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EDITED BY

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REVIEWED BY

Brooks A. Kaiser,
University of Southern Denmark, Denmark
Mirjam Perner,
Helmholtz Association of German
Research Centres (HZ), Germany

*CORRESPONDENCE

Naomi van der Most

✉ nvdmost@protonmail.com

Pei-Yuan Qian

✉ boqianpy@ust.hk

SPECIALTY SECTION

This article was submitted to
Marine Affairs and Policy,
a section of the journal
Frontiers in Marine Science

RECEIVED 12 October 2022

ACCEPTED 28 December 2022

PUBLISHED 25 January 2023

CITATION

van der Most N, Qian P-Y, Gao Y and
Gollner S (2023) Active hydrothermal vent
ecosystems in the Indian Ocean are in
need of protection.

Front. Mar. Sci. 9:1067912.

doi: 10.3389/fmars.2022.1067912

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Active hydrothermal vent ecosystems in the Indian Ocean are in need of protection

Naomi van der Most^{1*}, Pei-Yuan Qian^{2,3*}, Yan Gao⁴
and Sabine Gollner¹

¹Department of Ocean Systems (OCS), Royal Netherlands Institute for Sea Research (NIOZ), Texel, Netherlands, ²Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou, China, ³Department of Ocean Science, Hong Kong University of Science and Technology, Hong Kong, Hong Kong SAR, China, ⁴Department of Science and Technology and International Cooperation, China Deep Ocean Affairs Administration, Beijing, China

Deep-sea hydrothermal vent fields are among the most pristine and remarkable ecosystems on Earth. They are fueled by microbial chemosynthesis, harbor unique life and can be sources of precipitated mineral deposits. As the global demand for mineral resources rises, vent fields have been investigated for polymetallic sulfides (PMS) and biological resources. The International Seabed Authority (ISA) has issued 7 contracts for PMS exploration, including 4 licenses for vent fields in the Indian Ocean. Here, we provide a summary of the available ecological knowledge of Indian vent communities and we assess their vulnerability, sensitivity, ecological and biological significance. We combine and apply scientific criteria for Vulnerable Marine Ecosystems (VMEs) by FAO, Particular Sensitive Sea Areas (PSSAs) by IMO, and Ecologically or Biologically Significant Areas (EBSAs) by CBD. Our scientific assessment shows that all active vent fields in the Indian Ocean appear to meet all scientific criteria for protection, and both the high degree of uniqueness and fragility of these ecosystems stand out.

KEYWORDS

hydrothermal vent fields, Indian Ocean, deep-sea mining, vulnerable marine ecosystems (VMEs), ecologically or biologically significant areas (EBSAs), particularly sensitive sea areas (PSSAs), International Union for Conservation of Nature (IUCN)

1 Introduction

1.1 Ecology of hydrothermal vent ecosystems

Deep-sea hydrothermal vent ecosystems are exceptional habitats teeming with exotic life. Like oases in the desert, they are small but immensely productive hotspots on the otherwise barren seafloor. These dynamic ecosystems are located in geologically and tectonically active areas of the ocean, such as mid-ocean ridges, back-arc basins, and submarine volcanic arcs (Hannington et al., 2005; Beaulieu et al., 2013; Gollner et al., 2017). The release of geothermally heated fluid from the ocean crust supports chemosynthetic microbial communities that use reduced compounds from the vent fluids as energy to fix carbon

and produce organic compounds that sustain high growth of fauna. A vent field usually covers multiple active or (temporarily) inactive vent sites with a shared subsurface circulation (Jamieson and Gartman, 2020). When hydrothermal fluids come into contact with the cool ocean water, polymetallic sulfide deposits (PMS) are formed as minerals from the fluid precipitate (von Damm, 1995; Hannington et al., 2005). Differences in geophysical settings, fluid chemistry, and fluxes in vent flow lead to high spatial and temporal variations of geochemical and physical nature in vent fields (Lutz and Kennish, 1993).

Hydrothermal activity creates a mosaic of microhabitats with distinct faunal zonation along the physicochemical gradient (Marsh et al., 2012; Watanabe and Beedsee, 2015; Copley et al., 2016; Galkin, 2016). Chemoautotrophic microbes form the basis of the food web, supporting dense aggregations of chemosynthetic macrofauna and primary and secondary consumers (Grassle, 1987). Vent species are physiologically well adapted to the unstable and extreme vent environment, such as to rapid and intense temperature shifts, a low pH, low oxygen concentrations, and high heavy metal exposure (Minic et al., 2006; Ramirez-Llodra et al., 2007). High growth rates, high biomass, and low faunal diversity are typical for vent assemblages (Grassle, 1985). The vast majority of taxa are vent-obligate (endemic), and communities drastically change when hydrothermal discharging ceases (van Dover, 2001; Gollner et al., 2020).

The ecosystem description of a “hydrothermal vent” can be as broad as the description “forest” (Thaler and Amon, 2019). Forests range from tropical to boreal, and vent systems are as diverse in their chemical, geological, and physical properties. Although every vent field is unique, distinct biogeographic provinces do exist, which are characterized by their dominant species and overall community structure (Mullineaux et al., 2018). The Indian Ocean has been considered to be one of these biogeographic provinces (Moalic et al., 2012).

The Indian Ocean has four mid-ocean ridges with intermediate to ultraslow spreading rates (Moalic et al., 2012; Rogers et al., 2012). Kairei on the Central Indian Ridge was the first vent field discovered in this province at the beginning of the 21st century (Hashimoto et al., 2001). Since then, another 12 active vent fields have been discovered in the region (Figure 1). The Indian Ocean has been hypothesized as an ecological corridor between Atlantic and Pacific vent populations, with a closer relation to the West Pacific metacommunity (van Dover, 2001; Watanabe and Beedsee, 2015). The mussel *Bathymodiolus marisindicus* and shrimp *Rimicaris kairei* are two dominant species that closely resemble their Atlantic counterparts (Hashimoto, 2001; Watabe and Hashimoto, 2002). Other common fauna are bythograeid crabs, neolepas barnacles, alviniconcha snails, and actinostolid anemones, all reminiscent of the West Pacific. However, several species are unique to the Indian Ocean communities such as most notably the scaly-foot snail *Chrysomallon squamiferum* (Warén et al., 2003; Chen et al., 2014).

1.2 Exploration of polymetallic sulfide deposits and governance

Since the first discovery of a hydrothermal ecosystem in 1977, nearly 700 vents have been reported globally (Wang et al., 2021).

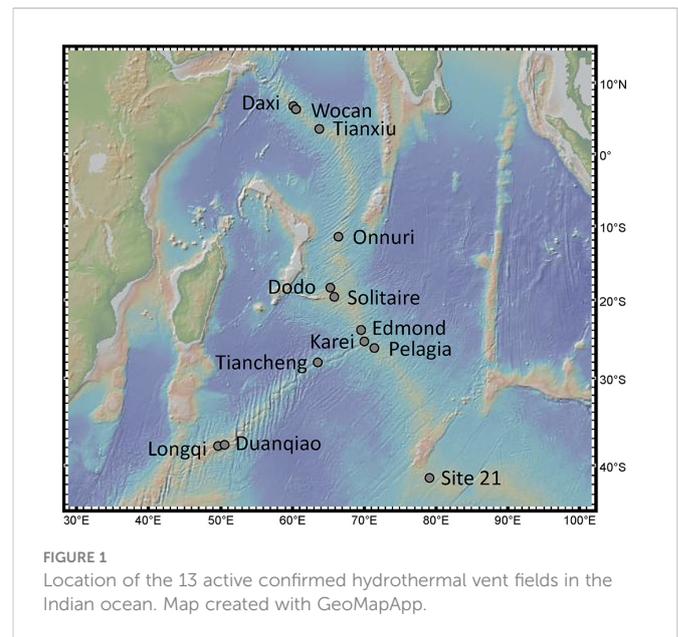


FIGURE 1
Location of the 13 active confirmed hydrothermal vent fields in the Indian ocean. Map created with GeoMapApp.

The interest for deep-sea mining has accelerated accordingly due to an increased metal demand (Wedding et al., 2015). At vent fields, mineral resources are found in the form of polymetallic sulfide (PMS) deposits, which are also known as seafloor massive sulfides (SMS) (Levin et al., 2016b). The International Seabed Authority (ISA) is in charge of regulating all mining-related activities in the Areas Beyond National Jurisdiction (the *Area*) under the United Nations Convention on the Law of the Sea (UNCLOS)¹. The ISA has the obligation to ensure that human activities in the international seabed are carried out for the benefit of humankind as a whole and to protect the marine environment from harmful impacts caused by resource extraction activities². At present, the ISA has issued three licenses for PMS exploration on the northern Mid-Atlantic Ridge and four licenses on the Indian mid-ocean ridges³. The four contractors are the German Federal Institute for Geosciences and Natural Resources (BGR), the China Ocean Mineral Resources Research and Development Association (COMRA), the Ministry of Earth Sciences from the Government of India, and the Government of the Republic of Korea. Each contract area covers 10,000 km² of which 75% will be relinquished. The contract areas of COMRA are on the South-West Indian Ridge, of the Government of India on the South-West Indian and the Central Indian Ridge, of BGR on the Central and South-East Indian ridge, and of The Government of the Republic of Korea on the Central Indian Ridge. Currently, 8 from the 13 confirmed active vent fields in the Indian Ocean (Longqi, Duanqiao, Tiancheng, Onnuri, Dodo, Kairei, Edmond, and Pelagia) are within those contract areas (Perez et al., 2021).

