Indian Ocean Hydrothermal Systems: Seafloor Hydrothermal Activities, Physical and Chemical Characteristics of Hydrothermal Fluids, and Vent-Associated Biological Communities

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Abstract

In the nearly 40 years since the discovery of the deep-sea hydrothermal vent site at the Galápagos spreading center, more than 300 sites of high-temperature hydrothermal venting have been discovered and investigated around the world. Surprisingly, however, most of these sites are located in the Pacific and Atlantic Oceans, whereas only five hydrothermal vent sites have been discovered in the Indian Ocean. During the TAIGA project, we conducted four research cruises to investigate four of the five Indian Ocean hydrothermal vent sites (two of which were newly discovered during one of the TAIGA cruises) located along the Central Indian Ridge (CIR). The results of geological and geochemical analyses demonstrate wide variation in fluid chemistry, reflecting the diverse geological background of the CIR hydrothermal vent fields. Although the CIR is an intermediate-spreading ridge, the geological and geochemical features of the Kairei hydrothermal field appear to be similar to ultramafic rock-hosted hydrothermal fields found along the slow-spreading Mid-Atlantic Ridge (MAR). By contrast, the Dodo hydrothermal field shares similarities with the hydrothermal vent sites found along the fast-spreading East Pacific Rise. The Solitaire and Edmond hydrothermal fields are characterized by high pH and Cl levels, respectively, although the geological background underlying the unusual chemistry of their hydrothermal fluids is still uncertain. Additionally, extensive microbiological analyses of the Kairei hydrothermal vent site revealed that its microbial communities are affected by the chemical characteristics of the hydrothermal vent fluids. Macrofaunal analyses also revealed new faunal data for the Indian Ocean hydrothermal vents, including novel genera and families that are potentially indigenous to the Indian Ocean hydrothermal systems. In particular, the discovery and characterization of a new morphotype of "scaly-foot" gastropod raises the question of the mechanism and physiological role of iron sulfide mineralization. The results of our investigations extended knowledge of the Indian Ocean hydrothermal systems including geochemical variations of hydrothermal fluids, their relationships to the geological

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background, the biodiversity and biogeography of the hydrothermal vent-associated microbial and faunal communities. This, in turn, will provide important insight into the relationships among geological backgrounds, hydrothermal processes, and biological activities, not only at the Indian Ocean hydrothermal vents but also in global mid-ocean ridge hydrothermal systems.

12.1 Introduction

Since the discovery of deep-sea hydrothermal vents at the Galápagos Rift in 1977 (Corliss et al. 1979), mid-ocean ridge (MOR) hydrothermal systems have attracted attention as key phenomena driving the geochemical cycles of many elements and sustaining unique biological communities in the ocean. A number of geological, geochemical, and biological studies have been conducted at MOR hydrothermal vent sites, providing important insight into the effect of MOR hydrothermal activity on ocean chemistry (e.g., Edmond et al. 1979, 1982; Von Damm et al. 1985a, b; Palmer and Edmond 1989; Elderfield and Schultz 1996), the limit, origin, and early evolution of life (e.g., (Jannasch and Mottl 1985; Nealson et al. 2005; Takai et al. 2006; Takai 2011) as well as the diversity and connections among different biogeographical provinces of hydrothermal vent faunas (e.g., Van Dover et al. 2002; Bachraty et al. 2009; Vrijenhoek 2010). However, most of the hydrothermal vent sites discovered and investigated thus far are located in the Pacific and Atlantic Oceans (German and Von Damm 2004), whereas only a few hydrothermal fields have been identified in the Indian Ocean (Gamo et al. 2001; Hashimoto et al. 2001; Van Dover et al. 2001; Tao et al. 2012; Nakamura et al. 2012). Thus, the geological, geochemical, and biological features of the Indian Ocean hydrothermal system remain poorly understood, and it appears highly uncertain which features are common to global hydrothermal systems and which are unique to the Indian Ocean system.

From 2008 to 2013, an interdisciplinary project (the TAIGA project) focused on interactions between the lithosphere, hydrosphere, and biosphere through the fluid circulation system beneath the seafloor was pursued (Urabe et al. Chap. 1). In this project, the Indian Ocean hydrothermal system was recognized as a major target because, at the beginning of the project, the geological, geochemical, and biological features of the Indian Ocean hydrothermal vent sites were observed to be quite diverse, even though they are located within the quite limited area of the Central Indian Ridge (CIR). In addition, this diversity appeared to be driven by different linkages among geological, geochemical, and

biological features (Urabe et al. Chap. 1). During this project, four research cruises using the R/V *Yokosuka*, R/V *Hakuho-maru*, human-occupied vehicle (HOV) *Shinkai 6500*, and autonomous underwater vehicle (AUV) *r2D4* were conducted to investigate the hydrothermal systems of the Indian Ocean. The cruises successfully discovered and explored two new hydrothermal vent sites (the Dodo and Solitaire hydrothermal fields) along the CIR and obtained additional detailed information on the two previously known hydrothermal vent systems (Kairei and Edmond hydrothermal fields). In this paper, we summarize the results of the investigations conducted in these Indian Ocean hydrothermal systems.

12.2 The Four Indian Ocean Hydrothermal Vent Fields Studied in the TAIGA Project

The four hydrothermal vent fields situated along the CIR (the Dodo, Solitaire, Edmond, and Kairei fields) (Fig. 12.1) were studied in the TAIGA project. The Edmond and Kairei hydrothermal fields were discovered previously (Gamo et al. 2001; Hashimoto et al. 2001; Van Dover et al. 2001), whereas the Dodo and Solitaire hydrothermal fields were newly discovered during the TAIGA project (Nakamura et al. 2012). Geological settings and geochemical characteristics of the four hydrothermal vent fields are summarized in Table 12.1.

