

Abstract. – Cephalopods were examined from more than 3000 zooplankton samples collected over a two-year period from coastal and estuarine waters of southwest Louisiana. In total, 270 cephalopods were taken in 164 of these samples; 267 specimens from 161 samples were *Lolliguncula brevis*. They were found in coastal waters from April through January, but in estuarine waters only in May, July, and August. Maximum standardized abundance was found in the nearbottom waters of the estuary in May. Overall, paralarval *L. brevis* were most often collected nearbottom in inshore coastal waters during May–June. This species was not collected in the estuary at salinities below 27×10^{-3} . Although they were found in coastal waters with lower salinities (22×10^{-3}), abundance was generally greatest in waters with salinities of about 26×10^{-3} . Somewhat surprisingly, paralarval *L. brevis* were collected throughout the range of dissolved oxygen concentrations sampled, including waters considered to be hypoxic, with $<2\text{ mL/L}$ dissolved oxygen. Contents of the digestive tract were examined in 50 paralarvae; 18% of these contained solid food while others were inflated with a semiliquid mush or clear liquid.

Observations on the Paralarval Ecology of a Euryhaline Squid *Lolliguncula brevis* (Cephalopoda: Loliginidae)

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The squid genus *Lolliguncula* is interesting from an evolutionary viewpoint because this coastal genus includes the only species of cephalopod known typically to inhabit low-salinity estuaries, *L. brevis*. Thus, it is a clear-cut example of adaptive radiation of the stenohaline Class Cephalopoda toward euryhalinity. Adaptation to an unusual environment may involve physiological or behavioral changes in an organism at any point in its life history. The physiology of euryhalinity in this species has been studied using trawl-caught squids from Galveston Bay, Texas (Hendrix et al. 1981, Segawa and Hanlon 1988, Wells et al. 1988). The distribution of adults and advanced juveniles has been reported from trawling studies of estuarine and coastal waters of Texas (Hixon 1980) and Florida (Dragovich and Kelly 1963 and 1967, Laughlin and Livingston 1982). Although morphological aspects of the development of this species have been described (Hall 1970, Hunter and Simon 1975, McConnathy et al. 1980, Vecchione 1982b), the only published report on the distribution of paralarvae (see Young and Harman 1988 for a discussion of the term) was a brief note on distribution near the northern limit of the species' range (Vecchione 1982a).

Studies of the early life history of cephalopods have been relatively infrequent because of logistical and taxonomic difficulties (Vecchione 1987). However, such studies should

eventually be useful for comparisons with other taxa in the development of early-life-history theory (Vecchione 1986). I report here on the distribution of paralarval *L. brevis* collected during two concurrent studies of zooplankton and associated hydrographic parameters in the coastal and estuarine waters of southwest Louisiana.

Vecchione (1987) concluded that starvation resulting from failure of first feeding may contribute substantially to cephalopod mortality and subsequent recruitment failure. Therefore, the contents of the digestive tracts in a subset of the specimens also were examined to determine whether paralarval feeding by *L. brevis* is amenable to study.

Materials and methods

Details of the collection methods have been presented by Vecchione et al. (1983). The collecting methods differed as described below, reflecting the two separate studies that were conducted concurrently over a two-year period.

The coastal study used a 60 cm opening/closing bongo sampler for triplicate one-minute tows at two discrete depths (three depths during February–April 1981) at nine stations monthly for 22 months, February 1981–November 1982 (Fig. 1, M and D stations). Towing speed was 1.5–2.5 knots. Most stations were located at the 10 m isobath and the

