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THE EGGS AND LARVAE OF *BRACHIOTEUTHIS* SP. (CEPHALOPODA : TEUTHOIDEA) FROM HAWAIIAN WATERS

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CEPHALOPODA
TEUTHOIDEA
BRACHIOTEUTHIS
EGGS
LARVAE
HAWAII

ABSTRACT. — *Brachioteuthis* sp. is the only squid outside of the family Enoploteuthidae that is known to spawn individual eggs into the plankton. Eggs captured off Hawaii were reared in the laboratory for several days after hatching. The hatchlings were identified by matching them to a size-series of larvae taken from plankton samples. As a result, the early life-history stages of the Hawaiian species of *Brachioteuthis* could be described. Peculiar aspects of the morphology of the larva include an elongate neck, an adjoining fluid-filled reservoir, an ocular appendage on the anterior end of each eye, large tentacles and very small arms. The larvae live in the upper 150 m of the open ocean during the day. The biology of this peculiar larva may bear some resemblence to that of a jellyfish.

CEPHALOPADA
TEUTHOIDEA
BRACHIOTEUTHIS
OEUFS
LARVES
HAWAÏ

RÉSUMÉ. — *Brachioteuthis* sp. est le seul Oegopsidé n'appartenant pas à la famille des Enopleuthidés qui pond des œufs individuels entre deux eaux. Les œufs ont été récoltés près de Hawaï, amenés à l'éclosion, et les jeunes animaux ont été maintenus en vie pendant quelques jours. Ils ont pu être identifiés par comparaison avec des séries de larves provenant d'échantillons de plancton. Les larves se distinguent par un « cou » allongé, un réservoir juxtaposé rempli de liquide, un appendice oculaire sur chaque œil, des tentacules très longs et des bras courts. Ces larves vivent en pleine eau au-dessus de 150 m, pendant le jour. Leur biologie assez particulière n'est pas sans rappeler celle des Méduses.

INTRODUCTION

Species of *Brachioteuthis*, the only genus in the family Brachioteuthidae, have a distinctive larval stage that is frequently caught in plankton tows. Because adults are rarely captured, taxonomy within the genus is based mainly on descriptions of larvae. The features of the larva, however, change dramatically as it grows. Since a complete growth series from a single species has never been described, problems in distinguishing morphological differences due to growth from those due to species differences have resulted in systematic confusion within the genus.

The eggs of *Brachioteuthis* sp. are occasionally found in Hawaiian waters (Young *et al.*, 1985). Individual eggs have been taken in plankton nets, indicating that adults spawn single eggs (as in species of the Enoploteuthinae) rather than egg masses (see Young and Harman, 1985, for information on the Enoploteuthinae). However, unlike members of the Enoploteuthinae, species of *Brachioteuthis* have nidamental glands which are thought to be responsible for producing egg-mass jelly (Jecklin, 1934). Apparently the spawning mechanism in this squid is unique. By rearing the eggs, the earliest larval stages can be obtained in perfect condition.

In this paper we describe a complete sequence of larval stages of the Hawaiian species. Although Berry (1914) identified this as *Brachioteuthis riisei*, we prefer not to use a specific name because of the systematic uncertainties within the genus. Our objective is not to present a detailed account of all potential systematic characters but to follow the basic morphological changes that take place during development through the larval stages, to point out some characters of potential systematic importance, and to speculate on some aspects of the biology of this peculiar larva.

MATERIALS AND METHODS

Eggs and larvae were taken as part of the sampling program described in Harman and Young (1985). Data on depth distribution during April, 1984 were obtained with an opening-closing 70-cm Bongo net with 0.505 mm mesh and during October, 1984 with an open 4-m^2 net with 0.505 mm mesh. The trawling regime is presented in Table 1. Depths given are depth ranges during the horizontal portion of the tow. The eggs were removed aboard ship from short, oblique plankton tows taken in the upper 150 m in oceanic waters near the island of Oahu, Hawaii. The eggs were placed in small containers of filtered seawater. After hatching, the young were transferred to one-liter holding jars which were placed on a rotator.

Table I. — Total volume of water sampled ($\times$ 1 000 m^3) by depth during the vertical distribution studies.

