J. Mar. Biol. Ass. U.K. (2003), **83**, 479–482
Printed in the United Kingdom

Aspects of the feeding biology of the pectinacean *Bathypecten vulcani*, a peri-hydrothermal vent bivalve

Gaël Le Pennec*, Peter G. Beninger[†‡], Marcel Le Pennec* and Anne Donval*

*UMR CNRS 6539, Institut Universitaire Européen de la Mer, Université de Bretagne Occidentale, 29280 Plouzané, France.
[†]Laboratoire de Biologie Marine, ISOMer, Faculté des Sciences, 44322 Nantes Cedex 3, France.
[‡]Corresponding author, e-mail: Peter.Beninger@isomer.univ-nantes.fr

The feeding biology of *Bathypecten vulcani*, a peri-hydrothermal vent pectinacean, was investigated using histological and scanning electron microscope studies of the gills and stomach contents of specimens sampled from the 9° and 13°N sites of the East Pacific Rise. Salient characteristics were compared with those of *Bathymodiolus thermophilus* from the same and similar habitats. The gills of *Bathypecten vulcani* displayed heterogeneous organic and mineral particles on their frontal surface. The digestive tract possessed well-developed structures (whose anatomical and cytological characteristics indicated full functionality), typically found in bivalves from littoral aerobic environments, as well as in *Bathymodiolus thermophilus*, which is capable of suspension-feeding: oesophagus, stomach, crystalline style, digestive gland, and intestine. Observations of stomach contents revealed diverse particles from the photic zone, including debris from diatoms and coccolithophorans. In contrast to *Bathymodiolus thermophilus*, bacteria were rarely observed in the digestive tract, indicating a more complete reliance on surface-originating particles.

INTRODUCTION

Bivalves from deep-sea hydrothermal vents present a host of morphological and cytological adaptations in their feeding and digestive systems, which differ in degree according to the extent of their reliance on endosymbionts (Le Pennec et al., 1995). To date, most research attention has been devoted to species close to the vent outflows, whereas the biology of small, peri-hydrothermal vent species such as *Bathypecten vulcani* (Superfamily: Pectinacea) has been largely ignored.

Based only on shell characters to date, the taxonomic position of *Bathypecten vulcani* has not yet been conclusively established (see references in Beninger et al., 2003), but its archaic characters may place it basal to the Pectinidae and the Propeamussidae.

Preliminary studies of the *Bathypecten vulcani* gill suggested a symbiotic relationship with bacteria present in only some bacteriocytes (Le Pennec et al., 1988), but this requires unambiguous confirmation. The peri-hydrothermal vent habitat of this species is intriguing, as it suggests a reduced influence of the vent environment. While it has not yet been possible to retrieve live specimens for observation and experimentation, the groundwork for an understanding of its feeding biology may be laid by appropriate investigation of material present on the gill and in the digestive tract, and by a comparison with the same data for species with a well-established endosymbiotic relationships in the same habitat. The present work therefore focuses on the digestive tract of *Bathypecten vulcani*, and compares relevant aspects to *Bathymodiolus thermophilus*.

MATERIALS AND METHODS

All *Bathypecten vulcani* specimens examined were collected by the research submersible 'Nautile' (IFREMER) at the East Pacific Rise. Three were obtained at 2630 m at the Genesis site (12°48′38″N–103°56′26″W) and three at 2528 m at the Tube Worm Pillar site (9°49′37″N–104°17′23″W) during the HOT 96 oceanographic cruise (February 1996). Three others were collected during the HOPE 99 cruise (April 1999): two at 2647 m at the Genesis site and one at 2515 m at the Mussel Bed site (9°50′37″N–104°17′31″W). All specimens were small: between 4.6 mm high (dorso-ventral axis) × 4 mm long (antero-posterior axis) and 10 mm high × 12 mm long.

The specimens were fixed in 10% buffered seawater formalin for 24 h prior to storage in 70% ethanol. Various parts of the digestive tract were dissected in the laboratory and embedded in paraffin after dehydration in an ascending ethanol series; 5 μm sections were stained with Masson's trichrome. Some histological sections were cleared in xylene and processed for scanning electron microscopy (SEM).

