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Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal

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Dispersal plays an important role in the establishment and maintenance of biodiversity and, for most deep-sea benthic marine invertebrates, it occurs mainly during the larval stages. Therefore, the mode of reproduction (and thus dispersal ability) will affect greatly the biogeographic and bathymetric distributions of deep-sea organisms. We tested the hypothesis that, for bathyal and abyssal echinoderms and ascidians of the Atlantic Ocean, species with planktotrophic larval development have broader biogeographic and bathymetric ranges than species with lecithotrophic development. In comparing two groups with lecithotrophic development, we found that ascidians, which probably have a shorter larval period and therefore less dispersal potential, were present in fewer geographic regions than elapod holothurians, which are likely to have longer larval periods. For asteroid and echinoid, both the geographic and bathymetric ranges were greater for lecithotrophic than for planktotrophic species. For these two classes, the relationships of egg diameter with geographic and bathymetric range were either linearly increasing or non-monotonic. We conclude that lecithotrophic development does not necessarily constrain dispersal in the deep sea, probably because species with planktotrophic development may be confined to regions of high detrital input from the sea surface. Our data suggest that more information is necessary on lengths of larval period for different species to accurately assess dispersal in the deep sea.

Key words: bathymetric range; biodiversity; biogeographic range; developmental mode; larval dispersal; lecithotrophy vs. planktotrophy.

Introduction

In ecological time, dispersal is integral to the establishment and maintenance of biological diversity both in shallow water and in the deep sea at all spatial scales (Sanders and Grassle, 1971; Sanders, 1979; Rex, 1981; Scheltema, 1986; Wilson and Hessler, 1987). For

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example, new colonization in an area of the continental slope where the biological community has been obliterated by a catastrophic disturbance, such as a turbidite, will depend on immigration of organisms during larval, juvenile or adult stages of their life cycle. Different species will arrive at different rates which in turn are determined by a complex suite of factors that may include dispersal ability, reproductive timing, fecundity, local currents, and the locations of reproductive source populations (Smith and Hessler, 1987). Once communities are established, life history traits and population processes will determine rates of local persistence and diversity. Offspring may disperse only short distances to repopulate locally, they may disperse long distances to establish or replenish another portion of the metapopulation, or they may be carried to inhospitable habitats where they may ultimately perish.

Dispersal is thought to have important consequences at both ecological and evolutionary time scales. In ecological time, dispersal potential can influence biological interactions such as competition (Levin, 1974; Chesson, 1985) and the ability of a species to persist in heterogeneous environments (Palmer and Strathmann, 1981), by allowing larvae to sample a range of potential environments (Strathmann, 1974). In evolutionary time, dispersal can increase geographic range allowing exploitation of new habitats (Scheltema, 1986), increase species longevity by damping extinction rates in variable environments (Hansen, 1978; Jablonski, 1982), reduce adverse effects of inbreeding depression, and maintain genetic continuity between metapopulations, thereby reducing rates of speciation (Wilson and Hessler, 1987).

Most of the advantages of dispersal assume temporal and spatial variability in habitat quality. The deep sea has more stable habitats than typical shallow-water systems, effectively negating some of the advantages. Etter and Caswell (1994) used a cellular automaton model to explore the circumstances under which long-distance dispersal was advantageous in deep-sea systems. Their model predicts that short-distance and long-distance dispersal are equally advantageous at low levels of disturbance (as would be expected on the abyssal plains) but that long distance dispersal becomes more advantageous at the intermediate disturbance frequencies that might be expected at slope and shelf depths.

One of the great surprises of the Challenger expedition was the finding that the abyssal fauna is similar everywhere in the world's oceans (Moseley, 1880). Indeed, many groups of deep-sea animals are known to have cosmopolitan species or genera. This originally was thought to result from uniform physical and chemical conditions throughout the deep sea, but may also reflect the virtual absence of dispersal barriers at bathyal depths (Wilson and Hessler, 1987). Evidence amassed during the past two decades has, however, revealed a much greater diversity of deep-sea habitat characteristics than previously suspected (reviewed by Tyler, 1995). In addition, recent work has shown a significant negative relationship of species diversity with increasing latitude in the North Atlantic for deep-sea isopods, gastropods and bivalves (Rex *et al.*, 1993). These findings underscore the importance of readdressing the potential role of pelagic larval dispersal in speciation and distribution of deep-sea animals.

