Modelling the interactions of the hydrothermal mussel *Bathymodiolus azoricus* with vent fluid

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ABSTRACT

In the 40 years since the discovery of the rich faunal community around hydrothermal vents, many studies have clearly shown that environmental conditions have a strong influence on species distribution in these habitats. Nevertheless, the mechanisms that determine the spatial and temporal dynamics of species' responses to vent conditions remain elusive. Metabolic studies to assess faunal interactions with vent fluid are particularly difficult to perform in the deep sea and are generally executed in isolation *ex situ*. Available data mainly concern foundation species, which visually dominate these ecosystems. This work uses a modelling approach to integrate biotic and abiotic data that have been acquired through the years on Eiffel Tower, a large sulphide edifice located on the Lucky Strike vent field on the Mid-Atlantic Ridge, and particularly on its dominant species, *Bathymodiolus azoricus*. A carbon-flux model was built using seven state variables: the biomass of mussels and their associated thiotrophic (SOX) and methanotrophic (MOX) symbionts and the ambient concentrations of oxygen, dihydrogen sulphide, methane and (particulate and dissolved) organic carbon. Temperature of the surrounding water and mussel density were the forcing variables in the system. Results showed no statistically significant differences between predicted and observed mussel biomass and estimates of energy partitioning within the mussel were in the range of available data.

Metabolic rates were generally rather low and greatly reduced by a temperature effect in the coldest samples. These low metabolic rates imply a long lifespan for *B. azoricus*. Simulations suggest that they would strongly hinder re-establishment and resilience of mussel biomass. However, because symbionts respond quickly to changes in vent fluid, mussels would be able to buffer strong variations in the hydrothermal fluid supply. The model showed that if mussels fed indifferently on both types of symbionts, coexistence of MOX and SOX cannot be reached, thereby likely favouring hypotheses of competition for space inside the mussel gills and/or a differential use of the production of each symbiont. Model predictions are highly dependent on current knowledge, and the results presented here highlight the need for more quantitative data on the biology of *B. azoricus* across different size classes, on its interactions with symbionts, and in varying environmental concentrations in its substrates.

1. Introduction

Hydrothermal vents are formed in areas where seawater penetrates the porous oceanic crust, heats up in contact with hot rocks and rises to the seafloor as hot emissions (up to 400 °C), rich in reduced compounds and heavy metals (Johnson and Tunnicliffe, 1985; Johnson et al., 1988a). In the plume of hydrothermal fluids, many reactions occur spontaneously or because of the activity of microorganisms. Some of these microorganisms use the energy from the reactions for primary production through chemosynthesis, supporting most of the food webs in hydrothermal ecosystems (Jannasch and Wirsen, 1979; Jannasch, 1995). The last 40 years of vent research has significantly increased our knowledge on the biology and ecology of the fauna living there. In most cases, dense faunal assemblages, visually dominated by a few invertebrate species, proliferate around fluid exits (Tunnicliffe et al., 1997; Tsurumi and Tunnicliffe, 2001; Govenar et al., 2005; Cuvelier

et al., 2009). Their spatial and temporal patterns are tightly linked to the intensity (Sarrazin et al., 1999; Luther et al., 2001; Gollner et al., 2010; Podowski et al., 2010; Marsh et al., 2012) and variability (Johnson et al., 1988b; Podowski et al., 2010; Cuvelier et al., 2011) of hydrothermal fluids. However, the mechanisms underlying the faunal response to this varying environment are still poorly understood. The need to better understand the functioning of vent communities is becoming more urgent as the industrial exploitation of sulphide deposits, formed by hydrothermal vent activity, is imminent.

Faunal response can be complex, and two types of interactions between hydrothermal species and their environment have to be considered. First, the hydrothermal fluids provide high concentrations of reduced compounds that may trigger high chemosynthetic primary production, potentially transferred up through the food web. Second, fluids are also characterized by high temperatures, high concentrations of potentially toxic compounds and high temporal variability (Johnson et al., 1988b; Barreyre et al., 2014). However, quantitative data on the biology of vent species and abiotic conditions are still scarce for hydrothermal ecosystems. Trophic networks have mainly been studied through the use of stable isotopes and fatty acids (e.g. Conway et al., 1994; Colaço et al., 2002; Léveillé et al., 2005; Bergquist et al., 2007; De Busserolles et al., 2009), but the high trophic opportunism of many hydrothermal species and the difficulty of obtaining isotopic signatures of the primary producers has limited the quantification and modelling of trophic flows through the entire ecosystem. Moreover, species tolerance to fluid physico-chemical characteristics have only occasionally been evaluated (Shillito et al., 2006; Henry et al., 2008) and very little is known about factors limiting faunal settlement.

