EARLY LIFE HISTORY STAGES OF ENOPLOTEUTHIN SQUIDS (CEPHALOPODA : TEUTHOIDEA : ENOPLOTEUTHIDAE) FROM HAWAIIAN WATERS

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HAWAII
LARVAE
CEPHALOPODA
ENOPLOTEUTHIDAE
SQUIDS
VERTICAL-DISTRIBUTION

ABSTRACT. — Species of the enoploteuthid subfamily Enoploteuthinae spawn individual eggs in the plankton. Eggs captured off Hawaii were reared in the laboratory for several days after hatching. The hatchings were matched to size-series of larvae taken from an extensive trawling program designed to catch squid larvae. The early life history stages of these species are described and systematic characters evaluated. Chromatophore patterns as well as photophore patterns were highly distinctive. In addition, all species, apparently, could be separated on the basis of sucker structure. A key to the identification of Hawaiian species is provided. Preliminary data indicate that vertical distribution patterns vary between species and, on a temporal basis, within species.

HAWAI
LARVES
CEPHALOPODA
ENOPLOTEUTHIDAE
CALMARS
DISTRIBUTION VERTICALE

RÉSUMÉ. — Les espèces de la sous-famille des Enoploteuthinés pondent des œufs individuels entre deux eaux. Les œufs récoltés près de Hawai ont été élevés pendant quelques jours après l'éclosion. Les éclosions ont été mises en rapport avec des séries de larves capturées au cours d'un programme de prospection. Les premiers stades post-embryonnaires de ces espèces sont décrits et les caractères systématiques sont évalués. Les livrées chromatiques (patron de chromatophores) et la disposition de photophores se sont révélées distinctes. De plus, les espèces peuvent être distinguées d'après la structure de leurs ventouses. Une clé de détermination est proposée pour les espèces de Hawai. Les données préliminaires semblent indiquer que les modes de distribution bathymétriques varient parmi les espèces, et à l'intérieur d'une espèce selon le temps considéré.

INTRODUCTION

Members of the squid subfamily Enoploteuthinae are among the most abundant small squids of the open ocean. The adults, where known, occupy the mesopelagic zone during the day and migrate into near-surface waters at night. They are the "myctophids" of the squid world. Adult females are thought to spawn individual eggs unlike most squids which spawn eggs in masses (Okiyama and Kasahara, 1975; Young, *et al.*, 1985). Although the spawning depths are unknown, both eggs and larvae of these squids are found in near-surface waters of the open ocean. The common occurrence of the eggs in surface waters has only recently been recognized (Young, *et al.*, 1985). Within the subfamily, only the eggs of *Watasenia scintillans* from Japan (Sasaki, 1914) and *Enoploteuthis reticulata* from Hawaii have been previously identified. The status of larval identification in the Enoploteuthinae barely surpasses that of the eggs. Only in a few places with a restricted enoploteuthin fauna (e.g., Japan and California) have some larvae been identified (Oku-

tani, 1968; Okutani and McGowan, 1969). As a result, ecological studies that would depend on knowledge of egg and larval abundances and distribution cannot be attempted on this group. The reasons for our meagre knowledge are obvious : larval identification requires accurate knowledge of the local adult fauna, and extensive collections that would provide size-series of larvae of all related species. Such circumstances are rarely encountered; the present study provides an exception.

This paper describes the early life history stages of members of the Enoploteuthinae found in Hawaiian waters, examines characters useful in identification and presents preliminary data on the distribution of the larvae.

MATERIALS AND METHODS

Samples were taken off the leeward side of Oahu, Hawaiian Archipelago (about 21°15'N, 158°20'W) during a series of cruises in 1983-1984 from the University of Hawaii's research ships R/V KANA KEOKI and R/V KILA (Fig. 1). Sampling consisted of both horizontal and oblique tows using both open nets and opening-closing nets. Two series of tows were made to examine vertical distribution. The first was taken in April, 1984 and consisted of 40 stratified oblique tows to a depth of 300 m with paired, opening-closing 70-cm bongo nets with 0.505 mm mesh. Each tow was designed to uniformly sample

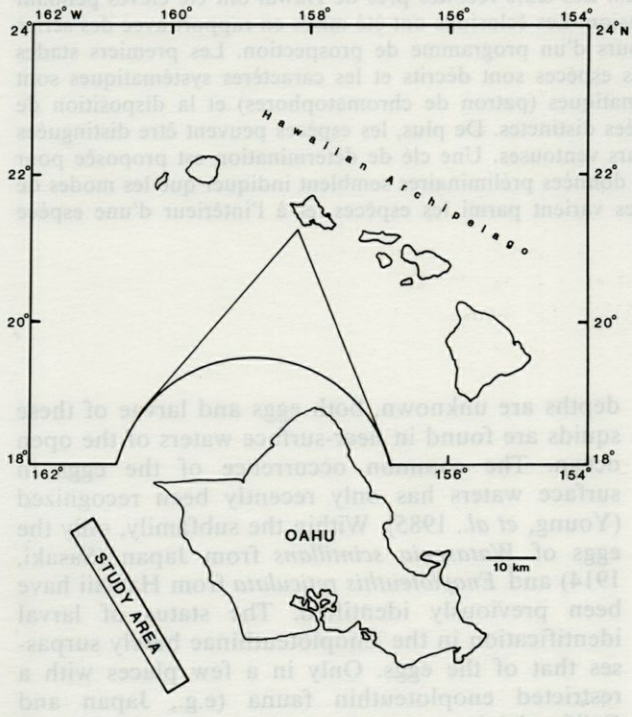


Fig. 1. — Location of study area.

a 50 m depth stratum in the upper 200 m and a 100 m depth stratum from 200 to 300 m. Placement of the nets was not precise as we lacked on-line feedback on net depth. Depth was determined with a Benthos time-depth recorder. During October, 1984 an open 4-m^2 net of 0.505 mm mesh was towed horizontally. We intended to sample at 5 m, 25 m, 75 m, 125 m and 200 m. Again net placement was not precise. A TSK flow meter was attached to all nets.

Vertical distribution data from the stratified-oblique series were compiled by apportioning the catch from each tow equally into 10 m depth increments over the depth range of the tow. The catch rate for a given depth increment was taken as the total catch in that depth zone divided by the total volume of water sampled in that zone for all tows. Subsequently, the increments were combined into 20 m depth zones. For the horizontal series, the entire catch for a tow was assumed to have been caught at the modal depth of the net during that tow. More details on the sampling program are given in Harman and Young, 1985. Table I summarizes the sampling effort for the April and October series.

Oblique tows (75 m or 150 m to the surface) for live eggs were taken with 1-m nets of 0.505 mm mesh. These samples were sorted on board ship using stereomicroscopes. Squid eggs removed from these samples were placed in 0.045 µm filtered seawater within the wells of tissue culture trays and were kept in an air-conditioned room (generally 22-24°C). After hatching, the larvae were placed in one-half or one liter bottles of filtered seawater which were then placed on rotators to prevent the squids from settling to the bottom of the jar.

Larvae were fixed in 4 % formalin and preserved in 40 % isopropyl alcohol. Fading of the chromatophore pigment was not serious in most cases. However, illustrations of chromatophore patterns must, except for hatchlings, be considered incomplete. Chromatophores can be selectively lost due to damage and some types of expanded chromato-

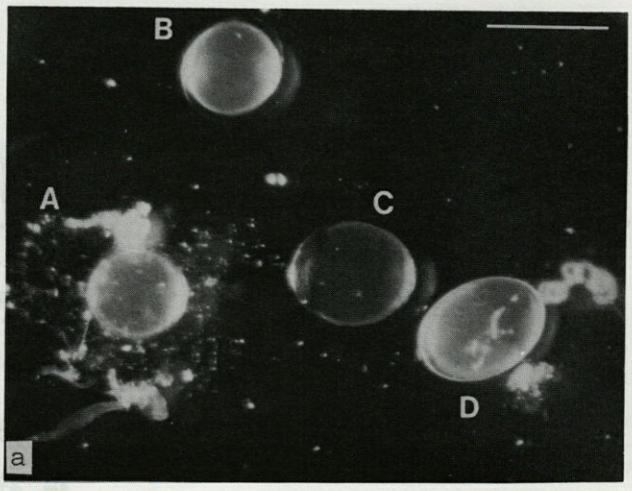
Table I. — Total volume of water sampled (× 1 000 m^3) by depth during the vertical distribution studies.

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				

phores can be difficult to detect especially if some fading has occurred. Even in good specimens, one cannot be certain that all chromatophores have been found. Details of the sucker structure were examined with an I.S.I. SS-40 scanning electron microscope. Access to the microscope limited the study to a cursory survey. The inner chitinous sucker ring in larval enoploteuthins only occasionally has teeth; its systematic value, therefore, is limited. The outer chitinous ring, however, exhibits an elaborate structure. This ring consists of three whorls of platelets called the inner (surrounds the aperature), the middle and the outer whorls. Typically the inner and middle whorls bear knobs. Since a platelet usually has only a single knob, platelet counts can often be taken more easily by counting knobs.

The term "hatchling" refers to young squids from the time of hatching until feeding begins. This stage, therefore, is comparable to the yolk-sac stages of fishes. The term "larva" is used as a convenient designation for the young stages of squids that are effectively caught by plankton nets. The term is not used to designate a well-defined growth stage (see Boletzky, 1974, for explanation). The term "band" is used to designate a transverse series of chromatophores or photophores. Bands on the mantle are numbered beginning anteriorly. The term "row" is used in a similar manner to refer to longitudinal series of chromatophores or photophores. The term "simple", used in conjunction with band or row, refers to a single line (= series) of photophores or chromatophores. The term "complex" refers to a band or row of more than a single series.

The Hawaiian enoploteuthin squids develop fins a few days after hatching in captivity, whereas, the newly hatched *Illex illecebrosus* (Ommastrephidae) have well developed fins at hatching (O'Dor *et al.*, 1982). Thus, the possibility exists that the Hawaiian squids could be hatching prematurely in the laboratory and that the early hatchlings illustrated here will not normally occur free in the plankton. We identified 2585 larval squids from the sampling program, of which 1069 (41 %) belonged to the Enoploteuthinae.