Other portions of the digestive tract and gonad were re-fixed in 2.5% glutaraldehyde in sodium cacodylate buffer, pH 7.3, 1100 mOsm, post-fixed in 2% osmium tetroxide in the same sodium cacodylate buffer, and processed for light microscopy of semi-thin sections and for transmission electron microscopy. Five specimens of *Bathymodiolus thermophilus* obtained at 2630 m in March 1982 and March 1984 from the 13°N site (EPR Biocyatherm and Biocyarise expeditions), fixed and prepared for histology and SEM following the procedure outlined, were studied for comparison.

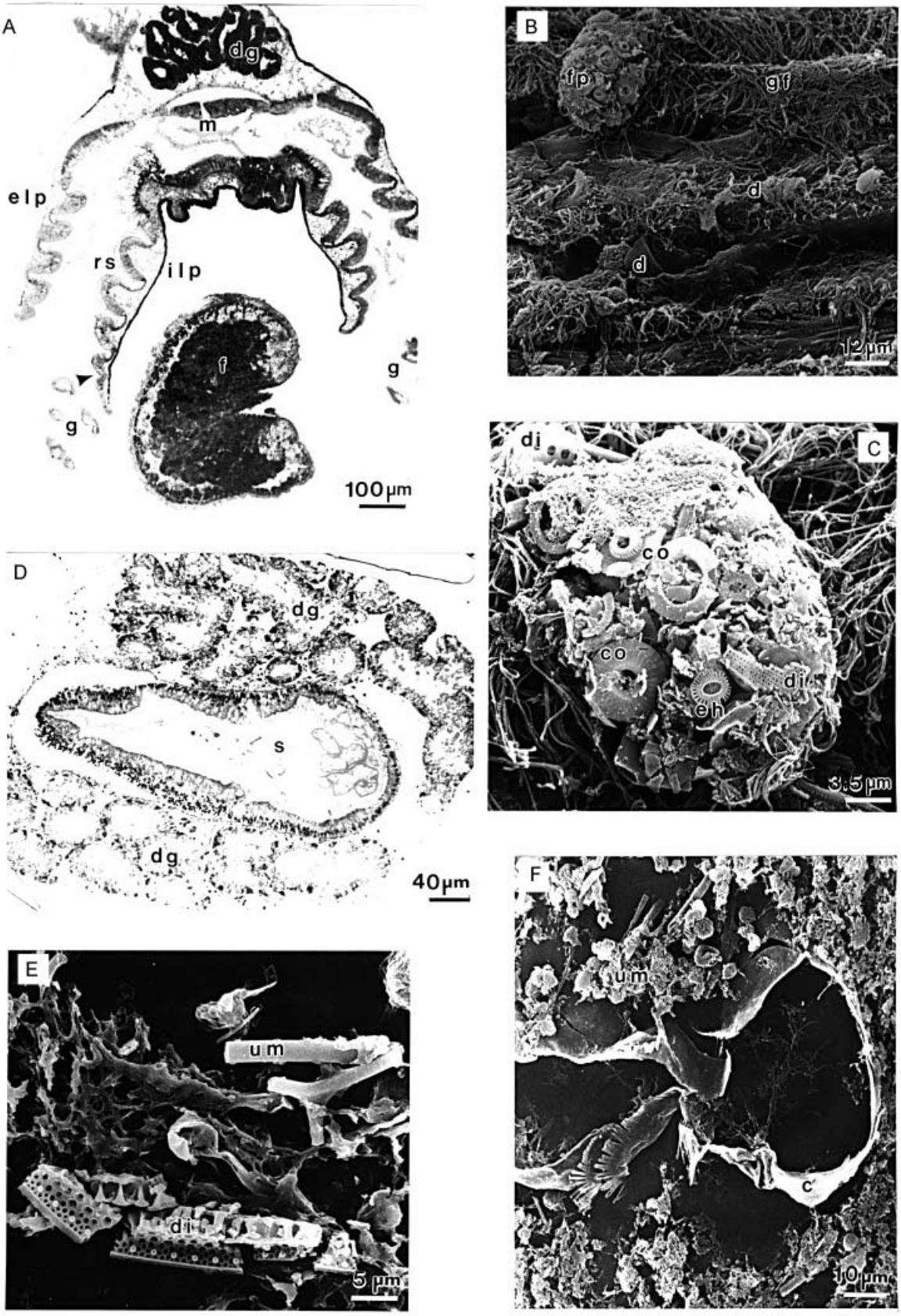

Figure 1. *Bathypecten vulcani*, photomicrographs of digestive system. (A) Transverse section of adult, showing the digestive gland (dg), mouth (m), external (elp) and internal (ilp) labial palps, whose outer surfaces are smooth and whose inner surfaces are ciliated and ridged (rs). The gills (g), located on either side of the foot (f) extend to the labial palps (arrow); (B) SEM of frontal surface of gill filaments (gf) showing various forms of unidentifiable debris (d) and a faecal pellet (fp) from a zooplankton organism; (C) SEM detail of faecal pellet showing coccolith (co) debris resembling *Emiliana huxleyi* (eh) and diatom (di) frustules; (D) semi-thin transverse section of *Bathypecten vulcani*, showing digestive acini (dg) surrounding the stomach (s); (E,F) SEM of *Bathypecten vulcani* stomach contents showing debris of diatom (di) frustules, crustacean (c) carapaces and unidentified material (um). Scale bars: as marked.

