

Research Article

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Faunal community of a new hot vent field on the Amami Rift

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Abstract

Deep-sea hydrothermal vents host chemosynthesis-based ecosystems inhabited chiefly by specially adapted animals that do not live anywhere else, and depth has been shown to be a major driver of species composition at vents around Japan. Though the Ryukyu region in southern Japan is home to many hot vents, only two – Minami-Ensei Knoll and Yoron Hole – have been found shallower than 1000 m. Here, we report the discovery of a new vent field on the Amami Rift northwest off Amami Ōshima at 630 m deep. A total of 29 macrofaunal species were recorded from Amami Rift, including 19 vent specialists. Comparison of species composition across the three shallow Ryukyu vents revealed only three shared species, highlighting that all three display distinct community structure. Amami Rift exhibits distinct zonation patterns and is generally more similar to Minami-Ensei than Yoron Hole, but the presence of key taxa such as the sulphide worm *Paralvinella* and the mussel '*Bathymodiolus*' *platifrons* as well as the absence of the symbiotic squat lobster *Shinkaia* and the limpet *Lepetodrilus* exemplify its difference with Minami-Ensei. Furthermore, the non-vent specific predators seen in these two sites were completely different. Overall, the Amami Rift vent field can be considered a shallow vent with a unique set of fauna, warranting future research on the mechanisms shaping disparate macrofaunal diversity between nearby shallow vents such as Amami Rift and Minami-Ensei. The unusual geological setting of Amami Rift at the converging point of Okinawa Trough and Ryukyu Arc may influence fluid chemistry to drive such differences.

Introduction

Hydrothermal vents are 'hotspots' of biology in the typically nutrient-poor deep ocean, powered by microbial chemosynthesis taking advantage of reducing chemicals in the hot vent fluid. The first hydrothermal vent in Japan, the JADE site of Izena Hole in Okinawa Trough, was discovered in 1988 by a joint German-Japanese cruise on-board R/V *SONNE* (Halbach *et al.*, 1989). Since then, at least 13 active vent fields have been located in the region of the Ryukyu subduction system, mostly in the Okinawa Trough and some on the Ryukyu Arc (Nakamura *et al.*, 2015; Brunner *et al.*, 2022). These vents are all located in a basin to the west of Ryukyu Islands (Figure 1A) (Mitarai *et al.*, 2016). With only two narrow, deep openings (Tokara Valley and Kerama Gap) along the whole system, this basin is largely enclosed for larval dispersal below 600 m depth (Kizaki, 1986). This has led to these vents together harbouring a unique set of specialist animal species distinct from other systems in the western Pacific (Brunner *et al.*, 2022).

The Amami Rift, previously known as the Amami Caldera, is located around 50 km northwest of Amami-Oshima, at the intersecting point between the volcanic front of the central Ryukyu Arc and rifting activity of the Okinawa Trough (Minami *et al.*, 2022). Surveys using ship-based and autonomous underwater vehicle (AUV) acoustic echo-sounding has revealed several rising gas plumes around 630 m depth, a typical feature of vent orifices in the Ryukyu region due to the rich gas content of their vent fluids (Nakamura *et al.*, 2015); further confirmed with smoke-like plumes visualised by the AUV's side-scan sonar imagery plus temperature anomalies (Minami *et al.*, 2022). Known active vent fields in the Ryukyu region mostly occur below 1000 m (Brunner *et al.*, 2022), making this a shallow site.

Depth is known to be a major factor driving biodiversity in the deep ocean, both directly by being an important physiological boundary for larval dispersal and settlement and also indirectly reflecting the influence of food availability, biotic interactions, among other factors (Rex and Etter, 2010). The species compositions of chemosynthetic ecosystems around Japan appear to be strongly influenced by depth along with vent fluid chemistry and sediment cover (Fujikura *et al.*, 2000; Kojima, 2002; Nakajima *et al.*, 2014; Watanabe and Kojima, 2015), while other factors such as lava type have also been shown to be major drivers in other vents (Podowski *et al.*, 2010; Beinart *et al.*, 2012). Only two Ryukyu vent fields at a similar depth to the Amami Rift acoustic anomalies have been reported with macrofaunal lists, including Minami-Ensei Knoll and Yoron Hole (Watanabe and Kojima, 2015). The faunal composition of Minami-Ensei at 600–730 m deep has been found to differ from other deeper systems due to the presence of numerous species only found in this site (Hashimoto *et al.*,



