

1995

The Early Life Histories of Three Families of Cephalopods (Order Teuthoidea) and an Examination of the Concept of a Paralarva

Elizabeth Keane Shea

College of William and Mary - Virginia Institute of Marine Science

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<https://dx.doi.org/doi:10.25773/v5-1wxh-6552>

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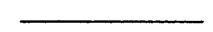
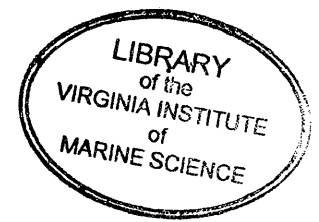
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THE EARLY LIFE HISTORIES OF THREE FAMILIES OF CEPHALOPODS
(ORDER TEUTHOIDEA) AND AN EXAMINATION OF THE CONCEPT OF A
PARALARVA



A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts




by
Elizabeth K. Shea
1995

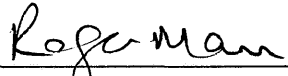
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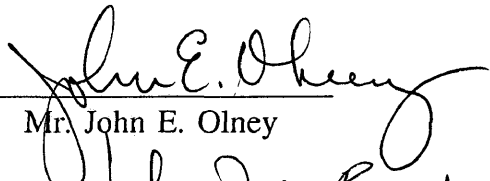
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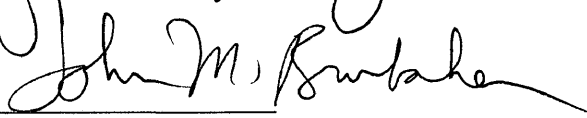
Elizabeth K. Shea

Approved, July 1995


Dr. Michael Vecchione
Committee Co-Chairman/Advisor


Dr. Roger L. Mann
Committee Co-Chairman/Advisor


Mr. John E. Olney


Dr. John M. Brubaker


Dr. Mark R. Patterson

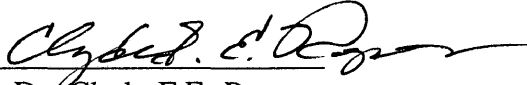

Dr. Clyde F.E. Roper
Smithsonian Institution
Washington D.C.

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ACKNOWLEDGMENTS

I very gratefully acknowledge and appreciate the constant support, guidance, and encouragement of my major professor, Dr. Michael Vecchione, during this research project. Identification of species, selection of methodologies and interpretation of results would have been impossible without his willingness to put down his own work and help me with mine. He is also a valued friend.

I would like to thank the other members of my Advisory Committee for their willingness to dive into a topic that was so far afield of their own interests, and for their patience with an absentee student. In particular, my thanks to John Olney, who was not only generous with his time and support, but also welcomed a fledgling squid researcher into his fish lab.

I would especially like to thank Dr. Clyde Roper for introducing me to the wonderful world of cephalopods, and for his continued support and direction over the last seven years. The Smithsonian "Squid Squad", in particular, Mike Sweeney, has been extremely helpful in allowing me access to the collection and in giving me work space during the waning phases of this thesis.

No acknowledgment section would be complete without thanking friends and family. Thank you for the long talks (SCIENCE!!), the parties, trips to the pub, lunchtime retreats, and marathon shopping trips. I have never had such good friends as those I found at VIMS. Mom and Dad, I know you think I'm crazy, but thank you for supporting me anyway. And finally, to Dennis. Thank you for always being there to listen, commiserate, and advise—you're the greatest!

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ABSTRACT

Controversy over the validity of describing newly-hatched cephalopods as "larvae" prompted the introduction of the term "paralarva" to describe the post hatching phase of life. This thesis examines the concept of a paralarva and describes the end of the paralarva stage for three families of squid (Cephalopoda: Teuthoidea: Oegopsida).

Specimens (n=2860) from the Amsterdam Mid North Atlantic Plankton Expedition (1980-1983) were examined and identified to family. Families were selected for further examination that were expected to exhibit gradual (Ctenopterygidae), moderate (Mastigoteuthidae) and radical (Brachioteuthidae) ontogenic changes in morphology.

Daytime and nighttime vertical distributions were used as an indicator of ontogenic change as required by the definition of a paralarva. Depth of capture for *Ctenopteryx sicula* increases gradually with increased dorsal mantle length (DML) during the day (ontogenic descent); all nighttime captures were in the upper 300m, regardless of size. All *Mastigoteuthis agassizii* specimens were caught >500m in day and night, regardless of size. All *Idioteuthis magna* were vertically spread between 0-1000m during the day, but in the upper 300m at night, regardless of size. *Brachioteuthis sp. 3* daytime distributions could not be accurately described because of malfunctioning collecting equipment; nighttime distributions were spread over the upper 300m. *Brachioteuthis sp. 4* captures were spread throughout the water column during both day and night.

Changes in the growth trajectories were found in all species; in some species, these growth discontinuities coincide with the onset of vertical migration. An inflection point in the growth trajectory describing the mantle opening width (MOW) and the fin length (FL) of *Ctenopteryx sicula* was found at 10-12mm DML; this size marks the beginning of ontogenetic descent. The MOW, FL, fin width (FW) and eye diameter (ED) of *Idioteuthis magna* changed at 6-7mm DML, which is the size at which night captured specimens are first found at depths greater than 100m. The head width (HW), head length (HL) and ED growth trajectories of *Mastigoteuthis agassizii* changed at 11mm DML; no concomitant change in day/night depth of capture was noted. The FL and FW of *Brachioteuthis sp. 3* changed at 15-18mm DML and again at 30mm DML, the funnel and head dimensions changed at 30mm DML; malfunctioning equipment precluded any observations as to the onset of diel vertical migration (DVM). Finally, the arm length (AL) tentacle length (TL), FL, FW, and MOW of *Brachioteuthis sp. 4* changed at 20-22mm DML with no concomitant change in day/night depth of capture.

The definition of a paralarva is broadened, and thus becomes applicable to species within the Teuthoidea, Octopoda and Sepioidea. The proposed definition is, "a cephalopod of the first post-hatching phase of life that has a distinctly different mode of life from that of older, conspecific individuals". The paralarva phase ends at the assumption of the adult niche (the end of the niche shift); concomitant changes in the growth trajectory are expected but not required and should not be relied upon to describe the paralarva phase of life in the absence of ecological data.

A generalized description of the early life history of cephalopods is proposed. A two stage paralarval phase, a two stage juvenile phase and a single stage adult phase of life is recognized, and both ecological and morphological indicators are required. Stage 1 of the paralarva phase (P1) begins at hatching and lasts until the beginning of the niche shift; stage 2 (P2) begins at the onset of the niche shift and lasts until the end of the niche shift. Stage 1 of the juvenile phase (J1) begins at the assumption of the full expression of adult ecology or behavior, and ends at when all adult morphological characters, *except mature gonads*, are present; stage 2 (J2) begins when all adult morphological characters are recognizable, and ends at the onset of gonad maturity. The adult phase begins at the time of reproductive organ maturation and ends at death.

Based on this new description, the P1 phase of *C. sicula* ends at 10mm DML, the size at which the first specimen is captured in daytime deeper than 100m; the P2 phase of *C. sicula* phase ends at 18.5mm DML with the onset of full adult diel vertical migration (DVM). The P2 stage of *I. magna* begins at 7mm DML with the first nighttime catch deeper than 100m. The paralarva stage of the remaining species could not be defined based on DVM, and results of multidimensional scaling did not provide good evidence for other potential ecological characteristics of importance.

In addition, changes in the number of rows of suckers on arms 1-3 in the Chtenopterygidae, in the eye position in the Mastigoteuthidae, and in the eye and internal organ position of Brachioteuthidae can be used to quickly and easily distinguish between the paralarval and juvenile phases of the life cycle.

"PARALARVA" IN THREE FAMILIES OF OEGOPSID CEPHALOPODS

INTRODUCTION

Life cycle research encompasses many seemingly disparate topics of study. Scientists who study distribution patterns, growth, energetics and diet all add pieces to the life cycle puzzle. But even with all these bits of merging information, the complete life cycles of most cephalopods remain a mystery. Although life cycle research has received increased attention in recent years, most of the emphasis has been on juveniles and adults. Only in the last 15 years have the early life histories have begun to be explored by many investigators. There are several reasons for this, including difficulties in identification, taxonomic confusion of newly-hatched and adult cephalopods, and disagreements over the terminology of life history stages. Early life histories are best known for commercially important species such as *Loligo pealei* (Haefner 1964, McConathy et al. 1980, Yang et al. 1980, Vecchione 1981) and *Illex illecebrosus* (Hatanaka 1986, Roper and Lu 1979, Vecchione 1979), which are found in relatively near-shore plankton samples; however, knowledge of even the most commonly investigated species contains large gaps. For example, the early stages of *Illex illecebrosus* have been described from the Middle Atlantic Bight (Roper and Lu 1979, Vecchione 1979), but the spatio-temporal details of spawning are unknown (Vecchione, pers. comm.). The tremendous gaps in knowledge of young cephalopods are outlined in an

extensive chapter on juvenile ecology (Vecchione 1987) in the second volume of Cephalopod Life Cycles (Boyle 1987). This work presents the most comprehensive review of literature on early life history published since the 1960s. Pre-1965 literature on early life history is summarized in detail by several authors including Clarke (1966) and Roper and Young (1975).

Identification and Taxonomy of Newly-hatched Cephalopods

In the mid-1980's, the Cephalopod International Advisory Council organized a workshop and symposium (CIAC-85) specifically to present new information on newly-hatched cephalopods and to focus attention on the problems of working with these small specimens. Several issues were emphasized that remain stumbling blocks to future life cycle research. The first impediment is the delicate nature of the tiny organisms. Specimens are easily damaged or ruined by nets or improper preservation. Often, the characters that are used to discriminate among species, genera, and families are those that are most easily damaged (tentacles, clubs, fins, skin, chromatophores). This problem will be solved only with improved collection devices and preservation techniques.

In cases where all diagnostic characteristics are intact, the researcher faces a second problem. Newly-hatched specimens have been historically identified based on the morphological characteristics of the adults. The considerable

taxonomic disorder of the adults (Roper 1983) is a hindrance to identification. When the adult identification is questionable, the newly-hatched specimen can not be identified with confidence.

Working with young cephalopods can also present several unique taxonomic problems. For many families, the young look similar to their adult counterparts, differing in the relative sizes of body parts and the development of features such as photophores and hooks (e.g., Enoploteuthidae, Onychoteuthidae); however, the adult and young of some families have more extreme differences in their morphology (e.g., Chiroteuthidae). These differences have led to several inappropriate generic designations by early authors. One very conspicuous example can be found in the family Ommastrephidae. Newly-hatched ommastrephids are easily identified by the fusion of their tentacles into a "proboscis". As the animal grows, the tentacles separate (Vecchione 1979). Although Chun (1903) suspected the specimens he assigned to the genus *Rhynchoteuthis* (subsequently changed to *Rhynchoteuthion* by Pfeffer (1908) because the generic name was preoccupied) were actually newly-hatched Ommastrephidae, he maintained the name (Chun 1910). Similar problems have been found with post hatching specimens of the family Chiroteuthidae. Newly-hatched *Chiroteuthis* are very distinctive, characterized by an elongate neck and brachial pillar not found in the adult (Young 1991). These newly-hatched cephalopods were placed in a separate genus (*Doratopsis*)

even after evidence was presented that they were young forms of *Chiroteuthis* (see Young 1991 for full discussion). Now they are known to be an early stage (the doratopsis stage), which is characteristic of the Chiroteuthidae. Young (1991) described the post-hatching, planktonic stages of the family Chiroteuthidae from Hawaiian waters, and redefined the family based on characteristics of the young.

Papers presented at CIAC-85 were published in a special volume of *Vie et Milieu: The Biology and Distribution of Early Juvenile Cephalopods* (*Vie et Milieu* 35(3-4) 1985). A second major publication from this workshop was Sweeney et al. (1992) which included a key for identification of newly-hatched cephalopods. Prior to the compilation of this key, researchers depended upon their individual knowledge of adult morphology to identify hatchlings and early juveniles. Whereas Sweeney et al. (1992) presented a comprehensive summary for many of the early life forms, problem areas still exist. There are many genera for which the newly-hatched specimens still have not been described (e.g., *Architeuthis*, *Neoteuthis*, *Lycoteuthis*, *Joubiniteuthis*) or have been described based on only a few specimens (Sweeney et al. 1992).

One of the most heated controversies that arose during CIAC-85 was the debate over the validity of the existence of a larval stage during cephalopod development. According to Geigy and Portmann's definition (1941), a larva

undergoes metamorphosis when larval parts are lost and adult parts form from embryonic rudiments. Based on this definition, Boletzky (1974a) argued that newly-hatched squids and octopods differed from the adults only in morphometrics, and therefore the term "larva" was not appropriate. In contrast, Nesis (1979) focused on the similarities between fish and cephalopod development, and considered metamorphosis to be an abrupt change in growth coefficients.

These debates led Young and Harman (1988) to introduce the term "paralarvae" (para-, Greek meaning closely resembling, or almost) to describe the planktonic young of cephalopods. They defined a paralarva as, "a cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctly different mode of life from that of older conspecific individuals". Thus, the inclusion of behavioral and ecological criteria uniquely defines a paralarval cephalopod. Young and Harman (1988) further stipulate that the subadult stage begins with the full attainment of morphological features used to define the species. This definition renders the juvenile as the life stage prior to the subadult stage, meaning that some juveniles may be called paralarvae. The adult stage is marked by the attainment of sexual maturity, a condition that may not occur in some cephalopods until extremely late in the life cycle.

Ecology of Newly-Hatched Cephalopods

Two types of distributions must be considered when discussing the ecology of cephalopods: geographic (or horizontal), and bathymetric (or vertical). Many neritic species are known to undergo extensive latitudinal and longitudinal migrations (e.g., *Illex illecebrosus*, *Todarodes sagittatus*). Vertical distributions are less well known. In fact, it was not until the 1960s and the advent of opening and closing nets that cephalopod vertical distributions could be accurately described (Clarke 1966). Roper and Young (1975) investigated the vertical migrations of adult cephalopods, but the newly-hatched cephalopods were not included in the analysis because, "the larvae of most species of pelagic cephalopods occur in the near-surface waters both during the day and night and as such do not demonstrate the same distributional patterns as their juvenile and adult forms (p.2)."

Vertical and geographical distribution of newly-hatched cephalopods must be pieced together from a variety of historical and recent documents; no review of the topic has ever been attempted. Distribution patterns for the most well known species show considerable variability, but some within-species generalizations of ranges can be made. For example, *I. illecebrosus* ranges from central Florida to Newfoundland (Lu 1973, Roper and Lu 1979) but the young seem to be most abundant in the northern Gulf Stream or Slope Water (Dawe and Beck 1985; Vecchione and Roper 1986). In the Middle Atlantic Bight, young

Loligo pealei generally are confined within the coastal boundary layer (Vecchione 1981). The distribution of the young loliginid *Lolliguncula brevis*, the only euryhaline species of cephalopod, is described in the Middle Atlantic Bight in a brief note on the northern limit of the species range (Vecchione 1982) and in a paper on the ecology of the young in the Gulf of Mexico (Vecchione 1991a).

Currently, very few papers describe the distributions of young squid that are not commercially important. Commercially important squid, such as the Loliginidae and Ommastrephidae, are found close to the continental margins. Squids from the open ocean are much more difficult to capture and for this reason, many potentially harvestable species remain unexploited. If fishing techniques evolve to permit easy, selective capture of these open ocean squid, it has been predicted that some families (for example, Gonatidae) may become commercially important food sources. Several papers from CIAC-85 as well as several papers resulting from the 1991 AMU/CIAC symposium in memory of Dr. Gilbert L. Voss, addressed these frequently neglected families. The newly-hatched enoploteuthid (Young and Harman 1985), and brachioteuthid (Young et al. 1985) distributions in Hawaiian waters were described, as were the Antarctic distribution of young cranchiids (Rodhouse and Clarke 1985) the world-wide distribution of young Octopoteuthidae (Stephen 1985), the Enoploteuthidae (*Abralia*: Burgess 1991) multiple families (Piatkowski and Welsch 1991, Nesis 1991) These families merit increased attention as they are abundant in the

worlds oceans and are important components of the oceanic food web (Clarke 1977, Rodhouse et al. 1992).

In addition to zoogeography, laboratory experiments on the growth and energetics of early stages of octopods and neritic squids are beginning to advance. Rearing squid through the life cycle has proven to be extremely difficult, and most studies have been descriptive rather than experimental (Forsythe and Van Heukelem 1987). Only recently have eggs and young been reared to sub-adult or adult specimens (see reviews in Boletzky and Hanlon 1983, Yang et al. 1986, Hanlon 1987). The culture of cuttlefishes and octopods with large eggs, however, has been more successful. For example, laboratory rearing of *Sepia officinalis* and *Octopus joubini* has been conducted since the late 1960s and 1970s, respectively. Richard (1966, 1975) pioneered work on comparative growth rates of juvenile *Sepia* raised in the laboratory at several different temperatures. Many of the near shore, commercially important species have been studied, and their growth is well described (Forsythe and Van Heukelem 1987); however, most studies have concentrated on changes in the overall size of the organism (DML or weight) with little attention paid to other characteristics. In general, these studies have concluded that newly-hatched cephalopods grow exponentially over the first 1-2 months of the life cycle (Teuthoidea: *Loligo opalescence* Yang et. al 1986; *Abralia trigonura* Bigelow 1992; Octopoda: *Octopus maya* Van Heukelem 1977; Multiple species Forsythe and Van

Heukelem 1987). Because these results are based on either DML or weight measurements, they do not provide much detail about the life history of the species. Perfecting these rearing techniques and modifying them for other species will allow future researchers additional insights into early life cycles. Until that time, collected samples and the associated station data must be used to infer ecological regimes and habits.

Thesis Problem

This thesis examines the early life history of five species (three families) of Oegopsid cephalopods. The utility of the concept of a "paralarva" as defined by Young and Harman (1988) is examined, and the end point of the paralarval stage is described. A revised definition of a paralarva is proposed and the paralarva phase of each family is redescribed.

Species-specific ontogenetic changes in morphology and ecology (diel vertical migration, DVM) are examined. Diel vertical migration was selected because a daytime v. nighttime difference in habitat is an intricate part of Young and Harman's 1988 definition. The onset of DVM is an indication of ontogenetic change because newly-hatched squids are not known to undergo vertical migrations and adults of many species are renowned for this behavior. Simple

morphological markers that may provide visual concordance with the end of the paralarval phase of the life cycle are examined.

MATERIALS AND METHODS

MATERIALS¹

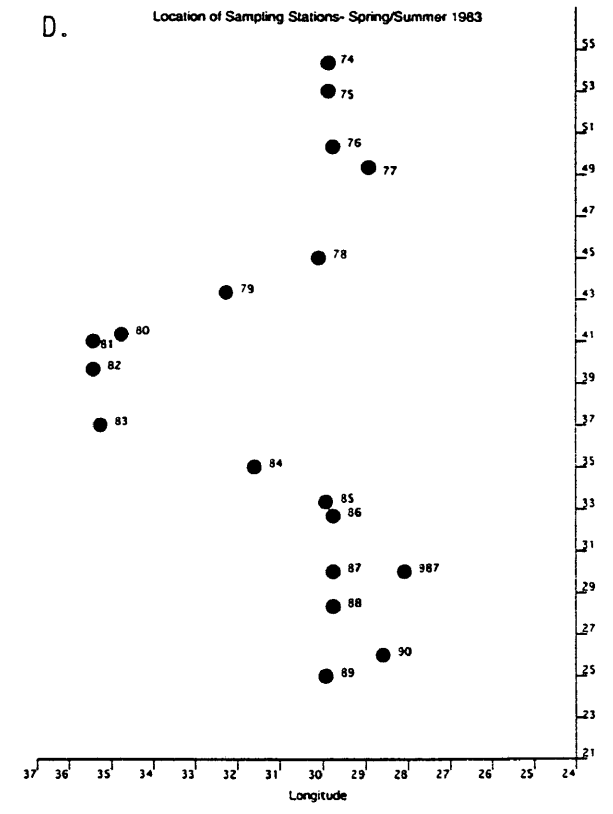
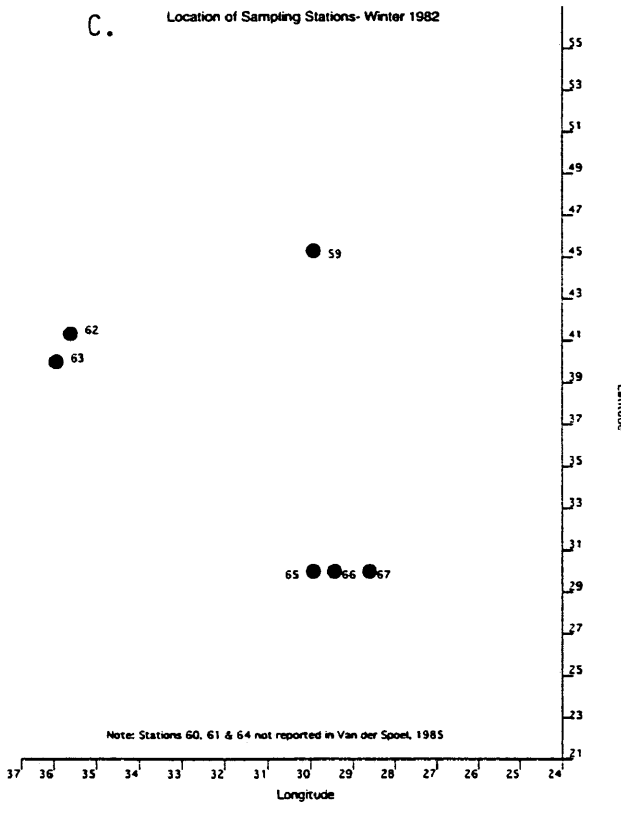
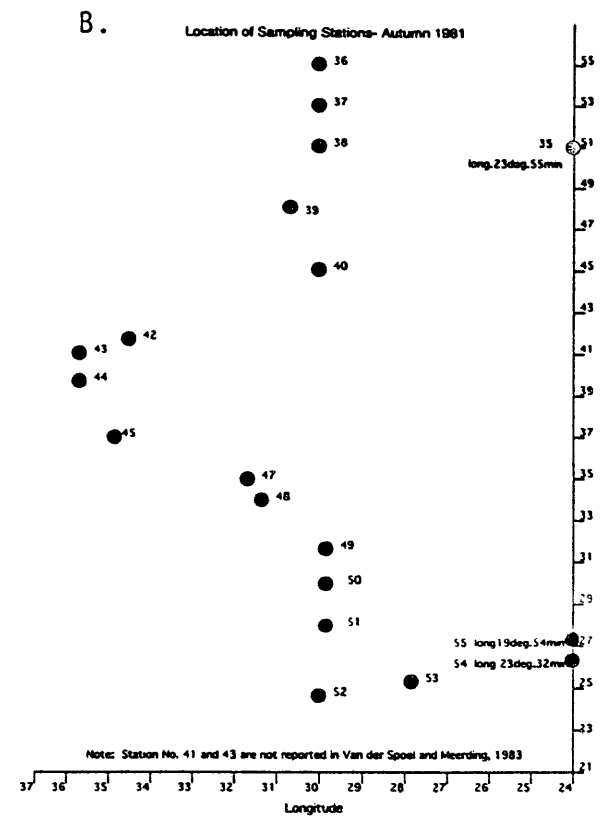
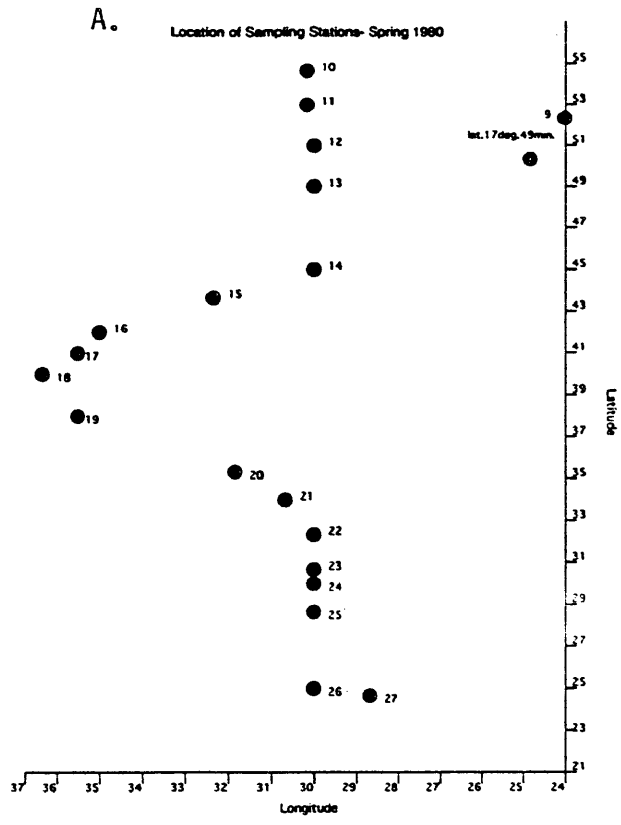
Cephalopods collected by the University of Amsterdam on the 1980-1983 cruises of the H.M.S. *Tydeman* (the Amsterdam Mid North Atlantic Plankton Expeditions (AMNAPE)) were examined. The University conducted collecting trips during four different seasons for the purpose of, "elucidating the patterns of latitudinal diversity, taxonomic variation below species level, vertical variation and the interaction of climate, hydrographic features and ecology on morphological variation of marine plankton" (p. 139 in Van der Spoel 1985). Cephalopods from these cruises were given to the Division of Mollusks, Smithsonian Institution, and they constitute one of the most comprehensive collections (approximately 1500 lots) of young cephalopods in existence.

Collecting Stations

Stations (Fig 1a-d) were located between 55°N and 25°N along the 30°W longitudinal line. The same approximate locations were sampled along this north-south transect at different seasons over a four year period in an attempt to understand the seasonal variation in the plankton assemblages. The 1981 cruise

¹ The following sections are compiled from van der Spoel (1981, 1985) and van der Spoel and Meerding (1983).

Figure 1. Location of sampling stations. a) Spring 1980 b) Autumn 1981 c) Winter 1982 d) Spring/Summer 1983. Multiple hauls were taken at each sample station; latitude and longitude of first haul is plotted.



also included east-west sampling (Stations 52-55) to "obtain information on neritic influences" (p. 77 in Van der Spoel and Meerding 1983).

Cruise Conditions

The 1980 (Fig. 1a) conditions (spring) were optimal for sampling and data retrieval, and effectively set the stage for the four-year sampling program.

Sample stations were located between 55°-25°N, approximately along the 30°W longitudinal line. Warm temperate and Sargasso Sea water dominated the upper 500m between 27°-50°N. The influence of the Canary Current was noted below 27°N, and the Subarctic polar water was found above 50°N. Arctic waters were found at depths > 500m (Van der Spoel 1981).

In the 1981 autumn cruise (Fig. 1b), an east-west transect (20-30° W) was added to the primarily north-south (24-55° N) cruise program to understand the influence of the African Shelf. Conditions were substantially different from the 1980 cruise, with the absence of a polar front and of Subarctic water in the northern section and a more pronounced thermocline in the upper 100m of water being the most obvious changes (Van der Spoel and Meerding 1983).

Weather conditions during the 1982 winter cruise (Fig. 1c) were extremely bad, and very little temperature and salinity data were collected. Station 62-63 were occupied close to North Atlantic Drift water, and all other stations were

taken from Sargasso Sea water (Van der Spoel 1985). Very few comparisons can be made between the winter and the other season cruises because of the lack of data.

Conditions in 1983 (summer, Fig. 1d) improved substantially and the majority of the samples were taken from North Atlantic Central waters. More specimens in all species except *M. agassizii* were found during this cruise than any other.

Collecting Gear- Nets

Discrete-depth and open-net hauls were taken at each station. Discrete-depth samples were obtained with the Rectangular Midwater Trawl (RMT1+8), an opening and closing net system developed by the Institute of Oceanographic Sciences, Great Britain. The RMT1 net (mouth area 0.8 m², mesh size 0.32mm) is positioned above the RMT8 (mouth area 8.0 m², mesh size 4.5mm, cod end linear mesh size 1.0mm); the nets are deployed simultaneously. Further discussion on the development and testing of the RMT 1+8 can be found in Baker et al. (1973) or Roe et al. (1980). Open oblique hauls were taken with an open RMT1 net. Other nets used include an open ringnet, designed specifically for this series of cruises, and open fine-meshed square nets (Van der Spoel and Meerding 1983). The ringnet was constructed with a circular mouth opening of 0.78 m² and was

made of conical sifting cloth with a mesh size of 0.18mm. Table 1 summarizes the collection data and gear for each of the 1980-1983 expeditions.

Collecting Gear- Physical Data

Physical oceanographic data were collected using expendable bathythermographs (XBTs) and Conductivity, Temperature and Depth collectors (CTDs), a net monitoring system for temperature at depth, satellite data (surface temperatures, supplied by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration), and sound velocity measurements (for calculation of salinity, supplied by the Hydrographic Office of the Royal Dutch Navy). Data from these sources were combined to create yearly vertical profiles of temperature (T), salinity (S), and vertical mixing, as well as T/S diagrams, and plots of sea surface T and S for the study area. Physical data are summarized in Van der Spoel (1981) (1980 cruise), Van der Spoel and Meerding (1983) (1981 cruise) and Van der Spoel (1985) (1982 and 1983 cruises).

METHODS

Collection Methods

All hauls, except for the small fine-meshed nets, were made from the stern of the ship. The sampling regime targeted depth intervals of 0-50m, 50-100m, 100-200m, 200-300m, 300-400m, 400-500m, and 500-1000m. The RMT1+8

Table 1. Summary of station and collection data for 1980-1983 cruises.

	1980	1981	1982	1983
Season	Spring	Fall	Winter	Summer
Dates	4/11-5/2	9/15-10/6	2/1-2/27	5/27-6/24
Latitude/Longitude	55-22oN, 30oW	55-24oN, 30oW 24oN 30oW - 27oN 20oW	55-22oN, 30oW	55-22oN, 30oW
No. Stations	19	21	7	18
Station Numbers	9-27	35-55	59, 62, 63, 65-68	74-90
Discrete Sampling				
Net Type	RMT1+8	RMT1+8	RMT1+8	RMT1+8
Number of Hauls	87	76	29	138
Depth Range (m)	0-1200	0-1200	0-1010	0-1760
Open Net Sampling				
Net Type	1) RMT1 2) Ring net 0.78 sq. m.	1) RMT1 2) Ring net 0.78 sq. m. 3) Fine mesh square net	1) RMT1 2) Ring net 3) Fine mesh square net 4) 2-0.25 sq m o/c nets 76 um & 202 um mesh (b)	1) RMT1 2) Ring net 3) Fine mesh square net 4) 2-0.25 sq m o/c nets 76 um & 202 um mesh (b)

Notes:

(a) Summarized from Van der Spoel 1981, 1983, 1985

(b) o/c = opening / closing

nets were opened at the top of the discrete-depth range and the layer was sampled in a downward direction.

All samples were sorted to major group on board ship and fixed according to methods specific to each animal group. Most frequently used fixatives were: 70% alcohol, propylene phenoxetol, and 2% or 4% formalin in seawater (Heyman 1981). Cephalopod specimens were stored at the Smithsonian Institution in 45% isopropyl alcohol according to protocol recommended by Roper and Sweeney (1983).

Identification

All cephalopods were sorted to family using adult and juvenile keys (Roper et al. 1969, Sweeney et al. 1992). Three families were chosen for detailed examination according to the following criteria. Families were supposed to have:

- 1) a relatively stable taxonomy in the study region;
- 2) a large number of specimens (50-100);
- 3) a range of recognizable ontogenetic stages;
- 4) specimens caught during both day and night hauls;
- 5) specimens caught at several depth horizons;

From the pool of families that met the above criteria, three were selected that were expected to represent gradual, intermediate and radical ontogenic changes in morphology.

Depth Distribution

Data were examined initially as a histogram of the number of specimens caught per haul in each depth horizon during separate day and night sampling periods. This graphing technique is typical for identifying vertical distributions of cephalopods (Clarke and Lu 1975, Lu and Clarke 1975a&b, Roper and Young 1975). Specimen records then were sorted by size to examine if trends in depth of capture with increasing size were evident.

Separate day and night graphs were created for each species. Because the sampling period spanned four years and four seasons, defining a consistent day and night time period was critical. Crepuscular periods were determined for each year of data using a marine navigation program (Twilight) based on the month, day and year of the sampling effort and the latitude and longitude at the sampling station. The program output was time of sunrise and sunset for that day at that latitude and longitude. Separate program runs were done for each station. The range of sunrises and sunsets was determined, and the median time of sunrise or sunset was used to identify the beginning of day or night for each year.

Latitude and Longitude Distributions

To understand the geographical and vertical distribution of the collected specimens, two sets of graphics were developed. The first presents the latitudes and longitudes where each of the three families were found. The occurrence of each species within the study families is broken down by year, to identify seasonal differences in geographic distribution.

The second group of graphs plots the depths of capture over the range of latitudes and longitudes. All occurrences (1980-1983) were graphed together for each species. These graphs were then compared with water column data (collected and summarized during the 1980-1983 cruises) to identify relationships between the species and its water mass.

Morphometric Data

Specimens from each species were examined under a stereomicroscope and measured using an ocular micrometer. Those specimens which were too large to be viewed under the microscope were measured with calipers. Dorsal mantle length (DML) was measured on all specimens. Mantle length is the standard for size determination in cephalopods, and according to Roper and Voss (1983), the mantle length is defined for squid as, "measured from anterior most point of mantle to posterior apex of mantle or tip of united fins, whichever

is longest". Dorsal mantle length was used as an indicator of the overall size and assumed relative age of the organism. Considerable variability in growth rates presumably occurs within cephalopod species. More precise aging methods are being developed for cephalopods, such as reading daily growth rings on statocysts, which are analogous to fish otoliths (Jereb et al. 1991). In the absence of ring number-to-growth correlations for each species, DML is the accepted measure of relative age in spite of its limitations. Other measurements were made for each species depending on the external morphology. For example, the tentacles of Mastigoteuthids often are lost during capture so tentacle length was not measured in that family. Features that appeared to change over time (such as neck length in the family Brachioteuthidae) were chosen. Growth trajectories of morphological characters plotted against DML that deviated from a simple, linear pattern are presented in the text. All remaining graphs are presented in Appendix A.

Changes in external morphology with ontogeny were described for each of the study species. Sizes were chosen to represent the time before, at, and after any described inflection point in the growth trajectories.

On several occasions there was a single specimen that was considerably outside the predominant size range. These single specimens provide interesting

anecdotal evidence, but can not be relied upon for interpretations and were eliminated from subsequent analyses.

Table 2 presents all character measurements taken within each family and their acronyms. Figure 2 (from Roper and Voss 1983) shows how each measurement was taken. Funnel dimensions are not commonly measured but are included in Figure 2.

Statistical Methods

For each species that did not appear to exhibit a diel vertical migration (DVM), morphometric characters and collection data were analyzed simultaneously using non-metric multidimensional scaling (Pielou 1984; Systat 1992) to provide insight into what other ecological data may be used as an indicator of the change in DML. Multidimensional scaling (MDS) refers to a group of statistical techniques that uses matrices of proximity data (how close one object is to another in n-dimensional space) to "uncover the 'hidden structure'" (Kruskal and Wish 1978) of a data set. The procedure fits a set of points into n-dimensions (2 or 3 dimensions usually provide the most interpretable results) so that the distances between points in the solution correspond as closely as possible to a given set of similarities or dissimilarities between a set of objects (Systat 1992). The techniques were developed for use in

Table 2. Morphometric characters measured in all species of each family.

Characteristic	Abbreviation	Ctenopterygidae	Mastigoteuthidae	Brachioteuthidae
Fourth Arm Length	4AL	X	X	X
Tentacle Length	TL	X		
Club Length	CL	X		X
Head Length	HL	X	X	X
Head Width	HW	X	X	X
Eye Diameter	ED	X	X	X
Neck Width	NW			X
Neck Length	NL			X
Funnel Width- Anterior	FunW-A	X	X	X
Funnel Width- Posterior	FunW-P	X	X	X
Funnel Length	FunL	X	X	X
Dorsal Mantle Length	DML	X	X	X
Mantle Opening Width	MOW	X	X	X
Fin Length	FL	X	X	X
Fin Width	FW		X	X

Figure 2. Measurements used for morphometric analysis (adapted from Roper and Voss 1983).

ED	= Eye diameter	HL	= Head length
FL	= Fin length	HW	= Head width
FW	= Fin width	ML	= Mantle length
FunL	= Funnel length	MW	= Mantle width
FunW-A	= Funnel width, anterior	TL	= Tentacle length
FunW-P	= Funnel width, posterior		

Funnel length (FunL), funnel width, anterior (FunW-A) and funnel width, posterior (FunW-P) are not generally measured, but are defined as follows:

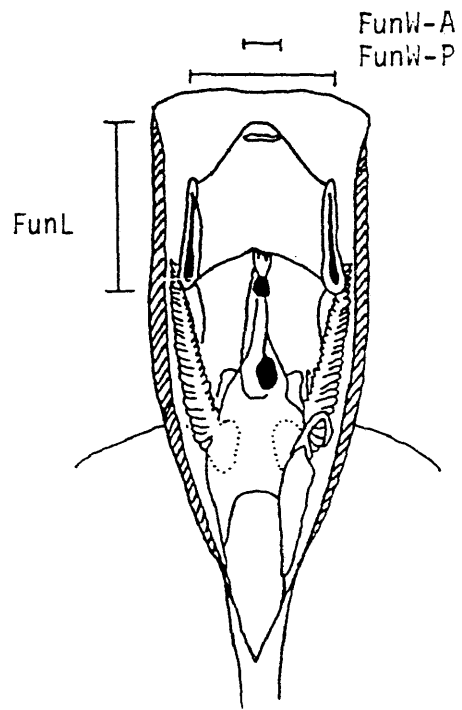
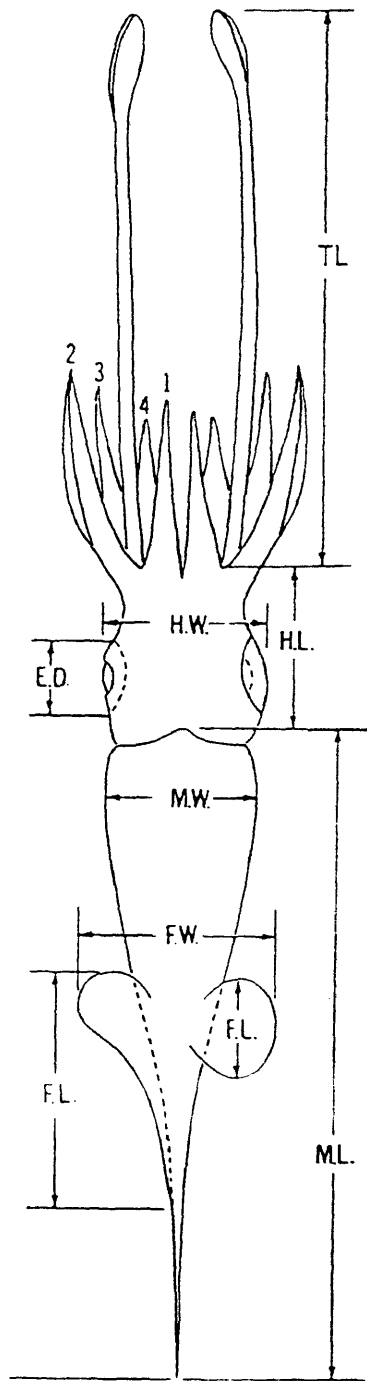
FunL: Length from the top of the funnel opening to the bottom, measured down the middle of the funnel to the bottom of the funnel locking cartilage.

FunW-A: Width of the top of the funnel, measured horizontally across anterior opening.

FunW-P: Width of the bottom of the funnel, measured horizontally across opening at the posterior end of the funnel locking cartilage.

The mantle opening width (MOW) was measured instead of the mantle width, and is defined as follows:

MOW: the maximum width of the mantle at the anterior most end.



the behavioral sciences, but have been applied successfully to biological data (Matthews 1978, Whittaker 1987, Prentice 1977). It is particularly useful when disparate (e.g. environmental and morphometric data) are used together to describe a set of objects.

Multidimensional scaling typically is divided into two types--metric and non-metric. In metric multidimensional scaling, the solution is based on a function described by a particular equation. In non-metric scaling, the solution function must describe a rising or falling pattern, but not any particular equation. The non-metric method does not depend on any arithmetic properties (sums, products, differences) of the proximity data. Instead, it depends solely on the rank order of the proximities and is considered a nonparametric method (Kruskal and Wish 1978).

No statistical distribution assumptions are necessary with MDS, because the method inputs are similarity / dissimilarity matrices. But, because MDS is a spatial model, the data must satisfy the following conditions (Systat 1992):

1. The distance from an object to itself is zero.
2. The distance from object A to object B is the same as that from B to A.
3. The distance from object A to C is less than or equal to the distance from A to B plus B to C (the triangle inequality).

There are several indicators of the "goodness" of the solution's final configuration that are generated for review by Systat for Windows. The two most important are the stress of the solution and the Shepard diagram. Stress is the goodness-of-fit statistic that MDS tries to minimize as it searches over many iterations for the best configuration. The larger the stress value, the worse the resulting configuration. Stress may approach zero, but stress = 0 implies that the distances on the MDS plot exactly equal the proximities, which is improbable. Problems associated with stress (e.g., reaching a local minimum instead of a global minimum) are further discussed in Kruskal and Wish (1978). Systat for Windows release 5.0 uses Kruskal's stress formula 1, which is the simplest and most commonly used formula (Kruskal 1964).