1 <https://www.isa.org.jm/about-isa>.

2 <https://www.isa.org.jm/>.

3 <https://isa.org.jm/index.php/minerals/exploration-areas>.

Mining activities may disturb vent ecosystems in an unprecedented manner on spatial and temporal scales (Gollner et al., 2017). Vent ecosystems on slow and ultraslow spreading ridges, such as those in the Indian Ocean, tend to be more stable and their biological communities are less exposed to natural disturbance events such as major volcanic eruptions than ones on fast spreading ridges (Gollner et al., 2017; van Dover et al., 2018). No disturbance experiments have been performed to mimic mining at vent ecosystems in the Area, but it is expected that mining would have severe consequences. Direct mining impacts may include removal of substrate and fauna, causing habitat loss, habitat fragmentation, and habitat modification, leading to loss of biodiversity at all levels: genetic, species, functional, and habitat (Levin et al., 2016b). Other direct mining impacts include light, sound, and electromagnetic exposure from mining equipment (Chen et al., 2021b) as well as changes in vent fluid flow (Kawagucci et al., 2013). Mining plumes can also create indirect mining impacts such as increased heavy metal load or high turbidities following sediment resuspension (Weaver et al., 2022). While it is expected that harm will be done to vent communities dependent on PMS as substrate, the ramifications extend beyond the local sphere (Levin et al., 2016a). Low recolonization of fauna in the vicinity of vents has been previously observed after a disturbance, likely due to lower resilience of those species (Gollner et al., 2015). In a wider region surrounding the vent, resuspension of potentially toxic sediment and returning plumes from the surface operational ship could affect both benthic and pelagic life.

The International Seabed Authority has been developing Regional Environmental Management Plans (REMP) for PMS at the northern Mid Atlantic Ridge (nMAR) and is planning to develop REMF for the Indian Ocean. A draft for the nMAR REMF has been released for stakeholder consultation on the 19th April 2022 (Lee, 2020), whilst a first workshop focusing on scientific issues related to REMF development in the Indian Ocean Region (IOR) has been co-organized by ISA, COMRA and Hong Kong University of Science and Technology.

In this study, we evaluate whether the confirmed active vent fields at the Indian mid-ocean ridges meet scientific criteria for protection from anthropogenic impacts, through a comprehensive review of the scientific literature, and a comparison of available baseline information of each vent field against criteria developed by the Food and Agricultural Organization (FAO) for Vulnerable Marine Ecosystems (VMEs), the Convention on Biological Diversity (CBD) for Ecologically or Biologically Significant Areas (EBSAs), and the International Maritime Organization (IMO) for Particularly Sensitive Sea Areas (PSSAs), following the same procedure as described in Gollner et al. (2021) for active vents fields under mineral exploration at the nMAR. All active vent fields of the IOR appear to be vulnerable and significant ecosystems.

2 Methods

In this study, we assessed 13 vent fields with confirmed activity from the Indian mid-ocean ridges from the Carlsberg Ridge (CR) to the Central Indian Ridge (CIR), the South-East Indian Ridge (SEIR), and the South-West Indian Ridge (SWIR): Daxi, Wocan, Tianxiu, Onnuri, Dodo, Solitaire, Edmond, Kairei, Pelagia, Tiancheng, Duanqiao, Longqi, and Site 21 (Figure 1).

The search engines Google Scholar and Scopus were used to collect scientific literature in November and December 2021, and June 2022, using English key words for our searches, which limited our search solely to publications in English. The following key words were used: “hydrothermal activity”, “hydrothermal field”, “vent fauna”, “vent-endemic biota”, “Indian Ocean”, “Indian mid-ocean ridge”, “deep-sea mining”, “polymetallic sulfide”, “mineral extraction”, “resilience”, the names of all Indian mid-ocean ridges, and individual vent fields. Additional literature used in this review was found through the references of initially selected articles. Furthermore, the search engine Ecosia was used to acquire general information from organizations such as the ISA, FAO, CBD, IMO, and IUCN, and to gain access to their online documents.

We first review the main ecological findings and shortly discuss i) the discovery and exploration of the vent field, ii) the geochemical setting, and then focus on iii) the biological composition. Regarding vent biodiversity, we focused on macro- and megafauna.

Scientific criteria for identifying hydrothermal ecosystems in the Indian Ocean in need of protection follow the determination as used in “Application of scientific criteria for identifying hydrothermal ecosystems in need of protection” for nMAR vents to evaluate ecosystem vulnerability and significance by Gollner et al. (2021) (Appendix 1). Criteria include 1) uniqueness and rarity, 2) functional significance, 3) fragility, 4) life-history traits of component species that make recovery difficult, 5) structural complexity, 6) biological diversity, 7) biological productivity, 8) naturalness, and 9) ecosystem services. The criteria have been derived from the guidelines for identifying VMEs from the FAO (FAO, 2009), EBSAs from the CBD (CBD, 2009), and PSSAs from the IMO (IMO, 2005). One PSSA criterion (social, cultural and economic criteria: Social or economic dependency, human dependency, cultural heritage) was not included in the scoring, but rather an Ecosystem Services criterion was proposed as a more relevant addition (Gollner et al., 2021). There is a precedent for applying ecosystem services in a deep-sea context, which entails supporting, provisioning, regulating, and cultural services (Earth Economics, 2015; Levin et al., 2016a; Le et al., 2017; van Dover et al., 2018; Turner et al., 2019; Orcutt et al., 2020).

Based on the literature review, both vent-specific and general information on 12 vents is used to determine if each vent field meets the scientific criteria for protection. For vent “Site 21”, there are only 2 references available – one on detection of plume anomaly and another on the collection of vent-endemic *Neolepas* barnacles with a dredge (Watanabe et al., 2018). Although these findings indicate that Site 21 shall be a confirmed active vent, we decided to exclude it in our assessment because of the lack of visual observation which complicates the scientific analyses of many criteria.

3 Results

3.1 Review of main ecological findings of IOR vent fields

An overview of different geochemical and biological characteristics for each vent field is listed in Table 1. The 13 active vents in the Indian Ocean occur across a depth range of ~2000 meters (from 1732 to 3690) along ~48° from the Northern to the Southern hemisphere, spanning four mid-ocean ridges.

TABLE 1 Selected attributes of 12 active vent fields in the Indian Ocean, based on the literature used in this review.

ATTRIBUTE	CR			CIR				SEIR	SWIR			
	Daxi	Wocan	Tianxiu	Onnuri	Dodo	Solitaire	Edmond					
Latitude	6°48'N	6°22'N	3°39'N	11°25'S	18°20'S	19°33'S	23°53'S	25°19'S	26°09'S	27°57'S	37°47'S	37°39'S
Longitude	60°18'E	60°31'E	63°45'E	66°25'E	65°28'E	65°50'E	69°36'E	70°02'E	71°26'E	63°32'E	49°39'E	50°24'E
Depth (m)	3450	2973-3105	3500	1990-2170	2745	2606	3290-3320	2415-2460	3680-3690	2682-2729	2755	1732
Host Rock	Basalt	Basalt	Serpentized harzburgite	Peridotite, gabbro	Fresh basalt	Basalt	Basalt	Basalt serpentized troctolite	n.d.	Basalt	Basalt	Basalt
Mineral	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide	Sulfide
Tmax (°C)	273°C	358°C	“high”	242°C	356°C	307°C	382°C	369°C	368°C	“high”	379°C	277°C
pHmin	n.d.	n.d.	n.d.	n.d.	3.3	4.4	3.1	3.3	3.2	n.d.	3.6	n.d.
[H2S]max	n.d.	n.d.	n.d.	n.d.	2.80	4.75	4.81	6.06	n.d.	n.d.	n.d.	n.d.
[CH4]max	n.d.	n.d.	“high”	n.d.	0.025	0.043	0.22	0.20	n.d.	n.d.	0.41	n.d.
[H2]max	n.d.	n.d.	n.d.	n.d.	2.2	0.43	0.12	8.5	n.d.	n.d.	0.21	n.d.
Taxa presence												
<i>Alvinoconcha</i> spp. snail	Absent	Dominant	Dominant	Dominant	Absent	Present	Present	Present	Dominant	Present	Absent	Absent
<i>Chrysomallon squamiferum</i> snail	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Present	Dominant	Dominant	Present
<i>Bathymodiolus marisindicus/septemdiarum</i> mussel	Absent	Present	Present	Dominant	Absent	Present	Absent	Dominant	Present	Dominant	Dominant	Dominant
<i>Neolepas marisindica</i> barnacle	Absent	Present	Present	Present	Absent	Present	Absent	Present	Present	Dominant	Dominant	Present
<i>Rimicaris kairei</i> shrimp	Dominant	Dominant	Dominant	Present	Dominant	Dominant	Dominant	Dominant	Dominant	Absent	Present	Absent
<i>Mirocaris indica</i> shrimp	Present	Present	Present	Present	Absent	Present	Present	Present	Present	Present	Present	Absent
<i>Austinograea</i> spp. crab	Present	Present	Present	Present	Dominant	Present	Present	Present	Dominant	Dominant	Absent	Absent
IUCN (critically) endangered or vulnerable species	Absent	Present	Present	Present	Absent	Present	Present	Present	Present	Present	Present	Present

[]: concentration in mmol kg⁻¹, end-member fluid; n.d.: no data.

