In situ observations on *Brachioteuthis beanii* Verrill: paired behavior, probably mating (Cephalopoda, Oegopsida)

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Abstract: A behavior that has never been seen in cephalopods was observed three times in a large aggregation of *Brachioteuthis beanii* Verrill, 1881. During a series of submersible dives off Cape Hatteras, North Carolina, eastern U. S., three pairs of *Brachioteuthis* were seen, and one pair was video-taped. In all three pairs one squid grasped the other by the posterior mantle in its arm crown. This paired behavior involved brief periods in which the grasped squid bent its head and body posteriorly and vigorously moved its arms around the head and mantle opening of the grasping squid. Although we were unable to capture any of the coupling pairs to determine their stage of maturity, we believe this unusual activity represents mating behavior.

Key words: Cephalopoda, squid, behavior, mating, *in situ* observations, submersible

The observations reported in this paper are based on a series of dives conducted by the Johnson-Sea-Link I submersible in September 1994 about 95 km off Cape Hatteras, North Carolina, in an area called The Point. The bottom topography is characterized by a series of parallel ridges and canyons that fan out seaward into deep water from the edge of the continental slope. The tops of the ridges where the dives took place were at about 700 m depth, and the walls of the canyons sloped off at angles of 50-70°.

The area of The Point is well known for its extremely high productivity, and the benthic biomass is an order of magnitude greater than in comparable areas (Schaff *et al.*, 1992; Felley and Vecchione, 1995). The ecosystem around The Point is well documented and is the site of ongoing environmental studies, especially as it is a potential location for oil exploration (Diaz *et al.*, 1994). Unpublished reports and video tapes from other submersible operations at The Point confirm that the abundance of cephalopods in the area is very high every year.

Our objectives during the dive series were (1) to test the hypothesis (Trites, 1983; O'Dor and Balch, 1985) that The Point is an area utilized by *Illex* spp. as a spawning ground, and (2) to observe and document occurrence and behavior of all species of cephalopods that were encountered during the cruise. This paper reports the observations on *Brachioteuthis beanii*, particularly on a behavior not previously observed in any species of deep-sea cephalopods. This continues the series of papers from our *in situ* observations on submersible and ROV data (Vecchione and Roper, 1991; Vecchione *et al.*, 1992; Roper and Vecchione, in press).

MATERIALS AND METHODS

The dive sites at The Point were located at 700-1000 m (bottom depth), beyond which the canyon floors sloped seaward into much deeper water. Bottom temperatures were approximately 4.5°C in the canyons.

Of the 15 dives conducted during the cruise, five yielded observations on *Brachioteuthis beanii*. In particular, Johnson-Sea-Link I dive 3745 provided the interesting results described here. This dive took place off Cape Hatteras at The Point on 08 September 1994 (35°13.513' N, 74°57.703' W; 1034-1329 hrs; maximum depth 800 m; surface temperature 28°C; thermocline at 80-120 m spanning 27-17°C; bottom temperature at 800 m, 4.58°C). Specimens of cephalopods were captured by the submersible and by a 2-m Tucker trawl.

Portions of the video sequences upon which this paper is based are presented within the "Cephalopods in Action" web pages through URL = http://nmnhwww.si.edu/cephs/.

RESULTS

In all, 13 species (12 squids and 1 octopod) were

observed from the submersible or captured by midwater trawl; large numbers of *Illex* were observed. Major new observations were filmed and recorded for *Mastigoteuthis magna* Joubin, 1913 (Roper and Vecchione, in press) and *Brachioteuthis beanii*. *B. beanii* was observed on five of the 15 dives at depths of 500 m, 700 m, two at 800 m, and 860 m. One specimen was captured in a midwater trawl, which enabled us to verify the specific identification. Individuals and aggregations occurred from about 5-60 m above the bottom. Most animals were seen in aggregations or schools; as many as 40-60 individuals were in sight from the submersible simultaneously, while others were more scattered. A single individual was seen on only one dive, just a few meters above the bottom. Several *B. beanii* were observed attacking prey consisting of myctophid and sternoptychid fishes.

