



## SYMPOSIUM

### Dispersal of Deep-Sea Larvae from the Intra-American Seas: Simulations of Trajectories using Ocean Models

Craig M. Young,<sup>1,\*</sup> Ruoying He,<sup>†</sup> Richard B. Emlet,<sup>\*</sup> Yizhen Li,<sup>†</sup> Hui Qian,<sup>†</sup> Shawn M. Arellano,<sup>2,\*</sup> Ahna Van Gaest,<sup>3,\*</sup> Kathleen C. Bennett,<sup>\*</sup> Maya Wolf,<sup>\*</sup> Tracey I. Smart<sup>4,\*</sup> and Mary E. Rice<sup>‡</sup>

<sup>\*</sup>Oregon Institute of Marine Biology, University of Oregon, Charleston, OR 97420, USA; <sup>†</sup>Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, USA; <sup>‡</sup>Smithsonian Marine Station at Ft. Pierce, Ft. Pierce, FL 34949, USA

From the symposium “Dispersal of Marine Organisms” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2012 at Charleston, South Carolina.

<sup>1</sup>E-mail: cmyoung@uoregon.edu

<sup>2</sup>Present address: Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

<sup>3</sup>Present address: Northwest Fishery Science Center, National Marine Fisheries Service, Newport, OR 97365, USA

<sup>4</sup>Present address: South Carolina Department of Natural Resources, Charleston, SC 29412, USA

**Synopsis** Using data on ocean circulation with a Lagrangian larval transport model, we modeled the potential dispersal distances for seven species of bathyal invertebrates whose durations of larval life have been estimated from laboratory rearing, MOCNESS plankton sampling, spawning times, and recruitment. Species associated with methane seeps in the Gulf of Mexico and/or Barbados included the bivalve “*Bathymodiolus*” *childressi*, the gastropod *Bathynnerita naticoidea*, the siboglinid polychaete tube worm *Lamellibrachia luymesii*, and the asteroid *Sclerasterias tanneri*. Non-seep species included the echinoids *Cidaridites blakei* and *Stylocidaris lineata* from sedimented slopes in the Bahamas and the wood-dwelling sipunculan *Phascolosoma turnerae*, found in Barbados, the Bahamas, and the Gulf of Mexico. Durations of the planktonic larval stages ranged from 3 weeks in lecithotrophic tubeworms to more than 2 years in planktotrophic starfish. Planktotrophic sipunculan larvae from the northern Gulf of Mexico were capable of reaching the mid-Atlantic off Newfoundland, a distance of more than 3000 km, during a 7- to 14-month drifting period, but the proportion retained in the Gulf of Mexico varied significantly among years. Larvae drifting in the upper water column often had longer median dispersal distances than larvae drifting for the same amount of time below the permanent thermocline, although the shapes of the distance–frequency curves varied with depth only in the species with the longest larval trajectories. Even species drifting for >2 years did not cross the ocean in the North Atlantic Drift.

#### Introduction

Planktonic larvae, which are found in the life cycles of most benthic animals (Thorson 1964), connect disjunct metapopulations on many spatial scales. The potential for dispersal at these various scales is critically important in understanding population dynamics and biogeography in the sea (Cowen et al. 2006; Cowen and Sponaugle 2009; McClain and Hardy 2010). The role of larval dispersal in maintaining the genetic structure of marine populations has been discussed from a theoretical standpoint ever since the discovery that some shallow-water larvae

can disperse across ocean basins (Scheltema 1968, 1971). The issue has taken center stage recently with the widespread recognition that larval transport influences recruitment, a process that is important in applied problems such as fisheries management, conservation, and the siting of marine protected areas. The present study deals with larval dispersal in the deep sea, a field that remains in its infancy.

Work on genetic connectivity at hydrothermal vents reveals little evidence for genetic structure on moderate to large scales along the axes of ridges (reviewed by Vrijenhoek 1997, 2010) but shows

significant structure on opposite sides of biogeographic barriers such as the Easter Island Microplate in the South Pacific (Won et al. 2003), the Blanco Transform Fault in the northeastern Pacific (Johnson et al. 2006; Young et al. 2008), and fracture zones on the Mid-Atlantic Ridge (O'Mullan et al. 2001).

Seamounts, which were once considered to be isolated habitats with high endemism (reviewed by Rogers 1994; McClain 2007), demonstrate a surprising level of genetic connectivity that probably reflects larval dispersal (Smith et al. 2004; Samadi et al. 2006). In contrast, invertebrates on homogeneous abyssal soft bottoms may have significant genetic structure on relatively small spatial scales (Zardus et al. 2006).

Recent work (reviewed by Cordes et al. 2007; Olu-Le Roy et al. 2007) reveals that several species-complexes of methane-seep invertebrates are found in both the eastern Atlantic (Gulf of Cadiz and Gulf of Guinea) and western Atlantic (Barbados Accretionary Prism, Gulf of Mexico, and Blake Plateau). However, genetic evidence (Olu-LeRoy et al. 2007) shows deep divergences among the morphologically similar ampho-Atlantic populations, suggesting infrequent connectivity. COI sequence data provide better evidence for connection among seeps in the southern Caribbean, northern Gulf of Mexico, and the Blake Plateau off the seaboard of North Carolina. Those species that have been examined in the well-studied seeps on the Louisiana Slope show minimal evidence of genetic structure (McMullin et al. 2003, 2010; Carney et al. 2006).

Although demographic factors, external environmental factors, and the distributions of disjunct habitats all play roles in determining genetic structure (Vrijenhoek 2010; Coykendall et al. 2011), larval or adult dispersal by oceanic currents is implicated as an important mechanism of connectivity in virtually every species that has been examined.

Biological factors such as ontogenetic vertical migration, buoyancy of embryos, predation, food availability, developmental rate, and physiological tolerances, all play roles in determining dispersal patterns, but these have been studied for relatively few deep-sea animals. However, by knowing just a single biological parameter, the length of larval life (planktonic larval duration [PLD]), and the speeds and directions of oceanic currents, one can estimate the likely upper limit of dispersal distance and relate probable dispersal trajectories to the biogeographic distributions of species. In the deep sea, simple dispersal models (progressive vector diagrams) using

Eulerian current data have been applied at hydrothermal vents (e.g., Chevaldonne et al. 1997; Marsh et al. 2001). Chevaldonne et al. (1997) used such models to explore a perceived discrepancy between lack of genetic structure in alvinellid polychaetes and the presumed absence of an effective dispersal stage. Later work on the embryos (Pradillon et al. 2005) revealed a mechanism, developmental arrest of embryos, which may explain this discrepancy. Marsh et al. (2001) used progressive vector models to predict that tube worm (*Riftia pachyptila*) larvae should disperse as much as 100 km during a 5-week planktonic period on the East Pacific Rise.

PLD is an important parameter for all dispersal models, but the estimation and use of this parameter are fraught with potential errors, especially when information on larval behavior is lacking (Shanks 2009). The problems are compounded for deep-sea species. For example, whereas shallow-water larvae may experience only minor fluctuations in temperature while dispersing, deep-sea larvae potentially can move into water of different temperatures (Young et al. 1996a, 1998), thereby experiencing changes in metabolism, feeding rate, and other vital processes. Four different methods have been employed for estimating PLD in the deep sea. The first is laboratory culture, which is non-trivial for deep-sea species because of the difficulty of maintaining correct conditions of temperature and pressure. Very few deep-sea species have been reared all the way to settlement. The second method is to compute PLD from metabolism and available energy stores. This method is only valid for lecithotrophs and requires assumptions about temperature and metabolic efficiency. The third method is to follow cohorts of larvae in the plankton. This is feasible only for species with discrete spawning seasons and is especially difficult for deep-sea species with long larval life. Finally, PLD may be estimated by comparison of settlement time and spawning time. In the deep sea, these two parameters are seldom known with certainty, so this method often requires back-calculation of settlement time using juvenile growth rates.

Even when PLD is known, it is easy to make large errors in estimating dispersal potential unless realistic oceanographic data are used. In a recent attempt to place upper and lower limits upon potential dispersal of larvae, McCain and Hardy (2010) plotted most of the known PLDs for deep-sea animals against rough estimates of high and low current speeds in the deep sea. Their plot showed that larvae dispersing in high currents could potentially go tens of thousands of kilometers during just a few months.

