



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.

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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 × 0.70 × 0.65 cm) equipped with two adjustable feet and was handled by the

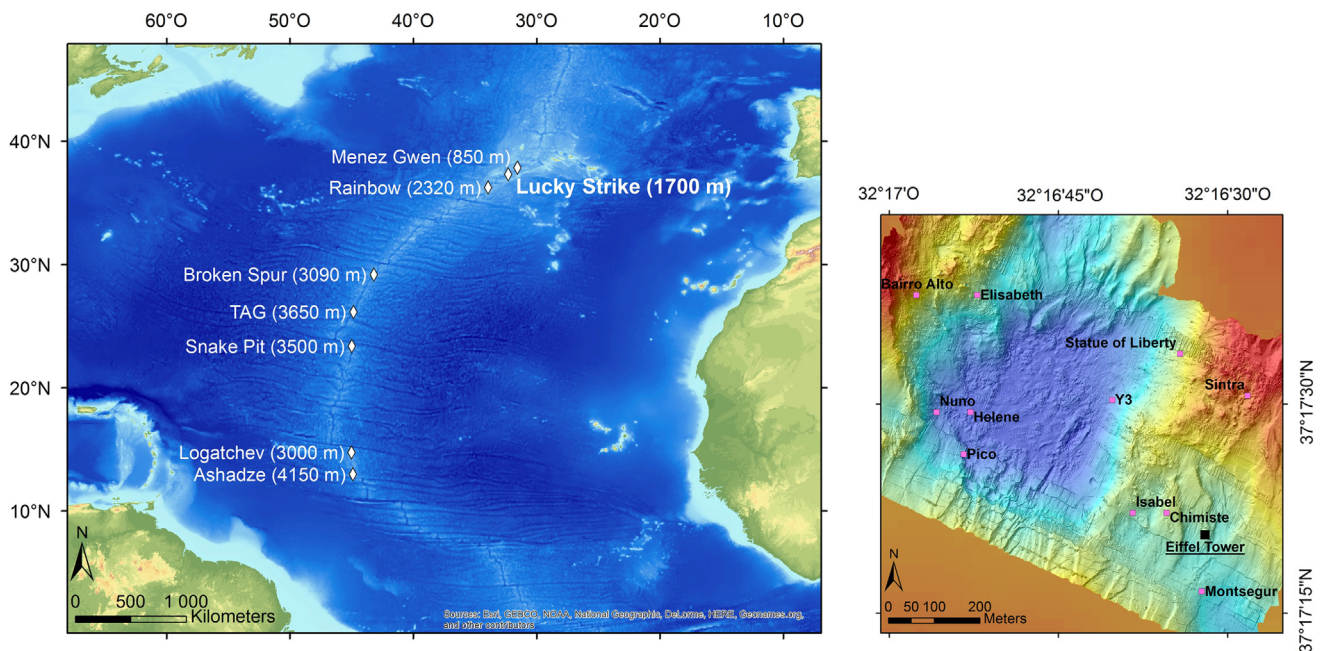


Fig. 1. Location of the Lucky Strike vent field on the Mid-Atlantic Ridge at 37°17.59N, 32°16.9W. Data from the MNT ETPO1 bedrock. The inset shows the hydrothermal vent field with several active sulphide edifices around a central lava lake, including the Eiffel Tower edifice in the south-east. Data from [Ondréas et al. \(2009\)](#).

submersible arm. The module was composed of an autonomous video camera (720 × 576 pixel) and two 35 W LED projectors, both protected by an anti-fouling system based on local chlorine generation. It also included a CHEMINI Fe *in situ* analyser ([Vuillemin et al., 2009](#); measuring total dissolved iron concentrations, called Fe hereafter), along with autonomous temperature probes (NKE, ST6000). During deployment of TEMPO, SEAMON communicated with the ROV via a contact-less serial interface (CLSI) and transmitted still images, allowing for optimal positioning of the camera view and the related environmental sensors.

During the 2006 deployment cruise, we dedicated considerable dive time to find the ideal location for the ~1 m³ TEMPO module. This location had to fulfill four requirements: a nearly flat area to position the module, the presence of a living faunal assemblage, a fluid source in the immediate vicinity (< 1 m), and accessibility for the ROV. After a few hours of surveying, TEMPO was positioned at the base of the south-east side of the Eiffel Tower edifice. A ledge colonised by *B. azoricus* mussels, featuring a diffuse flow zone with visible shimmering water was chosen for the temporal study ([Fig. 2](#)).

The camera was programmed to record 4 min of video footage twice a day along with temperature measurements every hour and Fe measurements every 12 h. TEMPO recorded data onto a hard disk drive for subsequent recovery of images (August 2008, MoMAR08 cruise with ROV *Victor6000*). The deployment calibration/set-up of the camera used more power than expected and the batteries only lasted 48 days, instead of the 365 days initially planned. In addition, although the module was initially programmed to record twice a day, it recorded haphazardly: sometimes it recorded twice a day, sometimes only in the morning or the evening, and sometimes it skipped a day or more. Overall, a total of 204 min (recorded over 48 days) of video images was analysed. The temperature probes recorded data for the whole duration of the mooring, and the CHEMINI Fe module operated for 4.37 months, i.e. until complete consumption of the chemical reagents available. An overview of the faunal and environmental data available for the duration of the video recordings (48 days) is shown in [Fig. 3](#). As the CHEMINI Fe module started recording with a 10 day delay, only 38 days of iron measurements were available for use in conjunction with video image analyses.



Fig. 2. The study scene as viewed by the TEMPO ecological observatory module at ~1692 m depth at the base of the Eiffel Tower edifice (Lucky Strike vent field, MAR). TEMPO was deployed in 2006 during the MoMARETO cruise and recovered in 2008 during the MoMAR08 cruise. The CHEMINI sample inlet and associated temperature probe can be seen on the left-hand side of the picture. The total studied surface covered approximately 0.1 m².

2.3. TEMPO image analyses

In a previous study of MAR hydrothermal ecosystems, several quantitative factors that can be accurately assessed from video images were identified by conducting a comparison with conventional faunal sampling ([Cuvelier et al., 2012](#)). These factors included the identification and quantification of a limited number of macrofaunal species, as well as the extraction of selected biological and environmental variables such as fluid flow rates, microbial coverage and biological rhythms ([Cuvelier et al., 2012](#)). Video images in this study were used to extract similar types of data.

Abundance—One still image of each video recording was used as a template to locate and count the relatively sedentary animals (i.e. *B. azoricus* mussels and *Pseudorimula midatlantica* limpets, [Table 1](#)). For the highly mobile shrimp species (*M. fortunata*), every 4 min of video recording was divided into 5 still images

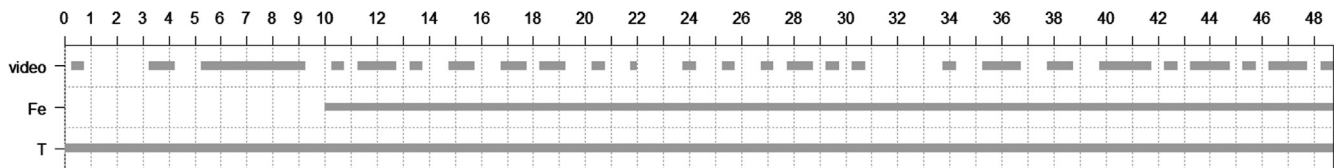


Fig. 3. Overview of data (video, iron concentrations (Fe) and temperature (T)) available for the duration of the video recording. Days are indicated on the top axis. The 48 day time-series was done between 04/09/2006 and 22/10/2006.