During JSL-I dive 3745, numerous individuals of *Brachioteuthis beanii* were first encountered at about 700 m in the box canyon with 70° sloping walls. The squids have a golden-colored body; arms and head are pink grading to whitish; the eyes each have a large, elongate anteroventral photophore that reflects the submersible lights brightly.

At about 60 m above the bottom, the submersible encountered loose aggregations of several dozen *Brachioteuthis* that continued to occur down through the rest of the water column. During the final descent to the bottom, two pairs of squid were observed coupled in tandem, as described below. The submersible stopped a few meters above the bottom directly in front of a third pair of already-coupled *B. beanii*. The pair was video-taped for 10 min, during which they remained coupled or in contact.

Because we were not present on that dive, no attempt was made to capture the two squid, each about 20 cm total length, which were still coupled when the submersible started its transect along the bottom. During this and other dives when *Brachioteuthis* were encountered, neither the aggregated individuals nor the three coupled pairs seemed to react to the submersible.

The following description is a summary of the 10-min video tape of the paired *Brachioteuthis beanii* begun after the squid were already coupled. The two were in a tandem position, head-to-tail, with the posterior squid firmly grasping the anterior squid with its arms along the fins and posterior mantle (Fig. 1a). Both squid remained quite still with no apparent attempts by the anterior partner to escape. Infrequently, the posterior squid angled its mantle dorsally, nearly 90° to the axis of the head and arms (Fig. 1b); this right-angle position was held for several seconds. At one point the two squid separated in a flurry of activity with vigorous arm waving and head movement (Fig. 2a). Then they oriented head-to-head, motionless, with their mantles parallel and adjacent for nearly a minute (Fig. 2b), followed by vigorous arm waving. The posterior individual

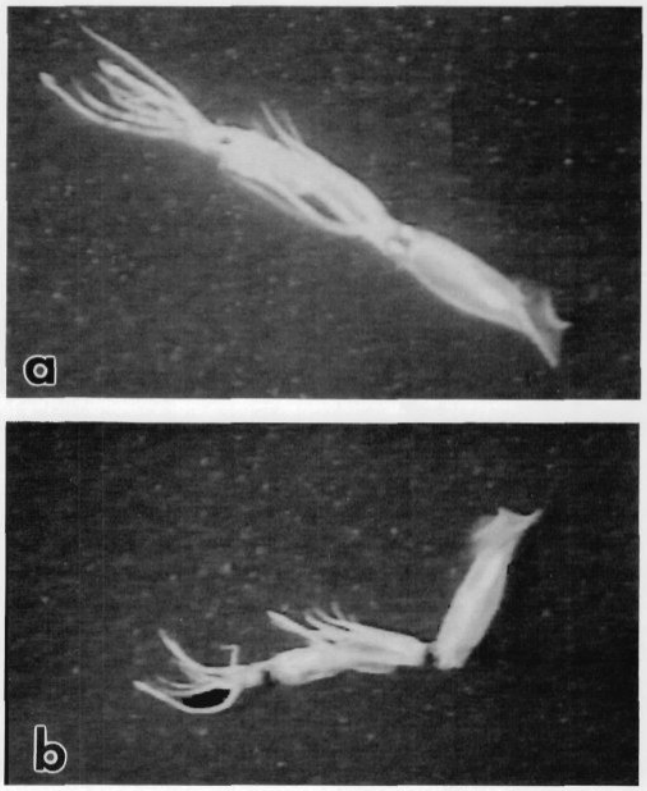

Fig. 1. a. Typical coupling behavior of *Brachioteuthis beanii*, showing posterior squid grasping anterior squid. Three couples were observed in this tandem position. (All figures are photographs made from video tapes). **b.** Coupled pair of *B. beanii* with head and mantle of the posterior squid held briefly in a right-angle position.

then eased back into the tail-holding position without a struggle. The next sequence involved activity in which the anterior squid underwent gyrations, then a rotating, twisting motion around the longitudinal axis of the body for about 45 sec while being firmly held by the posterior squid. Next followed about 2 min during which the anterior (grasped) squid bent its head and mantle posteriorly, forming nearly a circle, and manipulated its arms vigorously around the head and mantle opening of the posterior (grasping) squid (Fig. 2c). The final minute of observation showed the pair coupled quiescently in the head-to-tail tandem position (Fig. 1a).

