

Evidence of a sexual pause in *Bathymodiolus azoricus* (Bivalvia: Mytilidae) from hydrothermal vents of the Mid-Atlantic Ridge

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Histological sections of the gonad of *Bathymodiolus azoricus* from the Lucky Strike and Menez Gwen hydrothermal vent fields (Mid-Atlantic Ridge) demonstrated a spawning event in this species in May 1994, synchronous between the two vent fields located 60 km apart, and a sexual pause in gametogenesis. As reported for other vent mytilid species, *B. azoricus* from Lucky Strike and Menez Gwen could exhibit hermaphroditism.

In a recent paper, Comtet & Desbruyères (1998) showed that the recruitment of the mytilid bivalve *Bathymodiolus azoricus*, which dominate communities associated with hydrothermal activity of the Lucky Strike and Menez Gwen vent fields (respectively 37°17'N and 37°50'N) on the Mid-Atlantic Ridge (MAR) (Van Dover et al., 1996; Cosel et al., 1999), was discontinuous and synchronous between the two fields located 60 km apart. Such a discontinuous pattern may be related to discontinuity in larval availability, which could result from discontinuity in gametogenesis. However, previous studies on *Bathymodiolus thermophilus* Kenk & Wilson, 1985 from 13°N on the East Pacific Rise and the Galápagos Spreading Centre revealed that all gametogenetic stages occurred in the gonad of a single individual, both in males and females, suggesting continuous gametogenesis (Le Pennec et al., 1983; Le Pennec et al., 1984; Berg, 1985; Herry & Le Pennec, 1987). More recently, Le Pennec & Beninger (1997) reported a discontinuous component in the spermatogenesis of *B. thermophilus*, *B. puteoserpentis* Cosel, Métivier & Hashimoto, 1994 (from 23°N on the MAR) and *B. elongatus* Cosel, Métivier & Hashimoto, 1994 (from the north Fiji back-arc basin, south-west Pacific), based on differences in the relative proportions of the gonadal acini and the inter-acinal connective tissue. Discontinuous recruitment and continuous reproductive activity seem to be contradictory. The present work is aimed to check if the gametogenetic activity in *B. azoricus* from the Lucky Strike and Menez Gwen vent fields is continuous or discontinuous.

Sixty-one mytilids, ranging from 30 to 108 mm in shell length, were sampled during the two successive cruises DIVA 1 (May 1994, chief scientist Y. Fouquet) and DIVA 2 (June 1994, chief scientists A.-M. Alayse and D. Desbruyères), using the arm of the French submersible 'Nautilie', on the Eiffel Tower (1685 m depth), Isabel (1685 m) and Bairro Alto (1630 m) vent sites (Lucky Strike vent field), and on the Menez Gwen vent field (850 m). After on-board recovery, mytilids were fixed with 3% neutral formalin in seawater, and preserved in 70% ethanol. The gonad, located ventrally between the byssal gland and the posterior adductor muscle, and its extension located dorsally to the digestive gland were dissected. Tissue samples were dehydrated in increasing concentrations of ethanol (70, 95 and 100%), and in toluene. Samples were then embedded in paraffin wax at 60°C. Histological sections (5 µm) were dried (30°C, 24 h) and stained with haematoxylin–eosin following Gabe (1968).

Gonoducts observed in every individual have an heterogeneous structure composed of a semi-circled ciliated epithelium and a connective-like tissue (Figure 1A). This structure is similar to that described by Le Pennec et al. (1984) for the spermiducts of *B. thermophilus*. A single gonoduct with an homogeneous structure composed of only a ciliated epithelium, which could be also a spermiduct or an oviduct (Le Pennec et al., 1984) was observed. The occurrence of spermiducts in every individual would suggest that only males were collected, which is unlikely given the sampling size (61 individuals with length ranging from 30 to 108 mm). The observation of oocytes (Figure 1B) in sections showing spermiducts, i.e. in individuals identified as males, suggests that Lucky Strike and Menez Gwen mytilids could be hermaphrodites. Hermaphroditism has already been proposed for *B. thermophilus* (Berg, 1985) and *B. elongatus* (Le Pennec & Beninger, 1997). Thus it seems that hermaphroditism could occur, at least occasionally, in *Bathymodiolus*, as in its shallow-water related genera *Mytilus* and *Modiolus* (Lubet, 1959; Micallef & Tyler, 1988; Jasim & Brand, 1989).

