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The influence of larval migration and dispersal depth on potential larval trajectories of a deep-sea bivalve

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ABSTRACT

Many fundamental questions in marine ecology require an understanding of larval dispersal and connectivity, yet direct observations of larval trajectories are difficult or impossible to obtain. Although biophysical models provide an alternative approach, in the deep sea, essential biological parameters for these models have seldom been measured empirically. In this study, we used a biophysical model to explore the role of behaviorally mediated migration from two methane seep sites in the Gulf of Mexico on potential larval dispersal patterns and population connectivity of the deep-sea mussel *Bathymodiolus childressi*, a species for which some biological information is available. Three possible larval dispersal strategies were evaluated for larvae with a Planktonic Larval Duration (PLD) of 395 days: (1) demersal drift, (2) dispersal near the surface early in larval life followed by an extended demersal period before settlement, and (3) dispersal near the surface until just before settlement. Upward swimming speeds varied in the model based on the best data available. Average dispersal distances for simulated larvae varied between 16 km and 1488 km. Dispersal in the upper water column resulted in the greatest dispersal distance (1173 km ± 2.00), followed by mixed dispersal depth (921 km ± 2.00). Larvae originating in the Gulf of Mexico can potentially seed most known seep metapopulations on the Atlantic continental margin, whereas larvae drifting demersally cannot (237 km ± 1.43). Depth of dispersal is therefore shown to be a critical parameter for models of deep-sea connectivity.

1. Introduction

In marine systems, the exchange of dispersing larvae can drive the dynamics of marine metapopulations, resilience of populations to exploitation, and success of management strategies such as no-take marine reserves (Cowen and Sponaugle, 2009; Gaines et al., 2010; Puckett and Eggleston, 2016). The Planktonic Larval Duration (PLD), defined as the amount of time larvae and embryos spend in the water column, is often used to approximate dispersal distance. PLD may range from days to months. However, dispersal and connectivity patterns are influenced by PLD as well as numerous biological factors, including the location and timing of spawning relative to hydrodynamic features, the availability of suitable habitat for settlement, larval mortality, and larval swimming speed and direction (Young, 1987; Van Dover et al., 2002; Levin, 2006; Cowen et al., 2007; Eggleston et al., 2010; Pinsky et al., 2012; Mitarai et al., 2016). Behaviors occurring during the larval phase alter the vertical distribution of larvae in the water column, thereby exposing larvae to different hydrodynamic conditions at different depths (Sponaugle et al., 2002; Drew and Eggleston, 2006; Paris

et al., 2007; North et al., 2008; Butler et al., 2011). Behaviors that determine the depth of dispersal are likely to be especially important in the deep sea, where current speeds and directions differ significantly with depth in an extensive water column.

A major challenge in studying dispersal of deep-sea organisms is the availability of biological data for both adult and larval stages (Metaxas and Saunders, 2009; Hilario et al., 2015). Aspects of reproductive biology are known for many deep-sea animals (reviewed by Young, 2003), yet only a few species of deep-sea larvae have been reared in the laboratory (summarized by Hilario et al., 2015), and there are relatively few studies of in situ larval distributions in the deep sea (e.g. Kim and Mullineaux, 1998; Mullineaux et al., 2005; Arellano et al., 2014). Given the relatively sparse information on larval biology and spawning dynamics of deep-sea organisms, biophysical modeling has recently been used to explore potential larval dispersal and population connectivity patterns (e.g., Qian et al., 2015; Young et al., 2012; Mitarai et al., 2016). In this study, we focus on the deep-sea mussel *Bathymodiolus childressi*, a species for which some biological information is available.

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1.1. Biology of “*Bathymodiolus*” *childressi*

Mytilid mussels in the subfamily Bathymodiolinae (Gustafson et al., 1998) are found in deep-sea reducing habitats, and the genus *Bathymodiolus* includes species that are found at both hydrothermal vents and methane seeps. “*Bathymodiolus*” *childressi* is found throughout the Gulf of Mexico and Western Atlantic at depths from 200 m to more than 3000 m (Gustafson et al., 1998; Tyler et al., 2000; Carney et al., 2006; Cordes et al., 2009). We follow the recommendation of Jones and Vrijenhoek (2006) to use quotation marks around the genus name because of uncertainty about its taxonomic status. Spatiotemporal variation in population connectivity among subpopulations over ecological and evolutionary time scales can result from variation in the timing and location of spawning, hydrodynamic processes, larval behavior, and post-settlement processes such as emigration and mortality (Van Dover et al., 2002; Levin, 2006; Mitarai et al., 2016). Bathymodiolin mussels have been used as the model organism in the study of adaptation to extreme environments (Lorion et al., 2010; Thubaut et al., 2013). Recent work on mussels found on organic matter and wood falls challenges the “shallow to deep” evolutionary hypothesis and indicates a more complex, gradual evolution with multiple introductions to the deep-sea environment (Distel et al., 2000). Further more, molecular data demonstrate that vent and seep bathymodiolin mussels arose from multiple colonization events. The “*B.*” *childressi* species complex is widely distributed throughout the Western Atlantic at depths from 200 m to more than 3000 m (Gustafson et al., 1998; Tyler et al., 2000; Olu-Le Roy et al., 2007), but until recently, “*B.*” *childressi* was only known in the Gulf of Mexico (GOM). The most comprehensive regional study of genetic structure in seep mussel populations was undertaken in the GOM by Carney et al. (2006), who used two mitochondrial (ND4, COI) and six nuclear (one microsatellite, five RFLP) markers to look for structure between populations of “*B.*” *childressi* over a range of ~ 500 to 2200 m depth, and found genetic similarities across large geographic distances and depths in the GOM. Faure et al., 2015 also investigated the population connectivity of “*B.*” *childressi* in the GOM using COI and ND4 mitochondrial genes, with their results broadly agreeing with other studies that found considerable connectivity between subpopulations. However, it is important to note statistically significant genetic differentiation was found between two sampled populations in the central Gulf of Mexico, which is not consistent with the hypothesis of complete panmixia (Faure et al., 2015). These findings highlight the importance of understanding the physical oceanographic features and the role of larval dispersal in the region in combination with population genetic studies.