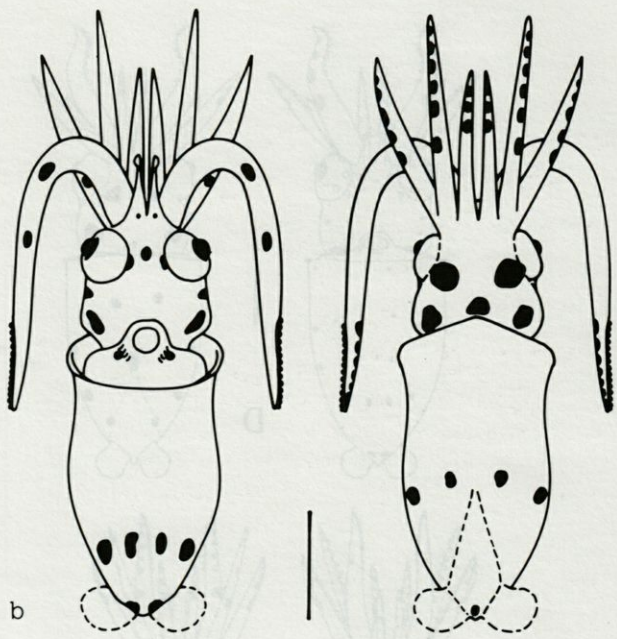


Fig. 2. — a, Photograph of living enoploteuthin eggs. A : *Abralia trigonura* (?), note jelly layer. B : *Enoploteuthis jonesis* (?). C : *Abraliopsis* sp. A. D : *Enoploteuthis reticulata*. Scale bar = 1.0 mm. b, *Abraliopsis* sp. A, 3.0 mm ML, showing unusual chromatophore pattern. Scale bar = 1.0 mm.

RESULTS

Abralia trigonura Berry, 1913

A. trigonura larvae were the most abundant larvae taken in this study : they comprised nearly 20 % of all squid larvae captured.

A. Eggs (Fig. 2a)

Shape and size : slightly ovoid, 0.9 ± 0.08 S.D. mm × 0.79 ± 0.04 mm. Color : usually a slight greenish tint, clear. Chorion : smooth; no pronounced perivitelline space. Jelly coating : sticky, clear, colorless, 0.5 mm thick.

B. Larvae (Pl. I)

1. *Chromatophores*

Advanced hatchling (Pl. IB) : ventral mantle — 4 simple transverse bands. Band III somewhat varia-

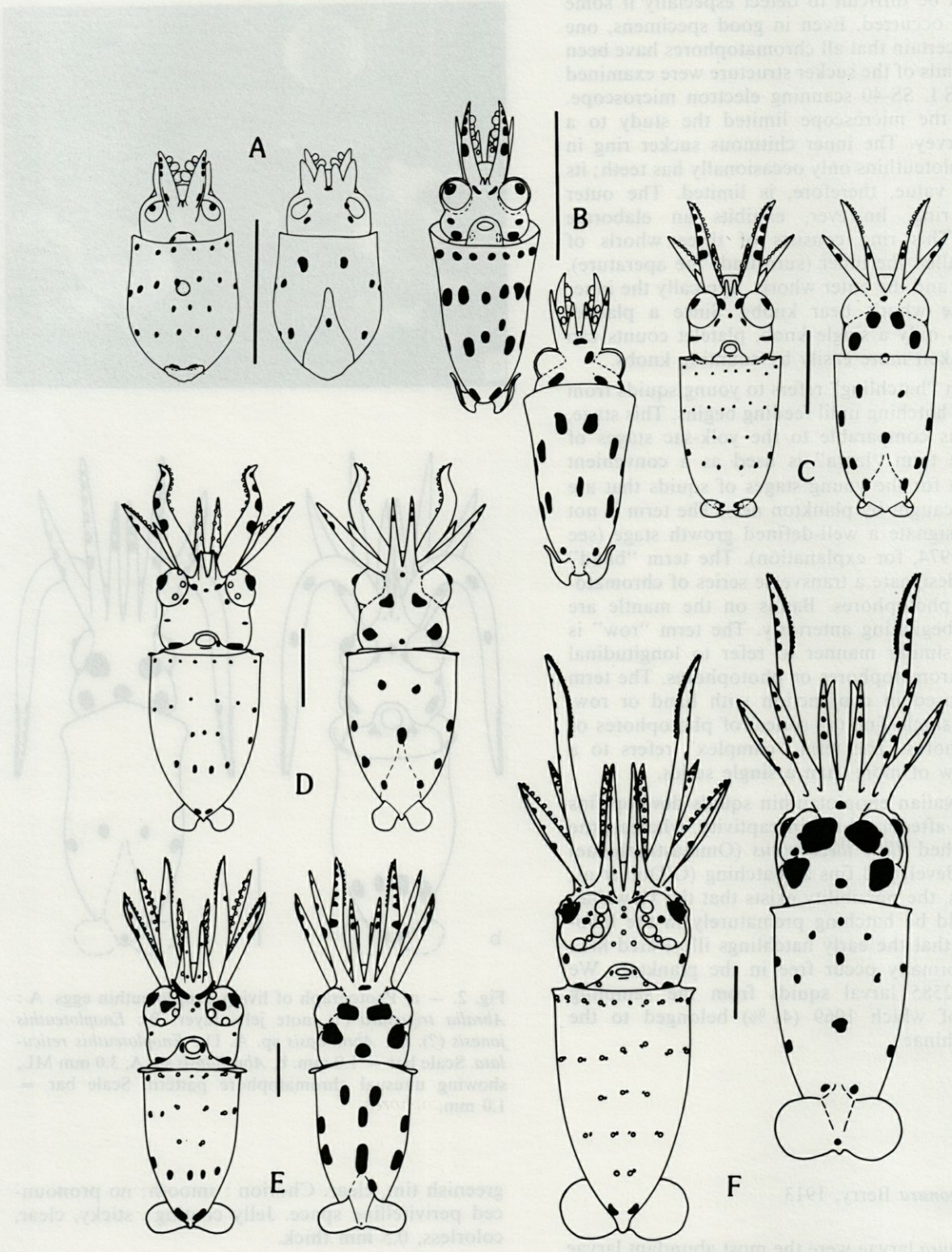


Plate I. — Larval stages of *Abralia trigonura*. A : 1.0 mm ML, at hatching. B : 1.3 mm ML, 7 days after hatching. C : 1.9 mm ML. D : 2.2 mm ML. E : 3.5 mm ML. F : 5.0 mm ML. Scale bars = 1.0 mm.

ble (e.g., Pl. IA, B) generally of only 2-3 chromatophores in mid-region of mantle. One pair of chromatophores at postero-ventral end of mantle. Dorsal mantle — terminal chromatophores of ventral mantle bands II and IV, 2 chromatophores near the anterior end of mantle, and 2 near the posterior end. These 8 chromatophores formed an approximate circle along margins of mantle. A single chromatophore within this circle on midline slightly posterior to mantle midpoint.

Head and brachial crown — tentacles with 3-5 chromatophores on distal half of each tentacle; one at base of each tentacle. (Although this tentacular pattern was not diagnostic, when combined with the large size and heavy pigmentation of these chromatophores, it often provided a valuable clue to the identification of damaged larvae).

5.0 mm ML : dorsal mantle and tentacles — chromatophores more numerous but hatchling pattern still recognizable.

2. *Photophores*

Ocular photophores : 3 large photophores on each eye at 2.2 mm ML (Pl. II). At 5.0 mm ML, 5 organs (large, small, large, small, large) (Pl. IF). (This pattern was diagnostic of the genus *Abralia* in Hawaiian waters). At 7.5 mm ML, posterior ocular photophore largest. (This feature was diagnostic of *A. trigonura* in Hawaiian waters.).

Integumental photophores : first on mantle at 3.4 mm ML. (Initially these photophores formed bands on the ventral mantle surface in same positions as the chromatophore bands). (Pl. IE, F).

3. *Sucker structure. 3 mm ML*

Tentacular sucker-platelet ratio = 16 : 23 : 86 (1 : 1.4 : 5.4) (inner whorl : middle whorl : outer whorl); outer platelets with free and pointed tips (Pl. IIA). Arm II, sucker 9-platelet ratio = 19 : 29 : 45 (1 : 1.5 : 2.4) (Pl. IIF). Arms I-III, most larger suckers with 1-2 large blunt teeth near distal margin of inner chitinous ring (Pl. IIF).

4. *Other larval characters*

Tentacular clubs compact, with small suckers of relatively uniform size; short, muscular arms and tentacles.

C. Vertical Distribution (Fig. 3a)

During the October series, *A. trigonura* had an abundance peak in the 50-70 m depth stratum during the day and in the 15-30 m stratum at night. Daytime capture rates (1.3 larvae/1 000 m^3) for the entire depth range sampled were similar to the night rates (1.5 larvae/1 000 m^3). The few specimens that were captured during the opening-closing net series in April provided little additional information.

Although data on abundance from different seasons are difficult to compare because of the sampling techniques, *A. trigonura* larvae seemed to be far less abundant in the April samples : Capture rates in October were 1.4 larvae/1 000 m^3 while during April capture rates were 0.09 larvae/1 000 m^3. In addition, during October these larvae ranked first in relative abundance among squid larvae taken while in April they ranked number 11.

Abralia astrosticta Berry, 1909

Since only 5 larvae of this species were captured, we do not have a complete size series. Unlike the other local members of the subfamily, the habitat of the adults is thought to be near the ocean floor on the steep slopes of the islands (Roper and Young, 1975).

A. Eggs

Eggs not found.

B. Larvae (Pl. III)

1. *Chromatophores*

3.2 mm ML (Pl. IIIA) : ventral mantle — 4 simple bands extended completely across mantle surface; two large chromatophores near fins. Dorsal mantle — two bands, continuations of ventral bands III and IV, extended across the dorsal mantle; anterior chromatophores damaged. Head and brachial crown — tentacle with distal series, large basal chromatophore and scattered intermediate chromatophores.

3.7 mm ML : ventral mantle pattern partially obscured by additional chromatophores. Dorsal pattern with 2 bands and complex row between bands and anterior mantle margin near midline. Tentacle with continuous series of chromatophores.

2. *Photophores*

Ocular photophores : 3 large photophores at 3.2 mm ML (Pl. IIIA); at 5.5 mm ML 5 ocular photophores (large, small, large, small, large) on each eye (In the adult the ocular photophores are approximately equal in size) (Pl. IIIB).

Integumental photophores (Pl. IIIB) : 2 on ventral mantle at 3.2 mm ML; at 5.5 mm ML numerous and unusually large. (The large size is diagnostic of a *A. astrosticta* in Hawaiian waters).

