

ASPECTS OF THE EARLY LIFE HISTORY OF *LOLIGO PEALEI* (CEPHALOPODA; MYOPSIDA)¹

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ABSTRACT The long-finned squid *Loligo pealei* was the most common squid collected in 2 years of zooplankton sampling over the Middle Atlantic Bight off New Jersey and Virginia. Planktonic specimens of *L. pealei* were found in that area during spring, summer, and fall; there were no indications of multiple stocks. This species was captured in waters with a salinity range of 31.5 to 34.0 ppt, and was confined to coastal waters except when current conditions, such as the passage of a Gulf Stream eddy, resulted in strong, offshore surface transport. While abundances were greater in night surface samples, larger specimens occurred in night subsurface samples indicating ontogenetic descent. Tentacle length was closely correlated with dorsal mantle length (DML) in preserved specimens of less than 4.5 mm DML, indicating that tentacles are noncontractile in newly hatched specimens. This may be part of a major discontinuity in the development of *L. pealei* which separates hatchlings from juveniles.

INTRODUCTION

The long-finned squid *Loligo pealei* Lesueur, 1821 is a commercially and scientifically important cephalopod species (Voss 1973). Although the biology of this squid has been studied for many years (Verrill 1882, Mesnil 1977) and is better known than the biology of most other cephalopods (Voss 1952), little is known of its early life history. Summers (1971) stated that two broods arise each year in the Middle Atlantic Bight, one an ubiquitous July brood, and the other a November brood which probably originates in the southern Middle Atlantic Bight. Mesnil (1977) suggested two, 20-month, alternating reproductive cycles occurred.

Although adults of *L. pealei* are demersal during the day and disperse vertically at night (Summers 1969), McMahon and Summers (1971) found that newly hatched specimens of *L. pealei* actively maintained position at the surface under all conditions of illumination. With impending petroleum resource development on the continental shelf of the Middle Atlantic Bight and the possible impacts of oil spills on surface biota, the research reported here was initiated to provide a descriptive summary of the distribution of planktonic juveniles of *L. pealei*. Specifically, I was looking for distributional discontinuities indicating the presence of multiple stocks in the Middle Atlantic Bight, and I wanted to determine the importance of the sea-surface layer in the early life history of *L. pealei*.

A standard set of measurements taken during this study showed surprisingly little variability of tentacle length in small specimens. I propose in this report an hypothesis to explain the apparent discontinuities in several parameters relating to the early life history of *L. pealei*.

MATERIALS AND METHODS

Squid were collected during a 2-year baseline study of zooplankton in the Middle Atlantic Bight, which was begun in the fall of 1975 and included four quarterly cruises per year. During the first year, six 24-hour stations were occupied on a cross-shelf transect off Atlantic City, NJ, extending from shallow inshore waters to the shelf break (Figure 1). At each of those stations surface collections were made every 3 hours using a neuston frame rigged with a standard 1 m, 505- μ m mesh net that sampled to a depth of approximately 12 cm. Subsurface oblique tows were made at night with 60 cm opening-closing bongo systems rigged with both 202- and 505- μ m mesh nets. The volume filtered during the subsurface collections was calculated from measurements made with General Oceanics flow meters; the volume filtered during the surface collections were determined likewise beginning with the third cruise (June 1976). Readings for each meter were compared in terms of revolutions per minute and outliers were discarded and replaced with the mean value for that meter.

During the second year, two stations to the north and a second transect of four stations off Wachapreague, VA, were added. Three of the original stations, D1, N3, and F2, were shortened with two subsurface tows and a single surface tow taken at night. Three additional replicates of the subsurface tows were collected at stations A2, B5, and E3. The filtered volumes were monitored similarly to the first year. Surface water temperatures and salinities were measured concurrently with all surface samples. All specimens were fixed and preserved in a 2 to 4% solution of formaldehyde in sea water buffered with borax.

Relative abundances in both surface and subsurface collections were calculated as numbers of specimens collected per 100 m³ of filtered water. Distributional statistics were computed based on all samples collected at stations where *L. pealei* was captured. Several pairwise comparisons between the most similar collecting methodologies (night,

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surface, 505- μ m mesh versus night, subsurface, 505- μ m mesh) are presented here. Because the t-test assumes equal variances, I used an F-test for equality of variances between the sets of observations to be compared. That test generally failed to demonstrate equality among the variances, so I chose to use the t' approximation (Sokal and Rohlf 1969, p. 374) for comparisons of observation sets. The comparisons were one-tailed with alpha significance set at 0.05.

