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BRUCE VONDRACEK

Wildlife and Fisheries Biology
University of California
Davis, CA 95616

LABORATORY REARING OF THE SQUID *LOLIGO PEALEI* TO THE JUVENILE STAGE: GROWTH COMPARISONS WITH FISHERY DATA

The common squid of the Northwest Atlantic, *Loligo pealei* Lesueur, 1821, is a valuable species that is exploited not only as a food for human consumption, but as an important research model in biomedicine (especially for the giant axon). Summers (1983) reviewed much of the ecological and fisheries literature in his description of the life cycle of *L. pealei*. There is an important gap in our knowledge of feeding, growth, and behavior during the early phases of the life cycle. In 1980, we reported the first data from young *L. pealei* reared to 40 d posthatching (Yang et al. 1980). We now present additional data on squid reared from hatching to 6 mo and compare existing laboratory growth data with estimates from fisheries data.

Materials and Methods

The squid were reared in closed system aquaria in artificial seawater (Instant Ocean¹). All details of system design and rearing techniques can be found in Yang et al. (1983, 1986). Wild-collected egg strands and laboratory-spawned eggs were obtained from the Marine Biological Laboratory in Woods Hole, MA and air shipped to Galveston, TX on 27 August 1985. Transit time was 30 h and the eggs were shipped in natural seawater (33 ppt). Upon arrival the water temperature was 16°C, pH 7.5, and NH₄-N 1.52 mg/L. The eggs were acclimated immediately and placed in a 1,600 L circular culture tank (CT) for incubation and early rearing. The major hatch occurred on 9 September 1985, and on 11 September (day 1 of the experiment) the spent egg capsules were removed. During this 14-d incubation

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

period water conditions were 13.8°C, 35.0 ppt, pH 8.01, and NH₄-N was <0.01 mg/L. The squid were initially fed three to seven times daily on assorted zooplankton that consisted mainly of copepods (0.5-2.5 mm body length). Subsequently, *Palaemonetes* sp. shrimp larvae, *Penaeus* sp. shrimp larvae, *Mysidopsis* sp. mysids, and fish larvae were offered. Once the squid attained 20 mm mantle length (ML), they were transferred to a 9,950 L raceway culture tank (RW) and their diet consisted of *Palaemonetes* sp. adults and small fish (*Menidia* sp.).

Results

Water quality data are listed in Table 1. Mortality was high during the first week despite many observations of active feeding by the hatchlings. The initial estimated population was 6,673 squid and 99%

TABLE 1.—Water quality of circular culture tank (CT) and raceway culture tank (RW) systems for *Loligo pealei*.

	CT system (days 1-124)	RW system (days 124-171)
Temperature (°C)		
Mean	15.8	21.3
(Range)	(13.2-19.5)	(18.2-22.9)
Salinity (ppt)		
Mean	33.8	36.1
(Range)	(33.0-35.0)	(36.0-36.5)
pH		
Mean	8.04	8.13
(Range)	(7.9-8.1)	(8.08-8.18)
Ammonia-nitrogen (mg/L)	<0.046	<0.046
Nitrite-nitrogen (mg/L)	<0.002	<0.002
Nitrate-nitrogen (mg/L)	<5.20	<16.30

of these died by day 5. By day 13 only three squid were alive and these survived to days 23, 130, and 172.

The types of food organisms offered to the squid and the periods they were fed are summarized in Figure 1. From days 1 to 57, the squid were fed wild-caught zooplankton (collected near shore and in the bays near Galveston Island). The copepods *Centropages velificatus*, *Temora turbinata*, *Eucalanus pileatus*, and *Labidocera aestiva* were the predominant species in the plankton, while crab zoea, sergestid shrimps, cladocerans, chaetognaths, and fish larvae were less common. We estimate plankton density at about 40/L during this period. There was certainly ample food available and feeding (mostly on copepods) was seen often from day 1 onward. Beginning day 22, palaemonid shrimp larvae (2-4 mm) were added to the tank and captured by squid. The squid were first able to capture mysid shrimp (2-8 mm) on day 51, and by day 57 benthic crustaceans (mainly *Mysidopsis* sp.) replaced zooplankton as the main diet. During this period food organism densities fluctuated between 2 and 10/L. As late as 44 d posthatching, squid (4-5 mm ML) were still seen eating copepods (*Labidocera aestiva*) as small as 1-2 mm long even with larger crustacean food available. After the transfer to the RW system, only benthic adult palaemonid shrimp and occasionally fishes were fed (<0.15/L).