12.2.1 Dodo Hydrothermal Field

The Dodo hydrothermal field (18°20.1′S, 65°17.9′E; depth of 2,745 m) is located in the Dodo Great Lava Plain in the middle of CIR segment 16 (Fig. 12.2a) (Nakamura et al. 2012). In this field, the active vents are situated on the spreading axis (Fig. 12.2b), in contrast to the hydrothermal vents of the other three hydrothermal vent fields (Solitaire, Kairei, and Edmond), which are all located in the off-axis region. The existence of seafloor hydrothermal activity in
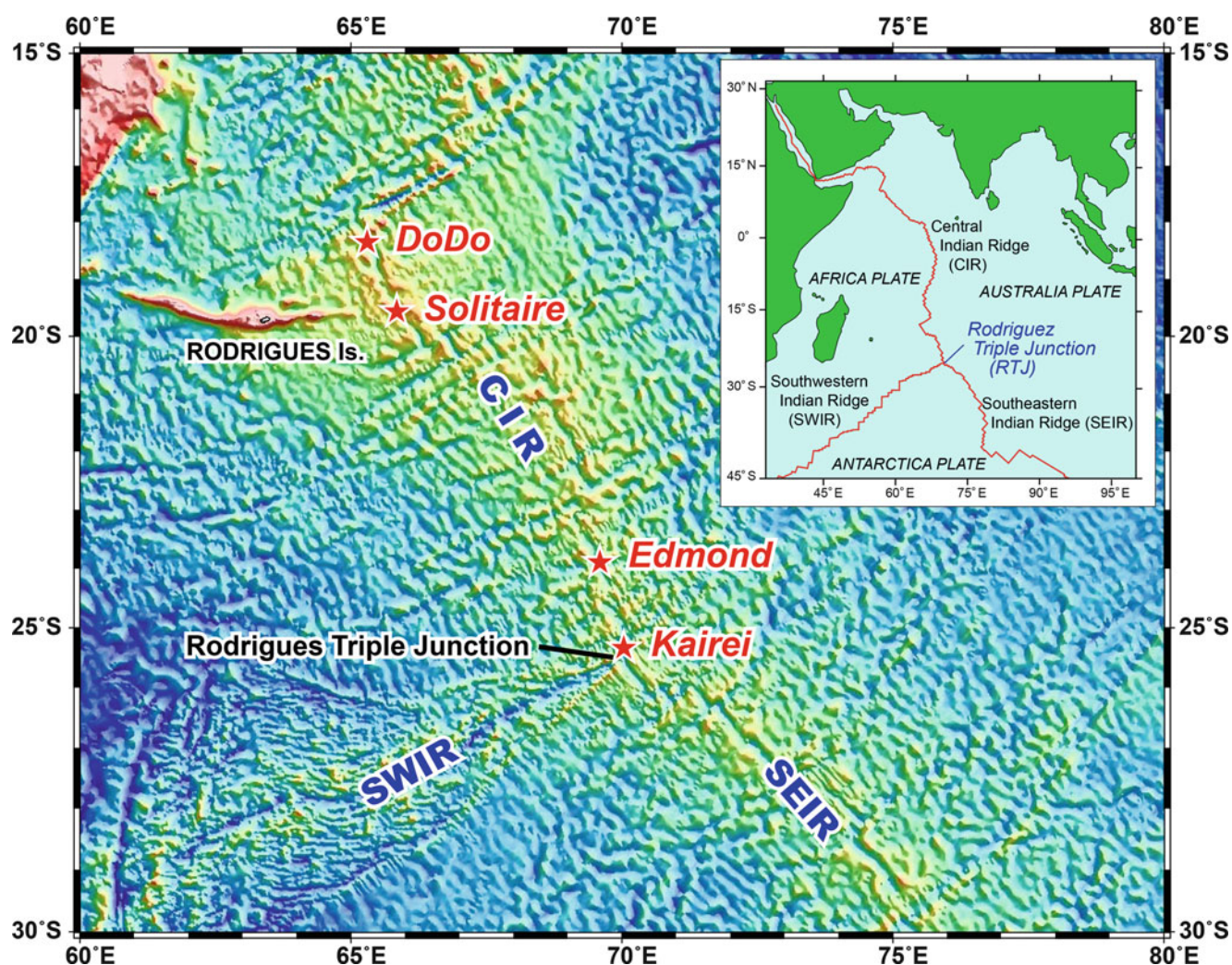
Fig. 12.1 Index map showing the locations of the four hydrothermal vent fields (Dodo, Solitaire, Edmond, and Kairei) along the Central Indian Ridge (CIR)

Table 12.1 Location, host-rock type, and hydrothermal fluid chemistry of the four CIR hydrothermal vent fields

Hydrothermal field	Dodo	Solitaire	Edmond	Kairei
Location	CIR-segment16 on-axis	CIR-segment15 off-axis	CIR-segment4 off-axis	CIR-segment1 off-axis
Host-rock type	E-MORB	E-MORB	N-MORB	Troctolite + D-MORB
Depth (m)	2,745	2,606	3,270–3,303	2,420–2,452
Temperature (°C)	356	296	382	369
pH (25 °C)	3.2	4.8	≤ 2.97–3.3	3.35–3.60
Cl (mmol/L)	~680	~500	926–973	571–623
H_2 (mmol/L)	~2.4	0.46	0.0556–0.1116	2.48–8.50
CH_4 (mmol/L)	~0.02	~0.05	0.233–0.415	0.123–0.203
CO_2 (mmol/L)	~4	~8	7.19–15.8	4.53–10.1
References	1	1	2, 3	2, 3, 4

CIR central indian ridge, *MORB* mid-ocean ridge basalt, *E-MORB* enriched MORB, *N-MORB* normal MORB, *D-MORB* depleted MORB
1. Nakamura et al. (2012), 2. Gallant and Von Damm (2006), 3. Kumagai et al. (2008), 4. Van Dover et al. (2001)
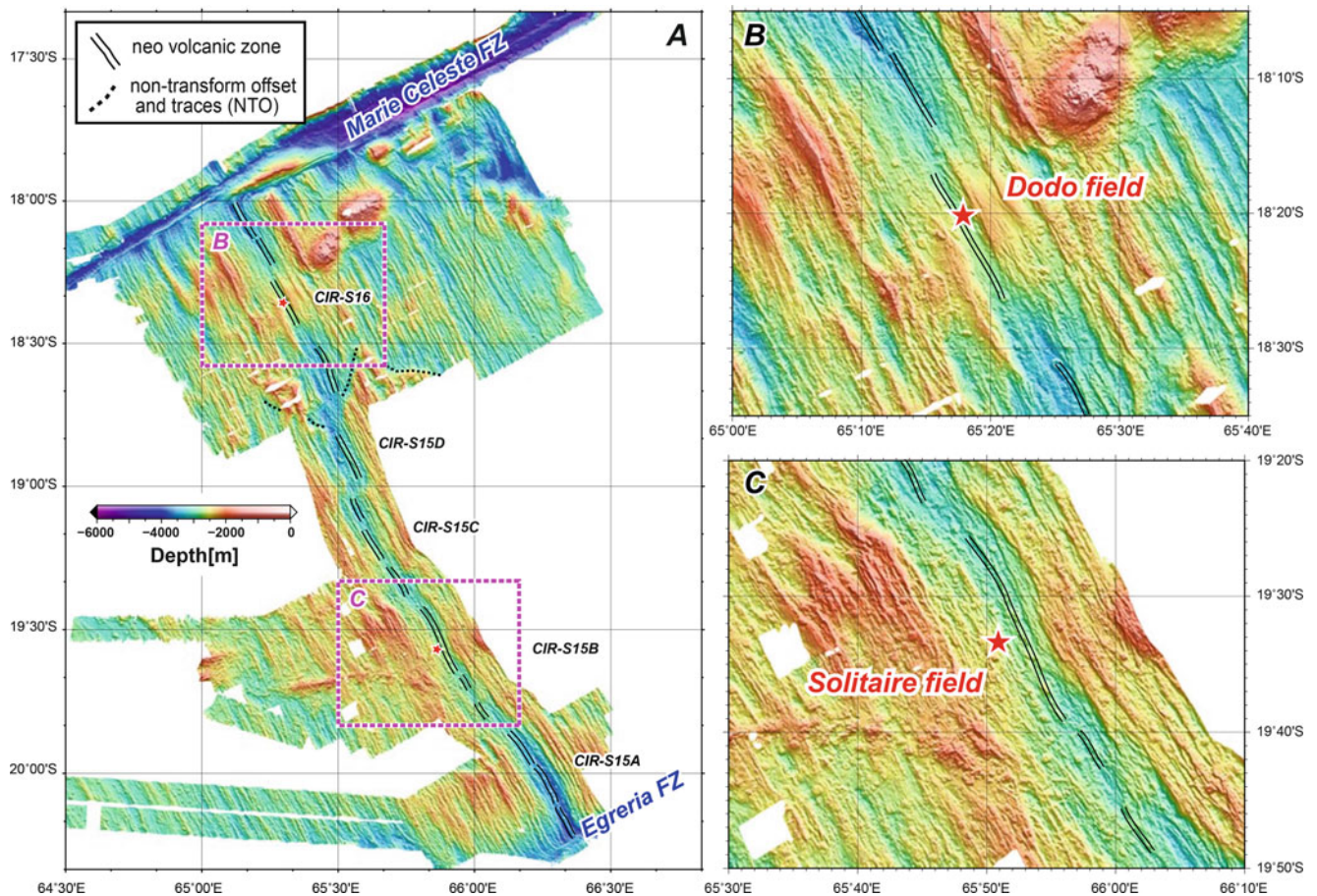
Fig. 12.2 (**a**) Bathymetric map of the Rodriguez segment area and detailed bathymetry maps around the (**b**) Dodo and (**c**) Solitaire hydrothermal fields (after Okino et al. Chap. 11)