The Shepard diagram (a scatterplot) provides a visual indication of the relationship between the distances between points in the MDS plot and the proximities of the points in space (for further discussion, see Kruskal and Wish, 1978). One of the fundamental assumptions of multidimensional scaling is that these two measures correspond to each other. In a perfect solution, there would be an exactly linear relationship; however, in all cases, the Shepard diagram should form either a smoothly rising or falling pattern, depending on whether the inputs were similarity or dissimilarity data. Any discontinuity (frequently manifested as a step-like configuration of points) or clumping in the Shepard diagram may indicate a degenerate solution has been reached. According to

Kruskal and Wish (1978), a degenerate solution occurs most often when: "1) nonmetric scaling is being used [when metric would be more appropriate], 2) the objects have a natural clustering".

To execute the MDS statistical procedure, several modifications of the original data were necessary. The following steps were taken to move from the measurement data to the final scaled configuration:

1. A text file composed of all measurement data, the depth horizon, the latitude & longitude, and the date and time of capture was generated from dBase3+.
2. Data were imported from dBase3+ into QuattroPro, segregated by species and crepuscular period, and saved as a Lotus 1-2-3 (.wk1) file. Salinity and temperature data were then keyed into the spreadsheet.
3. The spreadsheets were imported into Systat (version 5.01 for Windows) and standardized (variables were replaced with their z-scores), so that millimeters of dorsal mantle length were not compared with 1000s of meters in depth of capture.

4. Spearman's correlations were calculated to create a matrix suitable for input into multidimensional scaling. Spearman's technique was chosen because it, like nonmetric MDS, is a nonparametric method.

5. The resulting similarity matrix was used to perform the multidimensional scaling. MDS results were generated in two, three, four and five dimensions for comparison.

6. Resulting MDS configurations in 2,3, 4, and 5 dimensions were examined. The optimal configuration was chosen based on 1) minimization of stress; 2) shape and r^2 of the Shepard diagram; and 3) reasonable assignment of variables to the axes. The assignment of reasonable and easily interpretable variables often was the determining factor in choosing dimensionality. For example, a two dimensional configuration would be selected over a three dimensional result in the following situation:

2-Dimensions

stress = .107

Shepard's r^2 = .913

variable 1 = latitude/longitude

variable 2 = all morphological data

3-Dimensions

stress = .099

r^2 = .966

variable 1 = lat., long., temp.

variable 2 = FL, MOW, temp., salinity

variable 3 = DML, HW, FW, avg.depth

7. The degree to which each variable (e.g. DML, FL, salinity, latitude, etc) explained the resulting 2, 3, 4 or 5 dimensions was determined by running a second Spearman's correlation. This correlation compared the rank order of coordinates of the solution's configuration with the standardized measurement data.

8. Matrices generated by the second correlation in the day and night captures within each species were reviewed. Depending on the strength of the correlations, axes were assigned variables. A high correlation (generally greater than ± 0.750) implied that most of the variability along the axis was due to the selected variable(s).

The data set for the daytime analysis of *Brachioteuthis sp. 3* was too large for Systat version 5 to process. Several alternative methods of segregating the data (e.g., by year, and/or gear type) were considered and rejected because most of the specimens caught during the day were caught in the same haul. Three stations (Station 77-01 n=76; Station number unknown, n=22 Station 36-08, n=17) accounted for 44% of the captures of *Brachioteuthis sp. 3*; most of these specimens were similar in size. For these reasons, half of the specimens caught at these locations were selected using a random number table, and subsequently eliminated from the analysis. This method brought the number of specimens

down to a number that Systat could successfully process as previously described.

RESULTS

Specimens (n=2860) were examined and assigned to families within the Class Cephalopoda (Table 3). Most specimens (89.1%, n=2548) were identified to 24 families of the Order Teuthoidea (squids); 8.7% (n=250) were identified to 6 families of the Order Octopoda (octopods); 0.8% (n=22) were Order Sepioidea (cuttlefish) and 1.4% (n=40) were unidentifiable, usually due to the poor condition of the specimens. The families Ctenopterygidae, Mastigoteuthidae and Brachioteuthidae were chosen for further analysis based on the criteria outlined in the Materials and Methods section. Specimen from these families were further identified to species according to published keys for newly-hatched (Sweeney et al. 1992) or adult specimens (Ctenopterygidae: Roper et al. (1969); Mastigoteuthidae: Nesis (1987); Brachioteuthidae: Roper et al. (1984)).

Family Ctenopterygidae

Ctenopteryx sicula (Fig. 3)

Young: "Club suckers in distinctive circular pad (at <4mm ML), equals length of manus (at 6mm ML); single chromatophore occurs on aboral surface of club (at >=2mm ML); fins separate dorsally, fringe mantle laterally; hatchlings with transversely elongate fins, trabeculae (at 3.5mm ML); fin length increases with size; eyes small, widely separated" (Jefferts, p. 125 in Sweeney et al. 1992)

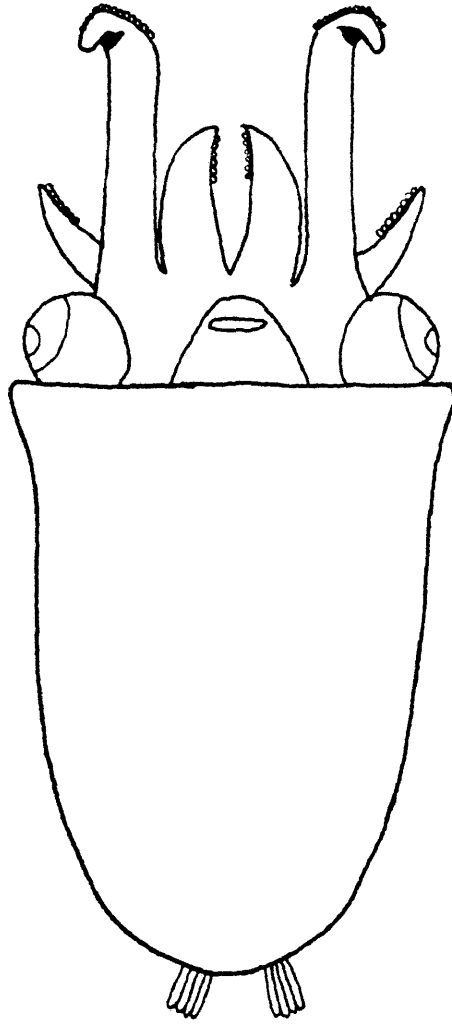
Table 3. Summary of families identified in the AMNAPE collection, the number of stations where these families were caught and the total number of specimens caught.

Family	1980		1981		1982		1983		Total	
	No. Stations	No. Specimens	No. Stations	No. Specimens	No. Stations	No. Specimens	No. Stations	No. Specimens	No. Stations	No. Specimens
<u>Order Teuthoidea</u>										
Ancistrocheiridae	1	1	0	0	0	0	0	0	1	1
Architeuthidae*	1	1	3	3	0	0	3	3	7	7
Argonauidae	2	2	5	5	0	0	1	1	8	8
Bathyleuthidae	1	2	0	0	0	0	2	2	3	4
Brachoteuthidae	17	46	9	27	6	6	43	180	75	259
Chroteuthidae	10	15	7	7	2	2	20	22	39	48
Cranchiidae	69	186	60	155	55	283	117	310	321	934
Chienopterygiidae	21	27	8	9	5	5	32	73	68	114
Cycloteuthidae	0	0	0	0	2	2	1	1	3	3
Enoplateuthidae	42	88	20	41	4	5	23	44	89	178
Goniatidae	25	74	0	0	0	0	11	30	36	104
Histioteuthidae	55	90	21	28	1	1	17	22	94	141
Joubiniteuthidae	2	2	0	0	0	0	0	0	2	2
Lampadoteuthidae	1	1	0	0	0	0	0	0	1	1
Lepidoteuthidae	3	3	0	0	0	0	1	1	4	4
Lycoteuthidae	2	2	0	0	0	0	0	0	2	2
Mastigoteuthidae	29	62	12	18	3	6	29	44	73	130
Neoteuthidae	5	6	1	1	0	0	1	1	7	8
Octopoteuthidae	12	17	4	4	8	8	13	16	37	45
Ommastrephidae	14	16	14	19	1	3	9	11	38	49
Onychoteuthidae	32	45	23	35	17	47	51	103	123	230
Pholidoteuthidae	2	2	0	0	0	0	0	1	1	3
Pyroteuthidae	54	125	27	54	13	36	37	58	131	273
Thysanoteuthidae	0	0	0	0	1	1	1	1	2	2
Total	420	813	214	406	118	405	413	924	1165	2548
<u>Order Octopoda</u>										
Allopsidae	1	1	0	0	0	0	0	0	1	1
Bolitaenidae	18	26	47	132	15	18	13	15	93	191
Octopodidae	2	2	0	0	0	0	4	4	6	6
Ocyropsidae	0	0	0	0	1	1	1	1	2	2
Tremoctopodidae	0	0	2	2	0	0	1	1	3	3
Vitreledonellidae	11	21	9	10	0	0	12	16	32	47
Total	32	50	58	144	16	19	31	37	137	250
<u>Order Sepioidae</u>										
Sepioidae	2	2	0	0	0	0	0	0	2	2
Sepioidae	7	13	1	1	0	0	4	4	12	18
Spirulidae	0	0	1	1	0	0	1	1	2	2
Total	9	15	2	2	0	0	5	5	16	22
Unidentified	15	20	8	10	0	0	6	10	29	40
Grand Total	476	898	242	562	134	424	455	976	1347	2860

Notes:
* = uncertain identification

Figure 3. Illustration of 2.7mm DML *Ctenopteryx sicula* (Station-haul: 54-09).

Ventral view.



Identification and Historical Synopsis

The most widely recognized and frequently assigned species in the family is *Ctenopteryx sicula* (Verany, 1851), although the type species of the genus was designated by *Ctenopteryx fimbriatus* (Appellof, 1889) which is a junior synonym of *C. sicula* (*vide* Clarke 1966). *Ctenopteryx cyprinoides* was described by Joubin (1894) and was synonymized with *C. fimbriatus* by Ashworth and Hoyle (1906). *Ctenopteryx sepioloides* Rancurel, 1970 was proposed because of a consistent variation in the mantle width to mantle length ratio noted in squid specimen collected from the stomach of *Alepisaurus ferox*. This species is maintained as separate from *C. sicula*, although the author himself expressed doubts about its validity. All squids with fringed or ribbed fins are assigned to *Ctenopteryx sicula*, pending a complete revision of the family.

In spite of some evidence for two morphotypes based on head width (see Fig. 6b), all specimens (n=114) were identified as *C. sicula*. Based on the morphological changes with ontogeny presented by Clarke (1966) and on comparisons between small and large specimens of the AMNAPE collection, this species was not expected to exhibit any radical morphological changes over time, and thus was designated as the "gradual" species (see Materials and Methods).

Depth and Areal Distributions

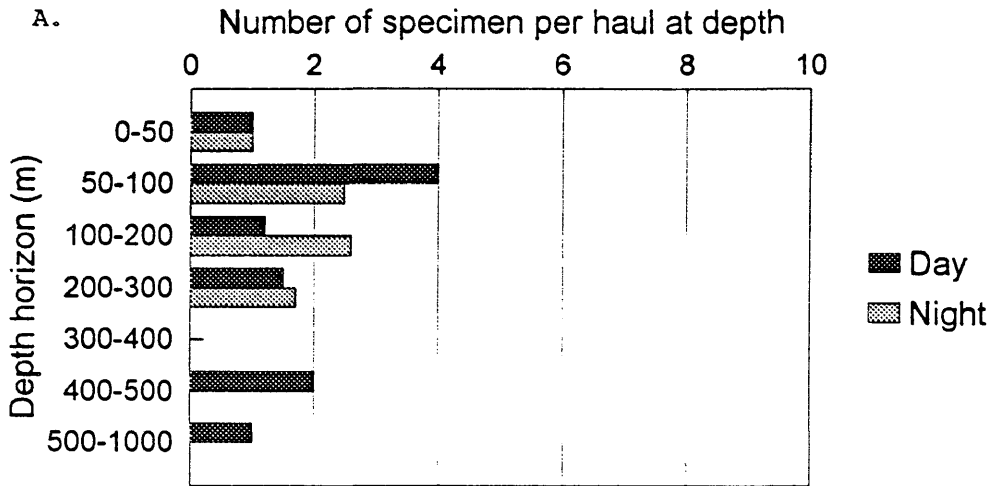
During the day, *C. sicula* was most frequently caught between 0-300m, with a peak capture per haul at 50-100m (Fig. 4a); five specimens were recorded at depths >400m. Night captures show specimens were evenly distributed throughout the 0-300m depth range with no deep captures recorded.

In the daytime samples, DML increased with depth of capture (Fig. 4b,c). The smallest specimens (3.2-9.8mm DML) all were caught in the upper 200m, except for a single 4.5mm DML specimen caught between 500-1000m. This specimen may represent contamination (e.g., a specimen entangled in the deeper net while going through the surface waters). Larger specimens were found at progressively deeper depths (50-300m), with the two largest specimens (18.5, 21.5mm DML) caught the deepest (600-1000m). At night, all specimens (2.2-41.7mm DML) were found in the upper 300m; most of these (43 of 48) were in the upper 200m.

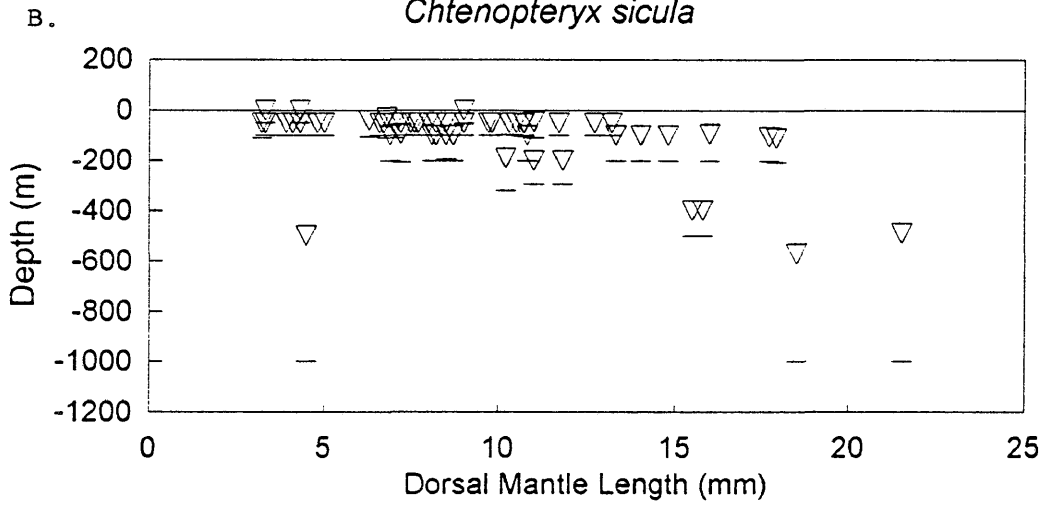
During the spring 1980 cruise (Fig 5a), *C. sicula* was most frequently captured in hauls along the 30° W longitudinal line south of 43°N, with a pocket of captures made at 35-36° W. All but one capture were taken from the upper 300m of water. Van der Spoel (1981) identifies the water masses at this depth as Canary Current water (at latitudes south of 27°N), Sargasso Sea water (27-40° N)

Figure 4. Depth distribution of *Ctenopteryx sicula*. a) Number of specimen per haul at each depth horizon during day and night b)day time depth of capture plotted against DML c)night time depth of capture plotted against DML. Net opened at triangle and closed at horizontal line. Each triangle/line combination represents one collected specimen. Note: Bottom depth is illustrated for 0-1000m depth horizon collected by malfunctioning opening/closing net.

Vertical Depth Distribution *Ctenopteryx sicula*



Depth vs. Dorsal Mantle Length (Day) *Ctenopteryx sicula*



Depth vs. Dorsal Mantle Length (Night) *Ctenopteryx sicula*

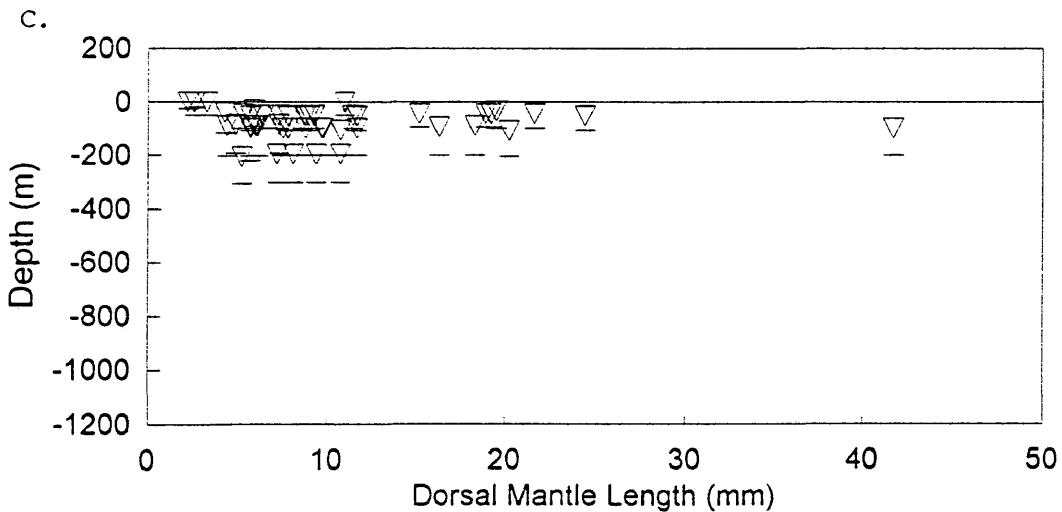
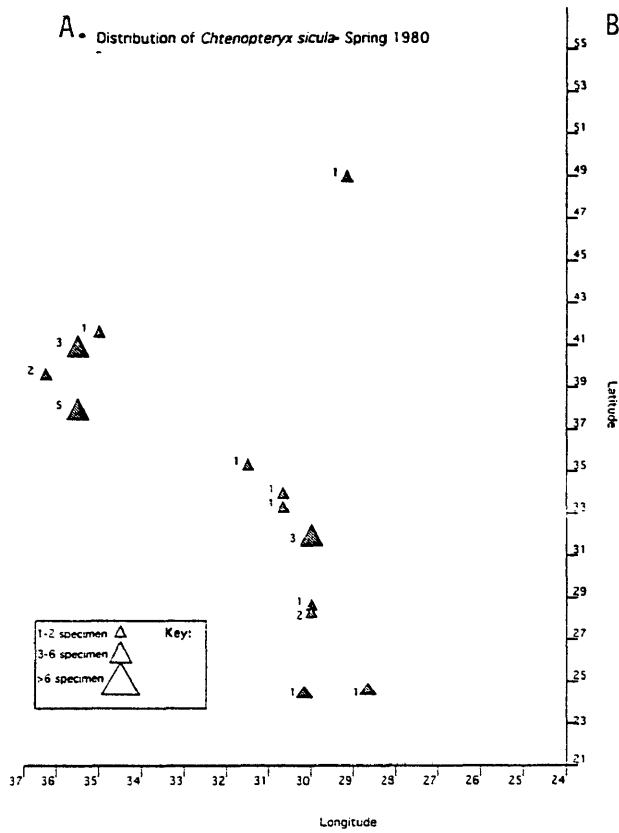
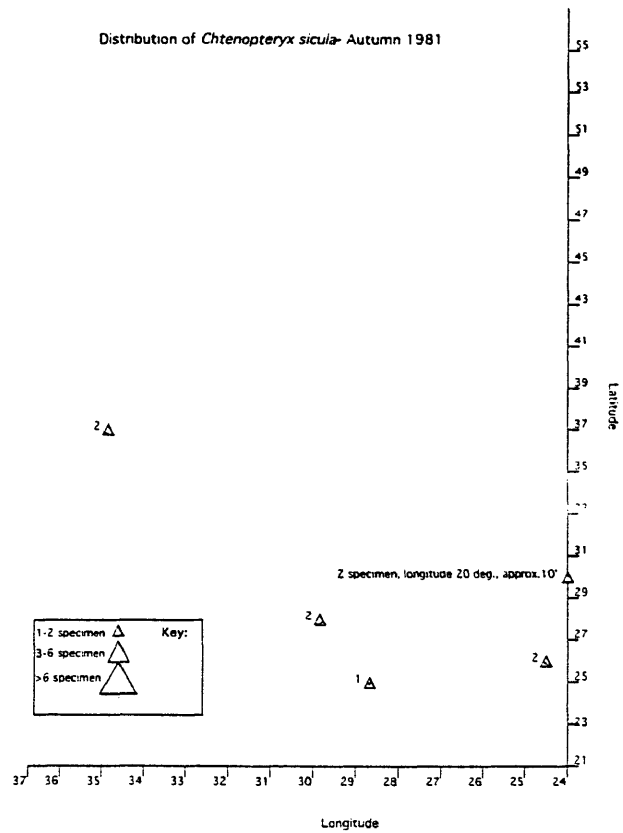


Figure 5. Areal distribution of *Chtenopteryx sicula*. a) Spring 1980 b) Autumn 1981 c) Winter 1982 d) Spring/Summer 1983. Center of the triangle marks the collection point. Overlapping triangles were combined and the number of specimens were added. North - South and East - West depth distributions of *Chtenopteryx sicula*. Hauls that contained cephalopods at each latitude and longitude are represented. Multiple specimen may have been caught in each depth horizon e) Spring 1980 f) Autumn 1981 g) Winter 1982 h) Summer 1983.

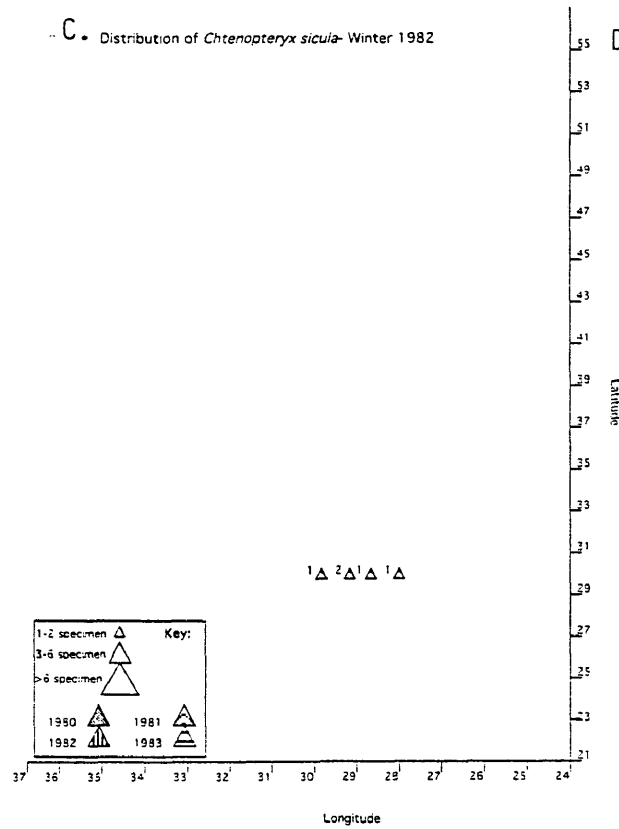
A. Distribution of *Chtenopteryx sicula*- Spring 1980



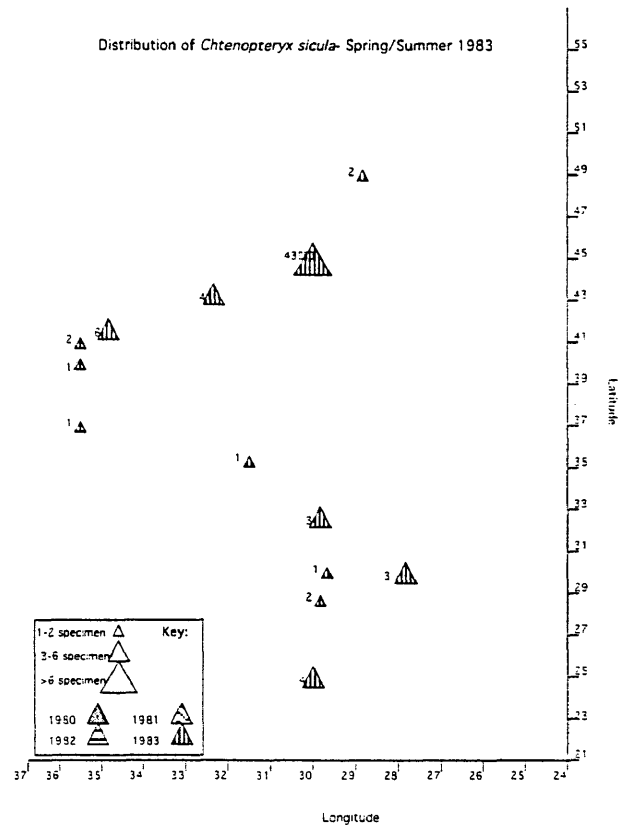
B. Distribution of *Chtenopteryx sicula*- Autumn 1981

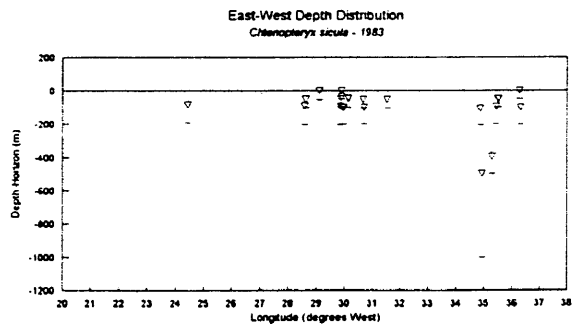
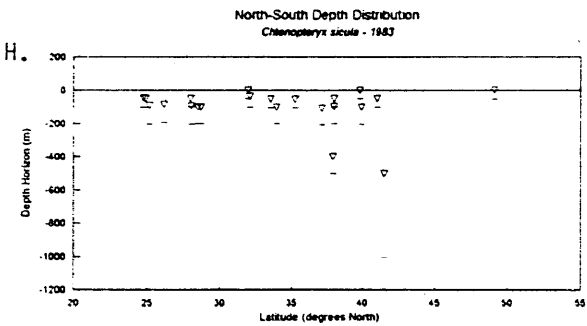
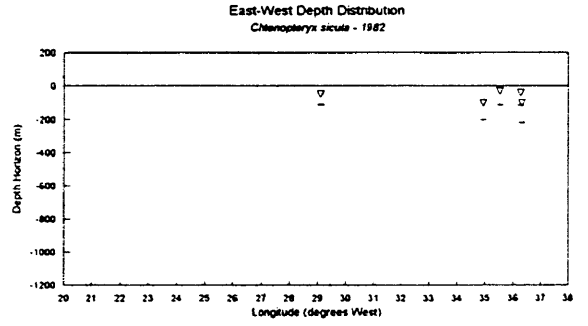
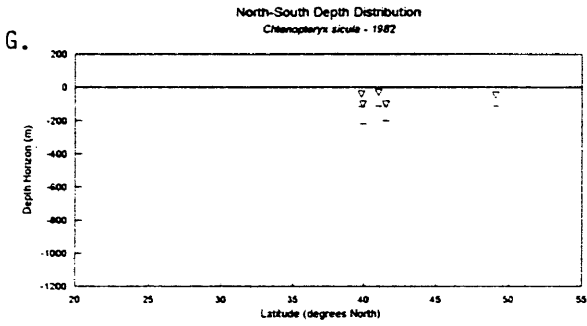
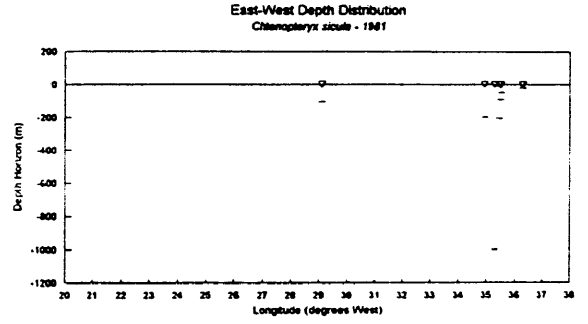
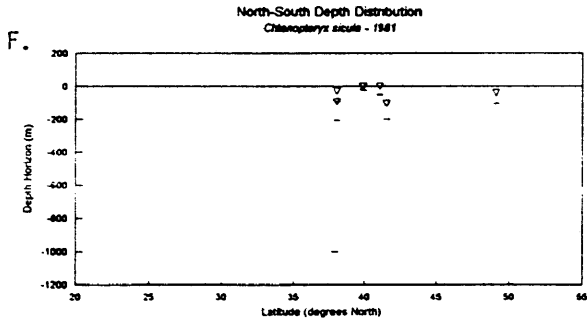
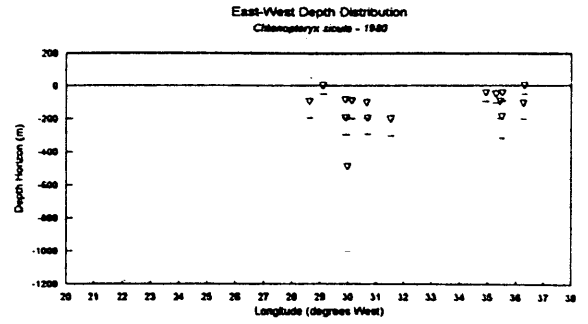
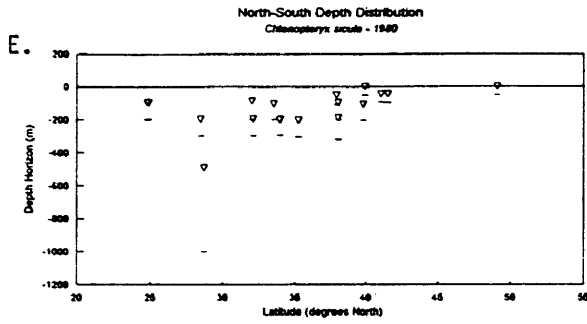


C. Distribution of *Chtenopteryx sicula*- Winter 1982



D. Distribution of *Chtenopteryx sicula*- Spring/Summer 1983





and Warm Temperate water (42-50° N). One specimen was taken from > 500m, in Arctic deep water (Van der Spoel 1981).

Captures of *C. sicula* were less frequent and more geographically dispersed in Autumn 1981 (Fig. 5b). All captures were south of 38° N, putting them in the Sargasso Sea water (Van der Spoel and Meerding, 1983), and all but one were from the upper 200m; 1-2 specimens were caught in each of the 6 hauls between 20-35° W. Depth of capture varied over the latitudes and longitudes, but most were caught in the upper 300m.

Only four specimens were captured during the winter 1982 cruise (Fig. 5c); all were at the southernmost stations between 27-30° W in the upper 200m in Sargasso Sea water (Van der Spoel 1985).

Most specimens were collected during the summer 1983 cruise (Fig. 5d). Captures were made all along the cruise track (49-24°N), with the highest concentration found at 45° N, 30°W. The depth of capture was predominantly in the upper 200m, (Sargasso Sea/ North Atlantic Central water) with two exceptions: one between 400-500m and the other from 500-1000m (N. Atlantic Deep water).

Morphometric Data

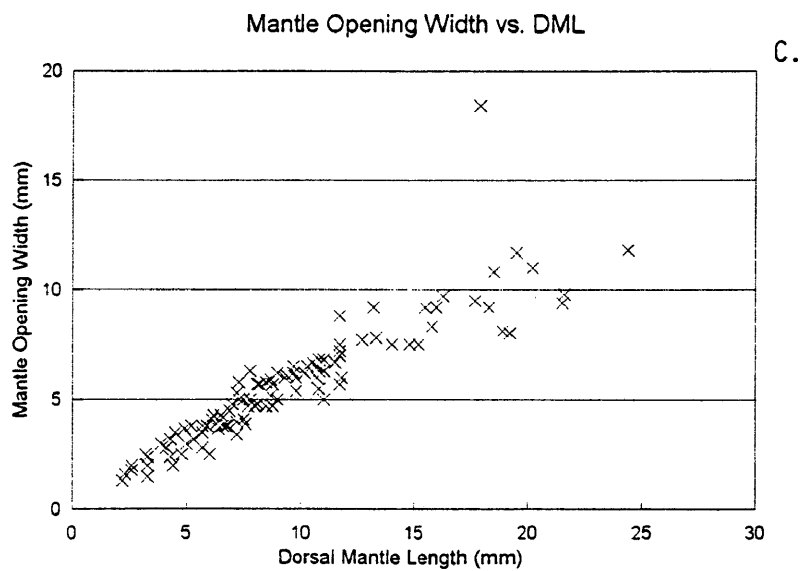
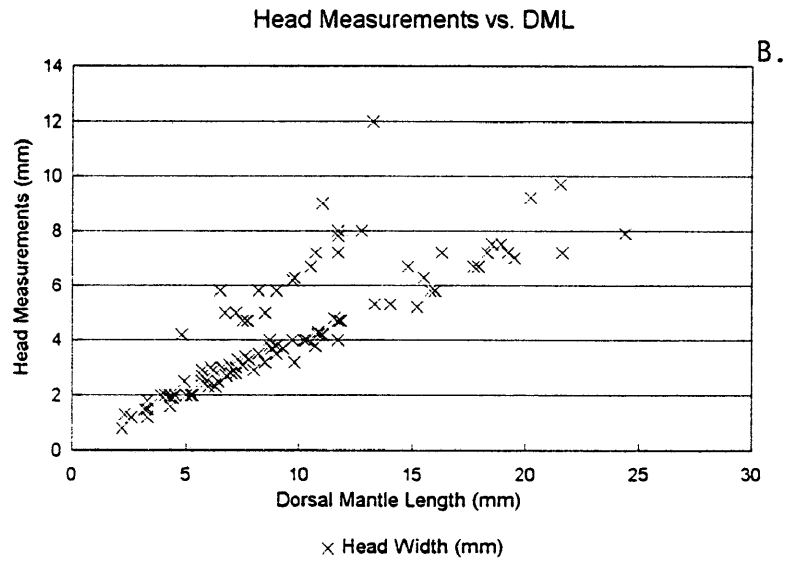
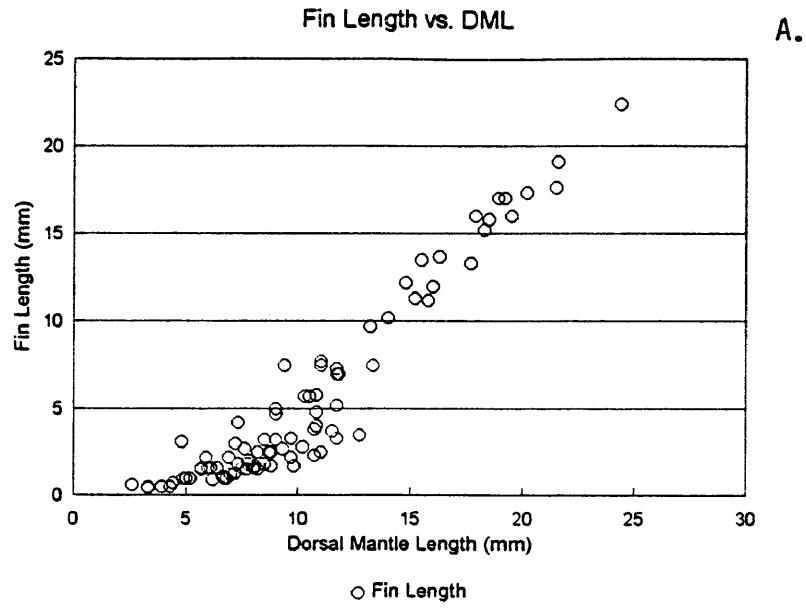
All but one specimen of *C. sicula* fell within the 2-25mm DML size range; this data sub-set is very robust, with many specimens spread over the entire range.

Fin length (Fig. 6a) was the only fin measurement taken because the ribs of the fins frequently were detached from the mantle and could not be reattached for accurate fin width measurement. At approximately 10mm DML, the slope of the growth trajectory doubles, indicating that the fin length begins to grow very quickly.

The *head dimensions* (Fig. 6b) show two different patterns. Whereas HL, ED (Appendix A) and HW (Fig. 6b) appear to remain linear over the entire size range, the head width graph shows a second parallel trajectory. This second trajectory may represent a gender difference, a second species, or unknown factors such as population variability.

Finally, the slope of the scatterplot for the *mantle opening width* (Fig. 6c) decreases with increasing DML, with the inflection point between 10-12mm DML.

Figure 6. Morphometric analysis of *Chtenopteryx sicula*. a) fin length b) head width c) mantle opening width.



Ontogenic Changes in External Morphology

4.4mm DML (station-haul 68-04, bottle no. ?): Mantle broad, almost U-shaped, no chromatophores evident because of skin damage. Funnel very large, anterior funnel projects past the base of the fourth arms; FBW = MOW. Eyes are small, anterior. All arms virtually equal in length; arm suckers small, stalked, and in two rows. Tentacles not much longer than arms, with circular "pad" marking beginning of club development; suckers and sucker buds beginning to grow from the "pad" causing the distal tip to bend. 5 rows of suckers on the club "pad"; no suckers on the tentacular stalk. Fins torn off.

5.1mm DML (station-haul 86-07, bottle no. 7106) All characters as above. Fins ribbed, present on posterior end only; FL = approximately 1/5 DML.

9.0mm DML (station-haul 77-01, bottle no. 8853): Characters as above with following exceptions: DML > ventral mantle length (VML) with a peak at the anterior end of the DML. Arm suckers are small, but plentiful; proximal end of all arms with 2 rows of suckers; distal end of arms 1-3 with 4-6 rows; swimming keel on both sides of 4th arm.

19.5mm DML (station-haul 81-08, bottle no. 8000): Same characters as above with the following exceptions: Fins run along entire lateral mantle. Eyes

antero-laterally directed. Funnel ends at base of the arm crown. Arm lengths can be differentiated, arm formula 2>3>4>1; arms 2 & 3 have developed a swimming keel on the ventral side.

Multidimensional Scaling

Because evidence of diel vertical migration was seen, a MDS analysis was not conducted.

Family Mastigoteuthidae

Young: "Mantle elongate; fins transversely oval; tentacular club with > 4 rows of suckers (6mm ML); tentacular stalk thicker than arms; stalk and club circular in cross section; club not expanded; eyes at front of head project diagonally anteriorly; gladius extends well posterior to fins as long, spike-like tail" (Roper and Sweeney, p.175 in Sweeney et al. 1992).

Historically, the family Mastigoteuthidae has been comprised of 18 species in 2 genera and 2 subgenera. Based on his earlier work (Nesis, 1977), Nesis (1987) presented a key with the family divided into two genera, *Mastigoteuthis* Verrill, 1881 which contained the subgenera *Mastigoteuthis* (s. str.) and *Mastigopsis* Grimpe, 1922, and *Echinoteuthis* Joubin, 1933. All but two described species (*M. Mastigopsis hjorti* and *E. danae*) were placed in the genus *Mastigoteuthis* subgenus *Mastigoteuthis*.

Recently, a new classification recognizing 8 species in 2 genera and 4 subgenera was proposed (Salcedo-Vargas & Okutani, 1994). The new classification resurrects the genus *Idioteuthis* Sasaki, 1916, collapses the subgenus *Mastigopsis*, relegates *Echinoteuthis* to subgeneric status, and creates a new subgenus *Magnoteuthis*, with the type species *Mastigoteuthis magna* Joubin, 1913. Salcedo-Vargas (1994) subsequently changed his mind and resurrected the genus *Echinoteuthis*, based on specimens from the Netherlands Indian Ocean Programme. In addition, Salcedo-Vargas & Okutani (1994) resolved the "grimaldii-group" (Nesis 1977, 1987). Rancurel (1971) first pointed out the similarities between *grimaldii*, *dentata*, *flammea* and *schmidti*. Nesis (1977, 1987) defined the "grimaldii-group" to include *grimaldii*, *schmidti*, *dentata* and *pyrodes*. Salcedo-Vargas and Okutani (1994) finally concluded that *grimaldii*, *dentata*, *flammea* and *schmidti* are all synonymous with *M. agassizii*.

Five different morphotypes of Mastigoteuthidae were identified in the AMNAPE collection using the key presented in Nesis (1987) and modified after Salcedo-Vargas and Okutani (1994). Four of the morphotypes were confidently identified to species - *Mastigoteuthis agassizii* (n=42), *Idioteuthis magna* (n=62), *Idioteuthis hjorti* (n=1) and *Echinoteuthis familica* (n=3). The fifth species, *Idioteuthis sp. A.* (n=7), was separated from *I. magna* based on the shape of the funnel locking apparatus (FLA). *Idioteuthis sp. A.* has a very long, narrow, straight FLA,

contrasting notably to the oval, almost pear-shaped FLA of *I. magna*. *Idioteuthis magna* Joubin, 1913 and *Mastigoteuthis agassizii* (Verrill, 1881) had enough specimens to allow further study. Based on historical literature, and the perceived change in fin shape over time when comparing adult and newly-hatched specimens, these two species were designated the "intermediate" species.

Idioteuthis magna (Fig. 7)

Depth and Areal Distribution

Histograms of specimens at depth show that during the day, *I. magna* is found in two groups; the first at 0-200m, with most specimens in 50-100m of water. The second group is found in waters >400m (Fig. 8a). During the night, most *I. magna* move up into the 50-200m range, with one exception (23.6 mm DML, 300-400m).

No trend in depth of capture is noted with increasing DML during the day (Fig. 8b). Specimens are generally distributed over the top 500m of the water column, with most specimens between 5-12 mm DML found between 0-100m. Two deep captures (>500m) were recorded. Night data (Fig. 8c) show a tremendous increase in the number of specimens at 50-100m. Specimens <7mm DML are caught only in the upper 100m. Specimens larger than 7mm are found in the upper 200m. The deepest capture depth was recorded for the largest

Figure 7. Illustration of 11.3mm DML *Idioteuthis magna* (Station-haul: 50-13).

