Hydrothermal vent octopuses of *Vulcanoctopus hydrothermalis*, feed on bathypelagic amphipods of *Halice hesmonectes*

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A feeding frenzy of 12 octopuses of *Vulcanoctopus hydrothermalis* was observed from the manned submersible 'Alvin' at Parigo, a 2620 m deep hydrothermal vent on the East Pacific Rise. The aggregated benthic octopuses at the active vent used their arms and webs to forage on bathypelagic amphipods, apparently targeting their attacks based on contact with the swarming amphipods. Individual octopuses wrapped their arms around the mantles of smaller octopuses, apparently in competition for prey. Although members of the prey species, *Halice hesmonectes*, are individually small (<5 mm long), the density of their swarms may make them attractive prey for the octopus. Inactive sulphide spires encircled part of this vent site; octopuses that climbed these spires had easy access to the dense prey swarms. The presence of the spires may uniquely enable this site to support simultaneous foraging by large numbers of octopuses.

INTRODUCTION

Among deep-sea octopuses, those of *Vulcanoctopus hydrothermalis* Gonzalez et al., 1998 are among the most frequently observed because their only known habitat, hydrothermal vents on the East Pacific Rise, are repeatedly visited by research submersibles each year. Evidence that these octopuses are specialized for vent habitats derives from the fact that the animals appear highly tolerant of sulphide exposure. They move freely across plumes of giant tubeworms (*Riftia pachyptila* Jones, 1981) that are bathed in toxic sulphide-rich vent fluids (personal observation). Mechanisms of sulphide resistance and other aspects of the biology of this species remain largely unknown.

Chemosynthesis sustains phenomenal accumulations of biomass at hydrothermal vents, suggesting that these octopuses have abundant prey, but what prey they take remains unknown. Based on their report of the holotype having a comparatively large, well-developed oesophageal crop, in contrast with that of most deep-sea octopuses, and of its stomach containing unidentified white cuticular fragments, González et al. (1998) suggested that octopuses of this species took comparatively large prey such as galatheid or bythograeid crabs. In over 30 min of video footage focusing on an individual octopus, no predation was seen, although the octopus' retreat from a comparatively large crab of *Bythograea thermydon* Williams, 1980 was concluded to be due to its having determined its potential prey was too large to handle (Rocha et al., 2002). Gut contents and feeding attempts of this species are otherwise unknown.

This paper reports over an hour of observations made from the manned submersible 'Alvin' of at least 12 individuals of *V. hydrothermalis* at Parigo, an active hydrothermal vent near 13°N on the East Pacific Rise. Gut content analysis supports observational evidence that the octopuses forage on swarms of the bathypelagic amphipod, *Halice hesmonectes* Martin et al., 1993 using their arms and

webs; observations indicate the octopuses also use their arms and webs to interact with each other, apparently while competing for access to prey.
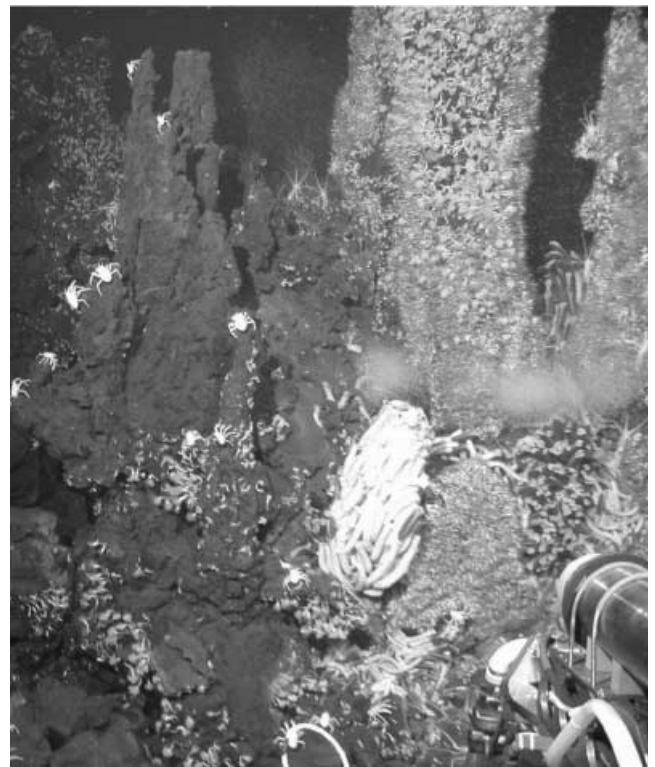

