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VIE ET MILIEU, 1985, 35 (3/4)

BIOLOGY AND DISTRIBUTION OF EARLY JUVENILE CEPHALOPODS

edited by K. MANGOLD and S.v. BOLETZKY

Travaux présentés au symposium « Biologie et Distribution de Céphalopodes Juvéniles Précoces » qui s'est tenu au Laboratoire Arago, Banyuls-sur-Mer, les 29 et 30 juin 1985, sous le patronat du Conseil International pour l'Avancement des recherches sur les Céphalopodes (C.I.A.C.), avec le soutien financier de la FAO, du PIROcéan, de l'IFREMER et de NATURALIA ET BIOLOGIA.

Papers presented at the symposium "Biology and Distribution of Early Juvenile Cephalopods", held at the Laboratoire Arago, Banyuls-sur-Mer, on 29 and 30 June 1985, under the auspices of the Cephalopod International Advisory Council (C.I.A.C.), funded by FAO, PIROcéan, IFREMER and NATURALIA ET BIOLOGIA.

Les référés suivants ont examiné les manuscrits publiés dans le tome 35. La rédaction leur exprime sa reconnaissance pour leurs analyses et leurs critiques.

The following persons have reviewed manuscripts published in volume 35. Their constructive comments have been valuable for the authors and are greatly appreciated by the editorial board.

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PREFACE

The symposium on BIOLOGY AND DISTRIBUTION OF EARLY JUVENILE CEPHALOPODS *was held at the Laboratoire Arago in Banyuls-sur-Mer on 29 and 30 June 1985. It followed a workshop on* EARLY GROWTH STAGES OF CEPHALOPODS *held from 17 to 28 June. Both meetings were organized under the auspices of the Cephalopod International Advisory Council* (CIAC), *which was founded in 1983 (see Appendix I).*

While the number of workshop participants was deliberately limited to 35 for practical reasons mainly regarding the constraints of benchwork on large collections of preserved specimens, the symposium was intended for a larger number of participants and was given a somewhat wider scope. Its title draws attention to aspects that led beyond the immediate goal of the workshop, which was the identification of early juveniles (with emphasis on the smallest so-called "larval" forms) of as many groups of cephalopods as possible. The result of this undertaking is a handbook that will be published separetely.

For the publication of the papers presented at the symposium, it was agreed that each manuscript submitted to VIE ET MILIEU *would be reviewed by two anonymous referees chosen from among the* CIAC *members, recognized specialists in one or several fields of cephalopod research. In addition to full-length papers, a few short notes and abstracts are published in this volume to provide the widest possible information on material presented at the symposium. Some of these short contributions were submitted as such, others are transformed articles that have been condensed following the advice of referees. Several talks presented at the symposium have not been submitted for publication in this volume.*

With some fifty participants (see Appendix II) presenting their papers in plenary sessions, the symposium was a compact meeting allowing everyone to have all the personal contacts desired. We refrain from subdividing the present volume into thematic sections. Such an editorial intervention would somehow do injustice to the truly interdisciplinary character of the whole meeting; indeed the biological oceanographer mainly interested in patterns of animal distribution in the sea freely exchanged ideas with the biologist more specifically involved in the analysis of patterns and processes occurring within the animal or among individuals of a given species.

This meeting was held almost exactly ten years after the first symposium on The Biology of Cephalopods (London, UK). In their Introduction to the special volume (Symp. zool. Soc. Lond., 38) composed of 22 articles covering a wide range of aspects of cephalopod biology, John Messenger and Marion Nixon remarked : "Although this Symposium was originally conceived simply as a tribute to Professor J.Z. Young, it soon became apparent that there had never been, so far as we could ascertain, a full-scale meeting devoted exclusively to [living] cephalopods". Since this statement was made, a number of meetings dealing exclusively with cephalopods have taken place in different parts of the world, sometimes more than one in the same year. In 1985, the CIAC *symposium was closely followed by the symposium "Cephalopods : Present and Past", which was organized by paleontologists of the University of Tübingen (F.R. Germany).*

However, no full-scale meeting devoted exclusively to young *cephalopods had hitherto been held. To organize this symposium in Banyuls was a true gratification to the resident teuthology group, thanks to the enthusiasm of all the people involved in the plan and its realization. It was also a token of grateful appreciation of a scientific tradition whose originator is no longer among us. Research on cephalopods has been carried out in Banyuls ever since Henri de Lacaze-Duthiers founded the Laboratoire Arago, in 1882, but it was with the work carried out here in the mid-twenties by the late Adolf Portmann, zoology professor at the university of Basel from 1928 to 1970, that the study of early life stages of cephalopods became firmly established at the Arago laboratory. Needless to say, Portmann considered this work to be naturally embedded in the more comprehensive study of the entire life cycle of cephalopods adapted to a variety of marine biotopes, a rather large assortment of which is found in the Banyuls area.*

We gratefully acknowledge the support and help provided by the Directors and the personnel of the Laboratoire Arago, the funds allocated to our meeting by FAO *and by two french institutions, namely the interdisciplinary oceanography program* PIROcéan *and the national institute of marine resources* IFREMER. *We also thank the association* NATURALIA ET BIOLOGIA *for a special grant covering part of the production costs of the symposium volume. Last but not least, we give our sincere thanks to all symposium participants for their cooperation throughout and beyond the meeting.*

Katharina MANGOLD and Sigurd v. BOLETZKY

VIE MILIEU, 1985, 35 (3/4) : 139-147

DISTRIBUTION AND SIZE OF JUVENILE SHORT-FINNED SQUID *(ILLEX ILLECEBROSUS)* (MOLLUSCA : CEPHALOPODA) SOUTH OF NEWFOUNDLAND DURING WINTER

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SQUID
DISTRIBUTION
SIZE
GULF STREAM SYSTEM

ABSTRACT. — The distribution of juvenile short-finned squid (*Illex illecebrosus*) in relation to water masses was examined from surveys carried out during February-March of 1981, 1982, 1984 and 1985. The pattern of juvenile squid distribution was somewhat variable among years but overall, juveniles were most abundant within either the northern Gulf Stream or Slope Water. They were only occasionally caught within the most seaward portion of the Gulf Stream or Sargasso Sea. Size distributions were consistent among years in showing a distinct increase in mean mantle length from the Gulf Stream landward toward the cooler water masses. Smallest juveniles for all years were those collected near the core of the Gulf Stream in 1981, supporting the proposed importance of the Gulf Stream in initial dispersal of young stages from an upstream spawning site.

CALMAR
DISTRIBUTION
DIMENSION
SYSTÈME DU COURANT DU GOLFE

RÉSUMÉ. — Distribution des Calmars juvéniles (*Illex illecebrosus*) pendant l'hiver. La distribution des Calmars juvéniles à nageoires courtes (*Illex illecebrosus*) par rapport aux masses d'eaux a été examinée à partir d'une étude réalisée au cours des mois de février et mars 1981, 1982, 1984 et 1985. La distribution semble varier quelque peu au cours des différentes années, mais en général les Calmars juvéniles sont plus abondants à l'intérieur du courant du golfe et du talus continental. Les Calmars juvéniles sont rarement capturés dans les zones situées au large du courant du golfe et de la mer des Sargasses. La répartition des dimensions est constante entre les années et indique une augmentation de la moyenne de la longueur du manteau allant du courant du golfe vers l'intérieur des masses d'eaux froides. Durant les quatre années étudiées les Calmars juvéniles les plus petits ont été capturés près de la partie centrale du courant du golfe en 1981, confirmant ainsi l'importance du courant du golfe pour la dispersion des juvéniles à partir du site de ponte.

INTRODUCTION

Although the exact northern and southern limits of distribution of *Illex illecebrosus* remain uncertain, the species is known to range between central Florida in the south and Newfoundland and Labrador waters in the north (Roper *et al.*, 1969; Lu 1973). Longevity is believed to be about one year (Hurley and Beck, 1979; Dawe *et al.*, 1985), with the major spawning period occuring in January-February (Squires, 1967; Hatanaka *et al.*, 1985; Dawe and Beck, 1985). Short-finned squid move from off-shelf waters onto the continental shelf in spring and are fished commercially, off the northeastern United States, on the Nova Scotian Shelf, and at Newfoundland during July to November.

Larval and small juvenile stages of *Illex* sp. were first described by Roper and Lu (1979) and since 1979 many surveys directed for these young stages have been carried out within the January-May period in the Gulf Stream and associated water masses (Fedulov and Froerman, 1980; Froerman *et al.*, 1981, Amaratunga 1981; Dawe *et al.*, 1982; Dawe and Beck, 1985; Hatanaka *et al.*, 1982, 1985; Arkhipkin *et al.*, 1983; Fedulov *et al.*, 1984; Rowell *et al.*, 1985). Based on laboratory experiments (O'Dor and Durward, 1978; O'Dor *et al.*, 1982; O'Dor and Balch, 1985) and the observed pattern of larval distribution (Hatanaka *et al.*, 1985; Dawe and Beck, 1985; Rowell *et al.*, 1985), it is felt that spawning probably occurs south of Cape Hatteras in close proximity to the Gulf Stream, which probably serves as the mechanism for dispersal of young stages (Trites, 1983). Larvae are most abundant in the northern part of the Gulf Stream or at the Gulf Stream frontal zone (Hatanaka *et al.*, 1985; Dawe and Beck, 1985) and, whereas newly-hatched larvae have been collected south of Cape Hatteras (Dawe and Beck, 1985; Rowell *et al.*, 1985), only more advanced larvae have been captured further to the northeast (Roper and Lu, 1979; Vecchione, 1979; Hatanaka *et al.*, 1985; Dawe and Beck, 1985).

The transformation from the larval to juvenile stage, which is characterized by separation of the fused tentacles, occurs within the 6-8 mm mantle length (ML) size range (Roper and Lu, 1979; Vecchione, 1979). Juveniles appear to be most abundant within the upper 100 m (Fedulov and Froerman, 1980; Hatanaka *et al.*, 1982; Froerman *et al.*, 1981) and there is some evidence of a diel vertical migration (Arkhipkin *et al.*, 1983). Depth distribution apparently varies somewhat and it has been reported that greatest juvenile abundance is in nutrient-rich waters above the oxygen minimum (Fedulov and Froerman, 1980).

In this paper, juvenile *Illex illecebrosus* areal distribution in relation to water masses is described from four surveys carried out within the Gulf Stream System south of Newfoundland during February-March of 1981, 1982, 1984 and 1985. The distribution of juvenile size-groups among water masses is also examined. Findings from surveys described here are compared with those from other surveys carried out since 1979. Relevant oceanographic features have been briefly reviewed by Trites (1983) and Dawe and Beck (1985) but more elaborate descriptions of the Gulf Stream System have been provided by other investigators (Iselin 1936; McLellan 1957; Stommel 1958; Gatien 1976; Worthington 1976; Fofonoff 1981).

MATERIALS AND METHODS

All four surveys were carried out aboard the Canadian research vessel GADUS ATLANTICA. The survey period, during February-March, was similar among years but survey design and sampling methodology varied considerably among surveys (Table 1). During all surveys midwater trawling was carried out along transects which extended true south, approximately normal to the general direction of Gulf Stream flow (Fig. 1). During the 1981 survey, sets were executed at several depths on each station whereas in later surveys sets were consistently at a depth of 100 m for 30 minutes each. It is recognized that juveniles may have been caught during retrieval of the trawl and so catches may have occured anywhere in the water column from the maximum depth to the surface. Therefore depth distribution of juveniles will not be addressed here.

Midwater trawls used to sample juveniles varied among surveys (Table 1). Initially during 1981 a

Table 1. — Summary of time, area and methods of sampling juvenile *Illex illecebrosus* during surveys carried out between 1981 and 1985

Year	Dates	Longitude range	Sampling Gear: Type	Liner mesh size (mm)	Depth (m)	No. sets
1981 :	21 Feb-6 Mar	56°W-50°W	Engels 400 mesh	15.0	100	6
			Midwater trawl (EMT-400)		300	6
					500	1
			Engels 80	12.0	100	15
			Midwater trawl (EMT-80)		300	16
					500	7
					1,000	7
1982 :	21 Feb-23 Feb	56°W	Engels 80	12.0	100	10
			Midwater trawl (EMT-80)			
1984 :	24 Feb-9 Mar	55°W-57°30'W	Diamond IX			
			Midwater trawl	12.0	100	57
1985 :	22 Feb -10 mar	55°-60°W	Diamond IX	12.0	100	95
			Midwater trawl			

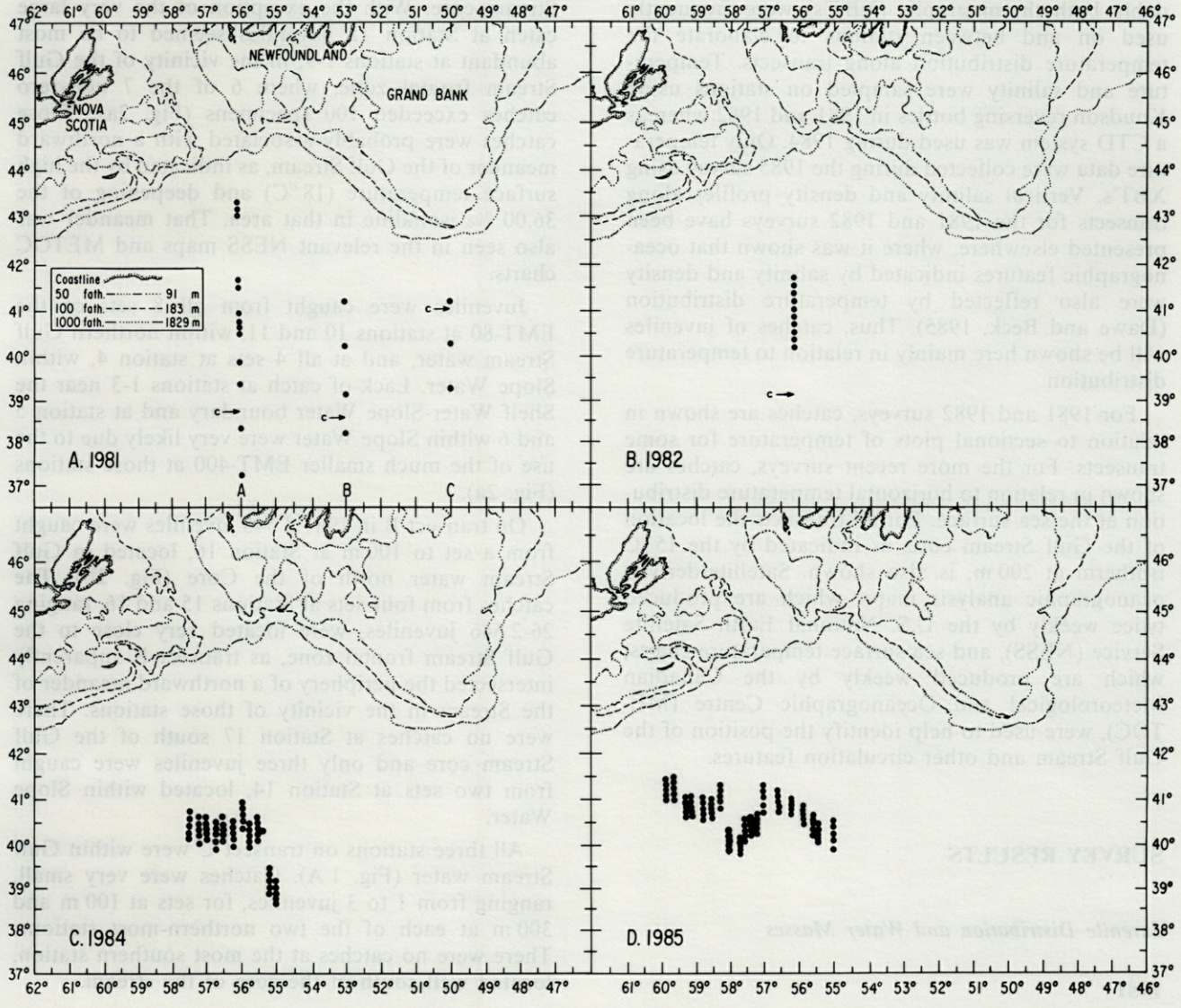


Fig. 1. — Location of stations on transects for surveys during February 21-March 6, 1981 (A), February 21-23, 1982 (B), February 24-March 9, 1984 (C) and February 22-March 10, 1985 (D). 'C' denotes the location of the Gulf Stream core on transects for 1981 and 1982.

small trawl, an Engels 400 mesh midwater trawl (EMT-400) was used but after 13 sets it had not succeeded in capturing any juveniles so the much larger Engels-80 midwater trawl (EMT-80) was used for the duration of the survey. That trawl was also used during the 1982 survey, but after 10 sets it became damaged beyond repair and midwater trawling was discontinued. It was concluded that the EMT-80 was impractical for extensive sampling due to its large size and so a Diamond IX midwater trawl was used during 1984 and 1985 surveys (Table 1).

Surveys in 1981 and 1982 were exploratory, sampling few transects but several water masses. The 1984 and 1985 surveys were aimed at developing an index of juvenile abundance based on catch rates. Toward that end the latter surveys sampled from the northern Gulf Stream northward toward the Shelf Water along randomly placed transects with five stations randomly placed on each transect. The 1981 survey sampled transects in the west to east direction, whereas the reverse was true for the 1985 survey. In 1984 every second transect was occupied while proceeding east to west during February 24-March 4 with the others being sampled during March 4-9 as the vessel returned, proceeding eastward across the survey area. Juvenile *Illex illecebrosus* were measured in dorsal mantle length to the nearest millimeter. Where catches were very large, a minimum of 100 specimens per station were measured.

Methods of oceanographic sampling also varied among the four surveys. During all surveys expen-

dable bathythermographs (XBT's) were frequently used on and between stations to elaborate the temperature distribution along transects. Temperature and salinity were sampled on stations using Knudson reversing bottles in 1981 and 1982 whereas a CTD system was used during 1984. Only temperature data were collected during the 1985 survey using XBT's. Vertical salinity and density profiles along transects for the 1981 and 1982 surveys have been presented elsewhere, where it was shown that oceanographic features indicated by salinity and density were also reflected by temperature distribution (Dawe and Beck, 1985). Thus, catches of juveniles will be shown here mainly in relation to temperature distribution.

For 1981 and 1982 surveys, catches are shown in relation to sectional plots of temperature for some transects. For the more recent surveys, catches are shown in relation to horizontal temperature distribution at the sea surface. For all transects the location of the Gulf Stream core, as indicated by the 15 °C isotherm at 200 m, is also shown. Satellite-derived ocanographic analysis maps, which are produced twice weekly by the U.S. National Earth Satellite Service (NESS), and sea surface temperature charts, which are produced weekly by the Canadian Meteorological and Oceanographic Centre (METOC), were used to help identify the position of the Gulf Stream and other circulation features.

SURVEY RESULTS

Juvenile Distribution and Water Masses

1981

For transects A and B sampled during the 1981 survey (Fig. 1 A), catches at maximum depth of tows are shown in relation to sectional plots of temperature in Fig. 2 and 3. The 35.00 ‰ isohaline is overlain to indicate the approximate position of the Shelf Water-Slope Water frontal zone, whereas the 36.00 ‰ isohaline outlines the distribution of Gulf Stream water.

For transect A (56°W, Fig. 2a) station positions were assigned relative to the 100 m sets only, since in some cases set positions for greater depths deviated from the station locations shown due to navigation problems. Juveniles were caught on Transect A in Slope Water and northern Gulf Stream water. The largest catch (3 462 individuals) was from a 100 m set at Station 12, very close to the Gulf Stream core of maximum surface velocity, where salinity exceeded 36.00 ‰ in the upper 200 m. Juveniles were caught from three of the four sets at that station but were not caught from any of the four sets at Station 13, located well south of the Gulf Stream core. With the exception of the very large catch at Station 12, juveniles seemed to be most abundant at stations 7-9, in the vicinity of the Gulf Stream frontal zone, where 6 of the 7 non-zero catches exceeded 100 specimens (Fig. 2a). Those catches were probably associated with a northward meander of the Gulf Stream, as indicated by the high surface temperature (18 °C) and deepening of the 36.00 ‰ isohaline in that area. That meander was also seen in the relevant NESS maps and METOC charts.

Juveniles were caught from all 8 sets of the EMT-80 at stations 10 and 11, within northern Gulf Stream water, and at all 4 sets at station 4, within Slope Water. Lack of catch at stations 1-3 near the Shelf Water-Slope Water boundary and at station 5 and 6 within Slope Water were very likely due to the use of the much smaller EMT-400 at those stations (Fig. 2a).

On transect B in 1981 2 546 juveniles were caught from a set to 100 m at Station 16, located in Gulf Stream water north of the Core (Fig. 2b). The catches from four sets at Stations 15 and 16, ranging 26-2 546 juveniles, were located very close to the Gulf Stream frontal zone, as transect B apparently intersected the periphery of a northward meander of the Stream in the vicinity of those stations. There were no catches at Station 17 south of the Gulf Stream core and only three juveniles were caught from two sets at Station 14, located within Slope Water.

All three stations on transect C were within Gulf Stream water (Fig. 1 A). Catches were very small, ranging from 1 to 3 juveniles, for sets at 100 m and 300 m at each of the two northern-most stations. There were no catches at the most southern station, located well south of the core of the stream.

1982

Only 10 stations were sampled using the EMT-80 during 1982, along a transect located at 56 °W (Fig. 1 B). All stations were located north of the Gulf Steam (Fig. 3). They extended from Shelf Water in the north (stations 1-4), through Slope Water (stations 5-9), to the periphery of a warm-core eddy. Catches occurred within Shelf Water and in association with the eddy periphery (station 10), but were greatest within Slope Water near the eddy periphery, ranging from 32 to 438 individuals at stations 7-9.

1984

For the 1984 survey station locations and catches are shown in relation to temperature distribution at sea surface (Fig. 4). No juveniles were caught during February 24-March 4 as the vessel sampled transects while proceeding westward (Fig. 4 aA). While returning eastward during March 4-9 (Fig. 4 aB), only

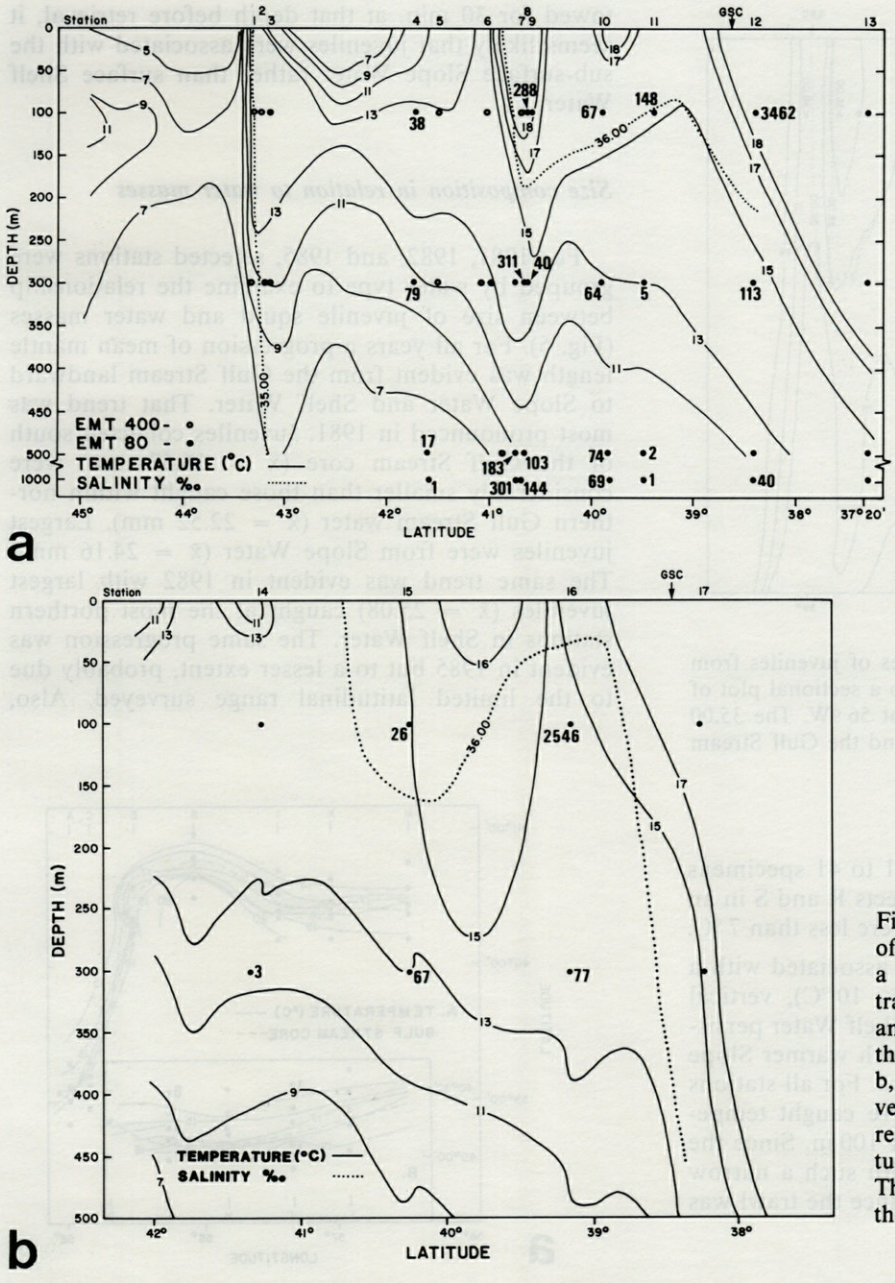


Fig. 2. — a, Location of sets and catches of juveniles during 1981 in relation to a sectional plot of temperature for transect A, located at 56 °W. The 35.00 and 36.00 ‰ isohalines are overlain and the Gulf Stream Core is labelled GSC. b, Location of sets and catches of juveniles from the EMT-80 during 1981 in relation to a sectional plot of temperature for transect B, located at 53 °W. The 36.00 ‰ isohaline is overlain and the Gulf Stream Core is labelled GSC.

8 juveniles were collected. A single specimen was caught south of the Gulf Stream core on transect J. The other 7 specimens were collected at two stations in Slope Water, where the temperature was 13 °C at the surface.

1985

During February 22-March 10, 1985 a section of the Gulf Stream System was surveyed between 55 °W and 60 ° (Fig. 4b). Only two juveniles were caught (transects C, D) within Slope Water, during February 22-March 1 between 55 °W and 57°08'W. However, later in the survey and to the west catches increased in magnitude and frequency. Also to the west, Shelf Water with temperature of less than 10 °C was prominent at surface (Fig. 4b). In that area, surface Shelf Water was in close proximity to the Gulf Stream, to the extent that the Slope Water at surface was generally characterized by a narrow band. Catches of 1-4 juveniles occurred at each of six stations within or very close to the Gulf Stream core on transects I, O, P, Q, and S (Fig. 4b) Some larger catches occurred in Slope Water, ranging from 1 to 19 juveniles on transects P, Q, and S. However, largest and most frequent catches occurred at stations where Shelf Water of less than 10 °C was present at surface. Catches associated with

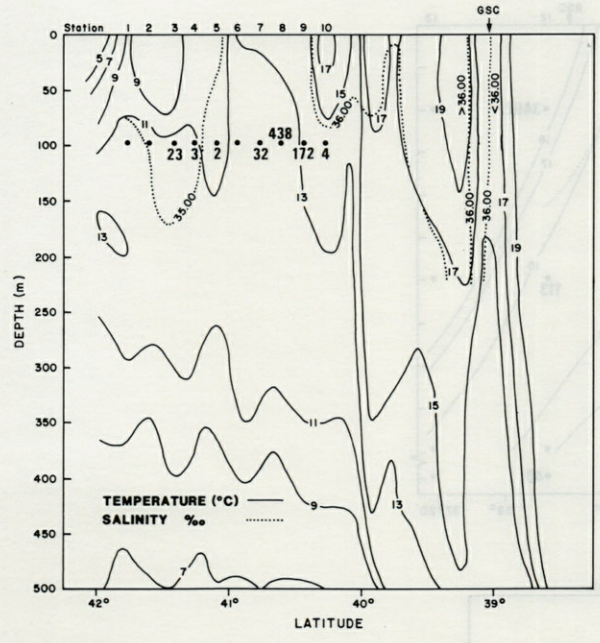


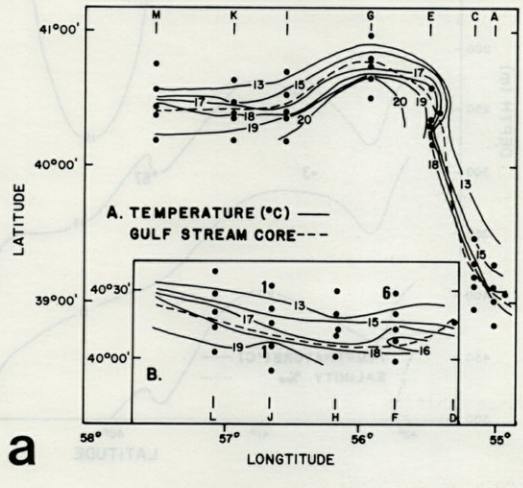
Fig. 3. — Location of sets and catches of juveniles from the EMT-80 during 1982 in relation to a sectional plot of temperature for the transect located at 56 °W. The 35.00 and 36.00 ‰ isohalines are overlain and the Gulf Stream Core is labelled GSC.

surface Shelf Water ranged from 1 to 41 specimens and were especially large on transects R and S in an area where surface temperatures were less than 7 °C.

Although greatest catches were associated with a region of surface Shelf Water (< 10 °C), vertical temperature profiles showed that Shelf Water persisted only to depths of 10-60 m. Much warmer Slope Water was evident at greater depths. For all stations where more than 5 specimens were caught temperatures ranged only 11.3-14.9 °C at 100 m. Since the largest catches were associated with such a narrow temperature range at 100 m, and since the trawl was towed for 30 min. at that depth before retrieval, it seems likely that juveniles were associated with the sub-surface Slope Water rather than surface Shelf Water.

Size composition in relation to water masses

For 1981, 1982, and 1985, selected stations were grouped by water type to examine the relationship between size of juvenile squid and water masses (Fig. 5). For all years a progression of mean mantle length was evident from the Gulf Stream landward to Slope Water and Shelf Water. That trend was most pronounced in 1981. Juveniles collected south of the Gulf Stream core ($\bar{x}$ = 16.57 mm) were considerably smaller than those caught within northern Gulf Stream water ($\bar{x}$ = 22.52 mm). Largest juveniles were from Slope Water ($\bar{x}$ = 24.16 mm). The same trend was evident in 1982 with largest juveniles ($\bar{x}$ = 25.08) caught at the most northern stations in Shelf Water. The same progression was evident in 1985 but to a lesser extent, probably due to the limited latitudinal range surveyed. Also,



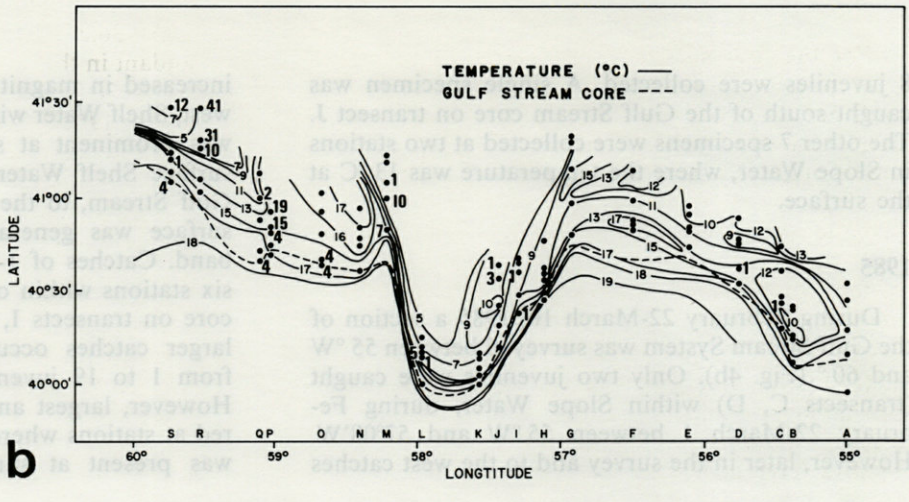


Fig. 4. — a, Location of stations on transects and catches of juveniles during 1984 in relation to surface temperature distribution as the vessel proceeded westward during February 24-March 4 (A) and as it returned eastward during March 4-9 (B, inset). b, Location of stations on transects and catches of juveniles during February 22-March 10, 1985 in relation to surface temperature distribution.

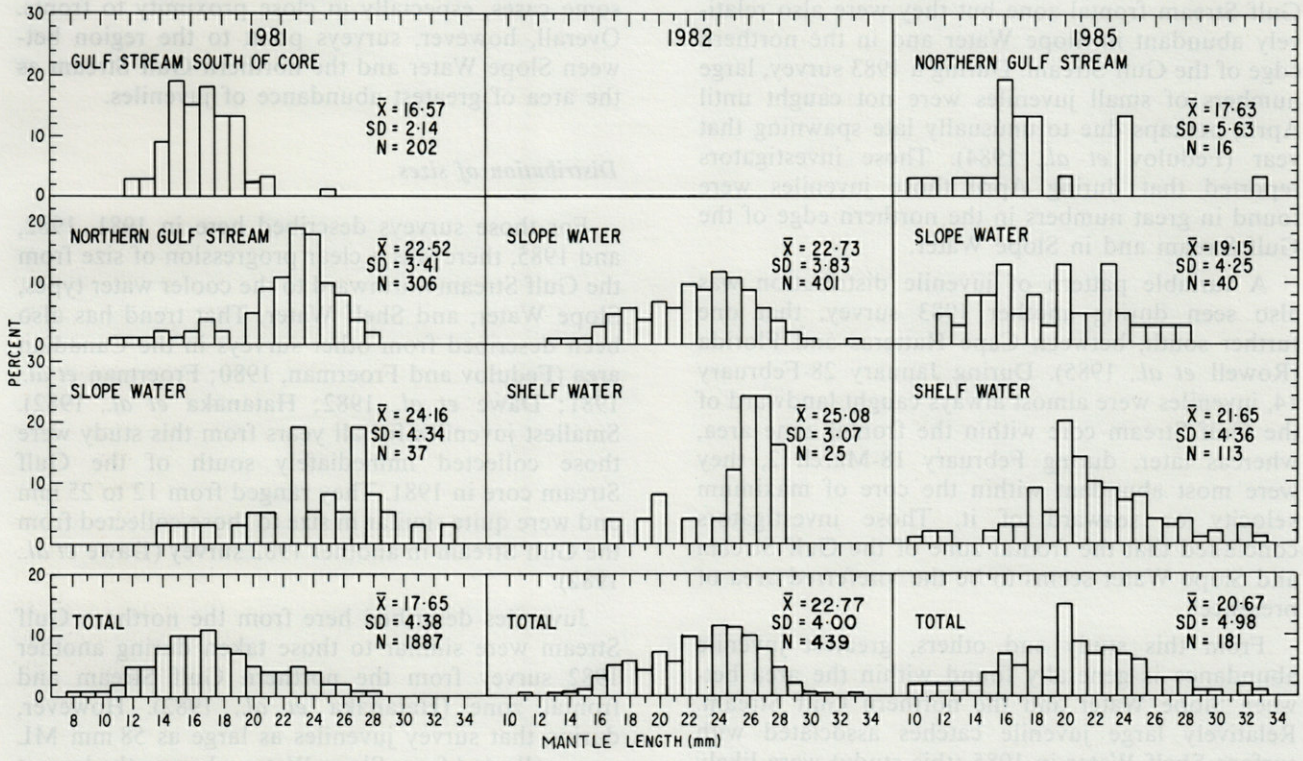


Fig. 5. — Length frequency distributions of juveniles for select stations by water mass and for total juveniles for each year; 1981 (A). 1982 (B) and 1985 (C).

juveniles associated with surface Shelf Water ($\bar{x}$ = 21.65 mm) were likely caught within sub-surface Slope Water. Mantle length ranges for total of juveniles were similar among years, overall ranging from 7 to 42 mm but for all years most juveniles were within the 8-33 mm length range (Fig. 5).

DISCUSSION

Juvenile distribution and water masses

For the four survey years overall, juvenile *Illex* were present in most water masses including the Gulf Stream, both north and south of the core of maximum velocity, Slope Water, Shelf Water, and in the periphery of a warm core eddy. Although the distribution pattern differed among years, greatest juvenile abundance was generally within northern Gulf Stream water, including northward meanders of the stream, or Slope Water immediately north of the stream. These water masses, collectively, include the relatively narrow Gulf Stream frontal zone.

Results of other surveys also describe somewhat conflicting distribution patterns of juveniles with certain similarities to those described here. Those surveys have generally indicated that juveniles are found in most water masses, including warm core eddies, Shelf Water, Slope Water, and the Gulf Stream (Dawe *et al.*, 1982; Fedulov *et al.*, 1984), but Hatanaka *et al.* (1982) reported that during January 16-March 5, 1982 juveniles were not found in the central Gulf Stream or the Sargasso Sea.

From the earliest such survey in Canadian waters during March 10-April 13, 1979 Fedulov and Froerman (1980) reported that juvenile *Illex* were most abundant in Slope Water and that the northern edge ot the Gulf Stream represents the seaward limit of their area of distribution. However, they noted that maximum abundance was associated with salinities of 35.80-36.25 ‰, indicating that juveniles were also abundant in the northern Gulf Stream where salinity exceeds 36.00 ‰. From a survey during March 3-May 4, 1981 Froerman *et al.* (1981) concluded that greatest juvenile abundance was within Slope Water in a zone 50-70 miles wide, close to the northern edge of the Gulf Stream. Within the same general area during a February 4-April 30, 1982 survey, abundance was also greatest within Slope Water, as well as the periphery of warm core eddies (Dawe *et al.*, 1982). Warm core eddies are derived from northward meanders of the Gulf Stream and peripheral areas of eddies are quite similar to the Gulf Stream frontal zone. From another 1982 survey (January 16-March 5), Hatanaka *et al.*, 1982 concluded that *Illex* juveniles were most abundant at the

Gulf Stream frontal zone but they were also relatively abundant in Slope Water and in the northern edge of the Gulf Stream. During a 1983 survey, large numbers of small juveniles were not caught until April, perhaps due to unusually late spawning that year (Fedulov *et al.*, 1984). Those investigators reported that during April those juveniles were found in great numbers in the northern edge of the Gulf Stream and in Slope Water.

A variable pattern of juvenile distribution was also seen during another 1983 survey, that one further south, between Cape Hatteras and Florida (Rowell *et al.*, 1985). During January 28-February 14, juveniles were almost always caught landward of the Gulf Stream core within the frontal zone area, whereas later, during February 18-March 2, they were most abundant within the core of maximum velocity or seaward of it. Those investigators concluded that the frontal zone of the Gulf Stream and Slope Water seems to be the 'preferred area of presence'.

From this study and others, greatest juvenile abundance is generally found within the area between Slope Water and the northern Gulf Stream. Relatively large juvenile catches associated with surface Shelf Water in 1985 (this study) were likely derived from sub-surface Slope Water, as also found by other investigators (Fedulov *et al.*, 1984; Hatanaka *et al.*, 1982; Arkhipkin *et al.*, 1983). However, later in spring (May-June), larger juveniles concentrate in Shelf Water and at the Shelf Water-Slope Water frontal zone (Fedulov *et al.*, 1984).

Although juvenile catches are generally few and small within and seaward of the Gulf Stream core, unusually large catches have occasionally occurred south of the core of maximum surface velocity. From this study the largest catch for all four years occurred immediately south of the core. Similarly during a 1979 survey, the greatest catch occurred south of the core (Fedulov and Froerman, 1980). Other investigators have also shown that very few but relatively large catches occurred south of the Gulf Stream core (Froerman *et al.*, 1981; Dawe *et al.*, 1982). All studies indicate that only rarely are juvenile specimens collected from the southern Gulf Stream or Sargasso Sea.

Accurate description of juvenile squid distribution relative to oceanography is difficult because of the dynamic nature of the Gulf Stream System. Oceanographic features such as current speed and direction, eddies, meanders and fronts are highly variable in time and space, making it frequently difficult to determine exactly were catches occurred. Uncertainty as to the exact depth of capture, using open trawls, adds to the problem. Discrete depth sampling, using opening and closing trawls, can address the problem of depth distribution (Hatanaka *et al.*, 1982), but it is recognized that the location of catches in relation to water masses is uncertain in some cases, especially in close proximity to fronts. Overall, however, surveys point to the region between Slope Water and the northern Gulf Stream as the area of greatest abundance of juveniles.

Distribution of sizes

For those surveys described here in 1981, 1982, and 1985, there was a clear progression of size from the Gulf Stream northward to the cooler water types, Slope Water, and Shelf Water. That trend has also been described from other surveys in the Canadian area (Fedulov and Froerman, 1980; Froerman *et al.*, 1981; Dawe *et al.*, 1982; Hatanaka *et al.*, 1982). Smallest juveniles for all years from this study were those collected immediately south of the Gulf Stream core in 1981. They ranged from 12 to 25 mm and were quite similar in size to those collected from the Gulf Stream in another 1982 survey (Dawe *et al.*, 1982).

Juveniles described here from the northern Gulf Stream were similar to those taken during another 1982 survey from the northern Gulf Stream and frontal zone (Hatanaka *et al.*, 1982). However, during that survey juveniles as large as 58 mm ML were collected from Slope Water whereas the largest juvenile described here from Slope Water and Shelf Water was 42 mm ML. Juveniles larger than those described here have commonly been collected during other surveys as well (Fedulov and Froerman, 1980; Froerman *et al.*, 1981; Dawe *et al.*, 1982; Fedulov *et al.*, 1984). That size disparity is likely related to more intensive sampling of cooler water types and sampling at depths greater than 100 m during other surveys. Arkhipkin *et al.* (1983) showed from a diel Shelf Water-Slope Water station that smallest juveniles were caught beneath Shelf Water at a depth of about 30-75 m, whereas larger juveniles were collected at greater depths.

The capture of smallest juveniles within the Gulf Stream and progression of sizes toward cooler water types is consistent with the observed pattern of larval distribution. Hatanaka *et al.* (1985) found that larvae were most abundant in the northern edge of the Gulf Stream and Dawe and Beck (1985) reported that larvae were caught only within northern Gulf Stream water. Thus, the distribution of juveniles, as well as larvae, supports the proposed importance of the Gulf Stream in the northeastward dispersal of young stages of *Illex illecebrosus* (Trites, 1983).

Surveys described here were carried out within a restricted time period, during February and March. However, the results of other surveys indicate that juveniles ranging approximately 1-4 cm in mantle length are generally found near the Gulf Stream frontal zone during January to April (Hatanaka *et al.*, 1982; Froerman *et al.*, 1980). This suggests that although most intense spawning may occur during January (Hatanaka *et al.*, 1982), spawning and

passive downstream dispersal of young stages occurs to some extent over a prolonged time period.

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DISTRIBUTION OF LARVAL AND JUVENILE *ILLEX* (MOLLUSCA : CEPHALOPODA) IN THE BLAKE PLATEAU REGION (NORTHWEST ATLANTIC)

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CEPHALOPODA
SQUID
ILLEX
LARVAL
JUVENILE
DISTRIBUTION
OCEANOGRAPHY

ABSTRACT. — Knowledge of the distribution of larval and juvenile short-finned squid *Illex illecebrosus* has increased rapidly since 1979 when the first large catches of these early life stages were taken along the northern edge of the Gulf Stream and in the adjacent Slope Waters between approximately 66° and 44°W. The role of the Gulf Stream system in the entrainment, transport, and dispersion of larval and juvenile *Illex* is discussed and recent evidence is presented for the existence of a major spawning area shoreward of the Gulf Stream Frontal Zone over the Blake Plateau. Larval and juvenile sizes and distribution patterns are analyzed in relation to macro- and meso-scale oceanographic features of the Gulf Stream Frontal Zone. Information is provided on meso-scale distributional differences between larvae and juveniles of *Illex* and also between various types of Rhynchoteuthion larvae.

CEPHALOPODA
ENCORNET
ILLEX
LARVE
JUVÉNILE
DISTRIBUTION
OCÉANOGRAPHIE

RÉSUMÉ. — Les connaissances sur la répartition de l'Encornet rouge, *Illex illecebrosus* aux stades larvaire et juvénile ont augmenté rapidement depuis 1979, c'est-à-dire depuis les premières récoltes importantes à des stades de vie précoces. Les prises ont eu lieu le long de la bordure nord du Gulf Stream et dans les eaux adjacentes du talus continental, entre 66° et 44 °W approximativement. Le rôle du Gulf Stream dans l'entraînement, le transport et la dispersion des Encornets larvaires et juvéniles est montré et des données récentes indiquant l'existence d'une zone de ponte importante du côté continental de la Zone frontale du Gulf Stream, sur le plateau de Blake, sont présentées. Les caractéristiques relatives à la taille et à la répartition des Encornets larvaires et juvéniles en fonction des caractéristiques océanographiques à grande et à moyenne échelle de la Zone frontale du Gulf Stream sont analysées. Enfin des informations indiquant des différences de répartition larvaire et juvénile entre les Encornets du genre *Illex* et d'autres larves de type Rhynchoteuthion sont présentées.

INTRODUCTION

The short-finned squid *Illex illecebrosus* is highly important to the fisheries of the northwest Atlantic both as a harvestable resource and as a major predator and prey species. Because of its relatively short life-cycle, estimated at 1-1.5 years (Squires, 1967), conventional methods of biomass projection have been impossible, as has the application of conventional fisheries management practise. Recognition of the need to develop a biological basis for management of the resource has Ied, since 1979, to major research efforts being directed at determining the essentially unknown early life history and distribution of the species. Prior to this, knowledge of the biology and distribution of *I. Illecebrosus* was largely restricted to the adult stage, from May through December, during the residency period on the shelf (Verrill, 1882; Mercer, 1969a, 1969b, 1973; Squires, 1967; Lange, 1980).

O'Dor (1983) has summarized the general biology and ecology of *I. illecebrosus,* while Rowell *et al.* (1984) and Trites and Rowell (1985) have reviewed the historical development of knowledge on the early life stages as well as recent research directed at determining the influence of oceanographic processes on their distribution. The discovery, during the winter of 1979 (Amaratunga *et al.,* 1980; Fedulov and Froerman, 1980), of large concentrations of small juveniles (approximately 15-80 mm Dorsal Mantle Length), as well as some larvae, between the Gulf Stream and the edge of the Scotian Shelf provided the first strong evidence in support of the suggestion of Roper & Lu (1979) that the Gulf Stream might play a role in the life-cycle of *I. illecebrosus.* Surveys in subsequent years provided additional distributional information and indicated that spawing probably occured upstream in the area south of, or immediately to the north of Cape Hatteras. Trites (1983) developed a larval dispersion model that would predict an idealized distribution of larval and early juvenile stages over a 1-2 month period after spawning. The model assumed bottom spawning, but appears equally valid for the pelagic spawning that we now consider more likely. Under this model, egg masses, larvae, and possibly juveniles are entrained by the Gulf Stream and transported at variable speed northeastward to areas seaward of the Continental Shelf along the northeastern U.S.A., the Scotian Shelf, and Grand Banks. During the course of this transport, the juveniles either passively, along with Warm Core Eddy formation, or actively leave the High Velocity Core of the Gulf Stream as it progresses northeastward and subsequently actively migrate shoreward to the Continental Shelf. Beginning in January 1983 a series of cruises was begun to examine the advection scenario as a mechanism for the transport of larvae and juveniles from assumed spawning areas over the Blake Plateau to the offshore area south of the Scotian Shelf and Grand Banks.

This paper provides a synoptic description of the distribution of Rhynchoteuthion type C' larvae and juveniles (Roper and Lu, 1979), believed to be *Illex illecebrosus,* in relation to the Gulf Stream and adjacent Slope Waters. Data are presented suggesting close proximity of a major spawning area to the region of Cape Canaveral, Florida. Information is also provided on the distribution of Rhynchoteuthion larval types A' and B' (Roper and Lu, 1979), believed to be *Ommastrephes bartrami,* and *Ornithoteuthis antillarum* and/or *Ommastrephes pteropus* respectively.

MATERIALS AND METHODS

Since March 1979 there has, in most years, been extensive sampling of the Gulf Stream and Slope Waters off the Scotian Shelf and Grand Banks between roughly 66° an 44 °W longitude.

There has been much less extensive sampling specifically directed at larval and juvenile *Illex* west of 66 °W. Dawe and Beck (1985) reviewed the distribution of larval *Illex* catches, including those from this more westerly area, for the period up to 1982, while Hatanaka *et al.* (1982) presented distributional information for both larvae and juveniles as far west as 74 °W. This paper draws on all of the available sources, including Amaratunga *et al.* (1980); Amaratunga & Budden (1982); Dawe *et al.* (1982); Fedulov *et al.* (1984). Data are also extracted from Rowell *et al.* (1984); and Trites and Rowell (1985) which include surveys by : the Alfred Needler, 28 January — 2 March 1983; the CSS Hudson, 11-15 December, 1984; and the Alfred Needler, 7-22 January 1985, and subsequently referred to in this paper respectively as Needler 83, Hudson 84 and Needler 85.

OCEANOGRAPHIC FEATURES AND DISTRIBUTIONAL PATTERNS OF EARLY LIFE STAGES

General Oceanographic Features

A dominant oceanographic feature in the North Atlantic is the Gulf Stream System, an intense western ocean boundary current present from the Straits of Florida to an area southeast of the Grand Banks (Fig. 1). Off the east coast of Florida the shoreward edge of the Gulf Stream (Slope/Gulf Stream Front), on average, can be delineated ap-

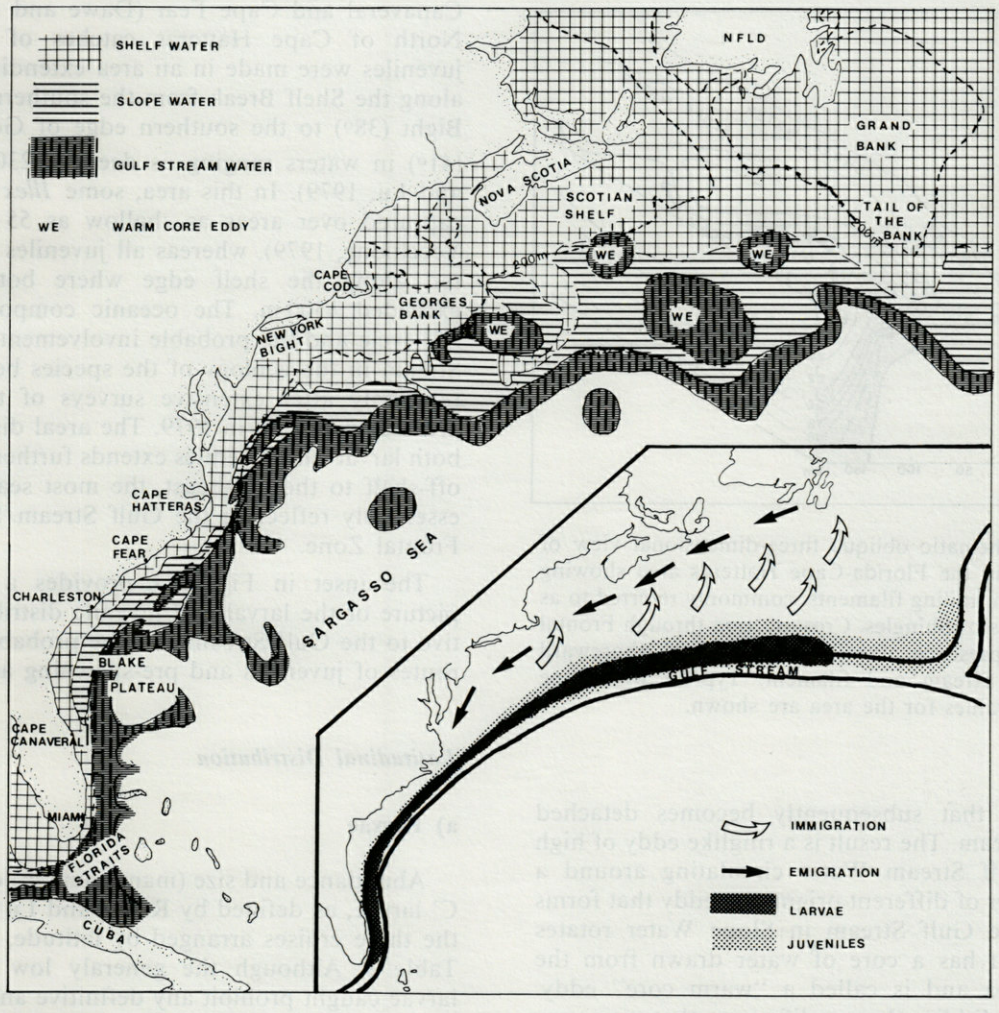


Fig. 1. — Map showing the Gulf Stream system off eastern North America, and major surface water-mass features for 4-5 January, 1985, (Extracted from United States National Weather Service NOAA/NESS satellite-derived oceanographic analysis maps). A schematic illustration of the suggested general life-cycle of *Illex illecebrosus* in relation to the Gulf Stream is shown in the inset.

proximately by the 200 m isobath. Further north, off South Carolina, the Stream tends to move further offshore, returning to about the 200 m isobath a short distance south of Cape Hatteras. Northeast of Cape Hatteras the Stream moves off the continental slope. The position of the Stream fluctuates.

Analysis of sea surface temperature maps, reveals that the standard deviation in the position of the Slope/Gulf Stream Front increases from a minimum of about 5 km off the east coast of Florida to a maximum of about 35 km off Cape Fear and then decreases to about 10 km off Cape Hatteras (Bane and Brooks, 1979). Downstream from Cape Hatteras, the amplitude of the meanders again increases rapidly, with the position of the northern edge of the Stream south of Nova Scotia varying by as much as 400 km.

In the Straits of Florida-Cape Hatteras area, the shoreward boundary of the Stream displays, in addition to meanders, a folded-wave pattern of Frontal Eddies (Fig. 2). Frontal Eddies of this type appear as tongue-like extrusions (filaments) of Gulf Stream Water, oriented upstream, nearly parallel to the Stream (and bathymetry). These Frontal Eddies tend to develop near the shoreward crest of a meander and usualy grow rapidly, developing a narrow, very elongated filament or "shingle" appearance (Lee *et al.*, 1981; Legeckis, 1979; Bane *et al.*, 1981). Frontal Eddies are short-lived phenomena, forming in only a few days and possibly dissipating on a comparable time scale. Satellite sea surface thermal imagery suggests that the total cycle takes place in 1 to 3 weeks, with wavelengths ranging from 90 to 260 km, and moving at speeds from 20 to 60 km/d in the general direction of the Gulf Stream (Legeckis, 1979).

Downstream from Cape Hatteras, the large meanders which develop in the Stream may form a

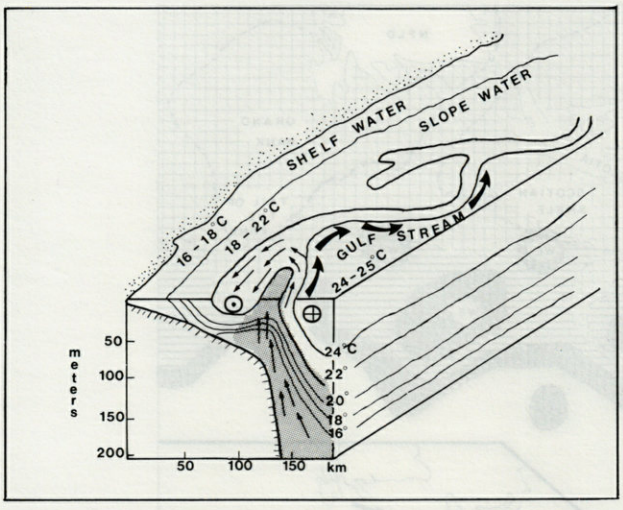


Fig. 2. — Schematic oblique three-dimensional view of Gulf Stream in the Florida-Cape Hatteras area showing meanders with trailing filaments, commonly referred to as Frontal Eddies or Shingles. Cross-section through Frontal Eddy shows presence of cold dome between shoreward edge of the Stream and filament. Typical wintertime temperature values for the area are shown.

major loop that subsequently becomes detached from the stream. The result is a ringlike eddy of high velocity Gulf Stream Water circulating around a core of water of different origin. An eddy that forms north of the Gulf Stream in Slope Water rotates clockwise; it has a core of water drawn from the Sargasso Sea and is called a "warm core" eddy. Warm Core Eddies, have a life-span that may vary from a few weeks to a year or more, and range in diameter from about 100 km up to 300 km.

The possible importance, as a transport-dispersion mechanism, of both the Gulf Stream, from Cape Hatteras northeastward, and the associated Warm Core Eddies have been examined by Trites (1983) in determining the distribution of larval/juvenile *Illex*. This paper will focus primarily on the distribution of early life stages of *Illex* in the area extending from Cape Hatteras southwestward to the Straits of Florida where the Gulf Stream and associated frontal eddies may play a key role.

General Distributional Patterns

General distributional knowledge of the early life stages of *Illex illecebrosus* has increased dramatically in recent years. The distributional information available prior to 1979 was all from areas either on the Continental Shelf or immediately along the Shelf Break suggesting an essentially neritic life-cycle. South of Cape Hatteras catches of larvae and juveniles were limited to an area along the 200 m isobath over the Blake Plateau between roughly Cape Canaveral and Cape Fear (Dawe and Beck, 1985). North of Cape Hatteras catches of larvae and juveniles were made in an area extending generally along the Shelf Break from the southern New York Bight (38°) to the southern edge of Georges Bank (41°) in waters ranging as deep as 2300 m (Roper and Lu, 1979). In this area, some *Illex* larvae were captured over areas as shallow as 55 m (see also Vecchione, 1979), whereas all juveniles were captured along the shelf edge where bottom depths exceeded 1500 m. The oceanic component of the life-cycle and the probable involvement of the Gulf Stream in the ecology of the species became apparent only after extensive surveys of the off-shelf areas commenced in 1979. The areal distribution of both larvae and juveniles extends further and further off-shelf to the northeast, the most seaward extent essentially reflecting the Gulf Stream/Slope Water Frontal Zone.

The inset in Figure 1 provides a generalized picture of the larval and juvenile distributions relative to the Gulf Stream and the probable migration routes of juveniles and pre-spawning adults.

Latitudinal Distribution

a) Larvae

Abundance and size (mantle length) data for type C' larvae, as defined by Roper and Lu (1979), from the three cruises arranged by latitude, are given in Table I. Although the generaly low numbers of larvae caught prohibit any definitive analysis, qualitatively, larvae are generally less abundant or are absent in the more northeasterly stations (Cape Hatteras area), as compared to the central area (off Charleston) with maximum catches taken in the Cape Canaveral area in the Needler 85 survey (Transect IV). Catch rates (Table IIA) are also low in the northeast and high along Transect IV. There is no clear geographical variation in size distribution. For the Hudson 84 and Needler 85 data there is some evidence of an increase in the median larval mantle lenght (ML) as well as an increase in minimum mantle lengths from southwest to northeast. In the more limited Needler 83 data there is a weak suggestion of the reverse during Leg I of the cruise, whereas Leg II data show smaller larvae to the south of those stations occupied in Leg I. These smaller lavae might represent a second brood. Sufficient numbers of larvae for lenght frequency histograms were taken only in Transects III, IV, and V on the Needler 85 survey and at a 22-h drogue-drift station located near Transect IV (Fig. 3). The most symmetrical distribution, with smallest size range, is found at and near Transect IV, with a strong mode at 1.8-1.9 mm ML. At Transects III and V the distribution is much flatter and has a wider range of sizes.

Table I. — Number and size (mantle length in mm) of Rhynchoteuthion type C' larvae in relation to latitude in February, 1983; December, 1984; and January, 1985.

	Needler (Feb. 83)				Hudson (Dec. 84)				Needler (Jan. 85)			
Latitude	Station No.	No. of Larvae	Mantle Range (mm)	Median Length (mm)	Station No.	No. of Larvae	Mantle Range (mm)	Median Length (mm)	Transect No.	No. of Larvae	Mantle Range (mm)	Median Length (mm)
Northeast												
36°00'N									I	2	3.2-6.4	4.8
35°00'					23	4	2.3-3.1	2.7				
34°41'					21	1	4.2	4.2				
34°30'									II	3	1.1-6.3	4.6
34°23'					20	1	2.4	2.4				
33°58'	44	1	2.5	2.5								
33°53'					18	1	1.8	1.8				
33°42'	53	2	3.5-4.8	4.1								
33°37'					16	1	2.2	2.2				
33°30'					15	2	2.0-2.7	2.4				
33°22'	65	3	3.5-3.9	3.7								
33°19'	66	1	3.5	3.5								
33°12'					13	1	1.8	1.8				
33°03'	69	1	3.0	3.0								
32°46'	82	1	3.0	3.0								
32°42'	83	2	3.0-4.9	3.9								
32°30'									III	39	0.8-6.0	1.8
32°17'	95	2	3.5-3.9	3.7								
32°12'					7	6	1.8-2.6	2.0				
32°11'	92	1	4.0	4.0								
32°11'					5	3	1.0- 2.0	1.8				
32°10'					6	3	1.0->1.7	1.6				
32°08'	88	1	3.3	3.3								
32°06'	106	1	>3.5	>3.5								
32°01'	107	3	2.8-6.4	3.2								
32°00'					4	7	2.2-3.8	2.6				
31°57'	108	3	3.0-5.4	5.0								
31°51'					3	23	1.6-4.2	2.2				
31°40'					2	2	>0.8-2.2	1.5				
31°23'	122	1	4.8	4.8								
31°13'	51*	1	1.0	1.0								
30°53'	131	1	>4.0	>4.0								
30°50'	129	1	>4.0	>4.0								
29°49'	8*	1	3.0	3.0								
28°50'	27*	2	1.0-2.0	1.5								
28°43'	33*	1	2.0	2.0								
28°30'									IV	123	1.0-3.4	2.0
25°25'									V	40	0.8-5.6	1.8
Southwest												

*Needler (Feb. 83 - LEG II)

b) Juveniles

The Needler 83 survey shows juvenile abundance to be highly variable latitudinally with no clear pattern, whereas the Needler 85 data reveal much higher numbers (and catch rates) in the southern three transects, being highest at Transect III (Tables IIA and III). We note that, if the high catch at station 45 of Transect III is deleted, catch rate increases progressively from Transects I through V. Interestingly, although the percentage of stations with catch shows little variation throughout the entire area, there appears to be a general progression as one proceeds southwestward. Although neither the 1983 nor the 1985 surveys provide any clear indication of a latitudinal progression in size of juveniles, the 1983 data do suggest the possiblity of increasing size towards the southwest when the median values for those stations having larger catches ($\geqslant 15$) are examined. In terms of length frequency patterns, the most peaked distribution occurred at Transect IV (Fig. 3).

Distribution Normal to the Gulf Stream Axis

The Needler 83 survey was designed to make many transverse sections approximately normal to the axis of the Gulf Stream (Fig. 4 A). The 15 °C isotherm, which is usually nested within a closely spaced set of isotherms at 200 m (Worthington, 1954; Webster, 1961; Fuglister, 1963) is frequently taken to indicate the geographic position of the High Velocity Core of the Gulf Stream. Stations where a catch of larvae and/or juveniles were made on Leg I of the Needler 83 survey (Fig. 4 C) were always located shoreward of the High Velocity Core of the

Table II. — Percentage of tows which collected *Illex*, catch rate, and ratio of larvae to juveniles from Needler 1985 survey; A) by complete transects; B) by segment of transect shoreward of the High Velocity Current (HVC), and; C) by segment of transects in the HVC.

A

Transect	Percentage of sets with catch: Larvae	Juveniles	Number/set: Larvae	Juveniles	Larval/Juvenile ratio
I	6	42	0.1	1.7	0.07
II	11	50	0.2	5.7	0.03
III	44	48	1.4	24.6 (8.4)*	0.06 (0.17)*
IV	94	62	7.4	10.5	0.70
V	76	59	2.4	17.3	0.14

* Catch rate and larval/juvenile ratio if the extremely high catch (415 juveniles) of station 45 is deleted.

B

Shoreward of the HVC

Transect	Percentage with catch: Larvae	Juvenile	Number/set: Larvae	Juvenile	Larval/Juvenile ratio
I	9	50	0.2	2.1	0.10
II	14	71	0.1	8.9	0.01
III	47	66	1.8	40.2 (12.5)*	0.04 (0.14)*
IV	100	40	10.0	16.2	0.62
V	86	50	2.7	20.7	0.13

* Catch rate and larval/juvenile ratio of the extremely high catch (415 juveniles) of station 45 is deleted.

