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Note

Are midwater shrimp trapped in the craters of submarine volcanoes by hydrothermal venting?

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Abstract

The biology of Kick'em Jenny (KEJ) submarine volcano, part of the Lesser Antilles volcanic arc and located off the coast of Grenada in the Caribbean Sea, was studied during a cruise in 2003. Hydrothermal venting and an associated biological assemblage were discovered in the volcanic crater (~250 m depth). Warm water with bubbling gas emanated through rock fissures and sediments. Shrimp (some of them swimming) were clustered at vents, while other individuals lay immobile on sediments. The shrimp fauna consisted of 3 mesopelagic species that had no prior record of benthic or vent association. We suggest that these midwater shrimp, from deeper water populations offshore, were trapped within the crater during their downward diel vertical migration. It is unknown whether they then succumbed to the hostile vent environment (immobile individuals) or whether they are potentially opportunistic vent residents (active individuals). Given the abundance of submarine arc volcanoes worldwide, this phenomenon suggests that volcanic arcs could be important interaction sites between oceanic midwater and vent communities.

Keywords: Hydrothermal vents; Seamount; Shrimp; Submarine arc volcano

1. Introduction

Volcanic arcs are common geological features, which total on a global scale about one-third of the entire length of mid-ocean ridges (Embley et al., 2004). Compared to the intense research on mid-ocean ridges, especially hydrothermal vents, submarine volcanic arcs have been relatively little

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explored. Geochemically, they are important because they inject hydrothermal fluids at many depths throughout the water column and are sites of potential ore deposits. Biologically, volcanic arcs may be important stepping stones geographically for vent and seamount fauna (Van Dover et al., 2002). Like seamount chains, each volcano in an arc is biogeographically an island surrounded by deeper water, but, in contrast to geologically inactive seamounts, there are vent dynamics and chemistry on the summit that affect organisms. Volcanic arcs, like seamounts, may also be important interaction sites between oceanic midwater and benthic communities.

Kick'em Jenny (KEJ) submarine volcano, located off the coast of Grenada in the Lesser Antilles (Fig. 1), is the most active submarine volcano in the Caribbean region (Sigurdsson and Shepherd, 1974; Devine and Sigurdsson, 1995; Watlington et al., 2002), last erupting in 2001. Bacterial mats and near-bottom floc, indicative of hydrothermal venting, were seen during 1989 submersible dives shortly after a 1988 eruption (Sigurdsson, personal observation). Here, we describe hydrothermal venting and an associated biological assemblage in the crater of the volcano at ~250 m depth that were observed by a remotely operated vehicle (ROV) in 2003. While the landward side of KEJ shoals towards Grenada, the western seaward side of the volcano slopes to ~1600 m depth. This suggests that midwater oceanic animals could encounter the summit of KEJ during their diel vertical migration. Thus, KEJ also provides an example of the complex interactions between midwater and vent communities that may be important in structuring faunal assemblages on volcanic arcs.

2. Materials and methods

Kick'em Jenny volcano was explored during cruise RB-03-03 on the NOAA ship *Ronald H. Brown* from 10 to 21 March 2003 as part of the NOAA Ocean Exploration Program (chief scientist H. Sigurdsson). Biological studies reported here were done on an ancillary basis. The *Eastern Oceanics* ROV was used for sampling and photography of the seafloor and benthos. Photography included color video, frame grabs from the video, and still photographs. A suction sampler with a single sample container was used to collect larger fauna, especially shrimp. Water and animals were vacuumed into the sampler via a tube and nozzle