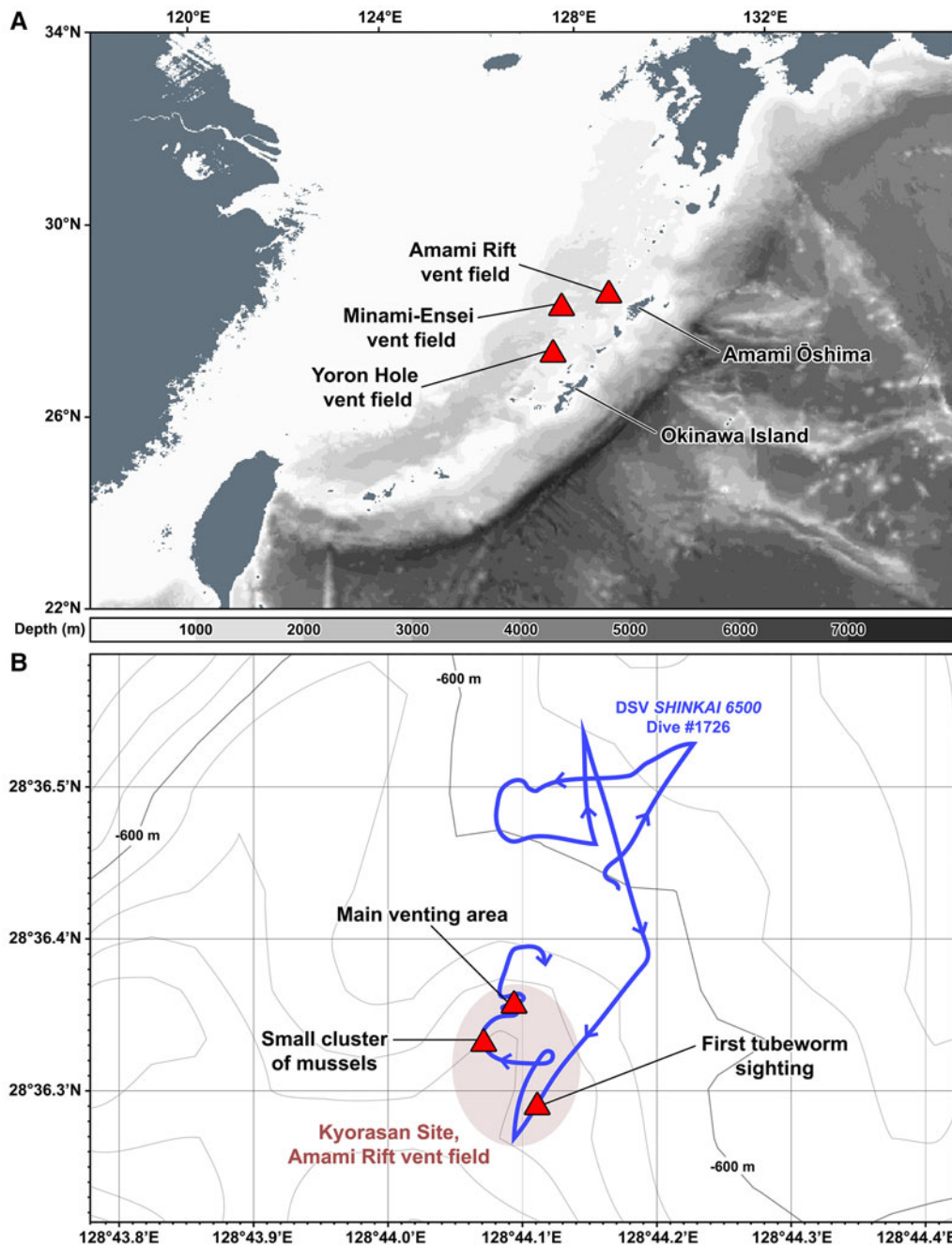


Figure 1. Maps of the Amami Rift hydrothermal vent field: A, Ryukyu region in southern Japan showing the general location of the Amami Rift, Minami-Ensei, and Yoron Hole vent fields; B, Close-up map showing dive track of HOV *SHINKAI 6500* dive #1726 and points of interest (bathymetric contours are 10 m apart); the light red oval indicates the estimated extent of the Kyorasan site, including the outskirts tubeworm colonies.

1995; Okutani, 2001; Watanabe and Kojima, 2015; Brunner *et al.*, 2022). Yoron Hole at 580 m deep is also unusual in having very low species richness (10 species) and without mussel assemblages (Watanabe and Kojima, 2015). The composition of animal communities on the Amami Rift may therefore also be peculiar. Here, we carried out the first submersible dive at the Amami Rift, confirming the presence of an active hydrothermal vent field and report its associated animals. We also compare this with other known nearby shallow sites, and discuss implications in terms of vent biogeography in the Ryukyu region.