APRIL			OCTOBER			
	Day	Night	Day		Night	
Depth (m)	vol.		Depth (m)	vol.	Depth (m)	vol.
0-20	3.8	4.6	0-20	23.5	0-20	25.2
20-40	3.8	4.6	20-40	30.0	20-40	24.1
40-60	5.6	5.0	50-70	14.7	40-60	9.5
60-80	6.0	6.8	75-95	13.4	60-80	8.9
80-100	5.1	3.6	95-115	21.5	95-115	46.6
100-120	5.3	7.0	120-140	34.0	120-140	11.2
120-140	6.1	6.8	220-220	24.4	140-160	32.0
140-160	5.3	3.6			165-185	20.5
160-180	4.7	3.6				
180-200	3.0	4.0				
200-220	2.3	3.2				
220-240	2.3	3.2				
240-260	2.0	2.4				

RESULTS

The *eggs* (Fig. 1 A) of *Brachioteuthis* sp. from Hawaiian waters were distinctive in being very

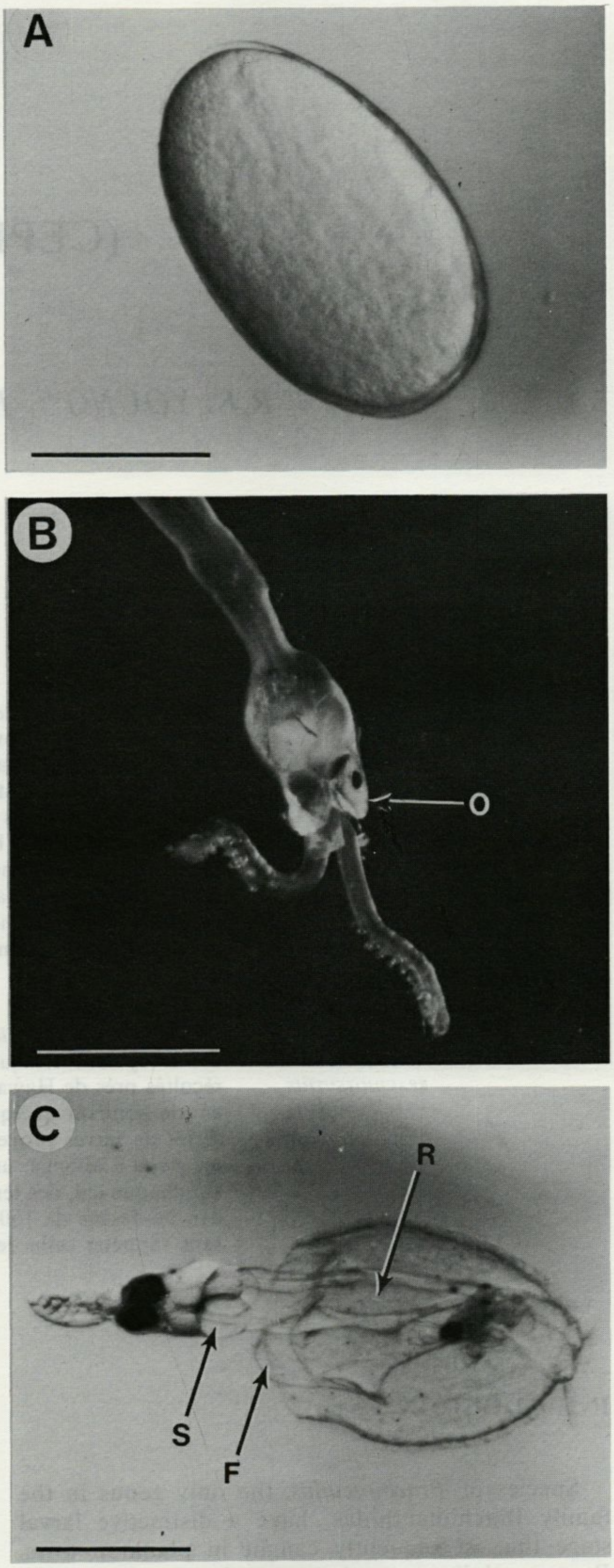

Fig. 1. — *Brachioteuthis* sp. A, Photograph of living egg. Scale bar = 0.5 mm; B, Photograph of freshly-captured 6 mm ML larva. O = ocular appendage. Scale bar = 2.0 mm; C, Photograph of living hatchling (2.0 mm ML) with neck partially contracted. F = funnel, R = reservoir, S = statocyst, Scale bar = 0.5 mm.

elongate, 1.2 ± 0.02 S.D. mm × 0.73 ± 0.03 S.D. mm which immediately distinguished them from the more nearly spherical eggs of the Enoploteuthinae. The eggs were not surrounded by a gelatinous envelope. A gelatinous layer, however, could have been lost during capture (see Young *et al.*, 1985). No pronounced perivitelline spaces were present. The chorion did not have obvious ornamentation. The eggs were infrequently caught in our sampling program.