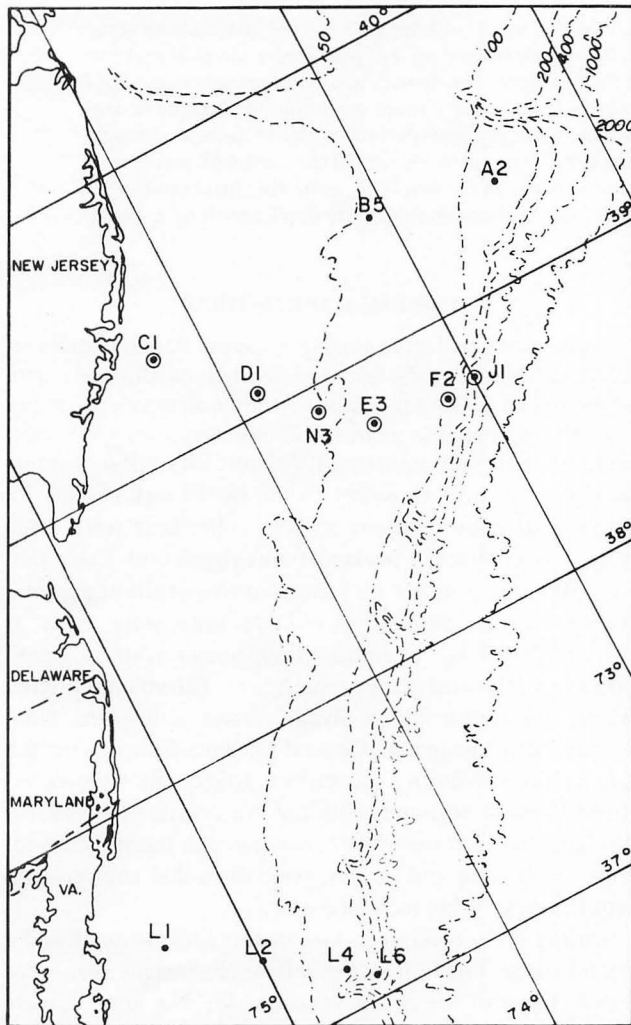


Figure 1. Stations sampled. Open circles: first year; solid dots: second year.

All measurements (Figure 2) were made to the nearest 0.05 mm using a dark-field dissecting microscope equipped with an ocular micrometer. Dorsal mantle length (DML) was measured on all specimens. Mantle width (MW), head length (HL), head width (HW), fin length (FL), width across fins (WAF), length of the third pair of arms (AL), and tentacle length (TL) were measured on 150 specimens for morphometric analysis. Although a few fairly large specimens were collected (up to 75 mm DML), a discontinuity in size distribution occurred at about 15 mm DML, so I have considered specimens ≤ 15 mm DML to be planktonic.

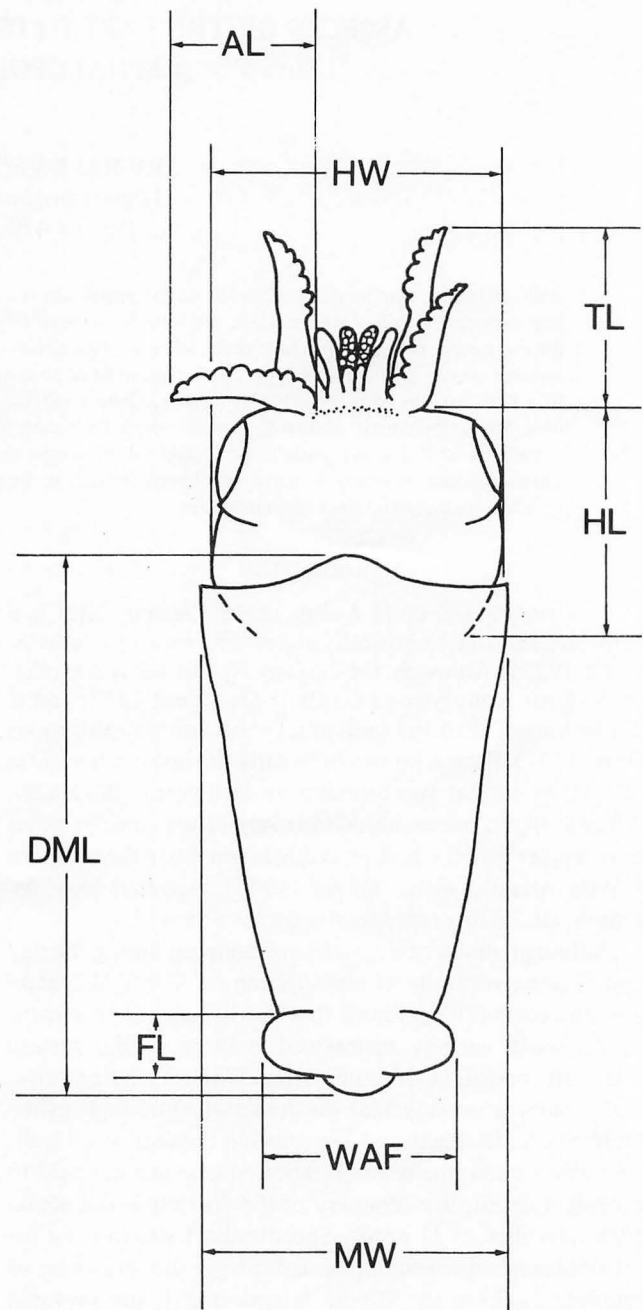


Figure 2. Morphometric characters used in this study: mantle width, MW; width across fins, WAF; fin length, FL; dorsal mantle length, DML; head length, HL; tentacle length, TL; head width, HW; and third arm length, AL.

RESULTS

The 635 loliginid specimens constituted the most numerous group of cephalopods collected during this study. Squids of the family Loliginidae that may occur in the study area include *Loligo pealei*, *Loligo plei*, and *Lolliguncula brevis* (Voss 1956, Cohen 1976). The last species was excluded from consideration because it is an estuarine spawner (Hall 1970). Of the *Loligo* species, *L. pealei* is by far the most

common in the Middle Atlantic Bight. *Loligo plei* reaches the northern limits of its geographic range in the study area (Cohen 1976), but is very rare north of Cape Hatteras (A. C. Cohen, National Museum of Natural History, Washington, D.C., personal communication, 1977). Circulation on the continental shelf of the Middle Atlantic Bight is a flow-through system from northeast to southwest (Beardsley et al. 1976, Bishop and Overland 1977) with only occasional short-term reversals of surface drift (Bumpus 1969). Thus, it is unlikely that many of the specimens drifted into the area from south of Cape Hatteras. McConathy et al. (1980) have described differences in chromatophore arrangements among species of hatchling loliginid squids and the smallest specimens collected in this study most closely matched their description of *L. pealei*. Therefore, I concluded that my loliginid specimens were *L. pealei*.

Planktonic specimens of *L. pealei* were collected during spring, summer, and fall cruises, but were absent from all winter collections (Figure 3). Peak abundances on both transects occurred in late summer. Although a few specimens were collected during the day, at those stations where *L. pealei* was most abundant, almost all were taken at night.

