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Corralling of larvae in the deep sea

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Large numbers of small individuals (pediveligers and juveniles <5 mm) are routinely recorded in size–frequency distributions of mussel samples collected from deep-sea chemosynthetic environments. If recruitment of invertebrates to deep-sea hydrothermal vent sites were via long-distance dispersal, as is typically assumed, one would expect recruitment 'events' recorded in size–frequency distributions to be difficult to detect, due to loss of larvae in an open system over large distances. If one imposes mesoscale oceanographic phenomena that minimize dilution of larvae (such as eddies shed from hydrothermal vent plumes) and episodic spawning, expression of this mesoscale corralling at the level of population structure would likely be limited to discrete records of recruitment events encountered serendipitously during haphazard sampling in space and time. The ubiquity of large numbers of post-larvae in mussel samples from a number of disparate sites is likely not serendipitous, but instead may reflect the importance of local sources and sinks of propagules in maintenance of mussel populations.

INTRODUCTION

Dense communities of invertebrates colonize deep-sea hydrothermal vents, but there is little understanding of how local vent populations are maintained. Vent communities are ephemeral, occupying geographically discrete sites in linear arrays along mid-ocean ridges (Van Dover, 2000). There is effective long-distance dispersal by larval stages of many species, including mussels, resulting in a high degree of gene flow between sites and species survival in the face of local extinctions (e.g. Black et al., 1994; Craddock et al., 1995; Vrijenhoek, 1997). This level of gene flow, however, can be accomplished with small numbers of individuals (<10) per generation (Vrijenhoek, 1997). Dispersal in an open system, where vast numbers of propagules are produced, seems a relatively trivial accomplishment for species with prolonged larval stages (Strathmann, 1985). More difficult to understand is how dense populations at a given site are maintained. Recognition of suitable habitat and behavioural responses to cues that allow propagules to settle at a site are critical but largely unexplored processes (Van Dover, 2000). Supply-side processes that deliver large numbers of larvae (Roughgarden et al., 1985; Underwood & Fairweather, 1989) are also unknown. Recently, Marsh et al. (2001) proposed one solution to the need for delivery of large numbers of propagules to vents, namely that larval lifespan in tubeworms may be optimized to limit average dispersal distances in a current regime that is characterized by periodic reversals. This solution does not preclude the possibility that occasional tubeworm larvae can be delivered to distant vent sites. A different sort of evidence is provided here to suggest that mussel larvae, too, must be effectively corralled and delivered to active hydrothermal vent systems and that sources and sinks for these corralled larvae may be predominantly (but not exclusively) local. There is scope for critical tests of these hypotheses.

The issue of larval supply is highlighted by the accumulating data on size–frequency distributions of mussels within chemosynthetic environments and the surprisingly large numbers of new recruits routinely observed.

MATERIALS AND METHODS

Washings of adult mussels from replicate samples within several vent sites and one seep site were sieved (250-μm screen) and all mussel adults, postlarvae (pediveligers; 350–400 μm), and juveniles (<5 mm shell length) were measured and tallied. Smallest individuals were recovered by sorting under a dissecting microscope. These samples arise from a larger study designed to yield quantitative measures of diversity within vent and seep mussel beds and were collected and processed following methods described in Van Dover & Trask (2000) and Van Dover (in press). Size–frequency distributions (Figure 1) were calculated for replicate samples of mussel clumps within study sites. Details of site locations, sampling dates, number of replicate samples per site, species, and numbers of individuals per replicate are provided in Table 1. Benthic or pelagic environments outside of the mussel-bed habitat were not sampled, so the presence or absence of mussel post-larvae cannot be assessed in these environments. These would be important samples in any design of a test of the models presented below.

RESULTS

Where venting is robust, mussel size–frequency distributions are strongly bimodal, with a sharp peak of recruits (postlarval and juvenile stages) and a more normally distributed apportionment of adults (Figure 1). The low abundance of individuals of intermediate length suggests that post-recruitment dynamics (predation, competition, etc.) are important in structuring the populations. This is consistent with observations by Rhoads et al. (1982) of heavy crab predation on intermediate size-classes of mussels.