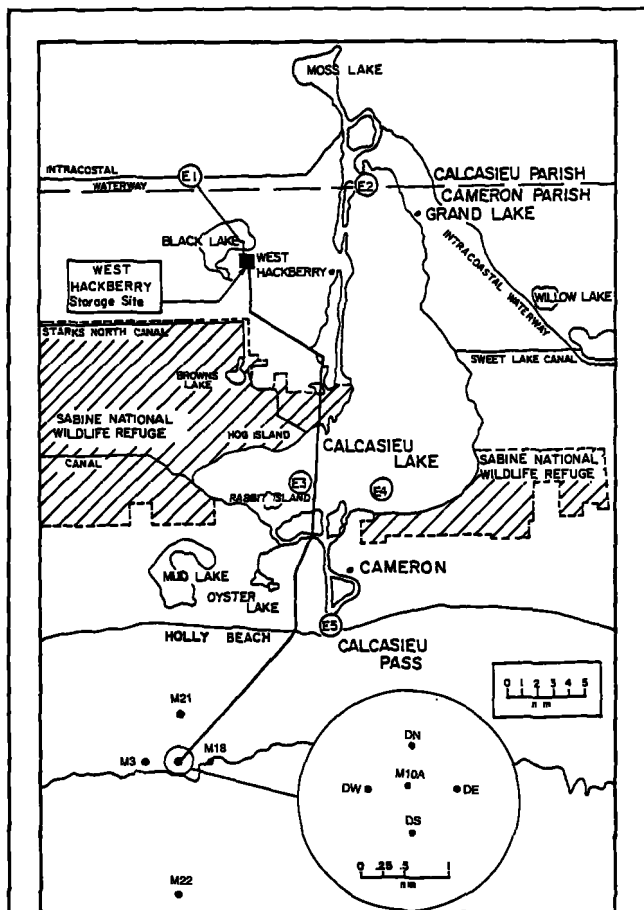


Figure 1

Locations of stations in southwest Louisiana. Estuarine stations are labeled E and coastal stations are labeled M and D. Station M18 was located on the 10 m isobath and station E5 was located at the coastline in Calcasieu Pass. Freshwater was diverted from the intracoastal waterway at station E1 and pumped to West Hackberry for solution-mining of a salt dome for a Strategic Petroleum Reserve storage site. A pipeline then transported the supersaturated brine to a diffuser at station M10A for discharge.

depths sampled were nearsurface (1–2 m depth) and nearbottom (~5–9 m depth). At the shallow station, M21 (5 m depth), and the deep station, M22 (14 m), the nearsurface tows were as described above but the nearbottom tows were modified to reflect local water depth. The bongo frame was rigged with 505 μm and 333 μm mesh nets, and both sides had flow meters mounted off-center inside the mouth to estimate the amount of water filtered for each sample. Most sampling was conducted during daytime because of contractual requirements. One station (M18) was resampled at night on the same day as regular monthly sampling for 9 months (June 1981, April–November 1982), to allow

diel comparisons to be made; station DW was also resampled at night for the final two months. Before sampling at each station, temperature, conductivity, dissolved oxygen, and pH were measured *in situ* with a Hydrolab 6000 probe at one-meter intervals from bottom to surface.

During the same time period, the nearby Calcasieu Estuary was sampled at 5–6 stations (labelled E1–E5 on Fig. 1) monthly for 21 months, February 1981–October 1982. This estuary is very shallow (average high-tide depth < 2 m), except in dredged channels, and sampling methods were constrained by the shallow stations (Stubblefield and Vecchione 1985). Triplicate one-minute samples were collected with two samplers described and figured by Stubblefield et al. (1984). The primary gear used at all stations was a half-meter ring net with 153 μm mesh mounted in a frame designed to eliminate avoidance due to bridle or boat wake. At three stations (E2, E3, and E4), an epibenthic pullsled rigged with 153 μm mesh netting was also used for 12 months, May 1981–April 1982, to examine vertical distribution in this very shallow water column. Flow meters were used with both samplers to estimate the amount of water filtered for each sample. At each station, physical parameters were measured similarly to the coastal stations. Sampling was timed to coincide with daytime high tide.

All samples were sorted for cephalopods. These were identified and individually measured (dorsal mantle length, DML). Standardized abundance in each sample was calculated as the number of *L. brevis* collected per 100 m³ of water filtered. The 12 samples collected at each coastal station filtered a total of about 150–250 m³ of seawater.

The questions that I wanted to address with these data can be grouped into two categories: (1) Description of large-scale patterns such as seasonal occurrence and overall distribution of the paralarvae with regard to temperature and salinity, and (2) statistical inference of small-scale patterns of abundance within waters in which the species occurs. Therefore, the data were treated differently depending on the category to be addressed.

In the first category, the description of paralarval distribution with respect to physical data (e.g., Fig. 3, the temperature-salinity diagram showing occurrence of *L. brevis*) is based on physical data at the sampled depths of all stations, including negative stations (where no paralarvae were taken), to contrast conditions under which they were collected from those where they were not, for all months in which *L. brevis* was collected at any station. Because the presence of paralarvae is limited in time to a brief period after seasonal hatching, including physical data for months in which they are not hatching would provide no infor-

mation on the abiotic dimensions of the paralarval niche.

