Behavioural observations of the cephalopod
Vulcanoctopus hydrothermalis

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Introduction

The hydrothermal vent ecosystem is inhabited by poorly known species of deep-sea octopuses (Lutz & Voight, 1994). *Vulcanoctopus hydrothermalis* González & Guerra, 1998, is the only described cephalopod from a hydrothermal vent (González et al., 1998). Little is known about this small benthic octopus, up to 35 mm mantle length, with a muscular and semi-translucent body, lack of any type of chromatic elements in the skin and eye with no trace of an iris (González et al., 1998). Its morphology was studied by González et al. (in press) but there have been no behavioural studies of this species to date.

Most observations of octopus behaviour in abyssal environments, mainly Cirroctopoda, have been described from videotape records (Boletzky et al., 1992; Villanueva et al., 1997; Vecchione & Young, 1997, among others). Live observations of animal behaviour at deep-sea hydrothermal vents are extremely difficult to carry out, mainly due to hostile environmental conditions such as pressure and darkness. The use of remotely operated vehicles (ROVs) or manned submersibles can impact the behaviour of the species being filmed (Spanier et al., 1994). In the abyssal zone, local conditions may change as a result of the spotlights, sounds, and turbulence of the submersible as well as the physical presence of a large object. However, video recordings, photographs, and direct observations using manned submersibles are the best means available to date for in situ studies of deep-sea animals behaviour (Hanlon & Messenger, 1996; Villanueva et al., 1997). The present paper reports the first observations on the behaviour of *V. hydrothermalis* based on video recordings.

Material and methods

The French manned submersible "*Nautile*" filmed several specimens of *Vulcanoctopus hydrothermalis* in their natural environment associated with high temperature hydrothermal vent in the East Pacific Rise (12°48.43'N-103°56.41'W; 2600 to 2650 m depth). Observations were carried out during the French cruise "HOPE 99" (7 April to 22 May, 1999) on board of the R/V *l'Atalante* and organized by the CNRS and IFREMER (URM7), Chief Scientist François Lallier. A total of 26 dives were undertaken on ten active hydrothermal vents. The video camera used was a Sony DXC 755 fixed on the submersible *Nautile*, with a Canon KRSBVP3 objective, (magnification 8.8, focal 6.48), recording onto S-VHS videotape.

The area studied is situated north to the site commonly known as Genesis, whose chemical and thermal characteristics were described by Sarradin et al. (1998). The temperature in the sampled area ranged from 1 to 2 °C in the surrounding seawater, between 1.6 and 10 °C around the *Riftia pachyptila* plumes, from 7 to 91 °C close to the alvinellid polychaete population, and finally between 262 and 289 °C in outflowing high-temperature vent fluid (Sarradin et al., 1998).

Octopus behavioural patterns were identified according to those defined by Hanlon & Messenger (1996).

Results

A total of 30'18" of sequences involving twenty-five specimens of *Vulcanoctopus hydrothermalis* were made between 2600 and 2650 m depth. Twelve specimens, mainly males, were observed on cliffs of basaltic rock covered by

oxidized sulphides and colonies of tubeworms *Riftia pachyptila* Jones, 1981, Alvinellidae polychaetes and mussels. Thirteen other specimens of *V. hydrothermalis* were observed on basaltic rock substrata around hydrothermal vent zones where crabs, galatheids and zoarcid fishes were also found.

Specimens of *V. hydrothermalis* were observed by pairs or in groups on basaltic rock bottoms in the vent periphery, while those filmed on tubeworms, Alvinellidae polychaete and mussels colonies were always found isolated.

Although all specimens showed open eyelids, mechanoreceptors (touch and pressure) and chemoreceptors (smell) seem to be the main sense organs employed by those deep-sea water octopuses. No responses or behavioural changes to submersible lights were observed.

Crawling pattern

A total of 13 sequences showed individuals "crawling" on bottoms. These octopuses were crawling slowly, with their arms extended. In all observations, the animals used their arms I (dorsal) and II (dorso-lateral) for tactile explorations, and arms III (ventro-lateral) and IV (ventral) for propulsion (Fig. 2). Individuals were also observed bearing their weight on their ventro-lateral (III) and ventral (IV) arms.

Defensive patterns

This behaviour was observed in two specimens as consequence of the disturbance generated by the submersible (Fig. 1). The "primary defence" of the
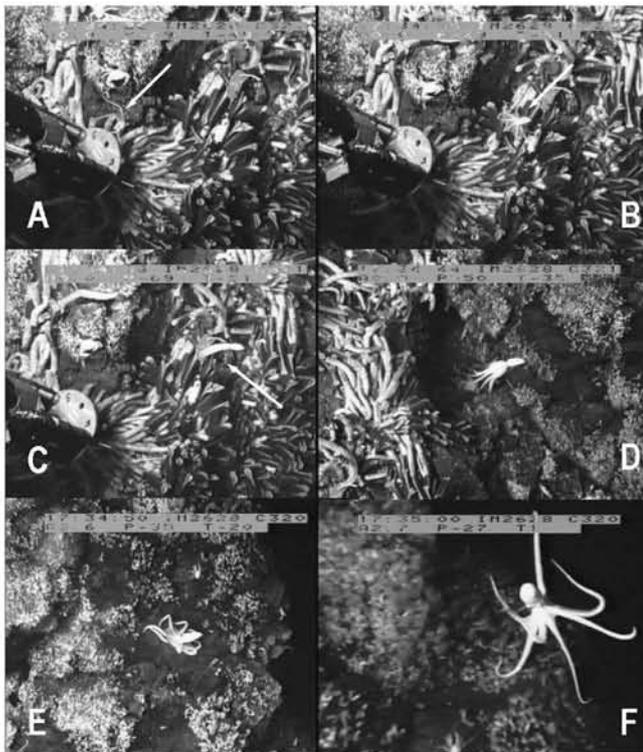