C

HVC

Transect	Percentage with catch: Larval	Juvenile	Number/set: Larval	Juvenile	Larval/Juvenile ratio
I	0	25	0	0.8	–
II	0	66	0	6.0	–
III	60	20	0.8	1.3	0.62
IV	88	75	4.6	7.0	0.66
V	66	66	0.7	1.3	0.54

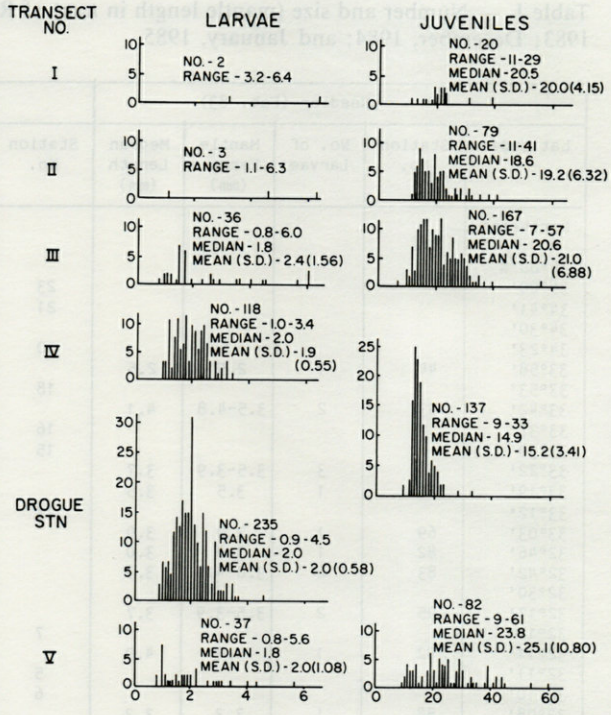


Fig. 3. — Length frequencies (mantle length in mm), range, and measures of central tendency, by transect, (see inset, Fig. 6) for larval and juvenile *Illex* for 7-22 January, 1985, cruise period.

Table III. — Number and size (mantle length in mm) of juvenile *Illex* in relation to latitude in February, 1983, and January, 1985.

	Needler (Feb. 83)								Needler (Jan. 85)			
	LEG I				LEG II							
Latitude	Station No.	No. of Juveniles	Mantle Range (mm)	Median Length (mm)	Station No.	No. of Juveniles	Mantle Range (mm)	Median Length (mm)	Transect No.	No. of Juveniles	Mantle Range (mm)	Median Length (mm)
Northeast												
37°39'N					120	2	23-30	26.5				
36°00'									I	20	11-29	20.5
34°38'	24	38	9-18	13.3								
34°30'									II	80	11-41	18.6
33°55'					84	126	14-86	32.3				
33°53'					86	3	24-43	31.0				
33°29'					70	20	16-30	23.5				
33°28'	65	7	13-27	16.0								
32°47'	82	5	21-53	24.0								
32°30'									III	~616	7-57	20.6
32°18'	95	4	19-23	19.5								
32°13'	94	15	7-30	13.0								
32°12'	92	34	7-30	10.3								
32°08'	88	4	9-13	12.5								
32°04'	107	1	29.0	29.0								
31°56'	108	1	24.0	24.0								
31°45'	114	5	44-56	47.0								
31°43'	112	5	14-24	22.0								
31°25'	122	4	11-27	22.5								
31°16'					55	4	19-76	44.5				
30°53'					45	7	20-68	43.0				
30°51'	129	5	15-37	20.0								
30°51'	131	29	13-72	31.0								
30°27'	137	359	9-66	30.9								
30°27'	139	1	36.0	36.0								
29°49'					8	4	20-51	35.0				
29°23'					16	1	22.0	22.0				
29°17'					20	64	19-92	31.5				
28°44'					31	2	32-37	34.5				
28°43'					33	13	18-35	22.3				
28°30'									IV	137	9-33	14.9
25°25'									V	~294	9-60	23.8
Southwest												

Table IV. — Percentage of stations including ommastrephids where A', B', C' Rhynchoteuthion types of larvae were caught either individually or in combination on a) Needler 1985 survey and b) Hudson 1984 survey.

		Percentage of stations with occurrence						
Transect	No of stations	A' only	B' only	C' only	A+B	A+C	B+C	A+B+C
a) Needler 85								
I	6	50	0	17	33	0	0	0
II	4	50	0	25	0	25	0	0
III	18	17	0	56	0	17	11	0
IV	28	0	0	32	0	14	36	18
V	15	7	0	20	7	27	27	13
All transects	71	13	0	33	4	17	23	10
b) Hudson 84								
All stations	16	13	6	38	6	13	31	0

Stream. On Leg II of the survey, however, catches were most frequently taken at or slightly seaward of the 15 °C isotherm, suggesting that they were principally in the High Velocity Core of the Stream. Larval catches on the Hudson 84 survey were most frequently taken at stations where the surface current was flowing at more than 1 ms^{-1} to the northeast (Fig. 5) and generally on the seaward side of the 15 °C isotherm at 200 m (Trites and Rowell, 1985). Larval and juvenile catch data for all stations of the Needler 85 survey are presented in Figure 6 with the estimated location of the High Velocity Core of the Gulf Stream. Although not clearly defined for all transects, the data suggest that highest catch levels tended to occur most frequently on the shoreward side of the High Velocity Core. To evaluate this further, catch data from each transect of the Needler 85 survey were lumped into two groups, one for all catches made shoreward of the Slope/Gulf

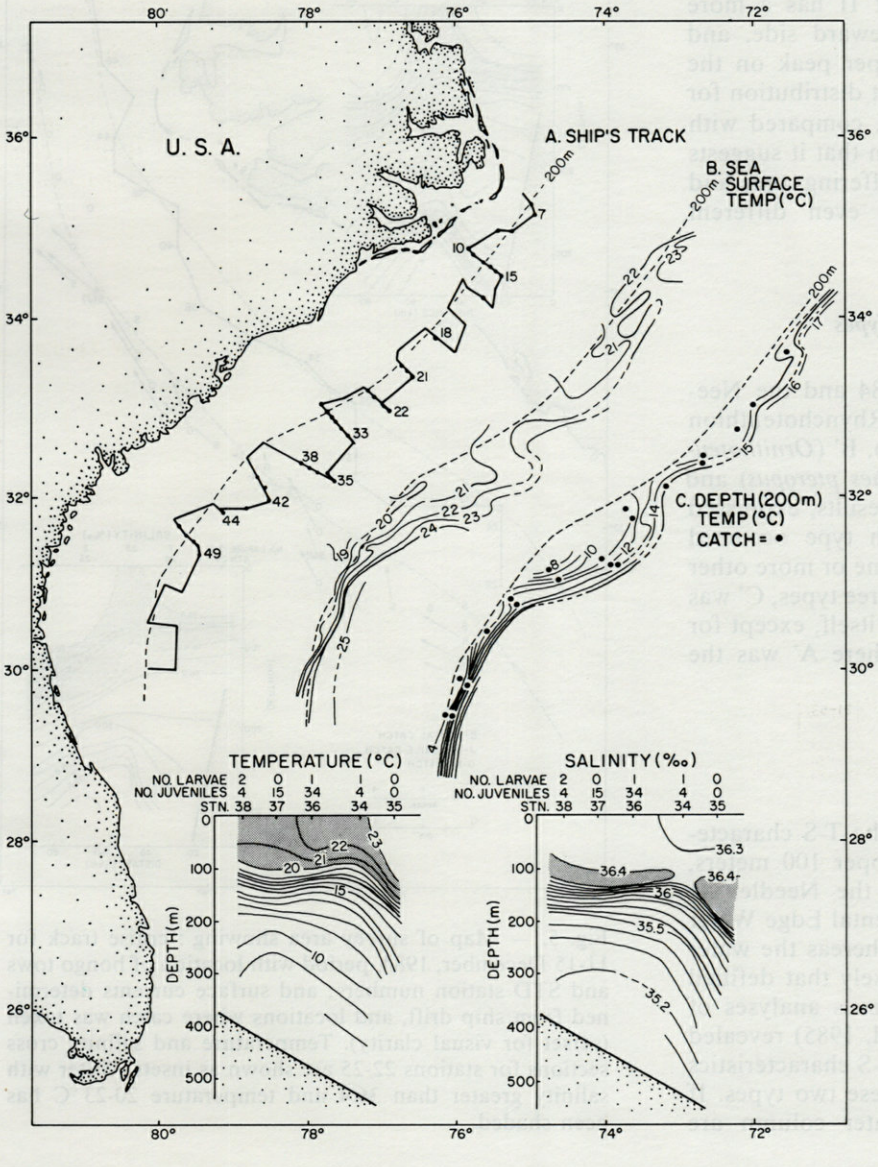


Fig. 4. — Map of survey area showing : (A) cruise track for 31 January-13 February, 1983 period with XBT's and station numbers of STD's; (B) sea surface temperature in °C; and (C) temperature at 200 m, including locations at which squid larvae and/or juveniles were caught. Figures B and C have been progressively offset for visual clarity. Temperature and salinity cross-sections for stations 34-38, off Charleston, are shown as insets. Water with salinity greater than 36.4 and temperature 20-23 °C has been shaded.

Stream Frontal Zone and the other for catches made in the High Velocity Core of the Gulf Stream (Table IIB and C). If larval catches in Transects I and II, which totalled only 5, are ignored, the percentage of stations having a catch range from moderate to high (47-100 %), with no clear pattern across the Frontal Zone. Abundance (catch/tow) of larvae is highest on Transect IV, with the shoreward catch rate twice that in the High Velocity Core. The pattern is similar for all transects. For juveniles, the percentage of stations with catch ranges from 40-71 in the shoreward side of the Frontal Zone, and from 20-75 in the High Velocity Core. Catch per tow is consistently higher in the shoreward side of the Frontal Zone by a factor ranging from 1.4 to 30.9.

Although the numbers of larvae caught in all but one transect are too small to determine size frequency distributional differences, it is clear in Transect IV that smaller larvae are concentrated shoreward of the High Velocity Core of the Gulf Stream (Fig. 7 A). For juveniles there is no clear overall pattern. However, Transect II has a more clumped distribution on the shoreward side, and Transect IV displays a much sharper peak on the shoreward side. The very broad, flat distribution for the shoreward side of Transect IV, compared with the other 4 transects is interesting in that it suggests a mixing of juveniles of widely differing ages and possibly developmental rates, or even different species of *Illex*.

Associated Rhynchoteuthion Larval Types

Samples taken on the Hudson 84 and the Needler 85 cruises were sorted for Rhynchoteuthion larval types A' (*Ommastrephes* spp.), B' (*Ornithoteuthis antillarum* and/or *Ommastrephes pteropus*) and C' (*Illex* spp.). A summary of the results, expressed as percent of stations where each type occurred separately of in combination with one or more other types, is given in Table IV. Of the three types, C' was the one most frequently present by itself, except for the two northernmost transects, where A' was the one most likely to occur by itself.

Catch in Relation to Water Masses

Rowell *et al.* (1984) found that the T-S characteristics of the water mass in the upper 100 meters, where catches were made during the Needler 83 survey, were very similar to Continental Edge Water as defined by Wennekens (1959) whereas the water further offshore matched more closely that defined as Yucatan Straits Water. Water mass analyses of Hudson 84 data (Trites and Rowell, 1985) revealed that catches were made where the T-S characteristics were generally midway between these two types. If only the upper 50 m of the water column are considered, then all Needler 83 catches were made at a temperature of approximately 22.0 ± 2.0 °C and a salinity of 36.3 ± 0.2, while the December, 1984, catches were made at a temperature of 24.0 ± 1.5 °C and salinity of 36.3 ± 0.1.

Catch in Relation to Upwelling

Physical oceanographic studies of the propagation of meanders, frontal eddies or filaments in the area between the Straits of Florida and Cape Hatteras indicate the presence of a cold dome underpinning the moving meanders (Bane *et al.*, 1981; Brooks and Bane, 1981, 1983; Lee *et al.*, 1981; Lee and Atkinson, 1983). Oceanographic sections off

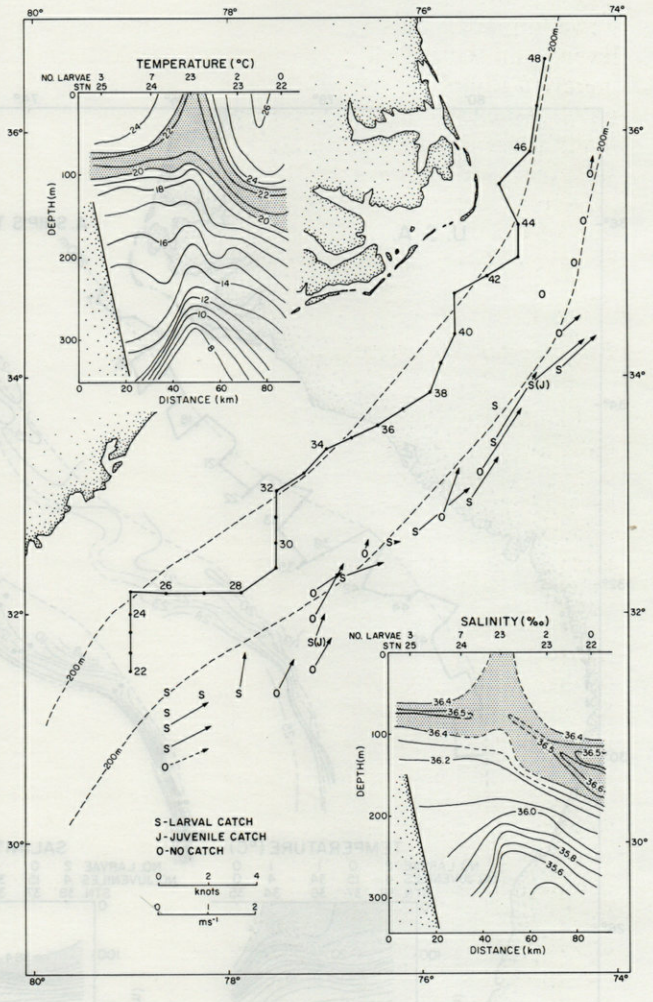


Fig. 5. — Map of survey area showing : cruise track for 11-15 December, 1984, period with location of bongo tows and STD station numbers; and surface currents determined from ship drift, and locations where catch was taken (offset for visual clarity). Temperature and salinity cross sections for stations 22-25 are shown as insets. Water with salinity greater than 36.4 and temperature 20-23 °C has been shaded.

the Charleston area, taken in the 1983, 1984, and 1985 cruises all show evidence of a cold dome on the shoreward side of the Gulf Stream (see insets, Figs. 4, 5 and 6). Although all three cruises showed relatively high larval/juvenile catches at most stations on the shoreward side of the High Velocity Core of the Gulf Stream in the Charleston area, highest concentrations occurred in or near the areas of upwelling. Lee and Atkinson (1983) concluded that the frontal eddies have considerable influence on primary production on the outer shelf. They concluded that upwelling in the cold dome, together with onshore flow in the cyclonic circulation, transports the deeper, nutrient-rich Gulf Stream waters into the euphotic zone for phytoplankton uptake. Rapid utilization of newly upwelled nutrients results in elongated patches of phytoplankton that propagate with the cold dome (Yoder *et al.*, 1981). The higher concentrations of larval *Illex* in and near upwelling areas may be associated with higher food levels and better survival rates or, alternatively, merely a sampling artifact. If larvae were preferentially associated with a particular water mass normally present only in a small deeper portion of the sampled water-column, then in upwelling areas this particular water mass occupies a much larger fraction of the column and hence a larger catch should be taken in the oblique tows (see insets, Fig. 5).

Evidence for Spawning in the Cape Canaveral Area

Examination of the larval size frequency spectra indicates that the smallest size range and nearly symmetric distribution occur in the Cape Canaveral area (Fig. 3). Examination of the larval/juvenile ratio for the 5 transects occupied between Cape Hatteras and Miami in 1985 (Table II A) indicates a value about an order of magnitude higher in Transect IV, off Cape Canaveral, than in any other transect. It is possible that a brood of larvae, hatched further south, may have been transported in the Gulf Stream and subsequently ejected out of the Stream by a Frontal Eddy in the Cape Canaveral area. However, the enormous alongstream diffusion produced by the shear in the Frontal Zone of the Gulf Stream, appears likely to diffuse larvae in a matter of a few days in the downstream direction on a scale comparable to the distance between transects, therefore, the uniqueness of Transect IV compared to III and V, supports the suggestion that a major local spawning area exists off Cape Canaveral.

Multiple Broods and Multiple Spawning Locations

The capture of recently hatched larvae on both the Hudson 84 and Needler 85 surveys indicates that spawning spans many weeks. Likewise, the presence of newly hatched larvae, less than 1 mm ML, and juveniles, greater than 60 mm ML, in the same area and time (e.g., Transect V, Fig. 3) indicates a relatively protracted spawning period. Although the extent to which spawning occurs as a series of "events", each concentrated over a short period of time, is unknown;, some of the size frequency diagrams (Figs. 3 and 7) do show more than one peak, suggesting a multiple brood composition. The possibility also exists, particularly in the more southern transects, that more than one species is involved.

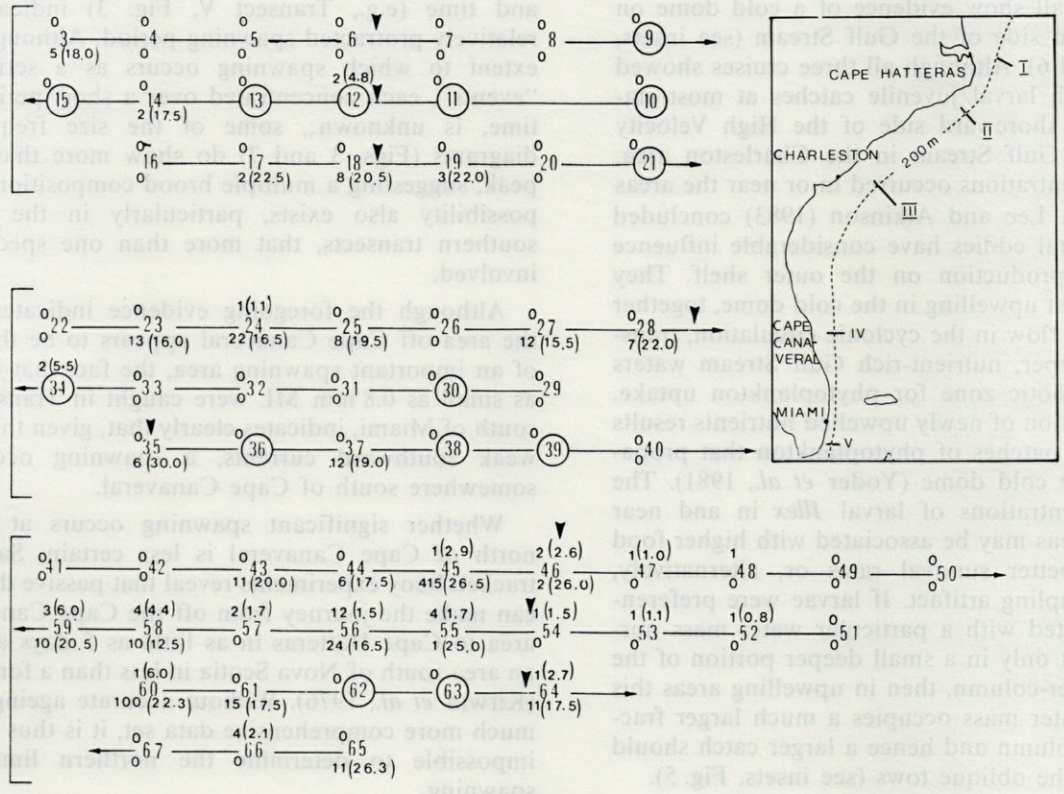
Although the foregoing evidence indicates that the area off Cape Canaveral appears to be the site of an important spawning area, the fact that larvae as small as 0.8 mm ML were caught in Transect V, south of Miami, indicates clearly that, given the very weak southward currents, a spawning occurred somewhere south of Cape Canaveral.

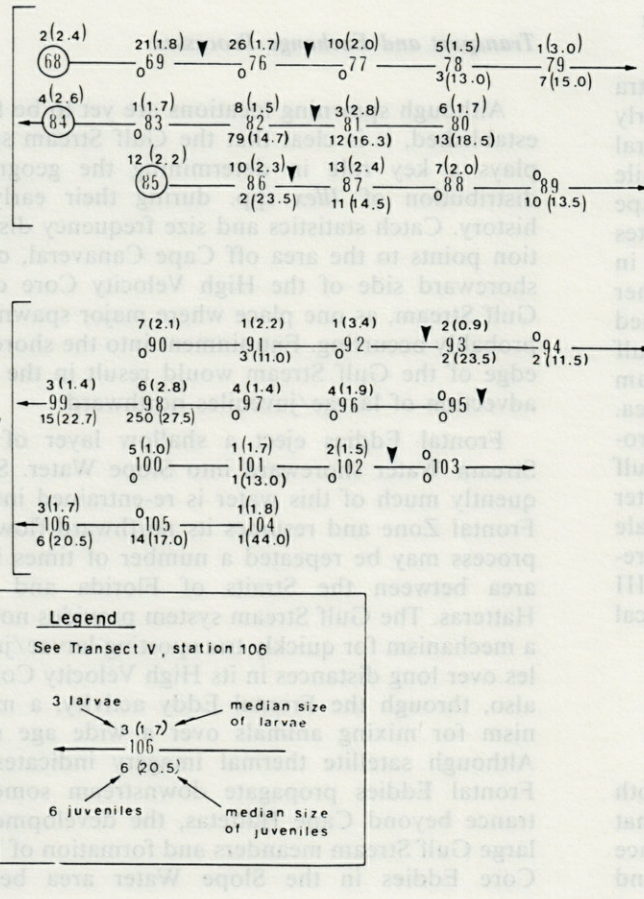
Whether significant spawning occurs at times north of Cape Canaveral is less certain. Satellite tracked buoy experiments reveal that passive drifters can make the journey from off the Cape Canaveral area to Cape Hatteras in as little as 5 days and to an area south of Nova Scotia in less than a fortnight (Kirwin *et al.*, 1976). Without accurate ageing or a much more comprehensive data set, it is thus as yet impossible to determine the northern limits of spawning.

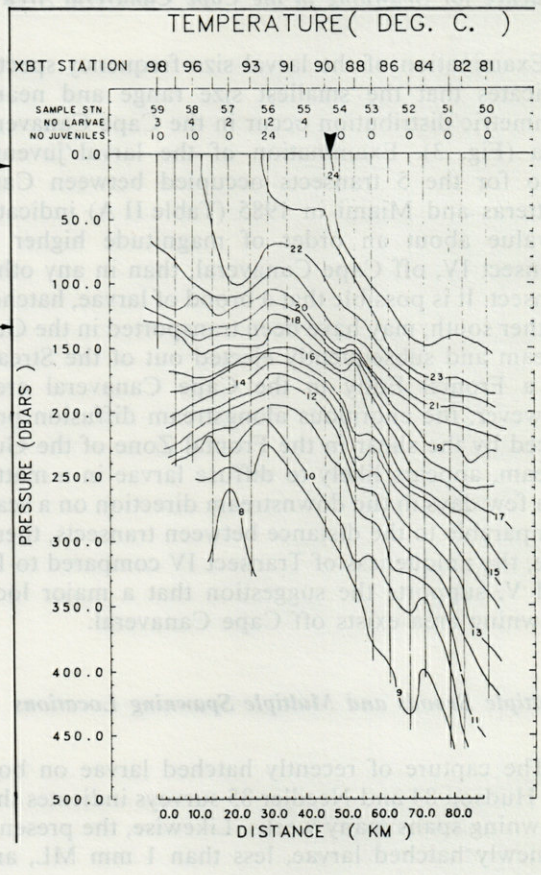
Transport and Exchange Processes

Although spawning locations are yet to be firmly established, it is cleat that the Gulf Stream system plays a key role in determining the geographic distribution of *Illex* spp. during their early life history. Catch statistics and size frequency distribution points to the area off Cape Canaveral, on the shoreward side of the High Velocity Core of the Gulf Stream, as one place where major spawning is probably occurring. Entrainment into the shoreward edge of the Gulf Stream would result in the rapid advection of larvae/juveniles northward.

Frontal Eddies eject a shallow layer of Gulf Stream Water shoreward into Slope Water. Subsequently much of this water is re-entrained into the Frontal Zone and resumes its northward flow. The process may be repeated a number of times in the area between the Straits of Florida and Cape Hatteras. The Gulf Stream system provides not only a mechanism for quickly transporting larvae/juveniles over long distances in its High Velocity Core but also, through the Frontal Eddy activity, a mechanism for mixing animals over a wide age range. Although satellite thermal imagery indicates that Frontal Eddies propagate downstream some distrance beyond Cape Hattetas, the development of large Gulf Stream meanders and formation of Warm Core Eddies in the Slope Water area between


I
II
III
CAPE HATTERAS
CHARLESTON
200m
CAPE CANAVERAL
MIAMI
I
II
III
IV
V


IV
V
Legend
See Transect V, station 106
3 larvae
3 (1.7)
106
6 (20.5)
6 juveniles
median size of larvae
median size of juveniles


TEMPERATURE (DEG. C.)
XBT STATION 98 96 93 91 90 88 86 84 82 81
SAMPLE STN 59 58 57 56 55 54 53 52 51 50
NO LARVAE 3 4 2 12 4 1 1 0 0
NO JUVENILES 10 10 0 24 1 0 0 0 0 0
PRESSURE (DBARS)
0.0
50.0
100.0
150.0
200.0
250.0
300.0
350.0
400.0
450.0
500.0
0.0 10.0 20.0 30.0 40.0 50.0 60.0 70.0 80.0
DISTANCE (KM)

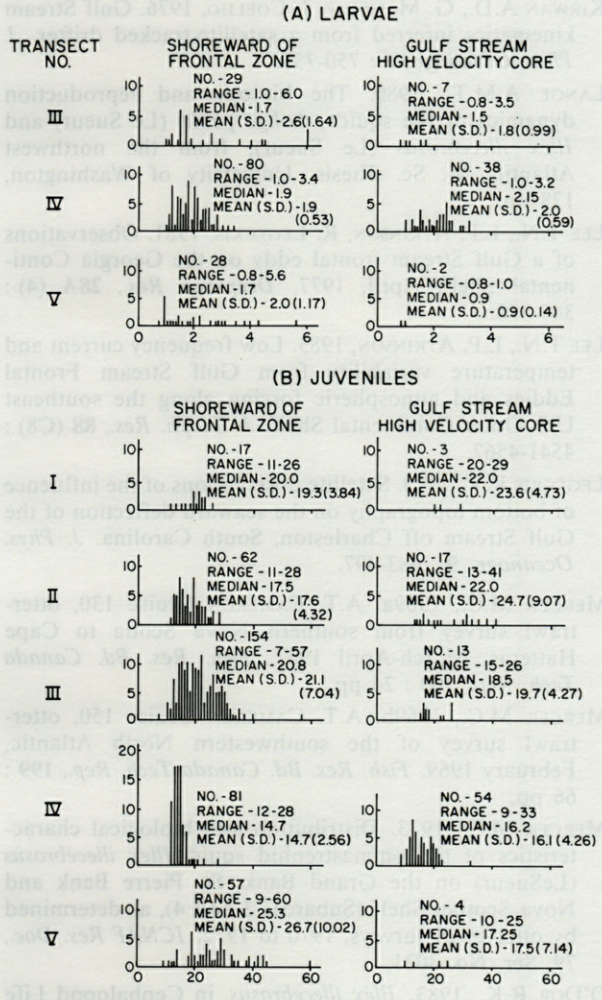


Fig. 7. — Length frequencies (mantle length in mm), range and measures of central tendency for larval captures (A) and juvenile captures (B) at grouped stations shoreward of Frontal Zone and in High Velocity Core of Gulf Stream, by transect (see inset, Fig. 6) for 7-22 January 1985 cruise period.

50-70 °W, provide a mechanism for transporting large volumes of larval/juvenile bearing water shoreward (Trites, 1983). Since Warm Core Eddy dimensions are typically 200-300 km in diameter and have a mean life span of 3-4 months (Trites and Drinkwater, 1985), they provide a mechanism potentially capable of removing large numbers of larvae/juveniles from the Gulf Stream and facilitate their subsequent migration onto the Continental Shelf between Newfoundland and Cape Cod.

Summary

1. Larvae and early juveniles are caught mainly in a narrow but very long strip of water centered in the Slope Water/Gulf Stream Frontal Zone extending from Florida to and beyond Cape Hatteras.

2. Both the Needler 83 and 85 data show more than one peak in the size frequency distributions suggesting that a sequence of brood hatching occurs.

3. A larval to juvenile catch ratio on a transect in the Cape Canaveral area on the Needler 85 survey, compared to transects to the north and south of it, together with the presence of very small larvae, and the more "compact" character of the length frequency distribution suggest that this may be near a major spawning area.

4. The presence of newly hatched larvae south of Miami, indicates that spawning also occurs south of the Cape Canaveral area.

5. The physical environment is probably a major factor determing larval/juvenile distribution in that : (a) The Gulf Stream provides a rapid transport system (as much as 1000 km/week). (b) Frontal Eddies eject surface-layer Gulf Stream Water shoreward into Slope Water, which is subsequently reentrained into the Stream. (c) Frontal Eddies produce upwelling of nutrient-rich water between the filament and the Gulf Stream proper, which in turn increases primary production in the Slope/Gulf Stream Frontal Zone. (d) Downstream from Cape Hatteras the formation of Warm-Core Gulf Stream Eddies eject large quantities of Gulf Stream Water into the Slope Water area south of Nova Scotia and the Grand Banks with eddy duration times typically of several months.

6. Higher catches in the upwelling zone may be : (a) The result of passive advection. (b) Related to increased availability of food and hence better survival rates. (c) A sampling artifact.

7. Recruitment success or failure may be critically dependent on the timing, location and number of Gulf Stream Frontal Eddies and Warm Core Eddies developing when larvae and/or juveniles are present.

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Fig. 6. — Larval and juvenile *Illex* catch taken on repeated occupation of stations along five transects (see inset for locations) during cruise period 7-22 January, 1985. Number of larvae, juveniles, and their median mantle length (mm) are shown at each sampling station. Temperature cross-section, taken during second occupation of Transect III, together with number of larvae and juveniles caught at each sampling station are shown in an inset. Vertical arrowhead denotes estimated location of High Velocity Core of Gulf Stream.

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GENERAL PATTERNS IN THE SUMMER DISTRIBUTION OF EARLY JUVENILE OMMASTREPHID SQUID OFF EASTERN AUSTRALIA (MOLLUSCA, CEPHALOPODA)

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CEPHALOPODA
OMMASTREPHIDAE
LARVAL SQUID
EASTERN AUSTRALIA
DISTRIBUTION

ABSTRACT. — Larval squid were sampled in three surveys off the eastern Australian coast in January, March and May 1983. Ommastrephid larvae were abundant and occurred at over 90 % of stations. Although identification to species level has not so far been possible for the majority of specimens, general patterns of distribution with respect to latitude and bottom depth are presented.

CEPHALOPODA
OMMASTREPHIDAE
LARVES
AUSTRALIE EST
DISTRIBUTION

RÉSUMÉ. — De jeunes Céphalopodes planctoniques ont été échantillonnés au large de la côte Est de l'Australie en janvier, mars et mai 1983. Les « larves » d'Ommastréphidés étaient abondantes et présentes dans plus de 90 % des stations. Bien que l'identification des spécimens au niveau de l'espèce n'ait pas été possible jusqu'ici, du moins pour la majorité des individus récoltés, quelques aspects généraux de la distribution des animaux en relation avec la latitude et la profondeur peuvent être dégagés.

INTRODUCTION

Eleven species of the commercially important squid family Ommastrephidae are known to occur off the eastern Australian coast (Nesis, 1979; Okutani, 1980; Lu & Dunning, 1982; Dunning & Brandt, 1985; Dunning, In Prep.). While the distribution and relative abundance of adults are now relatively well known, few studies have been directed at larval and early juvenile stages of these species in Australia waters.

Pelagic cephalopods collected by opportunistic plankton tows between the southern Great Barrier Reef and southeast Tasmania were described by Allan (1945). Ommastrephid larvae and early juveniles were outnumbered in the small collection only by "*Pyrgopsis pacificus* (Issel)" [probably *Leachia* spp.] and all were referred to the only ommastrephid species known from the east coast at that time, *Nototodarus gouldi* (McCoy, 1888). Because of the limited size of the collection, geographic and seasonal distribution patterns could not be described.

The study described here aimed to obtain preliminary information on the relative abundance of larval ommastrephid squid across the continental shelf and slope off central eastern Australia and to assess any changes in relative abundance with latitude and at different times during the summer. Because this area is dominated by a western boundary current, water mass associations were also expected to be important and detailed hydrographic information was sought.

Broad distributional patterns for species groups only are presented here; detailed species distributional patterns require identification of small larvae to lower taxonomic units than has so far been possible with this collection.

METHODS

Early juvenile cephalopods were collected during three eight-day surveys undertaken between 28° and 34°S off the eastern Australia coast in January, March and May 1983 (Fig. 1). Eight sampling stations were located along transects roughly perpendicular to the continental slope at each degree of latitude nominally at bottom depths of 50, 100, 200, 400, 1 000 and 2 000 metres and at stations 5 and 10 nautical miles east of the 2 000 m station. Concurrent 30 minute surface tows using 500 µm 50 cm paired Bongo nets and double oblique tows using a 500 µm 1 m bridleless larval tuna net (FAO, 1966) were undertaken at each station. Nominal towing speed was 1.5 m sec^{-1} (3 knots) with oblique tows to 150 m where bottom depths exceeded 200 m and to 10 m above the bottom in shallower water. Catches were standardized to numbers per 1 000 m^3 using Rigosha flowmeter counts from each net.

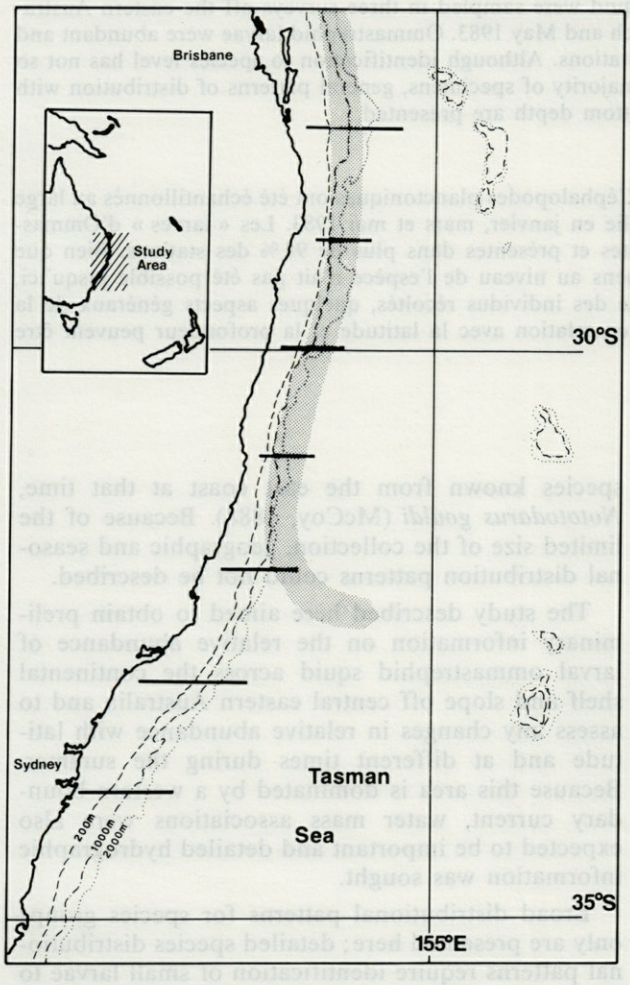

Fig. 1. — Study area showing the East Australian Current and the transects along each degree of latitude.

Unless otherwise indicated, standardized values are used throughout this paper.

Sampling was undertaken on each occasion from south to north to counter the possibility of towing in the same water mass in the southward flowing current. On transects at 34°, 32°, 30° and 28°S on the January and March surveys, paired day and night samples were taken at each of the eight stations during the same 24 hour period. Information on temperature, salinity, phosphates, nitrates, silicates and oxygen along each transect was obtained using expendable bathythermographs and a Neil Brown CTD with rosette sampler.

Larval ommastrephid squid are characterized by the fusion of the tentacles into a proboscis, persisting from hatching to "metamorphosis" at between 5 and 10 mm ML. Further identification was undertaken using the following characters :

1) the diameter of the lateral suckers on the proboscis tip;

2) the location and size of light organs on the ventral surface of the eyes and intestine;

3) the length of the proboscis relative to mantle length until the commencement of splitting to form the tentacles;

4) the length of the tentacles just prior to splitting relative to longest arm length.

Larvae with mantle lengths greater than 4 mm could generally be identified at least to genus using the above characters. However, the vast majority of the specimens collected during the study were less than 3 mm ML and these specimens have been separated into three major species groups as shown in the following table :

	Sucker diameters	Proboscis length	Species included
Group 1	≠	⩾ ML	***Ommastrephes bartrami***
			Ornithoteuthis volatilis
			Nototodarus hawaiiensis
Group 2	=	⩾ ML	***Sthenoteuhis* spp.**
Group 3	=	⩽ ML	***Eucleotheuthis luminosa***
			Nototodarus gouldi
			Todaropsis eblanae
			Todarodes pacificus

Larvae of *Todarodes filippovae* would fall into Group 3 morphologically but the known distribution of mature adults (Dunning & Brandt, 1985) makes it unlikely that this species is represented in the collections. No specimens of *Hyaloteuthis pelagica* (which have light organs present on the eyes and intestine from 1.5 mm [Harman & Young, 1985, this vol.]) were represented among the specimens less than 3 mm ML.

RESULTS

Oceanographic patterns

Throughout the sampling period, the area was dominated by the East Australian Current (EAC) (Hamon, 1965; Boland & Church, 1981), carrying tropical Coral Sea water southward along the offshore edge of the continental shelf to a point between 31° and 32°S where it turned eastward to form the Tasman Front (Stanton, 1981). During the January and March surveys, the EAC was evident at the slope as far south as 32° but in May, had moved away from the slope just to the north of 31°S. A temperature profile throught the current at 32°S in March is shown in figure 2. Anticyclonic warm core 'eddies' pinched off from the EAC often occur south of 32°S but were not encountered during the sampling period in the area surveyed.

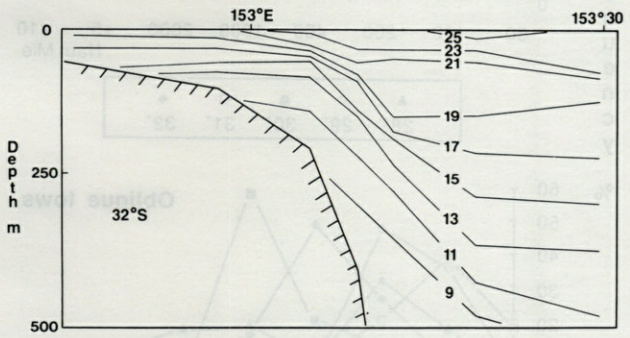

Fig. 2. — Temperature profile through the EAC at 32 °S, March 1983.

Surface currents were strongest in all three surveys at the edge of the continental shelf (400-1 000 m bottom depth) and decreased in velocity both shoreward and seaward. These southerly currents as measured by ship's drift reached 1.6 m sec^{-1} in January at 33°S, 2.05 m sec^{-1} in March at 31°S and 1.35 m sec^{-1} in May at 30°S. Between 30° and 32°S, especially during January, surface currents recorded at 50 and 100 m depth stations were typically northwest to northward at less than 0.5 m sec^{-1}.

Surface water temperatures varied by approximately 6 °C from north to south during each survey, with the major change at the temperature front to the south of the EAC at the point where it turned east. In March, a change of 4.7 °C was recorded over 1 nautical mile at the shelf edge at 32°S. The highest temperature recorded was 26.9 °C at the shelf edge at 28°S in March and the lowest, 19.6 °C on the shelf at 32°S in March.

Seasonal and latitudinal distribution of larvae

Numerically, ommastrephids were the dominant cephalopod larvae represented in the collections and occurred at over 90 % of the stations sampled. Larvae were more abundant in March than in either January or May with a mean overall catch rate from oblique tows of 15.7 individuals (standard deviation [SD] 28.5). This compared with 4.3 (SD 6.4) and 7.5 (SD 8.9) respectively in January and May. A similar pattern was evident in surface samples. In January, the average catch rate was 5.5 individuals (SD 8.4), in March 24.3 (SD 60.9) and in May, 9.2 (SD 13.9). The highest catch of 450 individuals per 1 000 m^3 was obtained from a surface sample taken at 32°S in 100 m depth in March.

Species group 1 overwhelmingly dominated samples from the first two surveys, comprising more than 99 % of all individuals. *Ommastrephes bartrami* and *Ornithoteuthis volatilis* were represented among the larger larvae and juveniles collected. By contrast, 44 % of specimens caught during the May cruise were from species groups 2 and 3 and larger specimens of *Ornithoteuthis volatilis* and *Sthenoteuthis* (probably *oualaniensis*) were positively identified. Representatives of species group 3 outnumbered those of group 2 by approximately 4 : 1 in this survey.

Mean catches combining all depth strata for each degree of latitude are shown in Table 1. In January, highest mean catches were at 33°S, in March at 32°S

Table I. — Mean catches standardized to 1 000 m^3 by latitude for the 1983 larval surveys.

Latitude	Oblique tows	Surface tows	Total
January survey			
28°S	4.7	3.2	4.0
29°S	5.8	4.6	5.2
30°S	2.1	1.4	1.7
31°S	2.6	2.0	2.3
32°S	5.5	11.0	8.3
33°S	11.2	18.0	14.6
34°S	0.7	2.9	1.8
March survey			
28°S	5.4	5.3	5.4
29°S	13.6	26.6	20.1
30°S	28.4	28.6	28.5
31°S	18.2	30.3	24.2
32°S	30.3	55.7	43.0
33°S	–	–	–
34°S	0.0	0.5	0.2
May survey			
28°S	3.1	4.6	3.9
29°S	10.1	6.5	8.3
30°S	17.5	21.6	19.6
31°S	15.3	17.5	16.4
32°S	3.7	1.1	2.4
33°S	1.8	12.7	7.2
34°S	1.5	1.4	1.4

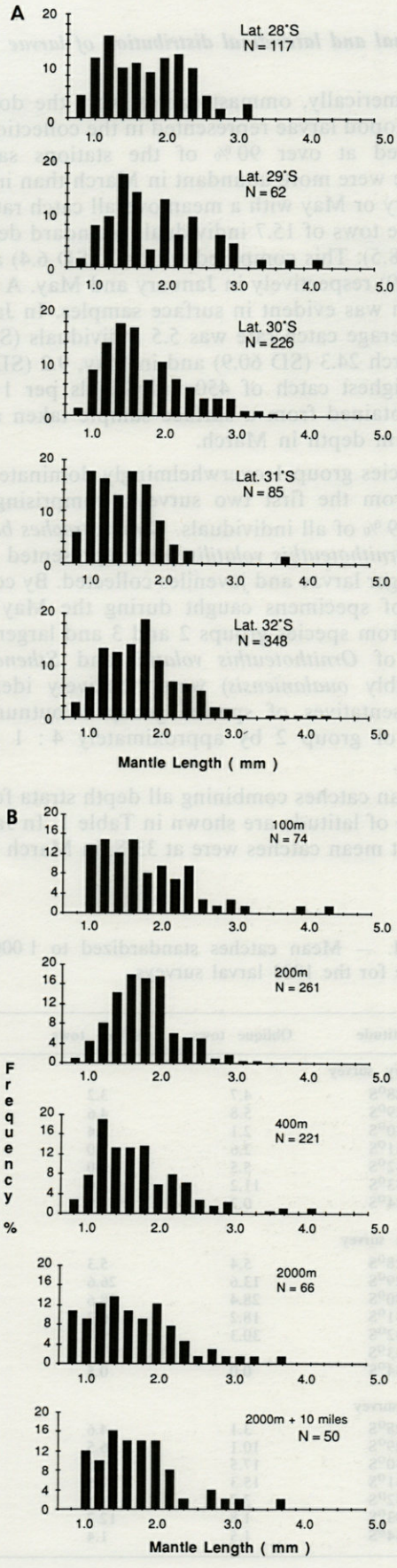

Fig. 3. — A, Size distribution of larvae in relation to latitude, oblique tows, March 1983. B, Size distribution in relation to bottom depth, oblique tows, March 1983.

and in May at 30°S. Lowest catches in all surveys were taken at 34°S.

For the March survey, size distribution along the latitudinal gradient was examined. Figure 3 A shows a possible indication of larger larvae north of 30°S. Larvae of 1.0 mm ML and less, sizes close to that at hatching for several ommastrephids, occurred throughout the area from 28° to 33°S during all surveys.

Distribution with respect to bottom depth

Larval abundance with respect to eight bottom depth strata was examined for the March survey.

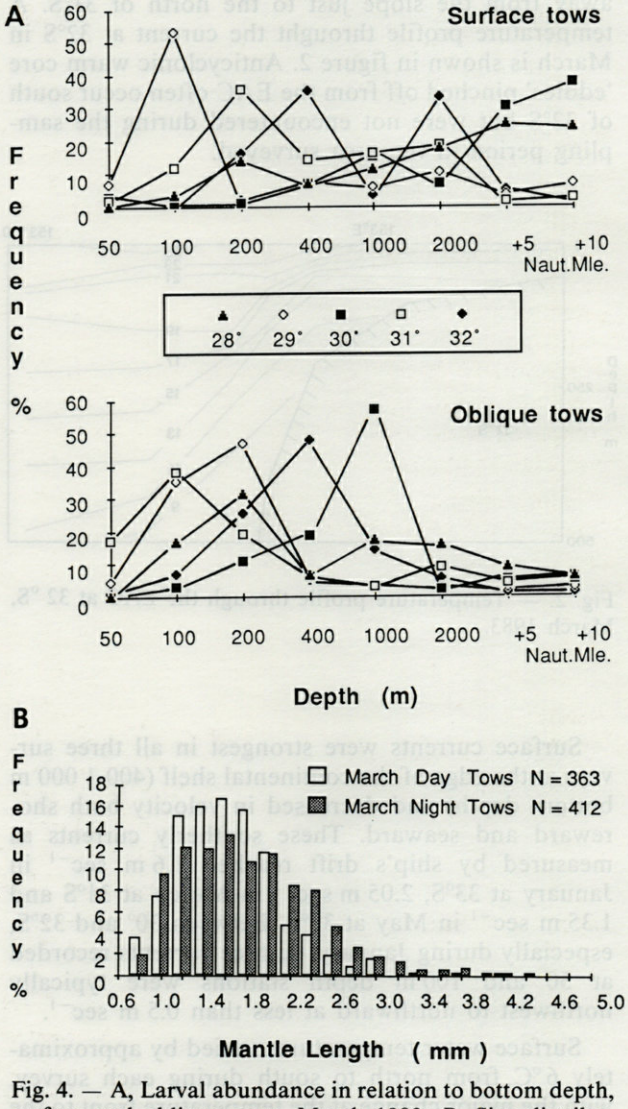

Fig. 4. — A, Larval abundance in relation to bottom depth, surface and oblique tows, March 1983; B, Size distribution, day and night oblique tows, March 1983.

Figure 4 A shows that although the pattern for each transect differs, catches were generally lower in oblique tows over depths greater than 2 000 m in contrast to surface tows which sometimes showed higher catches here. Both showed low catches at 50 m stations.

A broad spectrum of size classes was present at all depth strata examined with no clear relationship between size and bottom depth at the sampling station (Fig. 3 B). At stations deeper than 1 000 m and at 100 m, there is a slight indication of a higher proportion of larvae smaller than 1.5 mm ML.

Day — night comparisons

Size distribution of all specimens collected during the day in March versus those caught at night is presented in Figure 4 B. The distribution of specimens caught at night shows a slightly higher proportion of larger size classes than does that for specimens from day samples suggesting that differential net avoidance may be occurring.

Of the 32 stations from all surveys where comparisons could be made for oblique tows, 14 showed day catches higher than night catches (44 %). Day catches exceeded night catches in 7 of 23 surface tow comparisons (30 %). Day surface tows were less successful in January yielding higher catches than the comparable night tow on only 9 % of occasions compared with 50 % in March. Day tows were not undertaken in May.

Comparisons of mean catches for day and night samples from both the January and March surveys are shown below :

Survey	Oblique		Surface	
	Day	Night	Day	Night
January	2.07	5.2	1.3	6.8
March	15.1	15.5	30.9 (9.9*)	20.5

* Mean if catch of 450 individuals taken at the 100 m station is excluded.

DISCUSSION

Ommastrephid squid larvae were abundant and broadly distributed in East Australian Current waters from midsummer to early autumn but were less abundant in shelf and slope waters immediately to the south of the point where the current turns east (generally at or about 32°S near the shelf edge). Catches, both from surface and oblique tows were higher in March than in either January or May, corresponding to times of highest surface water temperatures and current velocities.

Larval ommastrephids were caught at more stations and in greater abundance in this study than reported by Sato (1973), Yamamoto & Hamada (1981) and Matsuda et al. (1972) for waters between Taiwan and southern Japan where similar ommastrephid species assemblages are present. Using 2 m nets, Matsuda *et al.* (1972) collected larvae at 31.5 % of stations sampled. A mean catch from midlayer tows of approximately 2.9 individuals was obtained and a maximum of 19 per 1 000 m^3 collected compared with 14.4 and 450 in this study.

In the western Arabian Sea in an area of significant upwelling, Nesis (1974) obtained ommastrephid larvae (83 % *Sthenoteuthis*) at less than 54 % of stations sampled compared with more than 90 % in this study. The mean catch rate was, however, higher than obtained from eastern Australian waters — 16.6 per 1 000 m^3 compared with a maximum of 15.7 for oblique samples taken in March 1983.

Little difference was evident in the size distribution of larvae caught in March either latitudinally or across the shelf from 50 m depth to 10 nautical miles east of the 2 000 m bottom depth contour. Larvae close to the expected size at hatching were evident throughout the EAC area in all surveys.

Significantly more ommastrephid larvae were caught at night than during the day in both surface and oblique tows during the January and March surveys. Diel vertical migration is unlikely to be a major contributing factor to this difference at stations in depths of less than 200 m where tows sample the entire water column. Evidence from other studies (Nesis, 1977; Nesis & Nigmatullin, 1979) suggests that even in deeper water, larval and early juvenile ommastrephids are predominantly found in the upper 200 m. Together with the difference in size composition between day and night samples observed, these data suggest that larval squid even at these small sizes are able to avoid plankton nets.

Available information on the seasonal and geographic distribution of juveniles and mature adults from the region is limited (Dunning & Brandt, 1985) and provides little corroboration of tentative identifications. Mature adults and small juveniles of *Ommastrephes, Sthenoteuthis oualaniensis, Ornithoteuthis, Hyaloteuthis* and *Eucleoteuthis* together with mature adults of *Nototodarus hawaiiensis and N. gouldi, Sthenoteuthis* sp., *Todaropsis* and *Todarodes pacificus* have been recorded between 27° and 35°S during March and April in previous years and many appear to have extended spawning seasons in east coast waters. The presence of juvenile specimens in all bimonthly trawl samples from off the northwest Australian coast in 1982-83 suggests that the population of *N. hawaiiensis* there spawns throughout the year (Dunning, in prep.) and this species may behave similarly off the east coast. In a series of 12 midwater trawl samples taken in late March 1981 in waters of from 200 to 800 m bottom depth near

34°30'S, juveniles of six genera were represented in the following abundances :

Ornithoteuthis....	279	*Sthenoteuthis*....	16
Eucleoteuthis.....	32	*Hyaleuthis*.....	2
Ommastrephes....	24	*Todaropsis*.....	1

If these genera are represented in similar relative abundances in the 1983 larval samples, it is probable that Group 1 is dominated by *Ornithoteuthis* larvae and Group 3 by *Eucleoteuthis luminosa* although *Nototodarus gouldi* may be more abundant in shallower shelf waters.

The larval species assemblage present in the 1983 summer catches changes late in the season with an increase in relative abundance of species groups 2 and 3. Combining positive identifications made from the material with the published data on adult and juvenile abundance, this change probably reflects an increase in the abundance of *Sthenoteuthis* spp., *Eucleoteuthis* and *N. gouldi* with group 1 species — *Ornithoteuthis, Ommastrephes* and perhaps *N. hawaiiensis* — increasing in abundance from January to March and then decreasing to a similar level in May as in January. Further clarification of species differences in larval abundance awaits identification of the 1983 collections to lower taxonomic levels than has so far been possible.

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JUVENILE PLANKTONIC CEPHALOPODS FROM NW AFRICA

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CEPHALOPODA, JUVENILE, PLANKTONIC, NW AFRICA

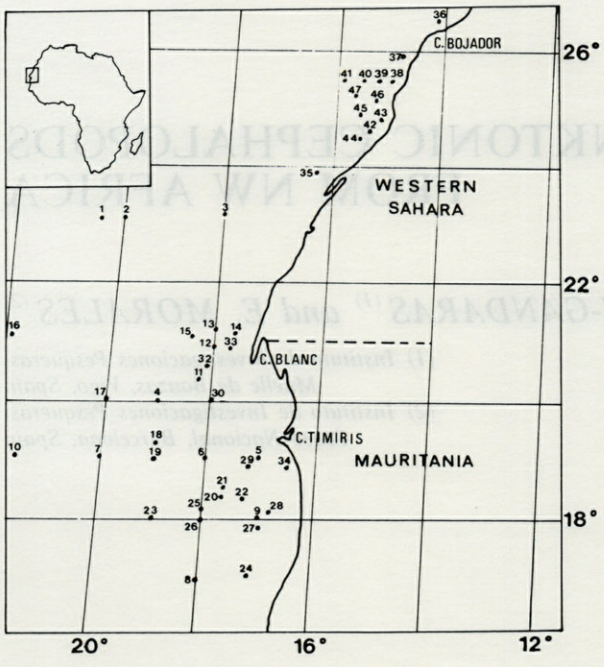
One hundred and ten early juvenile cephalopods were captured with WP2, Bongo nets of 300 and 500 µm mesh size, and Isaacs-Kidd Midwater Trawl (IKMT) by the R/V Cornide de Saavedra during the cruises "Sahara II" (August-September, 1971), "ATLOR II" (March, 1973), "ATLOR III" (April-

Table. — Species List.

C	S	TG	Family	Genus or stage	Species	Dorsal mantle length in mm
SII	1	WPS	Ommastrephidae	Rhynchoteuthion	–	4.2
»	2	»	Cranchiidae	–	–	1.7
»	3	»	Loliginidae	*Loligo*	sp.	1.4
»	»	»	»	*Loligo*	sp.	1.4
»	4	WP2	Ommastrephidae	Rhynchoteuthion		0.9
»	5	WP2	Enoploteuthidae	*Abralia*	*siedleckyi ?* Lipinsky,1983	12.4
»	6	WP2	»	*Abralia*	sp.	3.5
»	»	»	Octopoteuthidae	–	–	2.0
»	»	»	Ommastrephidae	Rhynchoteuthion	–	2.3
»	7	»	Brachioteuthidae	*Brachioteuthis*	sp.	7.2
»	8	»	Ommastrephidae	Rhynchoteuthion	–	1.6
»	9	»	Enoploteuthidae	*Pterygioteuthis ?*	–	1.6
»	10	»	Brachioteuthidae	*Brachioteuthis*	sp.	30.4
»	11	»	Enoploteuthidae	–	–	2.2
»	»	»	»	–	–	3.9
»	»	»	»	*Abralia*	sp.	3.1
»	»	»	Octopoteuthidae	–	–	2.5
»	»	»	»	–	–	2.3
»	12	WP2	Brachioteuthidae	*Brachioteuthis*	sp.	3.4
»	13	»	Enoploteuthidae	–	–	1.9
»	»	»	Brachioteuthidae	*Brachioteuthis*	sp.	2.0
»	14	»	Enoploteuthidae	–	–	1.6
»	»	»	Brachioteuthidae	*Brachioteuthis*	sp.	2.4
»	15	»	Ommastrephidae	Rhynchoteuthion	–	1.9
»	»	»	Enoploteuthidae	–	–	2.2
AII	16	WP2	Onychoteuthidae	–	–	4.0
»	17	»	Cranchiidae	*Teuthowenia*	*maculata* (Leach,1817)	32,6
»	18	»	Ctenopterygidae	–	–	2.0
»	»	»	Ommastrephidae	Rhynchoteuthion	–	1.1
»	19	»	»	»	–	1.3
»	20	»	Octopoteuthidae	–	–	2.1
»	21	»	Histioteuthidae	*Histioteuthis*	sp.	3.5
»	»	»	Ctenopterygidae	–	–	2.7
»	22	»	Cranchiidae	*Teuthowenia ?*	–	3.7
»	23	»	Ctenopterygidae	–	–	2.8
»	24	IKMT	Enoploteuthidae	*Abralia*	*verany ?* (Rüppell,1844)	26.4
»	»	»	Histioteuthidae	*Histioteuthis*	*reversa* (Verrill, 1880)	15.3
»	»	»	»	»	»	21.4
»	»	»	»	»	»	17.9
»	»	»	Ctenopterygidae	*Ctenopteryx*	sp.	21.3
»	»	»	Brachioteuthidae	*Brachioteuthis*	sp.	30.2
»	»	»	Cranchiidae	–	–	20.0
»	»	»	»	*Teuthowenia*	*maculata*	26.0
»	25	WP2	Ommastrephidae	Rhynchoteuthion	–	1.4
»	26	B500	Histioteuthidae	*Histioteuthis*	sp.	2.1
»	27	IKMT	Enoploteuthisae	*Abralia*	sp.	19.4
»	»	»	Octopoteuthidae	–	–	27.5
»	»	»	Histioteuthidae	*Histioteuthis*	*reversa*	18.0
»	»	»	Brachioteuthidae	*Brachioteuthis*	sp.	17.7
»	»	»	»	»	»	35.3
AII	28	B500	Octopoteuthidae	*Octopoteuthis*	sp.	10.1
»	»	»	»	»	»	12.0
»	»	»	Ommastrephidae	Rhynchoteuthion	–	4.0
»	29	IKMT	Histioteuthidae	*Histioteuthis*	*reversa*	22.5
»	»	»	Cranchiidae	*Teuthowenia*	*maculata*	21.0
»	»	»	»	»	»	35.6
»	»	»	»	*Galiteuthis*	sp.	15.0
»	30	WP2	Histioteuthidae	*Histioteuthis*	sp.	2.2
»	31	IKMT	Ctenopterygidae	*Ctenopteryx*	sp.	28.7
»	»	»	»	»	»	28.5
»	»	»	»	»	»	22.6
»	»	»	»	»	»	19.0
»	»	»	»	»	»	18.9
»	»	»	Brachioteuthidae	*Brachioteuthis*	sp.	28.5
»	»	»	»	»	»	33.0
»	»	»	»	»	»	35.0
»	»	»	»	»	»	29.1
»	»	»	Cranchiidae	*Teuthowenia*	*maculata*	24.0
»	»	»	»	»	»	20.7
»	32	WP2	»	»	»	6.3
»	33	»	Histioteuthidae	*Histioteuthis*	sp.	2.2
»	34	IKMT	Onychoteuthidae	–	–	22.2
»	»	»	»	–	–	21.1
»	»	»	»	–	–	11.7
»	»	»	Histioteuthidae	*Histioteuthis*	*reversa*	13.7
AIII	35	B300	Octopodidae	–	–	2.5
»	»	»	»	–	–	1.6
»	36	B500	Loliginidae	*Loligo*	sp.	2.5
»	»	»	»	»	»	2.1
»	37	B500	Sepiolidae	*Rondeletiola*	sp.	2.0
»	»	»	Brachioteuthidae	*Brachioteuthis*	sp.	1.8
»	38	»	Loliginidae	*Loligo*	sp.	2.3
»	39	»	»	»	»	3.0
»	40	B300	Sepiolidae	*Rondeletiola*	sp.	2.1
»	41	B500	Loliginidae	*Loligo*	sp.	2.1
»	42	B300	Sepiolidae	*Sepiola*	sp.	1.6
»	43	B500	Octopodidae	–	sp.	1.6
»	44	»	Loliginidae	*Loligo*	sp.	2.3
»	»	»	»	»	sp.	2.0
»	45	»	»	*Loligo*	sp.	2.4
»	»	»	»	»	»	2.5
»	46	»	»	»	»	2.6
»	»	»	Octopodidae	–	–	1.5
AV	47	B300	Octopodidae	–	–	1.5

C : cruise ; S : station number ; TG : type of gear («Working party 2» net with mesh aperture width of 200 µm ; Bongo nets with 300 and 500 µm mesh width, and Isaacs - Kidd midwater trawl).

Note added in proof : Due to an editorial error, one specimen in cruise AII, station 29. has been omitted : Ommastrephidae, *Todaropsis eblanae,* ML 19.7.



May, 1973) and "ATLOR V" (April, 1974) (Table 1). The area sampled extends from 16° to 26° of latitude North, and from the coast to 22 °00'W (Fig. 1).

The specimens were preserved in 4 % formalin in sea water. The observed proportion of represented families is : Sepiolidae 3 %, Loliginidae 11 %, Enoploteuthidae 10 %, Octopoteuthidae 6 %, Onychoteuthidae 4 %, Histioteuthidae 9 %, Ctenopterygidae 8 %, Brachioteuthidae 12 %, Ommastrephidae 9 %, Cranchiidae 10 %, Octopodidae 5 %, *incertae sedis* 14 %.

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Fig. 1. — Study area on the northwestern Africa coast (inset) and location of sampling stations.

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AN ANNOTATED LIST OF CEPHALOPOD LARVAE COLLECTED OFF THE MEDITERRANEAN COAST OF SPAIN, 1976-1981

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CEPHALOPODA
LARVAE
WESTERN MEDITERRANEAN
SPANISH COAST

ABSTRACT. — The identified cephalopod larvae come from biological samples collected during four surveys with a 40 cm diameter Bongo device fitted with 333 µm and 505 µm mesh size nets : Mediterraneo I (October 1976), Mediterraneo II (March 1977), Tanit (August 1979) and Maira I (December 1981). The area covered included the Mediterranean coast of Spain between Cabo Creus in the north and Cabo Palos in the south, and between Spain's mainland and the Balearic Islands. The following cephalopod taxa were identified : *Rossia macrosoma, Abraliopsis morisii, Thelidioteuthis alessandrinii, Onychoteuthis banksi, Ancistroteuthis lichtensteini, Histioteuthis reversa, Ctenopteryx sicula, Illex coindetii,* Rynchoteuthion larvae, *Galiteuthis* sp., *Octopus vulgaris, Octopus* sp., *Eledone cirrhosa, Macrotritopus* larvae, *Argonauta argo,* and some unidentified representatives of the families Sepiolidae, Loliginidae, Cranchiidae and Octopodidae.

CEPHALOPODA
LARVES
MÉDITERRANÉE OCCIDENTALE
CÔTE ESPAGNOLE

RÉSUMÉ. — Les larves de Céphalopodes identifiées ont été récoltées pendant quatre campagnes à l'aide de filets Bongo (mailles de 333 à 505 µm) : Mediterraneo I (Octobre, 1976), Mediterraneo II (Mars, 1977), Tanit (août, 1979) et Maira I (Décembre, 1981). L'aire d'étude est située entre le Cap Creus au nord et le Cap Palos au sud, et entre la côte espagnole et les îles Baléares. Les espèces suivantes ont été trouvées : *Rossia macrosoma, Abraliopsis morisii, Thelidioteuthis alessandrinii, Onychoteuthis banksi, Ancistroteuthis lichtensteini, Histioteuthis reversa, Ctenopteryx sicula, Illex coindetii,* Rynchoteuthion larvae, *Galiteuthis* sp., *Octopus vulgaris, Octopus* sp., *Eledone cirrhosa, Macrotritopus* larvae, *Argonauta argo,* et quelques représentants non identifiés des familles Sepiolidae, Loliginidae, Cranchiidae et Octopodidae.

We report here on identification and distribution of larval cephalopods collected during four survey cruises (1976-1981) conducted by the Instituto de Investigaciones Pesqueras de Barcelona.