For the second category, I wanted to determine average abundance within the water masses in which paralarval *L. brevis* were found, rather than average abundance throughout the entire geographic area. Because the paralarvae are planktonic and presumably stay within the water masses into which they hatch, average abundance would be artificially depressed if stations from other water masses (i.e., outside of the small-scale paralarval range) were included in calculations. For instance, physical conditions were sometimes very different at one or more stations because a coastal front divided the stations, so that *L. brevis* was collected in one group of stations but not in the other. Under those circumstances, including the water filtered at stations where the species was absent in the calculation of the number of *L. brevis* per m^3 of coastal water that month would not be an accurate representation of small-scale abundance. Descriptive statistics presented below are therefore based only on stations that collected *L. brevis*. For example, mean abundance for a month is the average of all samples, including negative ones, at all stations from which *L. brevis* were collected, but does not include negative stations. The statistical tests of hypotheses presented below were likewise based on the assumption that, if all twelve samples at a station failed to collect *L. brevis*, that station was extralimital for the paralarvae. For all tests of hypotheses, statistical significance was defined *a priori* as $\alpha = 0.05$.

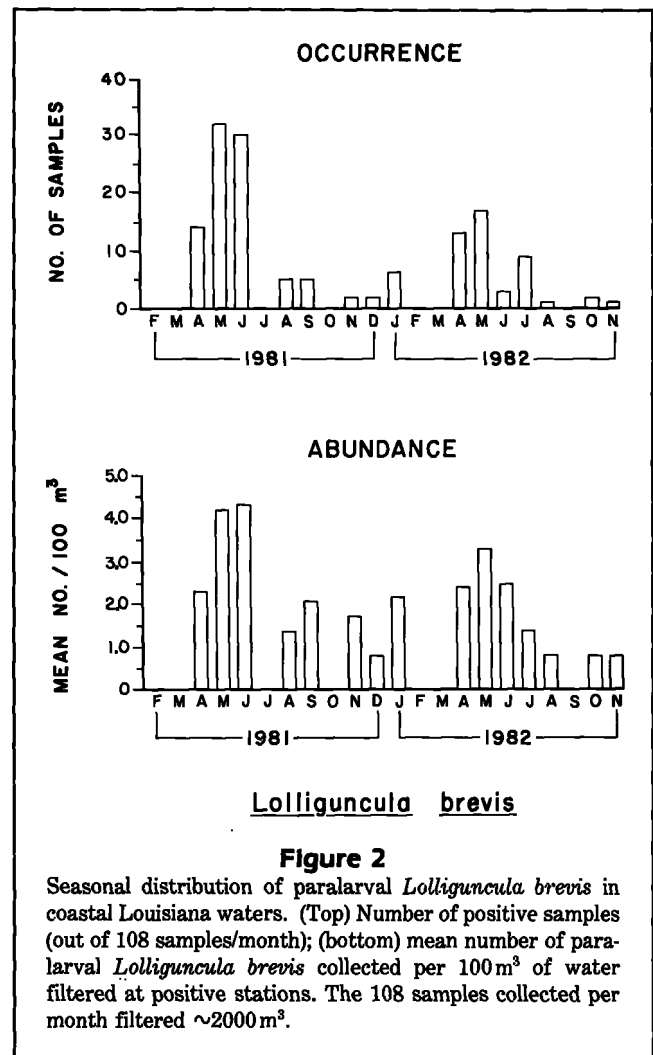
Fifty digestive tracts were examined. Specimens were selected arbitrarily to be representative of the paralarval size range. Specimens were cleared with trypsin and then transferred to glycerol, allowing direct examination of the intact esophagus, stomach, caecum, and intestine for food remains (Vecchione In press a).

Results

In all, 3159 zooplankton samples were collected. Two hundred seventy cephalopod paralarvae were collected in 164 samples. These included two *Loligo* sp., one *Illex* sp., and 267 *Lolliguncula brevis*. The *L. brevis* came from 161 samples and ranged in length from 1.1 to 13.6 mm DML.

