basin, the north of Hatton Bank, or south beyond the Whittard Canyon in the Bay of Biscay.

Linear correlations between presence-only rasters of dispersal extent are shown in Table 5. The correlation between estimate and modelled spatial extents was maximum 0.67 (HYCOM, Porcupine Bank, 700m simulations), and minimum 0.06 (POLCOMS, Rosemary Bank, 1500m simulations). Maps per location and depth (Figure 14-Figure 16) allow visualisation of these

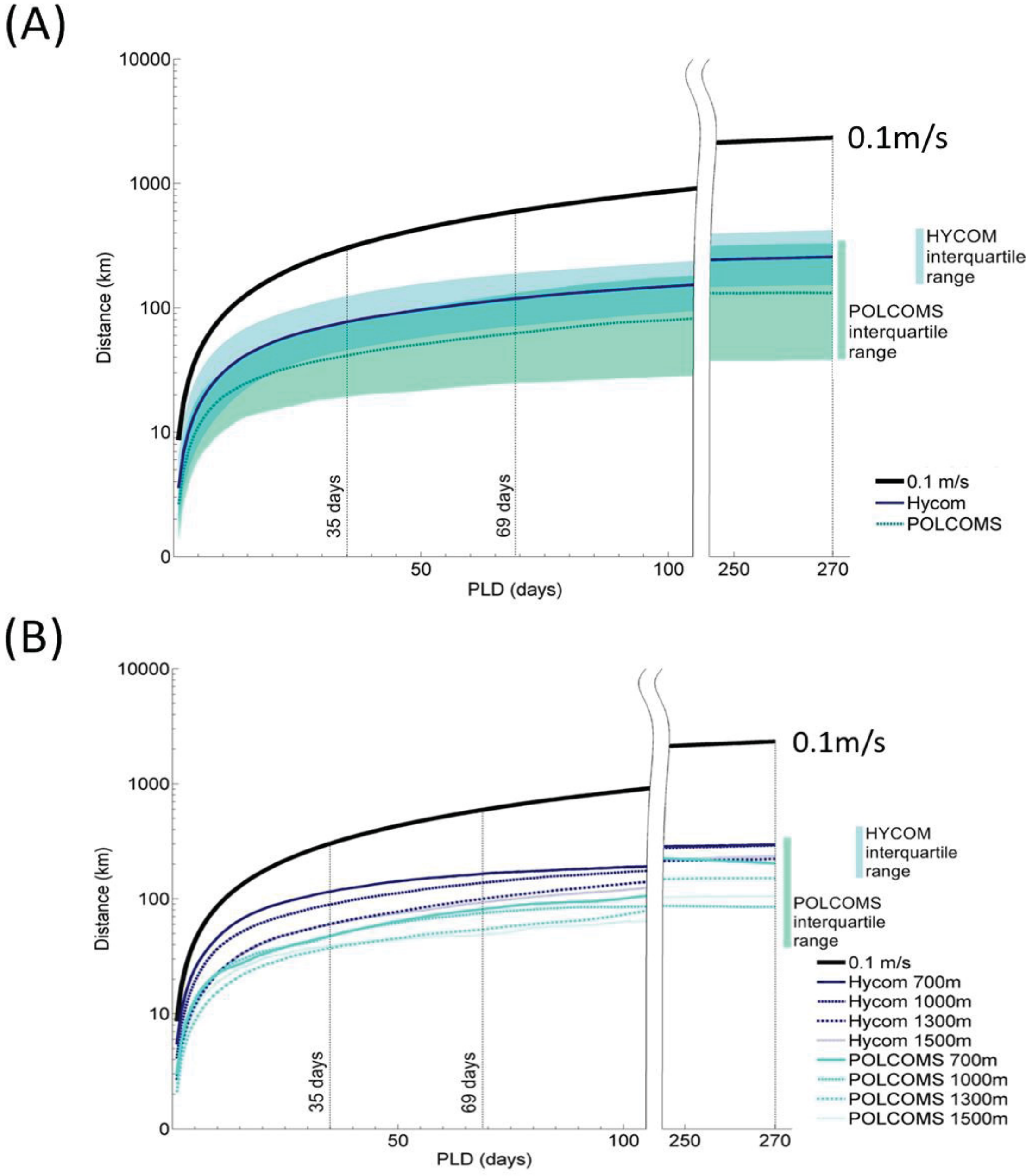


Figure 12 Plots of median dispersal distance over time for the estimate (after McClain and Hardy (2010)), and model predictions.

(A) Median values per model with shaded interquartile ranges inclusive of overlap. (B) Median values per depth band per model. Reference PLDs are highlighted in line with Hilario *et al.* (2015) and the PLDs representative of 50% (35 days) and 75% (69 days) of all known deep sea animals.

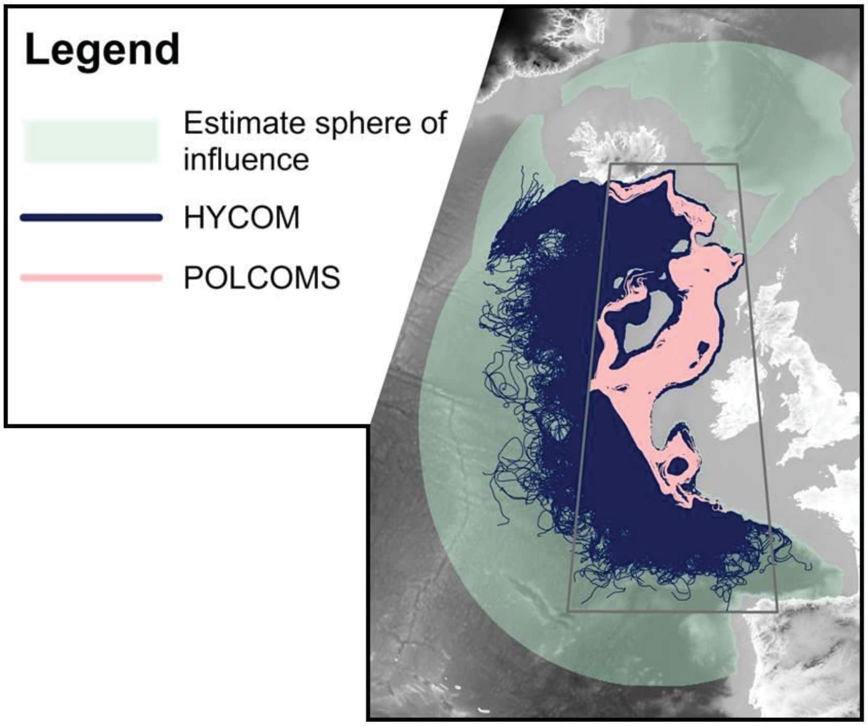


Figure 13 Plot of all simulated tracks in the HYCOM and POLCOMS models relative to the "sphere of influence" predictions of an average current speed based estimate (0.1m s^{-1}).

The grey box delineates the domain of the POLCOMS model: tracks simulated by the POLCOMS model are unable to exit this area.

	Depth	ROSEMARY BANK	ANTON DOHRN	PORCUPINE BANK	All depths and sites
POLCOMS Vs Estimate	700m	0.22	0.11	0.24	0.17
	1000m	0.19	0.13	**0.25**	
	1300m	0.16	0.15	0.21	
	1500m	***0.06***	0.1	0.24	
HYCOM Vs Estimate	700m	0.4	0.44	**0.67**	0.44
	1000m	0.39	0.41	0.6	
	1300m	0.28	0.29	0.59	
	1500m	***0.24***	0.25	0.66	
Model Vs Model (binary)	700m	**0.52**	0.25	0.34	0.36
	1000m	0.42	0.31	0.41	
	1300m	0.49	0.46	0.35	
	1500m	***0.18***	0.31	0.32	

Table 5 Linear correlation coefficients between presence-only rasters provide quantitative spatial comparisons between model and estimate predictions.

A comparison between the two models using this method is also shown to indicate correlations considering spatial spread without track density information. Minimum values are highlighted in bold italics, and maximum values in bold.

comparisons, with Porcupine Bank HYCOM simulations (Figure 16) filling the majority of the estimate spatial extent, except in the south towards the Spanish coastline, and at 1300m and 1500m with no connections to Rosemary Bank. This would make a difference to a marine manager who might want to know whether known fauna at 1500m depth can reach a protected area at Rosemary Bank: an estimate would say ‘yes’, and HYCOM would say ‘no’. The low correlation between the estimate and POLCOMS simulations from Rosemary Bank are displayed in Figure 14 where the estimate might expect connections between Rosemary Bank and anywhere in the Rockall Trough and Bay of Biscay to the south, while POLCOMS suggests larvae may not reach neighbouring Rockall Bank in the west. Therefore a marine manager asking whether there would be a dispersal connection between Rosemary Bank and Anton Dohrn Seamount would be told ‘yes’ from an estimate, and ‘no’ from POLCOMS simulations.

Overall HYCOM spatial extents were the most similar to the estimate, although the similarity was still less than 0.5 (0.44 across all depths and locations) (Table 5). The correlation between the estimate and POLCOMS simulations was very poor at 0.17 across all depths and locations (Table 5).

Both in terms of distance and spatial dispersal patterns, the estimate prediction was the least conservative and specific, with both modelled predictions being more retentive and spatially targeted. Therefore deep sea dispersal predictions obtained from Lagrangian models may be very different to those obtained from an estimate, even in the Rockall Trough which is an area of complex topography and therefore is more likely to be similar to an estimate due to the dispersive effect of the “horizontal pressure gradient error” (this error is exacerbated in complex topographic areas and is found in models using a terrain following vertical grid, as both HYCOM and POLCOMS do at these depths).

3.3.2 Do two different hydrodynamic models, each selected as potentially suited to larval dispersal simulations, give similar predictions of dispersal?

Plots of median dispersal distance over time show differences between the HYCOM and POLCOMS model predictions. Figure 12a shows the lower median dispersal distances and much larger interquartile range of the POLCOMS predictions when compared to HYCOM. An ANOVA comparing only the two models median distances per day confirms this difference ($p<0.0001$, $F(1,538)=276.8$). Plots of median dispersal distance broken down into median values per depth (Figure 12b) demonstrate that the shallowest simulations in the POLCOMS model on average travel less far than the deepest simulations in the HYCOM model.

Quantitative spatial comparisons using the linear correlation coefficients between rasters inclusive of track density values are displayed in Table 6. The maximum correlation between POLCOMS and HYCOM simulations was 0.46 (Rosemary Bank 1000m, Anton Dohrn 1000m, and Porcupine Bank 700m simulations), minimum 0.09 (Rosemary Bank 1300m simulations) and the average across all depths and locations only 0.35. (This can be compared to the spatial extent correlations without track density information which are shown in Table 5: max 0.52 (Rosemary Bank, 700m), min 0.18 (Rosemary Bank, 1500m), av. 0.36).

The maps in Figure 14- Figure 16 allow qualitative comparison between the HYCOM and POLCOMS predictions per depth and location. The spatial extent of simulations is clearly different between the two models, for example connections to the Iceland Basin are predicted in 1000m HYCOM Rosemary Bank simulations (Figure 14), but POLCOMS would not suggest this is possible.

While the 1500m Rosemary Bank simulations in HYCOM suggest connection to most of the Rockall Trough south of Rosemary Bank in complete contrast to the relatively small dispersal

Figure 14 - Figure 16 Maps per depth band of predicted larval dispersal as simulated from Rosemary Bank (Figure 14), Anton Dohrn Seamount (Figure 15) and Porcupine Bank (Figure 16). Simulations from HYCOM and POLCOMS models are displayed as track densities delineating between occasional and persistent pathways of dispersal. The estimate prediction area fills the POLCOMS domain but due to the 2D nature of simulations excludes areas of raised topography. Spatial correlations were conducted comparing the extent of modelled and estimated predictions (Table 5), and the extent and density information of each modelled prediction (Table 6)

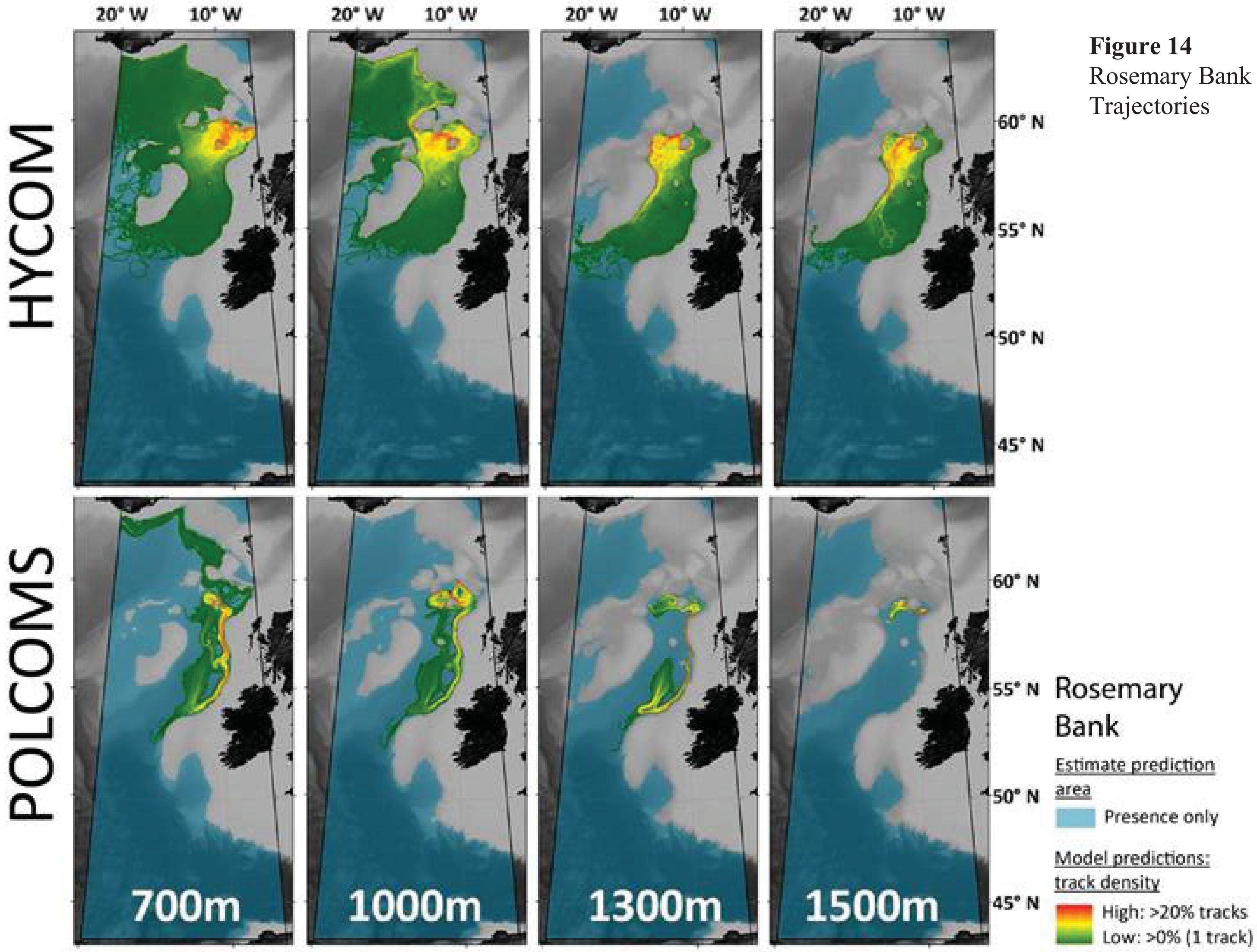


Figure 14 Rosemary Bank Trajectories

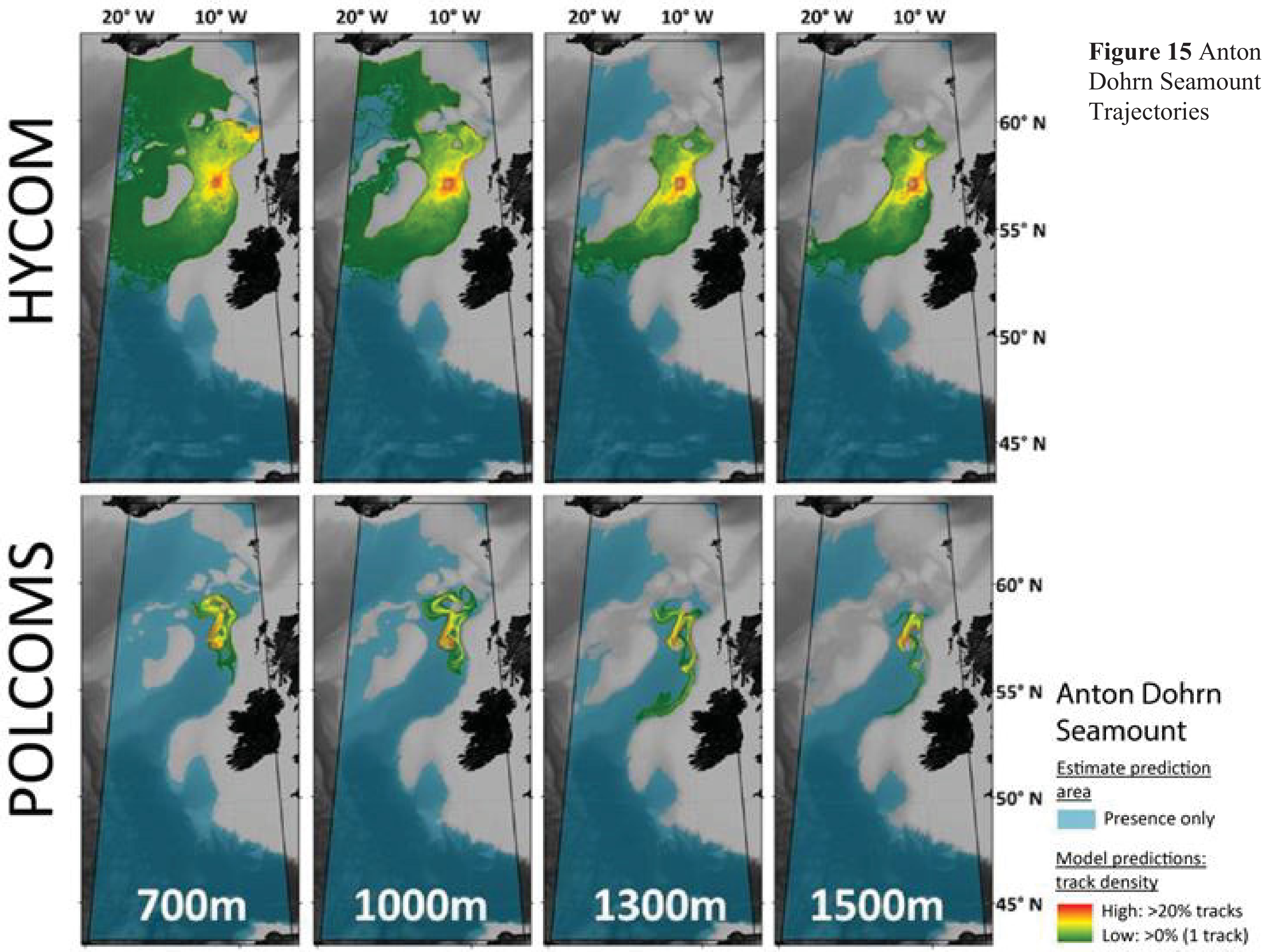


Figure 15 Anton Dohrn Seamount Trajectories

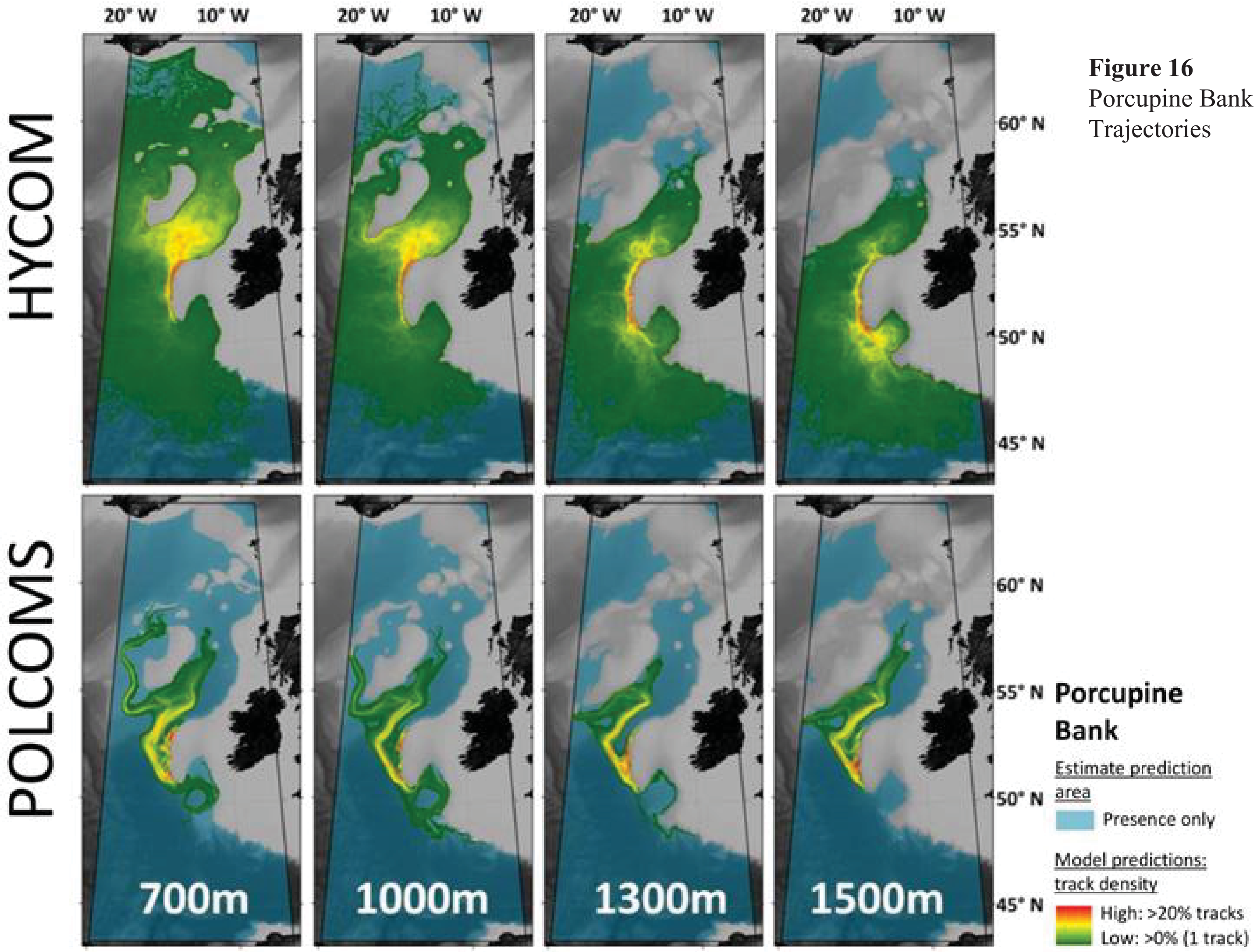


Figure 16
Porcupine Bank
Trajectories

	Depth	ROSEMARY BANK	ANTON DOHRN	PORCUPINE BANK	All depths and sites
Model Vs Model (track density)	700m	0.23	0.39	**0.46**	0.35
	1000m	**0.46**	**0.46**	0.37	
	1300m	***0.09***	0.35	0.45	
	1500m	0.19	0.33	0.35	

Table 6 Linear correlation coefficients between track density rasters provide a comparison between the POLCOMS and HYCOM model spatial outputs.

Correlations are sensitive to the full spatial spread as well as the locations of "dispersal highways". Minimum values are highlighted in ***bold italics***, and maximum values in **bold**.

range suggested by POLCOMS. Although correlations take into account track density information, to a marine manager the location of the high track density "highways of dispersal" (reds/yellows in Figure 14-Figure 16), and whether they are aligned between models may be the most useful information. Again Rosemary Bank simulations are the most dissimilar (Figure 14): for example 1300m southward trajectories in HYCOM show the "highways" extending west and down the flank of Rockall Bank, while POLCOMS simulations suggest most larvae would travel down the east of the Rockall Trough along a narrow corridor following the continental slope with no potential connections to Rockall bank. In contrast the results from Anton Dohrn Seamount (Figure 15) are more similar with the "highways" of high track density generally extending north-east towards Rosemary Bank in both HYCOM and POLCOMS simulations. Yet if a marine manager were to ask whether larvae from Anton Dohrn reach the Darwin Mounds to the north-east, HYCOM would say 'yes' and POLCOMS would say 'no'. Simulations from Porcupine Bank (Figure 16) might indicate a broad agreement that larvae will eventually reach the southern Rockall Bank, but the less direct "highways" in the POLCOMS model might reduce chances of larvae getting that far.

In summary, considering both distance and spatial analyses of dispersal, the two hydrodynamic models tested in this study would give different predictions of potential dispersal capabilities.

3.4 Discussion

3.4.1 Are deep sea dispersal predictions obtained from Lagrangian models different to simple estimates?

Yes, within this study area there is a difference between estimated and modelled predictions of larval dispersal.

It should be noted that we cannot yet comment on the accuracy of the modelled outcomes until some validation can be undertaken. Should the models be inaccurate, the modelled output could not be considered more useful than a basic estimate, however different they may be. There are more complexities found in deep sea hydrodynamics than most models allow for, most GCMs are built with the assumption that deep sea currents are entirely geostrophic in origin, affected only by topography and the earth's rotation, making them slow and consistent. However deep penetrating eddies have been found to affect larval transport from hydrothermal vents (Adams *et al.* 2011), GCMs are based on topography which is coarsely resolved and may omit many hydrographically influential features (Sandwell *et al.* 2014), and benthic storms are often observed with the ability to re-suspend sediments and potentially divert larval dispersal (Aller 1989, Harris 2014). GCMs, including those tested, unlikely account for such complexities, so ground truthing is absolutely vital before assessing whether models promote a more accurate representation than an estimate.

There may be some area and depth specific effects that promote the differences observed in this study. The complex topography of the Rockall Trough induces a lot of mesoscale activity (Holliday *et al.* 2000). If the estimate were similar to the modelled predictions this would suggest that the model simulates currents with fairly straight trajectories and constant speeds: something more likely to occur on a relatively featureless abyssal plain at 6000m.

This study's deep sea simulations are still in line with the findings of Shanks (2009) where average current speed based estimates of larval dispersal distances were the least conservative prediction. This would make the estimate method the most useful in studies of invasive species, for example, but if the aim is to inform conservation of a species, in line with the precautionary principle, a conservative modelled outcome would be the most useful (in the absence of a ground truthed accurate modelled outcome which would be the true ideal for both scenarios).

3.4.2 Do two different hydrodynamic models, each selected as potentially suited to larval dispersal simulations, give similar predictions of dispersal?

Although there were cases of mutual support (e.g. the location of the "highways" from Anton Dohrn simulations, Figure 15), in this study the two hydrodynamic models gave different predictions of dispersal. If the models were to be declared similar they would be able to be used interchangeably with equivalent results. However the fact that they could not give consistent answers as to e.g. whether Rosemary Bank was connected to south-east Rockall Bank at 1300m (Figure 14) means that these models must be considered different.

Model comparisons within ecology have been found to be a very helpful tool in assessing model choice, performance and reliability (Elith and Graham 2009, Downie *et al.* 2013, Putman and He 2013, Piechaud *et al.* 2015). The fact that these hydrodynamic models give different results when each are meant to be a reasonable and validated representation of reality, is due to the fact that both models will have been validated but only in the context of the purpose they were designed for: HYCOM as a global simulation of ocean hydrodynamics (i.e. validated globally, not locally), POLCOMS as a hydrodynamic model intending to be representative of the predominant UK shelf and coastal dynamics. These models have yet to be validated for the purpose of larval dispersal simulation, so a model comparison can help cross-validate and diagnose where each model's similarities and differences may lie in the context of simulating larval transport.

Much of the difference between the results of these two models is attributable to the difference in model horizontal resolution as well as the treatment of the dynamics in areas of steep topography. Putman and He (2013) advocate using the highest resolution model you can find, with increasing spatial and temporal averaging being responsible for dispersal tracks becoming progressively different from observations. This is due to the lack of small- and meso-scale processes being captured in coarser resolution models. Although both of these models would comply with Putman and He’s (2013) summary advice (i.e. to preserve physical processes on the scale of days and tens of kilometres), there is clearly enough difference between these models to alter predictions of larval dispersal on a scale relevant to a marine manager.

Lacroix *et al.*’s (2009) six-data-points-to-make-an-eddy highlights the differences attributable to horizontal resolution, surmising that POLCOMS would capture eddies of >64km, while HYCOM would capture eddies of >48+km. Local literature agrees that while the major eddies in the area may be over 100km in diameter (Sherwin *et al.* 2015), there are still some influential semi-permanent features within the Rockall Trough of 50-60km in diameter (Ullgren and White 2010, Booth 1988) which may have been overlooked by POLCOMS especially.

This in part would account for the more diffuse spread of the HYCOM predictions as the smaller eddies are liable to have a dispersive effect: something which you could correct for to some extent in the POLCOMS model by parameterising diffusion into the particle simulator, although this is unlikely to alter the “highways”. However as the HYCOM model appears more diffusive all over this difference between the models may be more attributable to the handling of horizontal pressure gradient errors. Both models have a scheme in place to handle these errors which occur in the presence of steep topography – something this study region is full of – but as different approaches are used in each model, one may be handling these errors better. Plots of current ellipses per model, per depth, can help highlight the differences here (see Appendix A2.1 (p167)), with the smaller ellipses and tight shelf edge current of the POLCOMS model suggesting a stricter handling of these errors.

The areas of agreement between models are still useful to highlight (e.g. Anton Dohrn predictions, Figure 15). These regions offer some cross-validation of larger-scale eddy features and lend some support to predictions before ground truthing is possible. The mismatch in resolution does mean that such a model comparison is not suited to the creation of an ensemble model (as might be done with species distribution models e.g. (Downie *et al.* 2013)) which would serve only to highlight areas of predicted smaller-scale eddy activity. There may also potentially be greater agreement when viewed over a larger inter-annual timescale.

Steps towards validation of the hydrodynamic models can be achieved first with comparison to local scientific literature: here, for example, the southward trajectories of POLCOMS larvae down the eastern side of the Rockall Trough from Rosemary bank at 700m - 1300m (Figure 14) are contrary to observations of northward transport down to 1000m, and below that southward transport down the western side of the Trough (Holliday and Cunningham 2013, Holliday *et al.* 2015). Furthermore the current speeds simulated in each model are different, with velocities in HYCOM being twice that in POLCOMS although both fall within the range of observed current speeds recorded in the shelf edge current (10-21 cm s^{-1}) (White and Bowyer 1997). Such broad-scale validation may allow a preliminary assessment of model reliability, something which can be done more thoroughly using sensitivity testing (see Chapter 2). However it is advisable to carry out such local hydrodynamic model validation as only a first step assessment: this is still insufficient to judge whether either model in this study was a suitable predictor of larval fates; only ground truthing with purpose-specific biological data (e.g. population genetic data or tagging) can fulfil this role.

3.4.3 Should we use Lagrangian models in studies of marine larval dispersal?

The answer may be a cautious yes: there can still be advantages of using Lagrangian models in spite of there being a high variability in model output. The obvious complexity of the marine environment necessitates the use of a method that does not assume constant current speed and direction, but what level of simplification is still representative of reality remains to be seen. Only ground truthing can assure the accuracy of a model.

The usefulness of Lagrangian models may also hinge on what the study is focussed on. Conservation efforts will benefit from the conservative predictions of dispersal offered by

Lagrangian models, but these must be interpreted as probabilistic in the meantime, and all models must still seek ground truthing for quantification of model accuracy.

If a deterministic, “final answer” type, model is what is sought then the difference between Lagrangian model predictions found in this study suggests that models cannot be relied upon until they are ground truthed in a purpose-specific manner. Such groundtruthing may also be beneficial to physical oceanographers as biological validation is currently not considered by model builders and could be incorporated at an earlier stage in the model building process.

The difference between models found in this study was largely attributable to a relatively small difference in model resolution and a difference in how the horizontal pressure gradient error is handled in the numerical set up of each model. Resolution issues could be overcome by identifying resolution needs *a priori* with knowledge of local mesoscale activity, while the technical handling of the horizontal pressure gradient error is a lot harder to mitigate against but a probabilistic interpretation will provide some diffusive error handling. These results do however offer a caution as to hydrodynamic model selection, an aspect that, in reality, is often limited by access restrictions.

The good news is that there has already been ground truthing success, particularly in comparing Lagrangian model results with seascape genetics (e.g. Foster *et al.* 2012, Liggins *et al.* 2013, Sunday *et al.* 2014). This approach can use model outputs to generate probabilities of gene flow to inform genetic projection models and compare results to observed genetic structure across the study region. Once ground truthed, a Lagrangian model could be incredibly useful across disciplines and purposes, allowing subsequent simulations (using the same model set up) to be run and trusted for multiple species provided that similar oceanographic features are important to larval fates.

4. Towards ‘ecological coherence’: assessing larval dispersal within a network of existing Marine Protected Areas

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The Convention on Biological Diversity (CBD) mandates the establishment of Marine Protected Area (MPA) networks worldwide, with recommendations stating the importance of ‘ecological coherence’. Part of this catchall term requires that MPAs are mutually supportive, including the exchange of benthic invertebrate larvae between MPAs. In the NE Atlantic the majority of offshore MPAs to date have been designated for the protection of the cold water coral Lophelia pertusa *(Linnaeus 1758), but we are yet to assess their ecological coherence in terms of larval dispersal. This study makes use of recently observed larval characteristics and freely available models to demonstrate how such an assessment can be undertaken. Predictions are derived from two null models of dispersal, allowing comparison of ‘passive’ (current driven) and ‘active’ (current driven with vertical migration) dispersal scenarios. The wider network (combining those established by the UK, Ireland and the North East Atlantic Fisheries Commission) appears to support some larval exchange, and has good local retention rates, but has some room for improvement, predominantly in Irish waters. The best performing MPAs are central to the network and are best placed to facilitate transport across local dispersal barriers. Passive and active dispersal simulations gave statistically similar results, providing encouragement to future network assessments where active characteristics are unknown or unavailable. However some site-specific differences in dispersal predictions between passive*

and active simulations are observed dependent upon whether local barriers can be surmounted by vertical larval movement.

4.1 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. The UK is a signatory to the Convention on Biological Diversity (CBD), and therefore is bound by its recommendations which states that species and ecosystems must be "conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas" (CBD 2010). Several further regional regulations cover a similar remit – e.g. the OSlo-PARis Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR 2003), the Marine Strategy Framework Directive (MSFD 2008), and the European Commission Habitats Directive (1992), which states the importance of an MPA network with "ecological coherence". The IUCN World Parks Congress (2003) also 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". Although a legal term which is hard to interpret, Ardron (2007) defines this 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"

Although there are many other aspects that need to be addressed to fulfil these criteria (e.g. maintaining the supply of particulate matter, maintaining environmental conditions, buffering the effects of destructive processes occurring near the protected areas (Roberts *et al.* 2003)) implicit within these requirements is a need to understand the interaction between designated MPAs and their wider environment, including the larval connectivity of the target species. Should designated MPAs within a network be ‘disconnected’, the network could not be self-sustaining or ‘ecologically coherent’. As a consequence, in extreme circumstances a protected ‘sink’ habitat (*sensu* Pulliam (1988): greater replacement of larvae than supply), could degrade due to lack of protection for its larval supply sites. In this instance further efforts to conserve the target species or habitat in a ‘disconnected’ ‘sink’ MPA would be rendered futile without protection of its larval sources.

Larval dispersal research has been integrated into MPA planning, primarily advising on MPA spacing (Botsford *et al.* 2001, Shanks *et al.* 2003, Gaines *et al.* 2003) , size (Botsford *et al.* 2001, Shanks *et al.* 2003), and persistence (Jessop and McAllen 2007, Burgess *et al.* 2014). There are also multiple suggestions for how to include these data in MPA network design (Walters *et al.* 2000, Gaines *et al.* 2003, Treml and Halpin 2012, White *et al.* 2014, Jonsson *et al.* 2016). Currently all advice is exclusively based on studies of shallow water taxa, and even then the advice is highly variable (Botsford *et al.* 2001, Shanks 2003, Halpern and Warner 2003, Jones and Carpenter 2009, Wedding *et al.* 2013).

Deep sea and offshore MPA networks are also being established under these governance frameworks, often adhering to the similar size and spacing rules as their shallow water and coastal counterparts (Wedding *et al.* 2013). This is predominantly due to a lack of species data in alternate locations, species-specific dispersal data, and time to seek new data whilst rushing to hit policy targets. Indeed, at present, offshore ‘networks’ comprise only a loose collection of MPAs, each having been selected due to having sufficient scientific data on which to base a designation. The following advice offered by OSPAR (2006) is a sensible approach for such data poor situations: “Habitat linkages and species movements can inform decision-making for the location of sites where information is available but, it should be accepted that in most cases our understanding of the connections between sites would emerge over time, especially for species whose ecology is poorly understood.”

At present, in UK and Irish offshore waters, the majority of deep sea MPAs have been designated in part for the protection of cold water coral reefs predominantly formed by the Scleractinian coral *Lophelia pertusa* (Linnaeus 1758). Although *L. pertusa* is commonplace as solitary colonies attached to hard substrate (Wilson,1979; Mortensen and Buhl-Mortensen 2004, 2005; Hovland 2005), certain conditions promote the aggregation of colonies into substantial reefs and carbonate mounds up to 300m high (Roberts *et al.* 2006; Howell *et al.* 2011) which themselves provide a habitat for many other species.

Offshore MPAs in the UK must be sized 30-60km in their minimum dimension, and 40-80km apart in spacing (Roberts 2010). The guidance explicitly states that “there is no detailed, reliable evidence of planktonic dispersal characteristics for any marine organism in England” (including inshore species), so this advice is based on a suite of proxy data including “oceanography, modelling, chemistry, population genetics, the rate of spread of invasive species, and the separation of known spawning and nursery grounds” (Roberts 2010).

Since the commissioning of the report for MPA sizing and spacing in the UK, and the subsequent designation of offshore MPAs, there has been some advance in our knowledge of deep water species larval data. Hilario *et al.* (2015) record 72 eurybathic and 21 deep sea species worldwide whose planktonic larval duration (PLD) has been estimated, although even fewer have known larval characteristics (in terms of their swimming ability, buoyancy, growth rates, vertical distribution, mortality, etc). Now *L. pertusa* has been added to this list with recent *ex situ* observations of *L. pertusa* larval behaviour and development (Larsson *et al.* 2014) supplementing previous reproductive observations about the species (Rogers 1999, Waller and Tyler 2005, Brooke and Jarnegren 2013).

This information, when teamed with the recent availability of freely accessible hydrodynamic model outputs (e.g. The HYbrid Coordinate Ocean Model (HYCOM), http://hycom.org), and biologically intentioned particle simulator models (e.g. Connectivity Modeling System, CMS https://github.com/beatrixparis/connectivity-modeling-system) means that it is now possible to estimate larval dispersal using modelled simulations.

The aims of this study are:

i. To conduct the first assessment of NE Atlantic offshore MPA networks, using a novel index to rank individual MPAs based on their performance as sources and sinks of *L. pertusa* larvae, and providing a network-wide assessment useful to marine managers.

ii. To compare active and passive dispersal scenarios to inform managers of the potential consequences of incomplete species understanding

iii. To generate a modelled null hypothesis of patterns of connectivity for *L. pertusa* among NE Atlantic MPAs for future validation using next generation sequencing.

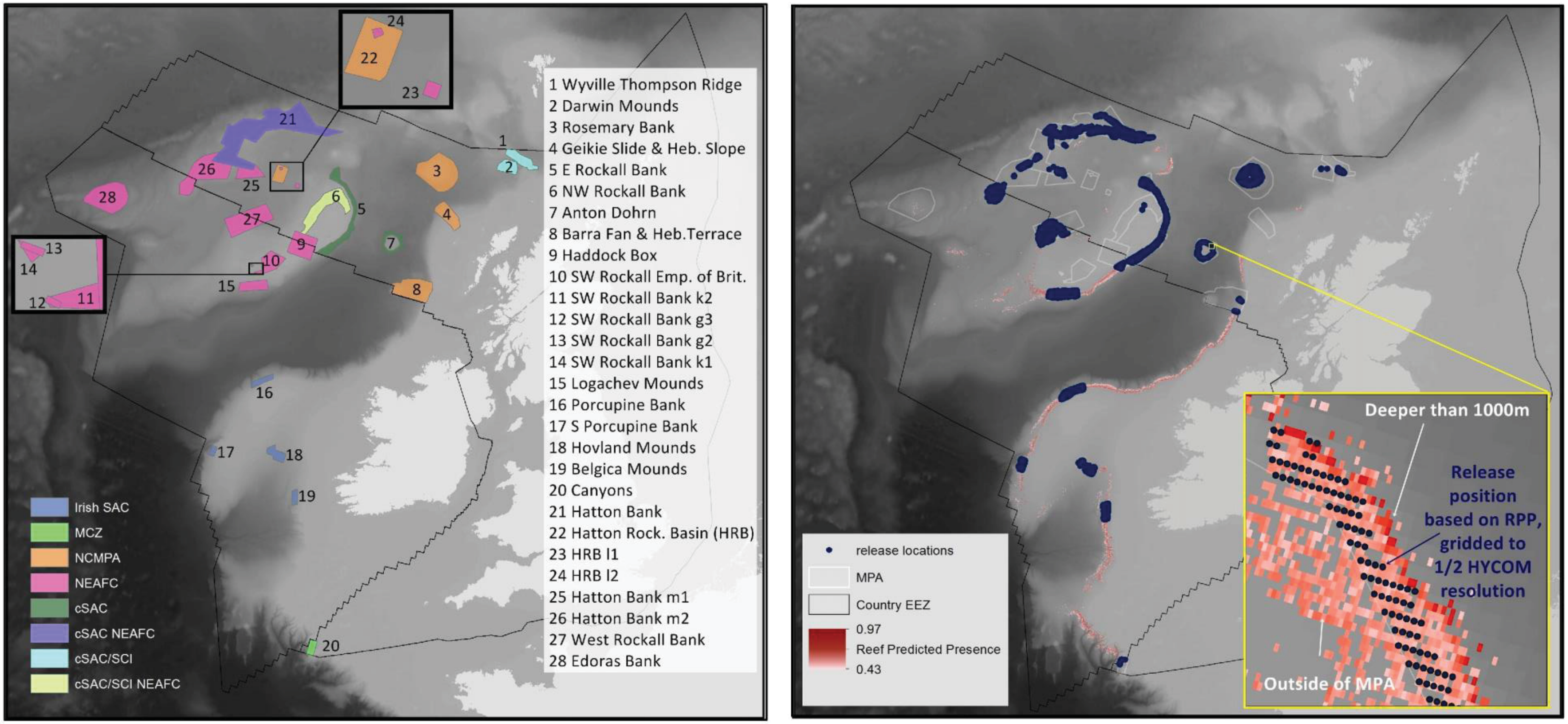
4.2 Methods

4.2.1 Study area

This study was undertaken in the NE Atlantic in the Extended Economic Zones west of UK and Ireland (Figure 17). Twenty-eight MPAs were considered in this region, designated by the UK's Joint Nature Conservation Committee (JNCC), Irelands National Parks and Wildlife Service (NWPS), and the North East Atlantic Fisheries Commission (NEAFC). Official terms for the different MPA types as highlighted in Figure 17 are: Special Areas of Conservation (SACs), candidate SACs (cSACs), Scottish Nature Conservation MPAs (NCMPAs), Marine Conservation Zones (MCZs), Sites of Community Importance (SCIs), or voluntary closures (NEAFC designated).

Figure 17 Location of study area, the wider MPA network, and larval release sites.

The left hand map displays the UK and Ireland EEZs, along with all the offshore MPAs considered in this study. All UK cSACs and NCMPAs designated by JNCC, and the Irish SACs designated by NPWS are EC Natura 2000 MPAs and are also part of the OSPAR MPA network. NEAFC MPAs are voluntary closures self-governed by the regional fishing community. The right hand map displays the location of modelled scleractinian Reef Predicted Presence (RPP) from Ross *et al.* (2015), and the interpreted release locations sited within MPAs and shallower than 1000m to ensure that reefs are dominated by *Lophelia pertusa*. (Linnaeus 1758).



4.2.2 Model set up

HYCOM is a hydrodynamic model of the world oceans gridded at 1/12° horizontal resolution. 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. This model supplies the velocity vectors which inform the advection protocols within the particle simulator. See Fossette *et al.* (2012) and North *et al.* (2009) for more information about different sources of velocity vector data. 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, as the NAO has been linked to the hydrodynamics of the Rockall Trough region (Holliday *et al.* 2000, Ullgren and 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 (see Chapter 2). Based on basic literature ground truthing, HYCOM appears to give more realistic outputs when compared to POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System, a regional hydrodynamic model), although this cannot be confirmed until quantitatively ground truthed in the future (See Chapter 3).

The CMS 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 a horizontal diffusivity of $7 m^2 s^{-1}$ every 4 hours in line with Wood *et al.* (2014, after Okubo 1971). No vertical diffusivity was parameterised as observations suggest that background vertical diffusivity would be in the order of 10^5 cm s^{-1} (i.e. 86.4cm per 100days, Von Storch (2010, after Munk and Wunsch 1998)) which would be negligible on the scale used in these simulations. Realistically heightened vertical velocities and diffusivity would be encountered when proximal to topography, but at present models of this scale are unable to parameterise this. In this study this error will be reduced by the topography often aligning with the location of an MPA where particles will be interpreted as settling rendering the complexities of the hydrodynamics there moot.

This study made use of the seascape module, allocating release locations to MPA polygons and tracking which MPA polygon the larvae settle in. Active larval dispersal simulations, where larvae undertook an ontogenetic vertical migration, also utilised the probability matrix of vertical migration. This matrix allows an Individual Based Model (IBM) approach where a cohort of larvae can have a range of vertical migration timings randomly assigned per individual. However without any data to inform proportions of larvae within different depth brackets, 100% of larvae were instructed to follow the vertical migration maximum as defined by Larsson *et al.* (2014) (a non- IBM approach).

4.2.3 Release locations

Release locations were derived from a high resolution habitat distribution model as published by Ross *et al.* (2015). The 250m multibeam-based Scleractinian reef model was thresholded to ≤1100m to exclude reefs which may be dominated by another cold water coral, *Solenosmillia variabilis* (Duncan 1873). The model output was then re-gridded to the horizontal sensitivity threshold defined in Chapter 2 (0.005°). Grid centroids of high reef probability located within offshore MPAs were used as release locations (Figure 17). Additional locations in the Darwin Mounds and NW Rockall Bank MPAs were added based on observational data (where reefs are 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.

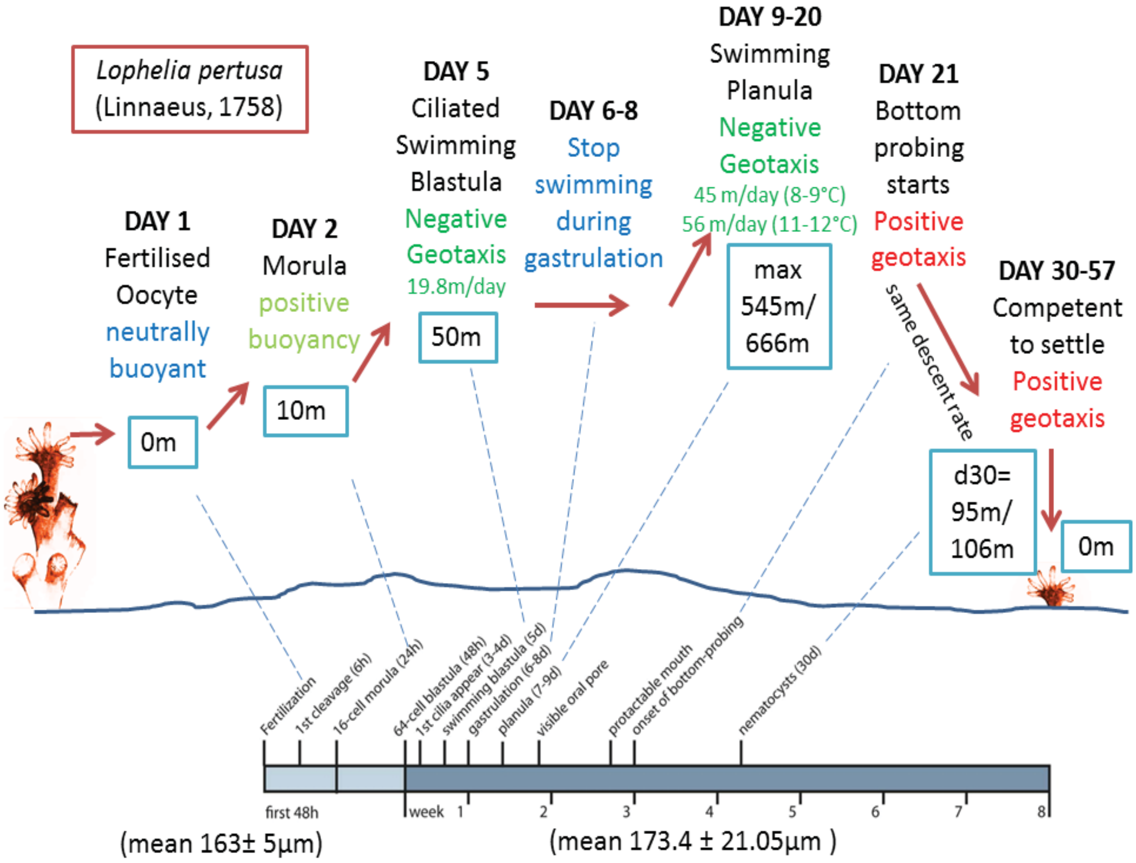


Figure 18 Vertical swimming profile for active larvae derived from Larsson *et al.* (2014).

100% of larvae were given the maximum swimming speeds suggested, when larvae are shallower than 550m they are assumed to have the 11-12°C swimming speeds, while deeper larvae adhere to the 8-9°C swimming speeds. All larvae (both passive and active) had a 57day PLD and were competent to settle from day 30.

4.2.4 Biological characterisation

Details of *L. pertusa*'s reproductive and behavioural characteristics were predominantly derived from recent studies by Brooke and Jarnegren (2013) and Larsson *et al.* (2014). Larval release was simulated daily from 4th January – 4th March in each year, capturing the seasonal reproduction period observed in Norway (Brooke and Jarnegren 2013) and in the NE Atlantic (Waller and Tyler 2005). Although it is likely there would only be one or two spawning events per season (Waller and Tyler 2005, Brooke and Jarnegren 2013), daily releases were performed to capture the full range of potential larval trajectories possible within this period.

Planktonic larval duration (PLD) was assumed to be 57days in line with the laboratory observations of Larsson *et al.* (2014), with larvae considered competent to settle from day 30. Figure **18** shows the maximal active vertical swimming speeds and timings which were also derived from Larsson *et al.* (2014) who observed *L. pertusa* larvae in the lab. Larvae below 550m depth (the conservative approximate depth of the permanent thermocline in February (White and 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. 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 probabilistic rather than realistic representation of larval fates.