The occurrence of seep species of mollusks, crustaceans, and other taxonomic groups across the Atlantic Ocean suggest broad connectivity (Olu-Le Roy et al., 2007; Cordes et al., 2007). Molecular *mtCOI* phylogenies for the deep-sea mussel “*Bathymodiolus*” *childressi*, suggest contemporary gene flow and population connectivity across known deep-water seeps in the southeastern Caribbean, central and eastern Gulf of Mexico and along the Western Atlantic (Cordes et al., 2007). Conversely, allozyme analysis of the deep-sea amphipod *Ventiella sulfuris* (Crustacea: Malacostraca Lysianassidae) shows strong isolation by distance (over an area of 1200 km²), likely due to the way in which it broods eggs (France et al., 1992; Vrijenhoek, 1997). Improved biophysical modeling techniques (Puckett et al., 2014; Qian et al., 2015) can predict potential larval dispersal and population connectivity among seep invertebrates with varying PLDs and larval behaviors and, thus, can help biological oceanographers understand how new populations are colonized and how present populations persist. These mechanisms can then be tested with molecular tools that identify the spatial scales at which genetic differentiation occurs (Carney et al., 2006; Thaler et al., 2011).

In the Gulf of Mexico, gametogenesis occurs synchronously, primarily in the fall (Tyler et al., 2007) though spawning has been induced artificially in earlier seasons (e.g., March) both in the Gulf of Mexico

and on the northwest Atlantic continental margin (Arellano and Young, 2009; Young, personal observations). Larval development described by Arellano and Young (2009), inferred planktotrophic development from the prodissoconch and estimated larval duration of up to 13 months by comparing the timing of spawning and settlement.

Early studies hypothesized, on the basis of egg volumes, that bathymodiolin mussel larvae might disperse demersally (Lutz et al., 1984; Turner et al., 1985). In support of this idea, mussel larvae of various sizes have been collected in bottom plankton traps (Young et al., unpublished data). Further more, recent collections using the AUV Sentry and SyPRID Sampler (see Billings et al., 2017 for details on SyPRID Sampler) have found bathymodiolin larvae of varying sizes within a few meters of the sea floor (Young, unpublished data). Vent polychaete and gastropod larvae have been shown to disperse demersally and in high abundance less than 15 m above the sea floor (Kim and Mullineaux, 1998). However, Arellano et al. (2014) identified “*B.*” *childressi* larvae in the upper 100 m of the water column while conducting MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) tows over the Brine Pool site in the northern Gulf of Mexico (650 m; 27°43′23″N, 91°16′30″W). Therefore, it is important to focus on the effects of dispersal depth on mytilid mussels to tease apart the possible dispersal strategies.

In this study, biological parameters relevant to larval dispersal models, including spawning date, swimming speed, planktonic larval duration, and vertical distribution in the water column were obtained from a combination of shipboard experiments, MOCNESS tows, and results from previous studies (Tyler et al., 2007; Arellano, 2008; Arellano and Young, 2009; Arellano et al., 2014). Because “*Bathymodiolus*” *childressi* larvae at similar stages of development have been found both in the water column and near the bottom, we used the best (yet still incomplete) biological information available to model the dispersal and connectivity consequences of three different plausible dispersal strategies for two metapopulations in the Gulf of Mexico.

2. Materials and methods

A climatological, hydrodynamic model was coupled with a Lagrangian particle-tracking model to predict dispersal paths for three possible larval behavioral scenarios. The output was used to compare the main and interactive effects for two spawning locations and three different larval dispersal behaviors for “*B.*” *childressi* with the response variable being mean dispersal distance.

2.1. Biophysical model and spatio-temporal scales

The hydrodynamic model used for this study is a configuration of the Regional Ocean Modeling System (ROMS) for the northwestern Atlantic Ocean (Zeng and He, 2016). The NW Atlantic model domain covers a large domain including the Caribbean and Intra-American Seas, Gulf of Mexico (GOM), U.S. South Atlantic, U.S. Mid-Atlantic and North Atlantic Bights, as well as the Sargasso with 7–10 km grid spacing and 36 terrain-following vertical levels (Fig. 1). Model spin-up used a five-year simulation of ocean currents, followed by six years of simulations for analysis that were averaged to three-hour intervals. The model is forced by long-term (1979–2009) monthly mean surface fluxes from the Climate Forecast System Reanalysis (CFSR; Saha et al., 2010), eight tidal constituents (M2, S2, O2, K2, O1, K1, Q1), and monthly-mean river discharge. Ocean conditions along the open eastern boundary of the model are provided by long-term monthly averages of the Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al., 2007).