Subintegumental photophores (Pl. III) : pair near posterior tip of ventral mantle. (This pair was in the

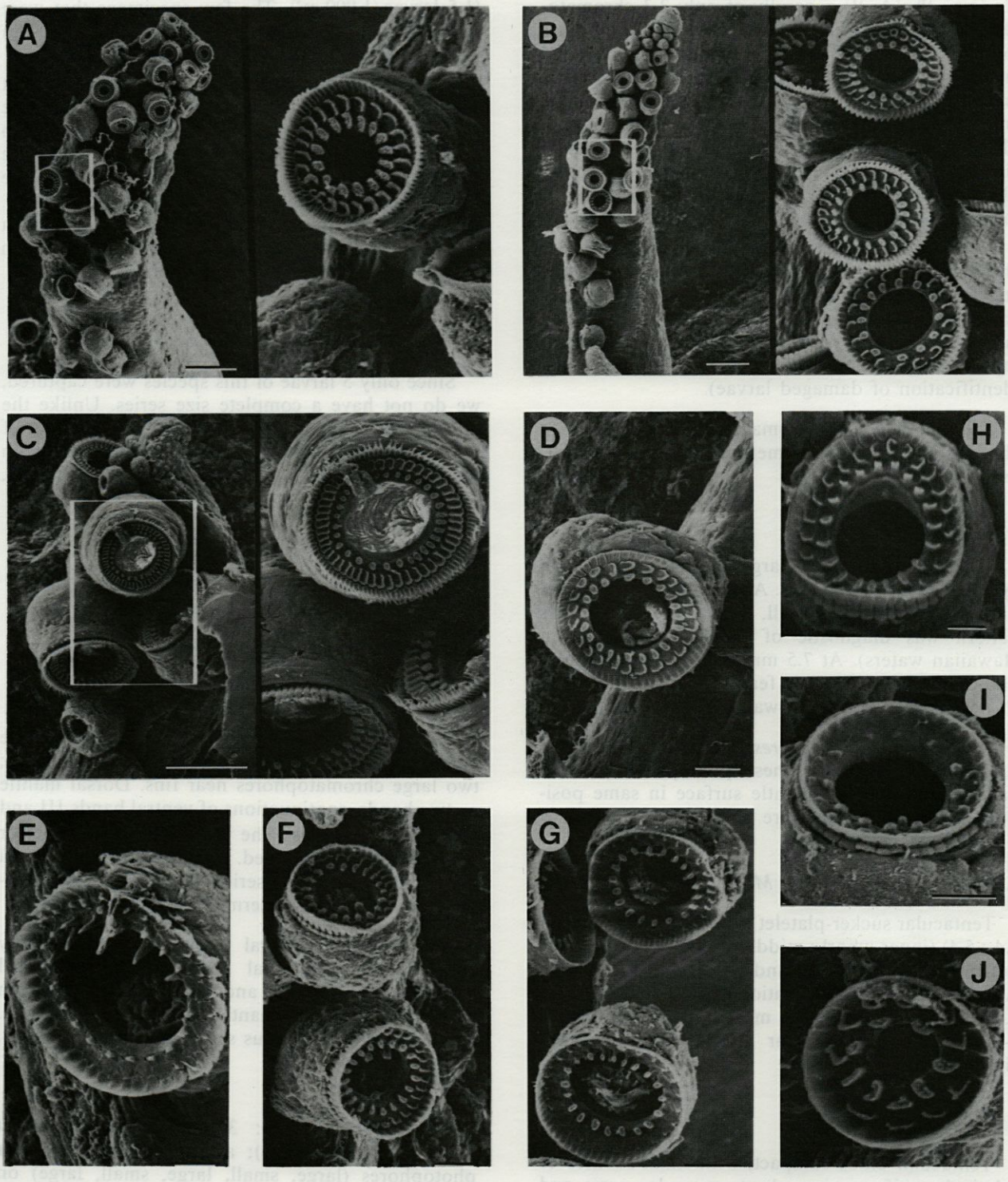


Plate II. — Scanning electron micrographs of tentacular clubs, club suckers and arm suckers. A : Tentacle club of *Abralia trigonura* (3.0 mm ML) with 5X enlarged sucker, scale bar = 1.0 mm. B : Tentacle club of *Abralia astrosticta* (3.5 mm ML) with 5X enlarged sucker, scale bar = 0.1 mm. C : Tentacle club of *Enoploteuthis higginsi* (2.0 mm ML) with 2X enlarged sucker, scale bar = 0.04 mm. D : arm II sucker of *E. higginsi* (4.6 mm ML), scale bar = 0.04 mm. E : arm II sucker of *Enoploteuthis reticulata* (3.3 mm ML), scale bar = 0.02 mm. F : arm II suckers of *A. trigonura* (3.0 mm ML), scale bar = 0.01 mm. G : arm II suckers of *Enoploteuthis jonesi* (3.0 mm ML), scale bar = 0.04 mm. H : arm III sucker of *A. astrosticta* (3.5 mm ML), scale bar = 0.01 mm. I : arm I sucker of *Abraliopsis* sp. B (3.0 mm ML), scale bar = 0.02 mm. J : arm II sucker of *Abraliopsis* sp. A (3.2 mm ML), scale bar = 0.01 mm.

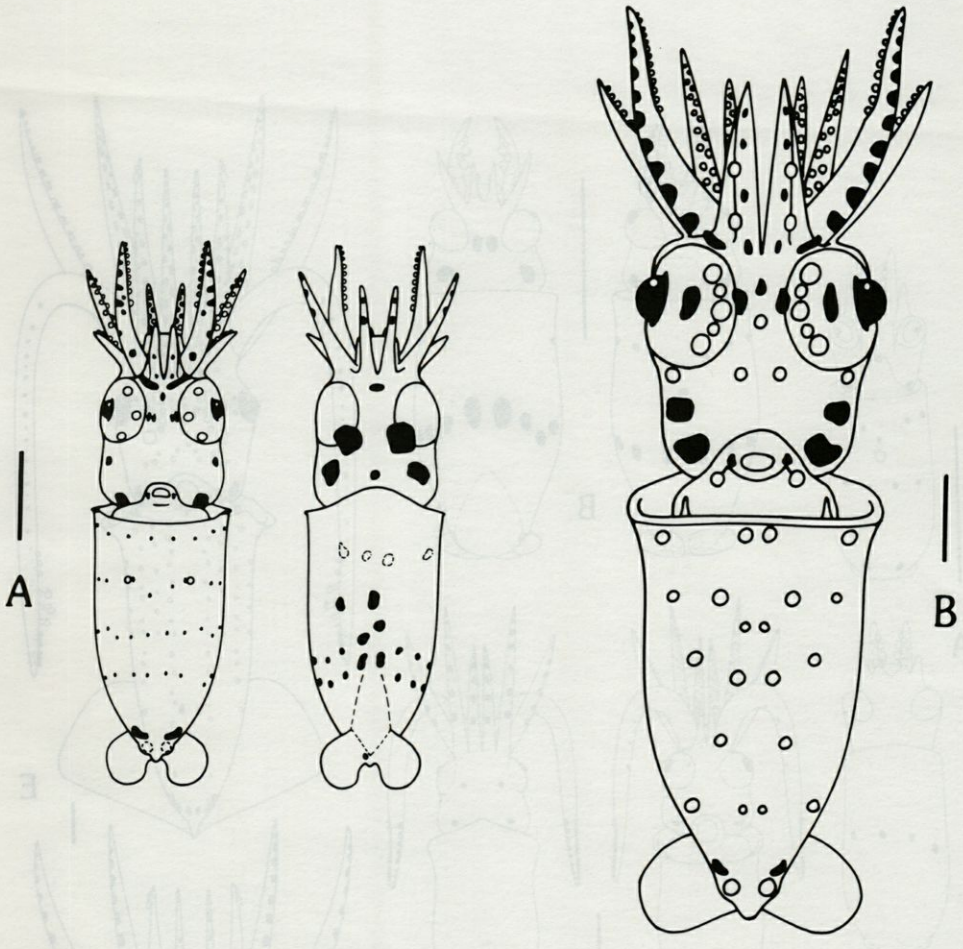


Plate III. — Larval stages of *Abralia astrosticta*. A : 3.2 mm ML. B : 5.5 mm ML. Scale bars = 1 mm.

initial stages of development at 3.2 mm ML and is diagnostic for this species).

3. *Sucker structure*

3.5 mm ML: 2 tentacular suckers — platelet ratios = 17 : 27 : 71 (1 : 1.6 : 4.2) and 13 : 18 : 64 (1 : 1.4 : 4.9); outer platelets with free, pointed tips (Pl. IIB). Arm III, sucker 5 — no teeth on inner chitinous ring; platelet ratio = 19 : 23 : 48 (1 : 1.2 : 2.5) (Pl. IIH).

4. *Other larval characters*

Tentacular clubs small, compact, with small suckers of nearly uniform size. Arms and tentacles relatively short, muscular.

C. Vertical Distribution

Data not available.

Abraliopsis

Three species in this genus are presently recognized from Hawaiian waters. We suspect that a variant of one of these is a fourth species. Two of the possible four species, however, are rare as adults and we recognize only two types of larvae at present.

Abraliopsis sp. A. Burgess (in manuscript)

Larvae of this species ranked 6th in overall abundance during the sampling program and comprised 5.2 % of all squid larvae taken.

A. Eggs (Fig. 2a)

Shape and size : ovoid, 1.01 ± 0.05 × 0.84 ± 0.04 mm. Color : colorless, clear. Chorion : smooth, no pronounced perivitilline space. Jelly coating : sticky, clear, colorless, thick. (In the later stages of embryogenesis the embryo oriented in the egg with the posterior end uppermost. If the egg was turned,