The work of Larsson *et al.* (2014) does not include *in situ* observations, or estimates of vertical distribution throughout the water column, leading to some uncertainty as to how the larvae may be found to behave in the wild (Metaxas and Saunders 2009). Maldonado *et al.* (2003, 2006) noted that lab-observed swimming abilities in sponge larvae were rarely observed in field observations. Therefore a null model of passive dispersal was also simulated, excluding the vertical migration characteristics from Larsson *et al.* (2014)). This facilitated a comparison of active *versus* passive dispersal strategies to inform marine managers as to the range of error which could be expected due to behavioural variability.

Larvae with vertical swimming abilities are thought to have the ability to enhance or reduce the dispersal ability of passive particles by using this ability to reach depths with differing current speeds and directions (Young *et al.* 1996, Sponaugle *et al.* 2002, Shanks *et al.* 2003, Young *et al.* 2012), along with accessing different temperatures which impact on larval metabolism and therefore development speeds (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. While Young *et al.* (2012) found a modest enhancement of dispersal ability by modelling the dispersal of the cold seep siboglonid worm *Lamellibrachia* *luymesi* (van der Land and Nørrevang 1975) with buoyant or vertically migrating properties. 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).

Active and passive dispersal of *L. pertusa* was therefore evaluated with a view to identifying differences and similarities in dispersal patterns to highlight areas of predictive confidence and to provide null model predictions which can be compared with genetic ground truthing data in the future.

As real dispersal patterns are likely to be neither entirely passive nor entirely active, the final 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.

4.2.5 Analysis

CMS connectivity outputs, based on MPA start and end polygons per trajectory, were compiled in the statistical software environment R (using a routine akin to the matlab processing script supplied with the CMS software). An MPA dispersal matrix was produced per year, per depth, per larval mode (passive/active, see Appendix A3.1 for example matrices from 2003 (p173)). A dispersal matrix is akin to an adjacency matrix in graph theory: all nodes (here MPAs) are listed as sources on the vertical plane and receivers on the horizontal plane, with values recorded within the matrix representing the number of larvae exchanged between source and receiver MPAs. Depth matrices were then stacked and larval counts summed to give a matrix per larval mode. The all depth matrix per year was then averaged across years to give the final passive and active results matrices.

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 also 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 (0.0416665^0) 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 for passive and active dispersal from the Darwin Mounds were also created. The Haversine formula was used to convert start and end latitude and longitude positions of particles into curved earth distances. Frequencies of dispersal distance were then plotted in Matlab.

MPA assessment metrics

Although larval dispersal should be integrated into the design of MPA networks, there is currently no advice on how to assess existing MPA networks on their ability to promote larval dispersal.

Lieberknecht *et al.* (2014) undertook a commissioned assessment of the ecological coherence of the UK's MPA network and openly admitted the lack of data and robustness in the connectivity component of their study: dispersal adequacy was captured by mapping 40km buffers around MPAs (in line with the upper 80km spacing limit recommended by Roberts *et al.* (2010)) and identifying areas of buffer overlap. Schill *et al.* (2015) assessed the dispersal of Caribbean corals between known reefs and identified the best connected unprotected reefs. The MPA assessment was secondary to the habitat assessment in their study, and the metrics used were based on network theory which is effective but harder for conservationists and policy makers to relate to. Melia *et al.* (2016) also approached the dispersal connectivity of the habitat sites and related this to conservation. Their study looked at ‘metacommunity connectivity’, addressing several species within different trophic levels, and developed metrics which define site connectivity ‘intensity’, ‘effectiveness’, and ‘persistence’.

None of these studies assess the MPA network directly: something which seems necessary if following OSPARs advice to develop our understanding of connections over time. Such an assessment can point out strengths and weaknesses in the network and offer guidance for future network coherence improvement.

This study developed a set of MPA assessment metrics based on a single combined dispersal matrix consisting of the average larval counts exchanged between MPAs across larval modes, years, and depths. Metrics were based on three qualities of importance to MPA and network performance:

a) Source performance: the ability to act as a source of larvae to the rest of the network and outside of the network
b) Local Retention: the ability to act as a source to itself (part of source performance, but should be emphasised due to its contribution to resilience)
c) Sink performance: the ability to retain settling larvae from other network sources

Each of these qualities is 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 source performance was quantified as an average ranking of several sub-criteria.

- The proportion of supplied larvae which go to non-protected sites
- The proportion of supplied larvae which are retained in other MPAs
- (The proportion of supplied larvae which are locally retained)
- The number of larvae supplied by source
- The number of MPAs supplied with larvae
- The evenness of strong supply across MPAs in the network

There are three potential fates for surviving larvae: supply outside of network, supply to another MPA within the network, and local retention. As all of these fates are important, in this example it was assumed that an ideal MPA, or network, would have a 3-way balanced split between these 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 allocations could be conceived if a particular quality should be deemed especially desirable: for example, individual MPA resilience may benefit from a higher percentage allocated to local retention.

Local retention was considered as part of the overall source performance ranking metric, but is highlighted due to its contribution to resilience and the ability for a network (or an MPA) to be self-sustaining should anything impact other MPAs in the network (in line with Ardron's (2007) fourth criteria of ecological coherence).

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 also contributes to network resilience as 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 source evenness metric was adapted from Simpson's Diversity Index (D) (Simpson 1949). 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). This means that strong connections are given more weight than those where only a few larvae are supplied/ retained, and ensures that the count of MPAs is not duplicated within the source performance index.

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

In this case n = the number of supplied larvae retained per MPA 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). Simpson's index is expressed here as 1/D in order that more even dominance gives a higher index.

Individual MPA sink performance was assessed under the following criteria:

- Number of larvae captured/retained
- Number of MPAs supplying larvae to retaining MPA

- Evenness of retainer’s sources

Similar to the source performance metric, these criteria again capture the diversity and strength of retaining MPA connections. Evenness again was assessed using Simpson’s 1/D, although n = the counts of larvae per source MPA (down a column from the dispersal matrix), and N = the total number of larvae retained in that MPA (column total).

For the eighteen MPAs which are both retainers and sources, two final assessment metrics are given:

- 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 all assessed rankings providing a final per MPA performance ranking. The ten MPAs without release points could not be included in source performance rankings, or final assessment metrics which depended on inclusion of this data.

MPA networks

An overall MPA network assessment is given for each of the sub-networks (Irish, NEAFC, UK) and the combined regional network. This is based on the ideal larval fates (i.e. proportions of MPA released larvae which were lost to outside the network, stayed within source MPAs, and were retained within the network) again using a 3-way balance split as an example target. The total number of larvae released, number of source MPAs, and number of retaining MPAs are also given per network for contextual comparison.

4.3 Results

Predicted MPA dispersal matrices are shown in Table 7-Table 9. All matrices can be read both left to right (assessing MPAs as larval sources) and top to bottom (assessing MPAs as larval retainers). As the MPAs are ordered roughly North to South, when assessing MPA sources larval counts in boxes to the right of the diagonal have drifted Southwards, and to the left Northwards. Sources in the Rockall Trough (white boxes) with larvae in grey shaded boxes have supplied MPAs to the west. Additional per depth matrices are available in Appendix A3.1 (p173).

4.3.1 Passive vs. active

Some qualitative difference was apparent when comparing the active (Table 7) and passive (Table 8) 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 7 further MPAs with active larvae. However, the majority of changes between 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 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 K.S test $D = 0.0434$ $p = 0.4523$; local retention only, both naïve & bootstrap adjusted K.S test $D= 0.0714$ $p =1$). If considering only mapped trajectories from the Darwin Mounds (Figure 19), passive and active dispersal

Table 7 Dispersal matrix of ACTIVE larval simulations.

Numbers recorded within the matrix are the number of larvae supplied from the source MPA (left-hand axis) to the retaining MPA (top axis). Read the matrix left to right to judge an MPA as a source, or top to bottom to judge an MPA as a retainer. Diagonal boxes therefore 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 <Q1, yellow =Q1-Q2(median), orange = Q2-Q3, red >Q3. MPAs are roughly

text did

	ACTIVE	RETAINING 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_l	HRB	HRB_l1	HRB_l2	HBm1	HBm2	WRockall	EdorasBank
SOURCE MPA	WTR	56171	18462	1680	0.333																								
	DarwinMounds	4370	6626	1063																									
	RosemaryBank	2E+06	6E+06	3E+07	4E+06	5E+05	2	1E+06	32316													68.67	17						
	GeikieS&HSlope																												
	ERockallBank	686.3	5747	2E+06	6E+05	7E+06	76105	2E+06	5E+05	6E+05	23858	8456	758.7		2.333	2E+05	1648					24230	3E+05	22570	142	3327	90.33	426.7	
	NWRockall_g	1	2.667	2140	107.7	10005	20528	924.3	8.333	473												23.33	71.33	382					
	AntonDohrn	4303	40639	6E+05	1E+06	5E+05	2	2E+06	6E+05	1972	1	4.333				5465	10.67						163						
	TheBarraF&HebTer	1900	2478	36408	2E+05	23450		2E+05	6E+05	79.67						298.3	0.667												
	HaddockBox	69.33	178	6346	27785	5E+05	24	66297	52398	3E+05	46941	18323	1785	0.333	4.667	2E+05	759.7											21	
	SWRockallEmpress																												
	SWRockall_k2																												
	SWRockall_g3k2																												
	SWRockall_g2k1																												
	SWRockall_k1																												
	LogachevMounds			365.7	2600	4E+05		68586	2E+05	51073	2E+05	1E+05	28553	49186	56909	5E+06	2566	5				3280	10226	96		1E+05	2E+05	4E+06	1E+05
	PorcupineBank			13.33	499	1E+05		21139	2E+05	14873	290.3					4E+05	4E+05	68.67									34	25069	
	SPorcupine					13552		608.3	9146	1795						2E+05	1E+06	32440										7681	
	HovlandMounds																0.667	5151	2E+06	6E+05									
	BelgicaMounds																8.667	28320	6E+05	2E+06									
	TheCanyons																				36584								
	HattonBank_l	307.7	3990	1E+06	9985	1E+06	444.7	21721	52.33		0.333					1						3E+07	2E+06	1E+05	11660	1E+06	1E+06	2E+05	1
	HRB																												
	HRB_l1																												
	HRB_l2																												
	HBm1			185	0.667	4407	0.667															93709	34647	1989	101.7	18156	6978	4724	
	HBm2																					1E+06	3590	4		26253	7E+06	2E+05	1E+05
	WRockall			1092		4E+05	9032			7379	29385	5206	897.7	23190	9076	11051						3E+05	2E+06	2E+06	872.7	2E+06	5E+05	9E+06	2777
	EdorasBank																												

Table 8 Dispersal matrix of PASSIVE larval simulations.

Details as in Table 7.

	PASSIVE	RETAINING 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_l	HRB	HRB_l1	HRB_l2	HBm1	HBm2	WRockall	EdorasBank
SOURCE MPA	WTR	2E+05	48282	5187																									
	DarwinMounds		10007	3722																									
	RosemaryBank	6E+05	2E+06	3E+07	3E+06	6E+05	2	1E+06	21993													11	4						
	GeikieS&HSlope																												
	ERockallBank	577.3	3093	1E+06	3E+05	1E+07	18	1E+06	4E+05	1E+05						1E+05	921.3					30776	4E+05	35974	55	5849	203.7	410.7	
	NWRockall_g		0.333	179.3	232.7	4432	36200	105	42.67	942														13					
	AntonDohrn	13	19503	5E+05	8E+05	5E+05		2E+06	6E+05	315.7						7030	57.33						1						
	TheBarraF&HebTer	1136	577.7	23415	39531	16020		1E+05	9E+05	102						435													
	HaddockBox	114.3	230.7	8797	17230	6E+05		45937	47336	2E+05						2E+05	103					0.333	10					0.333	
	SWRockallEmpress																												
	SWRockall_k2																												
	SWRockall_g3k2																												
	SWRockall_g2k1																												
	SWRockall_k1																												
	LogachevMounds			167.7	1354	2E+05		50698	59909	7471						6E+06	532	4				1358	4047	51		65278	1E+05	4E+06	25735
	PorcupineBank			20.33	2074	1E+05		26134	92709	12528						3E+05	1E+06	9									18	38417	
	SPorcupine				0.333	18255		569	13658	1722						2E+05	9E+05	14034										10557	
	HovlandMounds																	5.667	2E+06	8E+05									
	BelgicaMounds				0.333			0.667									5.333	19656	1E+05	3E+06									
	TheCanyons																	2			72083								
	HattonBank_l	96	201.7	8E+05	2952	8E+05		7586	1.667													4E+07	1E+06	41959	4002	7E+05	7E+05	79416	0.667
	HRB																												
	HRB_l1																												
	HRB_l2																												
	HBm1			22.33		361.7																70875	21811	300	86.33	26686	2085	2510	
	HBm2																					9E+05	1	4		6114	8E+06	45047	57416
	WRockall			12.67		1E+05				647						17611						1E+05	9E+05	2E+06	0.667	1E+06	4E+05	1E+07	1406
	EdorasBank																												

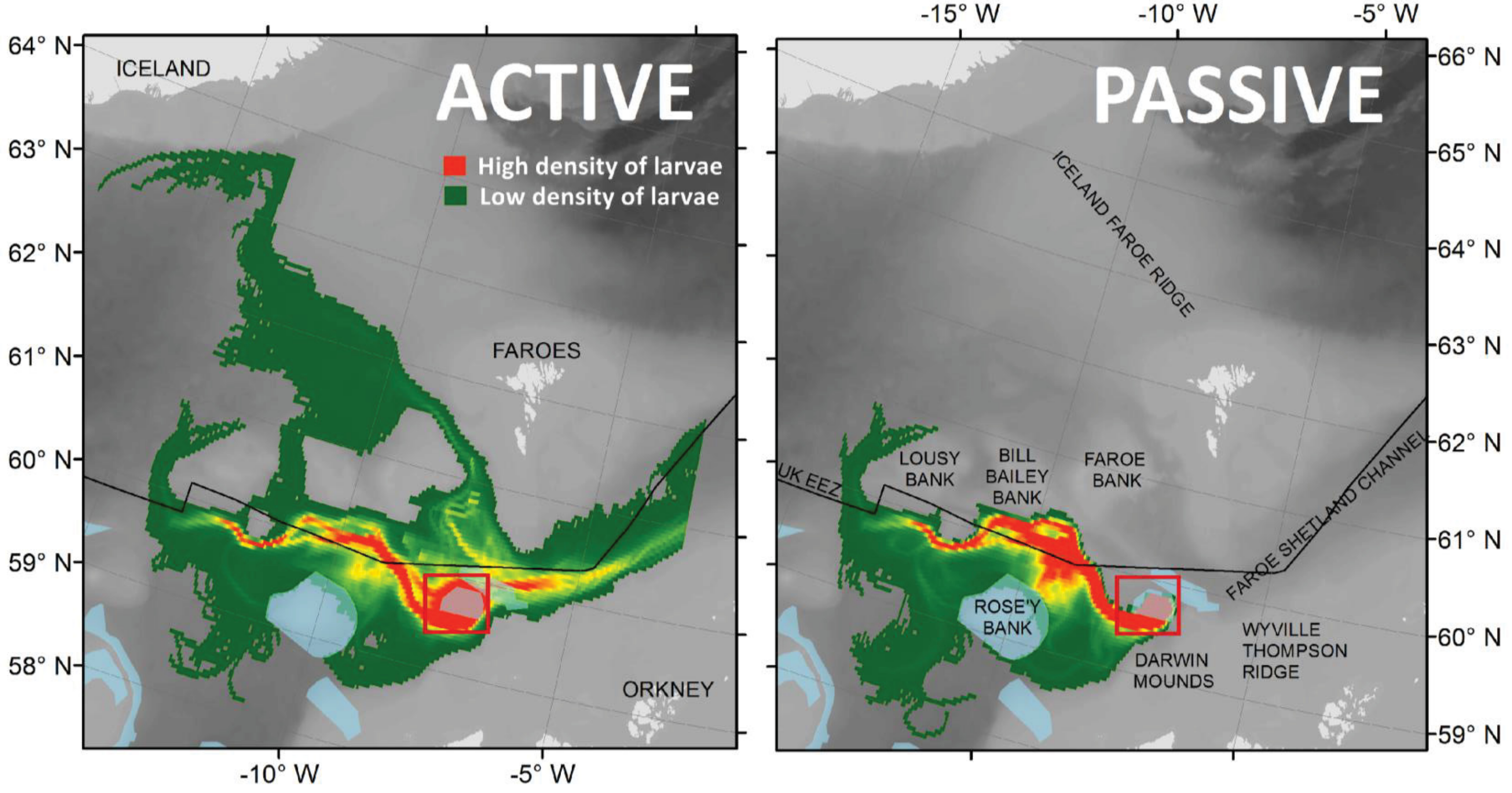
Table 9 Dispersal matrix of ALL larval simulations.

Details as in Table 7, however counts are averaged across larval modes (passive/ active) as well as simulation years.

	AVERAGE	RETAINING 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_l	HRB	HRB_l1	HRB_l2	HBm1	HBm2	WRockall	EdorasBank
SOURCE MPA	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	23988	351523	2E+06									
	TheCanyons																	1			54334								
	HattonBank_l	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_l1																												
	HRB_l2																												
	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						183238	1E+06	2E+06	436.67	2E+06	425345	1E+07	2091.5
	EdorasBank																												

Figure 19 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 (ie. 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 arguably shows that more active larvae are retained in the greater Darwin Mounds region (red box). This highlights the dependence upon definitions which may vary between studies. n = 70200 larvae released per larval mode.



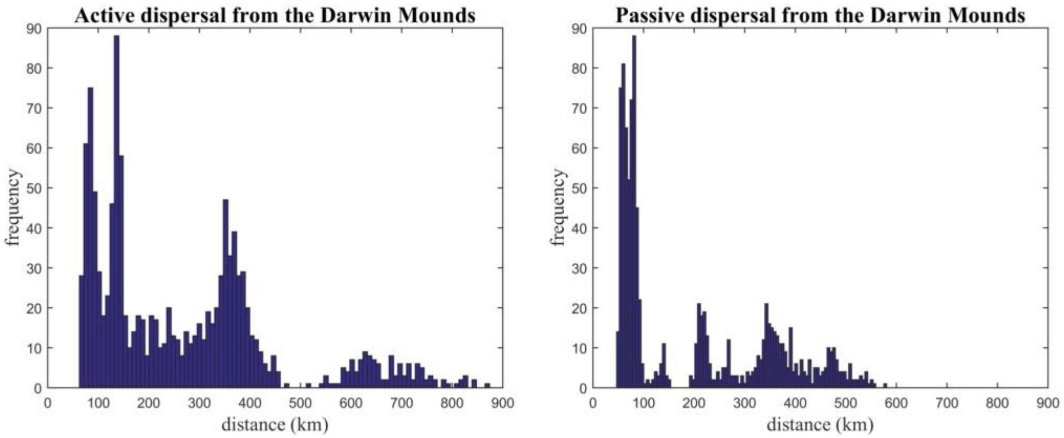


Figure 20 Dispersal kernels created from simulated trajectories at the Darwin Mounds MPA for both active (left) and passive (right) dispersal.

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. Arguably a greater number of larvae were retained within the region of the source MPA (marked with a square in Figure 19), but in practice the concentration of larvae retained within the MPA is lower for active larvae (Table 7, 19 878 larvae) than for passive (Table 8, 30 022 larvae).

Dispersal kernels of Darwin Mounds trajectories are shown in Figure 20. Passive dispersal was right skewed with the majority of settlement occuring near source (<100km dispersal distance) while others travelled up to 550km away likely settling in the region of Lousy Bank (Figure 19). 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 (Figure 19).

4.3.2 MPA assessment

The combined matrix of all simulations across all years, depths and larval modes is shown in Table 9. Colour coding according to quartiles gives a quick view of the strongest and weakest connections between source and retaining MPAs.

Larval flow appeared to be predominantly northwards in southern MPAs, both in the Rockall Trough and the Hatton Rockall Basin (grey rows) (i.e. high larval counts were generally to the left of the local retention diagonal boxes). Northern MPAs in both basins had a more even flow of larvae both northward and southward (high counts left and right of diagonal boxes). Flow between the Rockall Trough and Hatton Rockall Basin mainly came from Hatton Bank and West Rockall Bank flowing east, and East Rockall Bank and the Logachev Mounds flowing west. The majority of MPAs in the wider network performed well, with released larvae spreading to an average of 7 other MPAs, including an average of 3 strong (upper quartile) connections.

Individual MPA assessments

Metrics of individual MPA performance are shown in Table 10. Rankings B, C and F are based on proximity to 33.3% optima. A visualisation of MPA network connections is shown in Figure 21.

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

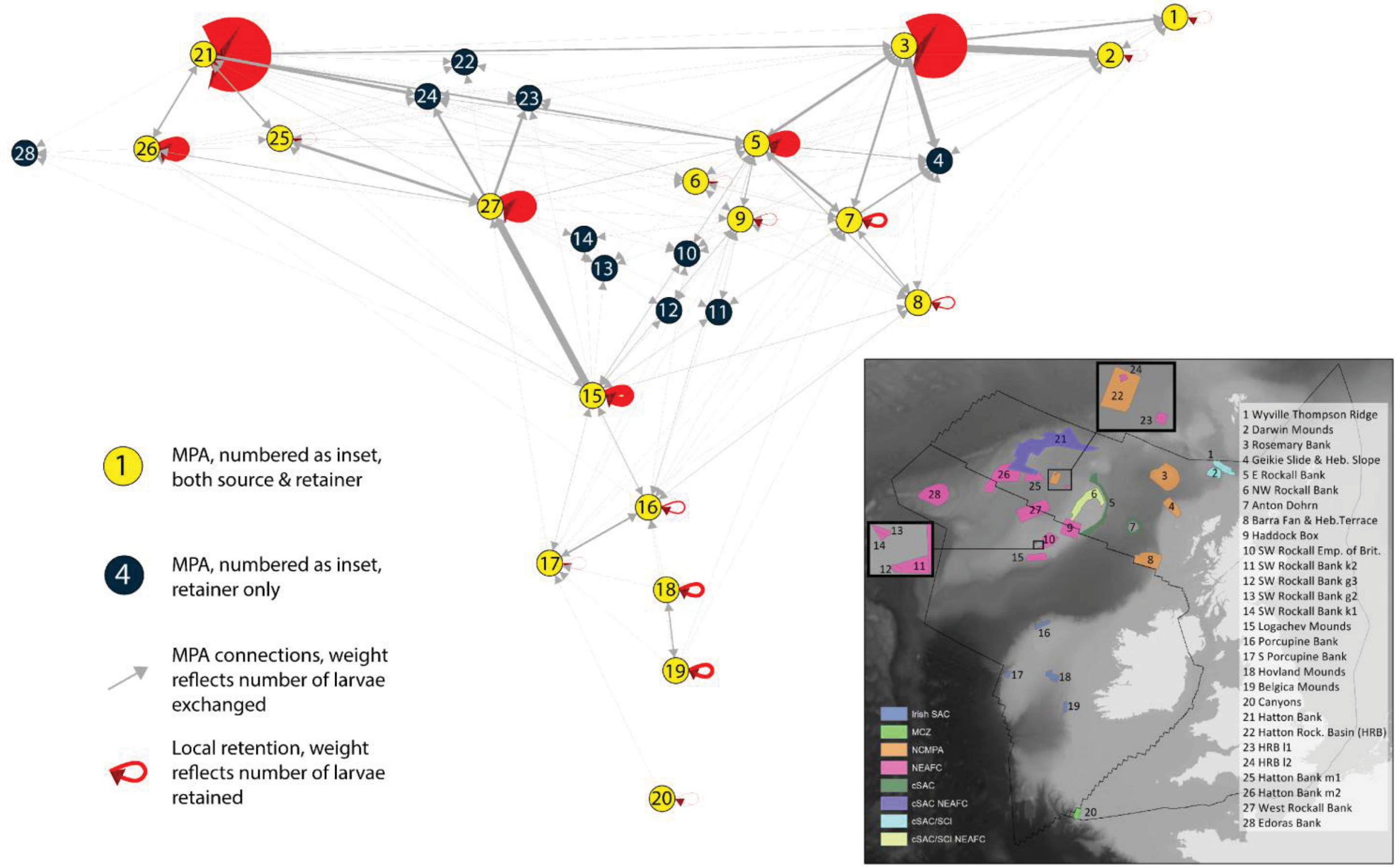
Table 10 MPA performance metrics.

Measures of source (including local retention), and recruiter performance are ranked (in grey columns) from 1 (best) to 18 (source performance) or 28 (recruiter performance, inclusive of 10 MPAs which did not supply larvae). Best (yellow) and worst (red) rankings are highlighted. Summary metrics are averages of cited rankings. MPAs are ordered by the overall MPA metric (last column) from best to worst performing MPA. MPAs which are recruiter only are excluded from metrics requiring comparison to source statistics, and are ordered by average recruiter ranking from best to worst performing MPA. Source performance measures in % are ranked with 33.3% as the target (best) proportion.

MPA	Sub-Network	MPA Size		SOURCE PERFORMANCE										Local Retention		Average source rank (A-F)	RETAINER PERFORMANCE								Average retainer rank (G-I)	MPA METRICS		
				Number of Larvae released/ supplied		Supplied larvae retained outside network		Supplied larvae retained by other MPAs (excluding local retention)		Number of MPAs supplied		Evenness of source's supply (1/Simpson's D, D= Σ(n/N)2)					Larvae retained			MPAs supplying retainer		Evenness of retainer's sources (1/Simpson's D, D= $\Sigma(n/N)^2$)			MPA net rating (Source, Sink, Balanced)		Average of source and retainer ranks (A-I)
		km^2	rank	count	rank A	% of larvae supplied by source	rank B	% of larvae supplied by source	rank C	count	rank D	Simpson's D	rank E	% of larvae supplied by source	rank F		count	% of all retained	rank G	count	rank H	Simpson's D	rank I		count retained/ supplied	net rating	
AntonDorhn	UK	1429	15	7569000	11	38.13	2	35.26	2	14	7	3.71	1	26.61	3	4.33	5125051.7	3.41	7	11	4	3.29	2	4.33	0.68	source	4.33
WRockall	NEAFC	5123	5	36959700	5	52.88	6	15.79	3	18	3	2.13	7	31.32	2	4.33	16124023	10.73	3	9	7	1.71	14	8.00	0.44	source	5.56
RosemaryBank	UK	6934	2	75376000	3	44.86	5	14.36	7	10	7	1.77	10	40.78	5	6.17	33942767	22.58	2	13	1	1.21	22	8.33	0.45	source	6.89
TheBarraF&HebTer	UK	4378	6	2034000	14	48.22	4	16.02	4	10	7	1.95	9	35.76	4	7.00	2139740.8	1.42	14	10	5	3.98	1	6.67	1.05	sink	6.89
ERockallBank	UK	3697	8	82791200	2	83.73	14	6.05	13	22	2	2.35	6	10.22	12	8.17	11888157	7.91	4	12	3	1.91	12	6.33	0.14	source	7.56
LogachevMounds	NEAFC	1600	13	51119400	4	78.30	9	10.32	8	21	1	2.38	5	11.38	11	6.33	6772359.5	4.51	6	9	7	1.35	18	10.33	0.13	source	7.67
HattonBank_I	UK/ NEAFC	15690	1	117725800	1	63.87	8	5.12	12	18	4	1.35	15	31.01	1	6.83	37760143	25.12	1	9	7	1.07	26	11.33	0.32	source	8.33
HaddockBox	NEAFC	3403	9	5508000	12	79.00	12	16.81	5	19	5	3.39	2	4.19	14	8.33	649425.5	0.43	18	9	7	2.22	6	10.33	0.12	source	9.00
HBm1	NEAFC	1474	14	234000	16	38.11	1	52.31	10	11	7	2.59	4	9.58	13	8.50	2896204.5	1.93	12	6	18	2.03	9	13.00	12.38	sink	10.00
PorcupineBank	Ireland	731	19	28746000	6	94.96	18	2.32	14	12	6	2.76	3	2.72	16	10.50	1838474.7	1.22	15	9	7	1.96	10	10.67	0.06	source	10.56
HBm2	NEAFC	6100	3	15354000	8	44.05	3	7.76	9	7	13	1.32	16	48.19	10	9.83	8865420	5.90	5	7	15	1.41	17	12.33	0.58	source	10.67
NWRockall_g	UK/ NEAFC	4368	7	45000	18	14.65	7	22.32	1	12	7	1.72	11	63.03	18	10.33	71179.167	0.05	22	8	14	2.23	5	13.67	1.58	sink	11.44
DarwinMounds	UK	1378	16	70200	17	81.63	10	6.52	11	3	16	2.09	8	11.85	9	11.83	4288765.5	2.85	9	9	7	1.04	27	14.33	61.09	sink	12.67
SPorcupine	Ireland	349	22	9531000	10	86.25	15	13.51	6	9	12	1.50	14	0.24	17	12.33	49848	0.03	24	6	18	2.21	7	16.33	0.01	source	13.67
BelgicaMounds	Ireland	514	21	15890900	7	83.05	13	2.36	15	6	13	1.32	17	14.59	7	12.00	3004510.3	2.00	11	2	26	1.54	16	17.67	0.19	source	13.89
HovlandMounds	Ireland	1086	18	12186000	9	76.34	11	5.66	17	4	16	1.57	13	18.01	6	12.00	2545882.2	1.69	13	2	26	1.31	19	19.33	0.21	source	14.44
WTR	UK	1741	12	3838800	13	96.10	17	0.96	16	4	15	1.62	12	2.94	15	14.67	1411486.2	0.94	17	9	7	1.19	23	15.67	0.37	source	15.00
TheCanyons	UK	660	20	432000	15	87.42	16	0.00	18	2	18	1.00	18	12.58	8	15.5	54333.833	0.04	23	1	28	1.00	28	26.33	0.13	source	19.11
GeikieS&HSlope	UK	2218	10	These MPAs do not supply larvae so cannot be assessed as sources													4953355.7	3.30	8	13	1	1.93	11	6.67	MPAs without source performance are not included in these metrics		
HRB	UK	1258	17														3689380.3	2.45	10	10	5	2.39	3	6.00			
EdorasBank	NEAFC	5879	4														177176.17	0.12	19	4	21	2.04	8	16.00			
SWRockallEmpress	NEAFC	2002	11														126510.17	0.08	20	7	15	2.38	4	13.00			
HRB_I1	NEAFC	120	24														1751589.3	1.17	16	7	15	1.14	25	18.67			
SWRockall_k2	NEAFC	129	23														73766.167	0.05	21	5	20	1.58	15	18.67			
SWRockall_k1	NEAFC	34	26														32995.667	0.02	26	4	21	1.31	20	22.33			
SWRockall_g2k1	NEAFC	22	27														36188.167	0.02	25	3	25	1.77	13	21.00			
SWRockall_g3k2	NEAFC	14	28														15997	0.01	27	4	21	1.25	21	23.00			
HRB_I2	NEAFC	42	25														8460.1667	0.01	28	4	21	1.16	24	24.33333			

Figure 21 Visualisation of MPA network connections.

MPAs are numbered and configured as shown in Figure 10 (inset here for ease of comparison). Yellow nodes represent MPAs which were both source and recruiter, while blue nodes are recruiter 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 source and recruiter) MPA overall, while The Canyons (20) performs the worst.



Hatton Bank has the best performing rate of both retention from any MPA source, and local retention; it is also the largest MPA and releases the most larvae. Larval retention ability (equivalent to rank G in Table 10) was correlated to MPA size (Pearson's r=0.81, n=28, p=<0.01). However Edoras Bank (also known as Edora's Bank) is the worst retaining large MPA (rank 4 size, rank 19 retention), and Belgica Mounds is the best retaining small MPA (rank 21 size, rank 11 retention).

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

MPA network assessment

Network assessment metrics were calculated for each individual network (defined by designating body) and for the combined wider network (Table 11**Error! Reference source not found.**). Based on an example ideal network criteria with a target three-way balanced split between local retention, larval supply to the rest of the network, and supply to non-protected areas outside of the network, the UK network performs the best (average rank 1.33), followed by the NEAFC closures (1.66), the combined network (3), and the Irish network (4). No network achieves the ideal balance, all networks

displaying a heavy bias towards supplying sites exterior to the network. Local retention rates were good for all networks except the Irish network which was comprised of only smaller than average sized MPAs (ranked 18, 19, 21, and 22 out of 28). The proportion of supply to the rest of the network was best in the UK network (8.59%), but was still less than a third of the ideal proportion (33.3%).

	Total number of larvae released	Number of source MPAs	Number of retaining MPAs	Network Assessment		
				Local retention %	Supply to rest of network %	Supply outside of network %
Irish	54167900	4	4	8.01	4.55	87.44
NEAFC	321923100	7	15	27.13	8.54	64.32
UK	207090800	9	11	27.13	8.59	64.28
COMBINED NETWORK	583181800	18	28	24.96	8.11	66.93

Table 11 Network assessment metrics**.**

In this example the ideal network would have a balance of 33.3% each to local retention, supply to rest of network, and supply to outside network.

4.4 Discussion

The results of this study offer the first assessment of NE Atlantic offshore MPA networks with regard to the larval dispersal component of their ecological coherence. This assessment is based on combined passive and active larvae null model simulations, offering an opportunity to compare the effect of behaviour on dispersal patterns. Both aspects of this study provide hypotheses which can be ground truthed in the future.

4.4.1 Passive vs. active

This study found no statistical difference between passive and active MPA dispersal matrices. It is important to note that this study was designed to be appropriate at a scale of relevance to marine managers. This means that when considering the effectiveness of an 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 generally this finding is at odds with the literature which often reports increased local retention in active swimming larvae. Paris and Cowen (2004), using a combination of observations and models, realised that damselfish larvae were using an increase in swimming ability during ontogenesis to swim downwards and stay in the bottom boundary layer if they were near suitable habitat. This trait was carried forward into Cowen *et al.*'s (2006) model which proposed the retentive effects of such behaviour when compared to passive larvae. Butler *et al.* (2011) also found greater retention when modelling active ontogenetic vertical migration in spiny lobster larvae, a species with a very long PLD (~170 days).

L. pertusa larvae nominally appear to have this trait as well, with Larsson *et al.* (2014) observing positive geotaxis from day 21 of their PLD (Figure 18), yet simulations showed no statistical difference between local retention counts in passive and active matrices. This finding may be attributable to the spatial frame of reference used. This study compares MPA matrices where differences between larval modes are only being tested on the 32% of released larvae which were captured within the wider MPA network, thereby excluding the 68% that settled in non-protected areas. A true ecological comparison would be better based on dispersal kernels such as those in Figure 20. The local retention metrics in Table 10 do provide a standardised area comparison between behaviours within one MPA, but matrix averages are based on MPAs of varying size. The Darwin Mounds case study shows lower local retention in active simulations based on matrix analysis, but Figure 19 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 which 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 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 on the basis of 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.

Examined in greater detail, the average lack of a difference between passive and active simulations on a network wide scale does not preclude site specific variation. The dispersal matrices (Table 7 and Table 8) show that in the Haddock Box local retention increase by a third when larvae were active, but at Porcupine Bank retention was two thirds reduced. The results from the Darwin Mounds alone (Figure 19 and Figure 20) also demonstrate a site specific effect of larval mode, concurrent with observations made by Butler *et al.* (2011), Young *et al.* (2012) and Edwards *et al.* (2007). Young *et al.* (2012) were simulating the effect of depth of release for a range of deep water invertebrates and simulated instances of enhanced, subverted and equivalent dispersal dependent on species, location and year of simulation. Edwards *et al.* (2007) found that the dispersal kernels of theoretical larvae on the US Georgia shelf would be more impacted by spawning time and location than by vertical positioning.

A site specific response is logical given the variability in topographic dispersal barriers, only some of those encountered by passive larvae can be overcome by larval vertical swimming ability.

Butler *et al.* (2011) also found that both active and passive simulations were bimodal with peaks at <400km from source and >1000km, and both peaks strengthened when larvae were active. This study observed a similar multi-modality in the example Darwin Mounds dispersal kernels

(Figure 20). The trimodal feature of the active Darwin Mounds dispersal kernels clearly reflects forks in the topography and hydrography – something which may also have been the case in Butler *et al.* (2011).

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 (Figure 20, not tested at other sites), again paralleling the findings of Butler *et al.* (2011). Young *et al.* (1996) 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 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 including mortality, availability of suitable habitat and conditions, competition with other species (e.g. *Madrepora oculata* (Linnaeus, 1758), or *Solenosmilia variabilis* (Duncan, 1873) below 1000m), survival rates, and settlement density estimates. 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 however 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 therefore there is potential for additional larval density diffusive effects in reality. Furthermore in reality dispersal kernels are liable to be smoother with greater mortality, greater individuality in larval characters, and the incidence of small scale oceanographic features which have dispersive effects not captured by the relatively low resolution hydrodynamic model.

Source population	Hypotheses	
Darwin Mounds SAC (UK)	Passive	Population related to Southern populations on **Faroe Bank, Bill Bailey Bank, Lousy Bank** and Northern populations on **Rosemary Bank**. Populations NOT closely related to **Wyville Thomson Ridge**. Vertical cline in relatedness.
	Active	Population related to Southern populations on **Faroe Bank, Bill Bailey Bank, Lousy Bank**, Northern populations on **Rosemary Bank** AND **Wyville Thomson Ridge.** No notable vertical cline in relatedness.
	Caveats	Darwin Mounds populations may not be sexually reproducing, if so Southern populations on **Faroe Bank, Bill Bailey Bank, Lousy Bank** and Northern populations on **Rosemary Bank** will NOT be closely related.
East Rockall Bank SAC (UK)	Passive	Population NOT closely related to those in **NW Rockall Bank, SW Rockall Empress of Britain Bank.** Vertical cline in relatedness.
	Active	Population IS closely related to those in **NW Rockall Bank, SW Rockall Empress of Britain Bank.** No notable vertical cline in relatedness.
Haddock Box Voluntary Closure (NEAFC)	Passive	Population NOT closely related to those in **SW Rockall Empress of Britain Bank, SW Rockall k2.** Vertical cline in relatedness.
	Active	Population IS closely related to those in **SW Rockall Empress of Britain Bank, SW Rockall k2.** No notable vertical cline in relatedness.
Logachev Mounds Voluntary Closure (NEAFC)	Passive	Population NOT closely related to those in **SW Rockall Empress of Britain Bank, SW Rockall k2, SW Rockall g3, SW Rockall g2, SW Rockall k1**. Vertical cline in relatedness.
	Active	Population IS closely related to those in **SW Rockall Empress of Britain Bank, SW Rockall k2, SW Rockall g3, SW Rockall g2, SW Rockall k1**. No notable vertical cline in relatedness.
West Rockall Bank Voluntary Closure (NEAFC)	Passive	Population NOT closely related to those in the **SW Rockall Empress of Britain Bank, SW Rockall g2.** Vertical cline in relatedness.
	Active	Population IS closely related to those in the **SW Rockall Empress of Britain Bank, SW Rockall g2.** No notable vertical cline in relatedness.

Table 12 Passive vs. active hypotheses for future ground truthing.

As one of the aims of this study is to generate modelled null hypotheses for future ground truthing,

Table 12 displays some hypotheses derived from this work which may be useful in discerning how much vertical migration is occurring within *L. pertusa* larval cohorts *in situ*.

4.4.2 MPA dispersal assessment

On the whole the wider MPA network for the protection of *L. pertusa* appears well interconnected (Table 9 and Figure 21). There were very few MPAs which appeared isolated from the network, and all source MPAs were succeeding in locally retaining a proportion of their own larvae, which is positive for future protection 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.

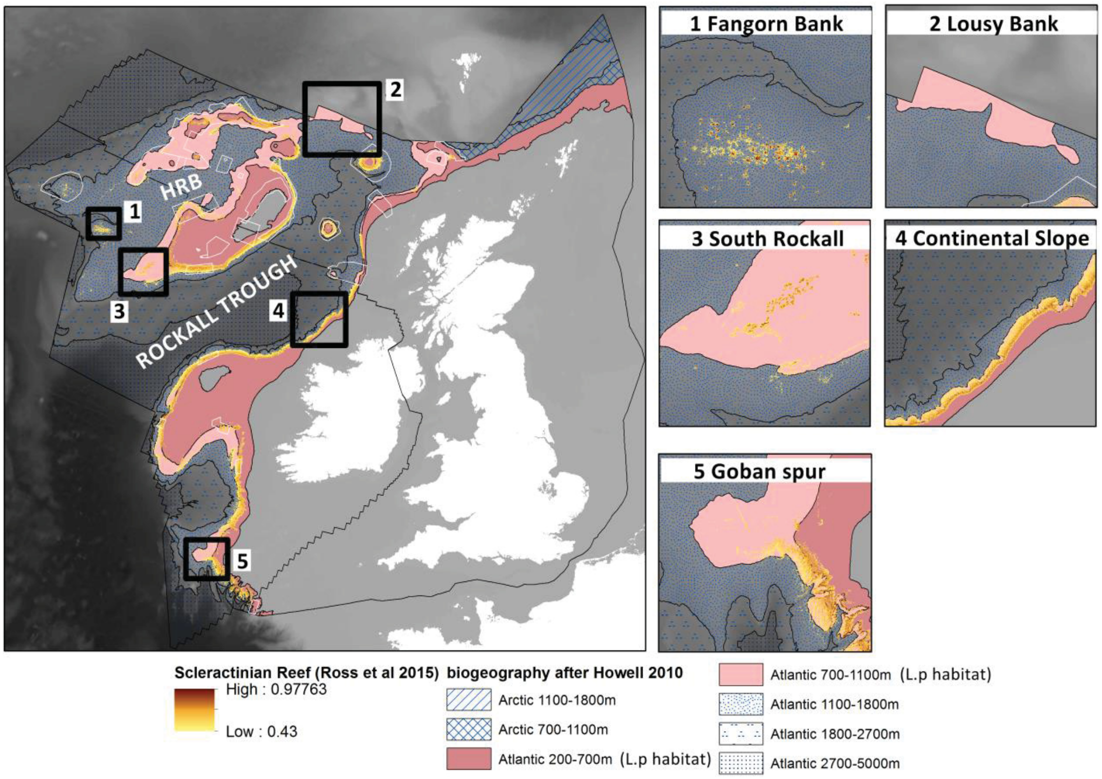


Figure 22 Habitat suitable for *Lophelia pertusa* species and Sclearactinian reef.

This highlights how much of the maximum area is currently protected, and considered in tandem with this study's network results (Figure 21), helps identify some areas where future protection may be beneficial. The Rockall Trough and Hatton Rockall Basin (HRB) are the main areas lacking suitable habitat. Scleractinian reef prediction from Ross *et al.* (2015: *L.pertusa* reef <1100m, *S.variabilis* reef >1100m), biogeography after Howell (2010).

It is important that both the failings and successes of the network be compared to what the maximum protection potential for the area could be, in terms of the area and extent of suitable habitat. For simplicity consider the topography and basic biogeographic provinces of the area (after Howell 2011) representing *L. pertusa* species's optimal depth range: Figure 22 highlights this area, along with the predictions for Scleractinian reef from Ross *et al.* (2015). The *L. pertusa* species depth range notably covers more ground than the predictions for reef presence, partly because this visualisation is simplified to only factor in depth and biogeography (there are many other factors which affect habitat suitability), but also because some areas maybe suitable to the species but not necessarily the reef habitat (Howell *et al.* 2011). The Ross *et al.* (2015)

Scleractinian reef model was also constrained to only predict into areas where high resolution bathymetry is available, so there may be reef suitable habitat in areas of the UK EEZ omitted due to lack of multibeam data (Rengstorf *et al.* (2013) have a higher resolution *L. pertusa* reef model available in Irish waters). MPAs within the highlighted depth range therefore have the potential to aid the network in the protection of *L. pertusa* reef, by offering protected habitat to either reef or individual colonies.

Figure 22 shows two large areas where there is no suitable *L. pertusa* habitat: the Rockall Trough and the Hatton Rockall Basin (HRB). Transiting these regions may therefore lead to the greatest loss of larvae where propagules may become trapped in mesoscale oceanographic features far from areas suitable for settlement. This may mean that the MPA network can never reach the example 33.3% target for larval exchange between network protected sites, as there will always be a proportion of larvae lost whilst crossing these divides.

This study does show that larval exchange is already likely to be occurring across these basins between existing MPAs. These simulations suggested that larvae being exchanged within the MPA network may be fording the Rockall Trough in two primary locations. The northern transit is aided by the protected seamounts (Anton Dohrn (the best MPA) and Rosemary Bank (the third best MPA) – MPAs 3 and 7 in Figure 21) which offer stepping stones between the continental slope and East Rockall Bank. The southern transit occurs between Porcupine Bank and the Logachev Mounds (MPAs 15 and 16 in Figure 21). The bridging of the Hatton Rockall Basin occurs predominantly at West Rockall Bank (the second best performing MPA – MPA 27 in Figure 21) offering a stepping stone connection between the various Rockall Bank and Hatton Bank protected areas.

Considered in tandem, Figure 21 and Figure 22 highlight the areas with the most room for improvement. Figure 22 shows that the UK network covers a lot of *L. pertusa*'s suitable depth range and consists of large MPAs with reasonable area coverage. The main area lacking protection is in the north of the study area, comprising Faroe Bank, Bill Baily Bank and Lousy Bank, with a major part of each feature falling under the jurisdiction of Denmark in the Faroe

Islands EEZ. A Small portion of Lousy Bank does extend into UK waters however, and this may be a useful area to explore for potential protection in the future, especially as this may aid the transit of larvae from the Darwin Mounds (ranked 6th worst performing of the 18 assessed MPAs) into the Hatton Bank region (Figure 19). Histological studies from the Darwin Mounds also bear consideration with regard to its performance as an MPA. Waller and Tyler (2005) explored the reproductive biology of *L. pertusa* at the Darwin Mounds and found an absence of sexually reproducing animals. Coupled with the work of LeGoff Vitry *et al.* (2004), who undertook a genetic study of the area and found very low genetic differentiation, this suggests that clonal reproduction (asexual budding & colony fragmentation) may be the dominant reproductive mode in this MPA. It is speculated that the nature of the patchy habitat at this site, comprised of mounds of raised substrate on a flat sedimented plane (made patchier through trawling destruction), may reduce the ability of immigrating larvae to settle, promoting clonal success in areas where retention is successful (LeGoff Vitry *et al.* 2004, Waller and Tyler 2005). Other speculations include the sterility induced by trawl damage, or polyp suffocation from dredging (Waller and Tyler 2005) or indeed repeat natural resuspension from storms and Wyville Thomson overflow events. Should this be the case at present, there may not be any onward dispersal of larvae from the Darwin Mounds MPA, and an amended matrix should be used removing this MPA as a source (row), but maintaining its ability to retain larvae (column).

The Canyons, also in UK waters, was the worst performing MPA as it is the most geographically isolated, but due to the shape of the UK and Irish EEZ boundaries and the underlying topography (Figure 22), improving the connections to this MPA will fall under Ireland's jurisdiction. France's EEZ is also proximate to the Canyons and given the northward flow of the European Shelf Current, reefs in French waters are the most likely to supply larvae to the Canyons MCZ, so we should also look to French waters to support this MPA. There may be weaknesses in the study predictions regarding the Canyons as the coarse underlying topography in the hydrodynamic model is unlikely to represent the canyon features well. However it is likely that any finer scale topography and associated hydrography would also have retentive properties. This MPA therefore warrants close monitoring, and site specific modelling in the future to better quantify its dispersal performance.

The Irish network has the greatest room for improvement, with only four relatively small MPAs situated on the continental slope. Thanks to the Irish National Seabed Survey all of Ireland's waters are mapped with high resolution bathymetry so the *L. pertusa* reef model prediction covers this entire EEZ (Ross *et al.* 2015) and even higher resolution models are available in this region (Rengstorf *et al.* 2013).

Figure 22 details the locations of suggested new sites for consideration in extending the network in this region. The huge area of Irish continental shelf which 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 be more promotional to 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 Hatton Rockall Basin.

At present only the NEAFC have provided any protection to habitat west of the continental slope in Irish waters. NEAFC voluntary closures currently support both national networks. Not all of these are closed for the protection of *L. pertusa*, but may do so incidentally (e.g. the Haddock Box). Note that Edoras Bank, and the Hatton Rockall Basin (inclusive of HRBl2) are not situated in areas of suitable depth for *L. pertusa*. These areas are protecting other species: Edoras likely hosts *S. variabilis* reef, due to the deeper waters, and HRB was designated for the protection of the Bird's Nest Sponge *Pheronema carpenteri* (Wyville Thomson 1869) sponge aggregations on polygonal fault geological features. These areas may be able to host small populations of *L. pertusa* species, but this remains to be seen. This study includes these regions on this basis, but if data is found to the contrary this may warrant their exclusion from future assessments of *L. pertusa* dispersal.

Should *L. pertusa* be supported in these deeper MPAs, Ireland may wish to consider Fangorn Bank as a potential area for future protection also. This site offers the only potential to improve connections to Edoras bank (the worst retaining large MPA). Both of these sites warrant consideration on behalf of *S.variabilis* even if *L. pertusa* is not supported.

Further advice on future areas of conservation value to the network can be explored using trajectory maps such as those shown in Figure 19. Dispersal models can be run both forwards and backwards in time, allowing detection of both larval fates and larval sources from any given location. Regions of trajectory overlap between forward and backward simulations can offer suggestions for areas worth investigating for future protection.

At present all of the advice offered by this study should be taken as tentative. This study could be extended over a longer timescale in order to account for inter-annual hydrographic variability (in line with the recommendations of Chapter 2) and modelled results are uncertain until ground truthed to ensure that predictions are reflecting reality and to quantify the margin of predictive error.

Biological ground truthing can also be undertaken by comparing these predictions to population genetics in the region. Le Goff-Vitry *et al.* (2004) assessed *L. pertusa* genetic connectivity in the NE Atlantic, including samples from La Chapelle (near the Canyons in the French EEZ), Hovland Mounds, the region of Porcupine Bank and Logachev Mounds, and the Darwin Mounds (as well as populations in Spanish and Norwegian waters). Of those tested, they detected a high degree of local retention at the Darwin Mounds (very high) and Hovland Mounds, concurrent with local retention rankings in this study. Although the Norwegian fjord sites were found to be the most genetically distinct, there was still structure detected between the continental slope sites relevant to this study, indicating only a moderate flow of genes between sites. 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 findings suggesting connection between all MPAs but at low levels compared with the amount supplied outside the network.

A more comprehensive population genetic study in the region is forthcoming, and will include "next generation sequencing" population genomics of *L. pertusa* and targeted ground truthing of this study. The new study will also investigate vertical (between depths) connectivity of populations which can be compared on a depth by depth basis to the results of this study (see supplementary matrices in Appendix A3.1 (p173)). Model results and genetics together will create a much more complete picture of what patterns of connectivity are occurring in the NE Atlantic, as well as the dispersal abilities of the species in general. Table 13 details some hypothesised source proportions derived from this study which can be used to test whether these predictions of dispersal are accurate. Particularly useful ground truthing targets may include:

- NW Rockall Bank which may be 63% self-recruiting. If a large proportion of recruits originate in E Rockall Bank MPA, larvae may have been vertically migrating. Interestingly in the study region NW Rockall is almost exclusively comprised of white colour morph *L. pertusa*. Most other sites are dominated by the orange morph but E Rockall Bank reefs display both morphs. Larsson *et al.* (2015) observed that oocytes of *L. pertusa* in Trondheim bore the pigment of the female they originated from so there may opportunity to test whether the colour morph at these sites are indicative of genetic relationship.
- 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 may disprove some of the predictions made by these models.
- The Canyons is predicted to be connected only to itself and non-protected areas. Any MPAs with a relationship to the canyons population would disprove tis prediction.