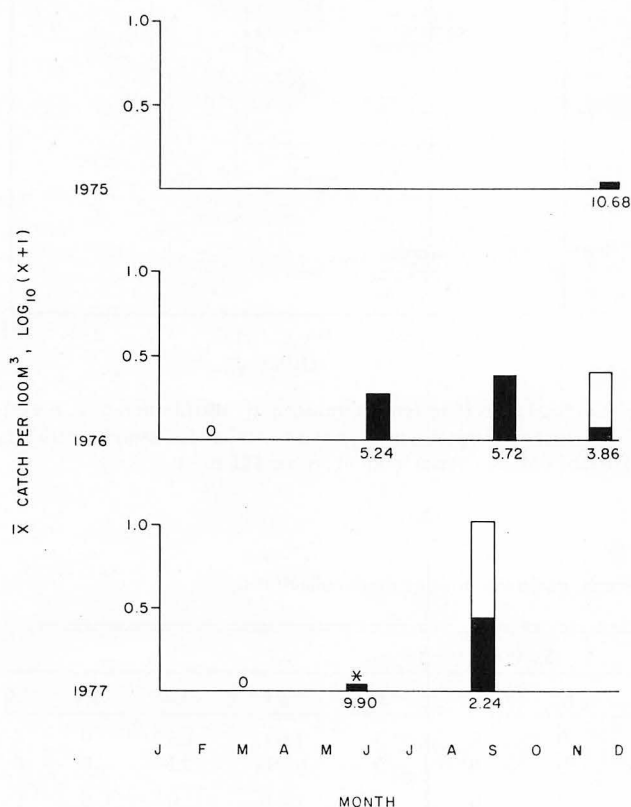


Figure 3. Seasonal distribution of planktonic *Loligo pealei*: solid bars, northern transect; open bars, northern and southern transects combined; *, southern transect value lower than that of northern transect; numbers below bars, mean dorsal mantle length (mm) for that cruise.

Abundance variability existed within the nighttime period but no pattern was apparent (Figure 4). The difference in mean DML between day and night surface collections was not significant.

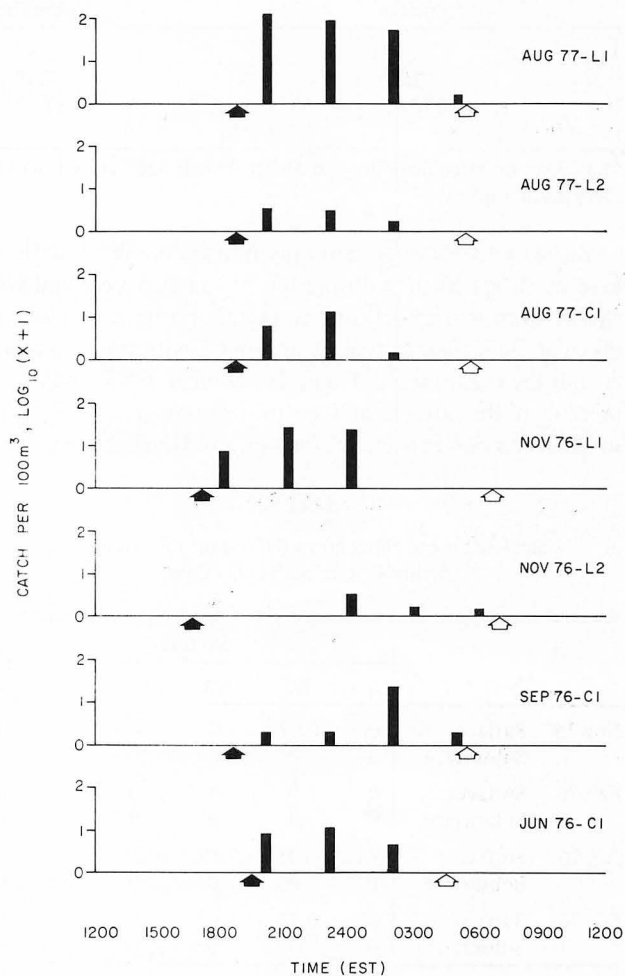


Figure 4. Diurnal variation in surface catch: \uparrow , sunset; \uparrow sunrise.

Relative abundance was significantly higher in surface samples taken at night than in night subsurface samples using the same mesh size (Table 1). Conversely, mean DML was significantly higher in subsurface (night, 505- μ m mesh) than in surface (night, 505- μ m mesh) samples (Table 2).

TABLE 1.

Comparison of surface and subsurface abundances¹.

	Surface	Subsurface
\bar{X}_{ab}	6.09	1.18
s_{ab}	18.77	3.75
N	58	20
t'	1.886	

¹Based on night collections with 505- μ m mesh nets. Abundances in N/100 m³.

TABLE 2.
Comparison of dorsal mantle lengths in surface and subsurface collections¹.

	Surface	Subsurface
\bar{X}_{DML}	2.47	3.87
s_{DML}	1.32	1.79
N	432	87
t'	6.926	

¹Based on night collections with 505- μ m mesh nets. Dorsal mantle lengths in mm.

Loligo pealei was present only in trace numbers (defined here as $< 1/100 \text{ m}^3$) during fall of the first year and was absent from winter collections. During spring, *L. pealei* was taken at the surface at coastal station C1 with trace numbers at midshelf stations N3 and E3. *Loligo pealei* was also present at the surface at C1 during summer, as well as in subsurface samples at inner-shelf station D1 (Table 3).

TABLE 3.
Calculated mean abundances ($N/100 \text{ m}^3$) for first year, night 505- μ m mesh collections.