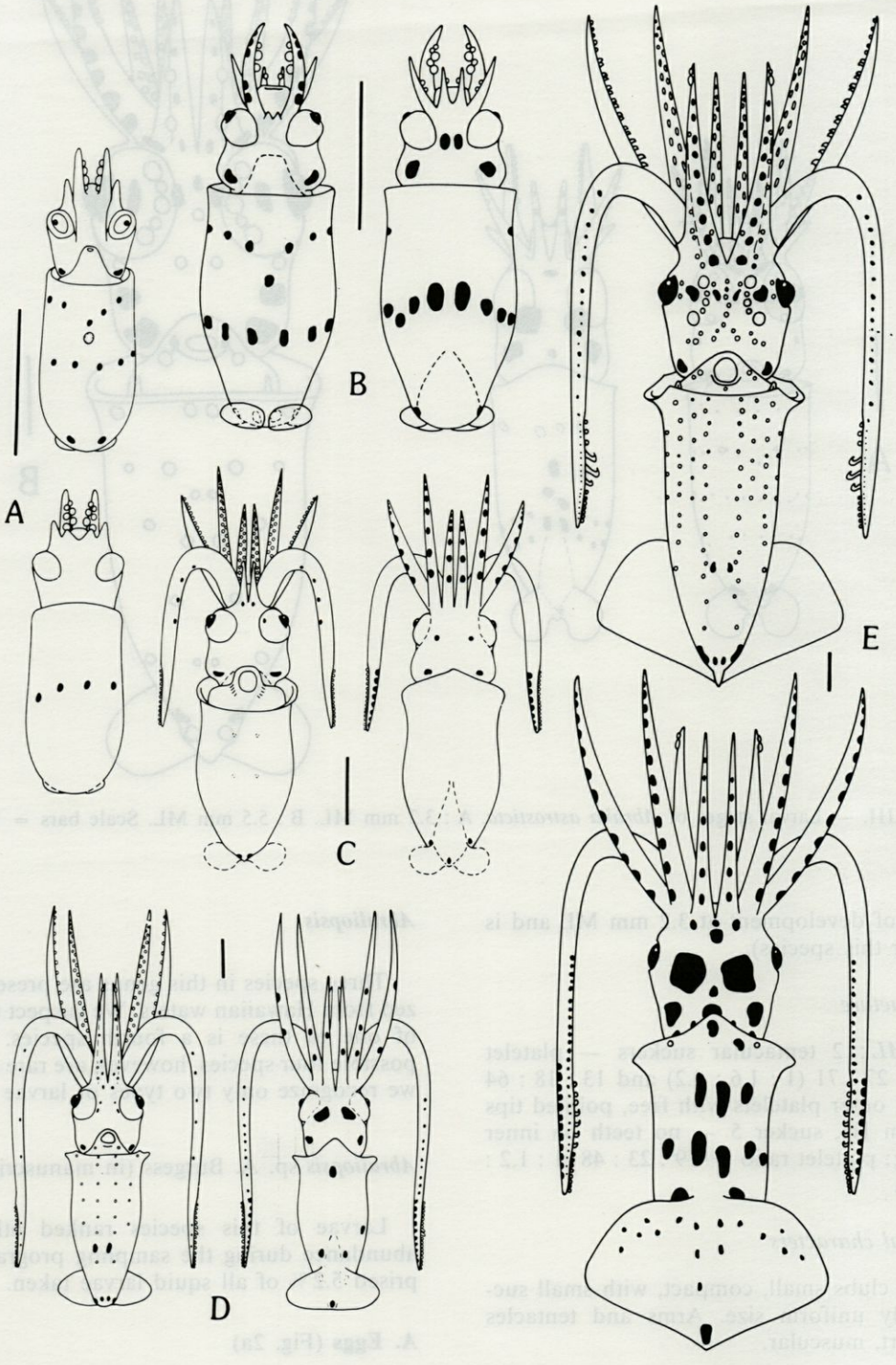


Plate IV. — Larval stages of *Abraliopsis* sp. A. A : 1.3 mm ML, at hatching. B : 1.6 mm ML, 6 days after hatching. C : 3.0 mm ML. D : 4.6 mm ML. E : 8.6 mm ML. Scale bars = 1 mm.

the embryo would quickly reorient. Embryos of all other species taken lay horizontally in the egg).

B. Larvae (Pl. IV)

1. *Chromatophores*

Advanced hatchling (Pl. IVB) : Ventral mantle — (band I near anterior end, simple, V-shape (apex of V points posteriorly); band II straight, simple, completely encircled mantle. Four chromatophores at posterior tip. Dorsal mantle — ventral band II with 2 larger chromatophores near the middorsal line. Head and brachial crown — 2 postero-lateral chromatophores ventrally on head, generally 4 dorsally; chromatophore series along each tentacle but none at tentacle base.

2.5 mm ML to at least 8.6 mm ML : posterior tip of dorsal mantle with single chromatophore. Otherwise, mantle pattern uncertain. Head and brachial crown pattern similar to hatchling but with additional chromatophores. (Unfortunately net- captured larvae almost invariably lost their distinctive mantle chromatophores due to damage. The chromatophores of the head and tentacles survived capture more frequently but selective loss of these chromatophores was a barrier to accurate identification. Pl. IV C and Fig. 4 illustrate the range of patterns seen for the 3.0 mm larva. We do not know if this variation is within the range of a single species or if an additional species is involved).

2. *Photophores*

Arm IV, terminal photophores : first at 2.0 mm ML, highly swollen.

Integumental photophores : first on mantle at 3.0 mm ML; about 4.5 mm ML 5 integumental photophores in each medial row on mantle well aligned. (The latter indicated the future rowed-pattern characteristic of *Abraliopsis* sp. A. This feature became more apparent at slightly larger sizes (e.g., Pl. IVD). Because of damage, development of ocular photophores could not be traced).

3. *Sucker structure*

1.9 mm ML : tentacular sucker (Pl. VA) (mid-club) — platelet ratio = 11 : 19 : 34 (1 : 1.8 : 3.1); outer platelets with attached, truncated ends; arm II, sucker 3 — platelet ratio = 7 : 8 : 16 (1 : 1.1 : 2.3).

3.2 mm ML : a distal tentacle sucker — platelet ratio = 12 : 19 : 30 (1 : 1.6 : 2.5); arm II, sucker 4 (Pl. IIJ) — platelet ratio = 8 : 10 : 19 (1 : 1.3 : 2.4).

5.6 mm ML : tentacular sucker (distal end of manus), platelet ratio = 12 : 21 : 52 (1 : 1.8 : 4.3), broad knob at proximal end of inner whorl; Arm II, basal sucker — platelet ratio = 10 : 11 : 23 (1 : 1.1 : 2.3).

4. *Other larval characters*

Both species of *Abraliopsis* : long, slender arms and tentacles, and slender mantles and heads; rapid growth of arms III compared to IV. (When arms III first approximately equal arms II in length, arms IV are about a third as long).

C. Vertical Distribution (Fig. 3b)

The October series indicated a peak depth during the day in the 75-95 m depth zone and in the 20-40 m depth zone at night. Although few specimens were caught during the April series, the absence of specimens in the upper 50 m at night was striking.

Abraliopsis sp. B. Burgess, in manuscript

This species ranked 5th in overall abundance and comprised 7.7 % of the larval squids taken.

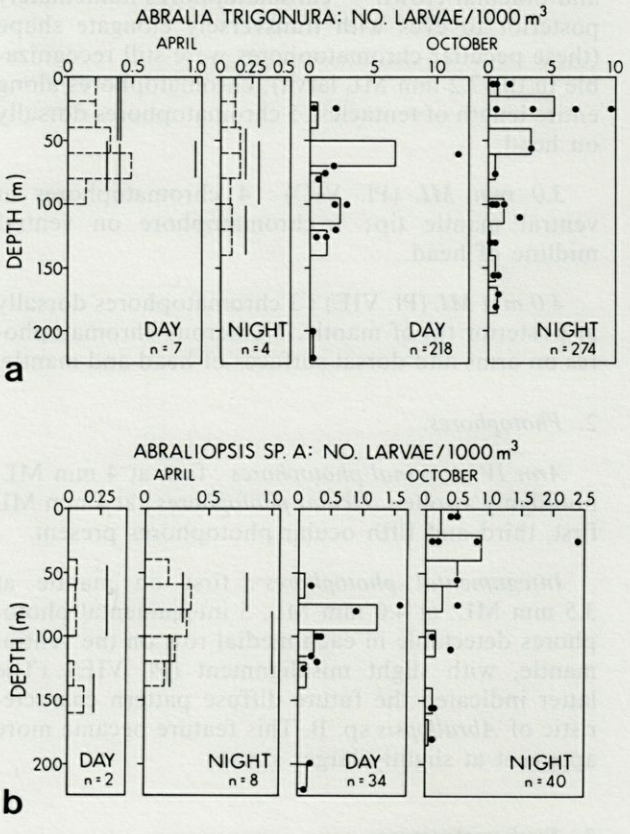


Fig. 3. — a : Vertical distribution of *Abralia trigonura*. In April series, vertical bars represent depth range and capture rates of *positive* opening-closing tows. In October series, dots represent modal fishing depth of *positive* open tows. Histograms represent average catch rates and, therefore, include negative tows not plotted. b : Vertical distribution of *Abraliopsis* sp. A.

A. Eggs

Eggs not examined.

B. Larvae (Pl. VI)

1. *Chromatophores*

Advanced hatchling (Pl. VIB) : ventral mantle — 2 chromatophores or 2 pairs of chromatophores or some combination of these (i.e., 1 : 2 or 2 : 1) in row on ventral mantle midline; 2 chromatophores at posterior end. Dorsal mantle — single pair of chromatophores near midregion; second pair at posterior tip. Head and brachial crown — ventral surface of the head with a chromatophore posterior to each eye and at each postero-lateral corner; dorsal surface of head with 3 or 4 chromatophores; tentacle with large chromatophore at base.

2.0 mm ML (Pl. VIC) : ventral mantle — single pair of chromatophores in mid-region. (Mantle chromatophores were rarely present in captured larvae due to damage. The ventral mantle row present in the hatchling was never observed). Head and brachial crown — chromatophores immediately posterior to eyes with transversely elongate shape (these peculiar chromatophores were still recognizable in the 7.2 mm ML larva); chromatophores along entire length of tentacles; 5 chromatophores dorsally on head.

3.0 mm ML (Pl. VID) : 4 chromatophores at ventral mantle tip; 1 chromatophore on ventral midline of head.

4.0 mm ML (Pl. VIE) : 3 chromatophores dorsally at posterior tip of mantle. Numerous chromatophores on arms and dorsal surfaces of head and mantle.

2. *Photophores.*

Arm IV, terminal photophores : first at 4 mm ML, not highly swollen. *Ocular photophores :* at 4 mm ML first, third and fifth ocular photophores present.

Integumental photophores : first on mantle at 3.5 mm ML; at 4.0 mm ML, 5 integumental photophores detectable in each medial row on the ventral mantle, with slight misalignment (Pl. VIE). (The latter indicated the future diffuse pattern characteristic of *Abraliopsis* sp. B. This feature became more apparent at slightly larger sizes).

3. *Sucker structure*

1.7 mm ML : most tentacular suckers with retort shape and narrow apertures; platelet formula not determined. Arm II, basal 2 suckers — platelet ratios = 8 : 13 : 18 (1 : 1.6 : 2.3) and 10 : 14 : 14 (1 : 1.4 : 1.4).

3.0 mm ML : tentacular sucker (Pl. VB) — platelet ratio = 12 : 26 : 42 (1 : 2.2 : 3.5); arm I, approximately sucker 8 — 12 inner platelets on inner whorl with larger knobs on distal portions, only distal knobs present on middle whorl, single bluntly rounded tooth distally on inner chitinous ring (Pl. II, I).

5.6 mm ML : tentacular sucker proximal to first hook — platelet ratio = 6 : 18 : 24 (1 : 3.0 : 4.0), one knob on inner whorl greatly elongate, outer platelets with truncated, attached ends; Arm II, basal sucker — platelet ratio = 8 : 8 : 25 (1 : 1 : 3.1).

4. *Other larval characters*

Appearance similar to *Abraliopsis* sp. A, but stubbier and more heavily pigmented in later stages.

C. Vertical Distribution (Fig. 4a)

In the October series, most captures were made between 50 m and about 125 m during the day and in the upper 60 m during the night. During the April series most larvae were caught in the upper 70 m during the day and in the upper 50 m at night.