Figure 1. Parigo Vent near 13°N on the East Pacific Rise at 2620 m depth photographed by the deep submergence vehicle 'Alvin' ('Alvin''s three-chip video camera is visible in the lower right-hand corner). Galatheid crabs are poised on the largely barren inactive sulphide spire to the left and eight octopuses of *Vulcanoctopus hydrothermalis* are visible on the central ridge and on the serpulid-covered sulphide spires to the right. Swarms of *Halice hesmonectes* appear as cloudy areas over the tubeworms.

MATERIALS AND METHODS

Deep submergence vehicle 'Alvin''s Dive 3939 located Parigo, a small vent near 12°48′N on the East Pacific Rise, with a fauna dominated by giant tubeworms of *Riftia pachpytilia*. Lying about 175 m south and east of the large vent Genesis, Parigo appeared to be isolated amid basalt talus dotted with abundant galatheid crabs. Large inactive sulphide spires towered over one side of the vent. Three spires were heavily colonized by serpulid polychaetes, heterotrophs that reportedly live in 2–5°C water (ten Hove & Zibrowius, 1986; Fustec et al., 1987). A fourth, more peripheral, spire had been heavily weathered and was nearly uncolonized. Serpulids had also colonized a slight rise beyond the spires in lower densities. Loosely defined amphipod swarms formed a discontinuous cloud over the tubeworms (Figure 1). Closer observation revealed at least 12 octopuses of *Vulcanoctopus hydrothermalis* on the serpulid-covered sulphide spires, on the tubeworms and at the edge of the spires. Other macrofaunal predators at the vent included a bythograeid crab and two individual fish, a zoarcid, likely *Thermarces cerberus* Rosenblatt & Cohen, 1986 and a liparid, *Careproctus hyaleius* Geistdoerfer, 1994.

'Alvin''s colour video cameras, including one 3-chip broadcast-quality camera and two single-chip video cameras, filmed the octopuses under illumination of the submarine's HMI (hydrargyrum medium arc-length iodide) lamps. Two Sony DSR-50 DVCam recorders recorded the video images. An externally mounted, forward-looking digital still camera also documented the area and associated fauna and the positions and behaviours of the octopuses. Two lasers on 'Alvin''s frame projected dots of light 10 cm apart, which provided a size-scale for use on videos and stills.