- At present directionality of genetic transfer is still difficult to detect, but if the Darwin Mounds do display a lack of sexually reproducing individuals (cf. LeGoff-Vitry *et al.* 2004, Waller and Tyler 2005), this will be an area where directionality can be inferred and therefore may prove useful in developing methods in this field. This will also mean that the directionality predicted by this study can be tested, and should recruits not be predominantly related to Rosemary Bank populations this could easily contradict predictions.

In spite of directionality issues, studies integrating marine genetic and dispersal modelling data have proven successful (e.g. Foster *et al.* 2012, Sunday *et al.* 2014) and may be useful to marine managers and ecologists in the future. These types of data are not an ideal match for cross-ground truthing: dispersal models predict only contemporary dispersal patterns while genetic data operates on generational timescales, and models rarely include mortality and therefore do not reflect the survival implicit in genetic exchange (Levin 2006, Metaxas and Saunders 2009, Liggins *et al.* 2013). However advice is available for undertaking and optimising such cross-comparison (e.g. Liggins *et al.* 2013), and discordance in results can also be informative in diagnosing areas where hydrography is not the only factor driving population structure (Galindo *et al.* 2010, Foster *et al.* 2012).

4.4.3 Conservation future

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 (2007) '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 Altantic Ocean, so a truly ecologically

Table 13 Hypothesised larval sources and proportions for future genetic sampling of MPAs.

(Left) Additional non-MPA genetic sources are likely, but predicted proportions between MPA sources could be tested. **Bold** MPA connections are active larvae only, *italic* passive only.

Wyville Thomson Ridge	88 %	Rosemary Bank	<1%	**Darwin Mounds**, ERockallBank, **NWRockall**, AntonDohrn, BarraFanandHebTerr., Hatton Bank
	11 %	Wyville Thomson Ridge		
Darwin Mounds	97 %	Rosemary Bank	2%	Wyville Thomson Ridge
			<1 %	self (sexual), ERockallBank, **NWRockall**, AntonDohrn, BarraFanandHebTerr., HattonBank
Rosemary Bank	86 %	Self	7 %	Hatton Bank
			6 %	ERockallBank
			<1 %	WyvilleThompsonRidge, DarwinMounds, NWRockall, AntonDohrn, BarraFanand HebTerr.,HaddockBox, LogachevMounds, HBm1, WRockall.
Geikie Slide and Hebrides Slope	83 %	Rosemary Bank	<1 %	**WyvilleThompsonRidge**, ERockallBank, **NWRockall**, BarraFanandHebTerr., HaddockBox, LogachevMounds, PorcupineBank, **BelgicaMounds**, HattonBank
	13 %	Anton Dohrn		
East Rockall Bank	74 %	Self	9 %	Hatton Bank
			5 %	Rosemary Bank
			3 %	Logachev Mounds
			3 %	Haddock Box
			2%	West Rockall
			2 %	Anton Dohrn
			<1 %	PorcupineBank, SPorcupineBank, NWRockall, BarraFanandHebTerr, HBm1
NW Rockall Bank	50%	Self	<1 %	Hatton Bank, **Rosemary Bank**
	36 %	E Rockall Bank		
	13 %	West Rockall		
Anton Dohrn Seamount	64 %	Self	5 %	Barra Fan and Hebrides Terrace
	16 %	Rosemary Bank	<1%	LogachevMounds, HaddockBox, PorcupineBank, HattonBank, NWRockall, SPorcupine, **BelgicaMounds**
	12 %	E Rockall Bank		
Barra Fan and Hebrides Terrace Seamount	31 %	E Rockall Bank	5 %	Porcupine Bank
	25 %	Self	3 %	Haddock Box
	21 %	Anton Dohrn	<1 %	RosemaryBank, SPorcupine, HattonBank, NWRockall.
	12 %	Logachev Mounds		
Haddock Box	81 %	E Rockall Bank	4 %	Logachev Mounds
	13 %	Self	<1 %	PorcupineBank, **WRockall**, NWRockall, SPorcupine, AntonDohrn, BarraFanand HebTerr.
SWEST Rockall Empress of Britain Bank*	76 %	Logachev Mounds	9 %	West Rockall
	11 %	Haddock Box	4 %	E Rockall Bank
SWEST Rockall k2*	89 %	Logachev Mounds	9 %	Haddock Box
			1 %	E Rockall Bank
			<1 %	West Rockall
SWEST Rockall g3*	95 %	Logachev Mounds	4 %	Haddock Box
			<1 %	E Rockall Bank, WRockall
SWEST Rockall g2*	93 %	Logachev Mounds	6 %	West Rockall
			<1 %	Haddock Box
SWEST Rockall k1*	97 %	Logachev Mounds	2 %	West Rockall Bank
			<1 %	HaddockBox, ERockallBank
Logachev Mounds	85 %	Logachev Mounds	4 %	Haddock Box
			4 %	Porcupine Bank
			3 %	S Porcupine
			<1 %	BarraFanandHebTerr., WRockall, NWRockall
Porcpuine Bank	84 %	S porcupine	<1 %	BelgicaMounds, LogachevMounds, HovlandMounds
	16 %	Self		
South Porcupine Bank	60 %	Belgica Mounds	<1 %	PorcupineBank, TheCanyons, LogachevMounds
	39 %	Self		
Hovaland Mounds	91 %	Self	9 %	Belgica Mounds
Belgica Mounds	99 %	Self	1 %	Hovland Mounds
Canyons	100%	Self	n/a	n/a
Hatton Bank	96 %	Self	2 %	HBm2
			1 %	West Rockall
			<1 %	HBm1, ERockallBank, LogachevMounds, RosemaryBank.
Hatton Rockall Basin*	66 %	West Rockall	<1 %	HBm1, ERockallBank, LogachevMounds, **HBm2.**
	31 %	Hatton Bank		
Hatton Rockall Basin l1*	99 %	West Rockall	<1 %	HattonBank, HBm1, LogachevMounds, **ERockallBank**
Hatton Rockall Basin l2*	92 %	Hatton Bank	6 %	West Rockall
			2 %	Logachev Mounds
Hatton Bank m1	67 %	West Rockall	7 %	Logachev Mounds
	24 %	Hatton Bank	<1 %	HBm1, HBm2, ERockallBank
Hatton Bank m2	88 %	Self	5 %	Hatton Bank
			4 %	Logachev Mounds
			1 %	West Rockall
			<1 %	HBm1, PorcupineBank
West Rockall Bank	68 %	Self	1 %	HBm2
	29 %	Logachev Mounds	<1 %	PorcupineBank, HattonBank, SPorcupine, HBm1, **HaddockBox, ERockallBank**.
Edoras Bank*	57 %	HBm2	<1 %	WRockall, HattonBank
	41 %	Logachev Mounds		

coherent network would span many nations' EEZs and the high seas ABNJ 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. Should genetic data become available for other species, this can also be compared to the *L. pertusa* null models in this study in order to derive larval characters where they are lacking. For example *Madrepora oculata* (Linnaeus 1758) is also a scleractinian reef building coral, and co-occurs with *L. pertusa* as a secondary reef habitat constituent in the region (Arnaud –Haond *et al.* 2015). Less is known about *M.oculata*'s larval characters, but preliminary evidence suggests that its population genetics may be structured differently to *L. pertusa* (Becheler *et al.* 2015). Upcoming work in our study region will be sourcing population genetic data for this species as well as *L. pertusa* allowing this data to be cross-compared with the predicted *L. pertusa* dispersal patterns. This would provide a means to ascertain its similarity to *L. pertusa*'s dispersal abilities. Differences and similarities will help us learn more about the PLD, spawning frequency, and vertical migration of both species. As results would also be relevant to the protection of the reefs in the area, *M. oculata* data should be integrated into MPA assessments in the future. There are many other species and habitats listed as protection targets in conservation legislation: these will require custom studies to ensure that the network is suitable for their protection also. The results of this study showing that passive and active dispersal give similar results in this region may allow these estimates to be suitable to many more species than previously thought, however differing PLDs will have an effect on how universally these assessments can be applied (see Chapter 2). 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 should therefore go towards testing the limits of the existing NE Atlantic network and its ability to support species with shorter PLDs. The low proportion of *L. pertusa* larvae being exchanged between networked sites as predicted by this study, is unlikely to improve for species with shorter PLDs, and 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 (2003) and Botsford *et al.* (2001).

5. Thesis discussion

The series of studies held within this thesis were performed to critically appraise the abilities of existing larval dispersal modelling tools, when applied within a deep sea context, to inform marine conservation.

To date, marine conservation has broadly overlooked larval dispersal in the establishment of marine protected area (MPA) networks. Only a small number of shallow water species studies (Botsford *et al.* 2001, Kinlan and Gaines 2003, Shanks 2003, Cowen 2006) have informed the size and spacing of MPAs in both coastal (Jones and Carpenter 2009) and offshore waters (Roberts *et al.* 2010, Wedding *et al.* 2013), leaving uncertainty as to whether MPAs have been designed for the adequate protection of species with unknown connectivity patterns.

Dispersal models are a well-established tool for discerning connectivity patterns in coastal waters, but there are still relatively few deep sea studies (especially based on non-vent benthic invertebrates) (Yearsley and Sigwart 2011, Young *et al.* 2012, Etter and Bower 2015). This field is now beginning to gain traction, but advice on dispersal model set up has a heavy shallow-water bias (North *et al.* 2009, Simons *et al.* 2012).

This thesis therefore aimed to inform future deep sea dispersal modellers, reviewing current dispersal investigation techniques (Chapter 1) and providing modelling guidance which is deep sea appropriate (Chapter 2). The reliability of dispersal model output was challenged, comparing model outputs to basic estimates and those driven by other hydrodynamic models

(Chapter 3). This advice was then applied to a real world scenario with the aim to inform future marine conservation management (Chapter 4).

5.1 Summary of findings and contribution to knowledge

All studies undertaken in this thesis have highlighted limitations within our knowledge and abilities, providing useful context and cautionary advice as to how to proceed further with deep sea larval dispersal modelling in the future.

Chapter 2 offers a step-by-step guide tailored to deep sea ecologists for sensitivity testing dispersal models (iterative permutations of model inputs to monitor the effect on model outputs). While other advice exists on sensitivity testing (e.g. Simons *et al.* 2012, Putman and He 2013), this study covers a greater depth range than any other, offers a new simple track distance separation over time technique, and relates the test analysis methods to ecologically recognisable concepts (autocorrelation tests, power analysis) which may aid greater understanding as to what these tests are detecting. Five input parameters were tested: timestep of particle simulator, horizontal and vertical separation of release points, release frequency, and temporal range of simulations. For all parameters sensitivity over the extended depth range reduced considerably as compared to the shallow water studies: a finding which can be related to both the structure of hydrodynamic model outputs files, and the watermass stratification in the region under study. Future ground truthing will be required to evaluate whether this simplified output structure is warranted in deep water. An increase in horizontal sensitivity (a reduction of the recommended distance separation of release locations) with increased Planktonic Larval Duration (PLD) was also observed. This is very relevant to deep sea studies where PLDs have the potential to be longer than in shallow water species (Shanks *et al.* 2003, McClain and Hardy 2010, Hilario *et al.* 2015). Additionally, the outcomes of each test were demonstrated to be useful in the set up and interpretation of future work in the study area (e.g.

an optimal arrangement of release locations can be found, no fewer than 52 releases per year should be used unless biologically informed, a minimum of 3 years of simulations incorporating climatic extremes may provide dispersal patterns with 90% similarity to 5 years of simulations).

Chapter 3 takes a look at the stability of model predictions. While the directional nature of currents makes models more likely to be useful than "sphere of influence" estimates (Gaines *et al.* 2003), if the variability in model output is high then a "sphere of influence" estimate may be as useful as a modelled prediction (at least until that prediction can be ground truthed). This is the first deep water study to undertake this comparison, extending observations from shallow water (Shanks 2009). The study compared the predictions from two hydrodynamic models and a "sphere of influence" estimate for a theoretical deep sea animal, with reference to a heavily caveated estimate used in a previous deep sea study (McClain and Hardy 2010). The results concur with shallow water observations, showing that models result in reduced predicted dispersal distances and can provide more spatially-explicit dispersal patterns than estimates. However this is the first study to demonstrate to ecologists the variability in model output between two equally 'sufficient' hydrodynamic models which might be chosen as the basis of an ecological study. The results emphasise the importance of ground truthing model predictions before trusting the conclusions which are drawn from them, highlighting a greater variability in hydrodynamic models than was previously understood by ecologists.

Chapter 4 follows sensitivity advice from Chapter 2, and proceeds with the 'winning' model from Chapter 3. This study uses a dispersal model to assess an already designated network of offshore MPAs in the NE Atlantic. Recently there have been other dispersal assessments published inclusive of an MPA network element (e.g. a network assessment against proxy dispersal values (Lieberknecht *et al.* 2014), an assessment of where new MPAs could be sited to complement an existing network (Schill *et al.* 2015), a metacommunity assessment of habitat connectivity intensity, effectiveness and persistence (Melia *et al.* 2016)), but none assess an existing MPA network's performance based on new connectivity data for the targeted conservation species.

Chapter 4 also includes a comparison of larval modes (passive *versus* active dispersal patterns), partly to compare how vertical migration may affect dispersal patterns, but also to provide a means to obtain an average dispersal pattern for a species (the cold water coral *Lophelia pertusa* (Linnaeus 1758)) where *in situ* observations of larval behaviour have not been obtained. The comparison of larval modes in Chapter 4 does not constitute a fully robust study of the effect of vertical migration, as the 'window of analysis' is restricted to larvae released from and being captured within MPAs. However this method does determine the conservation relevant effects of vertical migration, which may be less sensitive to differences than an objective analysis comparing the dispersal kernels of all released larvae. The 'net no difference' result between passive and active dispersal patterns for *L. pertusa* will be regionally relevant, provided these models perform well when ground truthed. This finding will vastly simplify the considerations when simulating dispersal for other species in this network. The results also lend greater support to there being only a site specific advantage offered by vertical migration, as the "net no deifference" result was a product of individual MPAs seeing opposing effects (i.e. vertical migration enhances dispersal potential in some MPAs and reduces dispersal potential in others) likely due to differing topographic restrictions. Although this is not a new theory (e.g. Edwards *et al.* 2007, Young *et al.* 2012), few studies discuss the physical topographic barriers which can be overcome by vertical migration, probably because of the shallow water bias to previous studies -shallow water species have less vertical distance to cover in order to be free of topographic impediment. This is the second deep water study to compare the dispersal patterns of different larval modes (Young *et al.* 2012), but this is the first to represent the changing vertical profile of a deep water species throughout the simulation, as opposed to comparing simulations run at two different depths.

All chapters cautioned against the generalisation of shallow water findings to deep water environments without prior testing. Chapter 2 demonstrated a decreased sensitivity of all parameters at a depth of 1500m. Chapter 3 conceded that model versus "sphere of influence" results were similar to the shallow water findings of Shanks (2009), but the complex topography of the study region may make this more likely than in an abyssal environment, for example.

Furthermore the variability of model versus model results could be interpreted as error enough to negate this finding, unless ground truthing can select one model as being more accurate than the other. Admittedly the shallow water study has not explored model output variability so similarity in this source of prediction error cannot be quantified. Chapter 4 showed that vertical migration may either enhance or reduce dispersal potential and this may be linked to the topography of the dispersal region and whether or not it may be surmounted by the species's vertical migration ability. Shallow water and coastal studies by definition will not cover more than 200m vertical distance; deep sea studies can span depth ranges measured in kilometres (potentially nearly 11km!). It is therefore logical that there may be some difference in the factors affecting dispersal in shallow/coastal and deep/offshore studies, inclusive of the scale of barriers, the complexity of the hydrography, and the availability and proximity of suitable habitat. This topic is yet to be addressed in the literature, but needs to be for the benefit of deep water marine conservation.

5.2 Limitations of the work

The biggest limitation of these studies, and modelling approaches in general, is the need for ground truthing to validate the voracity of model predictions. By definition a model is a simplification of reality with the aim to improve understanding. As every step has the potential to add error into predictions, ground truthing is necessary to discern whether a model does improve understanding or is an oversimplification.

All studies within this thesis have included a very basic level of ground truthing: a qualitative comparison to literature observations of local hydrography and any published genetic structures of target species. However this still does not quantify the error in results, so further work will be required to validate outputs. As ground truthing is dependent upon obtaining model-derived, spatially-targeted oceanographic and species-specific genetic data in the study area, additional funding and time would be necessary to undertake this process, such that it could not be completed during the course of this PhD. However a separate project, entitled "Deep Links", will be sourcing hydrographic and population genetic data in the study region this year (2016), so more robust ground truthing should be possible in the near future.

Several other factors restricted the scope and abilities of this project. Computing power, even when making use of Plymouth University's High Performance Computing cluster, placed many constraints on model set up, time, and data manipulation. Existing hydrodynamic models are still constrained in their representation of offshore environments, with limited deep water physical research expanding the field, persisting issues in resolving numerical equations in areas of steep topography, and computational constraints necessitating spatial and temporal averaging of model outputs. Deep sea biology is yet to find efficient ways of monitoring and identifying reproductive events and dispersal abilities, with issues identifying or tracking larvae, and restrictions associated with boat time and deep water long-term data collection. All of these aspects are lagging behind the resources available to shallow water studies.

While many restrictions still exist in the field of dispersal modelling (especially when applied to the data-poor deep sea) the existing tools may offer plenty of advancement to knowledge, at least in the honing of research questions and the provision of null models for future testing. However it is imperative that models are used responsibly with conclusions constrained to by the limitations of the models being used, and ground truthing data sought before any certainty is applied to model predictions.

5.3 Future work

The good news for deep sea science is that a long list of limitations leads to a similar list of future study topics. Although not exhaustive, the following are areas which require advancement before deep sea dispersal modelling can reach its full potential.

a) Biological and Oceanographic knowledge

Lophelia pertusa is comparatively well studied amongst deep sea taxa, many of which remain unstudied or even undiscovered. In order to accurately model larval dispersal for any species it would be optimal to have access to adult distribution, reproductive periodicity, larval behaviour, larval mortality, larval distribution, PLD, larval settlement, and larval survival data. As this thesis suggests at a minimum it would be preferable to have information on adult distribution (larval release locations and suitable habitat for settlement) and PLD, with these data null models can be created, and some of this information can be back-computed when used in tandem with ground truthing data.

However ground truthing the biology is only useful once the oceanography is sound. The first step is to improve general circulation models with higher resolution topographic data (there is already some available (Sandwell *et al.* 2014)). However if there is to be any dramatic improvement in hydrodynamic model performance further work must be done on the mitigation of horizontal pressure gradient error in regions of steep topography (Werner *et al.* 2007). Advances in data storage will be required to improve the accessibility of models with high temporal and spatial resolution which currently rely upon spatial and temporal averaging to overcome storage limitations. Improvements in high power computing may also allow the creation of higher resolution global coverage models which would be a big improvement for offshore studies which are not usually covered in smaller spatial scale high resolution coastal models. Deep sea dispersal models specifically would also benefit from greater attention to deep water oceanography inclusive of better understanding and simulation of deep water turbulent events. Although the Rockall Trough area, which was used as the location of all the studies in this thesis, is well researched (Holliday *et al.* 2013), the rest of the global deep ocean is not so fortunate and would benefit from exploration of watermass characteristics and identification of localised oceanographic phenomena which at a minimum could be used in the ground truthing of dispersal models in other regions (or globally).

b) Immediate work

Beyond the ground truthing study which will be undertaken soon, there are many advances which can be made with the tools which are currently available. Further to the findings of chapter 4, more targeted ecological work on deep sea passive versus active larval dispersal modelling could be undertaken. Hydrographic isolation is a topic yet to be covered in the literature which can be explored with models, and may result in reduced dispersal estimates measured in geographic distance. The science could be further aligned with conservation needs seeking to find multispecies assessments of MPA network connectivity, at present this would have to be theoretical in deep sea studies, exploring variable PLD, seasonality, and vertical migration scenarios to discern which species characteristics and combinations are supported by the existing network's connective potential. Finally the integration of dispersal model outputs into species distribution models (SDM) seems a logical next step with the *L. pertusa* data, to refine existing SDM predictions with data that is lacking from those based on environmental parameters alone (e.g. Ross and Howell 2013, Rengstorf *et al.* 2014, Piechaud *et al.* 2015, Ross *et al.* 2015). Areas predicted as suitable habitat in reality may be a species absence location due to the lack of connection to a larval pool, so integration of dispersal predictions into SDMs may reduce the area of suitable habitat on the basis of this disconnection. This had been planned as an additional chapter to this thesis but unfortunately time constraints have resulted in its postponement as future work. I am keen to continue my studies in this field.

Appendices

The following tables and figures can be found in these appendices:

Appendix 1: accompanying chapter 2

Appendix 2: accompanying chapter 3

Appendix 3: accompanying chapter 4

Appendix 1: accompanying chapter 2

A1.1 Standard release positions

The following release positions were used as the baseline locations for the Horizontal Positioning, Timestep, Release Frequency and Temporal Range tests (Table A1 - 1) and Vertical Positioning tests (Table A1 - 2). Vertical Positioning increments varied only in depth, not in latitude and longitude, and were located based on the deepest increment contour in each depth test (250m, 1050m, 1800m). The increment release locations for Horizontal Positioning tests are available in Table A1 - 3.

Table A1 - 1 Baseline locations for all tests except the Vertical Positioning test

Depth	Posn #	Long	Lat	Depth	Posn #	Long	Lat	Depth	Posn #	Long	Lat
700	1	348.640	57.257	1000	1	348.480	57.257	1500	1	348.400	57.257
700	2	348.686	57.257	1000	2	348.560	57.301	1500	2	348.475	57.339
700	3	348.733	57.257	1000	3	348.640	57.344	1500	3	348.573	57.388
700	4	348.779	57.257	1000	4	348.730	57.339	1500	4	348.684	57.388
700	5	348.800	57.231	1000	5	348.810	57.295	1500	5	348.796	57.388
700	6	348.828	57.213	1000	6	348.890	57.251	1500	6	348.894	57.337
700	7	348.875	57.213	1000	7	348.970	57.207	1500	7	348.984	57.274
700	8	348.880	57.172	1000	8	349.030	57.164	1500	8	349.062	57.192
700	9	348.880	57.126	1000	9	348.960	57.113	1500	9	349.007	57.082
700	10	348.834	57.126	1000	10	348.910	57.053	1500	10	348.921	57.017
700	11	348.788	57.125	1000	11	348.820	57.038	1500	11	348.823	56.963
700	12	348.741	57.125	1000	12	348.740	57.004	1500	12	348.715	56.950
700	13	348.694	57.125	1000	13	348.650	56.994	1500	13	348.604	56.950
700	14	348.648	57.125	1000	14	348.570	57.034	1500	14	348.501	56.983
700	15	348.639	57.164	1000	15	348.490	57.078	1500	15	348.403	57.036
700	16	348.639	57.211	1000	16	348.480	57.166	1500	16	348.400	57.146

Table A1 - 2 Baseline locations for the Vertical Positioning test

Depth	Posn #	Long	Lat	Depth	Posn #	Long	Lat	Depth	Posn #	Long	Lat
200	1	348.64	57.257	1000	1	348.48	57.257	1750	1	348.344	57.282
200	2	348.686	57.257	1000	2	348.56	57.301	1750	2	348.428	57.383
200	3	348.733	57.257	1000	3	348.641	57.344	1750	3	348.57	57.437
200	4	348.779	57.257	1000	4	348.73	57.339	1750	4	348.684	57.437
200	5	348.8	57.231	1000	5	348.811	57.295	1750	5	348.799	57.432
200	6	348.828	57.213	1000	6	348.891	57.251	1750	6	348.914	57.391
200	7	348.875	57.213	1000	7	348.971	57.207	1750	7	349.056	57.321
200	8	348.88	57.172	1000	8	349.029	57.164	1750	8	349.165	57.191
200	9	348.88	57.126	1000	9	348.96	57.113	1750	9	349.099	57.02
200	10	348.834	57.126	1000	10	348.907	57.053	1750	10	348.977	56.954
200	11	348.788	57.125	1000	11	348.82	57.038	1750	11	348.822	56.929
200	12	348.741	57.125	1000	12	348.737	57.004	1750	12	348.712	56.93
200	13	348.694	57.125	1000	13	348.648	56.994	1750	13	348.6	56.929
200	14	348.648	57.125	1000	14	348.567	57.034	1750	14	348.459	56.954
200	15	348.639	57.164	1000	15	348.487	57.078	1750	15	348.335	57.024
200	16	348.639	57.211	1000	16	348.48	57.166	1750	16	348.334	57.146

Table A1 - 3 Increment locations for the Horizontal Positioning test

Increment		baseline		0.001		0.005		0.01		0.025	
Depth	Posn #	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat
700	1	348.640	57.257	348.879	57.126	348.875	57.126	348.870	57.126	348.855	57.126
700	2	348.686	57.257	348.833	57.126	348.829	57.126	348.824	57.126	348.809	57.126
700	3	348.733	57.257	348.787	57.125	348.783	57.125	348.778	57.125	348.763	57.125
700	4	348.779	57.257	348.740	57.125	348.736	57.125	348.731	57.125	348.716	57.125
700	5	348.800	57.231	348.693	57.125	348.689	57.125	348.684	57.125	348.669	57.125
700	6	348.828	57.213	348.648	57.126	348.647	57.130	348.646	57.135	348.642	57.149
700	7	348.875	57.213	348.639	57.165	348.639	57.169	348.639	57.174	348.639	57.189
700	8	348.880	57.172	348.639	57.212	348.639	57.216	348.639	57.221	348.640	57.236
700	9	348.880	57.126	348.641	57.257	348.645	57.257	348.650	57.257	348.665	57.257
700	10	348.834	57.126	348.687	57.257	348.691	57.257	348.696	57.257	348.711	57.257
700	11	348.788	57.125	348.734	57.257	348.738	57.257	348.743	57.257	348.758	57.257
700	12	348.741	57.125	348.780	57.256	348.782	57.253	348.785	57.249	348.795	57.238
700	13	348.694	57.125	348.801	57.230	348.804	57.228	348.808	57.226	348.821	57.217
700	14	348.648	57.125	348.829	57.213	348.833	57.213	348.838	57.213	348.853	57.213
700	15	348.639	57.164	348.875	57.212	348.876	57.208	348.876	57.203	348.878	57.188
700	16	348.639	57.211	348.880	57.171	348.880	57.167	348.880	57.162	348.880	57.147
1000	1	348.480	57.257	348.480	57.256	348.480	57.252	348.480	57.247	348.480	57.232
1000	2	348.560	57.301	348.559	57.301	348.556	57.299	348.551	57.296	348.538	57.289
1000	3	348.640	57.344	348.639	57.344	348.636	57.342	348.631	57.339	348.618	57.332
1000	4	348.730	57.339	348.729	57.339	348.725	57.339	348.720	57.340	348.705	57.340
1000	5	348.810	57.295	348.809	57.295	348.806	57.297	348.801	57.300	348.788	57.307
1000	6	348.890	57.251	348.889	57.251	348.886	57.253	348.881	57.256	348.868	57.263
1000	7	348.970	57.207	348.969	57.208	348.966	57.209	348.961	57.212	348.948	57.219
1000	8	349.030	57.164	349.029	57.164	349.026	57.167	349.022	57.170	349.010	57.178
1000	9	348.960	57.113	348.961	57.113	348.964	57.116	348.968	57.119	348.980	57.127
1000	10	348.910	57.053	348.911	57.054	348.913	57.057	348.916	57.061	348.926	57.072
1000	11	348.820	57.038	348.821	57.038	348.825	57.039	348.830	57.040	348.845	57.042
1000	12	348.740	57.004	348.741	57.004	348.745	57.006	348.749	57.008	348.763	57.014
1000	13	348.650	56.994	348.651	56.994	348.655	56.994	348.660	56.995	348.675	56.997
1000	14	348.570	57.034	348.571	57.033	348.575	57.032	348.579	57.030	348.592	57.023
1000	15	348.490	57.078	348.491	57.078	348.494	57.075	348.499	57.073	348.512	57.066
1000	16	348.480	57.166	348.480	57.165	348.481	57.161	348.481	57.156	348.483	57.141
1500	1	348.400	57.257	349.062	57.191	349.060	57.188	349.058	57.183	349.051	57.170
1500	2	348.475	57.339	349.006	57.081	349.003	57.079	348.999	57.076	348.987	57.067
1500	3	348.573	57.388	348.920	57.017	348.917	57.015	348.912	57.012	348.899	57.005
1500	4	348.684	57.388	348.822	56.963	348.818	56.962	348.813	56.962	348.798	56.960
1500	5	348.796	57.388	348.714	56.950	348.710	56.950	348.705	56.950	348.690	56.950
1500	6	348.894	57.337	348.603	56.950	348.599	56.952	348.594	56.953	348.580	56.958
1500	7	348.984	57.274	348.500	56.983	348.497	56.985	348.492	56.988	348.479	56.995
1500	8	349.062	57.192	348.403	57.037	348.403	57.041	348.403	57.046	348.402	57.061
1500	9	349.007	57.082	348.400	57.147	348.400	57.151	348.400	57.156	348.400	57.171
1500	10	348.921	57.017	348.401	57.258	348.403	57.261	348.407	57.264	348.417	57.275
1500	11	348.823	56.963	348.476	57.339	348.479	57.341	348.484	57.343	348.497	57.350
1500	12	348.715	56.950	348.574	57.388	348.578	57.388	348.583	57.388	348.598	57.388
1500	13	348.604	56.950	348.685	57.388	348.689	57.388	348.694	57.388	348.709	57.388
1500	14	348.501	56.983	348.797	57.388	348.800	57.386	348.805	57.383	348.818	57.376
1500	15	348.403	57.036	348.895	57.336	348.898	57.334	348.902	57.331	348.914	57.323
1500	16	348.400	57.146	348.985	57.273	348.987	57.270	348.991	57.267	349.001	57.256

A1.2 Boxplots of TS, HS, VS for error estimation

Awareness of the distribution of these data can help when deciding upon model input values and provide some quantification of error when sub-optimal values must be used.

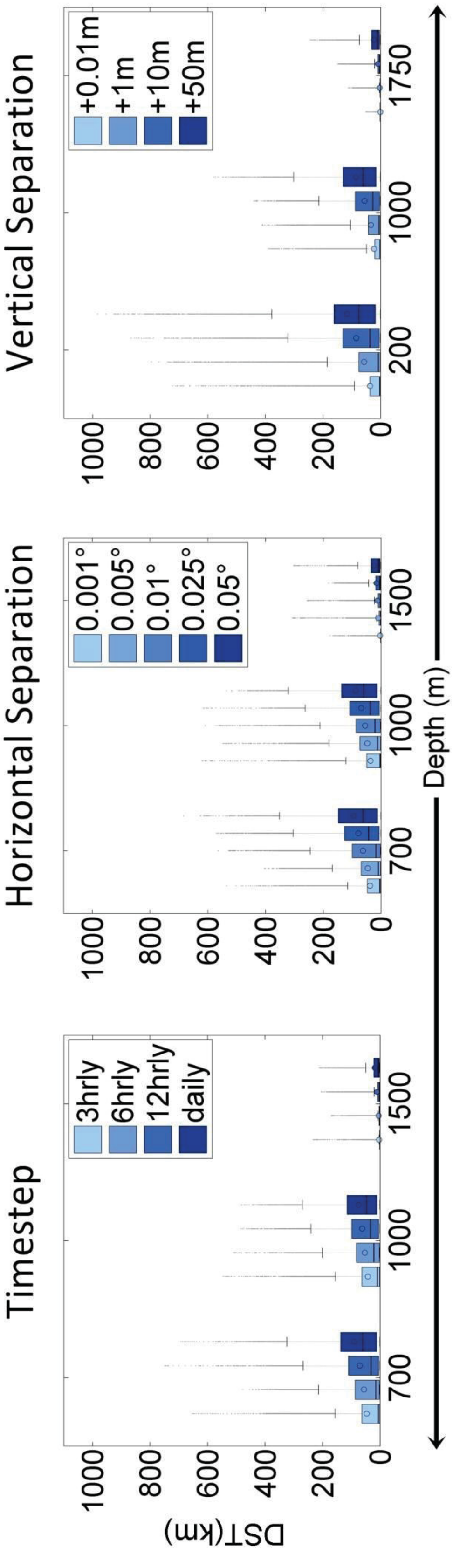


Figure A1 - 1 Boxplots of timestep, horizontal separation, and vertical separation increment test median, interquartile range, and outlier results.

A1.3 ANCOVA tests of increment and depth effect

The following GLMs were performed as ANCOVA tests of significance, confirming that the tested increments were having an effect on the straight line distance (sld) from baseline, and that depth also had an effect in each of the track dispersion technique tests.

The GLMs were performed in R, with increment (incr), depth, and day included in all ANCOVAs as factor variables (different inclusions were trialled, it just so happens they all ended up performing the best with those three as the predictors).

Post-hoc Tukey tests of factor (incr) and factor (depth) show the inter-relationship of factor levels and their respective significance.

"drop1" summaries are shown by way of summarising all the levels of a factor into an individual p value.

All tests resulted in the best GLM when straight line distance (sld) was included as square root transformed (sqrtsld).

HORIZONTAL

```
> summary(M2)

Call:
glm(formula = sqrtsld ~ factor(incr) + factor(depth) + factor(day),
    family = Gamma, data = m2)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.4419  -0.7769  -0.1865   0.3349   2.6224

Coefficients:
                    Estimate Std. Error t value Pr(>|t|)
(Intercept)        1.2403407  0.0200845  61.756  < 2e-16 ***
factor(incr)0.005 -0.0567097  0.0010646 -53.270  < 2e-16 ***
factor(incr)0.01  -0.0761433  0.0010140 -75.094  < 2e-16 ***
factor(incr)0.025 -0.0887582  0.0009907 -89.588  < 2e-16 ***
factor(depth)1000  0.0025041  0.0005788   4.326 1.52e-05 ***
factor(depth)1500  0.2393491  0.0014968 159.908  < 2e-16 ***
factor(day)1      -0.1372091  0.0269471  -5.092 3.55e-07 ***
factor(day)2      -0.0898570  0.0283419  -3.170  0.00152 **
factor(day)3      -0.1340915  0.0278430  -4.816 1.47e-06 ***
factor(day)4      -0.1951726  0.0271220  -7.196 6.22e-13 ***
factor(day)5      -0.2416328  0.0265915  -9.087  < 2e-16 ***
factor(day)6      -0.2803066  0.0261249 -10.729  < 2e-16 ***
factor(day)7      -0.3313541  0.0255574 -12.965  < 2e-16 ***
factor(day)8      -0.3882098  0.0249876 -15.536  < 2e-16 ***
factor(day)9      -0.4233234  0.0245957 -17.211  < 2e-16 ***
```

```
factor(day)10     -0.4650484  0.0241990 -19.218  < 2e-16 ***
factor(day)11     -0.5006132  0.0238305 -21.007  < 2e-16 ***
factor(day)12     -0.5329773  0.0235295 -22.651  < 2e-16 ***
factor(day)13     -0.5584487  0.0232809 -23.987  < 2e-16 ***
factor(day)14     -0.5879713  0.0230068 -25.556  < 2e-16 ***
factor(day)15     -0.6138355  0.0227722 -26.955  < 2e-16 ***
factor(day)16     -0.6396403  0.0225485 -28.367  < 2e-16 ***
factor(day)17     -0.6680682  0.0223314 -29.916  < 2e-16 ***
factor(day)18     -0.6872117  0.0221735 -30.992  < 2e-16 ***
factor(day)19     -0.7077957  0.0220174 -32.147  < 2e-16 ***
factor(day)20     -0.7307176  0.0218550 -33.435  < 2e-16 ***
factor(day)21     -0.7511900  0.0217073 -34.605  < 2e-16 ***
factor(day)22     -0.7708832  0.0215687 -35.741  < 2e-16 ***
factor(day)23     -0.7905628  0.0214357 -36.881  < 2e-16 ***
factor(day)24     -0.8103983  0.0213101 -38.029  < 2e-16 ***
factor(day)25     -0.8241237  0.0212230 -38.832  < 2e-16 ***
factor(day)26     -0.8392388  0.0211329 -39.712  < 2e-16 ***
factor(day)27     -0.8519978  0.0210586 -40.458  < 2e-16 ***
factor(day)28     -0.8655583  0.0209855 -41.246  < 2e-16 ***
factor(day)29     -0.8760881  0.0209219 -41.874  < 2e-16 ***
factor(day)30     -0.8885824  0.0208553 -42.607  < 2e-16 ***
factor(day)31     -0.8995508  0.0208006 -43.246  < 2e-16 ***
factor(day)32     -0.9102424  0.0207497 -43.868  < 2e-16 ***
factor(day)33     -0.9186687  0.0207072 -44.365  < 2e-16 ***
factor(day)34     -0.9264198  0.0206725 -44.814  < 2e-16 ***
factor(day)35     -0.9328998  0.0206421 -45.194  < 2e-16 ***
factor(day)36     -0.9387058  0.0206155 -45.534  < 2e-16 ***
factor(day)37     -0.9457545  0.0205849 -45.944  < 2e-16 ***
factor(day)38     -0.9531626  0.0205540 -46.373  < 2e-16 ***
factor(day)39     -0.9594909  0.0205273 -46.742  < 2e-16 ***
factor(day)40     -0.9659562  0.0205021 -47.115  < 2e-16 ***
factor(day)41     -0.9705591  0.0204827 -47.384  < 2e-16 ***
factor(day)42     -0.9769490  0.0204592 -47.751  < 2e-16 ***
factor(day)43     -0.9820915  0.0204395 -48.049  < 2e-16 ***
factor(day)44     -0.9866868  0.0204224 -48.314  < 2e-16 ***
factor(day)45     -0.9912714  0.0204069 -48.575  < 2e-16 ***
factor(day)46     -0.9948465  0.0203931 -48.783  < 2e-16 ***
factor(day)47     -0.9996330  0.0203773 -49.056  < 2e-16 ***
factor(day)48     -1.0040972  0.0203620 -49.312  < 2e-16 ***
factor(day)49     -1.0087442  0.0203469 -49.577  < 2e-16 ***
factor(day)50     -1.0126802  0.0203343 -49.802  < 2e-16 ***
factor(day)51     -1.0159710  0.0203231 -49.991  < 2e-16 ***
factor(day)52     -1.0193557  0.0203129 -50.183  < 2e-16 ***
factor(day)53     -1.0227211  0.0203030 -50.373  < 2e-16 ***
factor(day)54     -1.0251749  0.0202951 -50.513  < 2e-16 ***
factor(day)55     -1.0277357  0.0202875 -50.659  < 2e-16 ***
factor(day)56     -1.0302478  0.0202800 -50.801  < 2e-16 ***
factor(day)57     -1.0326331  0.0202732 -50.936  < 2e-16 ***
factor(day)58     -1.0349703  0.0202665 -51.068  < 2e-16 ***
factor(day)59     -1.0367660  0.0202610 -51.170  < 2e-16 ***
factor(day)60     -1.0393773  0.0202543 -51.316  < 2e-16 ***
factor(day)61     -1.0413156  0.0202488 -51.426  < 2e-16 ***
factor(day)62     -1.0436444  0.0202425 -51.557  < 2e-16 ***
factor(day)63     -1.0459105  0.0202363 -51.685  < 2e-16 ***
factor(day)64     -1.0477384  0.0202316 -51.787  < 2e-16 ***
factor(day)65     -1.0492598  0.0202275 -51.873  < 2e-16 ***
factor(day)66     -1.0508117  0.0202233 -51.960  < 2e-16 ***
factor(day)67     -1.0527463  0.0202186 -52.068  < 2e-16 ***
factor(day)68     -1.0547534  0.0202138 -52.180  < 2e-16 ***
factor(day)69     -1.0562203  0.0202100 -52.262  < 2e-16 ***
factor(day)70     -1.0580920  0.0202055 -52.367  < 2e-16 ***
factor(day)71     -1.0599845  0.0202009 -52.472  < 2e-16 ***
factor(day)72     -1.0619819  0.0201964 -52.583  < 2e-16 ***
factor(day)73     -1.0634689  0.0201928 -52.666  < 2e-16 ***
factor(day)74     -1.0649568  0.0201894 -52.748  < 2e-16 ***
factor(day)75     -1.0660806  0.0201868 -52.811  < 2e-16 ***
factor(day)76     -1.0674111  0.0201838 -52.884  < 2e-16 ***
factor(day)77     -1.0687169  0.0201812 -52.956  < 2e-16 ***
factor(day)78     -1.0700215  0.0201784 -53.028  < 2e-16 ***
factor(day)79     -1.0713876  0.0201752 -53.104  < 2e-16 ***
factor(day)80     -1.0728171  0.0201720 -53.183  < 2e-16 ***
```

```
factor(day)81     -1.0740684  0.0201693 -53.253  < 2e-16 ***
factor(day)82     -1.0753325  0.0201666 -53.322  < 2e-16 ***
factor(day)83     -1.0766590  0.0201639 -53.395  < 2e-16 ***
factor(day)84     -1.0776515  0.0201618 -53.450  < 2e-16 ***
factor(day)85     -1.0786049  0.0201599 -53.502  < 2e-16 ***
factor(day)86     -1.0795956  0.0201580 -53.557  < 2e-16 ***
factor(day)87     -1.0804462  0.0201563 -53.603  < 2e-16 ***
factor(day)88     -1.0811481  0.0201548 -53.642  < 2e-16 ***
factor(day)89     -1.0818946  0.0201533 -53.683  < 2e-16 ***
factor(day)90     -1.0826005  0.0201520 -53.722  < 2e-16 ***
factor(day)91     -1.0833290  0.0201505 -53.762  < 2e-16 ***
factor(day)92     -1.0841938  0.0201489 -53.809  < 2e-16 ***
factor(day)93     -1.0848968  0.0201475 -53.848  < 2e-16 ***
factor(day)94     -1.0858152  0.0201459 -53.898  < 2e-16 ***
factor(day)95     -1.0865534  0.0201444 -53.938  < 2e-16 ***
factor(day)96     -1.0872031  0.0201432 -53.974  < 2e-16 ***
factor(day)97     -1.0879391  0.0201419 -54.014  < 2e-16 ***
factor(day)98     -1.0885379  0.0201408 -54.046  < 2e-16 ***
factor(day)99     -1.0891227  0.0201397 -54.078  < 2e-16 ***
factor(day)100    -1.0896671  0.0201386 -54.108  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Gamma family taken to be 0.59243)

    Null deviance: 240337  on 198465  degrees of freedom
Residual deviance: 126610  on 198360  degrees of freedom
AIC: 885146

Number of Fisher Scoring iterations: 6

> drop1(M2, test = "Chi")
Single term deletions

Model:
sqrtsld ~ factor(incr) + factor(depth) + factor(day)
               Df Deviance     AIC scaled dev.  Pr(>Chi)
<none>              126610  885146
factor(incr)    3   132570  895199       10059 < 2.2e-16 ***
factor(depth)   2   152138  928232       43090 < 2.2e-16 ***
factor(day)   100   199210 1007491      122545 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> posth <- glht(M2, linfct=mcp(factor(incr) ="Tukey"), data = m2)
> summary(posth)

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(day), family = Gamma,
    data = m2)

Linear Hypotheses:
                     Estimate Std. Error z value Pr(>|z|)
0.005 - 0.001 == 0 -0.0567097  0.0010646  -53.27   <2e-16 ***
0.01 - 0.001 == 0  -0.0761433  0.0010140  -75.09   <2e-16 ***
0.025 - 0.001 == 0 -0.0887582  0.0009907  -89.59   <2e-16 ***
0.01 - 0.005 == 0  -0.0194336  0.0008020  -24.23   <2e-16 ***
0.025 - 0.005 == 0 -0.0320485  0.0007702  -41.61   <2e-16 ***
0.025 - 0.01 == 0  -0.0126149  0.0006930  -18.20   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)

> posth2 <- glht(M2, linfct=mcp(factor(depth) ="Tukey"), data = m2)
> summary(posth2)

         Simultaneous Tests for General Linear Hypotheses
```

```
Multiple Comparisons of Means: Tukey Contrasts


Fit: glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(day), famil
    data = m2)

Linear Hypotheses:
                  Estimate Std. Error z value Pr(>|z|)    
1000 - 700 == 0  0.0025041  0.0005788   4.326  3.1e-05 ***
1500 - 700 == 0  0.2393491  0.0014968 159.908  < 1e-05 ***
1500 - 1000 == 0 0.2368451  0.0014974 158.166  < 1e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

VERTICAL

```
> summary(M2)

Call:
glm(formula = sqrtsld ~ factor(incr)  + factor(depth) + factor(day), 
    family = Gamma, data = m2)

Deviance Residuals: 
    Min       1Q   Median       3Q      Max  
-2.4311  -0.8543  -0.2266   0.3426   2.6900  

Coefficients:
                    Estimate Std. Error  t value Pr(>|t|)    
(Intercept)        1.9807365  0.0501865   39.468  < 2e-16 ***
factor(incr) 1      -0.0937206  0.0016476  -56.884  < 2e-16 ***
factor(incr) 10     -0.1717578  0.0014749 -116.456  < 2e-16 ***
factor(incr) 50     -0.1956035  0.0014402 -135.820  < 2e-16 ***
factor(depth)1000  0.0179368  0.0005715   31.388  < 2e-16 ***
factor(depth)1750  0.2797534  0.0017164  162.987  < 2e-16 ***
factor(day)2      -0.3487920  0.0627993   -5.554 2.79e-08 ***
factor(day)3      -0.5295817  0.0593092   -8.929  < 2e-16 ***
factor(day)4      -0.6938567  0.0571408  -12.143  < 2e-16 ***
factor(day)5      -0.7843781  0.0558498  -14.044  < 2e-16 ***
factor(day)6      -0.8707881  0.0548405  -15.879  < 2e-16 ***
factor(day)7      -0.9389220  0.0541014  -17.355  < 2e-16 ***
factor(day)8      -1.0062962  0.0535258  -18.800  < 2e-16 ***
factor(day)9      -1.0562083  0.0531110  -19.887  < 2e-16 ***
factor(day)10     -1.1085402  0.0526947  -21.037  < 2e-16 ***
factor(day)11     -1.1511751  0.0523802  -21.977  < 2e-16 ***
factor(day)12     -1.1931260  0.0521112  -22.896  < 2e-16 ***
factor(day)13     -1.2267889  0.0518983  -23.638  < 2e-16 ***
factor(day)14     -1.2558864  0.0517256  -24.280  < 2e-16 ***
factor(day)15     -1.2840651  0.0515818  -24.894  < 2e-16 ***
factor(day)16     -1.3070769  0.0514575  -25.401  < 2e-16 ***
factor(day)17     -1.3268752  0.0513448  -25.842  < 2e-16 ***
factor(day)18     -1.3569154  0.0512236  -26.490  < 2e-16 ***
factor(day)19     -1.3827632  0.0511146  -27.052  < 2e-16 ***
factor(day)20     -1.4034143  0.0510265  -27.504  < 2e-16 ***
factor(day)21     -1.4214567  0.0509520  -27.898  < 2e-16 ***
factor(day)22     -1.4371849  0.0508878  -28.242  < 2e-16 ***
factor(day)23     -1.4564733  0.0508211  -28.659  < 2e-16 ***
factor(day)24     -1.4754799  0.0507566  -29.070  < 2e-16 ***
factor(day)25     -1.4891577  0.0507096  -29.366  < 2e-16 ***
factor(day)26     -1.5047478  0.0506639  -29.701  < 2e-16 ***
factor(day)27     -1.5143719  0.0506327  -29.909  < 2e-16 ***
factor(day)28     -1.5261789  0.0506003  -30.161  < 2e-16 ***
factor(day)29     -1.5362075  0.0505711  -30.377  < 2e-16 ***
factor(day)30     -1.5465411  0.0505431  -30.598  < 2e-16 ***
factor(day)31     -1.5564013  0.0505187  -30.808  < 2e-16 ***
factor(day)32     -1.5627339  0.0505007  -30.945  < 2e-16 ***
factor(day)33     -1.5703038  0.0504823  -31.106  < 2e-16 ***
factor(day)34     -1.5773831  0.0504649  -31.257  < 2e-16 ***
factor(day)35     -1.5842099  0.0504488  -31.402  < 2e-16 ***
factor(day)36     -1.5902437  0.0504345  -31.531  < 2e-16 ***
```

```
factor(day)37     -1.5974172  0.0504194  -31.683  < 2e-16 ***
factor(day)38     -1.6049091  0.0504038  -31.841  < 2e-16 ***
factor(day)39     -1.6107008  0.0503910  -31.964  < 2e-16 ***
factor(day)40     -1.6174542  0.0503772  -32.107  < 2e-16 ***
factor(day)41     -1.6243633  0.0503636  -32.253  < 2e-16 ***
factor(day)42     -1.6298799  0.0503524  -32.369  < 2e-16 ***
factor(day)43     -1.6357477  0.0503415  -32.493  < 2e-16 ***
factor(day)44     -1.6404633  0.0503325  -32.593  < 2e-16 ***
factor(day)45     -1.6449925  0.0503246  -32.688  < 2e-16 ***
factor(day)46     -1.6494104  0.0503167  -32.781  < 2e-16 ***
factor(day)47     -1.6537065  0.0503092  -32.871  < 2e-16 ***
factor(day)48     -1.6583434  0.0503013  -32.968  < 2e-16 ***
factor(day)49     -1.6630342  0.0502935  -33.067  < 2e-16 ***
factor(day)50     -1.6674524  0.0502864  -33.159  < 2e-16 ***
factor(day)51     -1.6717489  0.0502798  -33.249  < 2e-16 ***
factor(day)52     -1.6747389  0.0502750  -33.312  < 2e-16 ***
factor(day)53     -1.6780197  0.0502700  -33.380  < 2e-16 ***
factor(day)54     -1.6805168  0.0502661  -33.432  < 2e-16 ***
factor(day)55     -1.6832962  0.0502620  -33.490  < 2e-16 ***
factor(day)56     -1.6861891  0.0502579  -33.551  < 2e-16 ***
factor(day)57     -1.6889922  0.0502539  -33.609  < 2e-16 ***
factor(day)58     -1.6911365  0.0502508  -33.654  < 2e-16 ***
factor(day)59     -1.6931537  0.0502480  -33.696  < 2e-16 ***
factor(day)60     -1.6951100  0.0502453  -33.737  < 2e-16 ***
factor(day)61     -1.6978259  0.0502417  -33.793  < 2e-16 ***
factor(day)62     -1.7000039  0.0502388  -33.838  < 2e-16 ***
factor(day)63     -1.7026864  0.0502354  -33.894  < 2e-16 ***
factor(day)64     -1.7047105  0.0502328  -33.936  < 2e-16 ***
factor(day)65     -1.7066744  0.0502302  -33.977  < 2e-16 ***
factor(day)66     -1.7086063  0.0502278  -34.017  < 2e-16 ***
factor(day)67     -1.7107644  0.0502252  -34.062  < 2e-16 ***
factor(day)68     -1.7127213  0.0502228  -34.102  < 2e-16 ***
factor(day)69     -1.7147528  0.0502204  -34.145  < 2e-16 ***
factor(day)70     -1.7164884  0.0502184  -34.180  < 2e-16 ***
factor(day)71     -1.7179128  0.0502167  -34.210  < 2e-16 ***
factor(day)72     -1.7193622  0.0502150  -34.240  < 2e-16 ***
factor(day)73     -1.7210967  0.0502131  -34.276  < 2e-16 ***
factor(day)74     -1.7225846  0.0502115  -34.307  < 2e-16 ***
factor(day)75     -1.7239793  0.0502099  -34.335  < 2e-16 ***
factor(day)76     -1.7253364  0.0502084  -34.363  < 2e-16 ***
factor(day)77     -1.7267617  0.0502069  -34.393  < 2e-16 ***
factor(day)78     -1.7280259  0.0502056  -34.419  < 2e-16 ***
factor(day)79     -1.7295707  0.0502040  -34.451  < 2e-16 ***
factor(day)80     -1.7307706  0.0502027  -34.476  < 2e-16 ***
factor(day)81     -1.7320151  0.0502015  -34.501  < 2e-16 ***
factor(day)82     -1.7332405  0.0502002  -34.527  < 2e-16 ***
factor(day)83     -1.7343601  0.0501991  -34.550  < 2e-16 ***
factor(day)84     -1.7353862  0.0501981  -34.571  < 2e-16 ***
factor(day)85     -1.7362147  0.0501974  -34.588  < 2e-16 ***
factor(day)86     -1.7371466  0.0501965  -34.607  < 2e-16 ***
factor(day)87     -1.7380952  0.0501956  -34.626  < 2e-16 ***
factor(day)88     -1.7390056  0.0501947  -34.645  < 2e-16 ***
factor(day)89     -1.7397989  0.0501940  -34.661  < 2e-16 ***
factor(day)90     -1.7405362  0.0501933  -34.677  < 2e-16 ***
factor(day)91     -1.7412387  0.0501927  -34.691  < 2e-16 ***
factor(day)92     -1.7419088  0.0501921  -34.705  < 2e-16 ***
factor(day)93     -1.7425176  0.0501917  -34.717  < 2e-16 ***
factor(day)94     -1.7430452  0.0501912  -34.728  < 2e-16 ***
factor(day)95     -1.7434703  0.0501908  -34.737  < 2e-16 ***
factor(day)96     -1.7439483  0.0501904  -34.747  < 2e-16 ***
factor(day)97     -1.7445223  0.0501899  -34.758  < 2e-16 ***
factor(day)98     -1.7451703  0.0501893  -34.772  < 2e-16 ***
factor(day)99     -1.7456798  0.0501889  -34.782  < 2e-16 ***
factor(day)100    -1.7462689  0.0501883  -34.794  < 2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Gamma family taken to be 0.6641468)