		Station					
		C1	D1	N3	E3	F2	J1
Nov 75	Surface	0	0.07	0	0	0	0
	Subsurface	0	0	0	0	0	0
Feb 76	Surface	0	0	0	0	0	0
	Subsurface	0	0	0	0	0	0
Jun 76	Surface	4.95	0	0.48	0.25	0	0
	Subsurface	0	0	0	0	0	0
Sep 76	Surface	5.80	0.42	0	0	0	0
	Subsurface	0	1.06	0	0	0	0

During the fall of the second year, a few individuals of *L. pealei* existed at northern central-shelf stations B5, D1, and N3, but the greatest abundances were concentrated along the

southern transect at the surface at coastal station L1 and in subsurface samples at central-shelf station L2. This species was absent from winter collections. During spring, trace numbers were collected at southern stations L1 and L2, but larger numbers were taken at the surface at outer-shelf station F2 on the northern transect. Peak abundance during summer was found in both surface and subsurface collections from southern coastal station L1, and in surface collections from southern central-shelf station L2 and northern coastal station C1 (Table 4).

This species was confined to coastal water (based on a classification by Welch and Ruzicki 1979), but was fragmented into five separate areas of the temperature-salinity (T-S) regime (Figure 5). That fragmentation is more

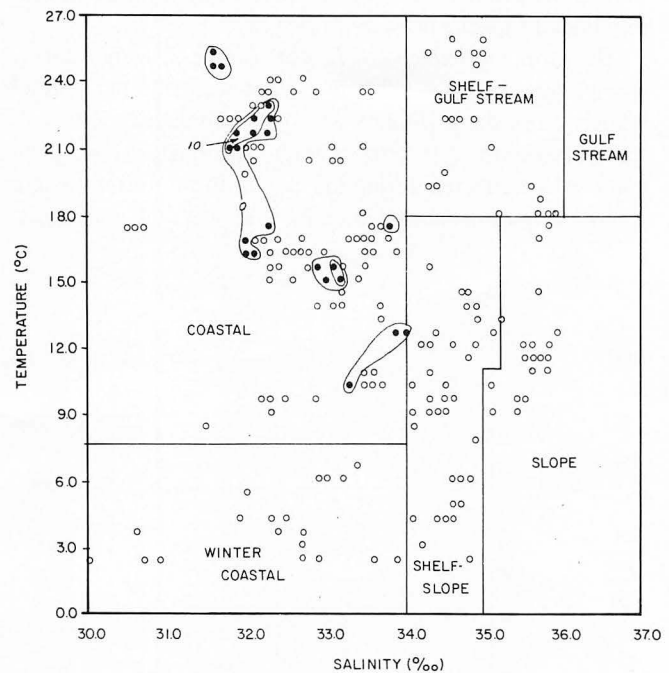


Figure 5. Night surface temperature-salinity distribution of *L. pealei*. Filled circles: samples with *L. pealei*; open circles: samples without. (Isoleths of abundance in numbers per 100 m^3 .)

TABLE 4.
Calculated mean abundances ($N/100 \text{ m}^3$) for second year, night 505- μ m mesh collections.

		Station											
		A2	B5	C1	D1	N3	E3	F2	J1	L1	L2	L4	L6
Nov 76	Surface	0	0.09	0	0	0	0	0	0	11.70	0.77	0	0
	Subsurface	0	0.14	0	0.46	0.56	0	0	0	0	2.64	0	0
Mar 77	Surface	0	0	0	0	0	0	0	0	0	0	0	0
	Subsurface	0	0	0	0	0	0	0	0	0	0	0	0
May 77	Surface	0	0	0	0	0	0	0.91	0	0.14	0	0	0
	Subsurface	0	0	0	0	0	0	0	0.33	0	0.21	0	0
Aug 77	Surface	0	0	4.39	0	0	0	0	0	58.57	1.16	0	0
	Subsurface	0	0	0	0	0	0	0	0	16.90	0.80	0	0

understandable when compared with the distribution of *Limacina retroversa* (Figure 6), an abundant boreal pteropod that is seasonally advected down the central-shelf region from the northeast (Vecchione 1979a). *Loligo pealei* was absent from waters in which *L. retroversa* was most abundant.

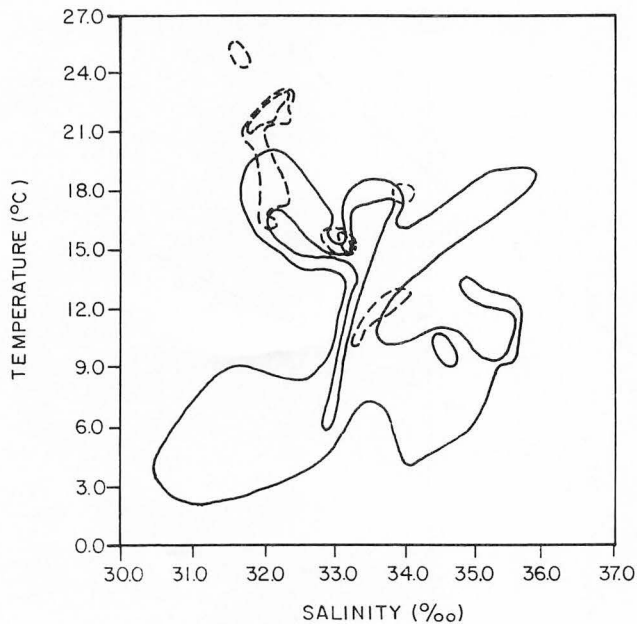


Figure 6. Comparison of night surface distributions in temperature-salinity regime. Solid lines: *Limacina retroversa*; dashed lines: *Loligo pealei*. Presence/absence and second highest abundance isopleths are shown for both species.

Based on limited size-frequency data from a series of samples taken 3 hours apart, mean growth rate at night was about 0.05 mm per hour (Figure 7). Although modal displacement indicated a similar overall rate of growth, the amount of modal increase was greater from 2400 to 0300 hours than from 2100 to 2400 hours.