Because the animals were not captured and because the resolution of the video tape was insufficient to show details of internal anatomy, we could not determine with certainty the sexes of the observed squid, even though they were of different appearance. The condition of the anterior specimen and visible differences in internal anatomy are worth noting and could provide hints about its sex. Close examination of the specimen in the video revealed that the mantle, fins, and tail are scarred and scratched, undoubtedly a result of being grasped and held by the posterior specimen. Furthermore, the region of the digestive glands and

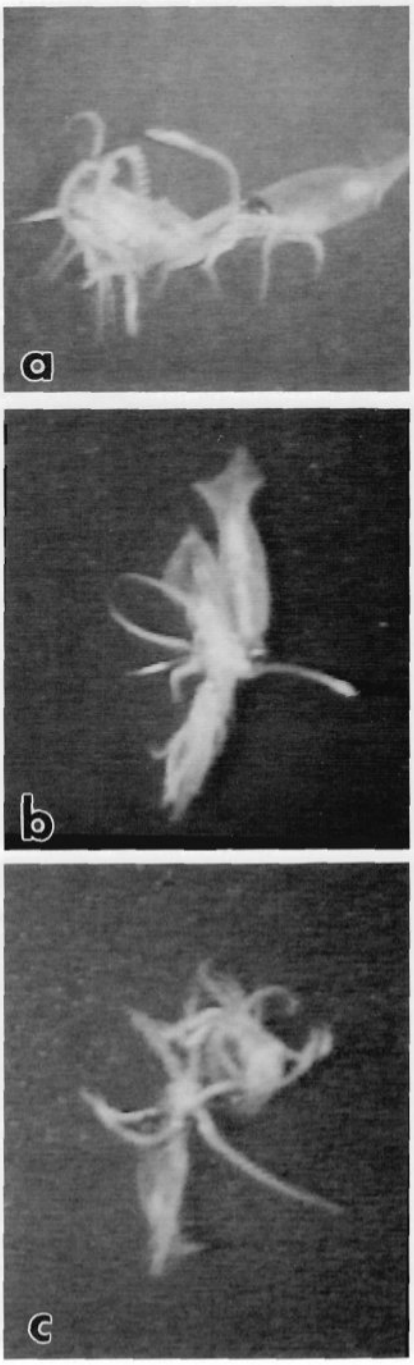

Fig. 2. a. Anterior squid (right) of paired *Brachioteuthis beanii,* waving arms and writhing. **b.** Pair of *B. beanii* lying head-to-head with mantles parallel and adjacent following activity shown in 2a. Anterior squid on left. **c.** Anterior squid (right) of coupled *B. beanii* with head and mantle bent posteriorly and vigorous arm movements.

especially the reproductive glands appears to be different. The major difference is that the anterior specimen has a distinct, broad, whitish, nodular mass dorsal to the digestive gland near the mantle opening (Fig. 3). This could be a mass of spermatophores deposited inside the mantle cavity on the internal mantle wall.

An immature male was captured on a later dive, and the reproductive organs, the spermatophoric apparatus, and testes were developing as asymmetrical structures in the posterior mantle as is shown by the coupled specimen in Fig. 3. There was no trace of a hectocotylus. We examined fully mature males of *Brachioteuthis* in the National Museum of Natural History collection; they had full Needham's sacs and no trace of a hectocotylus, as has been described as a character of the genus. No mature females were available for study and comparison with the video images.

Feeding behavior also was observed in several other *Brachioteuthis beanii* preying on myctophid fish. Further, observations were made on a resting position in which individuals typically were observed. This typical hovering posture has been observed and video taped on several occasions, both during this cruise and previously (unpubl.). The axis of the mantle, head, and arms lies in a horizontal plane; the arms are splayed out laterally in a fan-shaped arc. Very gentle mantle pulsations are seen, or no movement at all, and no forward or rearward locomotion occurs as a result of mantle expulsions. Some motion in the posterior direction occurs from fin flapping, but this is associated mostly with position-holding or slow swimming. During the upstroke the fins overlap dorsally. In some instances, the tentacular clubs are locked together.

