

REPRODUCTIVE PATTERNS OF DECAPOD CRUSTACEANS FROM HYDROTHERMAL VENTS

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Abstract.—The mode of larval development of four species of decapod crustaceans found at hydrothermal vents is determined from embryonic and/or larval material. Two of the species, the caridean shrimp *Alvinocaris lusca* and the brachyuran crab *Bythograea thermydron*, have planktotrophic larval development; the other two species, the squat lobsters *Munidopsis lentigo* and *M. subsquamosa*, have lecithotrophic larvae. The mode of larval development appears to be mainly a function of phylogenetic constraints. The vent habitat, per se, does not dictate a single life-history strategy.

The discovery in 1976 and subsequent years of hydrothermal springs at ocean-floor spreading centers in the eastern Pacific Ocean was accompanied by the discovery of extraordinary communities of animals associated with the venting sites (e.g., Lonsdale 1977; Corliss and Ballard 1979; Corliss et al. 1979). The nature of these communities has raised many questions regarding the means by which the animals circumvent the dual problems of 1) maintaining populations at geographically isolated and spatially restricted sites in the deep sea, and 2) providing adequate dispersal to ensure colonization of new vents and to escape the catastrophe of vent shutdown (Lutz et al. 1980; Berg 1985; Turner et al. 1985). The inaccessibility of the vent habitat, about 2500 m below the surface of the ocean, precludes rigorous methods of conducting life-history studies and of obtaining direct observations of the mode of larval development for many of the invertebrate species. In this report, we summarize what is known about the sequence of developmental events that link generations of decapod Crustacea occurring at the vents. Conclusions are based mainly upon the examination of embryonic material collected from gravid females and on larvae from sample washings and deep plankton tows. These life-history data are considered in light of the dispersal requirements of the animals and their phylogenetic constraints.

Three new species of decapods have been described from hydrothermal vent areas: the caridean shrimp *Alvinocaris lusca* Williams and Chace, 1982, from the Galapagos Rift, Rose Garden site (0°48.25'N, 86°13.48'W), the galatheid squat lobster *Munidopsis lentigo* Williams and Van Dover, 1983, from the 21°N study site (20°49.60'N, 109°06.00'W),

and the bythograeid crab *Bythograea thermydron* Williams, 1980, from the Galapagos Rift (see Williams 1980 for other Galapagos localities), 21°N, and 13°N (12°48.85'N, 103°56.60'W) study sites. These three species have been found only in association with other vent organisms and, thus, appear to be restricted to the vent ecosystem. In addition, a large galatheid identified as *Munidopsis subsquamosa* Henderson, 1885 (J. Ambler, pers. comm.), has been collected and/or observed at each of the three study sites.

Egg Size and Fecundity

In the Decapoda, as in many other invertebrates, egg size generally reflects the degree of abbreviation of larval development. Species producing small eggs have a shorter embryonic period (Wear 1974) and a greater number of larval instars (Rice 1980) than species with large eggs. Egg size in the vent decapod species varies considerably, from relatively small in *A. lusca* and *B. thermydron* to exceptionally large in *M. lentigo* and *M. subsquamosa* (Table 1, Fig. 1). Brood size is inversely related to egg size: the number of eggs per brood in the galatheids is two to three orders of magnitude less than that of *B. thermydron* (Table 1). These two extremes of egg size and fecundity suggest that at least two of the three main modes of larval development (Vance 1973) are represented in the decapod fauna associated with hydrothermal vents. Highly fecund species producing small eggs are most likely to have planktotrophic instars; the small number of large, yolky eggs of the galatheid species, presumably, either yield an abbreviated number of lecithotrophic instars or develop directly into juveniles.

Table 1.—Egg size, fecundity, and mode of larval development of decapod crustaceans associated with hydrothermal vents.

Species	Locality ¹	Number of eggs per female ²	Carapace size (mm) ³	Egg size (mm)	Mode of development ⁴
Caridea					
Bresiliidae					
<i>Alvinocaris lusca</i>	G	407	R-CL 11.45	0.34 × 0.50 ⁵	planktotrophic
Anomura					
Galatheidae					
<i>Munidopsis subsquamosa</i>	G, 13, 21, N	294	R-CL 48.8	2.2 × 2.3	lecithotrophic
<i>Munidopsis lentigo</i>	21	13	R-CL 15.4	2.0 × 2.2	lecithotrophic
Brachyura					
Bythograeidae					
<i>Bythograea therymydron</i>	G, 13, 21	33,550	CW 48.5	0.48 × 0.54	planktotrophic

¹ G = "Galapagos Rift," 13 = "13°N," 21 = "21°N," N = "non-vent" sites.