Although all morphometric parameters that I measured were significantly correlated (Pearson's r) with DML, a discontinuity appeared to exist at about 4.5 mm DML. The amount of variability in tentacle length was much greater in specimens larger than 4.5 mm DML than in the smaller specimens (Figure 8). Tentacle length in specimens less than 4.5 mm DML ranged from 21.1 to 54.4% of DML, whereas the range was 24.0 to 98.8% of DML in larger specimens. A similar increase in variability was not apparent in arm-length data (Figure 8), but an inflection downward in relative growth rates at about 4.5 mm DML was obvious in several parameters, including head length, head width (Figure 9), and mantle width (Figure 10).

DISCUSSION

Data from the National Marine Fisheries Service (NMFS) bottom trawl survey show great variability in catch of

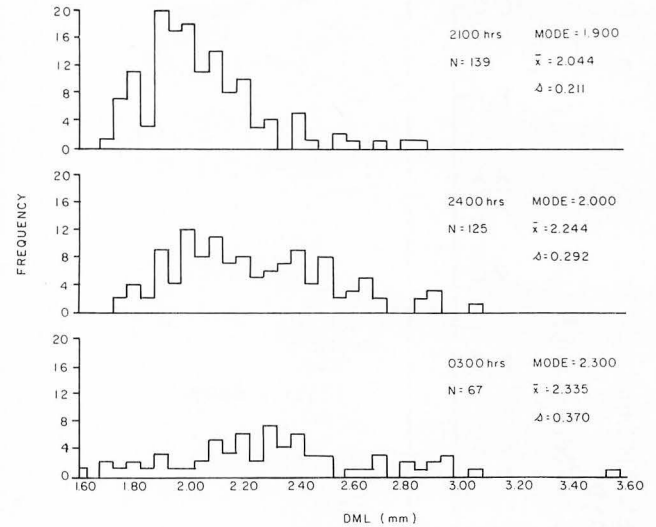


Figure 7. Size frequency histograms for collections made 3 hours apart.

Loligo pealei, both between geographical areas and within each area (Clark and Brown 1977). With increasing pressure on this species from foreign and domestic commercial fisheries (Lyles 1968, NMFS 1977), an urgent need exists to identify stocks, spawning areas, and seasons. The results presented here do not agree well with either Summers' (1971) finding of two separate broods or with Mesnil's (1977) alternating dual-cycle hypothesis. Based on data pooled from two years of collections, the only major distribution discontinuity noted was the absence of this species from winter samples. However, since the entire Middle Atlantic Bight was not sampled during this project, it is possible that separate stocks existed farther to the northeast. Within the New York and Chesapeake bights, though, it appears that hatching takes place continuously from early May through early November. Because embryonic development in this species takes from 257 to 642 hours, depending on temperature (McMahon and Summers 1971), it appears likely that spawning is also continuous in the area.

Most specimens of *L. pealei* were collected at night during this study. I believe that the paucity of specimens in day surface samples was a result of net avoidance rather than absence. Newly hatched specimens of *Loligo forbesi* have an escape speed of up to 25 cm sec⁻¹ (Mileikovsky 1973), whereas the neuston sampler, which draws approximately 12 cm, was towed at about 75 cm sec⁻¹. If *L. pealei* has an escape speed similar to that of *L. forbesi*, newly hatched young that are capable of detecting the sampler about 40 cm away, should have enough time to avoid it. Visual acuity in cephalopods is well documented (Wells 1966), and increased avoidance would be expected during daylight hours. The fact that some specimens were collected during the day may reflect a common avoidance reaction characteristic of *Loligo opalescens* which consists of simple

