



Dispersal and population connectivity in the deep North Atlantic estimated from physical transport processes



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ABSTRACT

Little is known about how larvae disperse in deep ocean currents despite how critical estimates of population connectivity are for ecology, evolution and conservation. Estimates of connectivity can provide important insights about the mechanisms that shape patterns of genetic variation. Strong population genetic divergence above and below about 3000 m has been documented for multiple protobranch bivalves in the western North Atlantic. One possible explanation for this congruent divergence is that the Deep Western Boundary Current (DWBC), which flows southwestward along the slope in this region, entrains larvae and impedes dispersal between the upper/middle slope and the lower slope or abyss. We used Lagrangian particle trajectories based on an eddy-resolving ocean general circulation model (specifically FLAME – Family of Linked Atlantic Model Experiments) to estimate the nature and scale of dispersal of passive larvae released near the sea floor at 4 depths across the continental slope (1500, 2000, 2500 and 3200 m) in the western North Atlantic and to test the potential role of the DWBC in explaining patterns of genetic variation on the continental margin. Passive particles released into the model DWBC followed highly complex trajectories that led to both onshore and offshore transport. Transport averaged about 1 km d^{-1} with dispersal kernels skewed strongly right indicating that some larvae dispersed much greater distances. Offshore transport was more likely than onshore and, despite a prevailing southwestward flow, some particles drifted north and east. Dispersal trajectories and estimates of population connectivity suggested that the DWBC is unlikely to prevent dispersal among depths, in part because of strong cross-slope forces induced by interactions between the DWBC and the deeper flows of the Gulf Stream. The strong genetic divergence we find in this region of the Northwest Atlantic is therefore likely driven by larval behaviors and/or mortality that limit dispersal, or local selective processes (both pre and post-settlement) that limit recruitment of immigrants from some depths.

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1. Introduction

Understanding how populations are connected through dispersal is of fundamental importance in ecology, evolution, conservation and management, and will play a crucial role in predicting how organisms might respond to contemporary anthropogenic stresses. From an evolutionary perspective, dispersal influences gene flow among populations, which in turn affects genetic diversity, phylogeographic patterns, adaptation to local selective pressures, and ultimately the likelihood of speciation (reviewed in Nosil, 2012). At an ecological scale, dispersal can influence demographic processes (Roughgarden et al., 1985), source-sink dynamics (Holt, 1985), metapopulation (Hanski, 1999) and

metacommunity persistence (Leibold et al., 2004), the maintenance of biodiversity (Mouquet and Loreau, 2003; Hubbell, 2001), the spread of invasive species (Neubert and Caswell, 2000; Byers and Pringle, 2006; Caswell et al., 2011) and play a vital role in management and conservation (Palumbi, 2003; Botsford et al., 2003, 2009; Gaines et al., 2003, 2010). Connectivity links dynamics at different scales and integrates local heterogeneity affecting regional-scale dynamics and long-term persistence. Quantifying the scale over which populations are connected is vital to understand the relative importance of various ecological processes, identify the appropriate scales of environmental influence in driving population dynamics and determine how local communities might respond to environmental change.

The extent to which populations are connected is determined by the scale, intensity, direction and frequency of dispersal among populations as well as post-settlement processes that influence the fitness of recruits. For many sessile marine invertebrates, dispersal occurs during the larval stage. Larvae (or gametes) are

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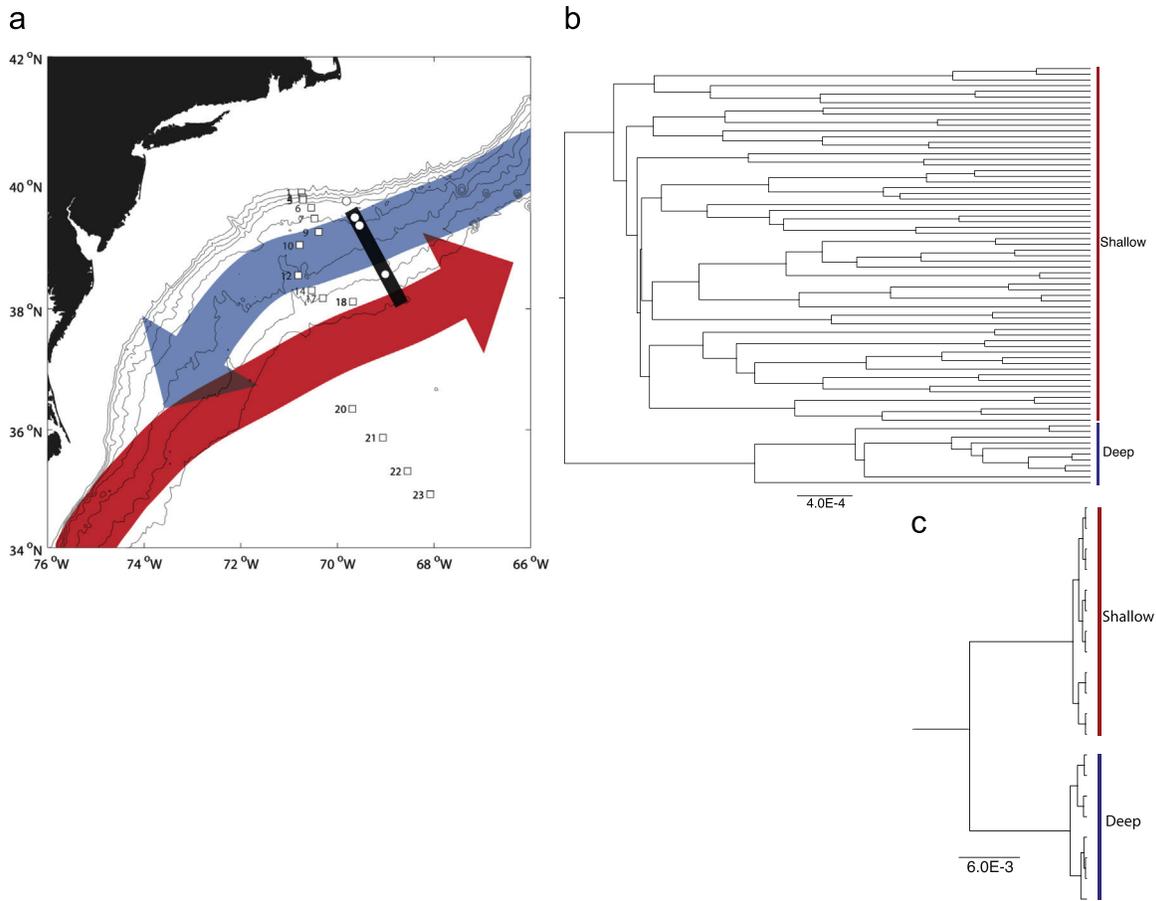


Fig. 1. (a) Map of the locations where previous genetic work was conducted (squares) with station numbers given next to each box and the locations where simulated trajectories were initiated for Lagrangian estimates of dispersal and connectivity (circles). The solid dark rectangle indicates the location of the Line W moored array (Toole et al. 2011). DWBC and Gulf Stream paths are illustrated schematically by blue and red block arrows, respectively. Isobaths are shown every 500 m. Note that the main genetic breaks in protobranch bivalves occurred between stations 9 and 14. (b) Multilocus phylogenetic relationships among individuals from shallow (stations 4, 5, 6, 7, and 9) and deep (10, 17, and 18) stations for *Deminucula atacellana* based on five loci (from Jennings et al. (2013)). (c) Multilocus phylogenetic relationships among individuals from shallow (6, 7, and 10) and deep (14, 17, and 18) stations for *Neilonella salicensis* based on three loci (from Glazier and Etter (2014)).

released into the water column where they are dispersed by the currents due to both advective and diffusive processes. The speed, variability and direction of the currents have a strong effect on where larvae move, especially if they exhibit little behavior and disperse essentially as passive particles. However, the interaction between larval behavior and physical transport processes (Paris et al., 2007; North et al., 2008; Sakina-Dorothée et al., 2010; Morgan, 2014) as well as environmental heterogeneity in productivity, local fecundity and larval mortality (White et al., 2014) can profoundly influence the patterns and magnitude of connectivity among populations. Post-settlement processes can also alter patterns of connectivity if recruits do not survive to reproduce or have reduced fitness. Connectivity thus represents the integration of both biological and physical processes and involves complex interactions between benthic and pelagic forces.