Table 1

Extraction of faunal and environmental data from the video footage recorded by the TEMPO module for 48 days (04/09/2006–22/10/2006) at ~1692 m depth at the base of the Eiffel Tower edifice (Lucky Strike vent field, Mid-Atlantic Ridge). The total studied surface covered approximately 0.1 m². Minimum and maximum values obtained for each temporal analysis are reported.

Faunal data	Species	Treatment	Results (min and max)
Abundance	<i>Bathymodiolus azoricus</i> , <i>Pseudorimula midatlantica</i> <i>Mirocaris fortunata</i>	1 still image twice a day (A.M., P.M.) 5 still images twice a day (A.M., P.M.) 10 × 20 s. video recordings (5 A.M., 5 P.M.)	40 to 52 individuals, 0 to 8 individuals 2 to 27 individuals
Valve opening	<i>Segonzacia mesatlantica</i>	4 min video recording twice a day (A.M., P.M.)	0 to 3 individuals
Changes in valve opening	<i>Bathymodiolus azoricus</i>	5 still images twice a day (A.M., P.M.) 22 × 4 min video recordings	16 to 53% of the individuals Caused by passage of other species (37.8%) or unobserved events (62.2%)
Microbial cover		1 still image every 5 days × 10	27.47 to 34.53%
Environmental data	Speed (cm s ⁻¹)	Treatment	Results (min and max)
Horizontal (current) and vertical (fluid flow) estimates in ordered classes			
1	0–1.49	4 min video sequence twice a day (A.M., P.M.)	0 to 10.5 cm s ⁻¹ for the current
2	1.5–2.49		0 to 7.5 cm s ⁻¹ for the fluid flow
...	...		
10	9.5–10.49		

A.M. morning; P.M. evening.

Table 2

Long-term changes in faunal and microbial abundances at the TEMPO site located at the base of the Eiffel Tower edifice (~1692 m) between 2006 and 2008 based on analyses of still images. The wide-angle views of the studied assemblage were assembled out of photographs taken by the ROV Victor6000 while the close-up views correspond to still images recorded by the TEMPO camera.

Taxon	Wide angle				Close-up			
	2006		2008		2006		2008	
	Abundance	Density (ind m ⁻²)	Abundance	Density (ind m ⁻²)	Abundance	Density (ind m ⁻²)	Abundance	Density (ind m ⁻²)
<i>Bathymodiolus azoricus</i>	734	739.5	768	879.7	51	508.5	75	782.1
<i>Mirocaris fortunata</i>	42	42.3	27	30.9	24	239.3	9	93.8
<i>Segonzacia mesatlantica</i>	6	6.0	3	3.4	2	19.9	0	0.0
	cm ²	%	cm ²	%	cm ²	%	cm ²	%
Microbial cover	4068.1	41.0	3933.8	45.1	371.6	37.1	354.1	36.9
Mussel cover	2618.5	26.4	3265.4	37.4	239.7	23.9	345.0	36.0
Total surface (cm ²)	9925.5		8729.9		1002.6		959.1	

(start, 1 min, 2 min, 3 min, and end at 4 min). Twenty seconds of video footage was also investigated around these time stamps to count the shrimp. For the *Segonzacia mesatlantica* crabs, the entire 4 min recording was analysed and abundance was recorded (Table 1).

Opened mussel valves were counted in five still images (start, 1 min, 2 min, 3 min and end) for each video recording (Table 1). Mussels were considered to have open valves when either the exhalant siphon or an opening between the two valves was visible. Counts were quantified as the percentage (%) of visible mussels with open valves. In addition, a random selection of 22 video recordings were analysed in detail for changes in mussel valve opening such as sudden closure reactions.

Microbial cover was assessed on a selection of 10 still images taken at 5 day intervals (Table 1). Microbial patches were manually marked

in white and the rest of the image was filled in black. The percentage (%) of the image covered by microbial mats was then measured using the ImageJ image analysis software (Rasband, 2012).

Vertical and horizontal components of water movement were estimated from on-screen tracking of particles. The particles travelling upwards were used as a proxy for hydrothermal fluid flow while those moving sideways were used to estimate currents. The distance travelled over time (cm s⁻¹) was estimated and these values were subsequently transformed to numerical classes (Table 1). The video recordings in which no particles could be observed were compared to other video recordings (using visual indicators of flow such as turbulence, shimmering water, etc.) and placed in the most similar corresponding classes. Since not all velocities were effectively measured (some were estimated from images), we used categorical values (classes) instead of numerical values.

Video images recorded at 8:00 UTC were referred to as A.M. (morning) while those recorded at 20:00 UTC were referred to as P.M. (evening).

2.4. Analysis of high-definition photographs taken in 2006 and 2008

High-definition photographs taken during deployment (1 September 2006) and recovery (12 August 2008) of the TEMPO module by the ROV *Victor6000* were used to monitor long-term variation in faunal distribution (23.3 months) (Table 2). Two sets of photographs were selected: wide-angle views of the scene (taken by the ROV), and closer views, corresponding to the images recorded by the TEMPO camera. The surface covered by each of these photographs was estimated using ImageJ with the length of the tip of the sampling inlet (29 mm) serving as a calibration reference (Fig. 2). The surface covered by mussels and microbial mats was evaluated along with mussel, shrimp and crab densities. As described above for the video still images, the surface covered by mussels and microbial mats was manually marked in different colours and the percentage (%) of coverage was measured.

2.5. Statistical analyses

All statistical analyses were carried out in R Development Core Team (2012). Pearson correlations with permutation tests (999 permutations), a valid test in the absence of normal error distribution, were calculated between all variables for the duration of the video recordings to determine which variables of faunal abundances or environmental factors showed similar or contrasting trends. Analyses of variance (ANOVA) with permutation tests (999 permutations) were conducted for shrimp abundance and the proportion of open mussel valves to examine how they changed within and between the video recordings.

Short-term variations in temperature for the duration of the video recording were analysed with correlograms. Rhythms and periodicities of temperature values and Fe measurements over longer terms were examined using Whittaker–Robinson periodograms (Legendre, 2012). Prior to periodogram analyses, data were tested for stationarity. When that condition was not met, a linear trend was extracted by regression to ensure stationarity and residuals were used for periodogram analysis. Missing values in the dataset were indicated by NA (not available). Whittaker–Robinson periodograms are based on a Buys-Ballot table, which folds a time series into a table along a period with maximum length of $n/2$. Buys-Ballot tables corresponding to periods of interest (e.g. diurnal cycles) can be constructed to test hypotheses (Legendre and Legendre, 2012). The statistic used in this function is the standard deviation of the means of the columns of the Buys-Ballot table (Legendre and Legendre, 2012). However, some degree of caution is necessary to interpret the results of significance tests in Whittaker–Robinson periodograms because harmonics of a basic period are often also found to be significant. Periodograms were calculated for the time period for which images were available (48 days) as well as for the long environmental time series collected after image recordings stopped (> 1 year).