    Null deviance: 254783  on 191135  degrees of freedom
Residual deviance: 134153  on 191031  degrees of freedom
```

```
AIC: 864470

Number of Fisher Scoring iterations: 6

> drop1(M2, test = "Chi") # for whether to drop one also for p value o
f main effect of factor
Single term deletions

Model:
sqrtsld ~ factor(incr)  + factor(depth) + factor(day)
              Df Deviance    AIC scaled dev.  Pr(>Chi)
<none>              134153 864470                      
factor(incr)     3   158017 900396       35932 < 2.2e-16 ***
factor(depth)  2   165429 911559       47092 < 2.2e-16 ***
factor(day)   99   197418 959530       95258 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> posth <- glht(M2, linfct=mcp(factor(incr) ="Tukey"), data = m2)
> summary(posth)

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(d
ay), family = Gamma,
    data = m2)

Linear Hypotheses:
                Estimate Std. Error z value Pr(>|z|)    
1 - 0.1 == 0  -0.0937206  0.0016476  -56.88   <2e-16 ***
10 - 0.1 == 0 -0.1717578  0.0014749 -116.46   <2e-16 ***
50 - 0.1 == 0 -0.1956035  0.0014402 -135.82   <2e-16 ***
10 - 1 == 0   -0.0780372  0.0010281  -75.91   <2e-16 ***
50 - 1 == 0   -0.1018829  0.0009766 -104.32   <2e-16 ***
50 - 10 == 0  -0.0238457  0.0006194  -38.50   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)

> posth2 <- glht(M2, linfct=mcp(factor(depth) ="Tukey"), data = m2)
> summary(posth2)

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(d
ay), family = Gamma,
    data = m2)

Linear Hypotheses:
                  Estimate Std. Error z value Pr(>|z|)    
1000 - 200 == 0  0.0179368  0.0005715   31.39   <2e-16 ***
1750 - 200 == 0  0.2797534  0.0017164  162.99   <2e-16 ***
1750 - 1000 == 0 0.2618166  0.0017322  151.15   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

TIMESTEP

```
> summary(M2)

Call:
glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(day),
family = Gamma,
    data = m2)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.3011  -0.7126  -0.1961   0.3128   2.6368

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)     1.4153516  0.0227323  62.262   <2e-16 ***
factor(incr) 21600     -0.0360491  0.0009790 -36.823   <2e-16 ***
factor(incr) 43200     -0.0644112  0.0009073 -70.995   <2e-16 ***
factor(incr) 86400     -0.0849766  0.0008628 -98.493   <2e-16 ***
factor(depth) 1000        0.0044278  0.0005232   8.462   <2e-16 ***
factor(depth) 1500        0.2634405  0.0012699 207.449   <2e-16 ***
factor(day)2   -0.2556197  0.0293241  -8.717   <2e-16 ***
factor(day)3   -0.3639115  0.0282276 -12.892   <2e-16 ***
factor(day)4   -0.4546708  0.0274111 -16.587   <2e-16 ***
factor(day)5   -0.5285107  0.0267660 -19.746   <2e-16 ***
factor(day)6   -0.5947293  0.0262091 -22.692   <2e-16 ***
factor(day)7   -0.6554506  0.0257520 -25.452   <2e-16 ***
factor(day)8   -0.7117822  0.0253333 -28.097   <2e-16 ***
factor(day)9   -0.7461221  0.0250736 -29.757   <2e-16 ***
factor(day)10  -0.7812083  0.0248419 -31.447   <2e-16 ***
factor(day)11  -0.8062077  0.0246781 -32.669   <2e-16 ***
factor(day)12  -0.8272296  0.0245420 -33.707   <2e-16 ***
factor(day)13  -0.8483648  0.0244178 -34.744   <2e-16 ***
factor(day)14  -0.8734081  0.0242695 -35.988   <2e-16 ***
factor(day)15  -0.8925951  0.0241652 -36.937   <2e-16 ***
factor(day)16  -0.9086135  0.0240730 -37.744   <2e-16 ***
factor(day)17  -0.9207697  0.0240060 -38.356   <2e-16 ***
factor(day)18  -0.9356316  0.0239296 -39.099   <2e-16 ***
factor(day)19  -0.9552016  0.0238305 -40.083   <2e-16 ***
factor(day)20  -0.9686523  0.0237634 -40.762   <2e-16 ***
factor(day)21  -0.9803764  0.0236999 -41.366   <2e-16 ***
factor(day)22  -0.9935839  0.0236429 -42.025   <2e-16 ***
factor(day)23  -1.0112543  0.0235628 -42.917   <2e-16 ***
factor(day)24  -1.0272939  0.0234938 -43.726   <2e-16 ***
factor(day)25  -1.0373365  0.0234504 -44.235   <2e-16 ***
factor(day)26  -1.0465864  0.0234116 -44.704   <2e-16 ***
factor(day)27  -1.0575608  0.0233681 -45.257   <2e-16 ***
factor(day)28  -1.0671806  0.0233295 -45.744   <2e-16 ***
factor(day)29  -1.0774290  0.0232919 -46.258   <2e-16 ***
factor(day)30  -1.0862412  0.0232579 -46.704   <2e-16 ***
factor(day)31  -1.0943747  0.0232283 -47.114   <2e-16 ***
factor(day)32  -1.1023334  0.0232011 -47.512   <2e-16 ***
factor(day)33  -1.1095071  0.0231772 -47.871   <2e-16 ***
factor(day)34  -1.1162006  0.0231547 -48.206   <2e-16 ***
factor(day)35  -1.1228262  0.0231314 -48.541   <2e-16 ***
factor(day)36  -1.1302602  0.0231076 -48.913   <2e-16 ***
factor(day)37  -1.1378160  0.0230838 -49.291   <2e-16 ***
factor(day)38  -1.1463744  0.0230584 -49.716   <2e-16 ***
factor(day)39  -1.1528995  0.0230391 -50.041   <2e-16 ***
factor(day)40  -1.1582806  0.0230233 -50.309   <2e-16 ***
factor(day)41  -1.1633059  0.0230091 -50.559   <2e-16 ***
factor(day)42  -1.1678536  0.0229962 -50.785   <2e-16 ***
factor(day)43  -1.1725445  0.0229834 -51.017   <2e-16 ***
factor(day)44  -1.1768159  0.0229719 -51.228   <2e-16 ***
factor(day)45  -1.1809410  0.0229613 -51.432   <2e-16 ***
factor(day)46  -1.1847969  0.0229515 -51.622   <2e-16 ***
factor(day)47  -1.1888055  0.0229413 -51.819   <2e-16 ***
factor(day)48  -1.1926098  0.0229316 -52.007   <2e-16 ***
factor(day)49  -1.1971475  0.0229212 -52.229   <2e-16 ***
```

```
factor(day)50  -1.2002038  0.0229134 -52.380   <2e-16 ***
factor(day)51  -1.2036305  0.0229056 -52.548   <2e-16 ***
factor(day)52  -1.2060171  0.0228998 -52.665   <2e-16 ***
factor(day)53  -1.2095028  0.0228919 -52.835   <2e-16 ***
factor(day)54  -1.2129432  0.0228842 -53.003   <2e-16 ***
factor(day)55  -1.2161284  0.0228772 -53.159   <2e-16 ***
factor(day)56  -1.2190321  0.0228710 -53.300   <2e-16 ***
factor(day)57  -1.2214450  0.0228660 -53.418   <2e-16 ***
factor(day)58  -1.2237505  0.0228611 -53.530   <2e-16 ***
factor(day)59  -1.2259941  0.0228564 -53.639   <2e-16 ***
factor(day)60  -1.2278951  0.0228525 -53.731   <2e-16 ***
factor(day)61  -1.2297690  0.0228488 -53.822   <2e-16 ***
factor(day)62  -1.2317148  0.0228449 -53.916   <2e-16 ***
factor(day)63  -1.2335782  0.0228412 -54.007   <2e-16 ***
factor(day)64  -1.2354386  0.0228377 -54.097   <2e-16 ***
factor(day)65  -1.2370878  0.0228345 -54.176   <2e-16 ***
factor(day)66  -1.2388519  0.0228312 -54.261   <2e-16 ***
factor(day)67  -1.2403546  0.0228283 -54.334   <2e-16 ***
factor(day)68  -1.2418853  0.0228255 -54.408   <2e-16 ***
factor(day)69  -1.2435735  0.0228224 -54.489   <2e-16 ***
factor(day)70  -1.2451845  0.0228195 -54.567   <2e-16 ***
factor(day)71  -1.2467598  0.0228167 -54.643   <2e-16 ***
factor(day)72  -1.2484741  0.0228136 -54.725   <2e-16 ***
factor(day)73  -1.2501990  0.0228106 -54.808   <2e-16 ***
factor(day)74  -1.2517625  0.0228079 -54.883   <2e-16 ***
factor(day)75  -1.2530891  0.0228057 -54.946   <2e-16 ***
factor(day)76  -1.2541738  0.0228039 -54.998   <2e-16 ***
factor(day)77  -1.2554087  0.0228018 -55.057   <2e-16 ***
factor(day)78  -1.2566027  0.0227998 -55.115   <2e-16 ***
factor(day)79  -1.2577496  0.0227979 -55.169   <2e-16 ***
factor(day)80  -1.2590500  0.0227958 -55.232   <2e-16 ***
factor(day)81  -1.2602485  0.0227939 -55.289   <2e-16 ***
factor(day)82  -1.2612693  0.0227923 -55.337   <2e-16 ***
factor(day)83  -1.2621679  0.0227909 -55.380   <2e-16 ***
factor(day)84  -1.2631172  0.0227894 -55.426   <2e-16 ***
factor(day)85  -1.2639498  0.0227881 -55.465   <2e-16 ***
factor(day)86  -1.2648473  0.0227867 -55.508   <2e-16 ***
factor(day)87  -1.2657073  0.0227854 -55.549   <2e-16 ***
factor(day)88  -1.2666241  0.0227840 -55.593   <2e-16 ***
factor(day)89  -1.2674879  0.0227827 -55.634   <2e-16 ***
factor(day)90  -1.2682465  0.0227816 -55.670   <2e-16 ***
factor(day)91  -1.2688751  0.0227807 -55.700   <2e-16 ***
factor(day)92  -1.2695793  0.0227796 -55.733   <2e-16 ***
factor(day)93  -1.2702604  0.0227786 -55.765   <2e-16 ***
factor(day)94  -1.2709903  0.0227776 -55.800   <2e-16 ***
factor(day)95  -1.2717404  0.0227765 -55.836   <2e-16 ***
factor(day)96  -1.2725325  0.0227754 -55.873   <2e-16 ***
factor(day)97  -1.2730863  0.0227746 -55.899   <2e-16 ***
factor(day)98  -1.2735419  0.0227739 -55.921   <2e-16 ***
factor(day)99  -1.2740967  0.0227732 -55.947   <2e-16 ***
factor(day)100 -1.2746975  0.0227722 -55.976   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for Gamma family taken to be 0.5478042)

    Null deviance: 250032  on 228563  degrees of freedom
Residual deviance: 124803  on 228459  degrees of freedom
AIC: 1000935

Number of Fisher Scoring iterations: 6

> drop1(M2, test = "Chi") # for whether to drop one also for p value o
f main effect of factor Chi for GLM F for lm (GAM use GAM summary)
Single term deletions

Model:
sqrtsld ~ factor(incr)  + factor(depth)  + factor(day)
            Df Deviance     AIC scaled dev.  Pr(>Chi)
<none>           124803 1000935
factor(incr)         3   131767 1013641       12712 < 2.2e-16 ***
```

```
factor(depth)          2   164921 1074166       73235 < 2.2e-16 ***
factor(day) 99   192834 1124926      124189 < 2.2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> posth <- glht(M2, linfct=mcp(factor(incr) ="Tukey"), data = m2)
> summary(posth)

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(d
ay), family = Gamma,
    data = m2)

Linear Hypotheses:
                     Estimate Std. Error z value Pr(>|z|)
21600 - 10800 == 0 -0.0360491  0.0009790  -36.82   <2e-16 ***
43200 - 10800 == 0 -0.0644112  0.0009073  -71.00   <2e-16 ***
86400 - 10800 == 0 -0.0849766  0.0008628  -98.49   <2e-16 ***
43200 - 21600 == 0 -0.0283620  0.0007804  -36.34   <2e-16 ***
86400 - 21600 == 0 -0.0489275  0.0007266  -67.33   <2e-16 ***
86400 - 43200 == 0 -0.0205654  0.0006207  -33.13   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)

> posth2 <- glht(M2, linfct=mcp(factor(depth) ="Tukey"), data = m2)
> summary(posth2)

         Simultaneous Tests for General Linear Hypotheses

Multiple Comparisons of Means: Tukey Contrasts


Fit: glm(formula = sqrtsld ~ factor(incr)  + factor(depth)  + factor(d
ay), family = Gamma,
    data = m2)

Linear Hypotheses:
                  Estimate Std. Error z value Pr(>|z|)
1000 - 700 == 0  0.0044278  0.0005232   8.462   <2e-16 ***
1500 - 700 == 0  0.2634405  0.0012699 207.449   <2e-16 ***
1500 - 1000 == 0 0.2590127  0.0012738 203.338   <2e-16 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Adjusted p values reported -- single-step method)
```

Appendix 2: accompanying chapter 3

A2.1 Current ellipses

Supplementary Figure A2 - 1 to : The following pairs of plots show current ellipses per model per depth for 200m, 700m, 1000m, 1300m[1], 1500m. The current ellipses use the two main principle components of modelled velocity data to represent the variability in current strength and direction over the entire simulated period (728 days for this study). Oval ellipses are oriented in the predominant direction of the current with the width representing variability in current direction (circles = highly variable, narrow ovals = little variability). Larger ellipses represent stronger current speeds. A current ellipse is plotted for every 5th grid point. 200m plots are shown in reference to the shelf edge current (which is more apparent in HYCOM at 200m).

HYCOM displays larger (= strong current speeds), and more circular (= high variability in current direction) ellipses. This higher variability throughout HYCOM plots suggests there may be a less strict handling of the horizontal pressure gradient errors than in POLCOMS.

Current ellipses were made with the assistance of Ricardo Torres at Plymouth Marine Laboratory.

---

[1] 1250m is shown for HYCOM as these are the nearest data points to the simulated 1300m larval tracks (the connectivity modeling system ran the simulation at 1300m in HYCOM by running an interpolation between the available data points).

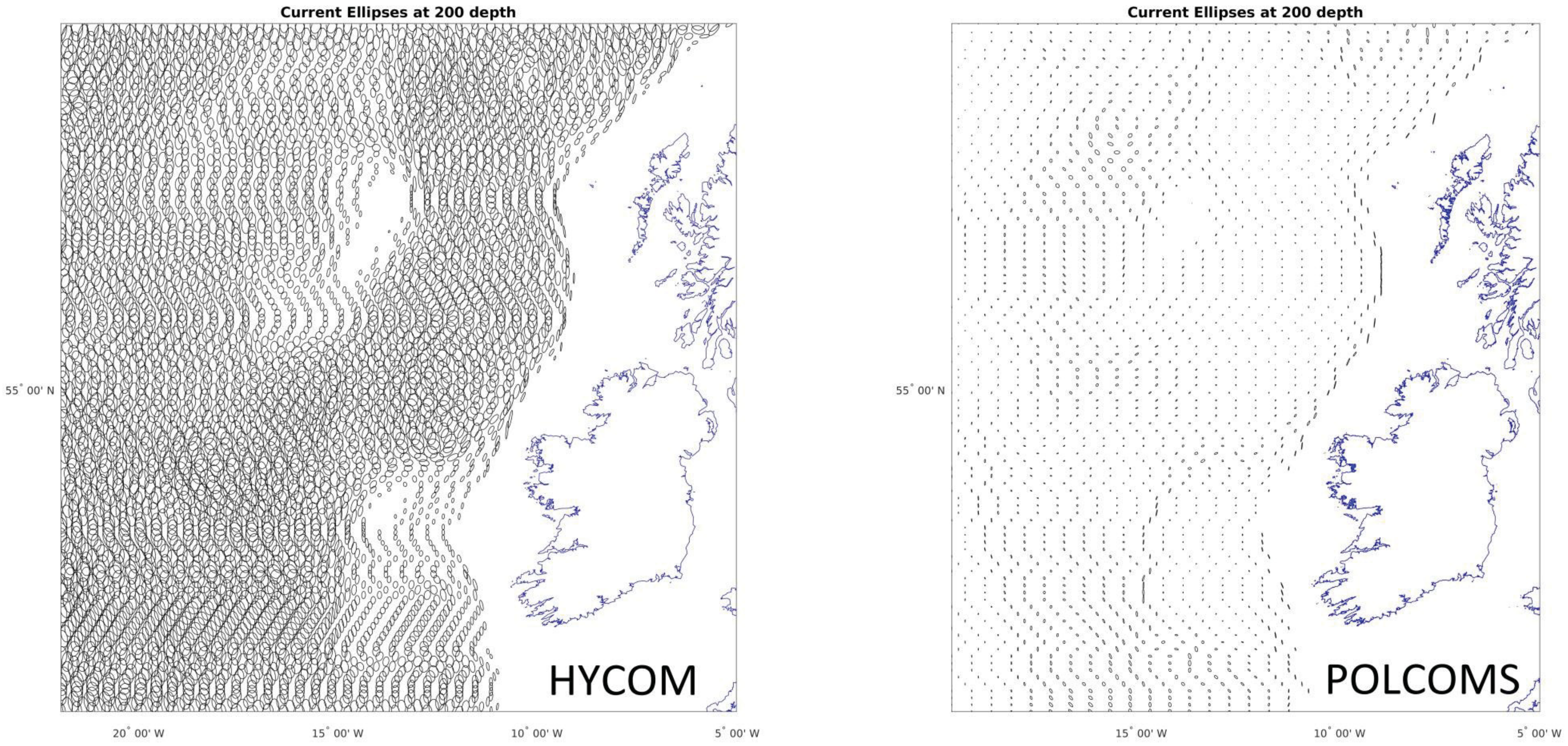


Figure A2 - 1 200m current ellipses

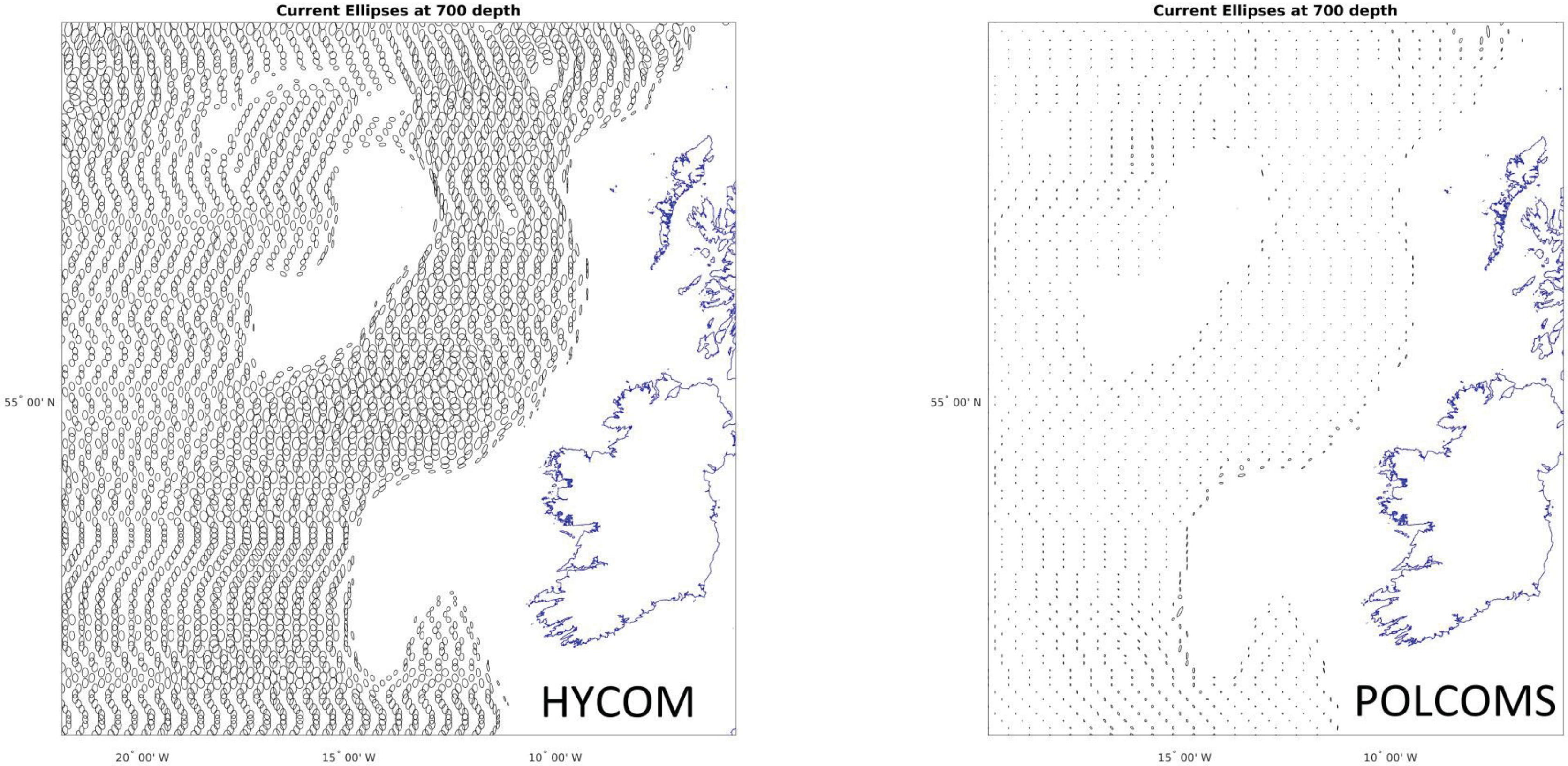


Figure A2 - 2 700m current ellipses

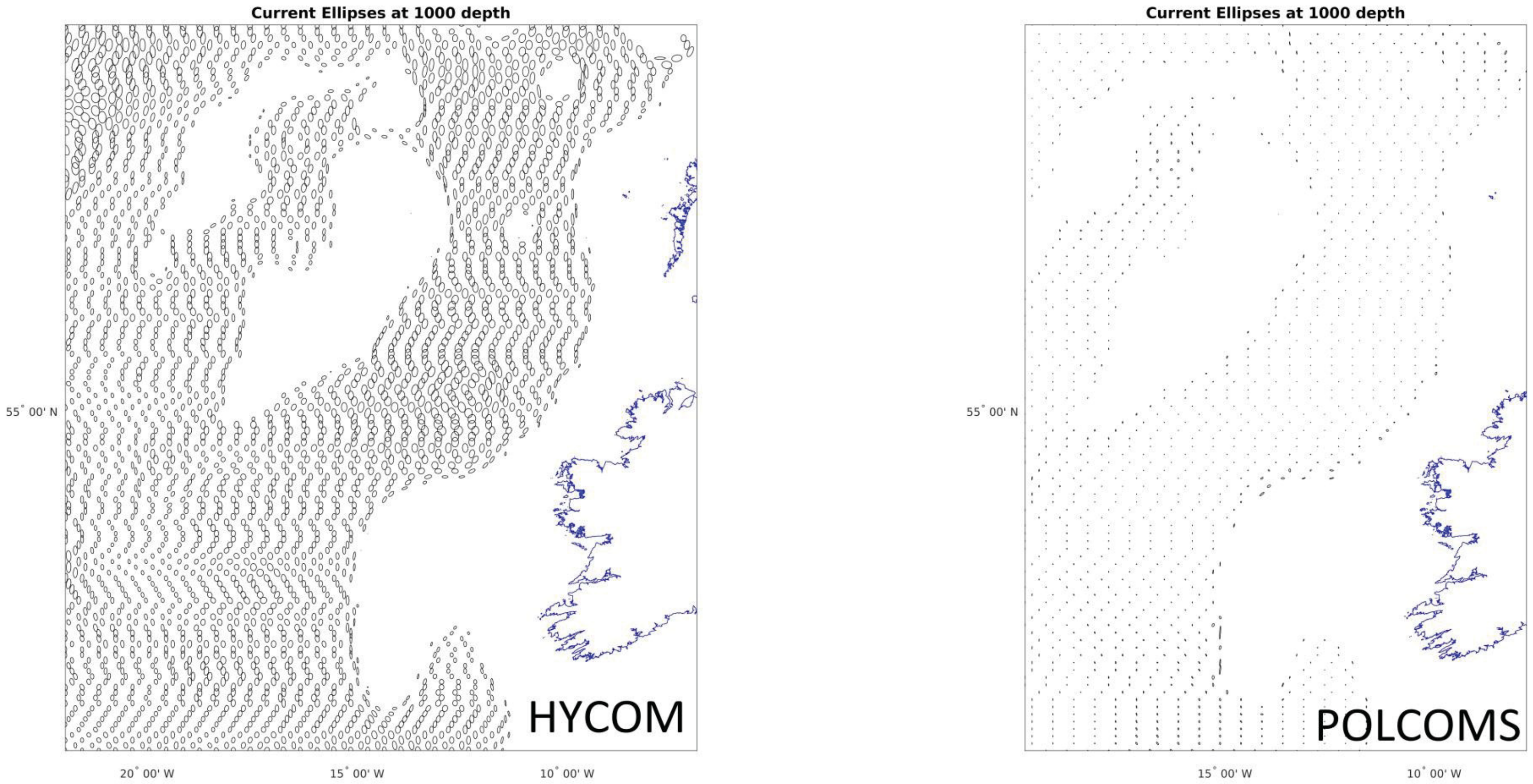


Figure A2 - 3 1000m current ellipses

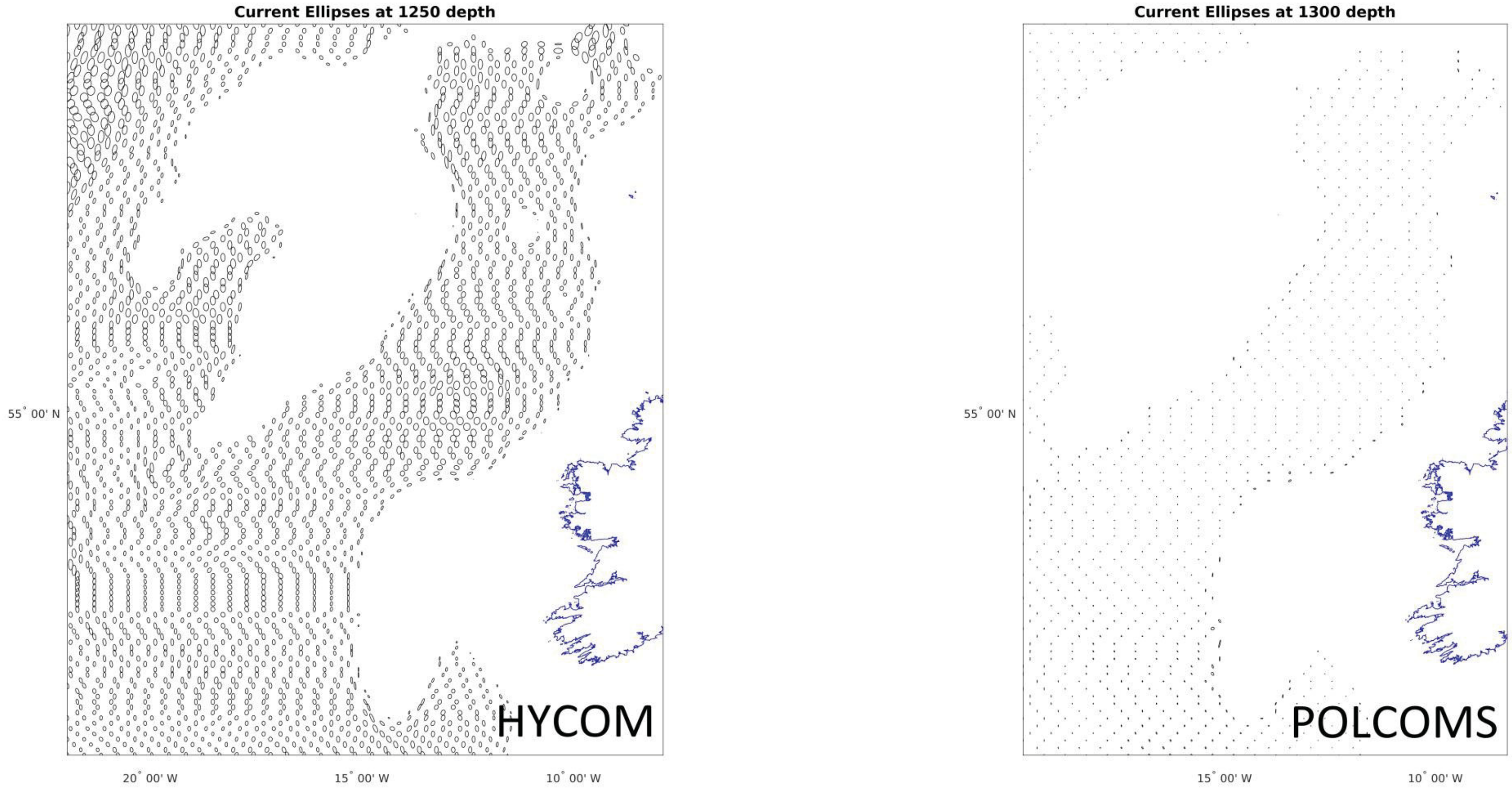


Figure A2 - 4 1300m current ellipses (HYCOM ellipses are from 1250m)

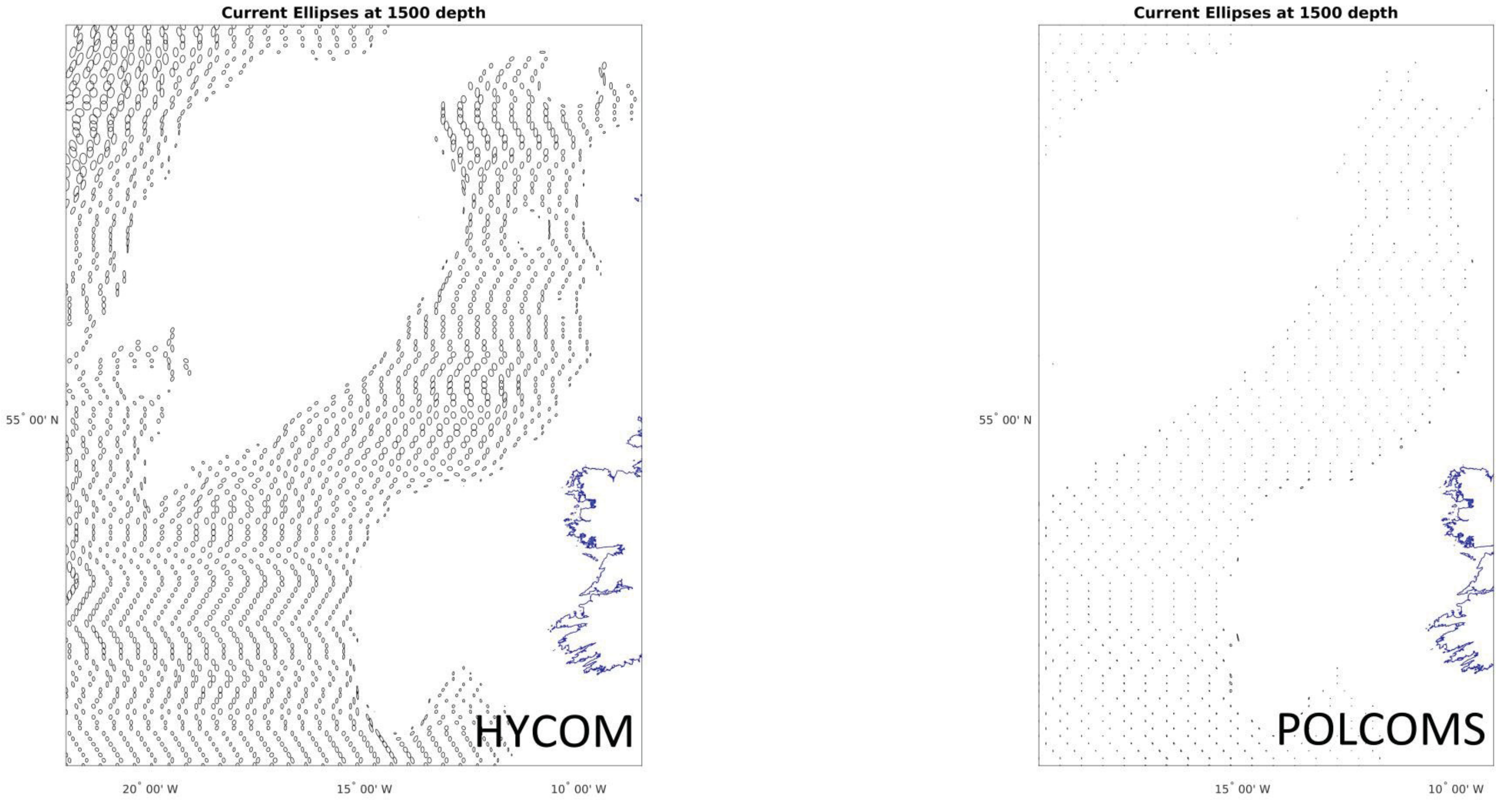


Figure A2 - 5 1500m current ellipses

Appendix 3: accompanying chapter 4

A3.1 Dispersal matrices per depth.

The following matrices (Table A3 - 1 to Table A3 - 32) form part of the basis of results matrices in Chapter 4. Individual per depth, per mode matrices are shown from the year 2003 as an example, although two further years of this data are also available (2007, 2010). Data was collected for all passive and active simulations per depth of simulation. This data may be useful in the future for depth specific ground truthing.

All matrices show raw data counts of larvae released from MPAs on the right hand side of the matrix, and retained in MPAs listed along the top of the matrix. Larvae were not released from all MPAs and MPAs span different depth ranges (but there is always at least one settling larvae visible in the matrix if the MPA did act as a source). Some MPAs were split into subdivisions in this raw data as the CMS model could not handle MPAs with holes in the middle. These subdivisions were summed in the final results shown in chapter 4.

Matrices are listed in depth order from shallowest (150m) to deepest (1000m), displaying first active, then passive results (all are labelled in the top left corner of the matrix).

Note there are no matrices for 250m or 300m depth as none of the MPAs had release cells at this depth (according to HYCOM – in reality they probably do!). All depths from 550m – 1000m were split into two halves when simulated due to computational restraints. Displayed here are the two halves summed into the per-depth matrix.

Table A3 - 1 150m Active Dispersal Matrix

150m Active		Retaining MPA																													
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	363	25	0	2	10024	0	52	632	0	0	0	0	0	0	0	0	0	9750	0	2558	0	0	0	0	0	0	0	0	0	0	24	0	0	3
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 2 150m Passive Dispersal Matrix

150m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_l	HBm1	HBm2	HRB_l1	HRB_l2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_l	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_l1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_l2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	1	0	0	0	3223	0	0	1538	0	0	0	0	0	0	0	0	0	20016	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 3 200m Active Dispersal Matrix

200m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_l	HBm1	HBm2	HRB_l1	HRB_l2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_l	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_l1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_l2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	9	9	0	1	3263	0	22	138	0	0	0	0	0	0	0	0	0	9769	0	2513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 4 200m Passive Dispersal Matrix

200m Passive		Retaining MPA																												
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	2	0	0	0	1402	0	0	50	0	0	0	0	0	0	0	0	0	16437	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 5 350m Active Dispersal Matrix

350m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2609	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 6 350m Passive Dispersal Matrix

		Retaining MPA																																	
	350m Passive	AntonDohm_N	AntonDohm_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohm_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohm_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4876	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 7 400m Active Dispersal Matrix

400m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	1176	563	0	47	5910	0	306	726	0	0	0	0	0	0	0	0	49	319	0	5260	0	0	0	0	0	0	0	0	0	0	1143	0	0	11
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	86	7	0	1864	58	0	653	0	0	0	0	0	0	0	0	0	0	0	0	3309	0	0	0	0	0	0	0	0	0	0	6	0	0	1044
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	265	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	446

Table A3 - 8 400m Passive Dispersal Matrix

400m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	861	145	0	14	8808	0	168	515	18	11	0	0	0	0	103	0	177	0	0	4574	0	0	0	0	0	0	0	0	0	0	656	0	0	4
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	RosemaryBank	108	2	0	1309	69	0	822	0	0	0	0	0	0	0	0	0	0	0	0	3991	0	0	0	0	0	0	0	0	0	0	2	0	0	501
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	245	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	73	0	0	0	0	0	0	0	0	0	0	0	0	0	1854

Table A3 - 9 450m Active Dispersal Matrix

	450m Active	Retaining MPA																																
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	24081	0	0	0	0	0	0	0	0	0	0	0	0	16644	0	0	16	0	6249	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	3551	1020	0	111	27011	0	1010	2071	113	4	0	0	0	0	137	0	276	3223	0	28991	0	0	0	0	0	0	2	0	0	2	2534	0	1	18
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	34	167	0	0	5108	0	4	896	0	0	17	0	0	0	0	0	8724	0	330	0	0	0	0	0	0	0	0	0	0	0	34418	0	315	0
	RosemaryBank	882	41	0	13937	518	0	6115	0	0	0	0	0	0	0	0	0	0	0	0	32011	0	0	0	0	0	0	0	0	0	0	62	0	0	9501
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	1749	461	0	88	120	0	8814	0	0	0	0	0	0	0	0	0	0	0	0	298	0	0	0	0	0	0	0	0	0	0	1096	0	0	661
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	1899	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	109	0	0	0	0	0	0	0	0	0	0	0	0	0	5232

Table A3 - 10 450m Passive Dispersal Matrix

		Retaining MPA																																
450m Passive		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	70855	0	0	0	0	0	0	0	0	0	0	0	0	9109	0	0	0	0	2085	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	3647	374	0	56	37053	0	461	811	53	28	0	0	0	6	1513	0	533	0	0	24674	0	0	0	0	0	0	0	0	0	0	1169	0	0	9
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	4	358	0	0	7006	0	9	1325	0	0	20	0	0	0	0	0	12978	0	1083	0	0	0	0	0	0	0	0	0	0	0	7330	0	3414	0
	RosemaryBank	783	40	0	9978	641	0	6001	0	0	0	0	0	0	0	0	0	0	0	0	38936	0	0	0	0	0	0	0	0	0	0	50	0	0	3563
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	3986	491	0	39	154	0	4585	0	0	0	0	0	0	0	0	0	1	0	0	522	0	0	0	0	0	0	0	0	0	0	4451	0	0	148
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WTR	0	0	0	3145	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	641	0	0	0	0	0	0	0	0	0	0	0	0	0	20003

Table A3 - 11 500m Active Dispersal Matrix

	500m Active	Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	87133	0	0	0	0	0	0	0	0	0	0	0	0	38236	0	0	0	0	12221	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	20768	1853	0	183	1E+05	0	3424	5638	1811	15	0	0	0	95	1483	0	2421	9365	0	2E+05	0	0	0	0	0	4	71	1	0	227	4968	0	0	79
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	984	433	0	0	20655	0	49	11021	0	0	0	0	0	0	0	0	12252	0	0	49	0	0	2	0	0	105	669	118	2	1614	3907	0	0	0
	HattonBank_I	2821	78	0	4963	3E+05	0	491	0	1E+06	66166	3290	605	1858	15757	91412	0	0	278	0	4E+05	0	0	0	0	0	0	0	0	0	0	0	0	7506	554
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	1299	1585	0	0	15771	2868	266	15773	49	1540	3780	72	0	7	7	0	2E+05	0	0	178	0	15853	5477	2601	244	3599	11639	1479	174	79066	18578	0	48342	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	41	638	0	0	17800	0	18	1501	0	0	30	0	0	0	0	0	18943	0	1283	0	0	0	0	0	0	0	0	0	0	0	47632	0	1860	0
	RosemaryBank	16335	841	0	3E+05	12071	0	2E+05	0	1	0	0	0	0	0	0	0	0	0	0	8E+05	0	0	0	0	0	0	0	0	0	0	2463	0	0	2E+05
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	1535	254	0	93	157	0	4107	0	0	0	0	0	0	0	0	0	0	0	0	240	0	0	0	0	0	0	0	0	0	0	402	0	0	412
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1455	0	0
	WRockall	0	0	0	0	29250	3	0	7731	2365	21376	681	74599	0	19646	8872	0	1	4203	0	274	0	4028	6	1193	21	0	2	0	0	21163	0	0	2E+05	0
	WTR	0	0	0	2679	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	117	0	0	0	0	0	0	0	0	0	0	0	0	0	6509

Table A3 - 12 500m Passive Dispersal Matrix

500m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	14080	0	0	0	0	3750	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	29318	996	0	129	2E+05	0	2229	2795	710	14	0	0	0	10	6758	0	4480	0	0	1E+05	0	0	0	0	0	0	0	0	0	0	3037	0	0	111
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	440	659	0	0	15989	0	34	4757	0	0	0	0	0	0	0	0	32520	0	0	58	0	0	0	0	0	0	0	0	0	0	2455	0	0	0
	HattonBank_I	149	1	0	324	69892	1	236	0	2E+06	40307	6960	82	32	12988	15513	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	528	237
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	1262	1914	0	0	22254	11	234	321	4	144	5555	0	0	2	0	0	4E+05	0	0	153	1	0	0	0	0	0	0	0	0	0	7362	0	75731	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	14	1051	0	0	16921	0	1	2285	0	0	0	0	0	0	0	0	45245	0	972	0	4	0	0	0	0	0	0	0	0	0	6243	0	7550	0
	RosemaryBank	14215	684	0	2E+05	19392	0	1E+05	0	1	0	0	0	0	0	0	0	0	0	0	1E+06	0	0	0	0	0	0	0	0	0	0	863	0	0	55422
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	2457	377	0	29	142	0	2101	0	0	0	0	0	0	0	0	0	1	0	0	251	0	0	0	0	0	0	0	0	0	0	1756	0	0	58
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	3159	0	0
	WRockall	0	0	0	0	14882	14	0	0	7653	53827	232	84321	0	28461	8793	0	14	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	3E+05	0
	WTR	0	0	0	16348	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	470	0	0	0	0	0	0	0	0	0	0	0	0	0	16746

Table A3 - 13 550m Active Dispersal Matrix

550m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	72011	0	0	0	0	12016	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	81119	13340	0	57	5E+05	0	11601	71271	3303	4	0	0	0	730	4811	0	27211	12707	0	4E+05	0	0	0	0	0	34	1391	45	0	2716	43851	0	0	47
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	7065	3287	0	0	1E+05	0	190	58842	0	0	0	0	0	0	0	0	94473	0	0	392	0	0	7	0	0	1289	9792	1527	10	17191	23238	0	10	0
	HattonBank_I	1756	117	0	236	5E+05	2	447	0	6E+06	4E+05	11023	2988	5373	71582	4E+05	0	0	0	0	5E+05	0	0	0	0	0	0	0	0	0	0	2	0	7110	156
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	11621	15649	0	0	2E+05	70880	1008	11701	2456	76387	1E+05	127	0	3557	0	0	1E+06	0	3	356	0	61787	48908	17694	575	38463	2E+05	13878	1967	2E+05	2E+05	0	5E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	20	1080	0	0	20173	0	56	1369	0	0	2	0	0	0	0	0	38007	0	3030	0	7	0	0	0	0	0	0	0	0	0	30980	0	4794	0
	RosemaryBank	46874	4733	0	7E+05	31102	0	4E+05	0	9	0	0	0	0	0	0	0	0	0	0	2E+06	0	0	0	0	0	0	0	0	0	0	6739	0	0	4E+05
	SPorcupine	0	6	0	0	707	0	0	114	0	0	0	0	0	0	0	0	5804	0	28339	0	1326	0	0	0	0	0	0	0	0	0	236	0	231	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	12836	1591	0	233	1103	0	35648	1	0	0	0	0	0	0	0	0	5	0	0	1445	0	0	0	0	0	0	0	0	0	0	10583	0	0	363
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	55544	914	0	1720	56386	3E+05	8494	4E+05	340	3E+05	84781	0	12	10382	0	310	0	6272	11	2194	19	1	2	0	0	27494	0	0	8E+05	0
	WTR	0	0	0	14611	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	654	0	0	0	0	0	0	0	0	0	0	0	0	0	41895

Table A3 - 14 550m Passive Dispersal Matrix

550m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	24817	0	0	0	0	7414	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	77646	7295	0	22	6E+05	0	5489	25137	1832	0	0	0	0	9	13311	0	34596	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	25737	0	0	64
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	3762	6287	0	0	1E+05	0	221	27911	0	0	0	0	0	0	0	0	2E+05	0	0	618	0	0	0	0	0	0	0	0	0	0	20428	0	0	0
	HattonBank_I	167	9	0	193	2E+05	1	104	0	7E+06	1E+05	21802	4860	190	54111	1E+05	0	0	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	6104	51
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	2980	1205	0	0	1E+05	223	769	326	1012	19823	53741	9	0	2296	0	0	3E+06	0	0	174	0	0	0	0	0	0	0	0	0	0	64606	0	9E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	6	2473	0	0	22917	0	0	1749	0	0	0	0	0	0	0	0	61147	0	4205	0	2	0	0	0	0	0	0	0	0	0	3938	0	12582	0
	RosemaryBank	38549	2298	0	4E+05	53771	0	3E+05	0	1	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	2356	0	0	1E+05
	SPorcupine	0	0	0	0	1027	0	0	151	0	0	0	0	0	0	0	0	8385	0	37589	0	1428	0	0	0	0	0	0	0	0	0	1124	0	254	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	18689	2460	0	13	772	0	8050	2	0	0	0	0	0	0	0	0	5	0	0	1726	0	0	0	0	0	0	0	0	0	0	32393	0	0	4
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	39471	653	0	0	1E+05	4E+05	1061	4E+05	2	2E+05	66385	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0
	WTR	0	0	0	73701	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2790	0	0	0	0	0	0	0	0	0	0	0	0	0	1E+05

Table A3 - 15 600m Active Dispersal Matrix

		Retaining MPA																																	
	600m Active	AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	60755	0	0	0	0	8572	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	47561	12054	0	12	3E+05	0	7806	97744	2100	0	0	0	0	505	2282	0	24462	10024	0	2E+05	0	0	0	0	0	55	1400	80	0	4190	38516	0	0	2
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	3576	1028	0	0	75227	0	74	21323	0	0	0	0	0	0	0	0	60902	0	0	121	0	0	0	0	0	588	6446	719	5	15348	12912	0	4	0
	HattonBank_I	676	102	0	109	4E+05	1	157	0	5E+06	4E+05	25820	6228	6021	1E+05	4E+05	0	0	0	0	4E+05	0	0	0	0	0	0	0	0	0	0	13	0	15337	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32726	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	5250	7176	0	0	74442	50533	917	5606	3069	69439	1E+05	84	0	11246	110	0	6E+05	0	0	168	0	24565	13996	6205	196	7239	39509	3592	340	35542	93162	0	5E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	1	1185	0	0	6938	0	3	748	0	0	0	0	0	0	0	0	29944	0	1365	0	2	0	0	0	0	0	0	0	0	0	13981	0	2878	0
	RosemaryBank	45984	5460	0	7E+05	49236	0	4E+05	0	3	0	0	0	0	0	0	0	0	0	0	2E+06	0	0	0	0	0	0	0	0	0	0	3576	0	0	3E+05
	SPorcupine	0	0	0	0	2923	0	0	344	0	0	0	0	0	0	0	0	31769	0	2E+05	0	5663	0	0	0	0	0	0	0	0	0	304	0	2946	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	17885	2307	0	434	1756	0	39606	1	0	0	0	0	0	0	0	0	8	0	0	2170	0	0	0	0	0	0	0	0	0	0	16879	0	0	129
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	25354	4289	0	51	60422	3E+05	8981	1E+05	60	2E+05	48586	0	0	565	0	81	0	15	0	24	0	1	0	1	0	651	0	0	5E+05	0
	WTR	0	0	0	8068	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	309	0	0	0	0	0	0	0	0	0	0	0	0	0	22511

Table A3 - 16 600m Passive Dispersal Matrix

		Retaining MPA																																	
	600m Passive	AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_l	HBm1	HBm2	HRB_l1	HRB_l2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	2	4E+05	0	0	0	1	0	0	0	0	0	0	0	0	32677	0	0	0	0	21824	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	29796	6834	0	21	5E+05	0	4436	8692	2269	0	0	0	0	1	3098	0	16218	0	0	1E+05	0	0	0	0	0	0	0	0	0	0	26825	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	1918	4351	0	0	78390	0	106	11818	0	0	0	0	0	0	0	0	84939	0	0	26	0	0	0	0	0	0	0	0	0	0	14471	0	0	0
	HattonBank_l	271	14	0	21	3E+05	0	6	0	6E+06	1E+05	6277	1168	670	47873	3E+05	0	0	0	0	4E+05	0	0	0	0	0	0	0	0	0	0	3	0	31950	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_l1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_l2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50759	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	1002	493	0	0	90544	1889	378	901	2029	36848	80271	144	0	5564	24	0	1E+06	0	0	6	0	0	0	0	0	0	0	0	0	0	49353	0	4E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	13	219	0	0	7238	0	4	221	0	0	0	0	0	0	0	0	20746	0	2664	0	2	0	0	0	0	0	0	0	0	0	2234	0	6611	0
	RosemaryBank	33381	1201	0	2E+05	48780	0	2E+05	0	2	0	0	0	0	0	0	0	0	0	0	2E+06	0	0	0	0	0	0	0	0	0	0	860	0	0	22362
	SPorcupine	7	0	0	0	5513	0	0	516	0	0	0	0	0	0	0	0	49034	0	1E+05	0	4873	0	0	0	0	0	0	0	0	0	8202	0	2212	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	17958	1321	0	0	1435	0	2770	6	0	0	0	0	0	0	0	0	2	0	0	1918	0	0	0	0	0	0	0	0	0	0	36604	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	9001	2165	0	0	53746	2E+05	13248	1E+05	0	89130	40171	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5E+05	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 17 650m Active Dispersal Matrix