A Lagrangian particle-tracking model was used to simulate the dispersion of simulated larvae released from two methane seep sites in the GOM. These sites are a part of a broader study of population connectivity of invertebrates among seep sites at Alaminos Canyon (26°21′17″N, 94°29′48″W) and Brine Pool (27°43′23″N, 91°16′30″W). The Larval TRANSport Lagrangian model (LTRANS, North et al., 2008) is an

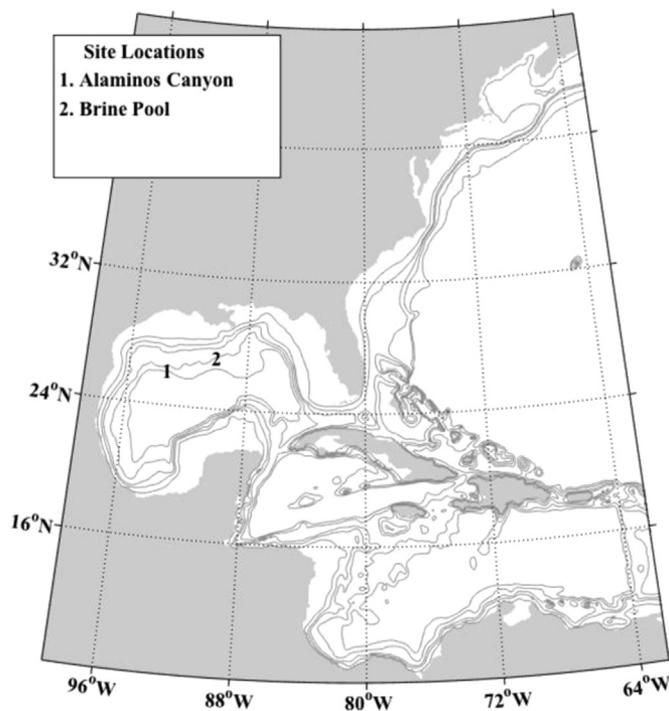


Fig. 1. Spatial domain of hydrodynamic ROMS model. Methane seep study sites are plotted on the model domain to match latitude, longitude, and depth of the actual locations: (1) Alaminos Canyon (26 21'17"N, 94 29'48" W, 1300 m) and (2) Brine Pool (27 43'23"N, 91 16'30"W, 660 m).

offline, particle-tracking model that predicts particle movement in three directions using advection, diffusion, and prescribed particle behavior (North et al., 2006). LTRANS interpolates 6 hourly sea surface height, water velocity, salinity, and temperature data from NW Atlantic model output, and utilizes a fourth-order Runge-Kutta scheme for particle advection. The similar modeling approach has been successfully applied in other previous analyses performed by members of our research team and proven to be a very effective way in delineating marine transport and connectivity (Pringle et al., 2017; North et al., 2015; Qian et al., 2015; Li et al., 2013; Putman and He, 2013).

2.2. Biological parameters for the models

Previous gametogenic studies indicate that *Bathymodiolus childressi* spawn mostly in the autumn (Tyler et al., 2007, Plowman and Young, in preparation), though spawning has been induced artificially by the injection of serotonin from late spring to fall (Arellano and Young, 2009, Breusing and Young, unpublished data, McVeigh et al., unpublished data), suggesting that some individuals could release gametes outside the peak fall spawning season. Because spawning has never been observed in nature, we chose a week near the estimated fall peak to “release” gametes in our models (Tyler et al., 2007).

The larvae of *Bathymodiolus childressi* have been collected at various depths, including the upper water column with MOCNESS tows at two sites in the Gulf of Mexico: Brine Pool (27° 43.4N 91° 16.8W) and Bush Hill (27° 47N, 92° 30W) (Arellano et al., 2014) and also in benthic larval traps (Arellano and Young, 2009), indicating that at least some larvae undertake long ontogenetic migrations. These observations justify inclusion of models that explore both demersal and planktonic dispersal.

Arellano and Young (2009) described development of the early larvae, showing that hatching occurs after two days and that the trochophore larvae swim weakly through day 10 when they become D-shell veligers. Arellano (2008) measured the swimming speed of trochophores in water-jacketed chambers at an average of 0.02 cm s^{-1} at

15°C , which is typical of the temperature below the permanent thermocline during the autumn spawning season (Arellano and Young, 2011). Arellano (2008) also showed that the trochophore swimming speed of a shallow-water mytilid mussel, *Mytilus trossulus*, was similar (0.06 cm s^{-1}) to that of “B.” *childressi* at the same temperature.

Swimming speeds have never been measured for D-shell or later veligers of *Bathymodiolus childressi* or any other bathymodiolin mussel. For the models, we used empirical values for early bivalve veligers of the confamilial shallow-water mussel *Mytilus edulis*, which are reported several times in the literature (Konstantinova, 1966; Sprung, 1984; Troost et al., 2008; Fuchs and DiBaco, 2011) and are consistently about an order of magnitude higher than the swimming speed of a mussel trochophore. In our models we used the speed of 0.2 cm s^{-1} estimated by Sprung (1984), who published detailed studies on all aspects of larval physiology.