Figure 2. Sequence (**A-D**) showing a specimen of *Vulcanoctopus hydrothermalis* using speculative hunting carried out on a prey, possibly the crab *Bythograea thermydron*. *Vulcanoctopus hydrothermalis* "crawling" on bottom with their arms extended. Note that the specimen used their pairs of arms dorsal (I) and dorso-lateral (II) for tactile exploration, and pairs of arms ventro-lateral (III) and ventral (IV) for propulsion.

Figure 1. *Vulcanoctopus hydrothermalis* defensive patterns. (**A**) Primary defence where the specimens hide in a *Riftia* bush or in the cracks of the substrate. (**B-F**) Secondary defence or escape manoeuvre that comprised strong pulsations generated by contraction of the brachial crown.
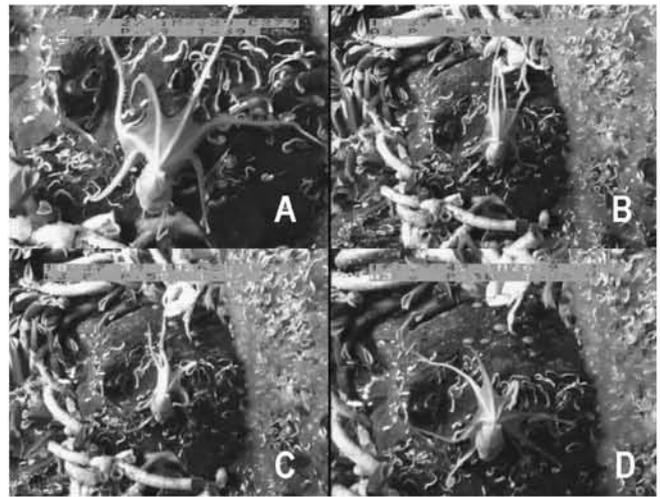
specimens was to hide in the *Riftia* colony or in cracks in the substratum (Fig. 1A) and maintain their positions within hiding places. No colour changes were observed in these specimens.

A "secondary defence" or "escape manoeuvre response" was observed when one specimen contacted the mechanical arm of the submersible. This behaviour is a "take-off" and consisted of strong pulsations generated by the arms contracting and pulling near the mantle, then straightening and pushing down with the web extended (Figs 1B-E). The animal pulled its body into a hydrodynamic fusiform shape to maximize the abrupt thrust provided by each pulse (Fig. 1C). Jet-propulsion through the funnel did not seem to be involved in this escape response. The elapsed time between each pulse was 3 to 4 seconds. A total of 4 pulses were observed during this escape manoeuvre, which displaced the specimen about 3 meters from the origin. This response ended when the octopus ceased pulsations and then floated with outspreaded arms. During flotation, the animal remained body up, its oral surface facing bottom, and fell slowly on the substratum moving its arms in all directions and maintaining the web contracted (Fig. 1F).

Tactile feeding pattern

"Tactile feeding" pattern was also observed in one specimen. This octopus was found crawling on the bottom and using its dorsal arms to detect potential prey. When the potential prey (a crab, *Bythograea thermydron* Williams, 1980) was located, the *Vulcanoctopus* tried to capture it using arms I and II. Arms III and IV were not utilized in the capture (Figs 2A-B). However, the attack was withdrawn when the animal detected the large size of the crab, and the octopod changed its displacement direction (Figs 2C-D).

Reproductive pattern

A group of five specimens was observed from the submersible during a long time sequence of 2'17", probably showing a reproductive pattern that consisted of a "mounting" and a "mating at distance" (Fig. 3). All specimens showed similar size and appeared clearly mature in the video images. Although specimens were not collected at the end of the observations, their sexual maturity could be estimated by the development of the gonad, which was observable across the transparent thin skin. Three specimens were mounting a fourth (female?) whereas the fifth octopus was mating at some distance, using its hectocotilized arm.

Figure 3. Group of five specimens of *Vulcanoctopus hydrothermalis* showing a probable reproductive behaviour comprising a mounting and a mating at distance.