650m Active		Retaining MPA																																
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	94865	0	0	0	0	3790	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	1E+05	33401	0	21	1E+06	0	17087	3E+05	7702	0	0	9	0	158	9404	0	73543	5561	0	5E+05	0	0	1	0	0	6	1951	16	0	10308	1E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	3420	1582	0	0	1E+05	0	245	27291	0	0	0	0	0	0	0	0	78319	0	0	90	0	1	0	0	0	828	8454	1032	8	18449	19691	0	2	0
	HattonBank_I	505	73	0	58	3E+05	0	120	0	5E+06	2E+05	8924	4308	4827	96703	3E+05	0	0	0	0	5E+05	0	0	0	0	0	0	0	0	0	0	5	0	9120	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	5870	11835	0	0	1E+05	63624	2038	9864	2532	1E+05	1E+05	1	0	11861	49	0	9E+05	0	0	111	0	15926	24271	6092	191	9330	31123	4580	538	14319	1E+05	0	9E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	2	2194	0	0	15248	0	7	590	0	0	0	0	0	0	0	0	39460	0	2460	0	1	0	0	0	0	0	0	0	0	0	23693	0	4372	0
	RosemaryBank	59727	5582	0	7E+05	74753	0	5E+05	0	0	0	0	0	0	0	0	0	0	1	0	3E+06	0	0	0	0	0	0	0	0	0	0	3247	0	0	2E+05
	SPorcupine	0	0	0	0	2526	0	0	398	0	0	0	0	0	0	0	0	37326	0	2E+05	0	3703	0	0	0	0	0	0	0	0	0	166	0	9183	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	16331	4168	0	332	1079	0	30912	4	0	0	0	0	0	0	0	0	1	0	0	1902	0	0	0	0	0	0	0	0	0	0	19382	0	0	15
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3856	0	0
	WRockall	0	0	0	0	31687	956	0	214	1E+05	3E+05	20210	2E+05	243	3E+05	1E+05	0	0	266	0	824	0	10	0	20	0	0	0	0	0	110	0	0	7E+05	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 18 650m Passive Dispersal Matrix

650m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	7E+05	0	0	0	0	0	0	0	0	0	0	0	0	31160	0	0	0	0	392	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	39283	23085	0	14	2E+06	0	8494	19982	3761	0	0	0	0	4	2057	0	41924	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	85630	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	4619	6602	0	0	1E+05	0	134	5797	0	0	0	0	0	0	0	0	1E+05	0	0	58	0	0	0	0	0	0	0	0	0	0	28649	0	0	0
	HattonBank_I	475	8	0	0	3E+05	0	121	0	6E+06	2E+05	8217	1338	882	31835	1E+05	0	0	0	0	6E+05	0	0	0	0	0	0	0	0	0	0	2	0	12232	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	28	82	0	0	19877	1885	1	171	918	89327	1E+05	0	0	3577	0	0	2E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	5690	0	8E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	33	92	0	0	10721	0	55	161	0	0	0	0	0	0	0	0	32373	0	1866	0	0	0	0	0	0	0	0	0	0	0	5825	0	25013	0
	RosemaryBank	78668	3423	0	3E+05	94294	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	1708	0	0	24069
	SPorcupine	7	0	0	0	6806	0	0	191	0	0	0	0	0	0	0	0	58370	0	1E+05	0	2589	0	0	0	0	0	0	0	0	0	5385	0	7437	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	11194	800	0	4	1221	0	2978	2	0	0	0	0	0	0	0	0	0	0	0	1977	0	0	0	0	0	0	0	0	0	0	54783	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7563	0	0
	WRockall	0	0	0	0	16783	937	0	0	37740	3E+05	32352	3E+05	0	2E+05	90193	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 19 700m Active Dispersal Matrix

	700m Active	Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	38426	0	0	0	0	1675	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	27419	10801	0	4	4E+05	0	6617	94179	2493	0	0	0	0	5	1445	0	19648	186	0	1E+05	0	0	0	0	0	1	204	3	0	1268	49601	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	362	203	0	0	9146	0	35	1757	0	0	0	0	0	0	0	0	7226	0	0	16	0	0	0	0	0	47	354	71	0	2457	2512	0	0	0
	HattonBank_I	145	27	0	16	77863	0	73	0	2E+06	25116	2450	293	210	11054	25600	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	3	0	178	0
	HBm1	0	0	0	0	1148	0	0	0	10062	859	423	26	16	921	2434	0	0	0	0	98	0	0	0	0	0	0	0	0	0	0	0	0	18	0
	HBm2	0	0	0	0	0	1002	0	0	2392	155	7172	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	565	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	554	4743	0	0	38226	31927	684	3464	240	29281	31566	0	0	2163	0	0	4E+05	0	0	1	0	2216	3103	586	30	3487	10065	2358	153	12755	39053	0	3E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	2	922	0	0	11931	0	21	322	0	0	0	0	0	0	0	0	35554	0	2651	0	4	0	0	0	0	0	0	0	0	0	13737	0	5352	0
	RosemaryBank	38188	2064	0	4E+05	71943	0	4E+05	0	3	0	0	0	0	0	0	0	0	1	0	2E+06	0	0	0	0	0	0	0	0	0	0	1690	0	0	80269
	SPorcupine	0	0	0	0	1409	0	0	100	0	0	0	0	0	0	0	0	29902	0	1E+05	0	2427	0	0	0	0	0	0	0	0	0	240	0	1409	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	29630	7560	0	124	2211	0	47416	2	0	0	0	0	0	0	0	0	2	0	0	3863	0	0	0	0	0	0	0	0	0	0	50962	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4697	0	0
	WRockall	0	0	0	0	2534	0	0	0	7757	15370	409	16185	3	17786	8126	0	0	0	0	148	0	0	0	0	0	0	0	0	0	0	0	0	29014	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 20 700m Passive Dispersal Matrix

		Retaining MPA																																
	700m Passive	AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AntonDohrn_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	BelgicaMounds	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	2964	0	0	0	0	54	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	8775	5587	0	0	6E+05	0	2592	5669	1209	0	0	0	0	0	134	0	1437	0	0	75627	0	0	0	0	0	0	0	0	0	0	51698	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	662	789	0	0	7929	0	19	522	0	0	0	0	0	0	0	0	8266	0	0	3	0	0	0	0	0	0	0	0	0	0	4203	0	0	0
	HattonBank_I	528	8	0	0	25669	0	32	0	2E+06	25093	1157	16	119	16443	28402	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	238	0
	HBm1	0	0	0	0	28	0	0	0	8901	5263	107	0	29	2486	3105	0	0	0	0	34	0	0	0	0	0	0	0	0	0	0	0	0	55	0
	HBm2	0	0	0	0	0	722	0	0	1207	23	10107	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	182	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	348	0	0	0	0	0	0	0	0	0	0	0	0	4E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	1	5	0	0	5334	7	0	86	75	15027	10439	0	0	222	0	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	1561	0	5E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	19	427	0	0	10786	0	163	200	0	0	0	0	0	0	0	0	37619	0	3970	0	7	0	0	0	0	0	0	0	0	0	12545	0	21792	0
	RosemaryBank	72759	2617	0	2E+05	69511	0	3E+05	0	3	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	1169	0	0	1996
	SPorcupine	0	0	0	0	5559	0	0	98	0	0	0	0	0	0	0	0	39473	0	86070	0	2637	0	0	0	0	0	0	0	0	0	4639	0	7145	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	25778	1499	0	7	1001	0	7238	0	0	0	0	0	0	0	0	0	2	0	0	5569	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7341	0	0
	WRockall	0	0	0	0	2581	0	0	0	1582	12354	544	16378	0	19859	4462	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50664	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 21 750m Active Dispersal Matrix

750m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	39417	21866	0	1140	11830	0	39065	16	0	0	0	0	0	0	0	0	29	0	0	17832	0	0	0	0	0	0	0	0	0	0	11638	0	0	25
	AntonDohrn_S	51709	36054	0	1204	14294	0	49149	34	0	0	0	0	0	0	0	0	7	0	0	19391	0	0	0	0	0	0	0	0	0	0	18379	0	0	13
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	14481	0	0	0	0	520	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	45830	20589	0	1	1E+06	0	11540	2E+05	12320	0	0	0	0	31	8498	0	61177	69	0	3E+05	0	0	0	0	0	0	110	2	0	873	1E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	1832	1769	0	0	68006	0	90	8736	0	0	0	0	0	0	0	0	48149	0	0	133	0	0	0	0	0	181	1559	305	0	5969	18274	0	0	0
	HattonBank_I	255	37	0	0	1E+05	0	135	0	4E+06	83225	66222	416	29	27571	41395	0	0	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	7	0	731	0
	HBm1	0	0	0	0	3777	0	0	0	79836	15235	834	642	157	6396	18216	0	0	0	0	375	0	0	0	0	0	0	0	0	0	0	0	0	240	0
	HBm2	0	0	0	0	0	65624	0	0	2E+05	16620	1E+06	0	0	212	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49979	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	2218	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	314	3979	0	0	50205	43121	68	3546	121	20445	22136	0	0	813	0	0	6E+05	0	0	0	0	9061	5554	2558	69	3644	8677	2752	192	21553	27391	0	6E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	8	633	0	0	12280	0	5	441	0	0	0	0	0	0	0	0	54934	0	2984	0	0	0	0	0	0	0	0	0	0	0	8197	0	9046	0
	RosemaryBank	69526	2716	0	6E+05	1E+05	0	7E+05	0	3	0	0	0	0	0	0	0	0	0	0	4E+06	0	0	0	0	0	0	0	0	0	0	2543	0	0	88818
	SPorcupine	0	0	0	0	2608	0	0	17	0	0	0	0	0	0	0	0	49865	0	2E+05	0	4250	0	0	0	0	0	0	0	0	0	1616	0	1241	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	21143	5587	0	34	1517	0	34619	0	0	0	0	0	0	0	0	0	2	0	0	4166	0	0	0	0	0	0	0	0	0	0	45911	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1996	0	0
	WRockall	0	0	0	0	55751	0	0	0	1E+05	4E+05	20427	2E+05	476	4E+05	1E+05	0	0	0	0	398	0	0	0	0	0	0	0	0	0	0	0	0	7E+05	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 22 750m Passive Dispersal Matrix

750m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	46191	30231	0	361	10691	0	31254	6	0	0	0	0	0	0	0	0	8	0	0	9367	0	0	0	0	0	0	0	0	0	0	10687	0	0	1
	AntonDohrn_S	54056	47401	0	347	13988	0	32628	3	0	0	0	0	0	0	0	0	10	0	0	10366	0	0	0	0	0	0	0	0	0	0	19800	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	1014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	12150	12790	0	0	2E+06	0	3135	19137	16137	0	0	0	0	94	375	0	3956	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	1254	3817	0	0	66839	0	127	3983	0	0	0	0	0	0	0	0	61864	0	0	43	0	0	0	0	0	0	0	0	0	0	19820	0	0	0
	HattonBank_I	167	5	0	0	23546	0	77	0	5E+06	37929	36062	83	18	19557	73540	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	827	0
	HBm1	0	0	0	0	14	0	0	0	69729	50455	3086	4	88	11000	21355	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	457	0
	HBm2	0	0	0	0	0	44084	0	0	1E+05	6706	1E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15123	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	2123	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	6508	0	0	51	11	15064	8882	0	0	28	0	0	1E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	7569	0	9E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	13	429	0	0	11525	0	28	54	0	0	0	0	0	0	0	0	31462	0	32192	0	0	0	0	0	0	0	0	0	0	0	10334	0	10849	0
	RosemaryBank	2E+05	3679	0	4E+05	99051	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	4E+06	0	0	0	0	0	0	0	0	0	0	1606	0	0	1271
	SPorcupine	0	0	0	0	5008	0	0	6	0	0	0	0	0	0	0	0	53205	0	2E+05	0	5458	0	0	0	0	0	0	0	0	0	3420	0	4754	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	19333	1056	0	18	439	0	9285	0	0	0	0	0	0	0	0	0	0	0	0	3824	0	0	0	0	0	0	0	0	0	0	89296	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1918	0	0
	WRockall	0	0	0	0	39107	0	0	0	35264	3E+05	16026	3E+05	0	3E+05	36997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 23 800m Active Dispersal Matrix

	800m Active	Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	1E+05	57198	0	399	22517	0	84520	0	0	0	0	0	0	0	0	0	111	0	0	44424	0	0	0	0	0	0	0	0	0	0	22355	0	0	0
	AntonDohrn_S	99475	67860	0	394	40864	0	1E+05	0	0	0	0	0	0	0	0	0	8	0	0	49985	0	0	0	0	0	0	0	0	0	0	38941	0	0	0
	BelgicaMounds	0	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	0	7700	0	0	0	0	202	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	33868	13984	0	0	5E+05	0	6627	78614	1094	0	0	0	0	19	374	0	22830	2	0	83929	0	0	0	0	0	0	8	0	0	16	68208	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	207	293	0	0	6485	0	12	2325	0	0	0	0	0	0	0	0	4372	0	0	26	0	0	0	0	0	0	55	0	0	302	2590	0	0	0
	HattonBank_I	68	4	0	0	33922	0	19	0	3E+06	38450	2E+05	11	4	3385	6016	0	0	0	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	0	4759	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	54872	0	0	2E+05	7271	1E+06	0	0	1297	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42757	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	7939	0	0	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	109	567	0	0	29776	22673	0	985	0	5740	8350	0	0	44	0	0	3E+05	0	0	0	0	6704	2057	2220	55	1509	1822	1255	51	2842	9453	0	3E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	24	343	0	0	6877	0	5	31	0	0	0	0	0	0	0	0	68346	0	2846	0	1	0	0	0	0	0	0	0	0	0	4388	0	15770	0
	RosemaryBank	82412	2312	0	3E+05	90172	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	2426	0	0	84762
	SPorcupine	0	0	0	0	785	0	0	16	0	0	0	0	0	0	0	0	28881	0	97922	0	2830	0	0	0	0	0	0	0	0	0	2205	0	273	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	2677	826	0	2	115	0	2754	0	0	0	0	0	0	0	0	0	0	0	0	914	0	0	0	0	0	0	0	0	0	0	5759	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4493	0	0
	WRockall	0	0	0	0	35896	0	0	0	74674	3E+05	9064	1E+05	197	2E+05	66440	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	6E+05	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 24 800m Passive Dispersal Matrix

		Retaining MPA																															
800m Passive		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	1E+05	70348	0	340	19861	0	52422	3	0	0	0	0	0	0	0	0	35	0	0	23189	0	0	0	0	0	0	0	0	0	0	32768	0	0	0
	AntonDohrn_S	1E+05	90701	0	319	56636	0	51155	4	0	0	0	0	0	0	0	0	136	0	0	21872	0	0	0	0	0	0	0	0	0	0	25652	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	36	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	8481	8893	0	0	8E+05	0	1146	17756	496	0	0	0	0	0	3	0	5607	0	0	38130	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	48	489	0	0	9619	0	6	388	0	0	0	0	0	0	0	0	194	0	0	1	0	0	0	0	0	0	0	0	0	0	2605	0	0	0
	HattonBank_I	2	0	0	0	4501	0	2	0	3E+06	331	1E+05	20	0	3080	1134	0	0	0	0	69944	0	0	0	0	0	0	0	0	0	0	0	0	1918	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	30756	0	0	1E+05	2933	2E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7432	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	2920	0	0	0	0	0	0	0	0	0	0	0	0	52101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	1467	0	0	106	0	9551	3018	0	0	21	0	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	4057	0	3E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	712	0	0	9358	0	0	203	0	0	0	0	0	0	0	0	40322	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	13917	0	10687	0
	RosemaryBank	98649	1812	0	1E+05	91738	0	4E+05	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	1740	0	0	0
	SPorcupine	0	0	0	0	836	0	0	6	0	0	0	0	0	0	0	0	23179	0	1E+05	0	3605	0	0	0	0	0	0	0	0	0	434	0	341	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	2357	200	0	0	86	0	1099	0	0	0	0	0	0	0	0	0	0	0	0	401	0	0	0	0	0	0	0	0	0	0	11642	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4991	0	0
	WRockall	0	0	0	0	1391	0	0	0	530	82649	6449	2E+05	0	85287	3282	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 25 850m Active Dispersal Matrix

850m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	3E+05	2E+05	0	261	28251	0	1E+05	0	0	0	0	0	0	0	0	0	155	0	0	75476	0	0	0	0	0	0	0	0	0	0	50489	0	0	0
	AntonDohrn_S	1E+05	76796	0	171	33796	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	0	54005	0	0	0	0	0	0	0	0	0	0	31448	0	0	0
	BelgicaMounds	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	13757	0	0	0	0	1543	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	1E+05	32218	0	0	2E+06	0	15209	1E+05	6122	0	0	0	0	59	3058	0	46436	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	253	378	0	0	8753	0	19	2866	0	0	0	0	0	0	0	0	4563	0	0	20	0	0	0	0	0	0	14	0	0	28	3194	0	0	0
	HattonBank_I	18	0	0	0	25807	0	18	0	3E+06	15667	2E+05	13	12	3246	5105	0	0	0	0	93244	0	0	0	0	0	0	0	0	0	0	0	0	13568	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	54375	0	0	3E+05	8217	1E+06	0	0	230	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58647	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	1662	0	0	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	23	196	0	0	70628	161	0	620	0	3765	19360	0	0	146	0	0	5E+05	0	0	0	0	3231	998	864	0	192	164	180	8	2483	3701	0	5E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	56	817	0	0	7168	0	0	114	0	0	0	0	0	0	0	0	79750	0	3620	0	0	0	0	0	0	0	0	0	0	0	6922	0	12855	0
	RosemaryBank	91645	2203	0	3E+05	1E+05	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	1967	0	0	1E+05
	SPorcupine	0	0	0	0	555	0	0	23	0	0	0	0	0	0	0	0	23786	0	98767	0	1737	0	0	0	0	0	0	0	0	0	1955	0	44	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	12040	3693	0	0	367	0	9799	0	0	0	0	0	0	0	0	0	1	0	0	3110	0	0	0	0	0	0	0	0	0	0	35678	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2708	0	0
	WRockall	0	0	0	0	1E+05	0	0	0	2E+05	8E+05	32894	4E+05	65	6E+05	1E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 26 850m Passive Dispersal Matrix

		Retaining MPA																																	
	850m Passive	AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	3E+05	2E+05	0	167	23620	0	64926	0	0	0	0	0	0	0	0	0	0	0	0	40825	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0
	AntonDohrn_S	1E+05	89035	0	169	72411	0	56636	0	0	0	0	0	0	0	0	0	46	0	0	29372	0	0	0	0	0	0	0	0	0	0	25558	0	0	0
	BelgicaMounds	0	0	4E+05	0	0	0	0	0	0	0	0	0	0	0	0	1907	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	19032	21238	0	0	3E+06	0	471	35649	16441	0	0	0	0	1	475	0	18852	0	0	93278	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	24	306	0	0	12456	0	0	694	0	0	0	0	0	0	0	0	215	0	0	0	0	0	0	0	0	0	0	0	0	0	2187	0	0	0
	HattonBank_I	0	0	0	0	10373	0	5	0	3E+06	4958	1E+05	15	0	5333	6254	0	0	0	0	51139	0	0	0	0	0	0	0	0	0	0	0	0	2484	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	33414	0	0	3E+05	1595	2E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9714	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	338	0	0	1	0	8478	2740	0	0	175	0	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	148	0	5E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	458	0	0	6552	0	0	93	0	0	0	0	0	0	0	0	31267	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	10763	0	3997	0
	RosemaryBank	1E+05	2268	0	1E+05	64045	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	4E+06	0	0	0	0	0	0	0	0	0	0	2139	0	0	0
	SPorcupine	0	0	0	0	67	0	0	1	0	0	0	0	0	0	0	0	21474	0	1E+05	0	7146	0	0	0	0	0	0	0	0	0	112	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	7889	680	0	0	264	0	4748	0	0	0	0	0	0	0	0	0	0	0	0	1920	0	0	0	0	0	0	0	0	0	0	60767	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4029	0	0
	WRockall	0	0	0	0	7673	0	0	0	11	1E+05	15094	3E+05	0	2E+05	2997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 27 900m Active Dispersal Matrix

	900m Active	Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	3E+05	2E+05	0	3	21903	0	1E+05	0	0	0	0	0	0	0	0	0	23	0	0	61141	0	0	0	0	0	0	0	0	0	0	49225	0	0	0
	AntonDohrn_S	1E+05	63489	0	0	26135	0	82545	0	0	0	0	0	0	0	0	0	9	0	0	45259	0	0	0	0	0	0	0	0	0	0	37165	0	0	0
	BelgicaMounds	0	0	57485	0	0	0	0	0	0	0	0	0	0	0	0	1971	0	0	0	0	53	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	4203	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1020	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	22639	13999	0	0	6E+05	0	4787	41707	3279	0	0	0	0	31	1012	0	13205	0	0	92373	0	0	0	0	0	0	0	0	0	0	50007	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	234	231	0	0	5497	0	14	1159	0	0	0	0	0	0	0	0	3112	0	0	2	0	0	0	0	0	0	0	0	0	0	2028	0	0	0
	HattonBank_I	0	0	0	0	734	0	0	0	1E+06	1177	59432	0	0	115	153	0	0	0	0	12201	0	0	0	0	0	0	0	0	0	0	0	0	1188	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	57018	0	0	2E+05	13231	1E+06	0	0	186	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50847	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	1461	0	0	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	47	0	0	12497	0	0	99	0	825	2129	0	0	11	0	0	2E+05	0	0	0	0	1641	857	1104	0	6	1	0	1	0	641	0	1E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	27	394	0	0	2659	0	0	59	0	0	0	0	0	0	0	0	27951	0	1999	0	0	0	0	0	0	0	0	0	0	0	2398	0	3333	0
	RosemaryBank	48684	3113	0	2E+05	71441	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	3165	0	0	88782
	SPorcupine	0	0	0	0	164	0	0	1	0	0	0	0	0	0	0	0	20756	0	1E+05	0	1332	0	0	0	0	0	0	0	0	0	144	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	24494	12391	0	0	997	0	16519	0	0	0	0	0	0	0	0	0	0	0	0	7063	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	35678	26	0	0	65637	5E+05	27501	3E+05	0	3E+05	42797	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 28 900m Passive Dispersal Matrix

900m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	4E+05	2E+05	0	0	8103	0	32260	0	0	0	0	0	0	0	0	0	0	0	0	34632	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0
	AntonDohrn_S	1E+05	60472	0	0	41477	0	47615	0	0	0	0	0	0	0	0	0	1	0	0	23619	0	0	0	0	0	0	0	0	0	0	30698	0	0	0
	BelgicaMounds	0	0	68440	0	0	0	0	0	0	0	0	0	0	0	0	135	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	4203	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1020	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	5277	6210	0	0	1E+06	0	340	459	3637	0	0	0	0	0	5	0	1384	0	0	35123	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	24	200	0	0	7735	0	1	426	0	0	0	0	0	0	0	0	47	0	0	0	0	0	0	0	0	0	0	0	0	0	1033	0	0	0
	HattonBank_I	0	0	0	0	110	0	0	0	1E+06	431	2544	0	0	203	1053	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	17726	0	0	1E+05	2697	2E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8390	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	5	0	0	0	0	1	0	0	0	0	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	5846	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	200	0	0	2140	0	0	1	0	0	0	0	0	0	0	0	16401	0	22481	0	0	0	0	0	0	0	0	0	0	0	1210	0	2	0
	RosemaryBank	63724	5461	0	23071	69750	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	3E+06	0	0	0	0	0	0	0	0	0	0	2162	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16076	0	74596	0	2070	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	23606	1100	0	0	841	0	6723	0	0	0	0	0	0	0	0	0	0	0	0	5278	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	73	0	0	0	0	46350	4015	1E+05	0	55627	293	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 29 950m Active Dispersal Matrix

950m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	2E+05	1E+05	0	0	14037	0	67605	0	0	0	0	0	0	0	0	0	1	0	0	31619	0	0	0	0	0	0	0	0	0	0	35107	0	0	0
	AntonDohrn_S	2E+05	1E+05	0	0	23955	0	1E+05	0	0	0	0	0	0	0	0	0	0	0	0	50244	0	0	0	0	0	0	0	0	0	0	98770	0	0	0
	BelgicaMounds	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	0	0	1643	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	4661	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	427	0	0	0	0	0	0	0	0	0	0	0	0	0	4518
	ERockallBank	36450	9888	0	0	1E+06	0	5836	51496	8651	0	0	0	0	24	417	0	9315	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	83653	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	1531	0	0	0	1E+06	427	16970	0	0	742	939	0	0	0	0	10629	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	32121	0	0	1E+05	2166	1E+06	0	0	250	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	82143	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	3	0	0	6956	0	0	37	0	518	227	0	0	1	0	0	5E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	105	0	4E+05	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	17	392	0	0	3445	0	0	66	0	0	0	0	0	0	0	0	35091	0	3887	0	0	0	0	0	0	0	0	0	0	0	2623	0	366	0
	RosemaryBank	54525	5280	0	2E+05	88618	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	4E+06	0	0	0	0	0	0	0	0	0	0	4592	0	0	45250
	SPorcupine	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	12065	0	65178	0	1038	0	0	0	0	0	0	0	0	0	2	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	34489	18824	0	0	984	0	30698	0	0	0	0	0	0	0	0	0	0	0	0	11719	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4407	0	0
	WRockall	0	0	0	0	9038	37	0	0	41183	5E+05	41401	3E+05	0	5E+05	29834	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 30 950m Passive Dispersal Matrix

	950m Passive	Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	2E+05	1E+05	0	0	2257	0	13839	0	0	0	0	0	0	0	0	0	0	0	0	18306	0	0	0	0	0	0	0	0	0	0	97304	0	0	0
	AntonDohrn_S	2E+05	92251	0	0	26495	0	59916	0	0	0	0	0	0	0	0	0	0	0	0	26035	0	0	0	0	0	0	0	0	0	0	97626	0	0	0
	BelgicaMounds	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	8169	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2164	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	5202	8200	0	0	2E+06	0	202	797	9722	0	0	0	0	0	22	0	359	0	0	48334	0	0	0	0	0	0	0	0	0	0	1E+05	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	176	0	0	0	2E+06	1491	4045	1	0	829	2450	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	10972	0	0	84735	67	2E+06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18307	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	6E+05	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	31193	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	25	0	0	1502	0	0	1	0	0	0	0	0	0	0	0	14752	0	55920	0	0	0	0	0	0	0	0	0	0	0	533	0	0	0
	RosemaryBank	1E+05	1082	0	3915	49326	0	8E+05	0	0	0	0	0	0	0	0	0	0	0	0	4E+06	0	0	0	0	0	0	0	0	0	0	1816	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5316	0	25842	0	1064	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	28010	449	0	0	771	0	4461	0	0	0	0	0	0	0	0	0	0	0	0	8048	0	0	0	0	0	0	0	0	0	0	3E+05	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8128	0	0
	WRockall	0	0	0	0	42	0	0	0	0	29384	3582	2E+05	0	72515	58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2E+06	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 31 1000m Active Dispersal Matrix

1000m Active		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	51890	28560	0	0	2139	0	16194	0	0	0	0	0	0	0	0	0	0	0	0	6353	0	0	0	0	0	0	0	0	0	0	10727	0	0	0
	AntonDohrn_S	49580	30398	0	0	6185	0	30706	0	0	0	0	0	0	0	0	0	0	0	0	13647	0	0	0	0	0	0	0	0	0	0	29151	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	1212	516	0	0	94262	0	60	5893	43	0	0	0	0	0	0	0	211	0	0	2604	0	0	0	0	0	0	0	0	0	0	5471	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	24262	0	4	0	0	0	0	0	0	0	0	84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	153	0	0	2269	3	13125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	72	0	0	0	0	19	0	0	0	0	0	0	19682	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4179	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	2	2	0	0	351	0	0	0	0	0	0	0	0	0	0	0	4409	0	637	0	0	0	0	0	0	0	0	0	0	0	164	0	5	0
	RosemaryBank	1975	64	0	3809	2209	0	23426	0	0	0	0	0	0	0	0	0	0	0	0	2E+05	0	0	0	0	0	0	0	0	0	0	137	0	0	553
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1469	0	7956	0	162	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	1	0	0	19	4683	459	2114	0	2523	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24527	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A3 - 32 1000m Passive Dispersal Matrix

1000m Passive		Retaining MPA																																	
		AntonDohrn_N	AntonDohrn_S	BelgicaMounds	DarwinMounds	ERockallBank	EdorasBank	GeikieS&HSlope	HaddockBox	HattonBank_I	HBm1	HBm2	HRB_I1	HRB_I2	HRB_S	HRB_N	HovlandMounds	LogachevMounds	NWRockall_g	PorcupineBank	RosemaryBank	SPorcupine	SWRockall_g2k1	SWRockall_k1S	SWRockall_k1NW	SWRockall_k1NE	SWRockall_g3k2	SWRockall_k2	SWRockall_k2S	SWRockall_k2W	SWRockallEmpress	TheBarraF&HebTer	TheCanyons	WRockall	WTR
Source MPA	AntonDohrn_N	47205	31153	0	0	562	0	4028	0	0	0	0	0	0	0	0	0	0	0	0	3269	0	0	0	0	0	0	0	0	0	0	20562	0	0	0
	AntonDohrn_S	97473	30252	0	0	4944	0	17900	0	0	0	0	0	0	0	0	0	0	0	0	6920	0	0	0	0	0	0	0	0	0	0	23779	0	0	0
	BelgicaMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	DarwinMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	ERockallBank	225	361	0	0	2E+05	0	17	0	0	0	0	0	0	0	0	0	2	0	0	338	0	0	0	0	0	0	0	0	0	0	7739	0	0	0
	EdorasBank	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	GeikieS&HSlope	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HaddockBox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HattonBank_I	0	0	0	0	0	0	0	0	30818	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HBm2	0	0	0	0	0	17	0	0	3083	0	15764	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_I2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HRB_N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	HovlandMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	LogachevMounds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26212	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	NWRockall_g	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	PorcupineBank	0	0	0	0	158	0	0	0	0	0	0	0	0	0	0	0	404	0	2620	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0
	RosemaryBank	5596	14	0	0	467	0	29078	0	0	0	0	0	0	0	0	0	0	0	0	3E+05	0	0	0	0	0	0	0	0	0	0	57	0	0	0
	SPorcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	2926	0	166	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g2k1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k1NE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_g3k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockall_k2W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SWRockallEmpress	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheBarraF&HebTer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	TheCanyons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	WRockall	0	0	0	0	0	0	0	0	0	1296	81	0	0	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28617	0
	WTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Glossary

Baroclinic – a stratified fluid where the gradients of pressure and density are misalligned. Instability of baroclinicity results in vorticity (eddies).

Barotropic – a stratified fluid where the gradients of pressure and density are aligned (isobaric surfaces are also isopycnal and isothermal, baroclinic vector is zero and motions of fluid are strongly constrained)

Geostrophy – currents flowing parallel to isobars as a result of the Coriolis force balancing the pressure gradient force. A geostrophic flow may be barotropic or baroclinic.

Halocline – the boundary (area of steepest gradient) separating two water masses of different salinity in a stratified fluid

Internal tides – occurs along pycnoclines, generated by tidal surface waters moving stratified water up and down sloping topography.

Internal waves – gravity waves occurring along pycnoclines. Can vary vastly in amplitude and frquency. Can be heightened by the lower water mass interfacing with rough topography.

Kelvin-Helmholtz instability – breaking internal waves, these occur when the Richardson number (the ratio of potential to kinetic energy) of a pycnocline drops below 0.25 (i.e. where the kinetic energy is high enough to break surface tension)

Pycnocline – the boundary (area of steepest gradient) separating two water masses of different density in a stratified fluid (may also be a halocline and/or thermocline)

Permanent Pycnocline – the boundary (area of steepest stable density gradient) which separates the upper waters where surface mixing occurs, and deeper waters. This can restrict transport of nutrients between upper and lower layers and can inhibit the vertical migration of plankton. This can be diffused by shear produced turbulence, creating areas of upwelling.

Reynolds Number – a metric to convey the ratio of inertia against viscosity. Low Reynolds numbers are viscosity dominated and characterise laminar flow, high

Reynolds numbers are inertia dominated and represent turbulent flows. Reynolds numbers can be applied to objects to assess the amount of drag they will experience.

Richardson Number – a metric to convey the ratio of potential energy (static stability) against kinetic energy (velocity shear). Where kinetic energy dominates the medium becomes unstable, e.g. waves break at high Richardson numbers (see *Kelvin-Helmholtz instability*).

Thermocline – the boundary (area of steepest gradient) separating two water masses of different temperatures in a stratified fluid

Upwelling – the upward movement of nutrient rich bottom waters towards the surface. Classically this is wind driven, but localised upwelling can occur as a symptom of the topography.

List of acronyms

ADS – Anton Dohrn Seamount

BBL – Bottom Boundary Layer

CBD – Convention on Biological Diversity

CMS – Connectivity Modeling System

DST – Distance Separation over Time

EEZ – Exclusive Economic Zone

ENAW – Eastern North Atlantic Water

FUV – Fraction of Unexplained Variance

GCM – General Circulation Model

HPC – High Performance Computing

HYCOM – Hybrid Coordinate Ocean Model

LDM – Larval Dispersal Model

MCZ – Marine Conservation Zone

MOW – Mediterranean Outflow Water

MPA – Marine Protected Area

NAO – North Atlantic Oscillation

NCODA – Navy Coupled Ocean Data Assimilation

NEAFC – North East Atlantic Fisheries Commission

OSPAR – OSlo-PARis Convention (aka "The Convention for the Protection of the Marine Environment of the North-East Atlantic")

PLD – Planktonic Larval Duration

POLCOMS – Proudman Oceanographic Laboratory Coastal Ocean Modelling System

PPD – Predicted Pathways of Dispersal

RT – Rockall Trough

SAC – Special Area of Conservation

SAIW – Sub-Arctic Intermediate Water

SDM – Species Distribution Model

SLD – Straight Line Distance

WTOW – Wyville Thomson Overflow Water

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Estimating dispersal distance in the deep sea: challenges and applications to marine reserves

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Population connectivity refers to the exchange of individuals among populations: it affects gene flow, regulates population size and function, and mitigates recovery from natural or anthropogenic disturbances. Many populations in the deep sea are spatially fragmented, and will become more so with increasing resource exploitation. Understanding population connectivity is critical for spatial management. For most benthic species, connectivity is achieved by the planktonic larval stage, and larval dispersal is, in turn, regulated by complex interactions between biological and oceanographic processes. Coupled biophysical models, incorporating ocean circulation and biological traits, such as planktonic larval duration (PLD), have been used to estimate population connectivity and generate spatial management plans in coastal and shallow waters. In the deep sea, knowledge gaps in both the physical and biological components are delaying the effective use of this approach. Here, we review the current efforts in conservation in the deep sea and evaluate (1) the relevance of using larval dispersal in the design of marine protected areas and (2) the application of biophysical models in the study of population connectivity. Within biophysical models, PLD can be used to estimate dispersal distance. We propose that a PLD that guarantees a minimum dispersal distance for a wide range of species should be used in the planning of marine protected areas in the deep sea. Based on a review of data on species found at depths >200 m, a PLD of 35 and 69 days ensures a minimum distance for 50 and 75%, respectively, of eurybathic and deep-sea species. We note that more data are required to enhance accuracy and address the high variability in PLD between and within taxonomic groups, limiting generalizations that are often appealing to decision-makers. Given the imminent expansion of resource exploitation in the deep sea, data relevant to spatial management are needed urgently.

Keywords: deep sea, connectivity, larval dispersal, biophysical models, marine reserve

INTRODUCTION

The deep sea, although the largest biome on the planet, remained unexplored until the late 19th century (Tyler, 2003) when the cosmopolitan occurrence of deep-sea fauna was established for the first time. Another 100 years of research and technological developments were necessary before the habitat heterogeneity (Ramirez-Llodra et al., 2010), high biodiversity (e.g., Grassle and Maciolek, 1992), and contribution to global ocean processes (Jahnke, 1996) of the deep sea challenged prevailing views and raised new ecological questions (Danovaro et al., 2014). In the last few decades, demand for deep-sea products, such as those from fishing, hydrocarbon extraction, and mining, has been rapidly expanding (Ramirez-Llodra et al., 2011; Thurber et al., 2014), and deep-sea ecologists are asked to provide solutions for the mitigation of exploitation impacts.

Although the deep seafloor includes some of the largest contiguous features of the planet, such as the abyssal plains and the sedimentary slopes of the continental margins (Ramirez-Llodra et al., 2010), many deep-sea populations are spatially fragmented, and may become more so as a consequence of human disturbance during resource exploitation and extraction. Concurrently, one of the main challenges of deep-sea ecology is the elucidation of the processes that lead to connectivity among spatially isolated populations, which would ultimately regulate their persistence and recovery after disturbance (reviewed in Cowen et al., 2007). Differences in population connectivity contribute greatly to the spatiotemporal patterns in the distribution of organisms and must be considered when defining spatial management strategies, including in the design of marine protected areas (MPAs) (Gaines et al., 2003).

Many marine benthic species have complex life cycles that include a pelagic larval stage and sessile/sedentary adults (Thorson, 1964). For these species, the main process that connects populations is larval transport; consequently, the factors that regulate larval dispersal and population connectivity have been receiving increased attention. Although Thorson (1950) predicted that deep-sea animals should brood their young or have direct development, recent analyses show that pelagic lecithotrophy, rather than brooding, is the main reproductive mode in the deep sea (reviewed in Young, 2003). Different approaches have been used to evaluate population connectivity by larval dispersal including: (i) measuring the hydrodynamic and biological processes involved in larval transport (e.g., Jackson et al., 2010; Thurnherr et al., 2011; Mullineaux et al., 2013); and (ii) deriving larval origins and dispersal pathways using genetic or geochemical markers (Levin, 2006; Cowen and Sponaugle, 2009), or a combination of the two (Foster et al., 2012). To achieve a mechanistic understanding of larval transport, the interaction of biological and physical processes on different spatial and temporal scales needs to be elucidated (Cowen et al., 2007). Because sampling over all relevant scales is presently not possible, numerical models that incorporate both physical dynamics and biological traits are increasingly being used to quantify larval transport and assess its role in regulating population connectivity (e.g., Cowen et al., 2006; Siegel et al., 2008; Nolasco et al., 2013). In coastal and shallow areas, such coupled biophysical models have provided information of relevance to decision-makers in determining the spatial arrangement of marine reserves (e.g., Guizien et al., 2012; Treml et al., 2012). However, in the deep sea, this field of research is still in its infancy and fewer than a handful of studies have explored this approach (Lavelle et al., 2010; McGillicuddy et al., 2010; Yearsley and Sigwart, 2011; Young et al., 2012).

Biological parameterization of the biophysical models presents a challenge even in well studied shallow-water systems (Metaxas and Saunders, 2009). Components, such as diel and ontogenetic vertical migration, buoyancy of embryos, mortality, food availability, developmental rate, and physiological tolerances, can play an important role in dispersal patterns, and should be incorporated in biophysical models. However, most of these factors have not been studied for many species, particularly in the deep sea. In contrast, the pelagic or planktonic larval duration (PLD), commonly defined as the developmental period of a species in the water column, has been estimated for a relatively large number of marine fishes and invertebrates (Shanks et al., 2003; Shanks, 2009) and is perhaps the most often cited biological variable potentially affecting population connectivity (Sponaugle et al., 2002). Although the validity of the long-standing hypothesis that species with long larval duration also have greater dispersal potential remains equivocal (Eckert, 2003; Siegel et al., 2003; Weersing and Toonen, 2009), PLD can be used to set an upper bound on dispersal distance (Selkoe and Toonen, 2011).

In this study, we firstly provide an overview of the current efforts in conservation associated with resource extraction in deep-sea seafloor habitats and evaluate the relevance of larval dispersal in the design of marine reserves. Secondly, we review the application of biophysical models to the study of population connectivity in the deep sea, and provide an evaluation of their performance. Lastly, we assess the extent of the current knowledge on PLD for deep-sea species as one of the main biological components consistently included in biophysical models. We then compare the available estimates from the deep sea with those from the closest taxonomic relatives that live in shallow systems to determine whether PLD is taxonomically conserved. Genetic tools have also been used in many studies to estimate dispersal distances and genetic connectivity, which we do not review here. A separate synthesis is underway, focused specifically on genetic-based estimates of deep-sea dispersal distances, including analyses of how different life-history factors may affect these estimates and that compare these estimates with those in shallow water (A. Baco et al in prep). These two syntheses are parallel products of the Population Connectivity working group of INDEEP (International Network of Scientific Investigations of Deep-Sea Ecosystems; www.indeep-project.org/). The ultimate goal is to provide recommendations for obtaining accurate estimates of larval dispersal and population connectivity that can be used on the spatial management of different deep-sea habitats.

USING LARVAL DISPERSAL IN THE DESIGN OF MARINE RESERVES IN THE DEEP SEA

With the depletion of mineral and biological resources on land and in coastal waters, resource extraction has been extending into the water column and the seafloor of the deep sea. Oil and gas have long been extracted offshore, in waters >200 m in depth. The *Deepwater Horizon* blowout in the Gulf of Mexico in 2010 was the largest oil spill in history (in terms of amount of oil spilled) and one that occurred directly on the seafloor of the deep sea. It impacted deep-water coral communities as far as 22 km away from the accident site at depths of 1850–1950 m (Fisher et al., 2014). The presence of some of these communities was unknown until surveys were conducted after the oil spill. The continuous expansion of oil and gas exploration onto the continental margins all around the globe is greatly enhancing the threat for similar accidents and impacts. Deep-water fishing has been occurring since the late 1950s but developed into a commercial industry in the last 40 years. The impact of bottom trawling on both deep-sea fish and benthic communities has been highlighted by a number of studies (Koslow et al., 2000; Bailey et al., 2009), and growing concern has resulted in recent proposals for a ban on deep-sea bottom trawling in European waters. An emerging potential pressure on the seafloor is through the development of deep-ocean industrial mining, which is rapidly gaining momentum. Deep-sea mining will potentially encompass polymetallic nodules in the abyssal plains, deposits of seafloor massive polymetallic sulfides (SMS) from hydrothermal vents, cobalt crusts from seamounts, among others. As of mid-2014, the International Seabed Authority (ISA) had granted 16 exploration contracts in the Atlantic, Pacific and Indian Oceans, covering all three types of resources (ISBA, 2014). However, deep-sea mining will occur both in national and international jurisdictions, and the laws and regulations that will apply to the industry are currently still under development.

Although the extraction methods can potentially be highly destructive, the spatial and temporal scales of their impact are not known. Additionally, both the biological communities and the drivers that regulate these communities are mostly unknown, particularly in the abyssal plains, but even at some of the hydrothermal vents and seamounts currently being targeted for exploration. A high probability of endemicity at some of these locations further underscores the potential impact of unfettered anthropogenic activities on these largely undescribed ecosystems. For these reasons, a recent call for the precautionary approach in the management of human activities in the deep sea includes plans for protection of the ecosystems, research to increase knowledge, and governance collaboration across sectors (Mengerink et al., 2014).

The strategies being considered for spatial management and protection in the deep sea are based on our existing practices from shallow waters: MPAs or other marine reserves partially or fully restricting certain human activities (Halpern, 2003). The spatial arrangements of marine reserves can vary from a single reserve to a network of many reserves within a habitat or region, but the target is usually a subset of habitats (or species) in a region (Hastings and Botsford, 2003; Sale et al., 2005). The selection of the subset of habitats to be protected is based on how representative they are within the region of interest, their uniqueness or rarity, their vulnerability to potential threats or presumed slow recovery from disturbance, whether they support high biodiversity or high productivity, or whether they are a key habitat for a particular stage in the life-history of species, particularly if the latter is threatened or endangered (CBD, 2007). Many of these selection criteria apply to habitats in the deep sea, particularly their vulnerability and presumed slow recovery from perturbation and high biodiversity (e.g., the abyssal plains), uniqueness (e.g., hydrothermal vents) and importance to certain life-history stages (e.g., seamounts). For a network of marine reserves or MPAs, additional criteria apply, such as maximizing connectivity between individual MPAs and maintaining viable populations across the network. These last two criteria are closely linked, particularly in spatially fragmented populations where persistence of a population will depend on either sufficiently large local replenishment in a single patch or, in its absence, sufficiently strong connectivity among patches in a network (Burgess et al., 2014). Since larval dispersal influences population connectivity (Cowen and Sponaugle, 2009), knowledge of the magnitude and pathways of dispersal can be critical elements in the design of effective marine reserves.

The concept of marine reserves in the deep sea in the face of potentially heightened exploitation is increasingly gaining support. An example from areas under international jurisdiction include an environmental management plan for the Clarion-Clipperton Zone (CCZ), generated by the International Seabed Authority (ISA) in which the Authority acknowledges its responsibility to afford effective protection of the environment from harmful effects of prospecting, exploitation and exploration activities (ISBA, 2011). The conservation objectives were to maintain regional biodiversity, ecosystem structure and ecosystem function across the CCZ, manage the CCZ consistently with the principles of integrated ecosystem-based management, and enable the preservation of representative and unique marine ecosystems. Based on environmental and ecological data, which included (presumed) faunal dispersal capabilities and distances, the ISA recommended the allocation of 9 areas of environmental interest, within each of 9 biogeographic subregions, each 400 × 400 km (a 200 × 200 km core area surrounded by a 100-km buffer zone) (ISBA, 2011; Wedding et al., 2013). The size of each area was presumed to be sufficient for each to maintain viable populations of species potentially restricted to a sub-region. Assessing the viability of a population requires the combined estimates of larval retention, reproductive output of the population, and population size at minimum (Burgess et al., 2014); this information largely did not exist when ISA made its recommendations. Further examples of marine reserves in the deep sea include the OSPAR network of MPAs in the North East Atlantic (OSPAR, 2003) as well as bottom trawl closures on the Mid Atlantic Ridge and various seamounts for the protection of vulnerable marine ecosystems (NEAFC, 2011). Within national jurisdiction, a few MPAs (or a national monument in the case of the US) have been established for the protection, at least in part, of deep-sea hydrothermal vents and they include the Endeavor Segment (Canada), the Marianas Trench region (USA), the mid-Atlantic Ridge off the Azores (Portugal), and the Guaymas Basin and Eastern Pacific Rise (Mexico). In addition, particularly within Europe and the USA, a number of MPAs have been established for the protection of vulnerable deep-sea habitats, principally cold water corals and deep-sea sponges. Generally, the conservation objectives and management plans of these align with those agreed upon in the Convention of Biological Diversity. As in the example with the CCZ, for all of the national MPAs, the information required to assess population connectivity and viability was weak to non-existent.

Recommendations on the spatial management through marine reserves have also been made by the scientific community directly. For example, the Dinard workshop, attended by stakeholders from various sectors and 14 countries provided a clear set of guidelines for setting up reserves in chemosynthetic environments (Ardron et al., 2011; Van Dover et al., 2012). The proposed design followed the same criteria as recommended for shallow water MPAs, including "ensuring connectivity" among reserves (Van Dover et al., 2012). Clark et al. (2014) assessed how each of the criteria for the selection of Ecologically and Biologically Significant Areas (EBSAs), described above in the context of MPAs, can be applied to deep-sea ecosystems, and provided a test case on seamounts in the Pacific Ocean. Other studies have addressed the management requirements and have made recommendations for conservation specifically with respect to mining SMS deposits, cobalt-rich crust regions on seamounts and manganese nodules in abyssal plains (Boschen et al., 2013; Wedding et al., 2013; Schlacher et al., 2014). Boschen et al. (2013) recommended the establishment of "preservation reference zones" during SMS mining, including upstream set-asides that can supply colonizing larvae, in addition to preserving an unimpacted section of the population. Wedding et al. (2013) provided a systematic framework for conservation in abyssal plains, including the incorporation of design principles utilized in shallow water, such as ecosystem-based management and networks of MPAs. The concepts of realized dispersal distances and the size of each MPA in the network, particularly as they relate to population viability, were addressed in the framework (Wedding et al., 2013).

While spatial planning is gaining attention in the context of deep-sea resource extraction, the data to support decisions are scarce. Classification systems of deep-sea habitat are being developed on which the criteria of representation of habitats within MPA networks may then be assessed (Howell, 2010; Howell et al., 2010), and species-area relationships have been used to inform baseline conservation targets for the deep North East Atlantic (Foster et al., 2013). Although recent science-based studies have started to address their relevance to the conservation of potentially vulnerable ecosystems in the deep sea (e.g., Rengstorf et al., 2013; Ross and Howell, 2013; Jackson et al., 2014; Nakajima et al., 2014), studies designed specifically to collect relevant data are still lacking. In addition to the attention being recent, the logistical constraints in collecting data from a remote environment, such as the deep sea, are great. Data on larval dispersal and population connectivity that are purported to be relevant in the design of marine reserves are particularly difficult to obtain, even in the more accessible shallow-water ecosystems (Burgess et al., 2014). Numerical models are one promising approach allowing the calculation of dispersal matrices under different scenarios, and their performance can be progressively improved with gaining biological and physical information.

APPLICATIONS OF BIOPHYSICAL MODELS TO LARVAL DISPERSAL

Lagrangian particle tracking methods, traditionally employed by atmospheric scientists and oceanographers, can be used to simulate the release of passive particles to track the fate of the advected drifters in the ocean. These passive drifters can be used to represent theoretical larvae in order to identify likely dispersal pathways, highlighting the oceanographic mechanisms and barriers to dispersal (Werner et al., 2007). Particles can also be given “behavior,” simulating swimming abilities such as diel vertical migration or ontogenetic buoyancy properties, to adjust predictions where dispersal is likely not passive (Levin, 2006; Werner et al., 2007).

Many of the biological parameters (e.g., planktonic larval duration, larval buoyancy, mortality over time, vertical migration, settlement probability, settlement behavior) included in the biophysical models cannot be estimated at this time for marine benthic species (in shallow or deep waters) (Metaxas and Saunders, 2009). Where these data are available, they may alter estimates of connectivity (Cowen et al., 2000). Many tracer parameters require data derived from biological traits, such as number of particles released (fecundity), particle release depth (spawning location), and particle tracking time (planktonic larval duration). The accuracy in these tracer characteristics along with rate of particle loss from the system (mortality) and “behavior” is the challenge that biologists face when they attempt to predict and validate dispersal pathways (Metaxas and Saunders, 2009).