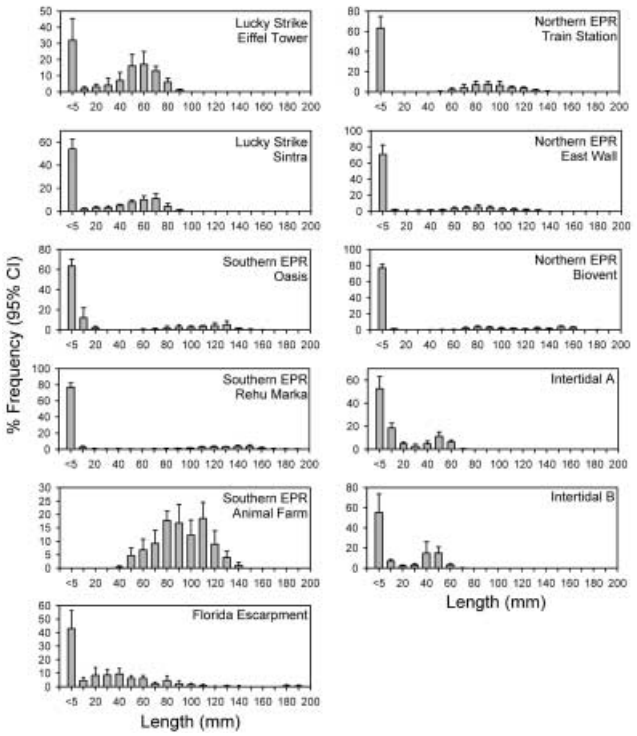

Figure 1. Mussel size–frequency distributions. Sites, species, sampling dates, number of replicates, and numbers of individuals are provided in Table 1. CI, confidence intervals (95%).

Mussel (*Bathymodiolus thermophilus* Kenk & Wilson) recruits are typically ~2–4× more abundant than adults at active southern and northern East Pacific Rise vents (Figure 1). A smaller mussel species, *Bathymodiolus azoricus* Van Cosel, Comtet, Krylova, occurs at the Mid-Atlantic Ridge vent field. Recruits dominate size–frequency distributions of *B. azoricus* at Lucky Strike in 1994 (Comtet & Desbruyères, 1998) and 1996 (Figure 1), but they make up a smaller proportion (30–50%) of the total population than at the East Pacific Rise. This is attributed to greater packing of adult *B. azoricus* per volume of mussel-bed habitat sampled. Recruits also dominate size–frequency distributions of *Bathymodiolus heckerae* Gustafson, Turner, Lutz, Vrijenhoek at the Florida Escarpment cold seep (Figure 1). No pediveligers or recruits were recovered from seven discrete mussel samples at a waning vent field (Animal Farm) on the southern East Pacific Rise (Figure 1). At Animal Farm, in contrast to active vents, there was no detectable temperature anomaly, ~50% of the mussel population was dead (based on the prevalence of empty shells), and mussel tissues were in poor, watery condition. Thus Animal Farm mussel beds, where there were no mussel recruits, have neither a local brood source (mussel gonad condition was poor) nor inorganic settlement cues (e.g. sulphide).

Of mussel recruits to northern East Pacific Rise vent sites, 59 ±15% are pediveligers. Rapid growth rates are reported for vent invertebrates (e.g. Lutz et al., 1994) and for vent mussels in particular (Rhoads et al., 1981, 1982). The ontogenetic growth curve for *Bathymodiolus thermophilus* is more similar to that of the fast-growing, shallow-water marsh mussel *Geukensia demissa* Dillwyn than to slow-growing deep-sea bivalves (Rhoads et al., 1982). There is as yet no experimental data on the duration of the pediveliger stage. If we assume that mussel pediveligers begin deposition of the juvenile shell within 2–3 days of occupying a mussel bed, then pediveliger delivery to a northern East Pacific Rise mussel bed would be on the order of 30,000 larvae d^{-1} 100 m^{-2} of habitat. This is based on the mean total number (289) of pediveligers collected in six quantitative samples (each 0.05 m^2; 0.3 m^2 total) from each of the three East Pacific Rise mussel beds. This larval delivery was observed twice in settlement traps deployed at the Rainbow site on the Mid-Atlantic Ridge (>2000 larvae collected over a two-week interval in three traps with sampling areas of 0.07 m^2=142 larvae d^{-1}× 0.21 m^2, or ~68,000 larvae d^{-1} to a 100-m^2 area; Comtet et al., 2000).

