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Influence of water temperature on the larval development of *Neoverruca* sp. and *Ashinkailepas seepiophila*—Implications for larval dispersal and settlement in the vent and seep environments

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ABSTRACT

Deep-sea hydrothermal vents and cold seeps are scattered and limited habitats, and species that are confined to these benthic habitats often have a planktonic larval stage in their life history to maintain dispersal and gene flow among discrete populations. We have reared the larvae of *Ashinkailepas seepiophila*, inhabiting inactive vents and active cold seeps, through their entire larval development under atmospheric pressure. Using two temperatures (4 °C, 10 °C) we examined whether larval development resembles other vent species in being affected by thermal stimulation. Under laboratory conditions, *A. seepiophila* completed larval development in 65 days at 4 °C. This is considerably shorter than the 100 days previously reported to be required at the same temperature by *Neoverruca* sp., a species confined to inhabiting active vents. Also in contrast to *Neoverruca* sp., *A. seepiophila* did not drastically shorten the developmental period from nauplius VI to cyprid when exposed to temperature of 10 °C. We conclude that there is no need for late naupliar stages of *A. seepiophila* to develop into cyprids more quickly at elevated temperatures because this species does not inhabit active vents. The difference in response to water temperature during larval development may contribute to the separated distribution of the two species at active vents (*Neoverruca* sp.) and inactive vents and cold seep (*A. seepiophila*) environments.

1. Introduction

Deep-sea hydrothermal vents are distributed on seafloor spreading centers and submarine volcanoes, while methane seeps are associated with both passive and active margins around the world (Levin, 2005). Both hydrothermal vents and methane seeps are patchy habitats and support rich and endemic biological communities (Sibuet and Olu, 1998; Van Dover, 2000). Organisms inhabiting hydrothermal vents and methane seeps in the deep sea face a problem in trying to maintain their populations over time. The scarcity and discrete distribution of their habitats would seem to favor direct development or an abbreviated pelagic larval development to insure that offspring are recruited into the local population rather than being lost by larval dispersal over long distances of inhospitable sea bottom. On the other hand, vents and seeps are relatively ephemeral. Species restricted to these habitats therefore need larvae that can disperse over considerable distances and found new populations before the parent population becomes extinct.

In general, cirripedes develop through a number of naupliar stages before they metamorphose into the terminal cypris larva, which is adapted for settlement (Høeg and Møller, 2006). In the deep sea, barnacles seem to employ four rather different larval development strategies (Fig. 1). Many scalpellids, such as *Ornatoscalpellum stroemii*, hatch at the cyprid stage and this enables the larvae to search for an attachment site immediately after release (Fig. 1D). By this means they avoid an inherently risky long distance dispersal that can entail significant mortality both during the naupliar phase and by failing to locate an original habitat when they reach the cyprid stage (Buhl-Mortensen and Høeg, 2006). Obviously, this strategy will only work in the long

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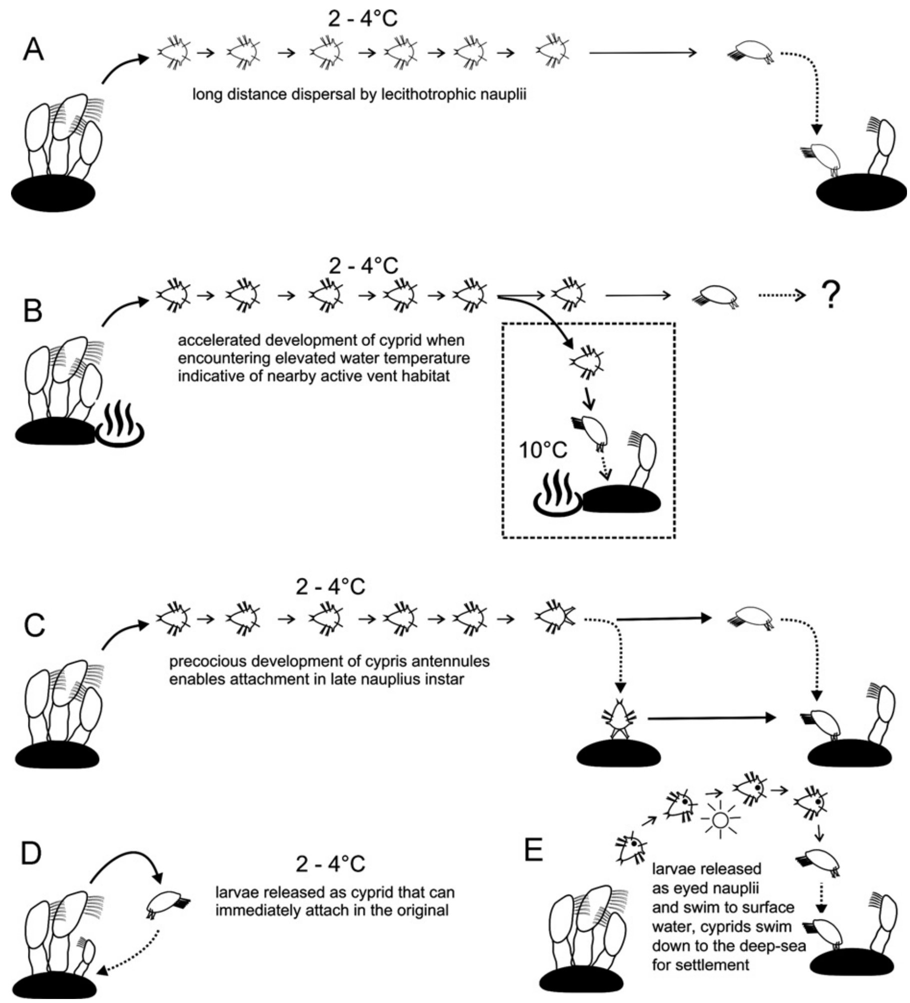