The *hatchling* (Pl. I A) was immediately distinguished by its elongate and highly contractile neck. When several days old, the hatchling had relatively large tentacles and short, stubby arms. Only arms I and II were present (an oegopsid characteristic) and each carried a single sucker (Pl. II A). The tentacles each carried 6 large suckers arranged in two rows.

The chromatophore pattern of the hatchling was distinctive. On the ventral surface of the mantle a simple band of chromatophores lay at the anterior margin. Slightly posterior to this band was a somewhat irregular, complex band. On the dorsal surface only the ends of the ventral anterior band could be seen. Otherwise, a cluster of four elongate chromatophores was present dorsally. On the ventral surface of the head a large chromatophore lay near the lateral edge of the head just posterior to each eye and a single chromatophore lay between the eyes at the base of the branchial crown. Several chromatophores were present on each tentacle. On the dorsal surface of the head just posterior to each eye was a large, slightly elongate chromatophore with an oblique orientation. A second pair of chromatophores lay above each eye and a single chromatophore lay on the midline at the base of the brachial crown.

The *2.6 mm larva* (Pl. I B) taken from plankton tows had a more elongate neck which, in preservation, was nearly as long as half the mantle length. The tentacles were slightly more elongate in this larva and each carried about five pairs of large suckers, a few smaller, developing suckers, and a distinct but bare stalk (see Pl. II B). The tentacular suckers had very small aperatures and the outer chitinous ring of one had a ratio of 12 : 24 : 38 (1 : 2 : 3.2) between platelets in the inner, middle and outer whorls. The inner chitinous rings were smooth. Each eye had a distinct silvery, pointed rostrum on its anterior end. This ocular appendage (i.e., a tapering extension of the silvery covering of the eye) was present in this location throughout the larval stages (see Fig. 1 B).

The chromatophore pattern was similar to that of the hatchling except that the ventral mantle chromatophores were more clearly organized into two separate bands, the four large dorsal mantle chromatophores were farther apart and several smaller ones were present, and the dorsal head chromatophores were larger. The other head and tentacle chromatophores seen in the hatchling could not be distinguished in this specimen.

At *5.4 mm ML* (Pl. I C), the neck was slightly shorter relative to the mantle. The tentacles were considerably larger and a manus was present. The chromatophore pattern was similar to the smaller larvae except that the chromatophores were more numerous. On the dorsal surface of the head, a very characteristic pattern of elongate and obliquely slanting chromatophores was present.

At *7.6 mm ML* (Pl. II C), the tentacles were very elongate and the tiny arms showed a slight increase in length. Each arm II had two suckers and one partially-developed sucker. Arms I still had a single sucker each. Small arms III were present and carried one developing sucker each. Arms IV were longer than arms III, but were still short and each carried a single large sucker. On each tentacle stalk, seven pairs of suckers were present; the manal suckers were in five irregular rows and the tip of the club bore numerous sucker buds. A tentacular sucker from the manus had a platelet ratio of 15 : 29 : 50 (1 : 1.9 : 3.3). On the largest sucker of the third arm we counted 13 inner plates but we were not able to distinguish platelets of the other whorls in our micrographs.

At *9.1 mm ML* (Pl. I D), additional chromatophores were present, but the dorsal surface of the head still had the distinctive elongate, oblique chromatophores.

At *16 mm ML* (Pl. II D) the tentacles were very long and carried numerous suckers on the club. Although the arms were more slender and elongate than at smaller sizes, they were still short. Many suckers were present on the arms. Each tentacle carried two series of suckers on the stalk, numerous suckers on the manus and large suckers on the dactylus. The clubs, therefore, had the basic structure found in juveniles and adults. Two tentaclar suckers had platelet ratios of 16 : 30 : 64 (1 : 1.9 : 4) and 15 : 35 : 54 (1 : 2.3 : 3.6) between the three whorls of platelets. The dorsal surface of the head still had the distinctive chromatophores found in smaller larvae.