Arellano and Young (2009) estimated planktonic larval duration (PLD) for *Bathymodiolus childressi* by back-calculating settlement times of field-collected juveniles using separate empirical measurements of juvenile growth rates. We used their maximum dispersal estimate of 13 months in our models.

2.3. Dispersal simulation scenarios for “B.” *childressi*

Three possible larval dispersal strategies (Fig. 2) were evaluated with simulations: (1) demersal drift, (2) dispersal near the surface early in larval life followed by an extended demersal period before settlement, and (3) dispersal near the surface. All dispersal simulations released 20 particles (“larvae”) every hour from each seep site, for a total of 14,880 particles released over one week from October 15 to 22. While the number of particles released is an underestimate of gametes released during a spawning event, the number of particles released in the three simulations provides statistically sound insight into the dispersal patterns of particles with each behavior type. Specific details on each simulation are as follows:

- (1) *Demersal drift* – The particles were programmed with demersal drift behavior, in which all particles stayed within one meter of the sea floor throughout the 395-day PLD (Fig. 2).
- (2) *Near surface dispersal followed by an extended demersal period* – Particles were programmed to exhibit no behavior the first two

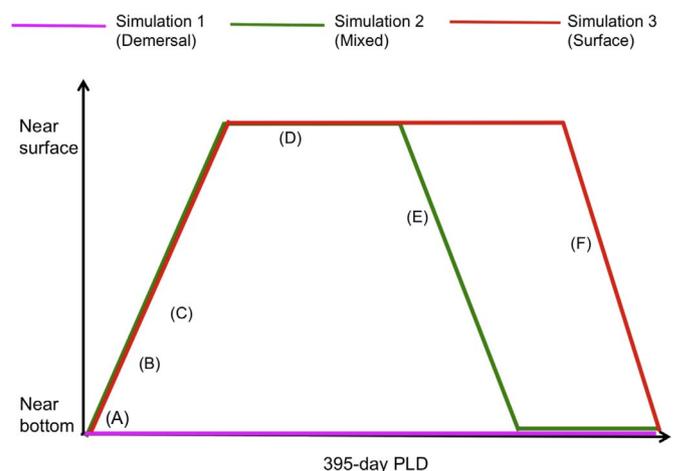


Fig. 2. Schematic diagram of specific larval behavior simulations for “B.” *childressi*. Simulation 1: larvae disperse near bottom for 395 days. Simulations 2 and 3 had the following simulation data: particles exhibited no behavior for the first two days (A), followed by weak upward swimming at 0.02 cm s^{-1} for days three to ten (B). Swimming then increased to 0.2 cm s^{-1} on day 10 (C). Simulation 2 larvae dispersed near 100 m depth 175 days (D) followed by 215 days of demersal drift (E). Simulation 3 larvae dispersed for 395 days near 100 m depth (F). All particles were programmed to arrive on the sea floor and settle by the end of their specific behavioral simulation.

days, followed by weak upward swimming behavior at 0.02 cm s^{-1} from day three to ten. On the tenth day, swimming speed increased to 0.2 cm s^{-1} . Particles remained near 100 m depth for 175 days, then began swimming downward at 0.2 cm s^{-1} on day 175, allowing up to 10 days for the particles to reach the sea floor by day 185. Once particles reached the seafloor, they drifted within one meter of the bottom until the end of the 395-day PLD (Fig. 2).

- (3) *Near surface dispersal* – Similar to the second simulation, particles exhibited no behavior the first two days, followed by weak upward swimming behavior at 0.02 cm s^{-1} from day three to ten. On the tenth day, swimming speed increased to 0.2 cm s^{-1} . Particles remained near 100 m depth for approximately 375 days, then began swimming downward at 0.2 cm s^{-1} on day 385, allowing up to 10 days for the particles to reach the sea floor by the end of their 395-day PLD (Fig. 2).

2.4. Hypotheses and statistical analyses

Deep ocean currents are generally an order of magnitude slower than surface currents (Dickson and Brown, 1994), although in the Gulf of Mexico there can be exceptions (Hamilton and Lugo-Fernandez, 2001). Therefore, we hypothesized that “*B.*” *childressi* with surface migration larval behavior would display the greatest average potential distance traveled, irrespective of release site. Statistically comprehensive Lagrangian Probability Density Functions (LPDFs) were used to characterize the dominant dispersal pathways of particles in the *US East* hydrodynamic model domain. Note that LPDF quantifies the probability of particles moving through a grid cell in the domain over the course of their PLD, which is distinct from simply analyzing dispersal trajectories. The main and interactive effects of spawning site and particle behavior were tested on mean dispersal distance with a one-way analysis of variance (ANOVA) model.