the area situated from 18–20°S on the CIR had been suggested by two previous surveys that detected hydrothermal anomalies in the water column (Jean-Baptiste et al. 1992; German et al. 2001). In December 2006, an extensive plume survey was conducted in the CIR region approximately 19°S during the KH 06–4 cruise on the R/V *Hakuho-maru* using vertical and tow-yo hydrocasts and the AUV *r2D4*. During the survey, evident plume signatures of hydrothermally derived CH_4, Mn, and ^{3}He abundance anomalies and a light transmission signal anomaly were detected in a ridge axial valley of the CIR at 18°20'S within the Dodo Great Lava Plain (Kawagucci et al. 2008). Three years later, in October 2009, detailed observations of the seafloor were performed using a deep-tow camera and the HOV *Shinkai 6500* during the YK 09–13 cruise on the R/V *Yokosuka*. During the cruise, a new hydrothermal field, named the Dodo hydrothermal field, was discovered (Nakamura et al. 2012). The Dodo Great Lava Plain, hosting the Dodo hydrothermal field, is characterized by a flat, smooth seafloor covered with sheet flow lavas stretching over 10 km along the axis, suggestive of high production rates of basaltic melt. These

morphological features are similar to those of typical fast-spreading ridges, such as the East Pacific Rise (EPR), rather than that in the spreading centers of the other CIR segments characterized by intermediate spreading rates.

Hydrothermal fluid emissions were observed within a small area (~15 m in diameter) in which many small black smoker chimneys (less than 1 m in height) sprout directly from cracks in the basaltic sheet flow lava. Three main chimney sites were observed: Potsunen, Tsukushi-1, and Tsukushi-2, among which the most vigorous black smoker discharges were observed at the Tsukushi-2 chimney site (Fig. 12.3a). Clear, diffuse fluid flows, either from tiny chimneys or directly from cracks and crevices in the basaltic sheet flow lava, were also detected around the black smoker chimneys. In addition to the active chimneys, several inactive chimneys were found near the Tsukushi-2 chimney site. Interestingly, there are many brownish spots with a small, collapsed crater-like structure on the basaltic sheet flow lava surrounding the hydrothermal vent sites (Fig. 12.3b), and cracks or crevices in pillowed lava and in the interpillow spaces are also stained a brownish color (Fig. 12.3c). The stained area extends more than 50 m along the N–S axis and

Fig. 12.3 Photographs of (**a**) the Tsukushi-2 chimneys on basaltic sheet flow lava at the Dodo hydrothermal field; (**b**) a brownish spot in the collapsed sheet flow lava; (**c**) cracks and interpillow spaces stained a brownish color; (**d**) inactive chimneys at the Tsukushi-2 chimney site without any fauna present, observed at the Dodo hydrothermal field in 2013; (**e**) the Toukon-3 chimneys in the Solitaire hydrothermal field; (**f**) a diffuse flow area issuing clear fluids in the Solitaire hydrothermal field; (**g**) large black smoker chimneys at the Nura Nura vent site, in the Edmond hydrothermal field; and (**h**) a small black smoker chimney at the Kali vent site, in the Kairei hydrothermal field
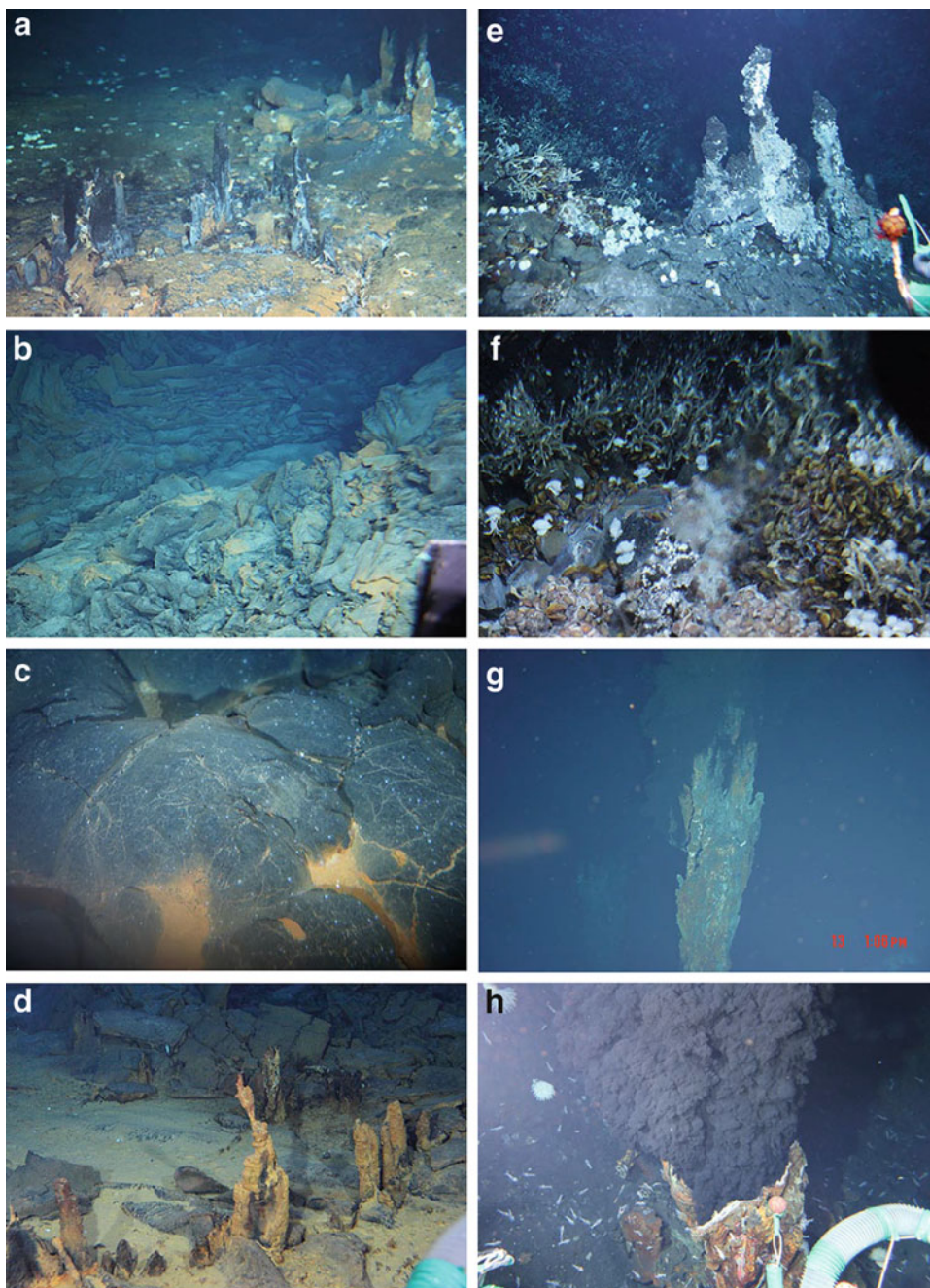

at least 200 m along the E–W axis. Recent observations made on the HOV *Shinkai 6500* in 2013 revealed that obvious hydrothermal fluid discharges at the Dodo field had stopped (Fig. 12.3d).