Biophysical models can be applied over a variety of time scales (Levin, 2006) and studies based on contemporary time scales can provide insight into current metapopulation management and demographic dynamics (Cowen and Sponaugle, 2009). Modeling can be used to define the average route and distance of dispersal paths from a release site (Cowen et al., 2007; Cowen and Sponaugle, 2009; Kool et al., 2013) and provide retention estimates and, thus, inform MPA networks (Paris and Cowen, 2004; Treml and Halpin, 2012). Most modeling studies are used to explore the effect of physical drivers on dispersal (Martins et al., 2010; Blanke et al., 2012; Soria et al., 2012; Young et al., 2012) but, in a system where knowledge of life-history traits is lacking, null models can test the effects of behavior on dispersal (Paris et al., 2007, 2009; Carr et al., 2008; Sundelöf and Jonsson, 2012), the relationship between PLD and dispersal ability (Siegel et al., 2003; Young et al., 2012), and the role of other abiotic/biotic factors in dispersal (Ayata et al., 2010; Martins et al., 2010; McGillicuddy et al., 2010; Treml and Halpin, 2012). The ability to run a model both forwards and backwards in time also allows for the prediction of both sources and sinks of propagules (Brickman et al., 2009). Results from these modeling efforts can then be compared to empirical data for biological validation (e.g., Foster et al., 2012), while also being used to constrain dispersal estimates within an ecological timeframe.

Because of the paucity of data on life histories of deep-sea fauna as well as deep-sea circulation, accurate modeling and precise validation are not feasible at this point. Basic models, which exclude life-history data can provide estimates of the bounds of dispersal ranges for future validation and hypothesis generation. Studies on population connectivity in the deep sea may benefit from biophysical modeling more than in shallow environments, given the inherent barriers of accessibility, scale and expense associated with the collection of samples. However, sampling is still required for validation of models and predictions.

CHOOSING PHYSICAL MODELS FOR DISPERSAL STUDIES IN THE DEEP SEA

Horizontal dispersal of planktonic propagules, such as larvae, is primarily passive, i.e., the greatest component of displacement is through advection by the oceanic velocity field. If the velocities are known across all scales of interest, dispersal reduces to a problem of advection. If, as is usually the case, knowledge of the velocity field is incomplete, the effects of the unknown velocities must be parameterized somehow. Often, the unresolved velocities are modeled as random-walk processes (e.g., Berg, 1993), which cause down-gradient fluxes proportional to the spatial gradients (Fickian diffusion), leading to advection-diffusion models.

There is a hierarchy of techniques that has been used to infer bounds on planktonic dispersal in the deep sea using advection-diffusion models, with the simplest ones being either purely advective or diffusive. The simplest advective model uses a representative “mean” velocity together with PLDs to estimate a dispersal distance (e.g., McClain and Hardy, 2010). As this model ignores both spatial and temporal variability in the velocity field, the relevance of the resulting estimates is restricted to temporal and spatial scales over which the circulation can be considered steady and homogeneous. On time scales that typically range from weeks to months and even years, horizontal dispersal across most of the deep ocean is either dominated or strongly affected by eddy diffusion (Speer et al., 2003), implying that advection-by-mean-flow models are not appropriate. Another simple technique that has sometimes been used to estimate dispersal distances is based on progressive vector diagram (PVDs) derived from Eulerian measurements (e.g., Marsh et al., 2001). While temporal variability of the velocity field is included in this method, spatial variability is not, restricting the relevance of the resulting estimates to the scales of the processes that dominate the velocities, such as eddies, Rossby waves, equatorial jets, and boundary currents. In particular near sloping topography (continental slopes, seamounts, mid-ocean ridges, etc.), the spatial scales of subinertial oceanic flows are often on the order of kilometers (e.g., Brink, 1995; Cannon and Pashinski, 1997; Stahr and Sanford, 1999; Thurnherr and Richards, 2001; McGillicuddy et al., 2010; Thurnherr et al., 2011), limiting the use of PVDs to temporal and spatial scales of days and 10 s of kilometers at most.

Given the difficulty of observing the velocity field in the deep ocean across a wide range of spatial and temporal scales, numerical ocean general circulation models (OGCMs) are often the only viable option for obtaining the velocities that are required to study larval dispersal. However, it is unlikely that all physical processes will be captured in a single OGCM: their greatest inadequacies are in relation to the processes occurring at the fine spatial and temporal scales which are of greatest relevance to a larva (Metaxas and Saunders, 2009). For example, Lacroix et al. (2009) suggested that a 3-km grid is required to resolve a 20-km eddy indicating the intensity of data coverage required to resolve sub-mesoscale and small scale processes. Because of the small scales involved, modeling the circulations near topography often requires dedicated regional models with high spatial and temporal resolution (e.g., Proehl et al., 2005; Mitarai et al., 2009; Lavelle et al., 2010; McGillicuddy et al., 2010), which can be hard to source. As even the highest-resolution regional models cannot resolve the small scales associated with mechanical turbulence, the effects of sub-gridscale processes on dispersal should be parameterized, in particular when vertical dispersal is to be investigated (e.g., Proehl et al., 2005).

Modeling of vertical dispersal requires sufficient vertical resolution in the velocity fields. The vertical resolution of most "general-purpose" models is typically quite coarse below the thermocline, where the vertical gradients of temperature and salinity, and the corresponding diffusive fluxes, tend to be small. Such models are less suitable for simulating vertical dispersal of tracers and propagules that are associated with strong vertical gradients, such as larvae released at the seabed, which set the diffusive vertical fluxes between adjacent grid cells or isopycnal layers. Within a grid cell or layer, diffusive vertical dispersal in a numerical model is instantaneous due to the standard assumption that any particles contained within a cell are distributed uniformly across its volume. In reality, it may take ∼a year for a tracer sheet to diffuse across a vertical distance of 100 m in the deep ocean, away from the immediate vicinity of topography (Ledwell and Watson, 1991; Ledwell et al., 1993, 2011). As a result, simulated vertical dispersal of propagules can be much more rapid than in the real ocean, even in models with accurate diffusive fluxes of heat, salt, oxygen, nutrients, etc. It is noted that fine vertical resolution is typically also required to simulate the small scales associated with the topographic flows discussed above. Such inaccuracies in this advective/diffusive vertical dispersion parameter will be exacerbated if any biological parameters are also used to modify vertical position within a model (e.g., buoyancy or vertical swimming behavior), so care must be used to minimize or acknowledge the error here.

Another important consequence of unresolved sub-gridscale processes in numerical models is that validation with velocity measurements is difficult, as the model velocities represent spatial averages over grid cells. As a result, direct comparisons between observed and modeled velocity time series often show sizable differences, even for high-resolution regional circulation models that have considerable skill in predicting dispersal as validated, for example, with tracer-release experiments (e.g., Proehl et al., 2005; Lavelle et al., 2010; McGillicuddy et al., 2010). In general, Lagrangian data from tracer and dye release experiments, and from float and drifter trajectories are more suitable for validating the dispersal characteristics of a model than Eulerian velocity measurements, because they integrate the effects of all processes affecting dispersal, regardless of their scales. While Lagrangian experiments are expensive and difficult to carry out, especially in the deep ocean, there are data available from previous and ongoing deep tracer-release experiments (e.g., Ledwell and Watson, 1991; Ledwell et al., 1993, 2000, 2011; Jackson et al., 2010) and float studies (e.g., Hautala and Riser, 1993; Hogg and Owens, 1999; Argo data http://www.argo.ucsd.edu/) that can be used to validate the dispersal characteristics of large-scale circulation models, at least in some regions of the deep ocean.

The choice of an appropriate OGCM, including subgridscale parameterizations, is key in the process of model parameterization. It should be recognized that OGCMs are generally not designed explicitly to estimate larval dispersal. Consequently, a model designed (and validated) to represent global thermohaline circulation may perform less well within particular regions (Fossette et al., 2012). Further complications arise in the choice of particle tracer. Online particle tracers run natively within the OGCM utilizing the full resolution model output to infer advection and diffusion, but access and computational restrictions can become prohibitive for repeated runs (North et al., 2009; Fossette et al., 2012). Offline particle tracer models (Supplementary Table 1) use outputs from OGCMs, with both the offline models and OGCM outputs being more accessible. However, outputs from temporally and spatially highly resolved OGCMs are often averaged to lower resolutions to reduce the required storage capacity. This averaging can in turn reduce the resolution of captured hydrographic phenomena, e.g., de-trending tides and smoothing eddies, potentially resulting in erroneous trajectory predictions (Putman and He, 2013). Sensitivity analyses can be very informative in terms of the limitations and predictive ability of an OGCM/particle tracer coupling, and can assist in model choices and discourage "black box" model usage (Simons et al., 2013). Coupled with study specific validation, sensitivity analysis is an advisable step prior to settling upon model choice and asking questions of dispersal (North et al., 2009).

PARAMETERIZING THE BIOLOGY FOR BIOPHYSICAL MODELS IN THE DEEP SEA: THE ROLE OF PLANKTONIC LARVAL DURATION

Most marine benthic species exhibit a biphasic life cycle, which includes a pelagic larva, but there are exceptions such as pericarid crustaceans and nematodes that have direct development. Hence, models of the distribution of benthic organisms typically incorporate species-specific biological parameters that account for this potentially dispersive larval phase. The most frequently utilized is the PLD during which larvae are susceptible to physical mixing and advection (Sponaugle et al., 2002; Treml et al., 2008). In spite of its reference to larval development, values of PLD provided in the literature often encompass the entire development between egg release and settlement, although such data would be best described as planktonic propagule duration (PPD; embryonic + larval phase). Because embryos (to late gastrula) may differ from larvae in physical properties (e.g., shape, buoyancy) and swimming capacity, a true PLD (restricted to the larval phase) may be distinguished from PPD, where such data are available (e.g., Brooke and Young, 2009; Selkoe and Toonen, 2011; Mercier et al., 2013). A clearer distinction enables the inclusion of passive vs. active dispersive phases (e.g., egg/embryos vs. larvae), as well as transient planktonic phases in species that undergo parental care or demersal development for a portion of the embryonic or larval phases (e.g., certain gastropods, polychaetes and anthozoans).

Taken as the length of the planktonic phase, PLD has long been a central variable of biophysical models (Sponaugle et al., 2002; Lett et al., 2010; Liggins et al., 2013). The simplest models assume that pelagic propagules are passive and that population connectivity is therefore inversely related to PLD (e.g., in reef fishes; Roberts, 1997). However, the strength of the relationship between PLD and dispersal is being debated (Paulay and Meyer, 2006; Strathmann, 2007; Shanks, 2009; Weersing and Toonen, 2009; Selkoe and Toonen, 2011; Mercier et al., 2013). The emerging view is that dispersal is not only determined by the length of the planktonic phase, but also by circulation processes (e.g., Watson et al., 2010) and larval behavior (e.g., Metaxas and Saunders, 2009; Shanks, 2009; Butler et al., 2011). Hence, the use of PLD in combination with other biological variables is now gaining favor in designing biophysical models of species recruitment and population connectivity (Sponaugle et al., 2002; Levin, 2006; Fiksen et al., 2007; Gilbert et al., 2010; Domingues et al., 2012; Treml et al., 2012; Kough et al., 2013; Nicolle et al., 2013; Nolasco et al., 2013). Fine predictions tend to include many biotic variables. For instance, the LARVAHS model proved to be effective at estimating recruitment success in clams, emphasizing the role of PLD, as well as habitat suitability, larval swimming behavior, wind patterns (seasons), spawning ground location and tidal phase at spawning (Bidegain et al., 2013). Nevertheless, simpler models can be relatively robust. A recent study of invertebrate and fish larvae showed that PLD and depth distribution explained 80% of total variation in dispersal distance, whereas spawning season, and geographic and annual variations in circulation had only marginal effects (Corell et al., 2012). Conversely, differences in reproductive seasons were determined to drive opposite source-sink dynamics in two congeneric mussel species (Carson et al., 2010). Testing various idealized larval behaviors also supported the role of vertical swimming/migration during planktonic development as a key determinant of nearshore settlement site (Drake et al., 2013).

While it may be desirable, the inclusion of several biotic variables, particularly behavioral traits, is generally more difficult for deep-sea than for shallow-water species. Even obtaining reliable estimates of PLDs can present a challenge; however, the coupling of PLD with oceanographic data can provide estimates of the upper bounds of dispersal distances (Young et al., 2012). To date, PLDs have been estimated for deep-sea species using four different methods: (1) larval culture in the laboratory, which presents several challenges in terms of maintaining appropriate rearing conditions, or in the field which may not allow for the completion of the life cycle; (2) computation of PLD from metabolic rates and available energy stores, which is valid only for lecithotrophic larvae; this approach also requires knowledge of the relationship between temperature and metabolic efficiency that for most deep-sea species can only be assumed; (3) tracking of larval cohorts in the plankton, an approach only possible for species with discrete spawning periods; and (4) calculation based on the timings of settlement and spawning times, which also may require back-calculation of settlement time using juvenile growth rates, seldom known for deep-sea species.

ANALYSIS OF EXISTING DATA ON PLANKTONIC LARVAL DURATIONS IN THE DEEP SEA

We assessed the current knowledge on planktonic larval durations (PLD) for deep-sea species and compared the available estimates with those from shallow-water species, using published observational and experimental PLD values for 305 species belonging to seven marine benthic phyla (**Table 1**, Supplementary Data): Cnidaria (12), Annelida (25), Sipuncula (1), Mollusca (31), Arthropoda (68), Echinodermata (167), Chordata (1). When multiple PLD values were available in the literature for the same species, only the minimum and maximum values were kept for analyses and used to calculate the median PLD; when only one value was available in the literature that value was used as minimum, maximum and median in all analyses.

Species were classified according to their bathymetric distribution into shallow (0–200 m), eurybathic (0–>200 m) and deep (>200 m). In total, PLD estimates were available for 212 shallow, 72 eurybathic and 21 deep-sea species (**Table 1**). Eurybathic—living below 200 m and deep-sea species were further categorized according to their habitat (**Figure 1**). The relatively high number of species from the sedimentary slope (excluding other specific sub-habitats found on slopes such as cold-water corals, cold seeps;

Table 1 | Number of species for which PLD has been estimated.

	Total	Cnidaria	Annelida, Polychaeta	Sipuncula	Mollusca	Arthropoda, Crustacea	Echinodermata	Chordata,Tunicata
Shallow	212	6	20	0	27	48	111	0
Eurybathic	72	3	1	0	2	14	52	0
Deep	21	3	4	1	2	6	4	1

$N = 75$), for which the PLD has been investigated is the result of numerous reproductive studies on echinoderms with a eurybathic distribution ($N = 52$); echinoderms are the best-studied group of deep-sea animals in terms of reproduction (Young, 2003) and are the taxonomic group for which many PLD values are available. Apart from these, PLD from species living below 200 m depth has been investigated mostly for polychaetes, molluscs, and crustaceans from chemosynthesis-based habitats (hydrothermal vents and cold seeps, $N = 12$) since questions related to how these insular and ephemeral habitats are maintained and new sites colonized by larvae have been of much interest in recent decades (Tyler and Young, 1999; Metaxas and Kelly, 2010). We examined differences in PLD among shallow, eurybathic and deep species (available values pooled within each of these three categories) with a Kruskal-Wallis test, followed by Dunn's multiple comparisons using the statistical software GraphPad Prism (version 6.0).

The ranges in minimum, maximum and median PLD were quite wide for all three bathymetric distributions (**Table 2**). Statistically significant differences were found between shallow and both eurybathic and deep species; PLD values of eurybathic and deep-sea species were not significantly different from one another (**Table 3**). Overall, shallow-water species present shorter PLD than eurybathic and deep species (**Figure 2**, **Table 2**).

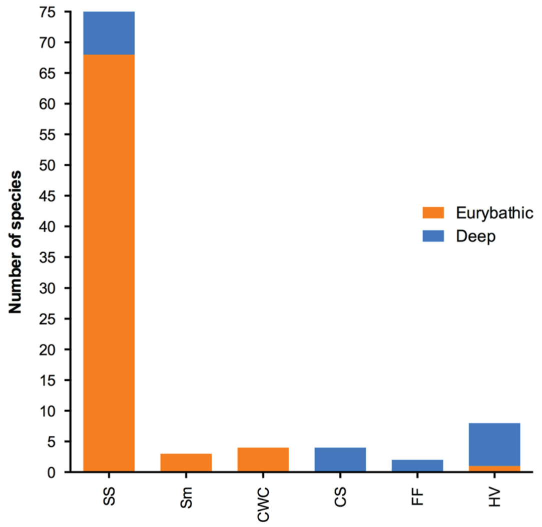

FIGURE 1 | Number of deep-sea and eurybathic species for which PLD has been estimated in different deep-sea habitats (SS, sedimentary slope; Sm, seamounts; CWC, cold water coral; CS, cold seeps; FF, food falls; HV, hydrothermal vents).

PLD estimates have been included in biophysical models to set boundaries on dispersal distances of individual species. However, in the context of spatial planning, connectivity is often not considered for single species, but rather between different areas. Models can estimate the durations that would be required to connect particular metapopulations; however, in most cases there is insufficient data on the distribution of deep-sea species to use this methodology. An alternative approach would be to incorporate in the models a PLD value that guarantees a minimum dispersal distance for a wide range of species. Based on the existing data, we propose that a PLD of 35 and 69 days ensures a minimum distance for 50 and 75%, respectively, of the eurybathic and deep-sea species in our study (**Figure 3**). Despite its potential utility, the paucity of data points and the high variability in PLD between and within taxonomic groups underscore the limitations of our proposal.

The current knowledge on the PLD of deep-sea species is scarce and unevenly distributed between habitats and taxonomic groups (**Figure 4**), limiting generalizations that are often appealing to decision-makers. More data on the larval ecology is undoubtedly necessary to develop effective conservation strategies for deep-sea habitats and species. Nevertheless, the few biophysical models integrating estimates of larval duration have already generated important information to understand dispersal and connectivity in the deep sea (e.g., Marsh et al., 2001; Yearsley and Sigwart, 2011; Young et al., 2012).

USING BIOPHYSICAL MODELS TO PREDICT DISPERSAL IN THE DEEP SEA

Only a handful of studies have attempted to model larval dispersal in the deep sea, and most of these have been limited by the availability of reliable estimates of biological parameters, including planktonic larval duration, spawning season, and dispersal depth. Consequently, most modeling exercises to date have been experiments that attempt to identify the biological values required to produce a given distributional or genetic pattern. In one of the earliest such studies, Chevaldonné et al. (1997) used a particle flux model to estimate the magnitude of dispersal required by larvae of

Table 2 | Descriptive statistics of the available minimum, maximum and median PLD values (days) for shallow ($N = 212$); eurybathic ($N = 72$) and deep species ($N = 20$; the value of 660 days determined for *Sclerasterias tanneri* was not included).

	Shallow			Eurybathic			Deep		
	Min.	**Max.**	**Median**	**Min.**	**Max.**	**Median**	**Min.**	**Max.**	**Median**
Range	0.17–293	0.17–293	0.17–293	1–167	5–167	3–167	1–240	10–420	10–315
Mean	25	30.35	27.68	43.13	53.26	48.14	73.40	119.9	96.63
St. Dev.	27.85	30.35	28	34.93	37.87	35	76.87	112.0	85
Median	18.00	24.00	22.75	33.50	46.50	42.00	44.50	94.00	66.25
Q_{25}	8.25	13.25	11.63	19.25	21.00	21.00	12.50	39.00	30.13
Q_{75}	33.75	40.75	36.38	64.00	78.75	74.75	120.0	151.8	143.3

Table 3 | Results of the Kruskal-Wallis and Dunn's multiple comparison tests used to investigate differences of minimum, maximum and median values between shallow, eurybathic and deep species.

	Kruskal-Wallis		Dunn's multiple comparison					
			Shallow vs. Eurybathic		Shallow vs. Deep		Eurybathic vs. Deep	
	K	*p*	Mean rank diff.	*p*	Mean rank diff.	*p*	Mean rank diff.	*p*
Min. PLD	24.39	<0.0001*	−53.00	<0.0001*	−58.18	0.0139*	−5.182	>0.9999
Max. PLD	43.93	<0.0001*	−58.10	<0.0001*	−106.7	<0.0001*	−48.46	0.0865
Median PLD	40.39	<0.0001*	−57.43	<0.0001*	−99.47	<0.0001*	−42.04	0.1753

**indicates statistically significant differences. The value of 660 days determined for Sclerasterias tanneri was not included.*

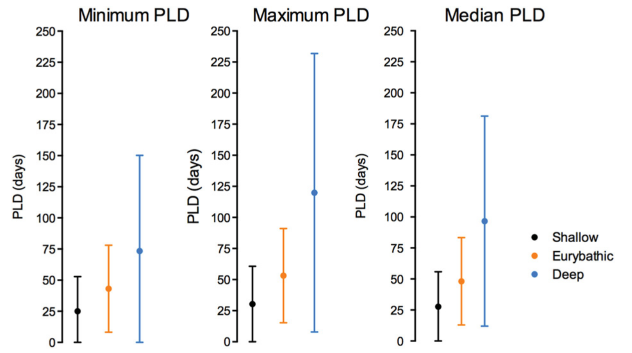

FIGURE 2 | Mean and standard deviation of minimum (left), maximum (middle) and median (right) PLD values for shallow, eurybathic and deep-sea species. The value of 660 days determined for *Sclerasterias tanneri* was not included.

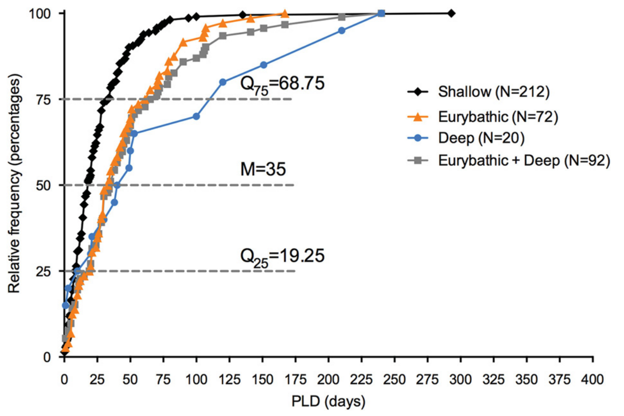

FIGURE 3 | Histogram of frequency of minimum PLD estimates available for shallow, eurybathic and deep-sea species. Median, percentile 25 and 75 are shown for PLD values of eurybathic and deep-sea species pooled together. The value of 660 days determined for Sclerasterias tanneri was not included.

the vent worm *Alvinella pompejana* to reach known vent sites on the East Pacific Rise (EPR). Short PLDs and lecithotrophic development were assumed based on circumstantial evidence, and the resulting simulations did not agree with an observed absence of genetic structure over large spatial scales. To explain the absence of genetic structure, the authors invoked spatially variable and frequent geological events, rather than the possibility that dispersal times were longer than assumed. Subsequent embryological studies with the same species (Pradillon et al., 2001, 2005) suggested a mechanism of developmental arrest at cold temperatures that could easily reconcile the genetic data with model predictions and confirming that lecithotrophic development does not necessarily result in short PLD (e.g., Shilling and Manahan, 1994).

Using progressive vector models based on Eulerian current measurements during a single year, Marsh et al. (2001) predicted the dispersal potential of the vent tubeworm *Riftia pachyptila* on the EPR. Reliable estimates of PLD were based on laboratory and *in situ* larval rearing, as well as metabolic measurements predicting the depletion rate of internal lipid stores. The models predicted peak dispersal distances at ~103 km, with high cumulative mortality by the terminal (presumably competent) larval stages. In a subsequent study, Brooke and Young (2009) showed that *R. pachyptila* disperse as unciliated embryos for the first 3 weeks of their 5-week development. If this observation is superimposed on the mortality schedule estimated by the simulations of Marsh et al. (2001), one must conclude that more than half of the individuals are lost from the vent system before they even become larvae. Brooke and Young (2009) also showed that ontogenetic migration by this species is limited by larval tolerance to the warm temperatures and low pressures that prevail in the shallower depths of the water column. The progressive vector approach of Marsh et al. (2001) was extended from 9°N to 13°N on the EPR by Mullineaux et al. (2002) who estimated dispersal distances for theoretical larvae with both shorter and longer PLDs than those determined empirically for *Riftia pachyptila*.

The dispersal of simulated larvae from hydrothermal vents as either passive particles or "balloonists" that migrate ontogenetically to and from the upper water column was modeled by McGillicuddy et al. (2010). The model was both driven and validated with data from moored current meters and particle trajectories based on larval releases every 12 min in all seasons of the year. The model assumed a 30-day dispersal period as predicted by Marsh et al. (2001) for *Riftia pachyptila*. This modeling exercise yielded several important conclusions, including the observation that larvae released at the crest of the EPR dispersed greater distances near the sea floor than higher in the water column. This result suggests that ontogenetic migration is not a viable strategy for increasing dispersal in this system and is in agreement with the physiological tolerances reported by Brooke and Young (2009).

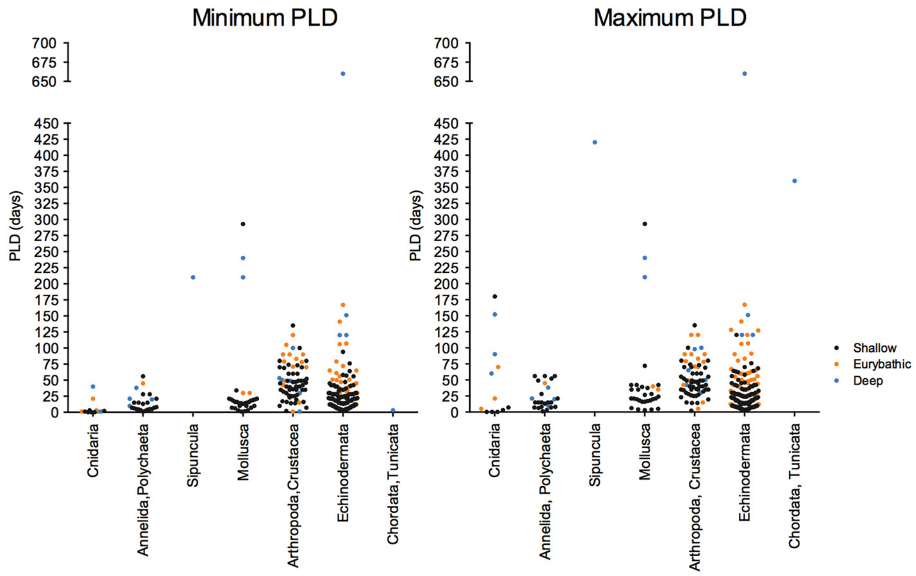

FIGURE 4 | Minimum (left) and maximum (right) PLD values available for shallow, eurybathic and deep-sea species of the different invertebrate phyla.

McGillicuddy et al. (2010) explained this pattern with reference to observed vigorous along-flank flows and high flow variability near the ridge axis, but were not able to test these hypotheses empirically with their moored current meter data. Another important conclusion was that the likelihood of successful settlement varied significantly with time of year. Larvae "released" in early summer were much less likely to find themselves near a suitable settlement site than ones released in winter. Lastly, the model showed that the period of precompetency may play a highly significant role in successful dispersal. As predicted by Jackson and Strathmann (1981), larvae that spend a higher percentage of their time being able to undergo metamorphosis will be more likely to encounter suitable habitat during that period. In the case of *R. pachyptila*, however, the developmental observations (Marsh et al., 2001; Brooke and Young, 2009) indicate that metamorphic competency is not attained until the very end of larval life.

In non-chemosynthetic habitats of the deep sea, Yearsley and Sigwart (2011) used a biophysical model to estimate connectivity among known populations of deep-sea chitons in archipelagos of the Southwest Pacific. Because there were no biological parameters available for any of the species examined, the models were based on several assumptions inferred from shallow-water species with known larval development. Because all known chitons from shallow water have lecithotrophic development, it was reasonably assumed that deep-water species would have the same developmental mode. Planktonic larval duration is unknown for any deep-sea chiton, and this important parameter was extrapolated from known shallow-water PLDs at relatively high temperatures. The assumption that the temperature/PLD curve is the same for shallow- and deep-water species is untested for this group and, based on observations in echinoderms and other phyla, may be unwarranted (Young, unpublished data). It was also assumed that dispersal occurred at approximately the same depth as where the adults are found. The observed dispersal kernels were likely too small to maintain connectivity among known populations within a single generation, suggesting the existence of additional undiscovered metapopulations that serve as stepping stones. The accuracy of the biological parameters used is questionable in the absence of empirical data, but because the authors intentionally overestimated dispersal by adding in a pre-larval dispersal phase of 50 days, the major conclusion may be robust.

A recent study used Lagrangian (LTRANS) modeling with regional ocean models system (ROMS) to predict dispersal trajectories of larvae with known PLD, either obtained from larval rearing studies or estimated indirectly from other types of biological data (Young et al., 2012). Dispersal trajectories were estimated for seven cold seep and non-seep species at each of two depths, originating from known adult locations off Barbados, in the Tongue of the Ocean Bahamas, and at seeps in the Gulf of Mexico. Planktonic larval durations ranged from 21 days in cold-seep tubeworms (*Lamellibrachia luymesi*) to nearly 2 years in bipinnaria larvae of the asteroid *Sclerasterias tanneri*. For those species with long PLDs, the models showed significantly greater dispersal at 100 m depth than at 500 m depth, although the actual ontogenetic movements are unknown for all species. For some species, simulations were run more than once a year, revealing highly significant temporal effects in dispersal distance and underscoring the importance of spawning time. Data on PLD had been measured for two Bahamian echinoids, *Stylocidaris lineata* and *Cidaris blakei* (Bennett et al., 2012), and an extended larval life had been documented for the sea star, which provided a conservative estimate of dispersal time. PLD also had been estimated for the tubeworm (Young et al., 1996) on the basis of larval rearing. For the other species, PLD had to be estimated from indirect methods. Based on data on the timing of spawning and seasonal recruitment, and on *in situ* growth rates of juveniles of *Bathymodiolus childressi* (Arellano and Young, 2009), settlement times of individuals were back-calculated. The number of days since the previous spawning peak to settlement was then determined as the PLD. A similar method was used for the sipunculan *Phascolosoma turnerae*, known to have a strongly seasonal spawning peak and for which a growth curve had been generated for laboratory-reared juveniles (Rice et al., 2012). Two species of seep molluscs, *Bathymodiolus childressi* and *Bathynerita naticoidea*, were collected in the water column during some seasons of the year. Because gametogenic cycles had already been documented for both species, it was possible to infer the approximate ages of the plankton-collected larvae to assist with the estimation of PLD.

The study of Young et al. (2012) demonstrates the value of incorporating various types of biological measurements into the estimation of dispersal distances. A major shortfall of this and all other deep-sea dispersal models is the absence of information on dispersal depth as determined by actual vertical distributions in the plankton (Arellano et al., 2014), or estimated by swimming speed, egg buoyancy, direction of swimming, and physiological tolerances.

MAIN DATA GAPS FOR ESTIMATING CONNECTIVITY IN THE DEEP SEA

Estimating connectivity in marine ecosystems requires the understanding of the biological and physical processes regulating larval dispersal, settlement and recruitment, which is hindered by the small size of larvae coupled with the vast and complex fluid environment. In the deep sea, the problem is magnified because of inherent barriers of accessibility and sampling constraints. Biophysical modeling approaches, an established technique in marine connectivity research, which incorporate key physical dynamics and biological traits, provide a partial solution to this problem. In the deep sea, however, knowledge gaps in both the physical and biological components are delaying the effective use of finely tuned biophysical models.

The physical components of biophysical models are limited by scale and computational capacity. Large scale processes are well understood and parameterized within model equations, but submesoscale ocean physics is an ongoing area of research. In any case, the phenomena at the small scales relevant to a larva are prohibitively expensive to parameterize within a large spatial scale model. For this reason, a sub-gridscale parameterisation is usually considered an adequate enough approximation for most purposes although this is difficult to estimate in itself. There are additional conflicts of resolution, such as poorly represented topography, and consequential flow modifications, that result from low resolution in bathymetry data. The best high-resolution models rely upon high quality bathymetry which is costly to acquire over large spatial scales, particularly at great depth and distance from shore. Accurate model performance requires the assimilation of and validation by high resolution observational data over large temporal and spatial scales.

Vertical velocity remains the most elusive component of both observed and modeled velocity fields, often reduced to secondary calculation in line with the conservation of energy. Without improved understanding of vertical velocities, the potential for passive vertical migration of larvae also remains elusive. In the end, numerical models should be taken for what they are—simplified approximations of reality offered as a best guess of average hydrographic conditions in the area concerned.

Biological processes that control larval dispersal include the reproductive effort of adults, which determines the timing and number of larvae in the water column, and larval development and behavior. Both these components determine how larvae interact with the oceanic circulation and influence the timing, distance and trajectory of larvae among habitats. Reproductive biology has only been studied for a small fraction of deep-sea species and most of the utilized knowledge on parental investment, egg size and fecundity has been extrapolated from a limited number of samples. Because time-series analyses are rare, measurements on reproductive synchrony and periodicity remains elusive for most deep-sea species. As a result, information on the initial factors controlling larval dispersal, "how many" and "when" larvae enter the water column is largely unavailable.

"How long" larvae spend in the water column is defined by the planktonic larval duration (PLD), a fundamental parameter in dispersal models that is unknown for most deep-sea species and highly variable among those for which it has been estimated. One of the biggest obstacles in acquiring accurate PLD estimates is the difficulty in culturing embryos and larvae in the laboratory. In addition, it remains difficult to assess whether and how pressure and temperature conditions may affect PLDs determined in culture. Studies on early life-history stages are scarce and hampered by sampling difficulties and the general lack of facilities available for long-term maintenance under appropriate conditions.

Lastly, "where" larvae are positioned in the water column is largely determined by their swimming behavior. Most larvae are poor horizontal swimmers, but they can alter their vertical positions actively through vertical swimming and/or passively through differential buoyancy; for deep-sea larvae, changes in vertical position may result in major changes in temperature and pressure, in turn resulting in major consequences in terms metabolic and feeding rates, and other vital processes. Further, because of the vertical structure in current velocity different dispersal pathways will also be affected. Ontogenetic changes in anatomical features can indirectly affect larval behavior, motility (speed) within the water column and nutritional reserves (or feeding regime), in turn influencing vertical positioning. However, detailed larval development characterization has only been achieved for few deep-sea species. Larval behavior and development studies are not only constrained by the difficulty in rearing deep-sea larvae in the laboratory, but also by the difficulty in identifying field collected larvae.

Recent technological advances can help expand our knowledge of reproductive and larval biology for deep-sea species. For example, increasing availability and development of new technologies, including pressure and temperature-controlled sampling vessels and holding facilities (e.g., Pradillon et al., 2004; Mestre et al., 2009, 2013; Ravaux et al., 2013) can facilitate the quantification of PLD and swimming behavior. Moreover, the development of sampling systems associated with larval identification by high-throughput molecular techniques allows direct observation of distribution of deep-sea larvae in the water column.

While many gaps exist in our ability to collect empirical data and use predictive models on the factors that regulate dispersal in the deep sea, anthropogenic pressure on this habitat for resource extraction is rapidly increasing. For most of the deep-sea regions currently under threat of major disturbances associated with fishing and mining, our limited understanding of the resident species and communities and the mechanism that regulate them can compromise our ability to manage them sustainably. Despite the cost in filling our knowledge gaps, there is an urgent need to do so.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fmars.2015.00006/abstract

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Supplemetary data. Published observational and experimental PLD values. Taxonomy according to WoRMS Editorial Board (2014). World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. (a) Subphylum; (b) Infraclass; (c) Infraorder. Depth category: D-Deep; E-Eurybathic; S-Shallow. Habitat when below 200 m: CS-Cold seep; CWC-Cold water coral; FF-Food fall; HV-Hydrothermal vent; Sm-Seamount; SS-Sedimentary slope.

Phylum	**Class**	**Subclass**	**Order**	**Family**	**Species**	**Min PLD**	**max PLD**	**midpoint PLD**	**Reference**	**Depth range**	**Depth category**	**Habitat below 200m**
Cnidaria	Anthozoa	Hexacorallia	Actiniaria	Hormathiidae	*Allantactis parasitica*	40	152	96	Mercier and Hamel, 2009	725-1100	D	SS
Cnidaria	Anthozoa	Hexacorallia	Scleractinia	Acroporidae	*Acropora cuneata*	0.17	0.17	0.17	Sammarco and Andrews, 1989	0-10	S	
Cnidaria	Anthozoa	Hexacorallia	Scleractinia	Acroporidae	*Acropora* sp.	1	3	2	Sammarco and Andrews, 1989	0-30	S	
Cnidaria	Anthozoa	Hexacorallia	Scleractinia	Acroporidae	*Isopora palifera*	0.17	0.17	0.17	Sammarco and Andrews, 1989	0-20	S	
Cnidaria	Anthozoa	Hexacorallia	Scleractinia	Caryophylliidae	*Lophelia pertusa*	21	21	21	Brooke and Janengren, 2013	20-6000	E	Sm, SS
Cnidaria	Anthozoa	Hexacorallia	Scleractinia	Pocilloporidae	*Pocillopora damicornis*	2	180	91	Richmond, 2005	0-40	S	
Cnidaria	Anthozoa	Hexacorallia	Scleractinia	Pocilloporidae	*Stylophora pistillata*	0.17	0.17	0.17	Sammarco and Andrews, 1989	0-40	S	
Cnidaria	Anthozoa	Octocorallia	Alcyonacea	Gorgoniidae	*Antillogorgia elisabethae*	3	7	5	Gutierrez et al., 2004	0-30	S	
Cnidaria	Anthozoa	Octocorallia	Alcyonacea	Nephtheidae	*Drifa glomerata*	1	60	30.5	Sun et al., 2010	350-1240	D	SS
Cnidaria	Anthozoa	Octocorallia	Alcyonacea	Nephtheidae	*Drifa sp.*	1	90	45.5	Sun et al., 2010	350-1240	D	SS
Cnidaria	Anthozoa	Octocorallia	Alcyonacea	Nephtheidae	*Duva florida*	1	5	3	Sun et al., 2011	100-300	E	SS
Cnidaria	Anthozoa	Octocorallia	Alcyonacea	Nephtheidae	*Gersemia fruticosa*	3	70	36.5	Sun et al., 2011	100-300	E	Sm, SS
Annelida	Polychaeta	Aciculata	Phyllodocida	Hesionidae	*Hesiocaeca methanolica*	20	20	20	Eckelbarger et al., 2001	500-600	D	CS
Annelida	Polychaeta	Aciculata	Phyllodocida	Nereididae	*Alitta virens*	4.5	15	10	Ushakova and Sarantchova, 2004	0-100	S	
Annelida	Polychaeta	Aciculata	Phyllodocida	Nereididae	*Hediste diversicolor*	2	8	5	Marty and Retiere, 1999	0-20	S	
Annelida	Polychaeta	Aciculata	Phyllodocida	Nereididae	*Platynereis dumerilii*	4	7	6	Fisher et al., 2010	0-20	S	
Annelida	Polychaeta	Aciculata	Phyllodocida	Polynoidae	*Harmothoe imbricata*	28	56	42	Pettibone, 1963	0-20	S	
Annelida	Polychaeta	Canalipalpata	Sabellida	Oweniidae	*Owenia fusiformis*	21	28	25	Thiebaul et al.,1992	0-20	S	
Annelida	Polychaeta	Canalipalpata	Sabellida	Sabellariidae	*Sabellaria alveolata*	28	56	42	Dubois et al., 2007	0-20	S	
Annelida	Polychaeta	Canalipalpata	Sabellida	Sabellidae	*Sabella spallanzanii*	15	21	18	Giangrande et al., 2000	0-10	S	
Annelida	Polychaeta	Canalipalpata	Sabellida	Serpulidae	*Circeis spirillum*	5	15	10	Ushakova, 2003	0-60	S	
Annelida	Polychaeta	Canalipalpata	Sabellida	Serpulidae	*Spirorbis spirorbis*	5	15	10	Ushakova, 2003	0-20	S	
Annelida	Polychaeta	Canalipalpata	Sabellida	Siboglinidae	*Lamellibrachia luymesi*	21	21	21	Young et al., 1996	300-1000	D	CS
Annelida	Polychaeta	Canalipalpata	Sabellida	Siboglinidae	*Lamellibrachia satsuma*	45	45	45	Miyake et al., 2006	82-300	E	HV
Annelida	Polychaeta	Canalipalpata	Sabellida	Siboglinidae	*Osedax japonicus*	10	10	10	Miyamoto et al., 2013	200-245	D	FF
Annelida	Polychaeta	Canalipalpata	Sabellida	Siboglinidae	*Riftia pachyptila*	38	38	38	Marsh et al., 2001	2000-2600	D	HV
Annelida	Polychaeta	Canalipalpata	Spionida	Spionidae	*Boccardia proboscidea*	15	15	15	Oyarzun et al., 2011	0-70	S	
Annelida	Polychaeta	Canalipalpata	Spionida	Spionidae	*Marenzelleria viridis*	56	56	56	Bochert, 2007	0-60	S	
Annelida	Polychaeta	Canalipalpata	Spionida	Spionidae	*Streblospio benedicti*	7	49	28	Levin, 1984; Pernet and McArthur, 2006	0-20	S	
Annelida	Polychaeta	Canalipalpata	Terebellida	Pectinariidae	*Pectinaria koreni*	15	15	15	Thiebault et al., 1996; Ellien et al., 2004	0-20	S	
Annelida	Polychaeta	Canalipalpata	Terebellida	Terebellidae	*Eupolymnia crescentis*	7	7	7	McHugh, 1993	0-10	S	
Annelida	Polychaeta	Canalipalpata	Terebellida	Terebellidae	*Eupolymnia nebulosa*	13	13	13	Nozais et al., 1996; Duchêne, 2004	0-10	S	
Annelida	Polychaeta	Canalipalpata	Terebellida	Terebellidae	*Lanice conchilega*	5	52	29	McHugh, 1993; Smith, 1989	0-100	S	
Annelida	Polychaeta	Canalipalpata	Terebellida	Terebellidae	*Thelepus crispus*	1	1	1	McHugh, 1993	0-100	S	
Annelida	Polychaeta	Canalipalpata	Terebellida	Terebellidae	*Thelepus extensus*	3	3	3	Nozais et al., 1996	0-20	S	
Annelida	Polychaeta	Scolecida		Arenicolidae	*Arenicola marina*	8	8	8	Farke and Berghuis, 1979	0-10	S	
Annelida	Polychaeta	Scolecida		Capitellidae	*Capitella capitata complex*	6	6	6	Mendez, 2002	0-10	S	
Sipuncula	Phascolosomatidea		Phascolosomatida	Phascolosomatidae	*Phascolosoma turnerae*	210	420	315	Young et al., 2012	500-700	D	FF
Mollusca	Bivalvia	Heterodonta	Myoida	Myidae	*Mya arenaria*	10	35	22.5	Strathmann, 1987	0-20	S	
Mollusca	Bivalvia	Heterodonta	Veneroida	Veneridae	*Venerupis philippinarum*	21	28	24.5	Bourne, 1982; Strathmann, 1987	0-10	s	
Mollusca	Bivalvia	Heterodonta	Euheterodonta	Pharidae	*Ensis directus*	16	16	16	Kenchington et al., 1998	0-100	S	
Mollusca	Bivalvia	Heterodonta	Euheterodonta	Pharidae	*Ensis magnus*	20	20	20	Da Costa et al., 2008	0-100	S	
Mollusca	Bivalvia	Pteriomorphia	Mytiloida	Mytilidae	*Bathymodiolus childressi*	240	240	240	Arellano and Young, 2009	650-2200	D	CS
Mollusca	Bivalvia	Pteriomorphia	Mytiloida	Mytilidae	*Mytilus edulis*	16	39	27.5	Bayne, 1965; Mestre et al., 2009	0-40	S	
Mollusca	Bivalvia	Pteriomorphia	Mytiloida	Mytilidae	*Perna perna*	15	20	17.5	Hicks and Tunnell 1995	0-10	S	
Mollusca	Bivalvia	Pteriomorphia	Mytiloida	Mytilidae	*Perna viridis*	14	37.5	25.75	Benson et al., 2001; Fajans and Baker, 2005	0-40	S	
Mollusca	Bivalvia	Pteriomorphia	Ostreoida	Ostreidae	*Crassostrea virginica*	10	18	14	Loosanoff and Davis, 1963	0-20	S	
Mollusca	Bivalvia	Pteriomorphia	Ostreoida	Ostreidae	*Ostrea lurida*	7	16	11.5	Loosanoff and Davis, 1963	0-70	S	
Mollusca	Bivalvia	Pteriomorphia	Pectinoida	Pectinidae	*Chlamys hastata*	34	42	38	Bernard, 1983; Hodgson and Bourne, 1988; Hodgson and Burke 1988	0-150	S	
Mollusca	Bivalvia	Pteriomorphia	Pectinoida	Pectinidae	*Pecten maximus*	18	42	30	Le Pennec et al., 2003	0-110	S	
Mollusca	Bivalvia	Heterodonta	Veneroida	Mactridae	*Spisula solidissima*	19	35	27	Loosanof and Davis, 1963	10-70	S	
Mollusca	Bivalvia	Heterodonta	Veneroida	Veneridae	*Tivela mactroides*	13	20.9	16.95	Garcia De Severeyn et al., 2000	0-10	S	
Mollusca	Gastropoda	Caenogastropoda	Littorinimorpha	Ranellidae	*Monoplex parthenopeum*	293	293	293	Scheltema, 1971	0-75	S	
Mollusca	Gastropoda	Caenogastropoda	Littorinimorpha	Vermetidae	*Dendropoma corallinaceum*	1	5	3	Hughes, 1978	0-10	S	
Mollusca	Gastropoda	Caenogastropoda	Neogastropoda	Muricidae	*Drupella cornus*	21	21	21	Johnson et al., 1993	0-20	S	
Mollusca	Gastropoda	Caenogastropoda	Neogastropoda	Muricidae	*Rapana venosa*	14	17	15.5	Harding and Roger, 1999	0-90	S	
Mollusca	Gastropoda	Heterobranchia	Cephalaspidea	Philinidae	*Philine aperta*	30	35	32.5	Hansen and Ockelmann, 1991	0-500	E	SS
Mollusca	Gastropoda	Heterobranchia	Cephalaspidea	Philinidae	*Philine auriformis*	30	40	35	Cadien and Ranasinghe, 2003	0-300	E	SS
Mollusca	Gastropoda	Caenogastropoda	Littorinimorpha	Calyptraeidae	*Crepidula fornicata*	14	42	28	Coe, 1949; Pechenik, 1984; Mestre et al., 2013	0-60	S	
Mollusca	Gastropoda	Caenogastropoda	Littorinimorpha	Calyptraeidae	*Crepidula plana*	18.1	71.9	45	Lima and Pechenik, 1985	0-70	S	
Mollusca	Gastropoda	Caenogastropoda	Littorinimorpha	Strombidae	*Lobatus gigas*	16	24	20	Davis et al., 1993; Davis, 1994	0-40	S	
Mollusca	Gastropoda	Caenogastropoda	Neogastropoda	Nassariidae	*Ilyanassa obsoleta*	10	21	15.5	Scheltema, 1967	0-20	S	
Mollusca	Gastropoda	Neritimorpha	Cycloneritimorpha	Phenacolepadidae	*Bathynerita naticoidea*	210	210	210	Young et al., 2012	500-700	D	CS
Mollusca	Gastropoda	Vetigastropoda		Haliotidae	*Haliotis asinina*	1.7	2.7	2.2	Sawatpeera et al., 2001	0-10	S	
Mollusca	Gastropoda	Vetigastropoda		Haliotidae	*Haliotis fulgens*	3	4	3.5	Leighton, 1974	0-20	S	
Mollusca	Gastropoda	Vetigastropoda		Haliotidae	*Haliotis rubra*	6	6	6	Prince et al., 1987	0-40	S	
Mollusca	Gastropoda	Vetigastropoda		Haliotidae	*Haliotis sorenseni*	7	18	12.5	Leighton, 1972	0-60	S	
Mollusca	Polyplacophora	Neoloricata	Chitonida	Mopaliidae	*Mopalia muscosa*	19.9	26.6	23.25	Pechenik, 1984	0-10	S	
Mollusca	Polyplacophora	Neoloricata	Chitonida	Mopaliidae	*Tonicella lineata*	2.7	3.8	3.25	Barnes, 1972	0-100	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Albuneidae	*Blepharipoda occidentalis*	40	40	40	Knight, 1968	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Diogenidae	*Paguristes turgidus*	15	15	15	Lough, 1974; Strathmann, 1987	30-450	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Lithodidae	*Cryptolithodes typicus*	35	35	35	Hart, 1964; Lough, 1974; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Lithodidae	*Haplogaster mertensii*	60	60	60	Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Lithodidae	*Lopholithodes mandtii*	60	60	60	Lough, 1974b; Strathmann, 1987	0-150	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus armatus*	73	73	73	Strathmann, 1987	0-110	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus beringanus*	70	70	70	Strathmann, 1987	0-350	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus capillatus*	71	71	71	Strathmann, 1987	0-450	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus dalli*	79	79	79	Strathmann, 1987	30-300	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus granosimanus*	70	70	70	Lough, 1974; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus hemphilli*	74	74	74	Lough, 1974; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus hirsutiusculus*	69	69	69	Lough, 1974; Fitch and Lindgren, 1979; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus ochotensis*	80	80	80	Lough, 1974; Strathmann, 1987	30-150	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Paguridae	*Pagurus samuelis*	70	70	70	Coffin, 1960; Lough, 1974; Fitch and Lindgren, 1979; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Porcellanidae	*Pachycheles rudis*	45	45	45	Boolootian et al., 1959; Knight, 1964; Gonor and Gonor, 1973; Lough, 1974	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Porcellanidae	*Petrolisthes cinctipes*	46	46	46	Boolootian et al., 1959; Gonor, 1970; Lough 1974a	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Porcellanidae	*Petrolisthes eriomerus*	60	60	60	Gonor, 1970; Lough, 1974	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Anomura (c)	Lithodidae	*Paralithodes camtschaticus*	90	90	90	From Shanks, 2009	0-250	E	Sm
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Bythograeidae	*Bythograea thermydron*	30	30	30	Epifanio et al., 1999	1800-2600	D	HV
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Cancridae	*Cancer productus*	100	100	100	Trask, 1970; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Cancridae	*Glebocarcinus oregonensis*	120	120	120	Lough, 1974a; Strathmann, 1987	30-450	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Cancridae	*Metacarcinus anthonyi*	40	40	40	Anderson, 1978	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Cancridae	*Metacarcinus gracilis*	49	49	49	Ally, 1975; Strathmann, 1987	30-200	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Cancridae	*Metacarcinus magister*	105	120	112.5	From Shanks, 2009	30-250	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Cancridae	*Romaleon antennarius*	36	36	36	Lough, 1974b	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Grapsidae	*Hemigrapsus nudus*	32	32	32	Boolootian et al., 1959; Lough, 1974a; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Grapsidae	*Hemigrapsus penicillatus*	16	55	35.5	Noel et al., 1997	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Grapsidae	*Hemigrapsus sanguineus*	16	55	35.5	Epifanio et al., 1998; McDermott, 1998	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Grapsidae	*Pachygrapsus crassipes*	135	135	135	Boolootian et al., 1959; Lough, 1974a; Schlotterbeck, 1976	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Majidae	*Chionoecetes bairdi*	90	90	90	Strathmann, 1987	30-475	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Majidae	*Chionoecetes tanneri*	90	90	90	Lough, 1974b; Strathmann, 1987; Jensen, 1995	30-475	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Majidae	*Oregonia gracilis*	42	42	42	Hart, 1960; Lough, 1974a, Strathmann, 1987	30-430	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Majidae	*Pugettia gracilis*	40	40	40	Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Majidae	*Pugettia producta*	49	49	49	Lough, 1974a; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Pinnotheridae	*Fabia subquadrata*	52	52	52	Lough, 1974b; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Pinnotheridae	*Pinnixa faba*	47	47	47	Pearce, 1966; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Pinnotheridae	*Pinnixa lattoralis*	47	47	47	Lough, 1974a; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Pinnotheridae	*Pinnixa longipes*	35	35	35	Lough, 1974a; Bousquette, 1980	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Portunidae	*Carcinus maenas*	80	80	80	From Shanks et al. 2003	0-100	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Xanthidae	*Cycloxanthops novemdentatus*	49	49	49	Knudsen, 1960	30-50	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Xanthidae	*Lophopanopeus bellus bellus*	35	35	35	Hart, 1935; Knudsen, 1964; Lough, 1974; Morris et al., 1980; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Xanthidae	*Lophopanopeus bellus diegensis*	35	35	35	Knudsen, 1959b; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Brachyura (c)	Xanthidae	*Paraxanthias taylori*	39	39	39	Knudsen, 1959a; Lough 1974	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Alpheidae	*Synalpheus pectiniger*	2	2	2	Weise, 1975	0-20	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Alvinocarididae	*Alvinocaris* sp.	50	50	50	Koyama et al., 2005	1157	D	HV
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Alvinocarididae	*Alvinocaris* sp. *or Chorocaris* sp.	100	100	100	Herring and Dixon, 1998	1650-3650	D	HV
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Crangonidae	*Crangon franciscorum*	35	35	35	DiBacco et al., 2001	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Crangonidae	*Crangon nigricuada*	27	27	27	Siegfried, 1989	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Pandalidae	*Pandalus jordani*	78	78	78	Modin and Cox, 1967; Strathmann, 1987	30-400	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Pandalidae	*Pandalus platyceros*	83	83	83	Strathmann, 1987	30-500	E	SS
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Caridea (c)	Alpheidae	*Alpheus immaculatus*	7	14	10.5	From Shanks et al., 2003	15-25	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Dendrobranchi	Penaeidae	*Penaeus monodon*	14	14	14	DiBacco et al., 2001	0-120	S	*Suborder
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Gebiidea (c)	Thalassinidae	*Neotrypaea californiensis*	49	49	49	Hornig et al., 1989	0-30	S	
Arthropoda, Crustacea (a)	Malacostraca		Decapoda, Gebiidea (c)	Thalassinidae	*Upogebia pugettensis*	30	30	30	Hart, 1937; Hornig et al., 1989	0-30	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Scalpelliformes	Eolepadidae	*Ashinkailepas seepiophila*	53	65	59	Yorisue et al., 2012	1150-1250	D	HV
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Scalpelliformes	Eolepadidae	*Leucolepas longa*	1	42	21.5	Tunnicliffe and Southward, 2004	1450-1850	D	HV
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Scalpelliformes	Scalpellidae	*Arcoscalpellum michelottianum*	49	49	49	Buhl-Mortensen and Hoeg, 2006	64	E	CWC
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Scalpelliformes	Scalpellidae	*Ornatoscalpellum stroemii*	1	5	3	Buhl-Mortensen and Hoeg, 2006	100-1600	E	CWC
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Scalpelliformes	Scalpellidae	*Pollicipes polymerus*	42	42	42	Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Scalpelliformes	Scalpellidae	*Scalpellum scalpellum*	10	15	12.5	Buhl-Mortensen and Hoeg, 2006	30-200	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Austrobalanidae	*Elminius modestus*	17	34	25.5	Crisp, 1958	0-10	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Balanidae	*Balanus glandula*	14	28	21	Schwindt, 2007	0-30	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Chthamalidae	*Chthamalus montagui*	19.5	19.5	19.5	Burrows et al., 1999	0-10	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Chthamalidae	*Chthamalus stellatus*	23	23	23	Burrows et al., 1999	0-10	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Chthamalidae	*Chthmalus dalli*	25	25	25	Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Chthamalidae	*Chthmalus fissus*	25	25	25	Hines, 1978; Strathmann, 1987	0-30	S	
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Neoverrucidae	*Neoverruca sp.*	49	98	73.5	Watanabe et al., 2004	1200	D	HV
Arthropoda, Crustacea (a)	Maxillopoda	Cirripedia (b)	Sessilia	Tetraclitidae	*Tetraclita rubescens*	26	26	26	Dawson et al., 2010	0-30	S	
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Pisaster ochraceus*	76	76	76	Strathmann, 1978	0-100	S	
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Asterias amurensis*	40	50	45	From Shanks, 2009	0-40	S	
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Asterias forbesi*	25	25	25	Costello et al., 1957	0-730	E	SS
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Asterias rubens*	28	56	42	Gemmill, 1914; Thorson, 1946	0-1200	E	SS
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Coscinasterias calamaria*	27	27	27	Barker, 1978	0-30	S	
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Leptasterias ochotensis similispinis*	12	12	12	Kubo, 1951	0-20	S	
Echinodermata	Asteroidea		Forcipulatida	Asteriidae	*Sclerasterias tanneri*	660	660	660	Young et al., 2012	500-700	D	SS
Echinodermata	Asteroidea		Forcipulatida	Astropectinidae	*Astropecten gisselbrechti*	4	4	4	Komatsu and Nojima, 1985	0-20	S	
Echinodermata	Asteroidea		Forcipulatida	Astropectinidae	*Astropecten latespinosus*	5	5	5	Komatsu et al., 1988	0-10	S	
Echinodermata	Asteroidea		Forcipulatida	Astropectinidae	*Astropecten polyacanthus*	3	4	3.5	Mortensen, 1937	0-200	S	
Echinodermata	Asteroidea		Forcipulatida	Astropectinidae	*Astropecten scoparius*	12	21	16.5	Mortensen, 1921; Oguro et al., 1976	15-65	S	
Echinodermata	Asteroidea		Forcipulatida	Astropectinidae	*Astropecten velitaris*	5	6	5.5	Mortensen, 1937	0-120	S	
Echinodermata	Asteroidea		Forcipulatida	Pycnopodiidae	*Pycnopodia helianthoides*	65	90	77.5	Strathmann, 1978; Strathmann, 1987	0-450	E	SS
Echinodermata	Asteroidea		Forcipulatida	Stichasteridae	*Stichaster australis*	38	38	38	Barker, 1978	5 - 600	E	SS
Echinodermata	Asteroidea		Paxillosida	Luidiidae	*Luidia alternata*	13	13	13	Komatsu et al., 1991	0-50	S	

Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia clathrata*	28	28	28	Strathmann, 1978; Komatsu et al., 1991	0-100	S	
Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia maculata*	64	64	64	Komatsu et al., 1994	0-130	S	
Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia quinaria*	36	36	36	Komatsu et al., 1982	10-150	S	
Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia savignyi*	12	12	12	Mortensen, 1938	0-50	S	
Echinodermata	Asteroidea	Paxillosida	Astropectinidae	*Ctenopleura fisheri*	15	15	15	Komatsu, 1982	40-200	S	
Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia ciliaris*	28	28	28	Komatsu et al., 1991	10-400	E	SS
Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia foliolata*	61	120	90.5	Strathmann, 1978	0-600	E	SS
Echinodermata	Asteroidea	Paxillosida	Luidiidae	*Luidia senegalensis*	18	18	18	Komatsu et al., 1991	0-40	S	
Echinodermata	Asteroidea	Spinulosida	Echinasteridae	*Echinaster purpureus*	4	4	4	Mortensen, 1938	10-50	S	
Echinodermata	Asteroidea	Spinulosida	Echinasteridae	*Echinaster echinophorus*	3	3	3	Atwood, 1973	0-80	S	
Echinodermata	Asteroidea	Spinulosida	Echinasteridae	*Henricia lisa*	30	60	45	Mercier and Hamel, 2008	100-4200	E	SS
Echinodermata	Asteroidea	Spinulosida	Echinasteridae	*Henricia sanguinolenta*	40	44	42	Mercier et al., 2013	20-2400	E	SS
Echinodermata	Asteroidea	Valvatida	Acanthasteridae	*Acanthaster planci*	12	14	13	Hoegh-Guldberg & Pearse, 1995; from Shanks et al., 2009	0-30	S	
Echinodermata	Asteroidea	Valvatida	Archasteridae	*Archaster typicus*	17	24	20.5	Mortensen, 1931; Komatsu et al., 2001	50-200	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Patiriella calcar*	10	22	16	Lawson-Kerr and Anderson, 1978; Byrne, 1991; Hoegh-Guldberg and Pearse, 1995	0-20	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Patiriella exigua*	22	22	22	Lawson-Kerr and Anderson, 1978	0-10	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Patiriella gunni*	12	16	14	Byrne, 1991	0-30	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Patiriella regularis*	47	70	58.5	Byrne and Barker, 1991; Hoegh-Guldberg and Pearse, 1995	0-100	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Aquilonastra batheri*	10	10	10	Kano and Komatsu, 1978	0-100	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Aquilonastra minor*	10	14	12	Komatsu et al., 1979; Soliman and Nojima, 1984	0-30	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Asterina coronata*	20	20	20	Komatsu, 1975	0-20	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Asterina gibbosa*	10	10	10	MacBride, 1896	0-150	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Cryptasterina hystera*	5	5	5	Byrne, 2005	0-50	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Cryptasterina pacifica*	28	28	28	Komatsu et al., 1990	0-50	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Cryptasterina pentagona*	6	10	8	Chen and Chen, 1992; Byrne et al., 2003	0-50	S	
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Patiria miniata*	26	50	38	Strathmann, 1987; Basch, 1996	0-300	E	SS
Echinodermata	Asteroidea	Valvatida	Asteropseidae	*Asteropsis carinifera*	30	30	30	Mortensen, 1937	0-20	S	
Echinodermata	Asteroidea	Valvatida	Goniasteridae	*Fromia ghardaqana*	24	24	24	Mortensen, 1938	0-40	S	
Echinodermata	Asteroidea	Valvatida	Goniasteridae	*Iconaster longimanus*	18	18	18	Laneand Hu, 1994	4-85	S	
Echinodermata	Asteroidea	Valvatida	Goniasteridae	*Mediaster aequalis*	38	128	83	Birkeland et al., 1971	0-500	E	SS
Echinodermata	Asteroidea	Valvatida	Odontasteridae	*Acodontaster hodgsoni*	106	106	106	Bosch and Pearse, 1990	20-300	E	SS
Echinodermata	Asteroidea	Valvatida	Odontasteridae	*Odontaster validus*	167	167	167	Pearse and Bosch, 1986	20-900	E	SS
Echinodermata	Asteroidea	Valvatida	Ophidiasteridae	*Certonardoa semiregularis*	21	21	21	Hayashi and Komatsu, 1971	0-10	S	
Echinodermata	Asteroidea	Valvatida	Ophidiasteridae	*Gomophia egyptiaca*	9	9	9	Yamaguchi, 1974	0-80	S	
Echinodermata	Asteroidea	Valvatida	Ophidiasteridae	*Linckia columbiae*	42	42	42	Hoegh-Guldberg and Pearse, 1995	0-100	S	
Echinodermata	Asteroidea	Valvatida	Ophidiasteridae	*Linckia laevigata*	22	22	22	Yamaguchi, 1973	0-60	S	
Echinodermata	Asteroidea	Valvatida	Ophidiasteridae	*Ophidiaster granifer*	9	15	12	Yamaguchi and Lucas, 1984	0-25	S	
Echinodermata	Asteroidea	Valvatida	Oreasteridae	*Pentaceraster mammillatus*	24	24	24	Mortensen, 1938	2-30	S	
Echinodermata	Asteroidea	Valvatida	Oreasteridae	*Protoreaster nodosus*	14	14	14	Yamaguchi, 1977	0-30	S	
Echinodermata	Asteroidea	Valvatida	Solasteridae	*Solaster endeca*	72	80	76	Mercier et al., 2013	20-1300	E	SS
Echinodermata	Asteroidea	Valvatida	Solasteridae	*Solaster stimpsoni*	50	50	50	Strathmann, 1987	0-610	E	SS
Echinodermata	Asteroidea	Valvatida	Solasteridae	*Crossaster papposus*	57	64	60.5	Mercier et al., 2013	0-50	S	
Echinodermata	Asteroidea	Valvatida	Poraniidae	*Porania antarctica*	65	65	65	Bosch and Pearse, 1990	0-900	E	SS
Echinodermata	Asteroidea	Velatida	Pterasteridae	*Pteraster tesselatus*	10	12	11	McEdward, 1992	10 - >200	E	SS
Echinodermata	Crinoidea	Isocrinida	Isselicrinidae	*Metacrinus rotundus*	10	12	11	Nakano et al., 2003	160-270	E	SS
Echinodermata	Echinoidea	Arbacioida	Arbaciidae	*Tetrapygus niger*	94	120	107	Fuentes and Barros, 2000	0-10	S	
Echinodermata	Echinoidea	Arbacioida	Arbaciidae	*Arbacia lixula*	26	26	26	George et al., 1990	0-50	S	
Echinodermata	Echinoidea	Arbacioida	Arbaciidae	*Arbacia punctulata*	20	40	30	Gordon, 1929; Cameron and Hinegardner, 1974; Herrera et al., 1996	50-200	S	
Echinodermata	Echinoidea	Arbacioida	Arbaciidae	*Arbacia stellata*	22	22	22	Emlet, 1995	0-90	S	
Echinodermata	Echinoidea	Aspidodiadematoida	Aspidodiadematidae	*Aspidodiadema jacobyi*	151	151	151	Young and George, 2000	350-850	D	SS
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Hemicentrotus pulcherrimus*	33	33	33	Emlet, 1995	0-50	S	
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Mesocentrotus franciscanus*	35	62	48.5	Strathmann, 1978; Cameron and Schroeter, 1980; Emlet et al., 1987	0-125	S	
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Strongylocentrotus droebachiensis*	29	51	40	Strathmann, 1978; Strathmann, 1987; Hart and Scheibling, 1988; Hart, 1995; Mercier et	0-1150	E	SS
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Strongylocentrotus fragilis*	141	141	141	Strathmann, 1978	100-1200	E	SS
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Strongylocentrotus intermedius*	30	35	32.5	Naidenko, 1996	0-35	S	
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Strongylocentrotus pallidus*	35	63	49	Strathmann, 1978; Emlet et al., 1987	5-1600	E	SS
Echinodermata	Echinoidea	Camarodonta	Strongylocentrotidae	*Strongylocentrotus purpuratus*	30	63	46.5	Strathmann, 1978; Cameron and Schroeter, 1980	0-65	S	
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Holopneustes inflatus*	8	8	8	Pers. comm. in Emlet, 1995	0-30	S	
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Mespilia globulus*	25	35	30	Onoda, 1936; Emlet, 1995	0-60	S	
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Salmacis bicolor*	23	24	23.5	Aiyar, 1935	0-100	S	
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Temnotrema sculptum*	26	26	26	Emlet, 1995	0-200	S	
Echinodermata	Echinoidea	Camarodonta	Toxopneustidae	*Lytechinus pictus*	21	27	24	Cameron and Hinegardner, 1974	0-150	S	
Echinodermata	Echinoidea	Camarodonta	Toxopneustidae	*Lytechinus variegatus*	10	12	11	Herrera et al., 1996	0-250	E	SS
Echinodermata	Echinoidea	Camarodonta	Toxopneustidae	*Nudechinus gravieri*	15	15	15	Mortensen, 1937	0-20	S	
Echinodermata	Echinoidea	Camarodonta	Toxopneustidae	*Tripneustes gratilla*	18	18	18	Mortensen, 1937	0-80	S	
Echinodermata	Echinoidea	Camarodonta	Echinidae	*Sterechinus neumayeri*	107	107	107	Bosch et al., 1987	0-850	E	SS
Echinodermata	Echinoidea	Camarodonta	Echinidae	*Echinus esculentus*	42	42	42	MacBride, 1903	0-100	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Echinometra lucunter*	23	23	23	Emlet et al., 1987	0-50	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Echinometra mathaei*	40	40	40	Onoda, 1936	0-150	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Echinometra vanbrunti*	18	18	18	Emlet et al., 1987; Emlet, 1995	0-50	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Echinometra lucunter*	14	14	14	Emlet, 1995	0-50	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Heliocidaris crassispina*	37	37	37	Onoda, 1931	0-85	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Heliocidaris erythrogramma*	4	5	4.5	Emlet et al., 1987; Emlet, 1995	0-35	S	
Echinodermata	Echinoidea	Camarodonta	Echinometridae	*Heterocentrotus mamillatus*	8	8	8	Mortensen, 1937	0-25	S	
Echinodermata	Echinoidea	Camarodonta	Mellitidae	*Encope michelini*	5	9	7	Herrera et al., 1996	0-100	S	
Echinodermata	Echinoidea	Camarodonta	Mellitidae	*Leodia sexiesperforata*	6	7	6.5	Herrera et al., 1996	0-60	S	
Echinodermata	Echinoidea	Camarodonta	Parechinidae	*Psammechinus miliaris*	58	58	58	Shearer et al., 1914	0-100	S	
Echinodermata	Echinoidea	Camarodonta	Parechinidae	*Loxechinus albus*	20	33	26.5	Fuentes and Barros, 2000	0-350	E	SS
Echinodermata	Echinoidea	Camarodonta	Parechinidae	*Paracentrotus lividus*	18	18	18	Cellario and George, 1990	0-50	S	
Echinodermata	Echinoidea	Camarodonta	Parechinidae	*Parechinus angulosus*	56	56	56	Cram, 1971a	0-180	S	
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Cidaris blakei*	120	120	120	Bennett et al., 2012	500-700	D	SS
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Phyllacanthus imperialis*	3	4	3.5	Olson et al., 1993	0-60	S	
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Phyllacanthus parvispinus*	5	5	5	Parks et al., 1989	0-80	S	
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Prionocidaris baculosa*	25	25	25	Mortensen, 1938	0-150	S	
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Eucidaris metularia*	30	30	30	Mortensen, 1937	0-500	E	SS
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Eucidaris thouarsii*	30	30	30	Emlet, 1988; Emlet, 1995	0-60	S	
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Eucidaris tribuloides*	25	30	27.5	Emlet et al., 1987; Parks et al., 1989	0-800	E	SS
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Evechinus chloroticus*	28	28	28	Dix, 1969	0-20	S	
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Goniocidaris umbraculum*	47	55	51	Barker, 1985	60-400	E	SS
Echinodermata	Echinoidea	Cidaroida	Cidaridae	*Stylocidaris lineata*	120	120	120	Young et al., 1992; Young et al. 1998	500-700	D	SS
Echinodermata	Echinoidea	Clypeasteroida	Clypeasteridae	*Clypeaster rosaceus*	5	7	6	Emlet et al., 1987; Herrera et al., 1996	0-300	E	SS
Echinodermata	Echinoidea	Clypeasteroida	Clypeasteridae	*Clypeaster subdepressus*	11	16	13.5	Emlet et al., 1987; Herrera et al., 1996	0-210	E	SS
Echinodermata	Echinoidea	Clypeasteroida	Dendrasteridae	*Dendraster excentricus*	21	68	44.5	Strathmann, 1978; Emlet et al., 1987	0-40	S	
Echinodermata	Echinoidea	Clypeasteroida	Echinarachniidae	*Echinarachnius parma*	28	35	31.5	Harvey, 1956	0-1500	E	SS
Echinodermata	Echinoidea	Clypeasteroida	Echinocyamidae	*Echinocyamus pusillus*	45	45	45	Theel, 1892	0-1250	E	SS
Echinodermata	Echinoidea	Clypeasteroida	Laganidae	*Jacksonaster depressum*	14	14	14	Mortensen, 1938	0-200	S	
Echinodermata	Echinoidea	Clypeasteroida	Laganidae	*Peronella japonica*	2.5	2.5	2.5	Dan, 1952; Okazaki, 1975	0-70	S	
Echinodermata	Echinoidea	Clypeasteroida	Mellitidae	*Mellita quinquiesperforata*	5	7	6	Herrera et al., 1996	0-180	S	
Echinodermata	Echinoidea	Clypeasteroida	Scutellidae	*Scaphechinus mirabilis*	28	30	29	Naidenko, 1996	0-125	S	
Echinodermata	Echinoidea	Clypeasteroida	Astriclypeidae	*Astriclypeus manni*	25	25	25	Tominaga, 1998	0-40	S	
Echinodermata	Echinoidea	Diadematoida	Diadematidae	*Diadema antillarum*	34	60	47	Eckert, 1998 from Levitan, 2000	0-400	E	SS
Echinodermata	Echinoidea	Diadematoida	Diadematidae	*Diadema mexicanum*	42	42	42	Emlet, 1995	10-100	S	
Echinodermata	Echinoidea	Diadematoida	Diadematidae	*Diadema setosum*	45	45	45	Mortensen, 1937	0-70	S	
Echinodermata	Echinoidea	Echinolampadoida	Echinolampadidae	*Echinolampas crassa*	41	41	41	Cram, 1971b	0-30	S	
Echinodermata	Echinoidea	Echinothurioida	Echinothuriidae	*Asthenosoma ijimai*	21	28	24.5	Amemiya and Tsuchiya, 1979	40-150	S	
Echinodermata	Echinoidea	Spatangoida	Loveniidae	*Echinocardium cordatum*	24	30	27	MacBride, 1913	0-230	E	SS
Echinodermata	Echinoidea	Spatangoida	Schizasteridae	*Brisaster latifrons*	33	67	50	Strathmann, 1978; Hart, 1996	20-1900	E	SS
Echinodermata	Echinoidea	Stomopneustoida	Stomopneustidae	*Stomopneustes variolaris*	28	28	28	Emlet, 2009	0-10	S	
Echinodermata	Holothuroidea	Apodida	Synaptidae	*Oestergrenia variabilis*	15	15	15	Komatsu et al., 2004	10-30	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Holothuria arenicola*	28	28	28	Mortensen, 1937	0-100	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Holothuria difficilis*	10	14	12	Mortensen, 1938	0-20	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Holothuria impatiens*	14	14	14	Mortensen, 1938	0-30	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Holothuria scabra*	14	17	15.5	Ramofafia et al., 2003; James, 2004	0-60	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Holothuria spinifera*	15	15	15	Asha and Muthiah, 2002	0-60	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Actinopyga echinites*	18	18	18	Chen and Chian, 1990	0-5	S	
Echinodermata	Holothuroidea	Aspidochirotida	Holothuriidae	*Actinopyga serratidens*	28	28	28	Mortensen, 1937	0-5	S	
Echinodermata	Holothuroidea	Aspidochirotida	Stichopodidae	*Apostichopus californicus*	51	127	89	Strathmann, 1978; Cameron and Fankboner, 1989	0-250	E	SS
Echinodermata	Holothuroidea	Aspidochirotida	Stichopodidae	*Parastichopus parvimensis*	28	45	36.5	Eckert et al., 2001	0-60	S	
Echinodermata	Holothuroidea	Aspidochirotida	Stichopodidae	*Apostichopus japonicus*	11	23	17	Suguri, 1965; Drozdov et al., 1991; Renbo and Yuan, 2004	0-200	S	
Echinodermata	Holothuroidea	Aspidochirotida	Stichopodidae	*Isostichopus fuscus*	22	27	24.5	Mercier et al., 2004	0-40	S	
Echinodermata	Holothuroidea	Aspidochirotida	Stichopodidae	*Stichopus* sp.	12	12	12	Hu et al., 2010		S	
Echinodermata	Holothuroidea	Dendrochirotida	Cucumariidae	*Aslia lefevrii*	42	46	44	Costelloe, 1988	0-30	S	
Echinodermata	Holothuroidea	Dendrochirotida	Cucumariidae	*Cucumaria frondosa*	44	48	46	Hamel and Mercier, 1996	20-270	E	SS
Echinodermata	Holothuroidea	Dendrochirotida	Cucumariidae	*Cucumaria miniata*	8	13	10.5	McEuen, 1986	0-225	E	SS
Echinodermata	Holothuroidea	Dendrochirotida	Cucumariidae	*Cucumaria piperata*	8	9.5	8.75	McEuen, 1986	0-140	S	
Echinodermata	Holothuroidea	Dendrochirotida	Cucumariidae	*Leptopentacta elongata*	9	9	9	Chia and Buchanan, 1969	0-100	S	
Echinodermata	Holothuroidea	Dendrochirotida	Cucumariidae	*Pseudocnus echinatus*	7	8	7.5	Ohshima, 1918; Ohshima, 1921	0-50	S	
Echinodermata	Holothuroidea	Dendrochirotida	Sclerodactylidae	*Eupentacta fraudatrix*	3	10	6.5	Dolmatov and Yushin, 1993	0-20	S	
Echinodermata	Holothuroidea	Dendrochirotida	Sclerodactylidae	*Eupentacta quinquesemita*	6.5	7.5	7	McEuen, 1986	0-60	S	
Echinodermata	Holothuroidea	Dendrochirotida	Phyllophoridae	*Pentamera populifera*	6	7.5	6.75	McEuen, 1987	0-260	E	SS
Echinodermata	Holothuroidea	Dendrochirotida	Psolidae	*Psolidium bullatum*	8	8	8	McEuen and Chia, 1991	0-200	S	
Echinodermata	Holothuroidea	Dendrochirotida	Psolidae	*Psolus chitonoides*	12	12	12	McEuen and Chia, 1991	0-250	E	SS
Echinodermata	Holothuroidea	Dendrochirotida	Psolidae	*Psolus fabricii*	51	59	55	Mercier et al., 2013	20-1200	E	SS
Echinodermata	Holothuroidea	Dendrochirotida	Psolidae	*Psolus phantapus*	56	61	58.5	Mercier et al., 2013	20 to >200	E	SS
Echinodermata	Holothuroidea	Dendrochirotida	Synaptidae	*Labidoplax buskii*	11	12	11.5	Nyholm, 1951	20 to >200	E	SS
Echinodermata	Holothuroidea	Molpadida	Caudinidae	*Caudina chilensis*	6	20	13	Inaba, 1930	0-990	E	SS
Echinodermata	Holothuroidea	Molpadida	Molpadiidae	*Molpadia intermedia*	6	7	6.5	McEuen and Chia, 1985	53-2900	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Amphiuridae	*Ophiodaphne formata*	21	21	21	Tominaga et al., 2004	70-450	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Amphiuridae	*Amphiura chiajei*	6	8	7	Fenaux, 1963, 1968	5-1200	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiactidae	*Ophiopholis aculeata*	30	83	56.5	Olsen, 1942; Strathmann, 1978	0-2040	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiocomidae	*Ophiocoma pumila*	79	91	85	Mladenov, 1985b	0-368	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiocomidae	*Ophiocomina nigra*	35	40	37.5	Narasimhamurti, 1933	0-400	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiodermatidae	*Ophioderma brevispina*	5	5	5	Webb, 1989	0-223	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiolepididae	*Ophiolepis elegans*	3	3	3	Stancyk, 1973	0-80	S	
Echinodermata	Ophiuroidea	Ophiurida	Ophiolepididae	*Ophioplocus japonicus*	6	6	6	Komatsu and Shosaku, 1993	0-2	S	
Echinodermata	Ophiuroidea	Ophiurida	Ophionereididae	*Ophionereis schayeri*	6	7	6.5	Selvakumaraswamy and Byrne, 2004	0-180	S	
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiothrix angulata*	19	19	19	Mladenov, 1976	0-540	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiothrix fragilis*	21	26	23.5	Thorson, 1946; MacBride, 1907; Morgan and Jangoux, 2005	0-150	S	
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiothrix oerstedii*	4	4	4	Mladenov, 1979	0-120	S	
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiothrix savignyi*	21	21	21	Mortensen, 1938	5-900	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiothrix suensoni*	42	42	42	Mladenov, 1985a	5-450	E	SS
Echinodermata	Ophiuroidea	Ophiurida	Ophiotrichidae	*Ophiomaza cacaotica*	12	14	13	Mortensen, 1937	0-80	S	
Chordata, Tunicata (a)	Ascidiacea	Phlebobranchia	Octacnemidae	*Megalodicopia hians*	3	360	181.5	Havenhand et al., 2006	200-5325	D	SS

Supplementary Material

Estimating dispersal distance in the deep sea: challenges and applications to marine reserves

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1. Supplementary Tables

Supplementary Table 1. Offline particle tracer software descriptions and compatibilities with considerations for ecological studies

Tracer	Description	Compatibility	Consideration for ecological studies	Supporting ecological references
ARIANE	FORTRAN based software able to be used on regional or global scales	Any volume conserving model (e.g. OPA, NEMO, ROMS), C grid required Linux system with FORTRAN library	Has been used with limited behavioral options (fixed depth and diel vertical migration through differing fixed depths at 12hr intervals). May be able to integrate more biotic/abiotic data given appropriate reprogramming. No random walk component instead relies upon turbulent sub-grid-scale parameterization in OGCM.	Bonhommeau et al., 2009a; Bonhommeau et al., 2009b, Pous et al., 2010; Berline et al., 2013
Connectivity modelling system (CMS)	Stochastic lagrangian model with biotic and abiotic optional modules and multi-nesting capabilities, with accompanying matlab routines for visualisation. Can use on-the-fly OGCM data via OPeNDAP.	Any A or B grid OGCMs (including HYCOM data assimilated transformation) Linux system with FORTRAN & NetCDF libraries.	Designed for easy use with ecological application, can be used for passive particles (with all modules off) or with biotic/abiotic components factored in. Random walk solved by 4th order Runge-Kutta discretization. Brand new, not much published testing yet.	Paris et al., 2013
Ichthyop	Java based IBM designed for ichthyoplankton dynamics, which can incorporate biotic and abiotic factors.	MARS, ROMS, NEMO, HYCOM	Useful where many factors are known (e.g. growth, movement, mortality), may require some simple recoding for species specifics requires a sufficiently limited spatial scale to warrant use of a regional OGCM. Tested by comparison to ARIANE and ROFF. Random walk elements integrated into movement sub-model, can be solved by either Euler or 4th order Runge-Kutta discretization.	Lett et al., 2008; Brochier et al., 2009: Martins et al., 2010; Yannicelli et al., 2012; Garavelli et al., 2012; Putman et al., 2012; Catalán et al., 2013; Putman and He, 2013

LTRANS	Larval transport lagrangian model	ROMS	Can simulate behaviors or passive, only couples with ROMS, random walk solved by 4th order Runge-Kutta	Schlag and North, 2012; Young et al., 2012; Li et al., 2014
MGET	ArcGIS related toolbox which can download OGCM data via OPeNDAP for connectivity analysis (designed for coral reef connectivity). Uses method developed by Treml et al. (2008)	Aviso (satellite), HYCOM (non-polar global or gulf of mexico), NOAA OSCAR (surface), ROMS-CoSiNE (pacific) ArcGIS, MGET, Python, PyWIN32, Matlab	Various restrictions of compatible OGCMs explained in help e.g. HYCOM depth restricted to 5500m. Probably one of the more user friendly methods. Requires input polygons and rasters which may make this more suited to the reef connectivity modelling it was designed for.	Treml et al., 2008; Mora et al., 2011; Treml and Halpin, 2012
ROMS OFfline lagrangian Floats (ROFF)	A subroutine code for ROMS for tracing drifters, with accompanying matlab routines for visualisation	ROMS	Has been used with limited behavioral options (fixed depth and diel vertical migration through differing fixed depths at 12hr intervals), only suitable for used with ROMS therefore with limited spatial scale.	Carr et al., 2008
TRACMASS	FORTRAN based similar to ARIANE based on the work of Kristofer Doos and Blank and Raynaud most recently updated in 2011	NEMO, ORCA, ROMS, POM, MICOM, IFS-ECMWF and EC-Earth Linux system with FORTRAN and NetCDF libraries	Can be set up to work to advect passive particles, at fixed depth, with added vertical velocity, or with “any specified depth function for bio-geochemical substances such as…larvae”.	Corell et al., 2012

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RESEARCH ARTICLE

Increasing the Depth of Current Understanding: Sensitivity Testing of Deep-Sea Larval Dispersal Models for Ecologists

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Abstract

Larval dispersal is an important ecological process of great interest to conservation and the establishment of marine protected areas. Increasing numbers of studies are turning to bio-physical models to simulate dispersal patterns, including in the deep-sea, but for many ecologists unassisted by a physical oceanographer, a model can present as a black box. Sensitivity testing offers a means to test the models' abilities and limitations and is a starting point for all modelling efforts. The aim of this study is to illustrate a sensitivity testing process for the unassisted ecologist, through a deep-sea case study example, and demonstrate how sensitivity testing can be used to determine optimal model settings, assess model adequacy, and inform ecological interpretation of model outputs. Five input parameters are tested (timestep of particle simulator (TS), horizontal (HS) and vertical separation (VS) of release points, release frequency (RF), and temporal range (TR) of simulations) using a commonly employed pairing of models. The procedures used are relevant to all marine larval dispersal models. It is shown how the results of these tests can inform the future set up and interpretation of ecological studies in this area. For example, an optimal arrangement of release locations spanning a release area could be deduced; the increased depth range spanned in deep-sea studies may necessitate the stratification of dispersal simulations with different numbers of release locations at different depths; no fewer than 52 releases per year should be used unless biologically informed; three years of simulations chosen based on climatic extremes may provide results with 90% similarity to five years of simulation; and this model setup is not appropriate for simulating rare dispersal events. A step-by-step process, summarising advice on the sensitivity testing procedure, is provided to inform all future unassisted ecologists looking to run a larval dispersal simulation.

Introduction

Dispersal has many important ecological functions in regulating the structure of a population. These functions have consequences for species survival and evolution [1]. Dispersal therefore has an impact upon conservation and management decisions and is a pivotal factor in the establishment of self-sustaining marine protected area networks worldwide.

Biophysical modelling is a well-established technique in shallow water dispersal studies. In this context biophysical modelling is defined as the use of hydrodynamic data (e.g. in situ ADCP data or the outputs of hydrodynamic models) combined with biological parameters to advect theoretical particles representing animals in order to predict dispersal patterns. This technique has been applied to studies of e.g. jellyfish [2], juvenile turtles [3], larval fish [4], and larval invertebrates [5] in order to discern the influence of ocean currents on faunal dispersal abilities. A number of review articles are available in this field to familiarise any ecologist with suitable methods and their requirements (e.g. [6–9], with [8] specifically addressing the bio-components such as mortality and larval behaviour—factors which are not addressed in this paper).

In the deep-sea however biophysical modelling is still in its infancy due to the paucity of well resolved biological (e.g. larval behavioural data, mortality estimates, swimming speeds, buoyancy, etc.) and oceanographic data required to drive dispersal simulations. To date, deep-sea studies are mostly focussed on vent and seep fauna (e.g. [10–13]), with a few more recent studies beginning to apply biophysical models in other settings (e.g. polyplacophoran wood-fall specialists [14], sedimented slope echinoids [13], protobranch bivalves [15], source-sink hypothesis [16]). Most of these studies required the assistance of a physical oceanographer to build and run the models.

Now, with the availability of reasonably resolved hydrodynamic model outputs and custom particle tracking software designed specifically to simulate larval dispersal, the number of deep-sea studies is likely to increase. Fossette et al. [17] provide an overview of potential sources of hydrodynamic data, and the supplementary data associated with Hilario et al. [18] reviews some of the offline particle tracking software suited to larval dispersal simulations. These tools could be used without the additional assistance of a physical oceanographer, but there is the risk that ecologists may be faced with a black box: a model which appears to work but whose inner workings are unknown, potentially resulting in misuse and misunderstanding of the models capabilities. This paper hopes to offer some guidance to those ecologists who, by design or necessity, choose to "fly solo".

While user manuals and literature written on specific model builds may elucidate many of the model's inner workings, sensitivity testing–the permutation of model input parameters to observe the result in model outputs–can provide practical insight into the workings of the model, define limits on input parameter values, and temper expectations of what conclusions can be drawn from simulations [19]. Furthermore existing publications provide some insight into shallow water sensitivity tests [20] and cautionary tales regarding model temporal and spatial resolution [21] but to date there is little advice catering to deep-sea model users who may encounter additional challenges.

There are three critical caveats of biophysical modelling that need to be understood before undertaking a modelling study: 1) by definition a model is a simplification of reality and therefore cannot be expected to represent every process adequately, 2) hydrodynamic models are usually built by and for physical oceanographers and therefore are not tailored to the needs of larval dispersal modelling and will require some compromise on the part of the ecologist, 3) there is usually a trade-off between model quality and computational power (and this applies to both the hydrodynamic model and the particle simulator). These issues are compounded when working in the deep-sea. The potential for longer planktonic larval durations due to metabolic constraints in cold deep sea waters [22–24] requires that models span larger areas, over greater depth ranges than shallow water/coastal studies. Furthermore these locations are usually offshore and therefore lacking in high resolution data. Hydrodynamic models which best fulfil this requirement are currently based on topographic maps derived from altimetry readings: a method with poorest topographic accuracy over areas of deep water and thick sediment seafloor. New topographic maps (not yet used in existing hydrodynamic models) were produced in 2014 improving existing maps by two to four times resolution, yet still these are only able to detect seamounts 1-2km tall [25]. As topography induces many hydrodynamic features, if the topography is inaccurate or coarsely resolved the hydrodynamics will also suffer. The need to cover large areas of ocean demands coarsened resolution due to computational restrictions necessitating temporal and spatial averaging. This averaging process further reduces the accuracy of the hydrodynamics [21] especially when considering the scales of relevance to a microscopic larva [8].

The environment at depth is often considered more stable than in surface waters but there are still many turbulent events. Benthic storms, which are caused by turbidity currents and deep penetrating eddies, may occur eight to ten times a year [26] but they are unlikely to be represented within dispersal simulations employing large scale hydrodynamic models. This simplified view of deep water is perpetuated in standard model output structures such as the Levitus convention of data structuring where the deeper you go the coarser the output resolution (in Levitus one data point is output every 50m at 150m-300m depth, every 100m at 300m-1500m, every 250m at 1500m-2000m, and every 500m from 2000m-5500m depth). Therefore biophysical models run from model outputs may result in decreasing sensitivity of parameters with depth due to the ever coarser resolution of output data points, between which the simulator must interpolate.

Beyond the trade-offs already built into the construction of the hydrodynamic model, the running of a particle simulator can place heavy demands on computational effort and analysis time [9]: a problem that would usually be the job of the physical oceanographer to solve, but which would fall to the ecologist if working alone. All of the parameters tested in this study affect the two most computationally intensive aspects of the simulation–the total number of particles being simulated and the number of velocity fields being loaded into the simulator. It should therefore be a high priority to optimise these parameters. The modeller’s aim is to find a balance between obtaining a saturated state within the model, where you have fulfilled the full potential of the models predictive power, whilst not including redundant autocorrelated simulations which are wasteful of computational power and analysis effort.

Knowing these caveats exist (and more besides, see [6–9, 18]), it is important that ecologists explore the capabilities and limitations of their model setup before undertaking an ecological study. The inputs should be tailored to the structure of the model and expectations should be tempered as to what model outputs may realistically represent. Complementing the work of Simons et al [20], this study explores the sensitivity of several parameters, all of which may be affected more severely than in shallow-water studies. Note that additional parameters are covered by Simons et al [20], and neither list is exhaustive of what could or should be tested. While other literature touches on the sensitivity testing of model parameters (e.g. [27–30]), the purpose of this study is to provide a more step-by-step approach for those ecologists faced with setting up their first larval dispersal model:

The aims of this study are:

1. To describe methods suited to detecting spatial autocorrelation due to model structure and assessing model saturation (which is similar to undertaking a power analysis)
2. To show how these methods can be used to optimise model inputs and assess model adequacy
3. To highlight the ecological consequences of parameter settings and identify deep-sea specific issues to benefit all future larval dispersal research

4. To provide a clear step-by-step procedure for other ecologists to follow when setting up their first larval dispersal model

Methods

Study Area

The Northeast Atlantic, in offshore waters west of the UK and Ireland, is used as a case study. The region (Fig 1), centred on the Rockall Trough (RT), has been a hotbed for deep-sea research for over a century and therefore offers a range of historic datasets which can be used for preliminary groundtruthing. The region's currents and water mass structures are well documented (e.g. [31, 32]).

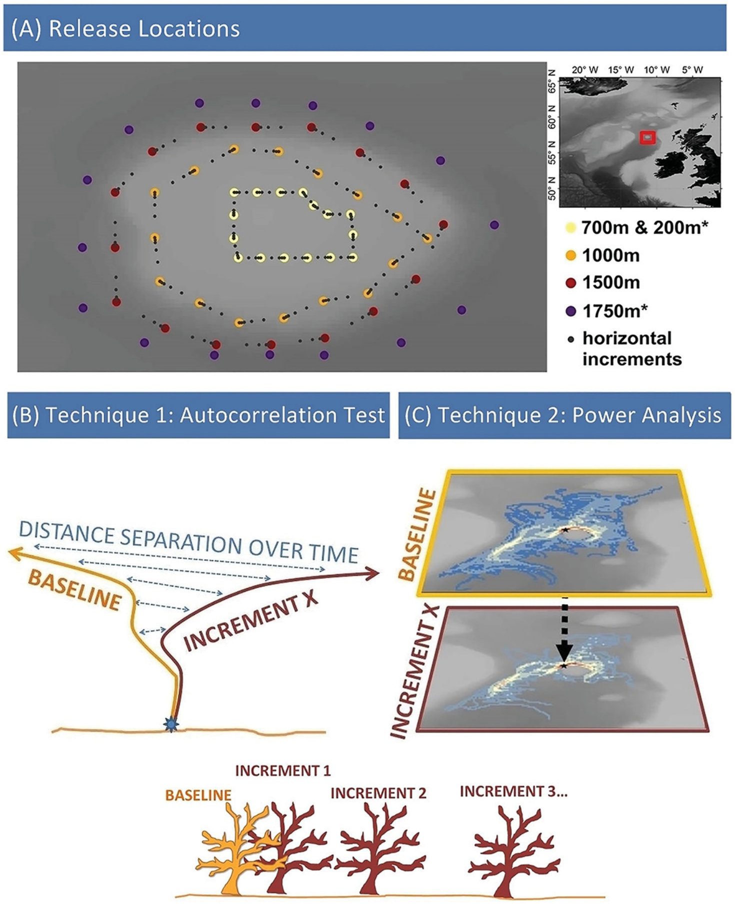

Fig 1. Methods used in this study. The study area (A) focused on Anton Dohrn Seamount (ADS) in the Rockall Trough region East of UK and Ireland. Release locations were defined based on model topography and equally spaced around the circumference of ADS at three standard depths (700m, 1000m, 1500m) with modified depths for the vertical separation test (200m and 1750m; marked with asterisk *) and increment locations shown for the horizontal separation test (coordinates given in S1 File). Two analysis techniques were used in this study: (B) The Autocorrelation tests are a comparison of each increment track with its corresponding baseline in terms of distance separation over time. (C) Power Analysis tests derive a linear correlation between rasters of track density, converting this into the fraction of unexplained variance metric (after Simons et al. [20]). Bathymetry and topography data were obtained online from the GEBCO Digital Atlas published by the British Oceanographic Data Centre on behalf of IOC and IHO, 2003 (GEBCO 30 arc-second grid, www.gebco.net).

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Situated in the centre of the RT, Anton Dohrn Seamount (ADS) was selected as the focal point for the study providing a site for amphi-directional releases across a wide depth range in order to best capture the currents in the area. ADS is a guyot (table mount) with a summit at 521m, and a maximal depth in the South at approximately 2100m, although within the coarse bathymetry of the hydrodynamic model it extends between 600m and 2000m depth. ADS is also a focal point in Holliday et al.'s [31] observational data for the region which spans 23 years of recordings at 22 full-depth standard location stations.

Hydrodynamic model

Freely available outputs from HYCOM+NCODA GLBa0.08 numerical model were used to provide the velocity fields which drive the particle simulator (hycom.org, [33]). Daily averaged data from 2008–2013 were used in the TR tests, while all other tests are based on the data from 2012–2013. HYCOM lends itself well to deep-sea studies due to its unique hybrid vertical grid structure within the native model (data is aligned with isopycnals in the open ocean, transforming to terrain-compressing (aka "sigma grid") layers over topography). The accessible outputs however average the native data into a list of depths (aka a "z-level grid"), specifically following the aforementioned Levitus depth structure. This study does not run a comparison between the native (online) and output-based (offline) particle simulation methods, but does explore the capabilities and limitations of this common output structure. The offline output-based method is the most accessible to deep-sea ecologists [17].

Vertical velocity is not output as standard from HYCOM, and is not available in the HYCOM outputs used by this study. It can be calculated separately based on the continuity equation, but this parameter is known to be noisy, problematic, and would be based on an interpolated grid (the output z-level grid) different from the native model structure (a hybrid grid). Therefore vertical velocity was consciously excluded from this study. This is further justified in this case due to average background vertical velocity in the deep ocean being estimated at 10^{-5} cm s^{-1} (i.e. <1m in 100 days) [34], but should this variable be available we would advise its inclusion, especially when conducting simulations in shallower water. Note that test results are likely to be affected by the inclusion of vertical velocity vectors.

The HYCOM Global analysis outputs project their data onto a Mercator horizontal grid for the majority of the world, but north of 47°N they adopt an atypical bi-polar grid. While the study area falls within this potentially problematic region, the particle simulator model used in this study has a facility to re-project the hydrodynamic data into a Mercator grid prior to simulations, and was tuned for use with HYCOM specifically (but can be used with other model outputs); this re-gridding facility was used during this study. Note that the more recently available HYCOM Global reanalysis data is already projected onto a Mercator grid north of 47°N.

Particle Simulator

The freely available Connectivity Modeling System (CMS) is a recently-developed offline Lagrangian particle simulator (https://github.com/beatrixparis/connectivity-modeling-system, [35]). It was especially developed for larval dispersal modelling, with multiple modules available for the integration of biotic and abiotic data, and is under continual development with additional modules becoming available for specialist uses. CMS has the facility to interface with the HYCOM servers and download hydrodynamic data directly. It can also utilise z-level stored hydrodynamic data whilst providing a re-gridding routine to adapt any data in problematic formats (e.g. uncommon non-orthogonal projections as mentioned above).

CMS and HYCOM together have already been used as the basis of multiple studies within different fields (including non-biological) and have been employed in studies of coral reef connectivity (e.g. [36–38]). This study uses the CMS in its simplest configuration: as a passive particle simulator. It uses a fourth order Runge-Kutta method of advection, and prioritises a tricubic interpolation method through space, although will alter this to tri-linear in the vicinity of land, or bicubic if run on a 2D basis (as is used here). A linear interpolation is run between time snapshots to advect the particle through changing velocity fields.

It should be noted that this study does not test the number of larvae released per spawning event as the model set up used here does not parameterise diffusivity. Without diffusivity all larvae released in one spawning event would follow identical tracks. It is possible to add diffusivity, but in the CMS it would require two arbitrary nest-wide values (one horizontal, one vertical) which themselves require sensitivity testing and careful study-specific consideration. Diffusivity should be tested and used in studies seeking to simulate multiple larvae per spawning event. It is not tested here as other particle simulators may handle this differently.

Parameters

The following parameters were selected for testing in this study:

- Timestep (TS) of particle simulator
- Horizontal Separation (HS) of release points
- Vertical Separation (VS) of release points
- Release Frequency (RF)
- Temporal Range (TR) of hydrodynamic data

The first three parameter tests (TS, HS and VS) aim to detect spatial autocorrelation as a product of model structure. In dispersal models, every particle run is expected to provide useful data, but particles released too close together may show related or identical outcomes entirely due to their spatial proximity. This is because model data is gridded (the model resolution defines the distance between data points) essentially causing data to act as if it is categorical rather than continuous. This is true for fine or coarse resolutions and for any interpolations applied; there will always come a point where a release location will be positioned within the same effective grid cell/category as another, thereby acting as a duplicate whose outcome is both unnecessary and unmeaningful. The aim of these tests is to ensure that all release positions simulated will represent independent samples from which ecological conclusions can be drawn. Therefore we ask: what is the highest resolution parameter setting that does not result in spatially autocorrelated outputs?

The TS of the particle simulator governs how often the simulator interrogates the hydrodynamic model for instruction to redirect the particle. This parameter is only dependent on the models used, and is not conditional upon the ecological question being studied. The aim here is to ensure the simulator asks for instruction frequently enough so that data is received from every grid cell along the dispersal pathway (as opposed to passing through several cells without "asking" for directions, Fig 2). As expected from the relationship between time, velocity and distance, TS is affected by the velocity range in the study area, and the resolution of the hydrodynamic model data (equivalent to distance). The Courant number (C) [39] is often used to test appropriate timesteps (ΔT) for a given grid resolution (ΔL) where average velocity ($\bar{V}$) is known:

$$C = \frac{\bar{V}\Delta \mathrm{T}}{\Delta \mathrm{L}}$$

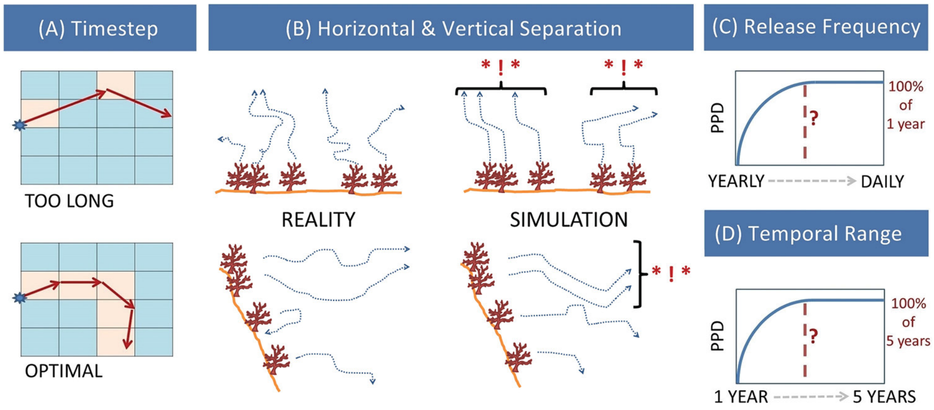

Fig 2. Descriptions of parameters tested in this study. (A) Timestep (TS) of the particle simulator governs how often the simulator asks for instruction. In this heavily simplified diagram, highlighted squares within the model grid have been asked for instruction–if the timestep is too long the resulting pathway may be very different from a timestep which is short enough to interrogate each grid square it encounters. (B) Horizontal (HS) and vertical separation (VS) of release points (spawning animals) in reality may be very small and yet result in different pathways of dispersal, but in a model simulation proximate release points may be spatially autocorrelated (here marked *! *) resulting in redundant simulations and a waste of computational power and analysis time. Both (C) release frequency (RF) and (D) temporal range (TR) tests act like a power analysis aiming to fulfil saturation of the models potential pathways of dispersal (PPD) either by simulating enough spawning events within a given period (e.g. daily within one year: release frequency), or by running simulations in enough years to be representative of a larger time period (e.g. five years: temporal range).

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This is a hydrodynamic modelling approach which can resolve questions about the TS [39], however an ecologist new to the world of hydrodynamic models may not be readily able to deduce average current speeds from model outputs, nor be able to identify the spatial and temporal range to average over. Should this be the case the test we offer here does not require prior knowledge of average velocity, but the results of the test can be used to back-compute average velocity. Ecologists who are not expert with NetCDF manipulation and Matlab may therefore benefit from this study's method, and can cross-check their results using a *post hoc* Courant test. Whichever approach is used, ideally a TS test should be the first sensitivity test run to ensure that the results of all other tests are not affected by using the wrong default TS.