At *21 mm ML,* the length of the neck was reduced to about 1/6 of the mantle length and arms II and III were elongate (length about 1/2 tentacle length). The chromatophore pattern appeared little-altered but most chromatophores were damaged in our specimen.

The most distinctive feature of *Brachioteuthis* larvae is their unusually long neck (Fig. 1 B). The head was found to be retracted to the level of the mantle opening in some larvae or extended about half the mantle length outward. The neck appeared to be a muscular, fluid-filled tube that was continuous with a large fluid-filled sac (reservoir) within the mantle (Fig. 1 C). The thin-walled reservoir appeared to have a thin muscular sheath and had

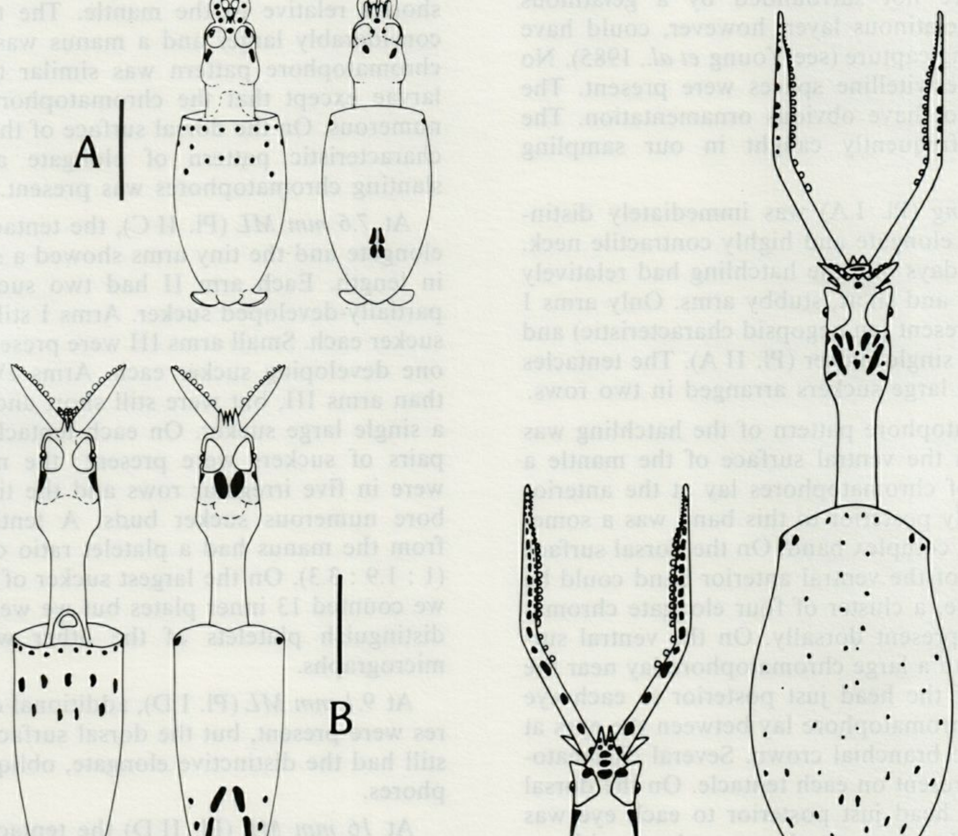

Plate I. — Larvae of *Brachioteuthis* sp. : A, 2.0 mm ML, 5 days after hatching; B, 2.6 mm ML; C, 5.4 mm ML; D, 9.1 mm ML. Scale bar = 1 mm.

