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Bathymodiolus growth dynamics in relation to environmental fluctuations in vent habitats

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ABSTRACT

The deep-sea mussel *Bathymodiolus thermophilus* is a dominant species in the East Pacific Rise (EPR) hydrothermal vent fields. On the EPR volcanically unstable area, this late colonizer reaches high biomass within 4–5 years on new habitats created by lava flows. The environmental conditions and growth rates characterizing the reestablishment of *B. thermophilus* populations are however largely unknown, leaving unconstrained the role of this foundation species in the ecosystem dynamics. A typical example from the vent field at 9°50'N that was affected by the last massive eruption was the Bio-9 hydrothermal vent site. Here, six years later, a large mussel population had reestablished. The von Bertalanffy growth model estimates the oldest *B. thermophilus* specimens to be 1.3 year-old in March 2012, consistent with the observation of scarce juveniles among tubeworms in 2010. Younger cohorts were also observed in 2012 but the low number of individuals, relatively to older cohorts, suggests limited survival or growth of new recruits at this site, that could reflect unsuitable habitat conditions. To further explore this asumption, we investigated the relationships between mussel growth dynamics and habitat properties. The approach combined sclerochronology analyses of daily shell growth with continuous habitat monitoring for two mussel assemblages; one from the Bio-9 new settlement and a second from the V-vent site unreached by the lava flow. At both vent sites, semi-diurnal fluctuations of abiotic conditions were recorded using sensors deployed in the mussel bed over 5 to 10 days. These data depict steep transitions from well oxygenated to oxygen-depleted conditions and from alkaline to acidic pH, combined with intermittent sulfide exposure. These semi-diurnal fluctuations exhibited marked changes in amplitude over time, exposing mussels to distinct regimes of abiotic constraints. The V-vent samples allowed growth patterns to be examined at the scale of individual life and compared to long-term records of habitat temperature and oceanographic mooring data in the years following the eruption. Both shell growth and habitat temperature at V-vent varied over the spring-neap tidal cycle and over longer periods of c.a. 60 days. The correlation of growth rate with temperature and, for some individuals, with current velocities supports the idea that tidal forcing impacts growth. Its influence on habitat conditions includes the spring-neap cycle, which is not reflected in current velocities but influences the venting rate. Additionally, it is expected that mesoscale eddies periodically passing across the ridge imprint shell growth through the influence of bottom current on the decimeter-thick mixing interface where mussels thrive. We conclude that diurnal-semidiurnal tidal fluctuations exert major abiotic constraints on *B. thermophilus* mussels and that low-frequency fluctuations act as significant determinants on growth. Finally, we postulate that the modulation of tidal fluctuations by large-scale hydrodynamic forcing ultimately constrains the capacity

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of this mussel species to form high biomass aggregations. This study indeed shows that the absence of these strong hydrodynamic drivers would limit the alternance of oxic and sulfidic conditions and significantly affect the growth rate of this species over time.

1. Introduction

Deep-sea vent mussels of the genus *Bathymodiolus* exploit a range of chemical resources available in their habitats in the form of dissolved reduced (H_2S, CH_4, H_2) and oxidized (O_2) compounds that are used for CO_2 fixation by flexible chemoautotrophic bacterial symbioses (Le Bris and Duperron, 2010). These mussels dominate the biomass of hydrothermal communities at several vent sites, thus playing a major role in energy transfer in these ecosystems (Van Dover, 2000). Diffuse vent environments display a complex combination of abiotic constraints with respect to the physiological requirements of these mussels (e.g. temperature limits, oxygen depletion and low pH limitation for carbonate mineralization) and the energy requirements of their symbionts (e.g. sulfide and oxygen availability, and alternative electron donors like methane or hydrogen in dual or mono-symbioses) (Johnson et al., 1994; Le Bris et al., 2006; Nees et al., 2009). A better understanding of the growth dynamics of these foundation species is thus needed if we want to appreciate their role in ecosystem functions. Furthermore, we need to elucidate the links between growth dynamics and habitat conditions. The capacity of recruits, not only to settle and survive but also to grow, ultimately governs the ability of this species to recolonize after vent habitat disturbances caused by volcanic eruptions or by anthropogenic impacts.