3.1.1 Vent fields of the Carlsberg Ridge

The CR, which is also referred to as the North-West Indian Ridge or the northern section of the CIR, is a divergent tectonic plate boundary between the Somatic plate and the Indian plate. It borders the CIR in the south and the Owen Transform Fault in the north and has a slow spreading rate of 22 - 32 mm per year (Ray et al., 2012). Daxi, Wocan, and Tianxiu active vent fields were found on the CR over the last 10 years. In total, 34 species have been recorded in these three vent fields (Zhou et al., 2022). The benthic communities in Tianxiu and Daxi fields appear to be subsets of those in Wocan, with a high genetic connectivity among the three vents (Zhou et al., 2022). It was suggested that biological communities in the CR vents form a separate province from those in the CIR and SWIR, based on differences in faunal composition and clear genetic clustering of species among these ridges (Zhou et al., 2022). Although the CR shares some community characteristics with the CIR, the prominent presence of polychaetes sets the CR metacommunity apart (Zhou et al., 2022). Interestingly, 2 polychaete species found on the CR have been grouped into clades with their East Pacific congeners, elucidating a direct biogeographic linkage between the CR and distant East Pacific metapopulation (Zhou et al., 2019).

3.1.1.1 Daxi (6°48'N, 60°10'E, 3450m)

The basalt-hosted Daxi vent field was discovered during the Dayang (DY33) cruise of COMRA in 2015 (Wang et al., 2021). Three mounts are located in this vent field and at least one of them accommodates clusters of active black smokers at the top (Wang et al., 2021). Eight chimney complexes ranging from several to more than 10 meters were seen, some discharged their fluids vigorously and others slowly (Wang et al., 2021).

The vent community at Daxi consisted of 15 recognized mega-faunal species which are a subset of the community at Wocan (Zhou et al., 2022), and was dominated by alvinocaridid shrimps, polychaetes, and crabs (Wang et al., 2021). The shrimp *Rimicaris kairei* was very dominant nearby hydrothermal activity while actinostlid anemones were common at the periphery. The alvinellid worm *Paralvinella mira* was endemic in the Daxi and Wocan vent fields, with lower abundances at Daxi (Han et al., 2021). The alvinellid strongly resembles 2 species, *P. hessleri* and an unnamed species *Paralvinella* sp. ZMBN, from the West Pacific (Han et al., 2021). *Austinograea rodriguezensis* crabs, *Munidopsis* lobsters, and shrimps resembling *Mirocaris indica* were also present at Daxi, while other typical Indian vent species, such as *Chrysomallon squamiferum* scaly-foot snails, *Alviniconcha marisindica* hairy snails, *Bathymodiolus marisindicus* mussels, and *Neolepas marisindica* stalked barnacles, were absent (Wang et al., 2021). A recently described novel neolepetopsid limpet, *Neolepetopsis prismatica* and a potentially new *Desbruyeresia* species were found so far exclusively in this vent field (Chen et al., 2021c; Zhou et al., 2022).

3.1.1.2 Wocan (6°22'N, 60°31'E, 2973-3105m)

Wocan was the first vent field discovered on the CR during the COMRA's DY28 cruise with the Research Vessel (RV) *Zhukezhen* in 2013 (Wang et al., 2017). TV-sled and TV-grab observations revealed the existence of two vent sites: Wocan-1 (~450 x 400 m) and ~1.7km to the northwest Wocan-2 (~200 x 400 m) (Qiu et al., 2021). During

the COMRA's DY38 cruise in 2017, a cluster of 17 active black smokers in Wocan-1 and a low-temperature diffuse flow area at Wocan-2 were confirmed (Qiu et al., 2021). Inactive (collapsed) chimneys, hydrothermal sediments, and sulfide talus were also found at Wocan-1 (Qiu et al., 2021).

Around the active vents, many vent-endemic species were discovered, including alvinocaridid shrimps, bythograeid crabs, actinostlid anemones, bathymodiolin mussels, and alviniconcha snails (Qiu et al., 2021). A potentially new shrimp species from the genus *Rimicaris* was recovered from Wocan (Zhou et al., 2022). The annelid *Amphisamytha wocanensis* was also found solely at Wocan, which surprisingly fell into a clade with species from the East Pacific (Zhou et al., 2019). A third polychaete observed at Wocan was the alvinellid worm *Paralvinella mira*, which was associated with *Alviniconcha* and *C. squamiferum* snails at this vent field (Han et al., 2021). Strikingly, *P. mira* and *Hesiolyra heteropoda* were highly abundant and form an alvinellid-/hesionid-polychaete worm dominated assemblage unique to the Indian Ocean (Han et al., 2021).

3.1.1.3 Tianxiu (3°7'N, 63°8'E, 3500m)

The ultramafic-hosted Tianxiu was also discovered during the COMRA's DY33 cruise in 2015 with a TV-sled and TV-grab (Chen et al., 2020). Black smoker chimney complexes, low-temperature diffuse vents, inactive massive sulfides, and hydrothermal sediments all occurred at Tianxiu (Zhou et al., 2022). A total of 12 megafaunal species were reported from the Tianxiu field, including *Alviniconcha marisindica* snails, *Neolepas marisindica* barnacles, *Bathymodiolus marisindicus* mussels, and a new crab species *Austinograea* sp. CR, and all of them were also found in the Wocan field (Zhou et al., 2022).

3.1.2 Vent fields of the Central Indian Ridge

Vent fields of the CIR are the most comprehensively studied among all the vents reported on the Indian mid-ocean ridges. The CIR borders the CR in the north and meets the SEIR and the SWIR at its most southern point in the Rodriguez Triple Junction (RTJ). The CIR has an average full spreading rate of 48 mm per year, which is moderate to slow spreading (Kumagai et al., 2008; Perez et al., 2021). To date, five active vent fields have been reported, including Onnuri, Dodo, Solitaire, Edmond, and Kairei (Hashimoto et al., 2001; van Dover et al., 2001; Tamaki, 2010; Nakamura et al., 2012; Ryu et al., 2019).

CIR vent communities show an immense diversity, including different morphotypes of *Chrysomallon squamiferum*. This scaly-foot snail hosts endosymbiotic sulphur-oxidizing bacteria (SOB) in its esophageal gland, which is rather unique among molluscs (Goffredi et al., 2004). Other characteristic CIR species are *Rimicaris kairei*, *Mirocaris indica*, and *Bathymodiolus marisindicus*, which are endemic to the Indian Ocean (Hashimoto et al., 2001; Watabe and Hashimoto, 2002; Komai et al., 2006). Furthermore, the vent-endemic polychaetes were discovered at Solitaire on the CIR (Nakamura et al., 2012). The copepod family Dirivultidae is the most species rich invertebrate family found in vent fields, yet members from this family have been hardly recorded at four Indian vent fields, three of which are located on the CIR (Gollner et al., 2010; Gollner et al., 2016; Lee et al., 2020; Sun et al., 2020). Onnuri, Solitaire, and Kairei

clearly emerge as extraordinary ecosystems, considering the exceptional diversity reported so far in these vent fields. Edmonds community seems to be a subset of Kairei's and may comprise source populations of both *R. kairei* and *Alviniconcha* sp. hairy snails on the CIR (Beedessee et al., 2013). Dodo is a relatively young vent field, which may explain its relatively low colonization by vent-endemic species (Nakamura et al., 2012). It was recently suggested that the CIR together with the northern SWIR (Tiancheng) forms a separate province from the CR and southern SWIR, with multiple vent sites that are of equal importance to the species pool (Zhou et al., 2022).

3.1.2.1 Onnuri (11°24'S, 66°25'E, 1990-2170m)

The Onnuri vent field was first explored with a TV-grab during a cruise on the RV *ISABU* from the Korean Institute of Ocean Science and Technology (KIOST) in 2018 (Kim and Lee, 2020). The field is ultramafic-hosted and was thought to have diffusive, clear, and low-temperature fluids from cracks in the seafloor (Kim and Lee, 2020; Kim et al., 2020). However, high temperatures were recorded during a re-visit to Onnuri (Suh et al., 2022).