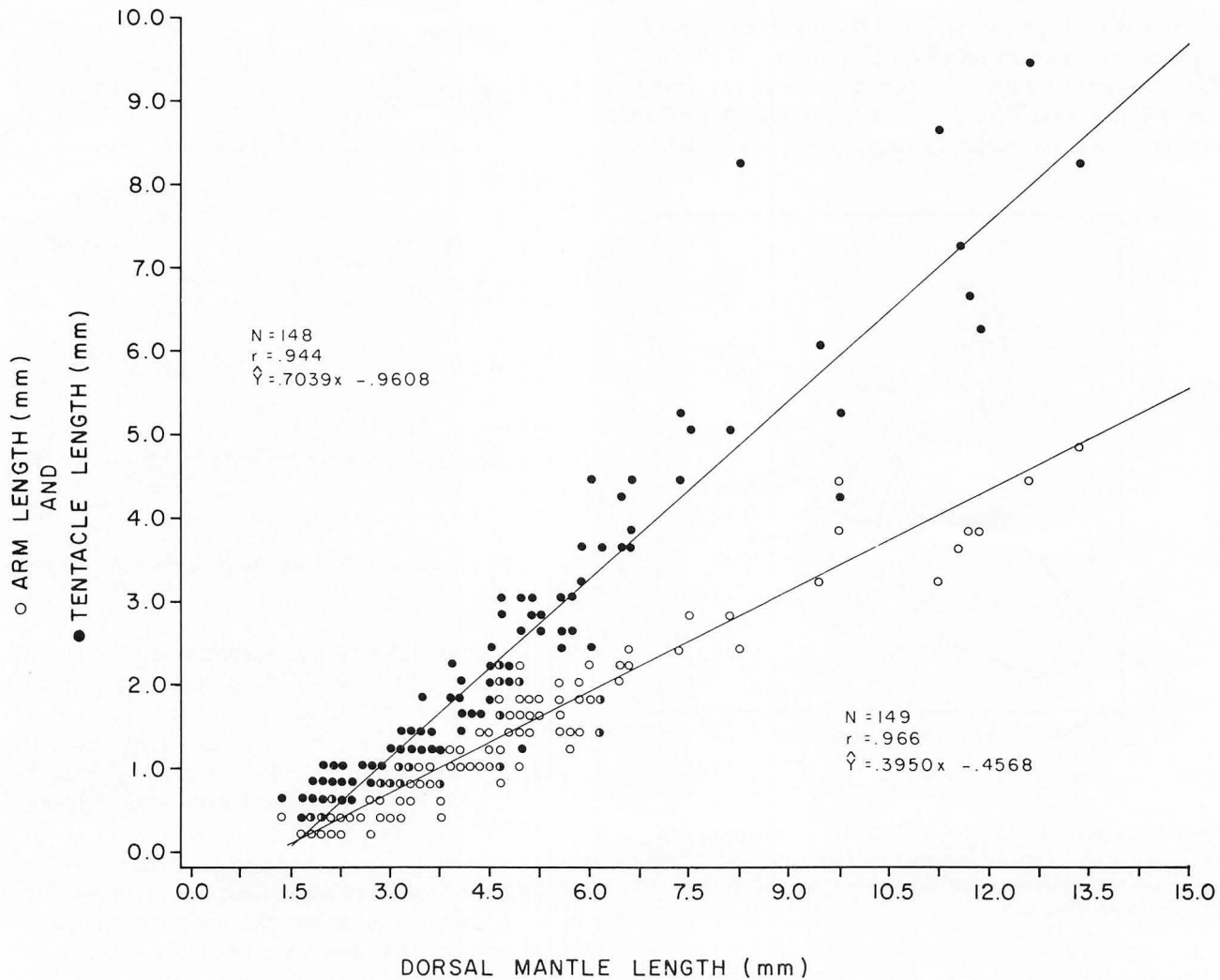


Figure 8. Linear regression of AL and TL with DML.

cessation of swimming so that the colorless animal sinks (Fields 1965). While such passive behavior could avoid visual predation, it would not prevent net-capture. Since hatchlings of *L. pealei* exhibit positive phototaxis in the laboratory (McMahon and Summers 1971), they are probably present at the surface during the day.

Loligo pealei was collected primarily at coastal and central-shelf stations, with greatest abundances consistently found at coastal stations. This nearshore distribution was reflected by the salinity range of the species, which was relatively narrow for the continental shelf of the Middle Atlantic Bight. Although a close relationship exists between the distribution of adult *L. pealei* and bottom water temperatures (Serchuk and Rathjen 1974), the planktonic stages were found across a moderately broad temperature range. At higher temperatures, *L. pealei* was collected at lower salinities and vice versa.

The mutual exclusion of *L. pealei* and *L. retroversa* on the temperature-salinity diagram (Figure 6) indicates separate origins of the two species even though the environ-

mental conditions in which they were found were similar. Based on distributional relationships with other planktonic molluscs, Vecchione (1979a) suggested that *L. pealei* was part of a distinct coastal-zooplankton community, perhaps confined within a coastal boundary layer (Beardsley and Hart 1978, Grant 1979). Boundary layer conditions would be subject to runoff and wind conditions because strong southwest winds and reduced runoff reduce the strength of alongshore surface flow (Bumpus 1969).

There are two possible explanations for the capture of *L. pealei* at the surface at outer-shelf station F2 in May 1977. West and southwest winds, which were common at that time of year and were recorded for 11 of the 14 days prior to the 23 May collection date (NOAA 1977), result in surface transport offshore (Boicourt 1973). Also, a warm-core Gulf Stream eddy was present (Figure 11) offshore of the shelf-edge front (Wright 1976), and such eddies have been shown to entrain shelf water along their trailing edges (Saunders 1971). Either phenomenon would result in offshore transport of surface fauna.