The first, "Mediterraneo I" on the B/O *Cornide de Saavedra,* was carried out in October 1976. The position of the 44 stations are shown in Fig. 1. We took 80 plankton tows; of these, 33 contained cephalopods.

The second cruise "Mediterraneo II", was made on the same vessel in March 1977. The station positions and station numbers are the same as "Mediterraneo I" except the southern and the offshore stations. We studied 28 stations, and 11 tows contained cephalopods.

"Tanit" in August 1979 on board the B/O *Garcia del Cid* covered part of this area. The last cruise was "Maira I" (December 1981) on board the B/O

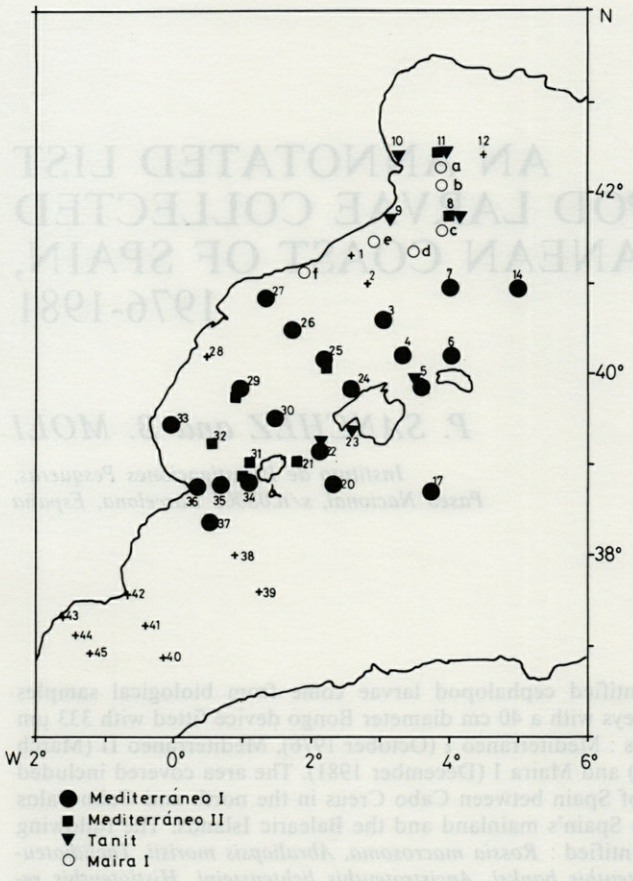

Fig. 1. — Distribution of stations and location of those at which cephalopods were captured (symbols other than crosses) in the four surveys.

Garcia del Cid; the study area (fig. 1) was smaller than for the previous cruises, it covered only the Catalonian coast. We caught cephalopods at 6 of the 20 stations visited.

Sampling procedures were identical, on all four cruises. Oblique tows were taken with a 40 cm diameter Bongo device fitted with 333 µm and 505 µm mesh size nets.

Rossia macrosoma (Delle Chiaje, 1829)

Mediterraneo II. — Station 29. One specimen of 2.05 mm ML was caught at night at 500-0 m.

Maira I. — Station a,e. Two specimens of 1.2 and 1.7 mm ML were caught at night at 500-0 m.

Maira I. — Station c. One specimen of 1.4 mm ML was caught during three day-time at 500-0 m.

Sepiolidae larvae

Mediterraneo I. — Stations 4, 24, 25. Three specimens ranging from 1.3 to 5.1 mm ML were caught at night at 200-0 m.

Mediterraneo II. — Stations 29, 32. Two specimens of 1.1 and 1.9 mm ML were caught at night at 500-0 m.

Abraliopsis morisii (Verany, 1837)

Mediterraneo I. — Station 25. One specimen of 3.8 mm ML was caught during the day-time at 200-0 m.

Thelidioteuthis alessandrinii (Verany, 1851)

Maira I. — Station f. One specimen of 2.3 mm ML was caught during the day-time at 100-0 m.

Onychoteuthis banksi (Leach, 1817)

Mediterraneo I. — Stations 3, 7, 14, 25. Nine specimens ranging from 3.2 to 8.9 mm ML were caught during the day-time at 200-0 m.

Tanit. — Stations 8, 11. Two specimens both of 3.1 mm were caught during the day-time at 300-0 m.

Tanit. — Station 22. Two specimens of 2.6 and 3.5 mm were caught at night at 300-0 m.

Ancistroteuthis lichtensteini (d'Orbigny, 1839)

Mediterraneo I. — Station 26. One specimen of 19 mm ML was caught at night at 200-0 m.

Histioteuthis reversa (Verrill, 1880)

Mediterraneo I. — Stations 7, 14. Three specimens ranging from 2.7 to 3.6 mm ML were caught during the day-time at 200-0 m.

Mediterraneo I. — Station 17. One specimen of 2.7 mm ML was caught at night at 200-0 m.

Mediterraneo II. — Station 8. One specimen of 2.1 mm ML was caught at night at 200-0 m.

Mediterraneo II. — Stations 21, 31. Two specimens of 4.5 and 8.0 mm ML were caught during the day at 200-0 m.

Mediterraneo II. — Station 34. One specimen of 3.5 mm ML was caught at night at 100-0 m.

Maira I. — Station b. Three specimens ranging from 2.2 to 2.8 mm ML were caught at night at 500-0 m.

Maira I. — Station d. One specimen of 2.5 mm ML was caught during the day-time at 500-0 m.

Ctenopteryx sicula (Verany, 1851)

Mediterraneo I. — Station 14. One specimen of 3.1 mm ML was caught during the day-time at 200-0 m.

Mediterraneo I. — Station 17. One specimen of 3.1 mm ML was caught at night at 200-0 m.

Illex coindetii (Verany, 1837)

Mediterraneo I. — Station 30. One specimen of 2.6 mm ML was caught during the day-time, at 200-0 m.

Mediterraneo II. — Station 31. Two specimens of 3.6 and 4.2 mm ML were caught during the day-time at 200-0 m.

Mediterraneo II. — Station 32. One specimen of 4.6 mm ML was caught at night at 500-0 m.

Rhynchoteuthion larvae

Mediterraneo I. — Stations 4, 6, 20, 22, 24, 35. Eleven specimens ranging from 1.5 to 3.5 mm ML were caught at night at 200-0 m.

Mediterraneo I. — Stations 5, 34. Four specimens ranging from 1.2 to 1.7 mm ML were caught during the day-time at 80-0 m.

Mediterraneo I. — Stations 25, 37. Three specimens ranging from 1.4 to 4.8 mm ML were caught during the day-time at 200-0 m.

Mediterraneo II. — Station 31. One specimen of 5.6 mm ML was caught during the day-time, at 200-0 m.

Mediterraneo II. — Station 32. One specimen of 3.1 mm ML was caught at night at 500-0 m.

Tanit. — Station 10. One specimen of 1.5 mm ML was caught during the day-time at 75-0 m.

Tanit. — Station 23. One specimen of 1.9 mm ML was caught at night at 50-0 m.

Galiteuthis sp.

Mediterraneo II. — Station 11. One specimen of 5.1 mm ML was caught at night at 500-0 m.

Cranchiidae larvae

Mediterraneo I. — Stations 25, 37. Three specimens ranging from 3.8 to 5.2 mm ML were caught during the day-time at 200-0 m.

Loliginidae larvae

Mediterraneo I. — Station 3. One specimen of 2.3 mm ML was caught during the day-time at 200-0 m.

Mediterraneo I. — Stations 26, 29. Two specimens of 1.9 and 2.4 mm ML were caught at night at 200-0 m.

Octopus vulgaris (Cuvier, 1797)

Mediterraneo I. — *Station 5.* One specimen of 4.5 mm ML was caught during the day-time at 80-0 m.

Mediterraneo I. — Station 36. One specimen of 3.1 mm ML was caught at night at 50-0 m.

Octopus sp.

Mediterraneo I. — Stations 4, 20. Three specimens ranging from 3.6 to 5.2 mm ML were caught at night at 200-0 m.

Mediterraneo I. — Station 37. One specimen of 2.6 mm ML was caught during the day-time at 200-0 m.

Octopodidae larvae

Mediterraneo I. — Station 22. One specimen of 1.02 mm ML was caught at night at 200-0 m.

Mediterraneo I. — Station 24. One specimen of 3.6 mm ML, possibly *Eledone cirrhosa* (Lamarck, 1798), was caught at night at 200-0 m.

Mediterraneo II. — Station 25. One specimen of 2.5 mm ML was caught at night at 500-0 m.

Mediterraneo I. — Station 27. One specimen of 2.5 mm ML was caught during the day-time at 200-0 m.

Mediterraneo I. — Station 33. One specimen of 2.06 mm ML was caught at night at 100-0 m.

Tanit. — Station 5. One specimen of 1.6 mm ML was caught at night at 75-0 m.

Tanit. — Station 9, 10. Three specimens ranging from 1.7 to 2.1 mm ML were caught during the day-time at 75-0 m.

Macrotritopus larvae

Mediterraneo I. — Station 22. Two specimens of 2.9 and 3.3. mm ML were caught at night at 200-0 m.

Argonauta argo (Linné, 1758)

Mediterraneo I. — Stations 3, 14. Two specimens of 1.2 and 2.9 mm ML were caught during the day-time at 200-0 m.

Mediterraneo I. — Station 17. One specimen of 1.2 mm ML was caught at night at 200-0 m.

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THE DISTRIBUTION OF LARVAE OF THE GENUS *OCTOPOTEUTHIS* RUPPELL, 1844 (CEPHALOPODA, TEUTHOIDEA)

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CEPHALOPODA
OCTOPOTEUTHIS
LARVAE
DISTRIBUTION
ONTOGENY

ABSTRACT. — While carrying out a systematic revision of the pelagic squid genus *Octopoteuthis*, the author examined 146 "larval" specimens of the genus from museum sources worldwide. Individuals could not be separated into species but morphometric and meristic characters were examined giving information on ontogenetic development. Specimens ranged in size from 1.3 to 27.0 mm dorsal mantle length (DML) and represented locations in the Atlantic, Pacific and Indian Oceans and also the Mediterranean Sea. Captures were made with a variety of trawls and plankton nets. The deepest record from a closing net was 1 200 m using a MOCNESS system. The largest group examined totalling 105 individuals was collected in the North Atlantic. In the Atlantic the highest larval occurence was found to be in March, April, and June (which may reflect higher sampling pressure in those months) but specimens were obtained in all months except January and December. Low numbers in each of the other oceans prohibited an evaluation of yearly larval distribution.

CEPHALOPODA
OCTOPOTEUTHIS
LARVES
DISTRIBUTION
ONTOGÉNIE

RÉSUMÉ. — Environ 150 spécimens de stades larvaires du genre *Octopoteuthis* provenant de nombreux musées du monde entier ont été examinés. Les spécimens ont été capturés à l'aide de différents types de chalut et de filets à plancton à des profondeurs variant entre 23 et 3 500 m. Le plus grand groupe d'individus provient de l'Océan Atlantique et totalise 106 individus. Même si les individus ne pouvaient être identifiés jusqu'à l'espèce, des caractères morphométriques et méristiques ont été examinés, permettant de préciser le développement ontogénique du genre. La longueur dorsale du manteau (DML) des spécimens provenant des océans Atlantique, Pacifique et Indien ainsi que de la Mer Méditerranée varie entre 1.3 et 27.0 mm. En Atlantique, le pic d'abondance des larves se situe aux mois de mars, avril et juin, ce qui peut être le reflet d'une pression au niveau de l'échantillonnage. Des spécimens sont présents toute l'année, à l'exception des mois de janvier et décembre. La faible taille des échantillons en provenance des autres localités empêche l'évaluation de la distribution des larves durant l'année.

INTRODUCTION

The circumglobal pelagic squid genus *Octopoteuthis* is represented by nine nominal species. The systematics of the genus is in considerable confusion because of species designations based on larval or early juvenile specimens, loss of type material, and the continued addition of new species without clarification of the status of earlier ones. The author has examined one hundred and forty-six *Octopoteuthis* larvae as part of an ongoing revision of the genus. Specimens of the genus *Octopoteuthis*, like other decapod squids, bear eight arms and two tentacles. The paired tentacles common to most squid are retained only during the larval period and

are autotomized at a dorsal mantle length (DML) of 25-30 mm, after which the stumps are gradually resorbed.

MATERIALS AND METHODS

The majority of specimens used in this study were borrowed from various institutions. Additional material was examined while on trip to the United States National Museum of Natural History (USNM), (Smithsonian Insitution), Washington, D.C. Measurements and counts used are those recommended by Roper and Voss (1983). All measurements to the nearest 0.1 millimetre (mm) were taken by means of metric calipers. Hooks and suckers were counted under a dissecting microscope. Figures of larval distribution were constructed using collection data accompanying the specimens and supplemented, where possible, with published cruise data (Schimdt 1912, 1929; Gibbs et al., 1971). Because of the low number of specimens available data on additional larval specimens were extracted from the literature.

RESULTS

In all 146 larval specimens from the Atlantic, Indian, Pacific Oceans and the Mediterranen Sea were examined. The adult characters normally used to separate species (photophore numbers and patterns and the presence or absence of accessory cusps on arm hooks) do not develop early enough to be useful for specific identification of larvae. At present no other characters have been found that can be used for specific identification of larval *Octopoteuthis*. All specimens discussed in this paper will, therefore, be referred to as *Octopoteuthis* spp.

The larvae of *Octopoteuthis* go through a great change of body proportions especially between 1 and 15 mm DML. Figure 1 shows ontogenetic changes of larval *Octopoteuthis* from 5.0 to 10.9 mm DML. Initially the eyes appear stalked but by the time specimens reach a DML of 10-15 mm the eyes have become sessile. Most specimes loose their tentacular clubs at or about 12 mm DML but this loss may be premature due to damage during capture. Only fifteen larvae had at least one complete tentacle, one of which had a DML greater than 12 mm. The tentacular clubs in all specimens exami-

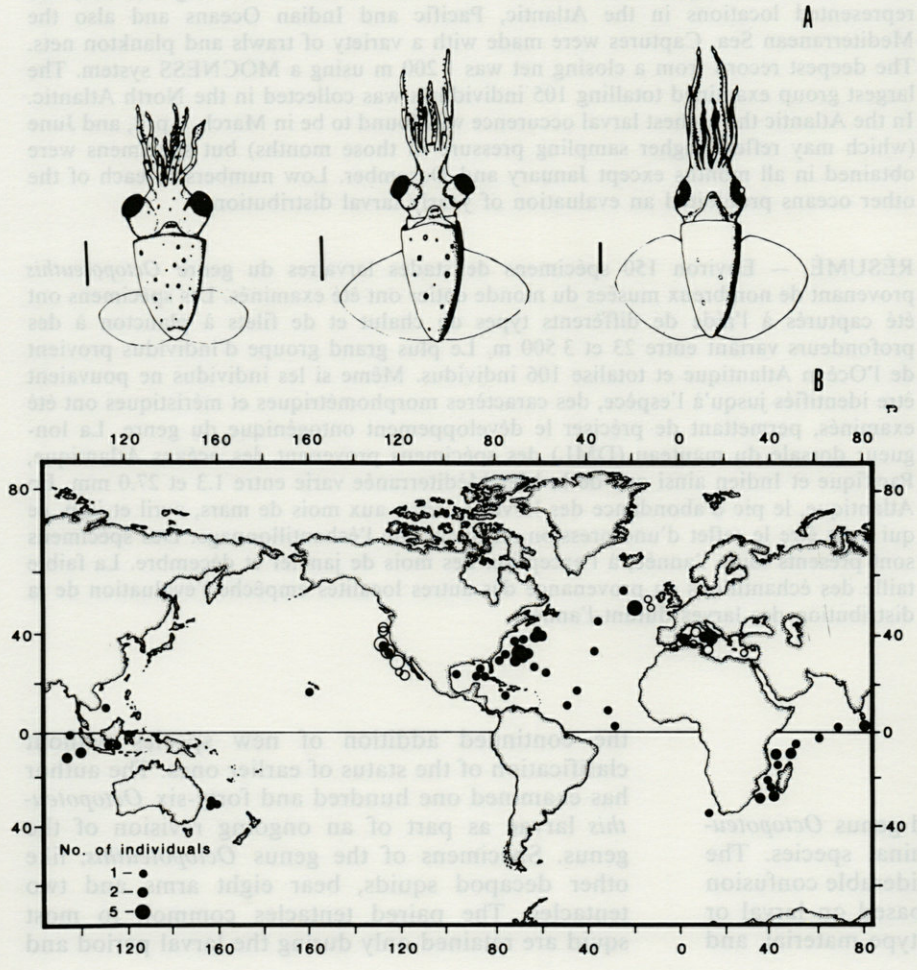


Fig. 1. — A, Diagram of three *Octopoteuthis* sp. larvae showing ontogeny (scale = 2 mm). B, distribution of larvae of *Octopoteuthis* reported on in this paper (filled circles — specimens from this study; empty circles — from literature).

ned bear 4 pairs of suckers; one very small pair on the carpus, 2 very large pairs on the manus and a second small pair on the dactylus.

Some brachial suckers have developed into hooks in specimens as small as 1.5 mm DML. Hooks initially appear in the mid-section of each arm with some suckers remaining both proximal and distal to them. In larger specimens, however, all the suckers, except 6-12 distally, have become hooks. In specimens of 5 mm DML, there are about 15-20 hooks and 6-10 suckers.

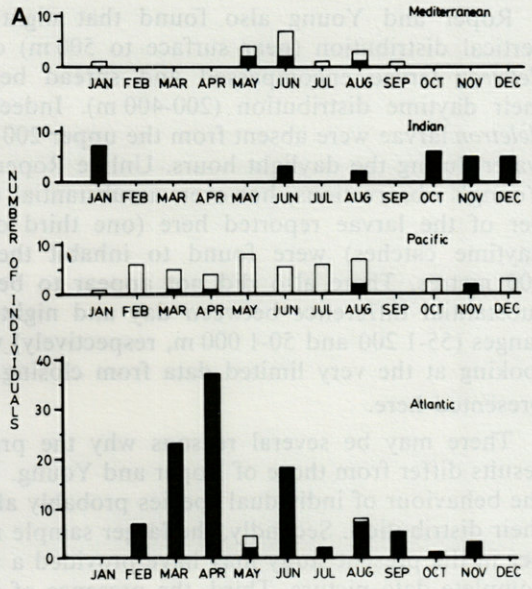
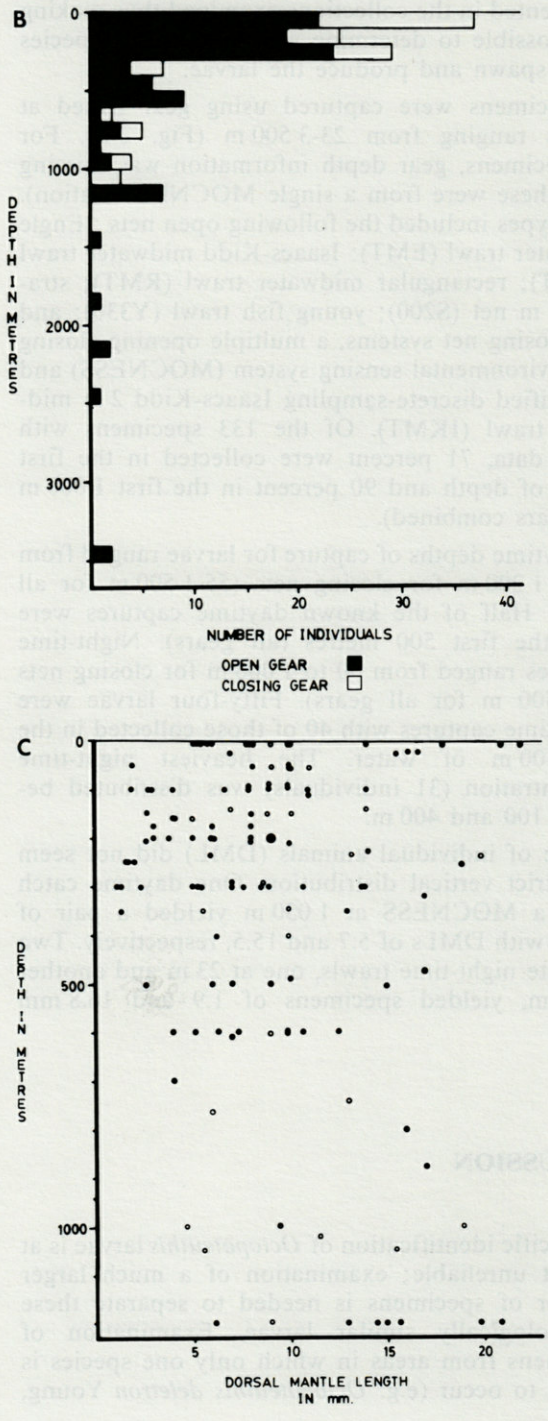


Fig. 2. — A, Monthly distribution of *Octopoteuthis* spp. larvae, by ocean based on collection data and literature records. B, Vertical distribution of *Octopoteuthis* spp. larvae from collection data. C, Vertical distribution of *Octopoteuthis* spp. larvae collected in the first 1 200 m depth plotted against dorsal mantle length (DML).

The largest number of specimens examined (105) came from the North Atlantic. A single specimen was from off the western coast of South Africa (Fig. 1B). Atlantic specimens were collected in all months except December and January with highest catches in March, April and June (Fig. 2 A).

Only 40 other specimens were examined, 6 and 29 from the Pacific and Indian Oceans, respectively, and 5 from the Mediterranean Sea (Fig. 1 B). Published literature sources were used to supplement these sparse data (Mediterranean : Degner,



1925, Issel 1925; Pacific : Okutani and McGowan 1969, Yamamoto and Okutani 1975; Atlantic : Cairns 1976, Massy 1909). Of the nearly 200 papers that mention the genus only a small number discuss specimens that could be identified as *Octopoteuthis* larvae and indicate collection data.

To aid in larval identification the author attempted to compare the monthly distributions with those of mature and near mature specimens (i.e. those having eggs or spermatophores) of various species. At least some mature members of each species could be found over the six to eight months represented in the collections examined thus making it impossible to determine when individual species might spawn and produce the larvae.

Specimens were captured using gear fished at depths ranging from 23-3 500 m (Fig. 2 B). For 13 specimens, gear depth information was missing (8 of these were from a single MOCNESS station). Gear types included the following open nets : Engle midwater trawl (EMT); Isaacs-Kidd midwater trawl (IKMT); rectangular midwater trawl (RMT); stramin 2 m net (S200); young fish trawl (Y330); and two closing net systems, a multiple opening-closing net environmental sensing system (MOCNESS) and a modified discrete-sampling Isaacs-Kidd 2 m midwater trawl (IKMT). Of the 133 specimens with depth data, 71 percent were collected in the first 500 m of depth and 90 percent in the first 1 000 m (all gears combined).

Daytime depths of capture for larvae ranged from 55 to 1 200 m for closing nets (55-1 500 m for all gears). Half of the known daytime captures were from the first 500 metres (all gears). Night-time captures ranged from 50 to 1 000 m for closing nets (50-3 500 m for all gears). Fifty-four larvae were night-time captures with 40 of those collected in the top 500 m of water. The heaviest night-time concentration (31 individuals) was distributed between 100 and 400 m.

Size of individual animals (DML) did not seem to restrict vertical distribution. One daytime catch using a MOCNESS at 1 050 m yielded a pair of larvae with DMLs of 5.7 and 15.5, respectively. Two separate night-time trawls, one at 23 m and another at 50 m, yielded specimens of 1.9 and 16.8 mm DML.

DISCUSSION

Specific identification of *Octopoteuthis* larvae is at present unreliable; examination of a much larger number of specimens is needed to separate these morphologically similar larvae. Examination of specimens from areas in which only one species is known to occur (e.g. *Octopoteuthis deletron* Young, 1972 from off California) may be useful in solving this problem.

Some of the present observations agree with those of Roper and Young (1975). They reported day and night trawl catches of 60 and 81 percent, respectively, of larvae of *O. deletron* in the first 500 m of water. The remainder of their specimens were collected in the next 700 m. In comparison, 4 specimens out of 146 reported here came from gear fished to depths greater than 1 200 m, but these deeper records are probably the result of catches made while the nets were being set.

Roper and Young also found that night-time vertical distribution (near surface to 500 m) of *O. deletron* larvae encompassed and spread beyond their daytime distribution (200-400 m). Indeed *O. deletron* larvae were absent from the upper 200 m of water during the daylight hours. Unlike Roper and Young's observations, however, a substantial number of the larvae reported here (one third of all daytime catches) were found to inhabit the top 200 metres. There also did not appear to be any substantial difference between day and night-time ranges (55-1 200 and 50-1 000 m, respectively) when looking at the very limited data from closing gear presented here.

There may be several reasons why the present results differ from those of Roper and Young. First, the behaviour of individual species probably affects their distribution. Secondly, the larger sample number in the present study may have provided a more complete data picture. Third, the presence of more than one species may have confused the pattern. Fourth, latitudinal variability may have also have confused the picture. Finally, a combination of biological and physical parameters such as light, temperature and productivity may be regulating distribution. However, neither Roper and Young's nor the present study had enough information on these parameters to qualify their affect on distribution.

It should be stressed that the above results are based on a very limited number of museum specimens, which may not reflect the total distribution of *Octopoteuthis* larvae either temporally or spacially. The sparsity of *Octopoteuthis* in collections forces the use of available data. As stated earlier only a portion of the depth records are useful. Truly accurate depth distribution figures will have to await data from much larger numbers of larvae collected in discrete-sampling gear types.

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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

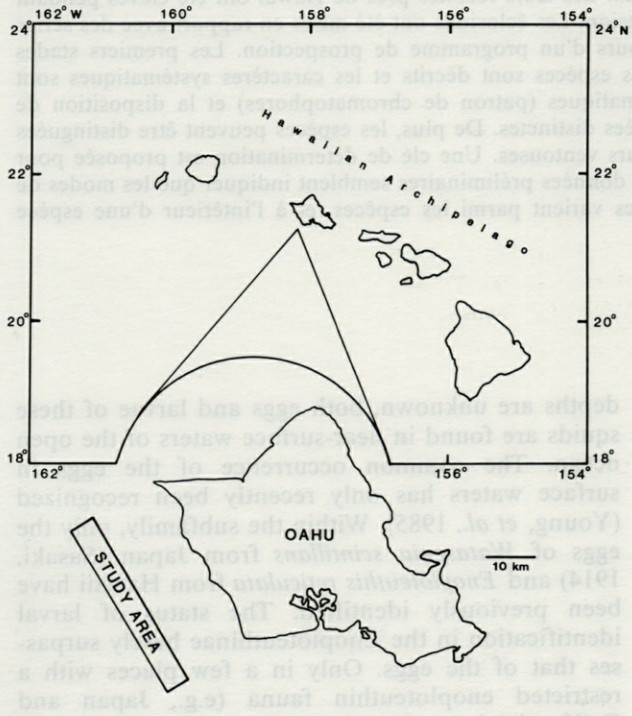


Fig. 1. — Location of study area.

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-

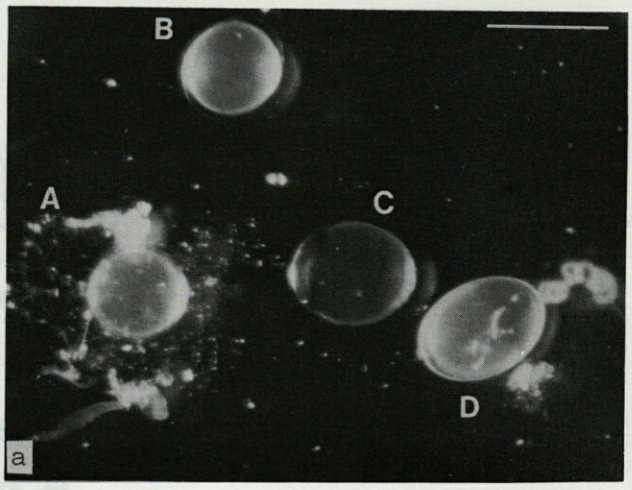
Table I. — Total volume of water sampled (× 1 000 m^3) by depth during the vertical distribution studies.

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.



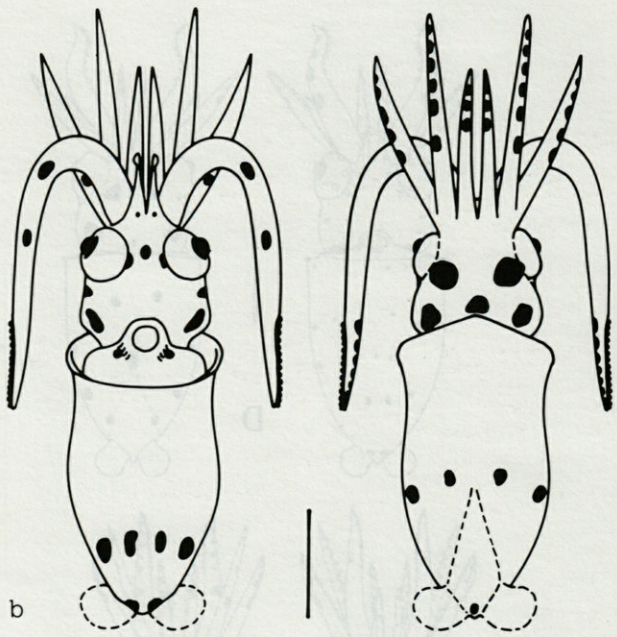


Fig. 2. — a, Photograph of living enoploteuthin eggs. A : *Abralia trigonura* (?), note jelly layer. B : *Enoploteuthis jonesis* (?). C : *Abraliopsis* sp. A. D : *Enoploteuthis reticulata*. Scale bar = 1.0 mm. b, *Abraliopsis* sp. A, 3.0 mm ML, showing unusual chromatophore pattern. Scale bar = 1.0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

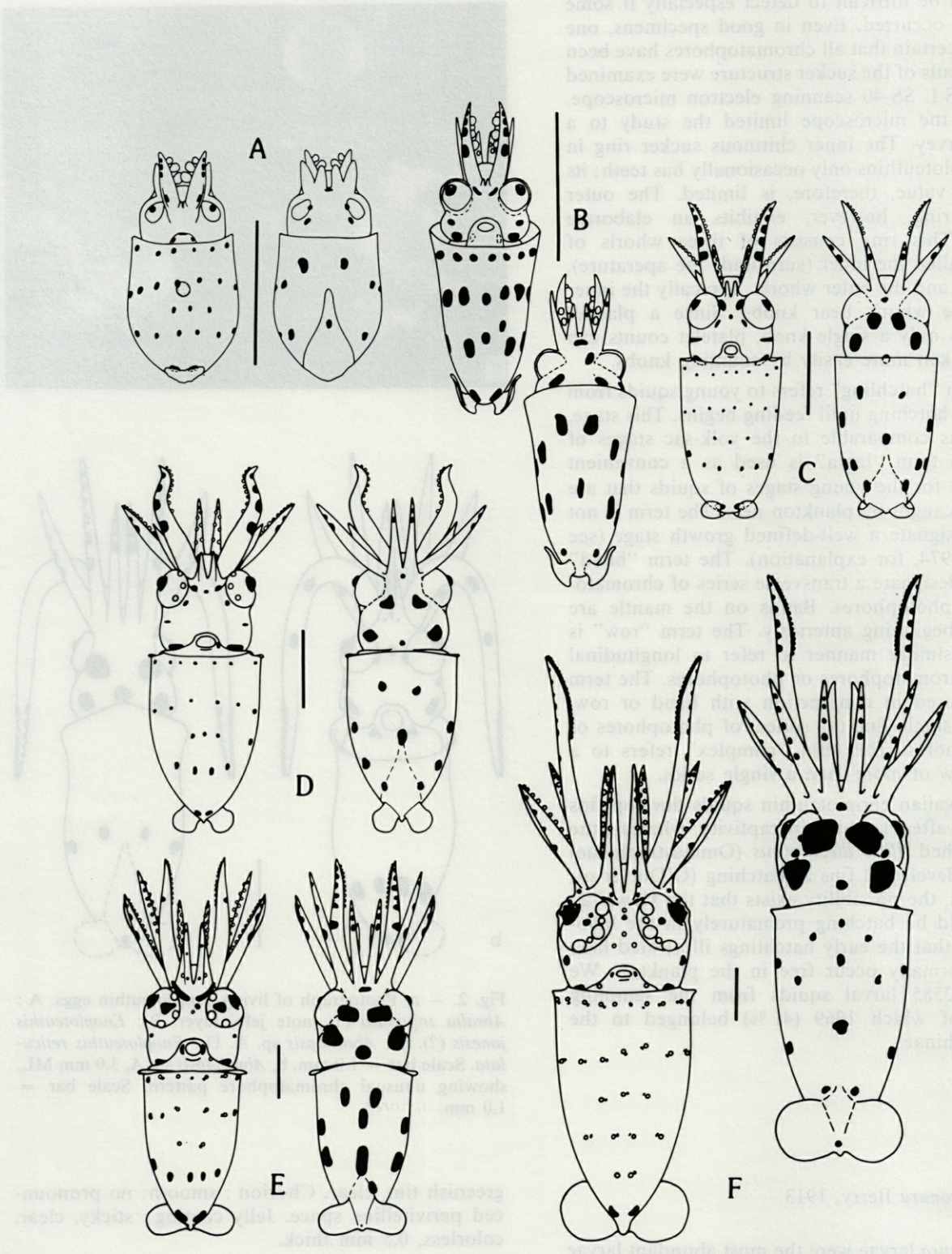


Plate I. — Larval stages of *Abralia trigonura*. A : 1.0 mm ML, at hatching. B : 1.3 mm ML, 7 days after hatching. C : 1.9 mm ML. D : 2.2 mm ML. E : 3.5 mm ML. F : 5.0 mm ML. Scale bars = 1.0 mm.

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

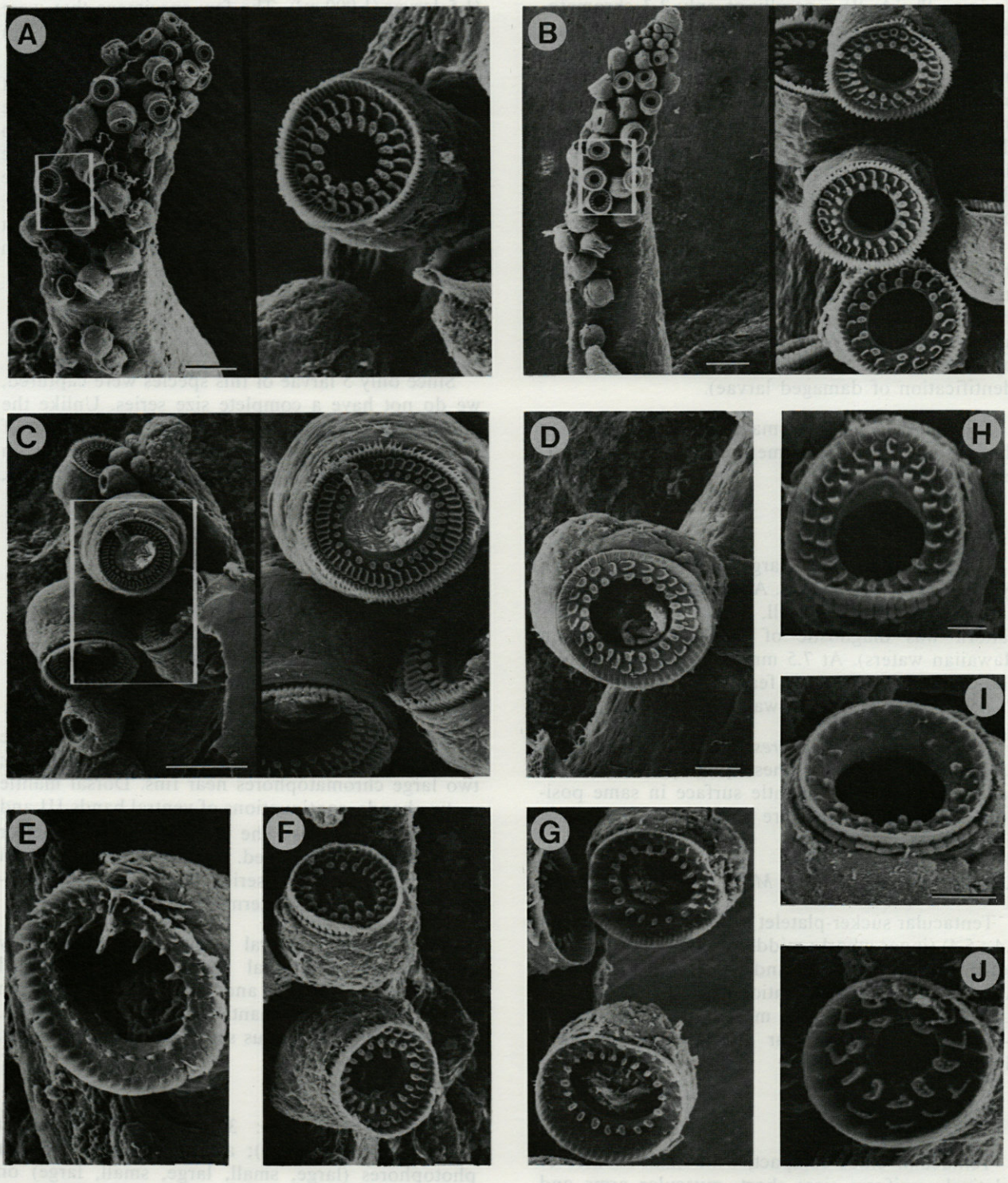


Plate II. — Scanning electron micrographs of tentacular clubs, club suckers and arm suckers. A : Tentacle club of *Abralia trigonura* (3.0 mm ML) with 5X enlarged sucker, scale bar = 1.0 mm. B : Tentacle club of *Abralia astrosticta* (3.5 mm ML) with 5X enlarged sucker, scale bar = 0.1 mm. C : Tentacle 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.

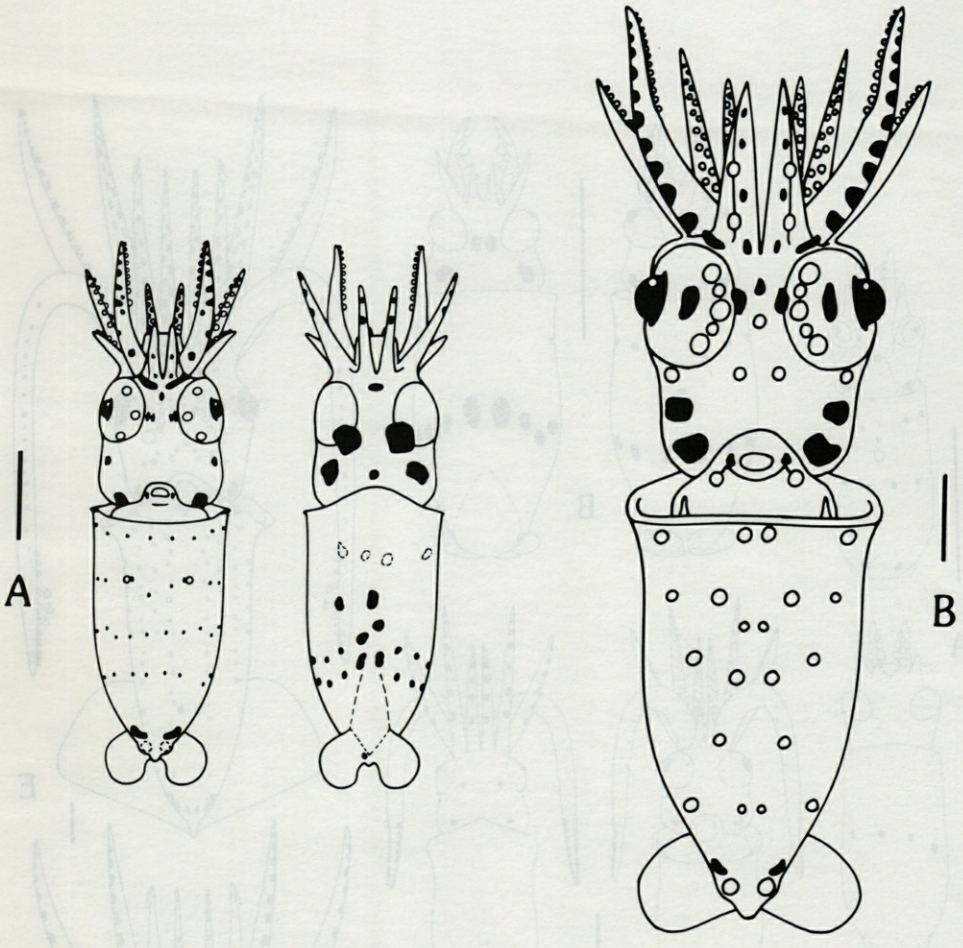


Plate III. — Larval stages of *Abralia astrosticta*. A : 3.2 mm ML. B : 5.5 mm ML. Scale bars = 1 mm.

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,

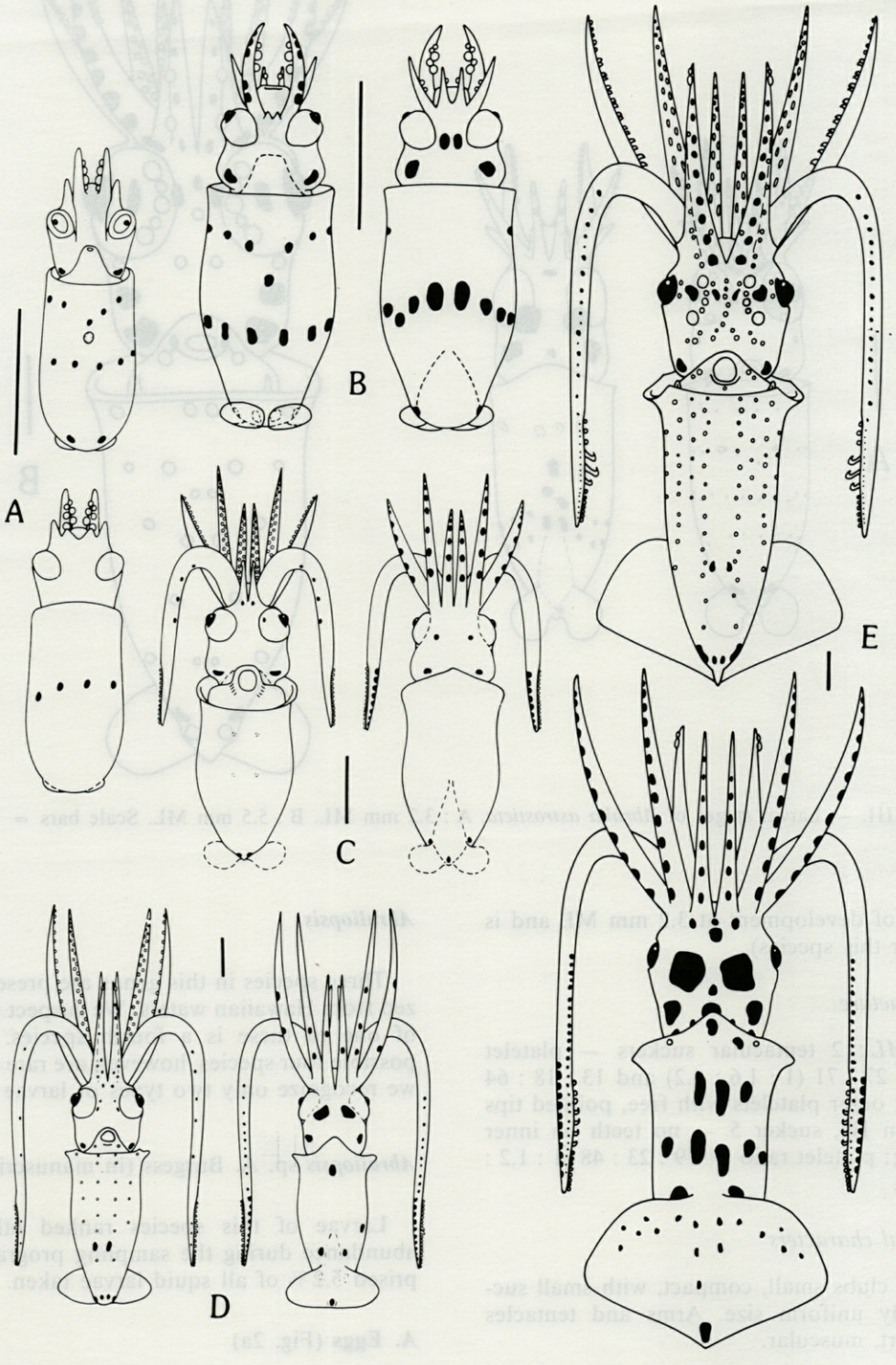


Plate IV. — Larval stages of *Abraliopsis* sp. A. A : 1.3 mm ML, at hatching. B : 1.6 mm ML, 6 days after hatching. C : 3.0 mm ML. D : 4.6 mm ML. E : 8.6 mm ML. Scale bars = 1 mm.

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.

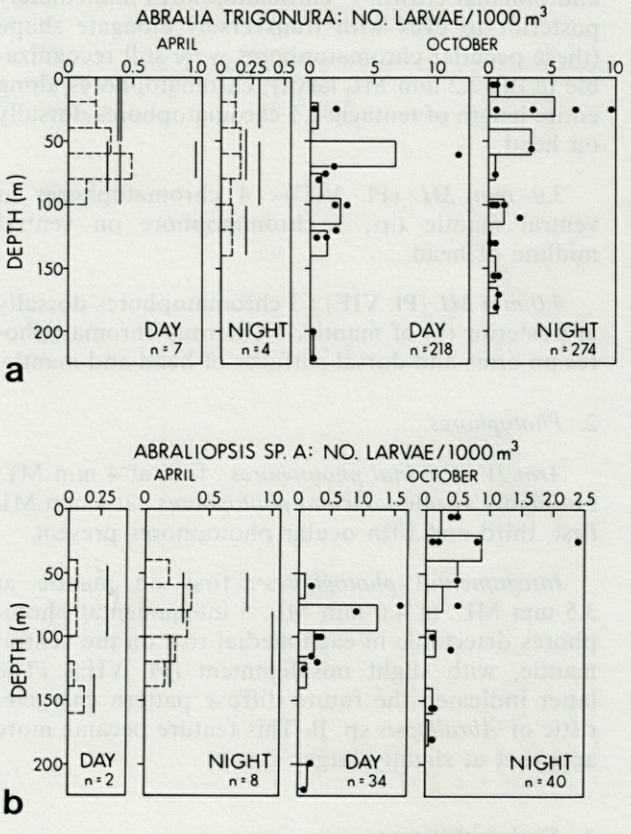


Fig. 3. — a : Vertical distribution of *Abralia trigonura*. In April series, vertical bars represent depth range and capture rates of *positive* opening-closing tows. In October series, dots represent modal fishing depth of *positive* open tows. Histograms represent average catch rates and, therefore, 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.

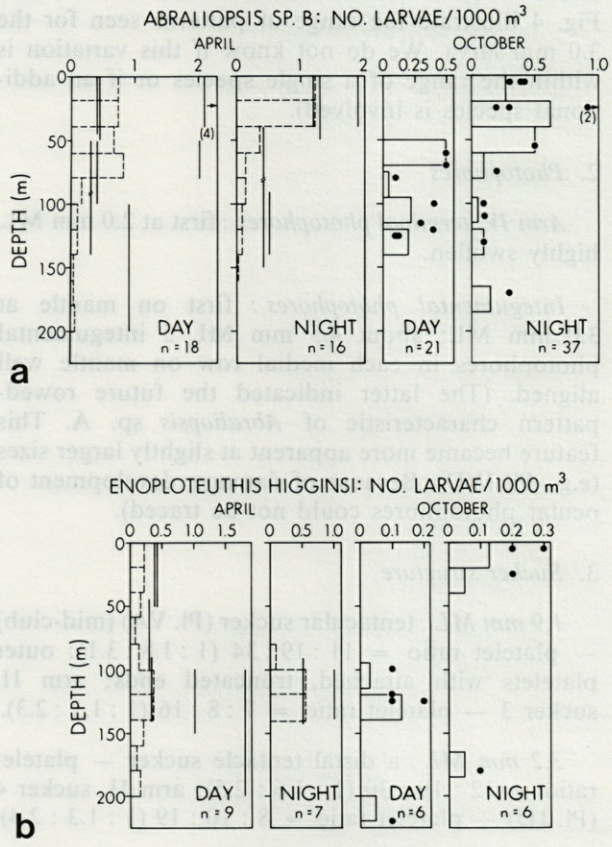


Fig. 4. — a : Vertical distribution of *Abraliopsis* sp. B. Symbols as in Fig. 3 b : Vertical distribution of *Enoploteuthis higginsi.* Symbols as in Fig. 3.

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.

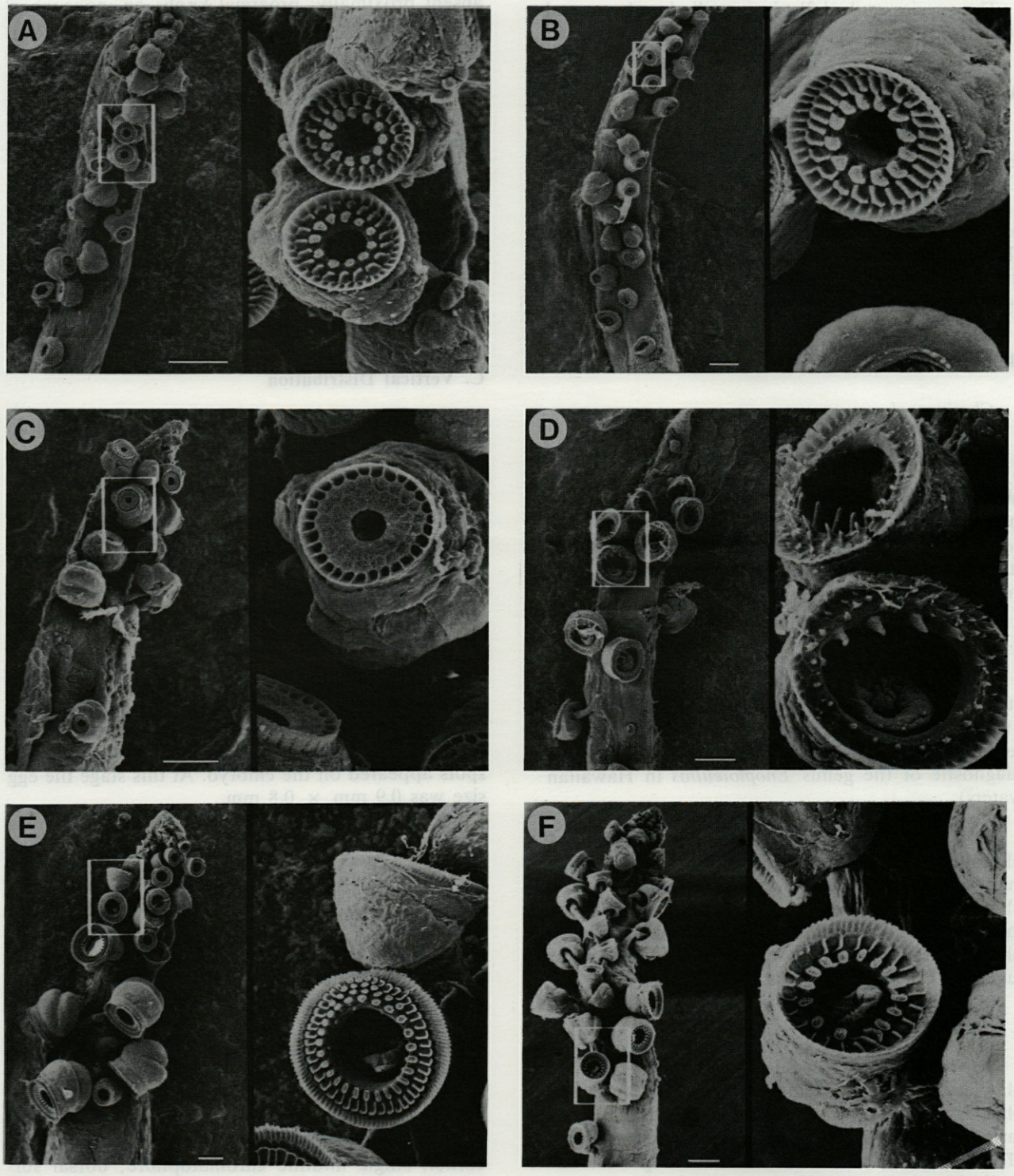


Plate V. — Scanning electron micrographs of tentacular clubs and club suckers. A : *Abraliopsis* sp. A (1.9 mm ML) with 5X enlarged suckers. B : *Abraliopsis* sp. B (3.0 mm ML) with 10 enlarged sucker. C : *Enoploteuthis reticulata* (2.3 mm ML) with 5X enlarged sucker. D : *E. reticulata* (3.3 mm ML)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

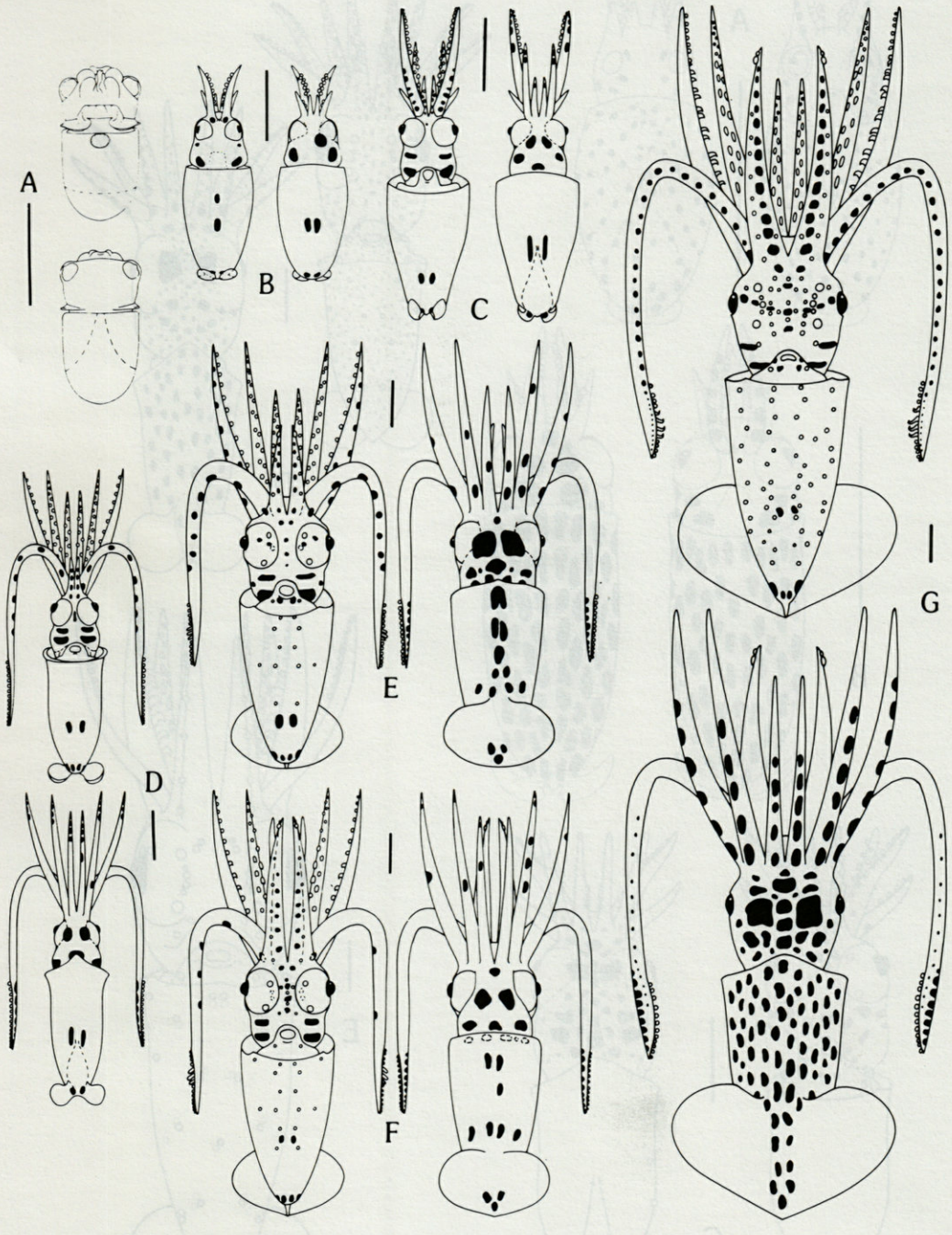


Plate VI. — Larval stages of *Abraliopsis* sp. B. A : 0.9 mm ML, 12 hrs after hatching. B : 1.6 mm ML, 3.5 days after hatching. C : 2.0 mm ML. D : 3.0 mm ML. E : 4.0 mm ML. F : 4.6 mm ML. G : 7.2 mm ML. Scale bars = 1.0 mm.

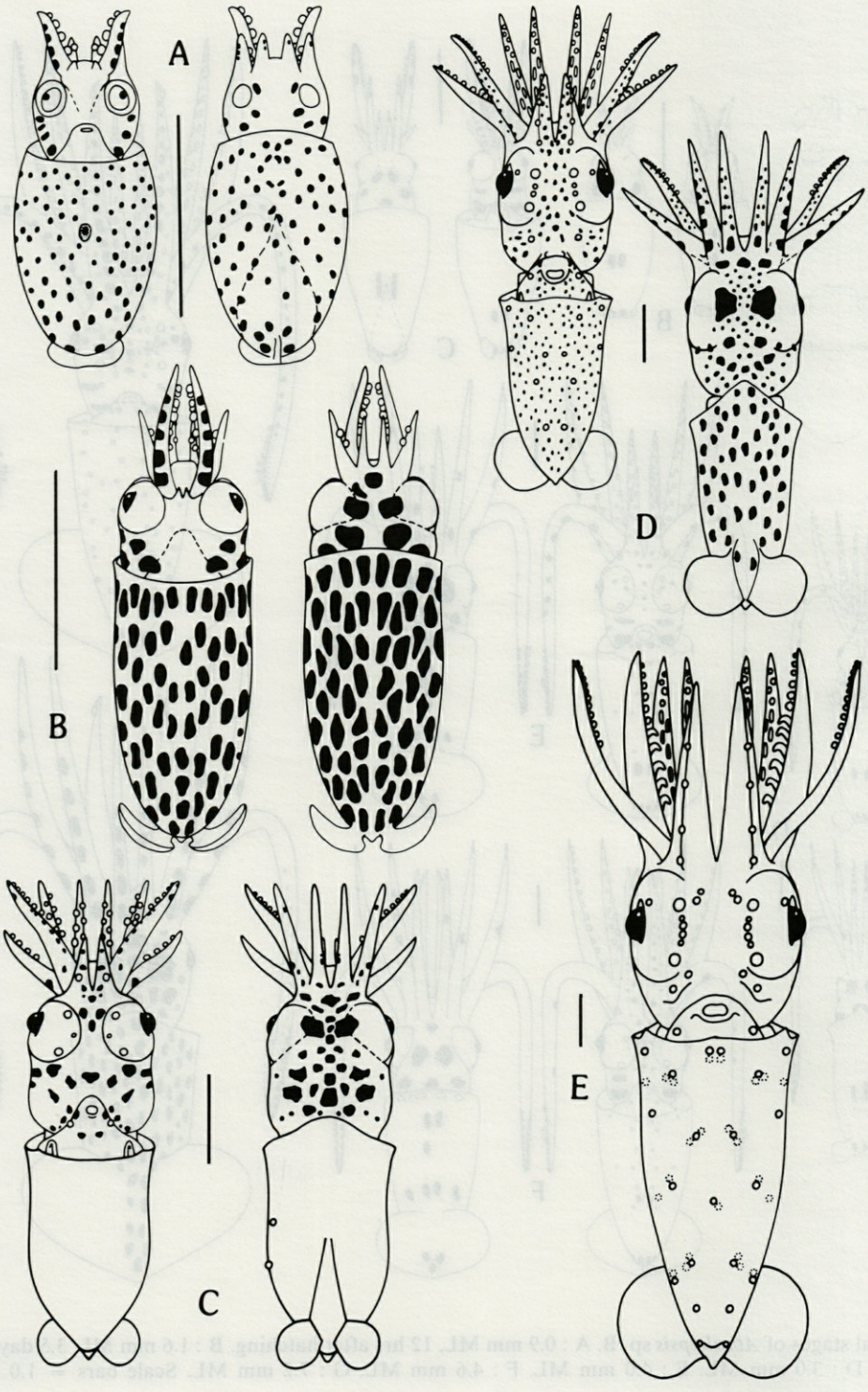


Plate VII. — Larval stages of *Enoploteuthis reticulata*. A : 1.2 mm ML, at hatching. B : 1.5 mm ML, 7 days after hatching. C : 2.8 mm ML. D : 4.1 mm ML. E : 6.8 mm ML. Scale bars = 1.0 mm.

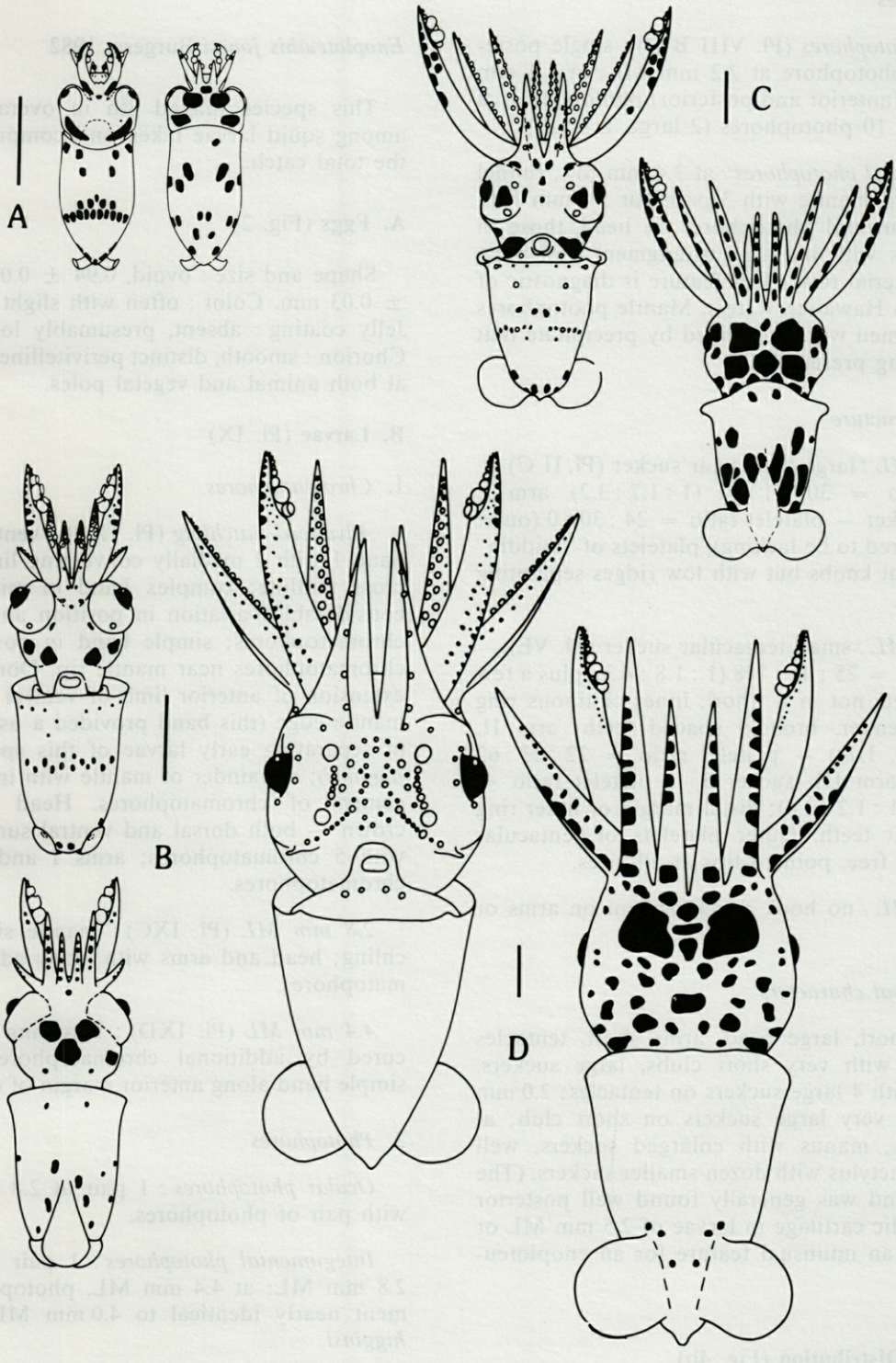


Plate VIII. — Larval stages of *Enoploteuthis higginsi*. A : 1.6 mm ML, 5.5 days after hatching. B : 2.2 mm ML. C : 3.4 mm ML. D : 5.8 mm ML. Scale bars = 1.0 mm.