Dorsal and ventral view.

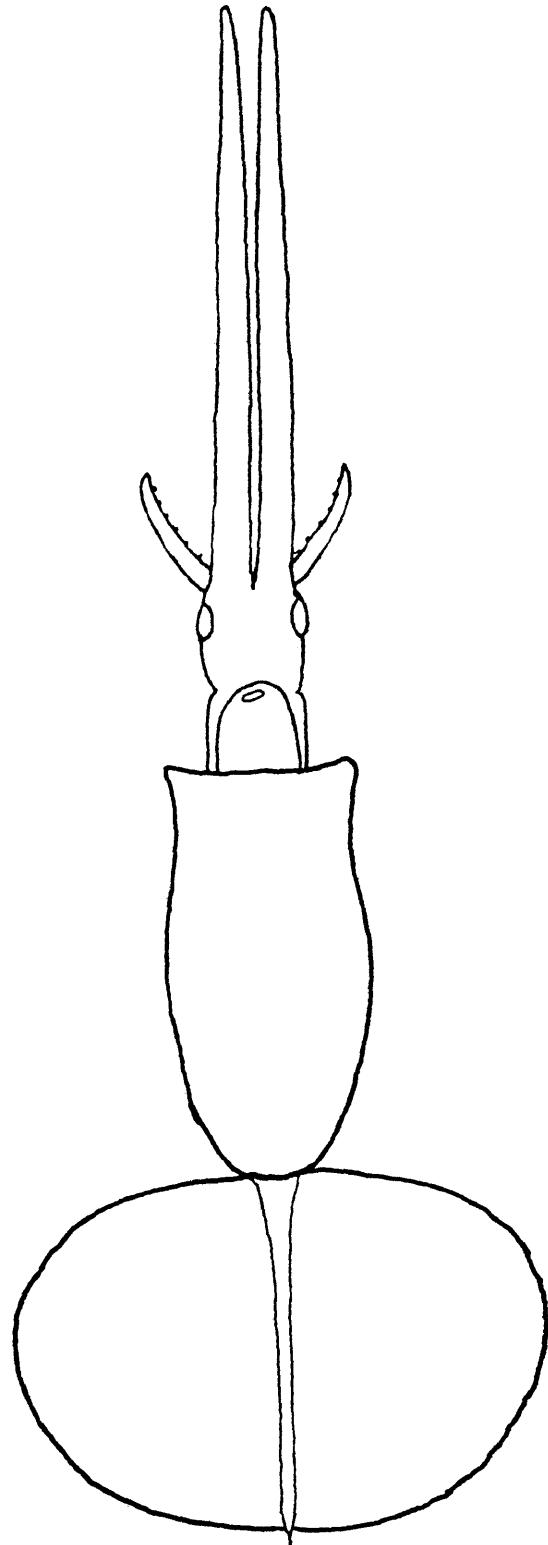
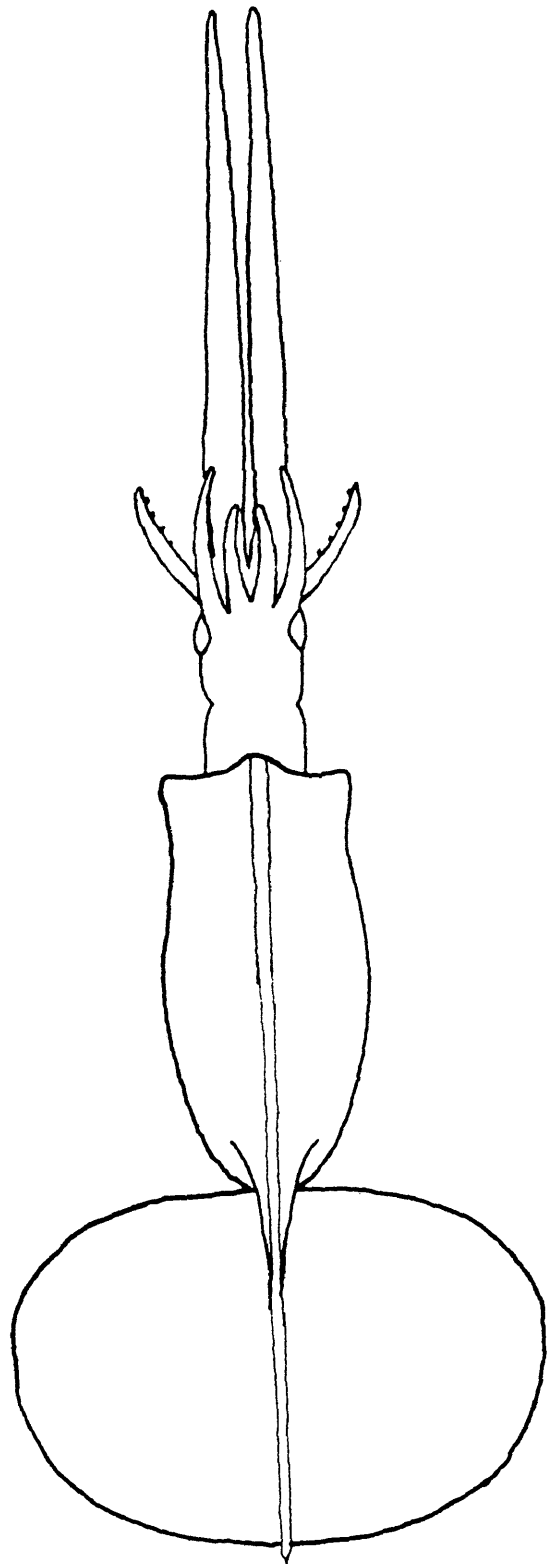
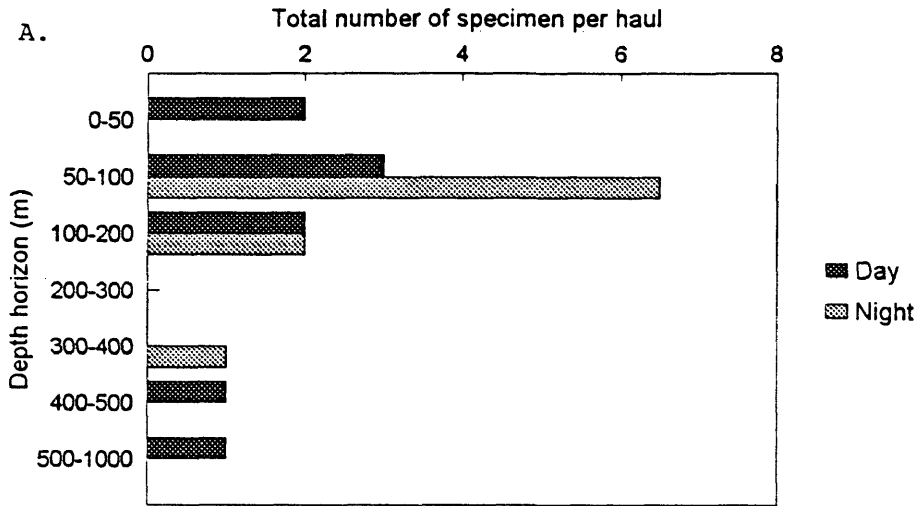
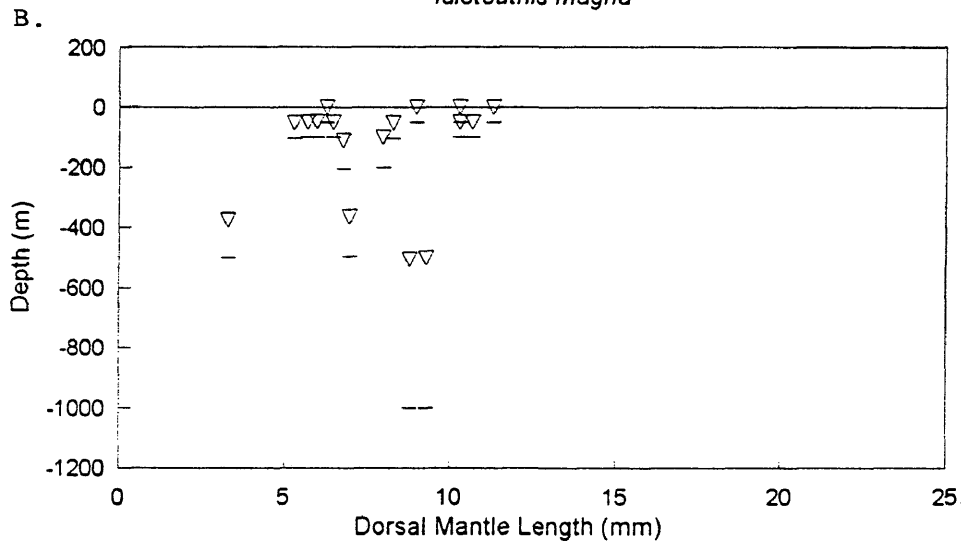


Figure 8. Depth distribution of *Idioteuthis magna*. a) Number of specimen per haul at each depth horizon during day and night b)day time depth of capture plotted against DML c)night time depth of capture plotted against DML. Net opened at triangle and closed at horizontal line. Each triangle/line combination represents one collected specimen. Note: Bottom depth is illustrated for 0-1000m depth horizon collected by malfunctioning opening/closing net.

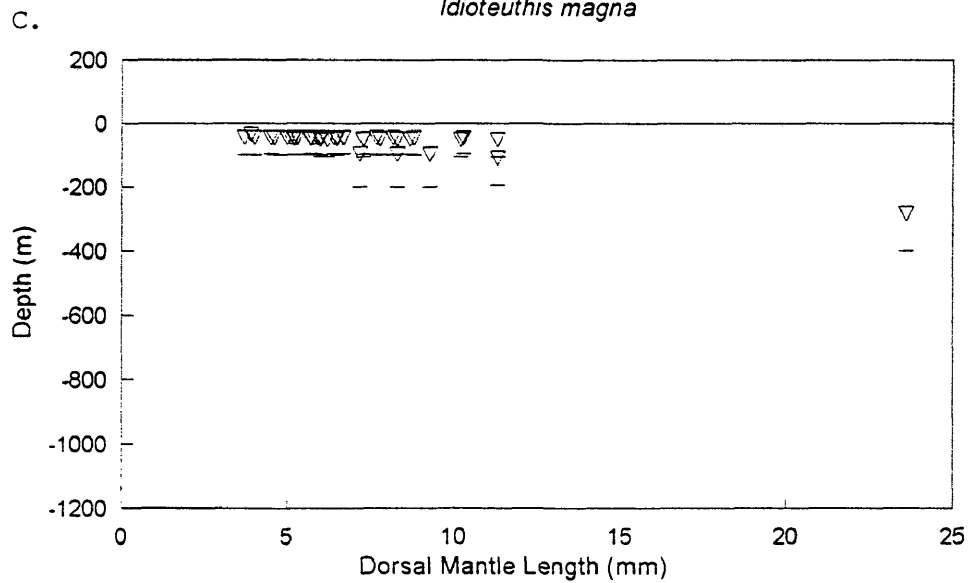
Vertical Depth Distribution
Idioteuthis magna



Depth vs. Dorsal Mantle Length (Day)
Idioteuthis magna



Depth vs. Dorsal Mantle Length (Night)
Idioteuthis magna



specimen, indicating a possible night time descent in depth of capture for larger specimen. Additional larger specimens are required to confirm this observation.

In the spring cruise of 1980, *I. magna* was caught in a very narrow latitudinal range, between 39-45°N, most in the upper 200m (Fig. 9a), with the largest concentration being caught at about 35°W. According to van der Spoel (1981), this location is a transition between the Sargasso Sea water mass and the Warm Temperate water mass. Water temperature at 200m [Figure 2 in van der Spoel (1981)] changes from 17°C at 39°N to 13-14 °C at 45° N. One of the hauls at the higher latitudes (40°N and 45°N) was in the 400-500m depth horizon. Van der Spoel (1981) identified this combination of depth and latitude as belonging to Arctic waters (<12 °C).

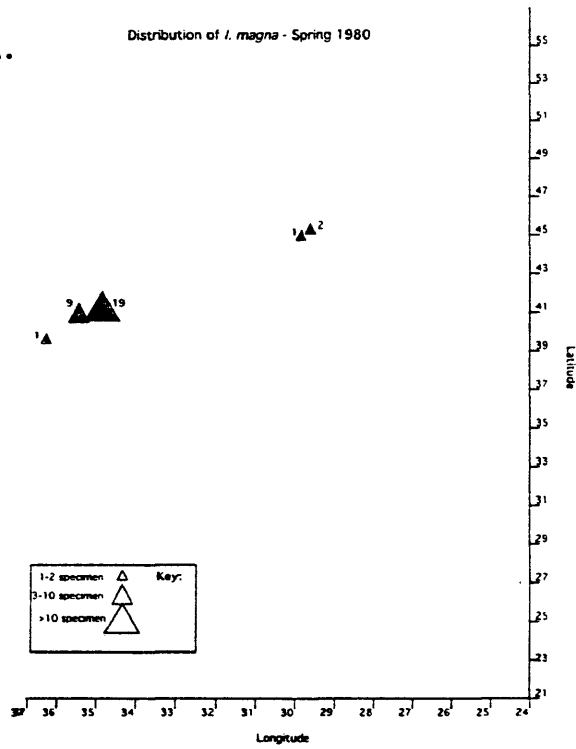
Only two specimens of *I. magna* were captured during the fall cruise of 1981 (Fig. 9b); both were found along the 30° W longitude line between 27-30° N (North Atlantic Central water), one from 100-200m, the other 300-400m. No specimens were captured during the winter cruise of 1982 (Fig. 9c).

Thirty-two specimens were caught during the 1983 summer cruise (Fig. 9d); most were captured between 41-45° N, although two tows were taken from 29-36° W. All but two hauls were taken from <200m in North Atlantic Central

Figure 9. Areal distribution of *Idioteuthis magna*. a) Spring 1980 b) Autumn 1981 c) Winter 1982 d) Spring/Summer 1983. Center of the triangle marks the collection point. Overlapping triangles were combined and the number of specimens were added. North - South and East - West depth distributions of *Idioteuthis magna*. Hauls that contained cephalopods at each latitude and longitude are represented. Multiple specimen may have been caught in each depth horizon e) Spring 1980 f) Autumn 1981 g) Winter 1982 h) Summer 1983.

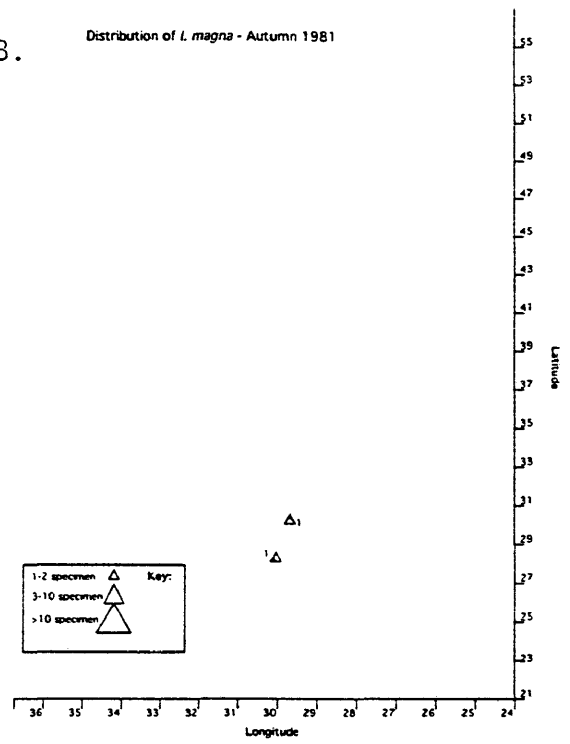
A.

Distribution of *L. magna* - Spring 1980



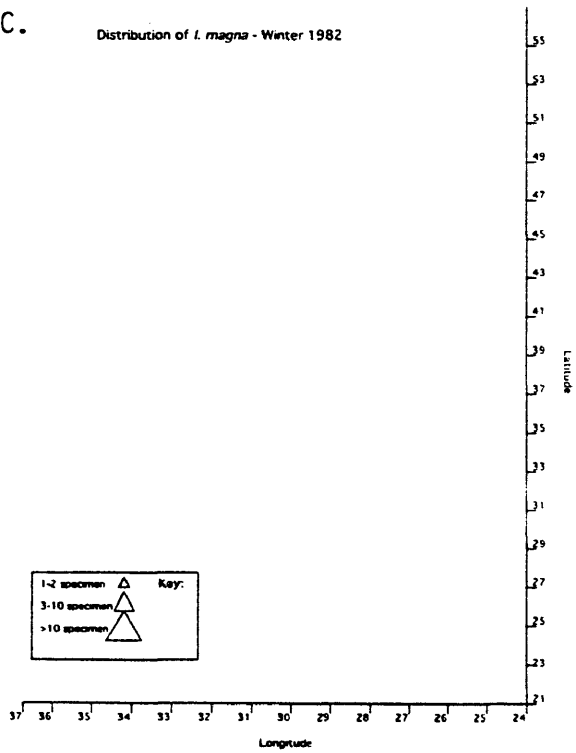
B.

Distribution of *L. magna* - Autumn 1981



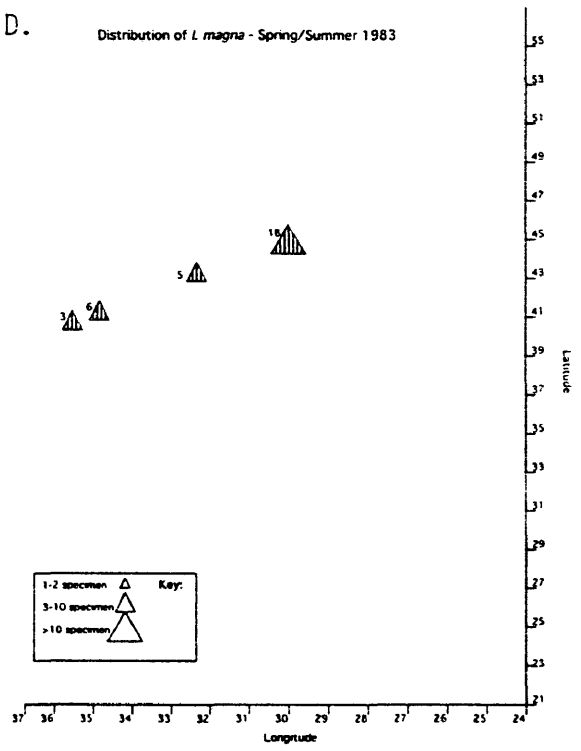
C.

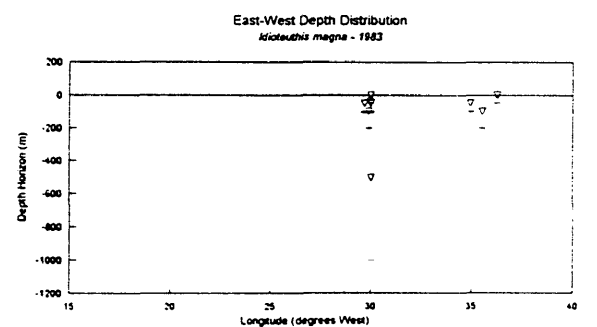
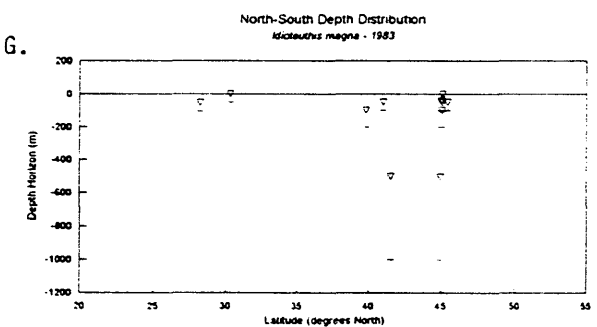
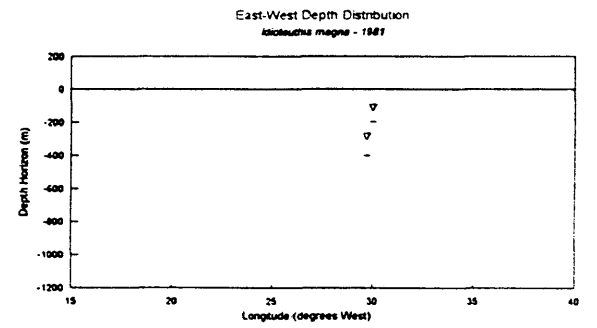
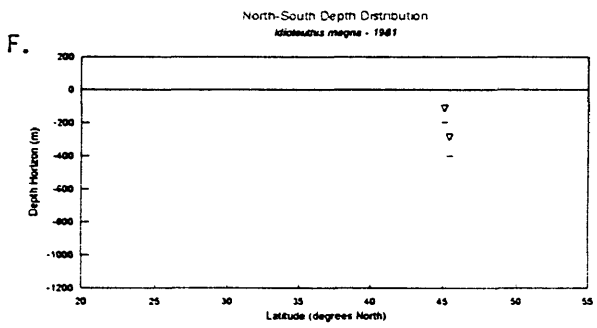
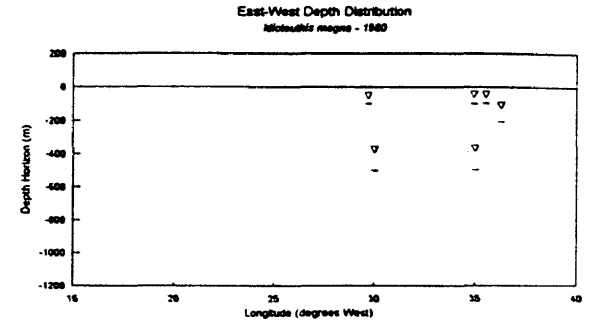
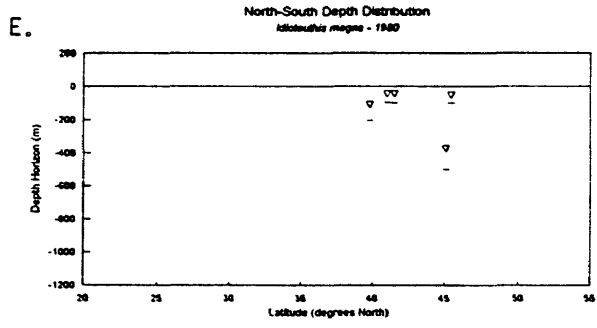
Distribution of *L. magna* - Winter 1982



D.

Distribution of *L. magna* - Spring/Summer 1983





water; the two deeper hauls were from 500-1000m, which had characteristics of both the North Atlantic Central waters and the North Atlantic Deep waters.

Morphometric Data

All but one specimen of *I. magna* fell within the 3-12mm DML size range; this data sub-set is very robust, with many specimens spread over the entire range.

The predominant pattern in *I. magna* is simple linear growth with a relatively low slope indicating that the DML grows faster than the other characteristics. Three exceptions occur, the fin dimensions, the mantle opening width, and the eye diameter.

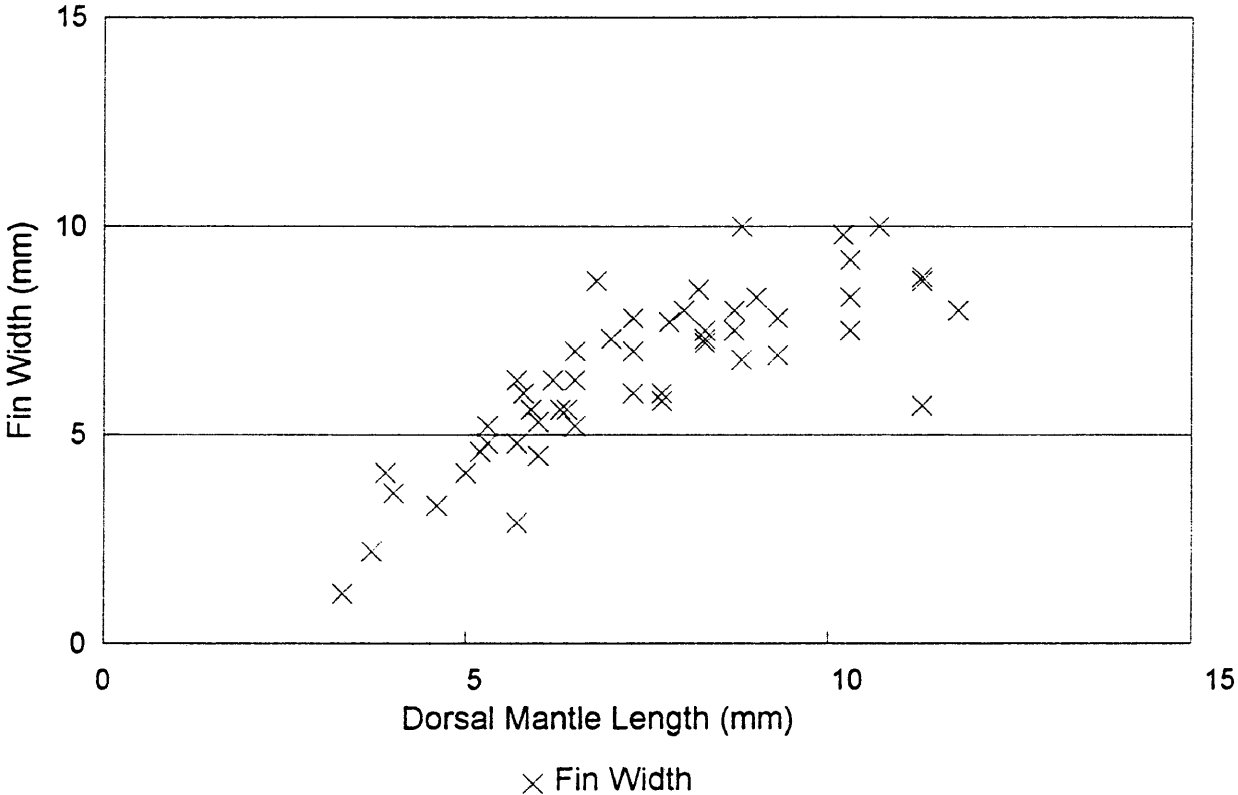
Fin measurement (Fig. 10a,b) data show a decrease in the slope of both width and length at about 7mm DML. Fin width is slightly larger than FL at all DML. At the largest DMLs, the FW grows to be approximately 80% of total DML, which is one of the species-diagnostic characteristics (Nesis 1987).

The *mantle opening width* (Fig. 10b) appears to level off after approximately 7mm DML, although there is considerable variation.

Figure 10. Morphometric analysis of *Idioteuthis magna*. a) fin width b) fin length
c) mantle opening width d) eye diameter.

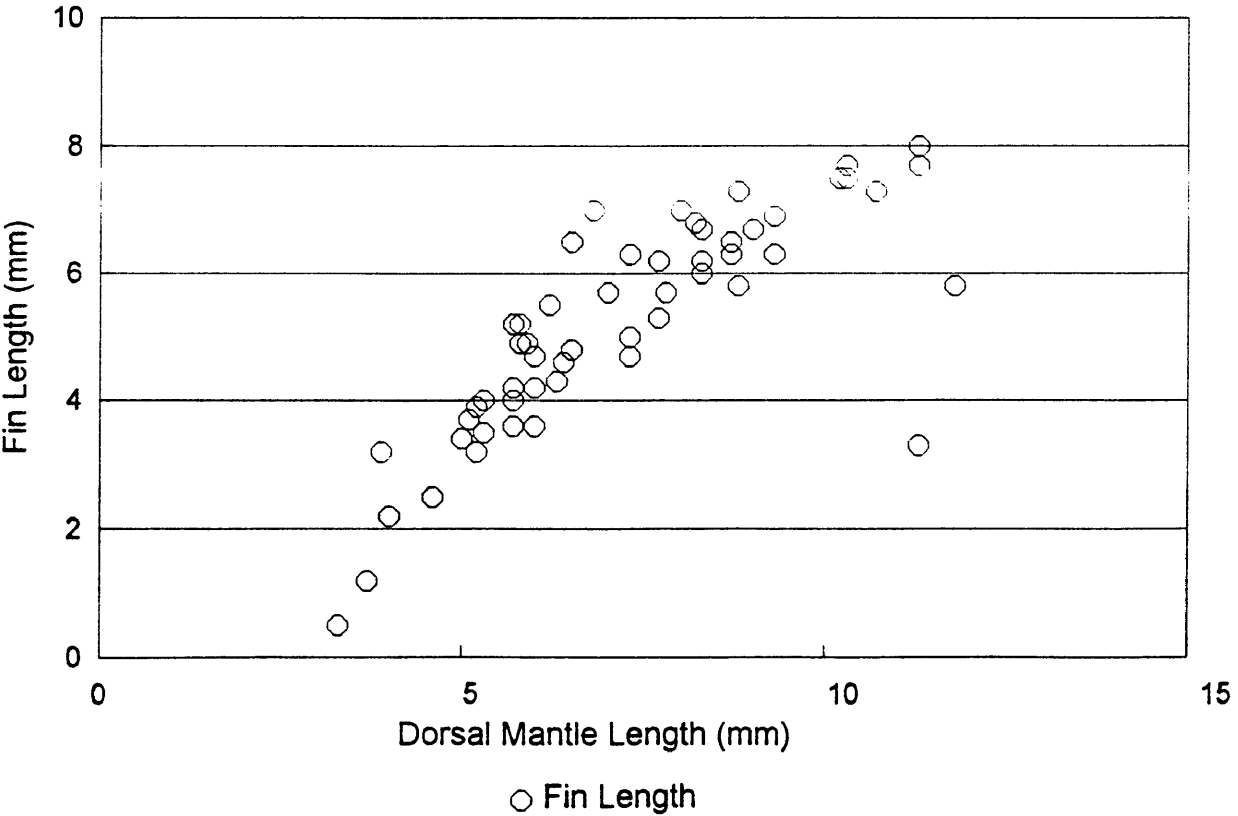
Fin Width vs. DML

A.



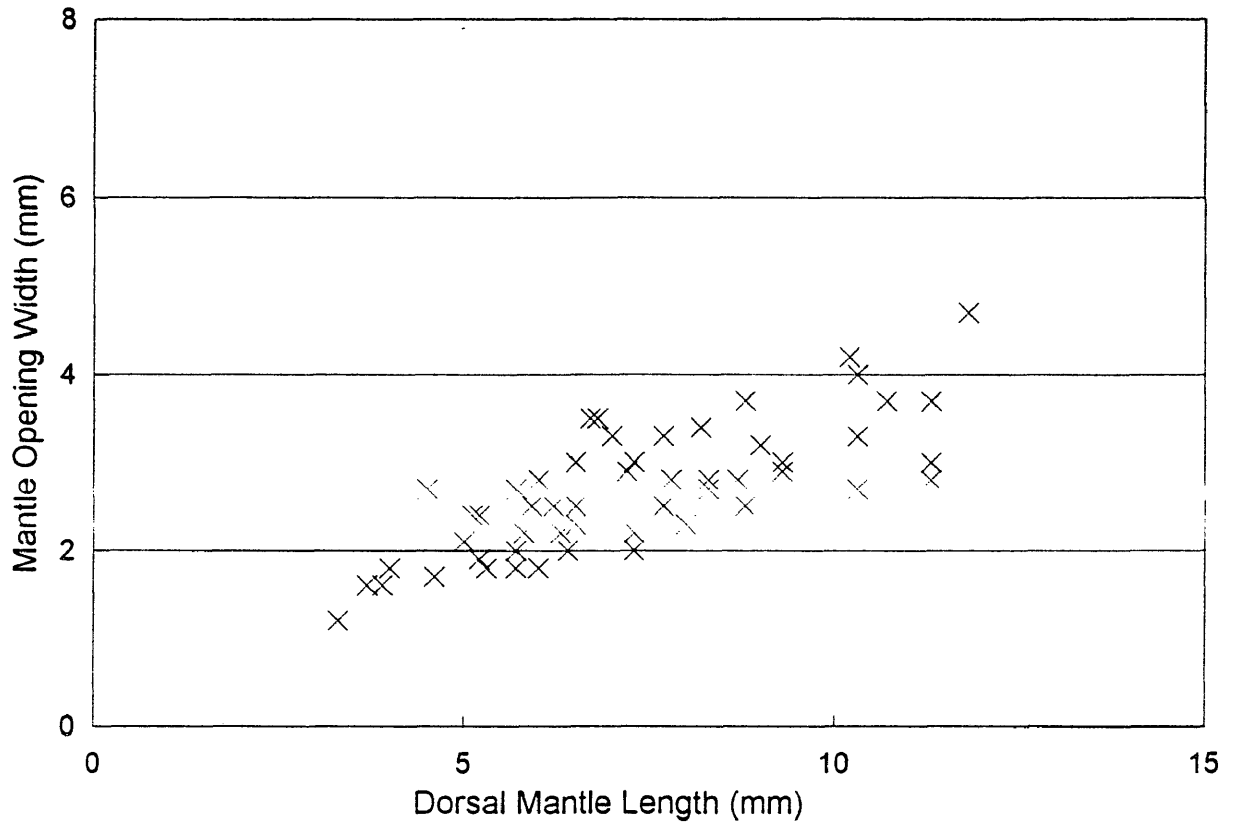
Fin Length vs. DML

B.



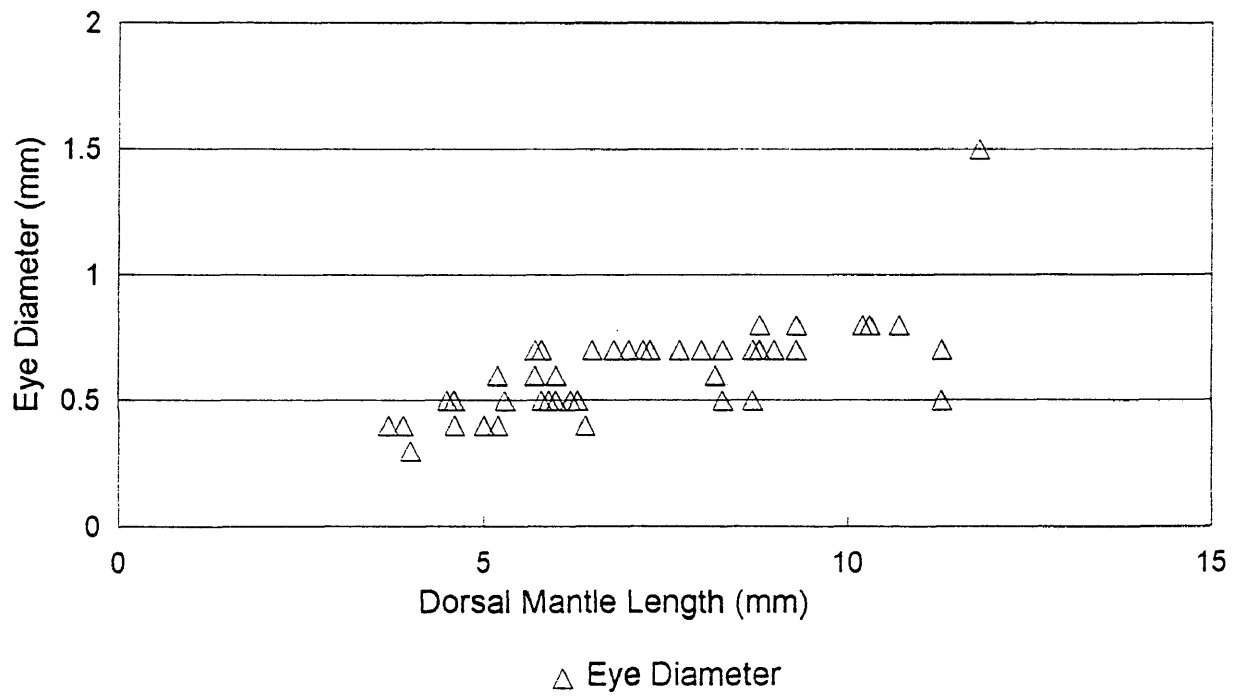
Mantle Opening Width vs. DML

C.



Eye Diameter vs. DML

D.



△ Eye Diameter

The *eye diameter* (Fig. 10c) trajectory appears to level off at approximately 6mm DML.

Ontogenic Changes in External Morphology

5.3mm DML (station-haul 14-10, bottle no. 544): Mantle moderately long, sack like, with large chromatophores along the dorsal midline. Head square, with statocysts large and clear; chromatophores on dorsal and ventral head, but pattern difficult to discern because of condition. Eyes small, anterior. Buccal apparatus large, with large beak. Tentacles missing. Arm formula 4>>2>1>3; swimming keel on fourth arm. Gladius extends considerably beyond the end of the mantle and beyond the end of the fins. Tail length approximately = to ML. Fins are large, circular; FL = 4/5 ML.

11.3mm DML (station-haul 50-13, bottle no. 3575): Characters same as before with the following exceptions: Eyes oriented antero-laterally. Arm formula 4>>2>3>1; arm suckers stalked; arm suckers on fourth arm are in 1 row, suckers on other arms are in 2 rows. Fin length has changed to 1/4th ML.

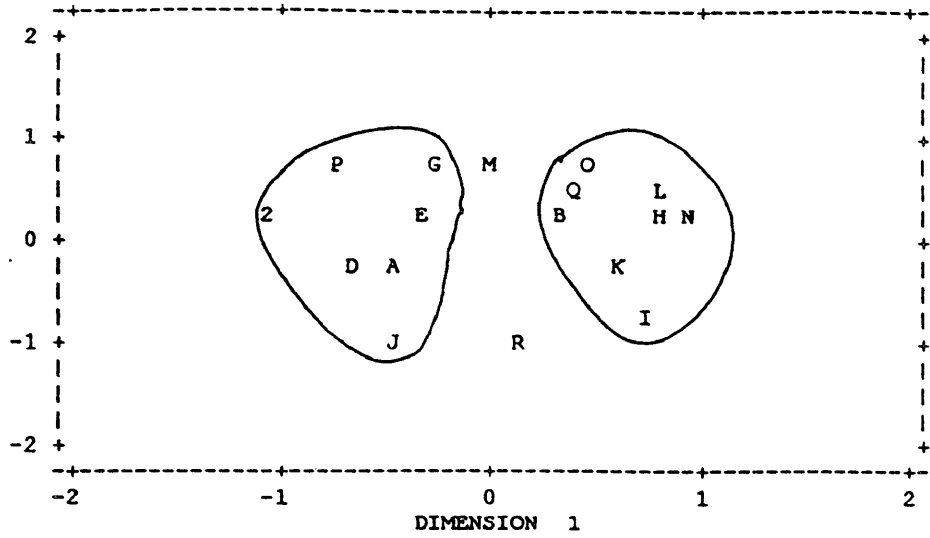
Multidimensional Scaling

The optimal configuration of both the day (Fig. 11a) and night (Fig. 11b) analysis was found in three dimensions, with stress equal to .107 and .126,

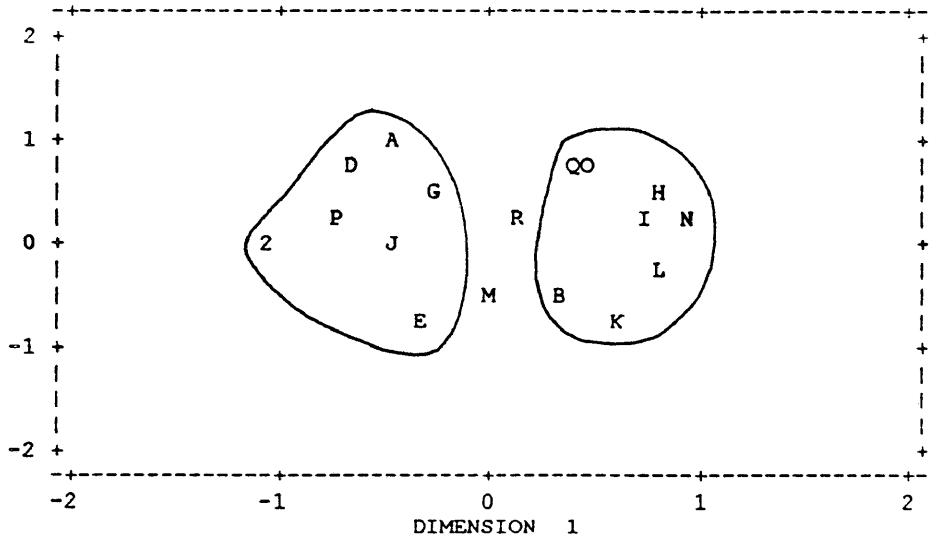
Figure 11. Multidimensional scaling analysis optimal configuration for *Idioteuthis magna*. Each letter represents one specimen. Axes described as follows, characters listed in order of importance. a) Day. Axis 1: latitude, longitude, ED, DML. Axis 2: HW, HL, salinity, temperature. Axis 3: funnel dimensions b) Night. Axis 1: DML, salinity, FL, FW, MOW, Funnel length. Axis 2: FL Axis 3: MOW.

DIMENSION 2

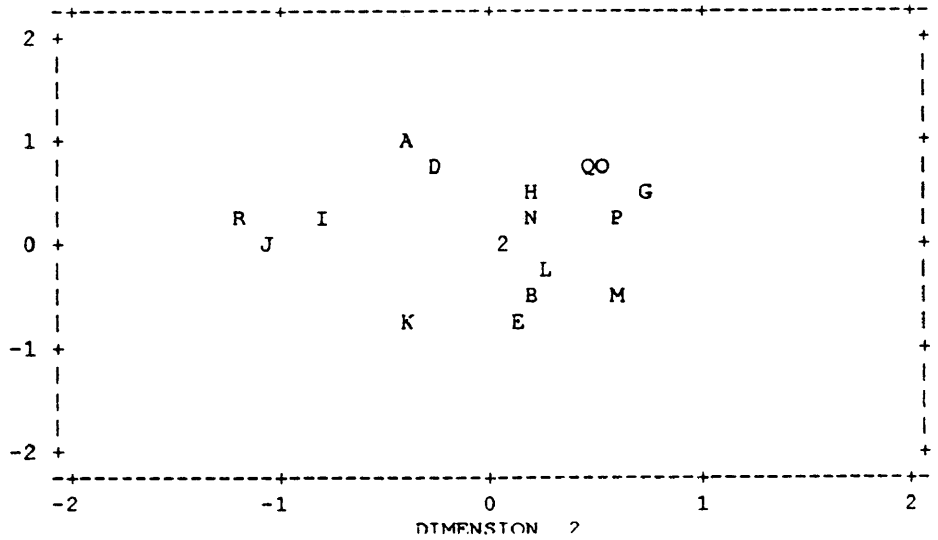
A.