Materials and methods

From the acoustic water column anomalies ('bubble plumes') detected in the Amami Rift, we targeted a northern cluster (called

'Area A' in Minami *et al.*, 2022: figs. 2b, 4d) of signals for ground-truthing. During R/V *YOKOSUKA* cruise YK23-16S (15–29 September 2023), we conducted a dive using the human-occupied vehicle (HOV) *SHINKAI 6500* on this area (dive #1726 on 19 September 2023; Figure 1A). A high-definition video camera (SONY FCB-H11, 1920 by 1080 pixels) and a digital still camera (Olympus E-PL6, 16 megapixels) mounted on the HOV *SHINKAI 6500* were used for *in situ* seafloor imagery. A CTD (conductivity, temperature, and depth) sensor (Seabird SBE-19) on top of the submersible was used to record the ambient water temperature approximately 2–3 m from the seafloor. Temperature of focused flow venting was taken using the HOV *SHINKAI 6500*'s temperature probe, while a RINKO III optical sensor (JFE Advantech Co., Ltd.) was used to measure the temperature of animal communities prior to sampling. Each

temperature measurement was taken over a two-minute period. Prior to the dive, seafloor bathymetry was obtained using a multi-beam echosounder (Kongsberg EM122) equipped on R/V YOKOSUKA and maps were drawn using the software Generic Mapping Tools (Wessel *et al.*, 2019).

Animals were collected using either a six-chambered suction sampler or directly collected using the submersible's manipulator into a bio box. Upon recovery on-board the research vessel, animal samples were immediately taken to a cold room (4°C). The animals were sorted, dissected, and identified morphologically under a stereomicroscope (Leica S9D or MS5). Specimens were fixed and preserved in 10% buffered formalin or directly in 99% ethanol. Macrophotography was carried out using digital single-lens reflex cameras including Canon EOS 5Ds R, Nikon D5600, and Olympus E-M1, and post-processed in Adobe Photoshop CC 2023.

Results

We successfully located a hydrothermally active area on the Amami Rift during HOV *SHINKAI 6500* dive #1726 (Figures 1 & 2), presumably responsible for the cluster of acoustic anomalies detected in 'Area A' of Minami *et al.* (2022). In the earlier part of the dive (Figure 1B), we explored an area around the northernmost acoustic anomalies in Area A (28°36.4'N-28°36.5'N, 128°44.1'E-128°44.2'E) but did not locate any signs of venting. Then we headed towards more southerly points where potential plume signals have been detected, and encountered an area where several tubeworms including *Lamellibrachia columna* and *Alaysia* sp. (Figure 2H) were growing on rocks (28°36.2905'N, 128°44.1053'E, 625 m deep). We continued south but soon the tubeworms disappeared, and we turned north instead. Eventually, chains of gas bubbles and a small cluster of '*Bathymodiolus japonicus*' mussels on pumice (28°36.341'N, 128°44.071'E, 626 m deep) appeared at approximately 100 m northwest of the point where we first saw tubeworms. From here the rocks became overgrown by more sponges, likely a result of increased organic input from the hydrothermal vent, combined with a higher density of tubeworms. Following these sponge-covered rocks, we soon discovered an active hydrothermal vent (Figure 2A) with dense aggregations of animals across an area of about 20 m by 30 m (28°36.360'N, 128°44.093'E, 628 m deep). We here name this the Kyorasan (meaning 'beautiful' in Amami dialect) site of the Amami Rift hydrothermal vent field. The average bottom water temperature measured by the submersible before arrival at the Kyorasan site was 10.46°C (SD = 0.10), but was elevated to 11.27°C (SD = 0.17) during our stay at the hydrothermally influenced area.

The Kyorasan site lacks discrete chimney structure, and instead vigorous venting takes place directly from a patch of flat seafloor at the centre of activity (about 5 m by 10 m in area). Diffuse flow venting is seen across the entire patch likely from porous substrate (Figure 2B), while focused venting was limited to some fissures within the patch. The highest temperature of the focused venting from a fissure was measured to be 260°C. This region (Figure 2B) appears white in colouration due to both dense aggregations of white nests constructed by the sulphide worm *Paralvinella* aff. *hessleri* and bacteria mat on top of what appeared to be thin sulphur crust. Due to vent fluid being emitted from this relatively large area, the entire Kyorasan site is covered in a layer of shimmering water. Other than *Paralvinella*, the alvinocaridid shrimp *Rimicaris leurokolos* is the only species abundantly occurring in this central region, both species aggregating around fissures with focused venting.