Unfortunately, these calculations did not take reversals of currents or variable velocities into account. The authors acknowledged that their calculations were preliminary and that better parameter estimates were needed. Here, we repeat these calculations for some of the same species, using realistic models of oceanographic currents for the actual places where the animals live.

It is expected that connections among distant populations would be facilitated by ontogenetic vertical migration, since dispersal distances should be greater in surface waters than in the slower currents of the deep sea (Young et al. 1996a). We know from laboratory studies that many species of deep-sea animals are confined to deeper waters because their larvae are incapable of tolerating the low pressure and high temperature found in the upper water column (Young and Tyler 1993; Young et al. 1996b, 1998; Brooke and Young 2009; Bennett et al. 2012). On the contrary, the larvae of some seep invertebrates have been reported near the surface (Van Gaest 2006; Arellano 2008), and some bathyal echinoderms have unexpectedly broad temperature tolerances (Young et al. 1996a; Young et al. 1998). The morphology of the protoconch (the initial shell of the larva) suggests that many abyssal gastropods are planktotrophic (Bouchet and Waren 1994) and data on oxygen isotopes indicate that some of these veligers migrate into warmer waters (Bouchet and Fontes 1981; Killingley and Rex 1985), observations that have been borne out by the collection of abyssal larvae in the surface plankton (Bouchet and Waren 1994).

In the present paper, we used velocities of oceanic currents computed by oceanographic hindcast models to assess potential larval-dispersal trajectories at two depths for invertebrates living in deep-sea wood falls (the sipunculan *Phascolosoma turnerae*), at cold methane seeps (the gastropod *Bathynnerita naticoidea*, the bivalve *Bathymodiolus childressi*, the siboglinid tube worm *Lamellibrachia luymesii*, and the asteroid *Sclerasterias tanneri*) and on sedimented bathyal slopes (the cidaroid echinoids *Stylocidaris lineata* and *Cidaris blakei*). With the exception of *S. tanneri*, whose larvae are currently being cultured in our laboratories, we have described aspects of larval development and reproductive ecology of all species used in the dispersal models (Rice 1985; Young and Tyler 1992; Young et al. 1996c, 1998; Van Gaest 2006; Arellano and Young 2009, 2011; Bennett et al. 2012; Rice et al., in press).

The approach was designed to answer the following questions using deep-sea species whose PLDs have been estimated from biological data: (1) What

is the relationship between PLD and dispersal potential for seep and non-seep slope animals in the intra-American seas? (2) How much does the dispersal potential vary from year to year because of variation in currents? (3) Do dispersal models demonstrate the potential for connectivity among distant deep-sea populations? (4) Do larvae migrating to the upper water column disperse significantly greater distances than do larvae remaining below the permanent thermocline? and (5) How do dispersal trajectories relate to known biogeographic distributions?

## Materials and methods

### Collection and rearing of animals

The seven species selected for dispersal models are from three bathyal sites, one each in the Gulf of Mexico, the Bahamas, and Barbados (Table 1), where we have worked extensively on reproductive and larval biology of deep-sea animals over the past 27 years, using Johnson-Sea-Link submersibles. Animals were collected carefully and transported to the surface in containers of cold seawater. Gametes were obtained using standard embryological techniques and larvae were cultured either in shipboard cold rooms or in our laboratories at Harbor Branch Oceanographic Institution (HBOI) in Florida, the Smithsonian Marine Station (SML) in Florida, or at the Oregon Institute of Marine Biology (OIMB). Direct observations of gonadal condition and of spawning were used in concert with gonadal histology to determine the appropriate time to initiate dispersal for the models.

### Estimating planktonic larval duration

Planktonic larval durations used in this article were determined by direct rearing of larvae or estimated by comparing settlement dates to known spawning times. In the latter cases, settlement dates were estimated by using measured growth rates of juveniles to back-calculate from the sizes of collected recruits.

Pelagosphaera larvae of the sipunculan *P. turnerae* were reared from gametes released spontaneously by adults maintained in refrigerated seawater tanks at Harbor Branch Oceanographic Institution, Florida, and cultured in refrigerated filtered seawater at the Smithsonian Marine Station in Florida (Rice et al., in press). Because we were not able to maintain these larvae to settlement, we estimated potential dispersal distances by indirect methods. Numerous spawning events were observed in the spring and summer months over several years (Rice et al., in press), with peak spawning occurring in May. We also deployed fibrous larval collectors on the bottom over a

**Table 1** Release sites (locations of adult populations), release dates (peak spawning or hatching dates), and run lengths (planktonic larval durations, PLDs) used for the dispersal models of the seven bathyal species studied. Adults of all species live at depths between 500 and 700 m

Species	Release sites	Release date	PLD (d)
Echinodermata			
<i>Sclerasterias tanneri</i>	GM <sup>a</sup>	October	660
<i>Cidaris blakei</i>	BR <sup>b</sup> , BA <sup>c</sup>	May	120
<i>Stylocidaris lineate</i>	BR <sup>b</sup> , BA <sup>c</sup>	May	120
Mollusca			
<i>Bathymodiolus childressi</i>	GM <sup>a</sup>	October	390
<i>Bathynnerita naticoidea</i>	GM <sup>a</sup> , BR <sup>b</sup>	May	210,390
Annelida			
<i>Lamellibrachia luymesii</i>	GM <sup>a</sup>	May	21
Sipuncula			
<i>Phascolosoma turnerae</i>	GM <sup>a</sup> , BR <sup>b</sup> , BA <sup>c</sup>	May	210,390

<sup>a</sup>Brine Pool, Louisiana Slope, Gulf of Mexico: 27°43.4' N 91°16.8' W.

<sup>b</sup>Off Hole Town, Barbados: 13°12.03' N 59°43.27' W.

<sup>c</sup>Southwest Reef, Tongue of the Ocean, Bahamas: 24°52.98' N 77°32.22' W.

3-year period, recovering the collectors at 3- to 6-month intervals. Growth rates of young individuals measured in the laboratory and in the field were used to generate a growth curve that allowed us to estimate the likely date of settlement for each individual recovered in the collectors. By counting back to the previous May spawning period, we obtained approximations of PLD.

A cold-seep mollusk, the gastropod *B. naticoidea* had a similar PLD as *P. turnerae*. *B. naticoidea* larvae hatch between February and July with a peak in May. Larvae identified by morphology and genetics were captured in mid-water MOCNESS tows in November and February, indicating a larval life that could be as short as 6–7 months from the May hatching peak or >12 months from the beginning of the spawning period through the following February (Van Gaest 2006).

Larvae of the cold-seep tube worm *L. luymesii* were cultured from zygotes removed by dissection from the terminal portion of females' oviducts (Young et al. 1996c; Hilario et al. 2005). Although the cultures never survived to metamorphosis, they generally survived for about 3 weeks. Predictions of duration of the larval stage based on metabolic rates and lipid stores (Leong 1998) provided independent confirmation of a three-week larval period. This is the only species we studied that had buoyant eggs.

The cold-seep bivalve *B. childressi* was spawned in the laboratory at OIMB by injection with 2 mM

serotonin and embryos were reared to the early larval stage in refrigerated seawater at 7°C. Because this species was not reared to settlement, we back-calculated settlement times for recruited individuals from growth rates of juveniles obtained from field outplant experiments (Arellano and Young 2009). As in *P. turnerae*, we counted back the months since the previous peak spawning period to estimate duration of the planktonic larval stage (Arellano and Young 2009).

Gametes of the asteroid *S. tanneri* from the Gulf of Mexico were obtained by injection of 100 μM 1-methyladenine during the October spawning season. The larvae of *S. tanneri* were cultured in incubators for >2 years without undergoing settlement. Water in cultures of bipinnaria larvae was changed by reverse filtration through 50 μm Nitex mesh and fed mixed cultures of the microalgae *Rhodomonas lens* and *Isochrysis galbana*. Similar culture methods were used for larvae of two Bahamian echinoid species, *C. blakei* (Bennett et al. 2012) and *S. lineata* (Young et al. 1998; T. I. Smart, R. B. Emler, and C. M. Young, unpublished data). Echinoid gametes were obtained by injection of 0.55 M KCl or 10 mM acetylcholine. The echinopluteus larvae were cultured through settlement in 0.45 μm filtered seawater held in cold-water incubators in Oregon.