Most biological data from these habitats involve large invertebrates which have a symbiotic association with bacteria (e.g. *Bathymodiolus septemdierum, Alviniconcha* sp. and *Ifremeria nautilei*, Henry et al., 2008; *Bathymodiolus azoricus*, Colaco et al., 2002; De Busserolles et al., 2009). This association ensures unshared primary production (Cavanaugh et al., 1981; Felbeck, 1981; Fisher et al., 1989; Girguis et al., 2002; Girguis and Childress, 2006) and offers a potential supplementary defence against fluid toxicity (Powell and Somero, 1985, 1986). These invertebrate species are referred to as "foundation species", because they significantly affect the habitat with the 3D structures they provide, favouring colonization by a wide range of associated species (Govenar and Fisher, 2007). Dayton (1972), who coined the term "foundation species", suggested that the study of these species would be a simple and efficient way of understanding an ecosystem's dynamics. Modelling is a widely used tool in marine ecosystem studies to integrate available quantitative knowledge, test hypotheses and predict the evolution of a system (Fennel and Neumann, 2014). A well-known hydrothermal edifice of the Lucky Strike vent field (Mid-Atlantic Ridge) is Eiffel Tower, dominated by the foundation mussel *B. azoricus*. To better understand the mechanisms underlying mussel spatial and temporal dynamics, we used available data to build a model mimicking the interactions between a *B. azoricus* assemblage and its environment. The objectives of our model were to (i) provide an estimate of the mussel energy budget, to gain insight on exchanges with the surrounding environment; (ii) determine factors that limit mussel growth in a given environment; (iii) predict the evolution of biomass of a settling mussel assemblage after an almost complete removal (direct disturbance) and also (iv) determine the response of an established assemblage to a flow interruption (indirect disturbance). Here, we used modelling to highlight gaps in our knowledge and guide future experiments.

2. Materials and methods

2.1. Ecological studies

Since the discovery of the Lucky Strike vent field in 1992 (Langmuir et al., 1993), several research activities including 27 oceanographic cruises and the set-up of the EMSO-Azores observatory in 2010 (http://

www.emso-fr.org/EMSO-Azores) have helped to compile a large amount of data on this particular area. The Eiffel Tower edifice is one of the most studied structures at Lucky Strike. It is visually dominated by the mussel *Bathymodiolus azoricus* (Van Dover et al., 1996; Desbruyères et al., 2000; Cuvelier et al., 2009) and a second assemblage dominated by shrimp in higher temperature areas has been identified (Sarrazin et al., 2015). Numerous studies on *Bathymodiolus* have shown that it probably owes its success to the presence of two phylotypes of symbionts in its large gills (Distel et al., 1995; Fiala-Médioni et al., 2002; Duperron et al., 2006): one that can produce organic carbon from the oxidation of methane (methanotrophic bacteria, MOX) and the other from the oxidation of sulphide (thiotrophic bacteria: SOX). This dual endosymbiosis, associated with a functional gut, gives the mussels high trophic plasticity, allowing them to survive across a wide range of environmental conditions (Page et al., 1991; Fiala-Médioni et al., 2002). Riou et al. (2008) observed that the carbon is first fixed by the bacteria and then transferred to the other mussel tissues, probably via intracellular digestion of the symbionts (Fiala-Médioni et al., 2002), as also observed in other deep-sea bivalves (Fisher and Childress, 1986; Streams et al., 1997). A recent study estimated that *B. azoricus* contributes on average to almost 90% of the total biomass on the Eiffel Tower edifice (Husson et al. 2017). In addition, *B. azoricus* exhibits properties specific to foundation species such as the provision of habitat through supplementary surfaces and complex 3D structure (Trask and Van Dover, 1999; Desbruyères et al., 2000; Cuvelier et al., 2009). However, its importance for the rest of the ecosystem is not well understood.

2.2. Sampling

This study used data from 15 sampling units collected during two cruises that took place in 2006 (MoMARETO, Sarradin and Sarrazin, 2006) and 2014 (MoMARSAT, Sarradin and Cannat, 2014), on the "*Pourquoi pas?*" research vessel, using the remotely operated vehicle (ROV) *Victor 6000*. During the MoMARETO cruise in 2006, 12 samples were collected (samples C1 to C12, mean mussel size from 20 to 78 mm, sampling procedure in Sarrazin et al., 2015). Three additional samples of medium and large mussels were collected during the MoMARSAT 2014 cruise (samples 14-2 to 14-4, mean mussel size from 35 to 58 mm, sampling procedure in Husson et al., 2017). During both cruises, temperature was measured prior to faunal sampling on several points over the assemblage. Mussel density, length-weight relationship and total surface area was reported for both cruises in Husson et al. (2017). The mussel body carbon-to-dry-weight ratio was measured on mussels collected during a third cruise (MoMARSAT 2015, R/V *Pourquoi pas?*) using the ROV *Victor 6000*, (Sarradin and Cannat, 2015; Khripounoff et al. 2016). Two estimates of the biomass were calculated on each sample by (i) applying length-weight relationship on each measured mussel length (B1) or (ii) applying length-weight relationship on the mean length of the sampled assemblage and multiplying by density (B2).

2.3. Model and equations

The model represents a square meter of hydrothermal substratum containing mussels that are flushed with hydrothermal fluid. The model has seven state variables (Table 1, Fig. 1): different potential food sources, i.e. particulate and dissolved organic carbon (OC in mol OC/L), methane (M in mol CH_4/L), dihydrogen sulphide (S, in mol H_2S/L), oxygen (O in mol O_2/L), mussel biomass (MUSSELS in mol C/m²) and their methanotrophic (MOX, in mol C/m²) and thiotrophic (SOX, in mol C/m²) symbionts.

The model acts as a chemostat, where concentrations of chemical species are renewed by the incoming flow (O_{input}, OC_{input}, M_{input}, S_{input}), consumed by the symbionts and mussels (OC_{uptake}, M_{uptake}, S_{uptake}, O_{uptake}^{SOX}, O_{uptake}^{MOX}, O_{uptake}^{MUSS}) and transported out of the system