Two observations from previous dives in the same area immediately preceding our cruise are relevant to the current discussion. Ophiuroid echinoderms occur in patches of great abundance on the soft sediments of the canyon walls and floor, often so abundant that their arms overlap. One extremely dense patch in this area required 4 min for the submersible to traverse its diameter (Felley and Vecchione, 1995). This phenomenon was observed on our cruise as well. A video sequence showed a cluster of ophiuroids, *Ophiura sarsii* Lütken, 1855, enveloping a *Brachioteuthis beanii* (Fig. 4a). The squid was still alive, as indicated by weak mantle pumping and fin beating, and it lay on its dorsal surface. A second video sequence showed a deep-sea red crab, *Chaceon* cf. *quinquedens* (Smith, 1879), grasping a *B. beanii* in one large cheliped with the posterior end of the squid held in its mouth (Fig. 4b); the maxillipeds were actively working.

DISCUSSION

While the status of the systematics of the Brachioteuthidae is quite confused and the family requires revision, we are confident that the species we observed, video taped, and captured is *Brachioteuthis beanii,* the type

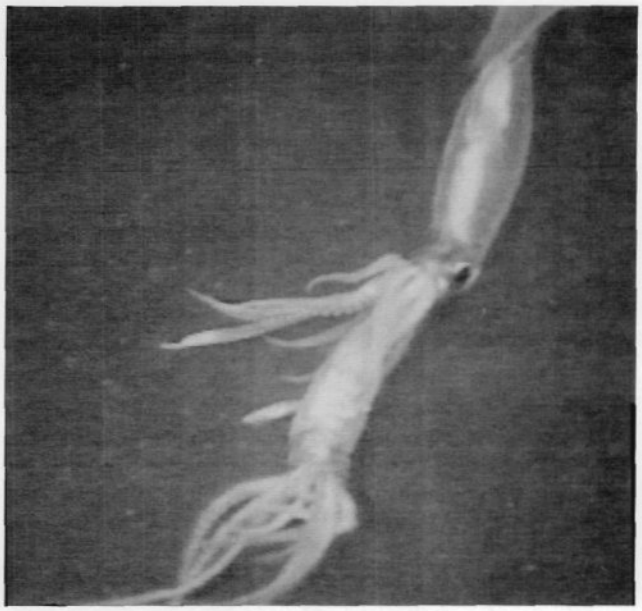

Fig. 3. Coupled pair of *Brachioteuthis beanii* showing different internal structures, having resumed tandem orientation following the activity shown in Figs. 2a-c. Posterior squid (top) with asymetrical reproductive apparatus, probably the male. Anterior squid (bottom) with broad, whitish, nodular mass dorsal to digestive gland in anterior mantle cavity, probably the female.

species of the genus. Our specimen conforms to the description and illustration of this species given by Verrill (1881) for the type specimens caught off Martha's Vineyard. It appears that the species is associated with the Gulf Stream system and that it is the only *Brachioteuthis* species currently known to occur in the northwestern Atlantic Ocean. Even more poorly known is *B. bowmani* Russell, 1909, from the northeastern Atlantic; the relationship between these two taxa is unknown (Nesis, 1987).

Brachioteuthis species are not abundant in collections; collection lots usually contain one or only a few specimens, and very few specimens are sexually mature. At least some species of *Brachioteuthis* develop distinctive dermal structures on the surface of the mantle at maturity (M. Sweeney, pers. comm.), but no such sculpturing was evident on any of the specimens observed during this cruise, nor from videos taken during previous cruises in the area.

In attempting to understand our observations of the previously unobserved coupling behavior in *Brachioteuthis beanii*, we offer two possible explanations:

(1) Cannibalism. The anterior specimen shows evidence of abrasion and external tissue damage on the posterior mantle, fins, and tail. But squids in general, to our knowledge, never have been observed to capture prey in the head-to-tail manner observed here. When squid attack prey, they usually strike in the region of the dorsal head-and-neck junction, to immobilize the prey with a lethal bite. In the three pairs of coupled *Brachioteuthis beanii* observed, the anterior specimen never appeared to struggle or to exhibit strong mantle contractions, as if in an effort to escape. Even when they decoupled and hovered parallel to each other, mantles adjacent and head-to-head, with no grasping action, no efforts to escape were observed. No partially devoured squid were seen. Several *B. beanii* were observed to attack myctophid and sternoptychid fishes which were