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).

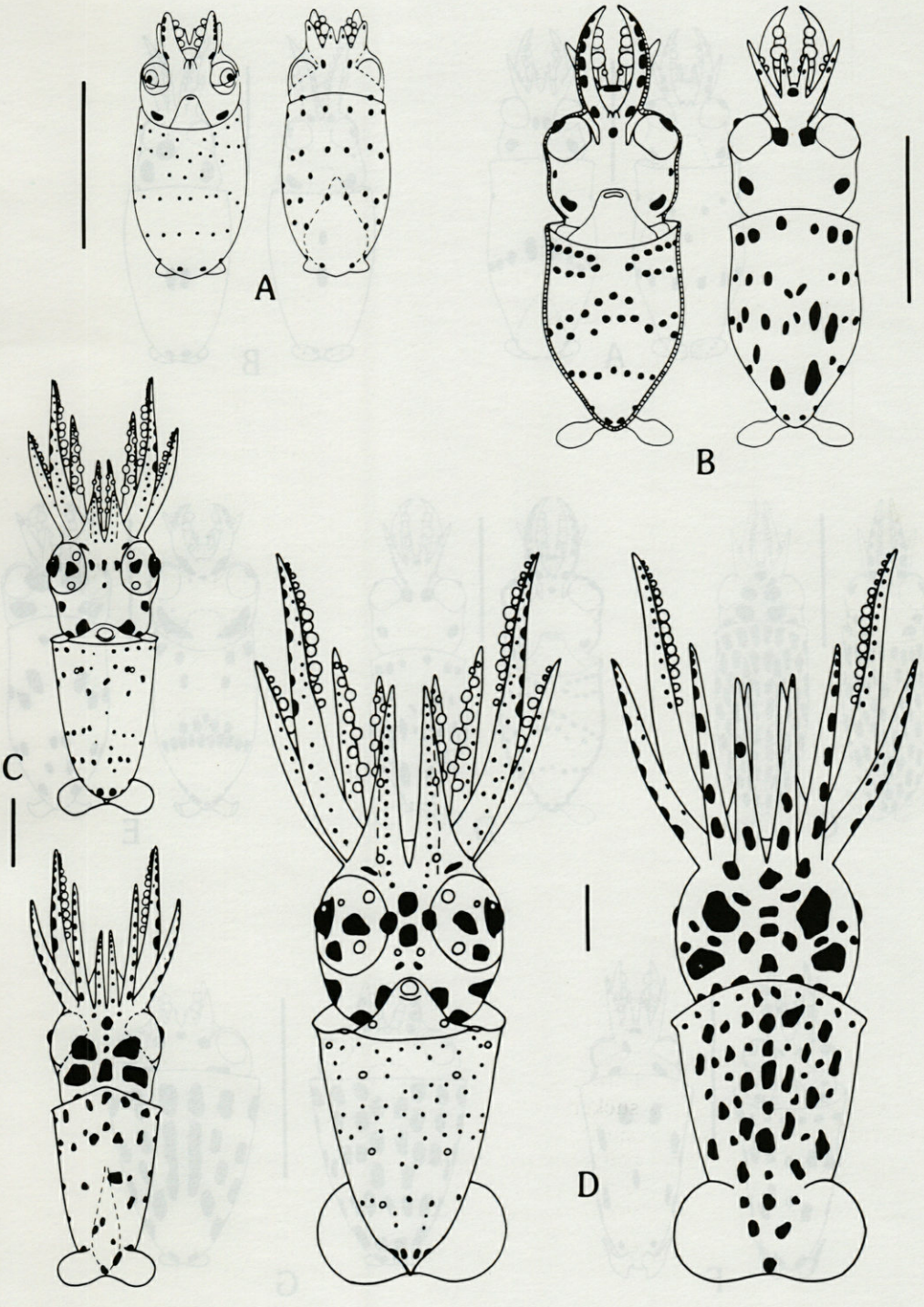


Plate IX. — Larval stages of *Enoploteuthis jonesi*. A : 1.1 mm ML, at hatching. B : 1.3 mm ML, 7 days after hatching. C : 2.8 mm ML. D : 4.4 mm ML. Scale bars = 1.0 mm.

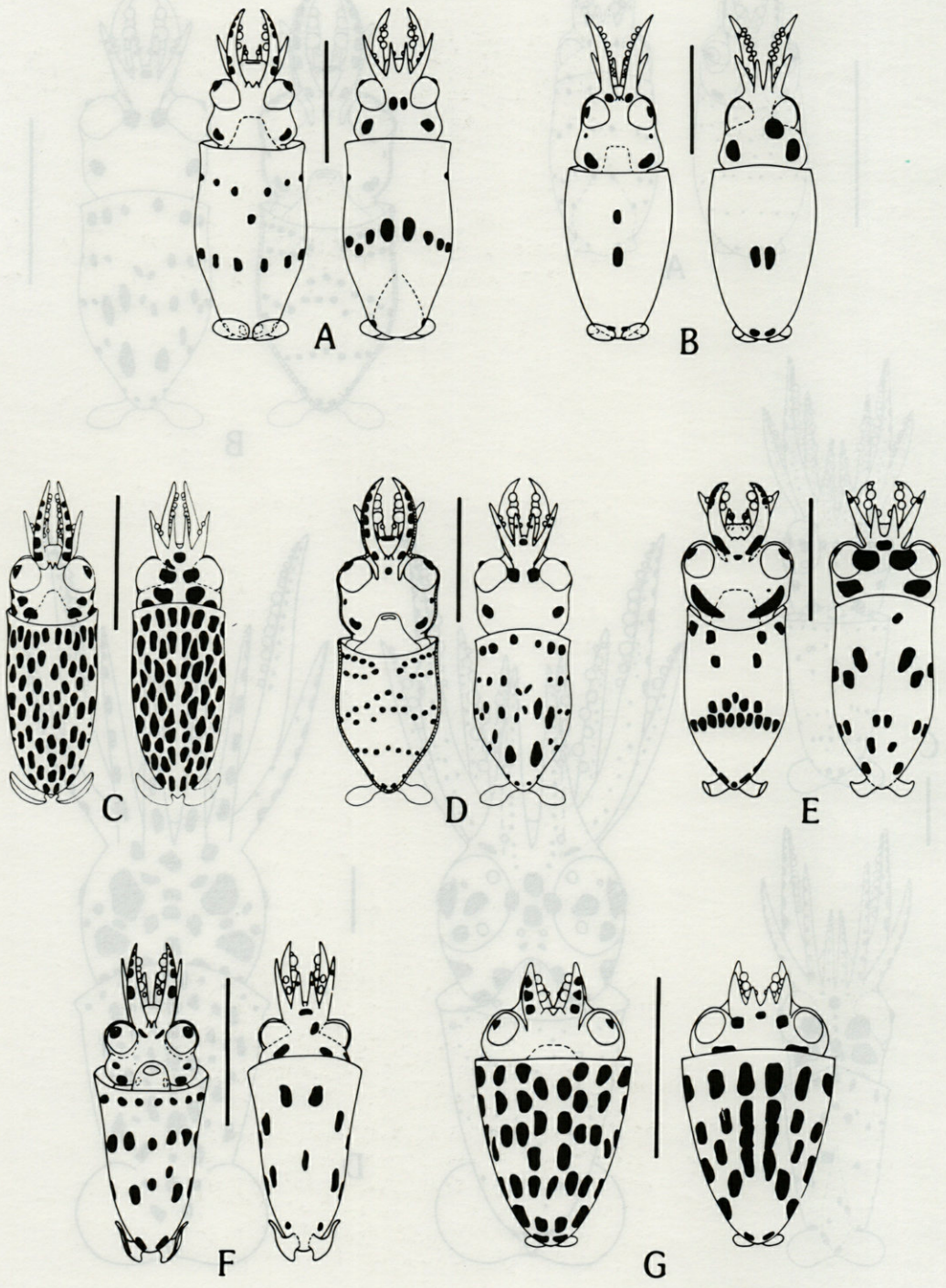


Plate X. — Enoploteuthin hatchling, several days after hatching. A : *Abraliopsis* sp. A (1.6 mm ML). B : *Abraliopsis* sp. B (1.6 mm ML). C : *Enoploteuthis reticulata* (1.5 mm ML). D : *Enoploteuthis jonesi* (1.3 mm ML). E : *Enoploteuthis higginsi* (1.6 mm ML). F : *Abralia trigonura* (1.3 mm ML). 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

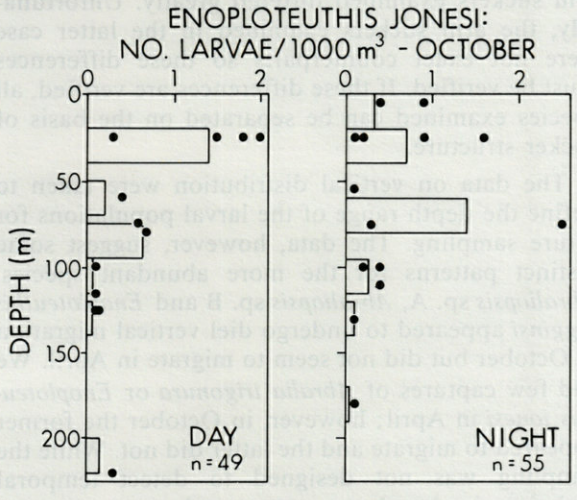


Fig. 5. — Vertical distribution of *Enoploteuthis jonesi.* Symbols as in Fig. 3.

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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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

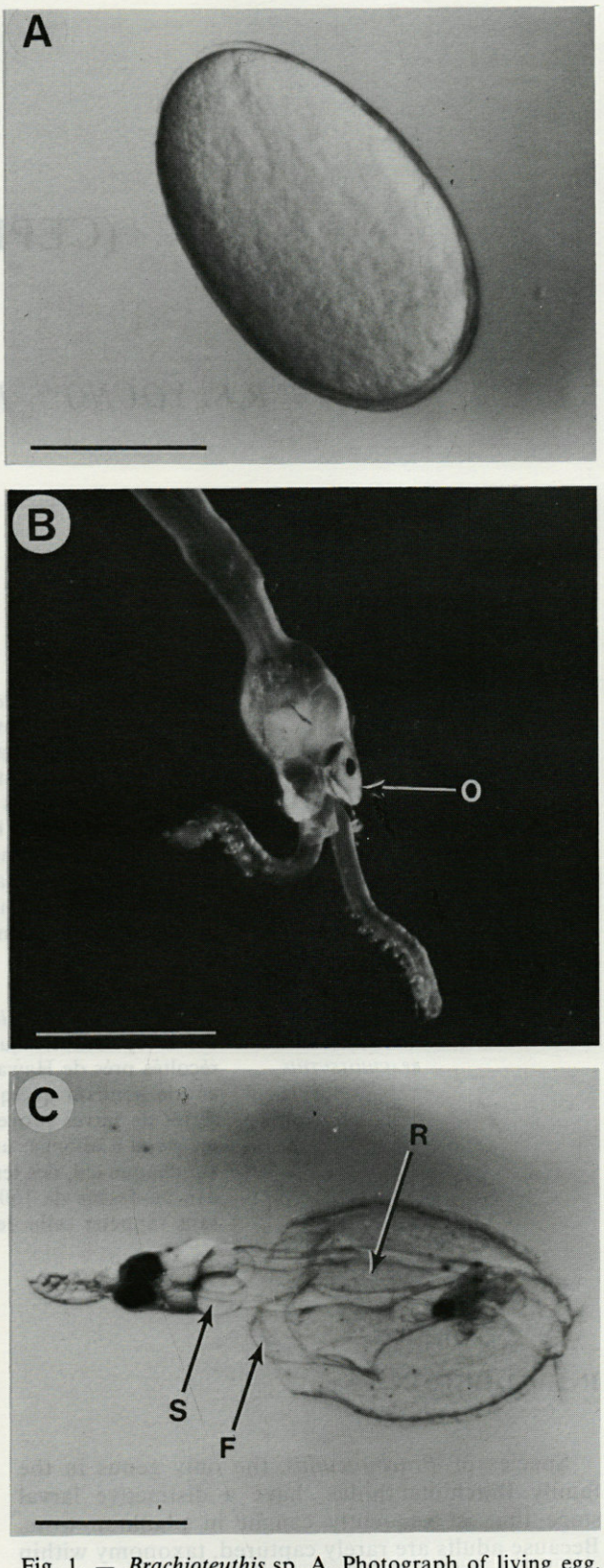

Fig. 1. — *Brachioteuthis* sp. A, Photograph of living egg. Scale bar = 0.5 mm; B, Photograph of freshly-captured 6 mm ML larva. O = ocular appendage. Scale bar = 2.0 mm; C, Photograph of living hatchling (2.0 mm ML) with neck partially contracted. F = funnel, R = reservoir, S = statocyst, Scale bar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

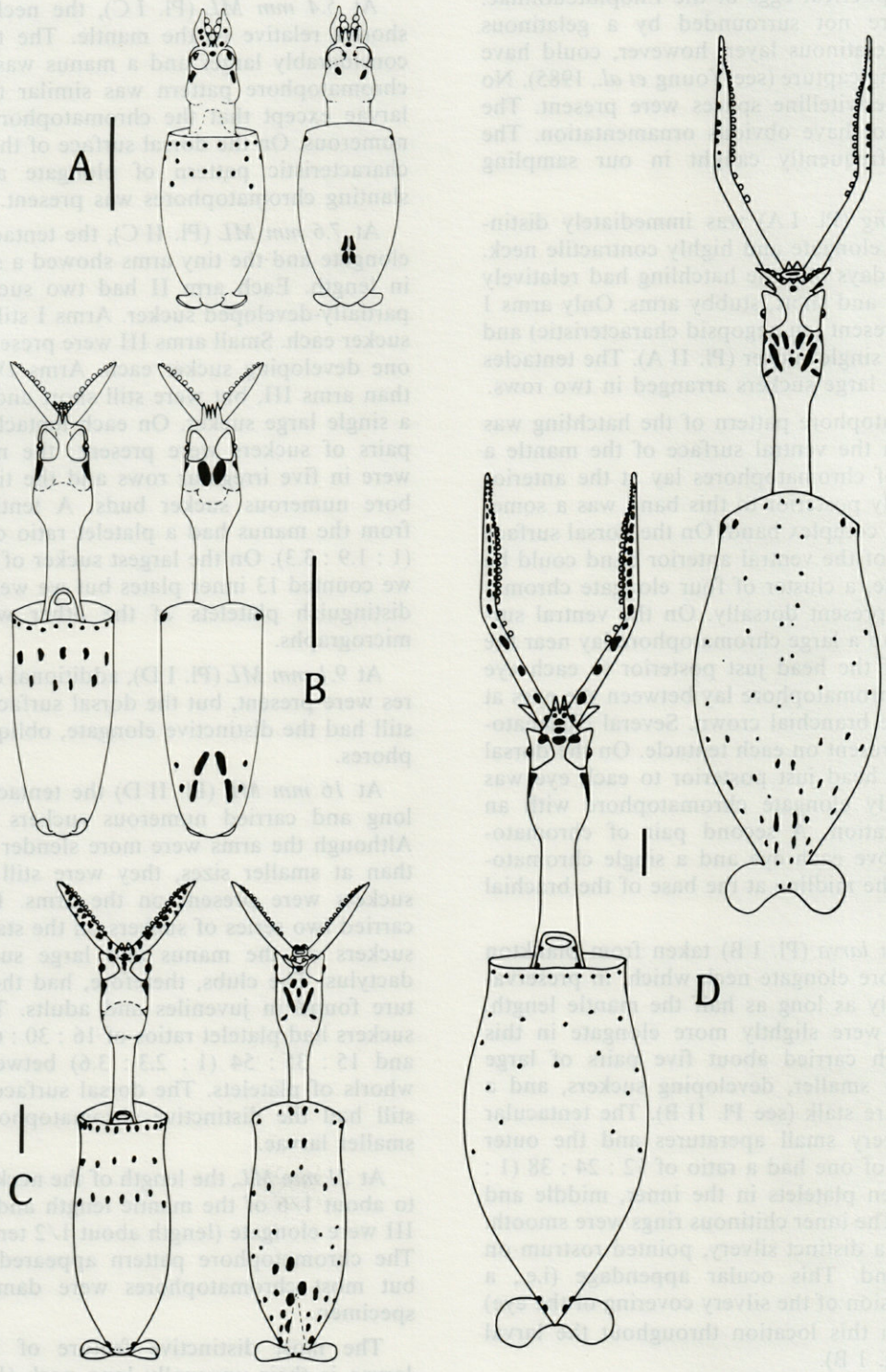

Plate I. — Larvae of *Brachioteuthis* sp. : A, 2.0 mm ML, 5 days after hatching; B, 2.6 mm ML; C, 5.4 mm ML; D, 9.1 mm ML. Scale bar = 1 mm.

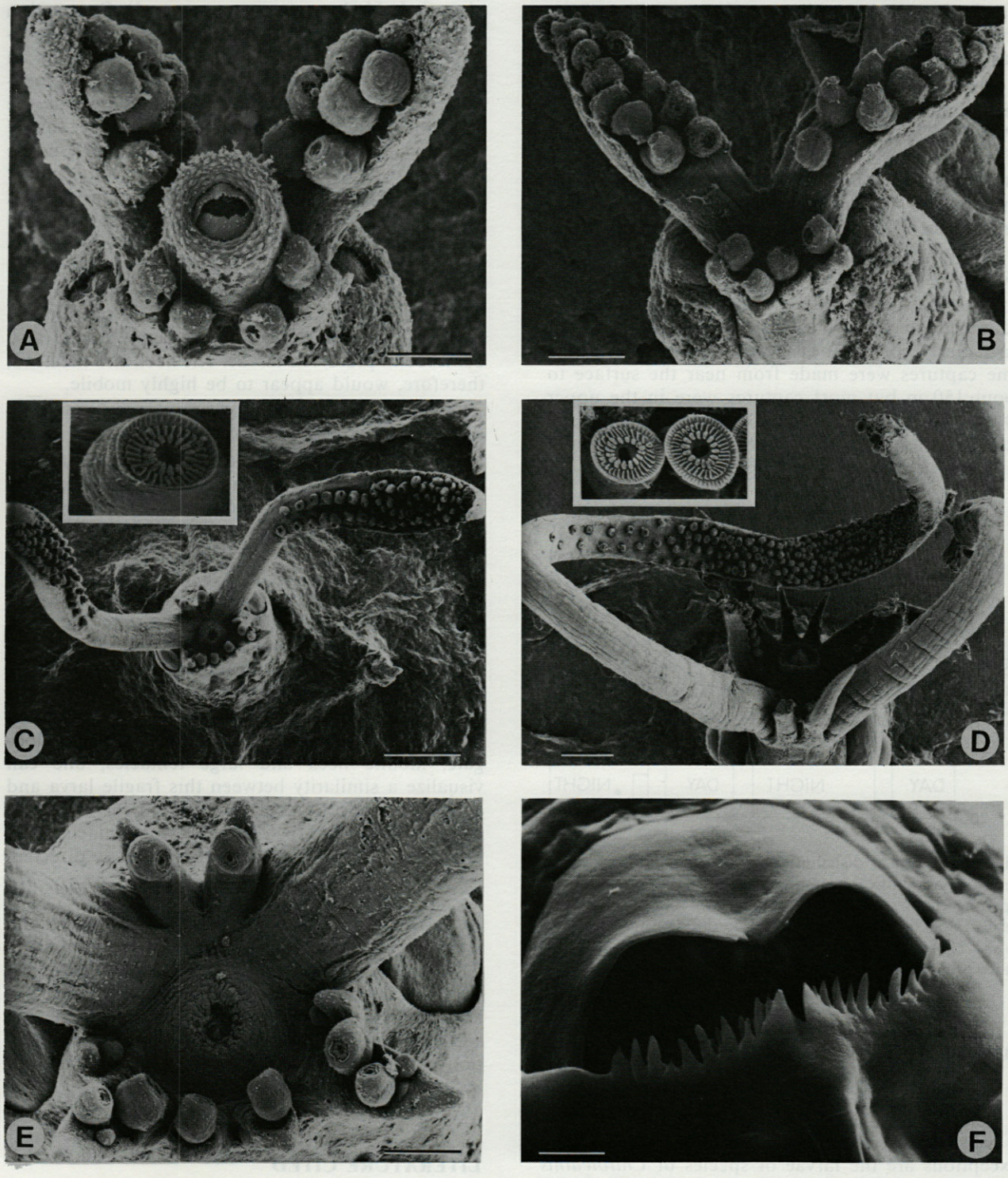

Plate II. — Scanning electron micrographs of *Brachioteuthis* sp. A, 2.1 mm ML hatchling, scale bar = 0.1 mm; B, 2.5 mm ML, scale bar = 0.1 mm; C, 7.6 mm ML, scale bar = 0.5 mm, insert is 10x enlargement of sucker from manus; D, 16 mm ML, scale bar = 0.5 mm, insert is 10x enlargement of sucker from manus; 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.

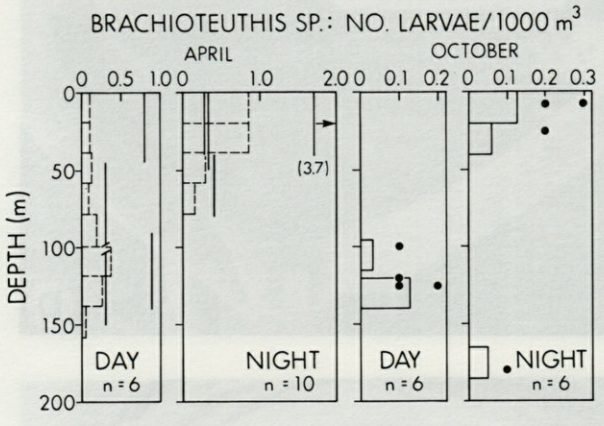

Fig. 2. — Vertical distribution of *Brachioteuthis* sp. April series : bars indicate depth range and capture rate of opening-closing tows; only positive tows shown. October series : dots indicate catch rate at modal depth for positive tows. Histograms indicate average capture rates and, therefore, include 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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THE LARVAE OF OMMASTREPHID SQUIDS (CEPHALOPODA, TEUTHOIDEA) FROM HAWAIIAN WATERS

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HAWAII
LARVAE
OMMASTREPHIDAE
CEPHALOPODA
VERTICAL DISTRIBUTION

ABSTRACT. — Rhynchoteuthion larvae of three species of ommastrephid squids from Hawaiian waters were identified, and aspects of their ecology examined. Important taxonomic characters for field identification include the number and location of photophores, length of the proboscis (fused tentacles), size at which the proboscis completely divides and the relative sizes of the suckers on the proboscis tip. Other taxonomic characters include sucker structure and chromatophore patterns. Variation among species were found in both temporal and vertical distributions.

HAWAI
LARVES
OMMASTREPHIDAE
CEPHALOPODA
DISTRIBUTION VERTICALE

RÉSUMÉ. — Des larves rhynchoteuthion de trois espèces d'Ommastrephidés des eaux de Hawai ont été identifiées, et leur écologie a été étudiée. Parmi les caractères importants permettant une identification rapide figurent le nombre et la disposition des photophores, la longueur de la trompe (tentacules fusionnés), la taille à laquelle les tentacules se séparent et la taille relative des ventouses placées à l'extrémité de la trompe. La structure des ventouses et la livrée chromatique (patron de chromatophores) constituent d'autres caractères taxonomiques. Des variations spécifiques existent quant à la distribution temporelle et bathymétrique.

INTRODUCTION

Squids of the family Ommastrephidae are among the largest and most numerous cephalopods in the open ocean. They are fast-swimming predators that feed in near-surface waters at night on fish, crustaceans and cephalopods (e.g., Wormuth, 1976). In turn, these squids are important prey (sometimes primary prey) for larger predators such as tunas (e.g., King and Ikehara, 1956), sharks (T. Clarke, 1971) and toothed whales (e.g., M. Clarke, 1980). Juveniles are heavily preyed upon by birds (e.g., Harrison *et al.*, 1983). Ommastrephids form the basis for the major squid fisheries of the world. Despite their importance, knowledge of the biology and ecology of these squids is very limited. Large information gaps result from our inability to effectively sample the fast-swimming juveniles and adults (e.g., Wormuth and Roper, 1983).

Three species of ommastrephids are resident in waters around the Hawaiian Archipelago : *Sthenoteuthis* (= *Symplectoteuthis*) *oualaniensis* (nomenclature follows Zuev *et al.*, 1975), *Hyaloteuthis pelagica* and *Nototodarus hawaiiensis*. A fourth species, *Ommastrephes bartrami*, is occasionally seen in Hawaiian waters, but apparently does not spawn there. The three common species are very different from one another in morphology and habitat. *S. oualaniensis*, which reaches about 315 mm ML in Hawaiian waters (Burgess, 1970), ranges throughout the oceanic tropical and subtropical Indo-Pacific region (Wormuth, 1976). *Sthenoteuthis* adults are often seen near the surface at night, and although their depth range, both during the day and night, is unknown (Young, 1975), this species is not generally found in waters where the bottom depth is shallower than 500 m. The presence of juvenile *Sthenoteuthis* in the stomachs of day-feeding seabirds suggests a shallow daytime habitat for that size class (Ashmole and

Ashmole, 1967). *H. pelagica,* which reaches about 85 mm ML in these waters (Burgess, 1970), is an oceanic, cosmopolitan, tropical and subtropical species (Wormuth, 1976); *Hyaloteuthis* has been caught at 100 m at night by trawl, but it has not been seen at nightlights around Hawaii. During the day it has been caught near 2 000 m, although its normal habitat is unknown (Young, 1978). *N. hawaiiensis* has been recorded only from neritic and slope waters of the Hawaiian Archipelago and eastern Australia (Dunning, this vol.). This species is associated with island land masses and has been caught near the bottom from 230 m to 710 m during the day and from the surface to 410 m at night (Yuen, 1979; Young, 1978). It reaches about 160 mm ML around Hawaii (Taguchi *et al.,* 1985).

Since the adults of these species cannot be quantitatively sampled with standard gear, assessment of larval abundance and biology could provide indications of adult population parameters. As a first step toward this objective, we examine here the taxonomy of the Hawaiian ommastrephid larvae and some general aspects of their ecology.

The larvae of ommastrephid squids are distinguished from those of other families by the fusion of the two tentacles into a proboscis. The tentacles, which are initially fused along their entire length, terminate with a disc bearing eight suckers. As the squid grows, the proboscis divides from the base, until the tentacles are separate and the suckers of the terminal disc (which also divides) become part of the developing tentacular clubs (Roper and Lu, 1979). The young squids are known as rhynchoteuthion larvae until the proboscis completes division.

Although ommastrephid squids have a distinctive larval type, species identification of larvae has proven difficult and, for most species, positive identification is not yet possible. Certain rhynchoteuthion larvae from Japanese and adjacent waters have been thought to be *S. oualaniensis* largely on the basis of their very elongate proboscis (e.g., Okutani and Tung, 1978; Matsuda *et al.,* 1972). Nesis (1979) also described larvae that he thought were *S. oualaniensis.* Otherwise, little is known about the identity of larvae of the three species found in Hawaiian waters. The limited number of species that spawn near Hawaii has simplified their identification.

MATERIALS & METHODS

Plankton tows were taken with a variety of gear types to investigate the temporal abundance of the three species and their vertical distribution. All of the stations occupied lay within the study area defined in Figure 1, which was 11-20 km off the Waianae coast of Oahu (approximately 21° 15' N × 158° 20'W), roughly over the 2 000 m depth contour. Additional specimens taken for taxonomic purposes came from other areas in the archipelago. Each of the nets used had 0.505 mm mesh, a TSK model 1201 flowmeter and a Benthos time-depth recorder. The specimens in this study were fixed in 4 % formalin and preserved in 40 % isopropanol.

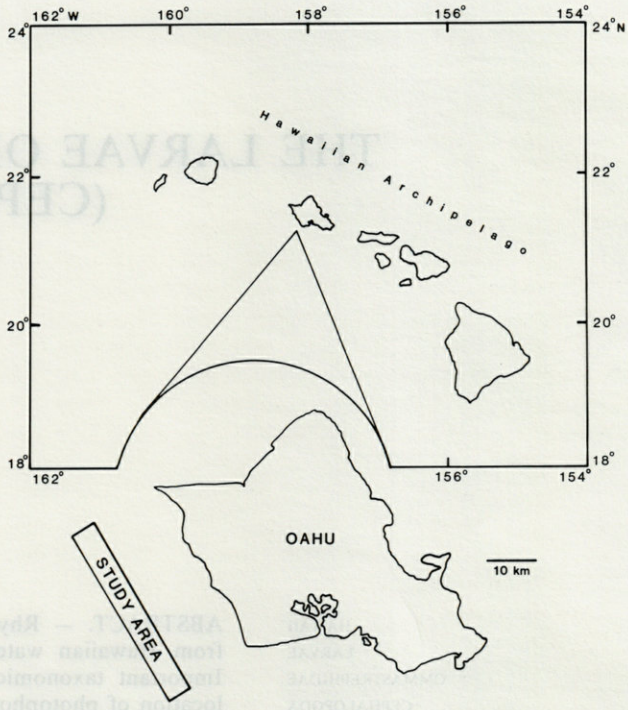

Fig. 1. — Location of study area within Hawaiian Archipelago.

The proboscis length was measured ventrally from the base (at the insertion of the tentacles near the third arms) to the tip (excluding the suckers), and proboscis indices (ratio of proboscis length to mantle length) were calculated for each species. Since the sizes of the proboscis suckers were affected by muscular contraction, sucker measurements were taken from the outer chitinous sucker rings. These rings possess three concentric whorls of platelets. The inner and middle whorls bear strongly-projecting knobs and the outer whorl does not. A Cambridge Stereoscan S-4 scanning electron microscope (SEM) was used for measuring the sucker rings and counting the knobs for three specimens of each species. The SEM was also used to look for differences in beak dentition. Differences in sizes and meristic counts were tested with t-tests or Mann-Whitney U-tests (Sokal and Rolf, 1981), and results of statistical tests were considered significant if p-values were < 0.05.

In December 1983, fourteen 30 minute horizontal and oblique tows were taken from the University of Hawaii's research ship R/V KANA KEOKI with an open 4-m^2 net and open, paired 70-cm Bongo nets,

ranging from the surface to 100 m. Although these tows were taken for other purposes, they provided some abundance data.

During April 1984, forty 30 minute tows were taken from the KANA KEOKI with opening-closing, paired 70-cm Bongo nets. The nets were towed obliquely through specific depth horizons during the day and night. This series was designed to uniformly sample 50 m depth strata in the upper 200 m and 100 m strata from 200-300 m. Placement of the nets was imprecise due to the lack of on-line feedback on net depth. Because of variations in the depth ranges sampled, the catch for each tow was divided into 10 m depth intervals for subsequent regrouping. Subdivision of the catch was based on the assumption that the catch rates were uniform over the entire depth range of the tow. Total catch rates were calculated by dividing the number of larvae caught in all tows in a given 10 m interval by the total volume of water sampled in that depth interval. These catch rates were then regrouped into 20 m intervals and plotted as histograms.

In August 1984, eight tows were taken from the University's research ship R/V KILA for seasonal and relative abundance data. These were 30-minute oblique tows from 150 m to the surface. All were taken with the open 4-m^2 net and all were taken during the day due to wire-time restrictions.

A second vertical distribution series was performed in October 1984 from the KILA. Forty 30-minute and 45-minute horizontal tows were taken with the open 4-m^2 net, ranging in depth from the surface to 220 m. The longer tows were taken at the deeper stations to insure that the time at depth was long compared with the transit time to and from this depth. Our intent was to sample depths of 5, 25, 75, 125 and 200 m, but our net placement was not precise. Samples were taken during both day and night. Analyses of these October vertical distribution data were somewhat different from the April data. The entire catch from a tow was assumed to have been caught at the net's modal depth during that tow. Both individual catch rates and histograms of mean catch rates were plotted by super-imposing the latter on the former in arbitrarily-located 20 m increments for each species. Table I shows the depths sampled and the total volume of water sampled at each depth for the April and October vertical distribution series.

Table I. — Total volume of water sampled ($\times$ 1000 m^3) by depth during vertical distribution series.

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 larvae collected fell into three distinct morphological groups, which could be followed through size-series to identifiable juveniles. Young larvae (about 2.0 mm ML) had dentition on the rostrum of the lower beak that was not distinguishible among the three species. By 4.0 mm ML, no trace of this dentition remained. The three species had identical dorsal and ventral head chromatophore patterns. As a result, neither of these characters was useful in species identification. Mantle chromatophore patterns were difficult to use due to frequent loss during capture. Juvenile and adult *S. oualaniensis* have fused funnel-mantle locking cartilages. Unfortunately, the fusion occurs at sizes of about 10-12 mm ML and larger and, therefore, is of no use in larval systematics.

Species Diagnoses

Nototodarus hawaiiensis (Berry, 1912)

1. Proboscis length (Fig. 2): typically short;

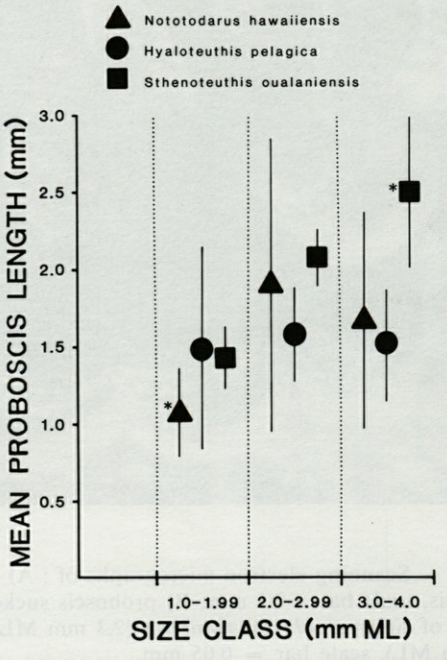

Fig. 2. — Mean proboscis length vs. mantle length by size class for specimens with non-dividing probosces. Bars are 95 % confidence limits. Asterisk denotes significant difference from others in the size class.

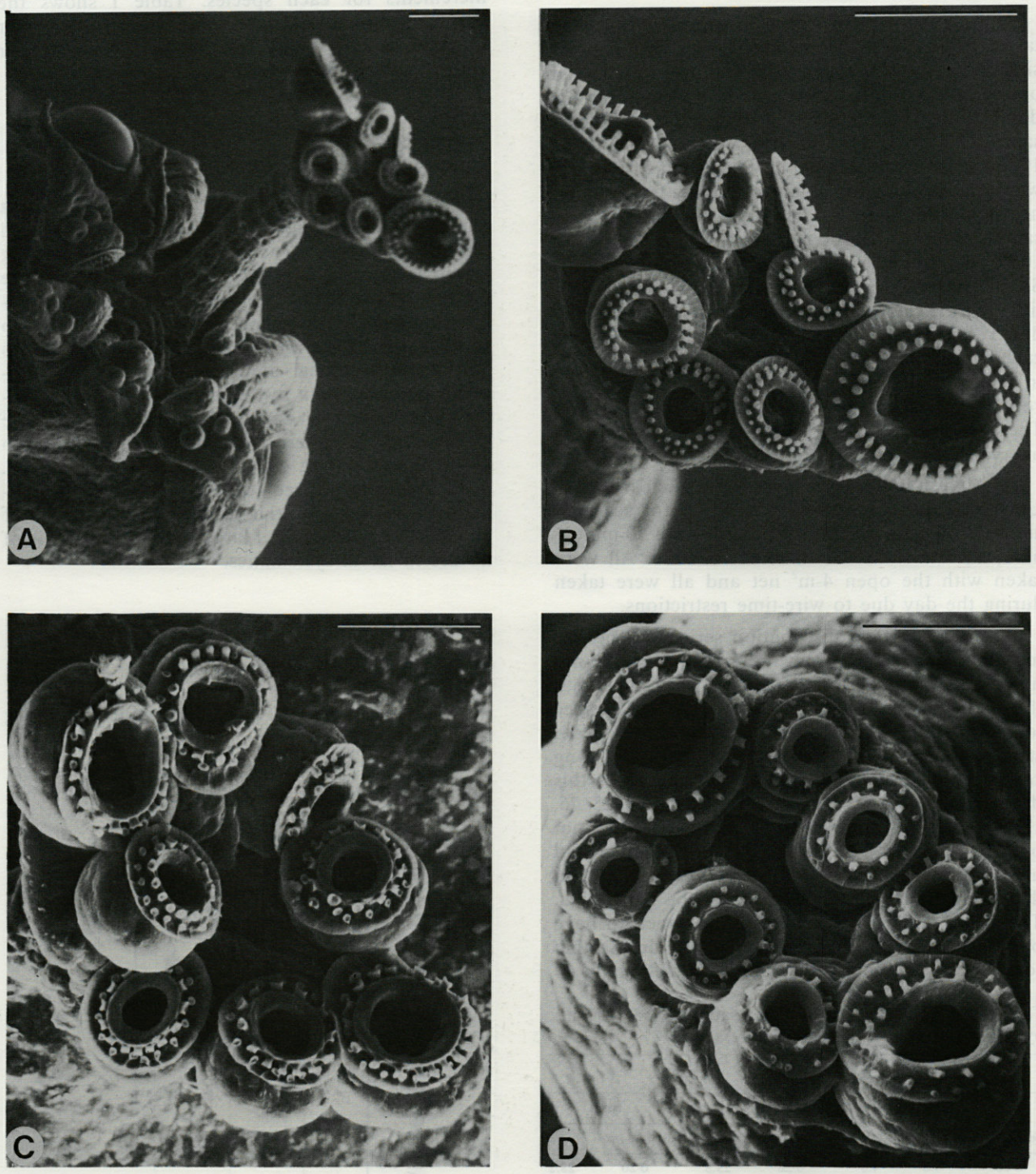

Plate I. — Scanning electron micrographs of : A) oral crown of *Nototodarus hawaiiensis* (1.1 mm ML) showing arms and proboscis, scale bar =0.1 mm; B) proboscis suckers of *N. hawaiiensis* (1.1 mm ML), scale bar = 0.1 mm; C) proboscis suckers of *Sthenoteuthis oualaniensis* (2.3 mm ML), scale bar = 0.05 mm; D, proboscis suckers of *Hyaloteuthis pelagica* (1.8 mm ML), scale bar = 0.05 mm.

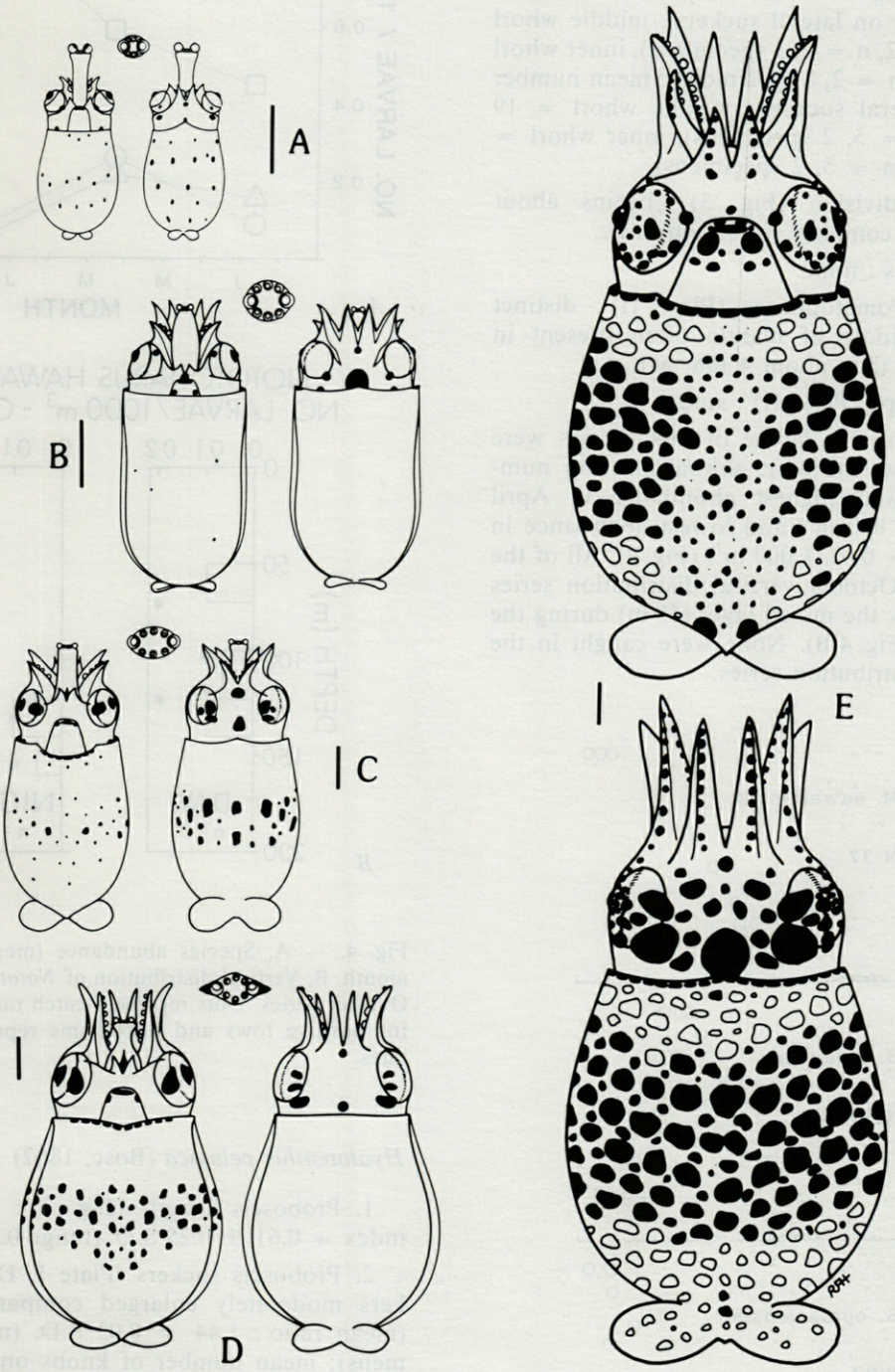

Plate II. — Larval stages of *Nototodarus hawaiiensis* (dorsal and ventral views) : A) 1.7 mm ML; B) 3.0 mm ML; C) 4.5 mm ML; D) 5.8 mm ML; E) 9.2 mm ML. Inserts show proboscis tips. Scale bar = 1.0 mm.

mean proboscis index = 0.56 ± 0.29 S.D. (range 0.24-1.14, n = 33).

2. Proboscis suckers (Plate I, B) : lateral 2 suckers greatly enlarged compared to medial 6 (mean ratio 1.67 ± 0.19 S.D., n = 32, 3 specimens); mean number of knobs on lateral suckers : middle whorl = 32 (range 31-32, n = 2, 2 specimens), inner whorl = 25 (range 25, n = 2, 2 specimens); mean number of knobs on lateral suckers : middle whorl = 19 (range 18-21, n = 5, 2 specimens), inner whorl = 17 (range 15-18, n = 5, 2 specimens).

3. Proboscis division (Fig. 3) : begins about 3.0-4.0 mm ML; complete by 8.5 mm ML.

4. Photophores : none.

5. Mantle chromatophores (Plate II) : distinct band around middle of mantle often present in specimens larger than about 4 mm ML.

6. Mantle shape (Plate II) : stout.

7. Distribution : the larvae of this species were present throughout the year, although in low numbers. They showed highest abundance in April (mean = 0.21/1 000 m^3) and lowest abundance in October (mean = 0.02/1 000 m^3) (Fig. 4). All of the captures in the October vertical distribution series were made below the mixed layer (50 m) during the day and night (Fig. 4,B). None were caught in the April vertical distribution series.

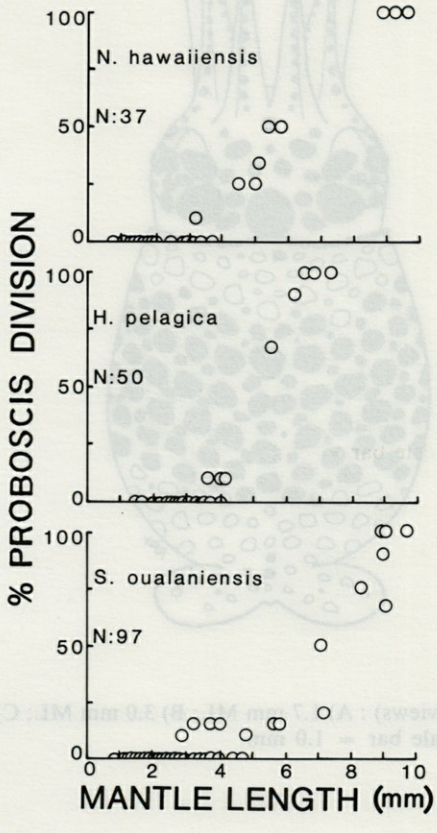

Fig. 3. — State of proboscis division by size.

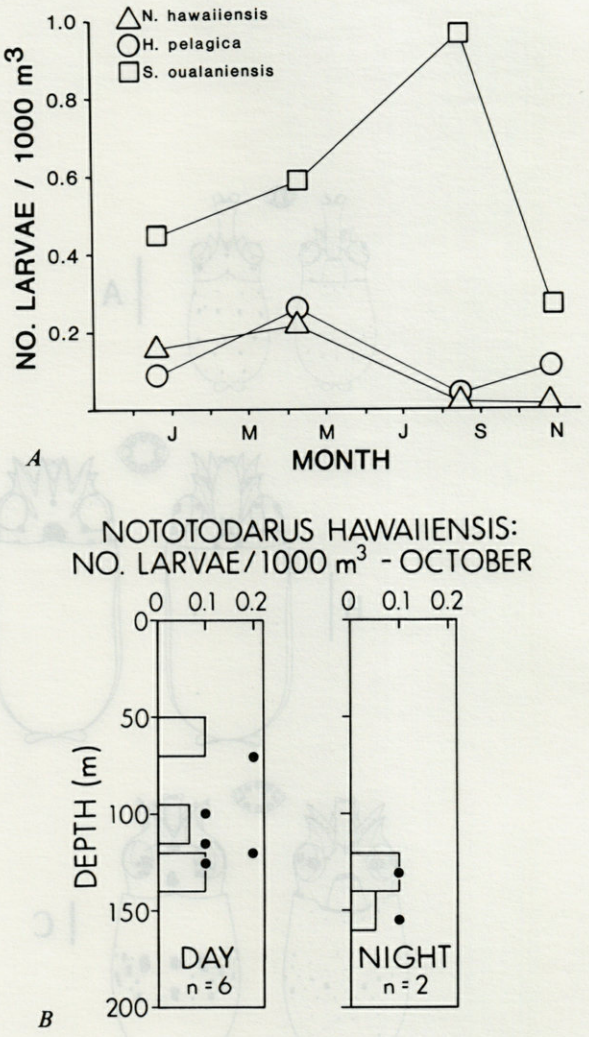

Fig. 4. — A, Species abundance (mean catch rates) by month. B, Vertical distribution of *Nototodarus hawaiiensis*, October series. Dots represent catch rates at modal depth for positive tows and histograms represent mean catch rates.

Hyaloteuthis pelagica (Bosc, 1802)

1. Proboscis length (Fig. 2) : mean proboscis index = 0.61 ± 0.25 S.D. (range 0.28-1.28, n = 44).

2. Proboscis suckers (Plate I, D) : lateral 2 suckers moderately enlarged compared to medial 6 (mean ratio : 1.44 ± 0.03 S.D. (n = 32, 3 specimens); mean number of knobs on lateral suckers : middle whorl = 18 (range 18-19, n = 3, 3 specimens), inner whorl = 15 (range 14-16, n = 3, 3 specimens); mean number of knobs on medial suckers : middle whorl = 12 (range 8-15, n = 7, 3 specimens), inner whorl = 9 (range 8-11, n = 7, 3 specimens).

3. Proboscis division (Fig. 3) : begins about 3.5-4.0 mm ML; complete by 6.5 mm ML.

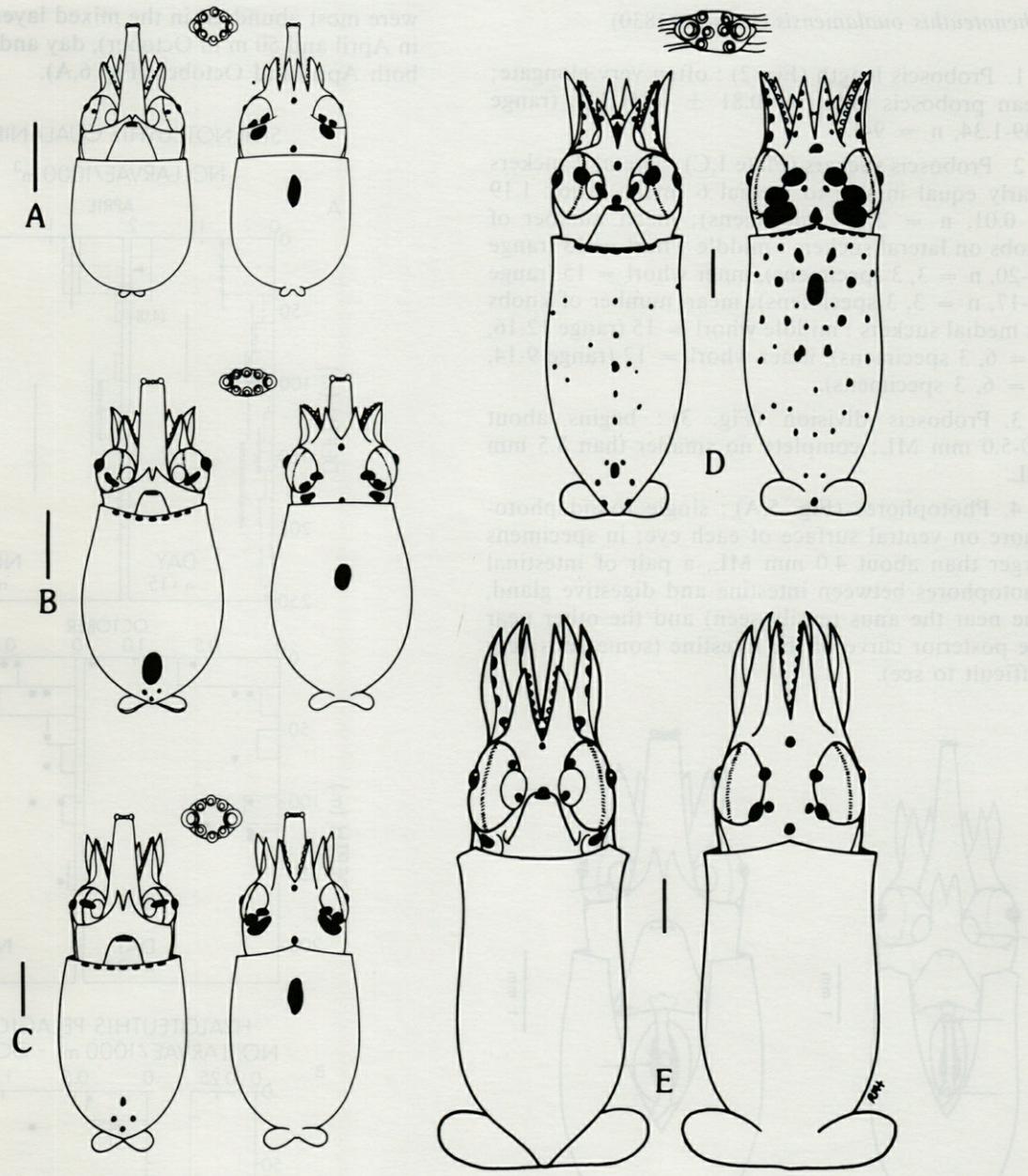

Plate III. — Larval stages of *Hyaloteuthis pelagica* (dorsal and ventral views) : A) 2.0 mm ML; B) 3.0 mm ML; C) 3.7 mm ML; D) 6.2 mm ML; E) 6.5 mm ML. Inserts show proboscis tips. Scale bar = 1.0 mm ML.

4. Photophores (Fig. 5, B) : single round photophore on ventral surface of each eye; single prominent photophore between intestine and digestive gland, about midway between anus and posterior curve of intestine; photophores present and well-developed in smallest specimens captured (1.4 mm ML).

5. Mantle chromatophores (Plate III) : pattern often obscured due to damage; cluster of 4 chromatophores sometimes visible on postero-ventral end of mantle.

6. Mantle shape (Plate III) : slender.

7. Distribution : the larvae of this species were present throughout the year. They showed highest abundance in April (mean = 0.26/1000 m^3) and lowest abundance in August (mean = 0.04/1000 m^3) (Fig. 4). During October at night, most of these larvae were taken in the mixed layer (upper 50 m) and during the day, none were caught shallower than 100 m (Fig. 6). In April, two specimens were caught in the upper 50 m at night and two were caught between 130-200 m during the day.

Sthenoteuthis oualaniensis (Lesson, 1830)

1. Proboscis length (Fig. 2) : often very elongate; mean proboscis index = 0.81 ± 0.25 S.D. (range 0.49-1.34, n = 94).

2. Proboscis suckers (Plate I,C) : lateral 2 suckers nearly equal in size to medial 6 (mean ratio : 1.19 ± 0.01, n = 27, 3 specimens); mean number of knobs on lateral suckers : middle whorl = 18 (range 16-20, n = 3, 3 specimens), inner whorl = 15 (range 12-17, n = 3, 3 specimens); mean number of knobs on medial suckers : middle whorl = 15 (range 12-16, n = 6, 3 specimens), inner whorl = 12 (range 9-14, n = 6, 3 specimens).

3. Proboscis division (Fig. 3) : begins about 3.0-5.0 mm ML; complete no smaller than 8.5 mm ML.

4. Photophores (Fig. 5,A) : single round photophore on ventral surface of each eye; in specimens larger than about 4.0 mm ML, a pair of intestinal photophores between intestine and digestive gland, one near the anus (easily seen) and the other near the posterior curve of the intestine (sometimes very difficult to see).

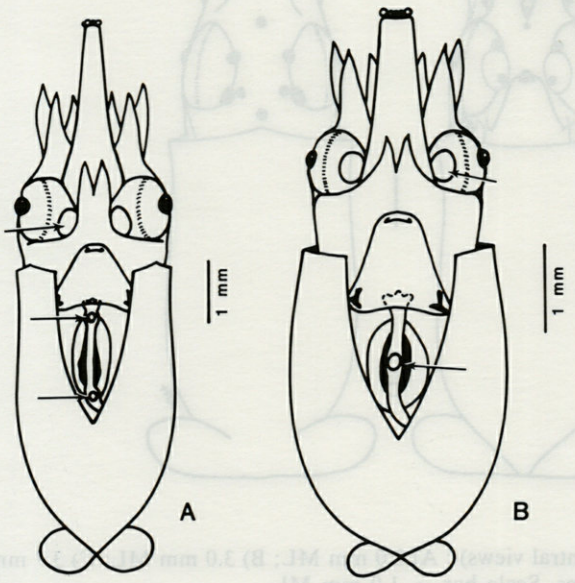

Fig. 5. — Photophore location in (A) *Sthenoteuthis oualaniensis* and (B) *Hyaloteuthis pelagica.*

5. Mantle chromatophores (Plate IV) : pattern often obscured by damage; pair of chromatophores sometimes visible on postero-ventral end of mantle.

6. Mantle shape (Plate IV) : slender.

7. Distribution : the larvae of this species were present in relatively high numbers throughout the year. They showed highest abundance in August (mean = 0.96/1000 m^3) and lowest abundance in October (mean = 0.27/1000 m^3) (Fig. 4,A). They were most abundant in the mixed layer (upper 70 m in April and 50 m in October), day and night, during both April and October (Fig. 6,A).

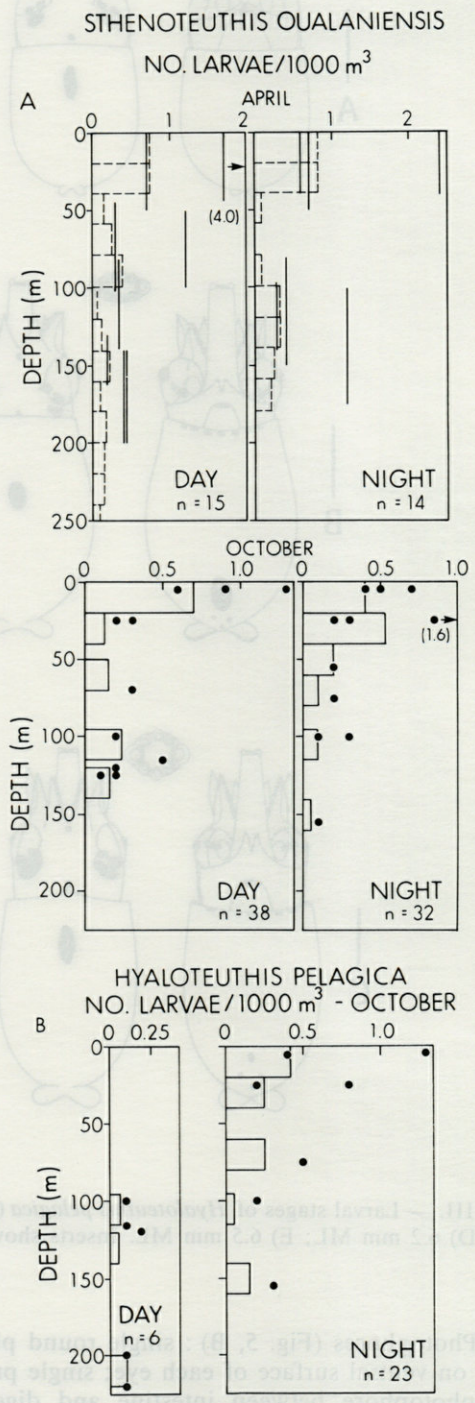

Fig. 6. — A, Vertical distribution of *Sthenoteuthis oualaniensis,* April and October series. In April, vertical bars represent catch rates and depth range for positive tows. In October, dots represent catch rates at modal depth for positive tows. Histograms represent mean catch rates, thus including negative tows. B, Vertical distribution of *Hyaloteuthis pelagica,* October series. Dots represent catch rates at modal depth for positive tows and histograms represent mean catch rates.

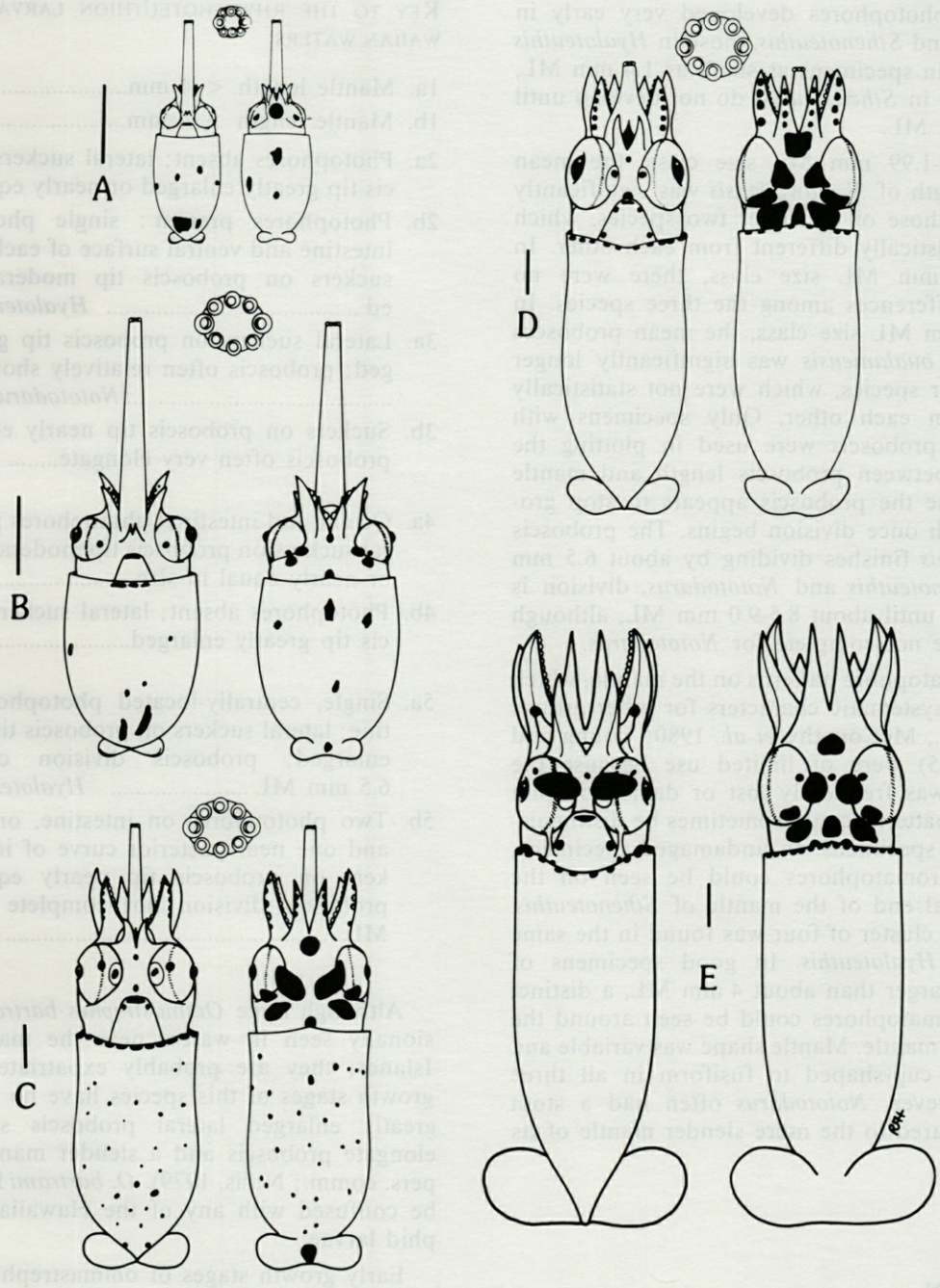

Plate IV. — Larval stages of *Sthenoteuthis oualaniensis* (dorsal and ventral views) : A) 1.4 mm ML; B) 2.3 mm ML; C) 5.8 mm ML; D) 7.1 mm ML; E) 9.1 mm ML. Inserts show proboscis tips. Scale bar = 1.0 mm.

Species Comparisons

Within-species variations in the size of the two lateral to the six medial proboscis suckers were not large and no individual measurements were statistically different from the mean ratio. However, between species, the means of this ratio were all significantly different.

On the outer chitinous sucker rings, the mean number of knobs in both the middle and inner whorls were significantly different between *N. hawaiiensis* and the other two species. There was no statistical difference between the mean number of knobs of *S. oualaniensis* and *H. pelagica*. Within a species, no significant difference was found in the number of knobs among specimens of different sizes (2.0 to 4.0 mm ML).

Although photophores developed very early in *Hyaloteuthis* and *Sthenoteuthis,* those in *Hyaloteuthis* were present in specimens as small as 1.4 mm ML, whereas those in *Sthenoteuthis* do not develop until about 4.0 mm ML.

In the 1.0-1.99 mm ML size class, the mean proboscis length of *N. hawaiiensis* was significantly shorter than those of the other two species, which were not statistically different from each other. In the 2.0-2.99 mm ML size class, there were no significant differences among the three species. In the 3.0-4.0 mm ML size class, the mean probosces length of *S. oualaniensis* was significantly longer than the other species, which were not statistically different from each other. Only specimens with non-dividing proboscis were used in plotting the relationship between proboscis length and mantle length because the proboscis appears to stop growing in length once division begins. The proboscis of *Hyaloteuthis* finishes dividing by about 6.5 mm ML. In *Sthenoteuthis* and *Nototodarus,* division is not complete until about 8.5-9.0 mm ML, although the results are not complete for *Nototodarus.*

The chromatophore patterns on the mantle, which are valuable systematic characters for other groups of squids (e.g., McConathy *et al.,* 1980; Young and Harman, 1985) were of limited use because the mantle skin was frequently lost or damaged upon capture, but patterns could sometimes be distinguished on good specimens. In undamaged specimens, a pair of chromatophores could be seen on the postero-ventral end of the mantle of *Sthenoteuthis.* In contrast, a cluster of four was found in the same position on *Hyaloteuthis.* In good specimens of *Nototodarus* larger than about 4 mm ML, a distinct band of chromatophores could be seen around the middle of the mantle. Mantle shape was variable and ranged from cup-shaped to fusiform in all three species. However, *Nototodarus* often had a stout mantle compared to the more slender mantle of its relatives.