Coastal distribution

Mesh comparisons Paralarval *L. brevis* were collected with 505 μm mesh in 75 samples and with 333 μm mesh in 77 samples. The Wilcoxon paired-sample, signed-rank test was used to compare both abundance and size of paralarval *L. brevis* in the two mesh sizes



of the bongo samples. Neither abundance nor size of the paralarvae differed significantly between mesh sizes. Therefore, in the following analyses the bongo samples are considered as a single data set regardless of mesh size.

Seasonal patterns Paralarval *L. brevis* were collected from April through January (Fig. 2). Both the highest average abundance (mean $N/100 m^3$) and the highest frequency of occurrence (number of samples that collected *L. brevis*) were found to occur in the spring (April-June) of both years. There appeared to be a slight tendency toward a bimodal seasonal distribution with a late-summer abundance minimum, similar to what I have found in many species of ichthyoplankton collected in these samples (unpubl. data).

Hydrographic relationships During the months in which *L. brevis* were collected, they were found

throughout the sampled temperature range, but were not collected at salinities of $<22 \times 10^{-3}$ (Fig. 3). Maximum abundance and frequency of occurrence were both associated with salinities of about 26×10^{-3} . Somewhat surprisingly, paralarval *L. brevis* were collected throughout the range of dissolved oxygen concentrations sampled, including waters considered to be hypoxic, with <2 mL/L dissolved oxygen (Fig. 4).

Diel variability Mean abundance and mean DML were compared between the night and day samples at the same stations on the same day. Abundance was somewhat greater during daytime (day $2.9/100\text{m}^3$; night $1.7/100\text{m}^3$), specimens caught at night tended to be somewhat larger (mean DML: day 2.0 mm; night 2.3 mm), but neither of these differences was statistically significant at the *a priori* α -level (*t*-test: abundance P 0.276, size [DML] P 0.600).

Vertical distribution Paralarvae were much more abundant nearbottom (mean abundance $4.7/100\text{m}^3$) than nearsurface ($0.7/100\text{m}^3$). Statistically, this trend was very significant (*t*-test, $P < 0.0001$). The paralarvae collected nearbottom were significantly larger (mean DML 2.1 mm) than those collected nearsurface (1.6 mm, *t*-test, P 0.049).

Variability among stations Abundance tended to be greater inshore at station M21 than farther offshore (Table 1) but, based on analysis of variance (ANOVA), this difference was not statistically significant (P 0.264). Similarly, paralarvae collected inshore tended to be larger than those offshore (Table 1), but this tendency also was not statistically significant (ANOVA, P 0.610). There was no obvious pattern of occurrence (number of samples) among stations, nor obvious patterns of changes in abundance or size alongshore.