During the first expedition scientists identified 21 macrofauna taxa and 65 nematodes, which were mainly distributed around cracks in the seafloor from which the hydrothermal fluids were emitted (Kim et al., 2020). Onnuri was visually dominated by three species of bathymodiolus mussels, *Bathymodiolus marisindicus*, *Bathymodiolus* sp.1, and *Gigantidas vrijenhoeki* as well as *Neolepas marisindica* barnacles (Jang et al., 2020; Kim et al., 2020). *G. vrijenhoeki* was associated with the scale worm *Branchipolynoe onnuriensis*, and both species were found exclusively at Onnuri (Jang et al., 2020). As the only member of the genus *Gigantidas* in the Indian Ocean, the *Gigantidas* mussel in Onnuri field is genetically closely related to two *Gigantidas* species from cold seeps in the Western Pacific (Jang et al., 2020; Ryu et al., 2021). This mussel species carries unique sulfur- and methane-oxidizing symbionts that differ in composition and are phylogenetically distinct from the symbionts of *B. marisindicus* at Onnuri (Jang et al., 2020). Besides *B. onnuriensis* and *G. vrijenhoeki* and their symbionts, many other organisms are only known from Onnuri. For example, Onnuri was the second Indian vent field from which copepods were retrieved so far, and the first with distinct species described alongside Solitaire (van Dover et al., 2001; Lee et al., 2020). This included a copepod species from the distant East Pacific, *Aphotopontius limatulus*, but also the novel species *Stygopontius spinifer* and *Aphotopontius kiost* which were found at Solitaire and Onnuri (Kim and Lee, 2020; Lee et al., 2020). Moreover, *Munidopsis lauensis*, *Smacigastes pumila*, *Alvinocaris markensis*, *Paralepetopsis ferrugivora*, *Lepetodrilus* sp. C, *Nereis* sp., and *Branchipolynoe seepensis* were absent at other Indian vent fields (Kim et al., 2020; Hwang et al., 2022). Three other taxa were known only from one other Indian vent field, *Archinome* sp. from Edmond (CIR), *Branchipolynoe* sp. from Kairei (CIR), and *Hesiolyra cf. bergi* from Longqi field (SWIR) (Kim et al., 2020). Besides the exceptional diversity of rare species, many taxa typical for Indian vents, including *Alvinocaris* shrimps, *Mirocaris* shrimps, *Austinograea* crabs, *Munidopsis* crabs, *Chrysomallon* snails, and *Alviniconcha* snails were present (Jang et al., 2020). Based on 16 retrieved taxa, seven trophic guilds, and four trophic levels have been recognized in the food web structure of Onnuri (Suh et al., 2022).

3.1.2.2 Dodo (18°20'S, 65°17'E, 2745m)

Dodo was visited during the cruise YK 09-13 on the RV *Yokosuka* of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) in 2009, following the detection of plume anomalies in 2006 (Kawagucci et al., 2008; Nakamura et al., 2012). The vent field is located amid the Dodo Great Lava Plain, which is a flat stretch of seafloor covered with sheet flow lava (Nakamura et al., 2012; Nakamura and Takai, 2015). Black smoker chimneys in a diameter of 15 meters were observed to emit hydrothermal fluids in 2009, but discharging was not observed in 2013 (Nakamura et al., 2012; Kawagucci et al., 2016). The system was hosted by fresh basalt and there were three main chimneys (Kawagucci et al., 2016).

Few vent megafauna species were found at Dodo, making this community emaciated in comparison to the communities of other CIR vents (Nakamura et al., 2012). However, sparsely distributed *A. rodriguezensis* crabs, patches of *R. kairei* shrimps on chimneys, some *Marianactis* sea anemones, lepetodrilid limpets and provannid snails were observed (Nakamura et al., 2012). The hydrothermal activity is suspected to be very young, which may explain the low biomass and faunal diversity (Nakamura et al., 2012). Microbial populations, however, were very abundant at Dodo (Kawagucci et al., 2016). The microbial density was several orders of magnitude higher than that at the neighboring Solitaire field and also significantly higher than those previously observed (Kawagucci et al., 2016).

3.1.2.3 Solitaire (19°33'S, 65°51'E, 2606m)

Like Dodo, the basalt-hosted Solitaire was explored during the JAMSTEC cruise YK 09-13 in 2009 after plume anomalies were detected in 2006 (Kawagucci et al., 2008; Nakamura et al., 2012). Hydrothermal fluids were emitted from a larger area (~50 x 50 m) than that of Dodo but the size was comparable to Kairei and Edmond (Nakamura et al., 2012). Three main chimneys of more than 5 m in height with mounds at their bases were present on top of talus, and extensive diffuse flows occurred from the permeable and thick talus throughout the field (Nakamura et al., 2012).

The lush vent community at Solitaire is rich in genetic, morphologic, and species diversity (Beedessee et al., 2013; Watanabe et al., 2018). For example, Solitaire was the first vent field outside of the Pacific where alvinellid polychaetes were found. Apart from Wocan, it remains the only field from which alvinellid worms have been described (Nakamura et al., 2012; Han et al., 2021). The alvinellid worms co-occurred with the *C. squamiferum* scaly-foot snail (Han et al., 2021). The white "Solitaire type" scaly-foot snail differed from the Kairei and Longqi morphotypes since they lack iron sulfide on their sclerites and shell, because Solitaire's vent fluids were iron-depleted (Nakamura et al., 2012). The scaly-foot snails and alviniconcha hairy snails at Kairei live near low-temperature fluids, whereas they were present at chimneys emitting high-temperature diffuse fluids at Solitaire (Nakamura et al., 2012). Other typical endemic vent species of Solitaire community include *R. kairei*, *M. indica*, *Bathymodiolus* mussels with lepetodrilid limpets attached, phymorhynchus gastropods, undescribed scale worms, and *Neolepas marisindica* and *Eochionellasmus* sp. barnacles (Nakamura et al., 2012; Watanabe et al., 2018). Noteworthy were the two cohorts of different sized *A. rodriguezensis* crabs at Solitaire, as they could be the source population of these bythograeid species for the CIR (Beedessee et al., 2013). The presence of copepods was another special feature of

this Indian vent community, as copepod species were previously described for only one other Indian vent field (Lee et al., 2020). The East Pacific *Aphotopontius limatulus* was shared by Solitaire and Onnuri, as well as the novel *A. muricatus* and *Stygiopontius spinifer* (Lee et al., 2020). However, the novel *Benthoxynus constrictus*, *S. horridus* and *S. geminus* were exclusively found at Solitaire (Lee et al., 2020). The first sessile barnacle of the family Chionelasmataceae outside of the Pacific was also found at Solitaire, and this novel species *Eochionelasmus coreana* has only been recorded here (Chan et al., 2020). Furthermore, the rare deep-sea snail *Desbruyeresia marisindica* was unique to Solitaire and Kairei (Watanabe and Beedessee, 2015). Other deep-sea taxa occasionally observed outside of the venting area included *Macrourid* fish, *Marianactis* anemones, *Munidopsis* squat lobsters and sea cucumbers (Nakamura et al., 2012).

3.1.2.4 Edmond (23°53'S, 69°36'E, 3290-3320m)

The basalt-hosted Edmond was the second active Indian vent discovered during the Voyage 162-13 with the RV *Knorr* and the Remotely Operated Vehicle (ROV) *Jason* in 2001 (van Dover et al., 2001). The vent field of 100 x 90 m is located in an area with cross-cutting ridge-crest structures reminiscent of the Trans-Atlantic Geotraverse (TAG) field on the nMAR (van Dover et al., 2001). Old, disaggregated sulfides, massive sulfide talus, and orange-brown iron-oxyhydroxide sediments are characteristic of Edmond, while chimney formations and venting styles varied greatly (van Dover et al., 2001).

Edmond supported a dense vent community with thousands of *R. kairei* shrimps swarming the black smokers and marianactis anemones dominating the vent periphery (van Dover et al., 2001). *R. kairei* populations between Edmond and Kairei sites showed no genetic differentiation and the former was suggested to provide the larval supply for other CIR vents since that population had the broadest size distribution (Beedessee et al., 2013). Edmond is also regarded as the source population of *Alviniconcha* sp. 3 snails (Beedessee et al., 2013). *A. rodriguezensis* crabs, *Mirocaris indica* shrimps, *branchinotogluma* scale worms, and *phymorhynchus* snails were also prevalent at Edmond (van Dover et al., 2001; Komai et al., 2006). The neolepetopsid limpet *Eulepetopsis crystallina* collected from the Edmond vent field was recently described (Chen et al., 2021c). Additionally, chemolithoautotrophic and heterotrophic bacteria not known to other vents have been isolated from Kairei and Edmond sulfides (van Dover et al., 2001).

3.1.2.5 Kairei (25°19'S, 70°02'E, 2415-2460m)

Kairei was the first active vent field discovered in the Indian Ocean during a JAMSTEC cruise with the RV *Hakuho Maru* and ROV *Kaiko* in 2000 and is one of the most visited vent fields (Hashimoto et al., 2001; van Dover et al., 2001; Komai et al., 2006). The hydrothermal activity covered an area of 40 x 80 m containing at least seven active vent sites with massive PMS deposits, including individual black smokers of more than 10 m in height (Hashimoto et al., 2001; Han et al., 2018).