An ecologist may expect to define the HS of release points using realistic positioning of individual animals or by release area e.g. habitat patches such as reefs. However within a model proximate populations may be spatially autocorrelated even if they would not be considered as such in real life (Fig 2).For example, simulating larval release from individual animals, which may access different turbulences and micro currents in real life, could produce identical predicted pathways of dispersal (PPDs) for 500 proximate animals. Existing studies have recognised this and coarsened their HS, either by using repeated simulations of larval release from randomly chosen coordinates within a release area (e.g. [13]), or by using centroids of subdivided area polygons with a size defined by the resolution of the hydrodynamic model [5, 20, 38]. While the resolution of the model may provide a reasonable guide as an HS upper limit, the interpolant of the particle simulator further refines the combined model resolution and may allow release points with a sub-grid scale HS to produce independent PPDs. By defining the HS at which spatial autocorrelation is no longer a concern, decisions about adequately positioning release points can be better informed. HS should be expected to be dependent upon the horizontal resolution of the hydrodynamic model, the interpolative ability of the particle simulator, and the TS of the particle simulator. The planktonic larval duration (PLD, equivalent to the length of time the simulation is run) is also likely to have an effect as the longer you track particles, the more chance they have to deviate from each other.

The same issue applies to VS: whether spawning animals are situated on a slope or a vertical cliff, the combined model's vertical resolution may affect the spatial autocorrelation of release points dispersed across depth bands (Fig 2). Simons et al. [20] tested this parameter between 2m and 30m from the surface, but in the deep sea there is much greater scope for varying sensitivity as the reference depth may be anywhere between 200m -11000m (i.e. from the edge of the continental slope to the bottom of an ocean trench).The vertical resolution of the model may vary with depth as it does when simulations are run within the native HYCOM model, or when running simulations based on model outputs with a stepped vertical structure (such as the previously mentioned Levitus convention). Results will likely be affected by the vertical data structure and the interpolative ability of the particle simulator. If vertical velocities and diffusion are included in model simulations, VS will also be affected by particle simulator TS.

For both the RF and TR tests we aim to assess model saturation and temporal autocorrelation. This is similar to a power analysis, for example defining how many quadrats would be required to represent the species composition of an area. In this case we search for the parameter values which maximise the potential of the models predictive power, aiming to find the coarsest resolution parameter setting which is still reflective of this asymptote. For the parameters tested this can be summarised as asking: how much temporal resolution can we lose while still adequately representing a high resolution baseline?

RF is akin to the number of spawning events in a given period of time (e.g. hourly, daily, etc.). Reality may define the spawning period (e.g. seasonal spawning may limit the simulation to a particular month), but the frequency of spawning events within that period is often unknown. Testing this parameter can offer a means to ensure that the maximum potential number of PPDs have been predicted whilst using the most computationally economic parameter setting (defining the point where the asymptote is reached, Fig 2). Equally if spawning periodicity is known (e.g. lunar periodicity [40] or annual planulation [41]), defining the point where RF reaches asymptote can show whether the model is capable of simulating your required setting, and whether there is a coarser setting which gives equivalent results. RF operates as a function of how temporally variable hydrodynamic conditions are within the model. If it is necessary to run a RF test, this should be done prior to HS and VS tests as it will affect whether you have captured the full variability of the modelled currents and therefore could affect the outcome of these tests. An inadequate RF is called an under-sampling/under-seeding problem [20, 42]. Other methods are available which offer similar results (e.g. [42]).

Ideally any modelling study will be representative of a longer period of time than actually simulated, for example Simons et al [20] used three years with different climatic extremes (El Niño/La Niña/normal) to encompass the maximal range of sensitivity and account for any chosen period of simulation in the study area. The TR test examines this sort of assumption by running a simulation over a longer period and checking whether any subset of years within this period (e.g. a set of three chosen based on climatic phenomena) could be deemed representative of the full simulation. In this test we especially aim to discover whether selecting years based on their North Atlantic Oscillation index (which would be a similar approach to Simons et al [20]) could give comparable results to running simulations over a longer period.

Sensitivity tests

Release locations were defined based on HYCOM output topography: identifying sites which interface with ADS at each depth in order to simulate the release of benthic larvae. Dispersal simulations were run from 16 release locations equally spaced around the circumference of

ADS at three different depths (700m, 1000m, 1500m) (Fig 1). The replicate 16 locations and three depths were used to control for differing states of hydrodynamic mixing. A planktonic larval duration (PLD) of 100days was used to capture the majority of known PLDs: Hilario et al [18] includes a study of known PLDs of eurybathic and deep-sea species stating that 50% would be accommodated by a PLD of 35d, and 75% by 69d, 100d equating to approximately 90% of species included in that study.

All sensitivity tests were carried out using multiple model runs with all parameters held the same throughout the test except for the parameter being permuted. All tests, unless otherwise stated, use: a particle tracking time-step of 1 hour, data from the year 2012 (4th Jan 2012 until 14th March 2013 to be inclusive of 100days tracking from 4th December 2012), the same 16 release positions per depth band at 700m, 1000m, and 1500m (see S1 File for exact release locations of each test), and a monthly RF as standard. Permuted increments for each test and custom setups which differ from the aforementioned standard are shown in (Table 1). HS increment locations were defined in ArcGIS 10.1 using buffers of appropriate radius centred on the baseline release locations, with final increment release locations placed along the seamount contour to maintain the interface with the seamount. All horizontal increments are subgrid-scale compared with the model resolution and are defined in degrees in order to be comparable to the model (projected distance e.g. kilometres would vary with latitude and be different in latitude vs longitude due to the model using grid cells defined in degrees). Standard baseline depths in the VS test were altered to best capture the different Levitus data resolutions. In Levitus, at 200m the next data point is 50m away, at 1000m it is 100m away, and at 1750m it is 250m away whereas at the standard depths used in other tests (700m, 1000m, 1500m) data points are all at the 100m resolution. The TR test was conducted over a five year period and all year combinations within this period compared (five 1 year, ten 2 year, ten 3 year, five 4 year, and one 5 year iterations). Year combinations were also assessed with respect to their North Atlantic Oscillation (NAO) state.

Table 1. Parameters tested in this study.

Sensitivity Test	Baseline (all increments compared to this)	Increment list		Customisation different from default
Timestep (TS)	*Individual spawning event* at default locations with TS = 1 hour.	3 hrs		n/a
		6 hrs		
		12 hrs		
		24 hrs		
Horizontal separation(HS)	*Individual spawning event* at default locations (= 0°)	+0.001°	Location modified by -	n/a
		+0.005°		
		+0.01°		
		+0.025°		
Vertical separation(VS)	*Individual spawning event* at modified standard depths (= 0m)	-0.1m	Depth modified by -	Depths were modified to monitor effect of Levitus structure (200m releases are above summit of seamount)
		-1m		
		-10m		
		-50m		
Release Frequency(RF)	*Multiple spawning events per individual location* from 365 releases (daily through 1 year)	183 releases (2 daily)		n/a
		104 releases (biweekly)		
		52 releases (weekly)		
		12 releases (monthly)		
		4 releases (seasonal)		
Temporal Range (TR)	*Multiple spawning events per individual location* from 5 years of releases (12 releases per year)	1 yr	Multiples are also permuted e.g. 3 yrs = year 1+year 3 +year 5	n/a
		2 yrs		
		3 yrs		
		4 yrs		

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Analysis

There are two analysis techniques used in this study relating to the two methodological aims set out in the introduction (Fig 1).

Detecting spatial autocorrelation due to model structure. Each of the three parameters (HS, VS, and TS) was tested with a track-by-track comparison method in order to detect increment spatial autocorrelation or independence when compared with test baselines. One track was used as a baseline, and each increment track was compared to this over time using the curved earth distance separation between them as a measure of independence/autocorrelation (hereafter termed Distance Separation over Time (DST), Fig 1B). 16 different release locations, three depths and 12 times were used as replicates to provide a median averaged result which controls for different current regimes in space and time. There were therefore 576 baseline tracks tested against their corresponding four increment tracks (192 per baseline depth band), totalling 2880 particles simulated per baseline/increment pairing. Analysis was performed in Matlab with DST curved earth distances derived using the haversine equation. All analyses were based on median averaged results as compared to a reference 10km threshold. This threshold represents the distance below which tracks would be deemed spatially autocorrelated. This is an arbitrary threshold value which should be defined within the context of the study: in this case 10km was selected as an example due to Foster et al [5] and Paris et al [35] agreeing this as a distance where competent larvae are likely to be able to detect and orient towards suitable habitat.

Supplementary ANCOVA tests of increment and depth significance were run in the statistical software environment R. As spatial autocorrelation tests detect the patchiness of hydrodynamic velocity instruction, example velocity fields from HYCOM were also plotted using Matlab in order to provide further context to test results.

Assessing model saturation. The two parameters (RF and TR) analysed to assess model saturation could not be compared using a track-by-track comparison as they trial different temporal frequencies and therefore contain multiple tracks per baseline or increment. There are therefore 16 replicates per baseline depth band, or 48 replicates total. This amounts to a minimum and maximum number of particles simulated per test of RF: 192 (seasonal) / 17520 (daily) and TR: 576 (1 year)/2880 (5 years), with the maxima representing the baselines. The method used for this comparison is similar to that used by Simons et al [20]). The simulator outputs each particle's position per day. These were converted into track lines in ArcGIS 10.1 and compiled into track density grids per baseline or increment. These grids were comprised of 2D spatial cells at half the resolution of the hydrodynamic model (~0.04°), with each cell displaying a count of the number of replicate tracks which pass through it. Track density plots differ from particle density distributions as no particle is counted twice per grid cell (representing numbers of tracks rather than repeated particle cell occupancy). The fraction of unexplained variance (FUV) was then found between each baseline/increment pairing: $= 1 - r^2$, where r is the linear correlation coefficient between track density rasters, as compared on a cell by cell basis and summarised as a single value per raster pairing. Following Simons et al.'s [20] example, a 0.05 threshold FUV variance was used to define the point where variance in FUV was minimal. At this point the increment was interpreted as giving effectively the same result as the baseline.

Results

Spatial autocorrelation tests

For all three tests, plots are shown of the median separation distance between each increment/baseline pairing (Fig 3). Results were averaged across all replicate locations and all days tracking and a piecewise cubic hermite interpolating polynomial line was fitted to the increment

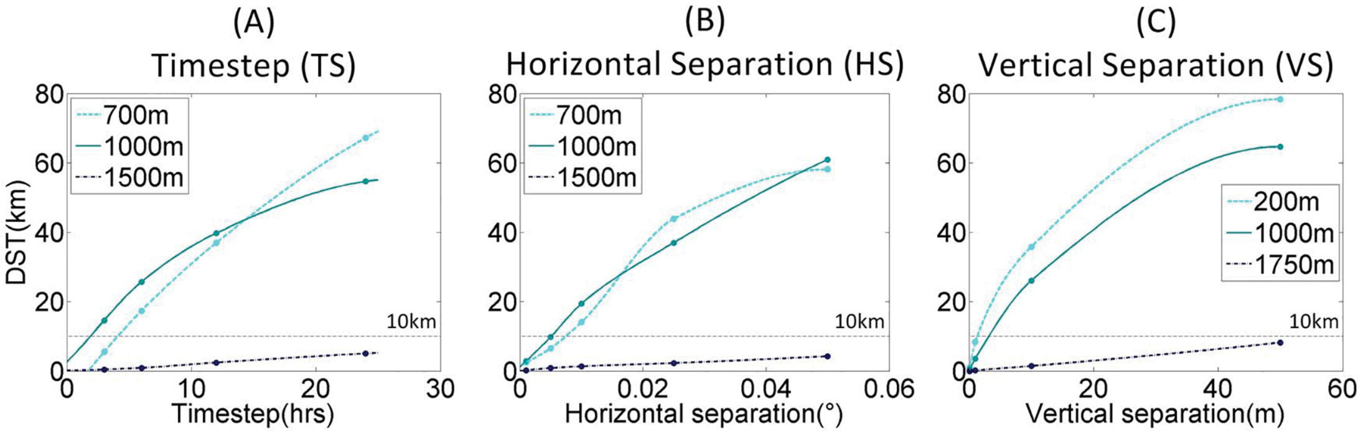

Fig 3. Results of spatial autocorrelation tests. Parameter increments from tests of (A) Timestep (TS), (B) Horizontal Separation (HS) and (C) Vertical Separation (VS), were plotted against median Distance Separation over Time (DST) with a piecewise polynomial interpolant applied between increment values of the same depth. A DST of 10km (based on records of larval habitat detection abilities) was taken as the autocorrelation/independence threshold allowing an optimal increment per depth to be derived from the intersection between the interpolant and the threshold. Optimal values derived from these plots are shown in Table 2.

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data per depth. These plots can be used to identify an increment value below which autocorrelation will occur. These values, hereafter referred to as 'optimal values', are shown in Table 2. S1 Fig includes boxplots of this data which are provided to give some scale of the variability in the data. This may be of use if, for example, rare dispersal events are important to the outcome of the study, or if suboptimal parameter values must be used and it is desirable to quantify the error that results. The results of ANCOVA tests of increment and depth significance can also be found in S1 File. Additional plots of median separation distance between each increment/baseline pairing over time (Fig 4) are shown for the HS test in order to show the effect of PLD on parameter sensitivity.

Table 2. Optimal value results of parameter sensitivity tests derived from plots in Fig 3 and Fig 5. All tests of spatial autocorrelation result in values less than the optimal value being spatially autocorrelated with the baseline (these tests define a high resolution baseline). All tests of model saturation (akin to a power analysis) result in values greater than the optimal value being temporally autocorrelated with the high resolution baseline.

Parameter	Test Type	Optimal Value	
Timestep (TS)	spatial autocorrelation	700m	4 hr
		1000m	2 hr
		1500m	48 hr (approx.)
Horizontal Separation (HS)	spatial autocorrelation	700m	0.0075°
		1000m	0.005°
		1500m	0.08° (approx.: this model resolution)
Vertical Separation (VS)	spatial autocorrelation	200m	1.5m
		1000m	3m
		1750m	60m
Release Frequency (RF)	model saturation	700m	150 releases per year
		1000m	160 releases per year
		1500m	75 releases per year
Temporal Range (TR)	model saturation	700m	4.3 yrs monthly releases
		1000m	4.3 yrs monthly releases
		1500m	4.1 yrs monthly releases

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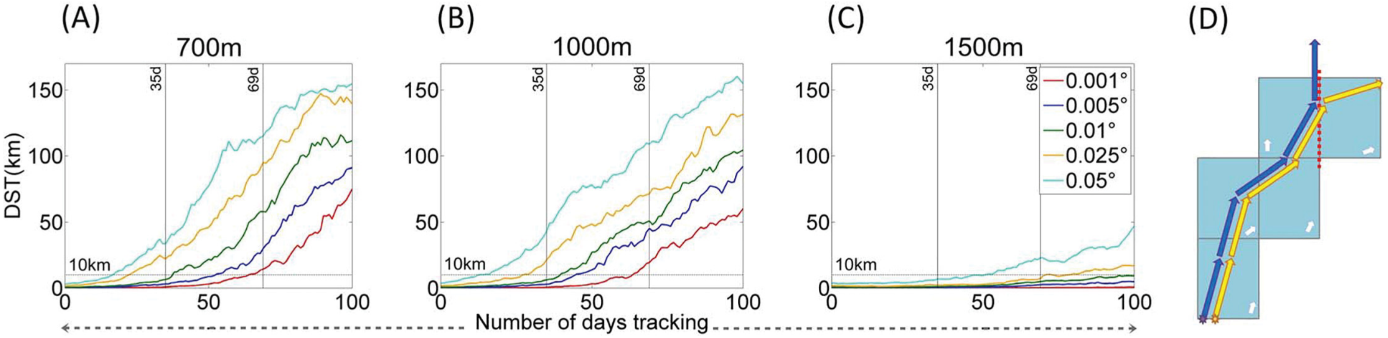

Fig 4. Plots, per depth, of Horizontal Separation (HS) increments Distance Separation over Time (DST) against tracking time (or Planktonic Larval Duration (PLD)). A 10km autocorrelation/independence threshold is shown and PLDs of 35days and 69days are marked reflecting PLDs which accommodate 50% and 75% of all known PLDs of deep-sea and eurybathic species (Hilario et al. [18]). Plots are shown for (A) 700m, (B) 1000m and (C) 1500m simulations. The right-hand diagram (D) demonstrates the possibility of two spatially autocorrelated tracks eventually accessing different instructions (represented by the white arrow in each grid cell) and deviating. This may account for the increased sensitivity over time, and may encourage interpretation as increased likelihood of error over time.

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Horizontal separation. The plot in Fig 3 shows that DST increases with horizontal distance between release points. At 1500m depth, all tested increments were autocorrelated with a median DST well below the example 10km threshold. At 700m and 1000m depth, track deviance increased beyond the threshold at 0.0075° and 0.005° horizontal distance respectively providing a minimum distance for HS at these depths.

Fig 4 shows the effect of PLD (tracking time) upon HS sensitivity, with Hilario et al.'s [18] benchmark PLDs marked as examples. By looking at the median DST per day of tracking, per increment, it is clear that in tests with different PLDs the HS sensitivity would be different. In this test all increments of HS would remain autocorrelated (stay within the example 10km independence threshold distance) every day for up to 18 days at all depths. This means that with this model set up you cannot model PLDs of less than 18 days at sub-grid scale spacing without spatial autocorrelation. At 1500m all increments of HS are autocorrelated up to 52 days PLD. In order to model dispersal of species with a PLD of 35 days (Hilario et al.'s [18] heuristic PLD to encompass 50% of known deep-sea species) our results suggest that at 700m and 1000m depth >0.01° separation between horizontal release locations is required with 0.025° being the first tested increment that fulfils this criteria. At 1500m all increments trialled are spatially autocorrelated and thus a horizontal separation distance of >0.05° (potentially equivalent to model resolution 0.08°) is required. However, to model dispersal of species with a PLD of 69 days (Hilario et al.'s [18] heuristic PLD to encompass 75% of known deep-sea species) horizontal release locations of 0.001° would provide spatially independent larval dispersal pathways at 700m and 1000m. At 1500m >0.025° degrees separation between horizontal release locations is still required with 0.05° being the only tested increment that fulfils this criteria.

Vertical separation. Again all increments tested at the deepest baseline depth (1750m) were considered autocorrelated if using the 10km threshold (Fig 3) although the polynomial interpolation suggests that the threshold for independence may be approached at approximately 60m separation. Therefore it may be advisable to stratify release locations by 60m depth separation when at around 1750m depth. At 200m and 1000m baseline depths, VS is considerably more sensitive, with release locations separated by only 1.5m and 3m vertical distance respectively expected to track independently from each other.

Timestep. All TS tests were compared to a baseline of 1 hr. The first (3 hrs) increment at 1000m depth was already independent from the 1 hr track with the polynomial suggestive of a threshold at approximately 2hrs. It would therefore be advisable to use at least a 2hr timestep at 1000m depth. Interestingly the threshold, and therefore advised timestep, at 700m was closer to 4hrs (Fig 3). At 1500m depth the largest increment (24 hrs) still resulted in autocorrelated tracks when using the example 10km threshold. In spite of this it is advisable to stick with at least a daily frequency as the temporal resolution of the hydrodynamic data is also daily. Basic checks against the Courant number calculation suggest that these results are more conservative than an arbitrary area-averaged Courant number. E.g. at 1500m, average velocity over the NE Atlantic is 0.02m/s, giving a $C = 0.46$ when $TS = 48$ hr. Results were closer to using the maximum velocity in a Courant calculation over the trajectory-only domain. E.g. at 1500m, a maximum velocity of 0.05m/s was encountered by trajectories, giving $C = 0.63$ for a 24 hr TS, C only approaches convergence ($C = 1$) at 40 hrs (average velocity in this domain is 0.01m/s, $C = 0.33$ at 48 hrs).

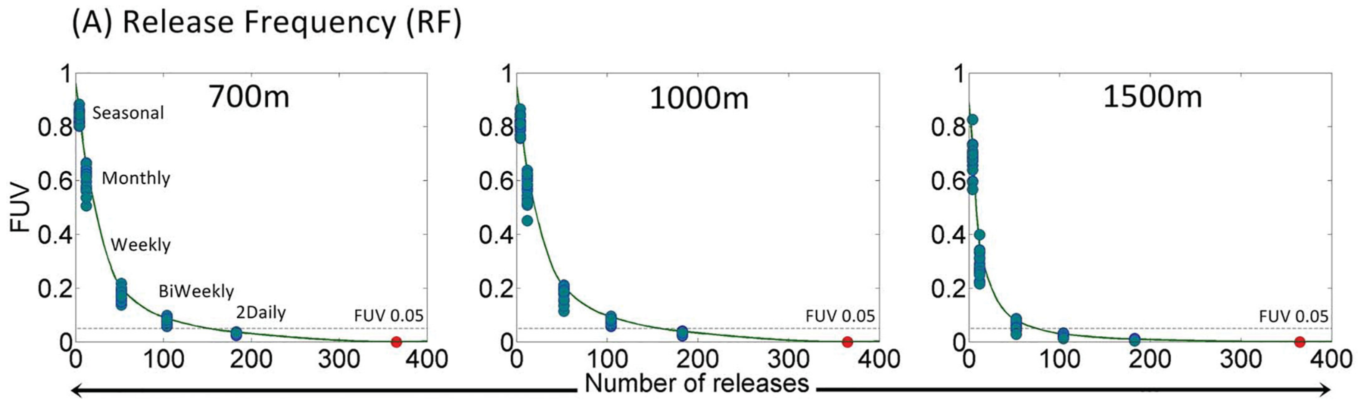
Hydrodynamic Model Plots. Matlab plots of the average velocity values for the standard 3 baseline depths are shown in Fig 6. The range of colours/velocity values in each plot shows that current velocities are more variable at 700m and 1000m than at 1500m. Closer inspection within the highlighted circles shows the 1000m depth slice as having the largest range in velocity values/colours, with patches of similar velocity covering smaller spatial extents than at the other two depths. These plots can be used to support.

Model saturation tests

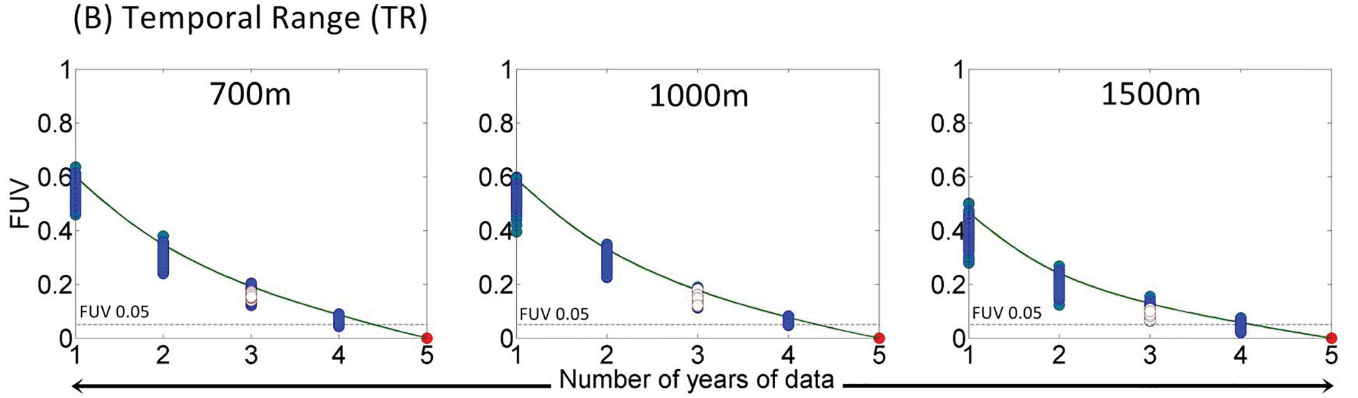
Each FUV value was plotted per increment and a piecewise cubic hermite interpolating polynomial line was fitted to the data in order that 95% of FUV values within each increment fell below it (Fig 5). This ensured that the polynomial was representative of the range of FUV values per increment and means that when the polynomial crosses the threshold 0.05 FUV the variance in FUV values should also have decreased below this value. The increment value where the polynomial crosses the 0.05 FUV threshold, hereafter referred to as the 'optimal value', is shown in Table 2.

Release Frequency. The FUV variance, or spread of points per increment, decreases steeply with the tested increment resolution (Fig 5). Seasonal releases do display little variance at 700m and 1000m, but have large FUV values indicating a correlation between maps of <0.36. The piecewise polynomial suggests that the FUV and 95% of its variance would decrease below the 0.05 threshold at 150–160 releases per year at 700m and 1000m. This result would mean that the track density plots derived from 150–160 releases in 2012 at these depths are effectively the same as track density plots from 365 releases in that year. At 1500m the variance in FUV values per increment is much higher, e.g. seasonal (four releases in a year) has a spread between 0.55 and 0.85 FUV (equivalent to a range of correlations from 0.70 to 0.28). At 1500m you would need at least 75 releases throughout the year to give an equivalent track dispersal plot to the daily release baseline.

Temporal Range. FUV decreases almost linearly with the number of years' data when compared with the full 5 yr track density plot (Fig 5). The intersection of the piecewise polynomial with the 0.05 threshold suggests that 4.3 years of data would be required to represent the full five years of data at both 700m and 1000m, although approximately 4.1 years of data would be adequate at 1500m. If an approach similar to that of Simons et al [20] was used in this study only the three years starred in Fig 7 would be used, representing the two NAO extremes and a non-NAO event year, with results corresponding to the data points highlighted in white on Fig 5. Only at 1500m do these values approach the threshold FUV value, although they are still greater than 0.05. This result suggests that the three NAO states which may be selected as representative of a longer period could not be considered equivalent to the track density plot of a full five years of releases.



(A) Release Frequency (RF)



(B) Temporal Range (TR)

FUV	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
COR	0.99	0.96	0.91	0.84	0.75	0.64	0.51	0.36	0.19	0

Fig 5. Results of temporal power analysis tests. Plots, per depth, for (A) Release Frequency (RF) and (B) Temporal Range (TR) tests, show increment values plotted against FUV scores. An FUV score represents one baseline/increment comparison, with a minimum of 16 replicates per increment (there are more in the temporal range test). A piecewise polynomial interpolant is fitted so that 95% of FUV scores fall below the line. The asymptotic threshold is defined as an FUV of 0.05 after Simons et al. [20]. Temporal range tests show FUV scores in white where three year datasets comprise years with optimal NAO indices (2009, 2010, and 2012 –see Fig 5). The table at the bottom shows the relationship between FUV and Pearson correlation values.

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Discussion

Optimal values

The optimal values shown in Table 2 are appropriate for: this commonly employed pairing of models (HYCOM Global 1/12° and Connectivity Modeling System), in the Rockall Trough region of the Northeast Atlantic, for a generalised species with a PLD of 100 days and monthly spawning events. Should any of these conditions be altered, different optimal values may be found.

The values shown are considered optimal as exceeding optimal value resolution (i.e. reducing distance or timestep, or increasing frequency or number of years of simulation) may result in a waste of computational and analysis effort although all PPDs will be represented. Coarsening optimal value resolution (i.e. increasing distance or timestep, or decreasing frequency or

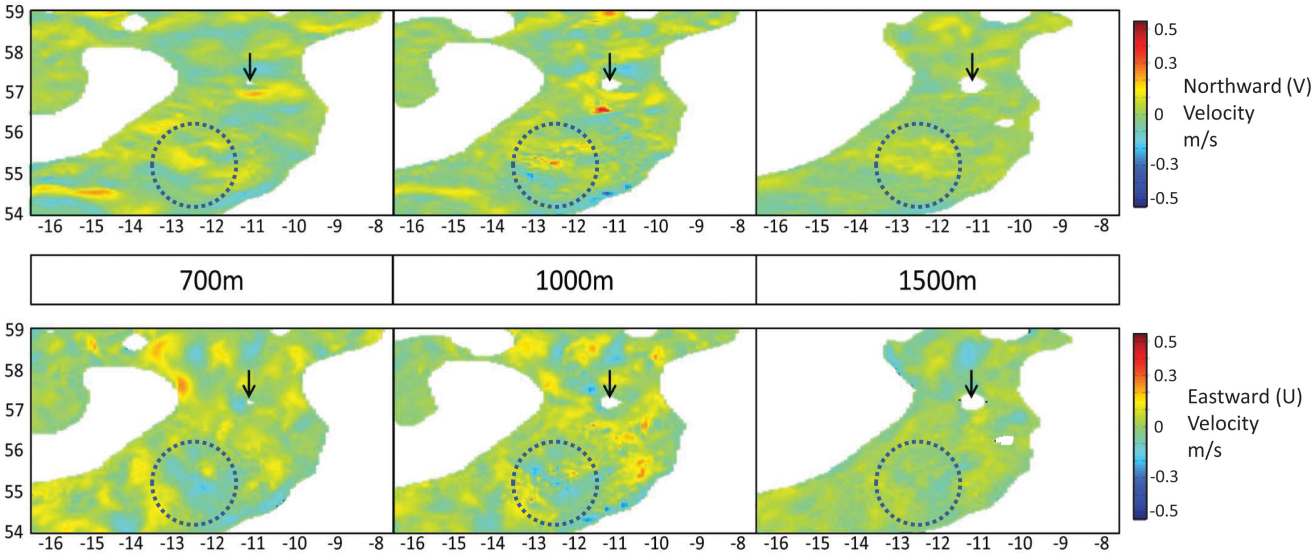

Fig 6. Example horizontal profiles of U and V velocity taken from one day in HYCOM (4th Jan 2012). HYCOM breaks down current velocities into directional components: U velocity measures current speeds in an East (+ve)/West (-ve) direction (top three plots), and V in a North (+ve)/South (-ve) direction (bottom three plots). Anton Dohrn Seamount is marked in each depth slice with an arrow. Areas of different velocity from the background values appear as coloured patches. A comparison of areas within the dotted circles shows that profiles from 1000m have the greatest variation in current velocities (a greater number of small coloured patches). Profiles from 1500m show the least variation in velocity. Topographic contours are derived directly from HYCOM velocity data.

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number of years of simulation) could result in PPDs being omitted which the model was capable of predicting, potentially to the detriment of study conclusions.

While it is always preferable to use optimal values (or a higher resolution), sometimes it is not possible to achieve this and coarser values must be used. In this situation the results of sensitivity tests can offer a means to quantify error due to sub-optimal parameter values. The FUV method offers the best error quantification technique as FUV values are derived from linear correlations (r). When the 95% of FUV values variance control crosses the FUV = 0.05 threshold used in this study (RF and TS tests, after [20]), this means that 95% of baseline/increment comparison replicates exceeded a correlation of 0.9975. If the 0.05 threshold was not met, a correlation could be derived from the 95% interpolation line at the point of the highest resolution increment which can be used. For example, the RF test optimal value in this study was 150 releases per year at 1000m, but perhaps a weekly release frequency is the highest resolution setting possible. In Fig 5 the weekly (52 releases per year) increment corresponds with an FUV of ~0.2 at 700m and 1000m, and ~0.1 at 1500m. This value can be used to back-compute a correlation between the weekly and daily PPDs as

$FUV = 1 - r^2$, so $r = \sqrt{(1 - FUV)}$ (a table is provided at the bottom of Fig 5 to make estimating this even quicker). As the FUV is read from the polynomial interpolation this represents the FUV that 95% of replicate FUVs fall below. Therefore at 700m and 1000m the correlation between a weekly and daily release frequency is ~0.96 or greater (FUV 0.2), and at 1500m is ~0.99 or greater. This may help decide or at least report the adequacy of the sub-optimal parameter setting which must be used in place of, and compared to, the optimal setting. As all of these FUV calculations are based on Simons et al.'s heuristic 95% variance control value, there is also scope for varying the 0.05 FUV threshold value in line with study aims (something which is also discussed in Simons et al. [20]).

Error/accuracy is not so easily quantified using the described spatial autocorrelation technique, but median DST values of sub-optimal increments could be cited relative to the

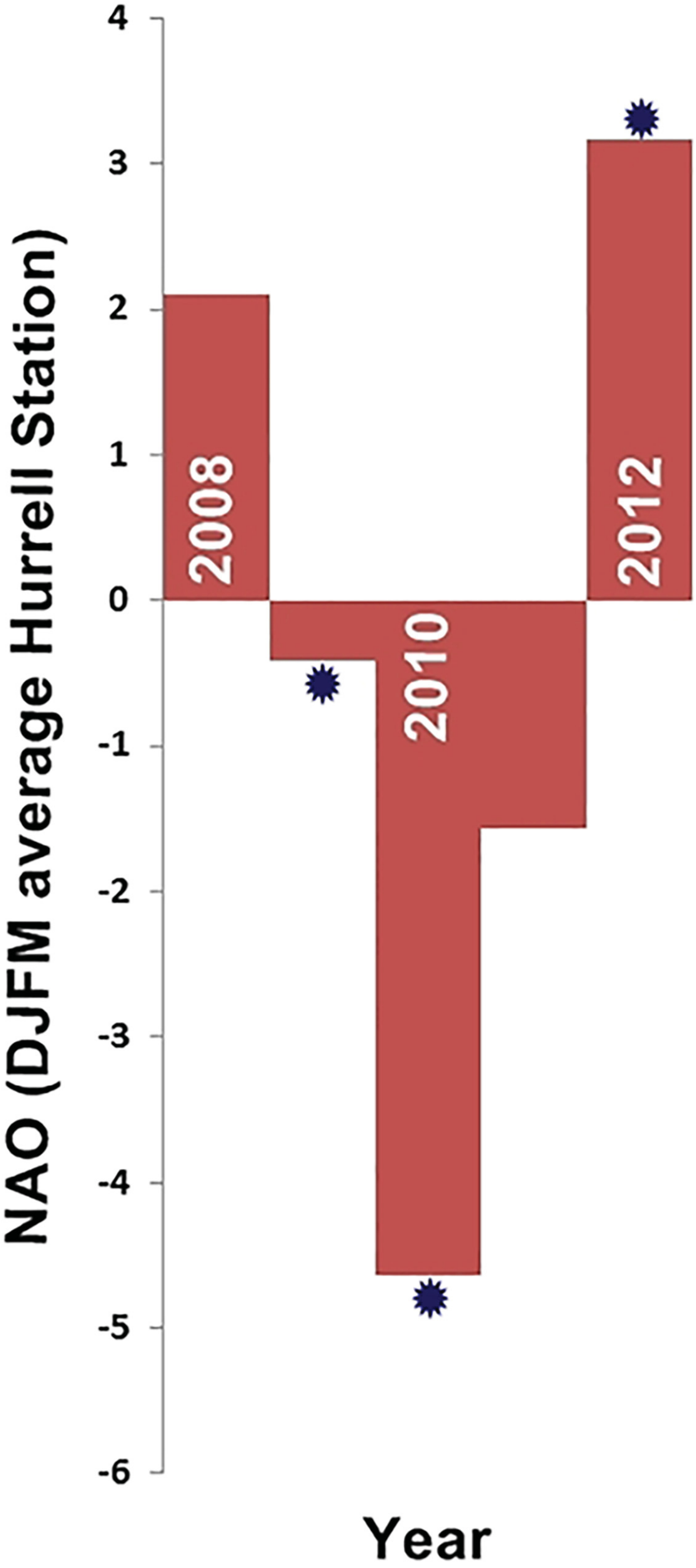
NAO (DJFM average Hurrell Station)
4
3
2
1
0
-1
-2
-3
-4
-5
-6
2008
2010
2012
Year

Fig 7. North Atlantic Oscillation (NAO) indices. Following Simons et al.'s [20] approach to El Niño, data from 2009 (NAO neutral), 2010 (strong negative) and 2012 (strong positive) should provide enough data to represent the full five years of simulations. Indices are plotted as December to March averages as recorded at Hurrell Station. Data sourced from http://climatedataguide.ucar.edu.

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threshold, and boxplots of all DST values per increment (available in S1 Fig) can provide benchmarks in terms of DST quartiles and outlier ranges. For example, a study undertaken at around 1000m depth would ideally have a VS of ~3m based on a 10km threshold distance according to Fig 3. If the resolution of depth recordings requires VS to be 10m (a sub-optimal value), then the plot in Fig 3 shows that at 1000m a 10m VS should be expected to, on average (median), be separated from a baseline track by ~25km (2.5 times the distance of the optimal value). You can also tell from the box plots in S1 Fig that a VS of ~1m (closest to the optimal value of 2m) would have an upper quartile at around 100km, but at 10m VS the upper quartile approaches 250km (also ~2.5 times the optimal value). So you could estimate the accuracy of a 10m VS to be 2.5 times worse than that of the optimal value.

Model Adequacy

As in Simons et al. [20], all tested parameters were affected by the strength of the mixing in the local system as portrayed within the hydrodynamic model. All tests can therefore provide insight into the hydrodynamic conditions within the chosen hydrodynamic model, and offer a means to ground-truth the combined hydrodynamic and simulator model's abilities and limitations.

The suite of tests run in this study serve to capture different aspects of the model hydrodynamics with two tests (HS, VS) detecting spatial variance, and two (RF, TR) testing temporal variance, while TS interacts with both. The resolution of the hydrodynamic model may inform some of the combined model limitations, but adjustments need to be made for the interpolation provided by the particle simulator.

Our findings suggest that with increasing depth, fewer sub-grid release positions are required in order to represent the full range of dispersal pathways it is possible to simulate (when using this particular pairing of models in this region). For this to occur, neighbouring data points at shallower depths must produce steep differentials allowing different particle movement instructions to be obtained from interpolated intermediate locations. For example, neighbouring cells instructing 0.9m/s Northeast and 0.8m/s South, may result in an interpolation instructing 0.1m/s East-Southeast midway between data points. This therefore suggests a high spatial variability in hydrodynamic data.

However our results at depth (1500m, 1750m) were less sensitive. The HS test revealed no independence of tracks until HS approached model resolution, and the VS test recommended separation at ~ ¼ model resolution. This lack of sensitivity at depth implies weak differentials between vertically neighbouring cells. For example, neighbouring cells instructing 0.7m/s Northeast and 0.8m/s Northeast, may result in an interpolation instructing 0.75m/s Northeast midway between data points which is very similar to the neighbouring instructions.

Further evidence of this interpretation can be gained from the horizontal slices through the hydrodynamic data. Fig 6 shows three example horizontal slices through HYCOM, detailing the current velocities and their variability. It is clear from these plots that current velocities are more variable at 700m and 1000m than at 1500m. Furthermore the greatest variability in current velocities is found at 1000m, which accounts for the switch in sensitivity between these 700m and 1000m depths in HS and TS tests. The smaller velocity patches at 1000m require particles to travel smaller distances between interrogations to ensure receipt of every new potential instruction. This resulting in the smaller optimal HS and TS values at 1000m.

Now, with some idea of how the currents behave within the combined model, a comparison to empirical data can offer qualitative groundtruthing of model predictions and provide an assessment of combined model adequacy. HYCOM as a global model has been validated on a global scale but may not adequately represent the study area, so this is worth reviewing.

In this study the literature reveals that all shallower simulations undertaken in this area would occupy the same watermass—the poleward moving Eastern North Atlantic Water (ENAW). ENAW extends down to 1200m and characteristically exhibits mesoscale activity and relatively high current velocities [31, 43, 44]. This could account for this study's predicted high variability of instruction through horizontal and vertical space at shallower depths. Winter convection in the area should also be expected to mix surface waters down to 600m typically, although this may extend to 1000m in severe winters [31].

Enhanced variation at 1000m may be due to a combination of factors. Eddies seen at shallower depths will have a smaller footprint at depth while the vorticity remains high, and the Hebrides Terrace Seamount summits at 1000m providing an additional stirring rod Southeast of ADS. There may also potentially be more interaction with intermediate water masses at 1000m. At this depth the core of Wyville Thomson ridge Overflow Water (WTOW) comes down from the north to the west of ADS, while Sub-Arctic Intermediate Water (SAIW) and Mediterranean Overflow Water (MOW) interact with the ENAW in a northward flow to the east of ADS [43].

As a result of this qualitative groundtruthing, the combined model in this study may be considered adequate when representing dominant water masses and mesoscale activity. However there is no obvious influence of SAIW or MOW in the model, so intermediate water masses probably remain largely un-parameterised (however the WTOW is visible in Fig 6 at both 700m and 1000m depths).

The results of the TS test can also be used to validate the model current speeds as the relationship velocity = distance/time can be related to the HS (distance) and TS (time) for each depth. For example, in this study:

- At 700m the recommended TS was 4 hrs (equivalent to ~500m/4 hrs based on 0.005° sensitivity) suggesting that local current speeds averaged around 0.4 m/s at this depth;
- The 1000m test recommends a maximum 2 hrs TS(750m/2 hrs based on 0.0075° sensitivity) equating to current speeds of 0.10m/s;
- The 1500m test may allow a TS >48 hr (8km/48 hrs based on 0.08° sensitivity) equivalent to maximum average current speeds of 0.046m/s (although this result is based on extending the polynomial interpolant far beyond the extent of the graph in Fig 3).

The literature does seem to bare out these predictions with Booth & Meldrum [45] recording currents with drifters (drogued between 66m and 166m) around Anton Dohrn as being up to 0.5m/s especially when caught in eddies, with a background flow of around 0.1m/s. Although derived from a different isopycnal model initialised from empirical data in the region, New & Smyth-Wright [46] estimate the Labrador Sea Water in the region (which only starts at 1500m) as ranging in current speeds from 0.004 m/s to 0.1 m/s, with some of the weakest of those current speeds recorded in the vicinity of ADS. ADS was the location of one of the observational transects in New & Smyth-Wright's study [46] and these observations are in line with empirical observations reported in Ellet, Edwards & Bowers [47]).

Checks against the Courant number showed that this study's TSs may be conservative, even when the velocity is averaged over only those grid cells encountered by trajectories. This is due to the 10km threshold introducing a maximum variance in result, while a Courant number could be based on an average over a large range of velocity values. Arguably a maximum velocity value could be used in Courant number calculations to approximate a similarly conservative result, but the method offered in this study has the benefit of inherently reflecting only the trajectory-encountered velocity values.

Both the RF and TR tests are representative of the variability in current velocities over time and can be used to assess this variability within the model. The RF result of 150–160 releases per year as equivalent to a daily release (at 700m and 1000m) suggest currents in this daily averaged model vary on the scale of roughly every two days. As tidal cycles are averaged out, this is representative of topographically induced mesoscale activity in the area. The TR result demonstrates high interannual variability in current velocities. This can be assessed against the North Atlantic Oscillation (NAO) data which is often attributed to driving large scale interannual hydrodynamic variability in the area due to its effect on convection regimes [46]. The test results show that the NAO dataset would not perform as well as the full test dataset if the 0.05 FUV variance threshold is deemed appropriate. Some literature agrees with this assessment, with NAO being linked to but not fully accounting for the interannual variability in the complex hydrodynamics of the Rockall Trough region [31, 43].This could have considerable consequence for the amount of data required to build PPDs valid over larger timescales, but at least the FUV and correlation scores can provide some quantitative estimate of how much is, or is not, captured within an NAO based dataset. As it stands using NAO selected years in this study would have a correlation to a five year baseline of approximately 0.92 (700m), 0.89 (1000m) and 0.95 (1500m) which may be considered adequate depending on the study premise.

This groundtruthing processes can inform the scenarios for future studies using this model set up; discerning whether the model set up should be used at all and further putting limits on the interpretations which can be drawn. The results of this study may suggest that HYCOM and CMS broadly agree with the observed hydrodynamics of the study area, but simulations cannot well represent rare dispersal events. Therefore all future studies using this model set up should be concerned with average PPDs and interpreted within this context. The lack of tides, sub-mesoscale, and even some mesoscale processes means that any results should be considered overestimates of dispersal abilities as the majority of these un-parameterised processes would have a retentive effect [48, 49]. Due to these inadequacies arguably the model would be better served as a statistical representation of dispersal probabilities rather than a deterministic model of larval fates.

The results of the HS over time test confirm that PLD will have an effect on positional sensitivity (Fig 4). These findings demonstrate the fact that autocorrelated tracks over time will eventually become free to deviate by accessing different instructions to the baseline (Fig 4, right-hand diagram). Therefore the longer the data is tracked, the more sensitive the parameter value becomes. This effect could be seen either as a need for a smaller separation distance when particles are tracked for longer, or as an increase in error with longer tracking times. Either way the result is informative as to how the model can be run and interpreted.

Ecological and deep-sea consequences of these results

Although primarily representative of model performance, many of these results can be interpreted within an ecological context and may inform directions of future research.

Kough and Paris [50] recently undertook a study of spawning periodicity, akin to the RF test, and interpreted the results in terms of the ecological consequences of different spawning strategies. Spawning periodicity was found to control the number and persistence of reef network dispersal connections, with larval behaviour stabilising these connections. They conclude that spawning periodicity should be accurately included within biophysical models of larval dispersal due to its large potential impact on dispersal ability. In the instance where the RF cannot accurately be determined, as is likely especially in deep-sea ecology, this study offers a method of statistically predicting PPDs as opposed to the deterministic approach made possible with accurate information. The range of PPDs generated by undertaking sensitivity tests can provide potential maximum and minimum bounds of dispersal or be combined into a single probabilistic PPD. This way a useful prediction can still be made even when species specific data is lacking.

The TR test further supplements conclusions drawn by Kough and Paris [50], particularly in the event of seasonal spawners (which do also occur in the deep sea e.g. *Henricia lisa* (Clark 1949, Echinodermata) [41] or *Lophelia pertusa* (Linnaeus 1758, Cnidaria) [51]). The interannual variation in hydrodynamic conditions exemplified by the TR test shows the potential for change in PPDs over time. In which case the larvae of seasonal spawners may sometimes be released asynchronously, accessing different current patterns from previous cohorts. This may impact upon population persistence or potentially even drive speciation events [52].

Of importance to deep-sea ecological research is the effect of depth on parameter sensitivity. As mentioned previously this sensitivity can be linked to reduced current speeds and variability at depth (at least in this study area). This may mean that organisms accessing deeper currents have reduced potential dispersal abilities, and therefore rely upon stepping-stone like dispersal within larger metapopulations. While there is some evidence in support of this (e.g. abyssal bivalves, [53]) there is yet to be enough empirical data to ground-truth this theory. The effect of depth on parameter sensitivity also means that empirical positional data does not need to be of as high quality/resolution at depth, which may be a relief to deep-sea ecologists faced with, for example, the positional data of a trawl's start and end points rather than a modern high resolution ROV location.

Summary and Recommendations

This study was undertaken in order to better inform future work in the field of biophysical dispersal models and to enable more deep-sea ecologists to perform such modelling studies. To this end we supply the following step-by-step process, to summarise our advice on sensitivity tests, with case study examples shown to demonstrate the thought process.

1. Start Point
   You will have:
   - Already chosen a model set up (comprising of hydrodynamic model(s) & particle simulator).
   - Identified your study area.
   - Recognised there are parameters you need where the optimal value is unclear, and/or have recognised you are unaware of the models capabilities and limitations.
   - Planned the sort of ecological questions you wish to be asking to ensure that thresholds and parameter choice are suited to future work, including the tracking time/PLDs.
     E.g. this study selected Hycom & CMS both of which are freely available and have previously been used in larval dispersal studies. Tests were performed in the Northeast Atlantic with the aim to pursue future work simulating passive larval release from benthic invertebrates within marine protected areas (MPAs) in the study area.
2. Identify parameters for sensitivity testing
   - It is worth performing sensitivity tests for as many parameters as possible, but if you need to prioritise then consider those where the optimal value is unclear, and at least select

  those which will test the modelled range of mixing strengths through space and time (i.e. representing x/y, depth, time) in your study area.

  - If biological individual based model parameters (e.g. behaviour) will be used in the final study, consider performing sensitivity tests on these also, especially where there is any uncertainty as to optimal values.
    E.g. this study considers 5 parameters, including horizontal separation (x/y), vertical separation (depth), and release frequency/temporal range/timestep (time). All parameters affect the two most computationally intensive aspects of the simulation–the total number of particles being simulated, and the number of velocity fields being loaded into the simulator. Additional parameters worth testing in our case may include diffusivity values and subsequently the number of particles released per spawning event, these will be tested but are excluded here as they are specific to this particle simulator.

3. Identify the methods required for each parameter

  - This paper offers methods which can be used either where there are individual track baselines, or where there are multitrack baselines. Consider the impact of your research aims upon the methods you use e.g. will you be interested in average dispersal pathways or rare dispersal events?
  - In deep-sea studies your research may span a large depth range, if so be sure to stratify your testing in order to test for sensitivity differences with depth.
  - If multiple PLDs will be used consider retesting for each different tracking time
  - Consider what factors may affect each parameter and how they affect each other before designing your tests and order of testing.
    E.g. our research will be interested in average dispersal pathways. Baseline tests were performed at 3 different depths which span the depth range included in future work. Aspects were considered such as the interaction between timestep and horizontal separation, and the impact of hydrodynamic model output structure on vertical separation. Tests against tracking time suggest recommendations will be different for different PLDs

4. Perform the tests and interpret the results

  - We recommend monitoring simulations (e.g. simulation time, record of memory usage) to gauge the parameter's impact upon computational effort.
  - The results should help you define input parameter values, gain an understanding of how mixing occurs in your study area within your model, and gauge your capability to fulfil the full predictive power of your model setup.
  - At this point some preliminary groundtruthing can be performed in order to assess the adequacy of your model in your study area. Comparison to existing literature or datasets (e.g. Argo floats) may reveal why your model performs the way it does (e.g. water mass structures) and/or flag your model as inadequate, in which case you must start the process again with a new model setup.
    E.g. results in this case inform the structuring of release grids from specific sites (marine protected areas)–now with optimised values for horizontal and vertical separation of points. Should this result in too many release points (decided by computational power), multiple simulations can be run at shallower depths, using the maximum sub-optimal number of releases still possible, with release location randomly varied at a minimum distance of 0.005° from previous simulations. The effect of depth may recommend a

stratification of simulations when performing ecological studies, with deeper MPAs requiring fewer (less separated) release points. Stratification will be informed by the watermass structure within the model. Timestep values did not greatly affect the time taken to run simulations so a timestep of one hour can be used throughout all future simulations. For species where no spawning periodicity is known, a release frequency per year will be set to weekly at a minimum (~90% correlation to a daily output), and will use at least three years spanning max/min/neutral NAO states (90% correlation to five years of simulated different NAO states).

5. Proceed to ecological studies using your model setup
    - You should now have a more intimate knowledge of the model setup workings and capabilities, allowing you to design your experiments appropriately and interpret your results responsibly.
      E.g. fortunately, as we are interested in average dispersal pathways this model setup should be adequate although this will not be proven until groundtruthed. Rare dispersal events will not be well represented especially at depth. Due to the lack of small scale hydrography represented, even in shallower water, results will likely be overestimates as sub-mesoscale and micro-scale hydrography would likely have promoted retention.
6. Repeat the process if the model set up or study area are changed
    - New model setups should be retested due to the effect of model resolution, structure, and strength and variability of modelled mixing, on the sensitivity of parameters.
    - As the strength of mixing in the study system (within the model) affects parameter sensitivity, different locations including different depths must be retested also.
      E.g. the results of this study are only suited to other dispersal research in the Rockall Trough region of the Northeast Atlantic using HYCOM and CMS ideally between 700m and 1500m (although some guidance is provided between 200m and 1750m due to the vertical separation test).

Supporting Information

S1 Fig. Boxplots accompanying timestep, horizontal separation, and vertical separation tests to provide a record of interquartile range and outliers per increment. This data may aid estimates of error if sub-optimal values must be selected.
(PDF)

S1 File. List of release location coordinates and results of ANCOVA tests of increment and depth effects.
(PDF)

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