Measuring connectivity in marine organisms with small propagules that drift for various lengths of time in the ocean is extremely difficult. Although the length of time larvae drift in ocean currents has been estimated, how that translates to distance and direction traveled and thus connectivity among populations is not well understood. Because of its obvious importance in ecology, evolution and conservation, a number of techniques have been developed to estimate dispersal based on a variety of complementary approaches including larval ecology, hydrographic models, coupled bio-physical models and empirical estimates based on genetics and geochemistry (reviewed in Levin (2006),

Thorrold et al. (2007), Cowen and Sponaugle (2009), Lowe and Allendorf (2010), Leis et al. (2011) and Kool et al. (2013)). Each technique has inherent advantages and disadvantages such that a combined approach, when possible, provides a more accurate estimate of connectivity and a more complete understanding of the forces that shape patterns of connectivity (Levin, 2006; Lowe and Allendorf, 2010; Leis et al., 2011).

While considerable advances have been made in estimating dispersal in shallow-water ecosystems (e.g. Kinlan and Gaines, 2003; Bradbury et al., 2008; Shanks, 2009; Selkoe and Toonen, 2011; López-Duarte et al., 2012; Riginos et al., 2014), much less is known about dispersal in the deep ocean, except perhaps around hydrothermal vents (e.g. Marsh et al., 2001; Mullineaux et al., 2002, 2010, 2013; Adams and Mullineaux, 2008; McGillicuddy et al., 2010). Recent estimates of the scale of dispersal in deep-sea organisms based on Planktonic Larval Duration (PLDs – e.g. Young et al., 2012) or genetic patterns of isolation by distance (Baco et al., 2014) suggest larvae can disperse 100s of km and are quite similar to shallow-water organisms in dispersal distance, despite lower temperatures that likely extend PLDs (e.g. O'Connor et al., 2007; Peck et al., 2007; Kelly and Eernisse, 2007) and weaker current velocities typically associated with increasing depth. In the deep sea, few have estimated dispersal based on physical processes (e.g. Yearsley and Sigwart, 2011; Young et al., 2012; Sala et al., 2013) and rarely have the predictions from physical transport models and/or PLDs been compared to inferences derived from patterns of

genetic variation (e.g. Henry et al., 2014). Such a combined approach provides a powerful framework to test the validity of various hypotheses and provides a more complete understanding of the potential explanations for observed patterns of genetic variation (e.g. Siegel et al., 2003; Sotka et al., 2004; Baums et al., 2006; Galindo et al., 2006, 2010; Weersing and Toonen, 2009; White et al., 2010; Alberto et al., 2011; Sunday et al., 2014). Here we use simulated Lagrangian particle trajectories based on an eddy-resolving ocean general circulation model (specifically FLAME – Family of Linked Atlantic Model Experiments) to estimate the nature and scale of dispersal at bathyal depths in the western North Atlantic and to test the potential role of the Deep Western Boundary Current (DWBC) in explaining patterns of genetic variation on the continental margin.

In particular, we test the hypothesis that the strong genetic divergence at bathyal depths in the western North Atlantic might be due to the DWBC impeding gene flow between upper and lower bathyal depths. Population genetic analyses of protobranch bivalves have repeatedly indicated strong genetic breaks along depth gradients in the western North Atlantic such that populations above and below approximately 3000 m are highly divergent (Etter et al., 2005; Zardus et al., 2006; Jennings et al., 2013; Glazier and Etter, 2014). Populations separated by as little as 40 km distance and 100 m depth exhibited pronounced divergence at multiple loci (see Fig. 1). The strong divergence at such small scales is very surprising because dispersal over that distance is likely within the dispersal window of their lecithotrophic larvae (Zardus, 2002; Scheltema and Williams, 2009) and no obvious topographic features exist in this region that would impede gene flow.

The present day DWBC flows equatorward along the continental slope between 700 and 4000 m (Fig. 2) with mean flows of 5–10 cm s⁻¹ (Pickart and Watts, 1990; Toole et al., 2011). The genetic break occurs within the DWBC, so one possible explanation for the observed divergence is that the relatively strong mean southwestward flow of the DWBC entrains passively (or weakly swimming) dispersing demersal larvae advecting them equatorward, preventing cross slope dispersal between the upper/middle slope and the lower slope or abyss. Despite the relatively strong mean flows oriented along the isobaths, neutrally buoyant free-drifting floats released at depth and Lagrangian simulations of particle trajectories in the DWBC suggest that circulation is highly complex and departs considerably from time-averaged mean

southwestward flow (Bower and Hunt, 2000a, 2000b; Bower et al., 2009, 2011, 2013; Lozier et al. 2013). Both empirical and simulated trajectories indicate considerable mesoscale variability with a high potential of cross-slope movement (i.e. between depth regimes), especially where the DWBC interacts with the Gulf Stream and its associated eddies. The highly complex mesoscale flows and the high probability of floats and simulated particles to move across-slope raises questions about whether the DWBC impedes larval exchange between upper and lower bathyal populations. To test the hypothesis that connectivity between populations from upper and lower bathyal depths might be precluded by the DWBC, we estimated dispersal trajectories of simulated passive larvae (neutrally buoyant particles) released along a depth gradient adjacent to our genetic samples in the western North Atlantic (Fig. 1). Specifically, we examined whether particles would move across slope and the distance they moved given certain PLDs.

2. Methods

2.1. Physical transport model

The ocean general circulation model used in this analysis to simulate particle trajectories is the highest resolution member of the Family of Linked Atlantic Modeling Experiments (FLAME) (Böning et al., 2006; Biastoch et al., 2008). This model uses a primitive equation, z-coordinate framework (Pacanowski, 1996) that includes isopycnal mixing, biharmonic friction and a bottom boundary layer parameterization for temperature and salinity (Beckmann and Döscher, 1997). In the vertical, the model domain is divided into 45 levels whose spacing increases from 10 m at the surface to a maximum of 250 m at the deepest levels. The ETOPO5 digital bathymetric database defines the seafloor for the model. This regional model spans from 18°S to 70°N on a Mercator grid with a resolution of 1/12° latitude × 1/12° cos(y) longitude, where y is latitude. The initial temperature and salinity fields of the model are specified by the superposition of January 1990 monthly mean anomalies (Levitus et al., 1994a, b) and annual means (Boyer and Levitus, 1997). During the simulation, sea surface salinity was restored to the monthly climatology with a 15-day time scale. At the open boundaries of the model, temperature and salinity were maintained at climatological values. Flow through the southern

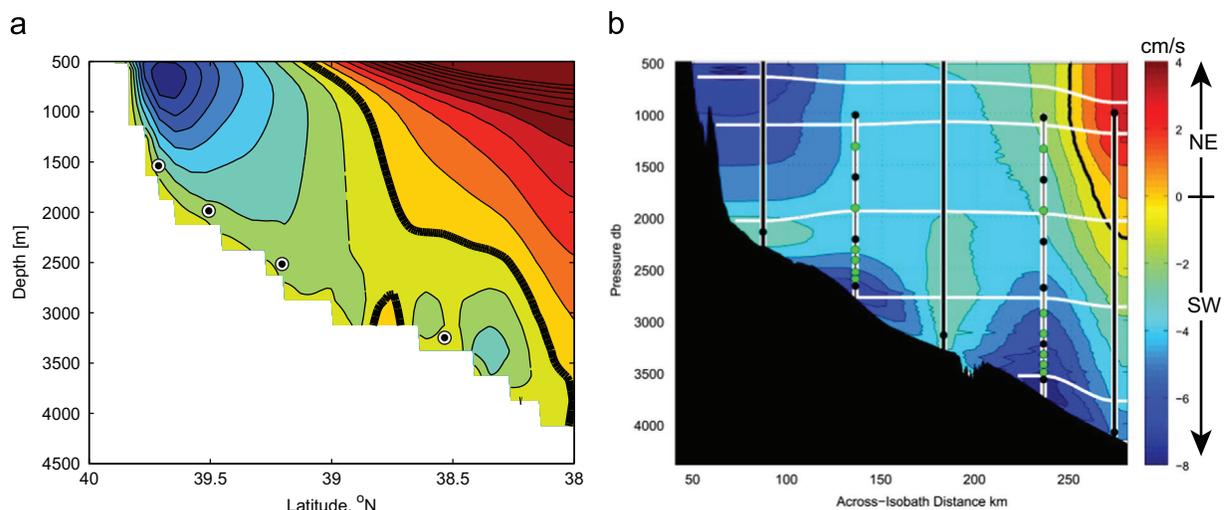


Fig. 2. (a) Section of time mean current speed perpendicular to the Line W section from 15-year run of FLAME. Circled black dots indicate model grid points where simulated trajectories were initiated. (b) Measured flows derived from the Line W array (From Toole et al. (2011); current meters are indicated by black dots, temperature/conductivity meters are indicated by green dots) across the same transect in (a). Velocity is color coded with negative values indicating southwestern flow and positive values northeastern flow. The similarity indicates that the major flow features are well characterized in the circulation model.