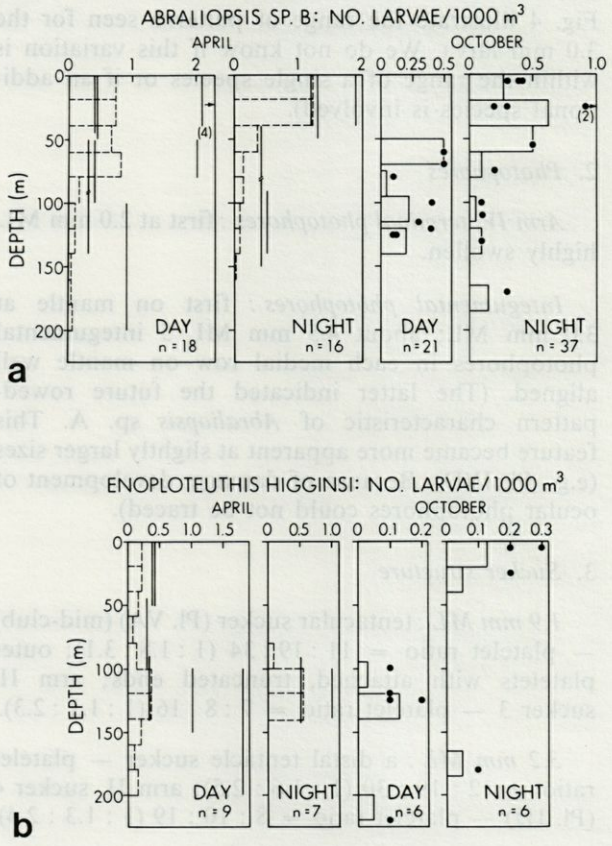


Fig. 4. — a : Vertical distribution of *Abraliopsis* sp. B. Symbols as in Fig. 3 b : Vertical distribution of *Enoploteuthis higginsi.* Symbols as in Fig. 3.

Enoploteuthis reticulata Rancurel, 1970

The species ranked 2lst in overall abundance and comprised less than 1 % of all squid larvae taken.

A. Eggs (Fig. 2)

Shape and size : ovoid, 1.08 ± 0.06 mm × 0.78 ± 0.07 mm. Color : colorless, slightly opaque. Chorion : covered with tiny pits which scatter light and give egg a slightly dull, silvery veneer; no pronounced perivielline space. (The peculiar pitted chorion was also found in mature eggs taken from the ovary of an adult female of this species). Jelly coating : clear, colorless, usually lost during capture.

B. Larvae (Pl. VII)

1. *Chromatophores*

Advanced hatchling (Pl. VIIB) : mantle — covered by numerous closely spaced chromatophores in no obvious pattern. Head and brachial crown — unusually large number of chromatophores. (The high concentration of chromatophores in all the larval stages distinguishes this from most other local enoploteuthin species).

2. *Photophores*

Ocular photophores : 2 large, 1 small on each eye at 2.8 mm ML (Pl. VIIC); at 6.8 mm ML, 4 small photophores between the larger terminal photophores on each eye (Pl. VII E) (this pattern was diagnostic of the genus *Enoploteuthis* in Hawaiian waters).

Integumental photophores : at 2.8 mm ML, 1 photophore on basal portion of each arm IV (the mantle was stripped of most integument but 2 photophores remained in a fragment of tissue stuck to the mantle side); at 6.8 mm ML, mantle photophore pattern identifiable with published patterns of juvenile (Pl. VI E) (Burgess, 1982).

3. *Sucker structure*

2.3 mm ML : Tentacular sucker (Pl. V C) — platelets of inner and middle whorls without knobs; platelets of outer whorl highly excavated; platelet ratio = 16 : 20 : 29 (1 : 1.3 : 1.8); aperture small. (The tentacular suckers of the hatchling were virtually identical). Arm II (?) — basal suckers same structure as above (platelet ratio = 16 : ? :28); sucker 7 aperture large, knobs present, inner chitinous ring with long slender teeth; platelet ratio = 18 : 24 : ?.

3.3 mm ML : tentacular suckers (Pl. VD) — 6 or 7 slender, pointed teeth on inner chitinous ring, long pointed knobs on distal platelets of innet whorl; typical knobs distally on the middle whorl but absent proximally; proximal knobs on inner whorl small; platelet ratio = 20 : 26 : 42 (1 : 1.3 : 2.1); outer platelets with attached and truncated tips on proximal portion of whorl, free and pointed tips on distal portion; arms II, sucker 5 (Pl. IIE) — similar to tentacular suckers; platelet ratio = 20 : 26 : 42; arms IV, sucker 4 — no teeth on inner chitinous ring, typical knobs on outer ring, few knobs on middle whorl.

4. *Other larval characters*

Tentacles short, about equal to arms I-III in length and thickness; large larvae with arms thicker than tentacles; head nearly rectangular in outline.

C. Vertical Distribution

The larvae were captured in the upper 200 m.

Enoploteuthis higginsi Burgess, 1982

This species ranked 14th in overall abundance among squid larvae captured and comprised 1.3 % of all specimens.

A. Eggs

The eggs of this species were not recognized in their earliest stages of development. However, by early organ formation, large diagnostic pigment spots appeared on the embryo. At this stage the egg size was 0.9 mm × 0.8 mm.

B. Larvae (Pl. VIII)

1. *Chromatophores*

Advanced hatchling (Pl. VIIIA) : Ventral mantle — band I (2 chromatophores on each side) at each antero-lateral margin joined with a posterior chromatophore to form an inverted L-shaped series; complex band just posterior to midregion; 5 chromatophores at posterior end. Dorsal mantle — scattered chromatophores, but no band at anterior margin. Head and brachial crown — ventral surface of head with large chromatophore at each postero-lateral corner, single midline chromatophore; dorsal surface of head with 5 chromatophores; each arm II with 1 chromatophore at tip; tentacle with chromatophore series on tip and large chromatophore at base.

2.2. mm ML : ventral pattern similar to hatchling but with more chromatophores; dorsal mantle pattern (Pl. VIII B) uncertain due to damage.

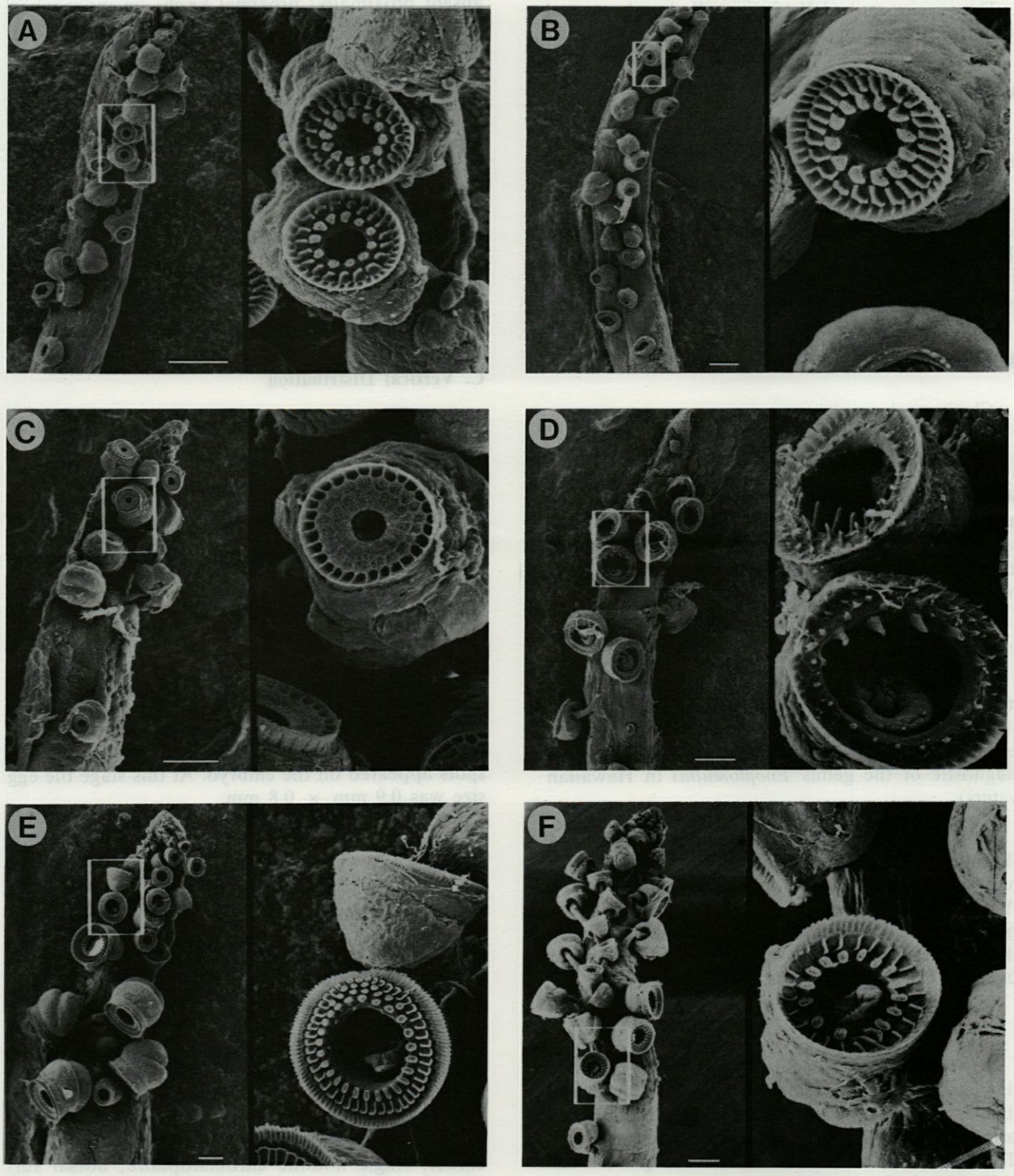


Plate V. — Scanning electron micrographs of tentacular clubs and club suckers. A : *Abraliopsis* sp. A (1.9 mm ML) with 5X enlarged suckers. B : *Abraliopsis* sp. B (3.0 mm ML) with 10 enlarged sucker. C : *Enoploteuthis reticulata* (2.3 mm ML) with 5X enlarged sucker. D : *E. reticulata* (3.3 mm ML) with 5X enlarged suckers. E : *Enoploteuthis higginsi* (4.6 mm ML) with 5X enlarged suckers. F : *Enoploteuthis jonesi* (3.0 mm ML) with 5X enlarged suckers. Scale bars = 0.1 mm.