Most of the research on the origin and zoogeography of the deep-sea fauna has centred on the speciose pericardid crustaceans, all of which reproduce by direct development (Hessler and Thistle, 1975; Hessler *et al.*, 1979; Wilson and Hessler, 1987) and hence have limited dispersal. Other studies have focused on taxa which were predicted to have limited larval dispersal, such as porcellanasterid sea stars (Madsen, 1961). Although it was long

thought that brooding and direct development should be the dominant modes of reproduction among deep-sea invertebrates (Thorson, 1950), we now know that this may be the exception rather than the rule. Planktonic larvae, especially but not exclusively lecithotrophic larvae, are commonly found in many deep-sea phyla (Rex and Warén, 1982; Bouchet and Warén, 1994; Pearse, 1994; Young, 1994). The potential roles of developmental mode (and hence dispersal ability) in speciation and biodiversity have been addressed in several reviews, all of which, however, emphasize the need for additional analyses (Sanders and Grassle, 1971; Rex, 1981, 1983; Wilson and Hessler, 1987).

Of the deep-sea species known to produce planktonic larvae, the Atlantic prosobranch gastropods are the best studied (Rex and Warén, 1982; Etter and Rex, 1990). Using bathyal (500–4000 m) prosobranchs as a model system, Stuart and Rex (1994) showed that the most important factors influencing local species diversity were regional diversity and the proportion of species with planktotrophic larvae in the regional species pool. A similar pattern has been demonstrated for shallow-water infaunal invertebrates in Scandinavian waters (Josefson, 1985).

In this paper, we consider whether the mode of larval development (and hence the dispersal potential of each generation) is related to the size of biogeographic (horizontal) and bathymetric (vertical) ranges in the deep sea. Range size is important in the context of biodiversity because endemism (restricted species range) is one of the major precursors of speciation. We focus on echinoderms that live in the Atlantic Ocean because reproduction has been studied in enough species to analyse large-scale patterns. For comparative purposes, we also include some data from the published literature on biogeographic patterns of ascidians, all of which produce larvae with very short distance dispersal and some of which are limited to hard substrata.

Developmental mode is related to zoogeographic range in shallow water animals (reviewed by Scheltema, 1986) and a similar pattern is expected for the deep sea (Wilson and Hessler, 1987). Here, we test the hypothesis that bathyal and abyssal species with planktotrophic development have broader vertical and horizontal ranges than species with lecithotrophic development. We assumed on the basis of shallow-water studies that dispersal of ascidians would be substantially less than dispersal of pelagic lecithotrophic echinoderm larvae, which in turn would be less than dispersal of planktotrophic echinoderm larvae.

Materials and methods

We obtained the egg size data from the published scientific literature, as well as from our own published and unpublished work. We (CMY, PAT) have reared the embryos or larvae of a number of bathyal echinoderms from the Caribbean region and the Rockall Trough and have determined egg sizes for many additional species. We supplemented this data set with information on echinoderm egg size and developmental mode summarized from the literature by Emler *et al.* (1987) and Sewell and Young (unpublished data). Where developmental mode (planktotrophy, pelagic lecithotrophy, brooding) was not examined directly, we assumed on the basis of data in Emler *et al.* (1987; Fig. 3) that echinoderm eggs with a diameter 300 μm or larger produced lecithotrophic larvae and smaller eggs produced planktotrophic larvae. We further assumed that lecithotrophic eggs developed into pelagic larvae unless brooding had actually been observed. Although development has not been described in detail for any deep-sea Atlantic ascidian, it is known from the

taxonomic literature that deep-sea colonial species brood larvae similar to those found in related shallow-water species (Herdman, 1882; Monniot and Monniot, 1973) and that solitary ascidians have egg sizes similar to those of shallow-water species. All known ascidian larvae are short-lived and lecithotrophic. All known colonial ascidians complete embryogenesis internally and release swimming larvae that remain in the water column for up to several hours or at most a few days before settlement. Although a few solitary ascidians brood their embryos, most are free-spawners that fertilize externally and complete larval development in less than one week (reviewed by Svane and Young, 1989).

We used the global scheme of abyssal zoogeography proposed by Vinogradova (1959) (Fig. 1) despite the existence of more recent and comprehensive schemes (e.g. Menzies *et al.*, 1973) because the data on ascidian distribution (Monniot and Monniot, 1973) were already tabulated in this scheme and because some of the biogeographic descriptions in the scientific literature (e.g. echinoid distributions in Mortensen (1927) and subsequent monographs) were not sufficiently detailed to categorize in a more complex scheme. We included in the data set each species that occurred in one of Vinogradova's Atlantic 'zones' (B1, B2a, B2b, B2c) and for which developmental mode could be inferred. This eliminated most of the exclusively Antarctic brooders and the few species with known egg sizes that occur only in the Indo-Pacific region. To qualify for inclusion, a species also had to have a known depth range with a lower boundary deeper than 500 m.

To avoid confusion, we will henceforth use the term 'zone' to refer only to bathymetric (vertical) distribution. The horizontal biogeographic 'zones' in the Vinogradova scheme will be referred to as 'regions'.