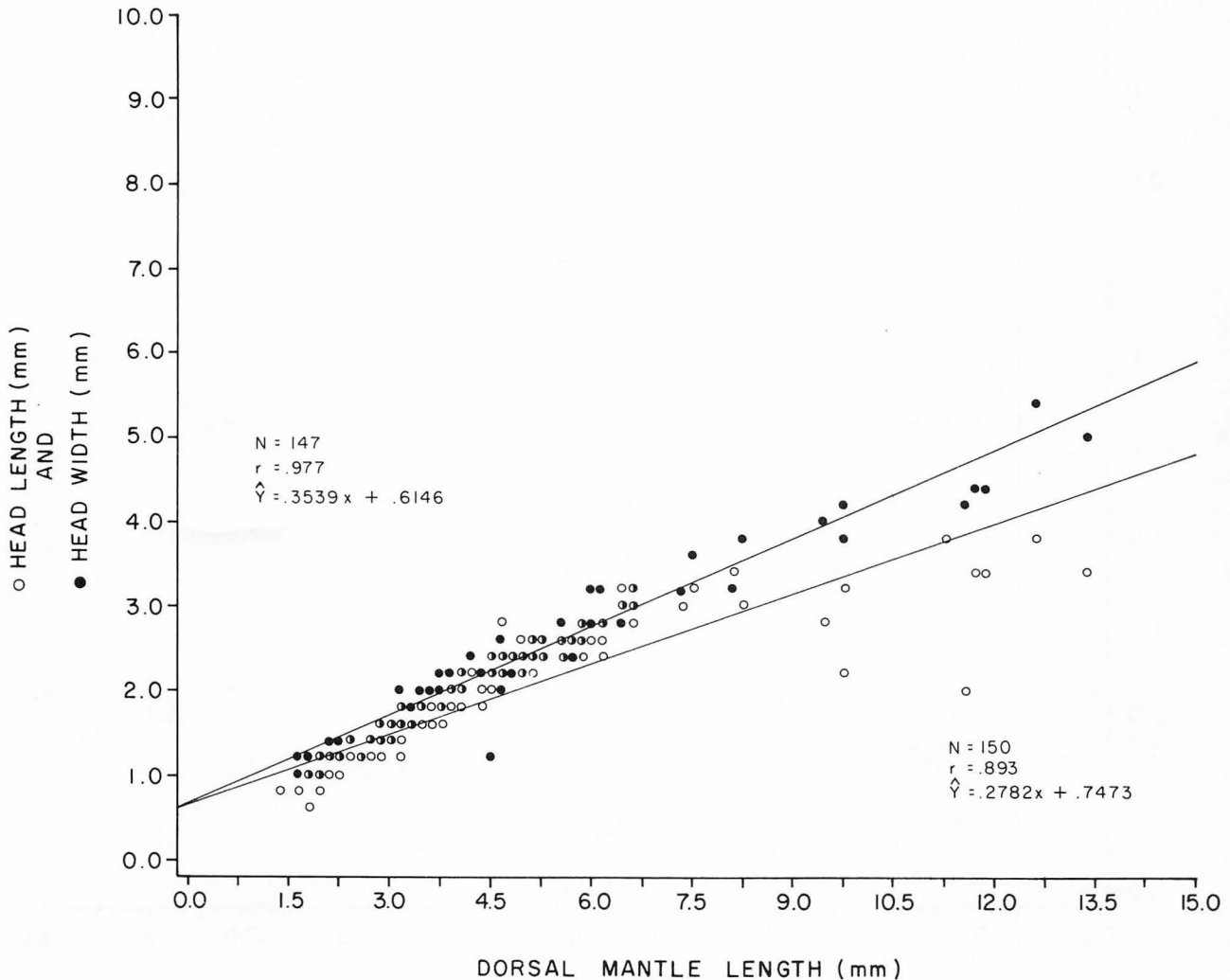


Figure 9. Linear regression of HL and HW with DML.

Ontogenetic descent through the water column is known for many species of oceanic cephalopods (Roper and Young 1975). The pattern of size distribution between surface and subsurface samples shows that a similar phenomenon occurs in this neritic species. The surface waters in continental shelf areas constitute an important biotope for feeding, particularly for the early stages of visual predators which require high-light intensities to find their food items (Hempel and Weikert 1972). The presence of comparatively large numbers of smaller specimens at the surface and small numbers of larger specimens in subsurface water indicates that hatchlings of *L. pealei* probably rise to the surface, feed for a short period, and then begin living deeper in the water column. They eventually assume the adult pattern of vertical distribution in which they are demersal during the day and dispersed at night (Summers 1969).

The overall growth rate of 0.3 mm in 6 hours presented here is consistent with Summers' (1968) estimate of 18 mm per month only if some modifying assumption is accepted. I propose two hypotheses, neither of which is strictly test-

able with this data set. Feeding and growth are probably not continuous throughout a 24-hour period. A visual predator such as *L. pealei* would not be consistently efficient in all light regimes. Periodicity in growth may follow feeding periodicity by an unknown time lag since digestion in adult *Loligo* is extracellular and rapid (Bidder 1966). The difference in increase in modal length between equal time periods shown in Figure 7 may be preliminary evidence of such noncontinuous growth.

An alternate hypothesis is that a change in overall growth rate occurs at some period of the early life history of *L. pealei*. A discontinuity existed in the morphometric growth of this species at about 4.5 mm DML. Particularly noteworthy is the close correlation between TL and DML in smaller specimens. This contrasts with the adult situation in which tentacles are highly contractile and, therefore, extremely variable in preserved specimens. I noted a similar lack of tentacle length variability in planktonic *Illex illecebrosus* (Vecchione 1979b), and Roper and Lu (1979) found this character sufficiently consistent to be of taxonomic use