3. Results

3.1. Data collected

Temperature and Fe data originating from the sampling inlet positioned within the camera's field of focus and on the mussel assemblage (Fig. 4A and B) were also used as explanatory variables of faunal variations. A 3 min delay was observed between

temperature and Fe measurements, precluding any test of correlation of the two data sets as originally planned (Vuillemin et al., 2009). On day 25 following TEMPO deployment, the sampling inlet was repositioned after a disturbance by a chimaeroid fish, identified as a male *Hydrolagus pallidus*, which passed between the module and the monitored faunal assemblage. The event was captured by the TEMPO camera. From day 1 to day 25, the probe had been positioned on the mussel bed and after day 25, it slid downwards about 6 cm into the diffuse flow area. Due to the significant difference in measured temperatures (a difference of almost 3 °C) (Fig. 4A), we considered these two periods as separate data sets for the statistical analyses.

The first temperature data set comprised days 1 to 25 (referred to as P1 from here on, 04/09/2006 to 29/09/2006); it was used as explanatory data in the study of faunal variation. Days 26 to 48 are referred to as P2 (29/09/2006 to 22/10/2006) corresponding to the second positioning of the probe until the end of the video recording. The P2 time series was not used for faunal interpretation (except for microbial mat coverage) because the inlet was no longer positioned on the studied assemblage. The third dataset (P3) featured the long-term time series of temperature values (22/10/2006 to 14/10/2007), adding up to 357 days (11.7 months). This period was used to determine significant periodicities in diffuse flow temperature. Unfortunately, the temperature data from August 2007 onwards could not be used because of a calibration problem.

As the *in situ* Fe analyser started recording with a ten-day delay and because the sampling probe slid at day 25, only 15 days of iron measurements were available for use in conjunction with image analyses (days 10 to 25 (P1), Fig. 3). The iron (Fe, Fig. 4B) data set spanned 133 days in total. 117 days, corresponding to 234 measurements in P2 and P3 -with 6 missing values- were considered for the study of long-term patterns.

3.2. Short-term variation

A total of 51 video recordings of 4 min each, spanning 48 days, were analysed. The scene filmed by TEMPO was characterised by the presence of three main areas with, from bottom to top: (1) a small diffusion zone with the presence of white anhydrites, (2) an elongated *B. azoricus* mussel assemblage bordered by (3) a rocky substrate with or without white microbial mats (Fig. 2). The sampling inlet (for temperature and Fe) was initially positioned directly on the faunal assemblage, as shown in Fig. 2. The total studied surface covered approximately 0.1 m².

Short-term changes were investigated for the fauna, temperature, Fe and other possible explanatory variables that were deduced from images such as flux and currents. Long-term variations of temperature and Fe concentrations are described in Section 3.3.

3.2.1. Environmental conditions

There was a noticeable increase in temperature values and Fe concentrations between P1 (4.87 ± 0.24 °C, 1.02 ± 0.22 μM) and P2 (7.87 ± 1.74 °C, 3.51 ± 3.08 μM), when the tip of the sampling inlet was moved as described above (Fig. 4A and B). Both temperature and Fe measurements recorded in the new sampling position P2 were significantly different from those registered during P1 (ANOVA with permutation tests: $F=145.24$, $p\text{-value}=0.001$ and $F=26.54$, $p\text{-value}=0.001$, for temperature and Fe, respectively; Fig. 4). This was taken into account when examining the relationships between the fauna and the environmental variables; we tested the faunal changes against the environmental variables only for P1, while P2 and P3 were analysed