boundary was specified by the Sverdrup relation while the northern boundary transport was based on output from a regional Arctic Ocean model (Brauch and Gerdes, 2005). The model was spun up from rest with 10 yrs of ECMWF (European Center for Medium-Range Weather Forecasting) climatological forcing. The model was then forced with a superposition of the 1990–2004 monthly anomalies of the NCEP/NCAR (National Center for Environmental Prediction/National Center for Atmospheric Research) reanalysis data (Kalnay et al., 1996) and the climatological forcing applied during the spin up. Model temperature, salinity, and velocity fields were stored as snapshots once every 3 days during the 1990–2004 period.

Numerical trajectories of Lagrangian particles were calculated offline by integrating the FLAME three-dimensional velocity field (Getzlaff et al., 2006; Hüttl-Kabus and Böning, 2008). More information about the trajectory calculation algorithm is documented in Gary et al. (2011). Since vertical velocity information was not stored during the original model run to conserve space, the vertical integral of the horizontal velocity divergence is used to determine the vertical velocity at each time step.

FLAME output has been shown to compare favorably with observations in several studies. Eden and Boening (2002) found good agreement in the width, maximum velocity and transport of the mean boundary currents (West Greenland and Labrador Currents) and with the spatial distribution, magnitude and seasonality of surface eddy kinetic energy (EKE) in the Labrador Sea. Böning et al. (2006) showed that FLAME reproduced the gradual increase in sea surface height in the Labrador Sea following the switch in the sign of the North Atlantic Oscillation (NAO) index after 1994 that was observed with altimetric sea surface height measurements (Hakkinen and Rhines, 2004), as well as the decadal trends in the transport of the DWBC observed with current meters at 53°N (Dengler et al., 2006). Getzlaff et al. (2006) found good agreement between FLAME and direct observations of the mean western boundary current transport at 53° and 43°N, as well as with subsurface EKE levels at 43°N, where the model captured about 90% of the observed variability at 1500 m depth.

FLAME has been used to investigate particle dispersal in the subsurface North Atlantic in a number of studies (Bower et al., 2009, 2011; Burkholder and Lozier, 2011a, 2011b, 2014; Gary et al., 2011, 2012, 2014; Lozier et al., 2013; Kwon et al., in press). Particularly relevant to the present study is a quantitative comparison between Lagrangian observations in the North Atlantic DWBC and simulated particle trajectories from FLAME by Lozier et al. (2013). These authors applied the Kolmogorov–Smirnov statistical test specifically designed for Lagrangian data by van Sebille et al. (2009) to compare (a) acoustically tracked subsurface float trajectories at 3000 dbar released in the DWBC between Newfoundland and Cape Hatteras in 1994 and 1995 (Bower and Hunt, 2000a, 2000b) to (b) similarly initiated numerical particle trajectories computed using FLAME. The time-varying test statistic, D_n , is the instantaneous maximum difference between cumulative probability distributions computed for the scatter of observed and simulated floats at each time step. If the trajectories in both ensembles are identical, $D_n=0$: the maximum value of D_n is 1. The power of the van Sebille et al. (2009) test is quantified by performing Monte Carlo iterations to determine the confidence level, α , around the test statistic. If $\alpha < 0.05$, we reject the null hypothesis that the trajectory ensembles come from the same spatial distribution. As documented in Lozier et al. (2013), visual comparison between the observed and simulated trajectories was favorable: the simulated pathways show evidence of offshore detrainment upstream of Cape Hatteras on a spatial scale comparable to the observed pathways. Also, the along-DWBC pathways simulated by the numerical particle trajectories were qualitatively similar to the observed trajectories. The time average value of

$D_n=0.26 \pm 0.05$ with a confidence level of $\alpha=0.92 \pm 0.08$. Lozier et al. (2013) concluded therefore that the spatial distributions of the observed and simulated trajectories were statistically indistinguishable. This result is consistent with a similar comparison between observed and simulated trajectories initiated in the DWBC near 50°N at 700 and 1500 dbar (Gary et al., 2011).

Fig. 2a shows the time-mean model current speed perpendicular to the transect shown in Fig. 1a, which coincides with “Line W”, a section that was occupied with a moored array including current meters, T/S sensors and moored profilers from 2004–2014 (first four years are described in Toole et al. (2011)). The four simulated particle release sites are shown by black dots with circle. The model DWBC is evident as negative mean flow blanketing the continental slope between the 400-m and 4000-m isobaths. The strongest mean DWBC flow exists at about 700 m, where it is more than 10 cm/s toward the southwest. A second velocity extremum is at 3400 m over the 3800 m-isobath, where mean current speed is about 4 cm/s. The strong northeastward mean model flow is indicative of the Gulf Stream, located just offshore of the DWBC in this location (Fig. 1a). For comparison, Fig. 2b shows the 4-year mean along-slope current speed from the Line W current observations. The shallow and deep DWBC velocity cores in Fig. 2a are also apparent in the observations: centered at about 600 m over the mid-slope, where peak southwestward speeds were about 8 cm/s, and above the 3700-m isobath, where the mean DWBC speed was about twice as large as in the model at 8 cm/s. A third slightly weaker velocity core not seen in the model was observed at about the 2750-m isobath. As in the model section, the opposing Gulf Stream flow was observed by the Line W array, although at a more offshore position. This data-model difference is not surprising: EGCMS are notorious for not accurately reproducing the exact Gulf Stream separation latitude. While this may impact the details of where exactly individual particles first encounter the Gulf Stream, it is not expected to significantly affect the general results for several reasons: (1) the release positions for the model particles are all well within the DWBC as defined in both the model and observations; (2) the more inshore position of the model Gulf Stream may in fact be more representative of the position of the Gulf Stream relative to the benthic sampling sites, which are closer to Cape Hatteras (Fig. 1a) where the Gulf Stream is closer to the slope; and (3) Lozier et al. (2013) showed good statistical agreement between simulated and observed trajectories at 3000 m in this region.

2.2. Particle release details

Particle trajectories were initialized at 4 depths across the continental slope (Fig. 1) in the deepest model layer at each location, which has a thickness of 250 m. Model velocity in this layer is representative of the flow above the frictional bottom boundary layer. Particles were released every 15 days from January 1, 1990 until the end of 2004 generating 360 simulated trajectories at each site. Their positions were recorded every 3 days. Releases were continuous throughout the years to better capture inter-annual variability in deep-water flows and because it more closely mimics the year-round reproductive biology typical of deep-water protobranchs (Tyler et al., 1994; Scheltema and Williams, 2009). Protobranch bivalves release perilympha larvae that are thought to disperse demersally for days to weeks (Zardus, 2002; Scheltema and Williams, 2009), although the low temperatures at bathyal depths may extend development rates and PLDs (O'Connor et al., 2007; Peck et al., 2007; Kelly and Eernisse, 2007). Recent estimates of PLDs for some deep-sea invertebrate larvae exceeded one year (Young et al., 2012). To estimate how larvae might disperse from sites on the continental slope near where bivalves have been sampled, we analyzed particle distributions and potential connectivity maps at 4 time scales; one month to

approximate the PLD time inferred based on shallow-water relatives, 6 months and 1 year to consider potential dispersal if development times are extended due to the lower temperatures at bathyal depths and 5 years to quantify patterns based on multi-generational stepping-stone dispersal.