Estuarine distribution

Whereas 237 *L. brevis* were collected in 152 coastal samples (5% of samples),

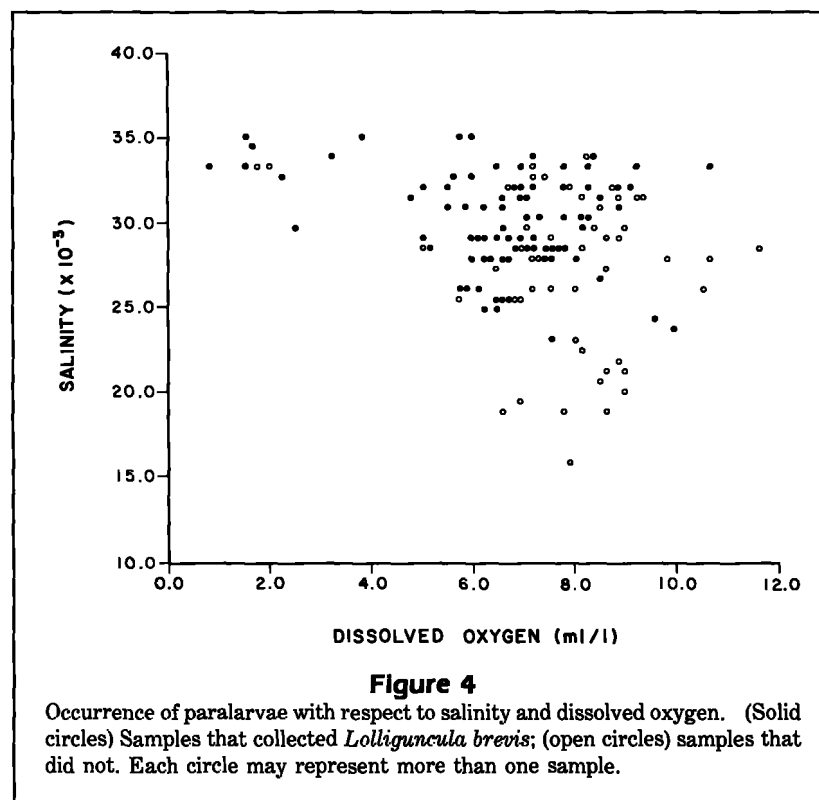
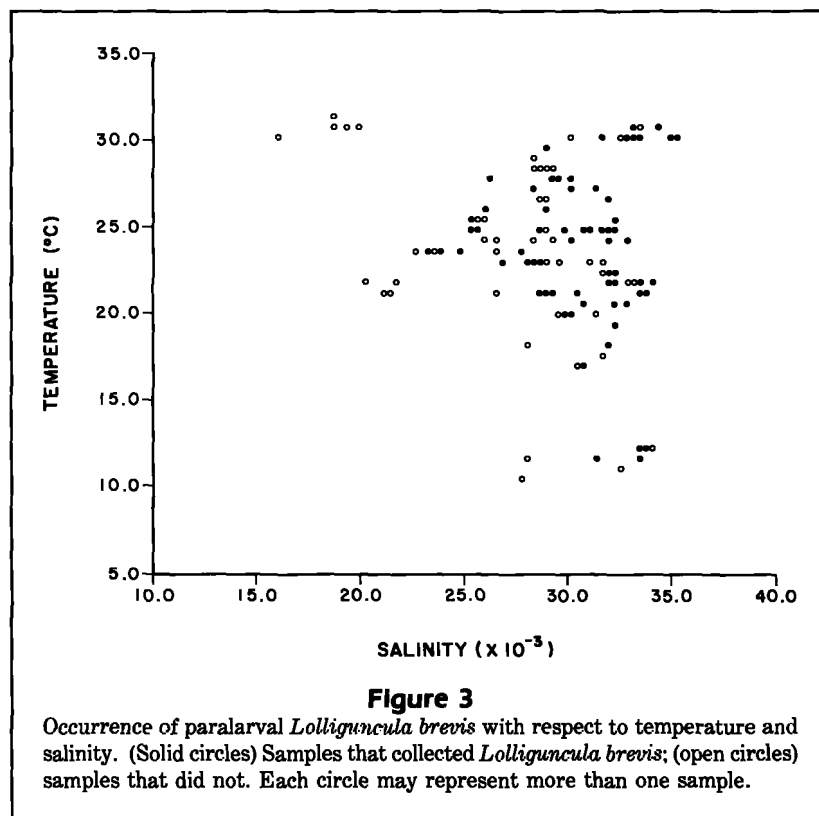


Table 1Distribution of paralarval *Lolliguncula brevis* at stations where paralarvae were present.

Station	Abundance ($N/100\text{m}^3$)		Size (mm DML)		Occurrence (N of samples)
	Mean	SD	Mean	SD	
Coastal					
M21	5.7	25.8	2.4	3.0	15
M18	2.8	5.9	2.0	0.9	29
DE	2.5	4.7	1.7	0.4	14
DN	3.3	6.3	2.8	2.2	10
M10A	1.5	3.6	2.2	1.3	12
DS	2.8	6.8	1.8	0.3	14
DW	1.7	3.8	2.4	1.4	12
M3	4.0	17.5	2.0	0.4	27
M22	2.1	4.3	1.7	0.3	19
Estuarine					
E5	4.4	5.3	2.1	1.1	4
E4	5.0	8.3	2.0	0.2	2
E3	78.3	105.9	3.4	4.1	3 (1 pulled) (all pulled)
E2	0	—	—	—	0
E1	0	—	—	—	0

only 30 were collected in 9 estuarine samples (2%; Table 1). The greatest abundance ($270/100\text{m}^3$) calculated during this study from either estuarine or coastal waters came from an epibenthic pulled sample taken at station E3 in May 1981; all pulled samples from that location and time included large numbers of paralarvae (Table 1). Also, paralarvae from estuarine waters were significantly larger (mean DML 2.5 mm) than those from coastal waters (2.0 mm; t -test, $P < 0.05$). Paralarvae were collected in the estuary only during May, July, and August. Although the estuarine sampling included waters that varied greatly in salinity, *L. brevis* were found there only in waters with salinities $>27 \times 10^{-3}$.