## Modeling

Dispersal patterns were simulated by the author He's Ocean Observing and Modeling Group at North Carolina State University. We modeled larval trajectories with the LTRANS Lagrangian larval transport model (North et al. 2006; Schlag et al. 2008) using oceanic circulation hindcasts produced by either the South Atlantic Bight and Gulf of Mexico (SABGOM) ocean model (Hyun and He 2010) or the global HyCOM/NCODA ocean model (Chassignet et al. 2009, <http://hycom.org/dataserver/glb-analysis/expt-90pt9>). Each simulation involved the passive particle releases of between 200 and 250 "larvae." For one species, *P. turnerae*, we ran the model for the Gulf of Mexico during the same time period in 3 different years to assess the importance for dispersal distance of inter-annual variability in circulation patterns. Other species were modeled only in a single year. For all species, we modeled the trajectories beginning at the times of known spawning peaks. Each run included more than 200 "releases" from various randomly chosen coordinates within 80 km of a site where adults are known to be abundant. We included no vertical migration behavior in the models; instead, we compared dispersal distances



unambiguously between two depths, 100 m (above the permanent thermocline) and 500 m (below the thermocline, ~100–200 m above the adult habitats of all species examined). This approach assumes that larvae quickly attain their dispersal depth and spend most of their larval life drifting at a particular height (isobarically) in the water column. Data on flotation rates of *L. luymesii* embryos (Young et al. 1996c) and swimming speeds of echinoderm and bivalve larvae (Arellano 2008) suggest that this assumption is not unreasonable, although the actual depths of dispersal in the sea are unknown.

### Analysis

All statistical analyses were performed using protocols in Systat 11 software. Median distances traveled at the two modeled depths (100 and 500 m) were compared for each run using the non-parametric Wilcoxon–Mann–Whitney test. Distances traveled obtained from oceanic circulation–dispersal models were also plotted as frequency histograms, and the shapes of the frequency distributions for shallow and deep water were compared with the Kolmogorov–Smirnov two-sample goodness of fit tests. To determine if there were significant differences in mean distances traveled among years and depths, we analyzed data for Gulf of Mexico models of *P. turnerae* using a 2-way fixed ANOVA with depth and year as the independent variables.

## Results

### A wood-dwelling opportunist: *P. turnerae*

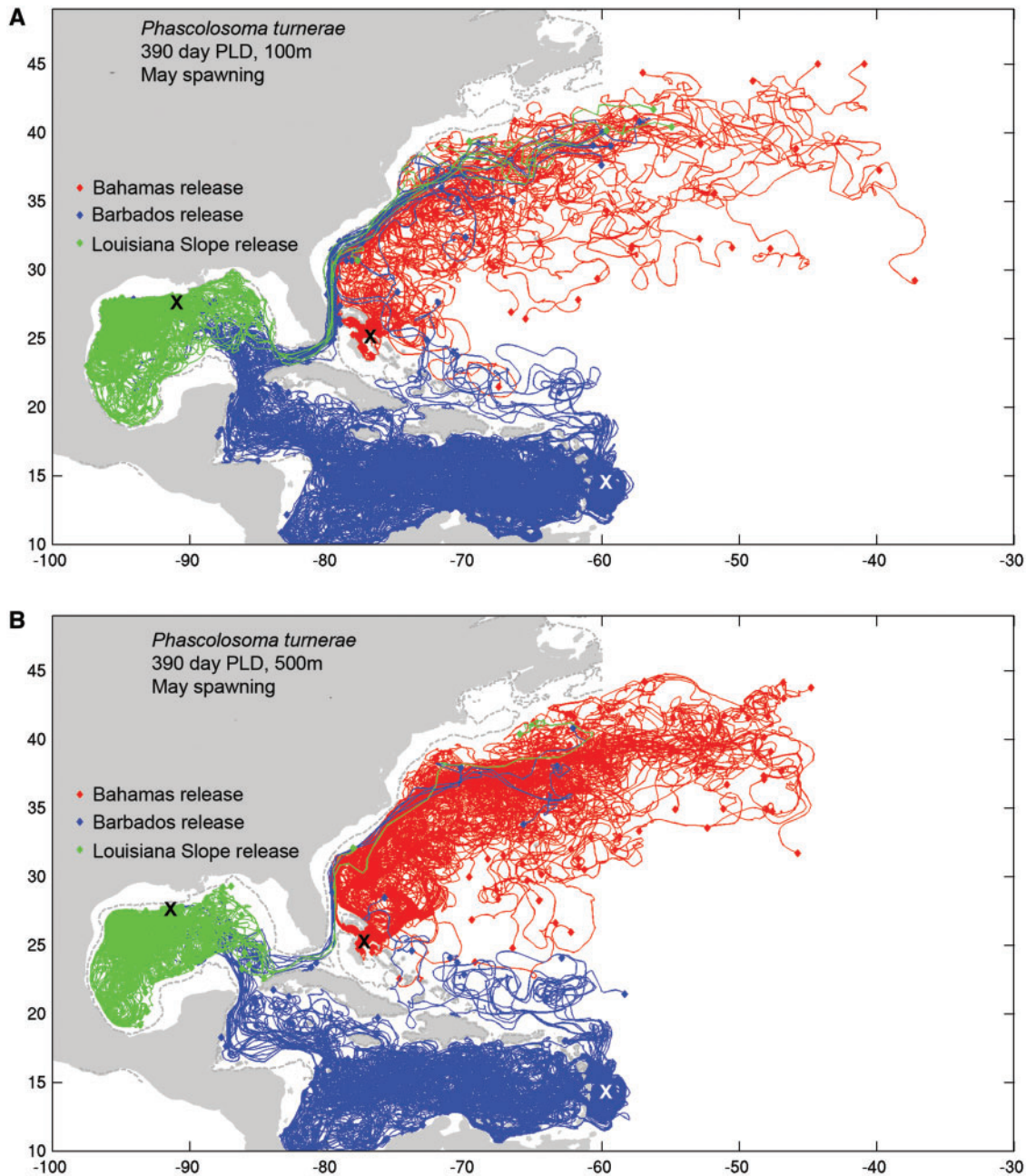
The sipunculan *P. turnerae* is the only species that occurs at all three release sites, so we ran more extensive analyses of this species than for the others. Figure 1 shows dispersal trajectories for larvae dispersing for a maximum estimated larval life of 13 months (Rice et al., in press). Larvae originating near Barbados had the potential of colonizing virtually the entire Caribbean area and the southeastern Gulf of Mexico, with most individuals being retained in the Caribbean. A few larvae entered the Gulf Stream and dispersed northward along the Atlantic seaboard. Larvae originating on the Louisiana Slope in the northern Gulf of Mexico dispersed throughout the Gulf and a significant number of them entered the Florida Current and dispersed up the east coast. A few larvae from the Northern Bahamas (Tongue of the Ocean) were retained in the local area, but none colonized Bahamian sites further south and most larvae from this area dispersed out into the North Atlantic, where many ended their larval life over much greater depths than those at which adults are

known to occur. As expected, transport from all sites was more-or-less unidirectional, following the overall flow pattern of the North Atlantic Gyre. However, there was sufficient retention in all areas, assuring that local populations could be reseeded. Frequency distributions of dispersal distances (Fig. 2) had distinctly different shapes at the different release sites. The distribution of Barbadian larvae (Fig. 2A) was unimodal in both deep and shallow water, with very few larvae being retained near the point of origin. Larvae released in the Gulf of Mexico (Fig. 2B) produced a bimodal distribution, with most being retained in the Gulf. In the Bahamas, those larvae that were not retained locally dispersed broadly and ended up many distances from the source (Fig. 2C). In none of these cases did the shape of the distribution differ between deep and shallow trajectories (Kolmogorov–Smirnov tests, Fig. 2).

The effect of depth on dispersal distance was evaluated by using nonparametric Wilcoxon–Mann–Whitney tests to compare median distances traveled at depths of 500 and 100 m (Table 2). When originating in the Bahamas or the Gulf of Mexico, larvae of *P. turnerae* from shallow water dispersed significantly greater distances than did those from deep water (Table 2). For larvae originating in Barbados, the median dispersal distance was greater in deep water than in shallow water, but the difference was not statistically significant ( $P=0.056$ ).

Larval trajectories of *P. turnerae* for 3 different years (Fig. 3) using a minimum PLD for this species showed significant inter-annual variation in dispersal distance, with many more shallow-water larvae entering the North Atlantic in 2009 than in 2007 or 2008. This effect was less apparent for larvae dispersing in deep water. A two-factor analysis of variance showed significant main effects for both depth and year, with a significant depth–year interaction (Table 3).

