

Egg Brooding by Deep-Sea Octopuses in the North Pacific Ocean

JANET R. VOIGHT^{1,*} AND ANTHONY J. GREHAN²

¹ *Department of Zoology, Field Museum of Natural History, Roosevelt Rd. at Lake Shore Dr., Chicago, Illinois 60605; and* ² *Martin Ryan Marine Science Institute, National University of Ireland, Galway, Ireland*

Abstract. Videotapes made from the submersible *Alvin* on Baby Bare, a 2600-m-deep North Pacific basalt outcrop, and at two other deep-sea localities document that octopuses of the genera *Graneledone* and *Benthoctopus* attach their eggs to hard substrate and apparently brood them through development. The behavior of brooding females was generally similar to that of shallow-water octopuses, but the genera showed apparent differences. In addition to the high density of brooding females observed at Baby Bare, which may relate to the increased availability of exposed hard substrates for egg attachment and of prey, females are suggested to increasingly associate with hard substrates as they mature. The biology of Baby Bare may seem unduly unique because the outcrop is isolated on a sedimented plain and is among the few exposures of hard substrate other than hydrothermal vents that have been explored by submersible. On the sediment-covered ocean floor, the availability of hard substrate may strongly affect the distribution of brooding octopuses. The size and shape of boreholes in 19 of over 400 thyasirid clam shells collected from Baby Bare support the hypothesis that octopuses had preyed upon the clams.

Introduction

Videotapes filmed from submersibles have documented the behavior of deep-sea squids (Moiseev, 1991; Vecchione and Roper, 1991; Roper and Vecchione, 1997) and cirrate octopods (Vecchione and Young, 1997; Villanueva *et al.*, 1997). However, such reports have provided virtually no new information on the benthic octopuses that form the Octopodidae, despite the occurrence of nine recognized

genera at depths greater than 1000 m (Voss, 1988a; González *et al.*, 1998). Laboratory studies do not compensate for the near-absence of *in situ* observations of deep-sea octopuses. *Bathypolypus arcticus* is the only species reported from below 1000 m that has survived trawling to be successfully maintained in the laboratory (O'Dor and Macalaster, 1983; Wood *et al.*, 1998). This species, however, is unusual among deep-sea octopuses (Voss, 1988a) in occurring at depths as shallow as 75 m at high latitudes (Wood *et al.*, 1998).

Trawl-collected octopodid specimens generally provide sparse information on behaviors such as maternal care or on the type of prey taken. Because we have had to rely almost exclusively on specimens collected in trawls, our knowledge of these fundamental aspects of deep-sea octopus biology is minimal. The rare discovery of isolated octopodid eggs in a trawl haul has required that generic identification be inferred from developing embryos (O'Shea and Kubodera, 1996), despite our scant knowledge of embryonic development in deep-sea octopodids. Although deep-sea octopuses are presumably predators, as are other cephalopods, the prey taken by hatchlings and adults remains generally unknown (but for exceptions see O'Dor and Macalaster, 1983; Nixon, 1987).

This paper reports submersible observations that document egg attachment and brooding by members of two octopodid genera, *Graneledone* and *Benthoctopus*, at depths greater than 2000 m in the North Pacific Ocean. Documentation of maternal egg care among deep-sea octopuses confirms the presence of this basic behavior in diverse members of the Octopodidae. The very high densities of brooding females discovered on the base and sides of Baby Bare, an 80-m-high basalt outcrop, suggest that substrate suitable for egg attachment may be extremely limiting. We also provide

Received 17 May 1999; accepted 25 October 1999.

* To whom correspondence should be addressed. E-mail: jvoight@fmnh.org

evidence to suggest that small octopuses drill the shells of clams on which they feed.

Materials and Methods

In situ observations

Videotapes made by the Deep Submergence Vehicle *Alvin* during dives in the North Pacific Ocean at Baby Bare outcrop (47° 42.64'N, 127° 47.15'W; 2640 m) in Cascadia Basin in August 1995, October 1997, and July 1998 form the bulk of the observations reported here. Additional data derive from an ROV *Jason* dive at Baby Bare in 1999, from *Alvin* dive videotapes taken in July 1994 (R. A. Lutz, pers. comm.) at Middle Valley (48° 27'N, 128° 42'W; 2400–2430 m), a sedimented hydrothermal vent described by Juniper *et al.* (1992), and from two still photographs shot from *Alvin* near the Oregon Subduction Zone in 1984 (J. C. Moore, pers. comm.).