² Estimated from females believed to be carrying full sponges of eggs.

³ R-CL = rostrum-carapace length, CW = carapace width.

⁴ As presumed from egg-size, fecundity, embryonic and/or larval data.

⁵ Williams and Chace (1982).

Embryonic and Larval Stages

Among ovigerous specimens of *B. therymydron* collected from Galapagos vent sites, several individuals bore eggs in which the embryonic development was almost complete, providing specimens very near the point of hatching. Dissection of these eggs revealed that *B. therymydron* emerges as a pre-zoea or 1st zoea with clearly unadvanced zoeal

characters. Several post-emergent, prezoal specimens, free of the embryonic membrane, were entangled in the egg mass of a female bythograeid crab from the 13°N vent site. The numerous long, filamentous processes on the abdominal segments and the elongate furcae and slender processes on the telson of these prezoae are distinctive features not previously described for any brachyuran zoea. A single brachyuran zoea was collected in a plank-

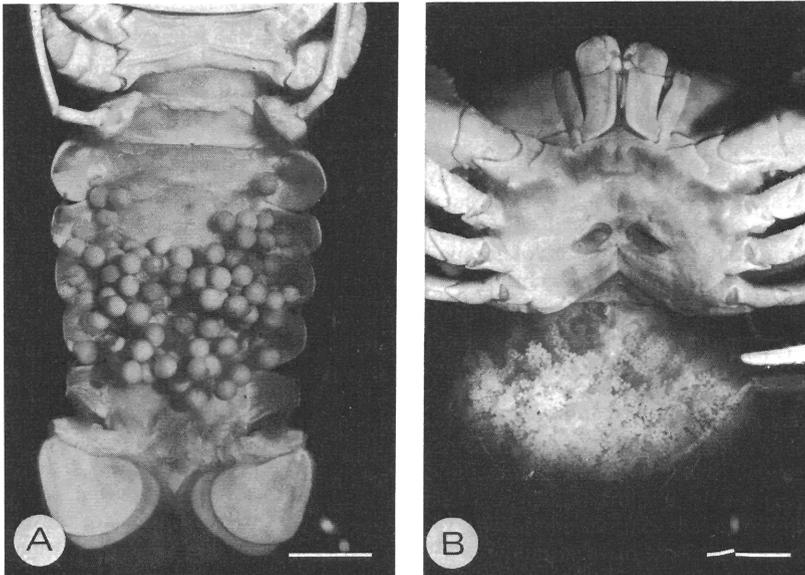


Fig. 1. Comparison of egg size and fecundity in ovigerous females of (A) *Munidopsis subsquamosa* and (B) *Bythograea therymydron*. Magnification of both approximately 1.1×. Scale bar = 1 cm.

ton net towed 1-3 m above the bottom at the 21°N site by DSRV *Alvin*; another zoea was sorted from sample washings of macrobenthic animals collected on the same dive by *Alvin*. Although it is impossible to confirm the identification of these zoeae at the species level, they share the distinctive features of the prezoae of *B. thermydron* and are, therefore, assigned to the family Bythograeidae. Both larval specimens are 1st zoeae, devoid of pigmentation except in the fixed eyes, and bear an extraordinary number of branched and unbranched processes on the carapace, abdomen, and telson. The mouthparts appear to be functional, with setose endites on the maxillae and maxillules. Setation of the exopodites of the 1st maxillipeds in both specimens is asymmetrical, suggesting that these larvae are aberrant in this respect, relative to typical brachyuran zoeae. A detailed description of the zoeae is provided in Van Dover et al. (1984).

Megalopae of *B. thermydron* were observed from a viewing port of *Alvin* at the Galapagos Rift study site and taken from washings of mussel clumps collected there. Williams (1980) characterized these large specimens as "crablike megalopae" with well-developed eyes and weak swimming ability.

No information is available concerning intermediate stages that must occur between the 1.5 mm (total length) 1st zoea and the 8.1 mm (carapace width) megalopa, nor where in the water column these stages might be found. Growth factors between instars in brachyuran larvae range from 1.05 to 2.70 (Rice 1968); if the growth factor of the larvae of the bythograeid crab is at the intermediate to upper end of this range, the difference in size between the 1st zoea and the megalopa may be accounted for without invoking an unusual number of larval instars or multiple megalopal stages. Despite the large size of the megalopa, there are no apparent modifications in the morphology of its mouthparts or locomotory appendages (Factor et al. 1982).