*Phascolosoma turnerae*, like wood-eating xylophagid bivalves in the deep sea, must locate ephemeral plant remains distributed in unpredictable places on the ocean floor. An important role of larval dispersal in such species must be the efficient “sampling” of the sea floor to assure that these rare habitats are located. The long larval life of this species assures thorough coverage of sea–floor habitats (Fig. 1). Some data on recruitment suggest that these larvae may be demersal, drifting very near the bottom where encounter with potential habitats is maximized (Rice et al., in press). If this is the case, then realized dispersal may be much lower than predicted in our models.

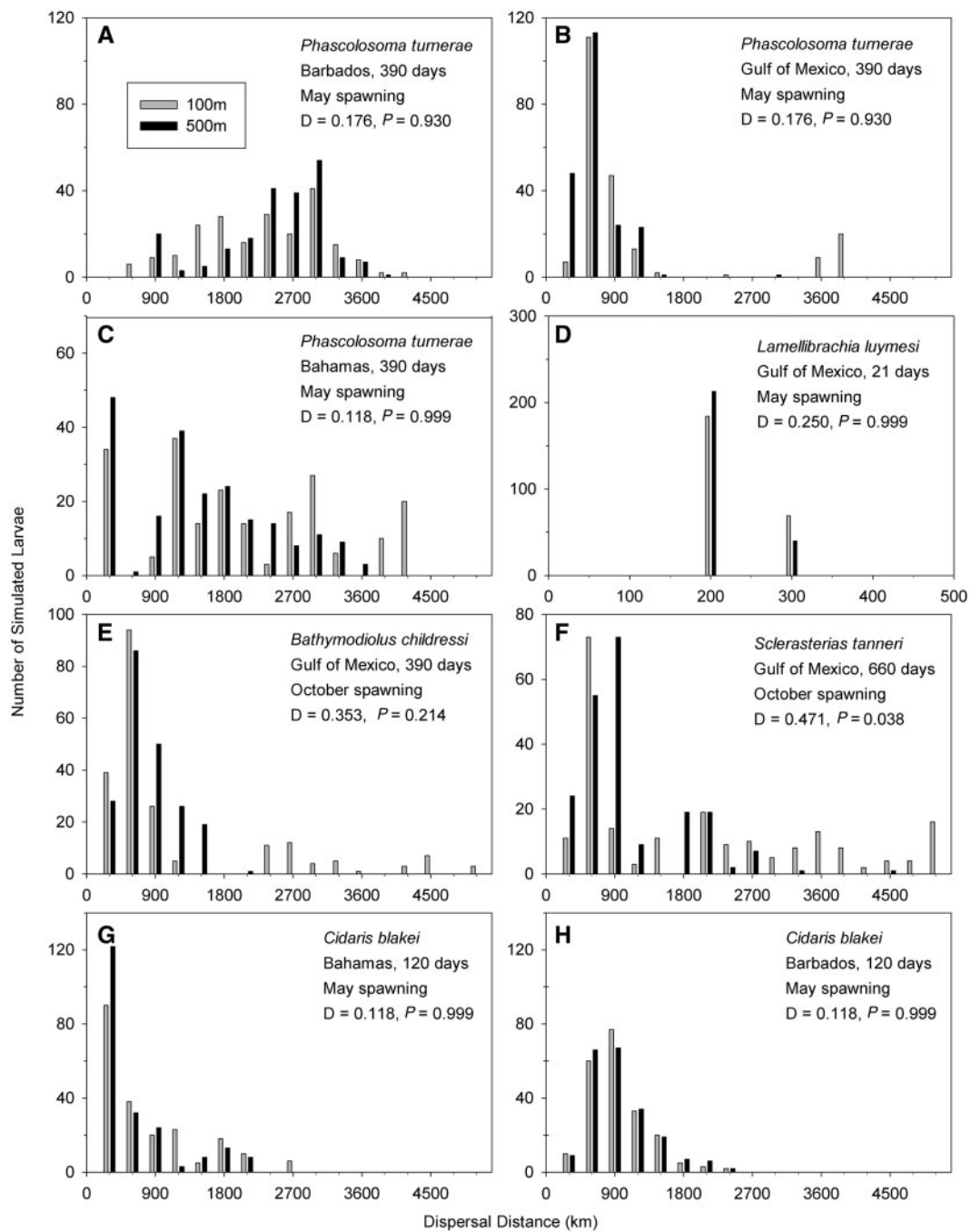


**Fig. 1** Simulated larval dispersal trajectories of the sipunculan *P. turnerae* at depths of 100 m (A) and 500 m (B) during 2010. The maximum estimated duration of the larval stage (390 days) was used. Larvae originating from each of the three release sites (Table 1) are color-coded. The trajectories originating at release sites off Barbados and in the Gulf of Mexico are also representative of the seep gastropod *B. naticoidea*. Beginning points, marked with “X,” also apply to subsequent figures.

**Methane-Seep Species: *B. naticoidea*, *L. luymesii*, *B. childressii*, and *S. tanneri***

The gastropod *B. naticoidea* is known to occur only at methane seeps on the Barbados Accretionary Prism and on the Louisiana Slope. Its larval lifespan covers approximately the same range as that of *P. turnerae* (6–12 months) and its larvae hatch from egg capsules during the same spring months as *P. turnerae* spawns, so the trajectories from Barbados and the Gulf of

Mexico depicted in Figs. 1 and 3 also predict the dispersal of *B. naticoidea*. Based on the south-to-north trajectories shown in the models, one might predict that the sink metapopulations in the Gulf of Mexico could be replenished in part by upstream source populations off Barbados (Fig. 1). However, most larvae that enter the Gulf of Mexico are entrained into the Florida Current without encountering the seeps on the Louisiana and Mississippi slopes.



**Fig. 2** Frequency histograms showing the number of “larvae” dispersing various distances at two depths. In all graphs but **D** (*L. luymesii*), histograms bars represent ending points grouped into 300-km bins. Numbers on the x-axis are upper limits of those bins. Data for *L. luymesii*, which has a relatively short larval life, are grouped in 100-km bins. Sample sizes are 253 for *L. luymesii* and 212 for all other runs. Kolmogorov–Smirnov *D* statistics comparing the shapes of the two depth curves are presented with *P*-values.

Unless there are many more seeps than presently known, most larvae produced off Barbados will be lost without finding a suitable habitat, whereas most larvae produced in the Gulf of Mexico will be retained in the Gulf with the potential of seeding local metapopulations on the slope from which they originated. Figure 4 shows the shallow and deep

trajectories for three species with very different PLDs all co-occurring at cold seeps in the northern Gulf of Mexico and released in 2010. The chemosynthetic tubeworm *L. luymesii*, whose known geographical range is confined entirely to the slope of the northern Gulf of Mexico, drifts as a lecithotrophic larva for only about 3 weeks (Young et al. 1996a).

**Table 2** Wilcoxon–Mann–Whitney U tests comparing median dispersal distances between two depths (100 and 500 m) in the simulation outputs

Release site species	Median dispersal distance (km)		U	Sample size	P
	100 m	500 m			
Louisiana Slope					
<i>Lamellibrachia luymesii</i>	102.60	113.50	32,257	253	0.878
<i>Bathymodiolus childressii</i>	423.29	507.03	19,929	210	0.088
<i>Sclerasterias tanneri</i>	1184.45	724.25	28,208	210	0.000
<i>Phascolosoma turnerae</i>	520.11	396.96	29,724	210	0.000
Bahamas					
<i>Cidaris blakei</i>	422.53	160.32	26,697	210	0.000
<i>Phascolosoma turnerae</i>	1570.35	1187.50	28,824	210	0.000
Barbados					
<i>Cidaris blakei</i>	642.88	617.54	21,689	210	0.772
<i>Phascolosoma turnerae</i>	2182.4	2376.6	19,670	210	0.056