Becker and Wheat (1995) and Mottl *et al.* (1995, 1998) describe the geology of Baby Bare. The extinct volcano is estimated to rise 300 m from a buried ridge crest, but extends only 70 m above the heavily sedimented, 2592-m-deep seafloor. Baby Bare is one of the few volcanic edifices that penetrate the nearly continuous layer of sediment that fills the northern Cascadia Basin between Juan de Fuca Ridge and the continent (Davis *et al.*, 1992a). Basalt exposures on steep, sediment-free slopes of Baby Bare occupy much less than 0.1 km² in total area (Mottl *et al.*, 1998). The Baby Bare fauna differs strikingly from that of the surrounding abyssal plain (Grehan *et al.*, 1995; Mottl *et al.*, 1998). Its abundant sponges and echinoderms are typical of the hard-substrate, filter-feeder-dominated seamount fauna, the composition and density of which may reflect the influence of the outcrop on local currents (*e.g.*, Tyler and Zibrowius, 1992; Genin *et al.*, 1992; Rogers, 1994). The fish fauna includes zoarcids, skates, and macrourids. In addition, at Baby Bare, thyasirid clams form locally dense aggregations near springs with water temperatures up to 25°C (Grehan *et al.*, 1995; Mottl *et al.*, 1998). Temperatures were recorded with the *Alvin* and *SUAVE* (SUBmersible System Used to Assess Vented Emissions) heat probes (Massoth *et al.*, 1995).

Octopuses were tentatively identified as members of the genus *Graneledone* if the videotape showed them to have many dorsal skin warts that are especially prominent over the eyes and arm suckers arranged in a single row. Individuals with skin warts in which the arm suckers formed a zig-zag row were also assigned to this genus. Octopuses with smooth skin and two sucker rows (in which the suckers were conspicuously smaller relative to the size of the octopus than in individuals referred to *Graneledone*) were assigned to the genus *Benthooctopus*. Internal examination of 10 specimens collected from Baby Bare, Middle Valley, and Axial Volcano (46°N 130°W, 1459 m) that were identified

on videotapes as members of *Graneledone* allowed this generic determination to be tested. These *Alvin*-collected specimens were compared to other North Pacific octopus specimens in the collections of the Field Museum of Natural History, the California Academy of Sciences, and the University of Miami Marine Laboratory, including seven paratypes of *G. pacifica* Voss and Percy, 1990.

The specimens lack an ink sac and crop, have irregular radulae and small posterior salivary glands, and the dorsal skin of their mantles and heads bears cartilaginous tubercles that are diagnostic of the genus *Graneledone* (Voss, 1988b). The zig-zag arrangement of arm suckers on some videotaped octopuses was attributed to the presence of more suckers that could be arranged in a strictly single row on arms of that length (Voight, 1993). The species determination is complicated by the possible synonymy of *Graneledone boreopacifica* Nesis, 1982, and *G. pacifica* Voss and Percy, 1990. Comparisons of the skin texture and sucker and gill counts of these specimens with seven paratypes of *G. pacifica* and extended study of Northeast Pacific specimens of the genus suggest that more than one species exists, probably segregated by depth (Voight, 1998). Because the 1350-m depth of the type locality of *G. boreopacifica* Nesis, 1982, contrasts sharply with the 2706-m depth of the type locality of *G. pacifica* Voss and Percy, 1990, the specimens from Baby Bare and Middle Valley are tentatively assigned to Voss and Percy's species, and the one from Axial to Nesis' species. The reproductive condition of four submersible-collected female specimens, including the female tentatively assigned to *G. boreopacifica*, is also reported.

Because no specimens that were identified from the videotapes as members of the genus *Benthooctopus* were collected, their identification remains unconfirmed. Although they might pertain to the genus *Bathypolypus*, the smooth dorsal mantle and the distinctly reversed countershaded coloration of these octopuses suggest otherwise. The apparent absence of octopodid genera other than *Graneledone* and *Benthooctopus* from the deep Northeast Pacific Ocean (Voss, 1988a; Voss and Percy, 1990) and the fact that the videotaped octopodids consistently show characters shared with those of specimens of *Benthooctopus* trawled from depths of over 2500 m off the Oregon margin (Voight, unpubl. data) strongly support this generic assignment.