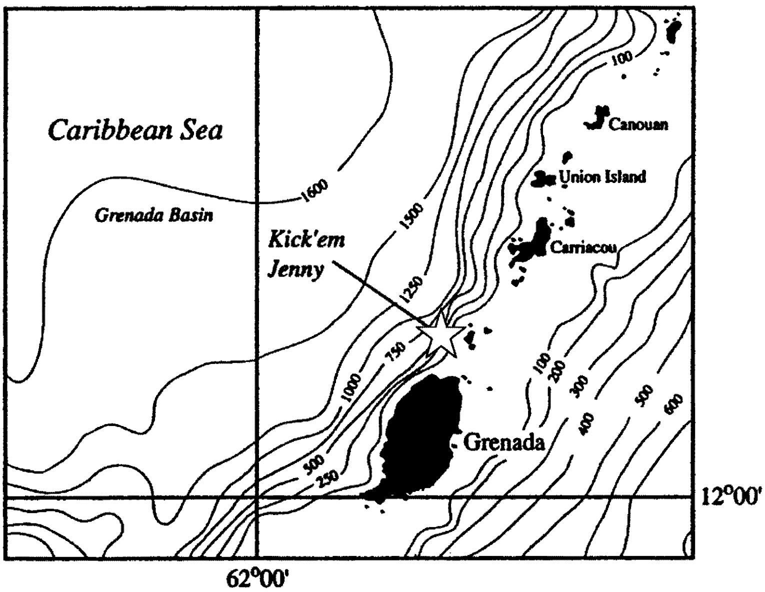

Fig. 1. Map showing the location of Kick'em Jenny volcano (contours in m). The star marks the location of the volcano.

held by the arm of the ROV and positioned near the seafloor. A temperature sensor was located at the end of the arm near the nozzle. The ROV was deployed only during daytime and retrieved 1 suction sample per dive. Three of the deployments targeted the central volcanic crater, and those 3 suction samples, taken near vents, contained shrimp. Shrimp were sorted by hand, rinsed with seawater on a 153 μm mesh sieve, preserved in 4% buffered formalin, and identified later in the laboratory. Food webs were investigated with stable isotopes ($\partial^{13}C$, $\partial^{15}N$) and gut content analyses (light microscopy) of selected specimens. Shrimp stable isotope values were measured by R. McKinney at the Narragansett EPA laboratory. $\partial^{13}C$ values were corrected for formalin effects by adding 1.65‰ to measured values (Sarakinos et al., 2002).

3. Results

3.1. Environmental setting of KEJ

KEJ lies beneath a warm (sea surface $T{\sim}26\,^{\circ}C$) tropical sea with a mixed layer depth of ~50 m. The floor of the main volcanic crater is ~250 m, while the shallowest part of the crater rim is ~180 m. Secondary cones and craters were noted outside the main crater. Venting, documented by ROV photographs and temperature measurements, occurred through fissures (up to tens of meters long) in the basaltic seafloor and also through fine-grained sediments and coarse-grained brecciated deposits (Fig. 2). Hydrothermal venting appeared to be confined to a small inner crater within the larger main crater of the volcano, especially along the base of the scarp that descended from the rim on the western side. Venting was not observed on the flanks of the volcano or in secondary craters. Bubbling gas was a notable feature of some, but not all, vents. Water near vent fauna was 14–17 °C (ambient $T = 14\,^{\circ}C$), while water emanating from fissures was up to 70 °C and hotter (~270 °C) in the sediments. Oxygen in the crater (250 m) was similar to that in the adjacent open ocean (115 μM/kg), and a prominent particle plume at ~230 m, seen in CTD transmissivity data, emanated downstream from the crater into the adjacent ocean basin (W.D. Wilson, personal communication).

3.2. KEJ biology overview

In 2003, the main KEJ vent crater had surprisingly few types of animals (several species of shrimp and worms). In contrast, the crater rim had abundant large suspension feeders (corals) and fish. Some inactive secondary craters outside the venting crater had a more diverse benthic and pelagic faunal assemblage, including urchins, crabs, sponges, corals, holothurians, pelagic and benthic fish, and pelagic gelatinous taxa. Within the main crater, some vents had shrimp, while others had none. Worm distributions near vents were poorly constrained since they were not usually visible photographically. A new spionid polychaete species, *Malacoceros jennicus,* was the most common worm (Graff et al., in preparation). White bacterial mats (presumably *Beggiatoa*) occurred near many vents and were the habitat of the worms; red flocculent material covered many surfaces on rocks and sediments near and away from vents. Although many animals were collected in a suction sample, locations of specific individuals relative to vents could not be ascertained.

