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High-resolution dynamics of a deep-sea hydrothermal mussel assemblage monitored by the EMSO-Açores MoMAR observatory

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ABSTRACT

Although the spatial distribution of hydrothermal vent assemblages in relation to environmental conditions has been assessed in several studies, there is little documented data on the temporal variation of the fauna and corresponding abiotic factors in a vent community. Here, we present one of the longest integrated (faunal and environmental data) time series ever obtained in a hydrothermal ecosystem. The data were acquired using the TEMPO ecological module that was deployed between 2006 and 2008 on the Mid-Atlantic Ridge, providing the first insights into the day-to-day variations in a *Bathymodiolus azoricus* mussel assemblage from the Lucky Strike vent field for the 48 days during which the video camera operated. The time-series yielded additional valuable information on longer-term variation in faunal distribution (comparing ~2 years), temperature (11.7 months) and iron concentrations (3.8 months).

Results from daily observations showed that the vent mussel assemblage was quite stable over the 48 days of the study, reflecting the relative stability of environmental conditions during this period. *B. azoricus* mussels appeared to thrive in areas of very limited hydrothermal fluid input in habitats that are, as in other deep-sea ecosystems, significantly influenced by ocean tidal signals. Variation in species abundance was observed but, with the exception of *Mirocaris fortunata* shrimp, no links could be established with measured environmental variables. Although we did not observe any clear tidal influence on vent fauna, it is likely that physiological processes and species' activities are influenced by these periodic variations. Longer time series are currently being acquired by different experiments deployed on the EMSO-Açores MoMAR observatory (2010–2013 and still recording). They should further improve our knowledge of the dynamics of hydrothermal systems and their associated faunal communities.

1. Introduction

Over the past 20 years, three major vent fields located in the northern part of the Mid-Atlantic Ridge (MAR), south of the Azores, have been repeatedly studied during oceanographic cruises involving international research teams. The Menez Gwen, Lucky Strike and Rainbow hydrothermal fields encompass different depth ranges and are characterised by the presence of different geological substrata and contrasting fluid chemistries (Fouquet et al., 1995; Charlou et al., 2000). Within these fields, Lucky Strike (LS) was selected for the deployment of one of the first deep-sea observatories (Cannat et al., 2011; Colaço et al., 2011). Part of this hydrothermally active zone is located within a Portuguese Marine Protected Area (Santos et al., 2003) that includes different types of marine ecosystems such as hydrothermal vents, seamounts and cold-water corals.

As in many hydrothermal ecosystems, the faunal assemblages of the LS vent field are distributed in mosaics spread across the various active sulphide edifices (Van Dover et al., 1996; Desbruyères et al., 2000, 2001). Two types of faunal associations are important in the LS field: the assemblages visually dominated by the vent mussel *Bathymodiolus azoricus* and one faunal assemblage visually dominated by the alvinocaridid shrimp *Mirocaris fortunata* (De Busserolles et al., 2009; Cuvelier et al., 2009, 2011a). Over the past few years, we have shown that the structure and composition of these assemblages are controlled by their positions

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in the mixing zone located between the hot hydrothermal fluids and cold surrounding seawater (Cuvelier et al., 2009; Sarradin et al., 2009). The mussel assemblages are found in the colder microhabitats (4.4–6.1 °C) of the ecosystem whereas the shrimp assemblages colonise slightly warmer microhabitats (5.2–9.5 °C), their temperature niche overlapping slightly with that of mussels (Cuvelier et al., 2011a). The environmental conditions found in the different vent habitats have a significant impact on microbial production because they influence the availability of energy sources (De Busserolles et al., 2009) and cause modifications in the proportion of endosymbionts in *B. azoricus* gills (Halary et al., 2008). In addition, they significantly influence the bioavailability of potentially toxic compounds such as sulphides and heavy metals (Cosson et al., 2008; Sarradin et al., 2009). The role of abiotic factors in controlling the structure and functioning of vent communities at the scale of a single edifice in this vent field was recently evaluated using multivariate analyses, and supplemented with biodiversity studies encompassing the meiofaunal compartment (De Busserolles et al., 2009; Cuvelier et al., 2011a; Sarrazin et al., unpublished data). In addition, long-term colonisation experiments have been initiated to obtain information on the role of hydrothermal activity in colonisation processes and species diversity (Cuvelier et al., 2014).