Fig. 1. Strategies for larval development and dispersal in deep sea cirripedes. Settlement occurs in the terminal, cypris stage, which in the cirripede ground pattern is preceded by six planktotrophic naupliar instars. (A) Long distance dispersal between patchily distributed habitats by lecithotrophic nauplii; common in species from the general deep sea environment where food items are scarce. (B) Acceleration of development into the terminal cypris stage, when nauplii encounter an elevated water temperature; found in species inhabiting hydrothermal vents such as *Neoverruca* sp. (C) Development of cypris attachment organs in the last nauplius instar, enabling precocious attachment to substratum if located before the cypris stage is reached; found in *Newmaniverruca albatrossiana* attaching to spines of deep sea echinoids. (D) Abbreviated development with hatching as cyprids that can settle immediately upon release into the parental habitat; found in some deep sea species from the family Scalpellidae. (E) Nauplii with eyes used for positive phototaxis; guiding them up to near surface waters for dispersal, while sinking down to near the bottom for settlement; found in the deep-sea barnacles *Verruca floridana* and *Paralepas pedunculat*a.

term if the mother habitat is stable and continues to offer settlement sites. Other barnacle species, such as *Arcoscalpellum michellottianum*, have very large lecithotrophic nauplii. This allows for a slow development using their copious nutrient stores, while dispersing over long distances in search of new settlement sites (Fig. 1A). A third and very interesting adaptation is seen in *Newmaniverruca albatrossiana*, which lives exclusively on spines of deep-sea urchins. Here the late stage nauplii have cyprid-like antennular attachment organs, which are believed to enable them to attach prematurely if they encounter their very rare habitat before reaching the cypris stage (Fig. 1C) (Watanabe et al., 2008). Nauplii of the deep-sea barnacles *Verruca floridana* and *Paralepas pedunculata* have a nauplius eye, normally used for positive phototaxis, and these species are believed to float up into near surface waters for dispersal, while sinking down to near the bottom for settlement (Bingham and Young, 1993; Fig. 1E).

Our previous studies showed that species of *Neoverruca*, a barnacle endemic to active hydrothermal vents, have a long developmental time with lecithotrophic nauplii, requiring ca. 100 days to attain the cyprid stage at 4 °C and under atmospheric pressure (Watanabe et al., 2004). But this normally long pelagic development can be accelerated if the nauplii encounter an elevated temperature (e.g., 10 °C) (Watanabe et al., 2006), indicative of the presence of a nearby active vent (Fig. 1B). This suggests an adaptation where settlement is accelerated when the larvae encounter the high water temperature associated with their vent environment, thus avoiding missing it by drifting by while still in the naupliar phase. Around Japan, *Neoverruca* sp. is found at active vent sites of the Myojin Knoll of the Izu-Ogasawara Arc, while *Ashinkailepas seepiophila* inhabits inactive vents and active methane seep environments (Fujikura et al., 2008; Kado unpublished). Here we study the larval development of *A. seepiophila*, and test whether a strong thermal response is present in the nauplii of this barnacle species that can inhabit both vent and seep environments. Details of the larval morphology of *A. seepiophila* will be described in separate publications.

2. Materials and methods

2.1. Sample collection

Adults of *Neoverruca* sp. and *A. seepiophila* were collected from hydrothermal vent sites of the Myojin Knoll (32°06′N, 139°52′E,