12.2.2 Solitaire Hydrothermal Field

The Solitaire hydrothermal field (19°33.413 S, 65°50.888 E; at a depth of 2,606 m) is located on the Roger plateau on the western ridge flank of CIR segment 15, at approximately 19°33′S (Fig. 12.2a), several kilometers from the ridge axis (Fig. 12.2c) (Nakamura et al. 2012). The location of the Solitaire hydrothermal field is approximately 150 km south of the Dodo hydrothermal field. As for the Dodo field, during the KH 06–4 cruise on the R/V *Hakuho-maru* in December 2006, an extensive plume survey was conducted using vertical and tow-yo hydrocasts and the AUV *r2D4* in the area where the existence of hydrothermal activity had been suggested by previous studies (Jean-Baptiste et al. 1992; German et al. 2001). During the survey, evident plume signatures of anomalies hydrothermally derived CH_4, Mn
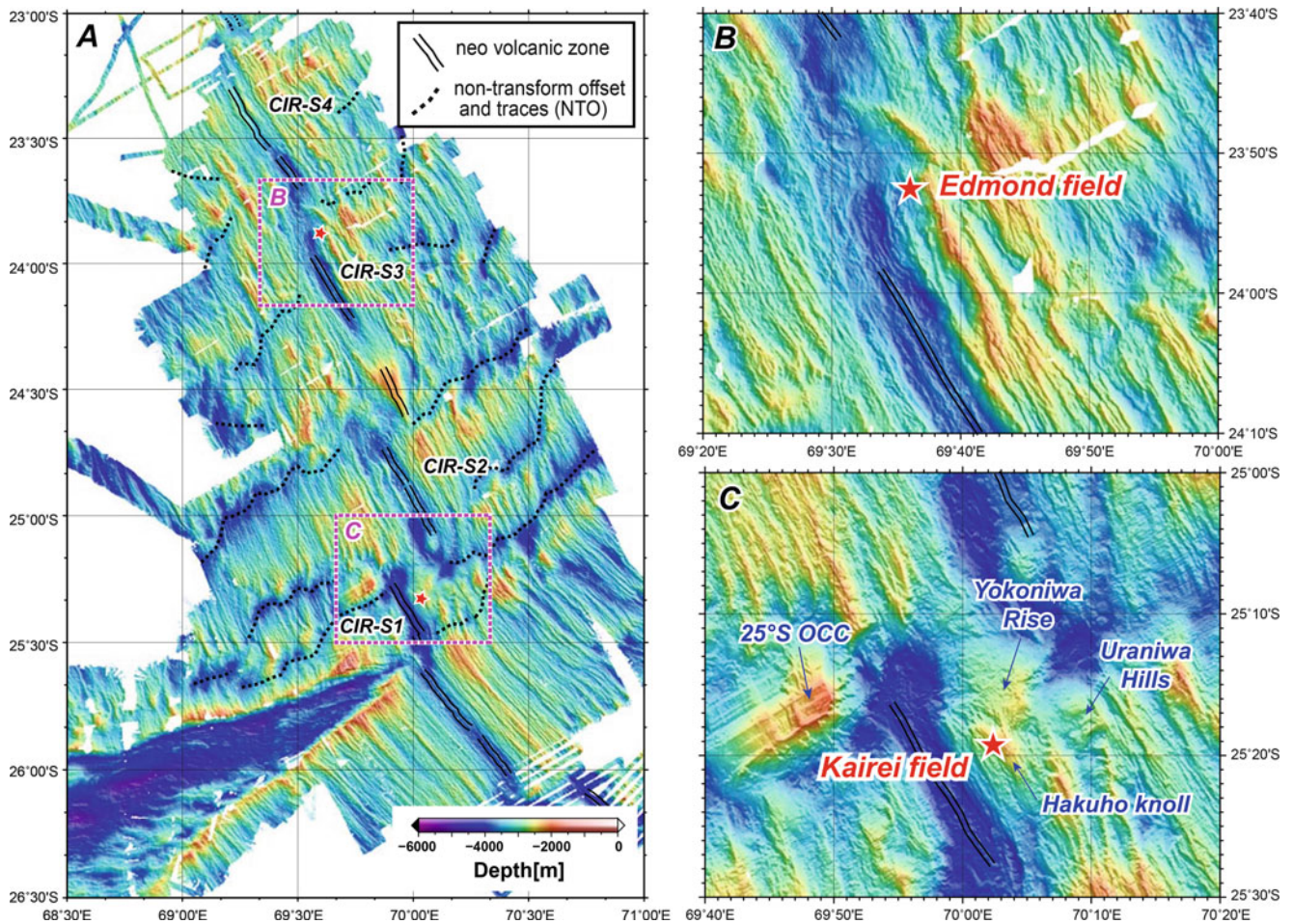
Fig. 12.4 (**a**) Bathymetric map of the CIR-S1 to S4 area and detailed bathymetry maps around the (**b**) Edmond and (**c**) Kairei hydrothermal fields (after Okino et al. Chap. 11).

and ^{3}He abundance and a light transmission signal anomaly were detected along the western off-axis slope of the CIR, at 19°34′S, on the Roger Plateau (Kawagucci et al. 2008). Finally, in October 2009, during the YK 09–13 cruise of the R/V *Yokosuka*, a new seafloor hydrothermal vent site, designated the Solitaire hydrothermal field, was discovered through deep-tow camera surveys and HOV dive observations.

The Solitaire field is situated on the talus at the base of a NNW-SSE-trending steep cliff regarded as a fault scarp. The area of hydrothermal fluid emissions was found to be approximately 50 × 50 m, which is significantly larger than the active venting area of the Dodo hydrothermal field but slightly smaller than those of the Kairei and Edmond hydrothermal fields. In the Solitaire hydrothermal field, three major chimney sites (Toukon-3, Tenkoji, and Liger) were identified. The observed chimneys were less than 5 m in height, with small mounds at their feet (Fig. 12.3e). Although several black smoker discharges were observed at the top of the Toukon-3 chimneys, most of the identified hydrothermal

emissions in the Solitaire field consist of clear fluids. In particular, numerous diffuse flow areas issuing clear fluids directly from the talus are a characteristic feature of the Solitaire field (Fig. 12.3f). It is likely that the extensive occurrence of thick and highly permeable talus results in a broad range of mixing zones in the subseafloor environments between the upwelling hydrothermal fluids and the infiltrated seawater.

12.2.3 Edmond Hydrothermal Field

The Edmond hydrothermal field (23°52.68′S, 69°35.80′E; at depths of 3,290–3,320 m) is located at the northern end of CIR segment 3 (Fig. 12.4a) (Van Dover et al. 2001). The location of the Edmond hydrothermal field is approximately 1,000 km south of the Solitaire hydrothermal field. The presence of active seafloor vents in this region was suggested by the results of hydrothermal plume surveys conducted in the 1980s (Herzig and Plüger 1988; Plüger et al. 1990). In

April 2001, detailed geological investigations were conducted through near-bottom water-column surveys by an American research team using the R/V *Knorr* and the remotely operated vehicle (ROV) *Jason*. The investigation resulted in the successful discovery of a hydrothermal vent field in an off-axis region of CIR segment 3 (Van Dover et al. 2001), where typical abyssal hills are observed (Kumagai et al. 2008) (Fig. 12.4b).

The main area of hydrothermal venting in the Edmond hydrothermal field covers ~100 × 60 m (Gallant and Von Damm 2006), which is larger than the other known CIR hydrothermal fields. The black smoker complexes are also larger (up to 35 m tall and 2 m in diameter; Gallant and Von Damm 2006) than any other known CIR hydrothermal field. The most vigorous black-smoker venting is located in discrete clusters of large chimneys at the Nura Nura vent site (Fig. 12.3g) (Kumagai et al. 2008). Similar to the Solitaire hydrothermal field, extensive areas of diffuse flows are present in the Edmond hydrothermal field, suggesting subseafloor seawater entrainment and mixing processes over a broad area. In addition to sulfide structures, orange-brown, iron oxyhydroxide sediments are also commonly observed around the Edmond hydrothermal field.