Clam shell collections

Biological collections made at Baby Bare during the three cruises included sediment scoops containing thyasirid clams and clam shells. The hypothesis that octopuses preyed on the clams (Mottl *et al.*, 1998) was tested by comparing boreholes made by shallow-water octopuses (Nixon *et al.*, 1980; Nixon and Maconnachie, 1988) to those discovered in clam shells from Baby Bare. Features characteristic of octopus boreholes are the round or ovoid shape, the beveled

cross-section with an external orifice larger than the internal orifice that penetrates the inner shell surface, and the location in or close to the myostracum (Nixon and Macconnachie, 1988). To test whether boring predators preferentially preyed on clams of a given size, the length of each valve collected in 1997 was measured, and median lengths of intact and bored valves were compared. The proportion of bored clam shells was calculated for each year's collection and compared across collections.

Results

In situ observations

DSV *Alvin* videotapes made both at Baby Bare and at Middle Valley show unusually high densities of octopuses, as Mottl *et al.* (1998) and Juniper *et al.* (1992) noted. Although octopuses are rarely seen during most submersible dives, 28 octopuses were videotaped during 11 dives at Baby Bare in 1995. One 3-min length of videotape from a 1997 dive shows 9 different octopuses, and 10 octopuses were videotaped by Jason in one pass from the outcrop's base to its summit. Observers at Middle Valley report that three or four octopuses could be seen at one time from the submersible, although rarely are such densities recorded on the videotape.

Both at Baby Bare and Middle Valley, octopuses of the genus *Graneledone* were seen moving across open, sedimented areas and sitting with the proximal half of their arms in contact with rocks. All six octopuses collected from open sedimented areas at Middle Valley were fully mature males with several spermatophores. The two nonbrooding female specimens were collected from hard substrate. The female specimen from Middle Valley was collected from beneath an Ocean Drilling Program (ODP) reentry cone that had been installed at Hole 858G in Dead Dog vent field in 1991 (see Davis *et al.*, 1992b; fig. 1). The female from Axial Volcano was collected from among basalt exposures on the caldera wall. Neither octopus was videotaped prior to collection.

Octopuses of *Graneledone* that were videotaped while positioned with their oral, sucker-carrying surface against rocks, or against rock crevices were, when viewed with sufficient detail, found to be brooding eggs attached to almost vertical rock faces or to rock overhangs (Fig. 1). Eggs were frequently only glimpsed above the female's dorsal web sector before they were covered by her web and arms. The eggs were attached to basalt, the only available hard substrate at Baby Bare. At Middle Valley, a brooding female *Graneledone* had attached her eggs to hydrothermally altered and lithified sediment (R. A. Zierenberg, pers. comm.) which also supported anemones, sponges, and ophiuroids, although these were absent from the immediate area of the eggs. A female *Graneledone* was photographed at the Oregon Subduction Zone on a large rock outcrop,

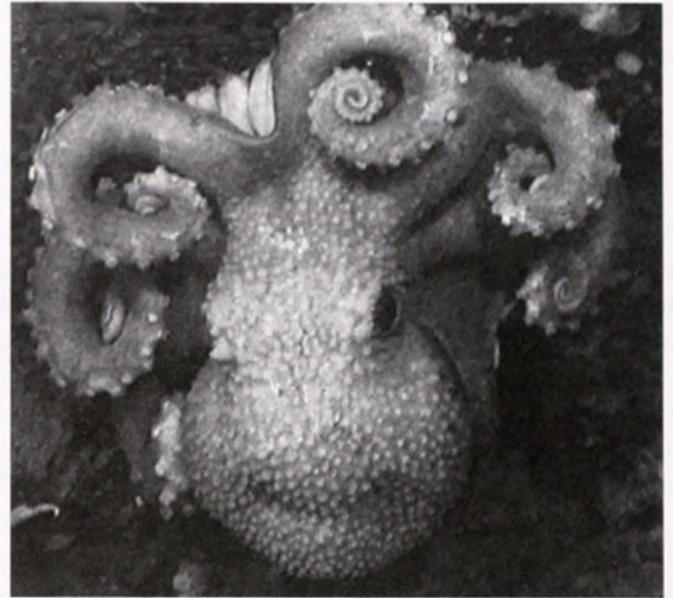


Figure 1. Still from a videotape of a female of *Graneledone pacifica* brooding eggs on a rock exposure at Baby Bare outcrop, *Alvin* Dive 2974, August 1995. Note the heavily textured dorsal mantle, prominent supraocular cirri, and comparatively few arm suckers. Eggs are seen suspended from the rock just above and to the left of the female's web.

roughly 1 km from the nearest cold seep (J. C. Moore, pers. comm.); although eggs can be seen near her upper web, the rock cannot be identified. Videotape from Mama Bare, another small basalt outcrop, also shows octopuses brooding eggs, although on the single dive there, fewer octopuses were seen than at Baby Bare.

