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Characterization of vent fauna at three hydrothermal vent fields on the Southwest Indian Ridge: Implications for biogeography and interannual dynamics on ultraslow-spreading ridges

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ABSTRACT

The Southwest Indian Ridge (SWIR) is an important section of the global mid-ocean ridge system providing a corridor for dispersion of vent fauna between the Pacific and Atlantic Oceans. However, very few studies focusing on the biodiversity and biogeography of this region have been performed. To better understand the biological baseline and biogeography of vent fields on SWIR, we have described the faunal assemblages at three hydrothermal fields on SWIR, the biogeographical relationships among the three fields and fields on neighboring ridges as well as community dynamics at Longqi on a short time-scale (3 years). Communities at two fields, Duanqiao and Tiancheng, were reported for the first time, and the Longqi community was characterized more comprehensively. Collected specimens, videos and images were examined and taxa identification was conducted by both morphological and molecular approaches (cytochrome oxidase I (COI) or 16 S ribosomal RNA gene). In total, 39 species were recorded, 18 of which were reported from SWIR for the first time. According to the multivariate analysis of occurrence of fauna from 16 vent fields on four ridge systems, the SWIR vent sites were generally more similar to Central Indian Ridge. Within Indian Ocean, Longqi and Duanqiao formed a subcluster, which appeared to be intermediate between the Central Indian Ridge, Mid-Atlantic Ridge and East Scotia Ridge. Distinct faunal zonation was described at Tiancheng and Longqi. Comparison of vent fauna discovered in 2011 and 2014/2015 revealed an interannual constancy in faunal zonation on most vents at Longqi, except DFF1 chimney, which displayed a successional change from an early stage featuring high-temperature venting and low species diversity, to a more mature stage characterized by diffuse fluid and more colonized taxa. Thus, the present study is the first interannual variation study on the ultra-slow spreading ridges, and will expand our understanding of biodiversity and biogeography of vent fields on SWIR.

1. Introduction

Deep-sea hydrothermal vents are extreme habitats, supporting dense fauna communities at intervals along the globe-encircling Mid-Ocean Ridges. The fragmented and unstable environment constrains the vent fauna to discrete habitats separated by barriers, resulting in a distinct spatial pattern (Ramirez-Llodra et al., 2007). Based on several decades of exploration and continuing accumulation of data, several biogeographic provinces have been identified in Pacific, Atlantic, Indian and Southern Ocean by comparing vent faunal composition at global scale (Bachraty et al., 2009; Moalic et al., 2012; Rogers et al., 2012). However, these results usually give inconsistent conclusions of vent biogeography for those regions with low survey effort, such as the Indian Ocean (Bachraty et al., 2009; Moalic et al., 2012; Rogers et al., 2012). Improved sampling of hydrothermal communities in these regions will shed new light on the understanding of the biogeography of chemosynthetic fauna.

Vicariance and dispersal are two main biological processes shaping biogeography (Tyler and Young, 2003; Vrijenhoek, 2010). Geological, chemical, and hydrographic factors that obstruct larval dispersal and result in vicariance events are called dispersal barriers; for example a microplate that interrupts the gene flow of vent organisms along ridge

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(Hurtado et al., 2004; Won et al., 2003). Factors that facilitate organismal dispersal are known as corridors, like the mid-ocean ridges in Indian Ocean (IR) (Watanabe and Beedessee, 2015) which connect the Mid-Atlantic Ridge (MAR) with Western Pacific (WP) fields. The IR is hypothesized to provide a pathway for taxa exchange between fields of the WP and MAR (German et al., 1998). However, because of its inaccessibility, most vent fields on the IR are unexplored and the fauna are still largely unknown.

The hydrothermal vent fauna in Indian Ocean was entirely unknown until the discovery of Kairei vent field on the Central Indian Ridge (CIR) in 2000 (Hashimoto et al., 2001). Shortly after that, a second vent field in Indian Ocean, Edmond, was discovered located about 160-km NNW of Kairei vent field (Van Dover et al., 2001). Most species found at the two vent fields showed evolutionary affinities with vent fauna in western Pacific and northern Atlantic, with the exception of the peculiar "scaly-foot" gastropod, *Chrysomallon squamiferum* (Van Dover et al., 2001). These findings provided the first set of evidence to address the biogeographic relationships of vent fauna in Indian Ocean. Two new vent communities, Dodo and Solitaire, were discovered on the CIR by Nakamura et al. (2012). Vent fauna discovered on the CIR were reviewed and updated by Watanabe and Beedessee (2015).

Mid-Ocean Ridges are categorized according to their full spreading rates: superfast (> 120 mm/yr), fast (80–120 mm/yr), intermediate (50–80 mm/yr), slow (20–50 mm/yr) and ultraslow (< 20 mm/yr) (Karson et al., 2015). Hydrothermal vent habitats are considered to be more stable on ridges with slower spreading rates (Desbruyères et al., 2001; Ramirez-Llodra et al., 2007). Compared with the slow- to intermediate-spreading CIR (23–47 mm/yr) (Okino et al., 2015), the Southwest Indian Ridge (SWIR) spreads much more slowly (about 15 mm/yr), and represents the longest section of very slow to ultraslow-spreading seafloor in the global mid-ocean ridge systems (Dick et al., 2003; Husson et al., 2015). Only a few vent communities have been described from this type of ridge system in other regions. Vent fields have been reported from the ultra-slow spreading Mid-Cayman spreading center (Connelly et al., 2012), Gakkel Ridge (Edmonds et al., 2003) and Mohn Ridge (Pedersen et al., 2005). However, these are all geographically isolated from neighboring ridge systems (Plouviez et al., 2015; Schander et al., 2010), and no specialized vent fauna have been recorded from the latter two regions (Schander et al., 2010; Shank et al., 2007). Unlike those faunal islands isolated from the neighboring ridges, the SWIR is an essential part of the geographic connection between WP/CIR and MAR. Therefore, the SWIR provides a good case for studying vent fauna on ultra-slow spreading ridge, which is also an important corridor for faunal dispersal between oceans (German et al., 1998) and may play an important role in shaping vent biogeography at a global scale. In 2003, the SWIR was chosen as one of the specific regions of the ChEss project (Biogeography of Deep-Water Chemosynthetic Ecosystems) due to its geographic significance (German et al., 2011).