Further away from the centre of activity (approximately 3–5 m) on weak diffuse flow, dense aggregations of bathymodioline

mussels (both '*Bathymodiolus japonicus*' and '*B. platifrons*') covers the surface of rocks (Figure 2C), with limpets (*Bathymacra nipponica* and *Pyropelta* cf. *yamato*) living on their shells. Temperature at the mussel aggregation was 12.37°C (SD = 0.43), slightly higher than the ambient temperature. The two bathymodioline mussel species generally tended to cluster separately, though in some aggregations they were mixed. The rocks occupied by the mussels were found to be sulphides, and this was the only area where sulphides were collected during this dive. The vent tonguefish *Symphurus thermophilus* lives in rather high density around the mussel colonies (Figure 2D) together with crabs (mostly a species of *Trichopeltarion*, occasionally *Gandalfus yunohana*). Aggregations of the alvinocaridid shrimp *Alvinocaris dissimilis* are also common around the mussels (Figure 2E), though many are also seen living inside the mussel clusters.

A third zone further away from the centre of activity (5–10 m) is dominated by the colloniid gastropod *Cantrainea jamsteci* (Figure 2F), with the sporadic occurrence of the mussel *Bathymodiolus aduloides* wedged between rock and sediment. The substrate in this third zone was mostly pumice boulders and rubbles scattered on a thin layer of sediment. No clear evidence of venting could be seen at this zone, though the posture of *B. aduloides* suggests weak diffuse flow is likely present underneath the rocks. Temperature of this zone was measured to be 11.46°C (SD = 0.01). In this zone we also sighted a chiton (Figure 2G) potentially in the genus *Deshayesiella* (Saito *et al.*, 2008), though this was not collected and the identification is tentative at best without a specimen. Even further away, the tubeworms *Lamellibrachia* and *Alaysia* live on rocks (Figure 2H), but we saw few large individuals.

Sorting of the biological material collected revealed a total of 26 macrofaunal species (Figure 3), including 10 molluscs (three bivalves and seven gastropods), 10 annelids, four decapod crustaceans, one sponge, and one fish. Three species including the siboglinid tubeworm *Alaysia* sp., the chiton, and the bythograeid crab *Gandalfus yunohana* were seen but not collected, to make a total of 29 species. Among these, 19 are identified as species or genera considered specialists of chemosynthetic habitats around Japan (Fujikura *et al.*, 2012; Brunner *et al.*, 2022), including: the bathymodioline mussels ('*B. japonicus*', '*B. platifrons*', and *B. aduloides*); the gastropods *Cantrainea jamsteci*, *Iheyaspira lequios*, *Puncturella parvinobilis*, *Bathymacra nipponica*, *Pyropelta* cf. *yamato*, and *Provanna clathrata*; the shrimps *Alvinocaris dissimilis*, *Rimicaris leurokolos*, *Lebbeus* cf. *shinkaia*; the crab *Gandalfus yunohana*; the tubeworms *Lamellibrachia columna* and *Alaysia* sp.; the sulphide worm *Paralvinella* aff. *hessleri*; the polynoid scale worm *Thermiphione* sp.; the amphinomid worm *Archinome jasoni*; and the tonguefish *Symphurus thermophilus*.

Discussion

The newly discovered Kyorasan site, Amami Rift hydrothermal vent field is among the shallowest deep-sea hot vent with known faunal composition in the Ryukyu region including the Okinawa Trough and Ryukyu Arc, along with Minami-Ensei Knoll and Yoron Hole (Fujikura *et al.*, 2012; Brunner *et al.*, 2022). The overall zonation pattern of the Amami Rift field with *Paralvinella* sulphide worms and *Rimicaris* shrimps in the warmest region surrounded by bathymodioline mussel colonies and tubeworms in the outskirts is consistent with the overall pattern in Ryukyu vents (Watanabe and Kojima, 2015; Yahagi *et al.*, 2015), though *Shinkaia* squat lobsters are missing. Compared to Yoron Hole at 580 m which only hosts 10 species and without a clear zonation pattern (Watanabe and Kojima, 2015), the Amami Rift field is certainly more similar to Minami-Ensei and other Ryukyu vents. The occurrence of a zone densely colonised