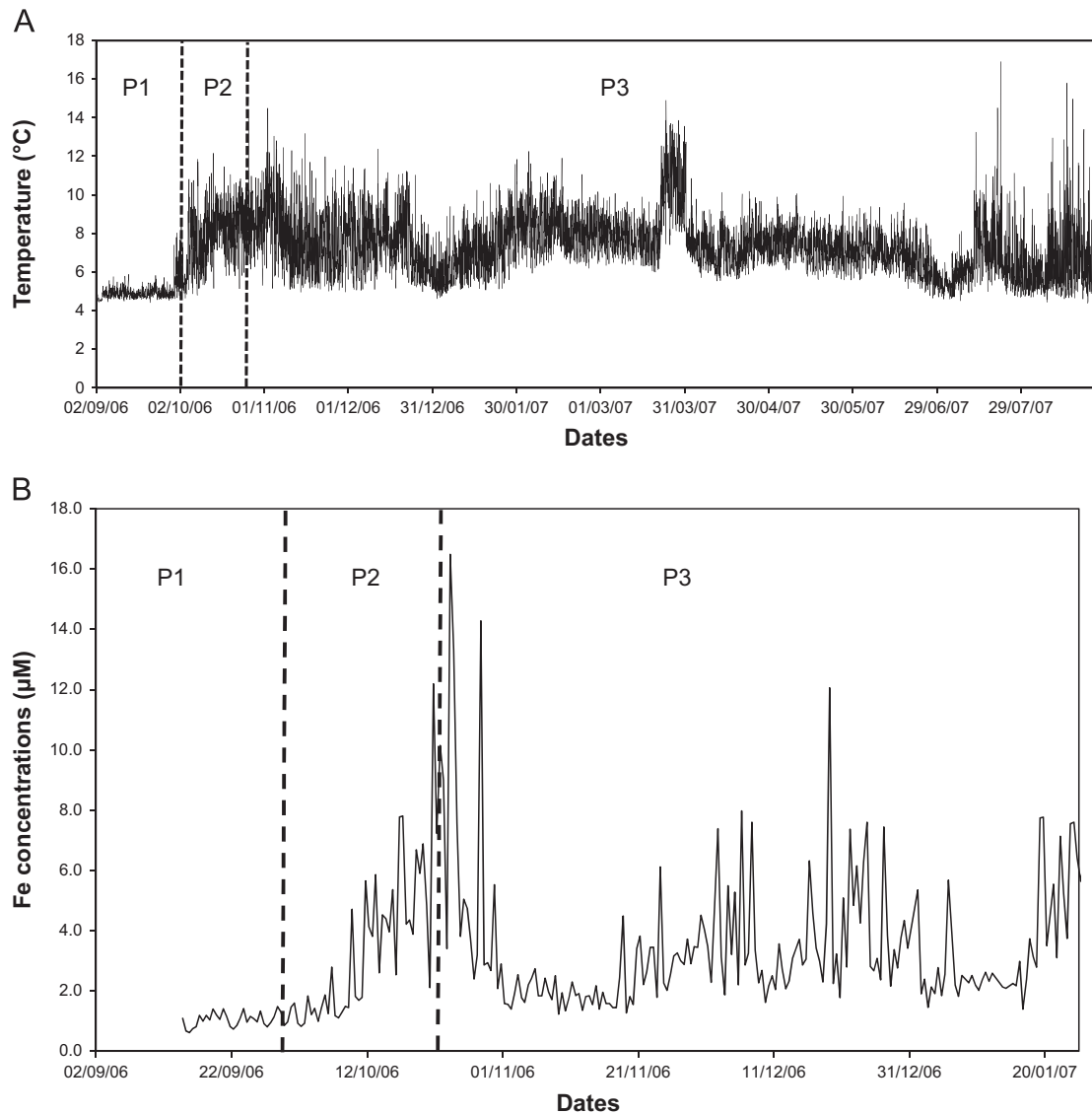


Fig. 4. Overview of the temperature (A) and Fe (B) data available and analysed. P1 represents the values measured on the *Bathymodiolus azoricus* mussel assemblage before probe displacement (day 0 to 25 for T °C and day 10 to 25 for Fe, indicated by the dotted line), P2 represents the remaining period for which video imagery was available (day 26 to 48) while P3 corresponds to the rest of the time series (day 48 to 405 for T °C and day 48 to 143 for Fe). The temperature series in (A) is 405 days long (04/09/2006 to 14/10/2007, 9720 h) and the Fe series in (B) is 133 days long (14/09/2006 to 25/01/2007, 3192 h).

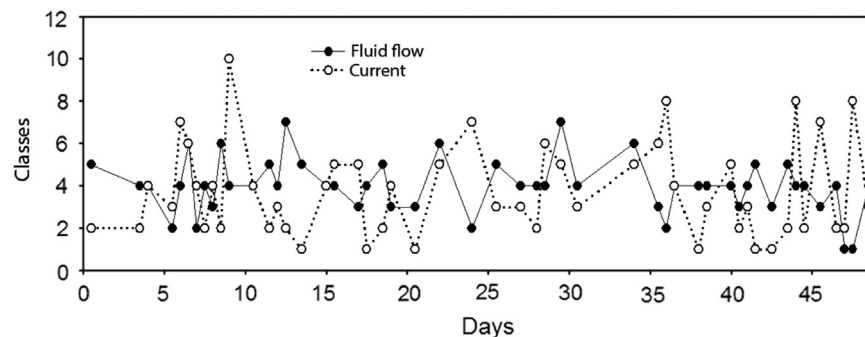


Fig. 5. Vertical (fluid flow) and horizontal (current) components of water movement measured through on-screen particle tracking, and then put classified into different classes (see Table 1 for details) based on the velocities observed during P1 (days 0–25) and P2 (days 26–48).

separately. The mean bottom seawater temperature in this area was 4.2 °C.

Vent-water flux (vertical particle velocities) and current speed (horizontal particle velocities) were assessed for the entire 48-day

time span (Fig. 5). They varied from 0 to 7.5 cm s⁻¹ for vent-water flux and from 0 to 10.5 cm s⁻¹ for current speed. They were coded into 10 classes (Table 1 for details). They were found to be negatively, but not significantly, correlated with each other

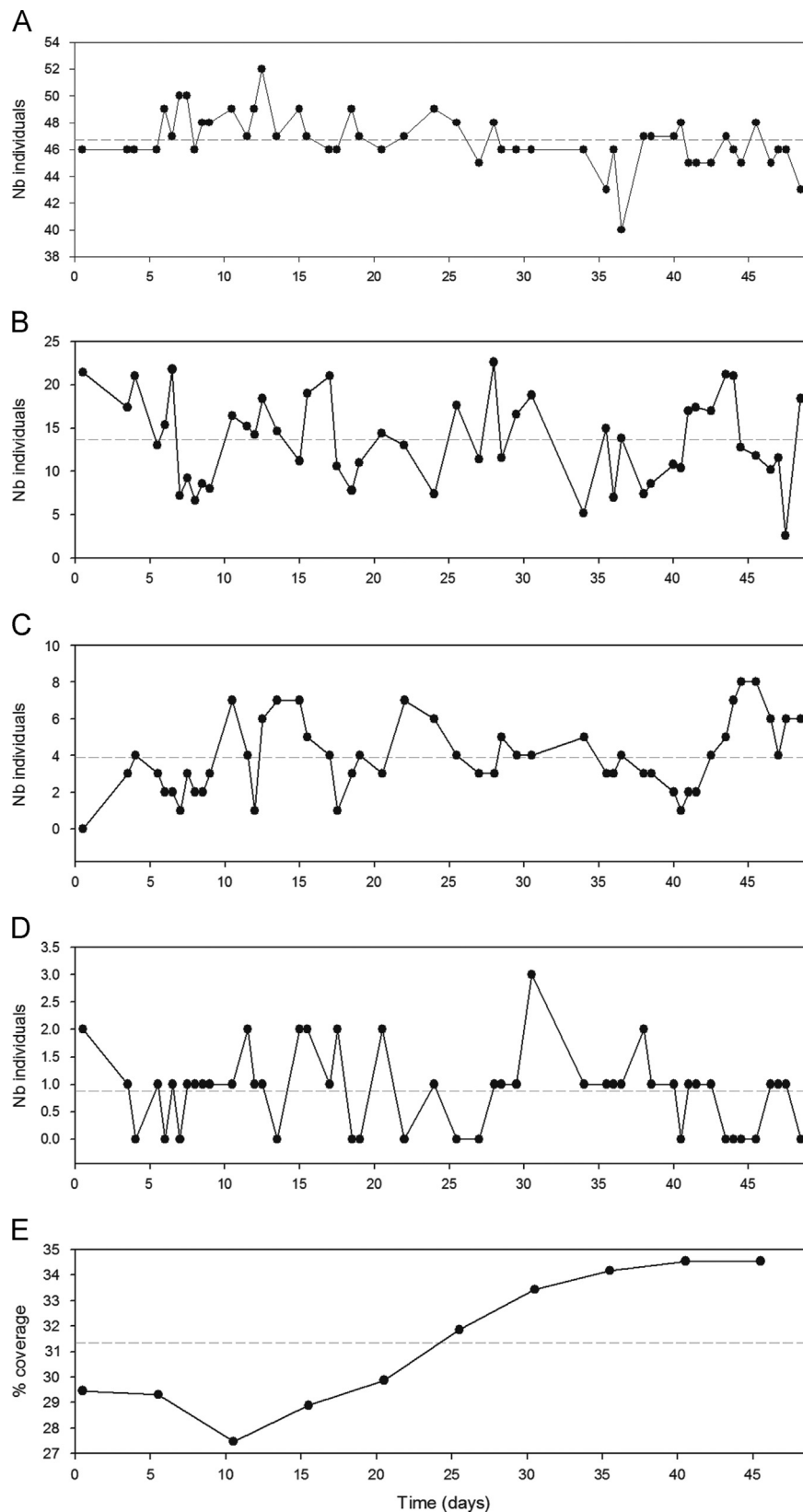


Fig. 6. Variation in faunal abundances: (A) *Bathymodiolus azoricus*, (B) *Mirocaris fortunata*, (C) *Pseudorimula midatlantica*, (D) *Segonzacia mesatlantica* and microbial coverage (E) as analysed from the video sequences, over the 48 days of video recording.