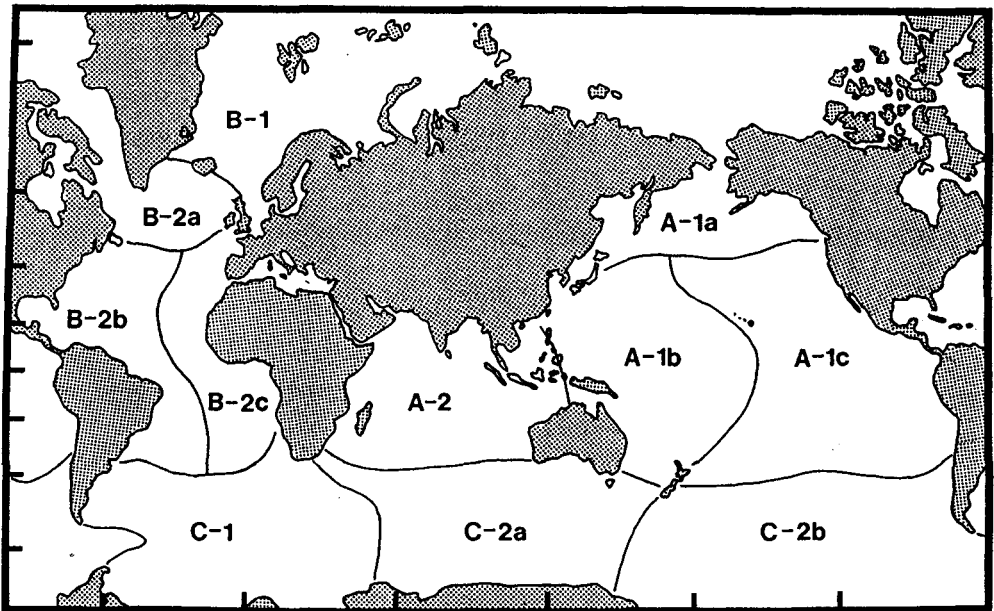


Figure 1. The scheme of abyssal biogeography proposed by Vinogradova (1959) and used in our study. Latitude and longitude lines are 20° apart.

We obtained most distributional data from taxonomic monographs that summarize a large part of the existing literature. Echinoid data were extracted from the classic works of Clark (1925) and Mortensen (1927, 1928, 1935, 1940, 1943a,b, 1948a,b, 1950, 1951) supplemented by newer information summarized by Gage *et al.* (1985) for the Northeast Atlantic, Serafy (1979) and Young (1992) for the Caribbean region and Tyler *et al.* (1995) for the genus *Echinus*. We obtained distributions of asteroids from Clark and Downey (1992) supplemented by our own work on the Bahamian asteroids (Young and Tyler, unpublished), and of elaspod holothurians from maps in Hansen (1975). Although we only included species that occur in the Atlantic, we tabulated for the analysis the total number of geographic regions worldwide in which these species occurred (maximum of 11 regions).

For asteroids and echinoids, we divided species by developmental mode (planktotrophs vs. lecithotrophs), and by the lower bathymetric limits ('slope' species: lower limit between 500 and 1000 m; 'deep' species: bathymetric limits > 1000 m). Differences in the frequency distributions of the number of geographic regions and the widths of bathymetric range (determined in 1-km increments) were examined for asteroids and echinoids by: (i) developmental mode (planktotroph vs. lecithotroph) and (ii) 'slope' vs. 'deep' species, using a Kolmogorov–Smirnov test. In these classes, we also examined the effect of developmental mode (two levels: planktotrophy, lecithotrophy) and maximum depth of occurrence (two levels: 500–1000 m, > 1000 m) on the number of geographic regions occupied by two-factor analysis of variance. For the same groups, we further examined the effect of developmental mode (two levels: planktotrophy, lecithotrophy) and number of occupied geographic regions (asteroids: five regions, echinoids: four regions) on the width of bathymetric range. For the analyses of variance, we used the general linear models of SAS.

We used linear and curvilinear regression to explore the relationships between egg size and the number of occupied geographic regions and between egg size and width of bathymetric range. We used the Sigmastat polynomial regression programs to determine the lines that best fit the data and we determined the significance of the relationships by analysis of variance.

Results

Geographic range

Pelagic lecithotrophic larval development is the major reproductive mode for both elaspod holothurians and ascidians. Ascidians are known to have very short larval development periods, whereas development time has not been measured for any elaspod. All of the 14 species of elaspod holothurians that live in at least one region of the Atlantic Ocean occupied more than one region, most occupied at least three and some species occupied as many as eight regions (Fig. 2). The species with the broadest geographic distributions (eight regions) have egg sizes ranging from 280 μm (*Elpidia glacialis*) to 4400 μm (*Psychropotes longicauda*). The pattern was strikingly different for Atlantic deep-sea ascidians, which were overwhelmingly limited to one or a few geographic regions (mostly less than four), generally within a single ocean basin (Fig. 2). A single species occupied six geographic regions.