DISCUSSION

Relatively few types of characters are useful in identifying these ommastrephid larvae. The most useful are : 1) the relative size differences of the proboscis suckers, 2) the number of knobs on the chitinous sucker rings, 3) the size at which photophores appear and the number of photophores, 4) the proboscis index, 5) the size at which the proboscis completely divides, 6) mantle shape and chromatophore pattern.

The following key is based on characters that are useful in routine identification :

KEY TO THE RHYNCHOTEUTHION LARVAE FROM HAWAIIAN WATERS

1a. Mantle length < 4 mm 2
1b. Mantle length > 4 mm 4
2a. Photophores absent; lateral suckers on proboscis tip greatly enlarged or nearly equal in size 3
2b. Photophores present : single photophore on intestine and ventral surface of each eye; lateral suckers on proboscis tip moderately enlarged ..... *Hyaloteuthis pelagica*
3a. Lateral suckers on proboscis tip greatly enlarged; proboscis often relatively short ..... *Nototodarus hawaiiensis*
3b. Suckers on proboscis tip nearly equal in size; proboscis often very elongate..... *Sthenoteuthis oualaniensis*
4a. Ocular and intestinal photophores present; lateral suckers on proboscis tip moderately enlarged or nearly equal in size 5
4b. Photophores absent; lateral suckers on proboscis tip greatly enlarged..... *Nototodarus hawaiiensis*
5a. Single, centrally-located photophore on intestine; lateral suckers on proboscis tip moderately enlarged; proboscis division complete by 6.5 mm ML ..... *Hyaloteuthis pelagica*
5b. Two photophores on intestine, one near anus and one near posterior curve of intestine; suckers on proboscis tip nearly equal in size; proboscis division not complete by 9.0 mm ML..... *Sthenoteuthis oualaniensis*

Although large *Ommastrephes bartrami* are occasionally seen in waters near the main Hawaiian Islands, they are probably expatriates. The early growth stages of this species have no photophores, greatly enlarged lateral proboscis suckers, very elongate proboscis and a slender mantle (Okutani, pers. comm.; Nesis, 1979). *O. bartrami* larvae cannot be confused with any of the Hawaiian ommastrephid larvae.

Early growth stages of ommastrephids were collected throughout the year, indicating year-round spawning. *N. hawaiiensis* and *H. pelagica* had peak abundances in April and *S. oualaniensis* showed a peak in August, which was a period of very low abundance for the other two species. From the samples used to compare temporal abundance, 245 *S. oualaniensis* were caught. This was considerably higher than the 55 *H. pelagica* and 37 *N. hawaiiensis* collected. The very high abundance of *Sthenoteuthis* in the August samples partially resulted from one unusually high catch, however, the median abundances showed that this species was still six times more abundant than either of the other species. These results differ from those of Boucher (1980),

who noted a Fall peak in abundance of ommastrephid larvae. Such differences would not be surprising if non-seasonal temporal variations are of greater magnitude than variation due to seasonal spawning.

If sampling in this study accurately reflected larval abundance and if larval growth and survival were similar for all three species, the higher abundance of *S. oualaniensis* throughout the year would suggest that the local adult population of this species was spawning more eggs than the other species during this study. However, we have no information on relative growth and survival and there is some doubt that we have accurately sampled the larval populations of all three species. *Nototodarus* was not caught in the mixed layer and was never very abundant in our samples. Although we have no knowledge of what the real abundance might be, most of the larvae of this neritic species could be distributed deeper than the depths that we sampled, or closer to the island masses, or at restricted location around the islands.

Sthenoteuthis larvae were most abundant in near-surface waters during both the day and night and there was no significant difference between the day and night catch rates during either sampling period suggesting no differential day-night avoidance. We probably sampled this species effectively. *Hyaloteuthis,* on the other hand, was abundant in near-surface waters at night, but was not caught shallower than 100 m during the day in October nor shallower than 130 m in April. Day vs. night catch rates differed significantly. Either *Hyaloteuthis* strongly avoided the net during the day or we did not sample the entire day habitat. The morphological similarities, however, between this species and *Sthenoteuthis* (which did not seem to show higher daytime avoidance) suggests that the latter alternative is the correct one. Indeed, ommastrephid larvae, in general, seem to be notoriously difficult to sample quantitatively (e.g., Nesis and Nigmatullin, 1979; Okutani and Watanabe, 1983). Perhaps the complexities of the larval habitat are partly resposible.

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GROWTH AND DISTRIBUTION OF YOUNG *MESONYCHOTEUTHIS HAMILTONI* ROBSON (MOLLUSCA : CEPHALOPODA) : AN ANTARCTIC SQUID

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ANTARCTIC
CEPHALOPODA
MESONYCHOTEUTHIS
GROWTH
DISTRIBUTION
HYDROGRAPHY

ABSTRACT. — Thirty seven juvenile specimens and one adult specimen of the cranchiid squid *Mesonychoteuthis hamiltoni* were captured by the opening and closing RMT8 net during RRS 'Discovery' cruise 100 (1979) in the Southern Ocean. The collection extends the size range of juveniles of this species previously described and illustrated. The small specimens resemble small juveniles of *Galiteuthis glacialis*, which also occur in most hauls, but are separated on the following characters : (a) *M. hamiltoni* lacks paired tubercles at the nuchal mantle fusion, (b) *M. hamiltoni* possesses a more capacious and thicker mantle, which is freer at the nuchal fusion and less constricted posterior to the opening; (c) juvenile *M. hamiltoni* up to a size of 26.5 mm (the largest in the present collection) have very small fins, while in *G. glacialis* of this size the posterior portion of the mantle has begun to extend into a tail and prominent fins appears; (d) *M. hamiltoni* has longer tentacles until it reaches a dorsal mantle length of approximately 25 mm. All specimens of *M. hamiltoni* were captured to the south of the Antarctic Convergence, and most were captured at depths between 20 m and 500 m apparently concentrated in the upper zone of 'Warm Deep Water' beneath the surface layer. Four newly hatched specimens were captured at 55°35'S between 20 and 500 m. The adult specimen was captured in a haul which had sampled a depth horizon from 2 000 m to 2 200 m.

ANTARCTIQUE
CEPHALOPODA
MESONYCHOTEUTHIS
CROISSANCE
DISTRIBUTION
HYDROGRAPHIE

RÉSUMÉ. — Trente-sept juvéniles et un adulte de *Mesonychoteuthis hamiltoni* (Cranchiidés) ont été récoltés à l'aide d'un filet fermant à double commande pendant la Campagne 100 (1979) du N/O « Discovery » dans l'océan Sud. Cette collection étend la gamme de taille des juvéniles décrits et illustrés de l'espèce. Les petits individus ressemblent aux petits juvéniles de *Galiteuthis glacialis* qui étaient présents dans la plupart des échantillons mais s'en distinguent par les caractères suivants : (a) *M. hamiltoni* n'a pas de tubercules pairs à la fusion nucale palléale; (b) *M. hamiltoni* a un manteau plus ample et plus épais, plus libre à la fusion nucale; il est moins resserré en arrière de son ouverture; (c) les juvéniles de *M. hamiltoni* jusqu'à la taille de 26,5 mm (le plus grand exemplaire de la collection) ont de très petites nageoires, alors que chez *Galiteuthis glacialis* de la même taille, le manteau s'étire en une queue portant des nageoires bien développées; (d) *M. hamiltoni* a des tentacules plus longs atteignant jusqu'à 25 mm environ. Tous les spécimens de *M. hamiltoni* ont été capturés au Sud de la Convergence antarctique, et la plupart d'entre-eux ont été pris entre 20 et 500 m de profondeur, apparemment concentrés dans la zone supérieure de l'« eau profonde chaude », situé en-dessous de la couche superficielle. Quatre individus nouveau-nés ont été capturés à 55°35'S, entre 20 et 500 m. Le spécimen adulte provient d'un coup de filet effectué entre 2 000 et 2 200 m de profondeur.

INTRODUCTION

The Antarctic squid *Mesonychoteuthis hamiltoni* Robson is a large, rarely caught species which grows to a maximum total length of 4 m (Roper, Sweeney & Nauen, 1984). It belongs to the family Cranchiidae, sub-family Taoniinae and is closely related phylogenetically to members of the genus *Taonius* and *Galiteuthis* (Voss and Voss, 1983). Of these, *Galiteuthis glacialis* (Chun) is the only other cranchiid squid known to occur in the Southern Ocean, south of the Antarctic Convergence. A detailed description of the systematics and morphology of *G. glacialis* is given by McSweeny (1978).

Until recently all known specimens of adult *Mesonychoteuthis hamiltoni,* including the type specimen, were taken from the stomachs of sperm whales. Juveniles have been caught by nets and a description of the juvenile, based on four specimens, 59-86 mm dorsal mantle length (DML), is given by McSweeny (1970). The genus is included in the generic revision of the Cranchiidae given by Voss (1980).

Mesonychoteuthis hamiltoni is a major prey item of sperm whales in the Southern Ocean (Klumov and Yukhov, 1975; Clarke, 1980). Beaks comprise 14 % of the numbers found in sperm whale stomachs from the Antarctic and, because of the large size of the species, this represents an estimated 77 % of the biomass consumed. At South Georgia the percentage of *M. hamiltoni* beaks by numbers was still higher at 23 %. It has not been found in the stomach contents of elephant seals or Weddell seals (Clarke and McLeod, 1982a, b), wandering albatrosses (Clarke, Croxall and Prince, 1981), black-browed or grey-headed albatrosses (Clarke and Prince, 1981), or emperor or Adelie penguins (Offredo, Ridoux and Clarke, 1985). Small numbers of beaks have been found in the stomachs of sooty and light-mantled sooty albatrosses (Berruti and Harcus, 1978). The rarity of the species in the stomach contents of predators, other than sperm whales, suggests that it is a relatively deep-living form that only occasionally, if ever, approaches the surface.

In this paper we describe and illustrate the change in form during growth of juvenile *Mesonychoteuthis hamiltoni* from a size of 4.8 mm to 26.5 mm DML emphasising those external features which separate this species from the other common cranchiid squid in the Southern Ocean, *Galiteuthis glacialis.* The distribution of juveniles, sampled by opening and closing rectangular midwater trawl, is given in relation to the hydrographic structure of the Southern Ocean, and the relation between body size of juveniles and water depth is examined.

MATERIAL AND METHODS

The track of RRS 'Discovery' cruise 100 (30 January to 4 April 1979) in the Southern Ocean and the sampling stations are shown in Fig. 1. All specimens of *Mesonychoteuthis hamiltoni* were caught in an RMT8 opening and closing net (Clarke, 1969). The samples were fixed in 5 % neutral formalin and stored in Steedman's solution. Capture rate is defined here as the number of specimens caught in any 100 m depth horizon, divided by the number of hauls which sampled that horizon. Where specimens were caught in a haul that spanned a horizon > 100 m it is assumed that capture rate is consistent throughout the vertical range of the haul and the catch divided by the number of 100 m horizons sampled. A section of the Southern Ocean showing hydrographic structure (after Deacon, 1937) is shown in Fig. 5.

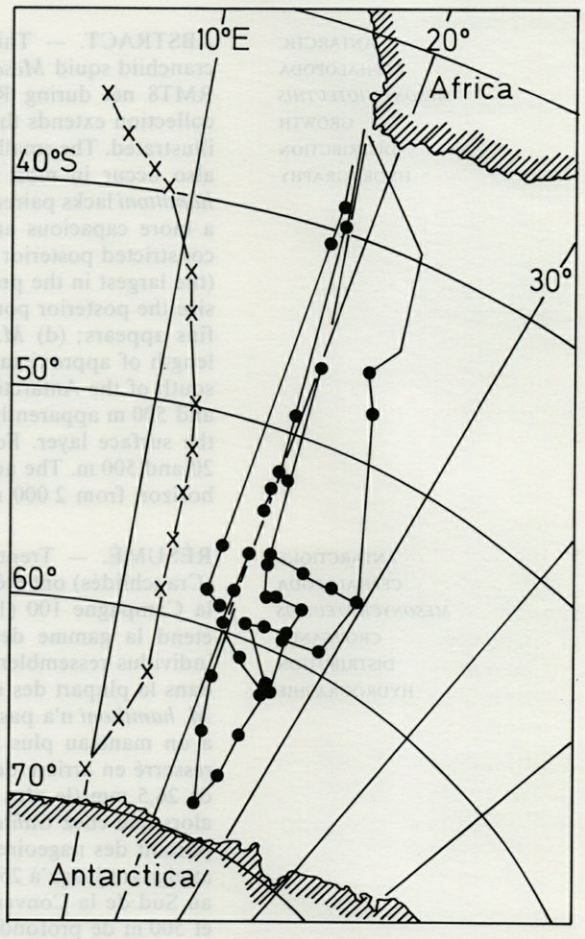


Fig. 1. — Sampling stations and track in the Southern Ocean of RRS 'Discovery' cruise 100 (1979). Stations marked by crosses are those upon which the section in Fig. 5 is based (after Deacon, 1937).

RESULTS

The size frequency distribution of the thirty seven juveniles captured (4.8 mm to 26.5 mm DML), is presented in Fig. 2. All but one sample that contained juvenile *M. hamiltoni* also contained juveniles of *G. glacialis*, and several of the samples also contained small numbers of juvenile *Alluroteuthis antarcticus*. One large, adult, female specimen of *Mesonychoteuthis* (1.17 m DML) was caught in a haul which had sampled a depth horizon from 2 000 m to 2 200 m.

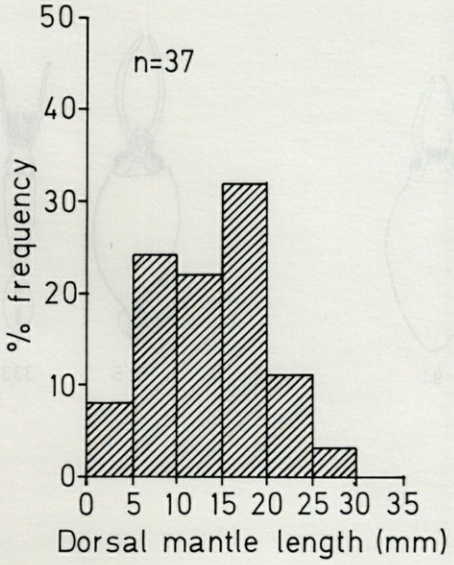


Fig. 2. — Size frequency distribution of *Mesonychoteuthis hamiltoni* captured during RRS 'Discovery' Cruise 100 in the Southern Ocean.

The change in form of juveniles during growth over the size range present in the collection is shown in Fig. 3, together with a series of *G. glacialis* juveniles, of the same size range. Because *M. hamiltoni* occurs sympatrically with *G. glacialis*, and small specimens of these two species resemble one another, it is important to emphasise the features by which they are separated :

1. Tubercles : a single tubercle occurs on the mid-line at the nuchal mantle fusion in juvenile *M. hamiltoni* (McSweeny, 1970). It is barely discernible in specimens > 20 mm DML and not visible in specimens < 20 mm DML. This feature contrasts strongly with *G. glacialis* which has paired tubercles on each side of the nuchal mantle fusion, these are apparent in individuals of all sizes.

2. Mantle : The form of the mantle in *M. hamiltoni* is more sac-like and capacious than in *G. glacialis*. The mantle is thicker in *Mesonychoteuthis* and less constricted posterior to the opening than in *Galiteuthis*. The mantle edge at the nuchal fusion is somewhat freer in *Mesonychoteuthis*.

3. Tail : In small *M. hamiltoni* (26.5 mm DML) the posterior portion of the mantle is not drawn out into a tail and the fins are very small. In *G. glacialis* the posterior portion of the mantle becomes drawn out into a tail in specimens > 20 mm DML and the fins increase in size at a much smaller DML than in *M. hamiltoni*. This feature immediately separates individuals > 20 mm DML.

4. Tentacles : The tentacles of small *M. hamiltoni* are longer than in *G. glacialis* (Fig. 4). The allometric equations relating tentacle length (TL) to DML are :

M. hamiltoni : $\log_{10}TL = 0.43 + 0.54 \log_{10}DML$ ($r = 0.899$; 18 df)

G. glacialis : $\log_{10}TL = -0.11 + 0.92 \log_{10}DML$ ($r = 0.920$; 18 df)

The t-test showed that the differences between slopes and intercepts are significant at $P < 0.01$. The lines intersect at a DML of approximately 25 mm.

The distribution of hauls, made with the RMT8 opening and closing net, and the catch of *M. hamiltoni* in relation to the hydrographic section of the Southern Ocean (Deacon, 1937), are illustrated in Figure 5. The section traverses the Southern Ocean from 35° S to 70° S and is based on data collected 5-15° west of the stations where net hauls were taken in 1979. Sampling was most intense to the south of the Antarctic Convergence. The maximum depth sampled was 3 000 m and two vertical series were taken; one at 57°30' S and the other at 68°30' S. No specimens of *M. hamiltoni* were caught north of 55° S and most individuals were caught in an area between 55° S and 59° S and in an area between 68° S and 69° S, close to the ice edge. The deepest haul to capture a juvenile sampled a horizon from 500 m to 995 m and the shallowest sampled a horizon from 0 m to 49 m. Three individuals were caught in hauls sampling 0-500 m and all other catches of juveniles were made between 20 m and 500 m. Twenty five juveniles were caught in a relatively narrow horizon immediately beneath the Antarctic surface layer which is characterised by a temperature of < 0.0° C and an oxygen tension of > 6.0 ml l^{-1} (Fig. 5). The three specimens caught in 0-500 m and the five specimens caught in 20-500 m may have been caught in this same water mass and so only three individuals are known to have come from the surface layer. Four specimens (4.8 mm, 4.9 mm, 5.2 mm, 5.9 mm DML) are apparently newly hatched from the egg. The mantles had a yolky appearance and in two specimens fragments of the chorion were still attached to the mantle. In all four specimens the head, arms and tentacles were enclosed in a membrane. These were captured at 55°35' S at depths between 20 and 500 m. The adult specimen was caught at a much greater depth, apparently in the cold bottom layer.

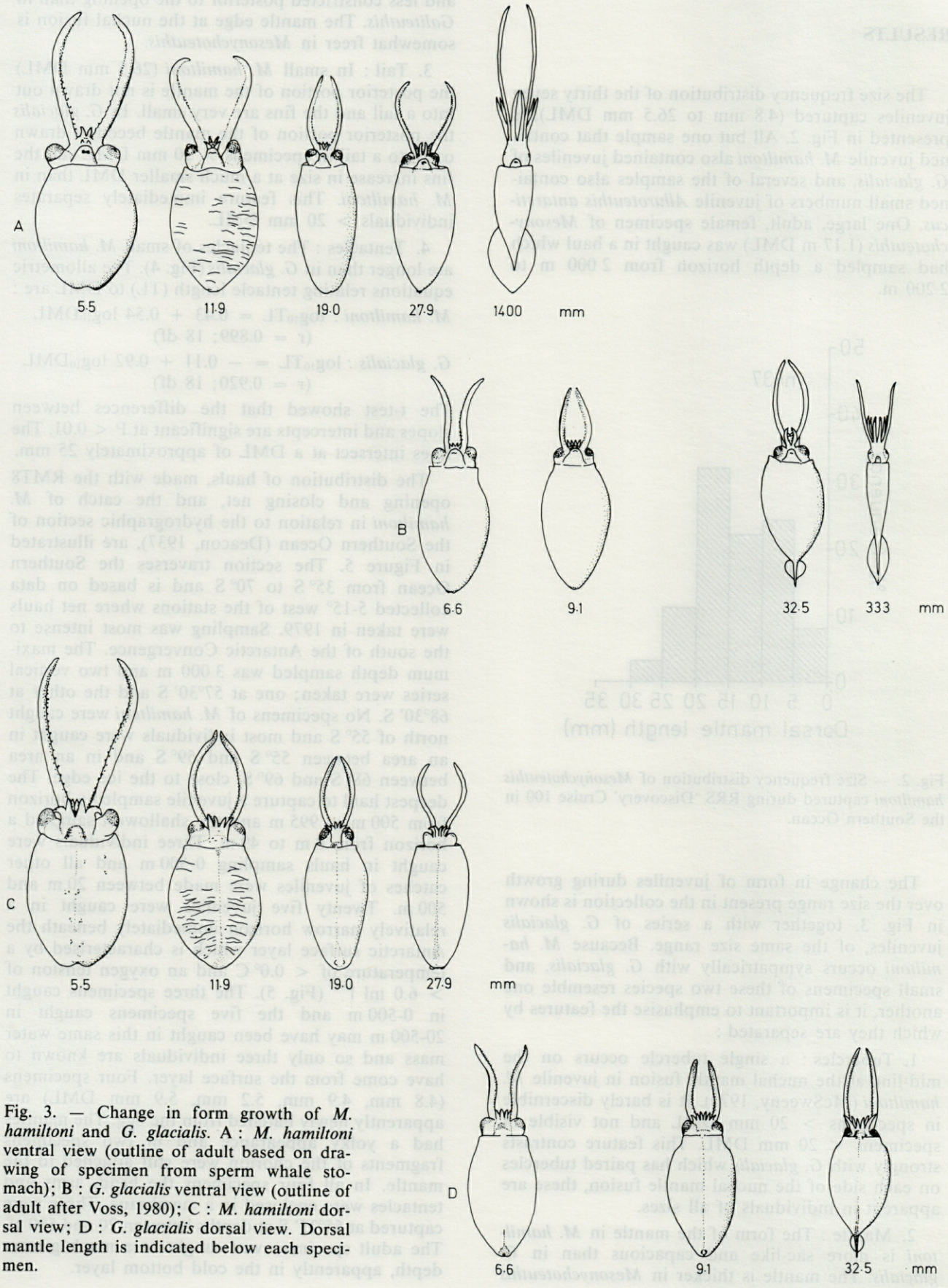


Fig. 3. — Change in form growth of *M. hamiltoni* and *G. glacialis*. A : *M. hamiltoni* ventral view (outline of adult based on drawing of specimen from sperm whale stomach); B : *G. glacialis* ventral view (outline of adult after Voss, 1980); C : *M. hamiltoni* dorsal view; D : *G. glacialis* dorsal view. Dorsal mantle length is indicated below each specimen.

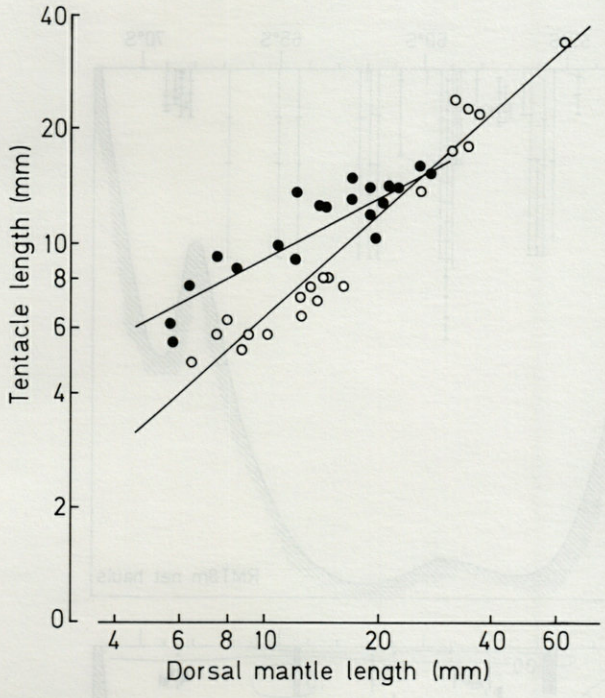


Fig. 4. — Tentacle length as a function of dorsal mantle length. Closed dots : *M. hamiltoni;* open dots : *G. glacialis.*

The number of hauls made through each 100 m depth horizon and the capture rate of juvenile *M. hamiltoni* are presented in Figure 6. The capture rate was low, despite high fishing effort, from the surface to 200 m, and was highest between 200 m and 500 m. Despite almost consistent fishing effort from 500 m to 2 000 m the capture rate below 500 m was very low.

The relation between size of juvenile *M. hamiltoni* and depth of capture is illustrated in Figure 7 (only juveniles caught within a 100 m-200 m depth horizon are included). The adult, which is the only adult known to have been caught by net, was captured at 2 000-2 200 m. It is premature to draw conclusions about the depth normally inhabited by adults.

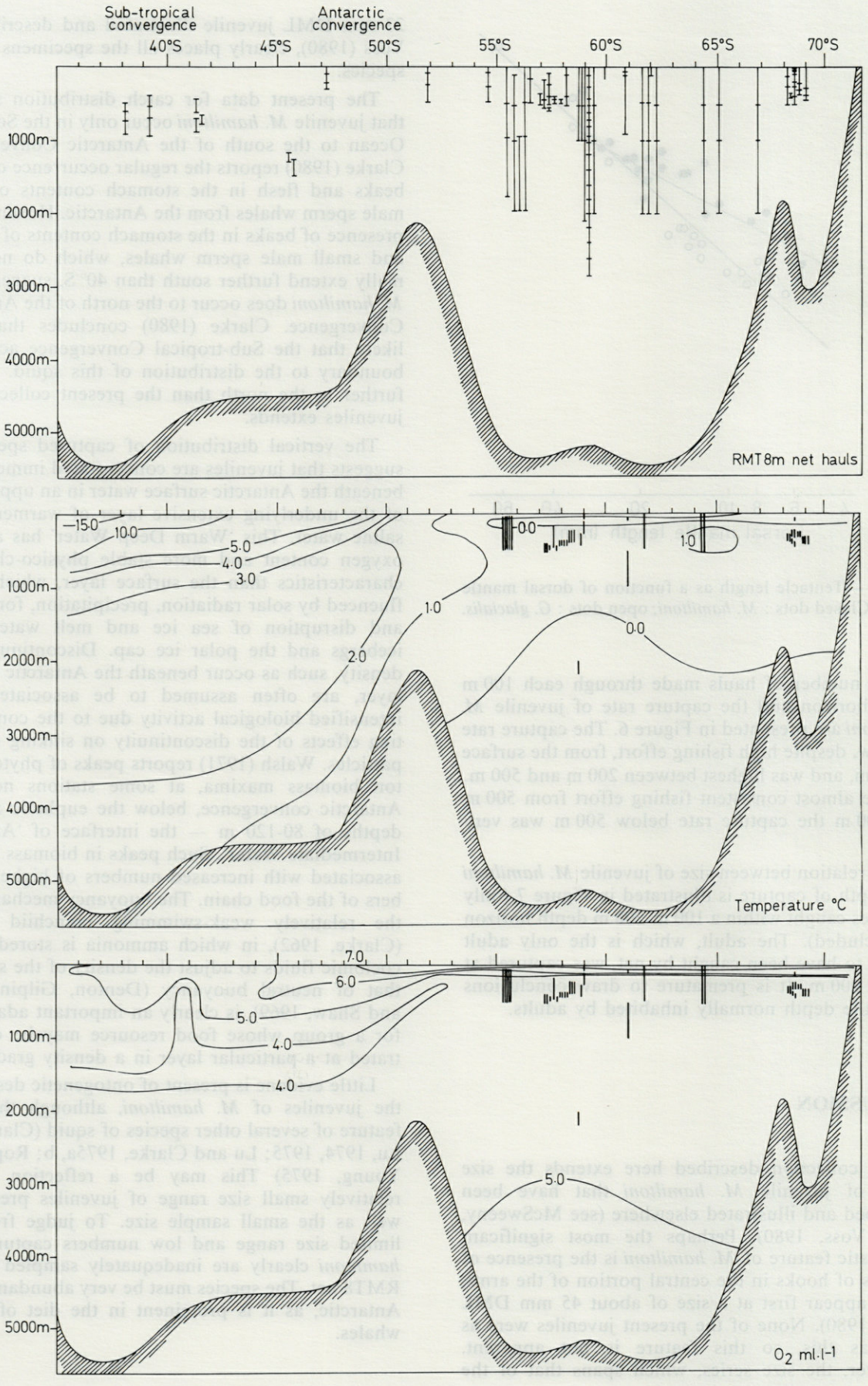
DISCUSSION

The collection described here extends the size range of juvenile *M. hamiltoni* that have been described and illustrated elsewhere (see McSweeny, 1970; Voss, 1980). Perhaps the most significant diagnostic feature of *M. hamiltoni* is the presence of a series of hooks in the central portion of the arms, which appear first at a size of about 45 mm DML (Voss, 1980). None of the present juveniles were as large as this, so this feature is not apparent. However, the size series, which spans that of the 23 mm DML juvenile illustrated and described by Voss (1980), clearly places all the specimens in this species.

The present data for catch distribution suggest that juvenile *M. hamiltoni* occur only in the Southern Ocean to the south of the Antarctic Convergence. Clarke (1980) reports the regular occurrence of adult beaks and flesh in the stomach contents of large male sperm whales from the Antarctic. However, the presence of beaks in the stomach contents of female and small male sperm whales, which do not normally extend further south than 40° S, suggests that *M. hamiltoni* does occur to the north of the Antarctic Convergence. Clarke (1980) concludes that it is likely that the Sub-tropical Convergence acts as a boundary to the distribution of this squid. This is further to the north than the present collection of juveniles extends.

The vertical distribution of captured specimens suggests that juveniles are concentrated immediately beneath the Antarctic surface water in an upper zone of the underlying extensive layer of warmer, more saline water. This 'Warm Deep Water' has a lower oxygen content and more stable physico-chemical characteristics than the surface layer, which is influenced by solar radiation, precipitation, formation and disruption of sea ice and melt water from icebergs and the polar ice cap. Discontinuities in density, such as occur beneath the Antarctic surface layer, are often assumed to be associated with intensified biological activity due to the concentrating effects of the discontinuity on sinking organic particles. Walsh (1971) reports peaks of phytoplankton biomass maxima, at some stations near the Antarctic convergence, below the euphotic zone at depths of 80-120 m — the interface of 'Antarctic Intermediate Water'. Such peaks in biomass may be associated with increased numbers of higher members of the food chain. The buoyancy mechanism of the relatively weak-swimming cranchiid squids (Clarke, 1962), in which ammonia is stored in the coelomic fluids to adjust the density of the squid to that of neutral buoyancy (Denton, Gilpin-Brown and Shaw, 1969), is clearly an important adaptation for a group whose food resource may be concentrated at a particular layer in a density gradient.

Little evidene is present of ontogenetic descent in the juveniles of *M. hamiltoni,* although this is a feature of several other species of squid (Clarke and Lu, 1974, 1975; Lu and Clarke, 1975a, b; Roper and Young, 1975) This may be a reflection of the relatively small size range of juveniles present as well as the small sample size. To judge from the limited size range and low numbers captured, *M. hamiltoni* clearly are inadequately sampled by the RMT8 net. The species must be very abundant in the Antarctic, as it is prominent in the diet of sperm whales.


Sub-tropical convergence
Antarctic convergence
40°S
45°S
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60°S
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1000m
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4000m
5000m
RMT8m net hauls
15·0
10·0
5·0
4·0
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1·0
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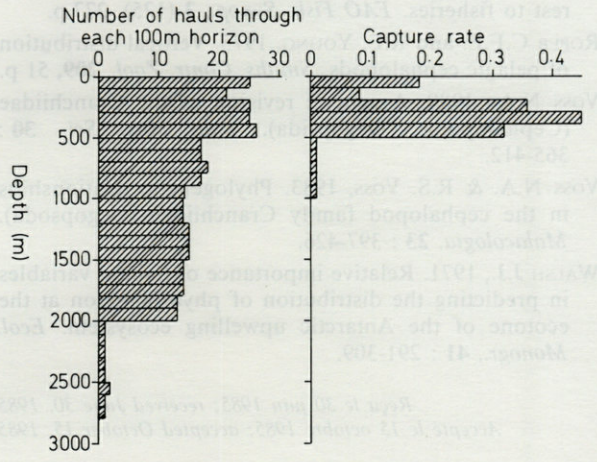

Fig. 6. — Number of hauls made through each 100 m depth horizon, compared with capture rate of *M. hamiltoni* during RRS 'Discovery' cruise 100.

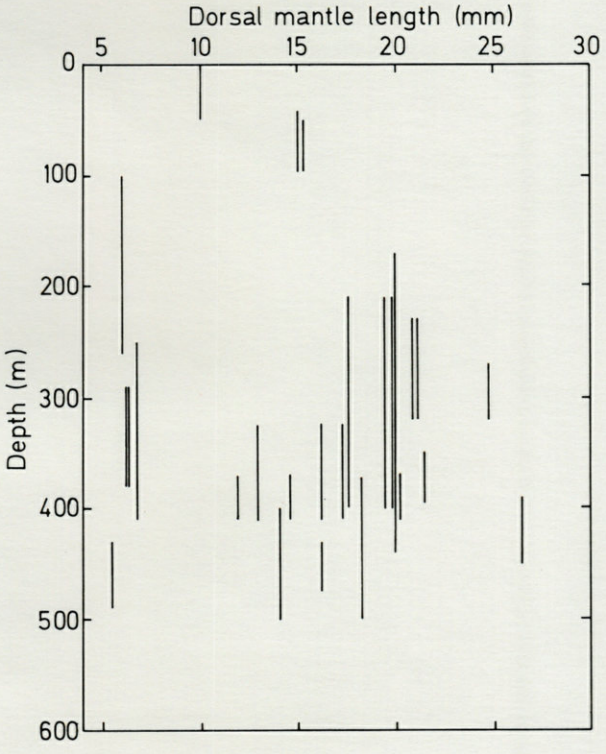

Fig. 7. — Depth distribution of *M. hamiltoni* as a functioon of dorsal mantle length. (Mostly specimens caught within 200 m depth horizon included).

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Fig. 5. — Section of Southern Ocean (after Deacon, 1937) showing position and depth of RMT8 net hauls and distribution of captured specimens in relation to temperature and oxygen. Each vertical line between tick marks represents a single haul (top section); each vertical line represents an individual specimen (centre and bottom sections).

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IN-SITU OBSERVATIONS ON THE SMALL-SCALE DISTRIBUTION OF JUVENILE SQUIDS (CEPHALOPODA : LOLIGINIDAE) ON THE NORTHWEST FLORIDA SHELF

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CEPHALOPODA
SQUID
LOLIGO
SUBMERSIBLE
VIDEO
DISTRIBUTION

ABSTRACT. — We examined 38 hours of videotapes recorded with a remote-controlled submersible at about 60 m depth on the northwest Florida continental shelf. Juvenile squids were among the most abundant organisms identified on the tapes. The larger individuals were identifiable as *Loligo* sp. Whereas behavior typical of obligate schooling was seen in adult *Loligo* in the tapes, the juveniles seldom were aggregated on a small scale (metres) and did not often appear to "orient" together. Consistent variability was noted, however on a larger scale of hundreds of metres. Variability in numbers of sightings along standardized sections of transects was usually independent of the total number of sightings per transect. Thus, as abundance increased, relative variability decreased. The juveniles seemed to be most abundant very near the bottom at night but were rarely seen during the day. While there are many advantages in working with videotaped observations from submersibles, problems remain to be resolved. These problems include standardization of submersible operation among different operators, identification of specimens, determination of size, and estimation of sightings per unit of effort.

CÉPHALOPODES
CALMAR
LOLIGO
SUBMERSIBLE
VIDÉO
DISTRIBUTION

RÉSUMÉ. — Nous avons examiné 38 heures de bandes vidéo enregistrées à bord d'un submersible téléguidé à une profondeur de 60 m sur la partie nord-ouest du plateau continental de la Floride. Les Calmars juvéniles figuraient parmi les organismes les plus abondants identifiés sur les bandes. Les plus grands individus ont pu être identifiés comme *Loligo* sp. Le comportement typique de la vie en banc des *Loligo* adultes a pu être observé, mais les jeunes ne montrent pas ce comportement grégaire, du moins pas dans un espace restreint (mètres). Les jeunes semblent être plus abondants près du fond pendant la nuit; ils ont été rarement vus pendant le jour. La méthode de travail, utilisant l'entregistrement sur bandes vidéo à partir d'un submersible téléguidé offre certains avantages, mais bien des problèmes restent à résoudre.

INTRODUCTION

Cephalopods do not undergo a true metamorphosis (Boletzky, 1974), but during development they do experience a change in ecology (Vecchione, in press) which is correlated with morphological changes (Vecchione, 1981; 1982). For loliginid squids, one aspect of this ecological change is the shift from the planktonic lifestyle of the early juveniles to the social structure of the adults, which are schooling demersal nekton.

Field studies using traditional methods have not successfully elucidated this shift in loliginid beha-

vior because it occurs at a size range at which the squids are large enough to avoid plankton nets, yet small enough to be extruded through the mesh of a nekton trawl. Furthermore, even very brief tows with either type of gear cannot be used effectively to distinguish distributional patterns on spatial scales of metres to hundreds of metres.

An approach to rectify this problem is direct observation, *in situ*. SCUBA has been used successfully to observe the behavior of cephalopods (e.g. Hanlon *et al.*, 1979; Griswold and Prezioso, 1981), but is of limited use for surveying distribution and relative abundance because of decompression requirements and limited mobility. Submersibles are particularly appropriate for such a study because they do not have the time-at-depth limitations of SCUBA. Observations on cephalopods from manned submersibles have been published (Waller and Wicklund, 1968) but are limited in number.

We analyzed squid occurrence and distribution in 38 hours of videotapes recorded by a remotely operated submersible on the northwest Florida continental shelf. This project allowed us a first look at the small-scale distribution of juvenile loliginids, as well as an opportunity to assess the usefulness and problems associated with such observations.

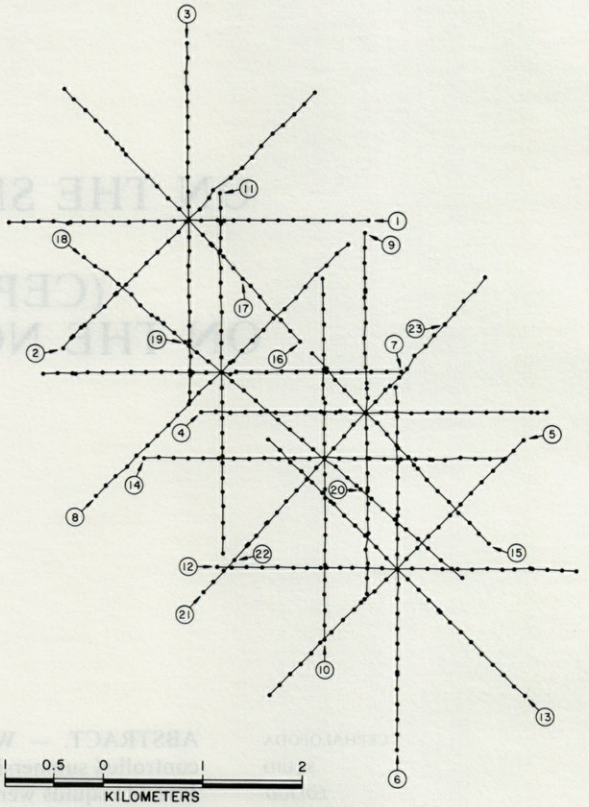

Fig. 1. — Path navigated by the remote-controlled submersible. Dots indicate high-resolution navigation fixes. Numbers designate start points for numbered transects.

MATERIALS AND METHODS

This study was designed as a photodocumentation survey for "live bottom" communities in an area leased for oil-drilling off the northwest coast of Florida (29°50' N, 86°05' W). The tethered, unmanned, 20 horsepower submersible was equipped with a 360 degree scanning sonar, black and white and color video, 35 mm still camera, four 500 watt variable-intensity flood lights, and a five-function manipulator. During September 1984, this submersible was navigated at ca. 1.9 km/h along a preplanned survey route (Fig. 1) by use of a surface console aboard a host vessel.

Position of the host vessel was established by a high-precision radio-positioning system. Position of the submersible was monitored relative to the host vessel by an acoustic reference system. The acoustic system and the surface radio-positioning system were integrated by on-board computer to establish the absolute position of the submersible. Real-time positioning coordinates of the submersible, its heading, and the time of day were then superimposed on the color video display.

The study area averaged 60 m depth. Coralline algae covered much of the sand bottom but small areas were characterized by emergent rocks of relic coral with "live-bottom" sponge-coral assemblages established on them.

After completion of the cruise, 38 h of videotapes recorded along the entire survey route were reviewed to note the occurrence and small-scale distribution of cephalopods. Because navigation fixes were recorded every 152 m along each transect, squid distribution was determined based on 152 m sections of transect along the surveyed bottom. The squids were subjectively categorized as small, medium, or large by comparison with objects of known size (discarded beer cans {12.5 cm length} and an abundant sea urchin, *Eucidaris tribuloides* {10-12 cm diameter}). Thus, we estimated these size categories to include squids of total length < 4 cm (small), 4-12 cm (medium), and > 12 cm (large). We also noted if the squids appeared to be schooling by defining schooling behavior as aggregation on a scale of 1-2 m and coordinated swimming or orientation of aggregated squids (Hurley, 1978; Mather and O'Dor, 1984).

OBSERVATIONS

In total, 1837 squids were sighted, the great majority of which (1657) were in the small-size

category. Sightings of medium-sized squids totaled 159, and 22 large squids were seen. Whereas 27 % of the large individuals appeared to be schooling (2 schools of 3 individuals each; 22 large squids sighted in all), and 23 % of the medium-sized squids were similarly aggregated (5 schools of 3-11 individuals per school; 36 schooling squids out of 159 individuals), only 9 % of the abundant small squids fit our definition of schooling (12 schools of 4-18 individuals per school; 149 total squids schooling from 1657 individual sightings). All of the large and many of the medium-sized squids were easily recognizable as the genus *Loligo*. The large squids often swam along with the submersible, sometimes in company with carangid fishes. However, such behavior was not observed in the medium or small individuals.

The remainder of this paper concerns the distribution of the small-sized juveniles, which also appeared to be *Loligo*. Considerable variability in numbers of individual sightings existed both among transects and among 152 m sections of each transect. Although almost half of the survey was conducted during daylight hours, only two probable squid sightings were recorded during the day. The high variability among night transects is demonstrated by the different scales on the vertical axes of graphs in Figure 2.

On all transects where small squids were seen, it appeared that the submersible was passing through patches of squids that extended over several 152 m sections (Fig. 2). Regardless of the total number of sightings per transect, the linear dimensions of these patches appeared to be fairly constant, approximately 610-1370 m. The consistency of this variability also can be seen by comparing the mean number of individual sightings per section along each transect with the standard deviation of the number of sightings per section (Fig. 3, A). Because this variability was independent of the number of sightings for nine out of twelve complete nighttime transects, the relative variability (coefficient of variability : CV = standard deviation/mean number of sightings per section on each transect) decreased as overall abundance increased (Fig. 3, B).

A few anomalies existed in these patterns, apparently a result of interactions between the small

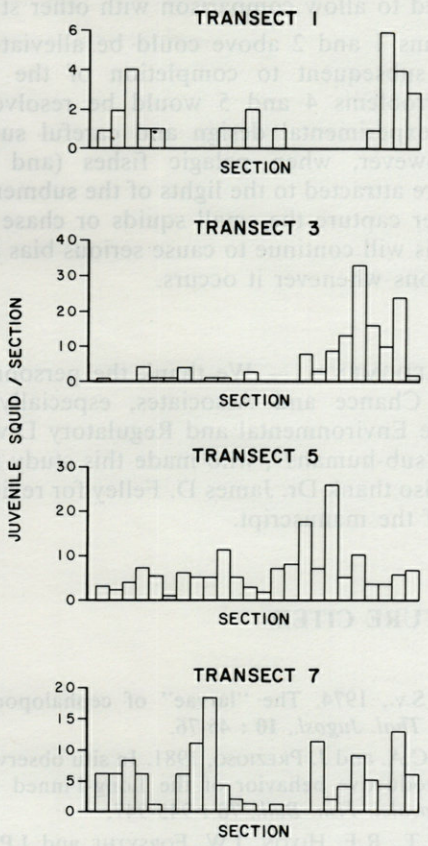

Fig. 2. — Distribution of sightings of small squids along selected night transects. Each vertical bar represents a 152 m section between navigation fixes. Note change of scale in vertical axes.

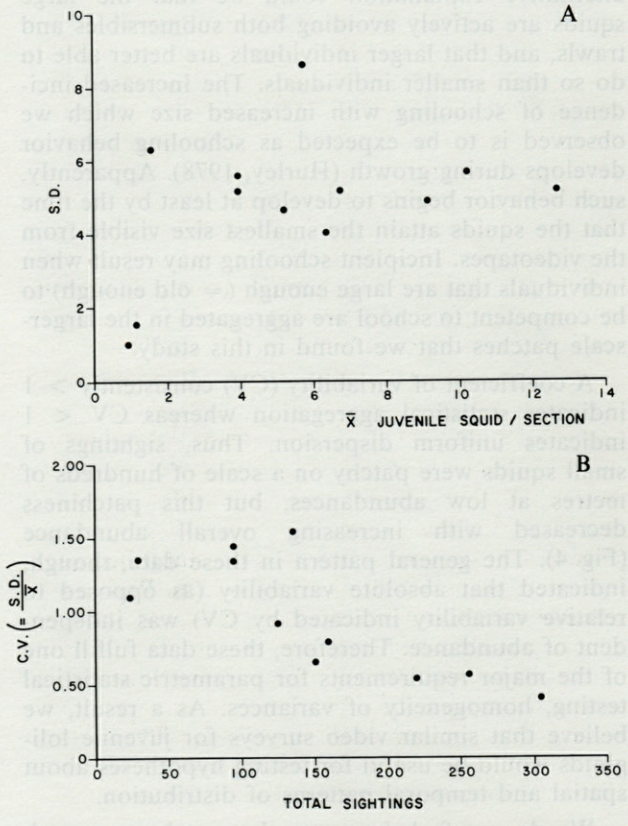

Fig. 3. — A, Mean and standard deviation of number of sightings of small squids per section. Each data point represents a transect. B, Comparison of total number of sightings of small squid along a transect with the Coefficient of Variability (standard deviation/mean number of sightings per section) for each transect.

squids and carangid fishes, which sometimes schooled in the lights of the submersible. Small squids were rarely seen on the few occasions when schools of carangids (and on one occasion, large squids) swam along ahead of the submersible. The small squids may have avoided the carangids or they may have been consumed by the carangids without being seen on the videotape. Another problem was that the operators sometimes experienced trouble controlling the submersible; no squids were seen on any of the occasions that the submersible gained altitude above the bottom.

DISCUSSION

Our observations, though limited in time and space, lead to some generalizations and to the development of several questions. The logarithmic distribution of sightings among size categories parallels the size-distribution pattern described for trawl-caught specimens (Summers, 1968) indicating that the observed distribution may result from age-dependent mortality rather than sampling error. An alternative explanation could be that the large squids are actively avoiding both submersibles and trawls, and that larger individuals are better able to do so than smaller individuals. The increased incidence of schooling with increased size which we observed is to be expected as schooling behavior develops during growth (Hurley, 1978). Apparently, such behavior begins to develop at least by the time that the squids attain the smallest size visible from the videotapes. Incipient schooling may result when individuals that are large enough (= old enough) to be competent to school are aggregated in the larger-scale patches that we found in this study.

A coefficient of variability (CV) consistently > 1 indicates statistical aggregation whereas $CV < 1$ indicates uniform dispersion. Thus, sightings of small squids were patchy on a scale of hundreds of metres at low abundances, but this patchiness decreased with increasing overall abundance (Fig. 4). The general pattern in these data, though, indicated that absolute variability (as opposed to relative variability indicated by CV) was independent of abundance. Therefore, these data fulfill one of the major requirements for parametric statistical testing, homogeneity of variances. As a result, we believe that similar video surveys for juvenile loliginids would be useful for testing hypotheses about spatial and temporal patterns of distribution.

We do not feel, however, that we have enough data from this study to test for statistical trends in spatial and temporal variability, although several patterns are suggested by these data. Variability among transects may be a function of time, with the squids aggregating very near bottom late at night after vertical dispersal during the early night. It was quite surprising that no squids were seen near bottom during the day, the time when *Loligo* presumably schools near bottom (Summers, 1969). Although several explanations of this paradox can be suggested (e.g. daytime avoidance of the submersible, burial in the sediment, chance that the submersible did not happen to be in the vicinity of any squids during the day, etc.), none are testable with the present data set.

We found that a videocamera-equipped submersible was a useful alternative to trawling as a method for surveying small-scale distribution of juvenile squids at an interface such as the sea bottom on the continental shelf. Several problems with this method were apparent, however :

1) Absolute determination of animal size was not possible.

2) Individuals could not be positively identified to species.

3) Pelagic fishes interfered with observations of juvenile squids.

4) Operation of the submersible (e.g., speed and altitude) lacked standardization among operators.

5) Units of sampling effort have not yet been established to allow comparison with other studies.

Problems 1 and 2 above could be alleviated by trawling subsequent to completion of the video survey. Problems 4 and 5 would be resolved by directed experimental design and careful supervision. However, when pelagic fishes (and large squids) are attracted to the lights of the submersible, they either capture the small squids or chase them away. This will continue to cause serious bias in the observations whenever it occurs.

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FIELD AND LABORATORY BEHAVIOR OF "MACROTRITOPUS LARVAE" REARED TO *OCTOPUS DEFILIPPI* VERANY, 1851 (MOLLUSCA : CEPHALOPODA)

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CEPHALOPODA
BEHAVIOR
DISTRIBUTION
OCTOPUS
LARVAE

ABSTRACT. — Seventeen advanced macrotritopus "larvae" from 7 to 15 mm mantle length were attracted to underwater lights in St. Croix, U.S. Virgin Islands. Their behavior was observed *in situ*, then seven were captured alive and one female was reared to an adult *Octopus defilippi*. The characteristic long arms of the planktonic young appear to function in flotation, feeding, crawling and defense. There is evidence that larger macrotritopus may be planktonic by night and benthic by day; thus the transition from a planktonic to benthic life may be controlled to ensure widespread distribution on to a suitable habitat. Morphological examination of 106 specimens from the Atlantic indicate that all macrotritopus "larvae" from this ocean are *O. defilippi*.

CEPHALOPODA
COMPORTEMENT
DISTRIBUTION
OCTOPUS
LARVES

RÉSUMÉ. — Dix-sept individus juvéniles « macrotritopus » ont été observés en mer, sous des projecteurs, et sept ont été capturés vivants. Une femelle a été élevée jusqu'au stade adulte. La troisième paire de bras, très longs, semble jouer un rôle dans la sustentation, la prédation, la locomotion au fond, et pour la défense. Certains indices permettent de conclure que les macrotritopus de taille relativement grande vivent entre deux eaux pendant la nuit et ne descendent au fond que sous l'influence de la lumière. Le changement de mode de vie peut ainsi être repoussé jusqu'à ce qu'un fond approprié soit trouvé, éventuellement loin du lieu d'éclosion. L'examen morphologique de 106 spécimens provenant de l'Atlantique permet de conclure que tous les macrotritopus de cette région appartiennent à l'espèce *Octopus defilippi*.

INTRODUCTION

Macrotritopus "larvae" are young planktonic octopods with the third arms longer than the others. There has been continued confusion over their identity before they were recognized in the Atlantic as the young of a known species, *Octopus defilippi*. We attempt in this report to address the following questions concerning macrotritopus : (1) is there a species complex characterized by a macrotritopus juvenile ? (2) what are the long arms for ? (3) how and why do relatively large macrotritopus stay in the plankton ? and (4) if this is a continental shelf octopod, why are the macrotritopus most often found in the open sea and not on the continental shelf ?

Grimpe (1922) proposed the genus *Macrotritopus* based upon a juvenile (11 mm mantle length, ML) pelagic *Octopus gracilis* Verrill, 1884 that had long third arms. Issel (1925) thought that macrotritopus "larvae" were *Octopus defilippi*, while Degner (1925) thought that they were the young of *Scaeurgus unicirrhus* because of a specimen 6.3 mm ML that

had a knob on the left third arm, which he viewed as a rudimentary hectocotylus. In 1929, Joubin and Robson described two species of *Macrotritopus* from the Mediterranean, Atlantic and Caribbean. In 1929, Robson placed *Macrotritopus* back as a subgenus of *Octopus*. Adam (1938) described *Octopus (Macrotritopus) elegans* from the Indo-Pacific and later (Adam, 1954) noted the similarity to *O. defilippi*. In 1954, Rees considered the "macrotritopus problem" and, based upon the radula and distribution, concluded that they were *Scaeurgus unicirrhus* (curiously he did not mention the paper by Issel, 1925 !). In 1964, Voss described *O. defilippi* from the western Atlantic. Meanwhile, oceanographic sampling worldwide produced macrotritopus "larvae" in nearly all tropical and temperate seas (e.g., Rancurel, 1970; Cairns, 1976; Lu and Clarke, 1975). Boletzky (1977a) described the young of *Scaeurgus unicirrhus* and confirmed that macrotritopus were unrelated. Hanlon *et al.* (1980a) and Nesis and Nikitina (1981) independently confirmed that macrotritopus in the Caribbean Sea are *O. defilippi*. The present paper expands and clarifies the latter two reports.

MATERIALS AND METHODS

Seventeen live macrotritopus were attracted to an underwater 1 500 watt mercury vapor light at depths of 15 to 40 m over both coral reef and sand plain bottoms in Salt River Canyon on the north shore of St. Croix, U.S. Virgin Islands (17°45' N, 64°45' W) between 1 and 7 September 1978. Deep water was immediately adjacent to the island. The octopods were observed and photographed *in situ* for several hours during saturation diving mission 78-5 in NULS-1 (NOAA's first Undersea Laboratory System; Hanlon *et al.*, 1980b). Seven animals were collected, two were transported live to the Marine Biomedical Institute (MBI) at Galveston and one survived to sexual maturity in a small closed seawater system (see system details in Forsythe and Hanlon, 1980).

Eighteen preserved specimens collected from four extensive MBI research cruises in the western Gulf of Mexico (November 1975, April 1976, March 1977 and August 1977) were examined. In addition, the 77 specimens of Nesis and Nikitina (1981) were examined as well as two specimens from the Discovery investigations (Station 7824) and two from the Albatross IV (73-2; Station 109). Seven very young individuals from South Africa were also studied. Geographically this material covers all the Caribbean Sea and Gulf of Mexico as well as the central and south Atlantic. Specimen sizes ranged from 1.3 to 15.0 mm ML. In addition, 20 specimens from the Indo-Pacific (Hawaii, Australia, Indian Ocean) were examined for general comparison with the Atlantic material. Nearly all of these specimens were collected with standard Bongo nets or 1 m and 2 m plankton nets with mesh sizes of 0.50 to 0.65 mm.

RESULTS

Behavioral observations underwater

During one night-lighting station (Station 10 in Hanlon *et al.*, 1980b), twelve macrotritopus were observed at 21 m in the lighted area within one hour. The water was clear, and large quantities of plankton were attracted to the light. Feeding by the macrotritopus was not observed. The octopods drifted in from offshore towards the light in midwater in a distinct posture (Fig. 1 A) in which all the arms were spread out radially; we term this the Spread-arm drift posture. In this position the octopods seemed almost neutrally buoyant; they would occasionally jet slowly backwards. They were observed in this position for at least 15 minutes at a time. Five other macrotritopus were observed at 18 other night-lighting stations ranging from 15 to 40 m.

Two other forms of swimming were seen. During slow swimming the octopods jetted backwards with the arms trailing in a V, the tips usually curled; we term this Backward-V swimming (Fig. 1 B). When the animals slowed, they drifted downward only very slowly in this posture. During fast swimming the octopods jetted rapidly backwards with all arms tapered straight behind into a point. When quickly approached by a diver the octopods would go swiftly from the Spread-arm drift posture to fast backward jetting with inking; these small octopods could easily cover 0.5 m per jet and could go at least three consecutive meters outswimming a diver. They usually then went to slow Backward-V swimming towards the bottom.

On two occasions octopuses were followed slowly to the substrate, in which case they spread the arms radially and landed oral surface first (Fig. 1 C). They moved upon the substrate very deftly and were well coordinated to walk or crawl around, over or under the varied objects on the coral reef. Both animals quickly slid into holes and disappeared from view. It was clear that the substrate was not alien to them.

Observations in the laboratory

After removal from the sea the octopods never again spent time in the water column of the small tanks. They became exclusively benthic and their activity pattern was strongly nocturnal. At dusk, they frequently crawled forward across the substrate with all arms spread radially while each searched the

bottom (Fig. 1 D). They often climbed vertical objects with the arms drooping downward while they observed the surroundings (Fig. 1 E). They ate small live mussels within two days and then small live crabs throughout laboratory rearing.

The surviving octopus grew from 10 to 90 mm ML in 151 days. For the first 4 weeks it buried itself in the oyster shell substrate (particle size approximately 5 × 3 × 2 mm) except during foraging and feeding. Thereafter it hid in small shells. On day 143 this female laid over 10,000 unfertilized eggs, mean length 2.1 mm, which she carried in her arms for 8 days until death. The specimen matched well the characters of *Octopus defilippi* described by Voss (1964) and it is deposited in the National Museum of Natural History, Division of Molluscs (USNM 730019), Washington, D.C. Details of behavior and color change will be the subject of a future publication.

DISCUSSION

The one reared female confirms that macrotritopus near the U.S. Virgin Islands are *Octopus defilippi.*

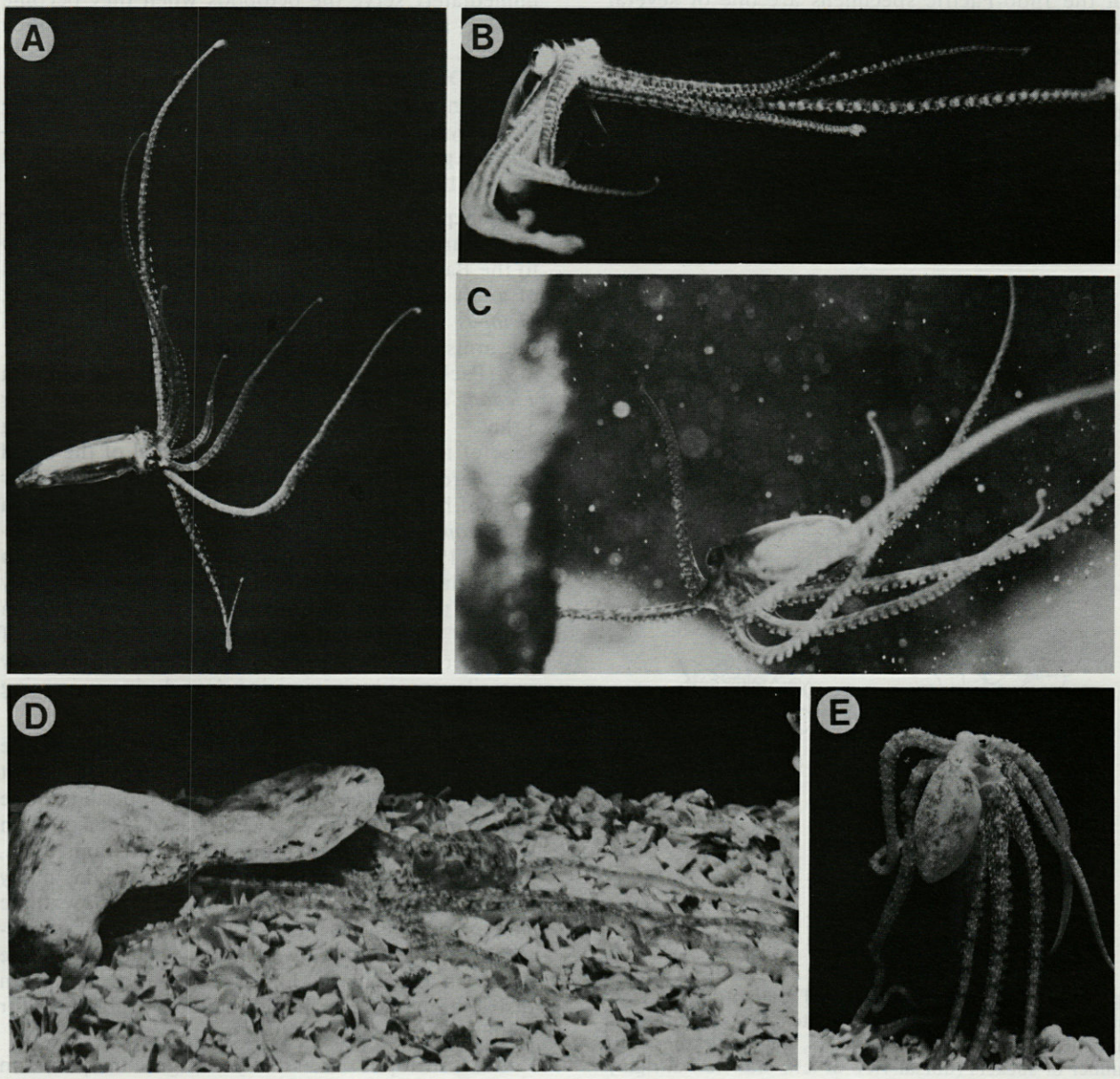

Fig. 1. — Behavior of macrotritopus "larvae" of *Octopus defilippi.* A, Spread-arm drift posture of a 9 mm ML octopod at 16 m underwater at night. B, Same octopod in Backward-V swimming. C, A 12 mm ML octopod about to land on the coral reef substrate at 15 m. D, Small field-caught female, 17 mm ML, after 2 weeks in the laboratory searching the bottom for food. E, Same female as in D at 25 mm ML in typical head-high sitting posture on the glass of the aquarium.

Inspection of 106 other macrotritopus from throughout the Atlantic indicate that all of them represent *O. defilippi.* The same conclusion was reached by Nesis and Nikitina (1981). The known distribution of *O. defilippi* (i.e., Caribbean, central and south Atlantic, Mediterranean) also supports this statement. The egg size, 2.1 mm, in the reared female corresponds to the smallest macrotritopus specimen, 1.3 mm ML after fixation. However, Indo-Pacific specimens appear to differ somewhat from Atlantic material in arm length ratios, funnel chromatophores and possibly other characters. Further study is required, but it seems likely that macrotritopus "larvae" represent a species complex worldwide and that the Indo-Pacific specimens are one or several species closely similar to *Octopus (Macrotritopus) elegans* (Adam, 1938, 1954) or *Octopus defilippi.*

In newly hatched macrotritopus, the ventrolateral arms (pair 3) are only very slightly longer than the other arms (Fig. 2). Subsequently, they outgrow arms 1, 2 and 4 very largely. The long, slender arms are obvious aids to flotation since they represent a large proportion of the surface area of the animal. The use of extended appendages to retard sinking is a well-documented fact in many pelagic organisms and our behavioral observations verify that macrotritopus can remain nearly stationary with little or no jetting. Long arms may also be useful in feeding upon larger plankton that stray into the extended arms during the Spread-arm drift posture. This type of "passive" and tactile feeding is not uncommon among octopods and is similar to the "speculative attacks" of *Octopus cyanea* (Yarnall, 1969) or *Octopus briareus* (Hanlon, 1975) and the "ambush" strategy of *Octopus burryi* (Hanlon and Hixon, 1980) and *Octopus joubini* (Mather, 1972). The long arms immediately serve the octopods when they become benthic, as we observed in the laboratory when they foraged the bottom with all arms spread radially (Fig. 1 D). The Spread-arm drift posture may also be useful in defense; it is strongly reminiscent of the Flamboyant defense pattern observed in young *Octopus* (e.g., Packard and Sanders, 1971; Hanlon and Hixon, 1980).

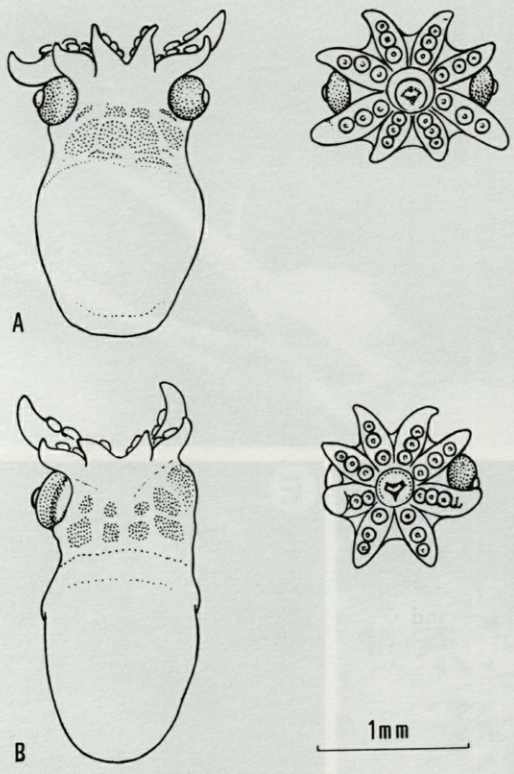

Fig. 2. — Preserved specimens of macrotritopus from South Africa. A, Very young post-hatching stage with third arms distinctly larger than others, but with the same number of suckers (dorsal view at left, oral view at right). B, Slightly more advanced stage, showing beginning formation of additional suckers only on arm pair 3 (dorsal view at left, oral view at right). NB : The extrusion of the eyeball is an artifact due to capture and fixation procedures.