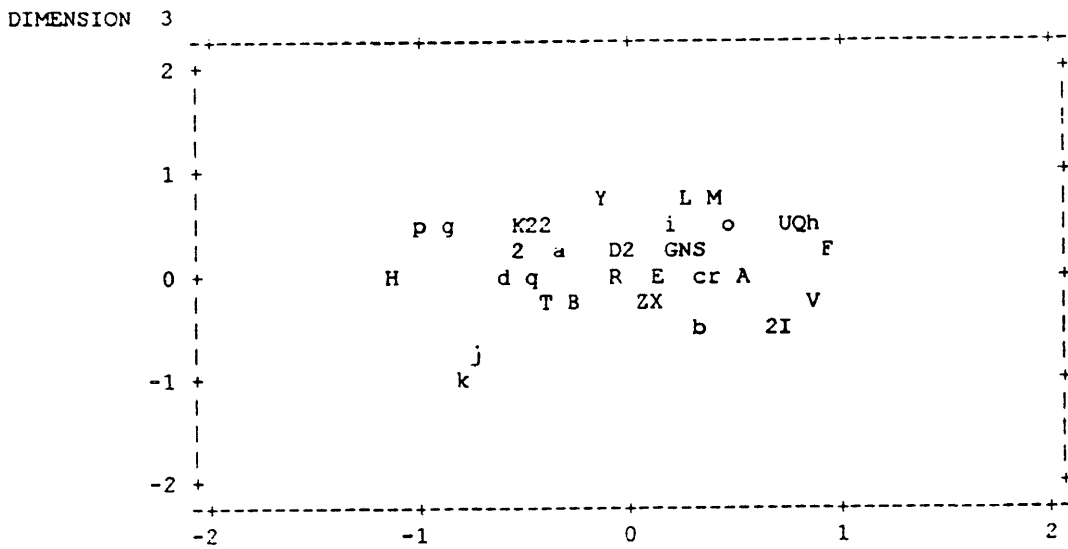
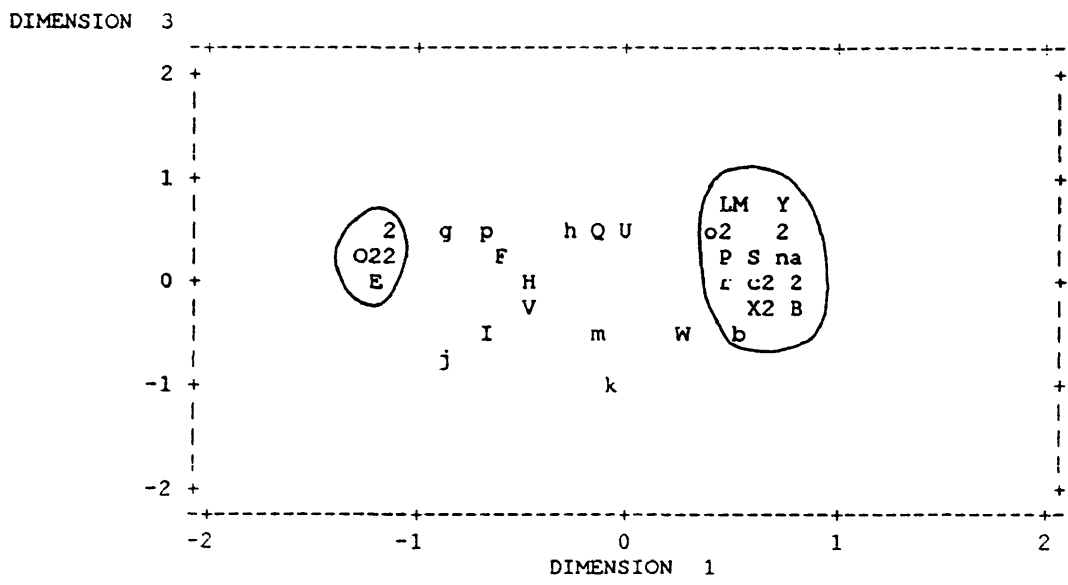
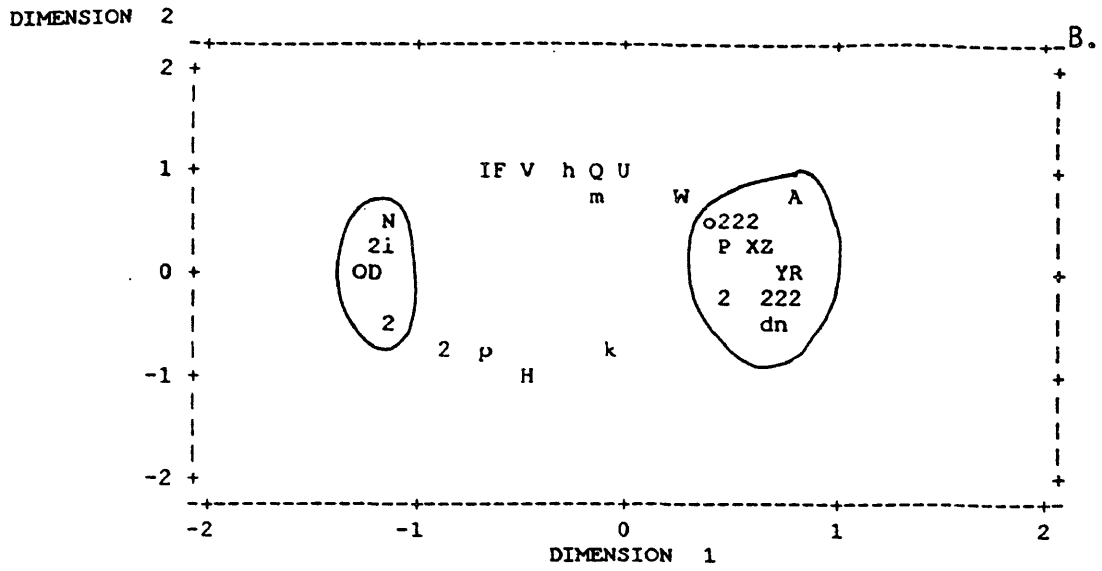


DIMENSION 3



DIMENSION 3





respectively. Shepard diagrams for both showed some variability, but the overall patterns were straight lines without any evidence of steps.

In the daytime, the first axis was described by the DML (-.769), ED (-.743), FL (-.673), HW (-.642), HL (-.650), latitude (-.686) and longitude (.627); the second axis by the HW (-.725), HL (-.699), salinity (.763) and temperature (.762); and the third axis by FunW-A (.796), FunW-P (.837) and FunLen (.885). The optimal configuration shows specimens fall out in two groups based on the first axis. Salinity and temperature were important in describing the variability but were not responsible for grouping the data. Average depth of capture did not describe the variability of the configuration at all.

At night, the DML (-.709), FL (-.643), FW (-.606), MOW (-.615), FunLen (-.600), and salinity (.670) describe the variability in the first dimension; fin length (.600) also describes the second axis. The MOW (-.627) describes the third axis. The variability of the optimal configuration is mostly described by the morphometric characters of the mantle (DML, MOW) fin (width and length) and the funnel length. Two groups of specimens are found based on the first dimension, as indicated in Fig. 11b; the difference between the two groups can be principally attributed to size differences in the captured specimens. The second and third dimension descriptors are also found describing the first

dimension, and the circular patterns seen are most likely artifacts of this duplicity.

Mastigoteuthis agassizii (Fig. 12)

Depth and Areal Distribution

Histograms of specimens at depth (Figure 13a) show that during the day, all specimens were caught between 500-1000m. Three were taken with a malfunctioning opening/closing net that fished a 0-1000m depth horizon. At night, a slight decrease in depth occurs, with some specimens found between 400-500m.

When the captures are sorted by DML (Figures 13b,c) the day time captures show that most specimens were caught between 500-1000m. No trend in depth of capture with increasing DML is evident. At night, one specimens (15.5 mm) was taken from the 0-500 depth horizon. The remaining 12 specimens (7.5-62.5 mm) were found between 500-1000m.

During the spring cruise of 1980, all specimen were found north of 35° N (Fig 14a), and almost all were found in water >500m depth. This combination of latitude and depth puts them squarely in the Arctic deep waters (van der Spoel 1981). In 1981, all specimens were caught above 41° N (Fig 14b). All but two specimens were caught between 500-1000m, again in the Arctic polar water (van

Figure 12. Illustration of 9.7 mm DML *Mastigoteuthis agassizii* (Station-haul:16-3, bottle 706). Dorsal and ventral view.

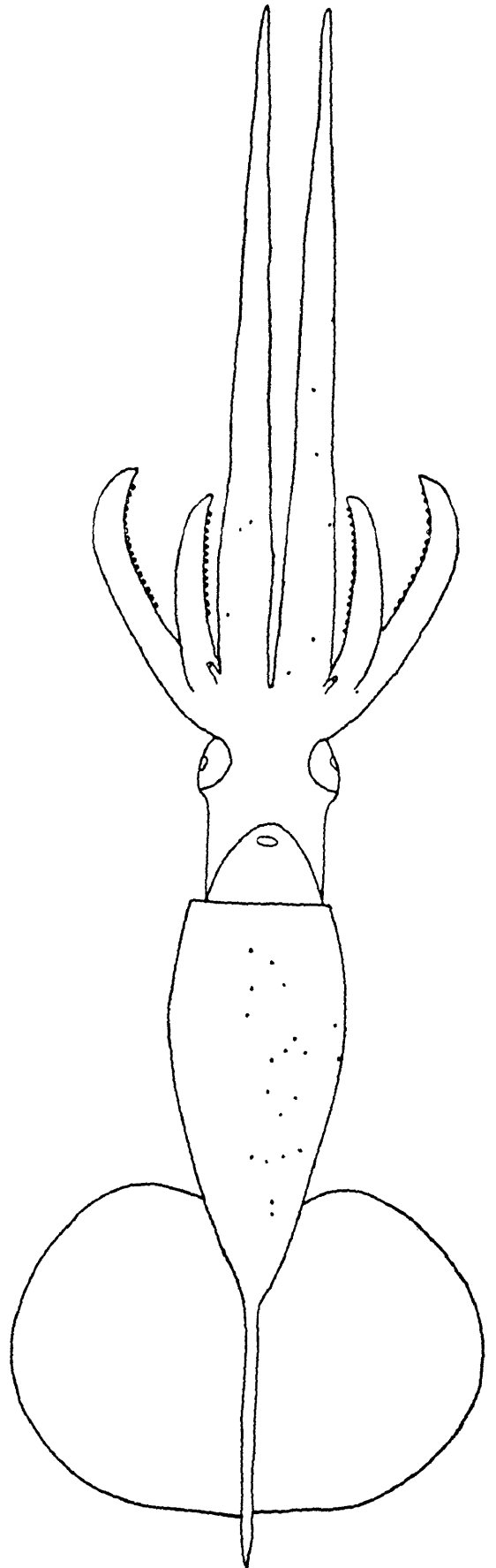
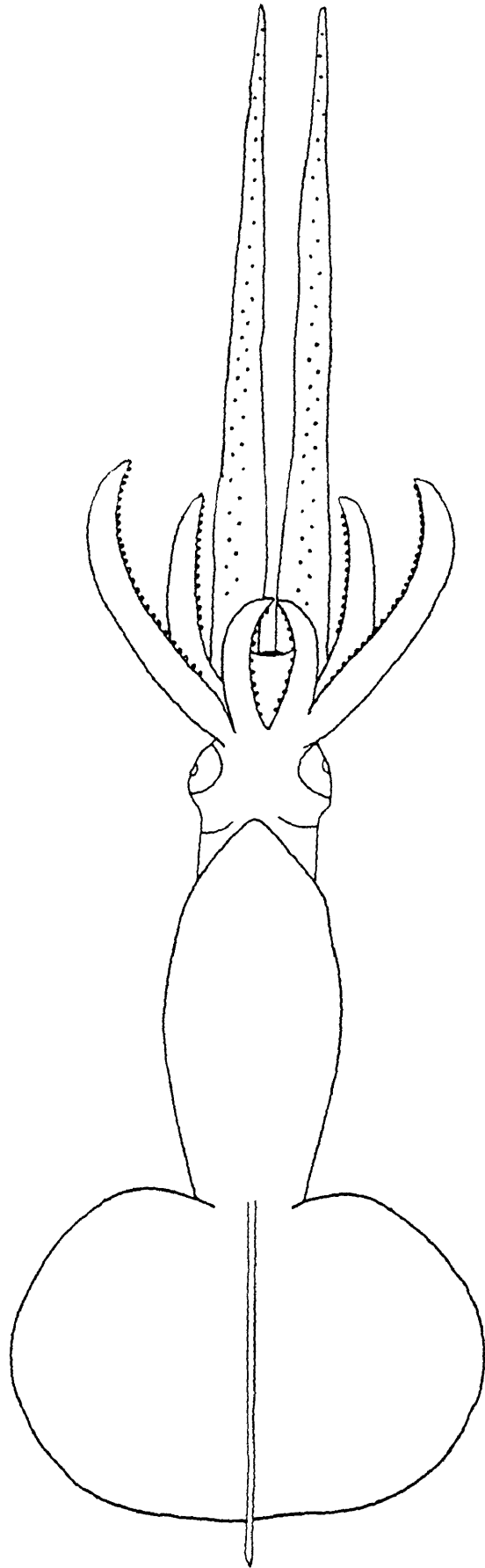
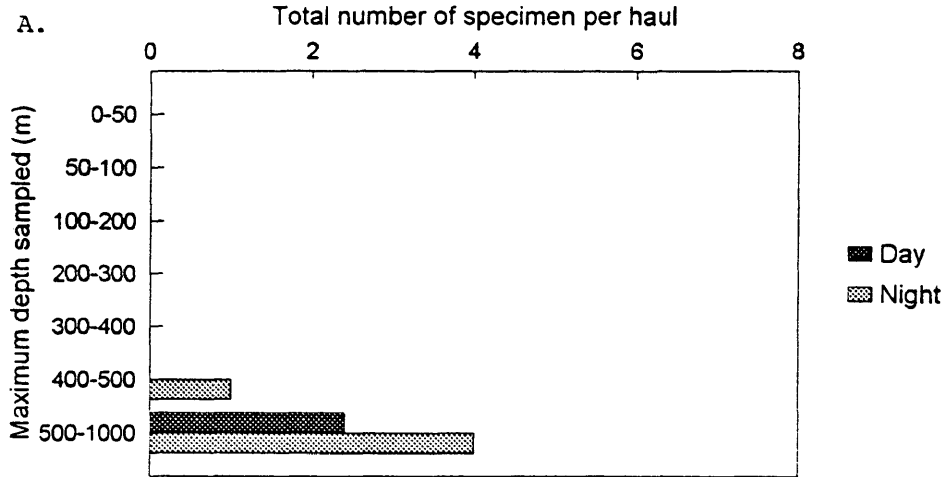
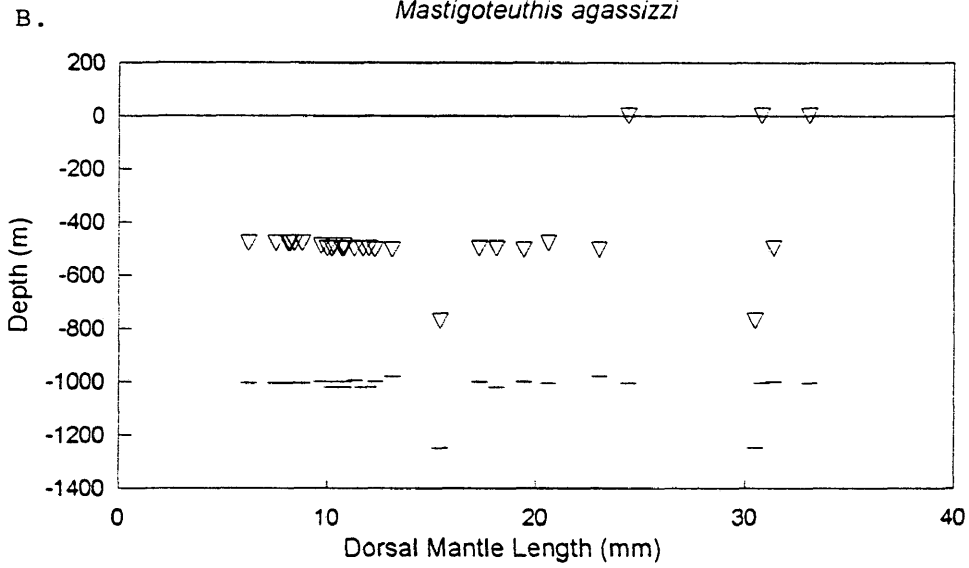


Figure 13. Depth distribution of *Mastigoteuthis agassizii*. a) Number of specimen per haul at each depth horizon during day and night b) day time depth of capture plotted against DML c) night time depth of capture plotted against DML. Net opened at triangle and closed at horizontal line. Each triangle/line combination represents one collected specimen. Note: Bottom depth is illustrated for 0-1000m depth horizon collected by malfunctioning opening/closing net.

Vertical Depth Distribution *Mastigoteuthis agassizzi*



Depth vs. Dorsal Mantle Length (Day) *Mastigoteuthis agassizzi*



Depth vs. Dorsal Mantle Length (Night) *Mastigoteuthis agassizzi*

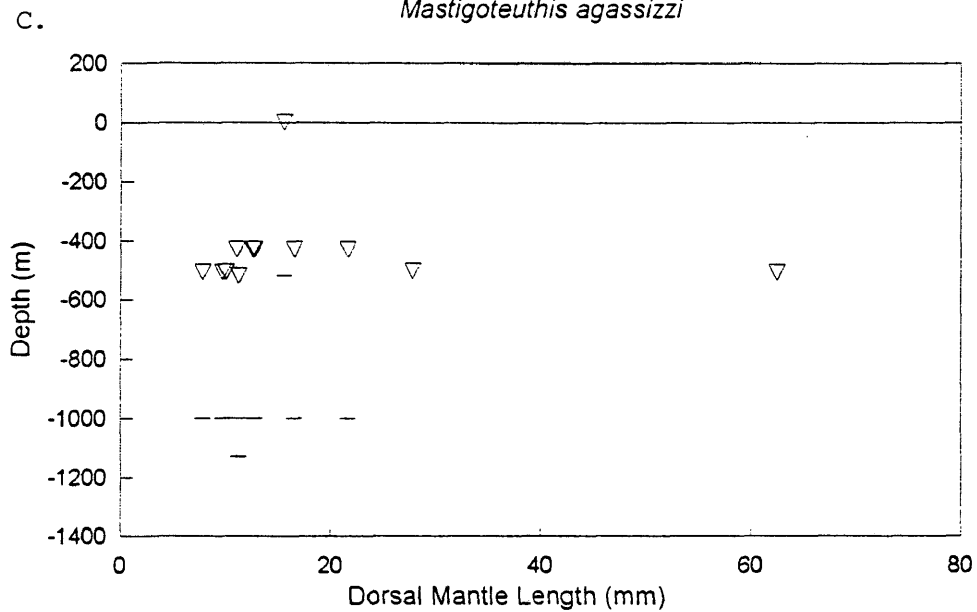
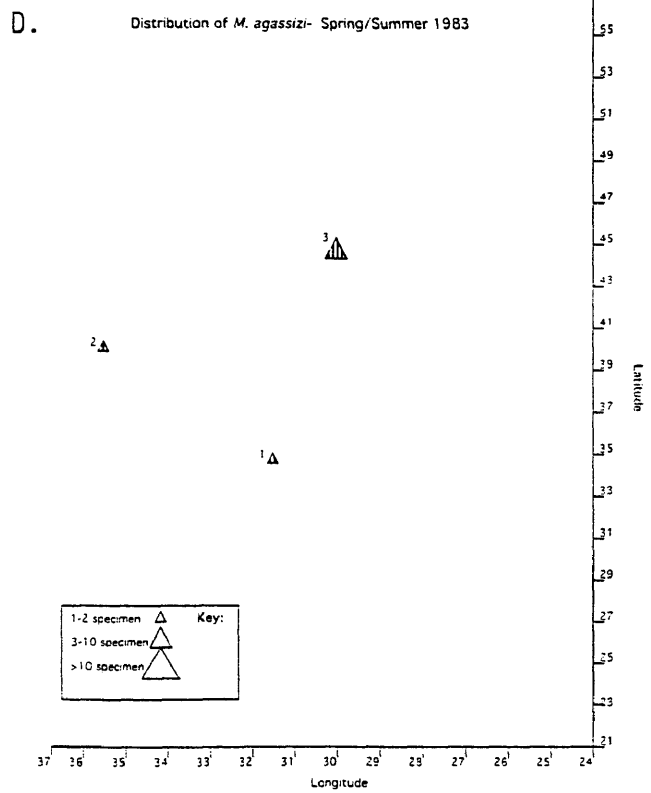
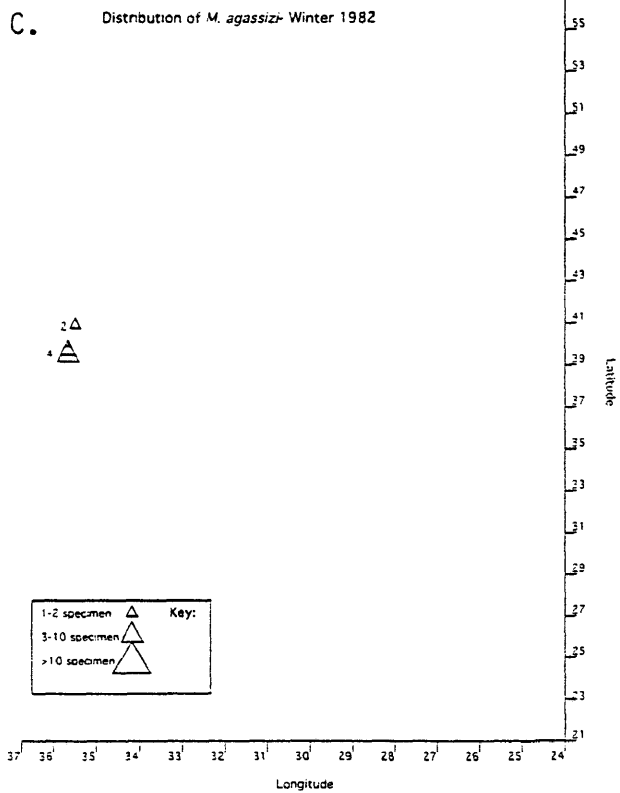
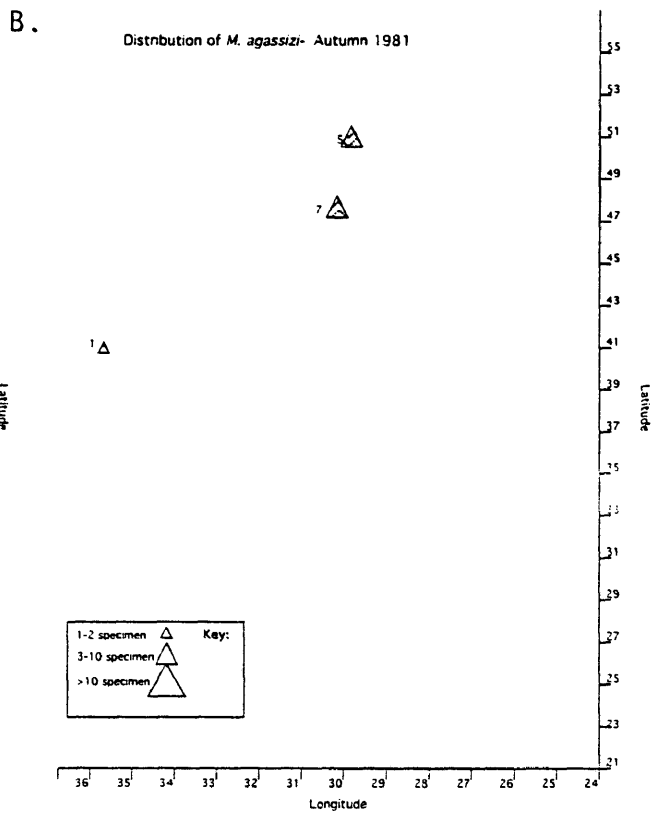
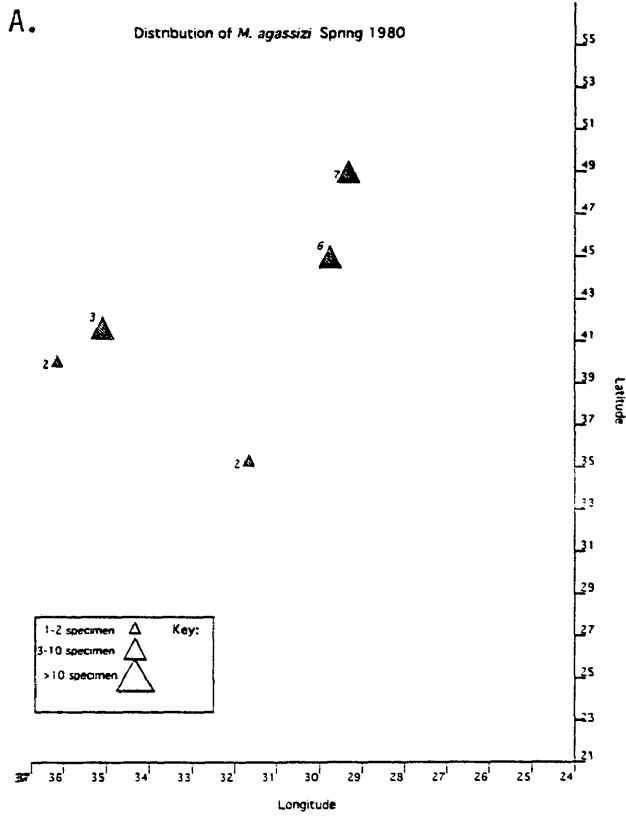
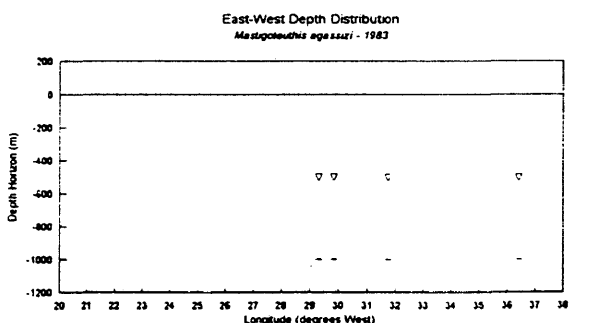
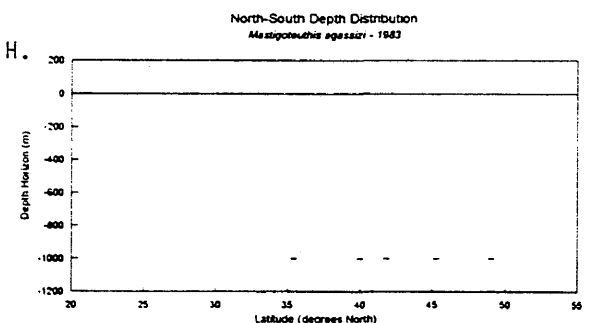
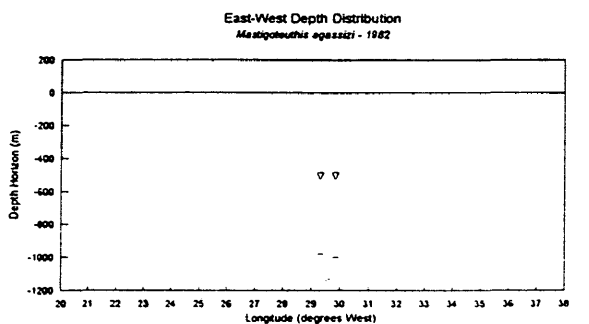
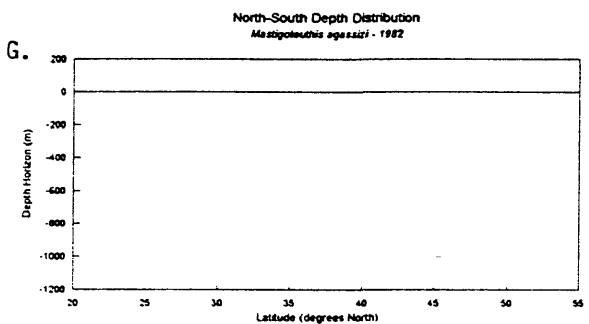
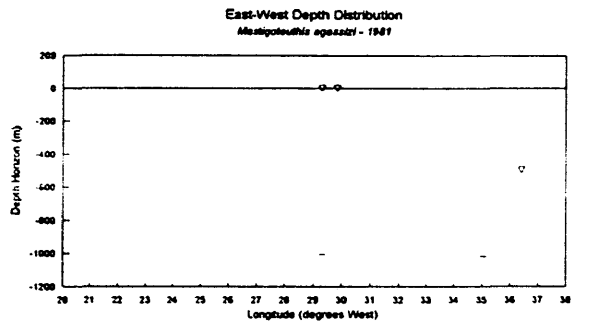
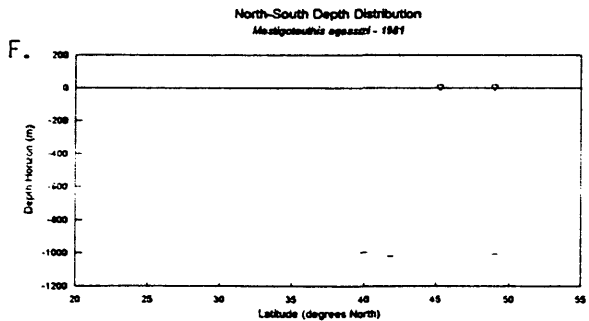
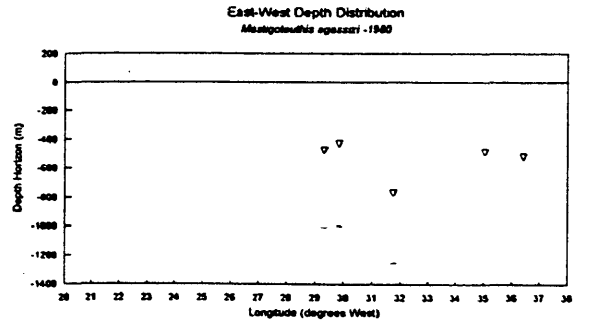
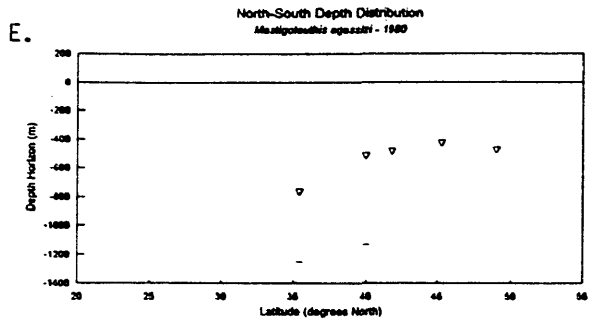


Figure 14. Areal distribution of *Mastigoteuthis agassizii*. a) Spring 1980 b) Autumn 1981 c) Winter 1982 d) Spring/Summer 1983. Center of the triangle marks the collection point. Overlapping triangles were combined and the number of specimens were added. North - South and East - West depth distributions of *Mastigoteuthis agassizii*. Hauls that contained cephalopods at each latitude and longitude are represented. Multiple specimen may have been caught in each depth horizon e) Spring 1980 f) Autumn 1981 g) Winter 1982 h) Spring/Summer 1983.





der Spoel and Meerding 1983). Because of the very strong trend for *M. agassizii* to be found in the deep waters, it is probable that these specimens were also taken from the deeper portion of the haul in the Arctic polar waters.

Six specimens were caught during the 1982 winter cruise between 39-41° N along the 36° W line, presumably from the North Atlantic Drift water (Van der Spoel 1985) (Fig. 14c). Depth of capture was 500-1000m. Six specimens were caught during the 1983 summer cruise, between 34-45° N in 500-1000m of water, in the North Atlantic Deep water (Fig. 14d).

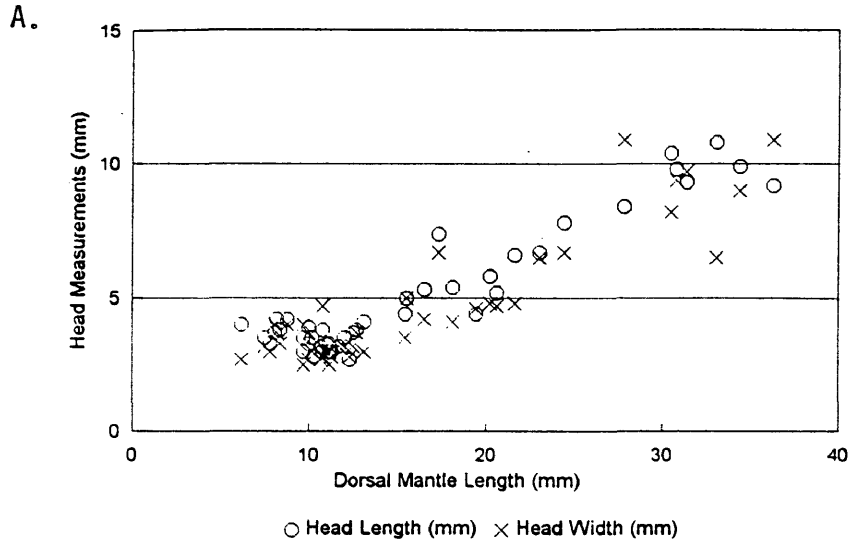
Morphometric Data

All but one specimens of *Mastigoteuthis agassizii* were between 3-40mm DML.

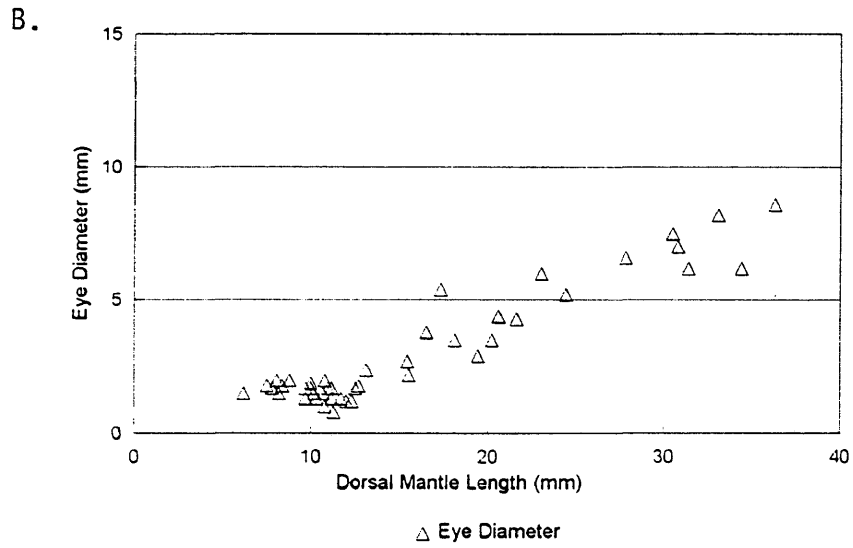
The *head and eye measurements* (Figure 15a,b) have the most dramatic changes apparent in the scatterplot. Head length and head width appear to be almost constant over the 3-11 mm DML range; at approximately 11mm DML a sudden increase occurs in the length and width with increasing DML. Throughout the entire size range, the length and width data are virtually superimposed on each other, indicating that they are not only equal in measurement, but also follow the same growth patterns. The eye diameter

Figure 15. Morphometric analysis of *Mastigoteuthis agassizii*. a) head measurements b) eye diameter c) funnel width vs. funnel length.

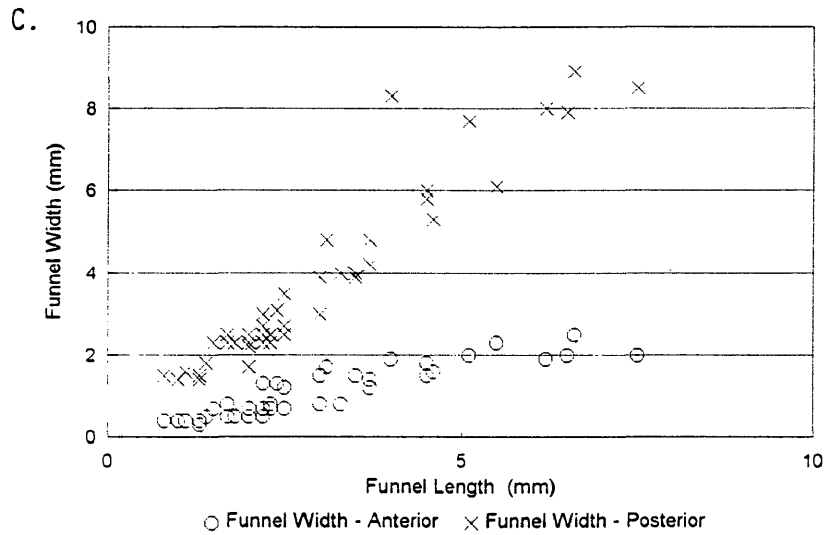
Head Measurements vs. DML



Eye Diameter vs. DML



Funnel Width vs. Funnel Length



follows the same patterns as described above with the inflection point at 11-12mm DML.

The anterior and posterior widths of the *funnel* (Fig. 15c) compared to the funnel length show a leveling off (FTW) or a decrease in slope (FBW) at approximately 2.5mm FunLen. A 4mm funnel length corresponds approximately to a DML of 12mm (see Appendix A).

Ontogenic Changes in External Morphology

9.7 mm DML (station-haul 16-03, bottle no. 706): Mantle sac-shaped, gelatinous. Chromatophores small, circular, dark brown to purple. HW = MOW. Eyes large, anterior. Arm formula 4>>>2>3>1.. Arm suckers very small in two rows. Arm suckers more densely packed on arms 1-3 than on arm 4. Buccal apparatus and beak large and protruding.

10.8 mm DML (station-haul 39-14, bottle no. 4532): Mantle long, gelatinous, tapered to a point at the posterior end. Mantle chromatophores small, densely spaced, red to purple. Gladius continues past end of mantle to form support for large, semi-circular fins; gladius extends beyond fins. Head square-ish, with dorsal and ventral chromatophores; statocysts very large. HW = MOW. Eyes large, anterior; ED = 1/2 HL. No reflective tissue on ventral eye. Buccal mass and beak very large. Arm formula 4>>2>3>1. Arm suckers small, stalked;

in 2 rows on arms 1-3, 2 rows then 1 row on arm 4. Remnant swimming keel noted on arms 4,3,2. No trabeculae present. Tentacles absent. Statocysts very large and obvious.

16.5 mm DML (station-haul 14-05, bottle no. 0537): Mantle long, gelatinous, becoming more sac-shaped. Posterior end of the ventral mantle getting thicker, as if mantle is growing into the fin area. Mantle chromatophores small, dense, red to purple. More chromatophores on ventral mantle than dorsal mantle. End of gladius broken. Fins very large and wide compared to mantle. HW = > MOW. Statocysts not noticeable. ED = 3/4 HL. Arm formula 4>>3>2>1. Buccal mass and beak are very large and reddish. Tentacles absent. Internal organs in upper 1/2 of mantle cavity, very near funnel.

27.8 mm DML (station-haul 81-06, bottle no. 7935): mantle long, gelatinous. Chromatophores over entire mantle and arm complex, small red to purple imbedded in skin. Fins very large, FL = ML and FW > ML. Head compact, statocysts not noticeable. HW > MOW. Eyes lateral and approximately equal to head length. Arm formula: 4>>2>3>1. Buccal mass large, but proportional to rest of body. Internal organs enlarged to encompass entire mantle cavity.