3.3. Shrimp

Shrimp were clustered in dense aggregations in some (but not all) venting fissures, including some with bubbling gas and some without gas bubbles (Fig. 2). Aggregations ranged in size from <1 m patches with tens of individuals to linear arrays along fissures with an estimated several hundred animals. Shrimp were also commonly observed dispersed as individuals lying immobile on their sides on top of sediment and in the crevices between rocks. They were not observed in inactive craters (without vents) on other parts of the volcano. It was unclear whether all the shrimp were alive. Shrimp in aggregations in and near active venting (shimmering water) were occasionally seen swimming in the video, but others

Fig. 2. Photographs (video frame grabs) of the KEJ vents and shrimp aggregations (260–261 m depth) and also a nearby area of the volcano covered with a reddish mat and without vents or shrimp (bottom right photograph, 231 m depth). Bubbles of venting gas can be seen in the top left photograph. The ROV suction tube (top photographs) is about 10 cm in diameter. Shrimp (white objects) are 5.5–6 cm long.

(especially solitary individuals on the sediment) did not respond even to direct contact. However, most shrimp brought onboard in suction samples were intact (not decomposed) and appeared to be alive (transparent with pigment, turning opaque soon after). Ovigerous females occurred. All shrimp species had eyes.

Three species of shrimp occurred (identified by the third author), all of them from groups normally considered midwater rather than benthic, and none previously reported from the vicinity of hydrothermal vents (Martin et al., 2005). The dominant species, constituting 93% of the 334 specimens, was the caridean shrimp *Janicella spinicauda* (family Oplophoridae) (A. Milne Edwards (1883), transferred from the genus *Oplophorus* by Chace (1986)). Ovigerous females had large orange eggs (2.7 × 1.6 mm), one characteristic of this genus. A second oplophorid, *Oplophorus gracilirostris* (A. Milne Edwards, 1881), constituted 3% of the specimens. The third shrimp species, from the family Sergestidae, was *Sergia* cf. *robusta* (Smith, 1882) and constituted 4% of the specimens. All species had carapace lengths of ~10–11 mm and total lengths (tip of rostrum to distal end of uropods) of ~5.5–6 cm. Voucher specimens have been catalogued in the Natural History Museum of Los Angeles County.

Gut contents of *Janicella spinicauda* (5 specimens) consisted of probable pelagic material including diatom frustules, spines and setae, crustacean exoskeleton pieces, and amorphous material. In contrast, sediment from the bacterial/polychaete mat was mostly black and other colored grains along with an occasional spine or diatom frustule, while non-vent sediment outside the crater was mostly light brown grains with abundant foraminiferan tests, gastropod shells, and some urchin spines. Mean corrected $\partial^{13}C$ for shrimp was -19.0 ± 0.5‰ and mean $\partial^{15}N$ was 6.2 ± 0.4‰ ($n = 6$).

4. Discussion

The number of vent-associated macrofaunal species at KEJ is small (three shrimp, one worm) compared to the species list at most vents and seeps (Sibuet and Olu, 1998; Tunnicliffe et al., 1998; Van Dover, 2000; Van Dover et al., 2002). This low diversity may be due to the limited area of suitable habitat, frequency of disruption by volcanic activity or outgassing and consequent lack of time for colonization and growth, or the geographic isolation of the volcano from the Mid-Atlantic Ridge system. Shallow vents elsewhere in the world also seem depauperate in the number of vent-specific metazoan species, although biomass can be high (Thiermann et al., 1997; Dando et al., 1999; Jeng et al., 2004).

The shrimp on KEJ are not from the usual vent-associated families, but from shrimp groups generally considered mesopelagic. Oplophorids are cosmopolitan, typically midwater, and feed mostly on metazoans, although gut contents also include protozoans and detritus (Hopkins et al., 1994). *J. spinicauda* is a strong vertical migrator (near surface at night, at 300–600 m during the day) (Ziemann, 1975). This species and *O. gracilirostris* are found widely in tropical seas, including the Sargasso Sea, Caribbean, and Gulf of Mexico (Chace, 1940; Hopkins et al., 1989, 1994; Frank, 1999), and above mid-Pacific seamounts (Allen and Butler, 1994; Seamounts Online Database, seamounts.sdsc.edu). *S.* cf. *robusta* has also been reported from these tropical Atlantic locations (Donaldson, 1975; Flock and Hopkins, 1992; Hopkins et al., 1994).