12.2.4 Kairei Hydrothermal Field

The Kairei hydrothermal field is located in the first segment of the CIR (25°19.23′S, 70°02.42′E; at a depth of 2,415–2,460 m) (Fig. 12.4a) (Gamo et al. 2001). The hydrothermal field was first recognized in 1993 through CTD hydrocasts and tow-yo surveys (Gamo et al. 1996) and was finally discovered by the ROV Kaiko in August 2000 as the first hydrothermal vent site in the Indian Ocean (Gamo et al. 2001). Based on the chemical characteristics of the detected hydrothermal vent fluids as well as basaltic rocks recovered in the vicinity of the hydrothermal vent field, the Kairei hydrothermal field was first recognized as a typical mid-ocean ridge basalt (MORB)-hosted hydrothermal system, despite the unusually high concentrations of H_2 found in its hydrothermal fluids (Gamo et al. 2001; Van Dover et al. 2001; Gallant and Von Damm 2006). However, subsequent bathymetric and visual observations performed using the R/V *Yokosuka* and HOV *Shinkai 6500* revealed that there are two well-defined oceanic core complex (OCC) structures (the 25°S OCC and Uraniwa Hills) consisting of peridotitic and gabbroic rocks within 20 km of the Kairei field (Kumagai et al. 2008) (Fig. 12.4c). More recent observations identified another peridotite-gabbro massif, designated the Yokoniwa Rise, just north of the Hakuho Knoll (Fig. 12.4c). Interestingly, it is generally accepted that OCCs occur only in slow- to ultra-slow-spreading ridges under magma-starved conditions (Escartin et al. 2003; Cannat et al.

2006), whereas the CIR has been classified as an intermediate-spreading ridge with a spreading speed of 47.5 mm/year (DeMets et al. 1994).

The main area of high-temperature vents extends for ~80 m along the rift wall and is ~40 m wide (Gamo et al. 2001; Gallant and Von Damm 2006). Several black smoker complexes with a maximum height of >10 m have been recognized in this area. The most vigorous black smoker discharges were observed at the Kali vent site (Fig. 12.3h) (Kumagai et al. 2008) in the westernmost part of the Kairei hydrothermal field. Although diffuse, lower-temperature flows along the sides and bases of black smoker chimneys are often detectable, broad areas of low-temperature simmering have not been observed in this hydrothermal field. In addition to the large active black smoker chimneys, large accumulations of weathered sulfides and inactive chimneys were also observed in this hydrothermal field.

12.3 Physical and Chemical Characteristics of Hydrothermal Fluids

In the Dodo hydrothermal field, the highest temperature measured was 356 °C, at the Tsukushi-2 chimney site. The lowest pH level of 3.2 was also recorded at this chimney site. These temperature and pH values are comparable with those of typical MOR black smoker fluids (German and Von Damm 2004). The Cl concentration in the hydrothermal fluid was found to be significantly (~20 %) enriched from that in seawater, suggesting subseafloor phase-separation and brine-phase enrichment. A notable feature of the Dodo hydrothermal fluids is their unusually high concentration of H_2 (>2 mmol/L). Such high H_2 contents in hydrothermal fluids are more similar to those found in ultramafic rock-hosted hydrothermal fluids (e.g., in the Rainbow, Logatchev, and Kairei fields), rather than basalt-hosted fluids. However, the morphological features of the Dodo Great Lava Plane clearly suggest a high production rate of basaltic melt, and indeed, no ultramafic rock has been identified around the Dodo hydrothermal field. Kawagucci et al. (2008) suggested a possible involvement of ultramafic rocks exposed in the Marie Celeste Fracture Zone (Hekinian 1982), approximately 50 km north of the Dodo hydrothermal field (Fig. 12.1). Although a model with large-scale hydrothermal circulation is not consistent with the fluid circulation pattern expected for the Dodo field (potentially an EPR-type, short-lived, relatively shallow circulating system), future investigations will be needed to determine the role of large fracture zones in the hydrothermal activity (especially in terms of fluid chemistry) of the neighboring segments. Conspicuous enrichment of K relative to Cl is also a distinctive feature commonly observed in the fluids of the Dodo field (Nakamura et al. 2012). It has been reported that the

basement MORB of the Dodo and Solitaire hydrothermal fields is highly enriched in alkaline and alkaline earth elements compared with typical MORB, due to the influence of plume components derived from the Réunion hot spot (Murton et al. 2005; Nauret et al. 2006). Therefore, it is reasonable to consider the high K/Cl ratio and, likely, other alkali element-to-Cl ratios of the Dodo hydrothermal fluids to reflect the distinct chemistry of the plume-influenced MORB at the base of the hydrothermal field.

In the Solitaire hydrothermal field, a significantly higher pH (4.8) was observed compared to the pH values of typical MOR hydrothermal fluids (3.3 ± 0.5) (German and Von Damm 2004). To explain the relatively high pH detected in MORB-hosted hydrothermal fluids, two primary possibilities are suggested: (1) the existence of highly altered basement rock lacking the ability to buffer the solution pH and (2) the presence of ammonium (NH_3/NH_4^+), serving to buffer the pH at a higher level (German and Von Damm 2004). However, these explanations seem to be unlikely for the Solitaire fluids because (a) the low accumulation of sulfide structures and lack of inactive chimneys imply a relatively young age of the hydrothermal field, and (b) there is no sedimentary component that could produce ammonium in the hydrothermal fluids. Instead, the relatively low temperature ($<300\ ^\circ C$) of the Solitaire vent fluids measured at the seafloor suggests another possibility, i.e., that subseafloor mixing between hydrothermal fluids and seawater causes the relatively high pH value of these fluids. The Solitaire fluids exhibit a content of chlorinities that is approximately 10 % lower than the ambient seawater, indicating subseafloor phase separation and segregation of a vapor-rich phase in the discharging fluids. As all of the other CIR hydrothermal systems (Kairei, Edmond, and Dodo fields) exhibit brine-rich hydrothermal fluids with higher chlorinity than the ambient seawater, this constitutes the first observation of discharges of vapor-rich hydrothermal fluids in the Indian Ocean. Despite the vapor enrichment of the Solitaire fluids, their H_2 concentrations (up to 0.46 mmol/L) are generally comparable with typical MOR hydrothermal fluids (McCollom 2008). In addition, similar to the Dodo fluids, the hydrothermal fluids from the Solitaire field are also characterized by a high K/Cl ratio relative to typical MORB-hosted hydrothermal fluids. Indeed, the basement MORB of the Solitaire hydrothermal field is reported to be influenced by the plume components from the Réunion hot spot and, thus, enriched in alkaline and alkaline earth elements (Murton et al. 2005). Therefore, the high K/Cl ratio of the Solitaire fluids is also likely to reflect the chemical characteristic of the plume-influenced MORB at the base of the hydrothermal fields, as in the Dodo hydrothermal field. Because the available hydrothermal fluid samples from the Solitaire field are very limited and the detailed chemical properties of these fluids are still largely unknown, detailed

ongoing and future studies of hydrothermal fluid chemistry will provide important insights into the question of how the large- and local-scale geological settings of the Solitaire field affect its unique hydrothermal fluid chemistry.

The maximum temperature of the Edmond hydrothermal fluids ($382\ ^\circ C$) (Gallant and Von Damm 2006) is the hottest temperature ever measured in Indian Ocean hydrothermal vents. The pH values of the Edmond fluids range from 2.97 to 3.3 (Gallant and Von Damm 2006; Kumagai et al. 2008), which are slightly lower than the Dodo, Solitaire, and Kairei fluids, but still within the range of typical MORB-hosted hydrothermal fluids (Gallant and Von Damm 2006). The Edmond fluids are characterized by quite high Cl concentrations, which are >70 % higher than in the local ambient seawater, indicating subseafloor phase separation and subsequent brine condensation. The water depth of the Edmond hydrothermal field is ~3,300 m, which corresponds to a hydrostatic pressure of 330 bar. This pressure at the seafloor is above the critical pressure of seawater, indicating that the phase separation of these fluids must occur under supercritical conditions. Furthermore, the data suggest that the temperature of the Edmond fluids must have exceeded $420\ ^\circ C$ to have undergone phase separation, even just below the seafloor. In spite of the notable brine enrichment detected, the H_2 concentrations found in the Edmond fluids (0.055–0.111 mmol/kg) (Gallant and Von Damm 2006; Kumagai et al. 2008) are comparable to those of typical MORB-hosted hydrothermal fluids observed elsewhere along the EPR and Mid-Atlantic Ridge (MAR). The vapor and brine phases produced through phase separation are known to be chemically very different from each other and from their parent fluid (e.g., gases are enriched in the vapor-dominated phase and depleted in the brine-dominated phase) (Butterfield et al. 2003). The parent fluid of the Edmond fluids is therefore considered to be more enriched in gases. In contrast to gaseous species, dissolved species that are primarily ionic (e.g., Na^+, Cl^-) are known to show a very strong affinity for the brine phase as a result of phase separation. Indeed, conspicuous enrichment of ionic species was observed in the Edmond fluids (Gallant and Von Damm 2006; Kumagai et al. 2008). However, the Edmond fluids are also characterized by alkali element-to-Cl ratios that are similar to those of typical MORB-hosted hydrothermal fluids (Gallant and Von Damm 2006; Kumagai et al. 2008). Kumagai et al. (Kumagai et al. 2008) reported the chemical composition of the basement basalt of the Edmond hydrothermal field, showing that the contents of alkaline and alkaline earth elements in the Edmond basalt are almost the same as those typically found in MORB (Sun and McDonough 1989).