3. Results

3.1. General particle trajectories

A total of 14,880 particles were tracked over a 395-day PLD. While there was variation in average dispersal distance, the overall trend was consistent. The greatest dispersal was observed for surface migration behavior (Simulation 3), followed by abbreviated surface migration behavior (Simulation 2), followed by demersal behavior (Simulation 1). Dispersal pathways and LPDFs also varied greatly according to release site; particles released from Alaminos Canyon in the eastern GOM had the lowest average dispersal distances, whereas particles released from Brine Pool in the Northern-central area of the GOM traveled throughout the eastern GOM and South-Atlantic Bight (Figs. 3 and 4). Particles with Simulation 1 behavior traveled along the bathymetric contours of the basin with the cyclonic flow of the deep-water currents when released from both Alaminos Canyon and Brine Pool (Figs. 3 and 4). When released from Alaminos Canyon, simulated larvae with Simulation 2 behavior spread throughout the western portion of the GOM (Fig. 3), whereas those released from Brine Pool traveled through the Florida Strait to the South-Atlantic Bight (Fig. 4). Finally, particles with Simulation 3 behavior traveled extensively throughout the GOM and South-Atlantic Bight when released from Alaminos Canyon and Brine Pool.

3.2. “*B.*” *childressi* Simulation 1

The mean distance traveled by particles varied significantly according to release site (one-way ANOVA; $F = 42,630$, $df = 1$, $29,759$, $p < 0.0001$). Mean distance traveled for particles with Simulation 1 behavior was higher when released from Brine Pool (Fig. 5; $413 \text{ km} \pm 0.04$), followed Alaminos Canyon (Fig. 5; $27 \text{ km} \pm 0.04$). In general, particles with demersal drift behavior did not disperse widely

throughout the GOM—rather they followed the bathymetric contours of the GOM with an easterly spread.

3.3. “*B.*” *childressi* Simulation 2

Mean distance traveled by particles also varied significantly with release site (one-way ANOVA; $F = 54,420$, $df = 1$, $29,759$, $p < 0.0001$). In general, mean distance traveled was higher when released from Brine Pool (Fig. 5; $1187 \text{ km} \pm 2.60$), followed by Alaminos Canyon (Fig. 5; $328 \text{ km} \pm 2.60$). Overall, particles with near surface drift followed by demersal drift behavior dispersed widely throughout the South-Atlantic Bight.

3.4. “*B.*” *childressi* Simulation 3

Mean distance traveled by prolonged surface drift particles also varied significantly with release site (one-way ANOVA; $F = 6,974$, $df = 1$, $29,759$, $p < 0.0001$). Mean distance was significantly higher when released from Brine Pool (Fig. 5; $1488 \text{ km} \pm 3.99$), followed by Alaminos Canyon (Fig. 5; $1016 \text{ km} \pm 3.99$). Particles with near surface drift also traveled widely throughout the GOM and South and Mid-Atlantic Bight.

4. Discussion

The study of deep-sea larvae and their dispersal to spatially isolated habitats remains one of the most challenging aspects of deep-sea science. This study used a coupled biophysical model to explore the roles of three hypothetical larval behaviors and spawning locations on potential larval dispersal and population connectivity for the mussel “*Bathymodiolus*” *childressi*. In general, “*B.*” *childressi* particles dispersed widely throughout the GOM, Florida Strait, as well as the South- and Mid-Atlantic Bights. Mean dispersal distances were much greater when larvae traveled in the euphotic zone than at relatively deep ($> 600 \text{ m}$) depths. For example, mean distance traveled for “*B.*” *childressi* Simulation 1 (demersal drift) was 220 km, whereas mean dispersal distances in Simulation 2 (near surface and demersal drift) and Simulation 3 (near surface) were 757 km and 1173 km, respectively (Fig. 5). Our results show that particles encounter other seep sites in the model domain, however this does not prove that there is a strong enough connection to influence population dynamics or genetic structure. To calculate the connection strength across the model domain, further analysis is needed to quantify the level of connectivity at both contemporary and evolutionary time scales between each of the seeps sites in our study system, as well as the level of self-recruitment.

Few studies have modeled larval dispersal behavior in the deep sea, with the greatest limitations in understanding due to dependable biological estimates of connectivity (Cowen and Sponaugule, 2009; Young et al., 2012; Hilario et al., 2015 and references therein, Mitarai et al., 2016). Hilario et al. (2015) reviewed the application of biophysical models in the study of larval dispersal and population connectivity in the deep sea, and found the majority of models did not incorporate any behavior (e.g., PLD and vertical migration). In one of the few studies that incorporated behavior, Young et al. (2012) released simulated larvae from randomly chosen coordinates within 80 km of a seep sites in the Intra-American Seas, where adult “*B.*” *childressi* were known to be abundant. Two depths of dispersal were tested, though no ontogenetic migration patterns were incorporated. Our current study builds upon the work of Young et al. (2012) by incorporating hypothetical vertical distributions and targeted releases from known methane seep sites.