To provide a statistical description of particle trajectories (potential connectivity) we created contour maps that depict the frequency of particle visits to a particular model location (defined by a box with the same resolution as the model, $1/12^\circ \times 1/12^\circ$) over a specified time scale (i.e. 30, 180, 360, and 1500 days). The position of each particle was recorded every 3 days and grid box counters were incremented by the number of particle visits in each box. This provides a contour plot of the particle positions (on 3 day intervals) integrated over the first 30 (180, 360 and 1500) days. Although this allows a single particle to increment a specific grid box more than once (either due to repeat visits resulting from convoluted trajectories or by slow advection where they remain in a single grid for more than three days) it represents a quantitative picture of the integrated potential connectivity. The probability that a larva settles within a particular spatial grid should be proportional to the particle visits. Since we do not know the exact PLDs of most deep-sea organisms or when they become competent to settle, it seems prudent to estimate connectivity using PLD “windows” (e.g. 0–30 days, 0–180 days, etc.).

3. Results

3.1. Trajectories

Individual particle trajectories indicated that neutrally buoyant particles did not typically remain trapped in the mean southwest

flow of the DWBC, but instead followed complex, highly convoluted paths that often resulted in cross slope transport (Fig. 3). While initial particle transport was often southwest, particles soon began to drift more eastward or westward moving across slope, indicating dispersal across depth regimes was possible. Off-shore transport appeared to be considerably more likely than on-shore, although both occurred.

3.2. Potential connectivity maps

The trajectory contour maps (Figs. 4–7) depict the frequency of particle visits at a specific model location providing an estimate of potential connectivity—where passive-dispersing larvae could have settled during a particular dispersal time frame (e.g. during the first 30 days). Essentially, these figures represent average (integrated over 15 years – 1990–2004) potential connectivity maps. Through time the contour maps show how the cloud of particles spread and how connectivity might change with different PLDs. The figures also include the position of particles (orange dots) at a specific time (30, 180, 360 and 1500 days).

After 30 days (Fig. 4), the connectivity maps and particles overlap among adjacent depths indicating they are likely to exchange some larvae despite the clear influence of the DWBC. The least overlap occurs between the two deepest stations, which were separated by somewhat larger distances (99 km). However, at longer time scales (Figs. 5–7) the density maps overlap considerably suggesting even the two deeper sites would be well connected.

The influence of the DWBC was most intense at the shallowest release points (1500 and 2000 m) and during the first 30 days as shown by the shape of the connectivity maps and the position of

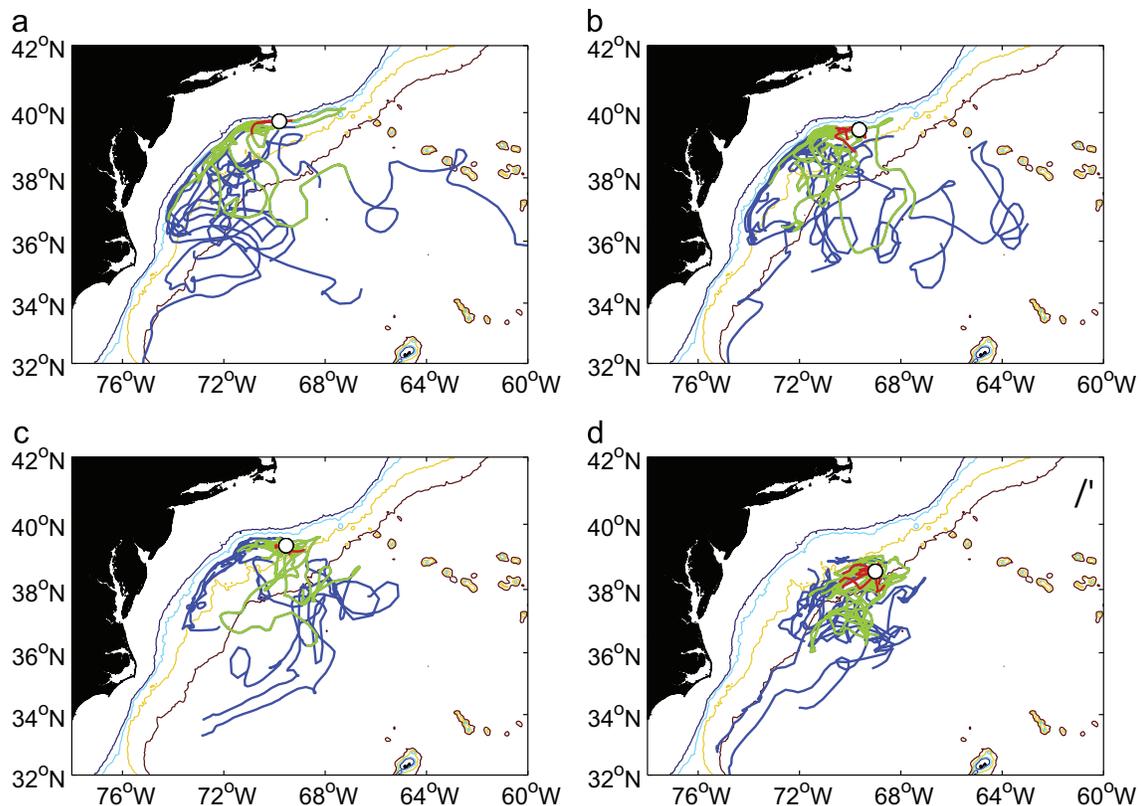


Fig. 3. Ten sample trajectories of neutrally buoyant particles released at 1500 m (a), 2000 m (b), 2500 m (c) and 3200 m (d) depth in the western North Atlantic. The open circle indicates the release point. Trajectories are color-coded based on time since release: 0–30 days – red, 31–180 days – green, 181–360 days – blue. Isobaths every 1000 m are color-coded black, cyan, yellow, and brown respectively.

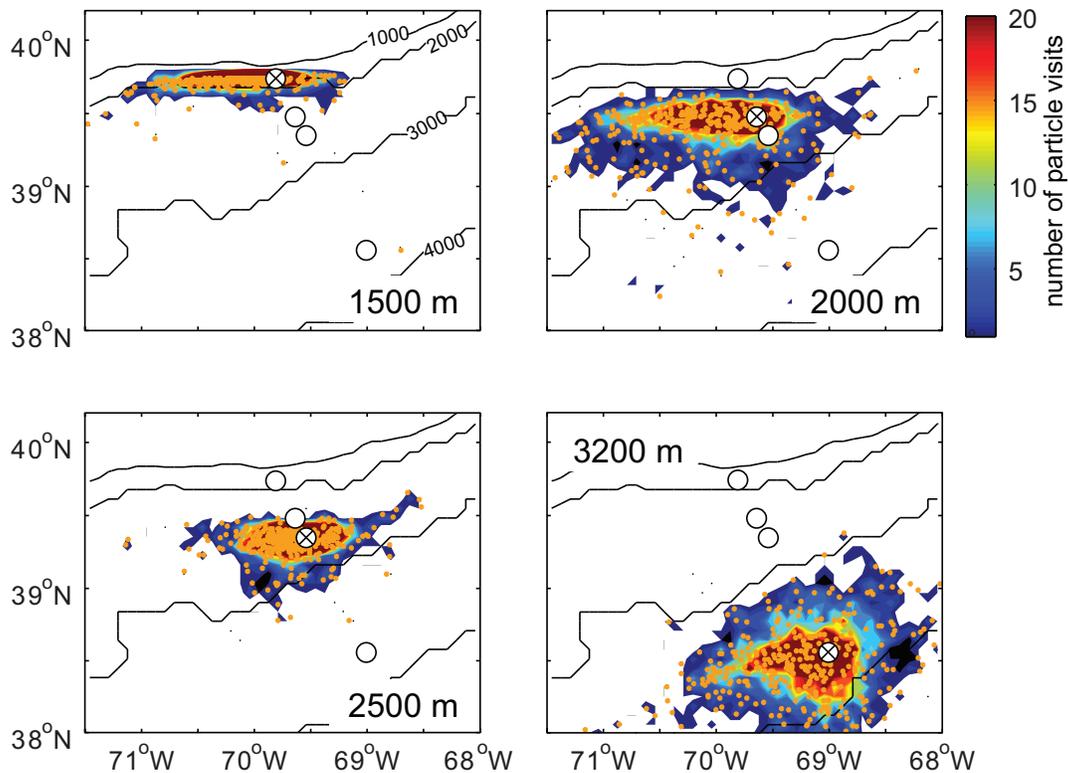


Fig. 4. Potential connectivity maps of 360 particles after 30 days for different release depths in the DWBC. The shading indicates the number of particle visits at a specific model grid point (defined by a box with the same resolution as the model, $1/12^\circ \times 1/12^\circ$) during the first 30 days after release. The warmer the color, the more particles visited that grid box. The position of each particle at 30 days after release is shown as an orange dot (note that panel axes were chosen so that the structure of the contours was clear, which meant that some orange end point dots fell outside the panel axes). A circle with an X indicates the release point. Open circles depict the other three release points used in the study. Isobaths are depicted by thin black lines every 1000 m.