The Longqi hydrothermal field is the first confirmed active field on SWIR (Tao et al., 2011). It is located at a high mound at the depth of about 2755 m, where the ridge valley meets a small non-transform offset. The surrounding area is characterized by complex seafloor topography, wide spread exposed basalt, lack of sediment, long-lived detachment faults and significant thinned crust (Tao et al., 2014). Although its hydrothermal activities were firstly observed during a Chinese expedition, DY19 in 2007, vent-endemic organisms were not comprehensively surveyed until the British expedition, RRS James Cook JC67 in 2011 (Copley, 2011; Copley et al., 2016). Subsequent studies focused on community description and biogeography (Copley et al., 2016), new species identification (Chen et al., 2015a, c; Zhang et al., 2017; Zhou et al., 2017), phylogeny (Herrera et al., 2015; Roterman et al., 2013) and connectivity (Chen et al., 2015b). A total of 21 taxa of macrofauna and megafauna in the community were revealed, forming different types of faunal assemblages, and a considerable fraction of which were probably new to science (Copley et al., 2016). Biogeographic analysis allied the Longqi with fields on CIR (Copley et al., 2016). Phylogenetic analysis based on *Kiwa*, *Neolepas* and some other species showed historical or current connections between Longqi and fields on neighboring ridges, supporting the hypothesis that SWIR acts/acted as a corridor for vent fauna between MAR/East Scotia Ridge (ESR) and CIR & WP vent fields (Chen et al., 2015c; Herrera et al., 2015; Roterman et al., 2013; Vereshchaka et al., 2015). However, the previous studies did not characterize the physical and geochemical properties of the hydrothermal fluid, and the revealed level of biodiversity at Longqi was rather lower than that at Kairei and many other fields on neighboring ridges. This might result from less extensive surveying (Copley, 2011). In addition, data from only one field are insufficient to represent the whole ridge, which is over 8000 km in length (Tao et al., 2014). Thus, more survey efforts are needed to find new vent communities, and to reveal the biodiversity, biogeography and specificity of vent fauna on SWIR.

From December 2014 to March 2015, about 3 years after the cruise JC67, 10 dives using Human Operated Vehicle (HOV) *Jiaolong* were carried out at Longqi by Chinese scientists, which provided more data on the composition, temporal and spatial variation of the community. In addition, some basic features of the fluid (such as temperature, and fluid chemistry) were characterized, providing valuable information of the habitats (Ji et al., 2017).

Besides Longqi, Tao et al. (2014) located another two vent fields — Duanqiao and Tiancheng on SWIR. The basaltic-hosted Tiancheng was located at 63°32′E /27°57′S, at a depth of about 2760 m, between the Melville transform faults and the Rodriguez triple junction, southwest of the relict Mt. Jourdanne hydrothermal field (Tao et al., 2014). Water temperature and turbidity anomalies were observed, but no sulfide was spotted or collected (Tao et al., 2014). Little was known about the fauna until the first biological sampling was carried out by the HOV *Jiaolong* in December 2014, providing the first set of materials for ecological analysis.

The Duanqiao field was located at 50°24′E/37°39′S, at the depth of about 1732 m. This field lay on the ridge axial high surrounded by flat seafloor and wide spread silica-rich sediment (Tao et al., 2014). As no temperature or turbidity anomalies were detected, it was initially thought to be an inactive field or at a late stage of hydrothermal activity (Tao et al., 2014). The typical vent fauna, such as "scaly-foot" gastropod, mussels and stalked barnacles, was not collected until the cruise DY34 in 2015.

The present study aims to integrate published data and the results of the surveys by Chinese scientists on SWIR, to characterize the three vent communities, and to address the biological baseline and biogeography of vent fields on SWIR.

2. Materials and methods

2.1. Faunal sampling and surveying

Video survey and sampling at the Tiancheng (Figs. 1, 3A–E) and Longqi vent fields (Figs. 1, 4A–F, 5A–G, 6A–B) were undertaken during the Chinese Cruise DY35 from December 2014 to March 2015, using the HOV *Jiaolong* equipped with a 7-function manipulator. Ten dives were carried out at Longqi and one at Tiancheng. At Longqi, the majority of specimens were collected from 4 diffuse vents: DFF1, DFF2, DFF5 and DFF11 (Figs. 2, 5A–G), while the rest were collected from one inactive chimney, DFF9 (Figs. 2, 6A-B). Materials were obtained at the venting sites or their direct vicinities. The survey at Duanqiao vent field was performed during the Chinese Cruise DY34 in April 2015. The TV-Grab was used to sample the vent animals on the top of the chimney structure.

After collection, samples of vent invertebrates were fixed and preserved in 95% ethanol. Videos and images were examined to identify uncollected taxa (e.g., fish) and analyze faunal distribution. Most of the materials are deposited in the Second Institute of Oceanography, State