A recent study by Faure et al. (2015) investigated the population connectivity of “*B.*” *childressi* across six sites in the GOM. The “*B.*” *childressi* network was found to be more highly structured than other bathymodiolin species in the study, and two subpopulations in the central GOM had statistically significant genetic differences that indicates reduced connectivity. The results of the study broadly align with

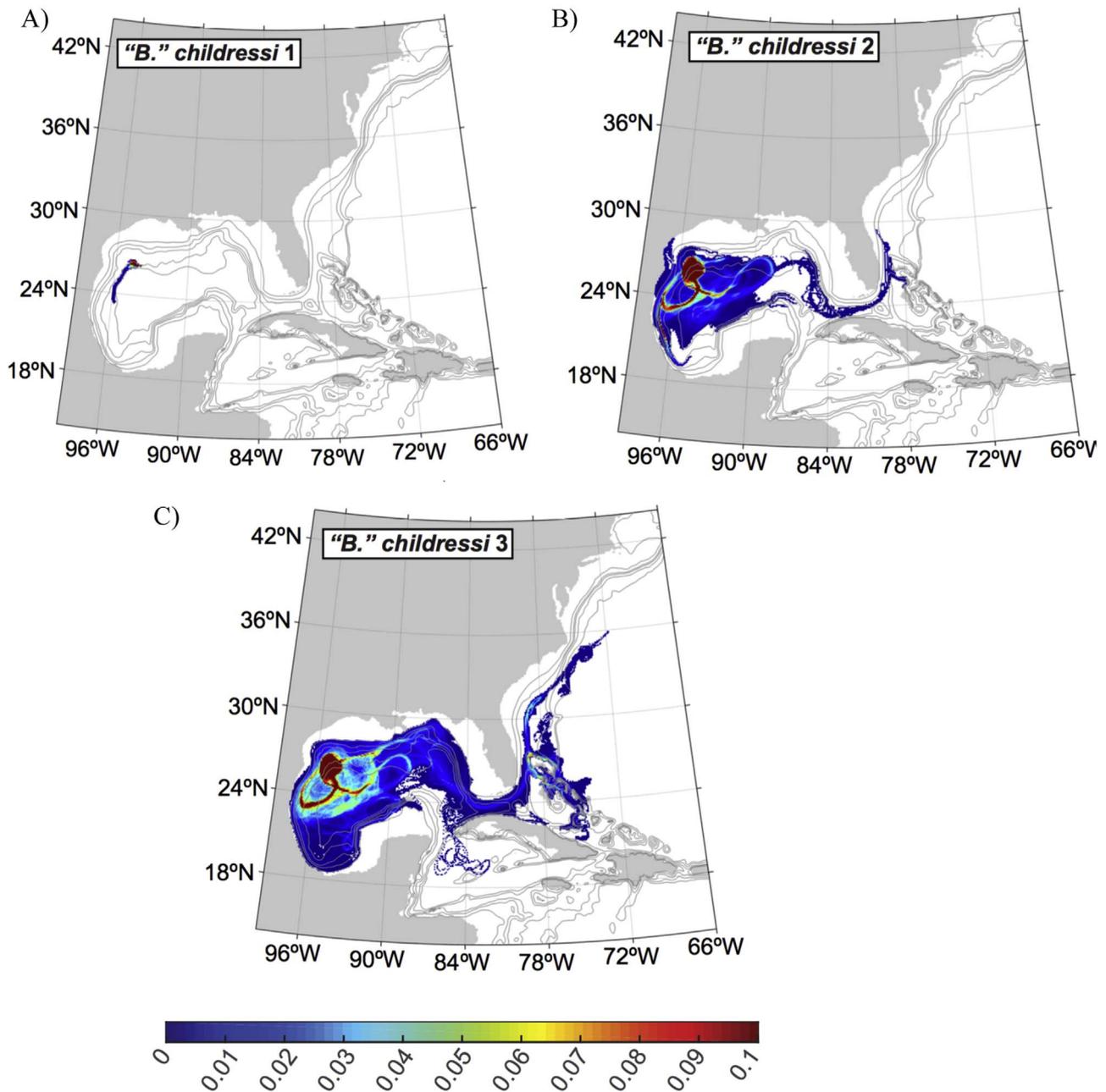


Fig. 3. Lagrangian Particle Density Functions (LPDFs) for a single release site, Alaminos Canyon, (site 1 as shown in Fig. 1) based on the trajectories of (A) "*Bathymodiolus*" *childressi* Simulation 1, (B) "*Bathymodiolus*" *childressi* Simulation 2, and (C) "*Bathymodiolus*" *childressi* Simulation 3. Warmer colors indicate a higher probability (for example, 10%) of a particle dispersing through a particular grid cell in the model domain, whereas cooler colors signify lower probabilities of particles dispersing through the grid cell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

current understanding of a well-connected population and previous research on population connectivity of "*B.*" *childressi* in the GOM (Carney et al., 2006); however, the genetic differentiation in the central GOM between two subpopulations indicates that biophysical factors influence connectivity over short distances. The results of the three simulated behaviors and genetic data from Faure et al. (2015) and Carney et al. (2006) show that it is not possible to have well-connected populations in the GOM with demersal drift behavior over a 13-month PLD. Therefore, it is likely that larvae are migrating into the water column in order to increase dispersal distance during their PLD. While it is possible to achieve higher levels of population connectivity with surface migration behavior, more research is necessary to characterize dispersal behaviors and oceanographic factors. Previous work has found some "*B.*" *childressi* larvae in the upper 100 m of the water

column (Arellano et al., 2014), but more sampling data is required to further understand the dispersal depths for the larvae over the course of their PLD.