Discussion

There have been no previous studies of the behaviour of the hydrothermal vent octopus *Vulcanoctopus hydrothermalis*. All behavioral patterns observed here are closely related to those reported for benthic species of incirrate octopus from other environments (Hanlon & Messenger, 1996) however, with some notable differences. The most remarkable is the lack of crypsis as defined by Hanlon & Messenger (1996). This is explained by the absence of chromatic elements in the skin of *V. hydrothermalis* (González et al., 1998). On the other hand, visual attacks were never observed in *V. hydrothermalis*. This may be due to a defective vision related to the absence of some features present in the eyes of other cephalopods (González et al., 1998), as well as to the adaptation to a lightless habitat, possibly related to its albinism. An alternative explanation would be that the relatively bright lights of the submersible caused eye damage at first approach, in which case the octopus would have been unable to respond or attack visually.

The behaviour of this species was also different from that of the deep-sea cirrate octopods, but this is not unexpected when morphological and habitats differences are considered

(e.g. Vecchione & Roper, 1991; Boletzky et al., 1992; Villanueva et al., 1997). *V. hydrothermalis* specimens were always found associated with the bottom and never swimming in the water column, as occurs in cirrate octopods living in abyssal environments. Swimming occured only as a secondary response or "escape manoeuvre" produced after the primary response of the specimen, which consisted of hiding within a *Riftia* bush or in cracks in the substratum. Crawling of *V. hydrothermalis* was different from crawling in cirrate octopods and similar to that used by shallow-water octopuses. Whereas *V. hydrothermalis* mainly used its dorsal (I) and dorso-lateral (II) pairs of arms for tactile explorations, and pairs of arms III (ventro-lateral) and IV (ventral) for propulsion, cirrate octopods, such as *Grimpoteuthis* sp., use all arms for crawling (Villanueva et al., 1997). These differences are due to distinct anatomical features, foraging strategies and the fact that these two types of octopuses occupy different ecological niches (Villanueva & Guerra, 1991; Gonzalez et al., 1998).

Villanueva et al. (1997) described the "take off" behaviour, observing it in *Cirroteuthis* spp. and *Grimpoteuthis* spp.. This mode of locomotion is quite similar to that observed in *V. hydrothermalis*. The only difference between this type of escape manoeuvre in cirrate octopus and that of *V. hydrothermalis* is that the former "takes off" with a single strong pulsation, whereas in *V. hydrothermalis* this behavior is composed of a sequence of three or four strong pulsations. This could be due to the absence of fins that allow "fin-swimming" (Villanueva et al., 1997) in the cirrate octopods. We agree with Villanueva et al. (1997) that the "pulsating style" or locomotion consisting of cycles of medusoid pulsations, observed in some cirrate octopods, may have been a repeated escape reaction, i.e. take-off caused by the stress produced by proximity of the mechanical arm of the submersible.

The mode of hunting observed in *V. hydrothermalis* could be considered an aborted "speculative hunt" (Hanlon & Messenger, 1996). This pattern is very similar to that used by shallow-water octopuses. In a completely speculative hunting, the animal firstly detects the prey with its arms, followed by a pounce with outspread web and then a feel around under the web for food. In the case described here, only the first step of this behaviour was observed. The animal did not complete the hunt probably because of the large size of the potential prey. In any case since only a single encounter with a large crab was observed this interpretation remains open.

The jet propulsion mode of locomotion observed in many kinds of cephalopods (Hanlon & Messenger, 1996) consists of forced expulsion of water through the funnel by contractions of the pallial muscles. Although this type of propulsion was not clearly observed in *V. hydrothermalis* this does not mean that the species cannot move using jet propulsion. Its mantle is muscular and the funnel is functional (González et al., 1998). However, the thinness of the mantle wall suggests that the contraction strength may be weak.

In the video records analysed, *V. hydrothermalis* was closely associated with colonies of *Riftia pachyptila* and

Alvinellidae polychaete, and more rarely with mussel beds; however no predation on these species was observed. Gonzalez et al. (1998) suggest that this octopus preys mainly on decapod crustaceans (probably galatheids). The observed aborted attack on a crab (*Bythograea thermydron*) is in keeping with the proposed dietary reliance on crabs, but further studies are needed to confirm this issue since other species of incirrate octopuses also prey upon polychaete and bivalves (Nixon, 1987).

Only one previous mating behaviour between two incirrate deep-sea octopods has been observed (Lutz & Voight, 1994). This observation corresponded to a rare "mating" of two males of different species, one of which appeared to be a mature male of *V. hydrothermalis*. Our observation on a group of five specimens reported here is the first mating behaviour observed and filmed in *V. hydrothermalis*. The "mating at distance" behaviour observed correspond with the reproductive patterns found in other incirrate octopus species (Hanlon & Messenger, 1996).

Vulcanoctopus hydrothermalis is to date the only incirrate octopus associated with hydrothermal vents. It was included in the family Octopodidae (González et al., 1998). However, its subfamily status is not clear and the authors suggested the possibility of a new sub-family, the Vulcanoctopodinae. The behavioural observations described in this paper show this species to be closely similar to other benthic incirrate octopus, but with characters that represent adaptations either to the deep-sea or to hydrothermal vent habitats. Whether it constitutes a form of the subfamily Bathypolypodinae, that has many deep-sea benthic species, or a new subfamily, is a point that could be elucidated using genetic analysis.

Acknowledgements

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