After 23 min of filming and observations, three sets of collections were begun to test whether the behaviours observed constituted foraging. Four octopuses were collected with 'Alvin''s multi-chambered suction sampler
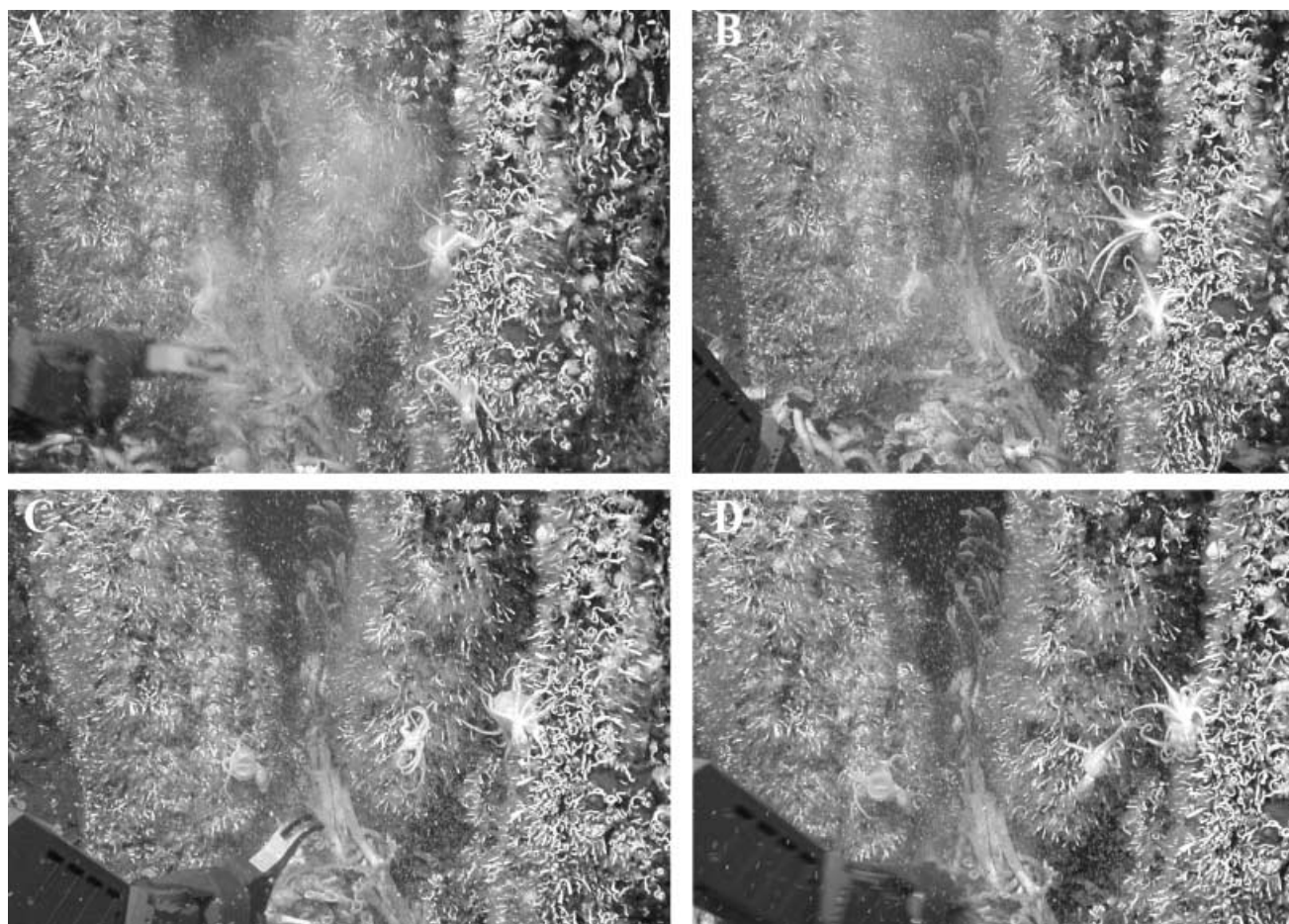

Figure 2. Images of octopuses of *Vulcanoctopus hydrothermalis* over a tubeworm mass at the base of the serpulid-covered sulphide spires of Parigo, taken at 20-s intervals by the forward-looking digital still camera on 'Alvin' while sampling is in progress. Amphipods of *Halice hesmonectes* are visible as particles in the water column. (A) Four octopuses continue to feed from the sulphide spires as the manipulator arm of 'Alvin' begins sampling. The octopus to the left (immediately above the manipulator arm) dangles from a serpulid tube as it pulls its arms together; the centre octopus is beginning to extend its arms in a starburst pattern and the arms of the upper right individual are ballooned. The fourth octopus is advancing from the lower right part of the image; (B) twenty seconds later, as the manipulator arm is lowered, the octopuses largely retain the same positions; the upper right octopus has begun to extend its arms as the lower right individual advances; (C) twenty seconds later, the octopus to the left has ballooned its arms and the centre octopus has maximally extended his arms. The octopuses to the right are in contact; the octopus from the lower right has engulfed the upper individual in its web; (D) after another twenty seconds, the arms of the left octopus remain ballooned, as are the arms of the centre octopus. The octopuses to the right are more readily discernible as the arms of the engulfed individual extend from beneath the upper octopus.

and part of the amphipod swarm was collected with its pelagic suction sampler. Isolating the apparent prey and predators in two separate suction samplers avoided any opportunistic post-collection feeding. In addition, 'Alvin''s manipulator arm collected tubeworms and associated fauna and placed them in a lidded box. The observations and collections occupied a total of 62 min.