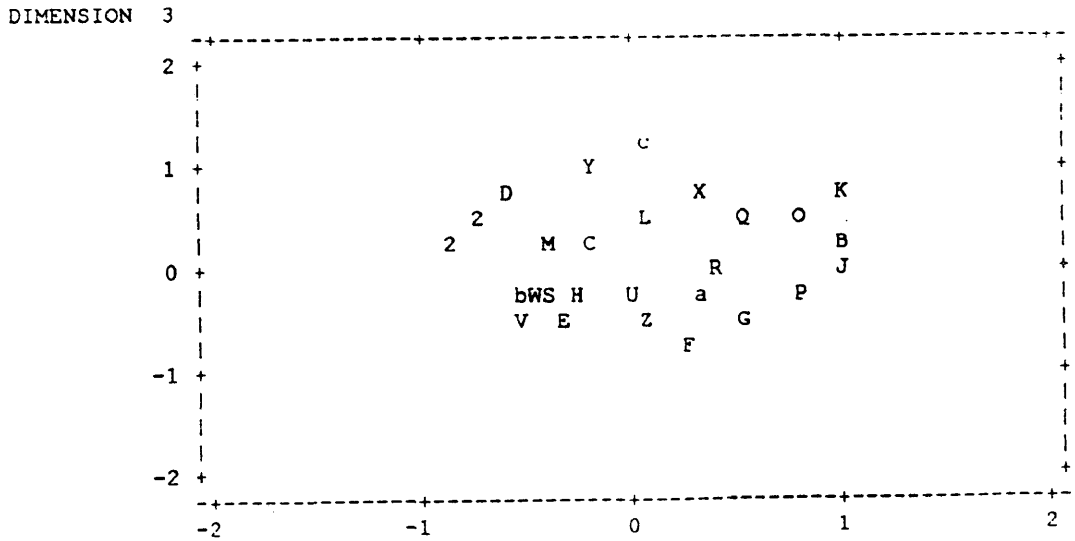
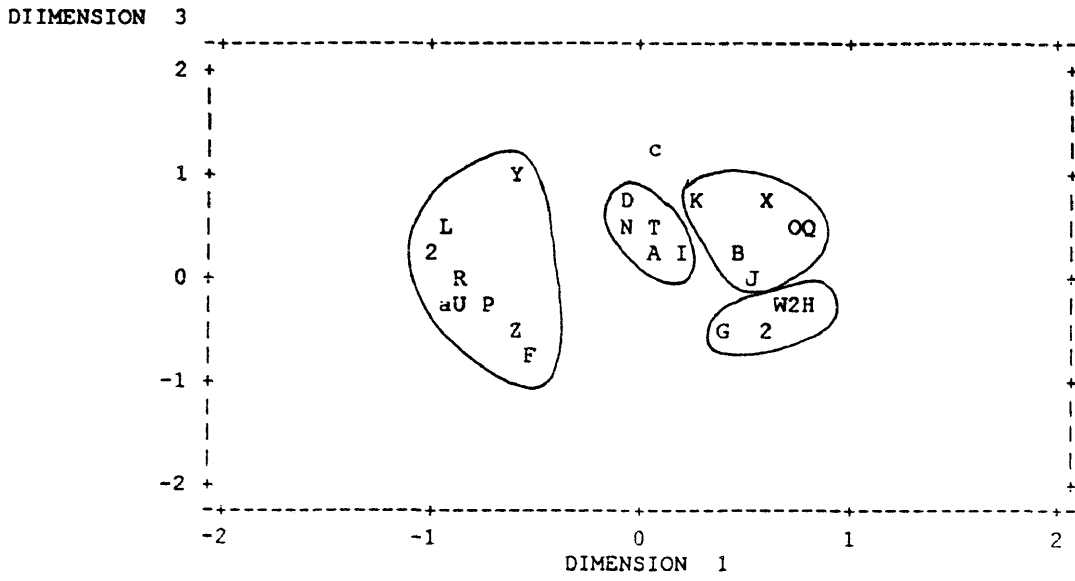
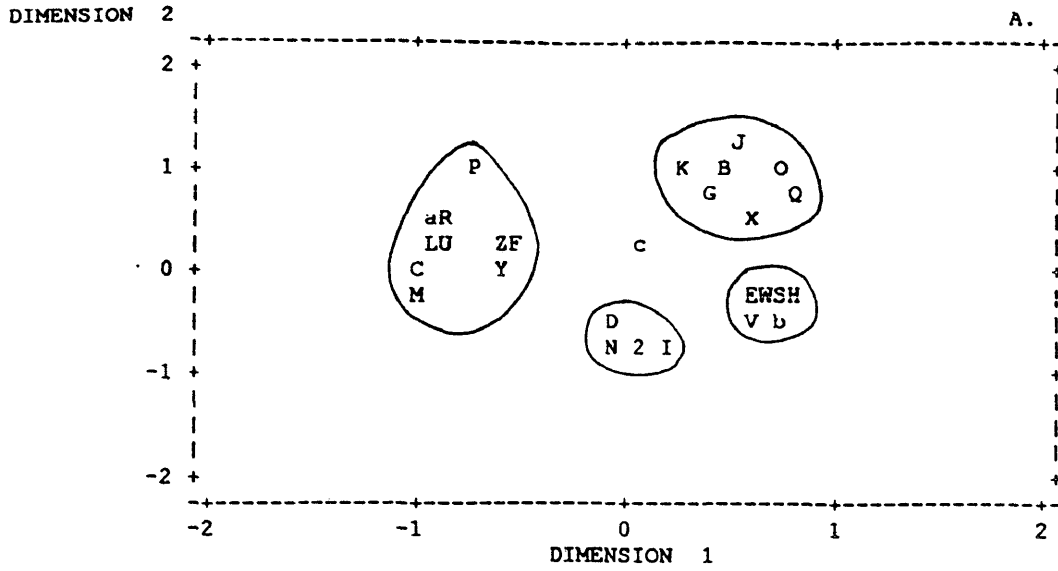
Multidimensional Scaling

Results of the daytime analysis (Fig. 16a) was best represented in three dimensions (stress= .085, Shepard diagram = straight); the night time configuration (Fig. 16b) was best in two dimensions (stress = .076, Shepard diagram = straight). The lack of night time salinity data is most likely the reason for this disparity in dimensionality, since the variability in the third dimension during the day was explained by the salinity data.

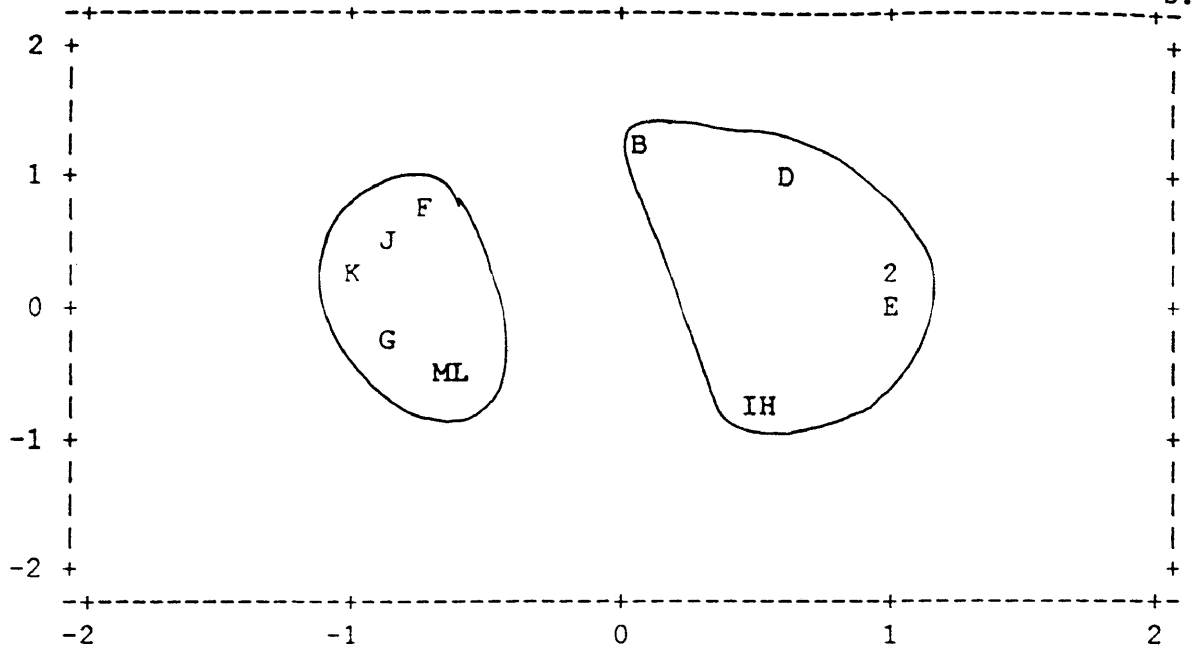
The first day time axis was described primarily by latitude (.850) and longitude (-.883) and somewhat by temperature (-.645) and depth (-.501). The second axis was described by all the morphological measurement data (range: DML = .721 to MOW = .858), and the third was explained by the salinity data (.663). Specimens are clumped into four groups based on the first axis (station data); one group incorporates considerable variation in morphology and salinity, the other three group according to differences in morphology and salinity.

The night time analysis showed similar results, with the latitude (-.956), longitude (.819) and depth (.819) explaining most of the variability of the first axis, and the morphological measurements explaining the second (range: DML = .613 to FW = .973). The resulting optimal configuration is a circular pattern which can be broken into two groups because of a discontinuity along the first axis.

Figure 16. Multidimensional scaling analysis optimal configuration for *Mastigoteuthis agassizii*. Each letter represents on specimen. Axes described as follows, characters listed in order of importance. A) Day. Axis 1: latitude, longitude, temperature and depth. Axis 2: morphological characters. Axis 3: salinity B) Night. Axis 1: latitude, longitude and average depth. Axis 2: morphological characters.



DIMENSION 2



DIMENSION 1

Family Brachioteuthidae

Young: Mantle elongate to elongate/bulbous; fins separate, terminal, paddle-shape, transversely oval; distinctive long, slender neck (no arm-crown stalk); eyes lateral but frequently occur toward ventral part of head; distinctive swelling on dorsal surface of head; mantle opening wide relative to neck; club suckers develop at hatching and adult-like pattern of numerous suckers on proximal manus well established by about 10mm ML; tentacles large, present at hatching, robust relative to arms" (Roper and Sweeney, p.158 in Sweeney et al. 1992).

The family Brachioteuthidae contains one genus (*Brachioteuthis*) and five species (*beanii*, *riisei*, *behnii*, *bowmanii*, and *picta*), but it is greatly in need of revision. Taxonomic confusion within the family can be attributed in part to poor original descriptions, and in part to the paucity of available mature specimens in good condition. A brief chronology of the family, and evidence that identifies two of the four morphotypes found in the AMNAPE collection follows.

A.E. Verrill erected the genus *Brachioteuthis* in 1881 and described its type species, *B. beanii*. Verrill used the similarity in external morphology (in particular, the rounded head and extended neck) to attribute the new genus to

the family Chiroteuthidae. No measurements were given within the text, but a life-size illustration of the dorsal arms, head and mantle was provided.

Steenstrup (1882) established a new genus, *Tracheloteuthis*, which he placed in the family Ommatostrephidae (Hoyle 1886, Pfeffer 1900). He went on to identify two new species attributed to the new genus, *Tracheloteuthis riisei* and *T. behni*. The species are separated based on the relative lengths of the fins and arms. In *T. riisei*, the fin length equals one-third the mantle length and the ventral arms equal two-thirds the lateral arms; the proportions of *T. behni* are very similar- fin length = $1/4$ mantle length and ventral arm length = $1/2$ lateral arms. Steenstrup ended his paper promising a more detailed description and figures later. Unfortunately, his next paper (Steenstrup 1898), which was published post-humously, reiterates the original description verbatim, and then adds an examination of the similarities and differences between *Verrillola* (Pfeffer 1884) and *Tracheloteuthis* (Steenstrup 1882). No additional characters were described to augment the original descriptions.

In 1905, Hoyle attempted to retrieve Steenstrup's type specimens to verify some of his own identifications. After deducing the identity of the type specimen, Hoyle addressed the usefulness of the diagnostic characters given by Steenstrup (1882), and he concluded that there is no reason to differentiate

between *T. riisei* and *T. behni*, "It will be seen that in several instances the same specimen would be placed in one species by the former criterion and in another by the latter. This is sufficient to throw grave doubt upon the efficacy of such features as diagnostic characters." (p. 96 in Hoyle 1905) Hoyle placed *behni* in synonymy with *riisei* maintaining the name *riisei* because it was the first species described by Steenstrup (1882); however, *T. riisei* and *T. behni* should be considered of dubious status because of their poor original descriptions, and because the designated type specimens are uncertain (Hoyle, 1905).

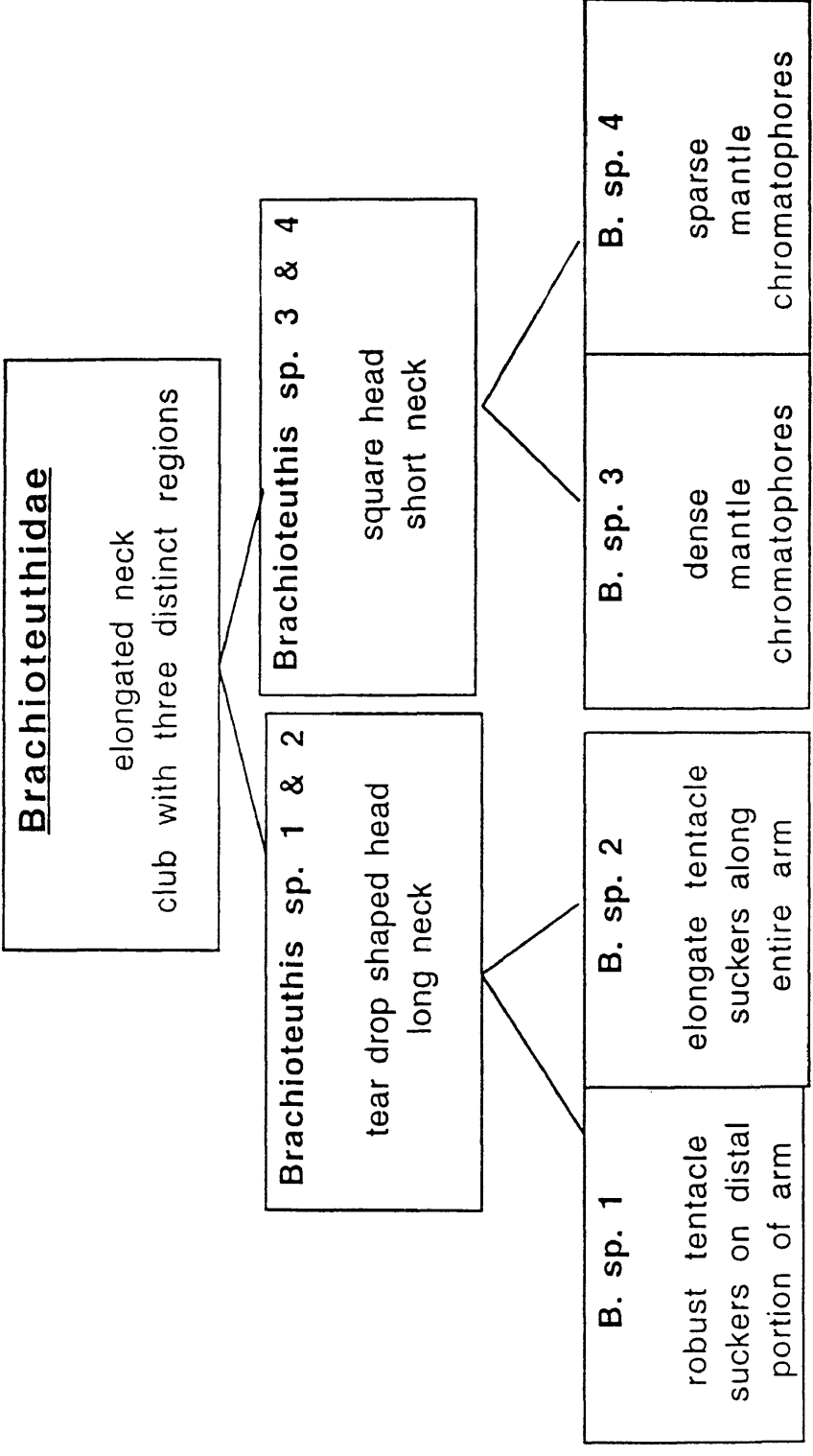
Mr. E.S. Russell described *Brachioteuthis bowmanii* (family = Brachioteuthidae) in 1909 from a single female of 61 mm ML caught at 61° 27' N, 003° 42'W (Russell 1909). He included a general description and measurements of external features. Russell (1922) gave a verbatim copy of the original description, but augmented the description with station data and six drawings. Russell believed that the specimen closely resembled *B. beanii*, but described it as new because it differed in "The great size of the head and eyes, the pigmented cornea, the shape of the anterior margin of the mantle, the peculiarities in the structure of the suckers and of the tentacular club" (p. 451). I believe that the specimen was sufficiently differentiated from other species, and that confident identification of new specimens to *B. beanii* is possible.

Soon after Russel's 1909 paper, Chun (1910) described the fifth and final new species, *Brachioteuthis picta*, from a 33 mm ML male caught in the Benguela Current (5° 6'N, 009° 58'E). His description provided a detailed examination of the external morphology as well as a brief treatment of the organs of the mantle cavity and the vascular system. In addition to the new description, Chun (1910) devoted the rest of this section to describing four specimens from three stations which "certainly belong to the developmental cycle of *Brachioteuthis*". Unfortunately, the first and best described specimen was later designated as the type specimen for *Histiochromius chuni* Pfeffer, 1912. Chun (1910) attributed the remaining three specimens to *B. riisei*, because they resembled the larva described by Hoyle (1886) as being *B. riisei*.

The selection of Brachioteuthidae as a representative family was initially thought to be straightforward, as *Brachioteuthis riisei* was the only species recognized in the region of the AMNAPE collections, however, based on the above chronology, *B. picta*, *B. beanii*, and *B. bowmanii* are the only adequately described species in the Brachioteuthidae.

Furthermore, a detailed examination of the specimens showed that four morphotypes (*Brachioteuthis* sp. 1-4) were consistently distinguishable (Fig. 17) based on the shape of the head, the mantle chromatophore patterns and the

Figure 17. Morphotypes of newly-hatched Brachioteuthidae.



Brachioteuthidae
elongated neck
club with three distinct regions

Brachioteuthis sp. 1 & 2
tear drop shaped head
long neck

Brachioteuthis sp. 3 & 4
square head
short neck

B. sp. 1
robust tentacle
suckers on distal
portion of arm

B. sp. 2
elongate tentacle
suckers along
entire arm

B. sp. 3
dense
mantle
chromatophores

B. sp. 4
sparse
mantle
chromatophores

shape of the tentacle. Only *Brachioteuthis sp. 3* (n=157) and *Brachioteuthis sp. 4* (n=31) had enough specimens to allow for further study.

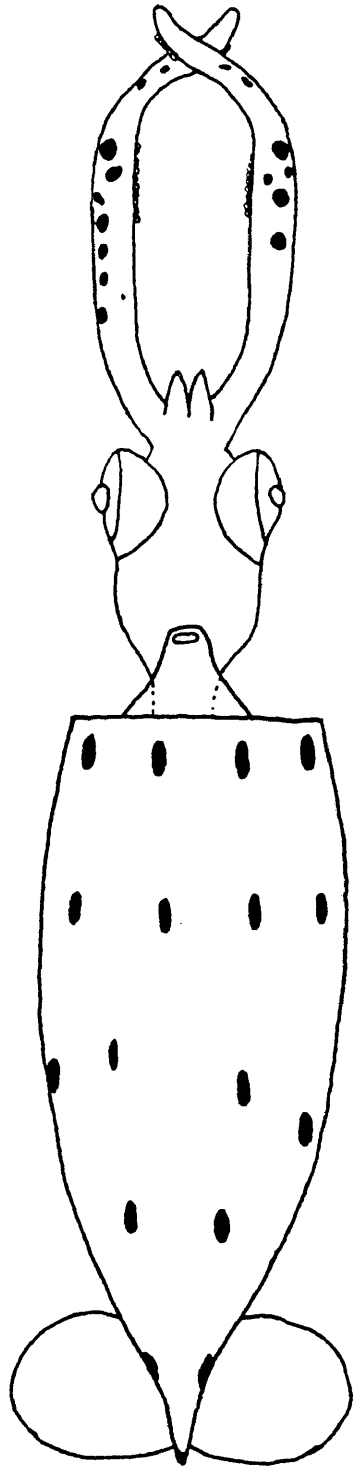
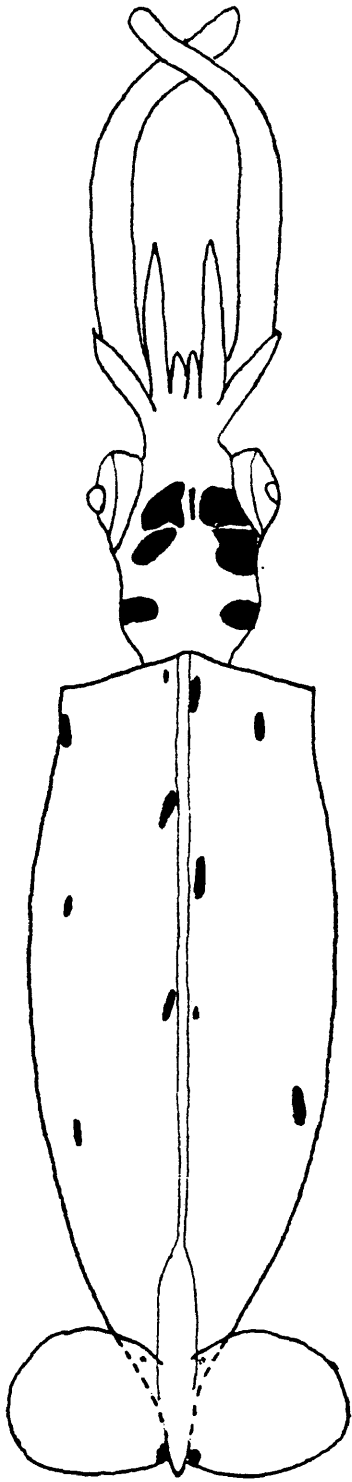
Table 4 summarizes the original description of several major diagnostic features of the well described Brachioteuthidae species and for *Brachioteuthis sp. 3* and *Brachioteuthis sp. 4*. A comparison shows that *Brachioteuthis sp. 3* is described similarly to *B. picta*, and *Brachioteuthis sp. 4* has many of the same characters as *B. bowmanii*. The two best characters for discriminating between species are the dentition of the sucker rings and the presence or absence of trabeculae. The use and interpretation of other, non-quantifiable characters (such as color, shape, or relative size) are subject to the past experience of both the author and the reader, as well as the growth stage of the specimen and the preservation technique used. The designation *Brachioteuthis sp. 3* and *Brachioteuthis sp. 4* will be maintained pending a complete revision of the Brachioteuthidae.

Based on historical (Chun 1910) and recent observations (Young et al 1985), brachioteuthid specimens were expected to undergo a substantial metamorphosis, especially in the length of the neck; therefore, this family was designated as the "radical" species.

Table 4. Comparison between original descriptions of *Brachioteuthis bowmanii*, *B. beanii*, and *B. picta* and characteristics noted in *B. sp. 3* and *B. sp. 4*.

	B. sp. 3 B. beani Veritt, 1881 Type location: off Martha's Vineyard, USA (based on 87mm DML male specimen) small, tapering to an acute posterior end dorsal mantle edge w/ broad obtuse angle	B. bowmani Russel, 1909 Type location: 610-27N 0030-42W (based on 81mm DML female specimen) fusiform, runs into sharp point behind anterior border of mantle free, not produced in obtuse angle	B. picta Chun, 1910 Type location: 50 6N 0090 58 E (based on 4.5 mm DML male specimen) long and narrow ending in long spine-like point	B. sp. 4 Location: 55-240N, 300W (based on composite of specimens approx. 10-22 mm DML) very long and thin, tapered posteriorly to a long, sharp point
Character body shape	caudal fin large in proportion to the body broad rhomboidal	shape resembles <i>O. sagittatus</i> posterior half of the mantle	FL = 1/2 ML heart shaped, nearly rhomboidal	attached to posterior end of dorsal mantle
fin	thickened at the bases of the arms.	very large, broader than mantle opening	rounded because of large protruding eyes	square shaped w/ 6 dorsal chromatophores
head	large w/ thin eye-lids	enormous, covered by skin	large and protruding light, glossy stripe on ventral side	small, approx. = 1/3 head length
eyes	1<4<2=3 long and slender	2<3<4<1 no web or keel (except 4th arms)	1<4<3<2 swimming keel on all arms	1<4<3<2 have trabeculae at base of pedicle
arms	none described???	honey ring higher in upper half, 5-6 w/ square teeth on upper, smooth on lower clint from pedicle, but are bound to the arm	none described???	swelling at base of sucker stalk
arm suckers	very long and slender TL=2xML few scattered, sessile suckers along whole length	slud, triangular in cross section sessile suckers in apr. 4 scattered rows half way down inferal face of tentacle- minute and sparsely scattered as reach middle	Relatively short, stalk flat on inner side, rounded on outside. Suckers single proximally, then 2 then 4 indistinct rows	short, stout. Suckers in 2 rows, then 4 then many. No single suckers on length.
tentacles	well developed long ovate, oblique, w/ a thick wrist flat or concave sucker-bearing face suckers small and numerous >= 18 rows w/ some middle larger than rest pedicels long and slender smooth and small swelling below base of sucker suckers had lost, honey rims sheaths: distal portion hood-shaped whilateral opening, basal part swollen laterally	thin and flattened from above downwards distal portion at right angle to proximal main body of club; numerous thin stalked suckers in 12-15 irregular rows suckers: cups hemispherical, horny rings have fine-pointed teeth in upper half. chromaloid at base of suckers dorsal view: like feather wharbs	not expanded, flat face CL=1/2 TL from point where suckers begin in > 1 row. pedicels long on outside edge, sessile on inside edge 3 sections on club delineated by sucker size	only 2 sections on club. sucker ring of outer suckers has a notch in the sucker ring at the top
club	small light purplish brown chromatophores uniformly scattered over the parts best preserved also on head, siphon and outer surface of arms and inner surfaces between suckers	pale red chroms on mantle (more on dorsal than on ventral) head brown and crimson with chroms esp. at antero-ventral border of eye chroms on arms and tent	purple brown background numerous, dense chromatols. dorsal more pigment than ventral 4 lg chrom. on dorsal head 3 on ventral head	chromatophores large and moderately spaced in small specimen. Very dense in large specimen. lots of chromatophores between suckers on club
body color:			chromatophores large & widely spaced 5 lg along dorsal midline 2 at posterior most end of dorsal fins on dorsal arms and tentacles more on ventral than on dorsal dark, red-purple	

Figure 18. Illustration of 9.5mm DML *Brachioteuthis* sp. 3 (Station-haul: 77-01, bottle no. 8853). Dorsal and ventral view.



Brachioteuthis sp. 3 (Fig. 18)

Depth and Areal Distributions

During the day, two groups of *Brachioteuthis sp. 3* are present: one at 0-200m and the other at >500m (most of these specimens were caught in 0-1000m hauls in malfunctioning opening and closing nets, and therefore may also have been in near-surface waters) (Fig. 19a). Most specimens in the first group were caught in the upper 50m in concentrated hauls. Night captures were not as plentiful, but all were made in the upper 300m.

When sorted according to DML (Fig 19b,c), the day captures show an intriguing, but inconclusive pattern. All specimens <30mm DML were in the upper 200m. Larger specimens were taken from 0-1000m depth horizon from a net with a malfunctioning net opening/closing mechanism.

Night captures show all specimens, regardless of size, in the upper 300m. Graphs of nighttime captures have more vertical spread than the day captures. Smallest specimens came from slightly deeper tows than larger specimens.

No specimens of *Brachioteuthis sp. 3* were captured during the spring cruise of 1980 or the winter cruise of 1982. The fall cruise of 1981 (Fig. 20a) caught a moderate number (n=24) of specimens, all of which were found north of 49° N, and along 30° W, putting them in North Atlantic Drift water (Van der

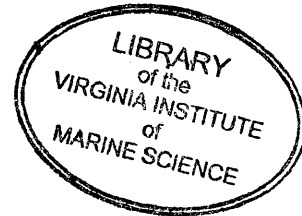
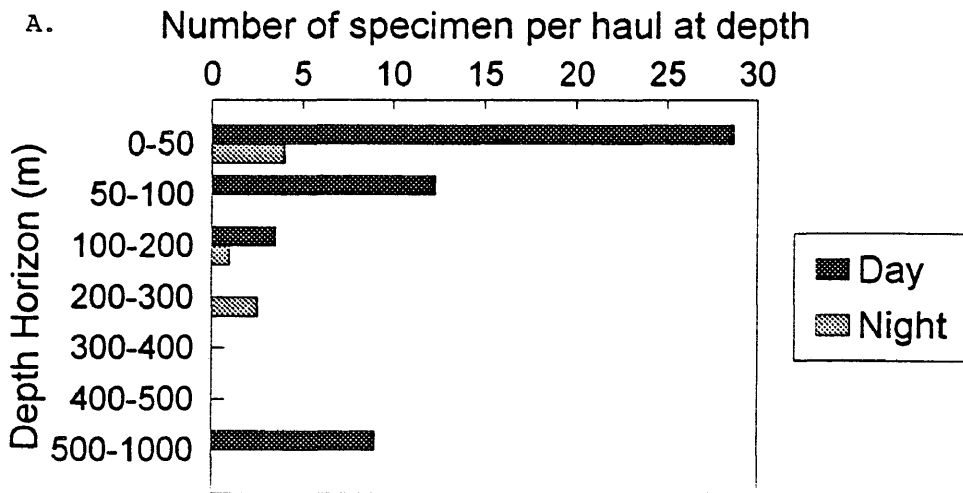


Figure 19. Depth distribution of *Brachioteuthis sp. 3*. a) Number of specimen per haul at each depth horizon during day and night b)day time depth of capture plotted against DML c)night time depth of capture plotted against DML. Net opened at triangle and closed at horizontal line. Each triangle/line combination represents one collected specimen. Note: Bottom depth is illustrated for 0-1000m depth horizon collected by malfunctioning opening/closing net.

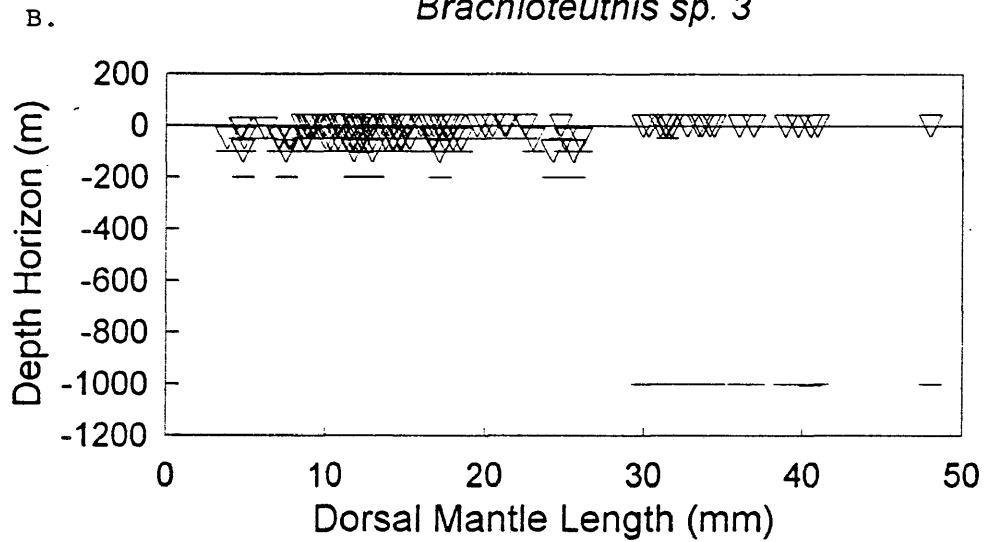
Vertical Depth Distribution

Brachioteuthis sp. 3



Depth vs. Dorsal Mantle Length (Day)

Brachioteuthis sp. 3



Depth vs. Dorsal Mantle Length (Night)

Brachioteuthis sp. 3

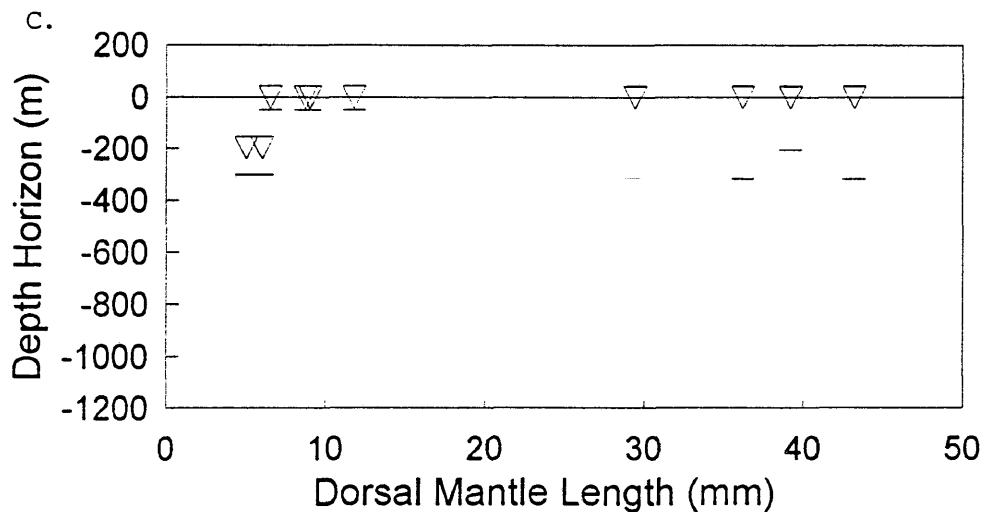
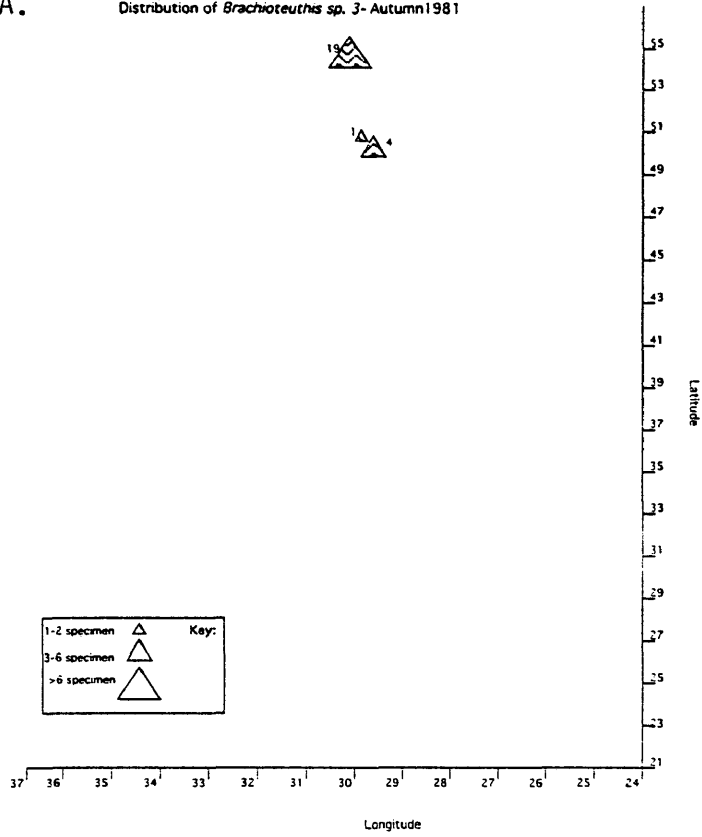


Figure 20. Areal distribution of *Brachioteuthis sp. 3*. a) Autumn 1981 b) Spring/Summer 1983. Center of the triangle marks the collection point. Overlapping triangles were combined and the number of specimens were added. North - South and East - West depth distributions for *Brachioteuthis sp. 3*. Hauls that contained cephalopods at each latitude and longitude are represented. Multiple specimen may have been caught in each depth horizon e) Autumn 1981 g) Spring /Summer 1983.

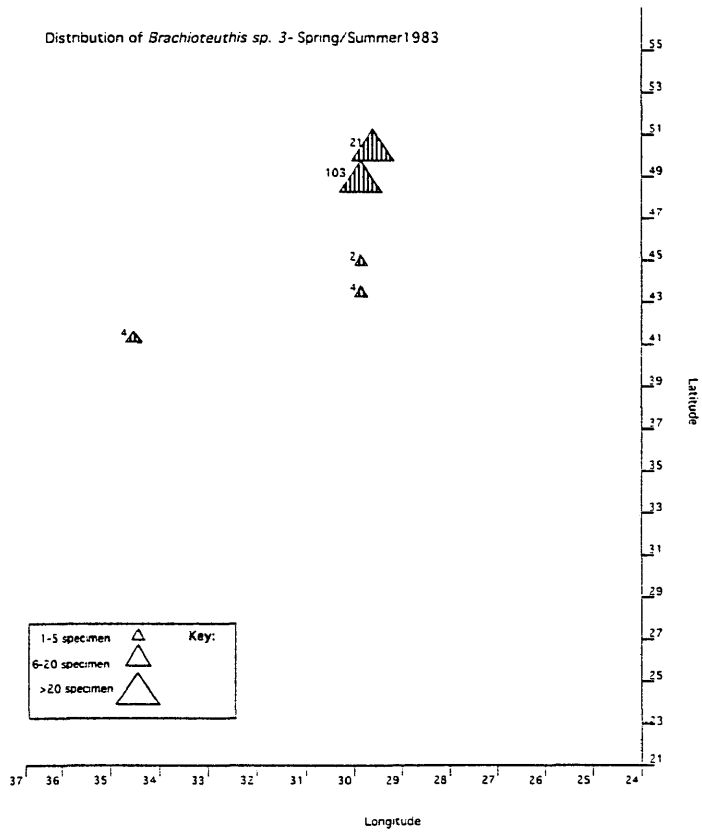
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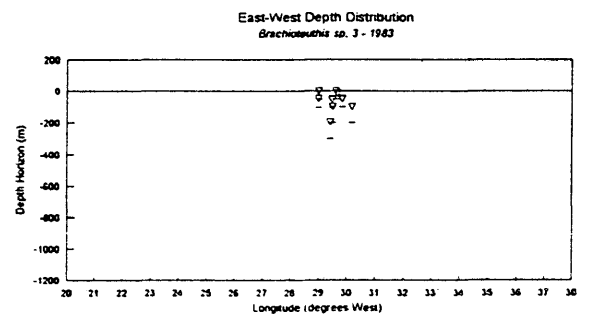
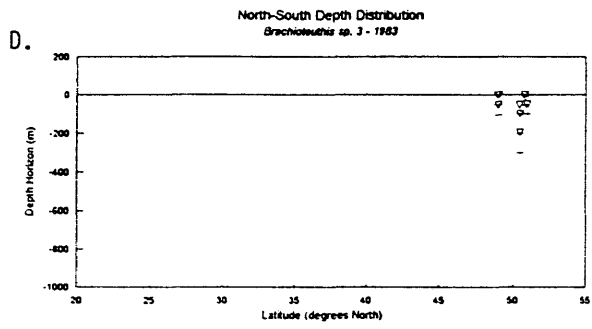
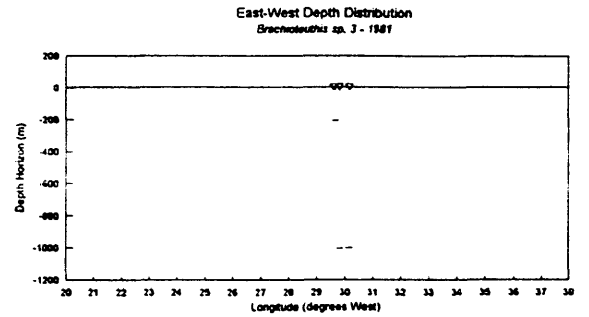
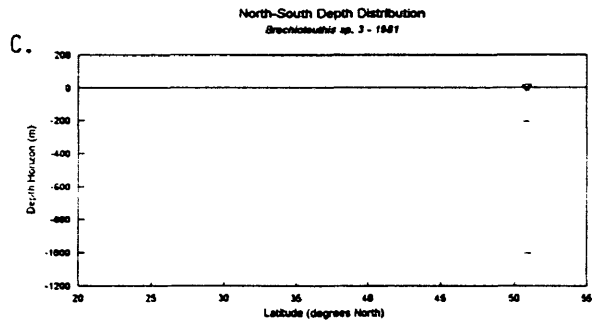
Distribution of *Brachioteuthis* sp. 3- Autumn 1981



B.

Distribution of *Brachioteuthis* sp. 3- Spring/Summer 1983





Spoel 1985). A large concentration of specimens was caught at 55° N, 30° W. All specimens were caught in the upper 300m in the Subpolar water mass (Van der Spoel 1985) .

The summer cruise of 1983 collected the largest number of specimens of this species by far (Fig. 20b). As in 1981, most were captured above 49° N in the upper 200m of North Atlantic Drift water (Van der Spoel 1985). An extraordinarily high concentration of specimens was caught at 30° W, between 48-50° N in the North Atlantic Drift water (Van der Spoel 1985). Most of the individuals of *B. sp. 3* were collected at stations 76 and 77 (approx. 49-50°N 29-29.5°W), from the upper 200m.

Morphometric data

Brachioteuthis sp. 3 had a very large size range of specimens (3-50mm DML) and number of specimens (n=114). No gaps exist in the size range, allowing for confident interpretation of the changes in the trajectory of the scatterpoints. In general, the characteristics measured resulted in an s-shaped growth trajectory with increasing DML. Thus, the trajectory can be divided into three sections. At the smallest sizes (<15mm DML), DML grows faster than the other individual characteristics; at approximately 15mm DML (inflection point A), the measured characters begin to grow much faster than the DML; at 30mm

DML (inflection point B), increases in the size of the character begin to decrease, with the resulting scatterplot more level.

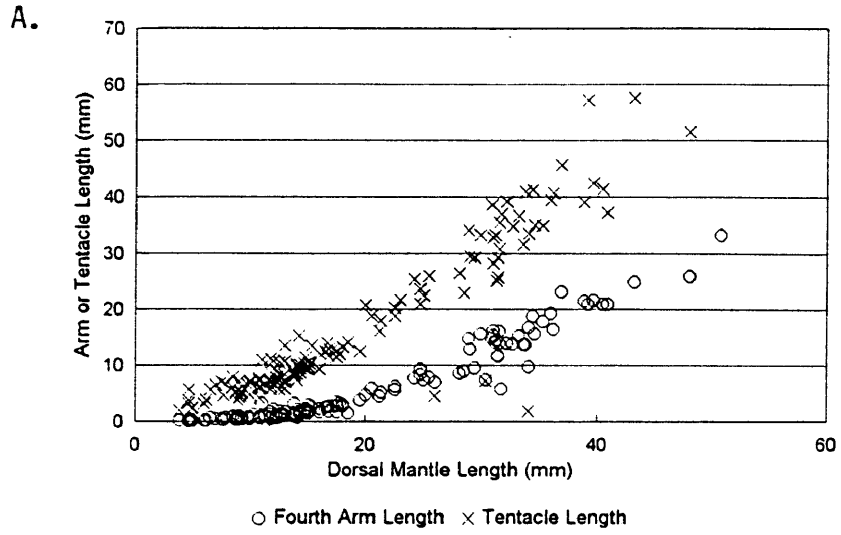
The *arms* and *tentacles* (Fig. 21a) appear to show exponential growth, with an inflection point at approximately 20mm DML. Both the arms and tentacles appear to grow in a similar manner, with the tentacles approximately twice as long as the fourth arm.