The question why the third rather than another pair of arms is accelerated in growth draws attention to the Backward-V swimming attitude that is typical of adult octopodids when swimming. For example, *Octopus vulgaris* in slow backward swimming trails the arms in two distinct bunches forming together a V (Packard, 1972), the outermost being arms 3. In *Eledone cirrhosa* it is the proximal half of arm pair 3 that — by its strong curvature — forms the leading edge of the "wings" that are so typical of the rapid backward swimming in this species. A very similar form of horizontal "stabilizer" has been observed in *Pteroctopus tetracirrhus* swimming backwards (Boletzky, 1976). The rapid growth of arm pair 3 in macrotritopus suggests an adaptation to rapidly achieve the adult hydrodynamic profile of the arm crown. Conversely, the slower allometric growth of the other arms may present advantages during early juvenile stages by minimizing drag during swimming (Boletzky, 1977 b).

Macrotritopus are capable of remaining in the plankton over a wide size range — from 1.3 to at least 15 mm ML. We estimate this period to be approximately 10 to 20 weeks based upon growth studies of young planktonic octopods (Itami *et al.,* 1963) and squids (Yang *et al.,* 1983). Like many young octopodids, the macrotritopus follow three phases in development — solely planktonic, planktonic/benthic and truly benthic — but the middle phase is particularly long, presumably to aid in distribution and reaching suitable substrate for settlement.

Macrotritopus are rarely caught in plankton samples over continental shelf areas (Rees, 1954; Clarke, 1969; Lu and Clarke, 1975; Nesis and Nikitina, 1981). This could be partially explained by the ability of larger macrotritopus to control their planktonic/benthic phase and thus settle as soon as

they reach shelf areas, but it may be due also to the preferred habitat of *O. defilippi*. Takeda and Okutani (1983) recently found *O. defilippi* from 328 to 600 m off Suriname and it is possible that this species is more common on the continental slope than on the shelf. Their ability to bury in the substrate (in the laboratory) indicates that they would be able to inhabit open sand and mud areas of the deep shelf and still find protection by burying.

Thus one might expect small macrotritopus to be carried to open ocean waters after hatching but to settle quickly when they reach the edge of a continental shelf. Rees (1954) described one specimen, 3.45 mm ventral mantle length, from the Discovery Expedition that was captured between 1 500 and 800 m and he suggested that it was seeking bottom to settle.

In summary, the "macrotritopus problem" (Rees, 1954) has been clarified substantially for the Atlantic Ocean. However, the presence of two variations of *O. defilippi* (Robson, 1929) remains a problem. In contrast to the "typical form" with a radula characterized by unicuspidate rhachidian teeth, the variation *dama* described by Robson based upon a specimen from the Mediterranean "has well-developed ectocones with a symmetrical seriation (A 3-4)". The same is noted by Adam (1938) for *O. elegans*, but later (Adam, 1954) the radula of *O. elegans* is described as "caractérisée par l'absence d'ectocones sur les dents médianes" ! Further clarification should result from analyzing the Indo-Pacific macrotritopus to uncover their similarities or differences with *O. defilippi*.

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LABORATORY REARING OF RHYNCHOTEUTHIONS OF THE OMMASTREPHID SQUID *ILLEX ILLECEBROSUS* (MOLLUSCA : CEPHALOPODA)

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OCEANIC SQUID
LABORATORY REARING
LARVAE
CEPHALOPODA

ABSTRACT. — A methodology is presented for obtaining egg masses from captive populations of the ommastrephid squid *Illex illecebrosus* and for incubating them intact under controlled conditions. Survival of rhynchoteuthion larvae for 9 days after hatching is the best reported to date, though it has not yet been possible to induce feeding. Factors critical to rearing success are discussed, e.g. tank size, stocking density, turbulence, light levels and photoperiod, as well as food type and concentration.

CALMAR OCÉANIQUE
ÉLEVAGE EN LABORATOIRE
LARVES
CEPHALOPODA

RÉSUMÉ. — Une méthode permettant d'obtenir des masses d'œufs à partir de populations captives du Calmar *Illex illecebrosus* (Ommastréphidés) et de les incuber, intacts, sous conditions contrôlées est présentée. La survie des larves (pendant 9 jours après l'éclosion) est la plus longue signalée jusqu'à ce jour, mais il n'a pas encore été possible d'obtenir que ces larves se nourrissent. Nous discutons les facteurs critiques pour le succès des élevages, tels que les dimensions des bassins, la densité de peuplement des larves, la turbulence, les niveaux d'éclairement et la photopériode, ainsi que la nature et la concentration de la nourriture.

INTRODUCTION

Research into the early life histories of ommastrephid squid has been hindered by the difficulties of obtaining field data on early stages and of rearing them in the laboratory. These difficulties are not unique to ommastrephids, but considerable advances have been made in rearing several other groups of cephalopods (see review by Boletzky & Hanlon, 1983). Several species in these groups have, in fact, been reared through their complete life cycles. Such has not been the case with open ocean ommastrephids. The larvae of only three species have been maintained in the laboratory : *Todarodes pacificus* (Hamabe, 1962), *Illex illecebrosus* (O'Dor *et al.*, 1982), and *Illex coindetii* (Boletzky *et al.*, 1973). However, except for *I. illecebrosus*, egg masses have been obtained only by chance, and for all species survival of the larvae has been extremely poor, the longest having been eight days (O'Dor & Durward, 1978). The most obvious factors implicated in such poor culturing success relate to difficulties in maintenance of the large gel egg masses and the inability to induce feeding by newly hatched larvae. The latter has been a problem common to the rearing of all small-egg cephalopods, eg. *Loligo pealei* (Yang *et al.*, 1980).

Capitalizing on the ability to maintain adult *I. illecebrosus* to maturity in the 15 m diameter pool tank of the Aquatron Laboratory, we have been able to develop methods for obtaining spawning, for incubating intact egg masses and for initiating the rearing of the resulting larvae. In addition to aiding rearing methodology, our observations can be related to the picture now emerging of the environ-

mental and behavioural characteristics of the early life histories of rhynchoteuthions.

METHODS

Two key factors in rearing *I. illecebrosus* rhynchoteuthions in the laboratory are the ability to obtain healthy adults from inshore waters close to the laboratory, and to maintain them in a holding facility large enough to allow survival to sexual maturity. The details of capture and of maintenance in the 15 m diameter pool tank of the Aquatron Laboratory of Dalhousie University, Halifax, Nova Scotia, Canada, are found in O'D'or *et al.*, 1977. Approximately 50 egg masses have been spawned in the tank and several techniques have been tested for observing and culturing the eggs : with intact egg masses in the tank; with whole or partial masses in small containers and with artificially fertilized eggs *in vitro*. However, since development of eggs separated from the egg mass gel appears not to be normal, it became apparent that maintenance and incubation of intact egg masses under controlled conditions would be required as a basis for successful rearing of larvae. This however poses problems, due both to the large size of some of the masses (up to 1 m in diameter and weighing 500 kg) and to the extremely tenuous nature of the gel itself. In addition, the density of an egg mass is close to that of the water in which it is spawned (O'Dor & Balch, 1985a), so that changes in density of the water flowing into the pool tank can result in masses either rising to the surface, being suspended on a mid-water density interface, or sinking to the bottom. Thus a capturing device was required which could be used to retrieve an egg mass from either of these strata in the tank. The resulting long-handled (6 m) scoop-net has a triangular metal funnel (1 m on an edge) tapering to a detachable mesh bag (dia. 48 cm, length 90 cm).

Once the egg mass is gently manoeuvred into the mesh bag, a 200 l cylindrical plastic tank (dia. 56 cm, height 85 cm) is brought up under it, lifted from the pool and taken to a controlled-temperature seawater lab. The tank then serves as an incubator for the egg mass, with constant temperature seawater flowing through it via a circular diffuser on the bottom (Fig. 1).

The 1.5 mm mesh size of the bag retains the gel but allows emerging larvae to move through it into the surrounding water. Larvae can then either be removed from the tank or retained in the cone-shaped collector through which overflow water passes to drain. The collector has a screen below its overflow which keeps larvae within the cone where they can seek out an appropriate level in the velocity gradient provided by the increasing diameter of the cone.

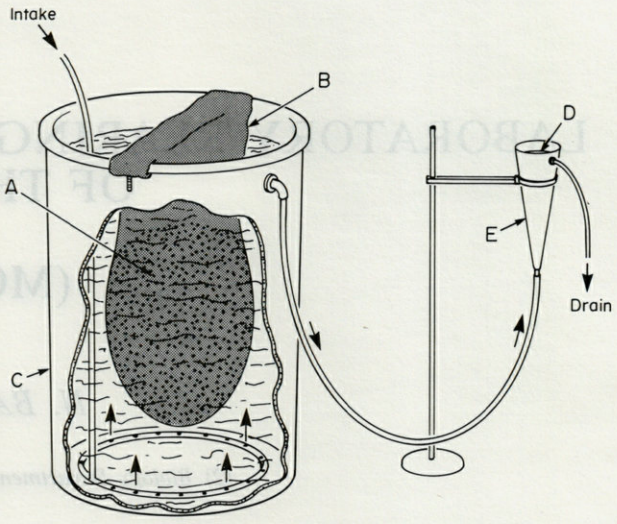

Fig. 1. — Incubation tank for a gel egg mass spawned by *Illex illecebrosus*. A. Egg mass, B. Mesh bag attached to rim of tank, C. Polyethylene tank (85 cm deep. 56 cm dia.), D. Retaining netting, E. Cone for collecting larvae.

The ability to control incubation temperature of the mass has allowed us to test the effect of temperature on hatching success. The following data were collected : egg mass size, number of eggs in mass, fertilization rate (% eggs which began development), and the number of larvae hatched. A 16 : 8 hr. light : dark photoperiod was imposed for the duration of the experiment. Some larvae were transferred to 4 l bottles for feeding experiments with two potential food sources : *Artemia* nauplii (250/l) and a unicellular alga, *Isochrysis* sp. (10^6/ml). Feeding bottles were rotated in a 20 °C temperature bath with the photoperiod given above. Each day the larvae were carefully removed from the feeding bottles, their guts were examined under a microscope for evidence of feeding and they were returned to new water and prey.

RESULTS & DISCUSSION

Table 1 outlines the results of the incubation experiment. Fertilization rates were low, all less than the maximum of 40 % reported for previous egg masses spawned in the Aquatron (O'Dor *et al.*, 1980)

Table I. — Effect of incubation temperature on hatching success from intact egg masses.

Temperature (°C)	Egg Mass Diameter (cm)	Number of eggs (x 10^3)	Fertilization Rate (%)	Number of Larvae	Hatching Success of Fertilized Eggs (%)
15	100	36	9	0	0
20	40	2.3	< 1	6	26
26	49	4.5	15	315	47

and 20 % for eggs artificially fertilized *in vitro* (O'Dor *et al.*, 1982). The almost total failure of fertilization in the 20 °C egg mass may be explained by the fact that it was probably spawned by the female which had previously produced the mass used in the 26 °C experiment. The first spawning could have exhausted her stock of spermatophores. In addition, there were few males in the captive school, a not uncommon problem, since schools captured inshore are often found to be segregated with respect to sex, sometimes with as few as 5 % males (O'Dor, 1983). Although it is unlikely that such low fertilization rates obtain in nature, speculation has been put forward on the potential impact of sexual mis-match at the time of spawning, resulting either from segregated schooling or from cannibalism of the males by the normally larger females (O'Dor, 1983). Since no observations have been made of schools close to spawing, the sex ratio of schools at the time of spermatophore implantation is unknown, though Amaratunga (1980) has reported late-season schools with as low as 26 % males. A further factor may be the possible effect of low temperature on sperm motility and viability, since fertilization of all masses took place at 15 °C, the operating temperature of the pool tank. We did not control the tank temperature so as to allow spawning at the higher temperatures used for subsequent egg incubation. The low fertilization rates in these large gel masses may also reflect a trade-off between fertilization success and the benefits derived from their flotation and anti-predation characteristics, i.e. the near-neutral density of a mass (O'Dor & Balch, 1985a) and the protection given by it against both planktonic and nektonic predators.

Although the lowest incubation temperature in this experiment (15 °C) was above the previously reported 12.5 °C minimum for normal egg developmen (O'Dor *et al.*, 1982), no eggs were successfully hatched at that temperature. Egg development stopped shortly after fertilization, a not uncommon occurrence in previous egg masses, though one which remains unexplained.

Clearly the most successful hatching was at 26 °C, the highest temperature yet reported for rhynchoteuthion larval rearing. In addition, although some did hatch prematurely at stage XVIII, after only five days, those which remained in the egg mass for seven days hatched at stage XX. Presumably this represents the most advanced stage possible at hatching, conferring on such larvae the best survival probability. The success of incubation at 26 °C supports the hypothesis that spawning may take place in the surface waters in or near the Gulf Stream, which can be as high as 26 °C. Indeed, the most recent field surveys have found larvae in Gulf Stream water up to 25 °C (Rowell & Trites, 1985).

From the perspective of designing a system for rearing rhynchoteuthion larvae, though the one described here has resulted in the best hatching success to date, it still does not provide an optimum environment for survival of the larvae. Of the 315 larvae hatched, only 13 % were collected alive and apparently healthy, the rest having been collected dead or moribund from the bottom of the tank. It is not clear what led to such poor post-hatch survival, but tank size and the degree of turbulence in the tank may be critical factors. The natural environment probably has relatively low levels of small-scale turbulence so that a rearing tank mimicking such an environment would be desirable. In addition, physical damage to the ciliature covering larvae probably results from the confined nature of the culture environment and may influence survival rates, perhaps mediated through disruption of ciliary feeding mechanisms (O'Dor & Balch, 1985b).

There was no apparent feeding on either of the two potential food sources over the nine days of the present feeding experiment, nor on a broad range of potential prey during previous tests. This suggests that we may be providing a combination of inappropriate culture conditions for the immediate post-hatch period. Factors such as container size, stocking density, turbulence, light levels and photoperiod, as well as the more obvious factors, food type and concentration, may all be critical for successful feeding. It is possible that the unique feature of rhynchoteuthions, the fused proboscis, is implicated in initial feeding in some important manner mitigated against by present culture conditions. Though post-hatch survival for nine days during the feeding experiment is the longest reported to date for rhynchoteuthions, there was no apparent development during that period. Survival was evidently based on utilization of yolk sac reserves, though some yolk remained at death even in the longest-lived individuals. Mortality during the transition from yolk feeding to active prey capture has been common in reared squid (Hanlon & Hixon, 1983). Factors such as light, vibration and, particularly, the type of movement exhibited by prey have been found to be critical (Yang *et al.*, 1983). On the assumption that squid larvae use one or a combination of chemo- or kino-receptors, or eyes, for prey detection, it will be important to refine culture conditions so as not to interfere with these sensing organs. This suggests the need for low densities both of larvae and prey, large container size, minimum turbulence, and low light levels coupled with appropriate visual backgrounds. Elucidating these factors may lead to an improved understanding of the mechanisms involved in initial feeding. This would serve not only to improve culture methodology but also to provide insights into this critical phase of rhynchoteuthion survival in nature. As Summers (1983) has noted for *Loligo pealei*, a similarly recalcitrant small-egg cephalopod, "what is needed is a revolutionary step in aquarium work, one directed toward the gentle management of planktonic organisms".

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BEHAVIOR, FEEDING AND GROWTH OF YOUNG *LOLIGO FORBESI* (CEPHALOPODA : MYOPSIDA) REARED IN THE LABORATORY

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CEPHALOPODA, *LOLIGO FORBESI*, REARING, JUVENILE BEHAVIOUR, GROWTH

Loligo forbesi is the largest known loliginid squid, an important biomedical research animal and a commercially fished species in the NE Atlantic. We reared this species from hatching to sexual maturity (140 mm ML) in 369 days at a mean temperature of 15 °C (s.d. 1.62). Eggs were obtained from England and France, air-shipped to Galveston, and hatched successfully (> 70 %) in both natural and artificial seawater in recirculating systems. The hatchlings were very large (3.2-4.0 mm ML) and were fed size-sorted zooplankton (mostly copepods) for the first 50 days. Mysidacean shrimps (1.3-5.3 mm) were mixed in with the zooplankton within 10 days and were the primary food from day 20 through 100; *Palaemonetes* sp. shrimp larvae (2.1-2.4 mm) were also eaten readily from day 10 to 80. One-week-old squids could capture and ingest prey of a wide size range, from less than 1 mm to 5.3 mm. Growth was rapid, exponential during the first two months. In 1983 (mean temperature 14 °C), the growth equation for live wet weight was :

$$\text{Weight} = 8.108e^{0.0541t} \quad (r^2 = 0.98)$$

and for live mantle length it was :

$$\text{Length} = 4.409e^{0.0182t} \quad (r^2 = 0.98)$$

This corresponds to approximately 5.4 % and 1.8 % increase in body weight and length per day, respectively. Slightly lower rates, 3.6 % daily weight increase and 1.3 % daily length increase, were obtained in a 1985 experiment (mean temperature 13.2 °C). In both experiments mortality was high : 94 % in 1983 and 97 % in 1985 by day 60, despite active feeding. By the time squids were approximately 12 mm ML and 0.2 g (approximately 30 — 60 days posthatching) they were capable of schooling together and maintaining their position in a current (2 cm/second). By comparison, *L. opalescens* in culture schooled at a size of 10 to 15 mm ML (Yang *et al.*, 1983, *Aquaculture 31* : 77-88). These results indicate that during the first 2 months of life, wild *L. forbesi* are subject to distribution by currents and can feed upon a wide variety and size of prey.

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BEHAVIOR, FEEDING AND GROWTH OF YOUNG LOLIGO FORBESI (CEPHALOPODA : MYOPSIDA) REARED IN THE LABORATORY

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ECOLOGICAL IMPLICATIONS OF LIFE STAGE TIMING DETERMINED FROM THE CULTIVATION OF *ROSSIA PACIFICA* (MOLLUSCA : CEPHALOPODA)

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ECOLOGY
TIMING
CULTIVATION
ROSSIA PACIFICA
SEPIOLID SQUID
CEPHALOPODA

ABSTRACT. — The sepiolid squid, *Rossia pacifica* Berry 1911, was trawled in the northeast Pacific ocean and brought into the laboratory where it is currently in cultivation. At seasonally varying temperatures, the generation is two years; 18-19 months from hatching to a spawning-related death, and 5-6 months for embryonic development. Growth in dorsal mantle length was slow for the initial one-half year, but increased at the time of spawning and death of the preceding year class. It continued through maturation to spawning at different rates for each sex. Repeated spawning was observed. Hatching of the eggs appeared to be keyed to the new moon and extended over more than two months. Low seawater temperatures may affect this process. The ecological significance of lunar cuing is discussed relative to predation. Long-term observation of overlapping, two-year life cycles from field data confirms measured growth in cultivation and suggests that two relatively independent year classes coexist on the same ground with little competition. The early life is characterized by low growth, adaptability and a conservative strategy. It is released by the semelparous death of the preceding year class to become more opportunistic, grow faster and become sexually mature. This life pattern may be homologous to other squid species.

ÉCOLOGIE
RYTHMES
ÉLEVAGE
ROSSIA PACIFICA
SEPIOLIDAE
CEPHALOPODA

RÉSUMÉ. — La durée d'une génération de *R. pacifica* soumise aux variations saisonnières de températures est de 2 ans : 18 à 19 mois de l'éclosion à la reproduction (suivie de la mort), et le développement embryonnaire se déroule en 5 à 6 mois. La croissance linéaire est lente pour les six mois suivant l'éclosion, puis augmente pendant la période où la « classe » de l'année précédente se reproduit et meurt. Après cette augmentation du taux de croissance, les taux divergent pour les deux sexes. Une même femelle peut pondre plusieurs fois en l'espace de quelques semaines. L'espèce peut être élevée en aquarium si des Crevettes vivantes de taille appropriée sont disponibles comme nourriture. Un fond de sable et un renouvellement continu de l'eau de mer dans les bacs d'élevage sont souhaitables. L'éclosion des jeunes semble liée aux phases lunaires et peut se prolonger sur plusieurs mois si les températures sont basses. L'influence de facteurs liés aux conditions artificielles doit également être prise en considération dans le déclenchement de l'éclosion.

INTRODUCTION

There are at least two compelling reasons for the determination of squid life cycles and the factors that cause them to progress. The most immediate of these is for the rational management of squid fisheries based on an assumption that conservation is desirable and that the squid stocks are not infinite. The second is more basic; it seeks to determine the ecological role of squid in marine ecosystems, noting that they are ubiquitous, ancient and never higher

than penultimate predators (Packard, 1972, Summers, 1983). The scientific establishment also places demands on squid as a source of giant axons (Baker, 1984) and as models for other biomedical research (National Research Council, 1985). Descriptions of a few, better-known squid life cycles (Boyle, 1983) suggest a partial dichotomy — some species have many small eggs and planktonic young that change form at relatively distinct life stages. Others have a few large eggs and hatch as functionally small adults (Boletzky, 1981). The former group is least well known.

The sepiolids are among the species with large eggs and an apparent direct development. They are widely distributed and can be cultivated (Boletzky and Hanlon, 1983). Furthermore, the sepiolids basically have only one life stage between hatching and death, and it is one that can be identified as a functionally generalized squid pattern, at least as far as neritic squids are concerned. Though more limited in sizes than some other squids, sepiolids cannot be considered small when compared with the majority of marine organisms. Because of cultivation, sepiolids may provide an experimental homology for the larger stages of other squid species.

An alternative to laboratory evaluation exists in long-term field studies where population statistics subtitute for precise determinations from known individuals. This approach is traditional in fisheries research and still necessary for those species that cannot be cultivated (e.g., Summers, 1971). The field study approach is inefficient and introduces possible errors due to sampling and migration; laboratory studies are prone to artifacts due to unnatural conditions.

In a recent paper, the author calls into question the widely used practice of equating size with the age of squid and raises the issue of elective behavior of individual squid at the latter stages (Summers, 1985). The purpose of this report is to describe some new information on life stage timing obtained during the first cultivation of *Rossia pacifica*. The ecological importance of timing is discussed.

MATERIALS AND METHODS

The common northeast Pacific sepiolid squid, *Rossia pacifica* Berry 1911, was caught regularly in Burrows Bay, Skagit County, Washington in June and July of 1983. Specimens were collected in 40 to 60 m depth with commercial shrimp trynets (10 foot otter trawls) from the R/V Leona III operated by personnel from the Shannon Point Marine Center. Examinations of about 30 specimens showed two distinct size groupings, the larger of which had a clear sexual dimorphism (females larger than males). Some of these were transferred to the laboratory near Anacortes, Washington and maintained in running seawater for a few weeks. All of the healthy animals fed readily on shrimp (approximately the same size as the squid), particularly various pandalid species. When sand was provided in the aquaria, the *Rossia* spent large portions of the daylight hours on the bottom covered with sand.

Cultivation

Seven of the smaller squid were placed together in a rectangular fiberglass aquarium with coarse sand (dimensions : 55 × 40 cm, filled to a depth of 35 cm). These were maintained together until March 1984, at which time sexual maturity was evident and pairs or individuals were isolated in various aquaria of the same or smaller dimensions (40 × 30 cm, filled to 30 cm depth) until all of them had died (a period extending from 10 April to 29 June, 1984). Of the seven, two were males and five females. One pair copulated on or shortly before 7 May; the female laid about 50 eggs (1 cm in diameter) on the aquarium wall approximately 1 June, and (after both were moved to a controlled temperature aquarium of about 95 L volume) another 35 eggs on 21 June. This female died four days later followed by the male five days after that.

Monthly mean temperatures varied seasonally from 6 to 12 °C. The controlled temperature aquarium was maintained at 10 °C, which is the approximate year-round mean temperature. This aquarium had regular, partial replacement of seawater rather than running seawater. Standard water quality parameters remained consistently high over the course of the cultivation (e.g., dissolved oxygen 7-11 ppm, pH 7.7-8.3, and both total and carbonate alkalinities 1.85-2.25 meq/liter).

Running seawater aquaria were situated in a north facing, roofed, but otherwise open and unheated room connected to the laboratory building. Artificial illumination was used irregularly during working hours, and rarely at night. Clear plastic sheeting was used to provide weather protection of the room during the most severe winter months. The temperature controlled aquarium was immediately adjacent to this room, but inside the building in a heated space. It received illumination through large windows and daytime artificial illumination. This aquarium was, in general, somewhat darker than the running seawater aquaria.

The animals were subjected to weekly photographic documentation, with a few lapses which include the period of embryonic development, beginning 3 August, 1983. Squid were photographed vertically from about one-half meter distance in shallow glass dishes placed on millimeter graph paper. The procedure was conducted quickly and with little apparent trauma using photoflood illumination. By later projection of color slides, it was possible to reliably

measure dorsal mantle length (and other dimensions) to less than one millimeter. It should be noted that this produces a good relative measure, but one which is foreshortened by the squid's upright posture and, to a lesser extent, by the photographic geometry.

The reliability of the photographic method was tested through a series of repeated photographs in a randomized complete block ANOVA design when the squid were half-grown (mean dorsal mantle length of 22 mm). As expected, the blocks (individual squid) were highly significant in photographic size determinations, but individual measurements of the same specimen did not vary significantly. Persons taking the measurements had a small, but consistent effect on the results.

Eggs were disturbed as little as possible, but were occasionally flushed with the flow of water from the intake hose to dislodge sediment and diatoms. The range of temperatures measured in the running seawater tank was from 15 to 6 °C over the period of embryonic development, with the greatest daily variation occurring in the summer. The temperature-controlled aquarium remained within one degree of the preset, 10 °C.

Following hatching late in 1984 and early in 1985, the young squid were transferred to floating plastic containers within the aquaria. After a few days the squid were released into all-glass aquaria of about 100 L capacity with a clean sand bottom. The squid in the temperature controlled aquarium were simply released in that tank which had coarse shell-sand as a bottom filter. Cultivation of second generation squid is continuing as of December, 1985.

RESULTS

The photographic sizes of the seven specimens and a representative number, or all, of the second generation is shown in Figure 1. A mean photographic dorsal mantle length is given in the figure; this should be taken as 80-90 % of the directly measured dorsal mantle length in relaxed live squids or fresh dead ones. It progresses from a measured hatching size of 6 mm dorsal mantle length (photographed at 80 %) to the largest females of 50 mm (photographed at 90 %). The photographic size range also increased from 2 mm during the hatching period to 12 mm at spawning; the last mostly due to sexual dimorphism.

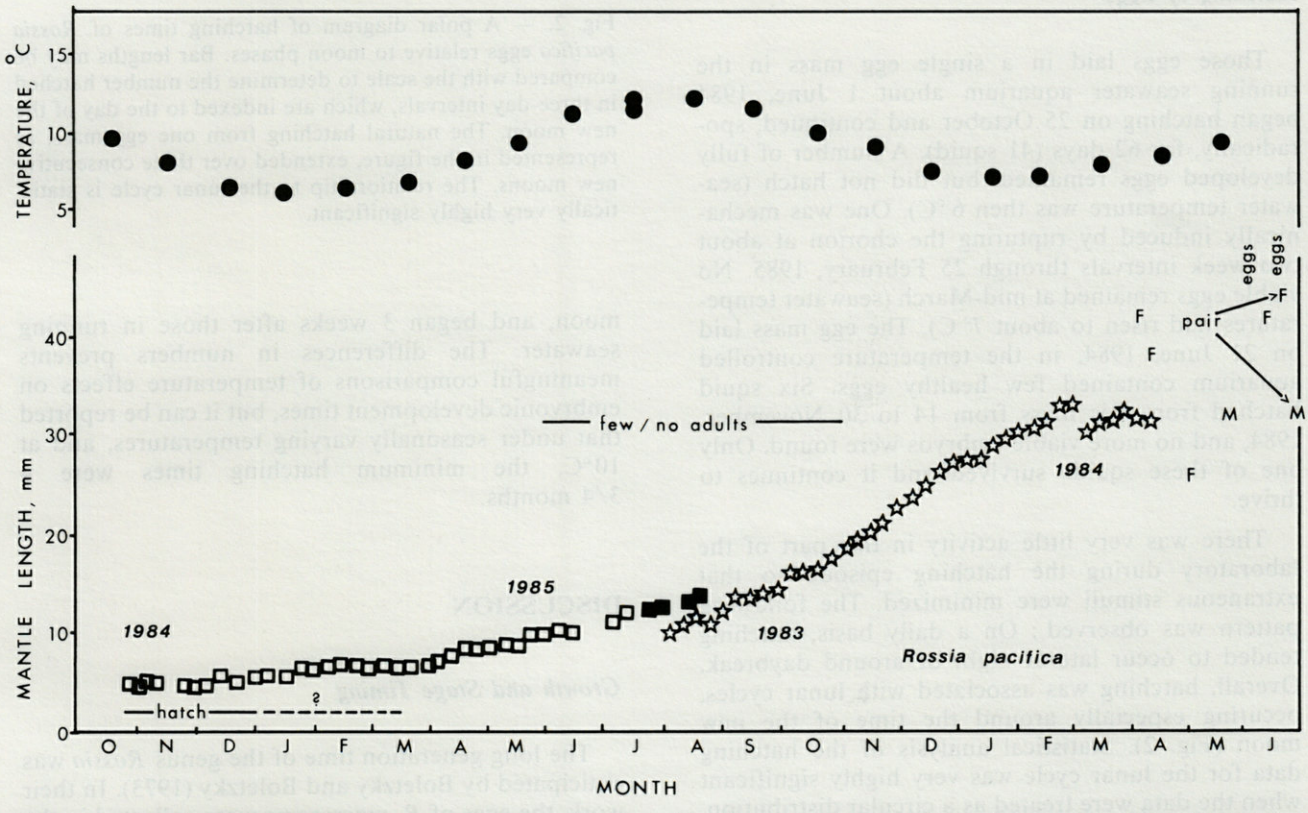

Fig. 1. — Growth of *Rossia pacifica* over a two-year life span. The figure is a transposition of mean dorsal mantle length data (photographic measurements) for seven specimens captured in June and July of 1983 (shown as stars) and all or a representative number of the subsequent generation (shown as squares). The ultimate sizes of the original seven are shown at the time of death as F (female) and M (male); one pair laid two batches of eggs as indicated. Monthly mean seawater temperatures are shown at the top-two data points in July represent a warmer season in 1985 compared with 1983. Filled squares are conservative size estimates from recent measurements.

Growth (Fig. 1) was continuous but not at the same rate through the one and one-half year life life span. Even after size correction for the photographic method — if such is necessary — it is clear that growth rates increase with age and size. This is opposite to the von Bertalanffy growth model. Field data and specimens of *R. pacifica* collected in the immediate area over the last decade readily fit this laboratory observation and further confirm that two age groups are typical. Food did not appear to be limiting in the laboratory because the numbers of shrimp consumed by the squid remained relatively constant throughout the cultivation (roughly 3/squid/week). In running seawater temperatures were seasonal and cycled twice over the total generation (life span plus embryonic development).

The cultivation determined that sexual maturity presages death in both sexes — with or without copulation and spawning. Thus, *R. pacifica* is semelparous as are other cephalopods (Boletzky, 1981) and it may spawn on more than one occasion over a period of weeks. Boletzky (personal communication) reported that *Rossia macrosoma* spawned over a period of two months.

Hatching of Eggs

Those eggs laid in a single egg mass in the running seawater aquarium about 1 June, 1984 began hatching on 25 October and continued, sporadically, for 62 days (41 squid). A number of fully developed eggs remained, but did not hatch (seawater temperature was then 6 °C). One was mechanically induced by rupturing the chorion at about two week intervals through 25 February, 1985. No viable eggs remained at mid-March (seawater temperatures had risen to about 7° C). The egg mass laid on 21 June, 1984, in the temperature controlled aquarium contained few healthy eggs. Six squid hatched from this mass from 14 to 30 November, 1984, and no more viable embryos were found. Only one of these squids survived and it continues to thrive.

There was very little activity in this part of the laboratory during the hatching episode so that extraneous stimuli were minimized. The following pattern was observed : On a daily basis, hatching tended to occur late at night or around daybreak. Overall, hatching was associated with lunar cycles, occuring especially around the time of the new moon (Fig. 2). Statistical analysis of the hatching data for the lunar cycle was very highly significant when the data were treated as a circular distribution. The estimated mean hatching time was one day after the new moon (approximately equal to the reporting delay based on 4-5 observations per week) with a standard deviation less than 6 days. Hatching in the temperature controlled aquarium spanned the new moon, and began 3 weeks after those in running seawater. The differences in numbers prevents meaningful comparisons of temperature effects on embryonic development times, but it can be reported that under seasonally varying temperatures, and at 10 °C, the minimum hatching times were 4 3/4 months.

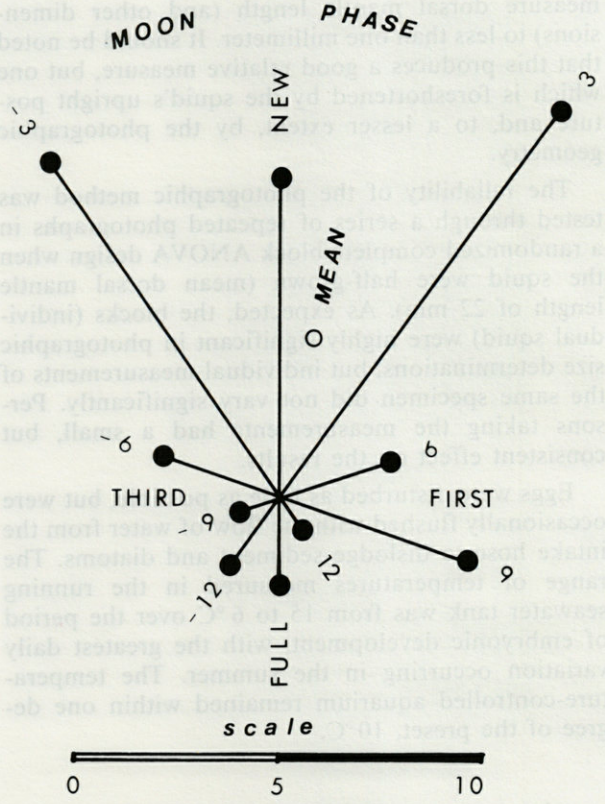

Fig. 2. — A polar diagram of hatching times of *Rossia pacifica* eggs relative to moon phases. Bar lengths may be compared with the scale to determine the number hatched in three-day intervals, which are indexed to the day of the new moon. The natural hatching from one egg mass, as represented in the figure, extended over three consecutive new moons. The relationship to the lunar cycle is statistically very highly significant.

DISCUSSION

Growth and Stage Timing

The long generation time of the genus *Rossia* was anticipated by Boletzky and Boletzky (1973). In their work, the eggs of *R. macrosoma* were collected in the western Mediterranean Sea, and maintained at 15 °C. A few specimens were raised at 15 °C and, later, 20-22 °C over a period of 240 days. These hatched at 6 mm mantle length and had reached 20 mm in 166 days. The increasing growth rate that

is reported here was not observed in Boletzky's work.

In a thesis dealing with the biology of *R. pacifica* in British Columbia, Brocco (1971) gave length-weight information for males and females larger than 10 mm mantle length. A scaling of those data suggests that the males have an increased ratio of weight to length at about 27 mm mantle length. This corresponds to Brocco's observation that 50 % had spermatophores at a size of 26 mm mantle length. Also, females had a more profound increase in the weight to length ratio at about 29 mm mantle length. He reported ovarian development beginning at 24 mm mantle length. Brocco speculated on a one year life span, which can be understood as an extrapolation of the right half of Figure 1 where the smaller specimens were not observed.

A seasonal growth pattern similar to Figure 1 is reported for North Sea plaice (Lockwood, 1974). Two separate von Bertalanffy growth curves were fitted to each age group in that case. Growth models aside, the ecological effect is the same in both species — two age groups live in close association with the bottom at the same time and place. They are distinctly different in size and, thus can avoid competition by partitioning the food resource. The North Sea plaice eventually migrates offshore and can live a long life and spawn repeatedly. *R. pacifica* invests all of its final energies in the production of a modest number of very large eggs. Apparently, it does not migrate far nor grow further except that dimorphism results in large females (for egg production).

In an ecological sense the spawning and death of the larger animals releases the subsequent year class to exploit the whole food resource. During the period of embryological development, this class doubles its size and reaches sexual maturity. If seasonal growth — or, better seasonal lack of growth — does occur in *R. pacifica,* it can only be attributed to the first half-year of very slow growth. Boletzky & Boletzky (1973) observed that newly hatched *R. macrosoma* live up to three months without feeding at 9 °C; these animals utilize muscle tissue for maintenance and neither grow nor survive. Perhaps *Rossia* has an unusually long life span precisely because, in an ecological sense, it hatches precociously, and it awaits a productivity opportunity before growing. One must question whether warmer or more favorable conditions promote early growth.

Hatching Times

The moon relationship in hatching was unexpected. Hatching occurred when day lengths were shortest (about 8 hours) and nights darkest. An animal vulnerable to visually oriented predators has maximum protection under these circumstances. Also of possible importance, lunar cuing spreads hatching over a long period, which provides an opportunity for areal distribution. Because the eggs are sizeable and the newly hatched animals are highly visible, a hatching strategy that minimizes vulnerability would be advantageous. An examination of data from an earlier cultivation of *Sepietta oweniana* (Bergström and Summers, 1983) showed that half of the few day long hatching events observed were at the time of the new moon.

Secondary keying factors cannot be discounted in the hatching of *R. pacifica.* The tidal amplitude, hence, water quality factors, cycle twice in each lunar cycle. Perhaps olfactory cues influence hatching. Mechanical stimulation may also occur as an indirect effect of tides, illumination or day length, perhaps through activity patterns of the embryos themselves. The unaided hatching was observed extending over three new moon events and may have been truncated by low seawater temperatures. Clearly, the hatching progressed at 10 °C and continued to nearly 6 °C. Eggs were mechanically induced over the next two months at seawater temperatures below 7 °C, but did not hatch spontaneously. It should be noted that embryonic duration had reached 9 months at this point and that yolk reserves remained.

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CAPTURE OF PREY, DIET AND FEEDING OF *SEPIA OFFICINALIS* AND *OCTOPUS VULGARIS* (MOLLUSCA : CEPHALOPODA) FROM HATCHLING TO ADULT

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CEPHALOPODA
SEPIA
OCTOPUS
PREY
FEEDING
HATCHLING
ADULT

ABSTRACT. — *Sepia officinalis* is large at hatching and resembles the adult. It hatches into the adult habitat and takes up the same nectobenthic habits. The buccal mass is large and well developed at hatching as are the arms and tentacles. Its first prey, a small shrimp, is captured with the tentacles as the adult takes a prawn. Benthic, nectobenthic and planktonic organisms are taken, bitten and paralysed with cephalotoxin; and much of their skeletal material is ingested. *Octopus vulgaris* is small at hatching, and has a very large buccal mass. The hatchling joins the plankton where it, presumably, feeds on very small organisms such as larval crustaceans. After several weeks it settles on the bottom in the adult habitat, where a great variety of benthic and nectobenthic animals are taken. For this it has specialised capturing and feeding methods. The prey is paralysed with cephalotoxin, spread of the toxin being aided by hyaluronidase, and musculo-skeletal and shell attachments are broken down by limited external digestion after which the flesh falls away for the octopus to eat. Little or no skeletal material is ingested.

CEPHALOPODA
SEPIA
OCTOPUS
PROIE
CAPTURE DE NOURRITURE
STADE D'ÉCLOSION
ADULTE

RÉSUMÉ. — Les nouveau-nés de *Sepia officinalis* sont relativement grands et ressemblent aux adultes dont ils adoptent l'habitat et le mode de vie necto-benthique. La masse buccale, les bras et les tentacules sont bien développés. Les Mysis, leur première proie, sont capturées avec les tentacules à la manière dont les adultes attrapent les Crevettes. Des organismes benthiques, necto-benthiques et planctoniques sont capturés, mordus et paralysés par la céphalotoxine. La matière squelettique des proies est ingérée en grande partie. Les nouveau-nés d'*Octopus vulgaris* sont de petite taille, mais leur masse buccale est très grande. Les animaux vivent entre deux eaux et se nourrissent probablement de petits organismes comme les larves de Crustacés. Après quelques semaines de vie planctonique, ils adoptent le mode de vie benthique des adultes et se nourrissent de proies benthiques et necto-benthiques très variées. La méthode de capture est spécialisée. Les proies sont paralysées par la céphalotoxine dont l'action est renforcée par la hyaluronidase. Les muscles sont détachés des parties squelettiques par digestion externe partielle, et les jeunes animaux mangent la chair ainsi libérée sans ingérer de matériel squelettique.

The many and varied studies of *Sepia officinalis* and *Octopus vulgaris* made during the past two decades permit us to follow some of their feeding habits from hatching to adulthood.

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SEPIA OFFICINALIS

The cuttlefish has a large egg (7.5 × 6 mm) and at hatching the young (5-9 mm mantle length) resembles the adult (see Boletzky, 1983). It is nektobenthic, and has similar habits to the adult. The yolk

is absorbed (see Boucaud-Camou *et al.*, this vol.) while the digestive system becomes functional and the animal begins to feed (see Boletzky, 1983). When a cuttlefish sees a live *Mysis* for the first time it will attack, after a delay of 10 s-10 min, using its tentacles to grasp the prey (Wells, 1958). Messenger (1968) analysed the capture of prawns by adult cuttlefish. Once sighted, the prey can be seized in as little as 2 s; the tentacles taking only 32 ms to traverse the distance to the prawn. The prey is withdrawn into the open arms in 150-320 ms, then bitten and saliva introduced. The saliva contains cephalotoxin (Ghiretti, 1959, 1960) which paralyses the prawn in about 5s. The prey is devoured completely except for the antennae and rostrum which are discarded (Messenger, 1968).

The mode of capturing other prey differs and no similarly detailed analyses are available. Cuttlefish usually jump on a crab from behind, to avoid injury from the chelae, and seize it with tentacles or the arms (Boulet, 1954; Messenger, 1968); the saliva induces paralysis (Ghiretti, 1959) within 9 s, and the prey is then eaten apart from the carapace, chelae and walking legs (Messenger, 1968). Some evidence suggests that cuttlefish take prey size into account when attacking crustaceans, since the remains of appendages in the stomach increase in size in relation to that of the cuttlefish (Guerra, Nixon and Castro, in prep.). Size selection is not necessary for prey without a hard exoskeleton, such as fish. In an aquarium the fry of *Mugil* were captured with the tentacles (Messenger, 1968) and, after attacking shoaling fish then several would be stored on the arms (Neill and Cullen, 1974). The saliva is toxic to fish (*Agonus catafractus* (Romijn, 1935)).

The stomach contents of wild caught *Sepia officinalis* include remains from a variety of prey (Najai and Ktari, 1974; Guerra, 1985) : the majority are bottom living (amphipods, brachyurans, isopods, porcellanids, lamellibranchs, gastropods, polychaetes and nemerteans), others are nektobenthic (teleosts (gobies and pleuronectids), cephalopods, Natantia and Portunidae) and a few are planktonic (copepods, ostracods and pteropods). Prey from such diverse habitats confirm the diel vertical migrations observed in the laboratory, that are aided by the buoyancy control system of the cuttlebone (Denton and Gilpin-Brown, 1961). Very young cuttlefish also move off the bottom to capture prey, and although at first they only respond to mysids (Wells, 1962), they come to attack other prey (Boletzky, 1983). This may be correlated with the development of the learning system of the brain; the vertical superior frontal system is initially poorly developed (Wirz, 1954; Wells, 1962; Messenger, 1973, 1977).

Crustacea form the main part of the diet of young cuttlefish, together with some fish and molluscs, but older animals with a mantle length of more than 100 mm tend to increase their intake of fish and molluscs, including their own kind (Najai and Ktari, 1974; Guerra, 1985).

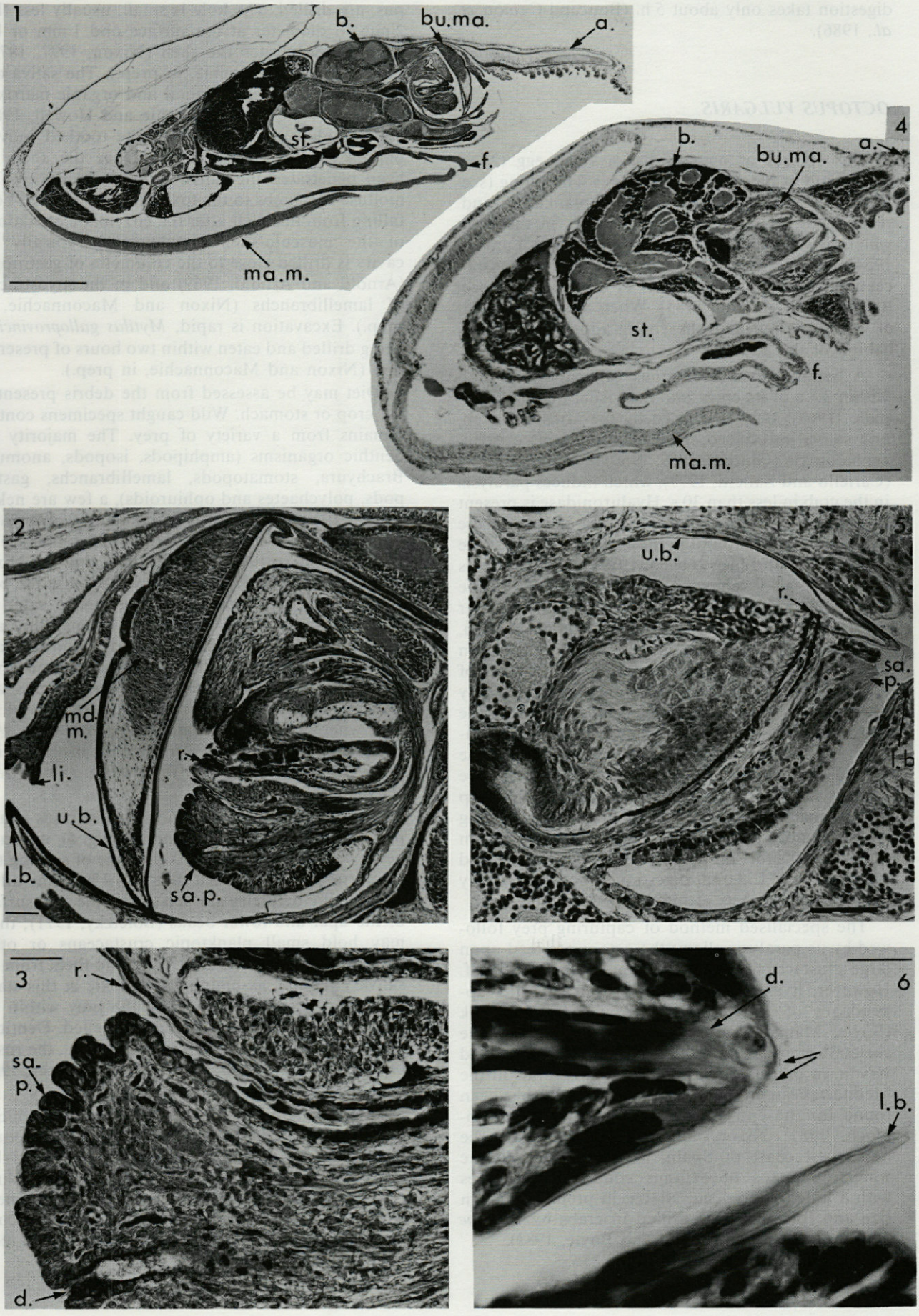
The buccal mass of a newly hatched cuttlefish is relatively large (Fig. 1). The upper and lower beaks are already tanned and have well developed rostra (Fig. 2). The upper beak has a large mandibular muscle. The buccal complex has many discrete structures which are readily identifiable (Fig. 2). The radular teeth are well formed and extend along the entire length of the ribbon. Beneath the radula is the large salivary papilla; this carries the duct from the posterior salivary glands and it appears to be fully functional at hatching (Fig. 3).

The length of the buccal mass is 28 % of the mantle at hatching, the proportion falling to 13 % in the adult. The upper and lower beaks, which are especially prominent in the hatchling, retain their sharply pointed rostra into adulthood (Mangold and Fioroni, 1966). The beaks are a chitin-protein complex as is the cuticle lining the digestive tract which extends along the oesophagus and into the stomach where it forms a gizzard-like grinding surface (Tompsett, 1939). The cuticle probably provides some protection against hard and sharp skeletal parts which are ingested. This material is broken up by the grinding action of the stomach. This is probably a lengthy process since many organs and skeletal parts can be recognized some time after a meal. In the adult digestion takes some 15 h at 20 °C (see Boucaud-Camou and Boucher-Rodoni, 1983) and rate of food conversion is high (40 to 50 %

Plate I. — 1-3, *Sepia officinalis* — newly hatched (Haematoxylin and eosin) : 1, median sagittal section through whole animal. Many organs are well developed. Bar 1 mm; 2, the buccal mass. Upper beak, partly tanned, has large mandibular muscle. The buccal complex is well developed. Bar 100 µm; 3, the salivary papilla and duct from the posterior salivary glands. Bar 50 µm.

4-6, *Octopus vulgaris* — newly hatched. (Haematoxylin and eosin.) : 4, Median sagittal section through whole animal. The brain and buccal mass are relatively very large. Other organs are poorly developed. Bar 200 µm; 5, The buccal mass. The radula has teeth along its length. The salivary papilla is also prominent. The buccal complex is poorly developed. Bar 50 µm; 6, the papillary shield, on the anterior face of the salivary papilla, has small teeth (arrowed). The duct from the posterior salivary glands appears functional. Bar 10 µm.

a, arm; b, brain; bu.ma., buccal mass; d, duct of posterior salivary gland; f, funnel; l.b., lower beak; li, lip; ma.m., mantle muscle; md.m., mandibular muscle; r, radula; sa.p., salivary papilla; st, statocyst; u.b., upper beak.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according to Pascual, 1978). In very young *Sepia* digestion takes only about 5 h. (Boucaud-Camou *et al.*, 1986).

OCTOPUS VULGARIS

This species of octopus has a small egg (2 × 1 mm) and at hatching the mantle is 2 mm long (see Mangold, 1983). The hatchling is planktonic and remains so for as long as eight weeks in the cold waters of the English Channel (Rees and Lumby, 1954) Hatchlings will feed on small larval crustaceans in the laboratory (Itami *et al.*, 1963; and see Boletzky and Hanlon, 1983). When a mantle length of 4-6 mm is reached, the young adopt the benthic habitat of the adult.

A benthic juvenile octopus can capture a crab within 3.8 s of its entry into the visual field (Maldonado, 1963). It is enveloped by the arms and web, and saliva introduced. The saliva contains a toxin, cephalotoxin (Ghiretti, 1959, 1960) in α- and β-forms (Cariello and Zanetti, 1977), which induces paralysis in the crab in less than 30 s. Hyaluronidase is present in the saliva (Romanini, 1952). This enzyme is the 'spreading factor' found in the venom of snakes (see Elliot, 1978) and bees (Owen, 1979) and depolarises hyaluronic acid, removing the chief obstacle to the spread of dissolved matter through the intercellular substances of loose connective tissue (see Ham, 1974). It is probably responsible for the breakdown of musculo-skeletal and arthropodial attachments of crabs which occurs within 20 min after capture by the octopus, leaving the flesh to fall away from the exoskeleton (Nixon, 1984), which is expelled separated but undamaged (Altman and Nixon, 1970). The octopus ingests the soft tissues and, it must be emphasised, these remain recognisable in the crop and stomach for up to two hours after feeding (Altman and Nixon, 1970); food may be present in the stomach for up to six hours (Andrews and Tansey, 1983). External digestion is not only strictly limited but also acts at highly specific sites.

The specialised method of capturing prey followed by its paralysis allows the octopus to feed upon large crustaceans, sometimes equal in size to itself. However, it also eats smaller crustaceans, the appendages of which can be broken by the beak (Boyle, Mangold and Froesch, 1979a), and some skeletal material may be ingested (Guerra and Nixon, in prep.). Crabs eaten by the octopus in the Mediterranean are paralysed but no orifice has been found for the entry of the toxin (Boyle and Knobloch, 1981; Nixon, unpub.). However, off the north-west coast of Spain, in the colder Altantic waters, middens of octopus contained carapaces with a hole (Guerra and Nixon, in prep.) similar in size and form to those drilled in crabs by *Eledone cirrhosa* in Scotland (Nixon and Boyle, 1982).

Shelled molluscs, not easily entered by the octopus, are drilled. The hole is small, usually less than 2 mm in diameter at the surface and 1 mm or less where it penetrates the shell (Nixon, 1977, 1979a; Nixon and Maconnachie, in prep.). The saliva acts chemically upon the mineral and organic matrix of the shell (Nixon, Maconnachie and Howell, 1980), and is aided in some way by the toothed salivary papilla (Nixon, 1979b, 1980). Once the shell has been penetrated the saliva can be introduced. The mollusc succumbs to the toxin, its soft, relaxed body falling from the shell after the enzymatic breakdown of the musculo-shell attachments. Typically the cavity is drilled close to the columella of gastropods (Arnold and Arnold, 1969) and in the myostracum of lamellibranchs (Nixon and Maconnachie, in prep.). Excavation is rapid, *Mytilus galloprovincialis* being drilled and eaten within two hours of presentation (Nixon and Maconnachie, in prep.).

Diet may be assessed from the debris present in the crop or stomach. Wild caught specimens contain remains from a variety of prey. The majority are benthic organisms (amphipods, isopods, anomura, Brachyura, stomatopods, lamellibranchs, gastropods, polychaetes and ophiuroids), a few are nektobenthic (fish, cephalopods and Natantia) and planktonic ostracods have also been found (Nigmatullin and Ostapenko, 1976; Guerra, 1978; and see Nixon 1986). There is evidence of diel variation in the prey eaten, crabs and some molluscs being eaten in daylight and fish in darkness (Nigmatullin and Ostapenko, 1976). In another study, temporal and regional differences in the prey taken were observed (Hatanaka, 1979). In shallow water shrimps and prawns formed 66 % and squat lobsters 33 % of the diet, whereas in deeper waters the proportions were reversed (Guerra, 1978). An increase in the variety of prey eaten occurs with growth (Smale and Buchan, 1981).

In *Octopus vulgaris* the buccal mass forms a large part of the newly hatched animal (Fig. 4), its length being 43 % of the mantle. At the time of settling this proportion is 23 % and it falls to 12 % in the adult. At hatching denticles are present on the oral surface of the uper and lower beaks (Boletzky, 1971); these may hold small planktonic crustaceans or other organisms whilst saliva is ejected onto them from the salivary papilla, assuming this is toxic at this stage, or perhaps the denticles retain the prey within the buccal cavity, while sea water is expelled. Denticles are absent in benthic juveniles and adults, the rostra of both beaks being short and smooth (Clarke, 1962; Mangold and Fioroni, 1966).

In the hatchling both beaks in the large buccal mass are thin and translucent (Fig. 5). The structures of the buccal complex are poorly developed but teeth are present along the length of the radular ribbon (Fig. 5) and the salivary papilla is prominent, with small teeth already present on the cuticular papillary shield (Fig. 6) (Nixon, 1979b). These teeth

are distinct in the juvenile and larger teeth are present on the everted tip of the duct from the posterior salivary glands (Nixon, 1979b, 1980).

All parts of the digestive tract, including the buccal mass, contain inherently rhythmic muscle (Andrews and Tansey, 1983), and a cycle of biting movements of the beaks lasting 19-27s has been recorded (Boyle, Mangold and Froesch, 1979a and b). The buccal complex exhibits co-ordinated movements of the radula, salivary papilla and lateral buccal palps (Nixon, 1968). These ensure the breakdown of food to a size suitable for passing along the oesophagus, where peristalsis carries it into the crop. The cuticular lining provides protection against most of the sharply pointed material although the small setae from the polychaete, *Hermione hystrix,* can penetrate into the brain (Nixon and Budelmann, 1984). The cuticle is a chitin-protein complex (Hunt and Nixon, 1981), chitin being in the α-form (see Rudall and Kenchington, 1973). The cuticle lining the stomach is thick and gizzard-like, aiding the physical breakdown of food. Hard skeletal structures ingested may remain recognisable while in the crop and stomach for up to two hours (Altman and Nixon, 1970), allowing identification. Digestion takes some 12 h at 18-19 °C (Bidder, 1966; Boucher-Rodoni and Mangold, 1977; Andrews and Tansey, 1983), and the conversion rate of food is high (Nixon, 1966).

DISCUSSION

The arms, tentacles and buccal mass of the cuttlefish are already well formed at hatching and are functional shortly afterwards when the first prey is captured and eaten. Very young cuttlefish feed only on *Mysis*; the response to *Mysis* 2-3 days after hatching is fixed and stereotyped and remains so for 5-6 weeks; at this age adult behaviour is evident and young cuttlefish take a wider spectrum of prey (Wells, 1962). Concurrent with such dietary changes is the ability to capture, handle and feed on this wider variety of animals while avoiding injury from them. These behavioural changes can be correlated with development of the central nervous system. The vertical lobe, an important part of the learning system (see Young, 1965; Messenger, 1977; Wells, 1978), is initially very small relative to the rest of the brain but almost doubles in relative size during growth (Wirz, 1954; Wells, 1962).

The newly hatched *Octopus vulgaris* has short arms with few suckers. The buccal mass although large is not well developed. The learning system of the brain is relatively small (Wirz, 1954) and appears poorly organised. The eyes and statocysts are large, and the mantle muscle thick while the funnel is large and extends far forward. These features suggest an animal able to make movements in pursuit of suitable prey which stimulates a response on entering the visual field even in the first few days of life. The dramatic change in lifestyle upon settlement to the bottom from the plankton must involve rapid learning to respond to different prey animals. These will be of diverse shape and form, and will evoke an attack based on vision (as with crabs) or on touch (for shelled molluscs). The organs involved in prey capture and feeding must also be suitably developed. The mode of feeding will depend upon the type of prey captured and it is perhaps surprising how quickly it becomes highly specialised, considering how poorly developed it was at hatching, especially when compared with the cuttlefish.

Investigations of the stomach contents reveal the versatility of *Octopus vulgaris* when feeding. Its diet changes with growth, with the depth of habitat and with the region in which it lives, as well as with seasonal availability of prey The specialised methods of feeding that largely avoid ingestion of hard skeletal material make it difficult to identify all the prey on which it feeds. The analysis of stomach contents together with the debris from the midden from the same animal will provide a better indication of diet. Even this may be incomplete, however, since the remains of crabs desintegrate rapidly and are washed away by local currents. The octopus may also scavenge as it accepts recently dead food in the laboratory. In *Sepia officinalis,* regional differences in diet have also been observed. These factors have important implications in studies of the trophic relations of these active carnivores so close to the top of the food web.

The octopus has decorated domestic ware since Minoan times. Both animals were familiar to Aristotle, who observed of the octopus that it '... gathers shell-fish, extracts the flesh and feeds on that; ... fishermen recognise their holes by the number of shells lying about' (see d'Arcy Thompson, 1910). We are now only beginning to understand something of how these two common coastal cephalopods capture their prey and feed on it, and much remains to be learned.

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FEEDING AND DIGESTION OF YOUNG *SEPIA OFFICINALIS* L. (MOLLUSCA : CEPHALOPODA) DURING POST-HATCHING DEVELOPMENT

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CEPHALOPODA
SEPIA OFFICINALIS
FEEDING
DIGESTION
POST-EMBRYONIC DEVELOPMENT
EARLY JUVENILE

ABSTRACT. — A whole variety of studies on feeding and digestion in very young animals has shown there are three phases in the life of the cuttlefish *Sepia officinalis*. During the embryonic phase, food is only provided by the yolk, which is digested by the intracellular enzymatic activities of the yolk syncytium. During the post-embryonic phase, which begins with the first meal, the embryonic mode of nutrition (yolk digestion) comes to coexist with the post-embryonic mode (capture of small crustaceans and extracellular digestion in the digestive tract). The progressive differentiation of the digestive gland is closely related to exogenous feeding. The transition to the juvenile-adult phase is characterized by changes in the diet (greater variety of prey) and by the acquisition of an « adult » pigmentation and physiology in the digestive gland. This time is marked by other changes (in the blood and nervous system) and seems to constitute a critical period in the life of *Sepia officinalis*.

CEPHALOPODA
SEPIA OFFICINALIS
NUTRITION
DIGESTION
DÉVELOPPEMENT
POST-EMBRYONNAIRE
JUVÉNILES

RÉSUMÉ. — Un ensemble de recherches sur la nutrition et la digestion chez les très jeunes animaux a permis de caractériser trois phases dans la vie de la Seiche *Sepia officinalis* L. Pendant la phase embryonnaire, la nutrition se fait uniquement aux dépens du vitellus, digéré grâce à l'activité enzymatique intracellulaire du syncytium vitellin. Pendant la phase post-embryonnaire qui commence au premier repas, les modes de nutrition embryonnaire (digestion intracellulaire du vitellus) et post-embryonnaire (capture de petits Crustacés et digestion extracellulaire dans le tractus digestif) vont coexister un certain temps. La différenciation progressive de la glande digestive est en relation étroite avec l'alimentation exogène. Le passage à la phase juvénile-adulte se caractérise par un changement de régime alimentaire (proies plus variées), l'acquisition d'une pigmentation et d'une physiologie « adultes » par la glande digestive. Il constitue dans la vie de la Seiche une période critique qui est marquée par d'autres changements au niveau du sang et du système nerveux.

INTRODUCTION

Although there is a lot of data available on the food and feeding habits of several young cephalopods that have been successfully reared in the laboratory (see the review of Boletzky and Hanlon, 1983, Boucher-Rodoni *et al.*, 1986 and Nixon, 1985), very little is known about the process of digestion in post-hatching cephalopods. Actually, most of the studies on digestion have been carried out on subadult and adult cephalopods (Boucaud-Camou and Boucher-Rodoni, 1983; Boucher-Rodoni *et al.*, 1986). The digestive gland has been shown to play an oustanding role in the digestive processes, being the main organ for both enzyme synthesis and digestive absorption. Moreover, conspicuous cytological changes in the gland can be related to the state of digestion (Boucaud-Camou and Boucher-Rodoni, 1983). Over the past years, our laboratory has

investigated the digestive processes of *Sepia officinalis* and made several studies of the early young (Yim, 1978, Boucaud-Camou and Yim, 1980, Yim and Boucaud-Camou, 1980, Boucaud-Camou, 1982, Tresgots, 1982), with various methods, such as histology, electron microscopy, histoenzymology and organ cultures using young *S. officinalis* reared in the laboratory under controlled conditions. We focused on the digestive gland because of its important role, and because it is the only digestive organ that is not fully developed at hatching. It is very different in colour and cytological structure when compared to the « adult » gland. This paper summarises all these results in an attempt to build a picture of the processes of feeding and digestion of an early juvenile cephalopod.

HATCHLINGS

Hatchling *Sepia officinalis* look like miniature adults and have the same benthic mode of life. The external yolk is fully digested but a large amount of yolk remains in the inner yolk sac. The space occupied in the adult by the digestive gland is largely occupied by yolk; the anterior lobe of the yolk sac, lined by the yolk syncytium, separates the paired lobes of the gland (Yim, 1978; Boucaud-Camou, 1982). The digestive cells are still undifferentiated; most of the cells are immature (Boucaud-Camou and Yim, 1980; Yim and Boucaud-Camou, 1980). At hatching, the digestive gland is still developing (multiplication stage) as shown by the many mitoses (Yim and Boucaud-Camou, 1980). Some « brown bodies » can also be seen; these are large inclusions in the cytoplasm, containing crystals. A few cells display synthetic activity, forming secretory granules : these are the « synthesizing cells » (Boucaud-Camou and Yim, 1980).