The frequency distributions of the number of geographic regions occupied by asteroids and echinoids did not differ significantly between developmental modes, when examined either separately or when the data for the two classes were combined (Fig. 3). For asteroids, ANOVA showed a significant effect of developmental mode on the number of

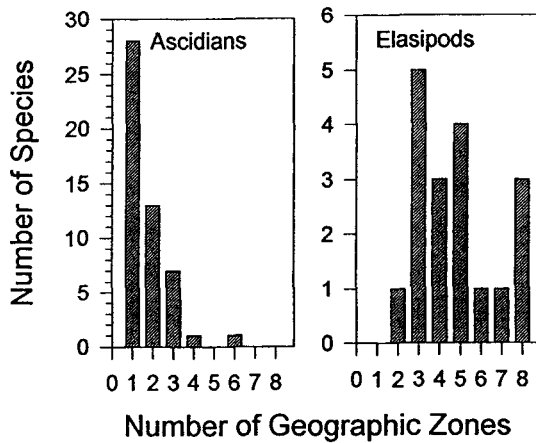


Figure 2. Frequency histograms of the number of geographic regions (Fig. 1) occupied by deep-sea ascidians and elaspod holothurians that occur in the Atlantic Ocean.

occupied geographic regions, and the number of regions occupied by lecithotrophs was significantly greater than that occupied by planktotrophs (Table 1). For this class, there was no significant effect of maximum depth of occurrence on the number of occupied regions. For echinoids, there was a significant interaction between the effects of developmental mode and maximum depth (Table 1), resulting from the large number of planktotrophic species at bathyal depths in the Bahamas which are limited to a single region (Fig. 3).

In both asteroids and echinoids, the frequency distributions of the number of occupied geographic regions differed significantly between species with a maximum depth of occurrence between 500 and 1000 m and species with a maximum depth of occurrence deeper than 1000 m (Fig. 3). This pattern also held when data from the two classes were combined (Fig. 3). In each case, deeper dwelling species tended to occupy a larger number of geographic regions than species found at a maximum depth of < 1000 m.

There was a significant relationship between egg diameter and number of occupied geographic regions for asteroids, but not for echinoids or elaspods (Fig. 4). In asteroids, a second order polynomial equation described best the relationship between the two variables, with the greatest horizontal ranges found at intermediate egg diameters (Fig. 4). When data were combined for echinoids, asteroids and elaspods, there was a significant positive linear relationship between egg diameter and geographic range (Fig. 4). This pattern is exactly opposite to that predicted from dispersal distances of shallow-water species (Scheltema, 1986). Some of the species with large egg sizes also have wide geographic distributions.

Bathymetric range

The frequency distributions of the widths of bathymetric range differed significantly between developmental modes when the data for asteroids and echinoids were combined, but not when the classes were examined separately (Fig. 5). In the combined data, most planktotrophs occurred over a vertical range of only 1–2 km, whereas the vertical range of lecithotrophs was often greater than 2 km, or as much as 6 km, wide. For asteroids, there