The inflection points of the *fin measurements* (Fig. 21b) are approximately the same as those of the arms and tentacles; inflection point A is at approximately 15-18mm DML, and point B is around 30mm DML. The fin width is slightly larger than the fin length at any given DML, but both characteristics appear to follow the same patterns of growth with increasing DML.

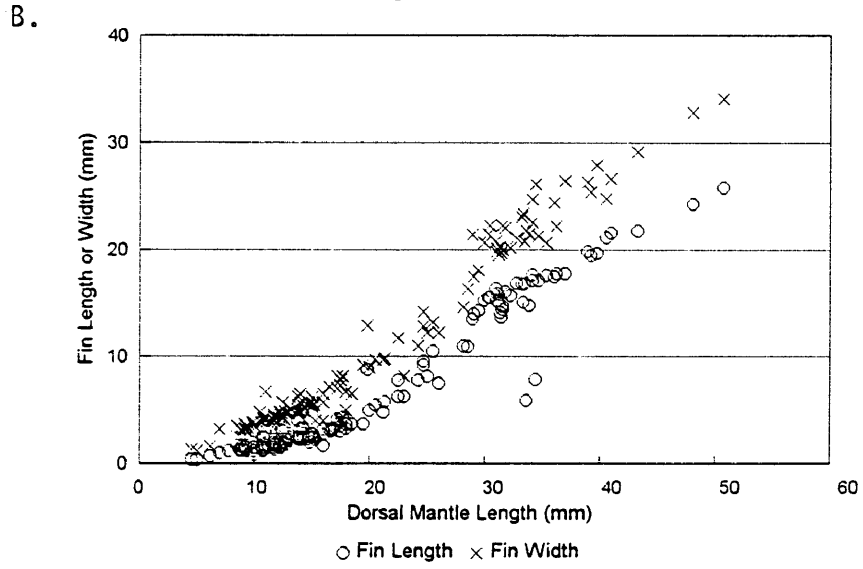
The *funnel dimensions* (Fig. 21c-e) present a pattern distinct from those previously discussed; however, the inflection points of the width measurements remain at approximately the same DMLs as previous measurements. The incremental change in the posterior funnel width (FW-P) (Fig.21c) over the first 18mm DML is greater than that of the middle portion, where it becomes more level. The third section of the graph shows a return to a rapid increase in the measurement with increasing DML. The anterior funnel width (FW-A) does not

Figure 21. Morphometric analysis of *Brachioteuthis sp. 3* a) arm and tentacle length b) fin dimensions c) funnel widths d) funnel length e) funnel length v. width f) head measurements g) eye diameter.

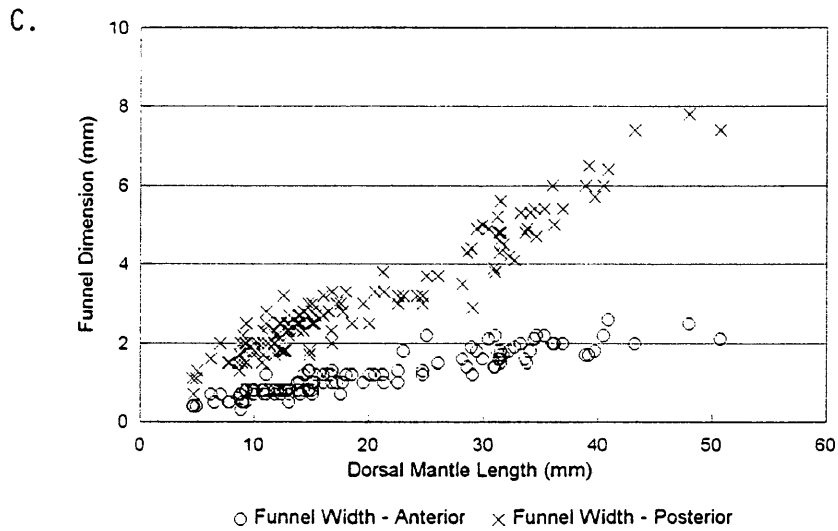
Arm and Tentacle Length vs. DML



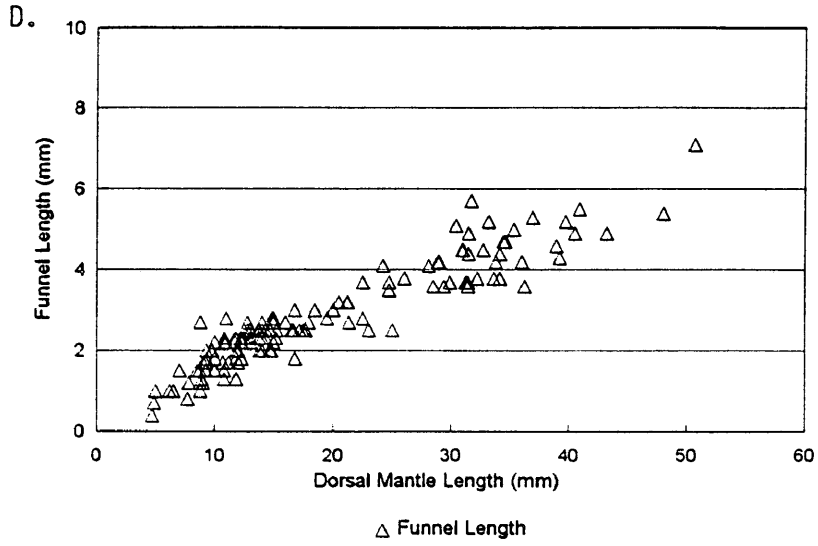
Fin Length or Fin Width vs. DML



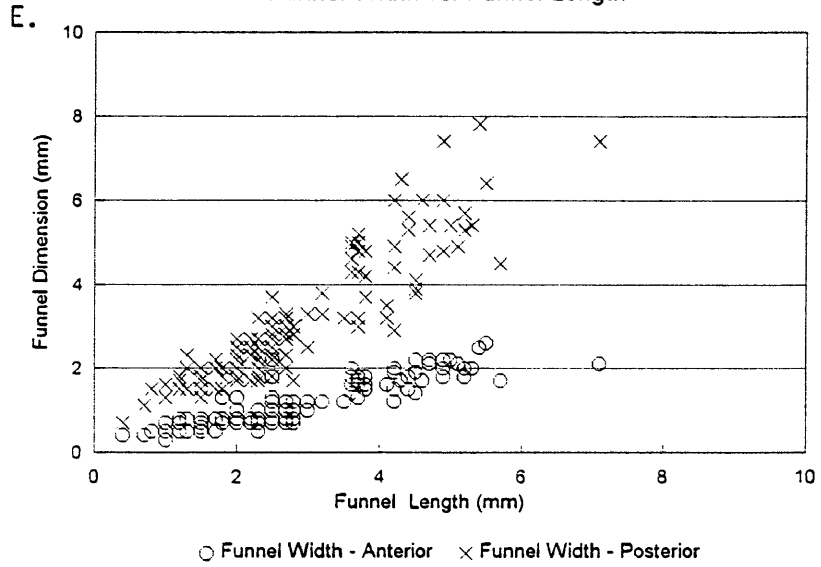
Funnel Dimensions vs. DML



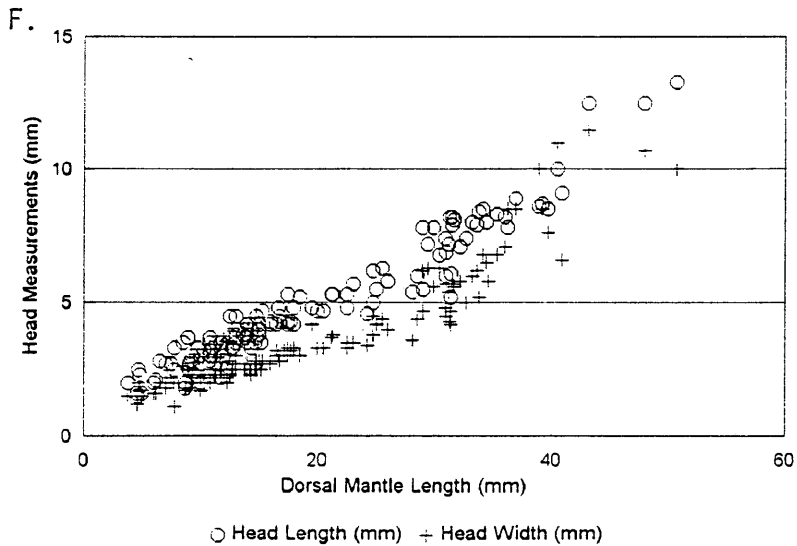
Funnel Length vs. DML



Funnel Width vs. Funnel Length



Head Measurements vs. DML



appear to have any inflection point across the range of DML; however, it does appear to level off at approximately 2mm FW-A at 30mm DML. The posterior width is almost exactly twice as large as the funnel top width at any DML. The funnel length (Fig. 21d) increases very slowly with increasing DML, and appears to level off at 4mm FL, at approximately 30mm DML. When the funnel widths are compared to the funnel length (Fig. 21e), the FW-P increases very rapidly with small increases in FL; the FW-A shows a less rapid increase.

Head and eye measurements (Fig. 21f,g) appear to have only one inflection point, again at about 28-30mm DML. Prior to 30mm DML, DML increases much faster than either the head length, the head width or the eye diameter. After 30mm, the HL, HW and ED begin to increase faster with respect to DML. In any case, the head length is always larger than the head width, which in turn is larger than the eye diameter. When comparing the head width with the head length, the length is significantly larger than the width up to approximately 7mm HL. At this point, the slope of the scatterplot increases and the width begins to increase in size faster than the length. At the largest DMLs, the head length is only slightly larger than the width.

Ontogenic Changes in External Morphology

10.1mm DML (station-haul 77-01, bottle no. 8852.5): Mantle long and moderately thin, with large, widely spaced chromatophores on the dorsal and

ventral sides; paddle-shaped fins very short with respect to DML ($FL=1/9ML$); head is square with four large dorsal chromatophores, 2 smaller ones at posterior end of dorsal-lateral head; eyes are anterior on the head, ED approx. $\frac{1}{2}$ HL; tentacles longer than arms, suckers begin half way up in one series, then 2, then 4, then many; distal tip of tentacle is sucker bud with 4+ rows of suckers; arm formula is $2>3>4>1$, Arm 1 & 4 with only one sucker, arm 3 with 1 sucker plus sucker buds.

26.0mm DML (station-haul unknown, bottle no. 6): Mantle long and moderately thin with large, widely spaced chromatophores; fins heart shaped, $FL=1/3 ML$; eyes anterior, but more lateral than in smaller specimens; head squarish with four dorsal chromatophores, and two additional smaller chromatophores at base of head; arm formula is $2>3>4>>1$ with arm suckers in 2 rows on stalks; swimming keel developing on fourth arm; tentacle long and thin, suckers start $1/3$ way up stalk in 1 series, then 2 series, then many; very small suckers on stalk; change from many, very small suckers to four rows of large suckers at distal end; three columns of 4-5 sessile suckers at the end of the tentacle, swimming keel forming at end of tentacle; digestive gland at the posterior mantle cavity.

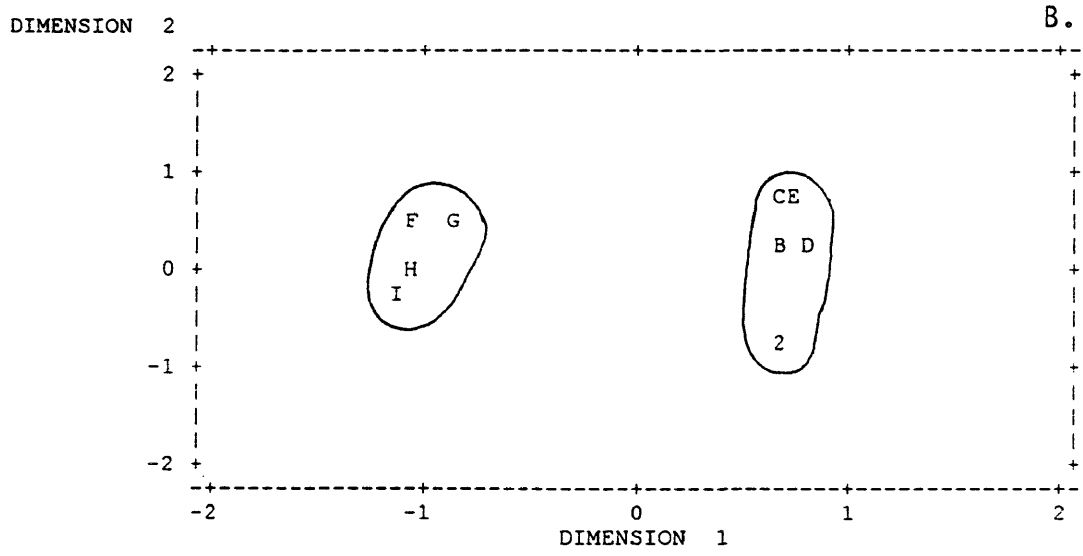
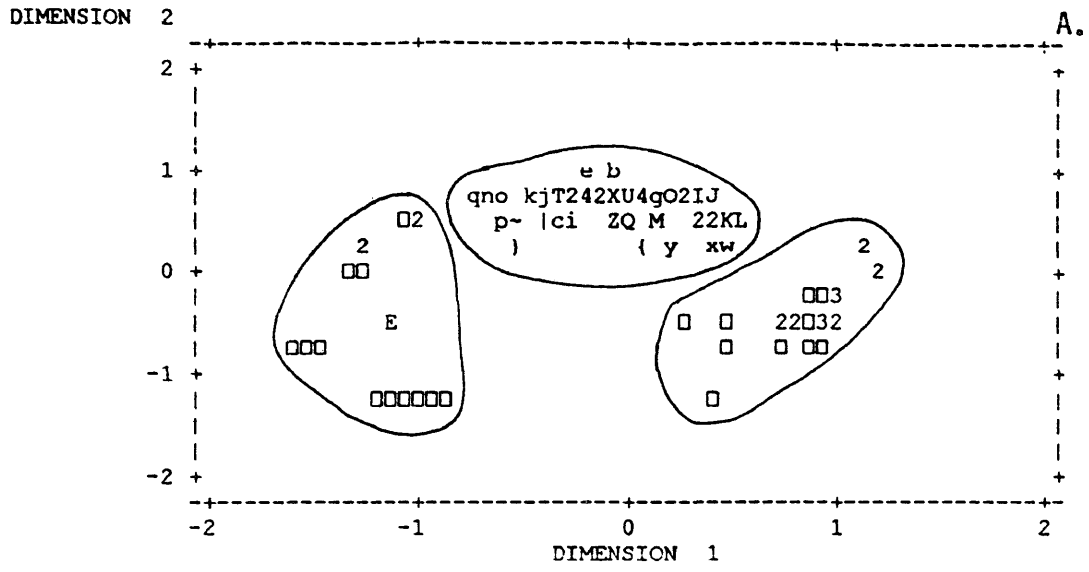
43.2mm DML (station-haul 38-14, bottle no. 4684): Mantle long and relatively thin; chromatophores on mantle are large and widely dispersed,

smaller more densely packed chromatophores have developed between larger chromatophores; head square with many chromatophores on dorsal and ventral sides, 4+2 "original" arrangement still recognizable; eyes large, equal to head length, lateral; arm formula 2>3>4>1, 1st arm has grown considerably; swimming keel present on all arms, arm suckers large, stalked, with trabeculae at base of arms 1-3; tentacle long and thin with small chromatophores along ventral midline; suckers tiny along stalk, at distal end change suddenly to four rows of larger suckers which are small on the ventral edge (inside) getting gradually larger towards the dorsal edge (outside); 4 sessile suckers at very distal end; digestive gland is near center of mantle cavity.

Multidimensional Scaling (Fig. 22a,b)

The optimal configuration for the daytime analysis was found in two dimensions. All morphological characters, except the NL, described the variability along the first axis (range: FunW-A = -.743 to FL = -.952); the remaining station data (depth latitude, longitude, and salinity), described the second axis, but the correlation was not very strong (either +/- .487 for each parameter). The daytime configuration was arch-shaped, but within this arch, three size clusters could be distinguished.

Figure 22. Multidimensional scaling analysis optimal configuration for *Brachioteuthis sp. 3*. Each letter represents one specimen. Axes described as follows, characters listed in order of importance. A) Day. Axis 1: morphological data, except NL. Axis 2: depth, latitude, longitude, salinity, temperature (very low correlation). B) Night. Axis 1: morphological characters, latitude, longitude, salinity, temperature. Axis 2: depth.



The optimal nighttime configuration was also found in two dimensions. The stress of the final configuration was .067 and the Shepard diagram was straight. The variability on the first axis was primarily described by the station data (latitude = -.873, longitude = .848, salinity = .848, temperature = .848), although all the morphological data was also slightly associated with the first axis (range: fourth arm -.582 to FunW-P = -.727). The variability on the second axis was associated with depth (.750). Two very distinct groups are formed based primarily on the station data.

Brachioteuthis sp. 4 (Fig. 23)

Depth and Areal Distributions

Depth distribution of *Brachioteuthis sp. 4* was almost continuous (Fig. 24a); several specimens were present at most depth horizons; the greatest concentration of specimens was from 0-200m. Specimens also were spread throughout the water column at night, with groups at 0-100m, 200-300m, and 400-500m.

When specimens are sorted by DML (Fig. 24b,c) the day captures show that most captures are made in the upper 100m, but there are exceptions. These exceptions do not follow any size-specific pattern. Night captures show a broader range of depths of capture over all DML; two of the largest specimens were taken from 0-500m hauls.

Figure 23. Illustration of 9.6 mm DML *Brachioteuthis* sp. 4 (Station-haul:80-21, bottle no. 8318). Dorsal and ventral view.

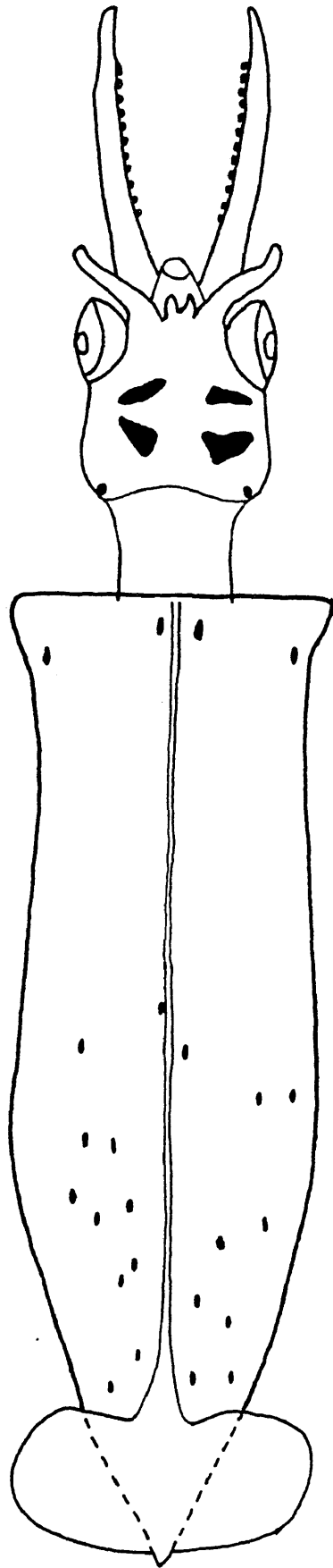
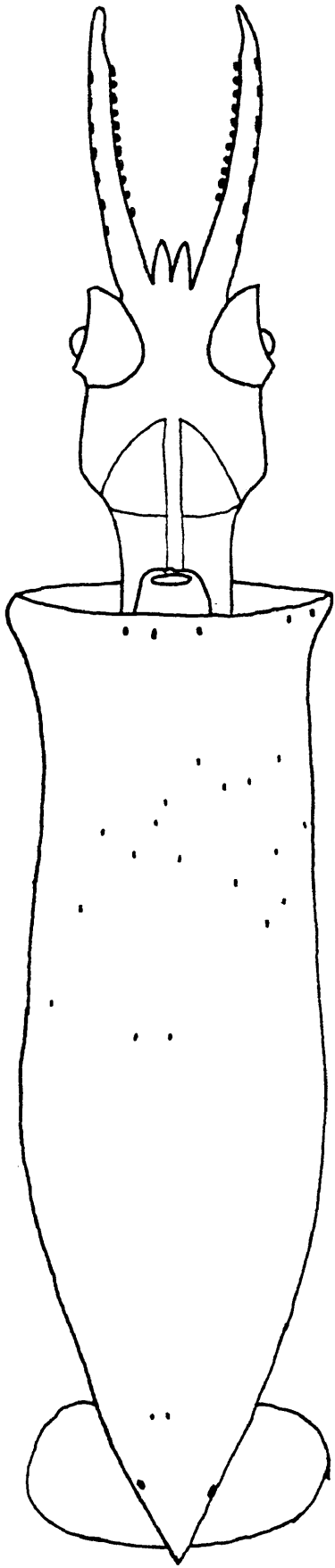
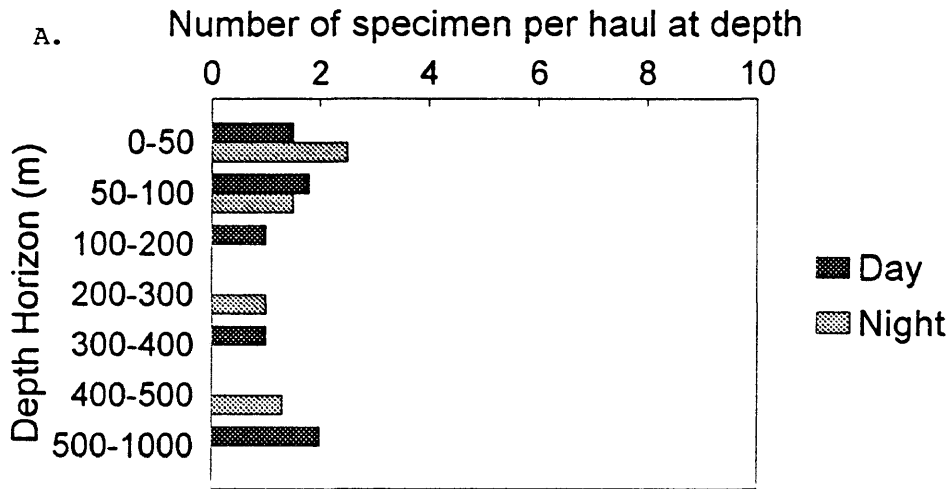


Figure 24. Depth distribution of *Brachioteuthis sp. 4*. a) Number of specimen per haul at each depth horizon during day and night b) day time depth of capture plotted against DML c) night time depth of capture plotted against DML. Net opened at triangle and closed at horizontal line. Each triangle/line combination represents one collected specimen. Note: Bottom depth is illustrated for 0-1000m depth horizon collected by malfunctioning opening/closing net.

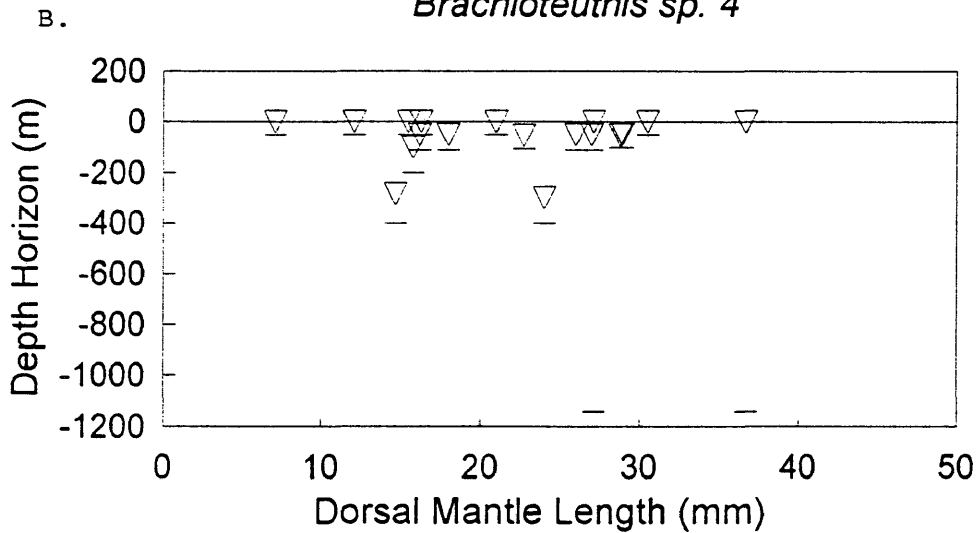
Vertical Depth Distribution

Brachioteuthis sp. 4



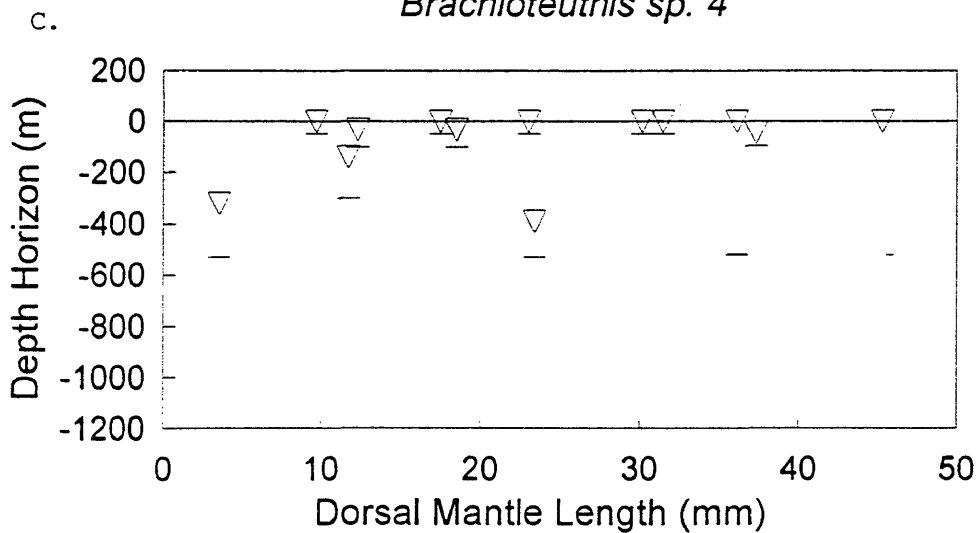
Depth vs. Dorsal Mantle Length (Day)

Brachioteuthis sp. 4



Depth vs. Dorsal Mantle Length (Night)

Brachioteuthis sp. 4



A few specimens of *Brachioteuthis sp. 4* were captured in spring 1980 between 33-43° N (Fig. 25a). Most of the captures occurred between 35-36° W, instead of around 30° W where most of the hauls were made. Depth of capture for *B. sp. 4* was more variable than for *B. sp. 3*; most captures were recorded in the upper 200m, but several were from the middle ranges, 300-500m. Hauls of 500m or less in the 33-43° window were taken primarily in the Sargasso Sea water mass. As discussed previously, the waters between 40-43° N are transitional between Sargasso Sea and Warm Temperate water masses. Hauls at depths >500m were from Antarctic polar waters.

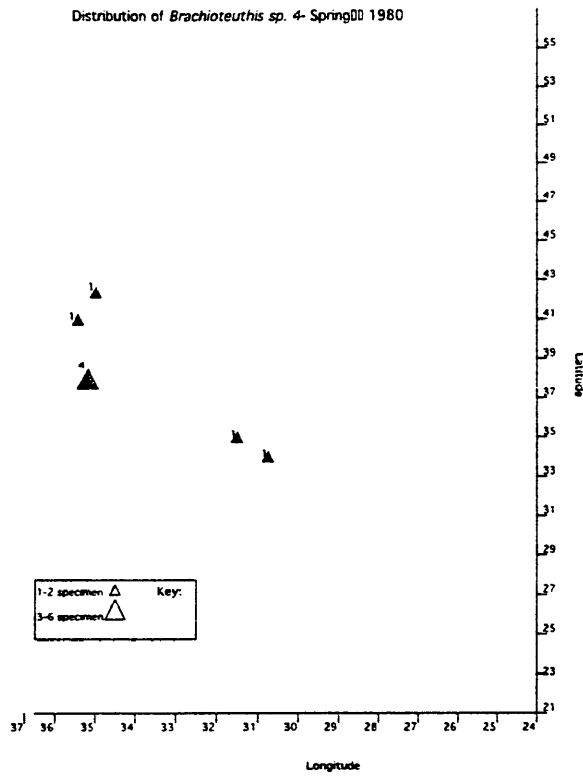
Only four specimens were caught during the autumn 1981 cruise (Fig. 25b). All of them were collected north of 49° N, along the 30° W longitude line. All were caught in the upper 200m, in Warm Temperate Waters (Van der Spoel and Meerding 1983). No specimens were caught during the winter 1982 cruise (Fig. 25c).

Most specimens of *B. sp. 4* were caught during the summer 1983 cruise (Fig. 25d). All captures were recorded between 39-45° N and 29-36° W, most in the upper 200m of water. This location and depth data places the specimens from the upper 75m in Temperate water, and the 75-200m specimens in North Atlantic Central Water (Van der Spoel 1985).

Figure 25. Areal distribution of *Brachioteuthis sp. 4*. a) Spring 1980 b) Autumn 1981 c) Winter 1982 d) Spring/Summer 1983. Center of the triangle marks the collection point. Overlapping triangles were combined and the number of specimens were added. North - South and East - West depth distributions of *Brachioteuthis sp. 4*. Hauls that contained cephalopods at each latitude and longitude are represented. Multiple specimen may have been caught in each depth horizon e) Spring 1980 f) Autumn 1981 g) Winter 1982 h) Spring/Summer 1983

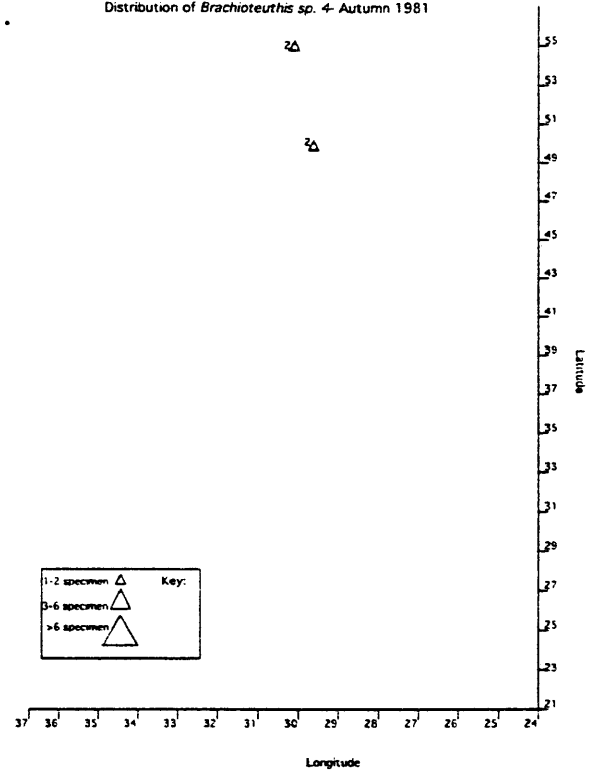
A.

Distribution of *Brachioteuthis* sp. 4- Spring 1980



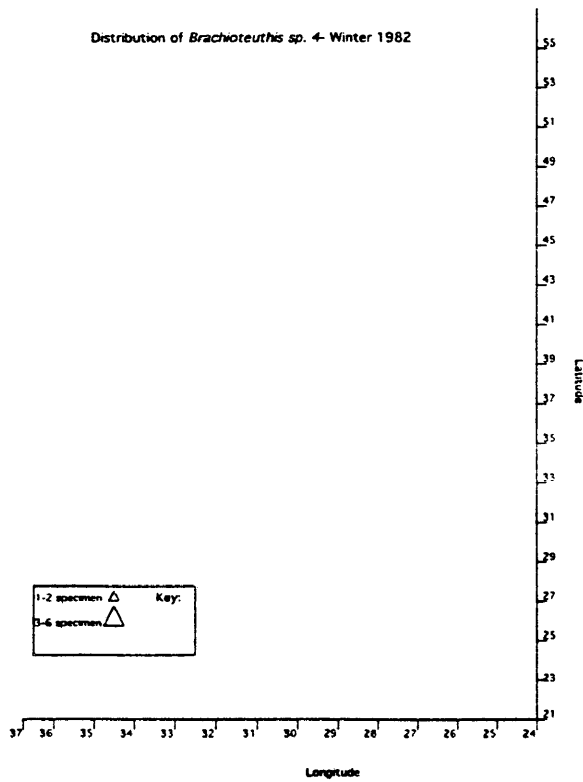
B.

Distribution of *Brachioteuthis* sp. 4- Autumn 1981



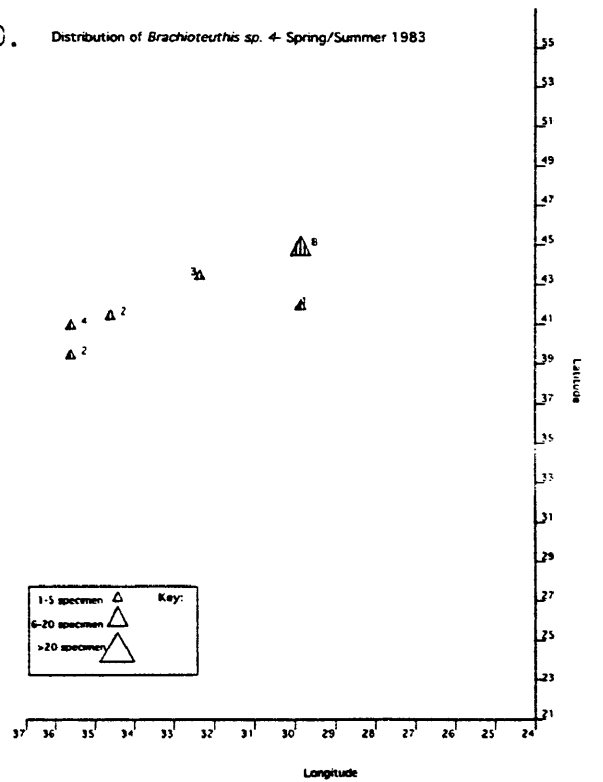
C.

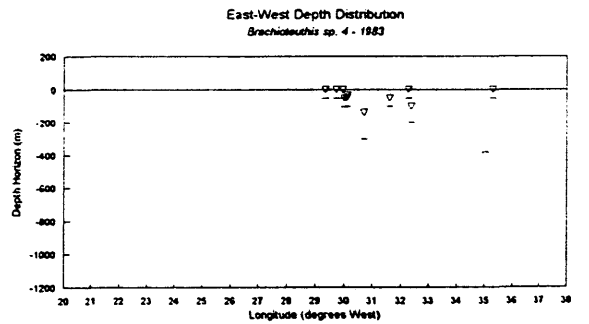
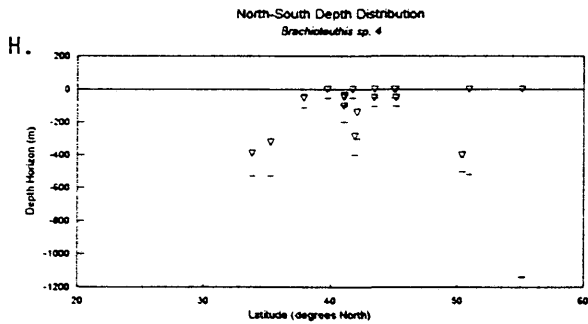
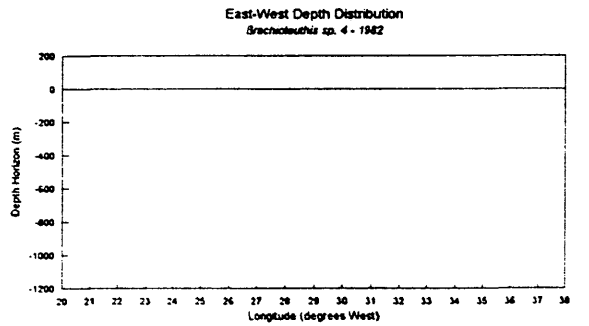
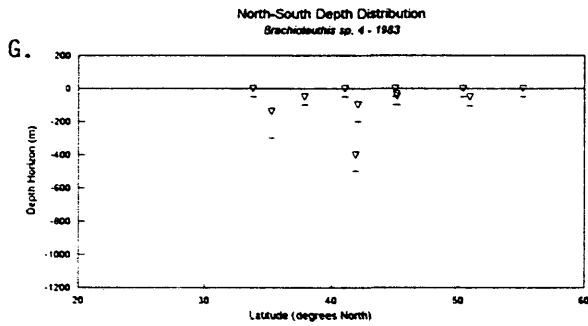
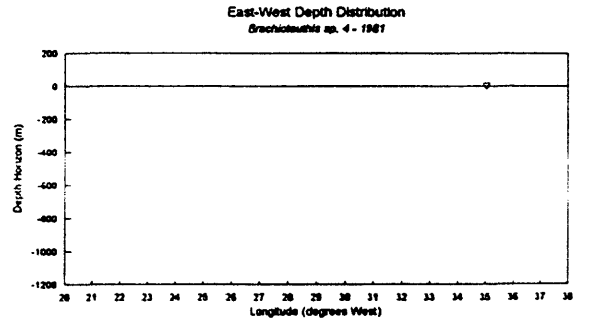
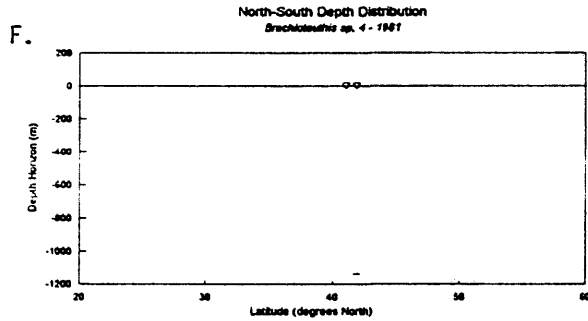
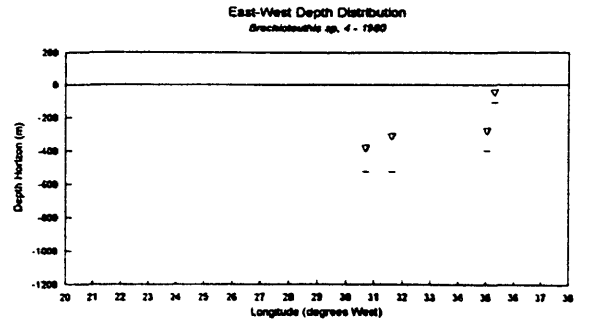
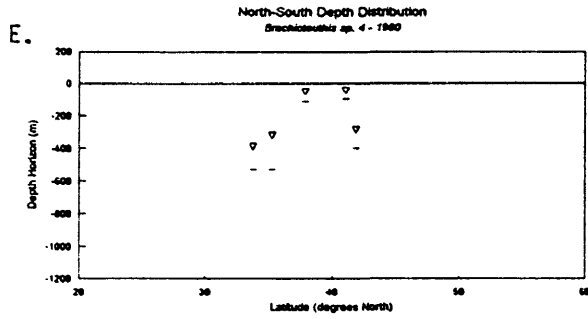
Distribution of *Brachioteuthis* sp. 4- Winter 1982



D.

Distribution of *Brachioteuthis* sp. 4- Spring/Summer 1983





Morphometric data

Brachioteuthis sp. 4 had a very large number of specimens between the size of 3-48mm DML. Specimens were well distributed over the size range. The lack of size gaps enabled solid interpretations of data. In general, most growth trajectories were either linear or exponential; only one inflection point was seen in any of the graphs of characteristics plotted against DML. This inflection point occurred at or about 20mm DML, and is the point at which the size of several measured characteristics began to increase rapidly with increasing DML.