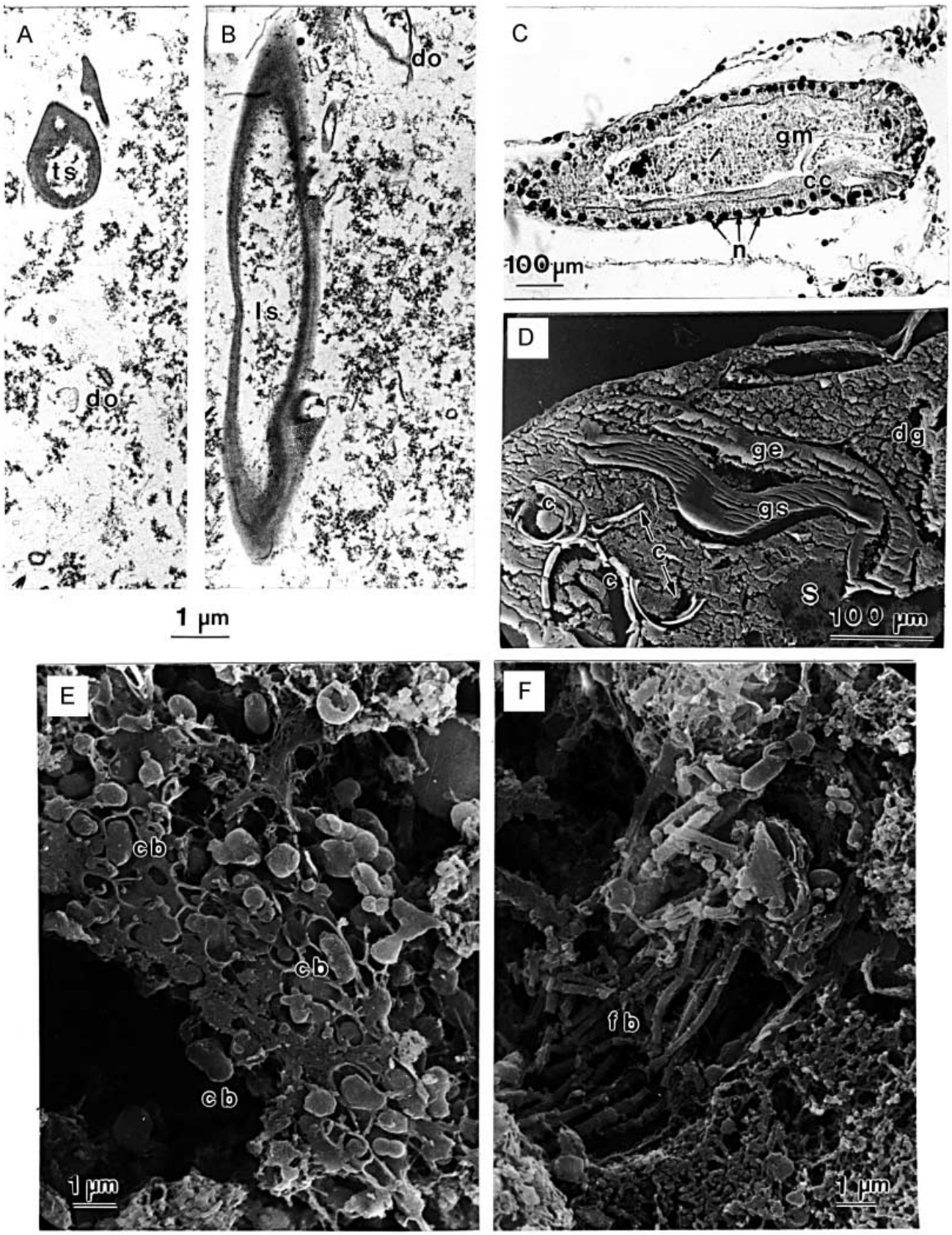

Figure 2. Photomicrographs of the digestive systems of *Bathypecten vulcani* and of the mytilid *Bathymodiolus thermophilus*, present on the same hydrothermal sites. (A) and (B) TEM of stomach contents of *Bathypecten vulcani*, showing debris of organisms (do), possibly including ciliates, seen in transverse (ts) and longitudinal sections (ls); (C) transverse thin section of the intestine of *Bathypecten vulcani*, showing a gastric epithelium composed of ciliated cells (cc) with basal nuclei (n). The intestinal lumen is filled with fine, granular material (gm); (D) SEM of 5 μm section of *Bathypecten vulcani* stomach, showing gastric epithelium (ge), thick gastric shield (gs), and stomach contents with prevalent crustacean carapaces (c). The stomach (s) is surrounded by the digestive gland (dg); (E,F) *Bathymodiolus thermophilus*. Coccoid (cb) and filamentous (fb) forms of bacteria observed in the stomach.

RESULTS AND DISCUSSION

The tubular gill filaments of *Bathypecten vulcani* were small in sectional diameter (approximately 30 μm), inconsistent with a trophic reliance on endosymbiotic gill bacteria. The mouth was crescent-shaped in the contracted (fixed) state (Figure 1A), and large (approximately 200 μm in length), indicating the potential to ingest particles beyond 200 μm along their shortest axis (given tissue shrinkage in histological preparation). Various particles were found on the frontal surface of the gill filaments, including zooplankton faecal pellets containing diatom and coccolithophoran tests (Figures 1B,C). As the *B. vulcani* gill does not appear capable of selection (Beninger et al., 2003), such a process, if it occurs at all, must be performed by the labial palps.