In the Kairei hydrothermal field, the maximum temperature of the fluid was reported to be $369\ ^\circ C$ at the Kali vent

(Kumagai et al. 2008). The pH levels in these high-temperature fluids (3.34 to 3.6) are comparable with those of typical MORB-hosted hydrothermal fluids (Gallant and Von Damm 2006; Kumagai et al. 2008). The Cl concentrations in the endmember fluids are significantly (up to ~14 %) greater than in the local ambient seawater, suggesting subseafloor phase separation and brine-phase enrichment. The first report of the chemical compositions of the Kairei hydrothermal fluids, by Gamo et al. (Gamo et al. 2001), noted a marked similarity between the Kairei fluids and other typical MORB-hosted hydrothermal fluids found along the EPR and MAR (Gamo et al. 2001). However, subsequent studies revealed distinct features of the Kairei hydrothermal fluids (Van Dover et al. 2001), including extraordinarily high H_2 concentrations, of 2.5–8.5 mmol/kg, compared to the concentrations found in typical MORB-hosted hydrothermal fluids (Van Dover et al. 2001; Takai et al. 2004a; Gallant and Von Damm 2006; Kumagai et al. 2008). H_2-enriched, high-temperature hydrothermal vent fluids, similar to the Kairei fluids, have been reported from several hydrothermal vent fields located along the MAR (e. g., the Rainbow, Logatchev I and II, Ashaze I and II, and Nibelungen fields) (Charlou et al. 2002, 2008; Melchert et al. 2008). It has generally been accepted that the H_2 enrichment of hydrothermal vent fluids is attributed to serpentinization of ultramafic rocks (e.g., abyssal peridotite) (Charlou et al. 2002; Douville et al. 2002). However, there was no geological evidence indicating the presence of ultramafic rocks at or near the Kairei hydrothermal field found in the initial investigation (Van Dover et al. 2001; Gallant and Von Damm 2006). Moreover, the Kairei hydrothermal fluids exhibit CH_4 and Si concentrations that are similar to those reported in typical MOR hydrothermal fluids (Gallant and Von Damm 2006), although the peridotite-hosted hydrothermal fluids observed along the MAR generally exhibit higher CH_4 and lower Si concentrations compared to typical basalt-hosted fluids (e.g., Charlou et al. 2002).

In 2006, detailed geological and geophysical investigations were conducted around the Kairei hydrothermal field using the HOV *Shinaki 6500* and R/V *Yokosuka* (YK05-16 cruise). During the research cruise, serpentinized gabbroic rocks (troctolite) were discovered at small topographic highs referred to as the Uraniwa Hills, ~15 km east of the Kairei hydrothermal field (Kumagai et al. 2008). Nakamura et al. (2009) performed geochemical reaction path model calculations to examine whether the reaction of seawater with the troctolitic rocks exposed in the vicinity of the Kairei hydrothermal field explains the high H_2 concentration measured in the hydrothermal fluids. The model results showed that the serpentinization of the Uraniwa troctolite can produce more than 16 mmol/kg of

H_2, similar to the H_2 concentrations detected in vent fluids derived from host basement rocks dominated by peridotite (Charlou et al. 2002; Schmidt et al. 2007). To explain the concentrations of the major dissolved components of the vent fluids other than H_2, Nakamura et al. (2009) produced an additional geochemical reaction path model incorporating both troctolite and basalt. The model calculations showed the following two results: (1) even limited interaction between the hydrothermal fluids (reacted with troctolite) and the basaltic wall rock could produce a high-SiO_2 content, similar to those found in basalt-hosted hydrothermal fluids; and (2) H_2 is not predicted to decrease notably during interactions with small amounts of basalt in a hydrothermal upflow zone. This basalt-troctolite hybrid model revealed that troctolite–seawater interactions in recharge and/or reaction zones are responsible for the remarkably high H_2 concentrations observed in the Kairei fluids, whereas the concentrations of other dissolved components of the vent fluids are controlled by the interactions with basalt in the subseafloor hydrothermal fluid flows (particularly in the discharge zone).

The low CH_4 concentration in the Kairei fluids cannot be explained by the hybrid model. Nakamura et al. (2009) noted that the Ni concentrations in olivine-rich gabbroic rocks (e. g., troctolite) are significantly lower than are found in typical mantle peridotite. Because the amount of Ni–Fe alloy directly affects the reaction kinetics of the reduction of CO_2 to CH_4 (Horita and Berndt 1999), the lower concentrations of Ni would reduce the catalytic rate of Fischer–Tropsch-type (FTT) or Sabbatier synthesis in the Uraniwa-Hills rocks, resulting in the lower concentrations of CH_4 relative to H_2 found in the Kairei fluids. However, it should be noted that even in typical peridotite-hosted hydrothermal systems, the CH_4 concentrations are not in equilibrium with the concentrations of H_2 and CO_2, and the real processes controlling CH_4 concentrations in hydrothermal fluids remain uncertain.

The Kairei fluids are also characterized by relatively low ratios of alkaline and alkaline earth elements-to-Cl compared with typical MORB-hosted hydrothermal fluids (Gallant and Von Damm 2006). Kumagai et al. (2008) noted the role of the chemical composition of basement rocks. It is well known that ultramafic rocks (including olivine-rich gabbroic rocks) are depleted in alkaline and alkaline earth elements compared to basaltic rocks. Furthermore, the basaltic rocks present around the Kairei hydrothermal field are also unusually depleted in these elements (Kumagai et al. 2008). Therefore, the chemical characteristics of the Kairei fluids are likely associated with the unique lithology of the Kairei hydrothermal field (involvement of olivine-rich gabbroic rocks and highly depleted basalt).

12.4 Biological Studies Conducted at the Four Hydrothermal Vent Fields

12.4.1 Microbial Communities and Microorganisms Isolated from the CIR Hydrothermal Systems

Among the four deep-sea hydrothermal systems explored along the CIR, only the Kairei field has been extensively studied with respect to the development of the deep-sea vent microbial community. In this section, we therefore summarize the results of the microbiological investigations conducted at the Kairei hydrothermal field thus far. Comprehensive characterizations of the microbial communities in hydrothermal fluids, chimney structures, and planktonic habitats in the mixing zones between the hydrothermal fluids and ambient seawater have been conducted in the Kairei field (Takai et al. 2004a, b; Suzuki et al. 2004; Nakagawa et al. 2004). In addition to microbial community development, the potential biogeochemical functions related to the subseafloor hydrothermal fluid flows and the associated microbial populations have also been addressed in a series of geomicrobiological and biogeochemical investigations (Takai et al. 2004a, 2006; Nakamura et al. 2009; Kawagucci et al. 2010).