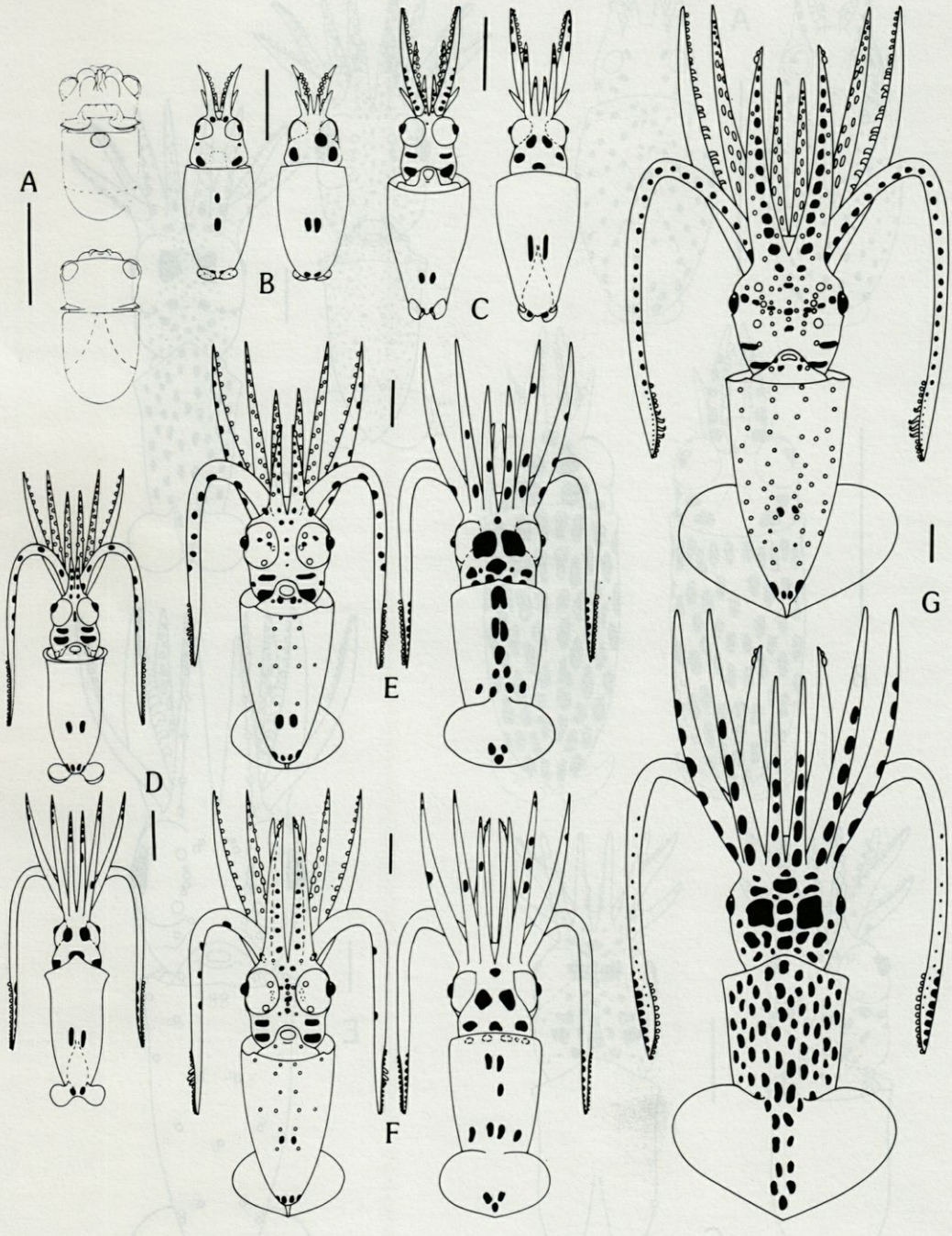


Plate VI. — Larval stages of *Abraliopsis* sp. B. A : 0.9 mm ML, 12 hrs after hatching. B : 1.6 mm ML, 3.5 days after hatching. C : 2.0 mm ML. D : 3.0 mm ML. E : 4.0 mm ML. F : 4.6 mm ML. G : 7.2 mm ML. Scale bars = 1.0 mm.

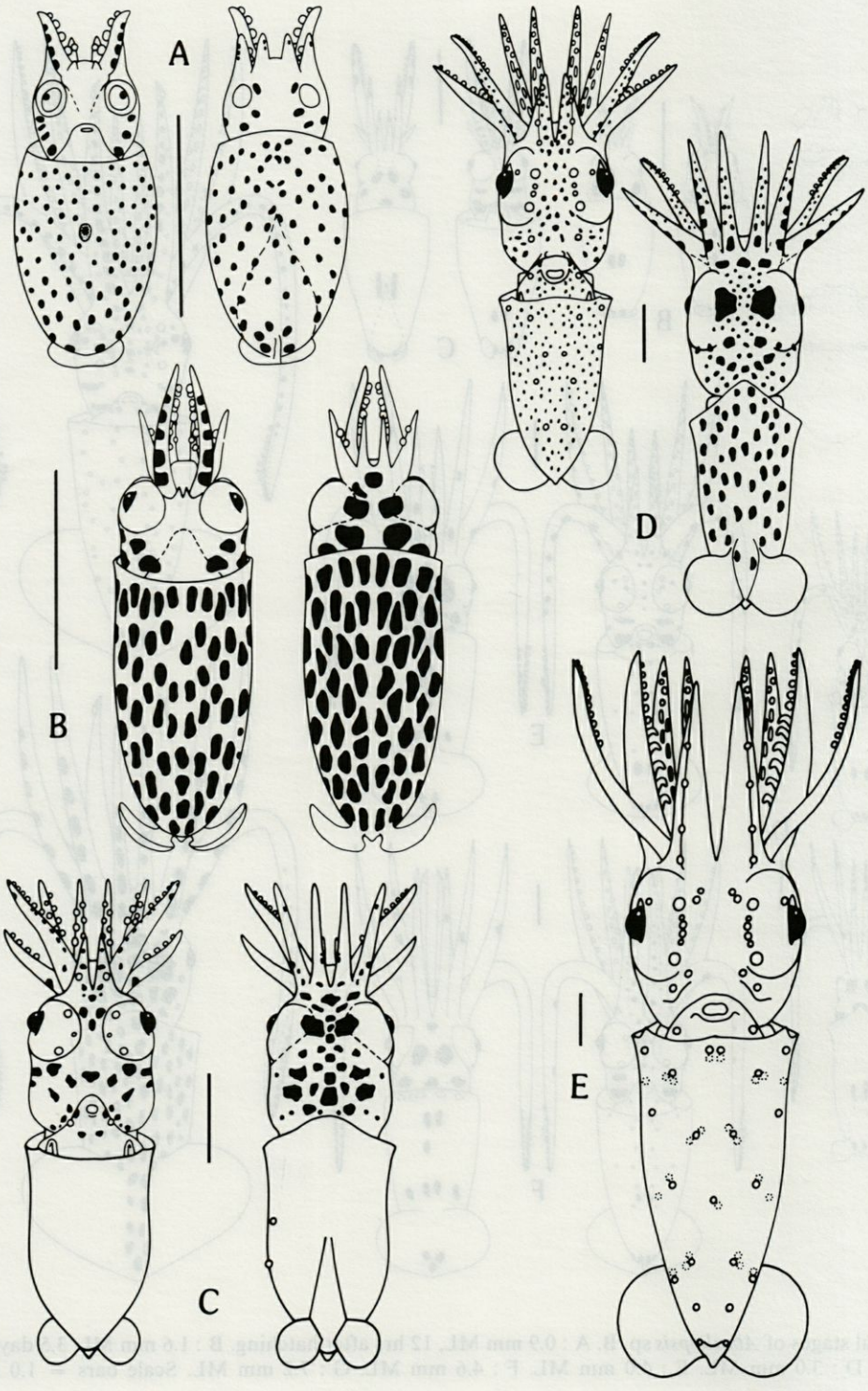


Plate VII. — Larval stages of *Enoploteuthis reticulata*. A : 1.2 mm ML, at hatching. B : 1.5 mm ML, 7 days after hatching. C : 2.8 mm ML. D : 4.1 mm ML. E : 6.8 mm ML. Scale bars = 1.0 mm.

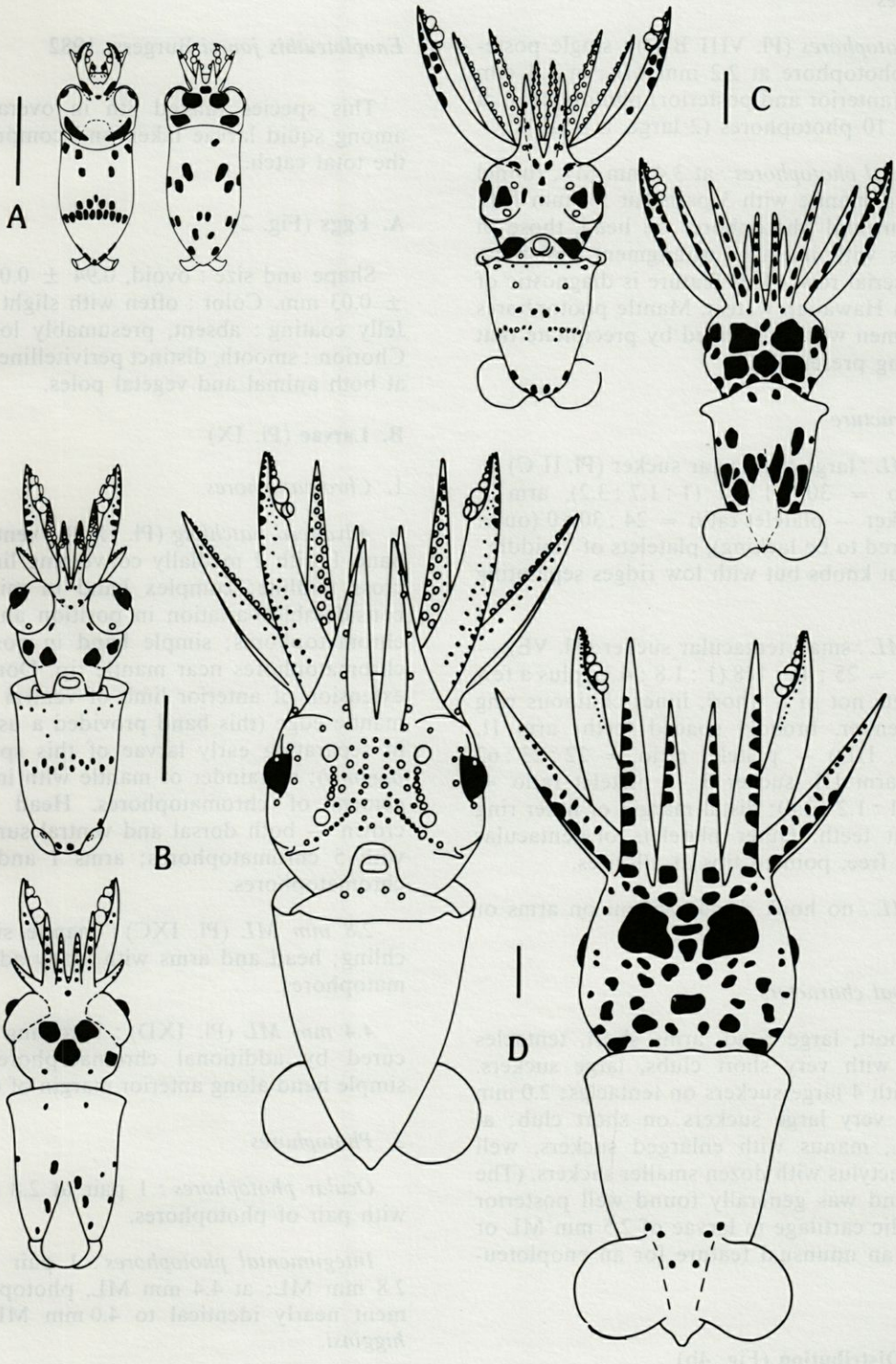


Plate VIII. — Larval stages of *Enoploteuthis higginsi*. A : 1.6 mm ML, 5.5 days after hatching. B : 2.2 mm ML. C : 3.4 mm ML. D : 5.8 mm ML. Scale bars = 1.0 mm.