The stomach and surrounding digestive gland of *B. vulcani* presented a typical bivalve histological profile, also found among hydrothermal vent species such as *Bathymodiolus thermophilus*, capable of a bivalent (suspension-feeding–symbiont) feeding strategy (Beninger & Le Pennec, 1991; Henry et al., 1991; Le Pennec et al., 1995; Figures 1D & 2C). There are very few published studies on bivalve gut contents, probably because of the great difficulty in identifying the partially-triturated remains of heterogeneous microscopic particles. However, zooplankton remains have been reported in the stomachs of littoral suspension-feeding bivalves (see Davenport et al., 2000 and references therein). The stomach of *Bathypecten vulcani* contained very heterogeneous particles, most of which were not identifiable (Figures 1E,F & 2A,B). However, diatom frustules were common, as were parts of zooplankton exoskeletons (Figures 1E,F & 2D). Similar profiles have been reported for littoral bivalves (see references in Beninger & Le Pennec, 1991) as well as for *Bathymodiolus thermophilus* (Le Pennec & Prieur, 1984; Le Pennec, 1988), which is known to present a bivalent trophic strategy (Le Pennec et al., 1995). The presence of diatom frustules indicates that surface-originating particles are ingested. The heterogeneity of gut contents argues for a non-selective diet, and at least a partial reliance on relatively scarce biodeposits, either originating from the surface or resuspended from the hydrothermal environment (Lampitt, 1985).