Free-swimming larvae of the galatheids have not been collected to date. The large eggs of ovigerous *M. lentigo* collected at 21°N were at a very early stage of development and showed no discernible larval features. Eggs of *M. subsquamosa* ranged from completely undeveloped to pre-emergent. Embryos of the latter were patently zoeal in form, not unlike the first zoeal stage of the shallow-water species *M. tridentata* (Esmark, 1857) described by Sars (1890). Reared in the laboratory, *M. tridentata* has an abbreviated number (three) of lecithotrophic zoeal stages; yolk reserves have been observed in the larvae throughout the zoeal development and, correspondingly, the mouthparts are nonfunctional (Samuelsen 1972). We suggest by analogy that this is the case in *M. lentigo* and *M. subsquamosa*, as well.

Discussion

We here report evidence that larval development of decapods associated with hydrothermal vents does not follow a single pattern: larvae may be either planktotrophic (*B. thermydron*, *A. lusca*) or lecithotrophic (*M. lentigo*, *M. subsquamosa*). Both of these modes are dispersive, but they may be fundamentally distinct: a planktotrophic larva has the potential of prolonging its pelagic life, through the use of extrinsic energy sources, until a suitable site for settlement is found. In contrast, lecithotrophic development prescribes a limit to the length of larval life as a function of the yolk reserve.

Does the pattern of adult distributions, insofar as we know them, correlate with the mode of larval development for each species? That is, are the geographically most widespread species the ones with larvae having the greatest dispersal potential? The data are ambiguous: adult *Bythograea thermydron* and *M. subsquamosa* have broad latitudinal distributions, occurring at Galapagos Rift, 13°N, and 21°N vent sites and, while the former has planktotrophic development, the latter has lecithotrophic larvae. *Munidopsis subsquamosa* is, in fact, part of a widespread, deep-sea species complex not restricted to the vent habitat (J. Ambler, pers. comm.). In this case, there would be no need for the larvae to seek out spatially discrete and/or geographically isolated vent sites in order to settle, and hence, no need for the ability to prolong larval life indefinitely.

Are the geographically most restricted species the ones with the least developed dispersive capabilities in the larvae? Again the data are ambiguous: adult *A. lusca* and *M. lentigo* have been collected only at the Galapagos Rift or 21°N vent sites, respectively, but, while *M. lentigo* has lecithotrophic development, we believe that *A. lusca* has planktotrophic larvae.

Interpretations of patterns of adult distributions and mode of larval development must be tempered with the knowledge that the data are minimal. Nevertheless, it is clear that the vent habitat, per se, does not dictate a single reproductive pattern in the decapod fauna. We suggest, instead, that the reproductive patterns of the vent-associated decapods are primarily determined by phylogenetic constraints. In support of this argument, we offer the observation that, in the genus *Munidopsis*, a highly successful deep-sea group, all of the gravid female specimens (representing more than 30 species), housed in the crustacean collection of the National Museum of Natural History, carry large, yolky eggs and, thus, presumably have non-planktotrophic larvae. In addition, it has been suggested that non-planktotrophs may be derived from planktotrophs, but not the reverse, resulting in a unidirectional trend in the evolution of life-history strategies

(Strathmann 1974; Hansen 1983). If so, this would preclude the derivation of a planktotrophic vent species from non-planktotrophic, non-vent species. The Brachyura, on the other hand, have been mostly unsuccessful in invading the deep sea (Hessler and Wilson 1983). Members of the brachyuran family Dorippidae have been found at depths greater than 2500 m. The egg sizes of two species of dorippids collected below this depth [*Ethusina faxonii* Rathbun, 1933, and *E. gracilipes* (Miers, 1886)] are on the order of 0.55 mm in diameter, comparable to that of *B. thermydron*, and suggest planktotrophic development in these species. The vast majority of shallow-water brachyuran species have planktotrophic larvae. It is likely, therefore, that the bythograeid crabs, presumably derived from shallow-water counterparts, are constrained to this mode of development on the basis of their phylogeny. The argument is less clear in the case of *A. lusca* which belongs to a poorly understood family with mostly shallow-water representatives, but with at least one deep-sea pelagic species (Williams and Chace 1982; Kensley 1983).

We conclude that populations of decapods at hydrothermal vents are established and maintained by recruitment of larvae which have passed through a series of either planktotrophic or lecithotrophic stages. The mode of larval development for a given species is determined primarily by phylogenetic constraints, rather than by the nature of the vent habitat itself.

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