The squid hatched at a mean size of 1.84 mm ML. The largest squid lived 172 d and attained a length of 35.4 mm ML and weighed 2.77 g. This female had a nidamental gland of 5.15 mm, indicating that the

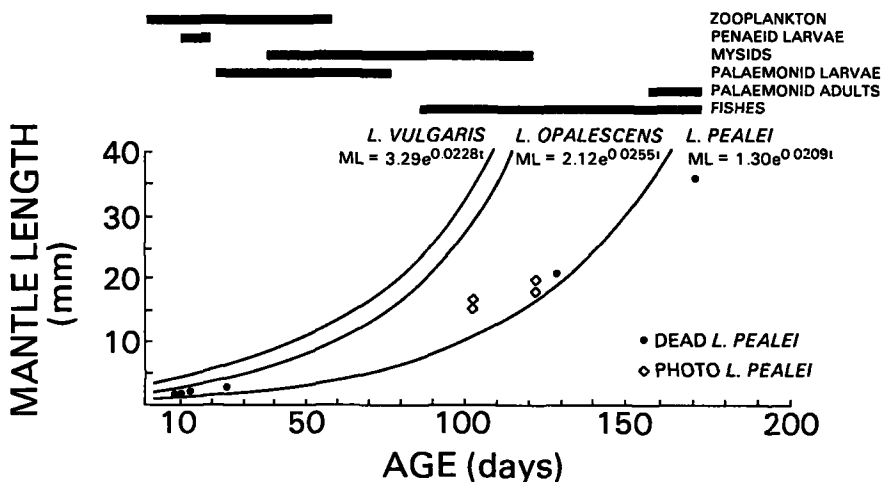


FIGURE 1.—Feeding and growth in *Loligo pealei*. Laboratory growth of *Loligo vulgaris* (Turk et al. 1985) and *L. opalescens* (Yang et al. 1986) is provided for comparison.

squid was immature but had developing gonads. Based upon 10 growth measurements (10 data points) from dead squid and several measurements obtained photographically from live squid (4 data points), the following exponential growth equation was generated for *L. pealei* (Fig. 1) during the first six months:

$$\text{Mantle length} = 1.30 e^{0.0209t}, r^2 = 0.98.$$

This indicates an approximate mean growth rate of 2% increase in mantle length per day.

Swimming and social behavior were observed carefully. A gentle circular flow (1-4 cm/s) was maintained in the CT system. Two squid 4 mm ML (41 d old) were able to maintain their position against a current of 1.8 cm/s. One week later (day 49), the squid could maintain their position in a current of 2.9 cm/s. On day 52, the two squid (approximately 5-8 mm ML) first showed schooling behavior by swimming parallel to one another throughout the day. They usually stayed in the darker areas of the tank but frequently moved into the lighter areas, probably to feed on the mysids that concentrated there. The final mortalities were caused by trauma and secondary infections that resulted from bumping the walls of the tank (Hulet et al. 1979).

Discussion

Since our first small-scale experiments with *Loligo pealei* (Yang et al. 1980), we have enlarged and refined our squid culture methodology enough to allow us to grow *L. forbesi* and *L. opalescens* through the life cycle (Hanlon et al. 1985; Yang et al. 1986). *Loligo pealei*, with its very small hatchling size (1.8 mm ML vs. 4.0 and 2.7, respectively for *L. forbesi* and *L. opalescens*), continues to be difficult to rear. Although our culture results in this report were poor numerically, they were a vast improvement over the many attempts in the past 100 yr to rear *L. pealei* (Verrill 1881; Williams 1909; Arnold et al. 1974). Significant improvements over our past *L. pealei* experiment include 1) increasing the culture tank size from 66 or 99 L to 1,600 L, 2) improved filtration capacity, and 3) feeding the squid many times daily (compared to twice) on different types and sizes of wild-caught zooplankton (compared to small copepods only). We cannot explain the high early mortality in the present experiment even though it is characteristic of all *Loligo* spp. rearing experiments thus far; feeding was observed often and the water quality remained in an acceptable range. Predation by wild zooplankton on squid hatchlings was possi-