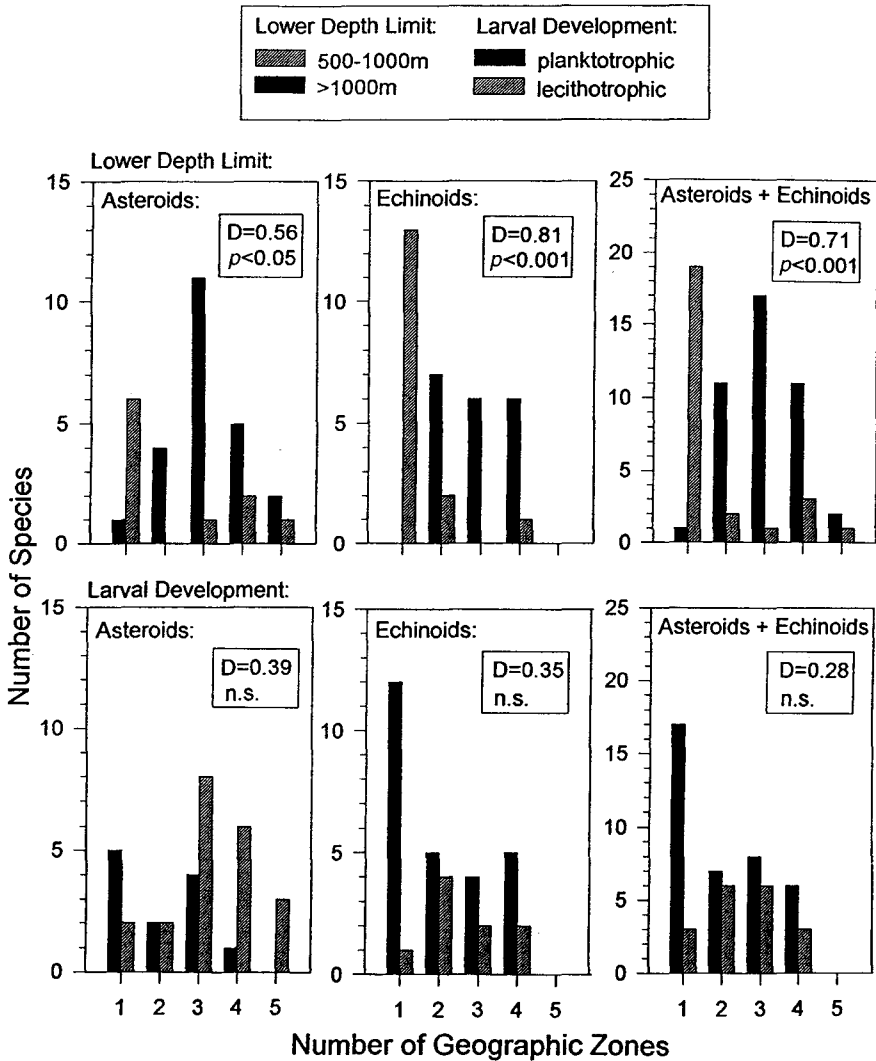


Figure 3. Frequency histograms showing the number of species of asteroids and echinoids occupying different numbers of biogeographic regions. The species are classified as either 'slope' or 'deep' species on the basis of the maximum depth of occurrence (see text for explanation), and as planktotrophic or lecithotrophic on the basis of larval rearing or egg size. 'D' is the Kolmogorov-Smirnov two-sample statistic and *p* values are for two-tailed tests.

was a significant effect of developmental mode on the width of bathymetric range which was greater for lecithotrophic than planktotrophic species (Table 2). There was a significant effect of the number of occupied geographic regions on the width of bathymetric range for both asteroids and echinoids (Table 2).

There was a significant positive linear relationship between egg diameter and width of bathymetric range for asteroids (Fig. 6), although the regression equation explained only 16% of the variance. As with horizontal range, the relationship was opposite to that

Table 1. Two-way analyses of variance examining the effects of developmental mode (two levels: planktotrophy, lecithotrophy) and maximum depth of occurrence (two levels: 500–1000 m, > 1000 m) on the number of geographic zones occupied by asteroids and echinoids (data illustrated in Fig. 3)

Source of variation	d.f.	Sum of squares	Mean square	F	<i>p</i>
Asteroids					
Maximum depth (A)	1	2.102	2.102	1.65	0.210
Developmental mode (B)	1	6.199	6.199	4.85	0.036
A × B	1	0.041	0.041	0.03	0.860
Error	29	37.03	1.277		
Echinoids					
Maximum depth (A)	1	5.504	5.504	9.70	0.004
Developmental mode (B)	1	0.728	0.728	1.28	0.266
A × B	1	4.779	4.779	8.42	0.007
Error	31	17.60	0.568		

predicted by conventional theory. Planktotrophic species appeared to have a more restricted distribution relative to lecithotrophic species, which had very wide ranges (Fig. 5). For echinoids, the data were best described by a third order polynomial equation which explained 40% of the variance. For planktotrophic species, the width of the bathymetric range increased with egg size. However, the relationship was not as clear for lecithotrophic species; some species with eggs > 1 mm have vertical ranges nearly as wide as those of the most widely distributed planktotrophs, whereas other species occur in ranges of less than 1000 m (Fig. 6). The combined data for asteroids and echinoids preserved the parabolic relationship found for echinoids, although there was more scatter around the line (Fig. 6). There was no significant relationship between egg diameter and bathymetric range width in elapsid holothurians (Fig. 6).

Discussion

Our major conclusion is that lecithotrophic development does not necessarily constrain dispersal in the deep sea. Comparison between ascidians with short-lived lecithotrophic larvae and elapsids which are likely to disperse longer distances demonstrates that geographic range is probably related to the distance of dispersal in the deep sea, as it is in shallow water. However, the prediction that species with planktotrophic larvae should be more widespread than species with lecithotrophic larvae does not hold for the deep Atlantic echinoderms. Indeed, the available data indicate that some of the most widespread species in the deep sea reproduce without the benefit of feeding larvae.