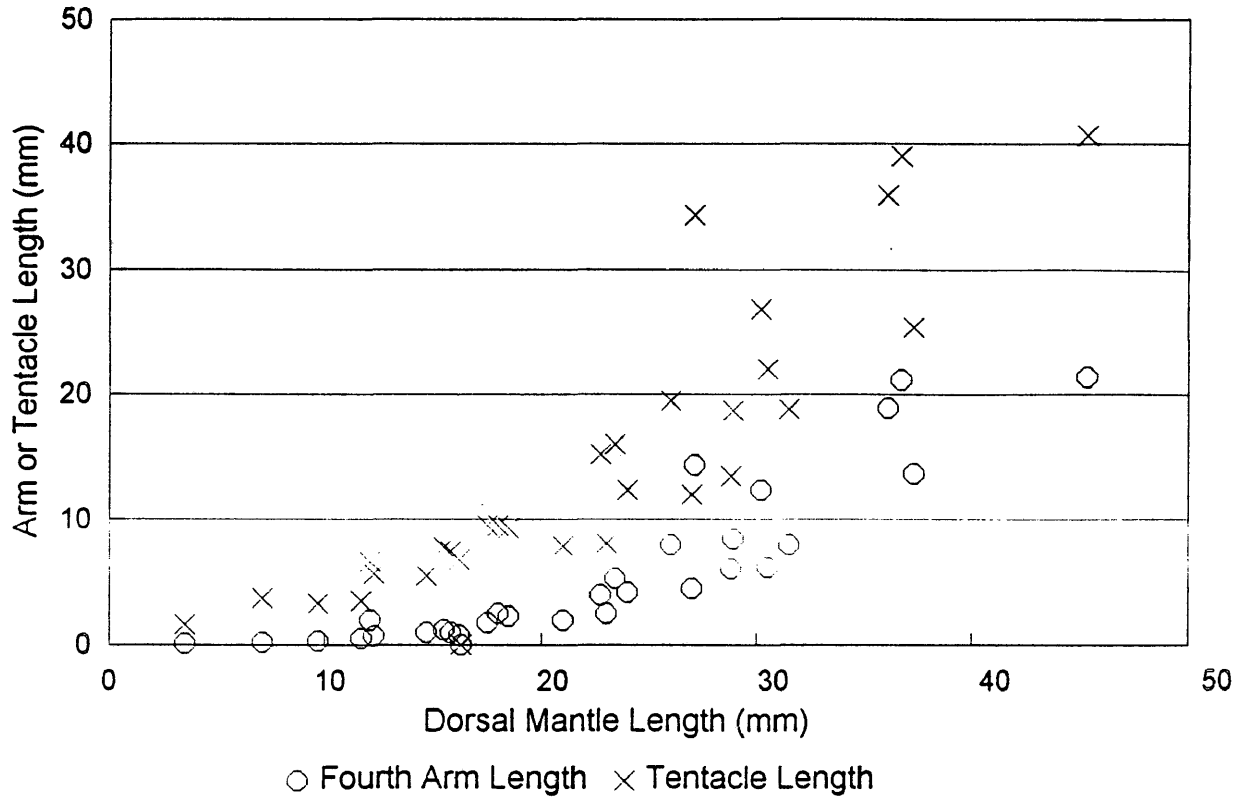
The *arm* and *tentacle length* measurements (Fig. 26a) show a change in the slope of the line at approximately 20mm DML. As expected, at any given DML, the tentacle length is longer than the fourth arm length. It is interesting that the TL and arm length appear to have the same pattern of changes with increasing DML, because tentacle lengths were expected to be more variable due to their elasticity.

The *fin measurements* (Fig. 26b) show a pattern similar to the arms and tentacles, with an inflection point seen at about 20mm DML. The fin length is just slightly larger than the fin width (although there is considerable variability), and the two measurements appear to change similarly with increasing DML.

Figure 26. Morphometric analysis of *Brachioteuthis sp. 4*. a) arm and tentacle length b) fin dimensions c) head measurements d) eye diameter e) mantle opening width.

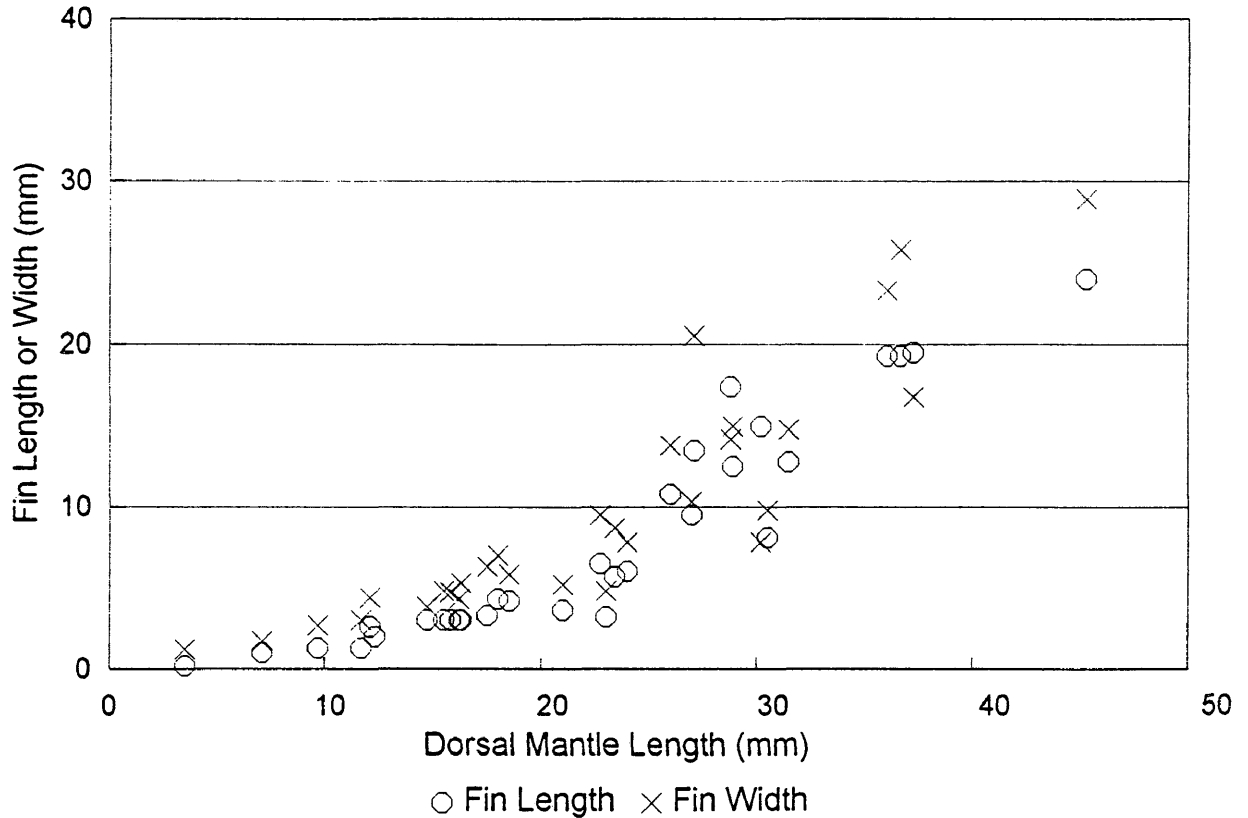
Arm and Tentacle Length vs. DML

A.

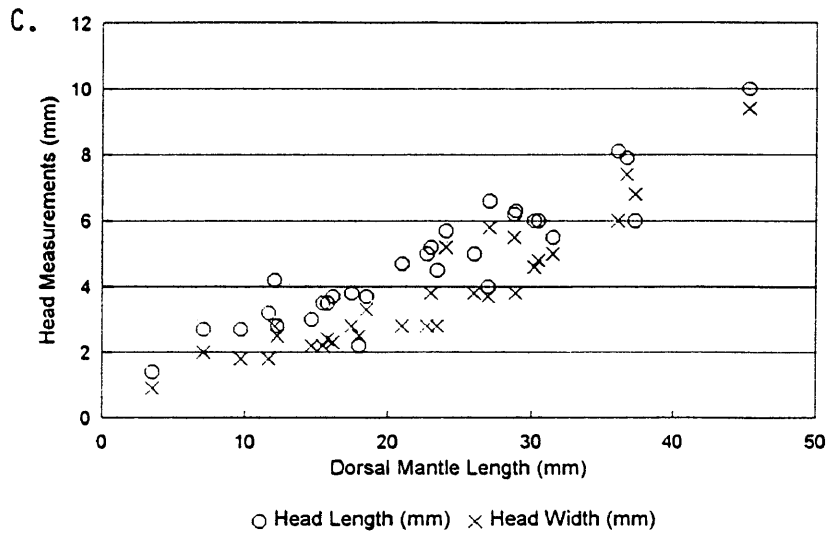


Fin Length or Fin Width vs. DML

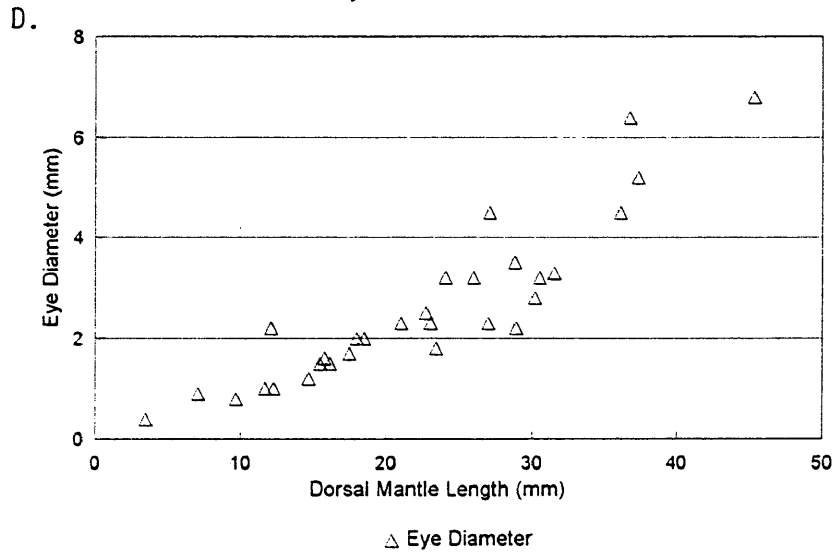
B.



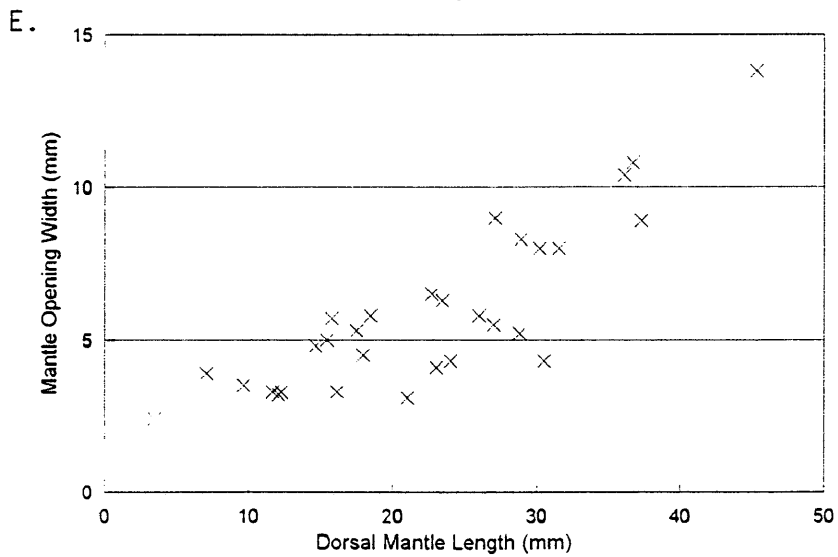
Head Measurements vs. DML



Eye Diameter vs. DML



Mantle Opening Width vs. DML



Head and eye measurements (Fig. 26c,d) indicate that the head length is usually larger than the width, and the eye diameter is generally smaller than either head measurement. At about 20-22mm DML, an inflection point in the eye diameter can be found; head length and width appear to increase linearly, with no leveling off evident.

The growth trajectory for the *mantle opening width* (Fig. 26e) shows an increasing rate of growth with increasing DML, with an inflection point at approximately 20-22mm DML.

Ontogenic Changes in External Morphology

14.6mm DML (station-haul 16-02, bottle No. 1297): Mantle long and thin, tapered at posterior end, gladius protrudes as a sharp point; anterior end also tapered to point on dorsal side; fins trapezoidal, very short compared to DML; chromatophores on dorsal and ventral mantle very small, close together; head is square with four large chromatophores on central dorsum, two medium dorsal posterior, close to neck; eyes anterior, $ED=1/2HL$; arm formula $2>3>4>1$; arm suckers are large, especially arms 2 & 3; tentacles stout, much longer than arms. Tentacle suckers start $\frac{1}{2}$ way up in 2 series, then 4, then many (>5), turning into sucker bud area with four tiny series on dorsal edge; distal end of tentacle has 3 rows of suckers, with ventral edge suckers much larger than dorsal edge suckers. Beginning of club portion of tentacle difficult to discern.

23.4mm DML (station-haul 21-03, bottle no. 1401): mantle very long and thin, anterior not pointed as before, chromatophore pattern not discernable; fins short compared to mantle ($FL=1/4-1/3ML$); gills very long and thin; head squarish; neck thick; arm formula $2>3>4>1$, keel developing on all arms, suckers on arm 1-3 very large and on stalks, arm 4 suckers smaller and not noticeably on stalks; tentacles moderately longer than arms, stout; tentacle suckers start $\frac{1}{2}$ way up stalk in 1 series, then 2, then 4 then numerous, then suckers too tiny to count columns; four series of suckers on distal end, small suckers on inner edge, large suckers on outer edge.

37.3mm DML (station-haul 17-01, bottle no. 749): Mantle long and thin, fins are much longer compared to mantle ($FL=1/2ML$); small, dense chromatophores all over body, with larger ones interspersed at broad intervals; head squarish with four large chromatophores on central dorsum and two smaller chromatophores at dorsal base of head; eyes lateral, ED approx. = to HL, reflective tissue on ventral eyeball; arm formula $2>3>4>1$ with swimming keel along length, arm 4 suckers are large like arm 1-3, arms 1-3 with trabeculae supporting membrane at base of stalk; tentacle stout, only slightly longer than 3rd arm; tentacle suckers start $\frac{1}{2}$ way up stalk in 1 column, then 2, then 4 (2 columns of 2 suckers), then many; sudden change at distal end, suckers 2-3x larger; at the terminal distal end, there are 3 distinct series of 5 suckers each.

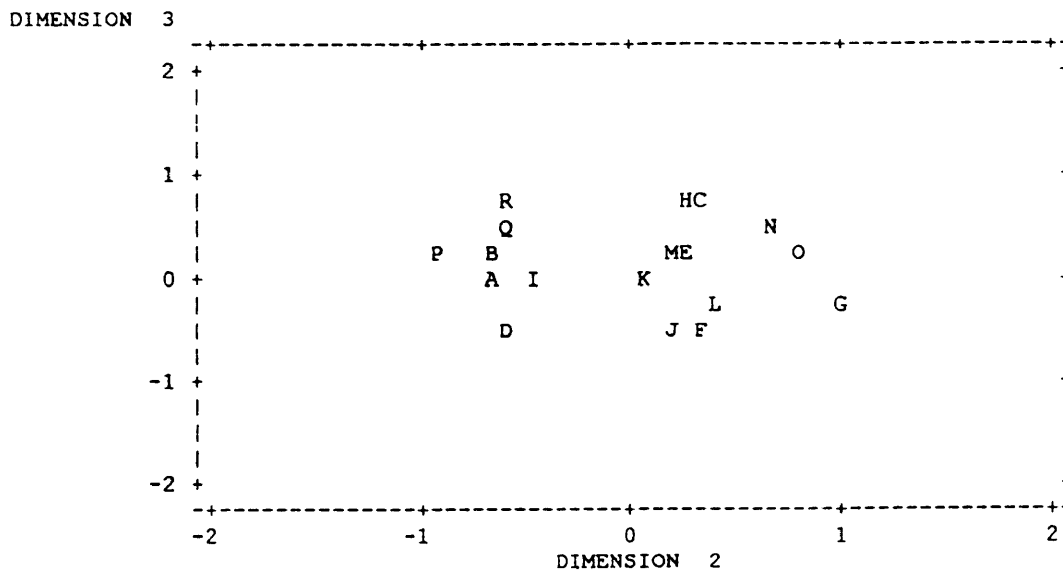
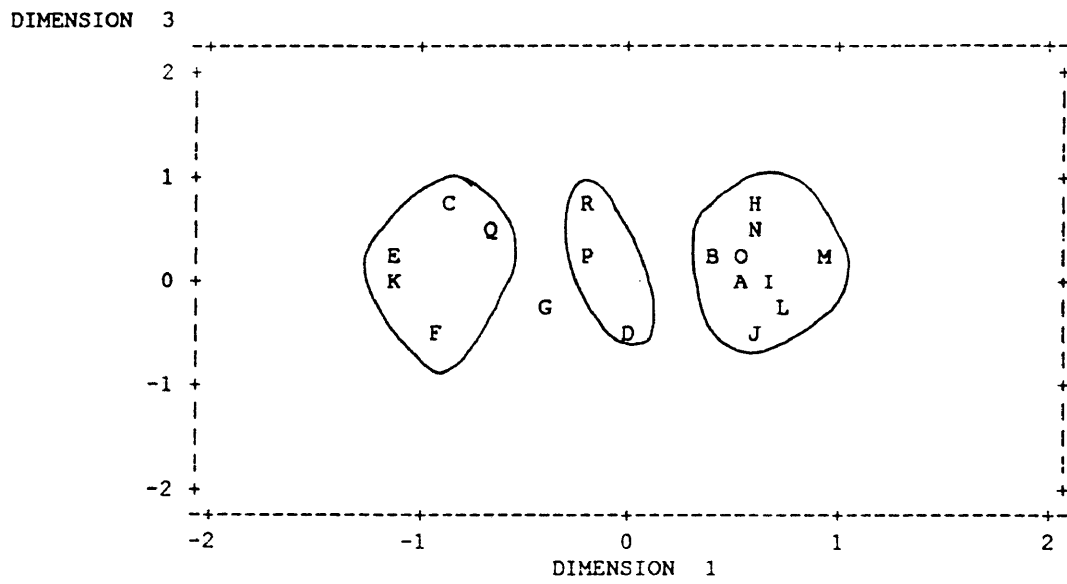
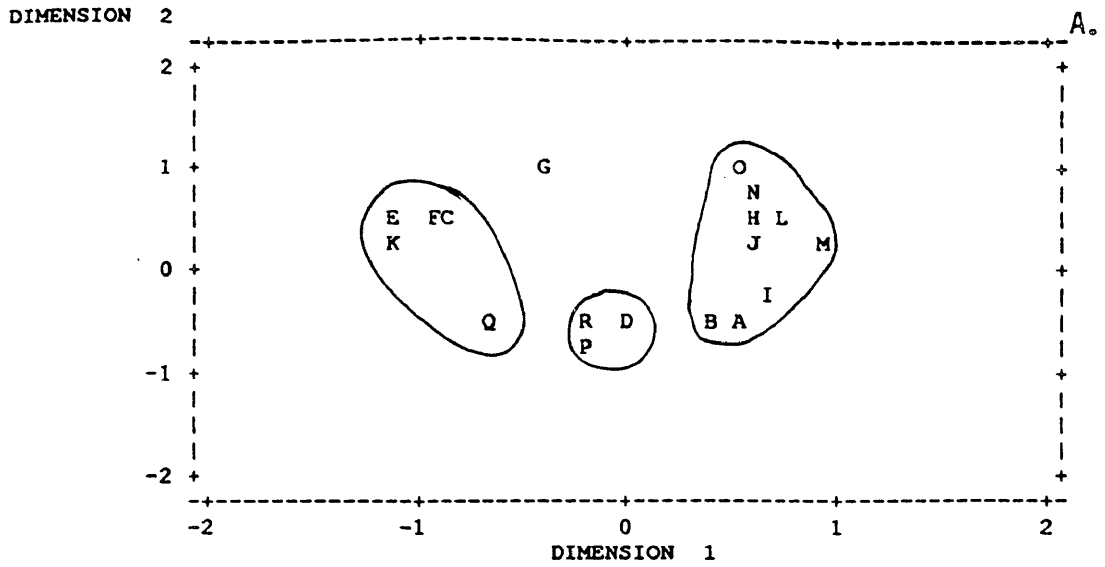
Multidimensional Scaling (Fig. 27a,b)

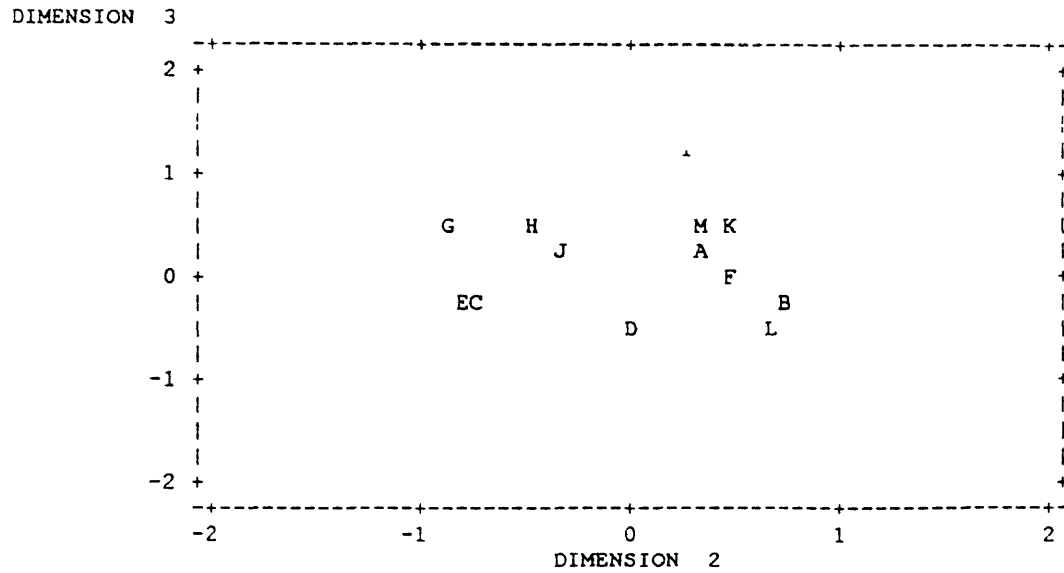
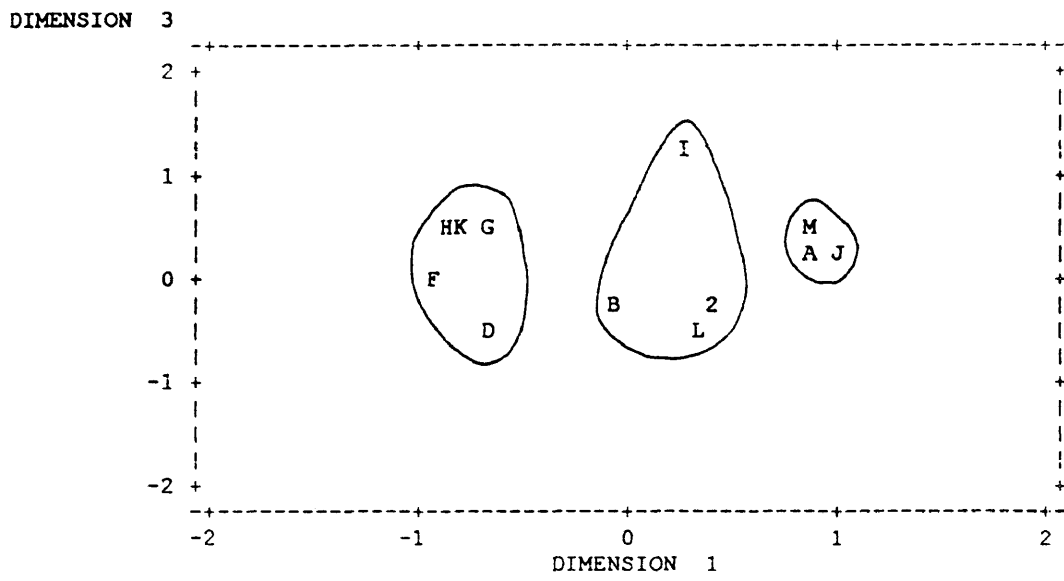
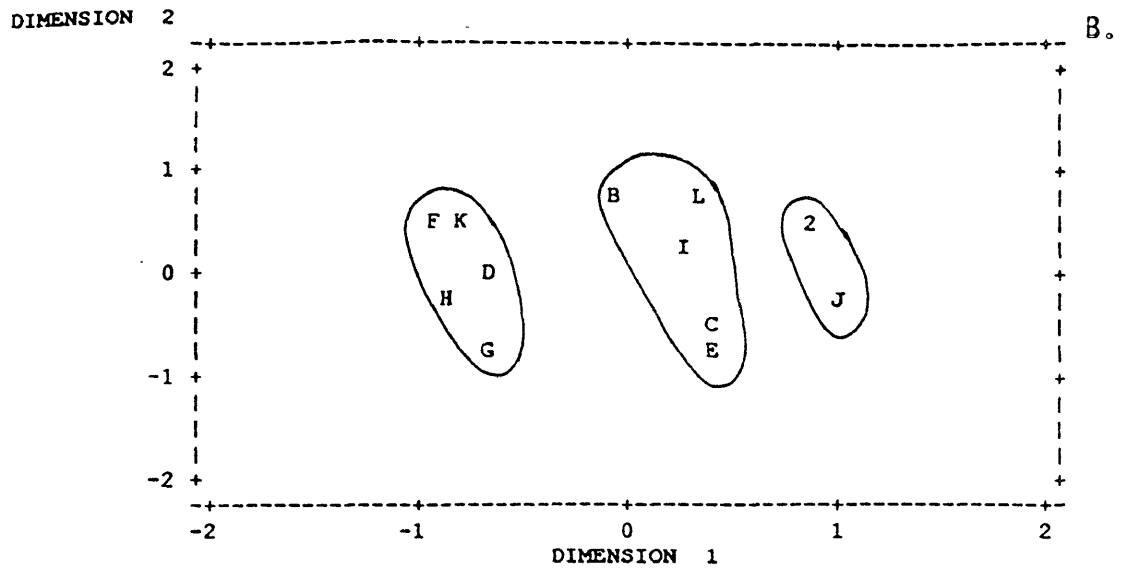
The optimal MDS configuration for daytime captures was three dimensional (stress = .159, Shepard diagram = straight); analysis of night captures was best interpreted in three dimensions (stress = .074, Shepard diagram = straight).

Most of the variability along the first axis of the day analysis is described by the latitude (-.857) and longitude (.781) of sample location, although CL (-.715), ED (-.656), HW (-.617), and HL (-.623) were also important descriptors. The variability of the second axis is best described by the remaining morphometric data (range: MOW = .532 to FunW-A = .889), with the notable exception of the NL (-.052). The third axis was described again by the morphology and the station data combined, but with a much lower range of correlation values (MOW = .070 to HW = .590). Several groups of specimens are evident in the resulting optimal configuration; the groups are based primarily on differences in areal distribution.

The night time configuration is very different from the day time configuration because the axes are very distinct. The first axis is described by the morphological characteristics except the NL (-.587) (range: CL = -.692 to FL = -.844), the second axis by latitude (-.781) and longitude (.859), and the third axis by salinity (-.740), temperature (-.784) and depth (.839). As in the daytime, the

Figure 27. Multidimensional scaling analysis optimal configuration for *Brachioteuthis sp. 4*. Each letter represents one specimen. Axes described as follows, characters listed in order of importance. a) Day. Axis 1: latitude, longitude, CL, ED, HW, HL. Axis 2: salinity, DML, FL, FW, 4AL, TenLen, NW, FBW. b) Night. Axis 1: morphological characters, except NL. Axis 2 latitude, longitude. Axis 3: salinity, temperature, depth.





nighttime optimal configuration shows four groups of specimens, but this time the groups are based on size differences.

DISCUSSION

A paralarva is defined as, " a cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctively different mode of life from that of older conspecific individuals" (Young and Harman 1988, p.202). According to the authors, "mode of life" can be inferred from "(1) major differences between the daytime habitat of the paralarva and that of older individuals and/or (2) distinct early discontinuities in growth patterns" (p. 202). The term was developed to be applied to oceanic Teuthoidea and Octopoda, because many species within these orders are found in the plankton early in life and in the deeper pelagic waters later in the life cycle.

Whereas this day/night planktonic/pelagic criterion is valuable for oceanic squids and octopods, it does not consistently apply to neritic or benthic species. Those cephalopods that do not follow this distributional pattern, including the entire order Sepioidea, challenge the usefulness of "paralarva" as a unifying terminology for the Cephalopoda. This flaw in the criterion was acknowledged by Young and Harman (1988). They recommended careful morphological examination to determine if developmental discontinuities exist, as being adequate to describe the end of a paralarval stage if planktonic / pelagic data are not available or applicable; however, this simple

recommendation makes the concept of a "paralarva" subject to the same debates as those that surround "larva". Calling morphological discontinuities in growth trajectories a metamorphosis has been a subject of much debate. These discontinuities can be used to suggest possible ecological changes, but they are not necessarily indicators of a lifestyle change. The inclusion of ecological elements that makes the definition of a paralarva unique; if the ecological data are not available or included, the usefulness of the definition is diminished considerably.

Several recent studies on the age and growth of paralarvae (Bigelow 1992, Vidal 1994) have used statolith or character measurements to describe ontogenic changes or discontinuities. Vidal (1994) for example, examined the changes in morphology of the arms, tentacles, fins, head and eyes over the early life history of *Illex argentinus*, a commercially important, neritic species of the family Ommastrephidae. As previously discussed (see introduction), when ommastrephid squids hatch, the tentacles are fused into a proboscis. This "rhyncoteuthion stage", as it is commonly known, is based solely on the fusion of the tentacles. The end of the paralarval phase has been expected to end at the separation of the proboscis into two tentacles. Vidal (1994) examined this event in detail and found, "No other morphological change, besides the proboscis division, takes place at the end of the rhyncoteuthion stage". She then suggested the paralarval stage of development in the Ommastrephidae ends at

the first discontinuity in the growth of the arms, suckers and fins (ca. 14mm DML) (Vidal 1994). This suggestion is contrary to the formal definition of a paralarva in that two critical components of the definition of a paralarva are missing: 1) differences in day-night habitat were not addressed; and 2) changes in morphology were not related to vertical distributions as required by the definition; instead they were attributed to changes in ecology (food type, survival ability, water masses). Equally important, actual ecological data that illustrated the proposed link were not analyzed.

Defining the end of the paralarval stage according to Young and Harman 1988, ideally would identify a change in niche from the planktonic to a mid- or deep-water mode of life, then a concomitant discontinuity in the growth trajectory. The onset of diel vertical migration is used as an indicator of this ecological change; however, areal distributions are also examined. If ecological data are unavailable, incomplete or do not show a change in day/night distributions, morphological data are used to define the paralarva phase of life, as allowed by the definition.

Family Ctenopterygidae

Ctenopteryx sicula

The geographic distribution of adult *C. sicula* generally is described as worldwide, but captures are most frequently recorded from the Mediterranean,

the North and South Atlantic between 40°N and 40°S and the North and West Pacific (Sweeney et al. 1992). The AMNAPE expedition sampled well within those boundaries, and the presence of newly-hatched and juvenile *C. sicula* is expected. No recent revision of the family exists.

The distinct difference between the frequent occurrence of *C. sicula* between 49-23°N in the spring/ summer and their virtual disappearance north of 37°N in the autumn/winter suggests that specimens are spawning, hatching, and growing during the warm months or the population moves south during the colder months (Fig. 5a-d). Winter captures may be biased low because of the poor collecting trip, but the autumn data support this trend. The number of specimens peaked in the spring/summer and was at a low point during the autumn/winter.

Roper and Young (1975) provided vertical distributional data (open net) that show adult *C. sicula* capture depths for larger specimens ranging from 0-850m during the day (38-62mm DML) and 100-200m at night (20-83mm DML). Because these were open net data, they give only a very broad indication of the depth horizons occupied by the species. Nevertheless, they classify the adult Chtenopterygidae as First Order Diel Vertical Migrators, meaning that they occur at moderate depths during the day (600-800m), but move to the surface waters (0-150m) at night. Young (1978) described open net captures from off

Hawaii at 675-800m during the daytime and 25-260 during the night, with 80% from 50-150m.

When the AMNAPE capture records are ordered according to increasing mantle length, an interesting pattern emerges, one of gradual ontogenic descent in the day time and a concentration of all sizes in the upper waters during the night. This finding contrasts with Roper and Young (1975), who indicate in their section on Ontogenetic Descent (p.2) that in most species of cephalopods, the larvae[sic] live in near surface waters and at a particular size abruptly descend into the adult habitat. In fact, the idea of a radical change from migrating to non-migrating behavior does not seem reasonable in cephalopods as a whole, as it implies that the instinct to migrate is somehow suppressed and then turned on at a particular size or under particular ecological conditions. A more likely scenario is that the newly-hatched specimens conduct micro-vertical migrations in the upper 100m of the water column, and as the organisms grow, they descend to deeper and deeper depths during the daytime hours. The sampling regime was not detailed enough to determine if the micro-vertical migrations occur in the upper 100m, but the gradual ontogenetic descent thereafter is evident in the Ctenopterygidae (Fig.4b,c). Therefore, for *C. sicula* several changes in ecology occur during the life history. The beginning of the ontogenetic descent occurs when the specimens of approximately 7mmDML first descend deeper than the upper 100m. Specimens of 10mm DML are collected in the 200-300m depth

horizon; and finally at 15mm from 400-500m. The squids finally begin to undergo the full or maximum vertical migration known for the adult of the species (as described by Roper and Young, 1975) at approximately 18mm DML.

The developmental pattern of *C. sicula* generally is characterized by linear growth over the 2-25mm DML range examined; however, two important exceptions exist. A change occurs in the relative growth rate of the fin length and the mantle opening width at approximately 10-12mm DML. The slope of the trajectory in the fin length after 12mm DML is almost double the slope before 12mm DML; conversely, the mantle opening width appears to grow quickly before 10mm DML, then to level off. Both the fins and the mantle opening are thought to be important in the locomotion of young cephalopods. Newly-hatched specimens are assumed to move by the same methods as the adults, although the actual mechanics of newly-hatched locomotion are unknown. It is interesting that the funnel measurements were linear over the entire range of DML (Appendix A). Lack of change in the growth trajectory of the funnel indicates that the funnel does not undergo any radical change in dimensions that may mark a beginning of adult style function, supporting the hypothesis that the mechanism of locomotion is the same in adult and newly-hatched specimens.

The change in fin and mantle growth trajectories in the AMNAPE collection occurs almost simultaneously with the first daytime capture of *C.*

sicula deeper than the upper 200m (10.2mm DML). Nighttime captures at depths greater than 200m begin at approximately 5mm DML. This contradiction indicates that even the smallest specimens have the ability to move into the deeper waters, but they have not yet assumed the adult behavior of ascending to the surface waters during the night, and descending during the day. The modes of life before and after 10-12 mm DML are distinctly different and the difference is marked simultaneously by a change in growth trajectories. According to Young and Harman's definition, the paralarval phase of the life cycle may be said to end at approximately 10-12mm DML in *C. sicula*, which is the size at which the morphology and ecology also change. The presence of a paralarval stage in *C. sicula* was predicted by Young and Harman (1988).

Family Mastigoteuthidae

The geographic distribution of adults in the family Mastigoteuthidae is worldwide, from tropical to boreal oceanic waters (Sweeney, et al. 1992). Mastigoteuthids are common inhabitants of the deep sea, but only rarely are more than 1-2 specimens taken at any one time (Young 1972). Thus, it is not surprising to find Mastigoteuthids in the AMNAPE collection but it is unusual to collect so many specimens with such a large size range.

The Mastigoteuthids are known to be deep water, open ocean squids. Nesis (1987) stated that the family Mastigoteuthidae contains bathypelagic and

meso-pelagic squids, with some benthic species. Adults of most species appear to be concentrated in the 500-1000m range during the day. This broad deepest-depth distribution is somewhat artificial, as sampling regimes frequently change from 100m discrete intervals of depth to 500m intervals at 500m depth, so the actual depth horizon of interest can not be firmly established. Some species may ascend to shallower depths at night (Roper and Young, 1975), while others are expected to stay in the deep waters throughout their diurnal cycle. Closing net, vertical distribution data are available for adult *M. magna* (NW Atlantic: Lu and Roper, 1979) *M. schmidtii* (=M.) (NE Atlantic: Clarke and Lu 1975, Lu and Clarke 1975) *M. pyrodes* (California: Roper and Young 1975) *M. hjorti* (Bermuda: Roper and Young 1975) and now for young *M. agassizii* and *M. magna* (Central Atlantic: this report). All reports, except for the AMNAPE specimens, have been based on very limited data sets.

M. agassizii

According to Nesis (1987), adult *Mastigoteuthis agassizii* are boreal and northern subtropical Atlantic, with northward extensions to the area south of Iceland. Geographic distribution of young and juvenile *M. agassizii* from the AMNAPE collection shows a relatively low frequency of capture and a tendency to be caught in the upper latitudes (>40°N) (Fig.14a-d). This finding contrasts with that of Lu and Clarke (1975a) in which the highest capture rate of *M.*

agassizii was from the lowest latitude (11°N) of their four-cruise study; at higher latitudes, the number of specimens declined drastically. Interestingly, all captures were made in the waters closest to the Azores, possibly indicating that oceanographic processes are concentrating *M. agassizii* around the islands, as Reid et al (1991) showed for Hawaii. Little variation occurs in the seasonal distributions-- the same areas of occurrence are found during each of the four cruises. This pattern suggests that the newly-hatched specimens do not undergo any large scale geographic migrations. This prediction is not surprising, based on the relatively bulbous body shape and gelatinous composition of the mantle of *M. agassizii*. Individuals of this species have not been considered to be strong swimmers.

The AMNAPE collection shows that *M. agassizii* specimens as small as 6.2mm DML are found in the 500-1000m depth horizon during both day and night, implying relatively newly-hatched and adult specimens share similar habitats. Lu and Clarke (1975) found that during the day, all specimens occurred deeper than 500m; during the night they found four specimens in the 50-100m depth horizon. They interpreted this as a diel spreading, but in light of the results of this study, the four specimens likely were "contaminants" from deeper hauls. *Mastigoteuthis agassizii* eggs, egg deposition, and hatching are undescribed at this time, but finding such small specimens at great depths suggests that hatching may occur in deep water. An alternative explanation is

that eggs hatch in the near-surface plankton and the newly-hatched young rapidly descend to the 500-1000m horizon. This scenario is unlikely because of the tremendous distance that would have to be traversed, and because the adults are not known to be strong swimmers. Lu and Clarke (1975a) describe a second trend that is not apparent in the AMNAPE data. As the specimens got larger, the upper limit of their depth horizon got deeper. In other words, as they grew (>40mm DML), they showed signs of an ontogenic descent into deeper waters.

The developmental pattern of *M. agassizii* is characterized by linear growth over the 6.2-62.5mm DML with two notable exceptions: the eye and head measurements have inflection points at approximately 11-12 mm DML. These inflection points do not coincide with changes in the depth of capture, which is 500-1000m over the 6.2-62.5mm size range regardless of the size of the specimen. Because no change develops in the depth of occurrence between the smallest and largest specimens, the end point of the paralarval stage of life can not be delineated based on ecology alone. In this situation, Young and Harman (1988) recommend using discontinuities in morphological growth trajectories as an indicator of the end of the paralarval stage. Thus, according to the definition *M. agassizii* does have a paralarval stage: those specimens < 12mm DML; but, since there is no obvious coincidental change in diel vertical distribution between the very small and the very large, the need for distinguishing between a paralarva

and non-paralarva is diminished. In fact, Young and Harmon (1988) predicted that *M. schmidti* (synonym of *M. agassizii*) would not have a paralarva.

The station data used in the MDS did not provide a good indication of what ecological parameters would be more applicable to use to mark the end of the paralarval phase. Depth describes the variability about the first axis for both day and night. In other groups, this might indicate considerable variability in depth of capture occurs over the size range during the daytime and nighttime. But, based on the depth vs. DML graph (Fig. 13b,c), it seems to be an artifact of the use of an average depth instead of the actual depth of capture. Salinity and temperature did not describe the variability of the optimal configuration at all. Predictions for important ecological parameters are then best based on morphological observations. The fins of the newly-hatched *M. agassizii* are very large with respect to the overall DML. This observation may indicate that there is some change in the animal with respect to its ability to move, or position itself to attack prey; it could be a change unrelated to the currently know method of locomotion in squids. Secondly, the head dimensions are the only measurements to change in their growth trajectories. This may indicate a change in visual acuity and possibly a new diet. Much more needs to be learned about these deep-ocean creatures before inferences can be made about the ecological specializations.

Idioteuthis magna

Idioteuthis magna occurs in the tropical and northern subtropical Atlantic and Indian Ocean and Tasman Sea (Nesis 1987). Depth distribution data have only been described once from few specimens, indicating that during the night, adult specimens are found in the 200-500m range; whereas daytime captures are from 700-800, and 0-1000m (Lu and Roper 1975).

The 1980 and 1983 areal distribution (Fig. 9a-d) shows several samples with moderate to large numbers of specimens, but in 1981 and 1982, virtually no specimens were caught. These seasonal differences suggest that the *I. magna* population migrates out of the area in the fall/winter and back into the NW Azores area during the spring/summer. This presence / absence pattern in *I. magna* is very distinct from that of *M. agassizii*, which is found in the same locality throughout the seasons.

Patterns in the depth distribution of newly-hatched *I. magna* are not as simple as those of *M. agassizii*. Specimens are collected during the day from a variety of depths; although most are found in the upper 200m, four were found below 200m, two of which were from the 500-1000m depth zone. At night, the smallest specimens (<7mm DML) were found in the upper 100m, with a gradual increase in depth of capture with increasing DML. This nighttime pattern is

similar to *C. sicula*'s daytime distribution, and again lends support to the idea that vertical migration is a behavior that may be manifested in the smallest specimens of some species. The day/night distribution patterns described are not consistent with any patterns described by Roper and Young (1975). A Diel Vertical Spreader as defined by Roper and Young (1975 p. 39) as when, "the night time vertical distribution... not only encompasses the daytime levels, but spreads well beyond the daytime limits." In the case of *I. magna*, the *daytime* vertical distribution encompasses the *nighttime* levels, and spreads well beyond them, just the reverse of the aforementioned definition. For this reason, I would propose calling them Reverse Diel Vertical Spreaders, even at the smallest of sizes.

The smallest of specimens appear to be spread out over the entire water column during the daytime, with the deepest specimens caught at about DML = 8-9mm. Although the data are not as convincing as for *C. sicula*, the inflection point does appear to coincide with the first records of night time captures at >100m (DML = 7.2mm). The scatter of depths found during the daytime is not found at night; instead, the specimens become very aggregated in the upper 200m, with those over 7.2mm being the only representatives of the 100-200m horizon.