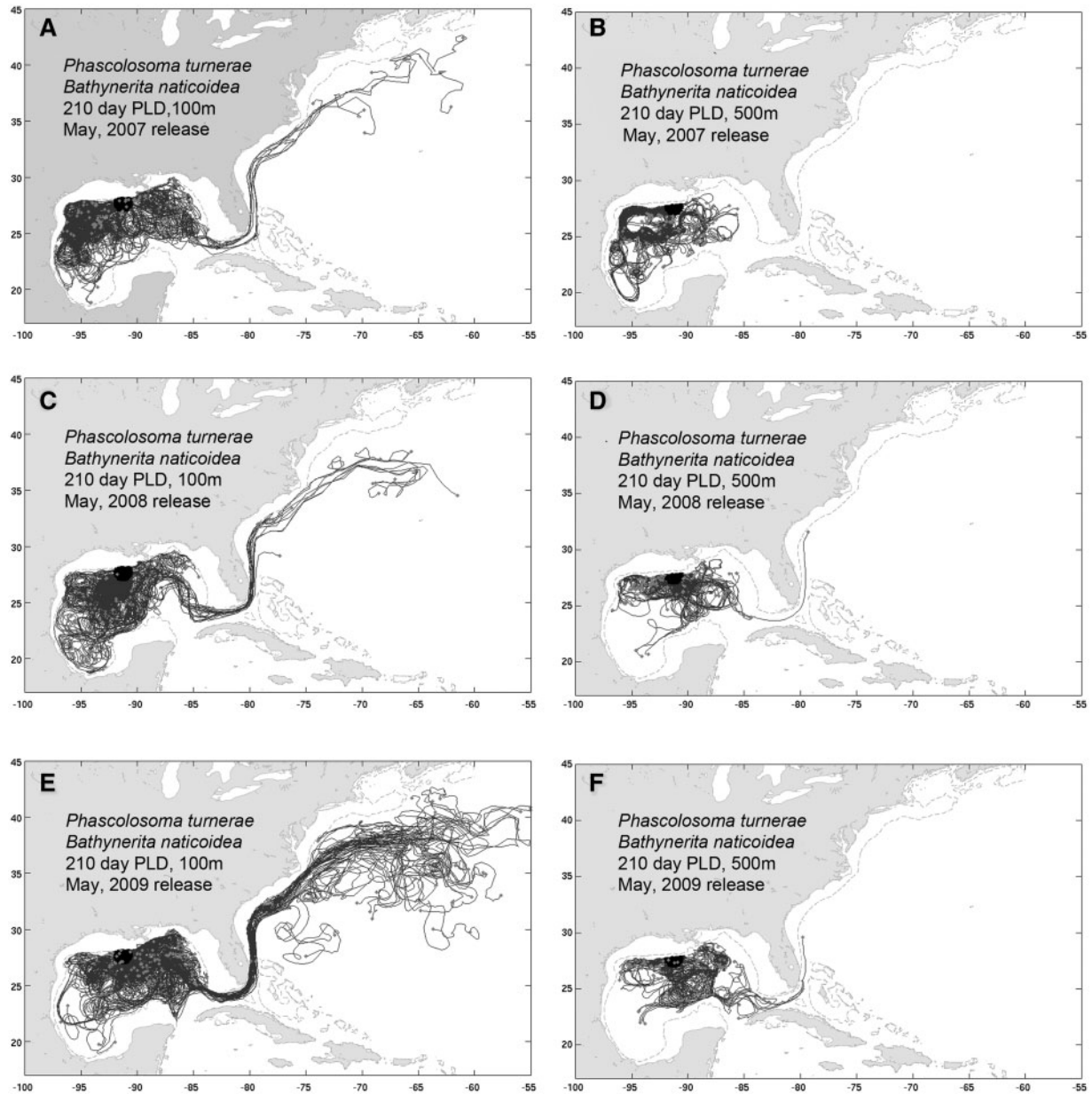
Larvae originating near the center of the species' range dispersed in both eastward and westward directions but were always retained in the Northern Gulf of Mexico, irrespective of dispersal depth. A few larvae dispersed as far as 300 km from the source, but the majority drifted between 100 and 200 km, with none being retained less than 100 km from the source (Fig. 2D). The shapes of the frequency curves of distances were not significantly different between depths, nor was there a significant effect of depth on the median dispersal distance (Table 2). The larvae of this species are strongly buoyant for the first days of their dispersal period, but become neutrally buoyant in the second week. Our unpublished data indicate that the larvae cannot tolerate temperatures above the thermocline. Because they do not feed (Young et al. 1996a) and because dispersal would not be enhanced significantly by migration through the thermocline, it is not surprising that these larvae have not evolved broader thermal tolerances. The life history seems well suited to maintaining small metapopulations in an environment with patchy slopes.

Simulated larvae of the seep mussel *B. childressii* dispersed throughout the Gulf of Mexico and many moved up the eastern seaboard, where they could potentially connect with cold seeps on the Blake Ridge (off North Carolina) and the Laurentian Fan (off Nova Scotia). It is surprising, therefore, that this species is not known from either of these seep systems in the western North Atlantic (Olu et al. 1996; Van Dover et al. 2003). Despite the fact that populations in the “B.” *childressii* clade are found on the other side of the Atlantic (Cordes et al. 2007; Olu-Le Roy et al. 2007),

simulated larvae from the Louisiana Slope did not connect with European or African populations during their 13 month drifting period when released in October of 2009. The models provided no evidence for the small-scale corralling of larvae that has been inferred from recruitment patterns of seep mussels (Van Dover et al. 2001), although most larvae were retained in the Gulf of Mexico within 1000 km of their point of origin (Fig. 2E). Studies of physiological tolerances (Arellano and Young 2011) indicate that these larvae could disperse above the permanent thermocline. In the models, however, the median dispersal distances were not significantly different between shallow and deep water (Table 2), nor did the shapes of the distance–frequency curves differ between shallow and deep water (Fig. 2E).

The species with the longest larval life studied (at least 32 months) was the asteroid *Sclerasterias tanneri*, which lives at seeps in the Gulf of Mexico and feeds on chemosynthetic mussels. It is also known from non-seep habitats at various depths off the eastern seaboard of the United States. Over a 2-year period, simulated larvae of this species dispersed widely in the North Atlantic Drift but did not make it as far as the European slope. The trajectory cloud of larvae originating in the Gulf of Mexico completely overlapped the known geographic range, which extends into the western North Atlantic as far north as Newfoundland (Clark and Downey 1991). Because the deep-water starfish of European seas are known very well (Clark and Downey 1991), we can say on the basis of both adult distributions and larval dispersal modeling that larvae of *S. tanneri* do