If dispersal distance is positively correlated with range size, then why are planktotrophs not more widespread in the deep sea? Conventional wisdom dictates that planktotrophic larvae should be capable of longer dispersal than lecithotrophic larvae because they can supplement the original energy allocated to the egg by feeding. Lecithotrophic larvae in shallow water often have relatively short lives. For example, larvae of bryozoans, ascidians

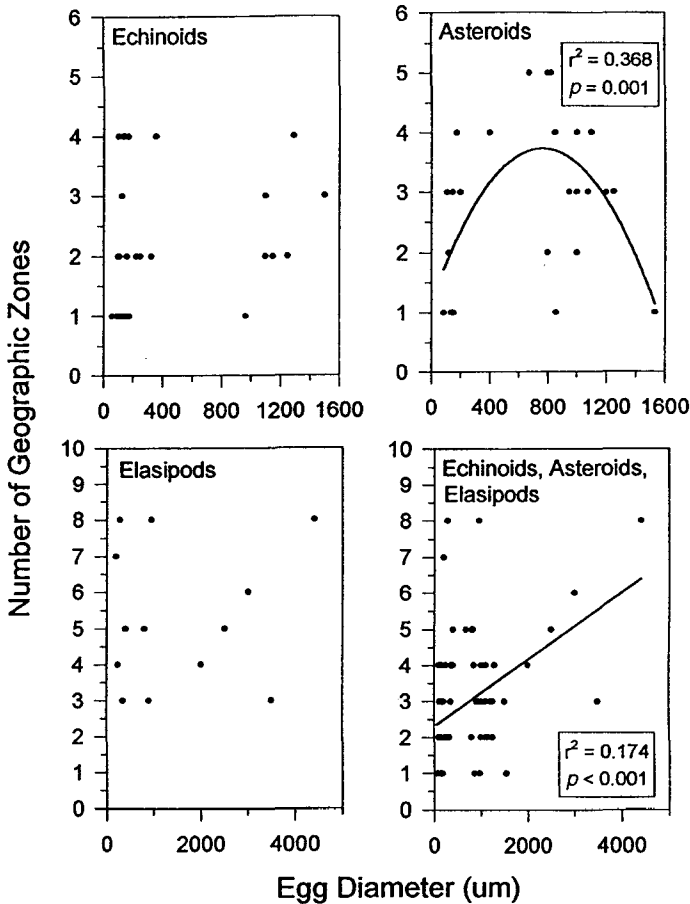


Figure 4. Scatter plots and regression analyses of the relationships between egg diameter and the number of geographic regions occupied by echinoderm species. Only significant regression lines are shown. The best-fit curves are: for asteroids, the second order polynomial equation $y = 1.192 + 0.007x - 4.381e^{-6}x^2$; for asteroids, echinoids and elaspipods combined, the first order linear equation $y = 2.359 + 8.784e^{-4}x$.

and many corals are brooded within the parent until larvae are ready to swim and settle. Shallow-water echinoderms that produce lecithotrophic larvae may complete development in just a few days, although pelagic periods as long as several weeks are common in temperate species. There is some evidence that lecithotrophic larvae have sufficient energy and nutrient stores to swim for long periods of time. For example, larvae of the temperate starfish *Mediaster aequalis* survived in culture for more than a year before settlement (Birkeland *et al.*, 1971). At low temperatures, the potential for dispersal without feeding is even greater because of low metabolic demand. Shilling and Manahan (1994) showed that the lecithotrophic larvae of some Antarctic echinoderms have low mass-specific respiration rates that may enable them to disperse for months, or even years, without depleting their energy reserves. We expect the same phenomenon to occur in the cold waters of the