(Pearson correlation with permutation tests, $r = -0.2145955$, $p\text{-value} = 0.125$). Current directions (left, right) also tended to change between video recordings. However, no distinct trends were revealed.

Results of the correlogram analysis of the temperature measured on top of the mussel assemblage during time interval P1 (25 days) with a resolution of one measurement per hour showed a significant cyclic periodicity of $\sim 24\text{--}25$ h,

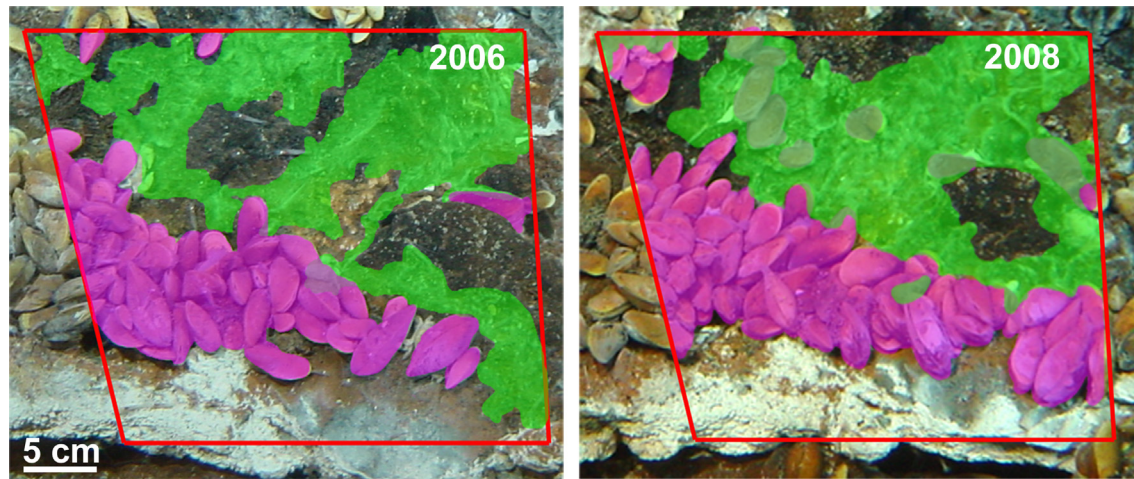


Fig. 7. Faunal coverage in 2006 and 2008 as observed on the close-ups. The red trapezoid-shape represents the camera view of TEMPO. The mussels are coloured in pink and the microbial mats are highlighted in green. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

corresponding to a diurnal/tidal frequency (Supplementary Fig. 1). A significant negative temporal correlation was found for a 12 h periodicity, corresponding to the semi-diurnal tidal periodicity (Fig. 6).

3.2.2. Fauna

3.2.2.1. Mussels—*Bathymodiolus azoricus*. Mussel abundance remained relatively constant over time in the video recordings (Fig. 6A). The number of individuals ranged from 40 to 52, although most (nearly 90%) of the recordings showed 45–49 mussels (Table 1). Nevertheless, the total area covered by the mussels decreased slightly (–1.5%), but expanded laterally (Fig. 7). During the timespan of the video recordings, one large individual died.

Overall, mussels showed a constant shell repositioning, apparently without breaking their byssus threads. Only one large movement (> 10 cm) by one individual was recorded. At any given time, in any given recording, approximately 37% of the mussels on the still image had their valves open, with a range of 16–53%. There were no significant differences in the number of open valves (log-transformed data) between the morning and evening video recordings (ANOVA *F*-test: *p*-value=0.384), but there were between the different recordings (*p*-value < 0.0001). Non-significant trends of negative correlations between the percentage of mussels with open valves and flux, as well as with crab abundances, were observed (Pearson correlations with permutation tests, $r = -0.17$, *p*-value > 0.1 and $r = -0.25$, *p*-value > 0.05, respectively).

Sudden valve closings were observed and were caused by shrimp (9.3%), limpets (0.5%) or polynoids (1%) approaching siphons and edges of mussel shells, a chimaeroid passing (22.3%), or crabs moving through the mussel bed (4.7%). There was no visible external trigger for the remaining 62.2% of the valve closings. For all events observed, reopening occurred within 10 s after the disturbance for 65% of the population.

3.2.2.2. Shrimp—*Mirocaris fortunata*. Shrimp abundances varied between and within video recordings, ranging from a minimum abundance of 2 individuals to a maximum of 27 individuals over the entire video recording period (Fig. 6B, Table 1). Shrimp abundances were positively and significantly correlated with vent-water flux (Pearson correlation with permutation test, $r = 0.35$, *p*-value < 0.05). There was a significant difference in shrimp abundance (log-transformed data) between the morning and evening (ANOVA with permutation test, $F = 7.75$,

p-value=0.0058), with a slightly higher abundance in the evening. There were also significant differences between observation recordings (*p*-value < 0.0001) although the factor(s) responsible for these differences remained unknown.

3.2.2.3. Limpets—*Pseudorimula midatlantica*. Abundances ranged from 0 to 8 visible individuals (Fig. 6C, Table 1). Only the individuals that could be unambiguously identified as *P. midatlantica* were counted. Hence, the abundance of this species is probably underestimated. Overall, there was an increase in *P. midatlantica* abundance over time at the beginning of the series, followed by a decrease from day 22 to day 40 and another increase towards the end. No significant links with the measured environmental variables could be established. Several individuals were seen moving around the mussel shells in the video recordings.

3.2.2.4. Crabs—*Segonzacia mesatlantica*. Abundances were low (up to 3 individuals, Fig. 6D). No links with other faunal or environmental variables could be established. Throughout the video recordings, crabs appeared to trigger valve closing in mussels when approaching them.

3.2.2.5. Polynoid polychaetes. A total of three polynoids were observed over all video recordings, probably all belonging to the species *Branchipolynoe seepensis*. Atlantic polynoid polychaete species are generally small in size (a few cm in length). Consequently, most of them were probably not visible in video stills. Therefore, these data cannot be considered representative.

3.2.2.6. Microbial mats. The percentage of the still image area covered by microbial mats increased steadily over the 48 days of the study (Fig. 6E). No significant correlation was observed between microbial mat coverage and temperature during the P1 and P2 periods (Pearson correlation with permutation tests, $r = 0.61$ and $r = 0.72$, respectively, *p*-values > 0.2). Moreover, there was no significant correlation between faunal abundance and microbial coverage.

3.3. Long-term changes in faunal distribution between 2006 and 2008

The surface area covered by the wide-angle photographs was 0.99 m² in 2006 and 0.87 m² in 2008. Our image analysis showed that there was a 11% increase in mussel coverage and a 4% increase

in microbial coverage between 2006 and 2008 (Table 2). The densities of the mussels also increased by $\sim 140 \text{ ind m}^{-2}$. Conversely, for shrimps and crabs, there was a decrease in densities from 42.3 ind m^{-2} to 30.9 ind m^{-2} for *M. fortunata* and from 6 ind m^{-2} to 3.4 ind m^{-2} for *S. mesatlantica*.