After 'Alvin' was brought onboard the RV 'Atlantis', the moribund octopuses were preserved in buffered-seawater–formalin and later transferred to 70% ethanol for storage. They are catalogued at The Field Museum (Chicago, IL) as FMNH 306500. The amphipods, identified as *Halice hesmonectes* by T.A. Haney, were preserved in 95% ethanol and are catalogued as FMNH 11029.

Four months after their collection, the oesophagus and stomach of each octopus were opened and their contents sent to T.A. Haney for identification. To assess the size of the octopuses collected, their mantle lengths were recorded; to estimate their maturity, the spermatophores stored in Needham's sac were counted.

RESULTS

Of 72 galatheid crabs visible on one digital still image taken during our approach to the vent, six occurred near vent fauna and two were near serpulids. The other 64 were peripheral to the vent, associated with the basalt talus. The seven octopuses of *Vulcanoctopus hydrothermalis* visible in the same image occurred on serpulids or rarely tubeworms; none were peripheral to the vent. Of the 12 octopuses estimated to have been observed, eight were closely associated with serpulids, four were on the slight serpulid-covered rise adjacent to the spires.

All individual octopuses exhibited a largely consistent behaviour that appeared to constitute foraging. Individuals extended six arms, typically the dorsal and both lateral arm pairs (Figure 2A,B) peripherally in a starburst pattern, and held this position for a variable amount of time. The web was then expanded before the free (unwebbed) arm tips were brought together in the water column. The water-filled web (Figure 2C) was then slowly deflated. Octopuses near the edge of the amphipod swarm were most often seen to perform this behaviour, however, octopuses were also seen performing it while dangling from a serpulid tube by one arm, sometimes a dorsal arm, while using other arms to forage. Occasionally, octopuses crawling forward with extended dorsal and lateral arms would move away from the amphipod swarm. As these individuals crawled with extended arms, their paths curved, returning them to denser amphipod aggregations where they brought their arm tips together.

The density of feeding octopuses at this site is unprecedented. Five octopuses are often seen in single video frames focused on the edge of the amphipod swarm. In one still image with 'Alvin''s paired lasers as a size-gauge, three octopuses occur within 50 cm of each other. Given the density of octopuses, contact among them was nearly inevitable and two basic interactions were seen. Twice, one octopus engulfed the mantle of a smaller one in its web and held it for about one minute; more frequently, interactions were brief arm-to-arm contact. Unfortunately, details of the interactions were frequently obscured by the density of the amphipod swarm.

During the observations, several octopuses left the area. However, at least four octopuses continued to feed within 15 cm of 'Alvin''s manipulator arm as it sampled *Riftia pachpytilia* and associated fauna (Figure 2). Even after the amphipod swarm became less dense, likely due to the physical disruption of the warm water by sampling activities, some octopuses remained and continued to forage.

All four octopuses collected were male. Their mantle lengths ranged from 42.9 to 51.8 mm. One individual had 22 spermatophores in Needham's sac, the others had one or none. The oesophagus and stomachs of all four octopuses contained only the remains of pelagic amphipods and yellow-orange oil droplets. These amphipods and those in 'Alvin''s pelagic sampler were identified as *Halice hesmonectes* (T.A. Haney, personal communication). Three of the four octopuses had the remains of at least nine amphipods in their oesophagi or stomachs; one had a minimum of five individuals.

DISCUSSION

These observations document aggregated benthic octopuses of *Vulcanoctopus hydrothermalis* using their arms and webs to engulf and then feed on bathypelagic crustaceans at 2620 m depth. Individually, amphipods of *Halice hesmonectes* are likely too small (<5 mm) to serve as octopus prey, but the density of their swarms, up to 1000 individuals/litre over warm (2 to 8°C) vents (Van Dover et al., 1992; Kaartvedt et al., 1994; Sheader et al., 2000), may make the species an attractive prey for the octopuses. Although most swarms occupy less than a cubic metre, they have been reported to extend over areas of up to 18 m^2 (Shank et al., 1998).