ble (e.g., crab megalops), but this factor alone did not cause the high mortality. The small hatching size of *L. pealei* may partly explain the greater initial mortality (compared with *L. opalescens* and *L. forbesi*) since providing food organisms within the proper size range was more difficult. The zooplankton offered to the squid during the first week was composed primarily of copepods ranging from 0.5 to 2.5 mm long, i.e., 25 to 110% the length of the squid. Nevertheless, squid hatchlings captured and fed upon copepods, often the largest ones. Occasionally, however, hatchlings avoided copepods and appeared startled by their jerky movements. Curiously, it is this same jerky motion that provides the behavioral stimulus for all *Loligo* hatchlings to feed upon copepods. However, if enough cannot be captured by the small *L. pealei*, they may not be able to meet the high energetic costs of pursuit, capture, and digestion of a mobile, armored prey. Another possible contributor to mortality may have been reduced levels of dissolved organic nutrients in our artificial seawater (which was physically, chemically, and biologically filtered; cf. Manahan and Stephens 1983) combined with a qualitatively restricted diet compared to nature.

The value of laboratory data is its potential to verify or refute hypothesized descriptions based on limited or discontinuous fisheries data. Although the number of individuals studied was low (only two squid after day 23), several growth and behavioral patterns can be described. For example, schooling behavior, which depends partly upon size and swimming strength, was observed at a similar size for cultured *L. pealei* (4-6 mm ML, 50-60 d; this report), cultured *L. vulgaris* (5-10 mm ML, 20-40 d; Turk et al. 1986), and cultured *L. opalescens* (8-11 mm ML, 40-50 d; Yang et al. 1986). The appearance of schooling behavior may be related to the transition from the planktonic phase to the juvenile and adult demersal (neritic) phase of the life cycle. Increased swimming ability associated with schooling would allow the young squid to migrate vertically and exploit other food sources during the night. Squid size seems to be a key, with all three species first exhibiting schooling behavior when the hatchlings are 5 to 10 mm ML. Age at schooling is more variable, as early as 20 d for *L. vulgaris* (the largest hatchling) and as late as 60 d for *L. pealei* (the smallest hatchling). These observations, while limited to two individuals, conform generally to estimates of the end of the planktonic period for *L. pealei* in nature. Vecchione (1981) estimated that a distinct change in morphometric growth in *L. pealei*, especially tentacle growth, occurred at 4.5 mm ML. A change in

lifestyle at this size is confirmed further by changes in chromatophore patterns from a ventro-dorsal to a dorso-ventral patterning gradient (McConathy et al. 1980; Vecchione 1981). Estimates based upon field data (Summers 1968, 1983; Vecchione 1981; Table 2) put the age of transition at <1 mo.

TABLE 2.—Growth rate comparisons for young *Loligo pealei*.

Species	Growth rate (mm/mo)	Mantle length increase (mm)	Temp. (°C)	Reference
Field				
<i>L. pealei</i>	28-46	2 to 30-48	15-19	Verrill 1881
<i>L. pealei</i>	14-18	2 to 70-90	—	Verrill 1881
<i>L. pealei</i>	9-14	2 to 62-100	8-15	Verrill 1881
<i>L. pealei</i>	11-28	2 to 45-110	7-19	Summers 1968
<i>L. pealei</i>	17-20	2 to 70-90	—	Mesnil 1977
<i>L. pealei</i>	36	2 to 40	10-24	Vecchione 1981
<i>L. pealei</i>	24	2 to 4	17-23	Harrigan 1985
Laboratory				
<i>L. pealei</i>	4-6	2 to 35	13-23	this report
<i>L. vulgaris</i>	19	3 to 75	12-23	Turk et al. 1985
<i>L. opalescens</i>	13	3 to 44	15-16	Yang et al. 1986

Growth of laboratory-reared *Loligo pealei* (Fig. 1) was slower than that of either *L. vulgaris* (Turk et al. 1986) or *L. opalescens* (Yang et al. 1986) reared in similar tanks at slightly colder temperatures. Growth of *L. pealei* in our previous culture experiment (Yang et al. 1980) was 3.1 mm ML at 40 d, and this datum fits with Figure 1 and the growth curve. Daily growth rate estimates (derived from the instantaneous growth rates) were 2.28%/day for *L. vulgaris*, 2.55%/day for *L. opalescens*, and 2.09%/day for *L. pealei*. Table 2 compares the published estimates of growth rate in *L. pealei*. It is clear that estimates from field samples are far higher than our laboratory results of 4-6 mm/month with *L. pealei* (temperatures are generally comparable). The fastest growth rates we have measured in laboratory-reared squid during the first three months have been 19 mm/month in *L. vulgaris* and 13 mm/month in *L. opalescens* (mean rates are closer to 7 and 6 mm/month, respectively). Extrapolating these data in either direction (field vs. laboratory) is difficult because growth rates must be calculated over short periods (i.e., <1 mo) and under similar circumstances to be compared directly. Our laboratory results with *L. pealei* are probably low estimates compared with its growth rate in nature; they are low compared even with *L. vulgaris* and *L. opalescens* grown in our laboratory. However, since growth is clearly exponential in form in these three squid species as well as other cephalopods (Forsythe and Van Heukelem in press), the numerical value of growth rate in milli-