The delineated surface area of the close-up photographs (Fig. 7) was approximately the same ($\sim 0.1 \text{ m}^2$) for 2006 and 2008. Similar to what was observed in the wide-angle photographs, image analysis showed an increase ($\sim 12\%$) in mussel coverage along with an increase in mussel densities between the two years (Table 2). However, the increase in microbial coverage observed in the wide-angle photographs was not detectable when analysing the close-up photographs (Fig. 7). Rather, there was a very slight decrease in microbial cover ($\sim 0.14\%$; Table 2) and mussels seemed to have replaced the microbial mats in certain areas (Fig. 7). The decrease in shrimp and crabs, described above (Section 3.2.2), was also observed in the close-up photographs with a decrease of 145.4 ind m^{-2} for the former and 19.9 ind m^{-2} for the latter.

3.4. Long-term changes in environmental variables

3.4.1. Temperature

Over the period of nearly one year of data analysed (P3), temperature values varied between 4.02°C and 18.33°C for a mean of $7.20 \pm 1.6^\circ\text{C}$ (Fig. 4A). 46.5% (3977) recorded temperatures between 4.20 and 6.99°C followed by 47.2% (4036) in the 7.00 – 9.99°C range; 6% (517) were recorded between 10.00 and 13.90°C and only 0.2% (18) were over 14°C . No significant linear trend was detected, but variations in temperature values were observed with several incursions over 10°C (Fig. 4A).

Whittaker–Robinson periodogram analyses were carried out on the 8548 hourly temperature values (P3), allowing a first preliminary assessment and a selection of possible periods of interest. Subsequently, various periodograms from periods of 1 to 50 h, 1 week, 1 month, 3 months and finally almost 6 months were calculated. The main significant periods in temperature variation found within a two-month time span are shown in Fig. 8. These periods accounted for significant harmonics found at higher frequencies. The first significant values were for the 12 h and 24 h periods (Fig. 8). Additional significant periods were found between periods $T=634 \text{ h}$ and 708 h , which correspond to between 26.4 and 29.5 days. A more pronounced grouping of significant periods in temperature variation was found between $T=1265 \text{ h}$ and 1392 h , or 52.7 to 58 days. Several harmonics of basic periods (e.g. semi-diurnal and diurnal) are visible within this two-month period, while some harmonics of low-frequency periods (e.g. lunar cycle) were

found in the periodograms spanning 3 months and 6 months (not shown).

3.4.2. Iron concentrations (Fe)

The entire Fe data set contained 259 measurements representing 133 days with measurements taken every 12 h (Fig. 4B). The mean Fe concentration was $3.2 \pm 2.4 \mu\text{M}$ with a maximum value of $16.5 \mu\text{M}$ and a minimum value of $0.62 \mu\text{M}$ (close to the detection limit). No significant linear trends were detected but a few incursions over $5 \mu\text{M}$ were observed. The periodogram was constructed for 117 days of measurements (P2 and P3). Significant periods were found around 30 days ($T=60$), which may correspond to the lunar cycle. One significant harmonic value was found at 55.5 days (Fig. 9).

4. Discussion

The TEMPO observatory experiment described in this study lasted nearly 2 years, with different levels of data acquisition. To our knowledge, the analysis presented here is one of the longest integrated (faunal and environmental data) time series obtained to date in a hydrothermal ecosystem. It provides the first insights on day-to-day variations in a *B. azoricus* mussel assemblage. Additional observations supply valuable information on longer-term variations in temperature and Fe concentrations, although these were not coupled with image data. The methodological approach developed for this experiment can serve as an example to determine what kind of information can be extracted from deep-sea observatories, and to explore the links between variables acquired at different spatial and temporal scales.

4.1. Short-term changes

The significant increase in measured environmental factors between the first (P1) and second (P2) periods of the video recording was due to a slight displacement of the water sampling inlet by a chimaeroid fish. This increase illustrates the high heterogeneity within habitats in the vent ecosystem, even at the scale of a few centimetres (Sarrazin et al., 1999; Cuvelier et al., 2009). Temperature readings (mean $4.87 \pm 0.24^\circ\text{C}$) along with iron concentrations (mean $1.02 \pm 0.22 \mu\text{M}$) measured on the mussel assemblage (P1) were representative of a very limited input of hydrothermal fluids. The temperature variations are in the same range as those observed by Khripounoff et al. (2008) 10 m above the seafloor in the LS vent field, outside the vent influence. They are also similar to the lower end of the temperatures measured in

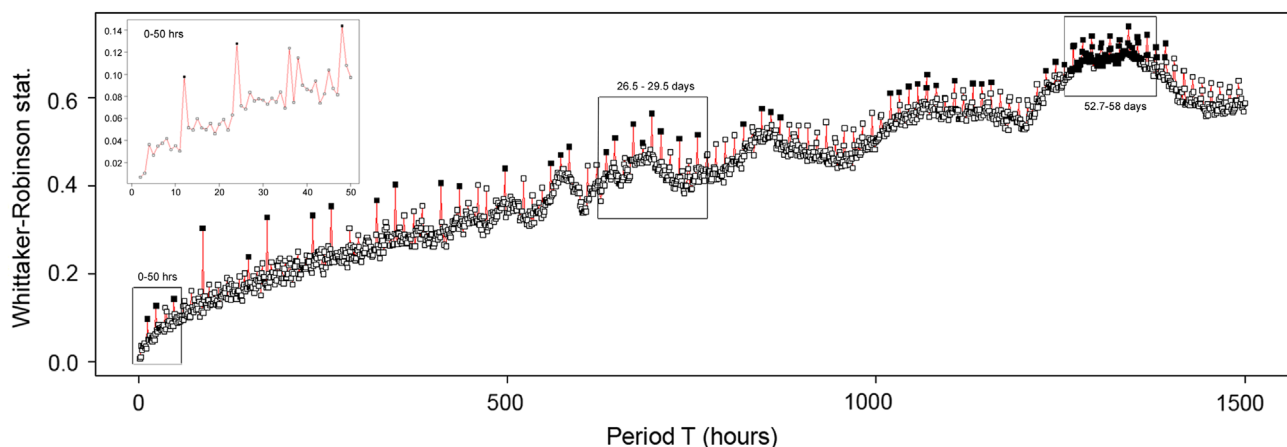


Fig. 8. Whittaker–Robinson periodogram computed for temperature, featuring periods comprised between 2 and 1500 h (approximately two months). Black squares indicate periods that are significant at the 5% level.