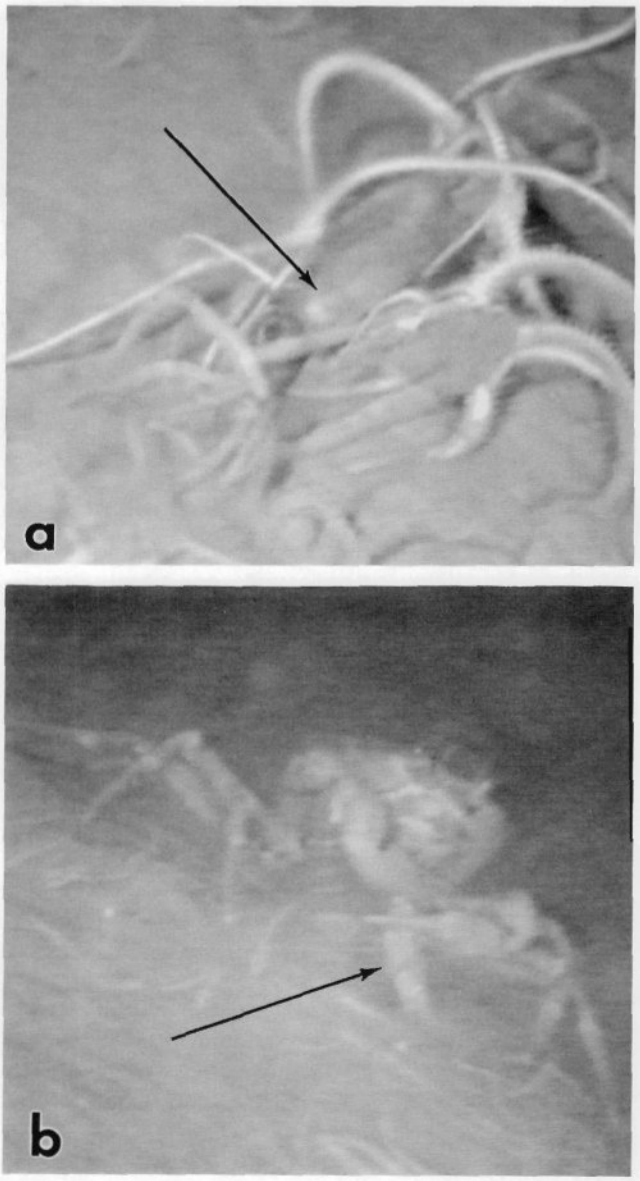

Fig. 4. a. A cluster of brittlestars, *Ophiura sarsii*, enveloping a live but weak *Brachioteuthis beanii* in apparent feeding frenzy. **b.** A deep-sea red crab, *Chaceon* cf. *quinquedens*, feeding on a dead *B. beanii* held in its cheliped.

abundant in the area, providing plenty of food. Cannibalism, therefore, seems unlikely.

(2) Mating behavior. Although the activity we describe here previously has not been observed in any deep-sea squid, we believe the observations can be explained as mating behavior. The coupled specimens were not captured to enable verification of sex and stage of maturity, but our hypothesis is supported by collateral evidence: (a) three pairs of *Brachioteuthis beanii* exhibited identical behavior; (b) the three grasped anterior squid made no attempts to escape; (c) the coupling period was of long duration, with alternating periods of quiescence and strong mutual action of the arms; (d) obvious differences in internal anatomy indicate different sexes; (e) four of the five dives that observed *B. beanii* recorded schools or aggregations of these squids within 60 m of the bottom in a highly productive environment; (f) the tissues of the mantle and fins of the anterior specimen are abraded and damaged, as is well documented for species of squids whose reproductive behavior is known (*e. g.* Hixon, 1983).