3.4 mm ML : ventral mantle chromatophore pattern of hatchling still recognizable (Pl. VIII C).

2. *Photophores*

Ocular photophores (Pl. VIII B-D) : single posterior ocular photophore at 2.2 mm ML; at 3.4 mm ML, 2 large (anterior and posterior) photophores, at 5.8 mm ML, 10 photophores (2 large, 8 small).

Integumental photophores : at 3.4 mm ML, funnel with one pair, mantle with 3 pairs; at 5.8 mm ML, many integumental photophores on head, those in medial series with irregular arrangment indicating future multiserial row. (This feature is diagnostic of *E. higginsi* in Hawaiian waters. Mantle photophores in this specimen were concealed by precipitate that formed during preservation).

3. *Sucker structure*

2.0 mm ML : large tentacular sucker (Pl. II C) — platelet ratio = 30 : 51 : 97 (1 : 1.7 : 3.2), arm I, mid-arm sucker — platelet ratio = 24 : 30 : 0 (outer whorl appeared to be lacking), platelets of "middle" whorl without knobs but with low ridges separating the platelets.

4.6. mm ML : small tentacular sucker (Pl. VE) — platelet ratio = 25 : 45 : 108 (1 : 1.8 : 4.3), plus a few distal platelets not in a whorl, inner chitinous ring with few slender, broadly spaced teeth; arm II, sucker 4 (Pl. IID) — platelet ratio = 22 : 23 : 62 (1 : 1 : 2.8); arm III, sucker 5 — platelet ratio = 18 : 22 : 62 (1 : 1.2 : 3.4); distal margin of inner ring with 4 blunt teeth. Outer platelets of tentacular suckers with free, pointed tips at all sizes.

7.6 mm ML : no hook developement on arms or tentacles.

4. *Other larval characters*

Mantle short, large head, arms short, tentacles large, thick with very short clubs, large suckers. Hatchling with 4 large suckers on tentacles; 2.0 mm ML, 4 or 5 very large suckers on short club; at 4.6 mm ML, manus with enlarged suckers, well developed dactylus with dozen smaller suckers. (The digestive gland was generally found well posterior to the cephalic cartilage in larvae of 2.5 mm ML or less. This is an ununsual feature for an enoploteuthid).

C. Vertical Distribution (Fig. 4b)

Although the number of captures were few, the October samples indicated a peak in the vertical distribution during the day between 100 and 125 m and during the night in the upper 25 m. The April series indicated a day peak in the same 100-150 m depth range although some specimens were captured in the upper 50 m. The night peak was also in the 100-150 m range.

Enoploteuthis jonesi Burgess, 1982

This species ranked 8th in overall abundance among squid larvae taken and comprised 4.3 % of the total catch.

A. Eggs (Fig. 2)

Shape and size : ovoid, 0.94 ± 0.07 mm × 0.77 ± 0.03 mm. Color : often with slight greenish tint. Jelly coating : absent, presumably lost in capture. Chorion : smooth, distinct perivitelline space usually at both animal and vegetal poles.

B. Larvae (Pl. IX)

1. *Chromatophores*

Advanced hatchling (Pl. IXB) : ventral mantle — band I with 2 medially converging limbs, does not cross midline; complex band in mid-region with considerable variation in position and numbers of chromatophores; simple band in posterior 1/3; 4 chromatophores near mantle tip. Dorsal mantle — extension of anterior limb of ventral band I along mantle edge (this band provided a useful character in separating early larvae of this species from *E. higginsi*); remainder of mantle with irregular arrangement of chromatophores. Head and brachial crown — both dorsal and ventral surfaces of head with 5 chromatophores; arms I and II with few chromatophores.

2.8 mm ML (Pl. IXC) : mantle similar to hatchling; head and arms with many additional chromatophores.

4.4 mm ML (Pl. IXD) : hatchling patterns obscured by additional chromatophores except for simple band along anterior margin of dorsal mantle.

2. *Photophores*

Ocular photophores : 1 pair at 2.8 mm ML; eye with pair of photophores.

Integumental photophores : 1 pair on mantle at 2.8 mm ML; at 4.4 mm ML, photophore arrangement nearly identical to 4.0 mm ML larva of *E. higginsi.*

3. *Sucker structure*

2.2 mm ML : large tentacular sucker — platelet ratio = 13 : 25 : 78 (1 : 1.9 : 6.0), outer platelets with free, pointed tips; arm II, sucker 6 — platelet ratio = 15 : 26 : 50 (1 : 1.7 : 3.3).

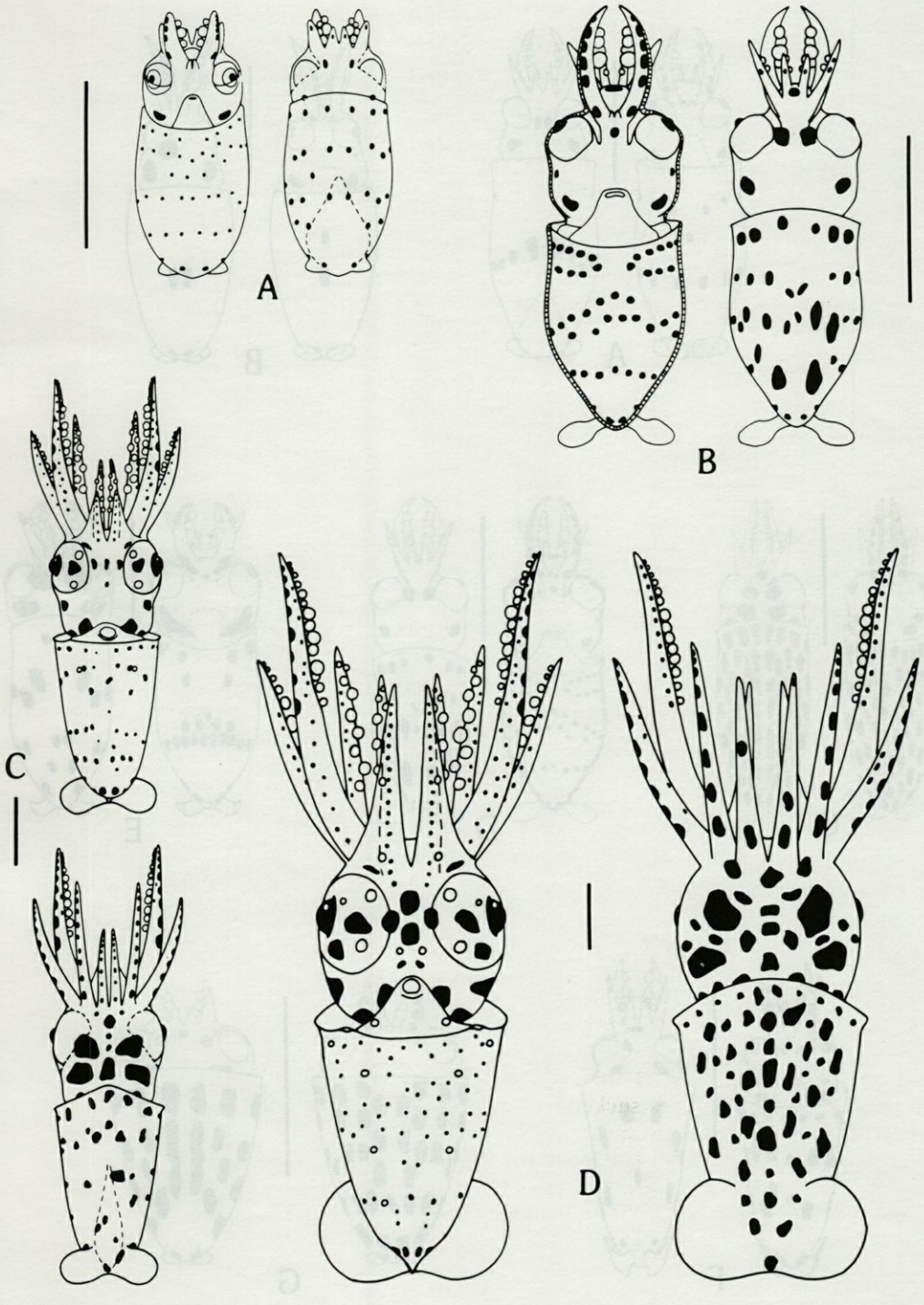


Plate IX. — Larval stages of *Enoploteuthis jonesi*. A : 1.1 mm ML, at hatching. B : 1.3 mm ML, 7 days after hatching. C : 2.8 mm ML. D : 4.4 mm ML. Scale bars = 1.0 mm.