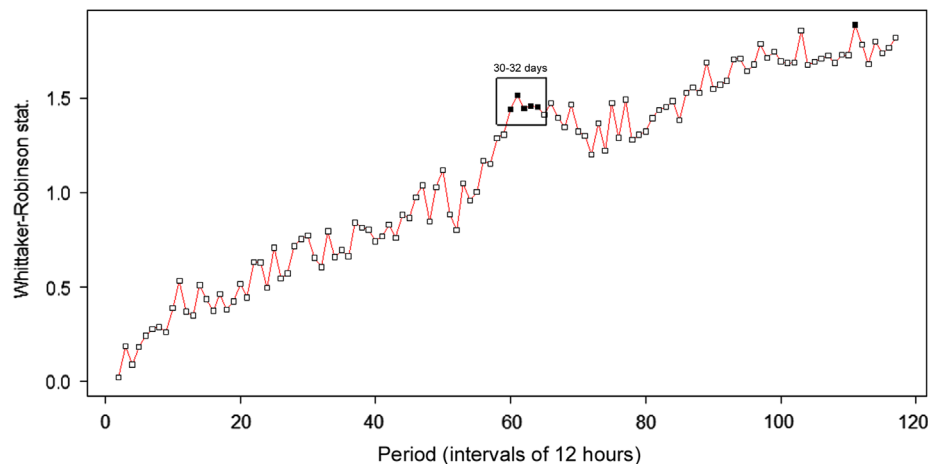


Fig. 9. Whittaker–Robinson periodogram computed for Fe concentrations measured at 12 h intervals for 117 days, featuring periods comprised between 2 and 117 time intervals of 12 h. The limit of the observation window of periodograms is the number of observation intervals divided by 2. Black squares indicate periods significant at the 5% level.

B. azoricus microhabitats on Eiffel Tower (De Busserolles et al., 2009; Cuvelier et al., 2009).

Patterns in temperature variation—Over the 25-day period (P1), the temperature time series showed a ~24–25 h cyclic periodicity and a negative temporal autocorrelation at 12 h. These values correspond to the tidal signal observed in the LS vent field at 25 h and to the semi-diurnal tidal oscillation at 12.30 h (Khrpounoff et al., 2000, 2008). They are also concordant with bottom pressure data acquired in the same area and for which significant periodicities matched the tidal signal and its harmonics (periodogram not shown; Ballu, unpublished data). For comparison, a 12.4 h periodicity in vent temperature time-series records has also been observed on the Juan de Fuca Ridge (Pacific Ocean), along with a 16–17 h inertial peak and a broadband peak centred at 4–5 days (Tivey et al., 2002). Variability in bottom temperatures and currents at LS also appear to be influenced, but to a lesser extent, by inertial oscillations (at about 20 h, Khrpounoff et al., 2008). Evidence for modulation of diffuse flow by tides has been provided by several temperature time-series measurements at hydrothermal vents (review by Tivey et al., 2002; Scheirer et al., 2006).

The potential mechanisms causing this tide-related variability include the modulation of seafloor and hydrostatic pressure fields by ocean tides, modulation of horizontal bottom currents by tides and solid Earth tide deformations (Schultz and Elderfield, 1997; Davis and Becker, 1999). While time-series records from low-temperature diffuse flow emissions indicate modulation of temperature by tidally induced changes in bottom currents (Little et al., 1988), high-temperature, high-flow vents (smokers) do not exhibit this tidal variability (Fornari et al., 1998; Tivey et al., 2002), suggesting that areas of higher fluid flow are less influenced by tides or that stronger flow variations may mask the tidal signal.

Links between faunal distribution and environmental conditions—Tidal cycles may have an impact on vent communities by modifying the degree of mixing of hydrothermal fluids with seawater, particularly in the near-bottom benthic boundary layer (BBL). Vent communities found at the BBL may be modified by rapid changes in tidal current direction and speed, inducing variation in temperature and related environmental conditions (Sarradin et al., 2009). Therefore, as the current speed varies between flood and ebb tides, the BBL shifts from a situation where the diffuse vent fluids are swept laterally along the seafloor towards one where plumes rise as a result of their buoyancy (Hautala et al., 2012). Visual observations of particle movements in our video images support this hypothesis: the particles flowed laterally when the

tidal current dominated and rose when the hydrothermal flux prevailed. Semi-diurnal variations of water flow and diurnal fluctuations of suspended particle loads have also been reported during a 6 day deployment on the Juan de Fuca Ridge (Johnson and Tunncliffe, 1985). Although not observed in our data, temporal variation in hydrodynamic processes may influence the availability of oxygen, chemicals and food resources for the fauna and can have significant effects on biological communities (Sarrazin et al., 1999; De Busserolles et al., 2009).

Little information and data on the effects of “moderate” environmental variation on the hydrothermal fauna are available for vent ecosystems. Several studies suggested that there is a strong link between faunal distribution, population dynamics and hydrothermal environmental conditions (Sarrazin et al., 1999, 2006; Govenar and Fisher, 2007; Cuvelier et al., 2009; Ivanenko et al., 2012; Sen et al., 2013), supporting the idea that the fauna respond quickly to “abiotically challenging” environments (Girguis and Lee, 2006). Modifications in fluid flow may influence resource availability (De Busserolles et al., 2009; Beinart et al., 2012) by inducing changes in microbial production (Guezennec et al., 1998; Sievert et al., 2000) and/or the abundance of symbionts (Halary et al., 2008; Robidart et al., 2011). Changes in fluid flow may also influence metal bioavailability (Cosson et al., 2008; Sarradin et al., 2009) and radionuclide exposure (Charmasson et al., 2009). Therefore, even moderate changes in hydrothermal habitats are expected to lead to a rapid response of the hydrothermal fauna, driven by their individual needs and tolerance.

In our study, the abundances of *B. azoricus* mussels and *S. mesatlantica* crabs were quite stable over time, reflecting the relative stability of environmental conditions during the 48-day video monitoring period. The abundances of *M. fortunata* shrimp varied with time and were significantly correlated with variations in hydrothermal fluid flow. A video camera deployed on the Trans-Atlantic Geotraverse (TAG) hydrothermal edifice (on the MAR) recorded an increase in shrimp densities, concordant with a local increase in temperature (Copley et al., 1999). The positive relationship of this species with the intensity of hydrothermal emissions (and temperature) is consistent with its distribution in the vicinity of active diffusers, in thermal conditions ranging from 2 to 25 °C (Segonzac, 1992; Gebruk et al., 1997; Polz et al., 1998; Van Dover et al., 1996; Desbruyères et al., 2001; Copley et al., 2007). Spatial distribution of *M. fortunata* shrimp can be explained by their nutritional requirements as they may feed on species relying on free-living bacteria (Segonzac et al., 1993; Gebruk et al., 2000; Colaço et al., 2002). Their high $\delta^{15}\text{N}$ values support the hypothesis

that they may be predators of bacterivorous and scavenger species (De Busserolles et al., 2009).

As in the case of most of the studied species, the abundance of *P. midatlantica* limpets varied through time, but no links could be established with environmental conditions. Similarly, no correlation between the abundance of buccinid gastropods and fluid temperature was observed on the Juan de Fuca Ridge (Martell et al., 2002). A significant increase in microbial cover was noticeable from day 10 to the end of the video recording period. A link with variation in hydrothermal fluid inputs was suspected, but this hypothesis was not statistically supported. Finally, although no significant influence of the tides was observed on the fauna, it is likely that physiological processes and species activities are influenced by these periodic variations. Longer time series, coupling video recordings and environmental data, are needed to test this hypothesis. Other physical and chemical data (current measurements as well as oxygen, sulphide and methane concentrations) would be useful additions to time-series analyses.

