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To cite this version:

R F Harman, R E Young. THE LARVAE OF OMMASTREPHID SQUIDS (CEPHALOPODA, TEUTHOIDEA) FROM HAWAIIAN WATERS. Vie et Milieu / Life & Environment, 1985, pp.211- 222. hal-03022113

HAL Id: hal-03022113 <https://hal.sorbonne-universite.fr/hal-03022113v1>

Submitted on 24 Nov 2020

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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 fïeld 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 océan. 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 ai,* 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 resuit 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 différent 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. peîagica,* which reaches about 85 mm ML in thèse 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 dise bearing eight suckers. As the squid grows, the proboscis divides from the base, until the tentacles are separate and the suckers of the terminal dise (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. Ail of the stations occupied lay within the study area defined in Figure l, which was 11-20 km off the Waianae coast of Oahu (approximately 21° 15' N \times

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

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.

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 électron 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 différences in beak dentition. Différences 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-m² 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 ail 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 intervais 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. Ail were taken with the open 4-m² 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 différent 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

Table I. $-$ Total volume of water sampled $(x 1000 m^3)$ **by depth during vertical distribution séries.**

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				

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.

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 spécimens with non-dividing probosces. Bars are 95 % confidence limits. Asterisk dénotes significant différence from others in the size class.

Plate I. **—** Scanning électron 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* $(1.8 \text{ mm} \text{ ML})$, scale bar = 0.05 mm .

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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.

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

2. Proboscis suckers (Plate I, B) : latéral 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; complète 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 m³) and lowest abundance in October (mean = $0.02/1000$ m³) (Fig. 4). All of the captures in the October vertical distribution séries 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; complète by 6.5 mm ML.

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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 welldeveloped 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 $= 0.26/1000 \text{ m}^3$) and lowest abundance in August (mean $= 0.04/1000$ m³) (Fig. 4). During October at night, most of thèse 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) : latéral 2 suckers nearly equal in size to medial 6 (mean ratio : 1.19 \pm 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 spécimens).

3. Proboscis division (Fig. 3) : begins about 3.0-5.0 mm ML; complète 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 = $0.96/1000$ m³) and lowest abundance in October (mean = $0.27/1000$ m³) (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 séries. 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 négative tows. B, Vertical distribution of *Hyaloteuthis pelagica,* October séries. Dots represent catch rates at modal depth for positive tows and histograms represent mean catch rates.

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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 différent from the mean ratio. However, between species, the means of this ratio were ail signifîcantly différent.

On the outer chitinous sucker rings, the mean number of knobs in both the middle and inner whorls were signifîcantly différent between N. *hawaiiensis* and the other two species. There was no statistical différence between the mean number of knobs of *S. oualaniensis* and *H. pelagica.* Within a species, no significant différence 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 signifîcantly shorter than those of the other two species, which were not statistically différent from each other. In the 2.0-2.99 mm ML size class, there were no significant différences among the three species. In the 3.0-4.0 mm ML size class, the mean probosces length of S. *oualaniensis* was signifîcantly 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 complète until about 8.5-9.0 mm ML, although the results are not complète for *Nototodarus.*

The chromatophore patterns on the mantle, which are valuable systematic characters for other groups of squids (e.g., McConathy *et ai,* 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 ail 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 différences 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 HA-WAIIAN WATERS

- la. Mantle length < 4 mm 2
- lb. 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 \ldots 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 complète by 9.0 mm ML *Sthenoteuthis oualaniensis*

Although large *Ommastrephes bartrami* are occasionally seen in waters near the main Hawaiian Islands, they are probably expatriâtes. 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 différences 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 ail 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 ail 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 différence 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 signifîcantly. 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.

ACKNOWLEDGMENTS **—** We thank the officers and crews of the R/V KANA KEOKI and the R/V KILA, as well as the many volunteers for their willing and able assistance during cruises. S. Ash, M. Inouye, G. Kubota, A. LeClaire and L. Yasukochi deserve special thanks for their assistance in sorting a large volume of plankton. This material is based on research supported in part by the National Science Foundation under grant numbers OCE 82-07754 and OCE 85-00664 to R.E.Y.

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Reçu le 26 août 1985; received August 26, 1985 Accept le 2 novembre 1985; accepted November 2, 1985