Paralarval feeding

Fifty paralarval digestive tracts were examined. Of these, 33 paralarvae were $<2\text{mm}$ DML, 12 were 2–3 mm DML, and 5 were $>3\text{mm}$ DML; the largest was 9.3 mm DML. The largest specimen had pieces of crustacean exoskeleton in the stomach and intestine but only fluid in the caecum. Of the other specimens $>3\text{mm}$ DML, one had nondescript solid chunks in its stomach, caecum, and intestine, one had fluid and ink in the stomach and caecum, and the digestive tracts of the other two were empty. In the 2–3 mm size-class, two contained solid chunks of unrecognizable food, four

had liquid and semiliquid mush in their digestive tracts, and six were empty. Of the smallest size-class, one contained crustacean appendages, four had amorphous chunks of food (usually in the combined stomach/caecum, although one specimen had a chunk of food in the esophagus), fifteen had one or more of the digestive organs inflated with fluid, and thirteen were empty. Therefore, of the total sample 18% of the paralarvae had solid food material in the digestive system.

Discussion

Distribution

Paralarval *L. brevis* do not seem to be as euryhaline as the adults. Trawl-caught *L. brevis* are osmoconformers that are known to tolerate salinities as low as 17.5×10^{-3} (Hendrix et al. 1981) and have been reported from estuarine waters with much lower salinities ($<10 \times 10^{-3}$, Laughlin and Livingston 1982). Paralarvae, however, were not found at salinities $<22 \times 10^{-3}$, and were most abundant at higher salinities. This may in part explain why the paralarvae were rare in the estuary as well as why they were most abundant in nearbottom samples where the salinity is higher than near the surface in both coastal and estuarine waters of Louisiana (Vecchione et al. 1983). The estuarine paralarvae were larger, and presumably older, than those of coastal waters. Thus, although estuarine paralarvae were not found in low-salinity waters, it appears that the distribution of this species shifts toward the estuary with growth, perhaps because of the onshore set of the nearbottom currents. Euryhalinity may develop ontogenetically late during paralarval development.

The spawning location for this species in Louisiana waters is not known. Whereas *L. brevis* eggs have been reported in trawl studies from Tampa Bay, Florida (Hall 1970) and from bay and coastal waters off Texas (Hixon 1980), extensive trawling (Vecchione In press b) at the same coastal and estuarine stations as the zooplankton projects reported here failed to collect any squid eggs throughout the same time period as this study. In Galveston Harbor, Texas, *L. brevis* attaches its egg capsules to hard surfaces, sometimes covering crab traps so thickly as to make them useless for their designed purpose (A. Landry, Texas A&M Univ., Galveston, pers. commun., 1984). The Louisiana trawling study avoided areas of hard substrate and thus probably missed local spawning areas. Hixon (1980) reported that *L. brevis* egg capsules were collected off Galveston from March through December in depths of 2–18 m with salinities of $21\text{--}35 \times 10^{-3}$ and tempera-

tures of 16–31°C. Paralarval seasonality in Louisiana is similar to that of the eggs off Galveston; therefore, in the northern Gulf of Mexico, *L. brevis* appears to hatch year-round except for the coldest months. This contrasts with the situation around the mouth of Chesapeake Bay, near the northern limit of the species' range, where paralarvae are found only during the warmest months of late summer (Vecchione 1982a).

Laughlin and Livingston (1982) concluded that fluctuations in the abundance of trawl-caught *L. brevis* in the Apalachicola Estuary, Florida are related to zooplankton biomass in the estuary, and they implied that this relationship results from the squid feeding on planktonic copepods. Juvenile and adult *L. brevis* actually feed on larger prey, mostly nektonic fishes and shrimps (Hanlon et al. 1983). Therefore, I believe that the correlation that Laughlin and Livingston (1982) described results from covariance of squid and zooplankton abundance with other independent factors such as salinity and current patterns. However, planktonic copepods are likely the natural prey for paralarval *L. brevis*. Copepods in the zooplankton samples reported here were abundant year-round, with spring and fall abundance peaks; even during midwinter, abundances $>1000/m^3$ were common. Although the concentration of natural food required for successful feeding by the paralarvae is not known, it does not seem likely that food limitations are responsible for the seasonal distribution found for the paralarval squids. It is possible, though, that factors such as seasonal storms that affect transport processes or patch dimensions of the prey are as important as temperature in controlling paralarval seasonality.