Kairei is characterized by a high biomass and high diversity with thousands of *R. kairei* shrimps living in the hydrothermally active zone and marianactis anemones occurring in the vent periphery, which is similar to those in Edmond. *R. kairei* shrimps partially feed

on sulfide-oxidizing filamentous epibionts in their branchial chambers, which were found to be the dominant primary producers in the Kairei community (van Dover et al., 2001; van Dover, 2002). Underneath the blanket of shrimps, bathymodiolus mussels, alviniconcha hairy snails and scaly-foot snails (*C. squamiferum*) formed clusters of hundreds of individuals (van Dover et al., 2001; van Dover, 2002). The scaly-foot snail was discovered in Kairei vent field and occurred only at Monju site (Nakamura et al., 2012). During the second excursion to Kairei, 36 invertebrate taxa were identified, with one-third of those species being found in the Pacific but many taxa belonged to new genera (van Dover et al., 2001). The recorded taxa include neolepas barnacles, actinostolid actinians, lepetodrilus limpets, bathymodiolus mussels, mirocaris shrimps, munidopsis lobsters, and many more (Hashimoto et al., 2001; van Dover et al., 2001; Watanabe and Beedessee, 2015). Further undescribed copepods, the new neolepetopsid limpet *Eulepetopsis crystallina*, and the new amphinomid polychaete *Amphisamytha marisindica* were collected at Kairei, all of which were found in a very limited number of Indian vent fields (van Dover et al., 2001; Zhou et al., 2019; Chen et al., 2021c). Furthermore, the lobster *Munidopsis laticorpus* and the snail *Iphinopsis boucheti* are unique to Kairei; and the snails *Bruceiella wareni* and *Desbruyeresia marisindica* are known only from Kairei, Wocan, and Solitaire (Cubelio et al., 2007; Watanabe and Beedessee, 2015; Zhou et al., 2022).

3.1.3 Vent fields of the South-East Indian Ridge

With a uniform spreading rate of 69 - 75 mm per year, the SEIR separates the Indo-Australian and Antarctic plates (Sempéré and Cochran, 1997) and meets the CIR at its most northwestern point in the RTJ and the Macquarie Triple Junction in the far east of the Pacific Ocean (Sempéré and Cochran, 1997). The SEIR is perhaps the less studied region of the Indian Ocean, with only two active vent fields reported so far.

3.1.3.1 Pelagia (26°1'S, 71°3'E, 3659m)

Pelagia was discovered during the INDEX 2014 cruise with the RV *Pelagia* by the German Federal Institute for Geosciences and Natural Resources (BGR) (BGR, 2015), and thereafter visited during the BGR INDEX 2016 cruise with the RV *Pourquoi pas?* and ROV *VICTOR 6000* (Han et al., 2018).

Consistent with other vents, strong faunal zonation was recorded at Pelagia. One study examining merely a single chimney complex recorded 17 megafauna taxa, which occurred in 4 zones of proximity to the hydrothermal activity (Gerdes et al., 2019). Common Indian species found at Pelagia were the snail *C. squamiferum*, the shrimps *M. indica* and *Alvinocaris solitaire*, and the stalked barnacle *N. marisindica* (Gerdes et al., 2019). The hairy snails *Alviniconcha marisindica* and the crab *A. rodriguezensis* were highly abundant nearest to black smoker fluids, followed by the shrimp *R. kairei* and thereafter the mussel *B. marisindicus* (Gerdes et al., 2019). Note that the bathymodiolin species *B. septemdiarium* and *B. marisindicus* cannot be distinguished based on the mCOI marker gene (Breusing et al., 2015). The community at Pelagia resembled those of other CIR vent fields, with newly described holothurian species (*Chiridota hydrothermoca* sp. inc) (Smirnov et al., 2000; Gerdes et al., 2021) and fish species (*Pachycara angeloi*) (Thiel et al., 2021), which were

reported from other CIR vents as Chiridotidae and Zoarcidae (Gerdes et al., 2019). Additionally, rare microbial strains were found at Pelagia and Kairei that distinctly differed from other mid-ocean ridge samples (Han et al., 2018). They were sampled at both active venting zones and inactive areas, with much larger proportions of novel operational taxonomic units than at chimneys in most other vent ecosystems (Han et al., 2018). Such rare species are likely dormant until better conditions for growth arrive and may be responsible for large element turnovers that affect large-scale biogeochemical cycling (Han et al., 2018).

3.1.3.2 Site 21 (41°15'S, 79°06'E)

Plume anomalies were detected at Site 21 near the Amsterdam-St. Paul Plateau, and a vent-associated barnacle belonging to the genus *Neolepas* was retrieved by dredge (Scheirer et al., 1998). However, no further publications have confirmed the activity of Site 21.

3.1.4 Vent fields of the South-West Indian Ridge

The SWIR is the second most slow spreading ridge in the world with an ultraslow spreading rate of ~15 mm per year (Patriat et al., 1997). Meeting the other Indian Ridges in the RTJ, the SWIR is a tectonic plate boundary between the Antarctic and African plate (Patriat et al., 1997). Three active vent fields from the SWIR have so far been reported, namely Tiancheng, Longqi, and Duanqiao.

The SWIR comprises of two separate clusters, the south-western Longqi and Duanqiao and the north-eastern Tiancheng (Sun et al., 2020). This appears to be the case for both community composition and genetic divergence since the *C. squamiferum* population of Longqi shows low connectivity to the CIR populations (Sun et al., 2020; Zhou et al., 2022). Tiancheng however showed a striking similarity to CIR vent communities, and transform faults on the SWIR possibly form a powerful barrier to gene flow among SWIR vents (Sun et al., 2020). Geological or hydrodynamic barriers thus could be a more important determinant of connectivity between these vent communities than ridge characteristics such as spreading rate. The Longqi and Duanqiao populations share community components with the CIR, the MAR, and the East Scotia Ridge, and have been suggested to be a separate province (Zhou et al., 2018; Reid et al., 2020; Zhou et al., 2022). The northern SWIR vent Tiancheng would be part of the CIR-nSWIR province (Zhou et al., 2022). Only four species so far occur at all the three fields: the mussels *B. marisindicus*, the scale worms *B. longqiensis*, the barnacles *N. marisindica*, and the scaly-foot snail *C. squamiferum* (Zhou et al., 2018; Sun et al., 2020). An interesting feature of all SWIR vents is the absence of alvinocarid shrimp dominance, which is typical for most CIR vents. Instead, mussels were highly abundant throughout the SWIR, even though there is a large bathymetric range between these vents (1732 - 2760m) (Zhou et al., 2018).

3.1.4.1 Tiancheng (27°57'S, 63°32'E, 2682-2729m)

The basalt-hosted Tiancheng vent field lies in the most northeastern section of the SWIR on the slope of the Tiancheng seamount (Chen et al., 2018; Fang and Wang, 2021). Three vent sites have been found, of which two diffuse flow areas and one high-temperature black smoker area (Sun et al., 2020).

An initial report identified 11 taxa at Tiancheng early on when only the diffuse TC-1 vent site was known (Zhou et al., 2018), with

dense aggregations of the mussel *Bathymodiolus marisindicus* in the center, actinostolid anemones in the periphery, and the presence of bythograeid crabs *Phymorhynchus* snails, *Mirocaris* shrimps, *Phymorhynchus* sp. "Tiancheng" snails, *Neolepas marisindica* barnacles, *Polynoidae* polychaetes, and *Ophiidae* fish (Zhou et al., 2018). However, a following visit to TC-2 and Tianchang recorded 12 additional taxa, including a distinct new morphotype of the snail *C. squamiferum* and the snail *Desbruyeresia* cf. *marisindica* (Sun et al., 2020). The "Tiancheng type" scaly-foot snail was dominant here and had reddish-brown zinc sulfide deposits on its dirty white scales and a brown shell (Sun et al., 2020). Some taxa that are uncommon in the Indian Ocean were recorded at Tiancheng, including undescribed copepods from the family Dirivultidae, the sea cucumber *Chiridota*, and the polychaete *Ophryotrocha* (Sun et al., 2020). Interestingly, Tiancheng's vent community was more similar to the CIR vent fields and had low connectivity to other SWIR vent fields (Zhou et al., 2018; Sun et al., 2020). Species that were reported for CIR vents but not at the other SIWR vents include the limpet *Eulepetopsis crystallina*, crab *A. rodriguezenis*, and mussel *B. marisindicus* (Sun et al., 2020; Chen et al., 2021c).

3.1.4.2 Longqi (37°47'S, 49°39'E, 2755m)

Longqi was the first active vent field discovered on an ultraslow mid-ocean ridge worldwide, and is by far the most explored vent field on the SWIR (Tao et al., 2012; Zhou et al., 2018). The basalt-hosted field has three vent sites that extend laterally over ~1000 m (Tao et al., 2012; Zhou et al., 2018). The first vent site was identified during the COMRA DY19 cruise in 2007 and two other vent sites were explored during the COMRA DY20 cruise in 2008/2009 (Tao et al., 2012). Temperature of discharging fluids was over 300°C but diffuse venting of clear fluids was also observed (Copley et al., 2016).