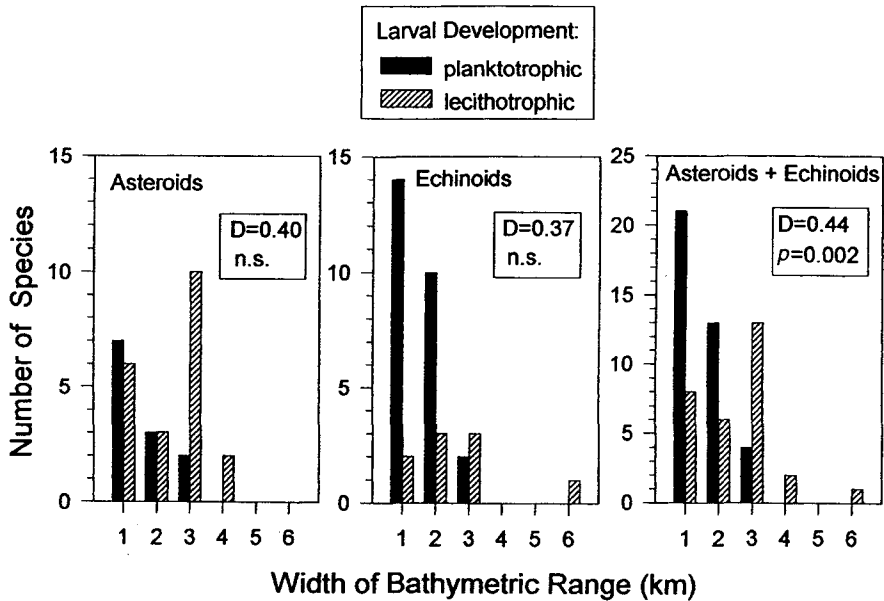


Figure 5. Frequency histograms showing the number of asteroid and echinoid species occupying bathymetric ranges of different sizes. Each range category on the x-axis represents the upper boundary of the class. ‘D’ is the Kolmogorov–Smirnov two-sample statistic and *p* values are for two-tailed tests.

deep sea. Thus, in the deep sea, planktotropic developers may not spend any more time in the plankton than pelagic lecithotrophs.

Recent studies on the genetics of hydrothermal vent organisms lends additional support to our finding that lecithotrophy does not limit deep-sea dispersal. Analysis of allozymes in two species of archaeogastropod limpets with lecithotrophic development failed to

Table 2. Two-way analyses of variance examining the effects of developmental mode (two levels: planktrotrophy, lecithotrophy) and geographic range (number of occupied zones) on the width of bathymetric range (data illustrated in Fig. 5)

Source of variation	d.f.	Sum of squares	Mean square	F	<i>p</i>
Asteroids					
No. zones (A)	4	10 466 246	2 616 561	4.76	0.006
Developmental mode (B)	1	2 741 263	2 741 263	4.98	0.035
A × B	3	1 953 279	651 093	1.18	0.337
Error	24	13 204 516	550 188		
Echinoids					
No. zones (A)	3	8 196 350	2 732 116	4.39	0.012
Developmental mode (B)	1	1 805 141	1 805 141	2.90	0.100
A × B	3	1 957 352	652 450	1.05	0.387
Error	27	16 820 627	622 986		

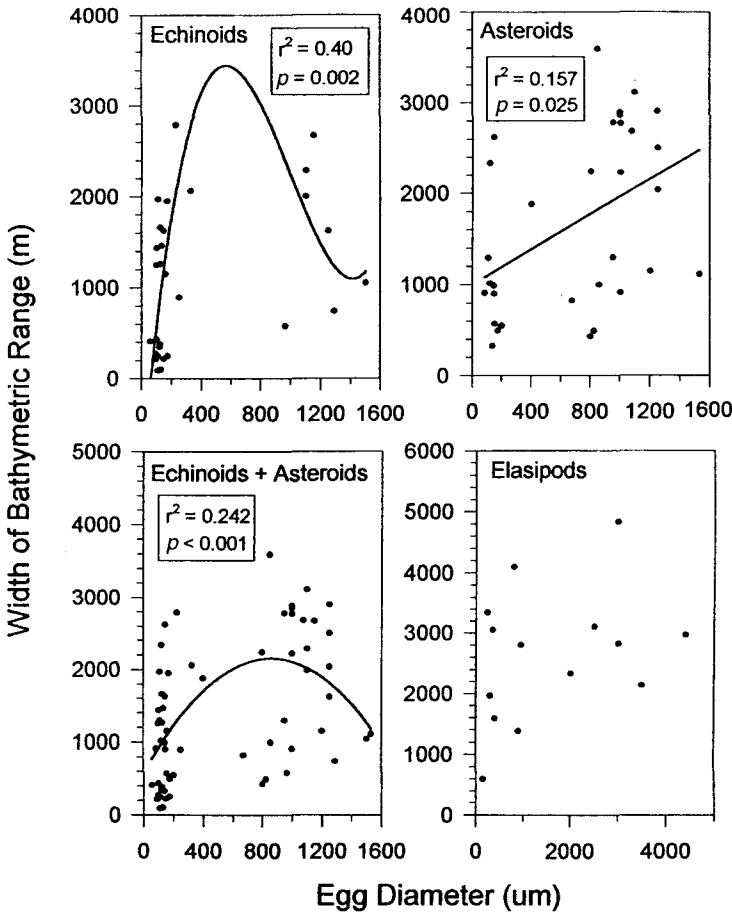


Figure 6. Scatter plots and regression analyses of the relationships between egg diameter and the widths of bathymetric range of echinoderm species. Only significant polynomial regression lines are shown. The best-fit curves are: for asteroids, the first order linear equation $y = 1050 + 0.869x$; for echinoids, the third order polynomial equation $y = -1.031e^3 + 18.34x - 0.023x^2 + 7.674e^{-6}x^3$; for asteroids and echinoids combined, the second order polynomial equation $y = 4.922e^2 + 4.245x - 0.003x^2$.