Changes in most of the characters measured in *I. magna* can be categorized as simple and linear. The slope of most trajectories is relatively small (exception = AL), indicating that characters grow slowly in relation to the overall body length (Appendix A). The exceptions to the linear developmental pattern (Fig. 10) are once again the MOW, and the fin dimensions which are better described as logarithmic with an inflection point at approximately 7mm DML. MOW measurements are variable, which is expected based on the plastic nature of the mantle.

The morphological inflection point at 7mm corresponds well with the nighttime descent. A DML of 7mm does not appear to have any special significance for the daytime captures, although specimens less than 8mm were always caught in the upper 500m. According to the definition, *I. magna* does have a paralarva: those specimens <7mm DM; however, the important ecological criterion was not the diel difference in vertical distribution as expected.

The station data used in the MDS did not provide a good suggestion of what ecological parameters would be more applicable than depth of capture to mark the end of the paralarval phase. Although the station data, with the exception of average depth of capture, do describe the variability within the day, the groups of specimens are based on areal distribution. Comparisons to Fig. 9 show that this result is an artifact of the sample collection locations.

The nighttime analysis showed several groups of specimens arranged in a circular pattern. Because the axes shared characters (e.g. the FL explained variability around the 1st and 2nd axes) the circular pattern that prevailed was most likely an artifact of the analysis. Salinity was the only station parameter that explained the variability of the data set.

Family Brachioteuthidae

The geographic distribution of the family Brachioteuthidae is worldwide (North and South Atlantic, the Mediterranean, the Indian Ocean, the Southwest Pacific, and the Southeast Pacific (based on *B. riisei*, Clarke 1966) between 60°N and 60°S (Pfeffer 1912).

The depth distribution of brachioteuthids is not well known, although species are suspected to undergo strong vertical migrations. Roper and Young (1975) presented depth distribution data for 6 large (38-42mm DML) specimens from Hawaii and show they are found in deep waters (830-1000m) during the day, and in the shallow waters at night (50-200m). No data for juvenile or newly-hatched specimens were available. Clarke (1966) cited evidence that adult specimens have been captured in open nets from the surface down to 3000m.

Brachioteuthis sp. 3

Juvenile and young specimens of *Brachioteuthis sp. 3* were caught only during the 1981 and 1983 seasons (Fig. 20a,b). All but 10 specimens were caught north of 45°N and most specimens were caught as part of a large aggregation. The presence of so many specimens of approximately the same size is a strong indication that the species aggregates in schools as juveniles. Since the specimens were of an intermediate size, they probably were not recently hatched. The vast seasonal differences at the same sampling locations may indicate that the schools make large scale seasonal migrations. This would not be surprising, as the body shape and musculature are consistent with other squids thought to undergo vast geographical migrations (for example, *Illex illecebrosus* and *Todarodes saggitatus*).

The interpretation of the daytime distribution of *Brachioteuthis sp. 3* is greatly diminished because the largest specimens were caught in malfunctioning opening and closing nets. But, the fact that only the larger (>30mm DML) specimens were caught in the malfunctioning nets is in itself interesting and other useful information can be gleaned from the graphs. At small sizes, the specimens are clustered in the upper depth horizons during both the day and night. No specimen smaller than 30mm DML was caught deeper than 200m during the day. In fact, in the daytime, almost all specimens smaller than 30mm DML were collected in the upper 100m of the water column. This pattern of distribution is similar to that found in *C. sicula*. Curiously, the nighttime data shows a vertical spreading of the smallest specimens down from the upper 100

meters to the 200-300m depth horizon. This fact shows again that even at the smallest sizes, the specimens are likely moving under their own power and exhibit a tendency to migrate vertically. Furthermore, specimens larger than 30mm DML are found in the upper 300m during the night. This finding is consistent with what has been suggested in the literature, but whether they have moved from much deeper depths and how the distribution changes with ontogeny remains to be examined.

In contrast to the Cthenopterigydae and Mastigoteuthidae, the developmental pattern of *Brachioteuthis sp. 3* cannot be easily categorized (Fig. 21). Each morphological character has a different growth trajectory; however, two different inflection points are repeatedly seen in the trajectories. The first is at approximately 15-18mm DML; the second at 28-30mm DML. No change in the depth of capture co-occurs with the first inflection point, and no accurate correlations with depth of capture can be made at the second inflection point due to the broken opening/closing net mechanisms. Based on the growth trajectories, specimens larger than 30mm DML are going through a time of decreased relative fin growth, but an increase in the trajectory of every other character.

The fact that the other species of this family do show signs of vertical migration would suggest that members of this family do vertically migrate.

Under the circumstances, the end of the paralarval stage of development can not be determined based on the ecology proposed by Young and Harman (1988). Better collection data of larger squids could potentially be pooled with these data to find the answer.

The identification of the end of the paralarval stage in *Brachioteuthis sp. 3* using morphology alone presents further problems. The growth trajectories change twice, at 15-18mm DML and at 28-30mm DML with no discernable change in ecology. If the depth distribution were known, it could give an indication of which to choose. This dilemma shows the weakness in using only morphology.

The station data used in the MDS did not provide a good suggestion of what ecological parameters would be more applicable than depth of capture to use to mark the end of the paralarval phase. The daytime analysis did not give any new information, showing only that there was a very large variability in the size and the shape of the organism captured; station data described the second axis, but the correlation values were low. Interesting, almost all of the parameters used in the analysis were important in describing the first axis; only average depth of capture was assigned to the second axis. The inclusion of depth on the nighttime configuration but not the daytime supports that there was some vertical spreading. The arc-shape of the optimal configuration may be

the result of interactions between the variables that described the first axis. The configuration can be broken into three sections, based but the sections are based on size and station data together, which makes predictions difficult.

Brachioteuthis sp. 4

The geographic distribution of *Brachioteuthis sp. 4* (Fig. 25a-d) is vastly different from that of *Brachioteuthis sp. 3*. *Brachioteuthis sp. 4* was caught in all but the winter seasons, when the weather precluded an extensive sampling regime. In contrast to *Brachioteuthis sp. 3*, most *Brachioteuthis sp. 4* specimens were caught singly or in small groups, in the waters around the Azores islands, generally between 43-33°N. The change in capture records from spring to summer to autumn implies that the population gradually moves from the Southwest side of the island complex to the north side, then due north. The winter catch records are hard to interpret because of the bad weather conditions; however, the fact that no *Brachioteuthis sp. 3* or *Brachioteuthis sp. 4* were caught during the winter may imply that brachioteuthids move out of the study area in the cold months.

Depth distribution data for *Brachioteuthis sp. 4* were also very different from those of *Brachioteuthis sp. 3*. Most of the specimens caught during the day (7.1-36.7mm DML) were found in the upper 100 m of water. At night, specimens

of all sizes spread out over the 0-500m depth horizon and, interestingly, some of the smallest specimens went to the deepest depths. According to the categorization of Roper and Young (1975), *B. sp. 3* should be considered Diel Vertical Spreaders, meaning that the nighttime vertical distribution encompasses and may spread beyond the daytime vertical distribution.

The growth trajectory of *Brachioteuthis sp. 4* is exponential over the 3.5-45.3mm DML size range. All measurements follow this trajectory except for the funnel length and width, eye diameter, and head length, which are linear. At each inflection point (10-15mm and 20mm DML), the slope of the line changes: before the inflection point DML grows faster than the measured character; after the inflection point the converse is true.

The first dramatic change that takes place in the life cycle is the increased relative growth of the tentacles length, head width and eye diameter. Along the growth continuum, the inflection point for each of these characters occurs between 10 and 15mm DML (Fig. 26). Changes in these characters may indicate an increased ability to focus on and capture prey (see Messenger 1968 for full description of the adult *Sepia* attack sequence). The next combination of characters to change (inflection point approximately 20mm DML) is the fin length and width, mantle opening width and arm length. The change in fin development may indicate a more active phase of life, perhaps one where prey is

more actively pursued, and the escape behavior becomes better developed. None of these morphological changes can be correlated with any particular change in the depth of capture. Specimens were spread vertically over the upper 400-500m regardless of size. The day and night vertical distribution data indicate that the newly-hatched specimens already may be able to migrate, even at sizes <20mm DML (Fig. 24). Funnel measurements without discontinuities further support this hypothesis. Two of the larger daytime specimen were captured between 0-1200m, but the suggestion that they were taken from the deepest depths are obscured by the presence of a larger specimen caught in the upper 50m. The rapid development of the arm length at this size may help in handling prey, or it may have some effect on making the squid more hydrodynamic.

Since the ecological data are inconclusive and both the juveniles/adults and paralarvae appear to inhabit the upper portion of the water column, even the "last resort" definition of a paralarva as, " young pelagic cephalopods that can be sampled quantitatively by standard plankton nets in near surface waters, during the day" (Young and Harman 1988, p.203) cannot be used. Once again, the paralarval phase must be delineated by changes in the growth trajectories alone. As in *B. sp. 3*, two possible sizes exist, 10-15mm DML or 20mm DML. Without good ecological data, the choice is arbitrary.

The station data used in the MDS did not provide a good suggestion of what ecological parameters would be more applicable than depth of capture to use to mark the end of the paralarval phase. The daytime results showed that species were taken over a large range of stations, and that there was very little variation in the average depth of capture. Conversely, the nighttime configuration is described, in part, by the average depth of capture. This difference suggests that the specimens may be clustered at one level during the day, but dispersed during the night, which is consistent with earlier data. Although the station data does not provide insight into the important ecological parameters, the fact that the head and eye measurements are responsible for much of the variability during the day may mean that the specimens were grouped based on visual acuity.

Utility of the Concept of a Paralarva

Cephalopods often are characterized as having direct development; fishes have been similarly labeled. This characterization does not mean that there are no differences at all between a newly-hatched and an adult cephalopod. In fact, several morphological and ecological characters can be used to differentiate between a newly-hatched and juvenile or adult form. For a example, the fins of most newly-hatched cephalopods have a characteristic "paddle" shape, and are attached dorsally to the distal end of the mantle. Newly-hatched cephalopods also have species-specific chromatophore patterns (e.g., *Octopus*, *Brachioteuthis*)

that are substantially different from the adult form. An ecological difference, as Young and Harman (1988) pointed out, is the planktonic vs. pelagic life style. Other ecological differences may include food preferences or geographic distributions. These ecological changes represent a significant change in the mode of life and are referred to here as niche shifts.

Whereas the 1988 definition was a positive first step towards a unifying concept describing the early life history of Teuthoid and Octopod cephalopods, expansion of the "paralarva" definition would allow the concept to be applicable to all cephalopods and potentially to all organisms that undergo direct development. It would also remove the need to rely on morphology as a "backup" indicator of the end of the paralarval stage.

For these reasons, I propose that the concept of a "paralarva" be simplified to the following, ecologically-based definition:

"a cephalopod of the first post-hatching life phase that has a distinctly different mode of life from that of older, conspecific individuals"

A "different mode of life" is intended to include species whose newly-hatched forms may exhibit the potential for, *but do not fully express*, a characteristic juvenile/adult mode of life (see Boletsky 1979). In these cases, the

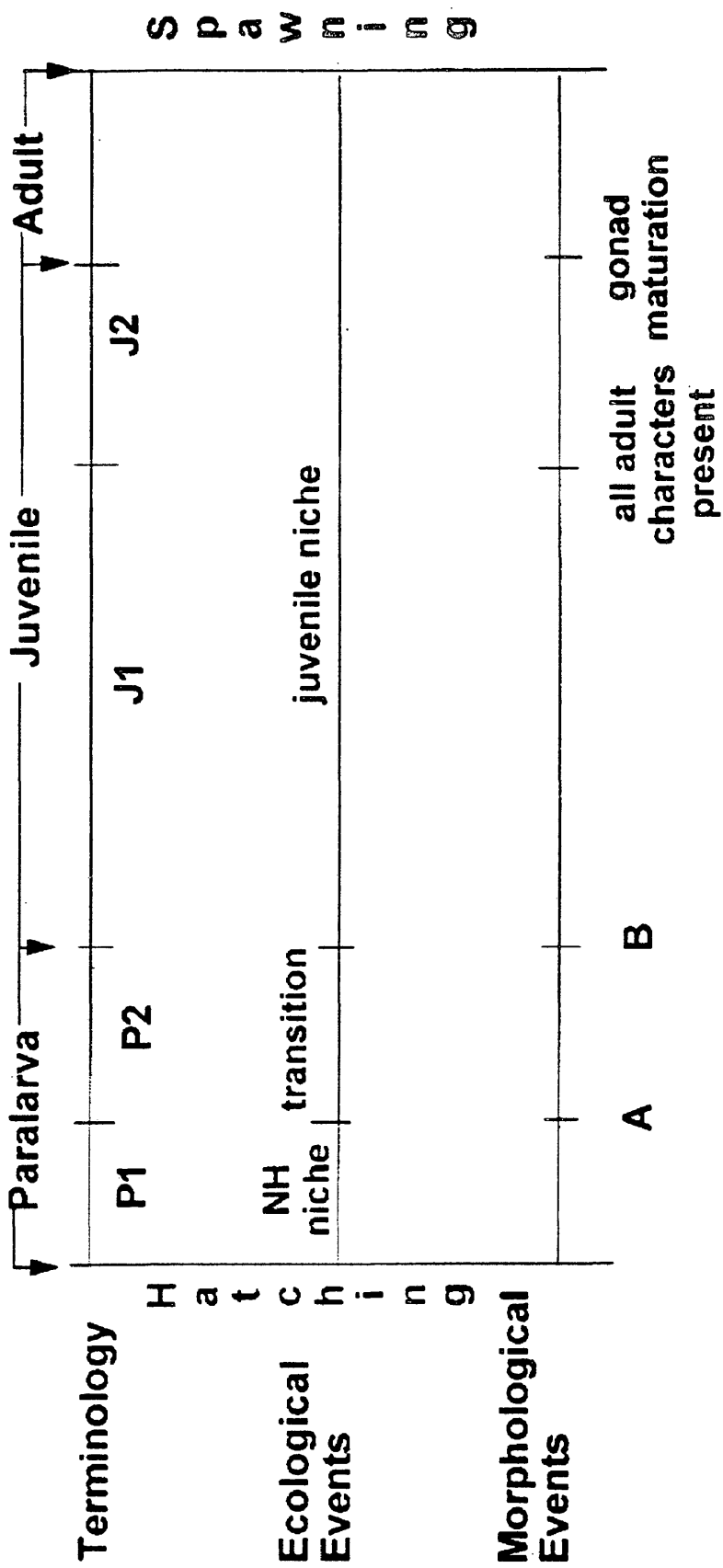
full expression of the juvenile/adult mode of life marks the end of the paralarval stage.

The life cycle of all cephalopods can be described according to this definition (Fig. 28). The paralarval life stage starts at hatching and ends at the full expression of the juvenile/adult niche. Two stages can be differentiated-- Stage 1 ends at the beginning of the niche shift; Stage 2 ends and the juvenile stage begins at the full expression of the juvenile/adult ecology/behavior. The juvenile phase can also be divided into two parts: Stage 1 ends at the time when all adult characters, except mature gonads, are present. Stage 2 ends at the onset of gonad maturation. Finally, the adult phase begins at the maturation of the reproductive organs.

This new description of the life cycle relies on both morphological and ecological criteria, as did the original description, but it also eliminates the possibility of a paralarva being called a juvenile (see Young and Harman 1988 for discussion). It has the additional benefit of eliminating the term "subadult" in cephalopod terminology. The definition for subadult of Young and Harman (1988) could be assumed for the Stage 2 juvenile.

Ecological niche shifts may be represented by the assumption of the juvenile or adult mode of life in any of the following categories: vertical

Figure 28. Schematic representation of the proposed description of the life cycle of the Class Cephalopoda.



distribution (Young and Harman 1988), geographical distribution, behavior (including but not limited to characteristic resting positions, banding patterns, or schooling (proposed by Hanlon et. al 1987), and predator-prey interactions (including attack sequence, manipulation of prey, escape methods. See Messenger 1978). This list must be augmented as new adult ecological or behavioral patterns are discovered. The niche shift will most likely, but not necessarily, be accompanied by a change in the growth trajectories of morphological features. Frequent changes noted thus far are in the dimensions of the fins, arms, tentacles or clubs. Additional characteristics that might be important include sucker counts and chromatophore patterns.

The literature on the age and growth of newly-hatched or paralarval cephalopods, regardless of the Order discussed, can be assimilated easily into the new life history description. Octopodid paralarvae already are considered to have two stages (Hochburg et al. 1992). Stage 1 includes those specimens that occur in the upper 200-300m and that do not have any developing sucker buds. Stage 2 specimens are caught in deeper water and have sucker buds. Possibly, stage 1 ends at the beginning of the change from the newly-hatched niche, and stage 2 ends at the final assumption of the juvenile/adult niche. Because the morphology of the arms of the stage 1 and stage 2 octopods is overtly different, prey capture and manipulation may be the ecological parameter of concern.

Newly-hatched Sepiolinae provide a behavioral example of a niche-shift. Immediately after hatching, Sepiodea (*Sepiola* and *Sepietta*) burrow in the sand just as the adults do (Boletzky et al 1971). However, the adult feeding behavior is not fully expressed until the organism waits until dusk to feed, regardless of the availability of food provided during the day (Boletzky et al 1971). Finally, a cellular morphology example can be given from the Teuthoidea. Cross-striated muscles are not present in the tentacles of *Sepioteuthis lessoniana* specimens less than 2 weeks after hatching (P1). Muscular differentiation begins at approximately 3 weeks (P2) and is fully formed by day 36 (J1). As a consequence of this lack of differentiation, newly-hatched *S. lessoniana* have a very different method of capturing prey. In general, adult squid capture prey with a tentacle "strike" and use their arms for prey manipulation. In contrast, *S. lessoniana* paralarvae use a burst of speed to overtake the prey, and use their arms for capture (W. Kier, personal communication, University of North Carolina at Chapel Hill).

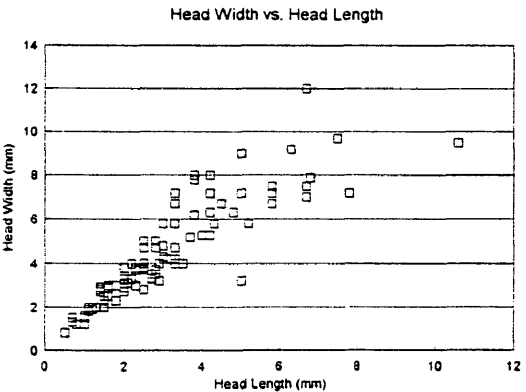
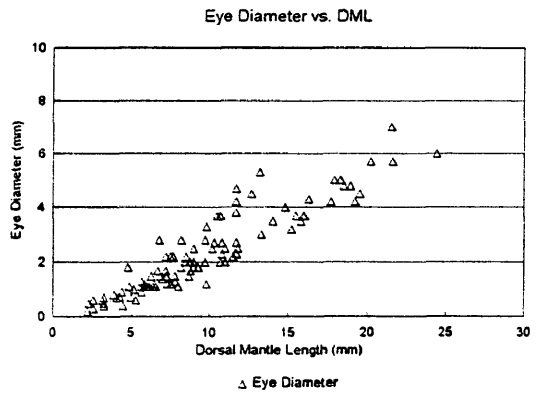
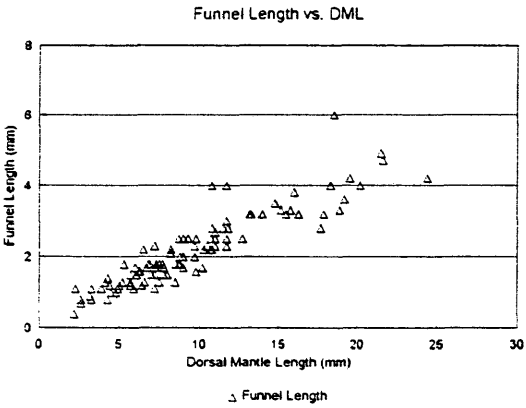
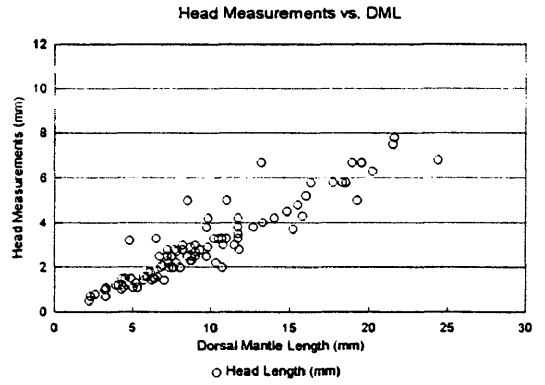
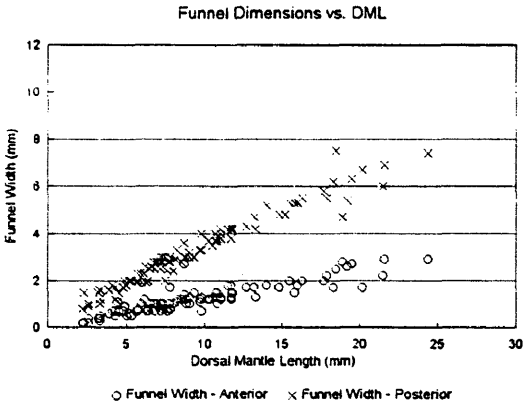
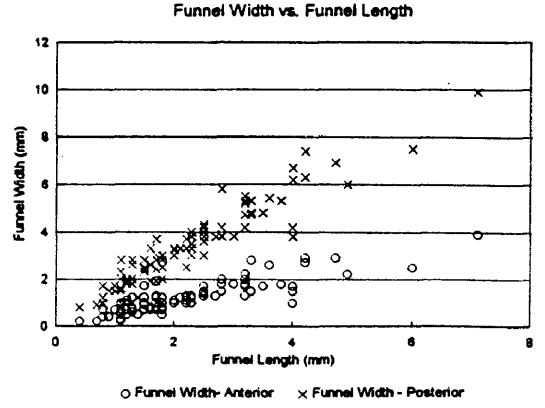
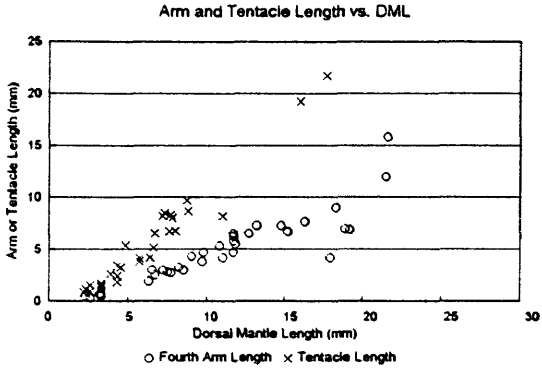
According to the new definition, the end of the paralarval stage for *C. sicula* takes place at the assumption of the full "adult" vertical migration range (18mm DML). In *Idioteuthis magna*, the P2 stage begins when the nighttime specimens are caught deeper than 100m during the night (7mm DML), but the end of P2 cannot be determined because of a lack of specimens. The paralarval

phase of the other species in this study can not be defined based on the vertical distribution.

Finally, each of these families appears to have an easily recognizable morphological marker of the shift from a paralarva to a juvenile. The position of the eye can be used as an indicator in all three families, as it apparently moves from the anterior-most position on the head (paralarva) to a lateral position (juvenile) that extends over most if not all of the length of the head. In the two *Brachioteuthis* species examined, the internal organs move from the posterior end of the mantle cavity (paralarva) to the anterior (juvenile). In *Chtenopteryx sicula*, the number of rows of suckers on arms 1-3 also can be used.

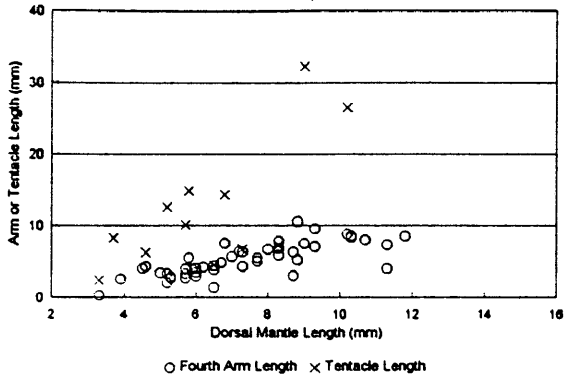
APPENDIX A. Ontogenic changes in morphology in *Ctenopteryx sicula*,
Idioteuthis magna, *Mastigoteuthis agassizii*, *Brachioteuthis sp. 3* and *Brachioteuthis sp.*

4.

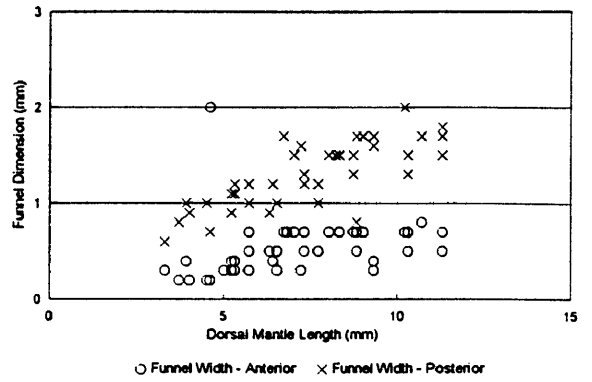


Ctenopteryx sicula

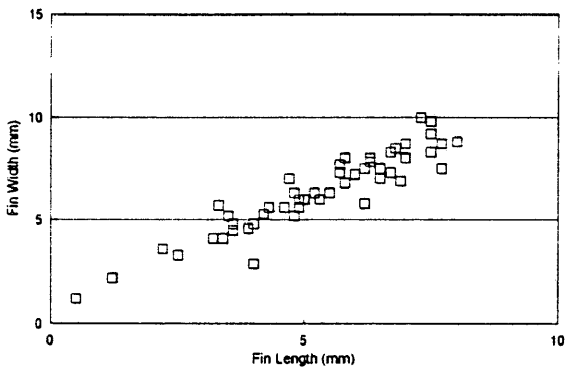
Arm and Tentacle Length vs. DML



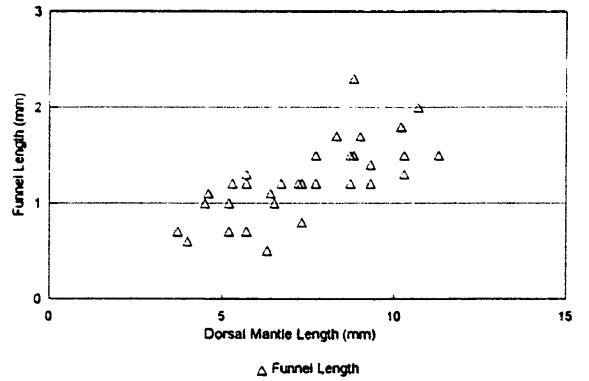
Funnel Dimensions vs. DML



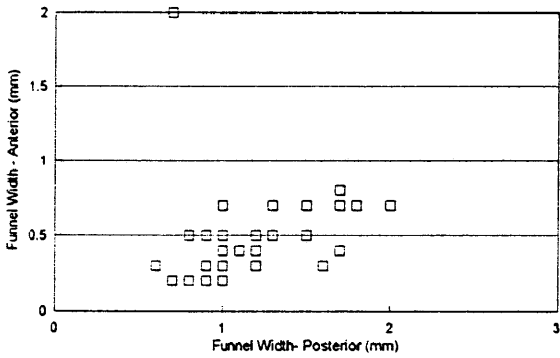
Fin Length vs. Fin Width



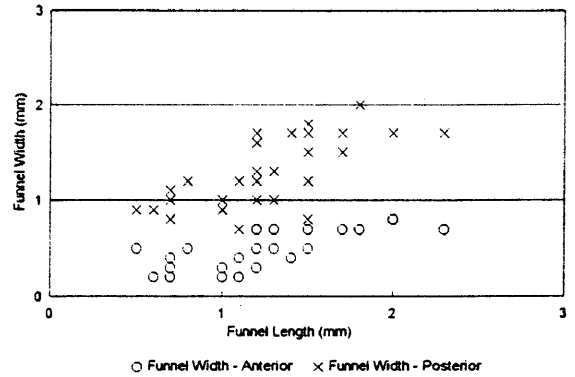
Funnel Length vs. DML



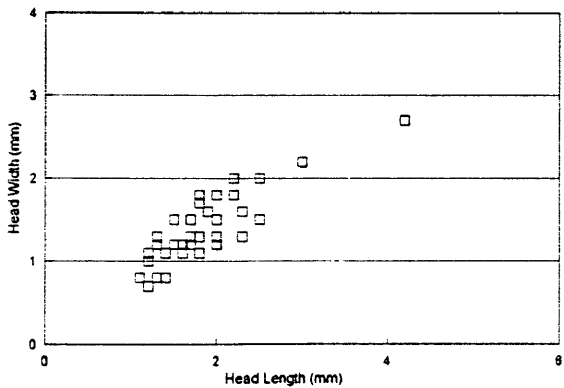
Funnel Width : Anterior v. Posterior



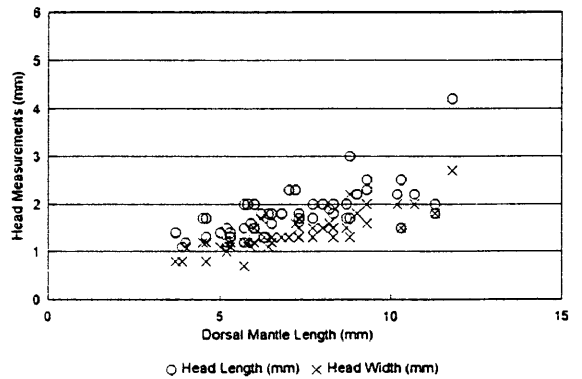
Funnel Width vs. Funnel Length



Head Width vs. Head Length

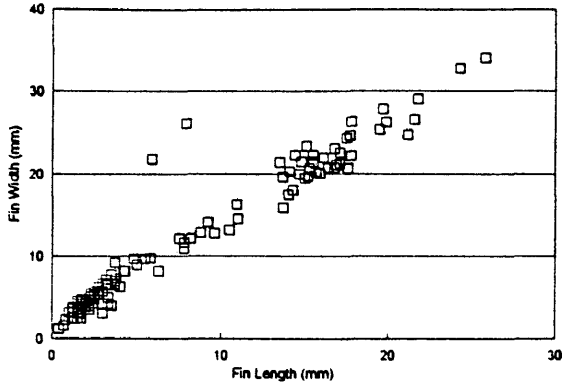


Head Measurements vs. DML

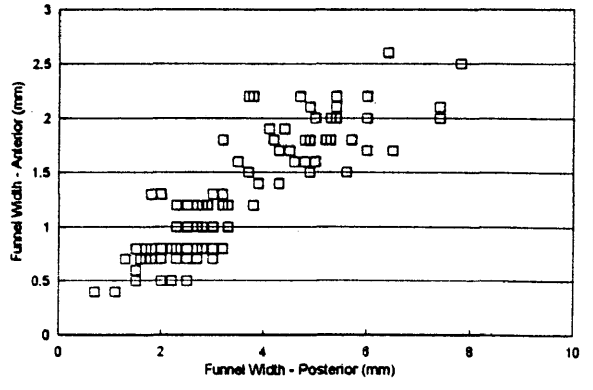


Idioteuthis magna

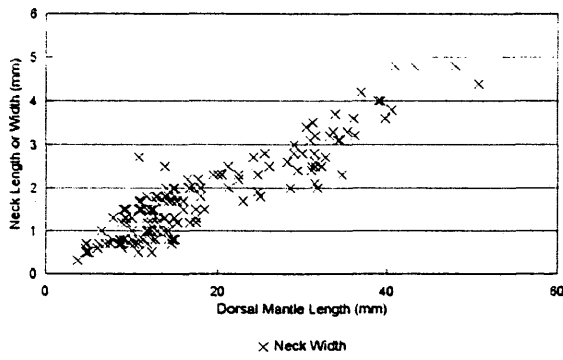
Fin Length vs. Fin Width



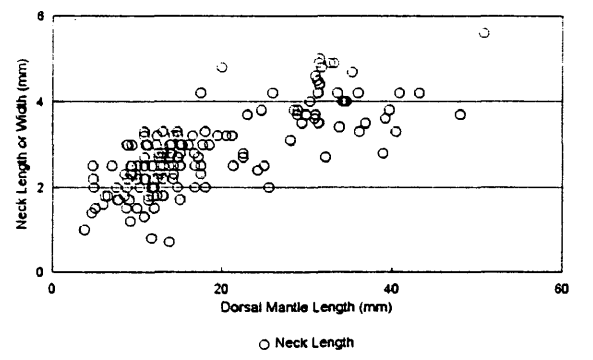
Funnel Width: Anterior vs. Posterior



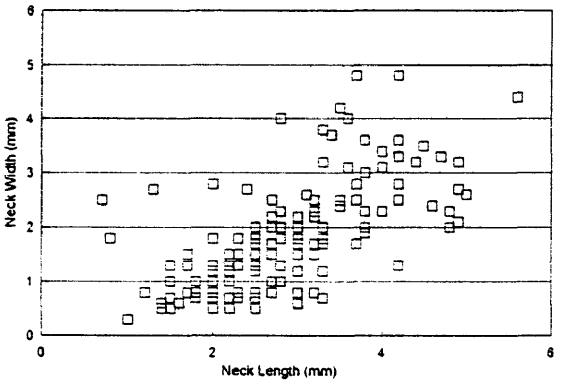
Neck Width vs. DML



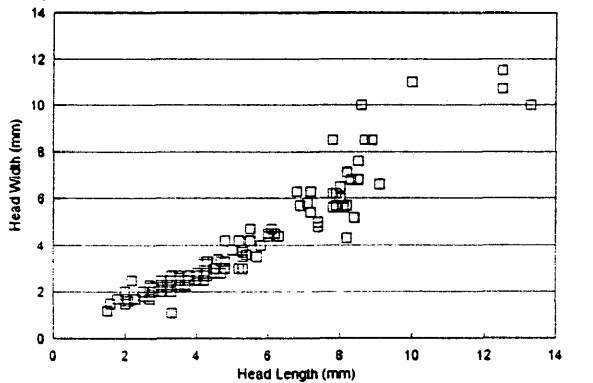
Neck Length vs. DML



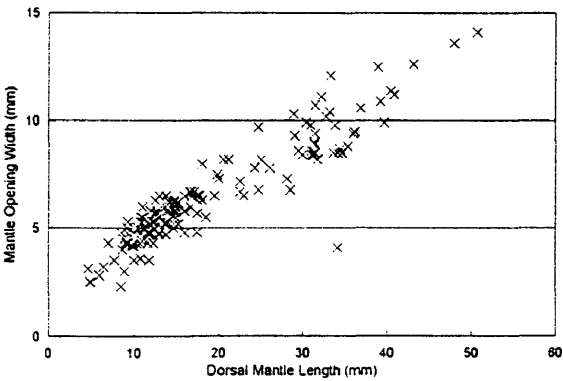
Neck Width vs. Neck Length

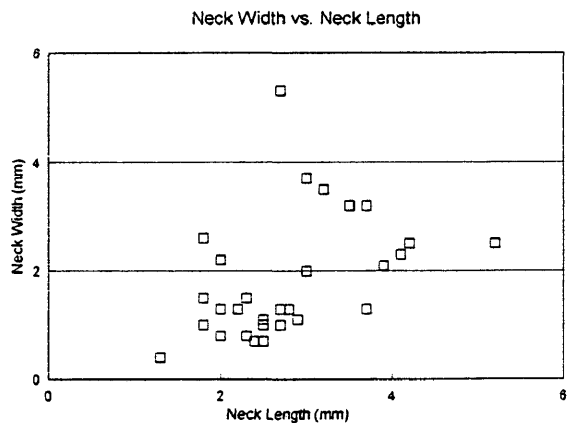
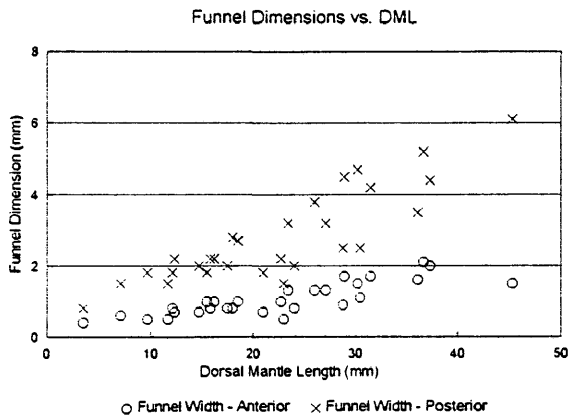
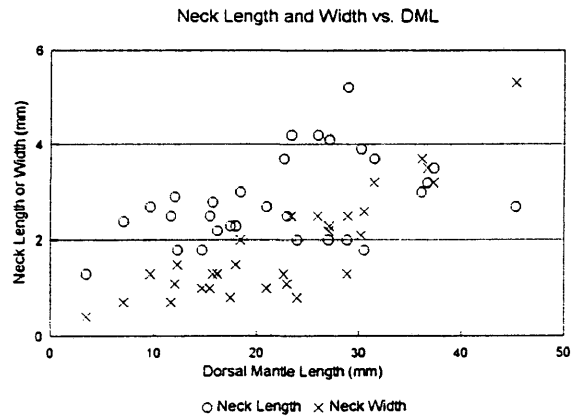
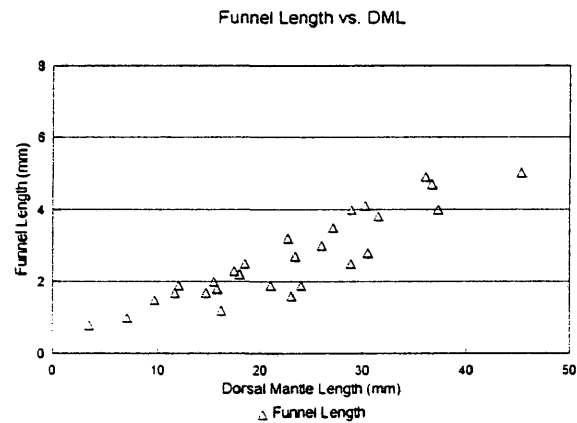
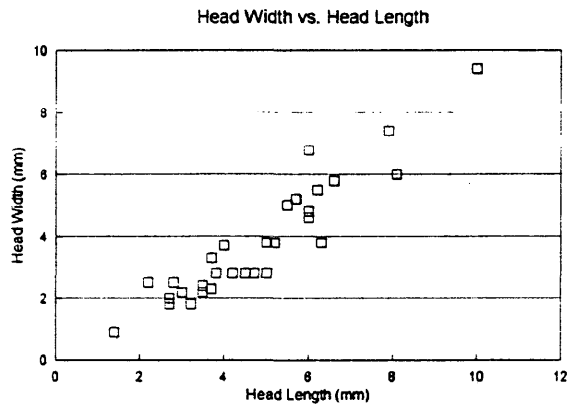
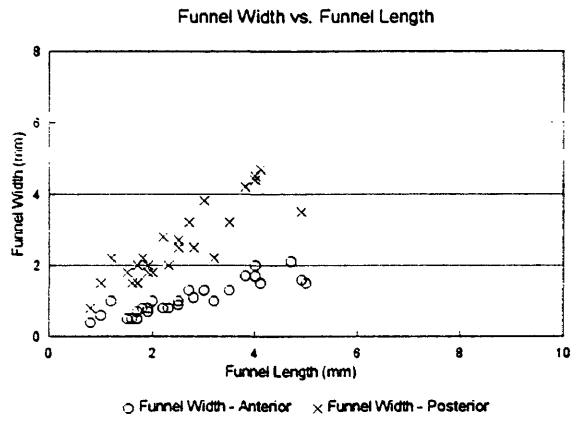
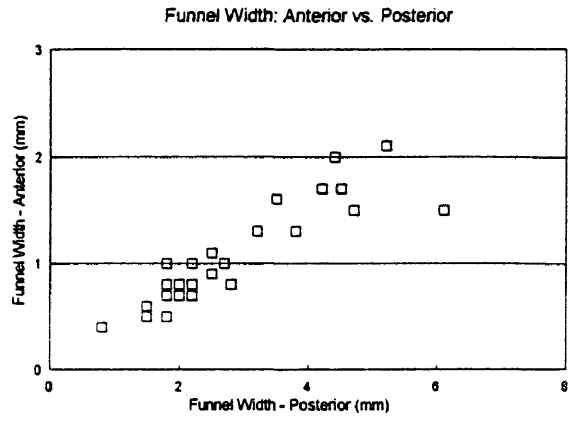
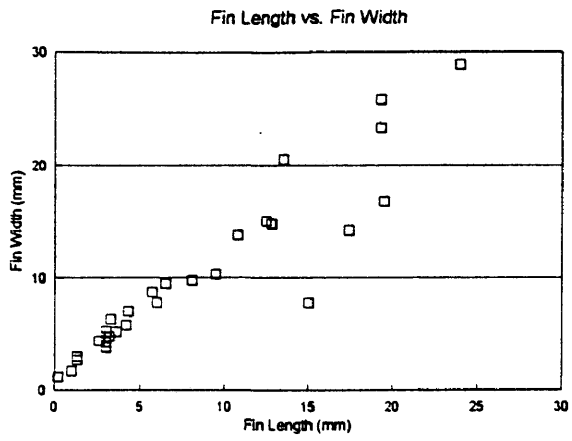


Head Width vs. Head Length



Mantle Opening Width vs. DML





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VITA

Elizabeth Keane Shea

Born in Boston, Massachusetts on July 11, 1967. Graduated from the Madeira School, Greenway, Virginia in 1985. Graduated from the College of William and Mary, Williamsburg, Virginia in 1989 with a BS in Biology.

Entered the Masters program at the College of William and Mary, School of Marine Science in August 1991.