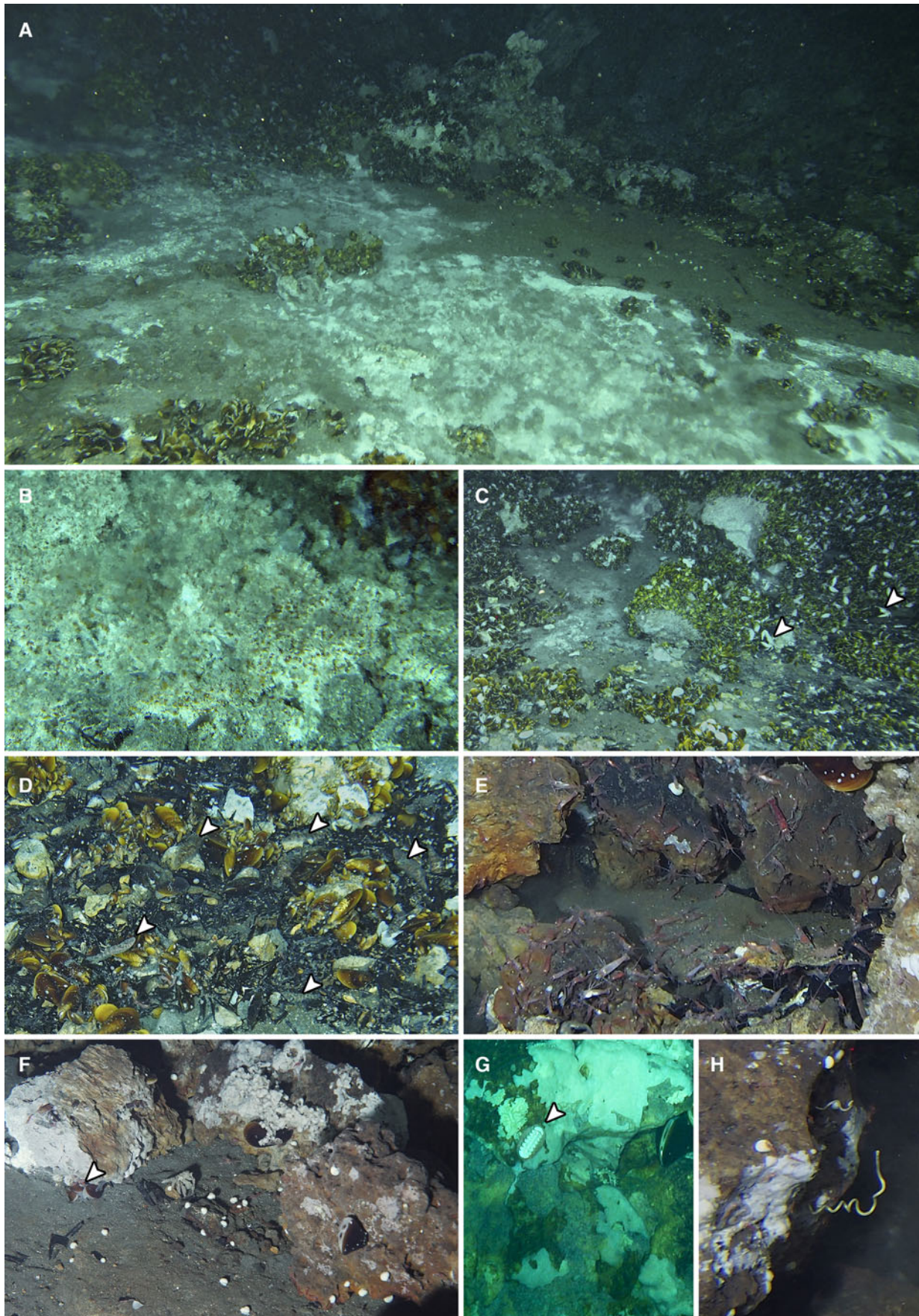


Figure 2. *In situ* photographs of the Kyorasan site, Amami Rift hydrothermal vent field: A, Overview of the main active area; B, Close-up of a *Paralvinella* colony on vent fluid emission; C, Dense colonies of bathymodioline mussels (white arrows indicate *Gandalfus yunohana* crabs); D, A cluster of the vent tonguefish *Symphurus thermophilus* (white arrows) on periostacal remains of bathymodioline mussels; E, An aggregation of the alvinocaridid shrimp *Alvinocaris dissimilis*; F, The peripheral zone colonized by the gastropod *Cantrainea jamsteci*, white arrow indicates several individuals of the burrowing mussel *Bathymodiolus adulooides*; G, A chiton (white arrow) potentially in the genus *Deshayesiella*; H, The tubeworm *Alaysia* sp. growing on rocks in the outskirts of the Kyorasan site. Photographs making up parts A-G were taken at the 'main venting area' in Figure 1B, while part H was taken at 'first tubeworm sighting'.