Longqi harbors a stunning vent community of about ~35 identified taxa to date with a unique biodiversity and a complex zonation pattern (Zhou et al., 2018; Zhou et al., 2019; Chen et al., 2021a; Chen et al., 2021c), including the scaly-foot snail *C. squamiferum*, alvinocaridid shrimps *R. kairei* and *M. indica*, stalked barnacle *N. marisindica*, and mussel *B. marisindica* (Zhou et al., 2018). At Longqi, dense shrimp aggregations occurred only in small quantities (Zhou et al., 2018). A lack of suitable substrate might have prevented the dominance of *R. kairei* at Longqi, since high-temperature fluids were only released from chimney summits (Zhou et al., 2018). Dominant species were, in distance from the venting, the scaly-foot snails *C. squamiferum*, peltospirid snails *Lepetodrilus* sp. "SWIR" and *Gigantopelta aegis*, mussel *B. marisindica*, and barnacle *N. marisindica* (Copley et al., 2016). The black *C. squamiferum* Longqi population was highly connected to the nearby Duanqiao population but exhibited low connectivity to the CIR populations (Chen et al., 2015; Zhou et al., 2018; Sun et al., 2020). Three polychaetes of the same genus occurred at Longqi: *Amphisamytha marisindica* which likely has an ancestor in the East Pacific, and *Amphisamytha collaris* and *Amphisamytha* sp. Longqi which were closely related to a Southwest Pacific species (Zhou et al., 2019). To date, at least 12 species have been recorded only in this vent field: the peltospirid snails *Dracogyra subfuscus*, *Lirapex politus* and *Lirapex felix*, *Phymorhynchus* sp. "SWIR", the lobster *Munidopsis* sp. "SWIR", the limpet *Neolepetopsis ardua*, and the polychaetes *Ophryotrocha jiaolongi*, *Amphisamytha collaris*, *Amphisamytha* sp.

Longqi, Polynoidae sp. 2, Polynoidae n. gen. n. sp. “655”, and *Laonice* sp. “Longqi” (Chen et al., 2017b; Zhang et al., 2017; Zhou et al., 2018; Zhou et al., 2019; Chen et al., 2021a; Chen et al., 2021c). The peltospirid snail *Gigantopelta aegis*, scale worm *Peinaleopolynoe* sp. “Dragon”, limpet *Lepetodrilus* sp. “SWIR”, and yeti crab *Kiwa* sp. “SWIR” occur only in one other vent field, the neighboring Duanqiao (Zhou et al., 2018). A unique feature of Longqi is the co-occurrence of five peltospirids snails, all within the same assemblage (Chen et al., 2021a).

3.1.4.3 Duanqiao (37°39'S, 50°24'E, 1732m)

The basalt-hosted Duanqiao vent field was discovered during the COMRA DY20 cruise (Tao et al., 2014). It was first believed to be an inactive field, until weak fluid emissions from a large sulfide edifice were observed with a TV-grab during the COMRA DY34 cruise in 2015 (Zhou et al., 2018). While only diffuse venting was observed from the manned submersible *Shenhaiyongshi*, high fluid temperatures were recorded during the same 2018/2019 cruise with the RV *Tansuoyihao* (Liao et al., 2019).

Duanqiao is less studied than the other two SWIR vents. However, 13 taxa were collected during the DY35 cruise (Zhou et al., 2018). Duanqiao shared ten of those taxa with Longqi, including the novel species *Gigantopelta aegis* snails, *Lepetodrilus* sp. “SWIR” limpets, and *Peinaleopolynoe* sp. “Dragon” scale worms that were so far not found at other vent fields (Zhou et al., 2018). *B. marisindicus* mussels and *Neolepas marisindica* barnacles were the most abundant species in both the Duanqiao and Longqi vent fields (Sun et al., 2020). At first glance, Duanqiao appeared to be a subset of the neighboring Longqi, yet multiple species were recorded at Duanqiao but not Longqi, including the gastropod *Desbruyeresia* sp. “SWIR” and the sea spiders *Sericosura bamberei*, *S. heteroscala*, and *S. duanqiaoensis*, of which the latter was a newly discovered species (Wang et al., 2018; Zhou et al., 2018). The scaly-foot snail *C. squamiferum* population at Duanqiao also differed from those in other vent fields, with a black shell and white sclerites (Zhou et al., 2018). This “Duanqiao type” snail showed very low genetic divergence from Longqi, and the morphotype is the result of Duanqiao’s distinct chemical environment (Zhou et al., 2018).

3.2 Generic and field-by field characteristics of active vent fields on the Indian Ocean ridges applicable to VME, EBSA, and PSSA criteria (Appendix 3)

By their very nature, vent fields globally, including those on the Indian Ocean Ridges, share fundamental ecological characteristics relevant to each of the 9 criteria assessed (Gollner et al., 2021). Criteria that are met by all vent fields include 1) Uniqueness and rarity, 2) Functional significance, 3) Fragility, 4) Life history traits of component species that makes recovery difficult, 5) Structural complexity, 6) Biological productivity, 7) Biological diversity, 8) Naturalness, and 9) Ecosystem services (Appendix 1, Appendix 2). Our scientific assessment of 12 vent fields on the Indian Ocean Ridges shows that all vent fields meet all scientific criteria for protection (Table 2 and Figure 2). A detailed field-by field analyses is also given in Appendix 3.

The Indian Ocean vent fields are unique and rare as they host small, island-like vent ecosystems with distinctive biotic and abiotic features (Han et al., 2018; Wang et al., 2018; Kim et al., 2020; Chen et al., 2021a; Han et al., 2021) (Table 1). Autotrophic microorganisms use chemosynthesis to fix carbon, as animal symbionts (e.g. *Alvinichona* or *Bathymodiolus* foundation species), bacterial mats or free-living cells (Dick, 2019). All active vents are of functional significance, as they support primary production by microorganisms, serve as discrete feeding area, and are essential for the growth, survival, reproduction, and persistence of vent-endemic species (van Dover, 2001; Mullineaux et al., 2018). The juveniles and adults of vent-endemic (vent-obligate) taxa are adapted to the extreme chemical and physical conditions of the vent habitat and thrive in these specialized (unique) ecosystems. Many animal species and microbial strains found in the Indian Ocean are endemic to this specific region, or even restricted to a single vent field (Han et al., 2018; Dick, 2019). Structural habitat complexity and local chemical gradients create niches that expand biodiversity on a genetic, morphological, functional, and species level (van Dover, 2001; Dick, 2019).

Various Indian vent-endemic species so far have only been found in a single vent field, like the limpet *Neolepetopsis prismatica*, the sessile barnacle *Eochionelasmus coreana*, and the sea spider *Sericosura duanqiaoensis* (Wang et al., 2018; Chan et al., 2020; Chen et al., 2021c). Even when a species is present at multiple vents, local fluid composition may influence phenological expression (Minic et al., 2006; Ramirez-Llodra et al., 2007). For instance, there are at least 5 different morphotypes of the scaly-foot snail *C. squamiferum* due to the different chemical profiles of Solitaire, Kairei, Tiancheng, Longqi, and Duanqiao vent fluids. Furthermore, all Indian vents sustain rich microbial communities that are mostly shaped by local geochemical circumstances, often with a large variability between vent sites from a single field (Dick, 2019). Symbiotic species, such as *Crysmallon squamiferum* and the mussel *Gigantidas vrijenhoeki*, are associated with novel microbial strains (Goffredi et al., 2004; Jang et al., 2020). Novel chemolithoautotrophic and heterotrophic microbes were isolated from sulfides, sediments, and plumes of the Indian vent fields (van Dover et al., 2001; Ding et al., 2017; Hu et al., 2020).

Many benthic species rely on pelagic larval stages to maintain population and genetic connectivity (Mullineaux et al., 2018; Chapman et al., 2019). There are many uncertainties surrounding recruitment relating to reproduction, larval development, larval dispersal, and settlement (Perez et al., 2021). However, some Indian-endemic species are thought to have low dispersal abilities due to negatively buoyant larvae or eggs, including the peltospirid snails *Chrysmallon squamiferum*, *Gigantopelta aegis*, *Dracogyra subfuscus*, and *Lirapex politus* (CR) (Chen et al., 2014), or the crab *Kiwa* sp. “SWIR” (Reid et al., 2020). Habitat degradation and fragmentation due to anthropogenic disturbance may lead to local loss of biodiversity (Pardini et al., 2017; van Dover et al., 2017; Niner et al., 2018) and ecosystem services (Le et al., 2017).

Currently, 11 vent species found in the Indian Ocean are on red list of the IUCN⁴, including the vulnerable mussel *Bathymodiolus*

⁴ <https://www.iucnredlist.org/search>

TABLE 2 Application of the scientific criteria for identifying hydrothermal ecosystems in need of protection at 12 Indian vent fields, based on the literature used in this review. Criteria definition follows Gollner et al. (2021) (see Appendix 1, 2).