support the prediction that dispersal should occur in a stepping-stone fashion (Craddock *et al.*, 1997). Gene flow did not decline as a function of distance between sampling sites, suggesting that the lecithotrophic larvae of these species are capable of very long distance dispersal (Craddock *et al.*, 1997). Based on the evidence available, alvinellid polychaetes, which are also endemic to hydrothermal vent systems, have lecithotrophic or direct development (Desbruyères and Laubier, 1986; Zal *et al.*, 1995). Genetic analysis of one such species, *Paralvinella grasslei*, nevertheless revealed evidence of substantial genetic exchange among distant populations (Jollivet *et al.*, 1995). A more recent model of alvinellid dispersal failed to reconcile this apparent paradox (Chevaldonné *et al.*, 1997). One possible explanation is that lecithotrophic alvinellid larvae have much greater dispersal potential

than currently assumed. Analysis of genetic exchange among distant populations of a species with planktotrophic larvae, the brisellid vent shrimp, *Rimicaris exoculata*, reveals a similar lack of population differentiation (Creasey *et al.*, 1996).

In the deep sea, species with planktotrophic larvae may be confined to regions where there is sufficiently high surface production to produce a significant amount of fine detrital food at bathypelagic and abyssopelagic depths. Planktotrophic larvae could be food limited in oligotrophic areas (but see Olson and Olson (1989) for counter-examples from shallow water), whereas lecithotrophic larvae may survive even if advected to areas of low productivity using energy stored internally. All planktotrophic echinoderms in the deep sea are also seasonal breeders, suggesting a strong link to seasonal patterns of surface productivity (Tyler and Young, 1992). In the Northeast Atlantic, we have found no seasonally breeding planktotrophic species south of 42°N, suggesting that a dispersal barrier, perhaps caused by food limitation, may be present in this area.

Planktotrophic species dominate the tropical bathyal fauna in the Caribbean region and these species tend to be endemic to that single geographic region. We suspect that temperature is a major cause of their limited distribution. Because they live at intermediate temperatures at slope depths, they are probably limited in some life history stage to certain latitudes because of geographic changes in temperature. By contrast, some of the deeper dwelling planktotrophs, such as *Echinus affinis*, occupy multiple regions, all of which have similar low temperatures at the appropriate depths. Pineda (1993) showed that the vertical range width of many slope species is significantly related to the mean depth of occurrence, apparently because their boundaries are constrained either by the sea surface or by the abyssal plain.

In the elasipod holothurians, it is important not to underestimate the dispersal of post-larval juveniles. Gebruk *et al.* (in press) have recently reaffirmed that pelagic juveniles of many elasipod species are found many thousands of metres above the sea bed. These juveniles have adult characteristics, but feed in the plankton rather than on benthic detritus. Thus, although elasipods have lecithotrophic larvae, the larval stage is not the only life history stage where dispersal may occur.

Developmental mode is not the only factor that determines dispersal distance. Larval advection depends on physical forcing mechanisms and such mechanisms may change from region to region. For example, small-scale eddies caused by local features of the seabed may retain eggs and larvae near the site of spawning in some regions, whereas larvae that spend comparable times in the plankton may disperse greater distances where the eddies are absent. On a larger scale, Taylor columns that occur over seamounts may retain reproductive propagules close to the seamount.

The flow of water in the deep sea is still relatively poorly understood compared to the surface circulation, so in most cases we cannot predict where larvae released at a particular location will go. On the basis of biogeographic distributions in the genus *Echinus*, Tyler *et al.* (1995) have hypothesized that the western boundary undercurrent, which transports North Atlantic Deep Water (NADW) south along the slope of the eastern United States, could have transported larvae from the centre of speciation in the North Atlantic to the South Atlantic and Pacific Oceans. Periods of weak NADW flow have probably resulted in allopatric speciation of isolated populations of *Echinus*.

Sanders and Grassle (1971) hypothesized that the rate of speciation in any particular deep-sea group is reflected by the number of extant species. They noted that the asellote isopods are very speciose and attributed this to genetic isolation caused by the lack of a

larval phase. Ophiuroids by contrast are not as diverse and many have long larval periods (Sanders and Grassle, 1971). Our data suggest that caution should be exercised in interpreting dispersal distances in the deep sea. If lecithotrophs can disperse as far, or perhaps farther, than planktotrophs, then inference of developmental mode from larval protoconchs of gastropods, prodissoconchs of bivalves, etc. may not accurately predict dispersal potential. Before we can relate dispersal potential to speciation rates, more empirical studies that address the actual lengths of larval life for deep-sea species are needed.

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