Coupled biophysical models can be valuable tools to study the general dispersal patterns of larvae and to better understand how behavior drives variation in dispersal and potential population connectivity. The LPDFs and mean dispersal distances from the three possible larval behavioral scenarios examined in this study are considered the best approximations to date of actual dispersal trajectories of "*B.*" *childressi* larvae under variable atmospheric and oceanographic conditions. Biological information, such as larval dispersal depth, behavior, and PLD remain unknown, however, model simulations enable an effective means to study the relative effect of directly observed behaviors of larvae on larval dispersal. Limited direct observations of

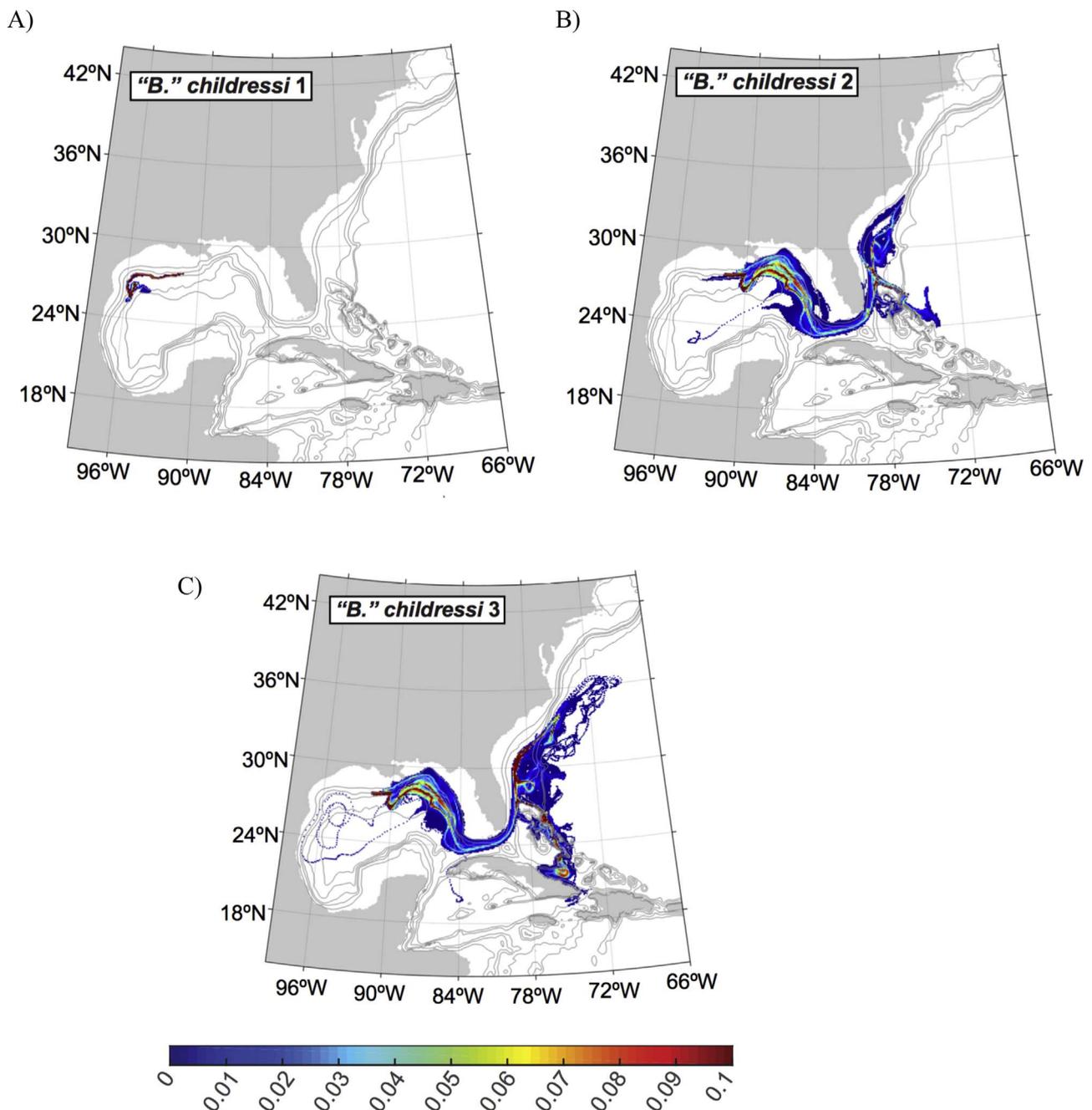


Fig. 4. Lagrangian Particle Density Functions (LPDFs) for a single release site, Brine Pool, (site 2 as shown in Fig. 1) based on the trajectories of (A) “*Bathymodiolus childressi* Simulation 1, (B) “*Bathymodiolus childressi* Simulation 2, and (C) “*Bathymodiolus childressi* Simulation 3. Warmer colors indicate a higher probability (for example, 10%) of a particle dispersing through a particular grid cell in the model domain, whereas cooler colors signify lower probabilities of particles dispersing through the grid cell. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

spawning events for vent and seep invertebrate species have found huge variation in the number of eggs released, with some species releasing only 200 eggs per individual, and others over 200,000 per individual (Tyler and Young, 1999). While egg production is distinct from the successful development of larvae, assumptions related to deep-sea fecundity are focused on total number of eggs for most species; hence, it was necessary to make estimates in this study. Additionally, the number of larvae will be correlated to the area of the seep and the number of fauna per unit area, as well as number of larvae released per individual species. The actual density of adult invertebrates at each seep site was not included in this study, and instead focused on the larval dispersal phase. The particles released in the simulations are an underestimate of larvae produced from a single spawning event, yet it still provides

insight into the dispersal of particles released from a known seep site. It is also computationally expensive to release large quantities of particles, which was taken into consideration during the experimental design of the simulation runs. With the current limitations in computing, it is not yet possible to simulate a spawning event from a dense seep community, and future work should mimic as best as possible the number of larvae created by seep communities with the use of high performance computers. Working with limited data provided an opportunity to explore the array of behaviors tested, and extensively study the effect of those behavioral parameters on potential dispersal. The monthly-averaged model forcing provides seasonal variations in ocean circulation patterns, resulting in predictions of average dispersal processes. However, short-term variability and the effect of synoptic-scale