During the first days of life, growth is still slow (Fig. 1). Newly hatched *Sepia* may not capture prey for up to three days while continuing nutrition (embryonic phase, Boucher *et al.*, 1986), the nutriments being provided exclusively from the yolk by the digestive activity of the yolk syncytium. This fact is illustrated by the strong proteolytic activity of the yolk syncytium, contrasting with the weak activity of the digestive gland (Boucaud-Camou, 1982). The digestive activity of the yolk syncytium is intracellular as shown by the strong positive reaction for such lysosomal enzymes as acid phosphatase (Boucaud-Camou, 1982) and dipeptidylaminopepti-

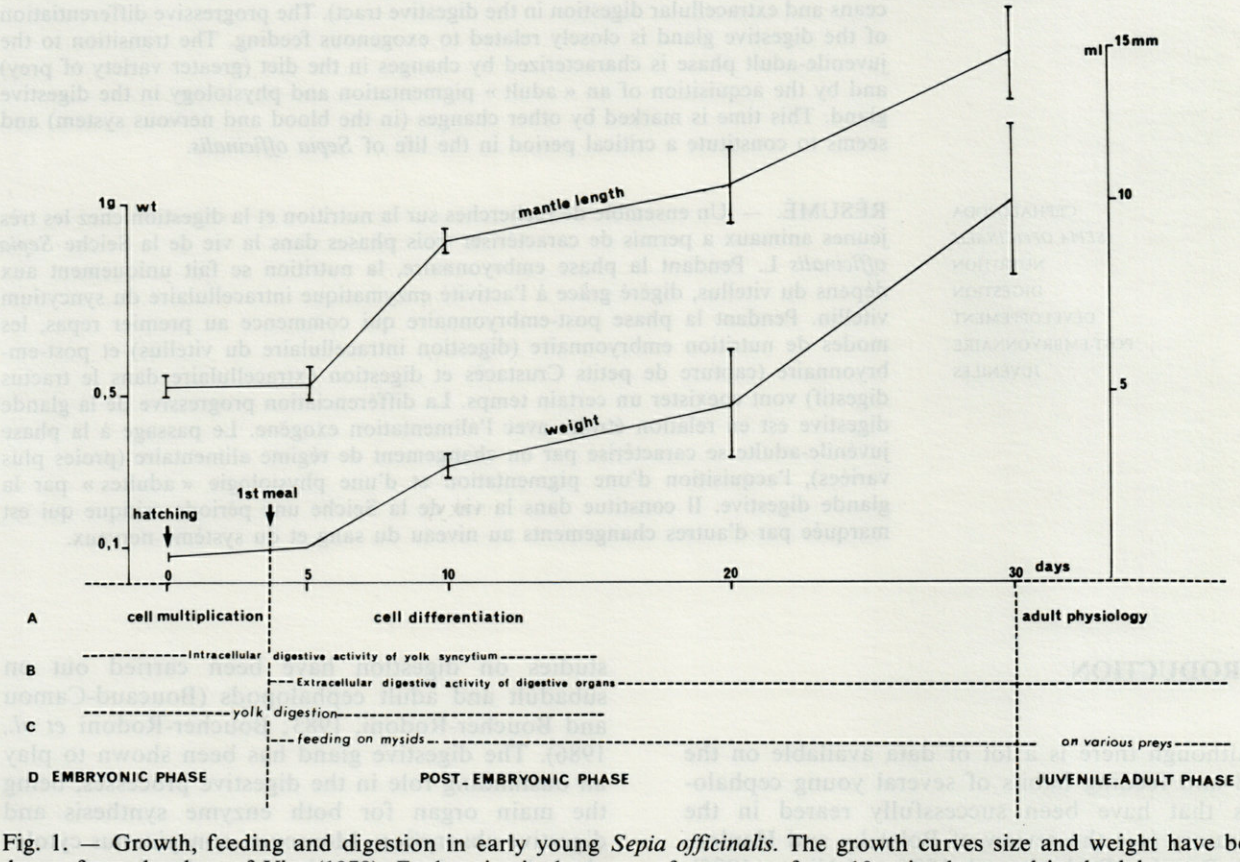

Fig. 1. — Growth, feeding and digestion in early young *Sepia officinalis*. The growth curves size and weight have been drawn from the data of Yim (1978). Each point is the mean of measures from 10 animals reared in the laboratory and fed on mysids. A : state of the digestive gland. B : mode of digestion; C : food; D : phases of the life cycle.
wt = fresh weight, ml = dorsal mantle length

dase II (Boucaud-Camou, unpublished results), and negative reactions for such extracellular enzymes as chymotrypsin (Boucaud-Camou, 1982).

POST-EMBRYONIC PHASE

This begins with the first meal (exogenous feeding). The favourite prey animals are mysids, which are plentiful in summer, in warm coastal waters. Prey capture by early juvenile *Sepia officinalis* has been extensively studied (Wells, 1958, 1962; Boulet, 1964; Messenger, 1968, 1977). Prey is digested far more quickly than in the adult (max. 5 hours at 25 °C, Yim, 1978).

The first meal releases the secretory activity of the digestive gland : so-called « boules » (proteinaceous inclusions characteristic of most cephalopods; Boucaud-Camou and Boucher-Rodoni, 1983) appear together with a secretion filling the lumen of the tubules of the gland, which has grown considerably at the expense of the inner yolk sac (Yim and Boucaud-Camou, 1980). The glandular secretion displays high proteolytic activity. However, yolk digestion continues, due to the digestive activities of the yolk syncytium (Boucaud-Camou, 1982).

During the following days, the two modes of nutrition, embryonic (yolk) and post-embryonic (prey capture), coexist. Yolk reserves would help very young *Sepia* to survive if the amount of food available were not sufficient. However, if there is enough food, the growth curve becomes exponential. During this post-embryonic phase, the digestive cells progressively differentiate and, about ten days after hatching, the four cell differentiation stages present in the adult can be recognized, i.e. in addition to the *immature cells* and the *synthesizing cells* already present at hatching, the *resting cells* and the *mature digestive cells* (Yim and Boucaud-Camou, 1980, Boucaud-Camou and Yim, 1980).

Apparently, the cell differentiation is triggered by exogenous feeding. The digestive glands of hatchlings or late embryos maintained in organ cultures for more than ten days do not display the conspicuous changes that appear after feeding (secretion, « boules », vacuoles). The most striking feature in these cultures is the great number of brown bodies (Tresgots, 1982). Moreover, the digestive gland of animals unfed since hatching looks inactive (Boucaud-Camou, unpublished results).

As first noticed by Richard and Decleir (1969), the digestive gland is not tinted at hatching and becomes progressively pigmented to reach the « adult » brown colour at the end of the first month of life (Yim, 1978). Obviously, the pigmentation is related to feeding : organ cultures of hatchling digestive glands remain unpigmented (Tresgots, 1982).

TRANSITION TO THE JUVENILE-ADULT PHASE

By the end of the first month of life, the digestive gland has the same coulour, the same histological structure and the same histophysiology (number of the « boules ») as in the adult (Yim, 1978, Yim and Boucaud-Camou, 1980). By now, the young *Sepia* will have reached an average mantle length of 15 mm (Yim, 1978) and be able to catch a greater variety of prey : small crabs, shrimps and fishes. At about this time there occur changes in blood composition (Richard and Decleir, 1969) and in the nervous system (Chichery, 1976). These seem to mark the transition to the juvenile-adult phase (Boucher-Rodoni *et al.*, 1986), a stage that seems critical in the life of *Sepia officinalis* at least in the laboratory. It is then that high mortality often occurs; it might also occur in nature, and it should be taken into account in recruitment studies.

DISCUSSION AND CONCLUSION

Under the aspects of feeding and digestion we have tried to define three phases in the life of *Sepia officinalis*. The *embryonic phase* corresponds to embryonic development and ends, not at hatching, but with the first meal. During this stage there is only yolk digestion; the digestive gland is still developing (cell multiplication) and has no digestive function. The *post-embryonic phase* is characterized by the beginning of exogenous feeding, which induces the start of exponential growth, and by the development of the digestive activity of the digestive gland (cell differentiation). Our post-embryonic phase corresponds almost exactly to the « période post-embryonnaire » of Richard and Decleir (1969) but is slightly longer. We have not used the term "larval", for there are no true "larvae" in cephalopods (Boletzky, 1974). Especially in *S. officinalis*, early juveniles have the same mode of life as the adults. The juvenile-adult phase begins (long before the onset of sexual maturity) with the physiological maturity of the digestive gland (adult physiology), a more varied diet and other metabolic and physiological changes, which make the end of the post-embryonic life a critical stage. These phases might, perhaps, be suitable for all cephalopods, as suggested in an earlier review (Boucher-Rodoni *et al.*, 1986). Certainly work on other species (especially those with a planktonic stage) is needed, considering the different feeding and digestive events of this period with respect to the three phases defined in Figure 1.

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CAN RHYNCHOTEUTHIONS SUSPENSION FEED ? (MOLLUSCA : CEPHALOPODA)

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CEPHALOPODA
OMMASTREPHID
SQUID
ILLEX ILLECEBROSUS
LARVAE
FILTER FEEDING

ABSTRACT. — The unique rhynchoteuthions of the ommastrephid squids are the smallest decapodan cephalopod hatchlings and have never been successfully reared. Based on anatomical and behavioural observations a mechanism of suspension feeding is proposed which depends on direct interception and inertial impaction on the mucus coated body surface. Mucus is transferred to the mouth area by ciliary motion and by observed cleaning behaviours. Suspension feeding is suggested to be a supplement to raptorial feeding but may be a critical "bridge" between small yolk reserves and the minimum development required for effective predation. Loss of ciliature through contact with vessel walls may prevent feeding in culture.

CEPHALOPODA
OMMASTRÉPHIDÉS
ILLEX ILLECEBROSUS
LARVES
FILTREUR

RÉSUMÉ. — La larve, ou rhynchoteuthion, des Calmars de la famille des Ommastrephidae est la plus petite de toutes celles des Céphalopodes Décapodes et n'a pas encore pu être élevée en aquarium. A partir d'observations d'anatomie et de comportement, il est suggéré que les larves pourraient se nourrir de particules en suspension. Les particules sont interceptées directement ou, dû à l'inertie même des particules, adhèrent à la couche de mucus couvrant la surface du rhynchoteuthion. Le mucus est transféré à la bouche par mouvements ciliaires et par un mode de nettoyage actif. Il est aussi suggéré que l'ingestion de particules en suspension supplémente l'alimentation par prédation mais peut aussi servir comme mécanisme intermédiaire entre les réserves alimentaires contenues dans le vitellus et le développement d'une prédation efficace. La perte de cils vibratils par contact avec les parois des bacs pourrait empêcher l'alimentation chez les larves en culture.

INTRODUCTION

The success of ommastrephid squid in the open ocean may result from reproductive adaptations which permit a life cycle isolated from land masses. They produce some of the smallest cephalopod eggs (ca. 0.8 mm) which yield unique « rhynchoteuthion » hatchlings less than 2 mm in total length with only two pairs of arms and a proboscis which later divides to form the tentacles of the adults. The small size of the eggs may be an adaptation to retaining the eggs in the upper water layers. All cephalopod eggs are probably denser than seawater, but ommastrephids produce neutrally buoyant egg masses by embedding small eggs in large volumes of gel produced by the nidamental glands (O'Dor & Balch, 1985). The advantages of small eggs may have provided a selective pressure producing embryos which hatch out too small to follow the usual cephalopod habits; rhynchoteuthions are the only cephalopod hatchlings which show sufficiently distinct developmental changes to make the term larvae attractive (Boletzky, 1974).

All cephalopod hatchlings which have been successfully reared begin to feed immediately as raptors (Boletzky & Hanlon, 1983), but all attempts to rear rhynchoteuthions on apparently suitable prey have failed (Balch *et al.*, this volume). Furthermore, no identifiable stomach contents have been found in wild-caught rhynchoteuthions. Based on extensive observations of rhynchoteuthion behaviour, but with

no direct evidence, this paper will examine a possible mechanism which would allow rhynchoteuthions to feed on suspended particles during the critical period of transition from yolk reserves to normal predation.

Labarbera (1984) has reviewed suspension feeding mechanisms and emphasizes that three types of processes are required : 1) water transport past feeding structures, 2) particle capture and 3) particle transport to the mouth for ingestion. He also argues that actual sieving by a mesh finer than the particles is a mechanism used often by biologists but infrequently by organisms because of its high energy cost. A surface covered with a sticky collector like mucus can be nearly as effective at a lower cost by capturing particles through « direct interception ». This is the key element in the present hypothesis.

MATERIALS AND METHODS

Illex illecebrosus rhynchoteuthions were obtained from egg masses spawned in captivity and incubated as described in Balch *et al.* (this volume). The specimens for light and electron microscopy hatched after 5 days at 26 °C. Specimens for scanning electron microscopy were fixed in Bouin's solution and dehydrated in acetone. After critical point drying, they were fixed to an aluminum stub and sputter-coated with a 60/40 mixture of gold/palladium. Photographs were taken with a Nanolab 2 000 SEM and Kodak Pan-X film.

Behavioural observations were made in either a plastic petri dish filled with seawater over a Zeiss inverted microscope or in a vertical flow-through swim chamber (3 mm square and 78 mm high, made from microscope slides) through a Zeiss dissecting microscope. In each set-up the ocular could be replaced with an RCA TC 2011/N low-light video camera connected to a Sony SLO-323 Beta recorder to make a permanent record. A Vicon Industries Model V240 Date/Time Display Generator added a time base to the nearest 0.1 s. Frame-by-frame analyses were made of behaviours. Over 20 hours of video were made from 80 hours of observation.

RESULTS

Rhynchoteuthions exhibited behaviours which could be associated with each of Labarbera's (1984) three processes. Since particle capture is the most critical step, and the type of capture determines the requirements for the other processes, it will be discussed first. Rhynchoteuthions have no obvious

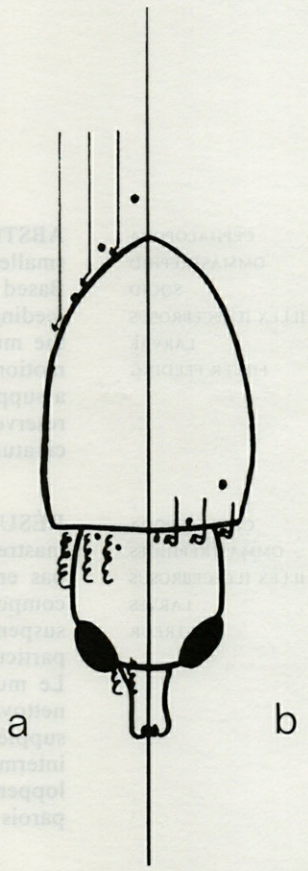
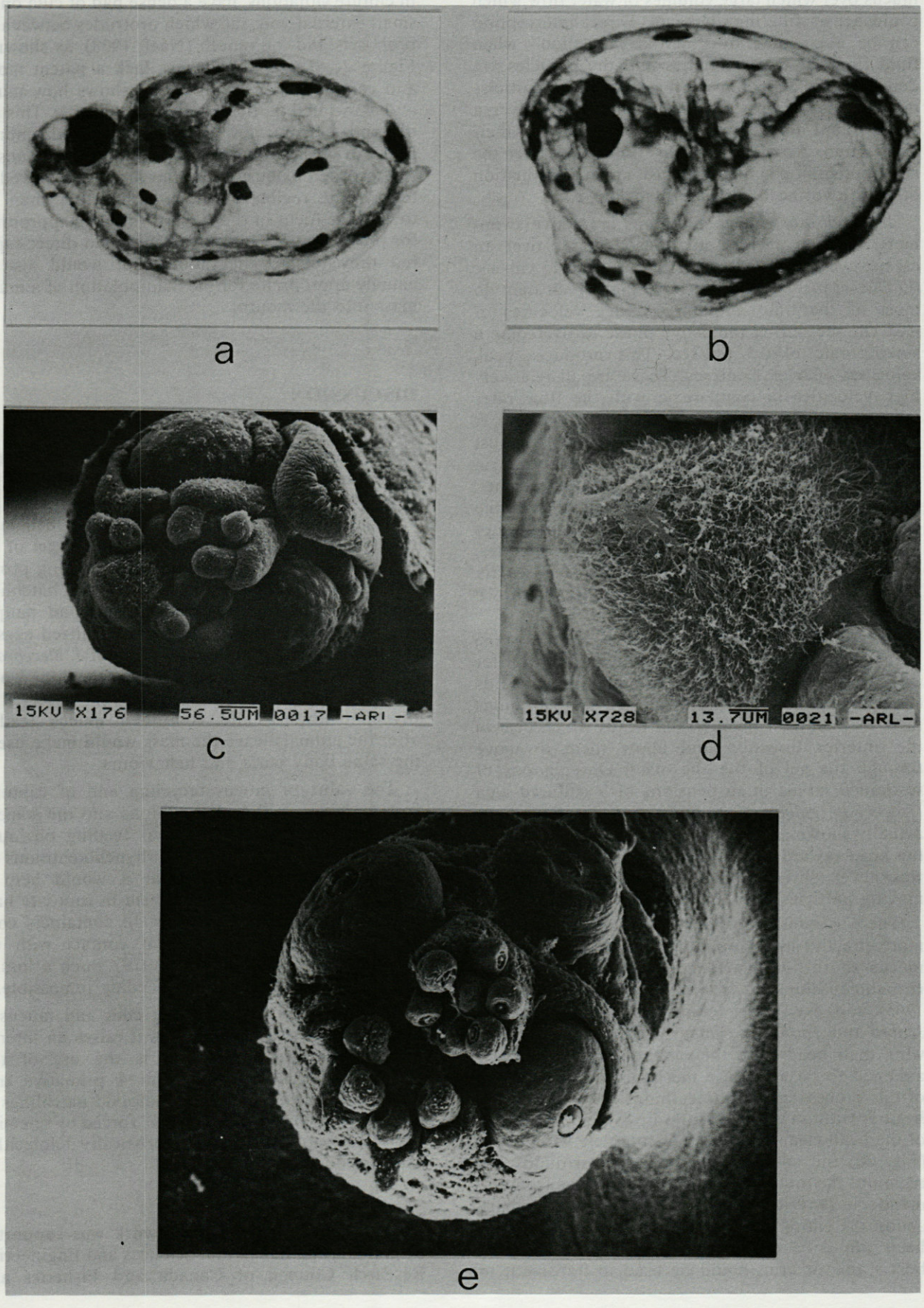


Fig. 1. — a, A schematic illustration of the streamlines and possible impaction points for particles on a rhynchoteuthion during jetting; b, of the flow pattern during mantle refilling.

Fig. 2. — a and b, A live sequence of a rhynchoteuthion withdrawing its head into the mantle. During withdrawal the mantle lip cleans the surface of the head, and when the head is fully withdrawn the lip, with accumulated mucus, lies directly over the mouth region. c, An overview of the ciliated pad on the yolk sac protruding between the proboscis and arms of a stage XVII embryo. d, A detail of the same specimen as in c showing accumulated mucus and particles on the ciliated pad. e, A similar view of a stage XX embryo after the pad has withdrawn (c-e SEM).


a
b
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c
15KV X728 13.7UM 0021 -ARL-
d
e

sieving structures but do have large areas covered in mucus over which large volumes of water flow which could act as filtering elements. Direct interception can be augmented by "inertial impaction" when fluid flows at high velocities and the particles are denser than the medium. In this mechanism particles move across streamlines as the fluid flows over a surface and impact on the surface due to their momentum. As will be shown, water flow over the rhynchoteuthion is relatively fast, and a combination of these two mechanisms is plausible.

I. illecebrosus rhynchoteuthions are active swimmers and can average up to 5.6 cm/sec over an escape cycle with peak velocities of up to 15 cm/sec (O'Dor *et al.*, 1985). Even hovering, which they do most of the time, requires average velocities of 0.62 cm/sec during the active phase to overcome a sinking rate of 0.5 cm/sec. This produces peak velocities of over 1 cm/sec. These are all relatively high velocities in comparison with the flow rates over most biological filter elements (Rubenstein & Koehl, 1977). It seems clear that some particles must adhere to the mucus coated mantle as shown in Figure 1a as the animal accelerates with each jet. The other likely place for inertial impaction is on the head near the lip of the mantle where the water being taken in changes direction and accelerates. The inertia of particles with densities significantly greater than water would cause impaction as shown in Figure 1b.

Accepting that there is water flow and some particle capture, a mechanism is required to transfer the particles to the mouth. Like other young squids (Boletzky, 1982), *I. Illecebrosus* rhynchoteuthions have cilia on their mantles and heads which beat in the anterior direction and allow them to move through the gel of the egg mass. Observations of restrained larvae in suspensions of a cultured alga *(Isochrysis galbana)* at high magnification have actually shown algae trapped in mucus moving over the head toward the mouth. Even though ingestion was never observed there is clearly a means of moving particles over the surface of the head.

There is another behaviour which may be even more effective in cleaning the head and transferring mucus to the mouth. There are reports of other rhynchoteuthions (*Todarodes pacificus*; Okiyama, 1965) and even large cranchiid squids (*Cranchia scabra* and *Taonius megalops*; Dilly, 1972) withdrawing their heads into their mantles. This has been assumed to be a defense mechanism. Observations of this process in rhynthoteuthions show that as the head is withdrawn the mantle lip wipes the surface of the head clean (Fig. 2a). On complete withdrawal (Fig. 2b) the contracted mantle lip surrounds the region of the mouth. Since all of the mucus from the mantle is moved toward the mantle lip by ciliary action the entire mucus collection from mantle and head would be collected at a site where the proboscis and/or arms could be used to transfer it to the mouth. Stage XVII embryos, which often hatch in culture situations, have a dense pad of cilia on the small external yolk sac which protrudes between the proboscis and the mouth (Naef, 1928), as shown in Figure 2c. These early stages lack a patent mouth and cannot feed, but Figure 2d shows how mucus and associated particles collect in this area. This pad disappears from view in more advanced embryos (Fig. 2e) but may still play a role in mucus transfer. All recorded extensions of the proboscis moved up toward the region of the mouth rather than out toward the focus of the eyes as would be appropriate for prey capture. This movement could direct captured prey toward the mouth, but would also be equally appropriate for the manipulation of a mucus mass into the mouth.

DISCUSSION

These observations do not prove that rhynchoteuthions are suspension feeders, but do provide circumstantial evidence that they have the capacity for it. There is also a logical progression of behaviour from the ciliary locomotion through the gel of the egg mass to the type of suspension feeding proposed. Durward *et al.* (1980) suggested that hatchlings might feed on micro-organisms, copepod nauplii, etc. which colonize the gel and unfertilized eggs in the large (up to 1 meter) egg masses of *I. illecebrosus* as they move to the outside. Such behaviour would certainly supplement the small yolk reserves of rhynchoteuthions, and continued mucus feeding after the animals leave the mass would make use of the same body parts and behaviours.

The value of mucus recycling and of captured food particles to rhynchoteuthions and the stage at which they change to raptorial feeding obviously require further investigation. If rhynchoteuthions are dependent on this mechanism it would help to explain why attempts to rear them in captivity have failed. Cephalopods kept in small containers commonly lose surface cilia from contact with the container walls (Hulet *et al.*, 1979). Such a loss of cilia would make suspension feeding impossible.

If suspension feeding using cilia and mucus is important for rhynchoteuthions it raises an interesting eveolutionary question : is the use of this common molluscan mechanism a primative trait retained by these smallest cephalopod hatchlings or is it a "re-invention of the wheel" forced by selection for small egg size to characteristically telolecithal cephalopods ?

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ASPECTS OF EGG DEVELOPMENT, POST-HATCHING BEHAVIOR, GROWTH AND REPRODUCTIVE BIOLOGY OF *OCTOPUS BURRYI* VOSS, 1950 (MOLLUSCA : CEPHALOPODA)

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CEPHALOPODA
OCTOPUS
BEHAVIOR
GROWTH
REPRODUCTION
CHROMATOPHORES

ABSTRACT. — Three live *Octopus burryi* were collected in the northwestern Gulf of Mexico allowing the first long-term laboratory observations of this species. The animals were maintained for up to 116 days in one 150 l closed seawater system using artificial sea water. A fertile brood of eggs laid in the laboratory required 26 days for embryonic development at 22 to 23 °C. Retinal pigmentation first appeared on day 9, the first chromatophores on day 16 and the second reversal of the embryos on day 23. Chromatophore development was documented. *Octopus burryi* produce small eggs (2.5 mm long) and small planktonic hatchlings (1.5 mm ML). Distinctive characteristics of hatchlings include approximately 205 chromatophores covering the body, two rows of chromatophores on each arm and four suckers per arm; these characters differentiate it from *O. vulgaris* hatchlings. Attempts to rear the hatchling through the planktonic phase were unsuccessful. Maximal survival was 16 days, and no growth was observed although hatchlings fed upon zooplankton. Two juveniles, weighing 0.8 and 1.2 g when collected, grew exponentially for the first month at rates of 8.5 and 9.8 % of body weight per day. When collected, the small juveniles could already show the full repertoire of body patterns described previously for adults. Both juveniles were males and developed hectocotyli at one month post-capture. Based upon mantle length growth, the juveniles were estimated to be 70 days old when collected. The larger male attained a maximum weight of 117 g and 75 mm ML after 116 days in the laboratory. Males are mature by an estimated age of 4 months post-hatching. A gravid female (204 g, 107 mm ML) laid a brood of approximately 35 000 eggs, which represented 45 % of her pre-spawning weight. The eggs were not attached to the substrate, but rather were carried by the female. Egg-laying occurred over a 2-week period. The life cycle of *O. burryi* is estimated to be 8 to 10 months at 22 to 25 °C.

CEPHALOPODA
OCTOPUS
COMPORTEMENT
CROISSANCE
REPRODUCTION
CHROMATOPHORES

RÉSUMÉ. — Trois *Octopus burryi* vivants ont été récoltés dans la partie nord-ouest du Golfe du Mexique et ont pu être maintenus au laboratoire jusqu'à 116 jours dans un bac de 150 l contenant de l'eau de mer artificielle. Une ponte a été déposée et l'éclosion a eu lieu 26 jours plus tard (22 à 23 °C). La pigmentation de la rétine était visible au 9^{e} jour de la vie embryonnaire, les premiers chromatophores ont été observés au 16^{e} jour et le second retournement a eu lieu au 23^{e} jour. Les œufs d'*O. burryi* sont petits (2,5 mm) et donnent naissance à des animaux planctoniques (1,5 mm ML). Les caractères typiques des nouveaux-nés, présence d'environ 205 chromatophores sur le corps, de deux rangées de chromatophores et de quatre ventouses par bras, permettent de séparer les jeunes de *O. burryi* et de *O. vulgaris*. Deux juvéniles benthiques mâles d'un poids de 0,8 et 1,2 g à la capture, ont montré une croissance exponentionnelle pendant le premier mois avec des taux de 8,5 et 9,8 % du poids total par jour. Ces

jeunes animaux possédaient déjà tout le répertoire de dessins et de postures connu chez les adultes. L'âge au moment de la capture a été estimé à 70 jours. Le plus grand mâle a atteint un poids de 117 g et une longueur de 75 mm ML après 116 jours. Les mâles sont probablement mûrs à l'âge de quatre mois. Une femelle a déposé une ponte d'environ 35 000 œufs, représentant 45 % de son propre poids avant la ponte. Le cycle de vie d'*O. burryi* est estimé à 8-10 mois à une température de 22 à 25 °C.

INTRODUCTION

Little is known about the biology and life history of *Octopus burryi* Voss, 1950 despite its fairly broad amphi-Atlantic distribution (reviewed in Hanlon and Hixon, 1980). *Octopus burryi* is known from approximately 45 specimens (including those described here) and since its description by Voss (1950) only Hanlon and Hixon (1980) have reported on aspects of the biology of this species. The data presented here are the first long-term laboratory observations of the live animal. Two sets of observations were made : the first of two juveniles collected in the surface plankton and subsequently reared in the laboratory; the second of a field-collected, gravid female and the viable eggs and hatchlings she produced in the laboratory. Baseline data are presented on (1) embryonic development, (2) hatchling morphology and behavior, (3) behavior, body patterning and growth of juveniles, (4) size at spawning, (5) fecundity and (6) brooding behavior.

MATERIALS AND METHODS

Three *Octopus burryi* were collected in the same area in the northwestern Gulf of Mexico (28° 20' N, 94° 10' W) approximately 110 km south-southeast of Galveston, Texas. Water depth in the immediate area ranged from 35 to 50 m. On 16 August 1980 two very small *O. burryi* were collected by dipnet at the sea surface under a bright night light (1000 watt quartz-iodide). A gravid female (204 g) living in a 3.8 l aluminium can was collected by bottom-trawl at a depth of 47 m on 22 February 1981.

All juvenile and adult octopuses were maintained and reared in closed (recirculating) aquarium systems of 150 l capacity using artificial sea water. The two juveniles were initially reared together in an enclosure measuring 25 × 15 × 10 cm. After 4 weeks, the larger of the two octopuses was moved to another enclosure (35 × 20 × 24 cm). A detailed description of these systems and their maintenance can be found in Forsythe (1984) and Forsythe and Hanlon (1980). The octopuses were fed *ad libitum* on live crabs (*Uca pugilator* and *Callinectes sapidus*), supplemented with live shrimps and fishes. The octopuses were periodically weighed and measured after being narcotized in a 2 % solution (by volume) of ethyl alcohol in sea water, and photographed regularly to document behavior and body patterning.

When the female octopus laid a fertile brood of eggs, six embryos were isolated to observe development. The embryos were filmed on video through a stereomicroscope at 48-hour intervals until hatching. When hatching was imminent, approximately 800 embryos were moved to the hatchling culture systems for observation of feeding and behavior. Hatchling octopuses were reared at 23 to 24 °C in a 1 m diameter dish-bottom tray, submerged in a larger 2000 l culture system (see Yang *et al.*, 1983). The dish-bottom tray had a maximum depth of 25 cm at the center and 10 cm depth at the outer wall. Water was added gently to the tray *via* two spray bars at the water's surface to create a slow rotation of the water column. Water left the tray by gravity *via* a central mesh-covered core (200 µm). The hatchlings were fed live (wild) zooplankton consisting primarily of copepods, larval crustaceans and fishes. The zooplankton was sorted only by size and when in short supply was supplemented with *Artemia* nauplii.

RESULTS

1. Embryonic development

Eggs, laid on 19 March 1981, were 2.2 to 2.5 mm long (excluding the stalk) and embryonic development took approximately 26 to 28 days at 22 to 23 °C. The first macroscopic signs of development were seen 5 days after egg-laying. Retinal pigmentation was visible as red after 9 days and turned brown by day 15. Chromatophore development is illustrated in Figure 1 A. The first chromatophores appeared on day 15, approximately stage XVI of Naef (1923/1928). All new chromatophores were yellow, and the early yellows (through stage XVIII) were curiously shaped with pigment missing in the middle. These youngest chromatophores were not able to open or close. Nearly all early yellows gradually turned darker until at hatching most chromatophores were brown. Only the ventral head remained unchanged from stage XVI to hatching, with only the two yellow chromatophores present. Through stages XVI and XVII, ventral chromatophores appeared faster, especially the double row of chromatophores along each arm. The first brown

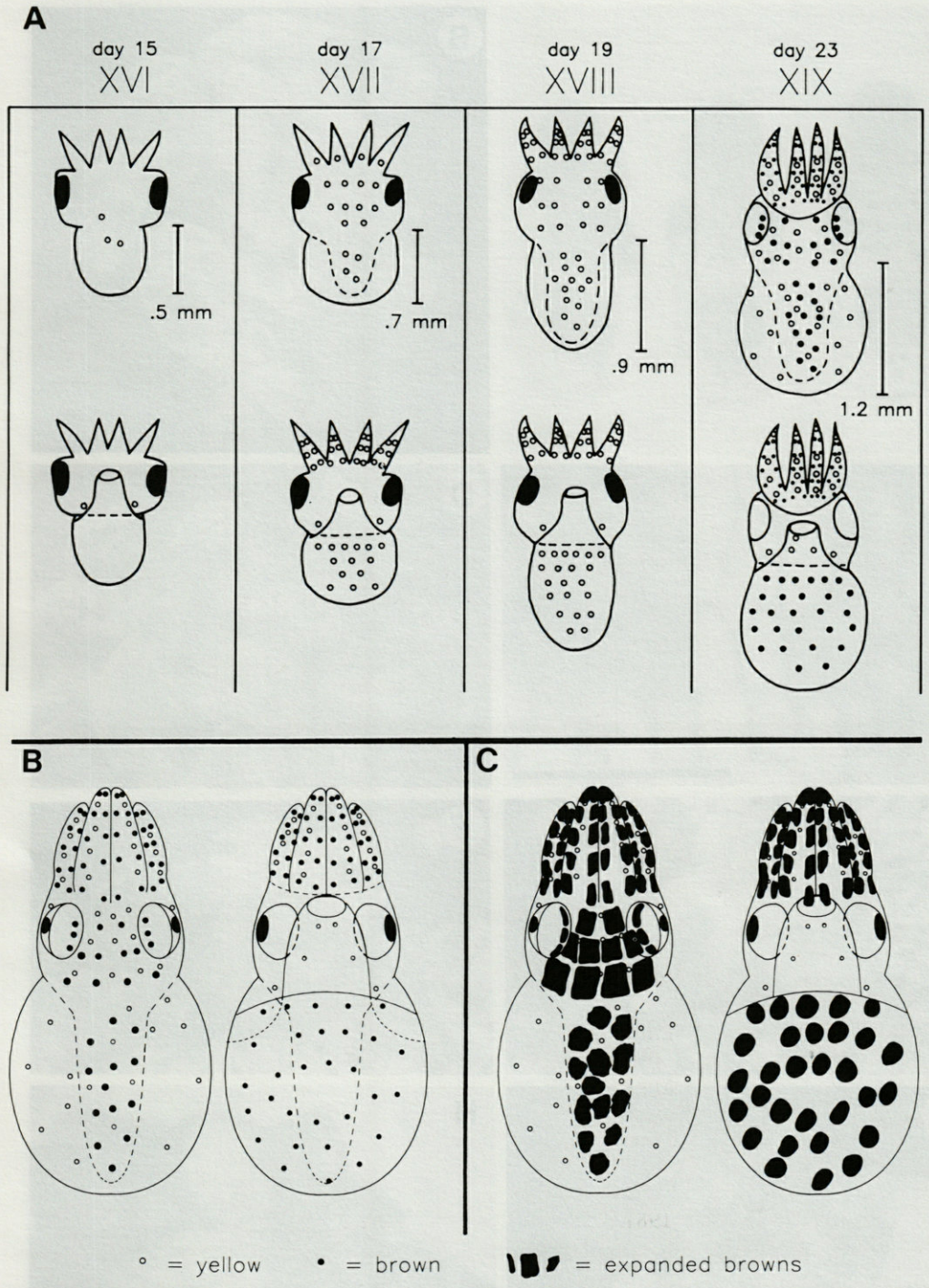

Fig. 1. — Chromatophore development, arrangement and patterning in hatchling *Octopus burryi.* A, Embryonic development of chromatophores. Placement, numbers and colors of retracted chromatophores are depicted accurately for six embryos at 22-23 °C. Stages according to Naef (1923/1928). Hatching occurred on day 26 (stage XX, Naef). Open circles : yellow chromatophores, closed circles browns. B, Typical chromatophore arrangement at hatching (stage XX, Naef). Of the 113 dorsal chromatophores, 56 are on the arms, 28 on the head and 29 on the mantle. Of the 92 ventral chromatophores, 56 are on the arms, 2 on the head, 4 on the funnel and 30 on the mantle. C, Typical dark body pattern of a live hatchling, with all brown chromatophores expanded and no yellows expanded. See text.

chromatophores were evident between stages XVIII and XIX, on day 21, and this coincided with the time that the chromatophores became functional (i.e., their radial muscle fibers were innervated and stimulated by chromatophore motoneurons). Figure 2 A illustrates the general morphology and chroma-

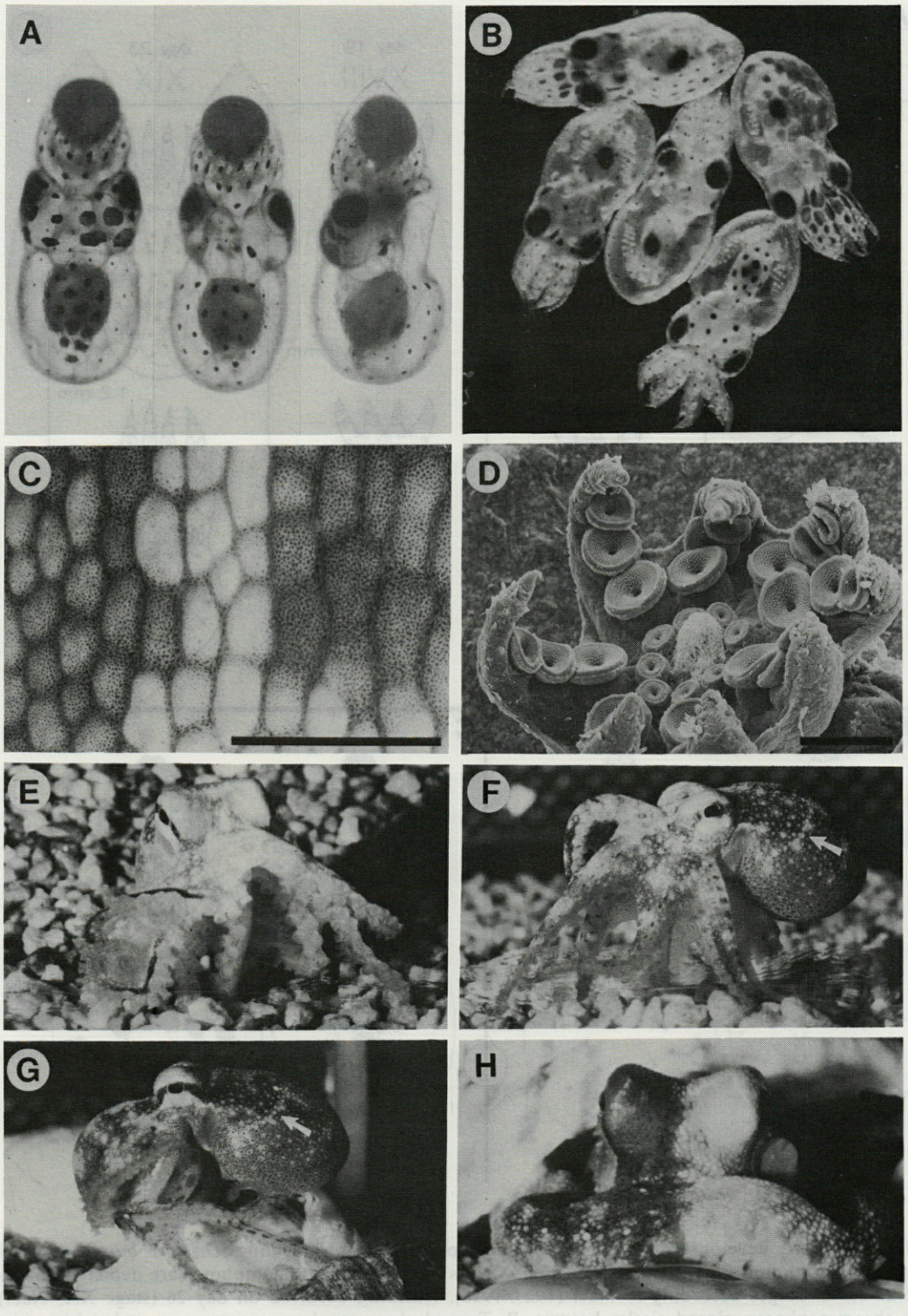

Fig. 2. — Young *Octopus burryi*. A, Dorsal, ventral and lateral view of a stage XIX embryo. Total length about 2 mm. B, Live hatchlings, 1.5 mm ML. Chromatophores and many internal organs are visible. Top four are ventral view, bottom animal is dorsal. C, Close up photograph of the patch and groove unit structure of the skin of a 75 mm ML male. Scale is 5 mm. See text. D, Scanning electron micrograph of sucker size and arrangement in a hatchling. Scale is 200 μm. E., F., G., H., Juvenile male, 16 mm ML, showing various chromatic components of body patterning. The Longitudinal arm stripe is conspicuous in E and expressed faintly in F. In F note some of the original large brown arm chromatophores from hatching. The Eye bar is obvious in E and G. The white Transverse streak is seen in F and G (arrows) and in G one of the very white Mantle spots is visible at the anterior edge of Transverse streak. In H the male shows a unilateral darkening pattern on the side toward the stimulus.

tophore arrangement of a stage XIX embryo on day 23, by which time the second reversal had taken place.

2. *Hatchling morphology and behavior*

The eggs hatched over a 10-day period. The hatchlings had a mean mantle length (ML) of 1.53 mm ± 0.048 mm (n = 35) and a mean total length of 2.51 mm ± 0.076 mm. General morphology of the hatchlings is shown in Figure 2 B, and the distinctive four suckers per arm are shown in Fig. 2 D. The arrangement of the 205 chromatophores of the hatchlings is depicted in Fig. 1 B. The animals were planktonic, swimming continuously, with a clear negative geo-taxis and weak positive photo-taxis. They maintained a 30 to 45 ° head-down body orientation, typically aiming mantle first into the current. No interactions between hatchlings were observed.

The hatchlings were fed sorted zooplankton between 150 and 400 µm for the first 10 days. Food size was gradually increased to 1 mm over the next 2 weeks. Large mortalities began on day 5, indicating that non-feeding hatchlings may survive only 3 to 4 days on internal yolk supplies. On day 7 the first hatchlings capturing food were seen, and thereafter voracious feeding was observed, with attacks being horizontal or slightly downward from a distance of 1 to 3 cm. Hatchlings would sometimes pursue food organisms for several centimeters before making the final lunging attack.

Despite heavy feeding, there was 80 % mortality by day 14. The last octopus died on day 26. Since hatching lasted until day 10, maximum survival was between 16 and 26 days. No growth in mantle length was observed.

3. *Feeding, growth and behavior of juveniles*

The two wild juvenile octopuses adapted well to the laboratory environment. They accepted live crabs immediately and grew rapidly (Table 1). When captured, they weighed 0.80 g and 1.20 g with dorsal mantle lengths of 15.6 and 16.1 mm, respectively. The smaller octopus attained a size of 23.9 g and 38 mm ML in 53 days, while the larger octopus grew to 117 g and 75 mm ML in 116 days. Both animals died by crawling out of the aquaria. Growth rates were highest during the first 4 weeks, with the overall instantaneous relative growth rate for the smaller and larger octopus being 8.5 % and 9.8 % of body weight per day, respectively. During this period of exponential growth, the octopuses doubled their weight every 7 to 8 days. Growth rates gradually diminished after the first month. Both animals were males, with the hectocotylus becoming clearly visible at a size of 5 g (25 mm ML). At the time of death both animals had fully formed spermatophores in the penis, indicating full sexual maturity.

Table I. — Growth of two field collected juvenile *Octopus burryi.*

Experiment day	*Octopus* # *1*			*Octopus* # *2*		
	WW (g)	ML (mm)	TL (mm)	WW (g)	ML (mm)	TL (mm)
3	1.19	16.1	–	0.80	15.6	41.8
9	2.79	22.7	59.5	1.82	19.4	52.5
16	5.17	28.5	80.0	2.80	22.9	60.9
23	10.22	33.6	100.5	5.13	25.7	76.0
30	18.60	42.7	124.0	8.72	31.0	93.1
44	40.70	54.5	170.0	19.05	38.0	122.0
52*	–	–	–	23.90	38.0	–
60	65.1	60.0	–	–	–	–
116*	117.6	75.0	225.0	–	–	–

* Measurements from freshly dead animal.

Although attempts to culture the hatchlings of this species were unsucccessful, it is possible to estimate the growth of *O. burryi* through its planktonic phase. Only the data of the larger octopus were utilized in this analysis since the growth of the smaller individual was inhibited by the aggressive behavior of the larger animal. By definition, the growth rate or slope remains constant during exponential growth (Brody, 1945; Forsythe, 1984). With a standard computerized, exponential curve-fitting program (see Forsythe, 1984), the slope of mantle length growth during the first 4 weeks in captivity was determined. Using the known hatchling mantle length of 1.53 mm as the y-intercept, the following exponential equation was generated : ML(mm) = $1.53e^{0.0335t}$; r^2 = 0.9840, where e = the natural log of 2 and t = age in days (Fig. 3). Assuming growth was constant from hatching at 22 to 23 °C, this octopus was about 70 days old when captured in the sea. Water temperature to a depth of 50 m in the northern Gulf of Mexico is equal to or greater than these temperatures during the summer and early fall (Hixon, 1980). The data for *O. vulgaris* (Itami *et al.*, 1963) through the planktonic phase and post-settlement are also shown in Fig. 3 and indicate that the assumptions made for planktonic growth of *O. burryi* are realistic.

Although these two octopuses were collected at the sea surface in relatively deep water, swimming was only rarely observed in the laboratory. The octopuses assumed a typical benthic lifestyle and swam only when startled or attacking food. The swimming attack upon crabs was remarkably fast. The octopuses would sight the prey from their lair and make a jet propelled, arm-first jump upon the prey. The octopuses jetted a distance equivalent to five to eight mantle lengths in less than a second. No speculative feeding searches were ever observed.

The larger octopus was always dominant over the smaller individual and would always feed first when

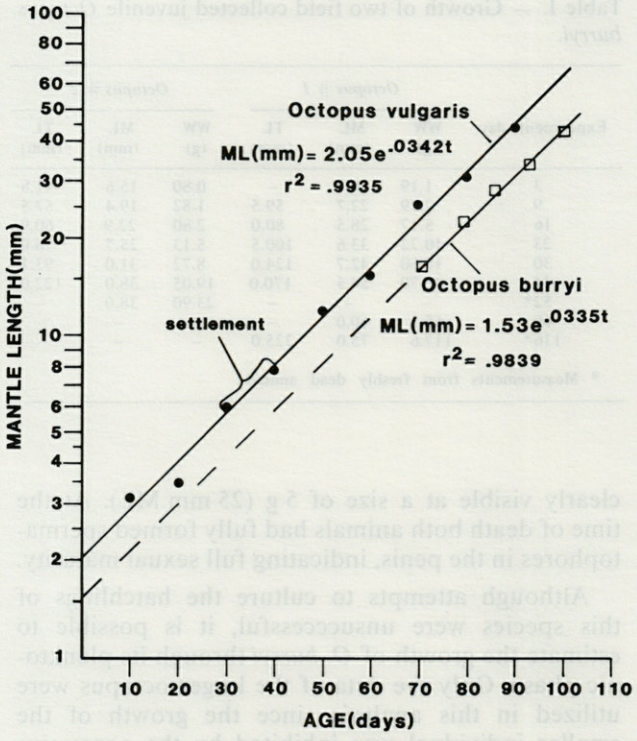

Fig. 3. — Comparative growth in mantle length of *Octopus burryi* and *O. vulgaris* through the planktonic phase and post-settlement.

crabs were added. If the smaller octopus tried to feed first, the larger animal would attack it and take its crab away. On several occasions the larger octopus actually attacked the smaller octopus, seemingly without provocation (i.e., not competing for food), chasing it around the enclosure. The larger octopus never inflicted any observable physical injury upon the smaller one; however, the slightly lower growth rates of the smaller octopus were probably due to the aggressive larger animal getting most of the food (cf. Mangold, 1983). After one month it became necessary to separate the two animals.

4. Body patterning

The elements of patterning — chromatophores and reflecting cells in the dermis — were different in hatchlings and juveniles. At hatching, only yellow and brown chromatophores were present, and only small, indistinct flecks of iridescence from scattered iridophore cells. By the juvenile stage (i.e., 16 mm ML in our wild-caught males), the skin structure was very complex. Yellow, red and brown chromatophores were present as well as iridophores (reflecting blue or green) and leucophores (reflecting white). The skin was well organized into discrete morphological units (Packard, 1982), each approximately 1 mm wide, that were delineated by grooves in the skin (Fig. 2 C). Individual units could vary from bright white (from underlying leucophores with no overlying chromatophores expanded) to yellow, red, brown or intergrading hues between yellow and brown. Combinations of morphological units in different states of chromatophore expansion resulted in different chromatic components being expressed. The combinations of chromatic components with skin texture (i.e., papillae in the morphological units) and postures produced the overall body pattern.

The planktonic hatchlings, with 205 chromatophores, could show only very simple body patterns. They could show the Clear pattern (no chromatophores expanded) or All Dark pattern (all chromatophores expanded), but they could also show a pattern in which all the large, deep brown chromatophores were expanded, but none of the yellows that were younger and shallower in the dermis (Fig. 1 C).

In contrast, the small wild-caught juveniles were already capable of a wide repertoire of patterning. The most species-characteristic component of patterning — Longitudinal arm stripes — was seen immediately in the 16 mm ML juvenile (Fig. 2 E, 2 F). The two young males showed 25 of the 26 components of patterning described for a 31 mm ML adult female by Hanlon and Hixon (1980). Only the chromatic component Dark-edged suckers (Component 6 in Hanlon and Hixon, 1980) was not observed in these two males. Some qualitative differences in other components are noteworthy. Most of the components were easily recognizable (e.g., the Transverse streak in Figs. 2 F, 2 G), but were less well-defined since fewer chromatophores and reflecting elements made up each component in these smaller animals. Yellow chromatophores and green iridescence were conspicuous on the mantle and arms, in contrast to the observations of Hanlon and Hixon (1980). One new chromatic component was observed — Dark splotches, each approximately 3 to 6 mm in diameter, widely dispersed on the arms and mantle and shown on a light overall pattern.

The same general body patterns (chronic and acute) were observed in these young animals as in the 31 mm ML female described *in situ* by Hanlon and Hixon (1980). Two exceptions were noted. The Flamboyant pattern was not seen in its fullest expression; the papillae were not greatly extented, probably due to the lack of textured visual stimuli in the laboratory environment. Secondly, the larger male, at 33 mm ML, showed a striking unilateral pattern in which the entire right side was dark and the left side very pale (Fig. 2 H). The apparent stimulus was the photographer's flash unit that was being moved in slowly on the right side of the octopus; thus the reaction was typical (Packard and Sanders, 1971), with the side toward the stimulus going dark.

5. Reproduction

The trawl-caught female *O. burryi* began laying fertile eggs 3 weeks after being brought into the laboratory. The female did not attach her eggs to the inner walls of the ceramic pot in which she resided, but rather carried the entire brood in her arms. This was accomplished by holding the eggs posteriorly, somewhat behind and beneath the mantle, in a « basket » formed by the aboral surface of the third and fourth pairs of arms. The female continuously ran her arm tips through the eggs and occasionally jetted water from the funnel into the brood. The brood consisted of numerous short strands of eggs (100-200 eggs per strand) ranging from 2 to 4 cm in length. Individual egg length ranged from 2.2 to 2.5 mm (excluding the stalk). After egg-laying the entire brood was removed from the female to estimate fecundity. Gravimetric and volumetric measurements of the brood gave estimates of 36 544 and 35 264 eggs, respectively. The female weighed 204 g (107 mm ML) 9 days prior to egg-laying. Thus the weight of the brood (91.36 g) represented 45 % of the female's pre-spawning weight. The female's mantle length diminished by 25 % (107 to 79 mm ML) one month after spawning. Only two strands of eggs were returned to the female and she produced no new eggs. Examination of the brood revealed that egg-laying occurred over approximately 2 weeks; there were three distinct groups of embryos differing in developmental stage by about one week. The female caught and completely ate a crab on three occasions while brooding eggs. She died 19 days after the last hatchings (115.7 g and 70 mm ML). There were fewer than 20 eggs left in the ovary at death.

DISCUSSION

1. Embryonic development and hatchling morphology

Octopus burryi is a small-egged octopus species with planktonic hatchlings. Egg length is essentially the same as *O. vulgaris* and *O. tetricus* (reviewed in Boyle, 1983) and represents 2 to 4 % of adult mantle length, which is typical of species with planktonic young (Boletzky, 1974). The duration of embryonic development (26 days at 23-24 °C) is also very similar to that reported for other small-egged species at these temperatures (Ambrose, 1981 : Fig. 4). The hatchlings of *O. burryi* (1.5 mm ML) are among the smallest reported in the subfamily Octopodinae along with *O. tetricus* (1.5 mm ML; Joll, 1976) and *O. defilippi* (1.3 mm ML; Hanlon *et al.*, this volume), yet this species shares some traits with species having hatchlings far larger. *Octopus burryi* has four suckers per arm at hatching like *O. bimaculatus* (Ambrose, 1981), *O. salutii* (Boletzky, 1977), *Scaeurgus unicirrhus* (Boletzky, 1984) and *Robsonella australis* (Brough, 1965). *Octopus burryi* has far more chromatophores at hatching (205) than similarly sized *O. tetricus* (ca. 48; Joll, 1976) and *O. vulgaris* (ca. 80; Fioroni, 1965), and more than *Hapalochlaena lunulata* (ca. 80-90; Overath and Boletzky, 1974) and *O. bimaculatus* (ca. 168; Ambrose, 1981), which are 50 and 70 % longer (ML) at hatching, respectively. *Octopus burryi* has nearly as many chromatophores as *O. maorum* (220; Batham, 1957), which is 300 % longer at hatching. Hatchling *O. burryi* thus have a far higher concentration of chromatophores compared to other planktonic octopods.

Octopus vulgaris occurs throughout the geographical range of *O. burryi* and the planktonic hatchlings of the two species can be differentiated by several features. *Octopus burryi* have far more chromatophores (205 vs. 80), and two rows of chromatophores on each arm versus one row in *O. vulgaris*. *Octopus burryi* has only two yellow chromatophores on the ventral head versus at least two dark red or brown chromatophores in *O. vulgaris*. On the dorsal mantle, only *O. burryi* has chromatophores (both have dark extrategumentals on the viscera). *Octopus burryi* has four suckers per arm, with the first sucker (nearest the mouth) the smallest and about half the diameter of the next sucker (Fig. 2 D); *O. vulgaris* has three equal-sized suckers per arm. Aside from chromatophore coloration, these features are clearly visible even on preserved material in reasonably good condition.

As reported from several other octopus species with planktonic hatchlings, the young of *O. burryi* readily attacked and fed on live zooplankton, yet survival was poor with little or no growth. In most attempts to culture planktonic octopod hatchlings, the live diets have provided some nutritional benefit in extending survival beyond that of unfed hatchlings, yet the diets have been apparently deficient in other important aspects (Mangold and Boletzky, 1973; Joll, 1976; Van Heukelem, 1976). The repeated failure to grow planktonic octopods to settlement since the early success of Itami *et al.* (1963) with *O. vulgaris* continues to be perplexing.

2. Early juvenile growth and behavior

One of the outstanding features of the early life history of *O. burryi* is the rapid growth potential of juveniles. The rate of sustained exponential growth in weight of the two benthic juveniles during the first month of captivity is surpassed only by that reported by Itami *et al.* (1963) for post-settlement *O. vulgaris* over the same size range. By the end of this rapid growth phase the two *O. burryi* had fully formed

hectocotyli. As with other octopus species (Forsythe, 1984) growth rates slowly decreased with the approach of sexual maturity, which was attained by the smaller male at 7 weeks post-capture.

In small-egged octopus species, settlement is probably not a distinct event in the change from a planktonic to benthic life style, but rather a period of gradual transition (Boletzky, 1977, Hanlon *et al.*, this volume). *Octopus cyanea, O. tetricus* and *O. vulgaris* become benthic in a size range of 0.2 to 0.5 g and 6 to 10 mm ML (reviewed in Boyle, 1983), although animals larger than this are occasionally collected in the plankton. If *O. burryi* settles out of the plankton in this size range it would be at a projected age of 40 to 60 days from hatching. In the early phase of settlement, *O. burryi* apparently assumes a diurnal planktonic/benthic behavior, swimming in the water column at night and living on the substrate by day.

3. Body patterning and behavior

Body patterning was noteworthy because of its diverse and complete form in such small animals. Juveniles of 6 mm ML can already do everything adults can, at an estimated age of only 70 to 80 days. This is remarkable considering that the hatchlings have only 205 chromatophores and are capable of showing only three very simple patterns : Clear (no chromatophores expanded), All dark (all yellows and browns expanded) and a variation of All Dark in which only browns are expanded (Fig. 1C). Since the brown chromatophores are very large, irregularly shaped and nearly overlapping with one another they can produce this distinctive third pattern, the behavioural significance of which is unknown. Neurophysiologically, the browns fire together, which implies that they developed morphologically at the same time and at the same approximate depth in the skin, and that the chromatophore motoneurons interconnected them during the same developmental period (Packard, 1982).

The browns on the viscera (called « extrategumental » by Fioroni, 1965) seem identical in structure, function, depth in the skin and neural connections as the ones on the dorsal head and on all the arms.

There is no conspicuous dorsal or ventral countershading gradient produced through chromatophore expansion. There are 113 chromatophores dorsally and 92 ventrally; among brown chromatophores (which contribute far more to darkening), 69 are dorsal and 70 ventral. Among other planktonic hatchling octopods there is no trend toward dorsal or ventral darkening as there seems to be in some loliginid squid hatchlings, which have many more chromatophores ventrally at hatching (cf., Naef, 1923/1928; McConathy *et al.*, 1980).

The most species-characteristic component, Longitundinal arm stripe, is strongly developed and conspicuous at 16 mm ML (Fig. 2 E). This component has not been described in other octopod species within the geographic range of *O. burryi* and is thus a useful identifying character for juvenile and adult animals. *Octopus vulgaris* darkens the frontal arm edges while the body is blanched white in the Dymantic pattern (Cowdry, 1911; Packard and Sanders, 1971), but *O. vulgaris* smaller than 1.0 g cannot produce this pattern. On larger *O. vulgaris* the Dymantic pattern is easily recognized while being absent as a pattern in *O. burryi.* Only *Octopus membranaceus,* an Indo-Pacific species, has been documented to have Longitudinal arm stripes similar to *O. burryi* (Voss and Williamson, 1971; Lam and Chiu, 1983). Other key identifying components of patterning are present and distinguishable by 16 mm ML. Specifically, the juxtaposition of white components and papillae on the mantle (i.e., white Head spots, Mantle spots and Transverse streak, and Long rounded head papillae and Long flattened dorsal mantle papillae) are exactly the same as depicted in Fig. 2 of Hanlon and Hixon (1980). It is remarkable how easily identified the Gulf of Mexico juveniles were, based upon the similarity in patterning with the adults described from the Virgin Islands, almost 3 300 km to the southeast. Thus the patterns have not only behavioral significance, but can be used as taxonomic keys for identification of live animals.

The most notable aspects of behavior involved feeding and intraspecific aggression. In the laboratory, *Octopus burryi* employed an ambush predator strategy by waiting for potential food organisms to enter the field of view. Food organisms were attacked at a relatively great distance, long before they were within arms' reach as reported by Hanlon and Hixon (1980); the animal they observed in the field may have been more cautious in the presence of two divers. No speculative benthic searching for food has been observed in the laboratory or field. The apparent diurnal departure from the substrate into the water column by juveniles may, however, be a speculative search for food.

The aggressive behavior of the larger juvenile *O. burryi* towards its smaller conspecific in the presence of abundant food suggests this species is not tolerant of crowding. The collection record of this species tends to support this, since about 80 % of the known specimens of *O. burryi* have been collected individually.

4. Reproductive biology

Most aspects of the reproductive biology of *O. burryi* differ little from those reported for other benthic octopods. *Octopus burryi,* along with *O. defilippi* (Hanlon *et al.*, this volume), *Hapalochlaena*

maculosa (Tranter and Augustine, 1973) and *Scaeurgus* spp. (Van Heukelem, unpub. observations from Hawaii) are the only benthic octopod species in the Family Octopodidae known to carry their eggs during embryonic development. Of these, only *Hapalochlaena maculosa* has large eggs and benthic hatchlings. Tranter and Augustine (1973) considered this type of special maternal care to be "an advanced evolutionary development"; however, the adaptive value of carrying a brood versus the more common behavior of egg attachment is unclear.

The gross fecundity of a small species like *O. burryi* is considerably less than larger species that produce eggs of similar size. *Octopus cyanea, O. tetricus* and *O. vulgaris,* which are 5 to 20 times larger at spawning, produce 100 000 to 700 000 eggs per brood (reviewed in Boyle, 1983) compared to the 35 000 of *O. burryi.* However, on a relative weight basis *O. burryi* shows comparable fecundity, producing approximately 175 eggs/g of body weight, compared to a range of 100 to 200 eggs/g for these other three species.

Finally, although the age of the female at the time of spawning was unknown, the larger of the two males would have attained the female's size in little more than a month had it not died prematurely. This would give the female an approximate age of 7 to 8 months from hatching.

5. *A proposed life cycle for* Octopus burryi

This life cycle is based upon growth and maturation observed at temperatures of 22 to 25 °C. *Octopus burryi* hatches at a size of 1.5 mm ML after a period of embryonic development lasting nearly a month. The hatchlings begin a 3-month period of extremely rapid exponential growth, doubling in weight every 7 to 8 days. The small octopuses are strictly planktonic during the first 4 to 6 weeks of this growth phase. Thereafter, they begin to gradually assume an adult-like benthic life style, although feeding forays into the water column can continue to an age of at least 10 weeks. Beyond an age of 3 months, growth rates gradually slow and males reach sexual maturity at an age of 4 months (ca. 38 mm ML as in our smaller mature male).

Females mature and spawn at 7 to 8 months of age. The full life cycle lasts 9 to 10 months, including embryonic development and egg brooding by the females. This scenario is probably valid for *O. burryi* throughout the Caribbean at depths of 50 m or less when temperatures remain above 20 °C year-round. One might expect little seasonality to spawning. In the northern Gulf of Mexico the life cycle may be closer to 12 months due to lower water temperatures and slowed growth in winter. More seasonality in spawning is likely.

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FECUNDITY OF THE CUTTLEFISH, *SEPIA OFFICINALIS* L. (MOLLUSCA : CEPHALOPODA), FROM THE GULF OF TUNIS

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CEPHALOPODA, *SEPIA OFFICINALIS*, INDIVIDUAL FECUNDITY, GLOBAL FECUNDITY

For fisheries purposes, fecundity of Cephalopod females is usually determined by counting the number of eggs contained in the ovary of mature individuals. The mechanisms of sperm storage and egg laying in Cephalopods ensure a very high rate of fertilized eggs, especially in species where eggs are laid singly, such as *Sepia officinalis*.

The individual and the global fecundity were determined from the spawning population in the Gulf of Tunis in 1980. The spawning period lasts from February to June (Najai, 1983). Smooth, mature eggs measure from 6 mm in diameter in the smallest individuals to 10 mm in females of the largest size classes. *Sepia officinalis* usually lays eggs over several days or weeks (Boletzky, 1983). In mature females, eggs of all developmental stages are present and it is not yet known how many eggs may become mature during a prolonged individual spawning period in nature. Laboratory observations, however, have shown that very small eggs may reach full maturity within a few weeks (Boletzky, in press), as surmised by Voss (1983). To estimate individual fecundity, smooth eggs and reticulated eggs of large size (6 to 10 mm, according to the size of the female) were counted (Ezzedine-Najai, 1984) for females of the size classes of 80 to 190 mm dorsal mantle length (Table I). Large females have more mature and near-mature eggs than small ones. However, the females of the small to medium size classes (90 to 150 mm ML) contribute more to the global fecundity of the spawning population than large individuals because they are more numerous (Table I). The number of eggs laid between February and June 1980 in the Gulf of Tunis was estimated at 16 millions. This might correspond to the effective fecundity of the spawning population, but one should keep in mind that the potential individual fecundity of *Sepia officinalis* is about four times higher (Boletzky, in press).

Table I. — Size distribution of *Sepia officinalis* females fished between February and June 1980 in the Gulf of Tunis, with corresponding fecundity values in terms of mean numbers of near-mature and mature ovarian eggs (based on a sample of 743 individuals).

Size class mm	Number of females (A)	Individual mean fecundity (B)	Deduced global fecundity (A x B)
80	2 388	99	236 412
90	9 553	163	1 557 139
100	12 737	181	2 305 397
110	17 115	228	3 902 220
120	10 747	235	2 525 545
130	6 766	230	1 556 180
140	4 776	195	931 320
150	3 980	383	1 524 340
160	1 592	345	549 240
170	1 194	365	**435 810**
180	796	420	334 320
190	398	543	216 114

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SIZES AND DISTRIBUTION OF CHROMATOPHORES DURING POST-EMBRYONIC DEVELOPMENT IN CEPHALOPODS

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CEPHALOPODS
CHROMATOPHORES
PATTERN-GENERATION
OCTOPUS
LARVA

ABSTRACT. — The spatial arrangements of chromatophores (spots) of cephalopods appear to be generated by processes of lateral inhibition (Meinhardt and Gierer, 1974) by which successive generations of spots are spaced out relative to previous ones. Spots arising later in development are smaller than those arising earlier. Spots do not disappear or die but their pigments change colour (become dark) with age. Details of these processes (positions and sizes of *founder* chromatophores and their relation to subsequent generations, rates of chromatophore production) are followed in the arm and mantle fields of *Octopus vulgaris* (and *Octopus dofleini*) both forwards in time by studying photographs of individuals during the first weeks after settling and backwards towards hatching. Knowledge of the processes enables hatchling and early juvenile chromatophore patterns to be recognized in later stages of ontogeny. Size-frequency histograms are constructed and attention is drawn to their value in systematics.