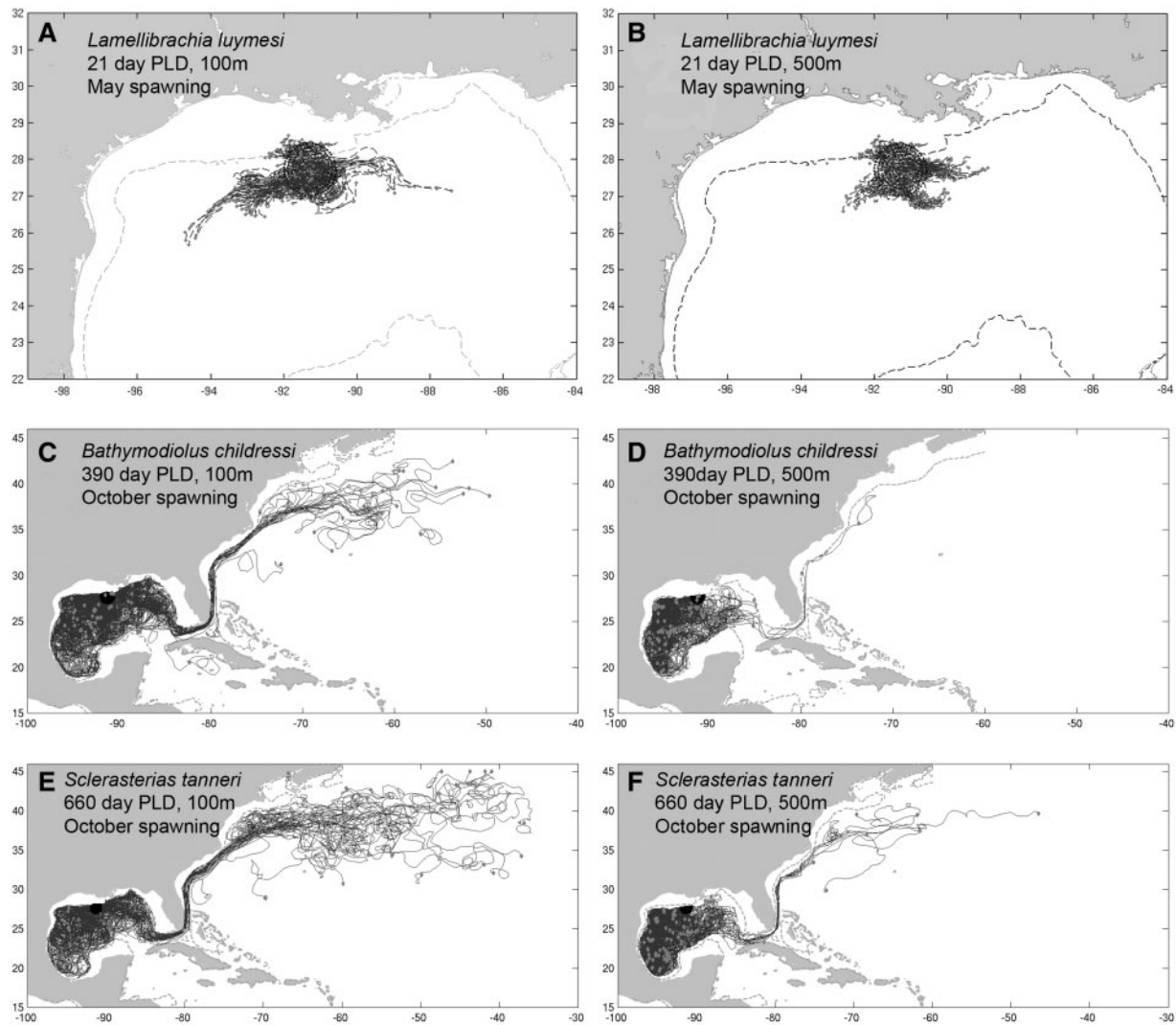




**Fig. 3** Simulated dispersal trajectories of *P. turnerae* and *B. naticoidea* originating in the Gulf of Mexico; the minimum calculated duration of the pelagic larval stage of 210 days was used. Depths are plotted in separate graphs for each of 3 years (**A** and **B**: 2007, **C** and **D**: 2008, **E** and **F**: 2009). These data may also be applied to the gaspod *B. naticoidea*, which has a similar hatching time and a similar PLD.

**Table 3** Two-factor analysis of variance testing the effects of year (2007–2009) and depth (100 and 500 m) on mean dispersal distance of larvae of *P. turnerae* or *B. naticoidea* during a 7 month duration as planktonic larvae

Source	Sum of squares	d.f.	Mean square	F-ratio	P
Year	4,079,904.757	2	2,039,952.378	6.125	0.002
Depth	50,348,500.000	1	50,348,500	151.163	0.000
Interaction	10,602,000.000	2	5,301,001.479	15.915	0.000
Error	417,675,000.000	1254	333,073.922	—	—



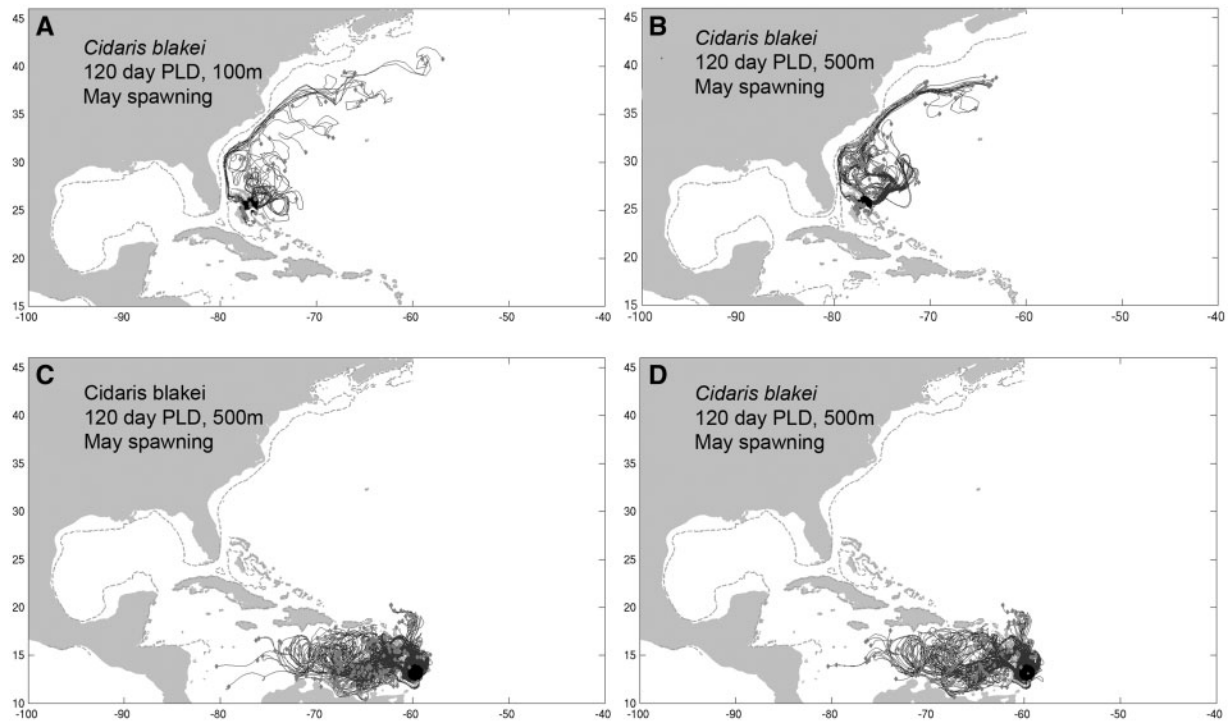
**Fig. 4** Simulated dispersal trajectories at two depths for three species living at methane seeps in the northern Gulf of Mexico: *L. luymesii* (A and B), *B. childressi* (C and D), and *S. tanneri* (E and F).

not drift across the Atlantic Ocean to colonize the European continental margin. Populations in the Northern Gulf of Mexico are probably self-sustaining or seeded by more southerly populations in the Caribbean. This was the only species studied that showed a significant difference in the shapes of distance–frequency curves between shallow and deep water (Fig. 2F), probably because more larvae above the thermocline than below it drifted away from the continental margin in the North Atlantic (Fig. 4).

#### Animals from island slopes: *C. blakei* and *S. lineata*

The two echinoid species from the Bahamas had similar PLDs (*S. lineata*: 3.5 months, *C. blakei*: 4 months); so, we used the same 4-month model to represent both of them. Simulated larvae

originating in Barbados were all retained in the Lesser Antilles region and did not supply metapopulations in the Bahamas (Fig. 5). Larvae originating in the northern Bahamas (Tongue of the Ocean) were either retained in the Bahamas (Fig. 2G) or exported through the New Providence channels into the North Atlantic, where populations are known along the eastern continental margins. Both species are limited, however, to depths of less than 800 m, so the model predicts that many larvae originating in the Bahamas are lost into deeper water where there are no suitable habitats for adults. There was a significant difference in median dispersal distance with depth for animals originating in the Bahamas but not in Barbados (Table 2). The shapes of the distance curves were not significantly different between depths. A full understanding of the role of dispersal for these species



**Fig. 5** Simulated dispersal trajectories at two depths for larvae of the cidaroid echinoid *C. blakei* spawned during May in the Tongue of the Ocean, Bahamas (**A** and **B**) and off Barbados (**C** and **D**) in 2010. The simulations used a PLD of 120 days. The data also approximate the dispersal trajectories of a second cidaroid, *S. lineata*, which spawns at the same time of year but has a slightly shorter PLD of about 106 days.

will require additional modeling to reveal how metapopulations on the slopes of various Caribbean islands might be connected.

## Discussion and conclusions

Dispersal influences not only geographic ranges of species (Scheltema 1986) but also the demography of marine species over ecological time scales (e.g. Caswell et al. 2011) and the longevity of species over geological time scales (Jablonski and Lutz 1983). Consequently, dispersal enters into virtually all discussions of biogeography, ecological resiliency (Gunderson et al. 2009), and conservation in the sea. The conservation of deep-sea communities has received increasing attention in recent years (reviewed by Thiel 2003) as highlighted by the 2010 Deep-Water Horizon oil spill in the Northern Gulf of Mexico (White et al., in press) and by efforts to establish marine protected areas on the high seas (Mills and Carlton 1998). The resiliency of a species to a local or regional disturbance such as a deep oil spill depends in part on the ability of larvae to disperse among suitable habitats. The present study, therefore, has potential relevance to the persistence of deep-sea populations impacted by human activities.