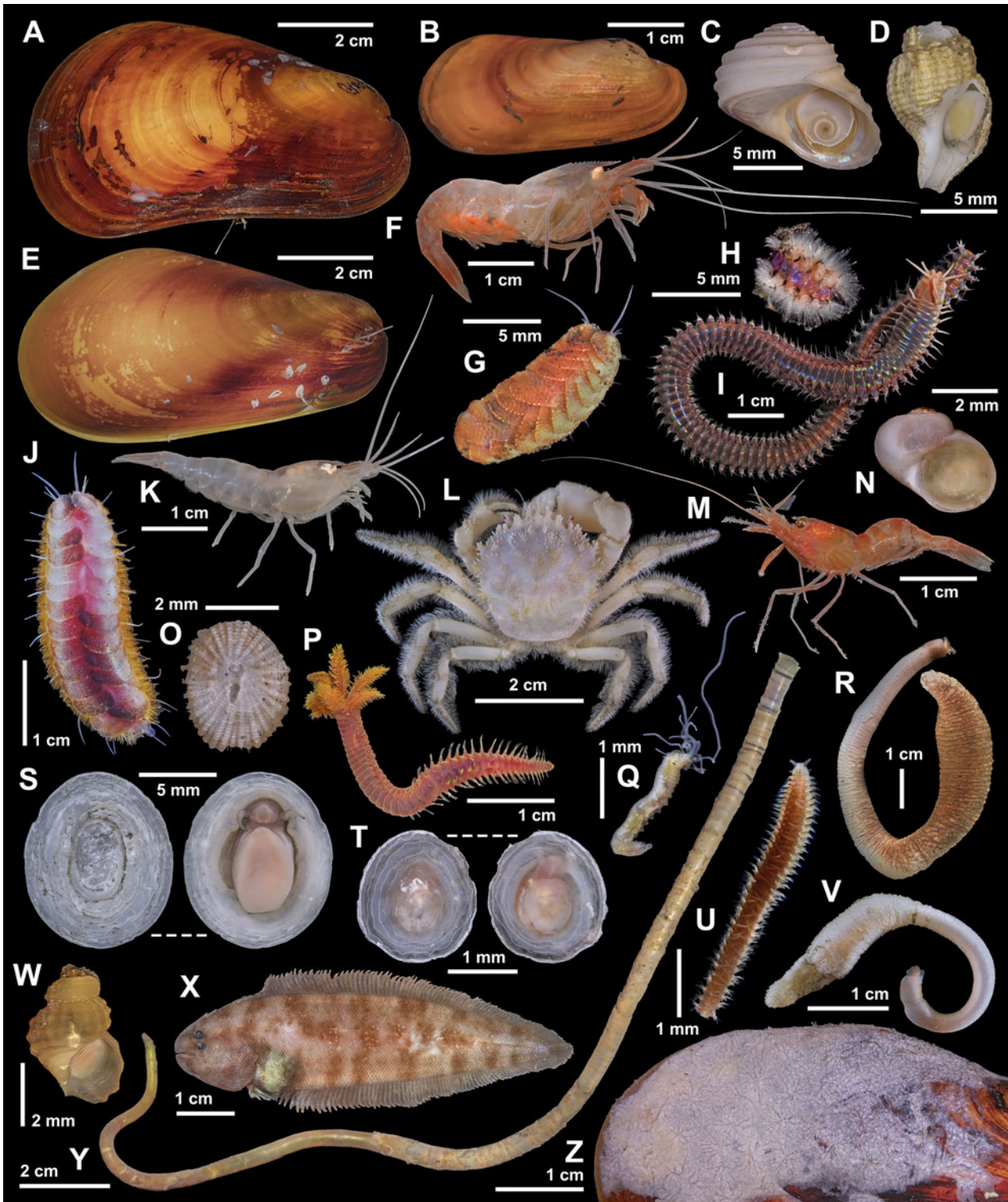


Figure 3. Macrofaunal animals collected from the Kyorasan site, Amami Rift hydrothermal vent field: A, *Bathymodiolus japonicus*; B, *Bathymodiolus aduloides*; C, *Cantrainea jamsteci*; D, the buccinid *Calagrassor cf. aldermenensis*; E, *Bathymodiolus platifrons*; F, *Alvinocaris dissimilis*; G, *Thermiphione* sp.; H, *Archinome jasoni*; I, *Eunice* sp.; J, Polynoidae indet.; K, *Rimicaris leurokolos*; L, *Trichopeltarion* sp.; M, *Lebbeus cf. shinkaiaae*; N, *Itheyaspira lequios*; O, *Puncturella parvinobilis*; P, *Paralvinella aff. hessleri*; Q, Terebellidae indet.; R, *Sipuncula* indet. 1; S, *Bathyacmaea nipponica*; T, *Pyropelta cf. yamato*; U, Dorvilleidae indet.; V, *Sipuncula* indet. 2; W, *Provanna clathrata*; X, *Symphurus thermophilus*; Y, *Lamellibrachia columna*; Z, Demospongiae indet. found living on mussel shells.