A single rock outcrop was visited in both 1998 and 1999. A female of *Graneledone* was present at the outcrop in both years. In 1999, her appearance was consistent with impending senescence: her posture indicated a deterioration of muscle tone, with her arms limply coiled; her skin was mottled and appeared to be flaccid. Unfortunately her clutch could not be examined.

Two eggs collected with the brooding female of *Graneledone* in 1995 (egg length = 25 mm; width = 12.25 mm) contained partially developed embryos. The embryos measured 9.5 mm in mantle length, with 7-mm-long arms that carried up to 30 suckers each. The similarity of these embryos to those reported and illustrated by O'Shea and Kubodera (1996) supports their assignment of the eggs and embryos to *Graneledone*. Embryonic structures were not yet visible in the seven eggs collected with the brooding female in 1998 (size range: 22.0 mm long by 11.2 mm wide to 24.8 by 12.2 mm).

Water temperatures near the brooding sites were recorded during two dives in 1995. The ambient temperature measured with the *SUAVE* probe was 1.83°C (G. J. Massoth, pers. comm.). At the base of a 1.5 m high basalt outcrop on which an octopus brooded eggs, the *Alvin* heat probe recorded a temperature of 3.0°C; within the crevice where the eggs were attached, the temperature was 1.83°C. Tempera-

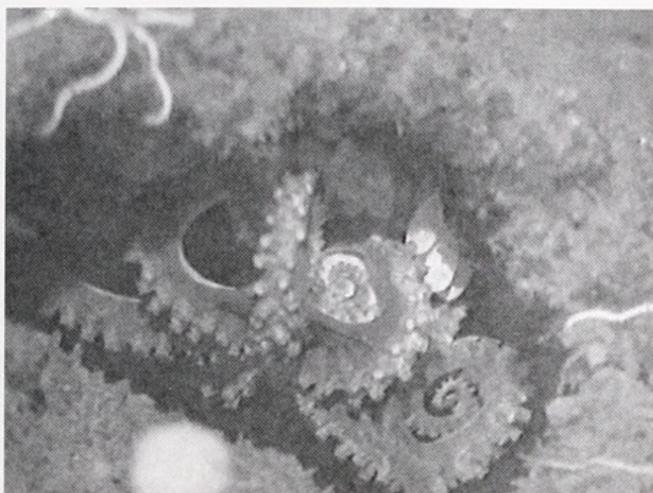


Figure 2. Still from a videotape of a female of *Benthoctopus* brooding eggs inside a rock overhang, *Alvin* dive 2974, August 13, 1995. Note the double rows of arm suckers, the dark ventral web surface, and the much brighter dorsal mantle surface. The oral surface of the animal is positioned away from the egg mass and the tear-shaped eggs are suspended from the roof of the rock crevice.

ture probes inserted into the sediment recorded temperatures as high as 4.5°C, but the water temperature just above the sediments was 1.84°C, only slightly elevated over ambient (G. J. Massoth, pers. comm.).

Brooding individuals of *Benthoctopus* were seen much less often than were those of *Graneledone*. Most members of *Benthoctopus* were observed partially hidden under ledges or in narrow crevices (Fig. 2), on one occasion within 5 m of a congener. Once in both 1995 and 1997, females of both genera brooded eggs in opposite ends of the same cleft in the rock face at Baby Bare. The sequence in which the females moved into the cleft could not be estimated because females of *Benthoctopus* were so deep in the recess of the rock that the developmental stage of their eggs could not be determined for comparison to those of *Graneledone*. Their proximity (within an arm's length) allowed the animals to be compared in size: females of *Benthoctopus* seen brooding at these depths of from 2400 to 2600 m were generally one-half to one-third the size of those of *Graneledone*. This differences in size and in how females were positioned—those of *Benthoctopus* were most often under rock overhangs or inside crevices while those of *Graneledone* were most often positioned against rocks—are likely to have strongly biased the observations toward members of *Graneledone* (e.g., 16 of 20 observations of octopuses in which the genus could be identified in 1995).