Vent topography may have contributed to the octopus aggregation. As noted, *Halice hesmonectes* swarm above the sea-floor (Van Dover et al., 1992; Kaartvedt et al., 1994), although assessing the height of a swarm above the sea-floor can be difficult given the down-looking views that submersibles afford. If swarms are typically high enough off the sea-floor to avoid an octopus' extended arms, a common posture of octopuses of *V. hydrothermalis* (Rocha et al., 2002; personal observation), they may escape detection. Because in this case, the amphipods swarmed among sulphide spires on which the octopuses were positioned, their height above the bottom offered no protection. Once they were detected, the octopuses could readily prey on the amphipods.

Observations of octopuses using their webs in foraging are not unique to *V. hydrothermalis*. Laidig et al. (1995) report that individuals of *Octopus rubescens* Berry, 1953 foraged at about 200 m depth on 10 mm long euphausiids in swarms and used their webs to secure their prey. More rarely these octopuses were considered to use vision to target individual prey. Laidig et al. (1995) report that the euphausiid swarms contained hundreds of individuals/m^3, but the octopuses did not aggregate; their density near the swarms was the same as in areas without swarms. A captive cirrate octopus ascribed to the genus *Grimpoteuthis* showed a seemingly similar behaviour, termed envelopment (Hunt, 1999). After a foodless week in an aquarium, the cirrate enveloped live *Artemia* that were poured over it as it swam near the top of its tank (Hunt, 1999). Later in

captivity, the octopus abandoned use of envelopment in favour of entrapping live adult *Artemia* against the bottom. More commonly, shallow-water incirrate octopuses use their webs in the 'speculative pounce', a behaviour that constitutes an octopus pouncing on a rock or coral head, enveloping it with the web, then closing the web with any potential prey inside (Yarnell, 1969). Although the behaviour may appear to be energetically demanding, individuals of *Octopus cyanea* Gray, 1849 reportedly make up to 111 such pounces in 25 min (Forsythe & Hanlon, 1997). The contrast between the speculative pounce and the behaviour of *V. hydrothermalis* reported here is that contact between the swarming amphipods and the octopuses' arms likely allowed the octopuses to target their attacks, reducing or even eliminating the element of speculation.

Although octopuses are generally regarded as solitary (Hanlon & Messenger, 1996), those of *V. hydrothermalis* have been observed in groups of up to five, in an apparent mating aggregation (Rocha et al., 2002). No copulatory behaviour was seen here, but with at least 12 octopuses observed, their density virtually assured intraspecific contact. Close contact among the conspecifics may contribute to the high incidence and levels of infections by the parasitic copepod, *Genesis vulcanoctopusi*, reported by López-González et al. (2000) in this octopus.

In what appeared to be the more aggressive interaction, seen only twice, one octopus wrapped its arms and web around the mantle of a smaller one, a very aggressive behaviour thought to interfere with respiration (Hanlon & Messenger, 1996). More often, octopuses would engage in arm-to-arm contact, which has been suggested to offer a means of assessing the size of a potential opponent (Hanlon & Messenger, 1996). If these interactions constitute dominance interactions or interference competition, which have not been previously reported in octopuses in the wild (Cigliano, 1993; Hanlon & Messenger, 1996), they may limit access to prey by smaller, more immature octopuses. The octopuses collected late in the observations were relatively immature, based on their few spermatophores compared with the average of 47 spermatophores in 16 males reported by González et al. (2002). If the octopuses that were seen to leave the area were the larger more mature individuals, their departure might have allowed these smaller octopuses to feed if intraspecific interactions affect individual behaviour. The fact that octopuses continued to feed in very close proximity to the considerable physical and acoustic disturbances that inevitably result from sampling with a hydraulic-powered suction sampler and an electronic arm (Figure 2), seems counterintuitive, and implies that their feeding had been previously restricted.

These observations do not support the hypothesis of González et al. (1998) that the large crop of *V. hydrothermalis* reflects routine exploitation of large hard-bodied prey, such as galatheid or vent-associated crabs, or shrimp or mussels. Although galatheids were abundant around the vent (Figure 1), their distribution was nearly exclusive of that of the octopuses. The preferred or normal prey of these octopuses, if any, remains unknown.

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