Paralarval *L. brevis* were found most often near the bottom in nearshore coastal waters. However, an important layer of the water column that was not sampled is the surface microlayer. Paralarval *Loligo pealei* in the Middle Atlantic Bight were far more abundant in neuston samples than in samples from subsurface waters, although they were larger in subsurface waters (Vecchione 1981). I inferred from this pattern that *L. pealei* hatchlings ascend to the surface for first feeding on the concentrated zooplankton of the neuston, and then shift ontogenetically to deeper waters. Paralarval *L. brevis* were also larger in bottom waters than near the surface. Neuston samples in waters of coastal Virginia collected paralarval *L. brevis* in comparatively large numbers (Vecchione 1982a). Thus, this species may undergo a similar ontogenetic vertical migration, but nighttime neuston sampling would be required to test this hypothesis.

It was somewhat surprising that paralarval *L. brevis* were found in waters considered to be hypoxic. Recent evidence (Wells et al. 1988, Vecchione In press b) indicates, however, that this species is capable of ad-

justing to low concentrations of dissolved oxygen by increasing oxygen uptake rates. Although no experimental evidence exists to show when in the life history this capability develops, my distributional data suggest that the paralarvae also have some means of coping with hypoxia. This would be a very important adaptation for a bottom-spawning species in coastal waters of the northern Gulf of Mexico. The bottom waters of this area seasonally become hypoxic during the salinity-stratified conditions of midsummer (Pokryfki and Randall 1987, Turner et al. 1987), causing catastrophic changes in the benthic fauna (Harper et al. 1981, Gaston 1985) and shifts in the distribution of nekton (Pavela et al. 1983).

Feeding

This is the first published analysis of stomach contents for paralarval cephalopods. The incidence of solid food material in the digestive organs may appear to be low but, when compared with feeding studies on trawl-caught squids, does not seem unreasonable. For instance, Dragovich and Kelly (1963) found that among 1684 adult and juvenile *L. brevis* trawled from Tampa Bay, 80% of the stomachs were empty; of those <40 mm in "body length," 94% had empty stomachs. Similar results have been found for other species of loliginids. One substantial difference between the paralarval stomach contents and those of larger squids is the dearth of recognizable hard parts in the ingested food of the paralarvae. This makes identification of the prey organisms even more difficult for paralarvae than for adults and juveniles, which bite their food into pieces and then swallow the pieces whole, including skeletal material. However, paralarvae of another loliginid, *Loligo vulgaris*, when feeding on small shrimp, can remove and ingest the soft tissue of the shrimp and discard the exoskeleton (S. v. Boletzky, Laboratoire Arago, Banyuls-sur-Mer, France, pers. commun., 1985). Recently, immunoassay methods have been developed to allow specific identification of very small samples of macerated food (e.g., Theilacker et al. 1986); such methods may be required for identification of gut contents in paralarval squids.

Determination of the number of animals that had fed was further complicated by the lack of differentiation between the stomach and caecum in small paralarvae and the frequent presence of either clear fluid or mush-like fluid in the combined stomach/caecum. This fluid is reminiscent of the caecal fluid in older squids that are well along in digesting a meal. Alternatively, the fluid may be largely seawater swallowed either naturally or during fixation or may be spontaneously secreted digestive fluids. Without knowing the dynamics of

digestion in paralarvae, distinguishing among these alternatives is impossible. Paralarval feeding is a subject greatly in need of study (Vecchione 1987, Vecchione and Hand 1989), especially because starvation of paralarvae has been proposed as a dominant factor affecting the large interannual variability in recruitment of cephalopods.

Acknowledgments

I thank the Brine Line Zoop Group for their labor in pursuit of this project. Funding was provided in part by U.S. Department of Energy Contract DE-AC-96-80P010228 to McNeese State University and partly by National Science Foundation grant OCE-8600541 to the author. Bruce B. Collette, Clyde F.E. Roper, Austin B. Williams, and Richard E. Young all reviewed drafts of the manuscript.

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