Videotapes show that in both genera the eggs are individually attached to the rock by short stalks that rapidly broaden to merge with the large chorion balloon of the egg. This outer egg membrane (chorion) is transparent, allowing the developing embryos to be seen. The developmental stages observed ranged from apparently undeveloped eggs to embryos in the second inversion (terminology of Boletzky, 1987). In clutches guarded by members of *Graneledone*, each egg stalk could be

seen to be attached to the rock by dark green cement similar to that reported for *Bathypolypus arcticus* (O'Dor and Macalaster, 1983). Regardless of the egg's stage of development, the color of the cement appeared to be the same. The number of eggs in any given clutch could not be determined.

Differences between the genera, in addition to the morphological characters used to distinguish them, were apparent. Octopuses of *Graneledone* behaved sluggishly, often showing virtually no response to the approach of the submersible. In contrast, individuals of *Benthoctopus* often jetted into the water column, sometimes toward the approaching submersible. While brooding eggs, octopuses of *Graneledone* positioned themselves with their dorsal surface away from the eggs and their oral surface nearest them. In contrast, octopuses of *Benthoctopus* positioned themselves with their oral, sucker-carrying surface facing away from their eggs and their mantle tip pointed toward them. Although observations are few, the eggs brooded by octopuses of *Graneledone* appeared to be more sausage-shaped and the eggs of *Benthoctopus* more teardrop-shaped.

The reproductive organs of all female specimens of *Graneledone* that were collected from hard substrate by submersible were enlarged, and the ovarian eggs of each showed some degree of enlargement (Table 1). The female brooding early-stage eggs collected from Baby Bare in 1998 had the smallest ovarian eggs. The oviducal glands of brooding females were smaller than those of nonbrooding females collected from hard substrate. No prey were apparent in the digestive systems of either brooding female, although the large mass of amber-colored oil in the proximal intestine of the female collected from Baby Bare in 1995 suggested a partially digested egg.

Clam shell collections

Small boreholes were discovered in between 3.8% and 5.1% of the thyasirid clam shells (tentatively identified as *Axinus* sp., near *A. grandis*, E. Southward, pers. comm.) collected (Table 2). Round or slightly oval boreholes were located most often on or near the umbo of the valves. Bored and intact valves do not appear to significantly differ in size (bored: median = 21.75 mm; intact median = 18.75 mm), nor are bored shells biased in handedness (right $n = 8$; left $n = 6$). The outer diameters of the boreholes range from 0.75 to 2 mm, and their inner diameters from 0.4 to 1.5 mm.

Discussion

In situ observations

The deep-sea octopus *Graneledone pacifica* and at least one species of *Benthoctopus* attach their eggs to hard substrate and apparently brood them during development. The high densities of brooding octopuses at depths below 2600 m at Baby Bare outcrop and Middle Valley hydrothermal vent field suggest

Table 1

Reported from preserved female specimens collected from hard substrates are mantle lengths in mm, the number and size of ovarian eggs and oviducal gland size and color

Specimen locality & Catalog number	Mantle length (mm)	Ovarian eggs Size (mm)** & appearance	Oviducal gland Size (mm)*; color
Non-Brooding Females			
MV-ODP cone 1994, #FMNH 278063	86.9	15 × 3.8 (<i>n</i> = 1), 8.5 × 2.5 (<i>n</i> = 65); Most weakly striated	12 × 7.3; Light orange
Axial 1998, #FMNH 282751	136.7	17.5 × 6 (<i>n</i> = 72); Filling, striated	14.4 × 9.3; Deep purple
Brooding Females			
Baby Bare 1995	99.3	21.5 × 9 (<i>n</i> = 3), 10 × 2.5 (<i>n</i> = 63); Flattened	7.4 × 6.2; Light orange
Baby Bare 1998, #FMNH 282750	80.9	8.25 × 2.5 (<i>n</i> = 90); Rounded, full	11 × 7.2; Light orange

* Length, measured parallel to the oviduct, by diameter, both in millimeters.