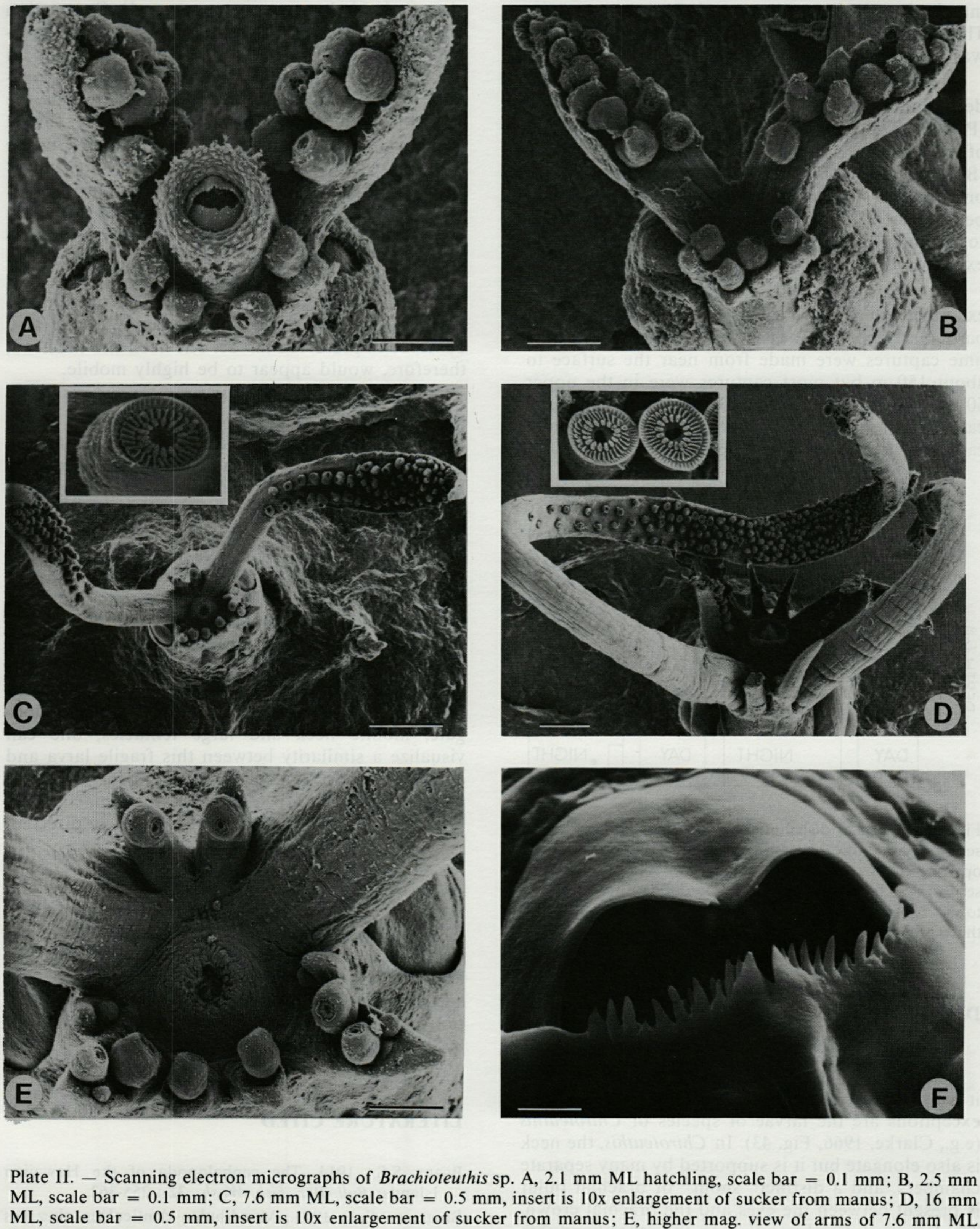

Plate II. — Scanning electron micrographs of *Brachioteuthis* sp. A, 2.1 mm ML hatchling, scale bar = 0.1 mm; B, 2.5 mm ML, scale bar = 0.1 mm; C, 7.6 mm ML, scale bar = 0.5 mm, insert is 10x enlargement of sucker from manus; D, 16 mm ML, scale bar = 0.5 mm, insert is 10x enlargement of sucker from manus; E, higher mag. view of arms of 7.6 mm ML larva, scale bar = 0.1 mm; F, beak from 7.0 mm ML larva, scale bar = 0.01 mm.

shapes varying from slender to balloon-like. The reservoir abutted against the digestive gland which was displaced posteriorly to a level about 2/3 of the mantle length from the anterior mantle margin. Therefore, much of the cone formed by the mantle was occupied by the reservoir.

Another unusual feature of this larva was the development of long teeth on the lower beak (Pl. 2 F). The presence of teeth on the cutting edge of the beaks is common in larval cephalopods (Boletzky, 1971). *Brachioteuthis* sp. was peculiar not only in the size of the teeth, but also in their persistence. They were well-developed in larvae up to 7.0 mm ML (beaks from larger larvae were not examined).