Histological sections of the gonad show two structural types: in the first, the gonad is mainly composed of empty spaces (Figure 1C) corresponding to empty acini, with remains of acini walls, and in the second, inter-acinal spaces in the gonad are mainly composed of adipogranular cells highly stained by eosin (Figure 1D). The majority of acini are empty, but several oocytes with well-differentiated nuclei are observed (Figure 1B & E). In some sections acini are filled with alveolar cells (Figure 1E) known to occur after spawning in several bivalve species (Lammens, 1967; Lucas, 1971). Numerous haemocytes occur both in the inter-acinal spaces and inside the acini (Figure 1E). All these observations indicate that the gonad of each individual is in a post-spawning phase. The low number of residual oocytes suggests that the gonad is in a completely- rather than partially-spawned stage. This indicates that a spawning event occurred before or during the sampling period, i.e. May 1994. This was confirmed by the occurrence of spermatozoa in the spermiduct of an individual collected the 10 May 1994 at the Eiffel Tower site (Figure 1F), and the presence of an oocyte inside the gonoduct of an individual collected the 22 May 1994 at the Menez Gwen field (Figure 1G). These results are consistent with the occurrence of newly recruited mytilids in June 1994 reported by Comtet & Desbruyères (1998). Moreover, no difference in the developmental

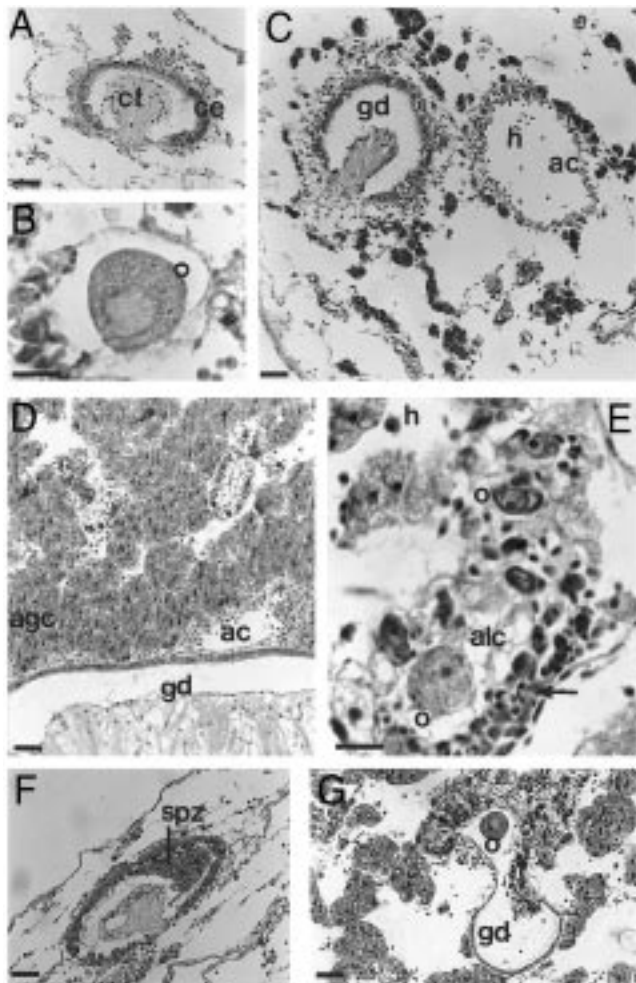


Figure 1. Histological sections in the gonad of *Bathymodiolus azoricus* from Lucky Strike and Menez Gwen. (A) Gonoduct with a semi-circled ciliated epithelium (ce) and a connective-like tissue (ct), Eiffel Tower, 10 May 1994. (B) Residual oocyte in the lumen of an acinus, Eiffel Tower, 7 May 1994. (C) General aspect of the gonad of an individual collected at Menez Gwen, 13 June 1994. (D) General aspect of the gonad of an individual collected at Eiffel Tower, 10 June 1994, showing the abundance of adipogranular cells (agc). (E) Acinus showing several oocytes and probably developing oocytes (arrow), Menez Gwen, 22 May 1994. (F) Spermatozoa (spz) observed in the spermiduct of an individual collected at Eiffel Tower, 10 May 1994. (G) Oocyte observed inside the gonoduct of an individual collected at Menez Gwen, 22 May 1994. ac, acinus; alc, alveolar cells; gd, gonoduct; h, haemocyte; o, oocyte. Scale bars: A, C, D, F, G, 50 μ m; B, E, 20 μ m.

stage of the gonad was observed between specimens of different sizes, nor between the different sites of Lucky Strike and Menez Gwen. This suggests that the spawning event was synchronous between the Lucky Strike and Menez Gwen vent fields, which could explain the synchronous recruitment hypothesized by Comtet & Desbruyères (1998).

Our findings also show the occurrence of a sexual pause in the gametogenesis of *B. azoricus* from the Lucky Strike and Menez Gwen vent fields, although in some sections, several cells are observed against the acini walls which could be oogonia or spermatogonia of the next gametogenesis (Figure 1E). This was never observed in other hydrothermal vent Mytilidae, even if a discontinuous component in the spermatogenesis of *B. thermophilus*, *B. puteoserpentis* and *B. elongatus* has been reported by Le Pennec & Beninger (1997). This contrasts with the general expectation of a

continuous reproductive activity for species living in stable feeding conditions through chemoautotrophic bacterial symbiosis, and confirms that it is not a unique reproductive strategy common to all the hydrothermal vent invertebrates [see Tyler & Young (1999) for a review].

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