** Length by width, both in millimeters.

that the availability of hard substrate and of potential prey strongly affect octopus distribution in the heavily sedimented deep sea. Boletzky (1994) theorized that maternal care is shared among the Octopodidae, although whether attaching eggs to hard substrates is a synapomorphy of the benthic octopuses remains unknown. A very few shallow-water octopodid species reportedly carry their developing eggs in their web instead of attaching them to substrate (Hochberg *et al.*, 1992), as some bathypelagic octopods are known to do (Young, 1972, 1995). Whether egg attachment is a synapomorphy of the Octopodidae that has undergone reversal in a few species or is a character that has evolved multiple times cannot be assessed because relationships within the family are poorly resolved (Voight, 1997).

The high density of octopuses at Baby Bare and Middle Valley had been linked to the availability of chemosynthetic clams as prey (Juniper *et al.*, 1992; Mottl *et al.*, 1998). The benefits that accrue to hatchling and maturing octopuses from the proximity of potential prey are clear, although mature and brooding individuals of most shallow-water species that have been studied generally reduce their prey intake (Wells and Wells, 1977). Because exposed hard substrate appears to be required for egg attachment, and the floor of the Cascadia Basin is covered by a thick layer of sediment (Davis *et al.*,

1992a; Mottl *et al.*, 1998), the availability in these areas of hard substrate may also attract octopuses.

Individual females may occupy brooding sites for years, as the limited data available indicate that cephalopod eggs develop extremely slowly. Egg size and ambient temperature appear to be the primary determinants of development rates (Boletzky, 1994; B. A. Seibel, pers. comm.). If these factors interact in the same way at temperatures typical of the deep sea—that is, if no compensating mechanism accelerates development at low temperatures—the 25-mm-long eggs of *Graneledone* are calculated to require almost 4 years to develop at ambient temperatures of near 2°C (B. A. Seibel, pers. comm.). Although warm (25°C) springs exist on Baby Bare (Mottl *et al.*, 1998), octopus eggs are brooded in rock crevices on the outcrop's flanks where the temperature is essentially unchanged from ambient. Although eggs attached to the warm basalt could gain heat by conduction, significant heat would probably be lost by radiation as the heat passed through the stalk.

Evidence of limiting substrate has been reported in another deep-water octopodid. The 11- by 6-mm eggs of *Bathypolypus arcticus* develop in about 400 days at temperatures of 5° to 11°C (Wood *et al.*, 1998). Eleven females of this species, and more than 100 eggs, were found enfolded in a single plastic sheet trawled from near Sweden (O'Dor and Macalaster, 1983). We did not observe congeneric females sharing a single substrate at Baby Bare, but females of different genera were seen within an arm's length of each other under the same ledge.

The distribution of maturing females in relation to substrate type appears to shift toward hard substrate. Both of the nonbrooding females collected from hard substrates had enlarged oviducal glands and large ovarian eggs (Table 1), evidence of reproductive maturation (Mangold-Wirz, 1963), but only 1 of the 14 trawl-collected female specimens in the type series (Voss and Percy, 1990) shows comparable enlargement of the female reproductive system. The small oviducal glands of brooding females compared to those of

Table 2

The total number of valves of thyasirid clams collected and examined each year and the number and frequency of bored valves

Year	Total (<i>n</i>) dead valves collected	Bored valves	
		<i>n</i>	%
1995	51	2	3.9
1997	272	14	5.1
1998	79	3	3.8
Total	402	19	4.7

The frequency of boreholes does not significantly differ among the collections: $G = 3.68$, $df = 5$, $P > 0.05$.

females that apparently have not yet spawned (Table 1) may be due to postspawning resorption. The small ovarian eggs in an "obviously exhausted" female of *Graneledone boreo-pacifica* (Nesis, 1989) may reflect this pattern. The contrast between the reproductive maturity of females collected from hard substrate and the immaturity of those trawled from soft substrate is startling and suggests that maturing females shift habitat preference to increasingly associate with hard substrate, perhaps to secure a brooding site. If increased prey availability were solely responsible for their advanced reproductive maturity, reproductively mature females would occur at a wide range of sizes rather than being among the largest specimens known in the species.