There is no previous indication of a benthic association for any of these species, and they have not previously been found at vents or seeps (Tunnicliffe et al., 1998; Van Dover, 2000; Martin and Haney, in press). Thus, their occurrence and abundance on KEJ is surprising. Caridean shrimp in other families (mostly alvinocaridids and hippolytids) are common or occasional endemics or vagrants in numerous hydrothermal vent regions including the western Pacific back-arc region, the Mid-Atlantic Ridge, and cold seeps on the southern Barbados prism and Gulf of Mexico (Williams, 1988; Olu et al., 1996; Shank et al., 1998; Tunnicliffe et al., 1998; Van Dover, 2000; Martin and Haney, in press).

It is uncertain to what extent the association between the shrimp and the KEJ vents is specific versus accidental or opportunistic. Aggregations of swimming shrimp around vents, and the absence of other (non-shrimp) pelagic fauna, suggested a deliberate association. However, other shrimp lay immobile on their sides on the sediment and around rocks. Given their typical midwater habitat and strong diel vertical migration, it appears likely that the KEJ shrimp were trapped within the crater as they descended during their diel vertical migration. The source populations were probably from the midwater community in the adjacent deeper water. Shrimp entering the crater may be incapacitated by vent emissions that could cause the apparently comatose state of some individuals. Gas chemistry was not analyzed, so we do not know if the bubbles were toxic (such as hydrogen sulfide), narcotizing (carbon dioxide), or merely hot (steam). At a shallow vent in the Okinawa Arc near Taiwan, Jeng et al. (2004) found that zooplankton killed by toxic vent plumes settled to the seafloor during slack tide and were fed upon by vast numbers of crabs. We do not presently know the timescale of the shrimp association at KEJ (since the ROV operated only during daytime). For example, it is unknown whether shrimp entered or left the crater daily or remained in proximity to vents once there. Shrimp were seen on all visits to the crater vents (3 different days).

A surprising observation was the absence of obvious predators (pelagic macroplankton, nekton, and fish) within the vent crater (based on video), although they were seen on the crater rim and in secondary craters along the flank. There are many diel vertical migrators in the tropical

Atlantic; if accidental trapping were the only mechanism involved, it is puzzling that other taxa were not observed in the aggregations or as detritus on the seafloor. The lack of predators and scavengers may contribute to shrimp abundance.

The KEJ shrimp do not appear to utilize directly any chemosynthetic production. Both gut contents and stable isotope values are consistent with normal pelagic feeding. Plankton and sinking particles elsewhere in the Caribbean have $\partial^{13}C$ values ranging from −18 to −23‰ (Woodworth et al., 2004), similar to the KEJ shrimp and in contrast to highly depleted chemosynthetic sources (Van Dover, 2000). Endemic Mid-Atlantic Ridge shrimp do utilize chemosynthetic food sources, although some species also use photosynthetically derived carbon (Gebruk et al., 2000; Pond et al., 2000; Van Dover, 2000; Colaço et al., 2002).

Seamounts function as biological oases within an ocean desert. They are sites of high biomass, abundance, biodiversity, and endemism of benthic and pelagic fauna (Boehlert and Genin, 1987; de Forges et al., 2000). Interactions between the height and shape of the seamount and currents elevate food concentrations, affect larval retention and dispersal, and create habitat complexity (Genin et al., 1986; Wishner et al., 1990, 1995; Mullineaux and Mills, 1997). Vertically migrating zooplankton in the surrounding oceanic waters may 'bump into' the seamount during their daytime descent, providing food for the seamount community; vertically migrating fish and zooplankton living on the seamount may rise at night to feed on plankton (Genin et al., 1994). KEJ (and presumably other submarine arc volcanoes) have features typical of seamounts as well as vents. Although wide expanses of relatively fresh lava both inside and outside the KEJ crater had no visible megafauna (Fig. 2), some non-vent locations had a diverse megafaunal assemblage characteristic of current-swept seamount ridges (on the crater rim), enriched basins (in an inactive crater), or deep coral habitats.

In conclusion, we suggest that the KEJ shrimp, presumably from midwater populations offshore, were trapped within the crater during their diel vertical migration. It is unknown whether they then succumbed to the hostile vent environment (immobile individuals) or whether they are potentially opportunistic vent residents (active individuals). Given the abundance of submarine arc volcanoes worldwide, this phenomenon suggests that volcanic arcs could be important interaction sites between oceanic midwater and vent communities.

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