the particles (Fig. 4). However, even at these depths and short time frames, some particles moved north and east from the release points, against the prevailing flow due to mesoscale variability. As with the individual particle trajectories (Fig. 3), these synoptic patterns indicate that initial dispersal is southwestward, but through time is strongly influenced by cross-slope processes that result in a more eastward spreading cloud (Figs. 5–7). For example, at 1500 m, particles drifted primarily southwestward along slope with little cross-slope transport for the first 30 days (Fig. 4). By 180 days (Fig. 5), cross-slope transport increased with many particles dispersing eastward from the release point. By 1500 days (Fig. 7), transport includes many trajectories that spread north and east, probably because they were entrained in the deep flows of the Gulf Stream and were advected northeast (see also Bower and Hunt (2000a, b)). Surprisingly, for particles released at 1500 m, relatively few trajectories made it south of 30°N .

In contrast, at 3200 m, the initial spread of particles (first 30 days) is much more uniform around the release point, probably because of the weaker bottom slope and/or weaker mean flows compared to the variability at this depth (Fig. 4). By 180 or 360 days (Figs. 5–6), dispersal appears largely similar to that at 1500 m, but with a somewhat reduced southwestward drift. Interestingly, by 1500 days, the deeper sites experience a much greater southwestward drift, with many trajectories moving south of 30°N , probably because the particles have slipped under the deeper flows of the Gulf Stream and were advected southwest by the DWBC (Bower and Hunt, 2000a, b). The trajectories at 3200 m also include a considerable number that have moved eastward and some that have moved westward onshore. Table 1 gives the percentage of particles at each release depth that are offshore (in deeper water) of their release isobath after each of the time steps

examined. Particles are transported offshore more quickly at the shallower depths, and after 30 days, the deepest site shows a slight onshore tendency. These results are consistent with the idea that the Gulf Stream presents a more formidable barrier to continuous southwestward transport along the slope in the DWBC for the shallower particles (Bower and Hunt, 2000a, b).

In general, advection to the southwest appears to be a function of depth, with greater southwest transport for the shallower sites during the first 360 days, especially the first 30 days (note the shape and dimensions of the red regions). By 1500 days, the pattern reverses with greater southwest transport for the deeper release points and a surprising northeastward spread for the shallowest site. At all depths, some trajectories moved across slope through time.

3.3. Particle displacement

If we consider only displacement from the release points, the distance traveled by particles varied with depth, but not in a simple predictable manner. The mean distance of particles from their release point after 30 days was greatest for the 2000 and 3200 m sites and least at 2500 m (Fig. 8). After 180 days, particles released at the two shallower depths (1500 and 2000 m) were displaced further than those at the deeper sites, and this was also true at 360 days. By 1500 days, displacements were similar for the 3 deepest release points and somewhat smaller for the shallowest depth.

The distribution of displacement distances typically had strong modes and were skewed right with a long tail of particles that dispersed much greater distances than the mean. After 30 days, the mean displacement was 27–58 km (depending on release

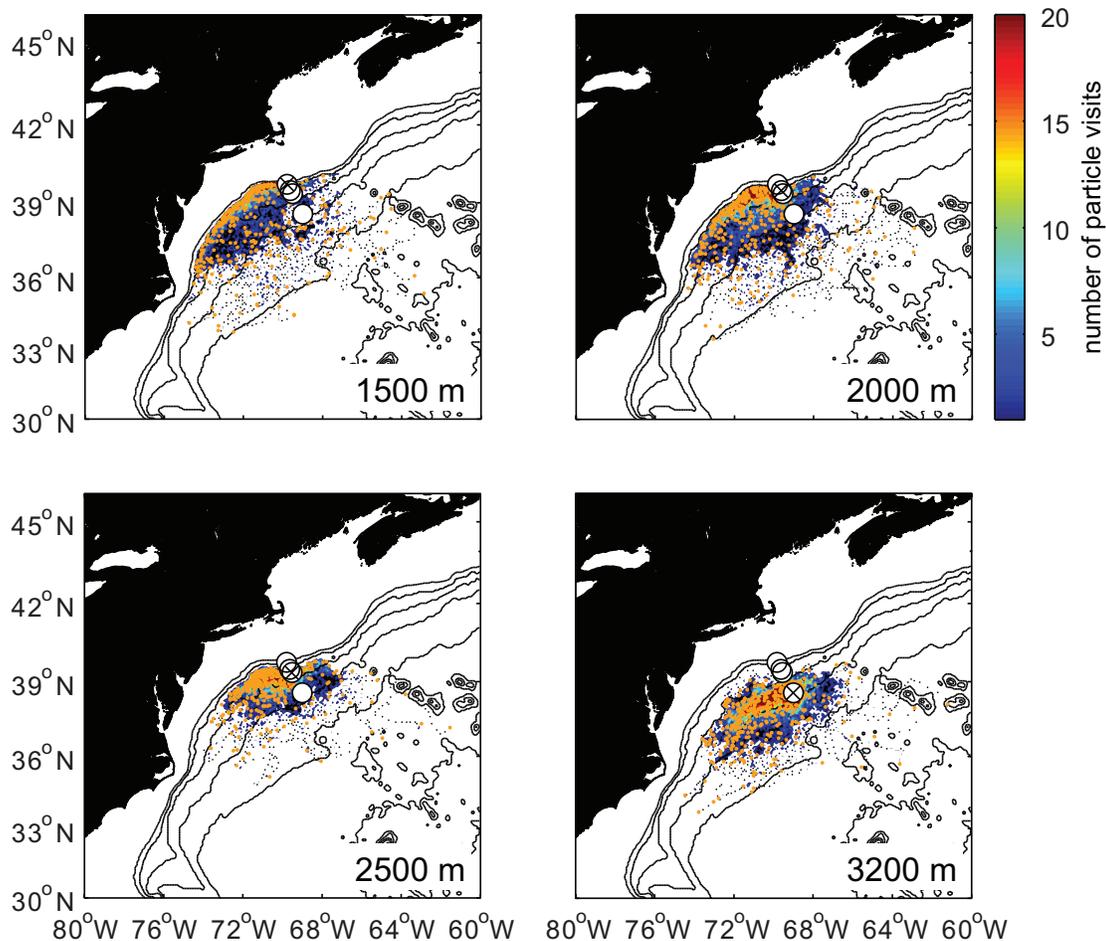


Fig. 5. Potential connectivity maps for different depths of release after 180 days. Details and color codes as described in Fig. 4.

depth), but some particles were more than 200 km from the release point. Similarly, after 1500 days, the mean displacement was ≈ 1100 – 1400 km, but some particles traveled nearly 5000 km from their release point.

4. Discussion

4.1. Dispersal rates and geography

Despite its importance to the ecology, evolution, and conservation of deep-sea organisms, little is known about how larvae might disperse at depth in the deep ocean and what implications that might have for the nature, scale and intensity of connectivity. Our results are based on passively dispersing neutrally buoyant particles that provide a qualitative picture of how the physics might move larvae, without any biology. Larvae are unlikely to remain passive or neutrally buoyant during development, so the results provide an important initial null model of how deep-water currents might affect dispersal.