The *vertical distribution* (Fig. 2) of the larvae was examined on two occasions. The larvae were not particularly abundant at either time. In April, daytime captures were made from near the surface to about 150 m but most captures were in the upper 50 m at night. During the October series, all day catches came from 100 to 125 m while most night captures were again in the upper 50 m.

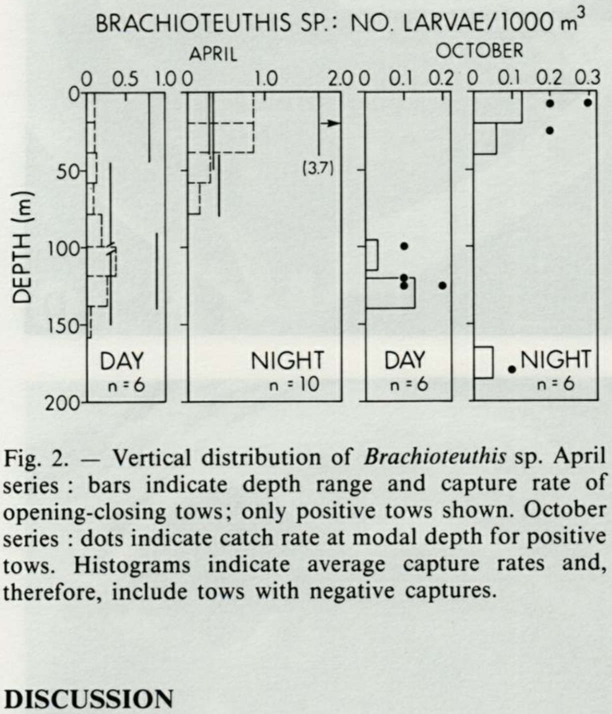

Fig. 2. — Vertical distribution of *Brachioteuthis* sp. April series : bars indicate depth range and capture rate of opening-closing tows; only positive tows shown. October series : dots indicate catch rate at modal depth for positive tows. Histograms indicate average capture rates and, therefore, include tows with negative captures.

DISCUSSION

The larva of *Brachioteuthis* is so distinctive that it cannot be confused with most other larvae. The exceptions are the larvae of species of *Chiroteuthis* (e.g., Clarke, 1966, Fig. 43). In *Chiroteuthis,* the neck is also elongate but it is supported by many separate chambers, and a distinct "snout" or brachial pillar is present between the eyes and the brachial crown. The larvae of *Brachioteuthis,* on the other hand, are characterized by an elongate, unpartioned neck, and no branchial pillar.

The peculiar morphology of this larva suggests an unusual biology. In the living hatchling, the head can be quickly extended or retracted. The mechanism probably has two components : 1) Contraction of the longitudinal muscles of the neck and relaxation of the reservoir muscles would result in an expanded reservoir and a shortened neck. Relaxation of the neck muscles and contraction of the reservoir would extend the neck. 2) The funnel retractor muscles which attach far posteriorly in the mantle cavity would, by contraction, pull the funnel and the attached neck well back into the mantle cavity in a position occasionally observed in preserved squid. The combination of these two processes can result in the retraction of the head to at least the level of the mantle opening. Because of the hydrostatic skeleton, contraction of muscles on one side of the neck will cause the neck to bend, a state also observed in preserved larvae. The neck and the head, therefore, would appear to be highly mobile.

A clue to the biology of these larvae is offered by the position of the ocular appendage. The ocular appendage in cephalopods aids in concealing the eye in well-lit environments such as that occupied by young *Brachioteuthis* (Young, 1975). The tapered shape of the appendage would reduce the intensity of the eye silhouette by the downward reflection of light (Denton and Nicol, 1965). To function properly, the appendage must be oriented with the pointed end downward. In most squids that have this structure, the appendage lies on the ventral surface of the eye. In *Brachioteuthis,* the appendage extends from the anterior end of the eye indicating that the larva generally orients in a head-down position. Hanging in such a manner with its elongate, mobile neck and large tentacles, one can visualize a similarity between this fragile larva and a jellyfish : a drifting bell with dangling tentacles. In contrast to the jellyfish, however, the tentacles with large eyes at their bases can be accurately directed.

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