The Kairei hydrothermal system exhibits slightly different hydrothermal fluid endmembers, influenced by subseafloor phase separation (Gallant and Von Damm 2006). The Kali vent site is a principal hydrothermal vent site hosting slightly brine-rich fluid, whereas the Fugen chimney site displays relatively gas-rich endmember fluid (Takai et al. 2004a; Gallant and Von Damm 2006). The Fugen chimney is located in the easternmost part of the hydrothermal field and is likely derived from the longest branched hydrothermal fluid path in the predicted subseafloor hydrogeologic structure (Gallant and Von Damm 2006). Although the Fugen chimney fluid is generally enriched with various gas components, the concentration of H_2 in the Fugen chimney fluid is lower than that in the Kali vent fluid (Takai et al. 2004a). The stable isotopic signatures of $\delta D(H_2)$, $\delta^{13}C(CO_2)$, and $\delta^{13}C(CH_4)$ vary between the Kali and Fugen hydrothermal fluids (Takai et al. 2004a; Kawagucci et al. 2010). Together with the observed variation in concentrations, the low $\delta D(H_2)$ value in the Fugen chimney fluid indicates a lower temperature isotopic equilibrium, likely promoted by microbial H_2 consumption. In addition, the high $\delta^{13}C(CO_2)$ value in the Fugen chimney fluid may be explained by isotopic fractionation during microbial consumption, and the significantly low $\delta^{13}C$ (CH_4) level in the Fugen fluid can be attained only through microbial methanogenesis (Takai et al. 2004a). All of these geochemical results are consistent with the composition and metabolic activity of the subseafloor microbial communities revealed through the microbiological characterization of the components entrained from the hydrothermal fluids (Takai et al. 2004a).

The microbial communities in the hydrothermal fluids and the chimney structures of the Kali and Fugen sites were characterized through the quantitative cultivation technique, 16S rRNA gene clone analysis, and FISH analysis (Takai et al. 2004a). Among the microbial communities trapped in the Kali vent and Fugen chimney fluids (the in-situ-colonization-system communities), members of *Thermococcus* and *Pyrococcus* represented the most abundant cultivated populations. The second most abundant cultivated population consisted of thermophilic and hyperthermophilic *Methanococcales* members, all of which represented hydrogenotrophic (H_2-trophic), methanogenic chemolithoautotrophs. The other cultivated microbial components were thermophilic and hyperthermophilic members of *Aquifex* and *Persephonella* (both H_2-trophic and/or thiotrophic chemolithoautotrophs) and *Archaeoglobus* (organotrophic and H_2-trophic, SO_4-reducing chemolithotrophs). *Thermodesulfatator* species were reported to be the dominant, H_2-trophic SO_4-reducing chemolithoautotrophic bacteria in the chimney microbial communities of the Kairei field (Moussard et al. 2004). In addition, certain populations of mesophilic and thermophilic *Epsilonproteobacteria*, such as *Hydrogenimonas* and *Sulfurimonas*, were found in the Fugen chimney fluids. These *Epsilonproteobacteria* are also H_2-trophic and thiotrophic chemolithoautotrophs. The microbial communities found in the Fugen chimney habitats were very similar to the community in the Fugen chimney fluid (Takai et al. 2004a).

Culture-independent molecular analyses (16S rRNA gene cloning and FISH analyses) have generally revealed similar compositions of the microbial communities found in the hydrothermal fluids and chimney structures (Takai et al. 2004a). However, FISH analysis clearly demonstrated the numerical predominance of *Methanococcales* populations in the microbial communities of the Kali and Fugen fluids and strongly suggested that hyperthermophilic H_2-trophic methanogens sustain the microbial communities as primary producers (Takai et al. 2004a). Thus, both geochemical and microbiological characterizations have pointed to the possible existence of a hyperthermophilic subsurface lithotrophic microbial ecosystem (HyperSLiME) beneath the Kairei hydrothermal field (Takai et al. 2004a).

In contrast to the microbial communities that are closely associated with the high-temperature hydrothermal fluid emissions of the Kairei field, the planktonic microbial communities found in the hydrothermal plumes and habitats in the vicinity of this field were not significantly different from those observed in other deep-sea hydrothermal environments (Takai et al. 2004b). Based on examination of the relative abundance of Marine Group I (*Creanarchaeota*

and *Epsilonproteobacteria*) populations in the planktonic microbial communities of the hydrothermal plumes, the communities in the Kairei field showed much less abundant *Epsilonproteobacteria* populations compared to the Iheya North field of the Okinawa Trough. However, microbial populations other than Marine Group I, such as the SUP05 group *Gammaproteobacteria*, a cosmopolitan microbial population that dominates hydrothermal plume communities (Sunamura et al. 2004; Dick and Tebo 2010), were not quantitatively estimated (Takai et al. 2004b). In addition, La Duc et al. (et al. 2007) reported that many of the heterotrophic bacteria isolated from the Kairei hydrothermal plumes displayed high multi-stressor tolerance to desiccation, peroxide exposure, and UV and gamma ray irradiation. However, it is still unclear whether this finding is specifically attributed to the microbial communities of the Kairei hydrothermal plumes or to global hydrothermal plume environments.

In the Edmond field, the microbial community of a sulfide chimney was characterized only via culture-independent, PCR-mediated 16S rRNA gene phylotype analysis (Hoek et al. 2003). The results of this analysis do not provide a quantitative estimation of the microbial community composition or potential functions and represent only qualitative compositional features. Compared to the 16S rRNA gene phylotype compositions obtained from various chimney habitats of the Kairei field, the phylotype composition in the Edmond sulfide chimney, exhibiting relatively high-temperature fluid, consisted mainly of bacterial phylotypes, such as *Epsilonproteobacteria* and *Aquificales*, and archaeal phylotypes, such as the *Aciduliprofundus* and *Thermococcus* genera (Hoek et al. 2003). These phylotypes were quite different from the phylotype compositions found in the Kairei chimneys and fluids, which were dominated by hydrogenotrophic *Methanococales* and sulfate-reducing chemolithotrophs (Takai et al. 2004a). Although quantitative characterization of the viable populations and metabolic functions of the microbial communities found in various Edmond hydrothermal field habitats remains to be conducted, the different patterns of the microbial phylotype compositions between the Kairei and the Edmond hydrothermal fields are likely associated with the different energy states of the microbially habitable (mixing) zones. These zones are primarily controlled by the physical and chemical characteristics of the endmember hydrothermal fluids, as suggested by Takai and Nakamura (2010, 2011).

Despite the poorly delimited patterns of microbial community development, many novel deep-sea vent microorganisms have been successfully isolated from the CIR deep-sea hydrothermal systems, likely due to the previously unexplored biogeographicity of these systems. Immediately after the discovery of the Kairei hydrothermal field, many new genera and species of deep-sea vent chemolithoautotrophs were isolated and described (L'Haridon et al. 2003; Moussard et al. 2004; Takai et al. 2004c, d, 2008). A hyperthermophilic hydrogenotrophic methanogen, *Methanocaldococcus indicus* (L'Haridon et al. 2003), and an extremely thermophilic hydrogenotrophic methanogen, *Methanotorris formicicus* (Takai et al. 2004c), identified in the Kairei hydrothermal field represent new species of *Methanococcales* and important primary producers of chemolithotrophic microbial communities. A thermophilic hydrogenotrophic sulfate-reducer, *Thermodesulfatator indicus* (Moussard et al. 2004), and a thermophilic hydrogenotrophic epsilonproteobacterium, *Hydrogenimonas thermophila* (Takai et al. 2004d), were new genera of deep-sea vent chemolithoautotrophs originally found in the CIR Kairei field. In addition, although it was not a new taxon of methanogen, the most hyperthermophilic living form identified thus far, *Methanopyrus kandleri* strain 116, was obtained from the Kairei hydrothermal fluid (Takai et al. 2008). The identification of such new taxa of deep-sea vent microorganisms was likely associated with the newly explored biogeographicity of CIR hydrothermal systems, and the unique physiological traits of these chemolithoautotrophs are related to the unique geological setting and hydrothermal fluid chemistry of the Kairei field.