The numerical simulations indicated that larvae would disperse on average about 1 – 2 km d^{-1} at mid to lower bathyal depths in the western North Atlantic. This is considerably less than dispersal estimates based on numerical simulations of coastal circulation in shallow water (< 200 m) (Siegel et al., 2008; Mitarai et al., 2009; Watson et al., 2010; Drake et al., 2011; Kim and Barth, 2011) and often less than what has been found at shallower bathyal depths

(Yearsley and Sigwart, 2011; Young et al., 2012; Sala et al., 2013). For example, simulated passive dispersal based on models of coastal circulation varied from 3 – 7 km d^{-1} , depending on depth (1 – 75 m), along the Oregon coast (Kim and Barth, 2011) and 2 – 8 km d^{-1} for depths < 20 m along the California coast (Drake et al., 2011). Even at deeper upper bathyal depths median dispersal rates were 1 – 6 km d^{-1} , depending on depth (100 or 500 m) and taxon, in the Northwest Atlantic and Gulf of Mexico (Young et al., 2012), while dispersal rates were 1 – 4 km d^{-1} at 800 – 1440 m in the tropical South Pacific (Yearsley and Sigwart, 2011) and only about 0.5 km d^{-1} at 600 – 2000 m in the Northeast Atlantic (Sala et al., 2013). At abyssal depths, dispersal rates are likely to be significantly less because the currents are substantially slower (Hogg and Owen, 1999). Dispersal rates in general appear to decline with depth, however, the distances larvae disperse and the degree of connectivity will also depend on PLDs, which are likely to be longer in the deep sea due to slower developmental rates at lower temperatures (O'Connor et al., 2007). The PLDs of some deep-water taxa are greater than a year and can exceed 600 days (Arellano and Young, 2009; Bennett et al., 2012; Young et al., 2012).

Although the mean distance our simulated particles dispersed was relatively small, the dispersal kernel was skewed strongly to the right with some particles dispersing much greater distances – up to 4-times the mean (Fig. 8). Rare long distance transport of larvae may have little impact demographically, but play an important role on longer time scales because it can maintain

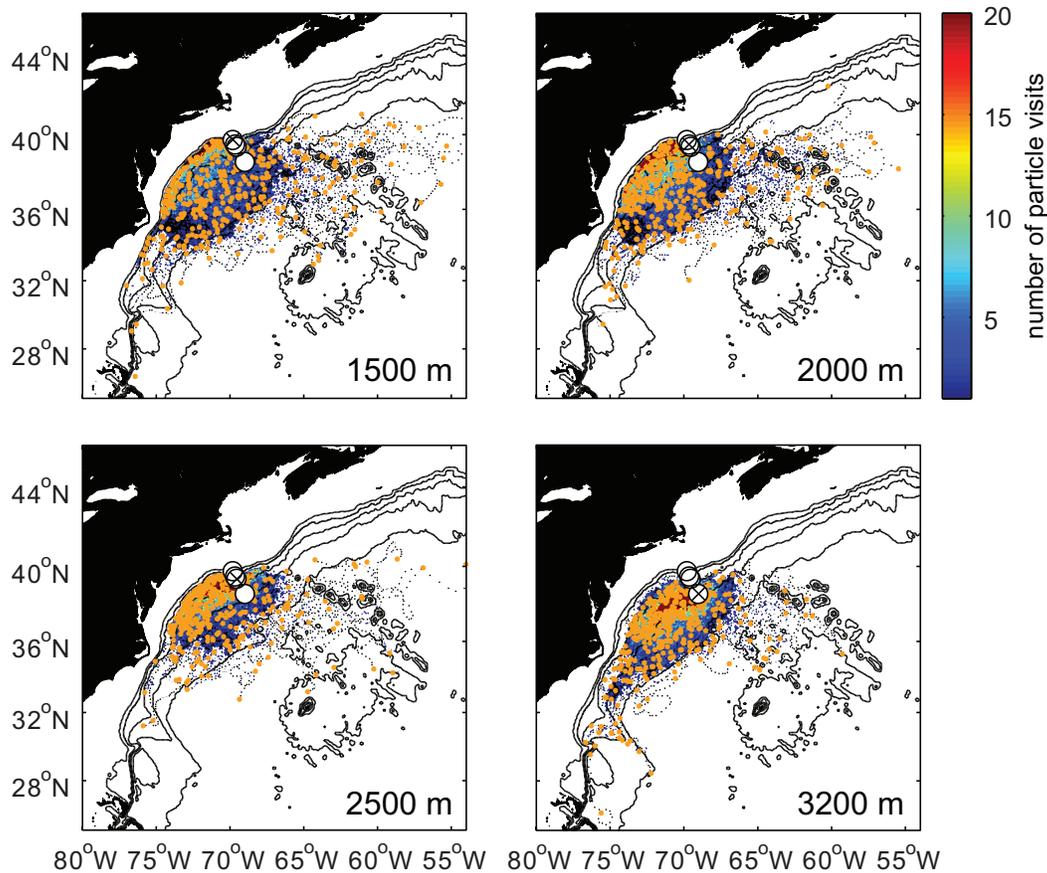


Fig. 6. Potential connectivity maps for different depths of release after 360 days. Details and color codes as described in Fig. 4.

evolutionary-connectivity among distant populations, affect the spatial and temporal scales of divergence, foster range shifts or expansions, enhance metapopulation and metacommunity persistence, and provide a mechanism to escape localized disturbances (Trakhtenbrot et al., 2005; Nathan, 2006; Hellberg, 2009).

4.2. Genetic patterns, connectivity and the influence of the DWBC

Both the individual particle trajectories and their distributions indicate that the DWBC is unlikely to impede larval exchange between upper and lower bathyal depths in this region of the Northwest Atlantic. This is consistent with empirical estimates of dispersal from floats released within the DWBC (Bower and Hunt, 2000a, b; Bower et al., 2009, 2011, 2013) and with simulated trajectories (based on FLAME) from thousands of e-floats released into the DWBC at various locations within the North Atlantic (Bower et al., 2009; Gary et al., 2011; Lozier et al., 2013). Most trajectories were highly convoluted and departed significantly from the mean southwestward flow of the DWBC. Movement across depths (east or west) was common indicating that the DWBC is unlikely to prevent the exchange among depths of passively dispersing larvae, assuming larvae survive the environmental changes (e.g. temperature, pressure, etc.) that attend changes in depth.

The cross-slope dispersal of particles documented here and in earlier work is not necessarily representative of the entire continental slope of the western North Atlantic, but nor is it unique.

The primary cause of the large cross-slope excursions in the vicinity of the bottom sampling sites is interaction between the DWBC and Gulf Stream. At about 35°N, the present-day Gulf Stream curves from its northward path toward the northeast and crosses the continental slope and proceeds generally eastward over deep water. This separation latitude is not fixed but wanders north and south due to meandering of the Gulf Stream. Particles being carried southwestward by the DWBC over the mid- and upper-slope north of the separation point are almost always entrained into the Gulf Stream as the two currents converge near the separation latitude. This results in particles being swept offshore into deeper water (see Bower and Hunt, 2000a, b).

On the other hand, particles being advected by the deeper part of the DWBC are frequently able to pass under the Gulf Stream and continue equatorward, but this too is accompanied by cross-slope motion: conservation of potential vorticity (approximated accurately at these depths by f/H , where f is the Coriolis parameter and H is the water layer thickness) dictates that the deep part of the water column slide down the slope by hundreds of meters in order to slip beneath the deep thermocline of the subtropical gyre (Hogg and Stommel, 1985; Bower and Hunt, 2000a, b). These particles may then continue equatorward over the slope but following a deeper isobath. This might also help to explain the genetic similarity between North and South Atlantic populations of the protobranch bivalve *Nucula ataccellana* at lower bathyal depths (Zardus et al., 2006).

Disruption of along-slope flow of the DWBC by another current has also been well-documented with observations around the