Role of catastrophic events—With the exception of the chimera-oid passage, which affected our data recording, no catastrophic event was observed during the 48-day period. Chimney collapses and landslides are frequent in the hydrothermal environment and can have significant destructive impacts on faunal communities (Johnson and Tunnicliffe, 1988; Tunnicliffe, 1991; Sarrazin et al., 1997). Our most recent TEMPO time series (2011) captured the growth of a small 4 cm chimney, but no immediate or visible effect was noticeable on the surrounding fauna (Sarrazin et al., unpublished data). Conversely, one of the rare continuous video records in the vent environment (26 days in 1986) filmed the growth and collapse of small anhydrite chimneys that caused the death of about 44% of the *Ridgeia piscesae* tubeworm (siboglinid polychaetes) community on the Axial volcano (northern East Pacific Rise; Tunnicliffe and Juniper, 1990). Mid-ocean ridge volcanic activity can also have significant effects on hydrothermal emissions, not only affecting areas of diffuse venting but also microbial coverage, as observed in 2001 during a major magmatic dike intrusion on LS (Dziak et al., 2004). Even though seismic activity is continuously recorded in the LS region through the EMSO-Açores MoMAR observatory (Cannat et al., unpublished data), its magnitude over the past decade appear to be too low to cause visible impacts on the geological structures and, consequently, on the mussel communities at large scales (Cuvelier et al., 2011b).

4.2. Long-term changes

Environmental conditions—During this study, temperature varied between ~4 and 16.9 °C in the study area. Significant periodicities in temperature were found, closely corresponding to the tidal (diurnal 24 h 50 min and semi-diurnal 12 h 25 min), lunar (a lunar month is about 29.53 days) and two lunar (52.7–58 days) cycles. Several harmonics of basic and low-frequency periods were also found in the longer periodograms. For Fe concentrations, only periodicities linked to the lunar cycle (30 and 55.5 days) were found. Longer time series as well as higher-frequency measurements, will be necessary to pinpoint significant periods.

Faunal changes—No drastic faunal changes occurred between the two years of the study. A slight increase in mussel and microbial coverage was observed between 2006 and 2008. Mussel densities also increased while those of shrimp and crabs decreased. With the exception of microbial coverage, similar patterns were observed in the close-up and wide-angle images, suggesting that the results obtained by a camera with a limited “observation” surface can be supplemented with observations at broader spatial scale. Individual growth rates could not be estimated, although this information would have been useful to better understand their relationships with variation in environmental conditions. Two recent studies have shown

that *Bathymodiolus* growth rates exhibit tide-related variability (Schone and Giere, 2005; Nedoncelle et al., 2013), possibly reflecting the variability of the mixing ratio between hydrothermal fluids and sea water and subsequently their influence on energy resources for symbionts (Nedoncelle et al., 2013). The addition of a laser grid on the camera could help us estimate growth dynamics from video images, although it would be a challenge to distinguish individuals without marking them.

4.3. Behavioural observations

To date, only a few studies have addressed behavioural issues in response to short-term variation in hydrothermal conditions in vent ecosystems (Tunnicliffe et al., 1990; Grelon et al., 2006) and only rare observations of species interactions are available. Clearly, continuous video monitoring associated with environmental sensing is a promising avenue of research to collect quantitative information on rates of change, biological rhythms and species interactions in these remote ecosystems. *B. azoricus* mussels show constant shell repositioning, but only one individual moved as far as 10 cm from its original position. At all times, about 37% of the mussels had their valves open, but no link with environmental conditions or the presence of other fauna could be established yet. Some mussels were observed reacting to the surrounding fauna by closing their valves when a contact was made. This immediate response to tactile stimuli, also observed in vent tubeworms (Tunnicliffe et al., 1990), suggests a protective mechanism against predators.

The *M. fortunata* shrimp were very active on the substrate. They appeared to be particularly attracted to the presence of diffuse venting and their densities varied with respect to changes in fluid flow. As suggested above, their higher occurrence in areas of stronger fluid emission may be linked to the presence of increased food sources. For example, Sievert et al. (2000) showed an increase in the abundance of microorganisms along a thermal gradient, indicating that microbial activity is stimulated by high temperatures and vent fluid flow. Similarly, Guezennec et al. (1998) observed a clear influence of fluid flow intensity on the development of biofilms at vents.

Very few direct interactions were observed between the vent species studied here, although aggressive behaviour was sporadically observed between crabs and shrimp. On a few occasions, the crabs chased the shrimp by moving towards them and displaying their claws, but these movements did not result in catching shrimp, suggesting that this behaviour was more territorial than predatory. Finally, although not significant, there was a negative correlation between the presence of vent gastropods and microbial coverage. We suggest that this may reflect grazing activity, with areas of abundant gastropod densities being cleaned of bacterial mats (De Busserolles et al., 2009). The acquisition of longer faunal time series will bring more insight into specific aspects of species behaviour, possibly leading to a better understanding of other important biological factors, such as growth and mortality.

5. Conclusions

Hydrothermal faunal assemblages at the LS vent field on the MAR are far more stable than anticipated and the relative steadiness of environmental factors was a surprise in an ecosystem characterised by extreme abiotic conditions. A key finding of this study is that the vent fauna of the filmed assemblage appear to be present in quite stable microhabitats, characterised by low hydrothermal inputs, where temperatures rarely exceed 20 °C.

The major limitation of our study arises from the fact that our analysis is based on a single faunal assemblage with only a few environmental measurements taken at small spatial scale, which is obviously not sufficient to describe the complexity of hydrothermal ecosystems. Although the observations made via a single deep-sea observatory are limited in spatial extent, they bring fundamental ecological insights into the dynamics of vent communities to which we did not have access previously. As shown by our long-term results, extrapolated from photographs taken in 2006 and 2008, these spatially-limited temporal observations may be supplemented with broader-scale video images repeatedly acquired by submersibles.

Recommendations for future work include the increase in spatial resolution of continuous temperature measurements (used as a proxy for hydrothermal inputs), which are essential to capture the small-scale heterogeneity of the habitat (2- or 3D mapping, Rinke and Lee, 2009). The acquisition of video data should be performed in triplicate (i.e. three cameras on three assemblages) and complemented by periodic ROV video transects at the edifice scale. Temporal studies should be designed to address a specific aspect of species behaviour, with the acquisition of higher-frequency data and continuous monitoring of key environmental factors. Finally, as all organisms are not visible on the image, the fauna associated with an assemblage similar to the filmed assemblage, should be sampled and its habitat characterised to supplement the data acquired by the observatory, providing an accurate portrait of the biodiversity.

In the near future, assessment of the effects of larger-scale environmental factors (such as seismicity, seafloor deformation, chemical variations, currents) on local environmental conditions as well as on the structure of vent communities is planned, using the integrated data sets acquired through the EMSO-Açores MoMAR deep-sea observatory deployed since 2010 (Cannat et al., 2011).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2014.04.004>.

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