Our data, the first to model dispersal of bathyal species in the Intra-American Seas using realistic biological data, show that most larvae are retained in the same geographic areas as the adults, but that the net transport of those not retained is essentially unidirectional. The southern metapopulations in the Caribbean and the western metapopulations in the Gulf of Mexico are more likely to be sources (*sensu* Pulliam 1988) and northern and eastern populations are more likely to be sinks. In the bathyal species that we studied, maximum dispersal distance was strongly related to PLD, ranging from 300 km in a tubeworm with a 3-week larval period to >5000 km in a starfish that disperses for >2 years. The release site played an important role in determining the shape of the distribution of distances attained. For example, long-lived larvae released in the Gulf of Mexico and finding their way into the Gulf Stream tended to have more bimodal distributions than ones released in Barbados or the Bahamas. Absolute distances were highly variable in all cases, and most of the data indicated that large numbers of larvae are retained in the general area of the adult habitat. Many larvae from Barbados were retained in the Southern Caribbean; exported ones could drift as far as the Gulf of Mexico and North Atlantic.

However, larvae released from the Northern sites never drifted far to the south; so, genetic exchange is expected to be unidirectional among the three sites studied.

Dispersal potential varied significantly among 3 years for the sipunculan *P. turnerae*, with mean dispersal distances highly dependent on year, especially in 100 m projections. The potential role of ontogenetic migration to the upper water column was more variable than expected, however. Larvae released in Barbados were less likely to disperse farther in shallow water than in deep water, and short-lived larvae such as *L. luymesii*, *S. lineta*, and *C. blakei* showed less of an effect of depth than did very long-lived larvae, such as those of *S. tanneri*.

Species living in the Bahamas are probably self-seeded by larvae retained in the Bahamas archipelago, but numerous larvae from this region are also exported into the Northwest Atlantic where they are most likely lost. From a conservation standpoint, these slope echinoderms with relatively long dispersal times, broad geographic ranges, and non-specialized (muddy slope) environments are probably not very vulnerable to extinction.

The cold-seep tubeworm *L. luymesii* may be the most vulnerable of the species we studied because of its very restricted geographic range, specialized habitat, and small dispersal potential. Major regional perturbations in the Northern Gulf of Mexico could have serious impacts on this species. By dramatic contrast, the sipunculan *P. turnerae* may be among the least vulnerable species. Its habitat, fibrous and woody materials of terrestrial origin, may be found virtually anywhere on the slope and the very long dispersal distances should provide good opportunities to locate these habitats. Interestingly, this species has been reported off the eastern coast of Australia (Edmonds 1985) as well as in the Bahamas, Caribbean, and Gulf of Mexico.

We saw no evidence that bathyal species from the Caribbean or the Gulf of Mexico could exchange genes from west to east across the Atlantic Ocean in either the equatorial current system or the North Atlantic Drift. Seeps recently discovered on the Nigerian and Gabon margins are all deeper than the known bathymetric range of *B. naticoidea*. If there are shallower seeps in that same region, they might well support metapopulations of this species. Van Gaest (2006) demonstrated that the larvae can tolerate tropical surface conditions and that their PLD is long enough to drift across the equatorial Atlantic. We can, therefore, speculate on the basis of these biological attributes that seeps off Africa or on the Brazilian margin could seed the Barbados

metapopulations of *B. naticoidea*. Westward dispersal in the equatorial current system could also provide some west-to-east trans-Atlantic exchange, but this hypothesis remains to be tested.

Although there are some genetic similarities between seep mussels on the two sides of the Atlantic (Cordes et al. 2007; Olu-Le Roy et al. 2007), our data suggest strongly that eastward drift in the North Atlantic is unlikely to carry larvae from North America to seeps in the Gulf of Cadiz or off Western Africa. If there is genetic exchange across the Atlantic, it is most likely unidirectional, from east to west in the equatorial current system.

## Acknowledgments

We thank the former ship and submersible crews at Harbor Branch Oceanographic Institution for outstanding support. This is Smithsonian Marine Station at Fort Pierce Contribution Number 881.

## Funding

This work was supported by National Science Foundation grants OCE-0527139, OCE-0119733, OCE-9633784, OCE-1029841, and OCE-1030453.

## References

- Arellano SM. 2008. Embryology, larval ecology, and recruitment of “*Bathymodiolus childressi*”, a cold-seep mussel from the Gulf of Mexico [dissertation]. [Oregon]: University of Oregon. p. 1–198.
- Arellano SM, Young CM. 2009. Spawning, development, and the duration of larval life in a deep-sea cold-seep mussel. *Biol Bull* 216:149–62.
- Arellano SM, Young CM. 2011. Temperature and salinity tolerances of embryos and larvae of the deep-sea mytilid mussel “*Bathymodiolus childressi*”. *Mar Biol* 158:2481–93.
- Bennett KC, Young CM, Emler RB. 2012. Larval development and metamorphosis of the deep-sea cidaroid urchin *Cidaris blakei*. *Biol Bull* 222:105–17.
- Bouchet P, Fontes JC. 1981. Larval vertical migrations in abyssal gastropods. Further evidence from isotopic analysis of larval and postlarval shells. *C R Seances Acad Sci, Paris (Ser III)* 292:1005–8.
- Bouchet P, Waren A. 1994. Ontogenetic migration and dispersal of deep-sea gastropod larvae. In: Young CM, Eckelbarger KE, editors. *Invertebrate reproduction, larval biology and recruitment in the Deep Sea Benthos*. New York: Columbia University Press. p. 261–83.
- Brooke SD, Young CM. 2009. Where do the embryos of *Riftia pachyptila* develop? Pressure tolerances, temperature tolerances, and buoyancy during prolonged embryonic dispersal. *Deep-Sea Res Part II* 56:1599–606.
- Carney SL, Formica MI, Divatia H, Nelson K, Fisher CR, Schaeffer SW. 2006. Population structure of the mussel “*Bathymodiolus childressi*” from Gulf of Mexico hydrocarbon seeps. *Deep-Sea Res Part I* 53:1061–72.