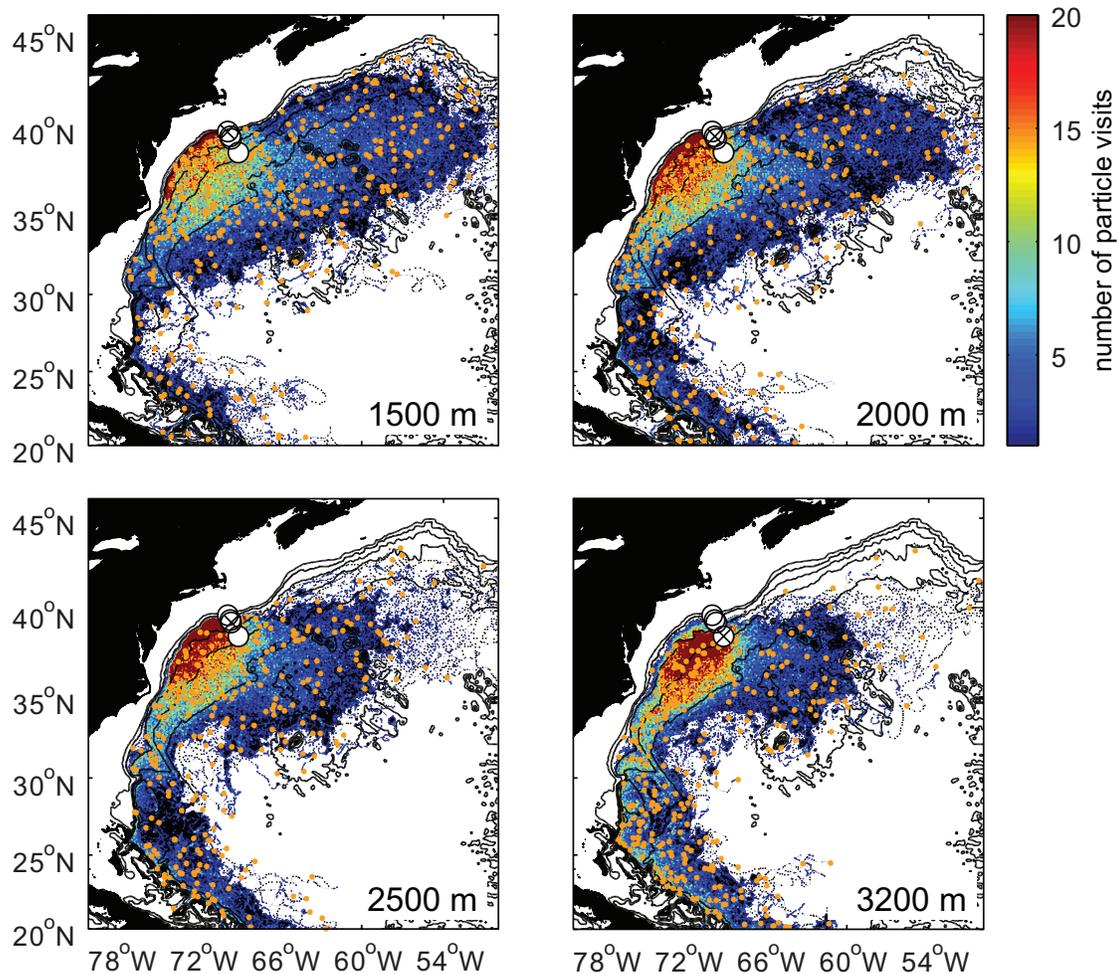


Fig. 7. Potential connectivity maps for different depths of release after 1500 days. Details and color codes as described in Fig. 4.

Table 1

Percentage of particles that are located offshore of release depth (i.e., in deeper water) as a function of release depth and time.

Release depth (m)	30 days	180 days	360 days	1500 days
1500	81	98	99	100
2000	90	92	98	98
2500	51	79	83	98
3200	38	55	68	92

Grand Banks of Newfoundland and Flemish Cap, where the Gulf Stream and its northward extension, the North Atlantic Current sometimes cross the continental slope and interact with the DWBC transport (Lavender et al., 2000; Fischer et al., 2004; Rhein et al., 2002; Bower et al., 2009, 2011). Sharp corners in the continental slope have also been shown to cause cross-slope motion of float trajectories in the DWBC and even detrainment of the particles from the DWBC entirely (Leaman and Vertes, 1996; Bower et al., 2013), likely due to inertial overshoot of the sharp corner (see Bower et al. (1997) and references therein). In between regions of current interactions and sharp bathymetric features, the DWBC in the western North Atlantic generally flows mostly uninterrupted for hundreds of kilometers over the continental slope, impeded from crossing the slope by potential vorticity (see examples in Leaman and Vertes (1996) and Bower and Hunt (2000a)). These are regions where the DWBC is most likely to impede larval exchange among depths. The locations of enhanced cross-slope

motions may have been different in the distant past when the Gulf Stream may have separated at more southerly latitudes (e.g., Keffer et al., 1988) with implications for how deep-water flows might influence connectivity over geological time.

Given the results from both modeled and empirical float estimates of dispersal, it seems unlikely that the strong genetic divergence we find among bivalve populations above and below 3000 m in the western North Atlantic (Chase et al., 1998; Etter et al., 2005; Zardus et al., 2006; Jennings et al., 2013; Glazier and Etter, 2014) reflects the restriction of gene flow by the DWBC. If populations at different depths are well connected and dispersal among depths is ongoing, how can such divergence emerge? The lack of obvious physical transport mechanisms that would impede larval exchange and the small scale over which divergence has occurred suggest selection may be involved.

Recent theoretical and empirical evidence clearly demonstrate that despite ongoing gene flow a variety of mechanisms can lead to diversification (reviewed in Nosil (2012)) and that these processes might be considerably more important for population differentiation and species formation in marine environments where physical barriers to gene exchange are less common (Bowen et al., 2013). For example, adaptation to local environmental conditions with ongoing gene flow (Doebeli and Dieckmann, 2003; Irwin, 2012) can lead to immigrant inviability (Nosil et al., 2005; Marshall et al., 2010), which will reduce gene flow and promote divergence. It is possible that larvae disperse among depths, but lack the necessary local adaptations to survive or reproduce.

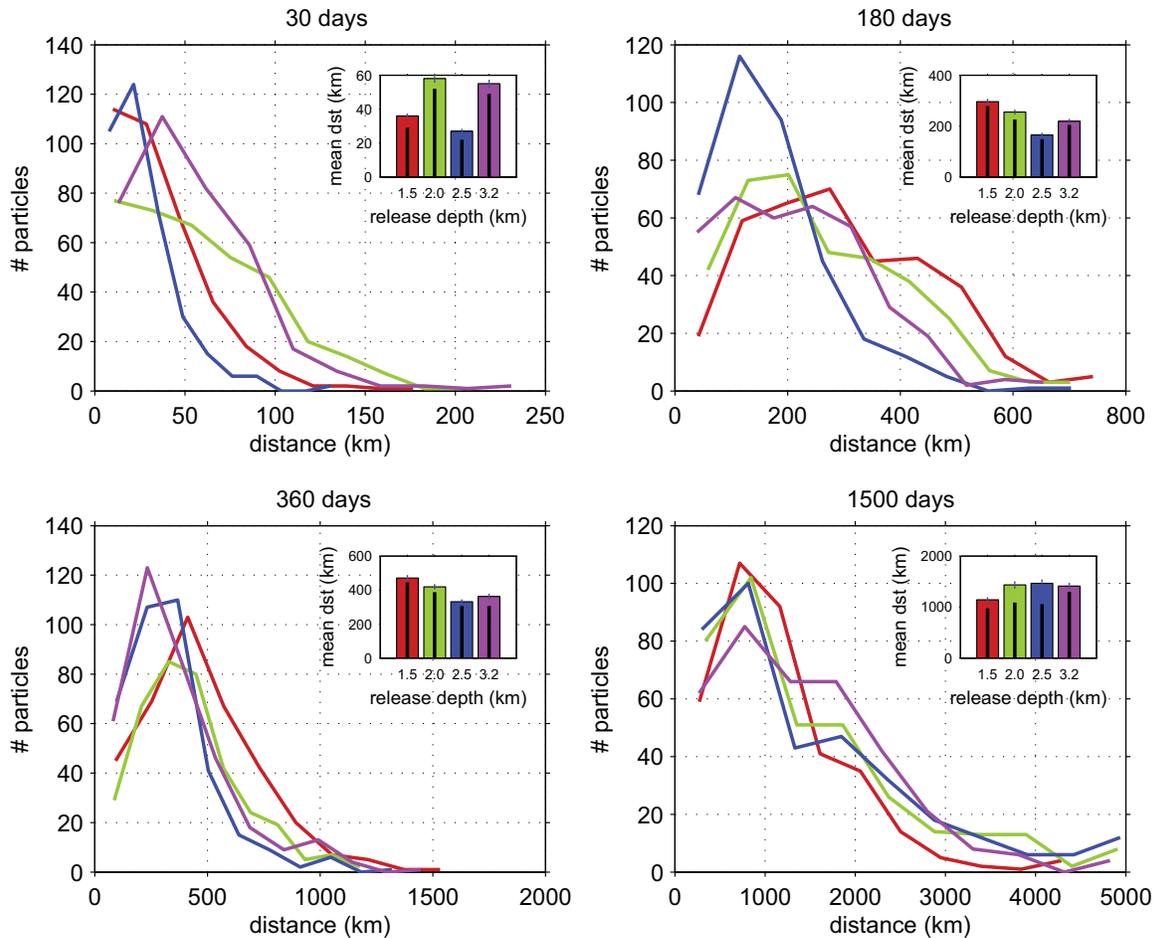


Fig. 8. Particle displacement distributions. The distance of particles from their release point (measured as a straight-line distance) after 30, 180, 360 and 1500 days. The lines indicate the number of particles at different distances from their release point and are color-coded based on release depth. Inset bar graphs indicate the mean and standard error (colored bars with blue error bars) and median (black lines) displacement of particles after a specific number of days as a function of release depth. (dst=distance).