Criterion	Subcriteria	Active vent fields known from the Indian mid-ocean ridges											
		Daxi	Wocan	Tianxiu	Onnuri	Dodo	Solitaire	Edmond	Kairei	Pelagia	Tiancheng	Longqi	Duanqiao
1. Uniqueness or rarity	1.1 habitats that contain endemic species	+	+	+	+	+	+	+	+	+	+	+	+
	1.2 habitats of rare, threatened or endangered species; only in discrete areas	+	+	+	+	+	+	+	+	+	+	+	+
	1.3 nurseries or discrete feeding, breeding or spawning areas	+	+	+	+	+	+	+	+	+	+	+	+
	1.4 unique or unusual biotic or abiotic features (chemical, physical, geological)	+	+	+	+	+	+	+	+	+	+	+	+
2. Functional significance	2.1 for survival, function (e.g. feeding), spawning/reproduction, or recovery of species	+	+	+	+	+	+	+	+	+	+	+	+
	2.2 for particular life history stages (e.g. nursery grounds or rearing areas, migratory routes for fish, reptiles, birds, mammals, invertebrates)	+	+	+	+	+	+	+	+	+	+	+	+
	2.3 for rare, threatened, or endangered marine species	+	+	+	+	+	+	+	+	+	+	+	+
3. Fragility	3.1 An area that contains a relatively high proportion of sensitive habitats, biotopes or species that are functionally fragile (highly susceptible to degradation or depletion by human activity or by natural events)	+	+	+	+	+	+	+	+	+	+	+	+
4. Life history	4.1 slow growth rates	-	-	-	-	-	-	-	-	-	-	-	-
	4.2 late age of maturity	-	-	-	-	-	-	-	-	-	-	-	-
	4.3 low or unpredictable recruitment	+	+	+	+	+	+	+	+	+	+	+	+
	4.4 long-lived species	=	=	=	=	=	=	=	=	=	=	=	=
5. Structural complexity	5.1 complex physical structures created by biotic and abiotic features	+	+	+	+	+	+	+	+	+	+	+	+
	5.2 ecological processes are dependent on these structured physical systems	+	+	+	+	+	+	+	+	+	+	+	+
6. Biological diversity	6.1 An area that contains comparatively higher diversity of ecosystems (including high diversity associated to complex structures), habitats, communities, or species, or has higher genetic diversity	+	+	+	+	+	+	+	+	+	+	+	+

(Continued)

TABLE 2 Continued

Criterion	Subcriteria	Active vent fields known from the Indian mid-ocean ridges											
		Daxi	Wocan	Tianxiu	Onnuri	Dodo	Solitaire	Edmond	Kairei	Pelagia	Tiancheng	Longqi	Duanqiao
7. Biological productivity	7.1 An area that has a particularly high rate of natural biological production. Such productivity is the net result of biological and physical processes which result in an increase in biomass	+	+	+	+	+	+	+	+	+	+	+	+
8. Naturalness	8.1 An area with a comparatively higher degree of naturalness as a result of lack of or low level human-induced disturbance or degradation	+	+	+	+	+	+	+	+	+	+	+	+
9. Ecosystem services	9.1 provisioning services, such as food, materials and energy, which are directly used by people (including marine genetic resources and bioprospecting, bioinspired materials, bioinspired processes)	+	+	+	+	+	+	+	+	+	+	+	+
	9.2 regulating services, that cover the way ecosystems regulate other environmental media or processes (including climate regulation, biological pump and carbon sequestration)	+	+	+	+	+	+	+	+	+	+	+	+
	9.3 cultural services that are related to the cultural or spiritual needs of people. These include spiritual services, aesthetic services, recreation, education (e.g. an area that offers an exceptional opportunity to demonstrate particular natural phenomena), and science (e.g. a research area that provides suitable baseline monitoring conditions because it is in near natural condition)	+	+	+	+	+	+	+	+	+	+	+	+
	9.4 supporting services, such as ecosystem processes and functions that underpin the other three types of services (including primary production, nutrient cycling)	+	+	+	+	+	+	+	+	+	+	+	+

Color codes for level of relevance for each criterion: Green (+): high, Yellow (=): medium, Red (-): low. Details of the scientific evidence supporting each score are provided in [Appendix 3](#).

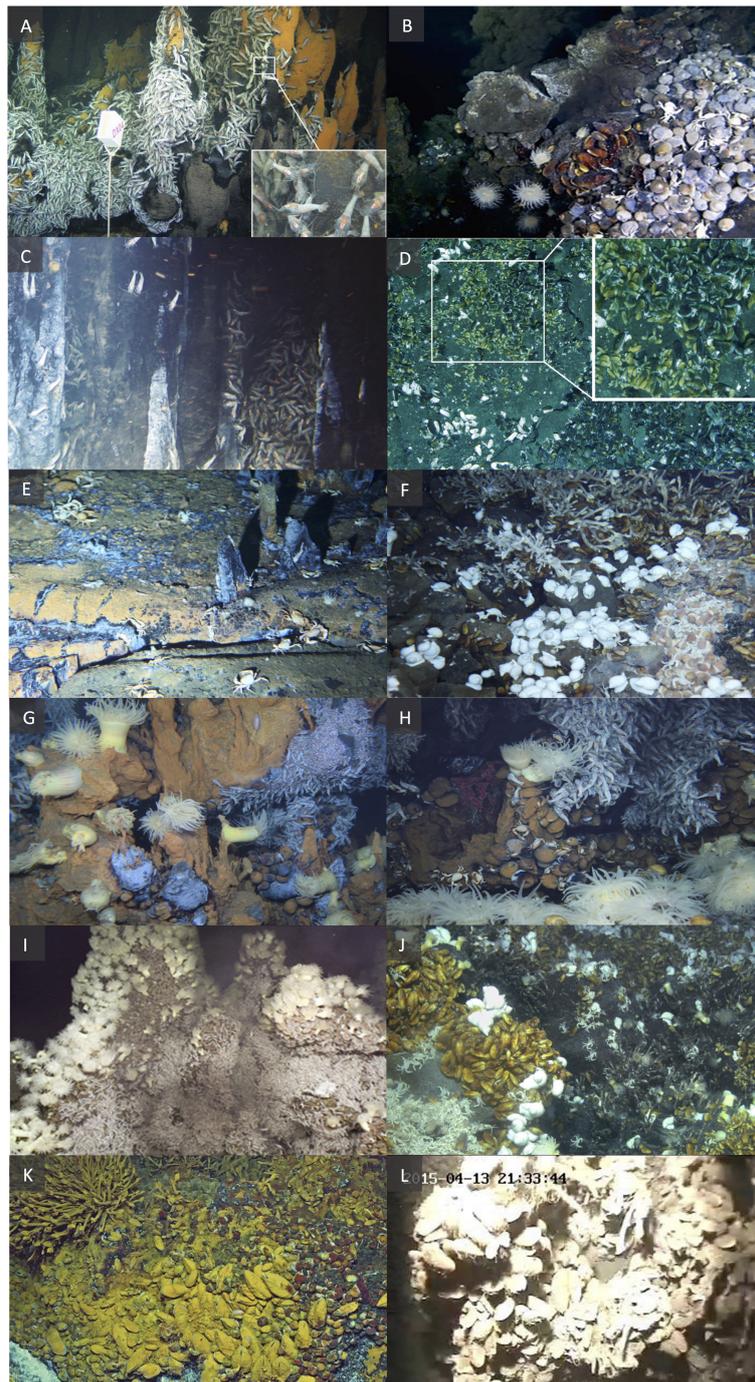


FIGURE 2

A selection of ecological features for each active Indian hydrothermal vent. (A) Extensive swarms of alvinocaridid shrimps at Daxi. (B) Snails, mussels, crabs, shrimps, and anemones near a black smoker at Wocan. (C) Alvinocaridid shrimp swarming on massive sulfide structures at Tianxiu. (D) Dominant mussel species *Bathymodiolus marisindicus* (yellow brown) and *Gigantidas vrijenhoeki* (dark brown) at Onnuri. (E) Sparsely distributed anemones and bythograeid crabs at Dodo. (F) Diffuse flow vent assemblage with mussels, different snails and barnacles at Solitaire. (G) Dense alvinocaridid shrimp aggregations surrounded by snails and anemones at Edmond. (H) High densities of shrimps, snails, crabs and anemones at Kairei. (I) Layered shrimp, mussel and anemone aggregations on a chimney structure at Pelagia. (J) Mussel beds with patches of snails, crabs and shrimps at Tiancheng. (K) Tiamat chimney dominated by peltospirid snails, alongside dense mussel and barnacle colonies at Longqi. (L) Mussel dominance at Duanqiao. Image credits; (A) Wang et al., 2021 (rightslink # 5441960651432); (B) Qiu et al., 2021 (rightslink # 5441961199302); (C) Zhou et al., 2022 (CC BY); (D) Jang et al., 2020 (rightslink # 5441970372620); (E, F, G, H) Beedessee et al., 2013 (CC BY); (I) Gerdes et al., 2019 (CC BY); (J) Sun et al., 2020 (CC BY); (K) Chen et al., 2021a. (rightslink # 5443111350852); (L) image from powerpoint presentation by Dr C.B. Soon at ISA workshop in Poland in 2018 (photo courtesy of COMRA).

marisindicus (VU), the endangered snails *Alviniconcha marisindica*, *Chrysomallon squamiferum*, *Debruyeresia marisindica*, and endangered mussel *Bathymodiolus septemdierum* (EN), as well as the critically endangered snails *Gigantopelta aegis*, *Iphinopsis*

boucheti, *Dracogyra subfuscus*, *Lirapex politus*, *Bruceiella wareni*, and the mussel *Gigantidas vrijenhoeki* (CR). The first three species are characteristic members of the Indian vent metacommunities, as are the bythograeid crab *Austinograea rodriguezensis*, the stalked

barnacle *Neolepas marisindica*, and the alvinocaridid shrimps *Rimicaris kairei* and *Mirocaris indica*. Although these species are common, they are absent at some vent fields (Table 1).