- Caswell H, Neubert MG, Hunter CM. 2011. Demography and dispersal: invasion speeds and sensitivity analysis in periodic and stochastic environments. *Theor Ecol* 4:407–21.
- Chassignet EP, Hurlburt HE, Metzger EJ, Smedstad OM, Cummings J, Halliwell GR, Bleck R, Baraille R, Wallcraft AJ, Lozano C, et al. 2009. U.S. GODAE: Global Ocean Prediction with the HYbrid Coordinate Ocean Model (HYCOM). *Oceanography* 22:64–75.
- Chevaldonne P, Jollivet D, Vangriesheim A, Desbruyères D. 1997. Hydrothermal-vent alvinellid polychaete dispersal in the eastern Pacific. 1. Influence of vent site distribution, bottom currents and biological patterns. *Limn Oceanogr* 42:67–80.
- Clark AM, Downey ME. 1991. *Starfishes of the Atlantic*. London: Chapman and Hall.
- Coykendall DK, Johnson SB, Karl SA, Lutz RA, Vrijenhoek RC. 2011. Genetic diversity and demographic instability in *Riftia pachyptila* tubeworms from eastern Pacific hydrothermal vents. *BMC Evol Biol* 11:96.
- Cordes EE, Carney SL, Hourdez S, Carney RS, Brooks JM, Fisher CR. 2007. Cold seeps of the deep Gulf of Mexico: Community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. *Deep-Sea Res Part I* 54:637–53.
- Cowen RK, Sponaugle S. 2009. Larval dispersal and marine population connectivity. *Ann Rev Mar Sci* 1:443–66.
- Cowen RK, Paris CB, Srinivasan A. 2006. Scaling of connectivity in marine populations. *Science* 311, 5760:522–7.
- Edmonds SJ. 1985. A new species of *Phascolosoma* (Sipuncula) from Australia. *Trans Roy Soc Australia* 109:43–4.
- Gunderson LH, Allen CR, Holling CS, editors. 2009. *Foundations of ecological resilience*. Washington (DC): Island Press.
- Hilario A, Young CM, Tyler PA. 2005. Sperm storage, internal fertilization, and embryonic dispersal in vent and seep tubeworms (Polychaeta: Siboglinidae: Vestimentifera). *Biol Bull* 208:20–8.
- Hyun KH, He R. 2010. Coastal upwelling in the South Atlantic Bight: a revisit of the 2003 cold event using long term observations and model hindcast solutions. *J Mar Systems* 83:1–13.
- Jablonski D, Lutz RA. 1983. Larval ecology of marine benthic invertebrates: Paleobiological implications. *Biol Rev* 58:21–89.
- Johnson SB, Young CR, Jones WJ, Waren A, Vrijenhoek RC. 2006. Migration, isolation, and speciation of hydrothermal vent limpets (Gastropoda; Lepetodrilidae) across the Blanco Transform Fault. *Biol Bull* 210:140–57.
- Killingley JS, Rex MA. 1985. Mode of larval development in some deep-sea gastropods indicated by oxygen-18 values of their carbonate shells. *Deep-Sea Res* 32:809–18.
- Leong PKK. 1998. *Metabolic importance of Na<sup>+</sup>, K<sup>+</sup>-ATPase activity during early development of marine invertebrates [dissertation]*. [California]: University of Southern California.
- Marsh AG, Mullineaux LS, Young CM, Manahan DT. 2001. Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. *Nature* 411:77–80.
- McClain CR. 2007. Guest editorial: seamounts: Identity crisis or split personality? *J Biogeogr* 34:2001–8.
- McClain CR, Hardy SM. 2010. The dynamics of biogeographic ranges in the deep sea. *Proc R Soc B* 277:3533–46.
- McMullin ER, Hourdez S, Schaeffer SW, Fisher CR. 2003. Phylogeny and biogeography of deep-sea vestimentiferan tubeworms and their bacterial symbionts. *Symbiosis* 34:1–41.
- McMullin ER, Nelson K, Fisher CR, Schaeffer SW. 2010. Population structure in two deep sea tubeworms, *Lamellibrachia luymesii* and *Seepiophila jonesi*, from the hydrocarbon seeps of the Gulf of Mexico. *Deep-Sea Res I* 57:1499–509.
- Mills CE, Carlton JT. 1998. Rationale for a system of international reserves for the open ocean. *Conservation Biol* 12:244–7.
- North EW, Hood RR, Chao S-Y, Sanford LP. 2006. Using a random displacement model to simulate turbulent particle motion in a baroclinic frontal zone: A new implementation scheme and model performance tests. *J Mar Systems* 60:365–80.
- Olu K, Sibuet M, Harmegnies F, Foucher J-P, Fiala-Médioni A. 1996. Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. *Prog in Oceanogr* 38:347–56.
- Olu-Le Roy K, von Cosel R, Hourdez S, Carney SL, Jollivet D. 2007. Amphi-Atlantic cold-seep *Bathymodiolus* species complexes across the equatorial belt. *Deep-Sea Res I* 54:1890–911.
- O'Mullan GD, Maas PAY, Lutz RA, Vrijenhoek RC. 2001. A hybrid zone between hydrothermal vent mussels (Bivalvia: Mytilidae) from the Mid-Atlantic Ridge. *Mol Ecol* 10:2819–31.
- Pradillon F, Le Bris N, Shillito B, Young C, Gaill F. 2005. Influence of environmental conditions on early development of the hydrothermal vent polychaete *Alvinella pompejana*. *J Exp Biol* 208:1551–61.
- Pulliam HR. 1988. Sources, sinks and population regulation. *Am Nat* 132:651–61.
- Rice ME. 1985. Description of a wood-boring sipunculan, *Phascolosoma turnerae*, new species. *Proce Biological Soc Wash* 98:54–60.
- Rice ME, Reichardt H, Piraino J, Young CM. In press. Reproduction, development, growth, and the length of larval life of *Phascolosoma turnerae*, a wood-dwelling deep-sea Sipunculan. *Invertebr Biol*.
- Rogers AD. 1994. The biology of seamounts. *Adv Mar Biol* 30:304–60.
- Samadi S, Bottan L, Macpherson E, De Forges BR, Boisselier M-C. 2006. Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. *Mar Biol* 149:1463–75.
- Scheltema RS. 1968. Dispersal of larvae by equatorial ocean currents and its importance to the zoogeography of shoal-water tropical species. *Nature* 217:1159–62.
- Scheltema RS. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shoal-water benthic marine gastropods. *Biol Bull* 140:284–322.
- Scheltema RS. 1986. On dispersal and planktonic larvae of benthic invertebrates: An eclectic overview and summary of problems. *Bull Mar Sci* 39:290–322.

- Schlag ZE, North EW, Smith K. 2008. Larval TRANSPORT Lagrangian model (LTRANS) User's Guide. Cambridge (MD): University of Maryland Center for Environmental Science, Horn Point Laboratory.
- Shanks AL. 2009. Pelagic larval duration and dispersal distance revisited. *Biol Bull* 216:373–85.
- Smith PJ, McVeagh SM, Mingoia JT, France SC. 2004. Mitochondrial DNA sequence variation in deep-sea bamboo coral (Keratoisidinae) species in the southwest and northwest Pacific Ocean. *Mar Biol* 144:253–61.
- Thiel H. 2003. Anthropogenic impacts in the deep sea. In: Tyler PA, editor. *Ecosystems of the deep ocean*. Amsterdam: Elsevier. p. 427–71.
- Thorson GL. 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. *Ophelia* 1:167–208.
- Van Dover CL, Jenkins CD, Turnipseed M. 2001. Corraling of larvae in the deep sea. *J Mar Biol Assoc UK* 81:823–6.
- Van Dover CL, Aharon P, Bernhard JM, Caylor E, Doerries M, Flickinger W, Gilhooly W. 2003. Blake Ridge methane seeps: characterization of a soft-sediment, chemosynthetically based ecosystem. *Deep-Sea Res I* 50:281–300.
- Van Gaest A. 2006. Ecology and early life history of *Bathynnerita naticoidea*: evidence for long-distance larval dispersal of a cold seep gastropod [Masters' Thesis]. [Oregon]: University of Oregon.
- Vrijenhoek RC. 1997. Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. *J Hered* 88:285–293.
- Vrijenhoek RC. 2010. Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Mol Ecol* 19:4391–411.
- White HK, Hsing P-Y, Cho W, Shank TM, Cordes EE, Quattrini AM, Nelson RK, Camili R, Demopolous AWJ, German CR, et al. In press. Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. *Proc Natl Acad Sci USA*.
- Won YJ, Hallam SJ, O'Mullan D, Pan IL, Buck KR, Vrijenhoek RC. 2003. Environmental acquisition of thiotrophic endosymbionts by deep-sea mussels of the genus *Bathymodiulus*. *Appl Environ Microbiol* 69:6785–92.
- Young CM, Tyler PA, Cameron JL, Rumrill S. 1992. Seasonal breeding aggregations in low-density populations of the bathyal echinoid *Stylocidaris lineata*. *Mar Biol* 113:603–12.
- Young CM, Tyler PA. 1993. Embryos of the deep-sea echinoid *Echinus affinis* require high pressure for development. *Limnol Oceanog* 38:178–81.
- Young CM, Devin M, Jaeckle WB, Ekaratne S. 1996a. The potential for ontogenetic vertical migration in larvae of deep-sea echinoids. *Oceanol Acta* 19:263–71.
- Young CM, Tyler PA, Gage JD. 1996b. Vertical distribution correlates with pressure tolerances of early embryos in the deep-sea asteroid *Plutonaster bifrons*. *J Mar Biol Assoc UK* 76:749–57.
- Young CM, Vazquez E, Metaxas A, Tyler PA. 1996c. Embryology of vestimentiferan tube worms from deep-sea methane/sulphide seeps. *Nature* 381:514–6.
- Young CM, Ekaratne SUK, Cameron JL. 1998. Thermal tolerances of embryos and planktotrophic larvae of *Archaeopneustes hystrix* (Spatangoidea) and *Stylocidaris lineata* (Cidaroida), bathyal echinoids from the Bahamian Slope. *J Exp Mar Biol Ecol* 223:65–76.
- Young CR, Fujio S, Vrijenhoek RC. 2008. Directional dispersal between mid-ocean ridges: deep ocean circulation and gene flow in *Ridgeia piscesae*. *Mol Ecol* 17:1718–31.
- Zardus JD, Etter RD, Chase RJ, Rex MR, Rex MA, Boyle EE. 2006. Bathymetric and geographic population structure in the pan-Atlantic deep-sea bivalve *Deminucula atacellana* (Schenck, 1939). *Mol Ecol* 15:639–51.