12.4.2 Hydrothermal Vent Fauna and Chemosynthetic Symbioses

The Kairei and Edmond fields have been found to host novel genera and families that are potentially indigenous to CIR hydrothermal systems as well as faunal species common to the Pacific and the Atlantic Oceans (Hashimoto et al. 2001; Van Dover et al. 2001). Based on the limited data obtained from these two hydrothermal vent sites, recent statistical work addressing the connections among biogeographical provinces (Bachraty et al. 2009) and population connectivities (Vrijenhoek 2010) has highlighted similarities between western Pacific and Indian Ocean vent communities. However, as the authors noted, the available information on the Indian Ocean hydrothermal vent faunas is still scarce, and additional faunal data from new Indian Ocean hydrothermal systems is required to improve our knowledge of the biodiversity and biogeography of the global deep-sea hydrothermal vent fauna. During the TAIGA project, we discovered and investigated two new hydrothermal vent sites, the Dodo and Solitaire fields (Nakamura et al. 2012), providing novel information about hydrothermal vent-endemic fauna in the Indian Ocean. The details regarding recent progress in understanding the distribution and genetic diversity of hydrothermal vent fauna and biogeographical and genetic population connectivities in the CIR hydrothermal systems are presented elsewhere in this book (Watanabe and Beedessee, Chap. 16). Here, we briefly

describe the results of the biological studies conducted at the CIR hydrothermal vent fields.

An important finding among the Indian Ocean vent fauna was the existence of two morphotypes of a "scaly-foot" gastropod. Since its first discovery in the Kairei hydrothermal field in 2001 (Van Dover et al. 2001), this gastropod has attracted particular attention because of its distinct features, including unusual black-colored iron sulfide dermal sclerites (Warén et al. 2003; Suzuki et al. 2006), an iron sulfide-plated armor shell structure (Yao et al. 2010), and the unique endo- and epi-symbioses found in its enlarged esophageal gland and sclerites, respectively (Goffredi et al. 2004). In October 2009, during the YK-09-13 cruise, a new morphotype of scaly-foot gastropod was found at the Solitaire hydrothermal field, which exhibits similar morphological and anatomical features to the previously reported type that inhabits the Kairei field but completely lacks an iron sulfide coating on its sclerites (Nakamura et al. 2012).

The new morphotype displays a brown shell and cream-colored sclerites, in contrast to the metallic black shell and sclerites of the type previously known from the Kairei field. Indeed, the sclerites of the Kairei morphotype exhibit the presence of a thick coating of iron sulfide minerals (e.g., greigite or pyrite), as previously reported (Warén et al. 2003; Suzuki et al. 2006), whereas no specific condensation of Fe and S was identified on the sclerites of the Solitaire morphotype. Surprisingly, however, phylogenetic and haplotype analyses clearly demonstrated that the two morphotypes of scaly-foot gastropod of different colors are genetically indistinguishable and should be classified as the same species (Nakamura et al. 2012). Furthermore, the non-iron-sulfide-mineralized sclerites of the Solitaire morphotype show greater mechanical strength of the overall structure compared to those of the Kairei morphotype (Nakamura et al. 2012), despite the fact that the iron sulfide mineralization of sclerites of the Kairei morphotype is believed to harden the sclerites for protection from predation (Suzuki et al. 2006). These findings from the new morphotype of the scaly-foot gastropod demonstrate that the mechanisms and physiological roles of iron sulfide mineralization are still fully uncertain.

A nutritional symbiotic relationship with chemosynthetic bacteria was also observed in the Kairei morphotype of the scaly-foot gastropod (Goffredi et al. 2004). There were different types of symbioses identified in different tissues, such as endosymbiosis of *gammaproteobacterium* in the greatly enlarged esophageal gland and episymbiosis of *Epsilonproteobacteria* and *Deltaproteobacteria* on the iron sulfide-coated sclerites. The nutritional transfer between the chemosynthetic symbiont and the host gastropod is likely sustained by the endosymbiosis in the esophageal gland (Goffredi et al. 2004). Very recently, the complete genome of a gammaproteobacterial endosymbiont found in the Kairei

morphotype of the scaly-foot gastropod has been determined (Nakagawa et al. 2013). Notable findings from this study include the presence and transcription of genes for flagellar assembly, through which proteins are potentially exported from the symbiont to the host (Nakagawa et al. 2013). This result indicates the possible nutritional transfer mechanism of this chemosynthetic symbiosis. In addition, the extremely low genetic individuality in the endosymbionts suggests that stringent symbiont selection by the Kairei morphotype of the scaly-foot gastropod prevents random genetic drift in the small population of horizontally transmitted symbionts (Nakagawa et al. 2013). The genomic analysis of the symbiont also suggested that the chemosynthetic symbiosis found in the Kairei morphotype of the scaly-foot gastropod was relatively recently established (Nakagawa et al. 2013).

Another novel chemosynthetic symbiosis was found in a hydrothermal vent gastropod (*Alviniconcha* aff. *hessleri*) predominantly living in the diffusing fluid flow zones of the Kairei field (Suzuki et al. 2005). *Alviniconcha* gastropods belonging to the family *Provannidae* inhabit deep-sea hydrothermal fields at the margins of the western and southwestern Pacific Ocean and along the CIR (Warén and Bouchet 2001; Nakamura et al. 2012). In the gills of the *Alviniconcha* gastropods from the Kairei field, an epsilonproteobacterial endosymbiont was identified for the first time using molecular ecological techniques. It was found that primary production by this species likely supports the nutrition of the host *Alviniconcha* gastropod (Suzuki et al. 2005). The complete genome of the *Alviniconcha* gastropod is being determined, and the energy, carbon metabolism, and nutritional transfer mechanisms of this symbiosis are being investigated through polyphasic physiological and molecular characterizations. The genetic evolution and ecophysiological functions of the chemosynthetic symbiosis found in the *Alviniconcha* gastropods will be clarified through multiple approaches in the future.

12.5 Future Prospects

During the TAIGA project, the exploration and assessment of four Indian Ocean hydrothermal vent fields, including two newly discovered hydrothermal fields, were significantly advanced. As shown in this paper, the results of these investigations greatly extend our knowledge of the geochemical variations of hydrothermal activity and their relationships to the geological background as well as the biodiversity and biogeography of the hydrothermal vent-associated microbial and faunal communities in the Indian Ocean. . The four studied hydrothermal vent sites were all located within the CIR; however, two other MORs in the Indian Ocean (Southeast Indian Ridge: SEIR and Southwest Indian Ridge: SWIR) remain to be explored.

Very recently, a new hydrothermal vent site was discovered along the SWIR and was explored by a Chinese scientific team (Tao et al. 2012). They found hydrothermal vent-endemic fauna, including scaly-foot gastropods at the vent site. However, the fluid chemistry and geological background of this site are still unknown, and detailed descriptions of the vent fauna have yet to be published. Moreover, several hydrothermal plumes indicating the existence of unseen hydrothermal vent sites have also been detected not only at the SWIR (German et al. 1998) but also at the SEIR (Wang et al. 2011). Because similarity between the Indian Ocean and Western Pacific Ocean vent communities has been noted by several researchers, the discovery and investigation of hydrothermal vent sites along the SEIR (a possible corridor for vent communities between Indian and Western Pacific Oceans) are particularly important. In the future, detailed geological, geochemical, and geophysical investigations as well as physiological, genetic, and trophic characterizations of hydrothermal vent-endemic fauna in uninvestigated hydrothermal vent sites will certainly provide important information contributing to our understanding the Indian Ocean MOR hydrothermal system and its relationship to the Pacific and Atlantic Ocean MOR hydrothermal systems.

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