To date, vent fields in the Indian Ocean remain among the most pristine ecosystems on Earth as they have been visited by scientists only in recent years (Menini and van Dover, 2019; Gollner et al., 2021). Moreover, these ecosystems have an outstanding potential to contribute genetic resources and inspire biomedical, biotechnological and commercial applications (Harden-Davies, 2017; Adam et al., 2020; Orcutt et al., 2020). For instance, the ‘armor design’ of *C. squamiferum* may lead to innovations in military equipment, vehicles, construction machinery or astronautics (Yao et al., 2010). These ecosystems also harbor rich microbial communities that are sources of natural pharmaceuticals since some unique bacteria and archaea have so far been reported only from SWIR and CIR vents (Thornburg et al., 2010; Han et al., 2018; Dick, 2019; Dasgupta et al., 2021). More novel operational taxonomic units have been found at Edmond and Kairei than at most other vents (Han et al., 2018).

4 Discussion

Hydrothermal ecosystems in the Indian Ocean were discovered and explored much later than those in other regions, yet the uniqueness and vulnerability of each active Indian vent stands out. The application of scientific criteria for protection of these vents highlights the need for protection of active vent ecosystems in the Indian Ocean.

4.1 The ecology of Indian Ocean vent fields

The present review outlines the historic role of this region in supporting population connectivity among biogeographic provinces and reveals the similarities and differences between vents of the Indian ridges. The Indian Ocean was hypothesized to be a corridor between the Atlantic and Pacific biological communities in the past. Here, we recognize the importance of the Indian population as both a copious source of unique vent species and a central point on the global ocean floor, with widespread connections to the Atlantic, Antarctic, West-, and East-Pacific (van Dover et al., 2001; Rogers et al., 2012; Watanabe and Beedessee, 2015; Perez et al., 2021). The Indian meta-population is much like a patchwork, with clear subpopulations that may even belong to separate provinces, and are strongly linked to particular regions (Sun et al., 2020; Han et al., 2021; Perez et al., 2021).

For example, both the nSWIR-CIR and CR have a bias towards the West Pacific meta-community, with taxa like neolepas stalked barnacles, alviniconcha snails, and bythograeid crabs common in both communities (van Dover et al., 2001; Watanabe et al., 2018). The CR was also suggested to have a direct biogeographic linkage to the East Pacific because different *Amphisamytha* polychaetes from the CR are genetically closely related to their East Pacific counterparts (Zhou et al., 2019).

While nSWIR-CIR and CR vents were dominated by *Rimicaris* and *Mirocaris* shrimp assemblages reminiscent of the MAR, except

Onnuri, sSWIR vents had high abundances of mussels and snails (Watanabe and Beedessee, 2015) (Table 1). Consistent with its relative geographical position, sSWIR vents seem to have strong ties to the East Scotia Ridge (ESR) in the Southern Ocean, characterized by high abundances of the stalked barnacle *Neolepas* spp., yeti crab *Kiwa* spp., and peltospirid snail *Gigantopelta* spp. (Chen et al., 2017a; Zhou et al., 2019). Similarity in community structure at species level to the ESR decreases over distance, as there is a clear continuum in community structure along the SWIR, CIR and CR (Sun et al., 2020). A proposed dispersal pathway from the Southern Pacific to the CIR via the SEIR was contradicted by molecular evidence on neolepas barnacles, indicating historic dispersal through the Southern Ocean was more likely (Watanabe et al., 2018). Still more research is needed, as the SEIR is the least studied Indian ridge and the only known active vent is merely 167 km away from Kairei, which may explain the high affinity between Pelagia and CIR vent communities.

The concept of “nearest vent, dearest friend” is further exemplified by the Tiancheng vent field, which is a nSWIR vent highly similar to CIR vents (Sun et al., 2020; Zhou et al., 2022). Besides the immediate proximity to the CIR vent fields and Kairei in particular, another important determinant of vent connectivity may be ridge continuity. Major transformation faults exist on the SWIR between Tiancheng and the other SWIR vents that presumably severely restrict larval dispersal (Sun et al., 2020). Previous genetic analyses in the East Pacific have also indicated animal dispersal is often constrained by geographical barriers common on mid-ocean ridges, such as trenches, transform faults, and microplates (Beedessee et al., 2013).

Consequently, future research should focus not only on biodiversity and functioning of single vent fields but also vent fields at a network scale. To date, only four studies have examined genetics across at least two Indian ridges and reported population connectivity of six different species (Chen et al., 2015; Watanabe et al., 2018; Sun et al., 2020; Zhou et al., 2022). However, recent work on population plasticity and genetic structure of the deep-sea mussel *Bathymodiolus platifrons* (Xu et al., 2017), the deep-sea limpet *Bathymacrea nipponica* (Xu et al., 2021), and the deep-sea squat lobster *Shinkaia crosnieri* (Xiao et al., 2020) clearly showed that populations of these species from vent and cold-seep fields thousands of kilometers apart in the west Pacific Ocean could be well connected. Hydrodynamics plays a more important role than habitats or geographic distance in driving the gene flow and divergence for these populations (Xiao et al., 2020; Xu et al., 2021). These findings (and unpublished data on population genetics and connectivity from Qian Pei-Yuan’s laboratory) clearly demonstrate that population genomic surveys should be applied to future population connectivity studies of deep-sea animals.

Furthermore, there are many inferred active vent fields that have not been thoroughly studied yet. Based on the Interridge database, biological communities of 3 vents on the CR, 16 vents on the CIR, 50 vents on the SEIR and 22 vents on the SWIR wait to be described, and even more wait to be discovered. Disturbances at single vent fields may affect entire metacommunities due to the source-sink dynamics of vent species (Vrijenhoek, 2010; Mullineaux et al., 2018). Yet mining is likely to target vent fields with the largest PMS deposits, which may often be older vent fields with more developed community structures.

Such vent fields can be the most diverse and likely serve as the sources of larval supplies for other vents. Before we decide on particular vent fields as representative management areas, characterization of individual locations must be done adequately while the paucity of knowledge on inter-vent connectivity within and between biogeographic provinces should also be addressed.

4.2 Governance

Previously, the International Guidelines of Deep-Sea Fisheries in the High Seas published by the FAO stated that vent fields and their associated communities “often display characteristics consistent with possible VMEs” (FAO, 2009). Lost City, Broken Spur, TAG, and Snake Pit are four active vent fields on the nMAR that have already been recognized as EBSAs by the CBD⁵ and in the same CBD report it was suggested other MAR vent fields should also be considered to be EBSAs. Moreover, an area of 135,688 km² comprising 2 inferred active vents on the CIR has already been designated and implemented as a Benthic Protected Area (BPA) by the Southern Indian Ocean Fishery Agreement (SIODFA). The SIODFA BPA protects from deep-sea and mid-water trawling (Menini and van Dover, 2019) but does not prohibit other human activities. These measures are in line with the mandate to take precautionary action when managing deep-sea hydrothermal vent ecosystems (Levin et al., 2017b; van Dover et al., 2018).

Ten Indian deep-sea hydrothermal vent species are currently red-listed by the IUCN, with more than half being Critically Endangered.⁴ This number is likely to increase, as more deep-sea species are considered by the IUCN, due to the imperiled status of Indian vents compared to other vents globally (Thomas et al., 2021). Gollner et al. (2021) suggested that active nMAR vents are ecosystems in need of protection. In this review, we conclude that all active vent fields in Indian Ocean are also in need of protection, calling for a global effort to protect these unique ecosystems.

5 Conclusion

Hydrothermal vents are extraordinary ecosystems that may be at risk of serious harm due to future deep-sea mining or other anthropogenic impacts. This review provides an overview of the unique geochemical and biological attributes of each confirmed active vent in the Indian Ocean. The Indian meta-population was long hypothesized to be a mixture of Atlantic and Pacific communities yet is instead composed of taxa known from other biogeographic provinces and vent species unique to the Indian Ocean. Criteria previously used to classify vulnerable and significant marine ecosystems were used to assess vents at the Indian mid-ocean ridges. All active vent fields in the Indian Ocean meet the scientific criteria for protection, and both the high degree of uniqueness and fragility of

these ecosystems stand out. This review and other scientific analyses underpin the important role of science in the ocean sector development. Future efforts should be focused on understanding population connectivity (gene flow), life-history, convergence, and divergence of deep-sea fauna in order to develop solid scientific evidence based regional environmental management plans for active hydrothermal ecosystems in the Indian Ocean.

Author contributions

NM drafted the article, P-YQ, YG, and SG contributed to the writing. All authors contributed to the article and approved the submitted version.

Funding

This work is supported by the UU-NIOZ project “Protecting deep seabed hydrothermal vent fields through area-based management tools” (to SG and Erik Molenaar), the grant from the Major Project of Basic and Applied Basic Research of Guangdong Province (2019B030302004), the Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou) [2021HJ01, SMSEGL20SC01], and GRF grant from the HKSAR government (16101822) to P-YQ.

Acknowledgments

The authors would like to thank Cindy L. van Dover and Terue Kihara for their valuable comments on a previous version of this manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.1067912/full#supplementary-material>

⁵ <https://chm.cbd.int/database/record?documentID=204107>

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