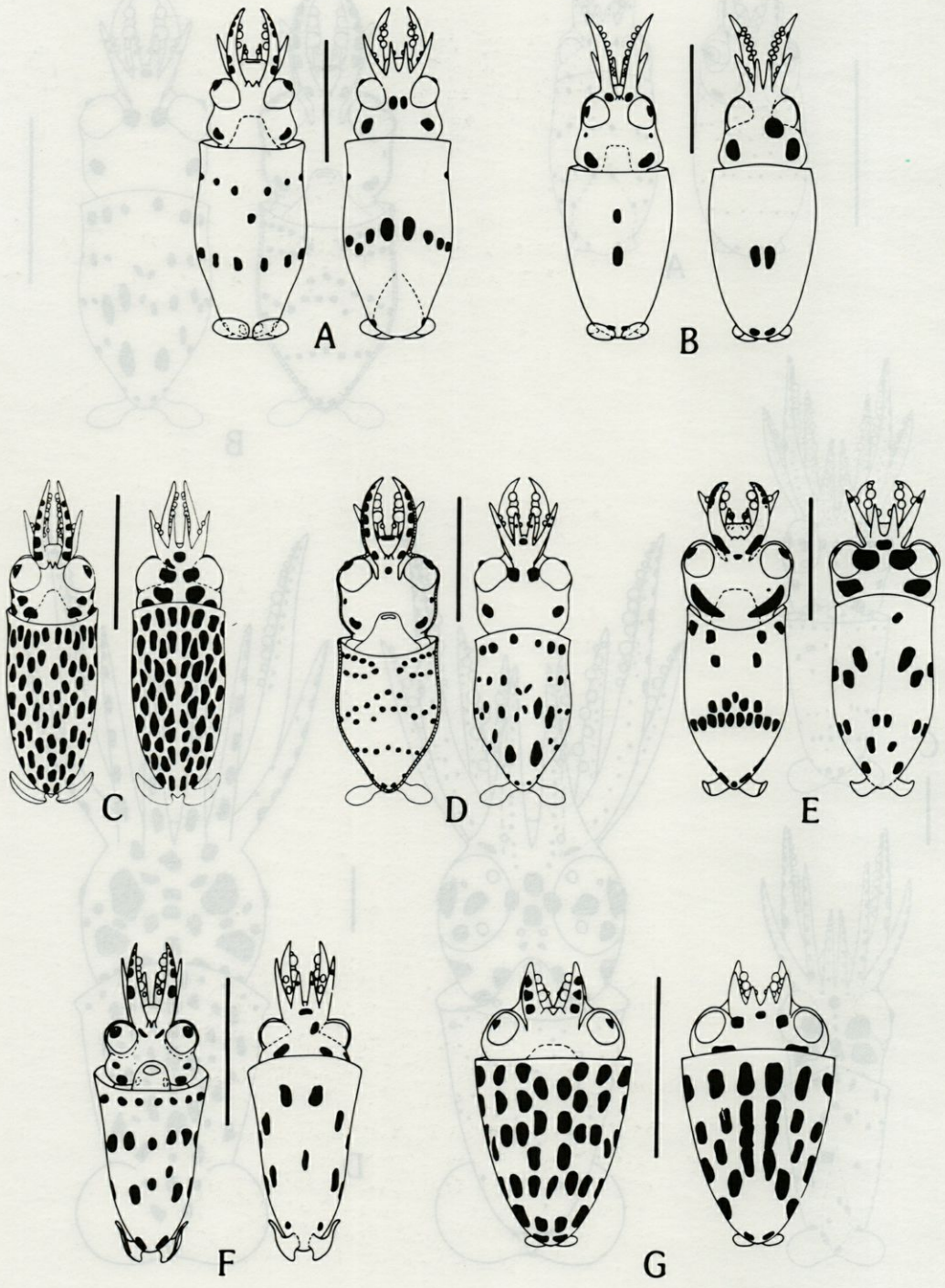


Plate X. — Enoploteuthin hatchling, several days after hatching. A : *Abraliopsis* sp. A (1.6 mm ML). B : *Abraliopsis* sp. B (1.6 mm ML). C : *Enoploteuthis reticulata* (1.5 mm ML). D : *Enoploteuthis jonesi* (1.3 mm ML). E : *Enoploteuthis higginsi* (1.6 mm ML). F : *Abralia trigonura* (1.3 mm ML). G : unknown genus and species (1.1 mm ML). Scale bars = 1.0 mm.

3.0 mm ML : tentacular sucker (Pl. VF) — platelet ratio = 15 : 24 : 76 (1 : 1.6 : 5.1); arm II, sucker 7 (Pl. IIG) — platelet ratio = 19 : 29 : ?, knobs only on distal portions of middle whorl; several slender teeth on distal margin of inner chitinous ring.

4. *Other larval characters*

Hatchling with few greatly enlarged suckers on tentacles; at 1.8 mm ML, generally with 7 or more suckers on manus and with well-developed dactylus with numerous sucker buds; at 2.2 mm ML, club elongate, suckers not greatly enlarged, club with distinct gradation from larger suckers on manus to smaller suckers on dactylus (Pl. VF). (This feature and the presence of long stalks on the tentacular suckers were useful in distinguishing this species from *A. trigonura*). The general form changed with growth. The early larvae were similar in shape to *Abralia trigonura* while the older larvae developed a stubbier appearance more like that of *E. higginsi.*

The digestive gland either abutted against the cephalic cartilage or was separated from it by only a narrow gap in young larvae. This larval series is identified to *E. jonesi* by process of elimination, this being the only remaining species of *Enoploteuthis* known from Hawaiian waters.

C. Vertical Distribution (Fig. 5)

The October series returned substantial catches in the upper 100 m during both the day and night.

Genus and species unknown (Pl. XG)

On several occasions we captured small eggs that developed into hatchlings that were different from

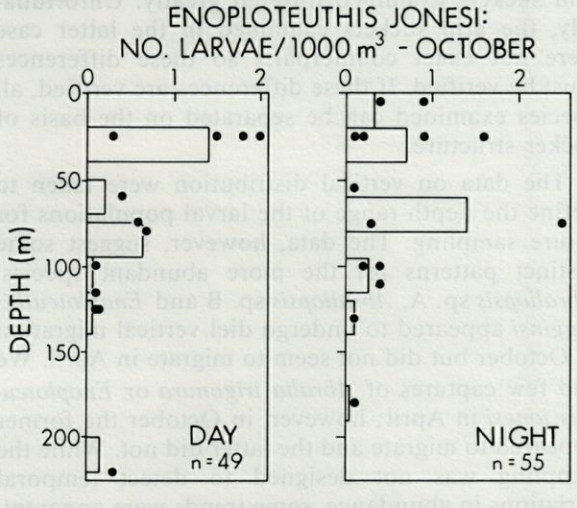


Fig. 5. — Vertical distribution of *Enoploteuthis jonesi.* Symbols as in Fig. 3.

others reported here. At present, the identity of this squid is unknown, and we cannot be certain that it belongs to the Enoploteuthinae.

A. Eggs

Egg spherical, chorion ovoid : 0.96 mm × 0.76 mm. Color : green tint. Chorion : smooth, perivitelline space at both animal and vegetal poles.

B. Larvae

1. *Chromatophores*

Hatchling : numerous chromatophores scattered over surface of mantle. Small region lacking chromatophores at postero-dorsal end of mantle. Head and brachial crown — 5 chromatophores on dorsal surface of head; 3 chromatophores on tentacle.

2. No photophores present.

3. Sucker structure not examined.

4. *Other larval characters*

Hatchling small (1.0 mm ML).

DISCUSSION

Our objective has been to describe the early life history stages of the species of Hawaiian Enoploteuthinae in sufficient detail to allow identification. The eggs of most Hawaiian enoploteuthins, however, are difficult to identify to species unless they are allowed to develop. The sculptured chorion of the eggs of *Enoploteuthis reticulata* made identifation of these eggs easy. Eggs of other species could be separated only by their size and color, but both of these features exhibit considerable variability. *Abraliopsis* sp. A, however, tends to have a larger egg that is generally colorless. The other species cannot be reliably identified, at present, prior to organ formation.

Identification of all larvae would be a simple task if they were captured in perfect condition. Unfortunately finding a perfect specimen in most plankton tows is a rare event. Identification, therefore, must depend on those characters that are not easily obscured by damage during capture. The following key attempts to use such characters.

KEY TO LARVAE OF THE ENOPLOTEUTHINAE FROM HAWAIIAN WATERS

1A. Arms and tentacles very long and slender.... 2
1B. Arms and tentacles not long and slender..... 3

2A. Chromatophores extend to base of tentacles; two transversely elongate chromatophores on ventral surface of head posterior to each eye; several (no. varies with size) chromatophores on ventral midline of head; arm IV tips not swollen until about 4 mm ML and then only slightly; at 4.0 mm ML or less, 2-3 chromatophores present at dorsal mantle tip ..... *Abraliopsis* sp. B

2B. Chromatophores absent from the basal 1/4 of tentacle; one chromatophore behind each eye (occasionally a second, small and more lateral chromatophore present) on ventral surface of head; generally 0 or 1 chromatophore on ventral midline of head; arm IV tips greatly swollen by 2.0 mm ML; at 2.5 to 8.6 mm ML a single chromatophore present at dorsal mantle tip ..... *Abraliopsis* sp. A

3A. Tentacular clubs short and bearing a few very large suckers ..... *Enoploteuthis higginsi* and young (< 2.0 mm ML) *E. jonesi.* (In the youngest stages, identification will rest with the chromatophore pattern, number of large tentacular suckers and position of the digestive gland).

3B. Tentacular clubs not unusually short, and lacking very large suckers 4

4A. Numerous chromatophores covering mantle and head ..... *Enoploteuthis reticulata*

4B. Only scattered chromatophores on mantle and head 5

5A. Tentacular clubs with small suckers of nearly uniform size; club suckers on short stalks; eyes with three large (when present) photophores 6

5B. Tentacular clubs with relatively large suckers on the manus that grade in size to small suckers on the dactylus; club suckers on moderately long stalks; eyes with two large (when present) photophores ..... *Enoploteuthis jonesi*

6A. Chromatophore pattern on dorsal mantle forming a circle with a single chromatophore at center; chromatophore band III on ventral mantle incomplete; integumental photophores small; no large subintegumental photophores near posterior tip of mantle.. *Abralia trigonura*

6B. Chromatophore pattern on the dorsal mantle with many midline chromatophores; chromatophore band III on ventral mantle complete; integumental photophores very large; two large subintegumental photophores near posterior mantle tip ..... *Abralia astrosticta*

Each species examined had a unique chromatophore pattern (Pl. X). The value of chromatophore patterns in identification has been demonstrated for some larval loliginid squids (McConathy *et al.*, 1980), and the considerable importance of the chromatophore patterns in the systematics of larval oegopsid squids is demonstrated here for the first time. The chromatophore patterns provide the single most valuable character for larval identification. However, some species are especially prone to the loss of chromatophores during capture. This was especially true of species of *Abraliopsis* in this study. The only way to reduce this problem is with careful capture and handling techniques. The functional significance of these distinctive patterns which are present at hatching is unknown.

The size and arrangement of photophores also provides many features that are of great value in identification. While photophore patterns generally are useful only in larger larvae, they are not as subject to trawl damage as are chromatophores. In this study, photophore characteristics, in most cases, were crucial in connecting larval and adult identifications. In *Abralia trigonura,* the ventral mantle photophore pattern initially appeared at the precise location of the chromatophore pattern : The photophores seemed to replace the chromatophores. This was not true in other species and its significance is unknown.

The structure of the chitinous rings has rarely been used in larval systematics (see Harman and Young, 1985, for another case). Since SEM micrographs are required, these features are of little value in routine identification. However, for verifying the integrity of a size-series, the value is great. Although the structure of the chitinous rings varies somewhat depending on the size of the larva and the sucker location on the brachial crown, clear differences were found nevertheless. The structure of the rings was unique in *E. reticulata* and could be easily traced from hatchling through early larval stages. The other two species of *Enoploteuthis* were easily separable on the basis of platelet ratios and dentition. While the tentacular suckers of the two species of *Abralia* were similar, the arm suckers differed in their dentition. In the two species of *Abraliopsis*, the tentacular suckers, also, were indistinguishable. However, the arm suckers examined differed greatly. Unfortunately, the arm suckers examined in the latter case were not exact counterparts so these differences must be verified. If these differences are verified, all species examined can be separated on the basis of sucker structure.

The data on vertical distribution were taken to define the depth range of the larval populations for future sampling. The data, however, suggest some distinct patterns for the more abundant species. *Abraliopsis* sp. A, *Abraliopsis* sp. B and *Enoploteuthis higginsi* appeared to undergo diel vertical migration in October but did not seem to migrate in April. We had few captures of *Abralia trigonura* or *Enoploteuthis jonesi* in April; however, in October the former appeared to migrate and the latter did not. While the sampling was not designed to detect temporal variations in abundance, some trends were apparent. *E. jonesi* was essentially absent in April but was abundant in October. *Abraliopsis* sp. A and *Abralia*

trigonura were also more abundant in October while *E. higginsi* was more abundant in April. *Abraliopsis* sp. B was abundant during both sampling periods. Clearly, if one wishes to investigate factors affecting reproduction and larval survival, intensive investigation of temporal variation in both abundance and vertical distribution is warranted.

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