by the colliiid snail *Cantrainea jamsteci* is atypical for Ryukyu vents but has also been reported from the Minami-Ensei Knoll (Hashimoto *et al.*, 1995) at a comparable depth of 600–730 m, indicating this species may prefer shallower depths. The presence of vent-specialist species so far only known from sites shallower than 1000 m like the shrimp *Alvinocaris dissimilis* (Komai and Segonzac, 2005; Methou *et al.*, 2023) and the tonguefish

Symphurus thermophilus (Tunnicliffe *et al.*, 2010) previously also recorded from Minami-Ensei suggests depth is indeed a factor shaping the diversity at the Amami Rift field.

The species composition of the Amami Rift field also exhibit several notable deviations from that of the Minami-Ensei Knoll (Hashimoto *et al.*, 1995). Most strikingly, Minami-Ensei Knoll lacks *Paralvinella* sulphide worms (Figure 3P; also present in

Yoron Hole) on its chimneys and '*Bathymodiolus platifrons*' (Figure 3E) in its dense mussel assemblages composed of only '*B. japonicus*' (Hashimoto *et al.*, 1995; Watanabe and Kojima, 2015). Previously, '*B. platifrons*' has only been sampled from over 900 m depth (Fujikura *et al.*, 2012) and indicated this could be due to depth partitioning – but as the Amami Rift is even shallower this cannot be the case and thus the reason for its absence in Minami-Ensei is unclear. The tubeworm *Alaysia* has also not been seen in Minami-Ensei, from which only *Lamellibrachia* was reported. The snail *Iheyaspira lequios* (Figure 3N), missing in Minami-Ensei, is present in the Amami Rift field, extending its bathymetric range by about 400 m (Fujikura *et al.*, 2012). The vent-specific bythograeid crab *Gandalfus yunohana* is extremely rare in the Ryukyu region with just one definitive record (Watanabe *et al.*, 2020) before ours at Amami Rift, but we note that 'Bythograeidae gen. sp.' recorded in Minami-Ensei (Hashimoto *et al.*, 1995) likely also refer to this species.

Among chemosymbiotic species found in Minami-Ensei, the vesicomyid clam *Akebiconcha kawamura* and the mussel *Gigantidas cf. horikoshii* (Hashimoto *et al.*, 1993) are conspicuously missing from the Amami Rift field, but this is likely because these are burrowing species requiring thick sandy or muddy sediments that are present in Minami-Ensei but not Amami Rift where only a thin layer of sediment was seen. The presence of such sediment in a number of vents in the Ryukyu region has been suggested as a major contributor to the relatively high species richness there (Watanabe and Kojima, 2015) and is certainly a factor behind the composition seen in Amami Rift. The absence of the symbiotic squat lobster *Shinkaia crosnieri* in Amami Rift is more puzzling, since it usually co-occurs between *Paralvinella* and bathymodioline mussels. In Yoron Hole, not just *S. crosnieri* but the entire mussel assemblage and its associated species were also missing (Watanabe and Kojima, 2015). This is not the case in Amami Rift. However, *Lepetodrilus* limpets which are considered to indicate the same zone as *Shinkaia* and also abundant in Minami-Ensei (Watanabe and Kojima, 2015) is lacking in Amami Rift, indicating that environmental conditions of this zone may be simply missing in Amami Rift. This may reflect differences in the vent fluid composition since Minami-Ensei is known to have a high methane output (Chiba, 1993; Brunner *et al.*, 2022), and methane concentration has been identified as another important driver of species richness at chemosynthetic ecosystems around Japan (Nakajima *et al.*, 2014).