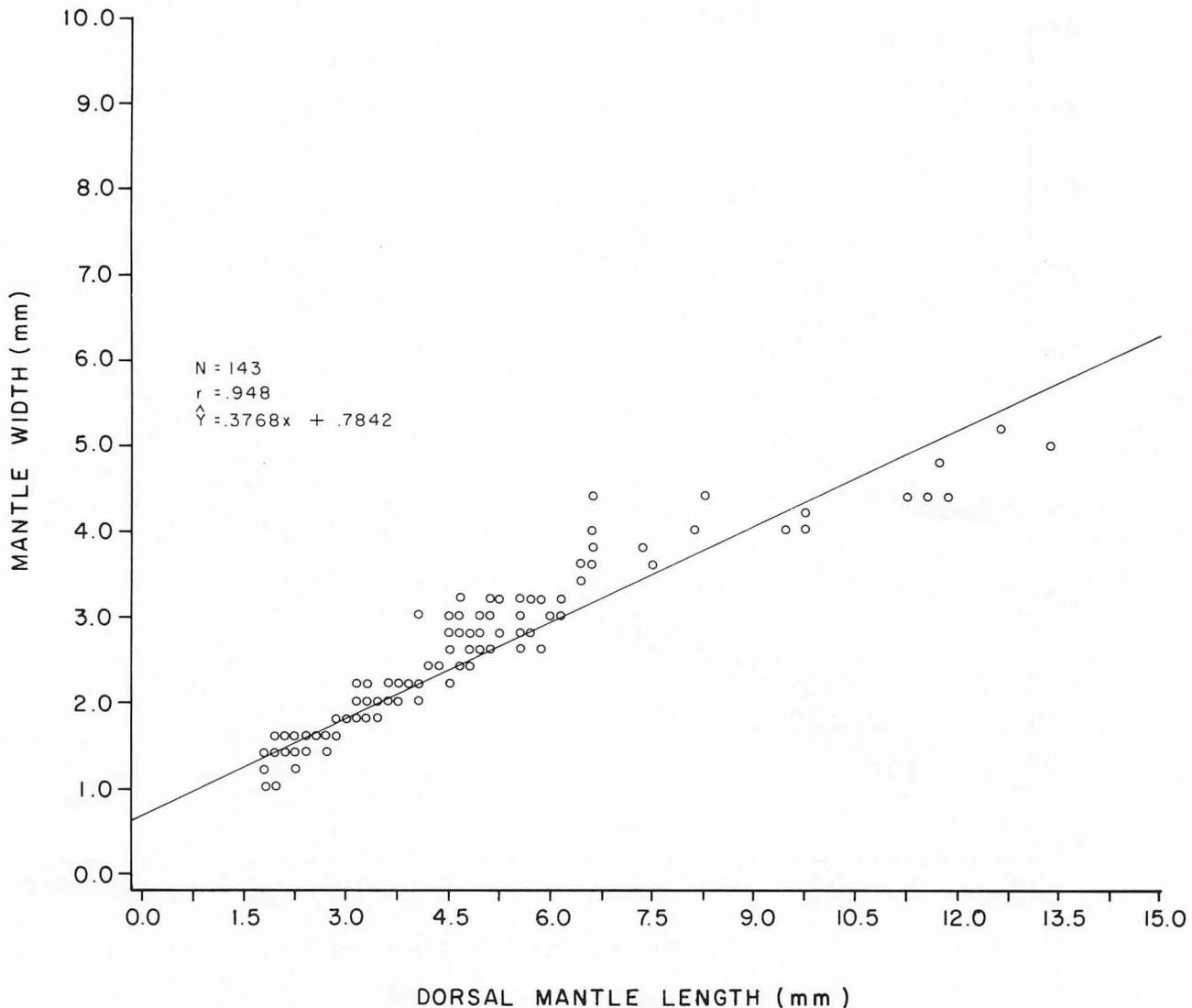


Figure 10. Linear regression of MW with DML.

in separating species of ommastrephid squid larvae. Although such lack of variability may result from uniform tentacle contraction in smaller specimens, the following statement by Boletzky (1974) indicates rather that the tentacles are not functionally contractile in hatchling squids:

“The attacking distance is smaller in young squids than in Sepioidea because the tentacles cannot be ejected like the tentacles of cuttlefish . . . Instead, the animal shoots forward when attacking.”

The morphometric discontinuity occurred at about the same size at which *L. pealei* undergoes ontogenetic descent. That is also approximately the size at which the pigmentation pattern of the young squids begins changing from reverse (ventro-dorsal) countershading to dorso-ventral countershading, another phenomenon as yet unexplained in loliginid development (McConathy et al. 1980). The simultaneous occurrence of all of these phenomena indicates strongly that a major discontinuity is occurring in the life

history of this species. A long-standing, although inconclusively proven, hypothesis on the early life history of fishes states that the first feeding after yolk absorption constitutes a critical stage in development (May 1974, Houde 1978). A similar critical stage may exist for hatchling squids which must feed at the surface until their tentacles become fully functional, at which time their behavior, distribution, appearance, and growth rate change.

CONCLUSIONS

1. No evidence was found of multiple stocks of *L. pealei* in the central and southern Middle Atlantic Bight. The species hatches continuously during the warm months throughout the study area.
2. Planktonic specimens of *L. pealei* are found within a relatively narrow salinity range reflecting their coastal distribution. That distribution is subject to perturbations by wind conditions or passage of Gulf Stream eddies

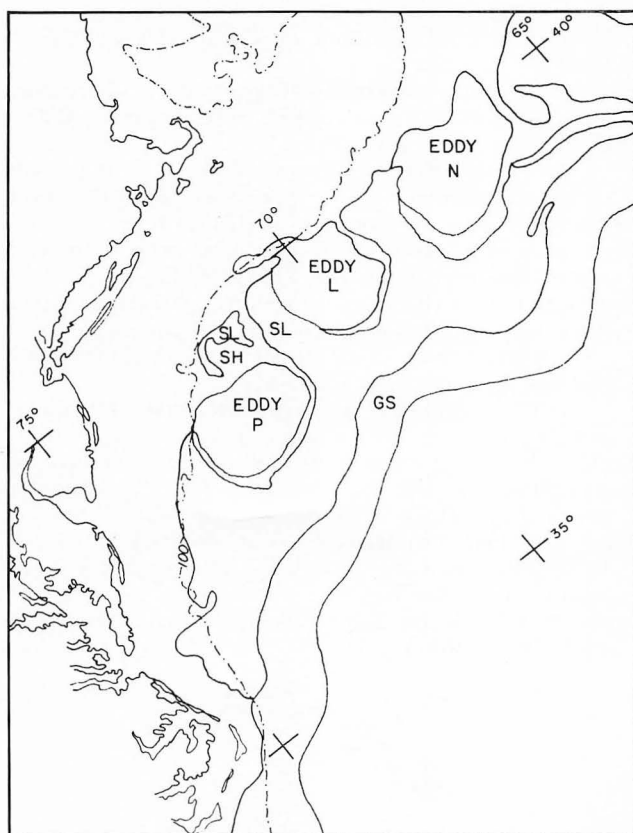


Figure 11. Locations of Gulf Stream and shelf-edge fronts on 1 June 1977, based on U.S. Naval Oceanographic Office Experimental Ocean Frontal Analysis (GS, Gulf Stream; SH, shelf water; SL, slope water).

which result in strong offshore transport of surface water.

3. The surface layer is extremely important to hatchlings of *L. pealei*; the hatchlings subsequently move deeper in the water column as they grow larger.
4. Tentacles of hatchlings may not be functionally contractile. This may be part of a major life history discontinuity which separates hatchlings (at the surface with reverse countershading and noncontractile tentacles) from juveniles (subsurface with dorso-ventral countershading and functional tentacles).

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