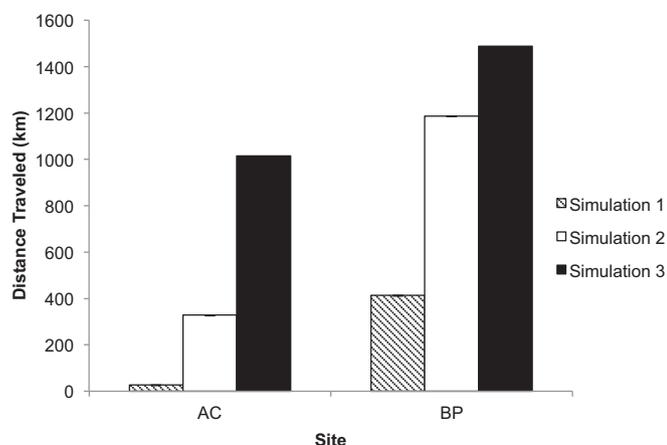


Fig. 5. Effects of (i) particle release site and (ii) larval behavior (demersal drift, surface to demersal drift, and surface drift) on mean (+SE) distance traveled (km) by “*Bathymodiolus*” *childressi* over 395-day PLD. AC = Alaminos Canyon and BP = Brine Pool. Simulation 1: larvae disperse near bottom for 395 days. Simulation 2: larvae disperse 175 days at the surface followed by 215 days of demersal drift. Simulation 3: larvae disperse the surface.

events such as storms, upwelling events, and tropical cyclones (which may greatly affect specific dispersal events) are not considered in this work. Spatially, the climatological model is limited by grid scale of 7–10 km. It is known that the larval tracking results are sensitive to the model grid resolution (Putman and He, 2013). A grid refinement is needed in a future study to better understand the movements of particles in the domain. This somewhat coarse spatial resolution is a necessary trade-off to cover such a large spatial domain (over 1000,000 km²).

The larval behavioral simulations presented are some of the most detailed performed to date for a deep-sea larva. Nevertheless, certain assumptions had to be made. It was assumed that “*B.*” *childressi* particles swim vertically and at a constant rate from days 3 to 10 at 0.02 cm s⁻¹, and then at 0.2 cm s⁻¹ for the remainder of their PLD. Little is known about their swimming behavior, nor how the larvae respond to light, pressure, and temperature over the course of their PLD. Previous laboratory observations (Arellano, 2008) show that “*B.*” *childressi* larvae do increase vertical swimming velocity with an increase in temperature (7–15 °C), and while it was beyond the scope of this study to manipulate swimming particle behavior in response to temperature, the particle swimming speeds were adjusted throughout the larval life to best match empirical data. The 13-month dispersal time is a realistic PLD for “*B.*” *childressi*; however, it is important to stress that the actual PLD is not known. Arellano and Young (2009) estimated larval life spans for “*B.*” *childressi* from estimated settlement dates and known spawning dates, and found PLD ranged from five months to 17 months. Other deep-sea invertebrates have prolonged PLDs, such as the gastropod *Bathynnerita naticoidea* (nearly one year; Van Gaest and Lea, 2006), and delayed development and metamorphosis until larvae encounter optimal environmental cues (Pradillon et al., 2001). The 13-month PLD was therefore chosen to understand the maximum potential dispersal potential for larval particles released from two sites in the GOM. The extensive distribution of larval particles with near surface dispersal behavior throughout the GOM and Florida Strait shows the maximum dispersal envelope and potential connectivity in the IAS. Future modeling research should vary the PLD to identify dispersal potential for the minimum and average PLD for “*B.*” *childressi*.

Further research of “*B.*” *childressi* larval dispersal throughout the Gulf of Mexico should focus on increasing the spatial scale of the model resolution to explore the effects of small-scale oceanographic features on large-scale dispersal patterns. The seasonal spawning of “*B.*” *childressi* may have a strong impact on potential dispersal, and further studies should compare mean dispersal distances among all four seasons to

determine if seasonal differences in spawning influence the dispersal and potential connectivity for simulated larvae with a 13-month PLD.

In summary, the amount of time spent in near surface waters for “*B.*” *childressi* larval particles had a significant effect on their dispersal throughout the Gulf of Mexico and U.S South Atlantic. These results suggest that obtaining values of the relevant physiological and behavioral parameters, such as PLD and dispersal depths of deep-sea larvae that can be integrated into biophysical models, should continue to take high priority in the study of deep-sea invertebrates and predictions of population connectivity.

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