Sections of the intestine of *Bathypecten vulcani* revealed only fine, granular material, suggesting efficient grinding in the stomach, presumably by the well-developed gastric shield (Figure 2C).

The lack of identifiable bacteria in the stomach contents of *B. vulcani* is in sharp contrast to the situation found in the *Bathymodiolus thermophilus* specimens examined from the same habitat, in which numerous coccoid and filamentous bacteria were readily observed (Figure 2E,F). These observations indicate a substantial difference in trophic sources and strategies between *Bathypecten vulcani*, which is located at the periphery of the vents, and *Bathymodiolus thermophilus*, which is found closer to the vent outflows (Desbruyères et al., 1982).

The feeding biology of *Bathypecten vulcani* thus appears to be characterized by a non-selective suspension-feeding regime, dependent upon particles originating from surface waters; the small whole size of this species, together with the relatively large size of the gill indicate that this species is food-limited in the peri-hydrothermal vent habitat. From the standpoint of feeding biology, these characteristics suggest that *B. vulcani* is a 'satellite' member of the deep-sea hydrothermal vent fauna, being largely dependent on organic particles originating from the surface and from the vents rather than on endosymbionts.

The authors are grateful to F. Gaill (CNRS-UPMC) for authorizing the study of *Bathypecten vulcani* specimens provided by P. Briand and M. Segonzac (IFREMER/Brest). Special thanks are due to J. Le Fèvre (CNRS-IUEM/UBO) and M. Segonzac for helpful discussions during the preparation of this article.

The HOT 96 and HOPE 99 cruises were respectively led by F. Gaill (CNRS/Paris) and F. Lallier (CNRS/Roscoff), with the support of INSU and IFREMER. This research was partially funded by the DORSALES programme.

REFERENCES

Beninger, P.G., Dufour, S., Decottignies, P. & Le Pennec, M., 2003. Particle processing mechanisms in the archaic, peri-hydrothermal vent bivalve *Bathypecten vulcani*, inferred from cilia and mucocyte distributions on the gill. *Marine Ecology Progress Series*, **246**, 183–195.

Beninger, P.G. & Le Pennec, M., 1991. Functional anatomy of scallops. In *Scallops: biology, ecology, aquaculture* (ed. S.E. Shumway), pp. 61–70. New York: Elsevier.

Davenport, J., Smith, R.J.J.W. & Packer, M., 2000. Mussels *Mytilus edulis* L.: significant consumers and destroyers of mesozooplankton. *Marine Ecology Progress Series*, **198**, 131–137.

Desbruyères, D., Crassous, P., Grassle, J., Khripounoff, A., Reyss, D., Rio, M. & Van Praet, M., 1982. Données écologiques sur un nouveau site d'hydrothermalisme actif de la ride du Pacifique oriental. *Comptes Rendus de l'Académie des Sciences de Paris*, **295**, 489–494.

Henry, M., Boucaud-Camou, E. & Lefort, Y., 1991. Functional micro-anatomy of the digestive gland of the scallop *Pecten maximus* (L.). *Aquatic Living Resources*, **4**, 191–202.

Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep Sea Research*, **32**, 885–897.

Le Pennec, M., 1988. Alimentation et reproduction d'un Mytilidae des sources hydrothermales profondes du Pacifique oriental. *Oceanologica Acta*, no. sp., 181–190.

Le Pennec, M., Beninger, P.G. & Herry, A., 1995. Feeding and digestive adaptations of bivalve molluscs to sulfide-rich habitats. *Comparative Biochemistry and Physiology*, **111A**, 183–189.

Le Pennec, M., Herry, A., Lutz, R. & Fiala-Médioni, A., 1988. Premières observations ultrastructurales de la branchies d'un bivalve Pectinidae hydrothermal profond. *Comptes Rendus de l'Académie des Sciences de Paris*, **307**, 627–633.

Le Pennec, M. & Prieur, D., 1984. Observations sur la nutrition d'un Mytilidae d'un site hydrothermal actif de la dorsale du Pacifique oriental. *Comptes Rendus de l'Académie des Sciences de Paris*, **298**, 493–498.

Submitted 1 July 2002. Accepted 3 March 2003.