While the spatial distribution of hydrothermal fauna is slowly being brought to light (Fisher et al., 1988; Sarrazin et al., 1997, 1999; Shank et al., 1998; Desbruyères et al., 2001; Luther et al., 2001; Cuvelier et al., 2011a; Marsh et al., 2012; Nye et al., 2013), there are very limited data on the temporal variation of vent communities and the corresponding abiotic factors (Glover et al., 2010; Tokeshi, 2011). Most temporal ecological studies at vents investigate recolonisation processes after disruptive events on fast and moderately spreading ridges (Tunnicliffe et al., 1997; Shank et al., 1998; Tsurumi and Tunnicliffe 2001; Shank et al., 2003; Nees et al., 2008; Marcus et al., 2009) and are based on yearly cruises rather than on continuous monitoring. A few studies have used time-series measurements at vents to monitor structural changes and variation of particle loads in low temperature hydrothermal deposit (Johnson and Tunnicliffe, 1985, 1988) and describe tube-worm behaviour (Tunnicliffe et al., 1990). Submersibles have also been used to acquire images at yearly intervals to follow variations in faunal distribution with the evolution of geological structures, observing the response of faunal assemblages to environmental changes or catastrophic events (landslide, cessation of venting, etc.) in specific areas (Van Dover, 1995; Sarrazin et al., 1997; Shank et al., 1998; Copley et al., 2007; Podowski et al., 2009; Gebruk et al., 2010; Cuvelier et al., 2011b). The effects of a drilling operation on a vent community have also been reported (Copley et al., 1997). Recently, a series of video images collected during 14 years of diving cruises on the LS vent field was used to evaluate the temporal changes in the distribution of faunal assemblages on the Eiffel Tower edifice; it demonstrated the relative overall stability on a decadal-scale (Cuvelier et al., 2011b). For the same period, the study of seafloor image mosaics at LS indicate a general decline in diffuse outflows throughout the vent field (Barreyre et al., 2012), although this could not be corroborated for the Eiffel Tower edifice (Cuvelier et al., 2011b).

At the spatial scale of a single edifice, the temporal variability of temperature, used as a proxy for hydrothermal inputs (Sarradin et al., 2009), has been investigated. Preliminary results show that hydrodynamic processes and spatial localisation influence the variability in recorded temperature data, suggesting that each microhabitat is constrained in space and time (Cuvelier et al., 2011b). Nevertheless, because most oceanographic cruises in the Azores region take place in the summer and operate over a short period of time, sub-annual variation in faunal communities, the associated environmental conditions and their interactions are difficult to assess. Therefore, knowledge about basic biological processes such as reproduction, recruitment, biological rhythms and species interactions remains limited.

The aim of the present study was to obtain basic knowledge about the day-to-day variation in biotic and abiotic factors in a hydrothermal mussel assemblage on an active sulphide edifice on the MAR, using data collected by the TEMPO temporal observatory module (Sarrazin et al., 2007), and to examine the links between faunal and environmental dynamics.

In the first part of the study, video images were used to evaluate changes in the structure of the monitored faunal assemblage at sub-annual scales. Video and screen-still images were analysed to identify the presence of biological rhythms and gain insights into species interactions. Imagery analysis of the fauna between the two years (2006–2008) was also carried out in order to assess variations at the deployment site. In the second part, video images and environmental monitoring data were coupled to examine the response of the fauna to variations in their habitats and in relation to catastrophic events. Temperature and total dissolved iron concentrations were used as proxies for hydrothermal inputs (Sarradin et al., 2009). The data collected have the potential to enhance our understanding of the temporal dynamics of hydrothermal ecosystems at sub-annual scales.

2. Materials and methods

2.1. Study site

The LS vent field is a well-known field with a central lava lake surrounded by more than 20 active hydrothermal edifices (Fouquet et al., 1995; Ondréas et al., 2009, Fig. 1). In the south-eastern section of the field, the Eiffel Tower hydrothermal edifice is an 11 m high structure. It is one of the most visited sites in the vent field, and has been the subject of several ecological studies (Desbruyères et al., 2000, 2001; Colaço et al., 2002; De Busserolles et al., 2009; Cuvelier et al., 2009; 2011a,b, 2012, 2014). The base of the Eiffel Tower edifice was extensively monitored during the MoMARETO 2006 cruise and deemed suitable for deployment of the MoMAR interdisciplinary deep-sea observatory. Primarily operated by French research teams, MoMAR is an international programme whose objective is to monitor hydrothermal vent processes at the MAR (37°18′N, ~200 km south of the Azores). This observatory combines long-term observations, detailed site studies and experimental work and includes a variety of seafloor and water column sensors. A subset of the data is periodically transmitted to a relay buoy moored nearby and then onshore via satellite. MoMAR has been active since 2006, with yearly maintenance cruises and regular upgrades (Cannat et al., 2011). It recently joined the EMSO European programme as the *EMSO-Açores observatory* (www.emso-eu.org).

2.2. The TEMPO ecological module

A prototype of the TEMPO ecological module (Sarrazin et al., 2007) was first deployed during the MoMARETO 2006 cruise at the LS vent field using the remotely operated vehicle (ROV) *Victor6000*. This prototype was composed of two main structures. The first one hosted the master electronics and the power supply (SEAMON, Blandin and Rolin, 2005). This SEAMON seabed station was used to support a local set of sensors, providing them with data storage, communication channels and power (8 kW h). The second structure (or sensor module) was moored jointly with the first one and was connected to the main module by a 15 m long cable. It was built on an aluminium frame ($0.85 \times 0.70 \times 0.65$ cm) equipped with two adjustable feet and was handled by the