Table 1. *Mussel bed (*Bathymodiolus *spp.) sampling information.*

Site	Mussel species	Sample date	Latitude, Longitude	Depth (m)	Number of replicates	Total number of mussels*
Mid-Atlantic Ridge (Lucky Strike)						
Sintra	*B. azoricus*	Jul 1996	37°17.5′N 32°16′W	1600	5	933
Eiffel Tower	*B. azoricus*	Jul 1996	37°17.5′N 32°16′W	1600	5	1911
S. East Pacific Rise						
Oasis	*B. thermophilus*	Feb 1999	17°25.4′S 113°12′W	2582	8	1297
Rehu Marka	*B. thermophilus*	Feb 1999	17°24.9′S 113°12′W	2581	7	1098
Animal Farm	*B. thermophilus*	Feb 1999	18°36.4′S 113°24′W	2675	7	218
N. East Pacific Rise						
Train Station	*B. thermophilus*	Nov 1999	9°49.6′N 104°17′W	2502	8	1077
East Wall	*B. thermophilus*	Nov 1999	9°50.5′N 104°17′W	2502	8	1725
Biovent	*B. thermophilus*	Nov 1999	9°51.0′N 104°17′W	2508	7	937
Florida Escarpment						
Site 1	*B. heckerae*	Oct 2000	26°01.8′N 85°55′W	3288	5	509

*, all replicates combined.

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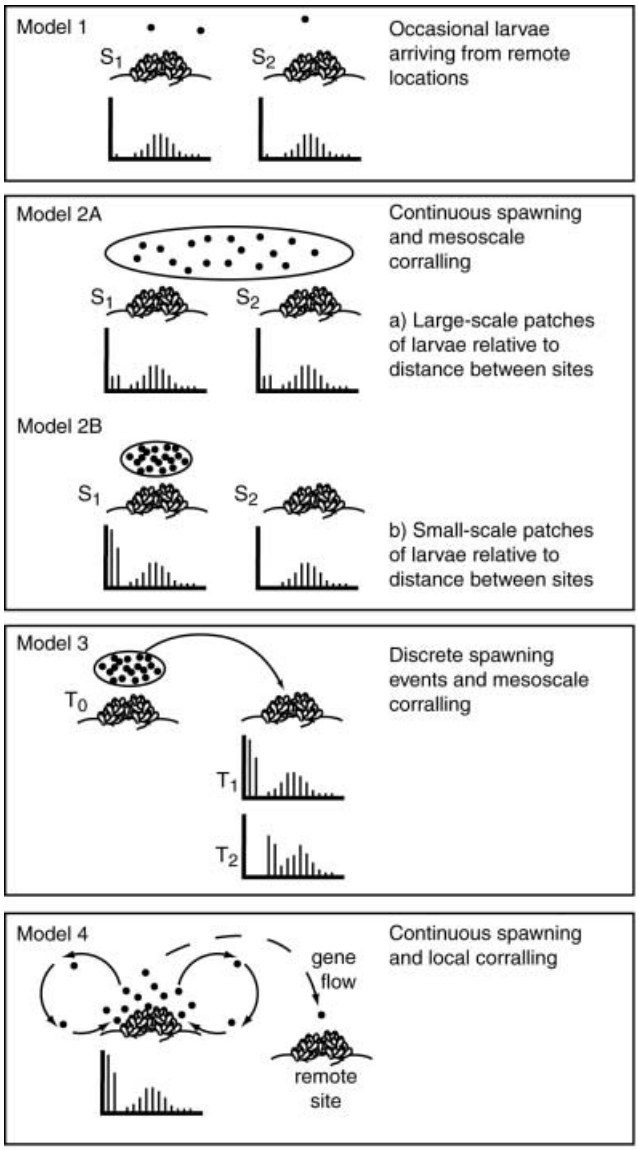

Figure 2. Models of larval dispersal and the resulting mussel size–frequency distributions in deep-sea hydrothermal vent mussel beds. S, Site; T, Time. See text for discussion.