If hard substrate suitable for egg attachment is limiting in the deep sea, high densities of brooding octopuses should be found at sites other than Baby Bare. Despite decades of study given to seamounts, such groups of octopuses have been unreported. The nature of the research that has been conducted at Baby Bare may make its fauna appear unduly unique. Baby Bare is one of the few non-hydrothermal vent structures in the deep sea that has been examined at depth with submersibles. The trawls, rock dredges, epibenthic sleds, and baited traps and hooks that have been most frequently used to sample seamounts (Wilson and Kaufmann, 1987) have focused on seamount summits rather than their bases. Even submersible explorations have most often focused on seamount summits. For example, the Canadian submersible *Pisces IV* documented the biota of Cobb Seamount at 180 m and above (Parker and Tunnicliffe, 1994), depths that are inaccessible to octopuses living at 2600 m. The bases of other seamounts surrounded by heavily sedimented seafloor must be observed to determine whether Baby Bare is unique in having high densities of brooding octopuses.

Clam shell collections

The similarity of the boreholes on thyasirid clam shells collected at Baby Bare to those drilled by shallow-water octopuses in bivalve shells (Nixon *et al.*, 1980; Nixon and Maconnachie, 1988) support the hypothesis that octopuses prey on the clams by drilling their shells. Two caveats reduce the confidence with which octopuses can be identified as predators of the clams. First, borehole morphology and size vary with prey species rather than octopus size (Nixon and Maconnachie, 1988). Second, because Baby Bare lies beneath the depth at which calcium and aragonite passively dissolve, the boreholes may have been enlarged and their edges obscured by shell dissolution. The edges of the boreholes were poorly defined when viewed with scanning electron microscopy (Voight, unpubl. data). Because, however, the boreholes are generally similar to those made by octopuses and no other deep-sea predators known to bore shells were collected during any cruise to Baby Bare, octopuses are concluded to have bored the clam shells. Whether

members of one, the other, or both genera bored the clams cannot be assessed. The octopus (an individual of *Benthocotopus*) reported to have grasped clam shells in three of its arms (Mottl *et al.*, 1998) was not observed to prey on them. The presence of crushed gastropod shells in the gut of the specimen of *Graneledone* from Axial Volcano (Voight, unpubl. data) suggests that these octopuses would not drill the thin shells of these clams.

The comparatively small size (28.5 mm or less) and thin shells of the Baby Bare clams indicate that they were bored by small octopuses. Shallow-water octopuses are known to prey on bivalves either by drilling the shell and injecting toxins through the borehole or by grasping the opposing valves with their suckers and forcing them open, usually without damaging the shells (McQuaid, 1994). Small octopuses are more likely to drill small bivalves than are large octopuses; large octopuses are more likely to force the valves apart, leaving little evidence of predation on the shells (McQuaid, 1994). In addition, greater predation pressure may be exerted by small or young octopuses, which may reach very high densities when clutches hatch, than by fully mature and possibly senescent adults. Nixon's (1987) review suggests that deep-sea octopuses opportunistically take small prey, although no evidence had previously suggested that abyssal octopuses prey on clams.

Further opportunities to directly observe the biology of abyssal octopuses may resolve questions raised by this research, including whether egg-brooding sites used by deep-sea octopuses are typically extremely localized, what is the duration of development of these large eggs, and do deep-sea octopuses drill hard-shelled prey such as clams.

Acknowledgments

M. Mottl, chief scientist of the 1995 cruise (supported by NSF grant OCE-93-14632), collected the brooding female with her eggs and shared videotapes. Co-chief Scientists of the 1997 cruise, K. Becker and H. P. Johnson, and J. Cowen, Chief Scientist in 1998 and 1999, graciously made opportunities available to expand earlier observations and make additional collections. R. A. Lutz provided videotape and octopus specimens from Middle Valley. C. J. Moore provided photographs of the Oregon specimens. Assistance of the *Alvin* and *Jason* groups and the crews of the R/V *Atlantis* and *Thomas G. Thompson* was essential in making observations on which this report is based. We thank R. A. Zierenberg, B. A. Seibel, G. J. Massoth, B. Loetel, R. Collin, N. Becker, F. E. Anderson, and two anonymous reviewers for their help. JRV's participation in the 1997 and 1998 cruises was supported by grants from the West Coast and Polar Regions Undersea Research Center at the University of Alaska Fairbanks and NOAA's National Undersea Research Program; her 1999 cruise participation was supported by Marshall Field Fund of the Department of

Zoology, The Field Museum. AJG's participation in the 1995 cruise was funded by a European collaboration grant awarded to Kim Juniper from the Association of Universities and Colleges of Canada.

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