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Growth increments and stable isotope variation in shells of the deep-sea hydrothermal vent bivalve mollusk *Bathymodiolus brevior* from the North Fiji Basin, Pacific Ocean

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Abstract

Bathymodiolus brevior [von Cosel, R., Métivier, B., Hashimoto, J., 1994. Three new species of *Bathymodiolus* (Bivalvia: Mytilidae) from hydrothermal vents in the Lau Basin and the North Fiji Basin, western Pacific, and the Snake Pit Area, mid-Atlantic ridge. *Veliger* 37, 374–392] a bivalve mollusk living at deep-sea hydrothermal vents, exhibits daily microgrowth structures in its shell. This interpretation is substantiated by various lines of evidence: (1) similar shell portions of contemporaneous specimens from the same locality contain almost the same number of microincrements; (2) the number of microincrements coincides with the expected number of days in which shell portions of *Bathymodiolus* spp. form; (3) the width of such microincrements compares well with daily growth rates estimated for the close relative *B. thermophilus* [Kenk, V.C., Wilson, B.R., 1985. A new mussel (Bivalvia, Mytilidae) from hydrothermal vents in the Galapagos rift-zone. *Malacologia* 26, 253–271]; (4) different specimens from the same site show similar microgrowth curves. In addition, we found support for tide-controlled shell growth. Daily shell growth rates fluctuate on a fortnightly basis. Some shell portions also revealed the typical tide-controlled microgrowth pattern commonly observed in intertidal bivalves. Based on the analyses of lunar daily growth increments, a growth curve for *B. brevior* was computed: $X_t = 14 \text{ cm} - (14 - 0.04 \text{ cm}) e^{-0.26t}$. This curve enables estimation of ontogenetic age from shell length. According to this equation, *B. brevior* reaches its maximum shell length of 14 cm at about age 18. Shell isotope analyses suggest that some major shell growth interruptions or retardations are related to extremely active hydrothermal venting activity. However, shell growth also stopped during periods of low venting implying physiological controls on shell formation. Results of the present study demonstrate that shells of *B. brevior* provide

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calendars and environmental data loggers that can complement or partly substitute for long-term observations of venting systems.

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1. Introduction

Age-structures of deep-sea hydrothermal vent (DHV) populations and dynamics of DHV ecosystems are still poorly understood. Such knowledge may provide important information on short-term hydrothermal activity. Although research on vent communities has dramatically increased since their first discovery in 1977 (Corliss et al., 1979), identification of ontogenetic ages of different organisms constituting hydrothermal vent communities is still rather problematic (Roux et al., 1985). Continuous monitoring of DHV ecosystems that could provide information on how fast organisms grow at such habitats is still scarce and expensive. In vivo experiments with living specimens from DHV communities have only recently been started (e.g., European program VENTOX).

Absolute dating techniques (e.g., Turekian and Cochran, 1981) have been used to infer approximate ages of shells of bivalve mollusks from DHVs. In the early 1980s, Rhoads et al. (1981) conducted mark-and-recovery experiments with shells of *Bathymodiolus thermophilus* (Kenk and Wilson, 1985) along the Galápagos Rift. Notched specimens were recovered after 294 and 297 days and the increase in shell length measured. Specimens of different initial shell lengths grew different amounts of new shell material during the experiment. This enabled the construction of an ontogenetic growth curve for *B. thermophilus*. Such growth curves are probably site-specific and species-specific. Although application to other bivalve mollusk species with different shell sizes is problematic, such growth curves may be of biological relevance for settlement, periodicity and death of hydrothermal biocoenoses. Similarly, staining experiments with the vestimentiferan tube worm *Ridgella piscesae* (Jones, 1985) were recently

completed and yielded information on skeletal growth rates (Urcuyo et al., 1998, 2003). In addition, shell dissolution rates have been used to determine ontogenetic ages of DHV shells (Lutz et al., 1985; Kennish and Lutz, 1999). Assuming that the outer shell layer of DHV bivalves dissolves at constant rates throughout the animal's lifetime, changes in its thickness from the umbonal shell portion toward the commissure can provide information on growth rates. However, this method only affords site-specific age estimates.

Sclerochronology (Buddemeier, 1975; Hudson et al., 1976), the analysis of skeletal growth patterns, can provide an alternative method for the determination of ontogenetic ages of DHV bivalves. This method is inexpensive and universally applicable to biogenic skeletons from different environmental settings (e.g., Jones et al., 1989; Pannella and MacClintock, 1968; Bourget, 1980). Numerous studies demonstrate that skeletal hard parts of a variety of different organism groups, including marine (e.g., Clark, 1974, 1975; Kennish and Olsson, 1975) and freshwater bivalve mollusks (Dunca and Mutvei, 2001), form by incremental growth, i.e., the periodic accretion of CaCO₃ along the ventral margin by mantle activity. Shell growth varies cyclically and results in the formation of distinct daily (Clark, 1975; Evans, 1972), fortnightly (Evans, 1972) and annual growth lines (Jones et al., 1978; Marchitto et al., 2000; Schöne et al., 2003a). Many bivalves from shallow marine and freshwater settings slow shell growth once per year during seasonal temperature extremes (Jones, 1983; Schöne et al., 2002), seasonal food scarcity (Schöne et al., 2003b) or annual reproduction cycles (Jones, 1980; Sato, 1995). Environmentally entrained biological clocks have been identified as pacemakers for some of these regular shell growth structures, in particular for circadian (24 h, solar day; Clark, 1975) and circalunidian (= on average