DISCUSSION

Four models of larval dispersal and the expected size–frequency distributions that would result are considered in Figure 2. In these models, assumptions are made regarding: (1) the timing of reproduction [continuous (defined here as a proportion of the population spawning at intervals of days rather than weeks), or discrete (spawning events separated by weeks, referred to elsewhere as synchronous, periodic, or 'seasonal')]; (2) the degree to which larvae are entrained by physical oceanographic processes; and (3) the scale of physical oceanographic processes. In Model 1, no corralling process operates (there are neither discrete spawning events, nor are there any physical oceanographic processes that concentrate larvae), and occasional larvae arrive at a mussel bed from remote locations. This would result in size–frequency distributions that lack any indication of a recruitment 'event' resulting from settlement of large numbers of larvae over short periods of time.

Where mesoscale (~1–10 km) processes might operate to transport larvae (*sensu* Kim et al., 1994; Kim & Mullineaux, 1998) and when spawning is continuous, the size of patches of corralled larvae determines the density of larvae within them and the probability that large numbers of larvae will settle at a given site. If patches of larvae are large relative to the distance between sites (Model 2A), size–frequency distributions between sites and in samples collected at different times are expected to be similar and to include a peak of small individuals. This is consistent with our empirical observations. If patch size is small relative to the distance between sites (Model 2B), then size–frequency distributions are expected to differ markedly across sampling sites with respect to the smallest size classes.

Where spawning occurs as discrete, synchronous events and there is mesoscale transport (Model 3), then, over time at a given site, differences in size–frequency distributions in the smaller mussel size-classes would be expected, reflecting the temporal variability of events. Collections taken at multiple sites should also sample this temporal variability. This is not consistent with observations at Lucky Strike on the Mid-Atlantic Ridge, where recruits dominate populations at multiple sites both within one sampling period and between sampling periods (Figure 1 and figures in Comtet & Desbruyères, 1998).

In Model 4, there is continuous spawning and local corralling of larvae. In this model, mussel size–frequency distributions always include a large number of small individuals, regardless of where or when samples were collected.

The size–frequency data do not allow discrimination between Model 2A, where large-scale patches of larvae are always available to colonize mussel beds, and Model 4, where the scale of larval patchiness is local.

The bias is that high densities of recruits in mussel beds everywhere is difficult to attribute to mesoscale transport processes operating on large patches of larvae, given what is considered to be inevitable losses of larvae from the patches by predation, starvation, dilution, and by the imperfect predictability of the track of mesoscale patterns. Furthermore, while mesoscale corralling processes relating to the thermal buoyancy of vent fluids and generation of convection cells can apply to hydrothermal systems, these thermally driven processes can not be invoked as mechanisms for larval corralling at the Florida Escarpment cold seep site.

Delivery of large numbers of pediveligers in both space and time must be important for maintenance of dense vent-mussel populations. Remarkably and consistently high densities of mussel recruits within active mussel beds lead to consideration of whether local mussel populations are largely derived from local sources. Grassle (1985) observed that 50% of recruits to mussel beds at two Galapagos vent sites separated by 8 km (Rose Garden and Mussel Bed) share the same genetic background (based on allele frequencies) as 60% of the adults at the same sites. Brood sources for Rose Garden or Mussel Bed recruits could, based on these data, be the local adult populations, although alternative remote brood stocks could also be postulated.

There may be a trophic advantage to local corralling. The larval mussel shell suggests planktotrophic development (Lutz et al., 1980) and previous studies emphasize

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the long-distance dispersal potential of mussel larvae (Lutz et al., 1980; Craddock et al., 1995; Vrijenhoek, 1997). Symbiont transmission may be vertical, imparting a chemoautotrophic potential at fertilization (Cary & Giovannoni, 1993, but see also LePennec & Beninger, 1997; Eckelbarger & Young, 1999). Even if transmission is horizontal, the timing of acquisition of symbionts and the degree of reliance of mussel larvae and pediveligers on symbiont primary production is as yet unknown. An optimal larval strategy may be local retention of larvae within environments where symbionts can thrive and contribute to larval and/or post-larval growth. Inevitable loss of larvae from the local system would generate the gene flow required for maintenance of regional populations in patchy environments.

Studies of dispersal in vent systems to date have focused on mesoscale oceanographic processes that entrain larvae for delivery to distant locales and that facilitate gene flow. While long-distance dispersal is critical for maintenance of vent species, consistently high abundances of recruits to mussel beds suggest that effective corralling of larvae in the deep sea facilitates maintenance of high population densities in suitable habitats.

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