meters per month will increase disproportionately fast as the animal gets larger; thus the *L. pealei* data extrapolated to 60 or 90 mm ML would compare more favorably with most other growth estimates in Table 2. The growth rate estimates of Vecchione (1981), Harrigan (1985), and the first estimate by Verrill (1881), all based upon size-frequency data, seem to be excessive in view of laboratory and field growth data on cephalopods (Forsythe and Van Heukelem in press). Based upon our rearing experience with *Loligo* spp., we estimate that *L. pealei* in nature could grow as fast as 20 mm/month during the first few months if conditions were optimal.

Acknowledgments

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ROGER T. HANLON
PHILIP E. TURK
PHILLIP G. LEE
WON TACK YANG

*The Marine Biomedical Institute
The University of Texas Medical Branch
200 University Boulevard
Galveston, TX 77550-2772*

CHANGES IN THE POPULATION STRUCTURE OF MALE STRIPED BASS, *MORONE SAXATILIS*, SPAWNING IN THE THREE AREAS OF THE CHESAPEAKE BAY FROM 1984 TO 1986

The striped bass, *Morone saxatilis*, supported important commercial and recreational fisheries until recently. Population declines over the past 15 years have prompted fishing restrictions in most states along the Atlantic coast of the United States and a complete moratorium in Maryland. Spawning success of *M. saxatilis* has been poor since 1970, except for 1982 when the juvenile index reported by the Maryland Department of Natural Resources which was near the 50-yr average for Chesapeake stocks (Boone and Uphoff 1983).

Knowledge of the population structure of the striped bass is important to restoration efforts. Many attempts have been made to identify distinct stocks along the Atlantic coast and within Chesapeake Bay.

Morphological studies have found evidence of discrete stocks within the Chesapeake system (c.f. Setzler et al. 1980 for review), while studies of allozyme variation have been ambiguous (Morgan et al. 1973; Grove et al. 1976; Sidell et al. 1980). Electrophoretic studies have found only limited allozyme variation and, thus, discrimination of stocks has been problematical. To further understand the reproductive patterns of striped bass in the Chesapeake Bay, an analysis of mitochondrial DNA (mtDNA) genotypes among spawning individuals was initiated in 1984. For the most part, mtDNA is maternally inherited and provides information concerning matriarchal ancestry. The results of this analysis for the overall striped bass fishery will be reported elsewhere, but support the conclusion that distinct stocks exist in the Chesapeake Bay. As part of this survey, it was deemed important to examine the distribution of mtDNA genotypes of striped bass among 1982 year class individuals as they recruited into reproducing populations and to determine if the distribution of these genotypes changed in subsequent years. I report here on the distribution of mtDNA genotypes in 1982 year class males during their first (1984) and third spawning seasons (1986).

Methods

Striped bass were gill netted from the Chesapeake Bay at the mouth of the Sassafra River (Worton Point, 23, 24, 26 April 1984 and 7, 9 May 1986), the Potomac River (2 May 1984 and 29 April 1986) and Choptank River (9 May 1984 and 13 May 1986) during the spawning season. Age and sex determinations were made by counting scale annuli and visually inspecting the gonads, respectively. The accuracy of scale annuli for aging striped bass was reviewed by Setzler et al (1980). MtDNA was isolated from the livers according to the methods of Chapman and Powers (1984) and digested with the restriction endonucleases *Hind* III, *Eco* RI, and *Bcl* I. The digested mtDNA fragments were separated on 0.8% agarose gels. To insure consistent scoring of genotypes, 1984 samples were rerun against 1986 samples. Homogeneity of mtDNA frequencies within localities and among years was tested by G^2 tests with pooling of expected classes less than five (c.f. Sokal and Rolf 1969).

Results and Discussion

Variation in *M. saxatilis* mtDNA was characterized by fragment length polymorphisms that can be