The nuchal area is known to be a site for attachment of spermatophores in other oceanic squids, *e. g.* enoploteuthids (Burgess, in press). If the white mass dorsal to the digestive gland observed in our video tape is a deposit of spermatophores, the coupled specimens are different sexes and the anterior specimen would be the female, while the posterior specimen, with its asymetrical reproductive apparatus, would be the male. The female would not have to be fully mature to mate and receive spermatophores; this would be similar to the case in *Illex coindetii* (Verany, 1839) (Mangold-Wirz, 1963). It could be a selective/evolutionary advantage for an early-maturing male to have his spermatophores in place and available for fertilization of the eggs the moment they become ripe. Retention of viable sperm is known in females of other species of cephalopods (Mangold, 1987).

Scavenging by ophiuroids and a *Chaceon* crab on weak or dead *Brachioteuthis beanii* is additional evidence that spawning followed by death occurs in this area. There seems no possibility that ophiuroids or *Chaceon* crabs could capture a healthy mesopelagic or bentho-pelagic squid, even if it were resting on the bottom. Although *Illex* commonly rests on the bottom, we never have observed *Brachioteuthis* to do so. We suggest that the squid were spent and dying individuals that had sunk to the bottom after spawning as is known for other cephalopods (Mangold, 1987). Spent, dying squids that sink to the bottom could provide a significant source of energy to the deep benthic fauna.

We believe that the most reasonable explanation for these observations on *Brachioteuthis beanii* is that they demonstrate, for the first time, mating behavior in deep-sea squids.

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LITERATURE CITED

Burgess, L. A. In press. A survey of seminal receptacles in the Enoploteuthidae. *In: Systematics and Biogeography of Cephalopods,* N. A. Voss *et al.*, eds. *Smithsonian Contributions to Zoology.*

Diaz, R. J., J. A. Blake, and G. Randall Cutter, Jr., eds. 1994. Topical studies in oceanography. Input, accumulation and cycling of materials on the continental slope off Cape Hatteras. *Deep-Sea Research II* 41(4-6):705-982.

Felley, J. D. and M. Vecchione. 1995. Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles. *Fishery Bulletin* 93(2):262-273.

Hixon, R. 1983. *Loligo opalescens. In: Cephalopod Life Cycles. Vol. I, Species Accounts,* P. R. Boyle, ed. pp. 95-114. Academic Press, London.

Mangold, K. 1987. Reproduction. *In: Cephalopod Life Cycles. Vol. II, Comparative Reviews,* P. R. Boyle, ed. pp. 157-200. Academic Press, London.

Mangold-Wirz, K. 1963. Biologie des cephalopodes benthiques et nectoniques del la Mer Catalane. *Vie et Milieu (suppl.)* 13:1-285.

Nesis, K. N. 1987. *Cephalopods of the World. Squids, Cuttlefishes, Octopuses, and Allies.* T. F. H. Publications, Neptune City, New Jersey, 351 pp.

O'Dor, R. K. and N. Balch. 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *Northwest Atlantic Fisheries Organization, Scientific Council Studies* 9:69-76.

Roper, C. F. E. and M. Vecchione. In press. *In situ* observations test hypotheses of functional morphology in *Mastigoteuthis* (Cephalopoda; Oegopsida). *Vie et Milieu.*

Schaff, T., L. Levin, N. Blair, D. DeMaster, R. Pope, and S. Boehme. 1992. Spatial heterogeneity of benthos on the Carolina continental slope: large (100 km)-scale variation. *Marine Ecology Progress Series* 88:143-160.

Trites, R. W. 1983. Physical oceanographic features and processes relevant to *Illex illecebrosus* spawning in the western North Atlantic and subsequent larval distribution. *North Atlantic Fisheries Organization, Scientific Council Studies* 6:39-55.

Vecchione, M. and C. F. E. Roper. 1991. Cephalopods observed from submersibles in the western North Atlantic. *Bulletin of Marine Science* 49(1-2):433-445.

Vecchione, M., B. H. Robison, and C. F. E. Roper. 1992. A tale of two

species: tail morphology in paralarval *Chiroteuthis* (Cephalopoda: Chiroteuthidae). *Proceedings of the Biological Society of Washington* 105(4):683-692.

Verrill, A. E. 1880-1881. The cephalopods of the north-eastern coast of America. Part II. The smaller cephalopods, including the "squids" and the octopi, with other allied forms. *Transactions of the Connecticut Academy of Sciences* 5(6):259-446.

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