CÉPHALOPODES
CHROMATOPHORES
RÉPARTITION
GÉNÉRATION
OCTOPUS
LARVE

RÉSUMÉ. — Chez les céphalopodes, la répartition spatiale des chromatophores semble généralement s'opérer par inhibition latérale (Meinhardt et Gierer); les générations successives de chromatophores se répartissent en fonction de celles qui les précèdent. Les chromatophores qui apparaissent plus tardivement au cours du développement sont plus petits que leurs prédécesseurs. Les chromatophores ne disparaissent pas, mais changent de couleur (s'assombrissent) avec l'âge. Les détails de ces opérations (position et taille des chromatophores *primitifs* et leur relation avec les générations suivantes, la vitesse de production des chromatophores, etc.) sont examinés dans le temps au niveau des champs morphogénétiques des bras et du manteau d'*Octopus vulgaris* (et d'*Octopus dofleini*), en étudiant des photographies de spécimens prises pendant les premières semaines de vie benthique et en déduisant la répartition au moment de l'éclosion. Les histogrammes tailles-fréquences ont été construits et l'attention est attirée sur leur intérêt heuristique pour les études de classification.

INTRODUCTION

If we are to discover whether the distinctive patterns of chromatophores (spots) on the head, arms, mantle and funnel of hatchling squids and octopods have any function other than to provide systematists with a god-given means of identifying larval cephalopods in plankton hauls, we shall need to bear two things in mind. 1) Chromatophores are visual effectors under neuro-muscular control; spots flash on and off — by expansion and retraction — and create visual effects tuned to eyes : eyes that have much in common with the systematist's, eyes for recognizing members of one's own species and for gathering information about food or for alerting

to potential danger, and eyes that can be tricked. 2) The initial arrangement of spots influences all subsequent arrangements.

F.G. Hochberg has discovered that hatchling octopods can be simply keyed down to the species (? genus) level by the characteristic number and positions of chromatophores. (Similar criteria were used by McConathy *et al.* (1980) for distinguishing hatchlings of *Loligo* and *Lolliguncula*). It has, however, not been generally realized that these hatchling spots persist throughout the weeks of « larval » life and into the months of benthic life that follow. They do not die or disappear, and thus they furnish an invaluable way of linking early planktonic stages with much later stages of the life history the intermediates of which may be completely absent from plankton collections or are difficult to relate using other characters. *Octopus vulgaris* has a maximum of eight tegumental chromatophores on the dorsal mantle surface at hatching (Fioroni, 1965, Fig. 33) — a forward pair (but sometimes 3 or 4) at the boundary between mantle and head and a posterior pair (but rarely 3 or 4) — yet even after this tiny individual has grown ten-thousand fold in size (from 3 mg body weight to 30 g) these *founder chromatophores* can still be discerned, embedded amongst the hundreds of thousands of spots that have arisen in the intervening space and time unaltered in size, shape and relative positions (see Plate Ia).

As we shall see, there is a spacing principle at work by which the locations of spots of subsequent generations is influenced by the spots already present. Put another way, this means that *chromatophore arrangements are always patterned,* never random, and the patterns are *spatio-temporal.* Pictures through the surface of the skin in which all four dimensions are collapsed into two, offer as much information about the ontogenetic history of the organism as does a section through the trunk of a tree or a scale from a fish, but unlike these the developing structure does not need to be sacrificed in the process.

One very simple kind of pattern resulting from this spacing principle is illustrated in Figure 1a, b of a 1-week-old *Sepiola robusta.* The new, small, chromatophores (« generation II ») are arranged around and between the larger, older, spots (« generation I »). The best model that I have encountered for understanding these kinds of regular/irregular pattern is Meinhardt and Gierer's (1974) theory of *lateral inhibition.* It involves activator and inhibitor substances each with its own diffusion range and has been mathematically formulated in two simultaneous equations. Figure 1c shows the locations of

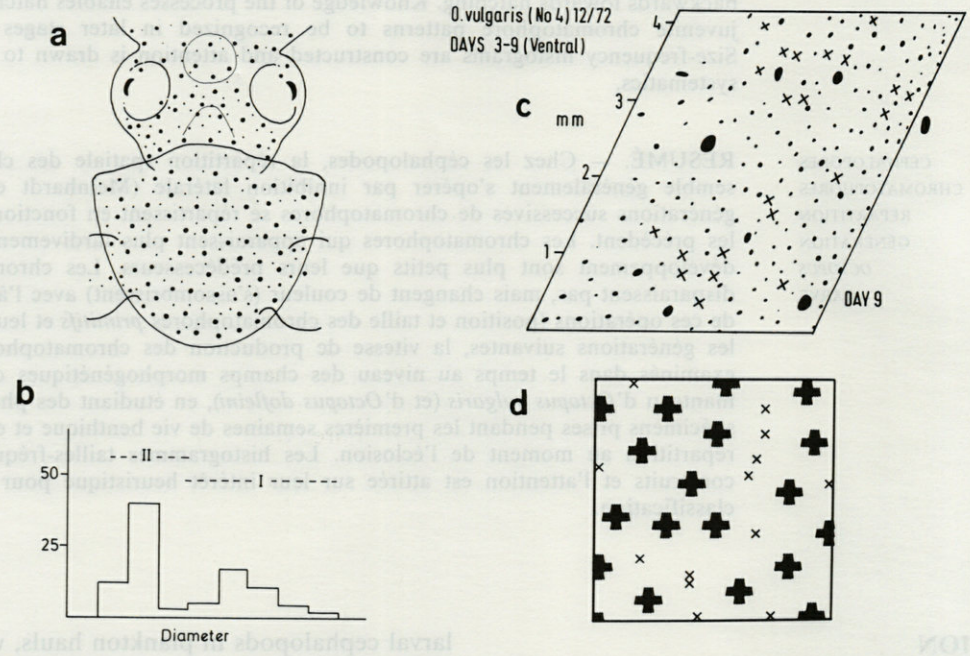


Fig. 1. — a, Arrangement of spots (retracted chromatophores) on the dorsal mantle surface of 1-week-old *Sepiola robusta.* (From a photograph by J. Lecomte taken for R. Hanlon.) Dorsal mantle length 6.5 mm. b, Size histogram (resting diameters) of spots in this photograph. c, Drawing (from photograph) of part of the ventral mantle surface of an early benthic *Octopus vulgaris* showing new spots (x) that have arisen over a 6-day period in spaces between extant ones (•). Note that some appear in pairs and that extant chromatophores range in size. d, Computer model by H. Meinhardt of regular/irregular arrangement of extant spots (+) and a new generation (x) arising between them, some as a pair or in a row, based on principle of lateral inhibition (see text). Both illustrations first published in *Biological Pattern Formation* by H. Meinhardt (1982).

new chromatophores arising, some of them as pairs, in a field already occupied by spots. Meinhardt's computer model of this, employing the principle of lateral inhibition, is shown alongside (Fig. 1 d) (Meinhardt, 1982).

I have published the general rules underlying the generation of chromatophore patterns as « Rules for the conduct of young chromatophores » in Packard, 1982. Figure 1 illustrates the rule that young chromatophores should never grow larger than neighbours already established. The resulting *hierarchy of sizes* reflecting age classes is perhaps the most valuable single key to the correct analysis of chromatophore patterns in cephalopods.

A more detailed example of the operation of the age/size hierarchy and of associated rules is illustrated in Figure 8 (see main text).

METHODS

Animals

Early benthic octopuses (*Octopus vulgaris* Lamarck) were obtained from local fishermen through the live animal supply service of the Naples Zoological Station and maintained in small black perspex tanks with transparent lids and fed at intervals on *Carcinus maenas* or the marine isopod *Sphaeroma* between sessions of photography.

Planktonic (? immediate post-hatching) *Octopus dofleini* were caught at the night light at the Friday Harbor Laboratories of the University of Washington in December and January initially by Claudia Mills and kindly transported by her to Canada (University of Victoria) where they were kept in circulating seawater. Others were studied at the Friday Harbor Laboratory.

Anaesthesia, photography, measurement

All analyses have been on photographs of the intact skin of live animals working both backwards in time and forwards. *Single individuals* were followed at magnifications and resolutions sufficient to identify single chromatophores. The photographs that served for analysis of resting sizes and recruitment of chromatophores were taken with a Leica back on a Leica Panphot in the reflecting microscope mode with the lowest power (× 3.8) water immersion lens (illumination mercury vapour lamp) using Kodacolor negative film (ASA 100) and Ektachrome (100 ASA). The anaesthetic used was urethane (ethyl carbamate) 0.5 — 1.0 % in seawater (depending on size of animal). The aim of anaesthesia is to reduce movement and to obtain chromatophores in the retracted (resting) condition. (N.B. I have subsequently found that the popular invertebrate relaxant magnesium chloride ($MgCl_2$ isotonic, 1 part + seawater, 1 part) is a better anaesthetic and does not have the long-term toxic effects of urethane). Anaesthetized animals were held (sometimes for up to one hour) in a small bath at room temperature on a soft polystyrene foam bed cut to the shape of the animal and areas to be photographed were either flattened under glass (large microscope slide) or directly by the condenser of the water immersion condenser/objective. Areas of photographic prints and slides to be sampled were inspected either with head lenses or under the × 6 and × 12 objectives of a Wild dissecting microscope and chromatophores were drawn by light tube (*camera lucida*). Final linear magnifications achieved ranged up to × 70.

GENERAL

The studies of Naef (1921-28) on late embryological stages were extented in detail by Fioroni (1965) for the development of chromatophore patterns (Musterentwicklung). Their data and mine are combined in what follows. Terms are those of current developmental terminology.

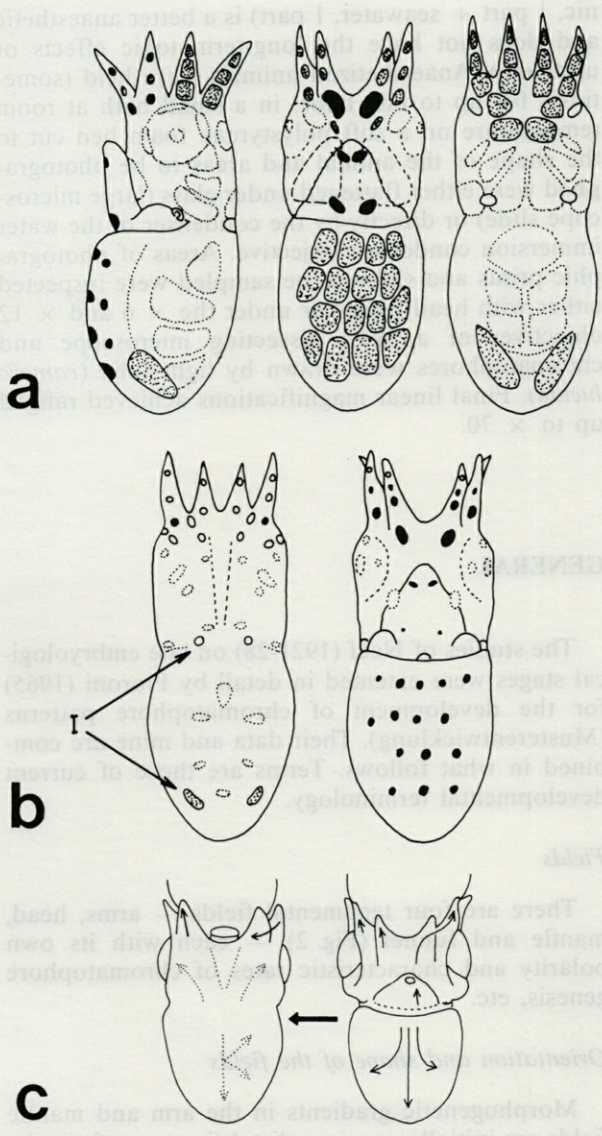
Fields

There are four tegumental fields — arms, head, mantle and funnel (Fig. 2) — each with its own polarity and characteristic rates of chromatophore genesis, etc.

Orientation and shape of the fields

Morphogenetic gradients in the arm and mantle fields are initially proximo-distal (i.e. away from the brain) and either dorso-ventral or ventro-dorsal (see Fig. 2). Edge-effects are common especially in early stages of development. As previously empty fields become occupied by recruitment of chromatophores their polarity may invert one or more times. For instance, in *Octopus vulgaris* at hatching there are many more tegumental chromatophores on the ventral mantle surface (Fig. 2) than on the dorsal, and this condition persists until the "larva" settles from the plankton; but in all benthic stages of this animal there are more on the dorsal mantle surface. The build-up of the gradients producing these effects is illustrated diagramatically in Figure 3. Presumably in this species the early gradients collapse or convert to inhibitory ones once the planktonic phase is over.

Octopus dofleini (Plate Ib) hatches with many tegumental spots dorsally but none ventrally — i.e. the reverse of the situation in *O. vulgaris* — indicating that reversal of gradients is one of the epigenetic variables that can be played upon by evolutionary processes.



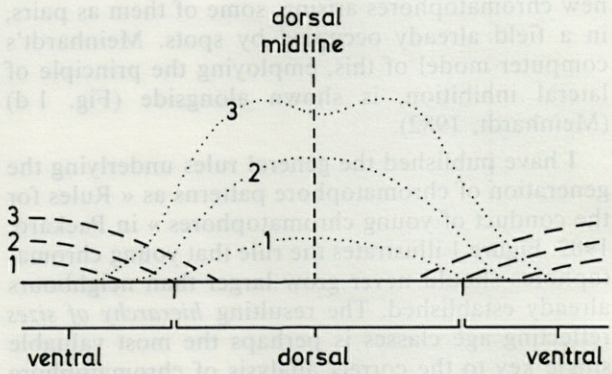
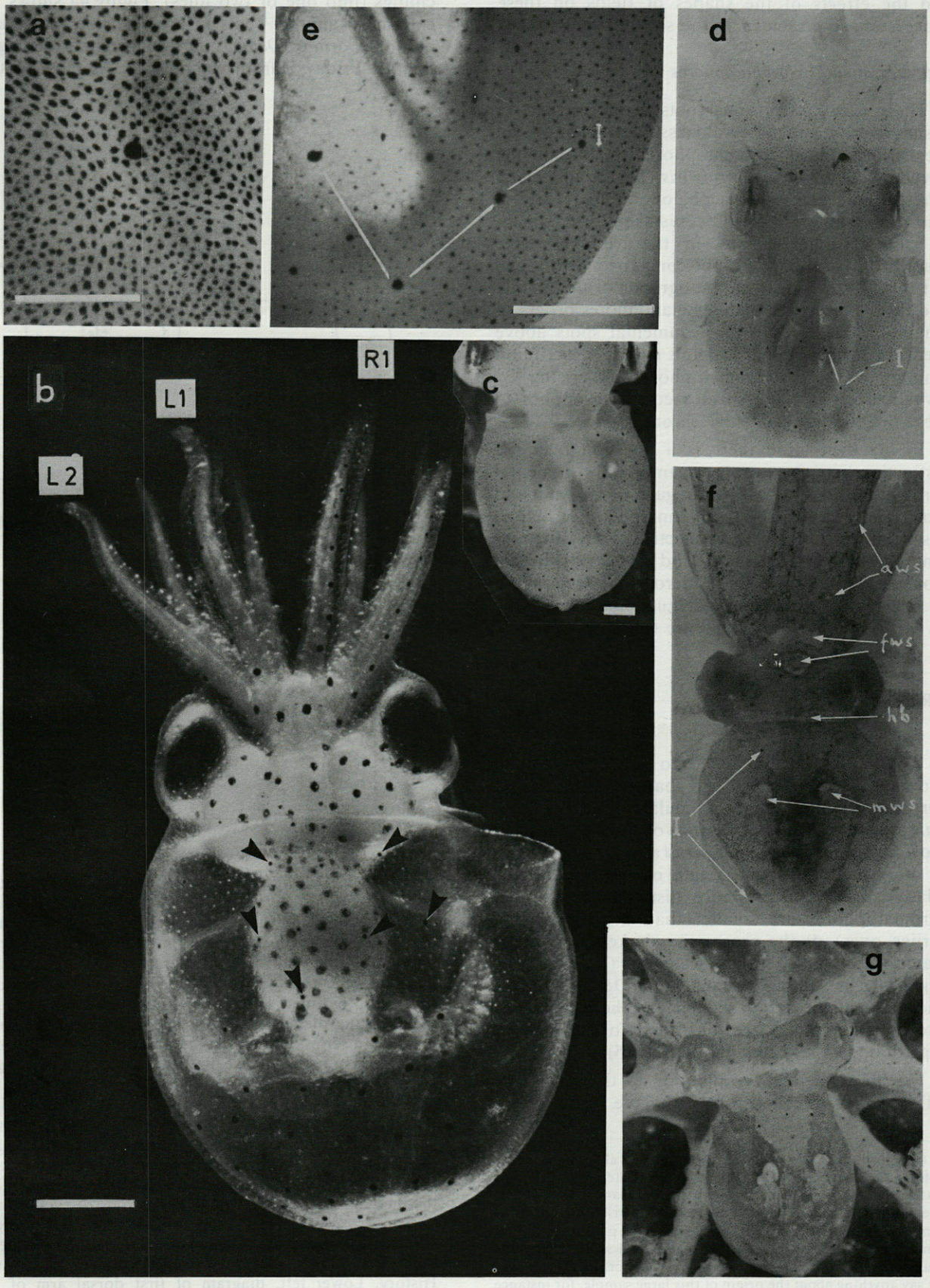


Fig. 3. — Gradients of spot production on the dorsal and ventral mantle surfaces of *Octopus vulgaris* as indicated by sizes and numbers of chromatophores with time (1, 2, 3) during planktonic life (dashed lines) and early benthic life (dotted lines).

Fig. 2. — Hatching dress (*Schlüpfkleid*) of *Octopus vulgaris* emphasising founder chromatophores of tegumental series in the arm and mantle fields (extrategumental spots dotted outlines). Pigment density indicated by shading. a, Expanded, lateral, ventral and dorsal, b, Retracted (left is dorsal, right, ventral). I = newly formed anterior and posterior pairs of founder chromatophores at edges of dorsal mantle field. c, Sequence of appearance of tegumental founder chromatophores (full arrows) and of extrategumental series (dotted arrows) during late embryogenesis. (All three figures from Fioroni, 1965, modified).

Plate I. — a, Low power photograph of skin taken by reflecting microscope at left anterior margin of dorsal mantle field of juvenile *O. vulgaris* (30 g body weight, d.m.l. 46 mm) to show single large chromatophore of original hatching series ("founder" chromatophore) surrounded by populations of smaller chromatophores (see text). Smallest spots (grey) are orange/red in life. All chromatophores in resting condition. Note the "patch" and "groove" arrangement characteristic of these late stages of ontogeny. Densities in the patches are higher, and chromatophores smaller, than in the grooves. Scale bar = 0.5 mm. b, Dorso-lateral aspect of anaesthetized *Octopus dofleini* caught at the night light showing founder chromatophores on arms and mantle (some of the smaller anterior mantle chromatophores indicated by arrows). Buccal mass, eyes, brain, visceral mass and overlying extrategumental chromatophores all conspicuous, also pallial connectives, stellate ganglia, gills and hearts. Bright points in the dorsal skin of mantle and head are Kölliker's bristles. Note absence of founder chromatophores on ventro-lateral (and ventral) surface part of which is seen at right of photograph. Scale bar = 1 mm. c, Ventral view of mantle of early benthic *O. vulgaris* "No. 2" (anaesthetized) analysed in Fig. 6a and 7d (Body weight 0.3 g). All chromatophores in retracted condition. Large ones belong to original hatching series (see text and caption to Fig. 6). Scale bar = 1 mm. d, Ventral view of early benthic *O. vulgaris* "No. 4" analysed in Fig. 7a and b. Four of the founder chromatophores (I) linked by lines. e, Detail of the middle of the mantle (right side) of specimen "No. 4" showing the extensive population of small chromatophores already recruited during benthic life. Note wide zones of inhibition round some of the "founder" and marker chromatophores (up to 500 µm across, far left and lower right) and tendency of chromatophores to arise in rows. Minimum nearest neighbour distances to founder chromatophores 100 µm). All chromatophores in resting condition. Scale bar = 1 mm. f, Dorsal view of "No. 2" (see c this Plate) under glass anaesthetized. Some of chromatophores expanded, especially in area of skin in contact with glass. Note anterior and posterior pair of large "founder" chromatophores (I) on mantle and conspicuous double row on dorsal (aboral) aspect of arms. Mantle-frontal and arm-white spots (m.w.s., f.w.s. and a.w.s.) and white head bar (h.b.) also well established. g, Same specimen, partially anaesthetized in natural posture, pale (all chromatophores retracted).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Evidence for *metamerism* and *field sub-division*, and the effects of the shapes of fields on these processes, are presented in the sections that follow.

Extrategumental chromatophores

These very conspicuous spots in the connective tissues overlying the visceral mass, head and eyes are the earliest dorsal chromatophores to arise in the development of *Octopus vulgaris* (Fig. 2) and many other forms, and since cephalopod larvae are so transparent they can often be mistaken for tegumental chromatophores lying in the true skin (see Plate Ib). My studies are not concerned with them, but they often appear in photographs of the mantle and head skin as enormous melanophores orders of magnitude larger than the tegumental spots above them (1). It may be that Joubin's curious description (Joubin, 1892) of chromatophores as arising by invagination from the surface ectoderm applies to these large extrategumental chromatophores.

In my own mind there is a question over the distinction between extrategumental and tegumental chromatophores at least with regard to the head and arms. The founder series of arm spots (see below) lies deep, on top of the connective tissue surrounding the arm musculature, and appears, whether looked at in life or in light microscopic sections, to be continuous with the extrategumental spots lying on top of the head musculature (see Naef, 1928).

ARMS

The arm field, subdivided into 8 (or 10) sub-fields shows the influence that field shape and size has on chromatophore genesis : particularly a) the *sequential* (proximo-distal) appearance of spots as the arms grow from the tips, b) their *serial* arrangement in one or more lines down the length of the arms, c) the relative *age/size rule* (more distal, later, founder chromatophores are smaller than more proximal, earlier, ones), d) the progressive darkening of chromatophores with age, the latest spots (near the tips) being always yellow or orange/red. Details of these and of the pigmentation sequence of the arms during late hatching stages are illustrated for the various cephalopod families by Fioroni (1965).

Hochberg has drawn attention to the systematic differences between octopuses in the linear arrangement of founder spots down the arms of hatchlings (into one or two lines). Figure 4a shows an extreme example : spots in a single line (uniserial) on dorsal arm of *Octopus dofleini* caught at the night light at Friday Harbor Laboratory. As most of the

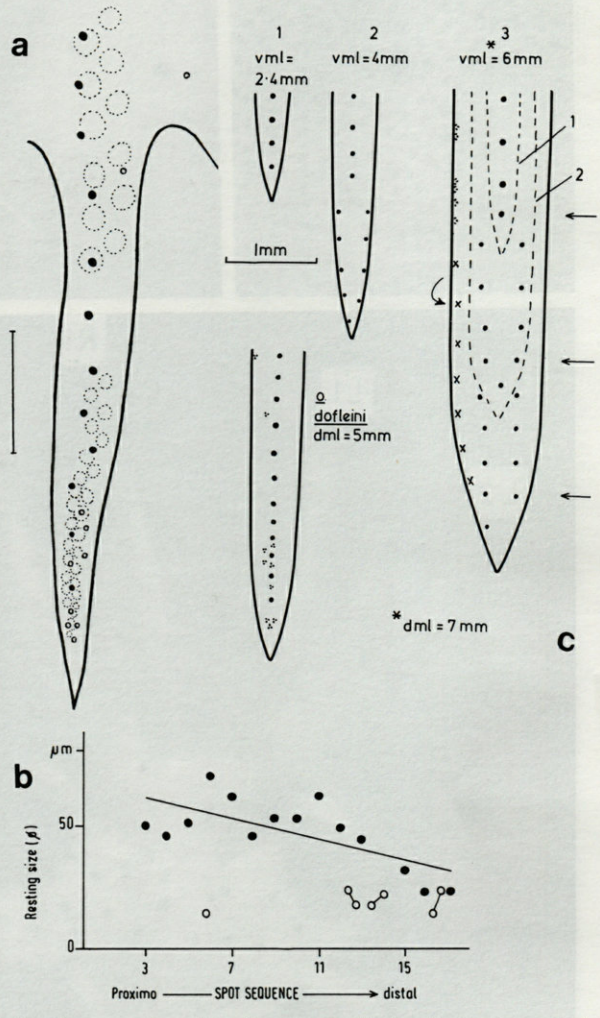


Fig. 4. — a, Drawing from two Kodacolor prints of the dorsal surface of Arm 1 right of anaesthetized post-hatching *Octopus dofleini* showing 14 uniserial founder chromatophores (•) being succeeded near the tip by a paired series (o). Note that there are members that are intermediate between the two series. Suckers, seen by transparency, also outlined. Scale bar 0.5 mm. b, Chromatophore sizes (resting diameters) in this specimen plotted against position in series. Regression line fitted for uniserial spots (•). Other spots (o). c, Idealized diagram of the arrangement of chromatophores on the first dorsal arms (left) of Rees's three "larval" *O. vulgaris* (Rees, 1950) representing three successive stages (1, 2, 3) with ventral mantle lengths (v.m.l.) indicated. In 3) the contributions of earlier stages to the additive growth of the third are indicated by the hatched lines 1 and 2. × Ventral (aboral) series shown on the medial surface only. Spots on the rims of suckers not shown. Arrows, levels at which *arm white spots* will appear. All drawn to the same scale and checked on the specimens themselves kindly loaned by British Museum of Natural History. Lower left, diagram of first dorsal arm of *O. dofleini* to the same scale (from a).

(1) Fioroni's (1965) counts, and the mean values given in his tables and figures, always include the extrategumental spots, usually on the visceral mass. In his table 15 and Figure 33, he gives complete details of the numerical distribution of these (range 5-10) along with the arrangements of the posterior two (but sometimes 3 (28 %) or 4 (3.8 %)) of tegumental spots at hatching in a sample of 1116 hatchling *O. vulgaris*. Unfortunately he does not say anything about the origin of this large sample, for instance whether they were all from the same brood or not.

specimens caught at the night light have about nine dark chromatophores (the same as the number in Gabe's (1975, Fig. 2) on the first dorsal arms, they are assumed to be freshly hatched. This specimen has 12 dark red spots and 11 orange/red. Most of the orange/red (which will in turn become dark) are the beginning of a second series of spots, smaller than the first, forming a double row. The regression in size of the sequentially produced uniserial spots is shown in Figure 4b.

Figure 4c is a composite diagram from Rees's three *Octopus* "larvae" in the British Museum. In this species (supposed to be *O. vulgaris*) the double row is added distally, as the arm grows in length, after four (sometimes only three) uniserial spots. There are 4 1/2 'pairs' at a ventral mantle length (v.m.l.) of 4 mm and 8 1/2 'pairs' by the late planktonic stage (v.m.l. 6 mm). An even later — immediate pre-benthic — stage is illustrated in Adams (1937). In his drawing, there are four uniserial spots on Arm 1 left and three on Arm 1 right. The double row on Arm 1 left consists of 13 pairs of spots.

The long double row is still conspicious on the arms of benthic stages of *Octopus* (Plate Ia, f and g) and can be traced well into juvenile life so long as the skin is pale (overlying chromatophores retracted). While evidently in two rows (biserial), these founder spots are usually unevenly staggered and therefore not really in pairs. Subsequently appearing spots are also shown in Figure 4c including a distally running ventral (oral) series in two single lines just above the suckers (shown on the medial side only in Fig. 4 c). The members of these two oral rows are smaller, but not much smaller, in size than their companions aborally and their spacing indicates that they belong to the same generation as the aboral series produced as a result of the extension outwards (from the middle of the arm sub-field), of the same morphogenetic influences that gave rise to the initial double row, directly paralleling what happens to the mantle field at this same stage (see above and Fig. 3). Fig. 4c (3) also shows the first members of a proximal series in a single row but smaller in diameter and closer together than the others, belonging to a subsequent generation.

Nearest neighbour distances between founder chromatophores on the arms are typically 0.15 mm expanding to 0.25 mm by the benthic stage as the arms and skin grow.

MANTLE

On the mantle, as on the arms, the original hatching pattern of chromatophores, or "*Schlüpfkleid*" (= literally hatching dress, Fig. 2) can still be seen in benthic *Octopus* showing through the later dress. The spots composing the original dress are identifiable because they are larger in resting size than any subsequent sets of chromatophores, and as the mantle grows throughout its surface (and not terminally like the arms), they retain, by and large, their original positions (i.e. configuration) relative to each other and to the mantle fields as a whole.

Ventral mantle

In Figure 5a I have identified the 16 founder chromatophores (resting diameters > 70 μm) of the original hatching dress on the ventral mantle surface of an early benthic *O. vulgaris*, and an adjacent drawing (Fig. 5b) shows them as they would have appeared in this specimen when it hatched. The figure also illustrates the genesis of spots. Founder chromatophores are shown alone on the left side of Figure 5a, and together with subsequent generations on the right. A photograph of this animal appears as Plate Ic.

The mantle field of *Octopus* exhibits edge-effects

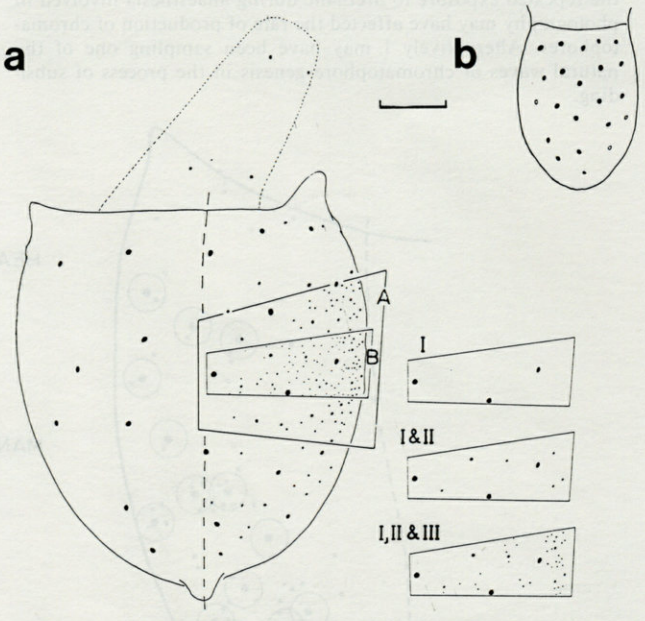


Fig. 5. — a, Details of pattern on the ventral mantle surface of an early benthic *Octopus vulgaris* (body weight 0.3 g) with all the larger chromatophores drawn at correct scale and shape. The figure is drawn from an original photograph in such a way as to show on the left (right side of mantle) only the largest (founder) chromatophores (mean diameter > 65 μm), and on the right (left side of mantle) the founder chromatophores (I) plus the succeeding generation (II) (mean diameters 35-65 μm) while inset A includes the third generation (III) (mean diameters ~ 30 μm) and inset B includes the latest generation (IV) (mean diameter < 25 μm). The successive recruitment of these categories of spots within area B is shown alongside. Note also the four founders on the funnel. Compare with Figure 1. b, All the founder spots in this specimen (with sizes, shapes and relative positions conserved) as they will have appeared in the original ventral mantle hatching dress. To same scale.

but no obvious proximo-distal sequence or serial arrangement of spots presumably because the mantle field, unlike the arms, is broad and short. Squids such as *Alloteuthis* (see Fioroni 1965) and *Illex* with long narrow mantle do show serial arrangements down the length of the mantle. Nevertheless in *Octopus* spots tend to *cluster* and to arise in *rows*, presumably as a result of activator and inhibitor influences emanating from extant chromatophores of the kind mentioned above. The tendency to form rows was noticed by Fioroni (1965), who shows various arrangements on the ventral surface of *O. vulgaris* at hatching (his Fig. 32 and Table 14); it persists into later stages of ontogeny and can be detected in Plate Ie. Clustering of new chromatophores is revealed in the analysis (Fig. 6a) of the recruitment of spots into the ventral skin of an individual (seen in Plate Id and e) over a 6-day period. During this period the total population of chromatophores grew by just over 10 % (2). As explained in the caption, nearly half arise in the neighbourhood of extant founder and marker chromatophores; they are, however, distanced from them by a minimum nearest neighbour distance of 100 µm again suggesting lateral inhibitory influences.

Rates of chromatophore production evident in these analyses are higher laterally (and posteriorly) than in the middle of the ventral surface (where they reach zero). They are part of the outward extension of the large wave of chromatophore production that appears in the middle of the dorsal mantle field at the transition from planktonic to benthic life (Fig. 3).

Dorsal Mantle

The dorsal mantle field is more complex than the ventral. Until the post-planktonic wave appears, chromatophores on the dorsal surface seem to owe their production to an extension (laterally and posteriorly) of the wave (Fig. 3, dashed lines) that originates midventrally in the late embryo and continues to operate during planktonic life (see also Adams' (1937) drawings and photographs but omitting the large dorsal extrategumental spots on the visceral mass). When *Octopus vulgaris* settles from

(2) The increase was 5.5 % over the first two days of this period. As noted in the Methods, urethane has toxic effects and the repeated exposure to urethane during anaesthesia involved in photography may have affected the rate of production of chromatophores. Alternatively I may have been sampling one of the natural waves of chromatophore genesis in the process of subsiding.

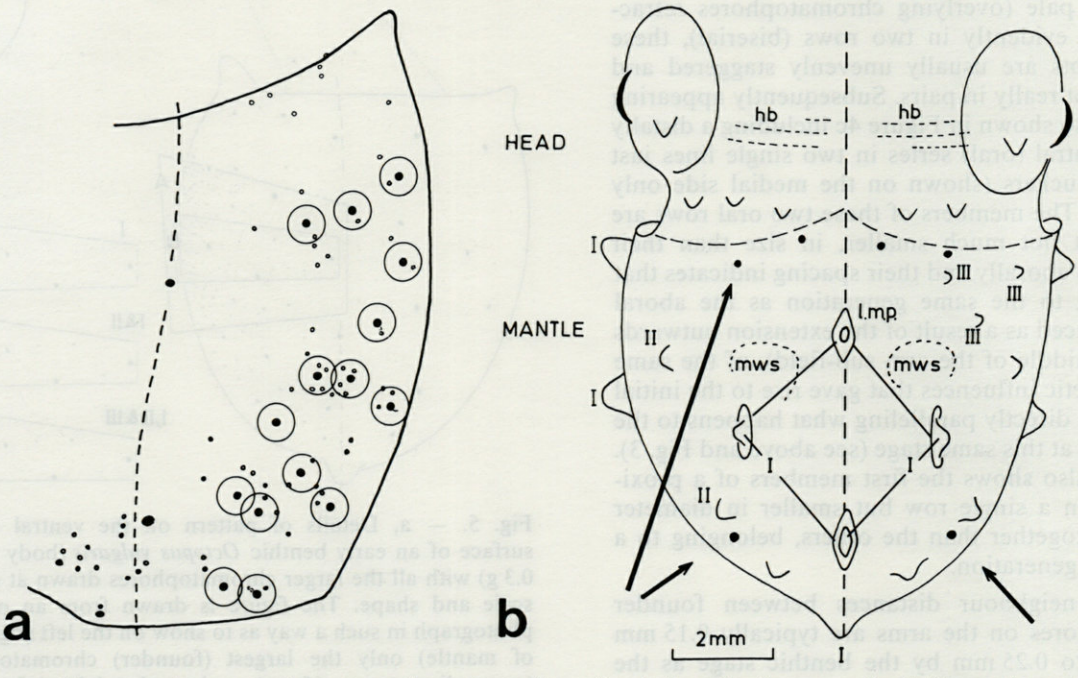


Fig. 6. — a, Chromatophore genesis on ventral mantle surface of early benthic *Octopus vulgaris* (drawn from photograph). The incidence of new spots (○) is shown in relation to founder and other marker chromatophores (●) on the anterior seven eighths of the left mantle surface of an 0.3 g body weight ("No. 4") *O. vulgaris* between days 3 and 9 of observation. The circles drawn round founder and marker spots cover a total of 15 % of the area analysed. 43 % of new chromatophores fall within these circles. Note also « edge effects » at anterior mantle margin. Area analysed approximately 17 mm^2. Total number of all chromatophores in this area on Day 3 was 580; total number of new by Day 5 was 52 (5.5 % increase in two days) and by Day 9 was 61 (10.5 % increase in six days). Sampe specimen as Plate Ic. b, Relationship of mantle founder chromatophores (anterior 4 and posterior 2 indicated by arrows) to other features of skin patterning in an early benthic *O. vulgaris*. Boundary between head and mantle fields indicated by dashed line. The diamond-shaped group of four primary long *papillae* (l.m.p.), or cirri, is linked by lines; lateral and posterior long papillae indicated by the Roman numeral I. Seconday and tertiary papillae (II & III) also indicated. Note relationship of these to *mantle white spots* (m.w.s.). h.b., head bar (from photograph).

the plankton, the rate of chromatophore genesis into the otherwise empty dorsal mantle field rapidly overtakes the rate of recruitment into the ventral field, with three results : i) chromatophores are smaller dorsally than ventrally, ii) local densities become and remain much higher dorsally than ventrally, iii) the progressive decrease in the size of individual chromatophores with each generation (age/size rule) produces more members in the different size classes dorsally than ventrally, particularly in the smallest size class. The dorsal spurt in chromatophore genesis at the end of the planktonic phase is so dramatic as to hint at something like metamorphosis. It is as if the skin were waiting for its owner to settle on the sea floor before bringing out the fine-grain dress that is going to serve for the rest of its life, and replace the coarse-grain set of extra-tegumental spots (on the surface of the viscera) that served during the transparent planktonic phase. I have not been able to follow the initial details of this process. It has already begun by the time the earliest benthic stages become available as occasional catches in dredges or on the nets of fishermen. But I have analysed the size-histogram for expanded chromatophores in the anterior third of the dorsal mantle field of the earliest stage available to me : a specimen of 0.25 g body weight (DML 8 mm). All tegumental chromatophores in the area were still immature (i.e. orange or red, not brown or black) and in the same state of expansion. The size spectrum and accumulated totals of successively smaller size categories are shown in Figure 7a & b. The latter curve gives the putative increase in the population of spots with age in this part of the mantle (see Discussion and Conclusions).

As mentioned in the Introduction all the founder chromatophores of the original hatching dress can still be seen during these and later stages. In Plate II there are six, four anterior (resting diameters ~ 100 μm) and a posterior pair (resting diameters ~ 140 μm). The spectrum of sizes of mature (dark) chromatophores, and their red/brown precursors, in a specimen of similar stage has been analysed for an area in the anterior mantle field (Fig. 7c). The histogram has the same shape as Figure 7a and analyses a similar population of spots, but now in the mature (and resting) condition.

Figure 8 shows the typical spatial arrangement and behaviour of mature and immature spots over a 14-day period of development : i.e. during the period of recruitment represented by the left-hand end of the histograms. Although the figure shows less than 0.2 mm^2 of the original skin surface, it illustrates all the main rules of pattern generation given in this paper (see caption). They are rules that apply not only to the dorsal mantle surface but, with modifications of the variables, to all parts of the

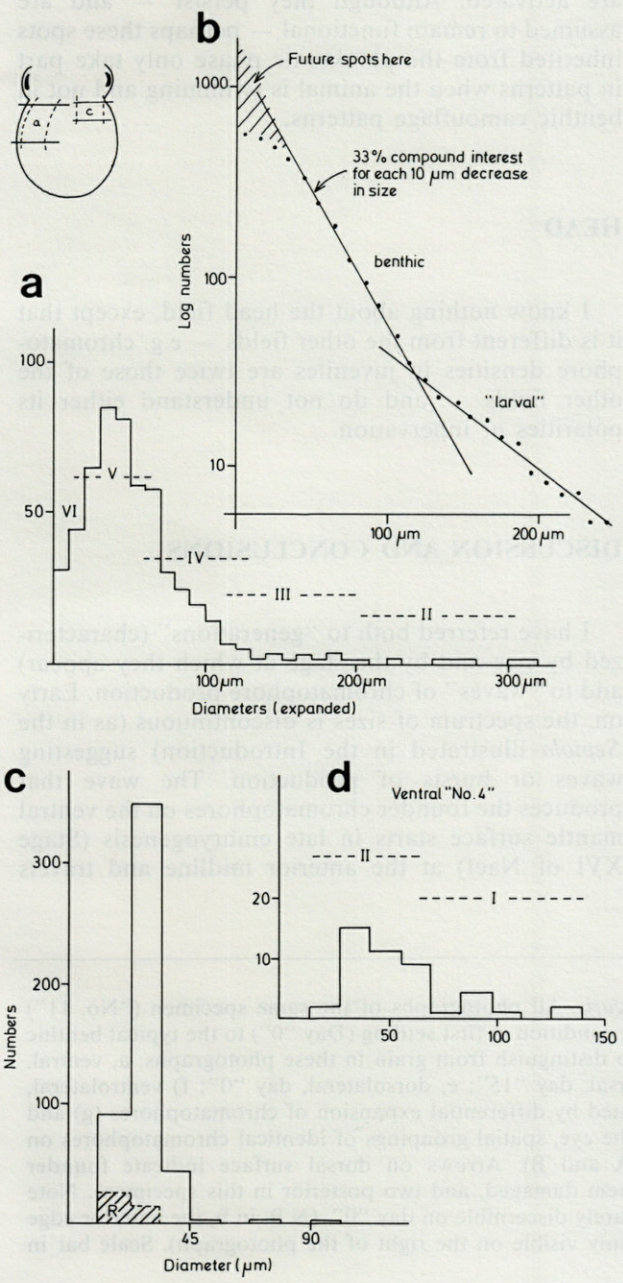


Fig. 7. — a, Spectrum of sizes (expanded state) of all chromatophores in dorsal mantle area (indicated as 'a' in inset) of early benthic *O. vulgaris* (body weight 0.25 g) from photograph. b, Accumulated totals with decreasing size plotted semi-logarithmically (same data as (a)) to show rates of recruitment of chromatophores (as a function of their size) with clear transition between planktonic and benthic phases and area for future recruits. c, Size histogram (resting diameters) of all dark dorsal mantle chromatophores (melanophores and their immediate red precursors R) in area of skin (indicated as 'c' in inset) for later benthic stage (1.2 g body weight) of *O. vulgaris* (from photograph). d, For comparison, histogram of founder and marker chromatophores (generations I and II) of ventral surface of specimen analysed in Fig. 6a.

skin. As far as is known they continue to operate throughout ontogeny (3).

When looking at the array of relaxed or uniformly expanded chromatophores in an area of skin — whether of an octopus or a squid — it is perhaps easier to accept the finding that the smaller chromatophores are the latest (and youngest) arrivals on the scene than to use this knowledge to read the ontogenetic time dimension embedded in the spectrum of sizes that each scene contains. In principle it is possible to do this simply by looking from a distance, or as it were with fuzzy spectacles, and not resolving in the scene chromatophores below a certain size. The lower his resolving power the further back the viewer goes in ontogenetic history. In Plate I f and g, and Plate II, the only individual spots easily resolved on the mantle by the eye at a distance of 1 metre from the photograph are the anterior and posterior pair : i.e. the only tegumental chromatophores present at hatching. At normal reading distance the next generations can be perceived, while the most recent generation require a lens or are apparent only as grain in this reproduction. I have mimicked the "fuzzy spectacles" process (of selected size resolutions) in the analysis given for ventral chromatophores of one of these specimens (Fig. 5). Figure 7 d gives the size-histogram (resting sizes) of the first two generations of ventral chromatophores in this specimen; corresponding early generations of spots in the size-histogram for the dorsal surface (Fig. 7 a, b) are tentatively assigned Roman numerals.

Relation of mantle to other features of patterning

Finally, as chromatophores are part of a larger system consisting of other features (or components) of body patterning (see Packard & Hochberg, 1977) — notably of papillae raised by dermal muscles and of white spot areas underlain by leucophore material — I show the spatial relationship of these to founder chromatophores (arrowed) on the dorsal mantle surface of an early benthic octopus (Fig. 6b). There is also an epigenetic relationship between chromatophores and white spot areas (see Discussion).

It is interesting to note that although papillae can be raised and lowered and chromatophores be switched on and off to produce nervously coordinated body patterns at this stage, in none of my photographs are the founder chromatophores expanded. In Plate II g the specimen figured in this plate is wearing a dark mottle produced by expansion of chromatophores but it is notable that neither the founder chromatophores (anterior and posterior) nor the second generation (marker) chromatophores are activated. Although they persist — and are assumed to remain functional — perhaps these spots inherited from the planktonic phase only take part in patterns when the animal is swimming and not in benthic camouflage patterns.

HEAD

I know nothing about the head field, except that it is different from the other fields — e.g. chromatophore densities in juveniles are twice those of the other fields — and do not understand either its polarities or innervation.

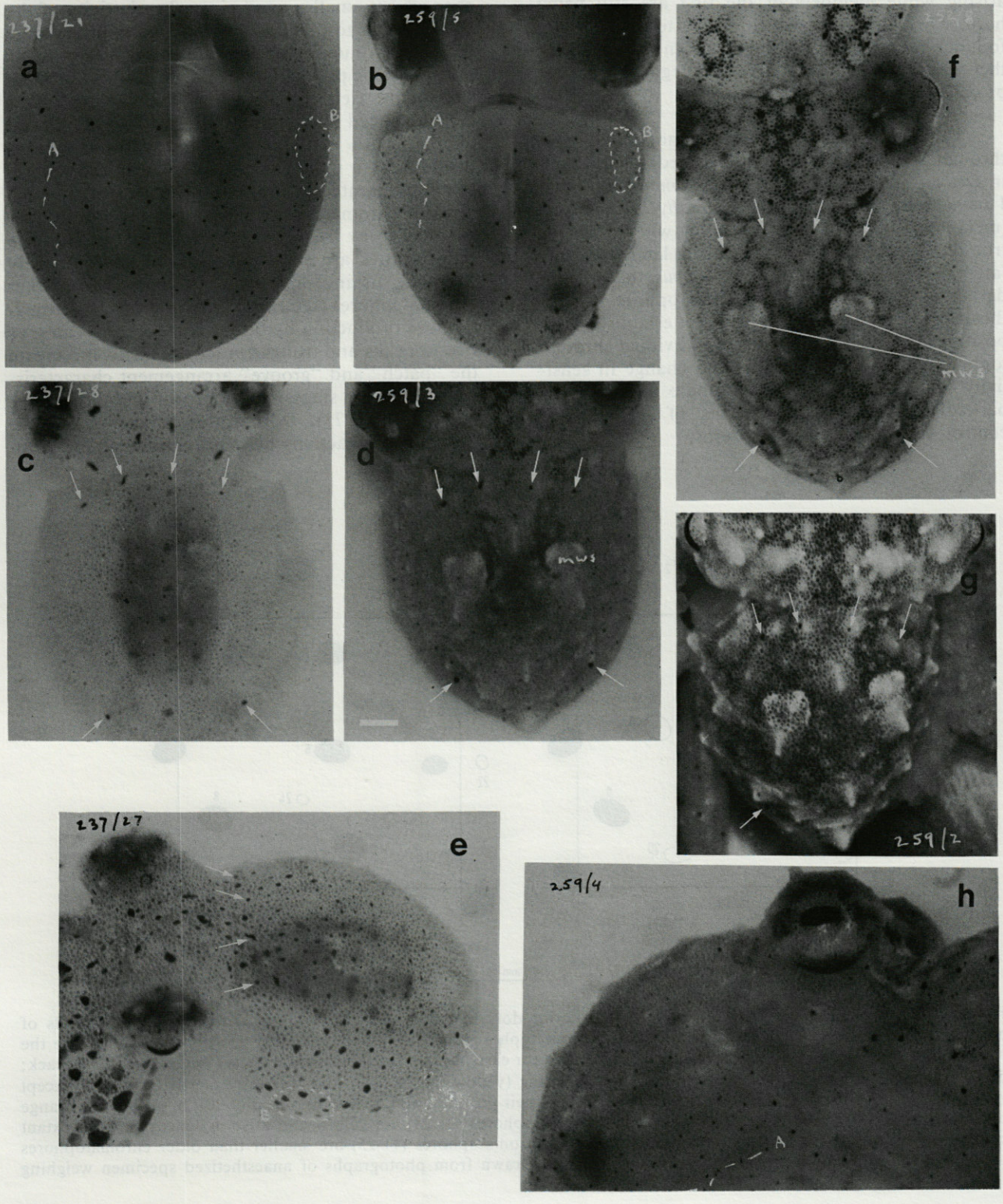
DISCUSSION AND CONCLUSIONS

I have referred both to "generations" (characterized by size and by the stage at which they appear) and to "waves" of chromatophore production. Early on, the spectrum of sizes is discontinuous (as in the *Sepiola* illustrated in the Introduction) suggesting waves or bursts of production. The wave that produces the founder chromatophores on the ventral mantle surface starts in late embryogenesis (Stage XVI of Naef) at the anterior midline and travels

(3) An additional rule, bearing on the pharmacological and physiological properties of chromatophores, is illustrated on the left (Day 1) of Figure 8, namely that young (yellow) chromatophores have different sensitivity to anaesthetics than older (dark) chromatophores. Yellow spots are not relaxed (their muscles are contracted), while other spots are in the resting condition (muscles relaxed).

Plate II. — Pattern differentiation in early benthic *Octopus vulgaris*. All photographs of the same specimen ("No. 11") showing developmental changes in mantle dress from transparent condition at first settling (Day "0") to the typical benthic condition two weeks later. Youngest chromatophores difficult to distinguish from grain in these photographs. a, ventral, day "0"; b, ventral, day "15"; c) dorsal, day "0"; d and g, dorsal, day "15"; e, dorsolateral, day "0"; f) ventrolateral, day "11". Also shown, examples of physiological pattern generated by differential expansion of chromatophores (g) and (h) and by papilla-raising before anaesthetic has acted. To aid the eye, spatial groupings of identical chromatophores on ventral and dorsal surfaces are ringed or linked by lines (A and B). Arrows on dorsal surface indicate founder chromatophores or original hatching dress (4 anterior, one of them damaged, and two posterior in this specimen). Note the differentiation of the mantle white spots (m.w.s.) which are barely discernible on day "0". (N.B. in b, the anterior edge of the ventral mantle is withdrawn into the mantle cavity and only visible on the right of the photograph). Scale bar in d = 1 mm.

outwards and backwards. It continues after hatching so that many of the chromatophores that result from it arise laterally and posteriorly during planktonic life spreading up on to the dorsal surface. The later spots are smaller than those arising near the centre of pattern generation — as if the power of the wave were subsiding — but since they have the same characteristic spacing (nearest neighbour distances) as the earlier spots I place them in the same size-frequency envelope as the rest of the ventral



founder series. The generation that follows, arising between them, has characteristically different spacing and size. Similar considerations apply to the arms where the wave starts in the middle of the aboral surface proximally and spreads distally and laterally onto the oral surface of each arm. As in other kinds of populations, the waves or (generations) may overlap in time, with a new generation arising while members of the first are still being born. On the arms, which grow terminally, the founder series is still being laid down distally when the next generation has already begun to appear proximally.

All dark chromatophores (melanophores) pass through a pale (yellow or orange/red) phase. And in *Octopus all yellow and orange chromatophores* that I have followed from birth *eventually become dark* (melanophores). But I do not know whether this is true of squids, or of *Octopus* during later ontogeny (after 50 g body weight). In *Octopus* the *rate* of darkening varies from one chromatophore to another, depending in some way not yet established, on position. The change in colour of individual chromatophores with age (and associated change in sensitivity to anaesthetics, see footnote 3 above) is particularly interesting in terms of the nervous control of chromatophore patterns.

Obviously the skin expands in size and changes shape during ontogeny — and I have attempted to show the effect of this on the placing of spots between hatching and early benthic stages in Figure 5 a and b — but I have not followed changes in size and shape of the fields in any detail for the simple reason that during the days or weeks of early benthic life with which this paper is concerned these changes are small — and given the elasticity of the skin difficult to observe — compared with the large increases in number and absolute densities of spots over the same period. On the dorsal surface, subdivision of the fields begins soon after settling and is well advanced by the time 1.0 g body weight (dorsal mantle length 13 mm) is reached. Subdivision takes the form of a number of circular areas each representing separate pattern-generating centres in which rates of chromatophore production are locally higher than away from the centres. At first appearance these centres are empty and spaced approximately the same distance apart as the founder and marker chromatophores (see Figures). Variations in chromatophore production by only a few per cent can give rise to peaks and troughs in local density and create the "patch" and "groove" arrangement characteristic of all later stages (see Plate I a and Froesch & Messenger, 1978). During this process there are evidently interactions between chromatophore pro-

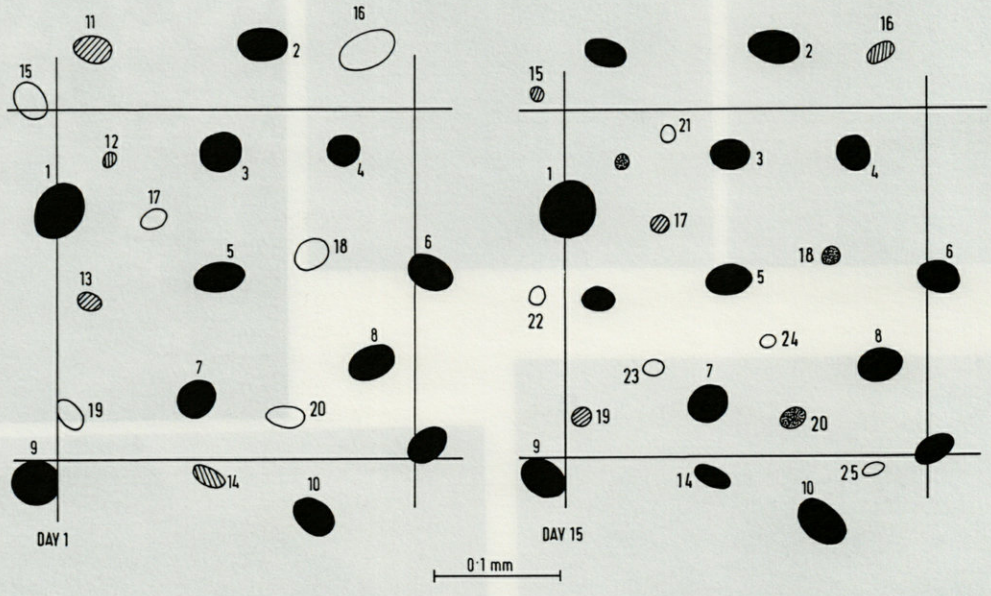


Fig. 8. — Genesis of chromatophore pattern in anterior dorsal mantle surface of young *Octopus vulgaris*. Details of positions, shapes, sizes, and colour of individual chromatophores on Day 1 (left) and Day 15 (right) that illustrate the rules of *pattern generation* in this species. Spots numbered for ease of identification; mature spots ("melanophores") black; depth of pigmentation of other spots indicated by shading (yellow, unshaded); all spots in retracted condition (except yellow on Day 1). Rules : a, extant chromatophores retain their positions and do not disappear (1-20); b, yellow and orange chromatophores darken with age (11-20); c, new chromatophores (21-25) are yellow and arise in spaces between extant chromatophores (non-random distribution); d, younger chromatophores (11-25) are smaller than older chromatophores (1-10) and the population forms an age/size hierarchy. (Drawn from photographs of anaesthetized specimen weighing 1.4 g).

duction and other pattern-giving elements, particularly iridocytes and leucophores. In the earliest benthic stages I have studied (0.25 g body weight), the Anlagen of the white spots appear as clusters of iridocytes. One of these, which will form the mantle white spot, is just visible as a crescent of iridocytes that will later be followed by leucophore material as the white spot enlarges backwards (compare also Plate II c with Plate II d and f). Rates of chromatophore production in the tissue overlying these and other white spots are lower than in the area immediately in front of the crescent (resulting in local densities twice as high on the proximal side of the boundary as on the distal). Chromatophore genesis is being locally inhibited either by leucophores or by the morphogens that induce white spot development.

It needs emphasising that all the main findings in this paper come from the practice of following single individuals : individual chromatophores in individual animals. The value of this as a technique can not be overstressed. It is the classical comparative method in which the individual serves as the base of comparison with itself at another stage. The amount of fine-tuned information available in a pair of pictures of even a small area of skin — so long as they are of the *same* area at different points in ontogeny — is illustrated in Figure 8. What I have called "Rules" are derived from observation. During the process of comparison the eye makes predictions none of which have been falsified in hundreds of hours of analysis of such pairs of photographs. The only chromatophores that I have ever seen disappear during ontogeny are occasional damaged ones (broken or oddly shaped).

Having established that, in any one part of the skin, successive generations of chromatophores have smaller resting diameters than their predecessors and are pale when they first arise, it is no longer strictly necessary to take a second photograph at a later stage to predict earlier states of the skin. A single photograph will do.

The general interpretation of the size-frequency histograms that can be constructed from a photograph is shown in Fig. 9. The slope and position of the curve of accumulative totals should be species-specific so long as original dimensions are preserved.

Whether systematists and seagoing and field biologists will learn to use the potential information about the developmental history of an individual embedded in a single photograph of its skin will depend on whether they are prepared to anaesthetize and photograph a specimen *before* fixing. Once captured on film, the information does not decay.

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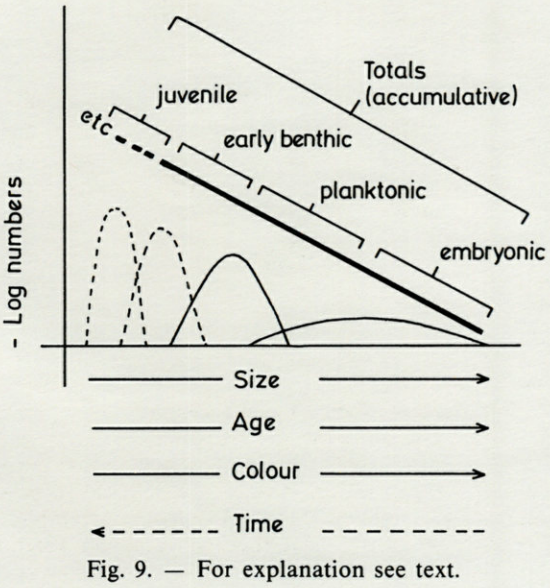

Fig. 9. — For explanation see text.

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APPENDIX I

C.I.A.C.

Cephalopod International Advisory Council

Executive Secretary : Dr Malcolm R. Clarke FRS

Founded in September 1983 C.I.A.C. consists of nine executive members and nine alternate or substitute members. The rules of election and length of service are designed to ensure a progressive evolution of membership to reflect trends in living cephalopod research while retaining a stability in the general aims of the founding council. Membership will respresent broad international interests and all aspects of cephalopod research except squid giant axon research and palaeontology.

The present council includes members from Australia, Canada, England, France, Japan, South Africa, Spain and the U.S.A. whose research interests include systematics, ecology, behaviour, embryology, parasitology, physiology, culture, capture and fisheries.

Background

Research effort. There are probably less than 50 established "full time" cephalopod researchers (excluding giant fibre physiologists and palaeontologists). Two continents each only contain one such specialist !

The *importance* of cephalopods to man is increasing in several directions. Their proportion in world fisheries has increased over several decades although their inclusion in fisheries statistics as "shellfish", "molluscs" or "by-catch" partly obscures this increase. Their potential as food is very considerable. They have an increasingly recognised value as experimental animals for fundamental research in cell, sensory, neurophysiological, pharmacological and behavioural processes.

They are now known to be extremely important in oceanic and shallow sea food webs.

Their study is extending our knowledge of the physiological alternatives open to marine animals in such things as locomotion, buoyancy, camouflage and perception.

Aims of C.I.A.C.

These are to stimulate, speed up and influence the direction of cephalopod research, to provide help and advice on aspects of cephalopod biology and to spread information on past and current research.

Methods to be adopted

To fulfill the aims of C.I.A.C. it is proposed that :

1. Workshops involving the examination of data and material should be held every second year starting in 1985.
2. Handbooks including the results of every workshop will be published.
3. Training courses will be given, e.g. on the identification of beaks (for predator specialists) and an introduction to cephalopods for fisheries biologists (including identification, anatomy; measurements, age determination, etc.).
4. Advice and help will be provided by consultants in any particular field or geographic region.
5. A computational bibliography with a multiple retrieval system will be produced.
6. A self-financing newsletter on living cephalopods will be produced.
7. Translation available will be listed and C.I.A.C. will actively seek translations of key works and will collect a small library of rare or key works.
8. Research will be stimulated by publishing or circulating "state of the art" or "position" papers in currently important areas of research.

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APPENDIX II

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Symposium, Banyuls, 29-30 June 1985

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VIE ET MILIEU : Volume 35

TABLE DES MATIÈRES — *TABLE OF CONTENTS*

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INSTRUCTIONS AUX AUTEURS

TEXTE

Les manuscrits, dactylographiés en double interligne sur le recto seulement des feuilles numérotées (ne pas excéder 20 pages) sont présentés en trois jeux complets, sous leur forme définitive.

Le titre du manuscrit doit être le plus court possible; il est suivi du prénom et du nom de l'auteur (ou de chacun des auteurs) ainsi que de l'adresse (ou des adresses) du Laboratoire dans lequel a été effectué le travail.

Chaque manuscrit comportera :

— un résumé en français de 15 lignes maximum figurant en début d'article, suivi de sa traduction en anglais,
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— un titre abrégé pour haut de page (60 signes et espaces au plus),
— la traduction anglaise du titre de l'article,
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Les noms scientifiques (genres, espèces, sous-espèces) figurent en italiques ou soulignés d'un seul trait.

Les références bibliographiques des auteurs cités dans le texte sont regroupées à la fin du manuscrit dans l'ordre alphabétique des noms d'auteurs; elles doivent être conformes aux modèles suivants :

GRIFFITHS C.L. and J.A. KING, 1979. Some relationships between size, food availability and energy balance in the Ribbed Mussel *Aulacomya ater. Mar. Biol,* **51** (2) : 141-150.

EAGLE R.A. and P.A. HARDIMAN, 1977. Some observations on the relative Abundance of species in a benthic community. *In* Biology of Benthic Organisms. Edited by B.F. Keegan, P.O. Ceidigh and P.J.S. Boaden, Pergamon Press, Oxford-New York, 197-208.

Le titre des périodiques doit être abrégé d'après les règles internationales (World list of Scientific Periodicals).

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ILLUSTRATIONS

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La revue publie gratuitement 2 planches au trait pleine page et 1 seule planche en simili; les illustrations supplémentaires ou en couleurs sont facturées aux auteurs.

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INSTRUCTIONS TO AUTHORS

TEXT

The manuscript should by typed double-spaced on one side of white paper, format A4, pages numbered (max, 20 pp), and sent in definitive form, in triplicate, to the editor.

The title of the paper should be as concise as possible; it is followed by the first and second name of the author(s) and address of the laboratory at which the work was done. Each manuscript should include :

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Line drawings should be prepared with India ink on heavy tracing paper, bristol board, white drawing-cardboard or graph paper (blue grid). Letters and numbers on figures should be large enough to be easily readable after reduction; use letter transfer equipment, preferably Futura characters. As far as possible, figures should be grouped in plates of 17 × 24.35 cm final size (generally the explanations are included in this frame); the width of a single column is 8.1 cm. Prepare figures using the "homologous rectangles" rule; indicate the number of the figure and the author's name with blue pencil on the back of the figure. Do not write explanations on the figure.

Photographs and half-tone drawings must always be grouped as plates. Scale bars are reduced with the figures. Number plates and tables in roman numbers on the back. Limit total number of tables to an absolute minimum of items indispensable for clear presentation.

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VIE ET MILIEU, 1985, 35 (3/4)

BIOLOGY AND DISTRIBUTION OF EARLY JUVENILE CEPHALOPODS

edited by K. MANGOLD and S.v. BOLETZKY

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