The non-vent specific animals recovered from Amami Rift also clearly differ from those found in Minami-Ensei. A number of predators from surrounding normal deep-sea floor have been reported to be common in Minami-Ensei, including the anomuran crab *Paralomis*, the buccinid snail *Neptunea insularis*, and the asteroid *Ceramaster misakiensis* (Hashimoto *et al.*, 1995). Furthermore, the outskirts of Minami-Ensei was densely covered in bouquets of a branching sponge in the order Poecilosclerida (Fujikura *et al.*, 2012). All of these are absent from Amami Rift. Instead, the trichopeltariid crab *Trichopeltarion* sp. (Figure 3L) was numerous in both bathymodioline mussel and *Cantrainea* snail assemblages. Trichopeltariids have not been recorded from hot vents, and our species is morphologically closest to *Trichopeltarion janetae* from seamounts and hydrocarbon seeps ranging from eastern New Zealand to Tasmania, Australia between 830–1700 m deep (Ahyong, 2008; Tavares and Cleva, 2010). The presence of *T. janetae* in several New Zealand seeps indicates members of this genus have some tolerance to chemosynthetic environments, and are able to invade them to take advantage of the increased food availability there. We did recover a species of buccinid snail (*Calagrassor cf. aldermenensis*; Figure 3D), but it is rare at the Amami Rift field unlike *Neptunea* which

was common in Minami-Ensei (Hashimoto *et al.*, 1995). Notably, we also collected two species of sipunculan worms (Figure 3R, 3V), but as they were found in crevices of sulphide deposits and pumice, they may have been simply missed by previous sampling efforts in Minami-Ensei. The cause of these differences in non-vent specific fauna is unclear, but fluid chemistry or species composition of the surrounding non-vent seafloor may be key contributing factors.

Overall, our study reports a new hydrothermal field on Amami Rift whose zonation pattern of dominant species generally resemble those of other vents in the Ryukyu region, but with an unusual species composition. The species richness of 29 is high for a hydrothermal vent in the Ryukyu region and only surpassed by two others (Sakai and Iheya North vent fields) in this region (Brunner *et al.*, 2022). In addition to first records from vents (e.g., the crab genus *Trichopeltarion*), our records also represent bathymetric range extensions for many vent-specialist species (e.g., *Iheyaspira lequios*, '*Bathymodiolus platifrons*'). The only three taxa shared across Minami-Ensei, Yoron Hole, and Amami Rift are the shrimps *Rimicaris* and *Lebbeus* as well as eunicid polychaete worms (Watanabe and Kojima, 2015), exemplifying that each shallow Ryukyu vent field explored thus far have a unique set of macrofauna. Community analyses have repeatedly recognised shallow sites like Minami-Ensei as distinctive (Nakajima *et al.*, 2014; Brunner *et al.*, 2022), which can also be expected of Amami Rift.

The discovery of the Amami Rift hydrothermal vent field paves the way for follow-up studies toward a better understanding of how disparate community structures arise in nearby shallow vents. Vent fluid composition may be a key driver, and that of Amami Rift could be distinct from other Ryukyu vents due to its unique geological background at the intersection of Ryukyu Arc and Okinawa Trough (Minami *et al.*, 2022). Biogeochemical characteristics of underwater volcanism in the Ryukyu region remains understudied (Shinjo and Kato, 2000), and how lava type and depth influence vent fluid chemistry in this region requires further research. Ryukyu vents even shallower than Amami Rift have been hinted by turbidity, water chemistry, and dredges containing bathymodioline mussels between 275–300 m deep on Daiichi-Amami Knoll (Minami and Ohara, 2016; Wen *et al.*, 2016) only about 20 km northwest of Amami Rift field, an interesting target for exploration. Just south of Okinawa, the Kueishan Island (also known as Gueishandao or Turtle Island) site off northern Taiwan host very shallow vents between 15–323 m deep (Komai and Chan, 2009; Wang *et al.*, 2014; Mellado *et al.*, 2022). While the sublittoral Kueishan vents comprise mainly non-vent endemics except the crab *Xenograpsus testudinatus* (Chen *et al.*, 2018), the upper bathyal (200–323 m deep) vents are dominated by vent endemics not found in any of the three shallow Ryukyu vents such as the mussel '*Bathymodiolus taiwanensis*', in addition to *X. testudinatus* (Wang *et al.*, 2014). An overarching study analysing the links between community structure, fluid chemistry, and underlying geology of these shallow vents in and around the Ryukyu region is warranted in the future.

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Authors' contributions. CC conceived and designed the study. CC, HN, and HK collected, sorted, and identified the macrofauna. CC interpreted the results and drafted the original manuscript which was edited by HN and HK. All authors agreed with the submission and publication of this manuscript in its present form.

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Competing interest. None.

Ethical standards. We have followed all applicable international, national, and/or institutional guidelines for the care and use of animals.

Data availability. All data generated or analysed during this study are included in this published article.

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