Emerging phylogeographic patterns in the deep sea suggest that environmental gradients paralleling changes in depth may provide one of the primary mechanisms mediating population differentiation and species formation in deep-water ecosystems (Etter et al., 2005; Baco and Cairns, 2012; Jennings et al., 2013; Quattrini et al., 2013). Depth differences are associated with changes in a wide variety of environmental variables including temperature, hydrostatic pressure, oxygen, POC flux, habitat heterogeneity, trophic complexity and the nature and amount of food (reviewed in Gage and Tyler (1991)). These environmental changes have been invoked as key forces in regulating bathymetric distributions (Carney, 2005), altering ecological processes (Levin et al., 2001), shaping major macroecological patterns (reviewed in Rex and Etter (2010)), fostering adaptation (e.g. Somero, 1992; Levin and Gooday, 2003; Brown and Thatje, 2014), and promoting diversification (Etter et al., 2005; Jennings et al., 2013). Widespread and consistent divergence across depth gradients suggests depth and its concomitant environmental gradients may also play an important role in the origin and evolution of the deep-sea fauna.

4.3. Paleo-oceanography

Our estimates of dispersal and connectivity are based on the contemporary hydrodynamics of the North Atlantic. The probability that larval exchange occurs among depths is a function of

the intensity of the DWBC and the strength of cross slope processes. The oceanography of the North Atlantic and in particular the intensity of the DWBC (Boyle and Keigwin, 1982; Keigwin and Pickart, 1999; McManus et al., 2004; Lippold et al., 2012) and the position and strength of the Gulf Stream (Keffer et al., 1988) have varied through time. It is possible that a more intense DWBC in the past disrupted gene flow between depth regimes long enough for populations to diverge in regions where cross-slope processes are weak (e.g. away from sharp bathymetric features or interactions with the Gulf Stream). If divergence in the past was sufficient to prevent recruitment of larvae from contrasting depth regimes, then even though the contemporary flows of the DWBC allow larval exchange between depths now, gene flow might be precluded due to migrant inviability (sensu Nosil et al. (2005)). Molecular clock estimates of the observed genetic divergence between upper and lower bathyal populations in the protobranch *Nucula ataccellana* suggest a recent split 1 mya (Jennings et al., 2013), during which time the DWBC varied considerably in intensity (Boyle and Keigwin 1982; Keigwin and Pickart, 1999; McManus et al., 2004; Lippold et al., 2012). The protobranch *Neilonella salicensis* also exhibits a strong genetic break between depths in the same general vicinity, but molecular clock estimates of divergence between shallow and deep clades indicate gene flow has been absent for more than 15 million years (Glazier and Etter, 2014). Interestingly, the formation of the North Atlantic Deep Water, which drives the DWBC, has progressively weakened over

the past 3 million years and was considerably stronger from 3 to 14 mya (Frank et al., 2002). Our estimates of divergence time in these bivalves coincide with this period of stronger export. As global climate shifted historically and thermohaline circulation waxed and waned the DWBC may have periodically disrupted gene flow among populations at different depths fostering repeated rounds of species formation. If true, we should expect other taxa with distributions that span the DWBC to exhibit diversification at similar times. In addition, the waxing and waning of the DWBC might act essentially as a speciation pump by repeatedly disrupting gene flow in regions of weak cross-slope forces, which might help explain the well known peak in diversity at bathyal depths in the western North Atlantic (Rex, 1981; Etter and Grassle, 1992).

4.4. Caveats

Although the estimates of dispersal presented here represent a reasonable first approximation of how larvae might disperse at depth, a number of factors have not been included that are likely to alter dispersal and the scale and intensity of connectivity. They were excluded for simplicity and because we lack reasonable estimates of those factors. For example, larval behavior such as tidal, diurnal or ontogenetic migration can dramatically alter the scale and direction larvae disperse (Drake et al. 2013; Morgan, 2014). This often depends on stratified water columns where vertical migration over relatively small scales allows larvae to modulate dispersal by exploiting water masses moving at different rates or directions. In the deep sea, stratification is less, environmental cues are less pronounced (e.g. diurnal and tidal) and larvae would in general need to migrate over much greater distances to find water masses that differ significantly in speed or direction (e.g. DWBC vs Gulf Stream, Fig. 2). We know little about the behavior of deep-sea larvae, but recent evidence identified bathyal mussel larvae (*Bathymodiolus*) in the surface waters (Arellano et al., 2014), suggesting such vertical migrations are possible. Larvae of other deep-sea taxa have also been found in surface waters (Reviewed in Scheltema (1994), Bouchet and Waren (1994) and Young (2003)). The scale and geography of dispersal for larvae in the surface currents would be substantially different than those dispersing at depth. While dispersing in the surface currents might be possible for some deep-sea taxa, many species are confined to deep water because their larvae cannot tolerate the low pressure and high temperature of near-surface waters (Young and Tyler, 1993; Young et al., 1996; 1998; Brooke and Young, 2009; Bennett et al., 2012). Demersal larvae might also exploit the slower flows of the benthic boundary layer to limit dispersal away from natal sites.

Another important factor not included in our simulation is how and when larvae descend through the water column to settle, which might involve considerable changes in depth and water masses for larvae that migrate ontogenetically to surface waters or for those advected from the slope into deeper waters. Settlement might be active (e.g. swimming) or passive (e.g. density changes) (reviewed in Young (2003)), and could alter dispersal and how populations are connected. Better estimates of dispersal and connectivity in the deep sea will require more details about larval behavior and development at depth. In addition, spatial variation in fecundity, mortality during the larval phase and larval physiological tolerance needs to be included because they can influence dispersal and population connectivity (Trembl et al., 2012; White et al., 2014).

Our estimates of dispersal and connectivity are also dependent on the quality of the hydrographic model driving dispersal. It is important to keep in mind that the resolution of the physical transport model might be inadequate to capture all the forces affecting dispersal on the scale of minute larvae. Biophysical models

can be enormously insightful in understanding how transport processes might influence dispersal (e.g. Xue et al., 2008; Siegel et al., 2008; Inzce et al., 2010; Watson et al., 2010; Drake et al., 2011) and to explore how larval behaviors and life histories might affect connectivity (Drake et al., 2013; Morgan, 2014; Trembl et al., 2012; White et al., 2014). However, before using them directly to estimate potential impacts of contemporary environmental issues (e.g. resource exploitation, mining, etc.) or to guide conservation strategies (e.g. MPA design), they need to be empirically validated on both ecological and evolutionary time scales (reviewed in Levin (2006); Kool et al. (2013)). Trace element signatures using calcified structures (e.g. López-Duarte et al., 2012) or genetic analyses of early recruits (e.g. Jones et al., 2005) could be used to estimate connectivity on ecological (demographic) time scales. On longer evolutionary time scales, estimates of population genetic divergence (e.g. Siegel et al., 2003; Galindo et al., 2006, 2010; Weersing and Toonen, 2009; White et al., 2010; Alberto et al., 2011) can provide insight into average long-term connectivity.

5. Conclusions

The results presented here provide one of the first estimates of how passive larvae might disperse at deeper bathyal depths in the western North Atlantic and quantifies the scale and geography of how populations might be connected. Unraveling how populations are connected is critical for explaining biogeographic patterns of diversity (Levin and Dayton 2009; Gooday et al., 2010), predicting how deep-sea ecosystems might respond to climate change (Danovaro et al., 2008, 2009; Glover et al., 2010), developing conservation and management strategies to mitigate the intense exploitation of deep-sea resources (Ramirez-Llodra et al., 2011; Levin and Sibuet, 2012; Mengerink et al., 2014; Pusceddu et al., 2014) and identifying appropriate locations and scales for MPAs (Harris and Whiteway, 2009; Clark et al., 2011; Watling et al., 2013; Hilaro, et al. 2015).

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