Bathymodiolus brevior and *Bathymodiolus thermophilus*, two species from Pacific hydrothermal vents, have been shown to grow according to a von Bertalanffy model (Schöne and Giere, 2005; Nedoncelle et al., 2013). With a shell growth rate up to 4 cm per year in the juvenile stage, these species form large mature beds on the seafloor within a few years, reaching an asymptotic size at about 18 years. These studies also revealed spring-neap periodicities in the daily shell growth rate of the two species (i.e. 14–28 days) and proposed periodic changes in the mussel habitat conditions as the probable cause of this variability. As temperature records near diffuse venting sources commonly show, the fluid-seawater mixing conditions in diffuse vent habitats exhibit periodic variations, with spring-neap tidal cyclicity or modulation over longer periods (Chevaldonné et al., 1991; Johnson et al., 1994). No detailed mechanism was however established to support the relationship between growth cyclicity and habitat temperature fluctuations and explain the inferred tidal effects on growth rates. More generally, very little is known on the abiotic factors influencing growth in vent habitats.

Bathymodiolus thermophilus is an endemic species of the East Pacific Rise (EPR), an area that undergoes frequent volcanic eruptions, with massive lava flows leading to the local extinction of invertebrate populations established around vents (Shank et al., 1998; Mullineaux et al., 2012). The 9°50′N vent field was disturbed by massive eruptions in 1991 and in January 2006 (Soule et al., 2007). In early 2006, the massive volcanic eruption eradicated *B. thermophilus* from an area measuring several square kilometers, while dense mussel beds persisted at the periphery of the lava flow (Fornari et al., 2012). After a delay in larval recruitment (Mullineaux et al., 2012), mussel populations reestablished on new habitats. This recolonization sequence, similar to that observed 15 years earlier (Shank et al., 1998), provided an opportunity to better understand how growth dynamics are influenced by environmental conditions at different time scales.

In this paper, we examine the temporal characteristics of the mussel habitat along with shell growth variations on specimens collected from two large populations from the 9°50′N area; a new population at the Bio-9 site that was covered by lava during the last eruption and a second population at the V-vent site, 5.8 km south of Bio-9, that was not reached by the lava flow. The size distribution of a large sample from the new Bio-9 population was examined in the context of the von Bertallanfy shell growth model. Based on a sclerochronology method calibrated with *in situ* fluorescent marking (Nedoncelle et al., 2013), the daily growth rate was assessed for individuals from the two sites over periods of several days, and compared to short-term fluctuations of environmental variables (temperature, sulfide, oxygen and pH). The comparison between oceanographic data and temperature recorded during the post-eruption monitoring program (NSF Ridge 2000) and shell growth records of V-vent samples was used to examine how growth can be modulated over the long-term by hydrodynamic forcing at regional and ridge scales. A first analysis of the potential links between physico-chemical constraints in the mussel habitat and growth patterns is proposed on this basis, paving the way for future experimental investigation of abiotic influences on growth and, therefore, on the reestablishement of high-biomass populations of these foundation species in disturbed hydrothermal environments.

2. Materials and methods

2.1. Mussel collections

Individuals of *Bathymodiolus thermophilus* used for size-distribution and sclerochronological analyses were collected during three cruises using the deep-sea manned submersibles Nautile (R/V Atalante cruises MESCAL1 in April–May 2010 and MESCAL2 in March 2012) and Alvin (R/V Atlantis cruise AT2610 in January 2014). Biological sampling was conducted on two vent sites of the EPR: V-vent (09°47.3′N, 104°17.0′W, 2513 m depth) located at the southern exterior edge of the lava flow that covered the area in early 2006 and Bio-9 (9°50.3′N, 104°17.5′W, 2508 m depth) located within the area impacted by the eruption (Soule et al., 2007) (Suppl. Fig. 1a).

In 2010, 35 mussels were collected at V-vent from a single large mussel bed covering about 50 m^2 of a diffuse vent area on the basaltic seafloor. The area had been previously visited in 2007 by Mullineaux et al. (2012), who reported large mature mussel beds representing pre-eruption populations (Suppl. Fig. 2a). This same bed was sampled in 2010 as described in Nedoncelle et al. (2013) (Suppl. Fig. 2b).

In 2012, individuals were collected from a large mussel bed surrounding a *Riftia pachyptila* bush at Bio-9 (Suppl. Fig. 1b), within a few tens of meters from a black smoker complex. Four collections composed of 43, 67, 84 and 28 individuals were collected in bioboxes from three different locations in this area (Suppl. Table 1). The mussels used for sclerochronological analyses belong to the first and third mussel collections.

A size-distribution analysis was performed on the 222 individuals of *B. thermophilus* collected at Bio9. Each shell was measured along its maximum growth axis, from the ventral margin to the hinge. The age of the most abundant class was estimated from the growth model previously established using in situ calcein marking of shells at V-vent (Nedoncelle et al., 2013). We similarly