Deep-sea ecology

Developmental arrest in vent worm embryos

Temperature is a key factor in controlling the distribution of marine organisms and is particularly important at hydrothermal vents, where steep thermal gradients are present over a scale of centimetres[1]. The thermophilic worm *Alvinella pompejana*, which is found at the vents of the East Pacific Rise (2,500-m depth), has an unusually broad thermotolerance (20–80 °C) as an adult[2,3], but we show here that the temperature range required by the developing embryo is very different from that tolerated by adults. Our results indicate that early embryos may disperse through cold abyssal water in a state of developmental arrest, completing their development only when they encounter water that is warm enough for their growth and survival.

We obtained early embryos of *A. pompejana* by *in vitro* fertilization, and reared them at temperatures ranging from 2 °C to 20 °C under atmospheric and deep-sea pressures. We monitored mortality (diagnosed by the breakdown of the plasma membrane or by production of irregular cytoplasmic blebs) and zygotic cleavage during early development.

Embryos kept at 20 °C and one atmosphere of pressure all died within 24 h (Fig. 1a), although many completed the first cleavage. At 14 °C and 10 °C, 70–90% of zygotes cleaved, with rates varying as a function of temperature. At 2 °C, oocytes and embryos remained intact, without cleaving, for 72 h (Fig. 1a) and for at least a further 8 days, when we stopped the experiment.

As low hydrostatic pressure inhibits cleavage in other deep-sea invertebrates[4], some irregular cleavages in our one-atmosphere incubations were not unexpected. When we repeated the incubation experiments at *in situ* pressures (250 atmospheres), we obtained qualitatively similar results (Fig. 1b), with fewer abnormalities.

To investigate whether cold-water developmental arrest is reversible, we maintained zygotes at 2 °C for 72 h, exposed them to a 10 °C heat pulse for 45 min, and incubated them at 2 °C for a further 24 h. Although embryos maintained at 2 °C never underwent cleavage, those exposed to a short heat pulse resumed development, and cleavage continued even after the embryos were moved back into cold water (Fig. 1c).

The large difference in temperature tolerance between adults (20–80 °C) and embryos (2–20 °C) precludes the possibility of embryonic development inside adult worm tubes. Optimal temperatures for development (10–15 °C) are found close to the bases of hydrothermal-vent chimneys. As eggs are negatively buoyant upon release, some embryos probably develop on or near the sea floor, just below the adult habitat. However, it is likely that at least some embryos are dispersed by currents and carried to new sites through cold (2 °C) abyssal sea water, as occurs in other vent species[5,6]. Our results show that embryos of *A. pompejana* survive but do not develop at this temperature.

It has been suggested that dispersing larvae of hydrothermal-vent bivalves[7] and polychaetes[8] may delay their development until they encounter warm water. Our results provide empirical evidence for such reversible developmental arrest in a vent species; a similar phenomenon has been reported in larvae of the bathyal echinoid *Linopneustes longispinus*[9]. Although we do not know how long the embryos of *A. pompejana* remain viable at low temperatures, this temperature-sensitive mechanism for controlling development may result in

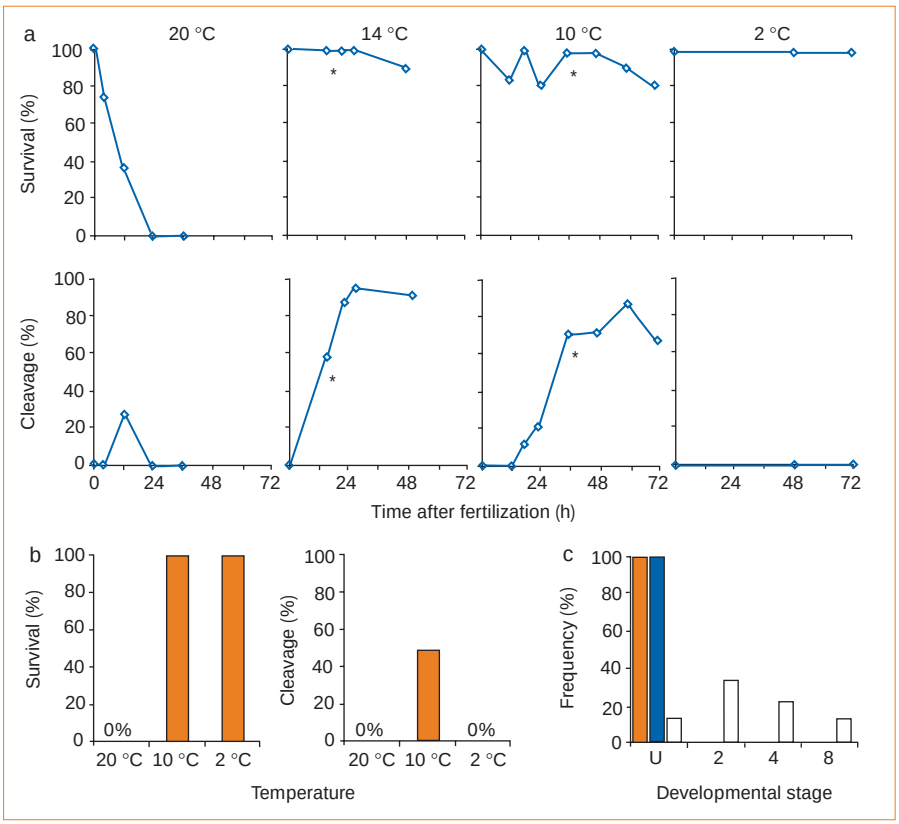

Figure 1 Effects of temperature on early embryos of *Alvinella pompejana*. **a,** Percentage of embryos surviving (top) and cleaving (bottom) when incubated at one atmosphere of pressure and at temperatures of 2–20 °C. At least 20 embryos were scored per sample, except for 2 samples (asterisks), which contained fewer embryos. **b,** Survival and cleavage at the indicated temperatures after 48 h at a pressure of 250 atmospheres. **c,** Distribution of cleavage stages in embryos incubated at 2 °C for 24 h (orange bar) and 8 days (blue bar) and in 72-h embryos exposed to a 45-min heat pulse at 10 °C (white bars), then transferred back to 2 °C for a further 24 h. Developmental stages are two- to eight-cell stages. U, uncleaved.

very long dispersal distances.

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