ASPECTS OF LARVAL ECOLOGY OF *SQUILLA EMPUSA* (CRUSTACEA, STOMATOPODA) IN CHESAPEAKE BAY

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ABSTRACT

Larvae of *Squilla empusa* were collected from the plankton and were laboratory-reared in 16 combinations of temperature and salinity to determine their tolerances. Larvae survived longer and molted more frequently when reared at 25‰ and 20° or 25° C, which corresponds to the natural conditions of Chesapeake Bay when the larvae were collected.

A 2-yr planktonic survey conducted in the lower region of the bay by the Virginia Institute of Marine Sciences was compared with a survey made at the bay mouth in 1976. The seasonal occurrence of *Squilla empusa* larvae extended from the last week of July until the first week of October with a peak abundance occurring about the first week of September. The peak abundance in the lower region of the bay was 0.37 larva/m^3 in 1971 and 0.59 larva/m^3 in 1972. Four of the nine stages were not captured. Collections taken at the bay mouth in 1976 with a ½ m net captured all stages and the peak abundance was determined to be 0.27 larva/m^3. The larvae were more abundant in the higher salinity waters of the channel areas and eastern portion of lower Chesapeake Bay. A large-mouth plankton net with relatively coarse mesh should be towed at night to ensure the collection of all larval stages since the larger larvae are apparently able to avoid small nets.

The Order Stomatopoda is a small group of primitive, specialized crustaceans which reside primarily in shallow tropical marine waters. Of the 350 species (Caldwell and Dingle 1976) only a few extend into temperate waters, *Squilla empusa* among them. This mantis shrimp, which attains a length of 20 cm, is found from Massachusetts to northern South America and is quite abundant throughout its range, including Chesapeake Bay (Brooks 1878; Cowles 1930; Wass 1972).

Stomatopod larvae are often found in great swarms, particularly in tropical waters where adults are most abundant. The planktonic larval stages compose a substantial portion of the neritic plankton and constitute a considerable part of the diet of reef fishes, jacks, scads, herrings, snappers, and commercially important pelagic fishes such as tunas and mackerel (Sunier 1917; Fish 1925; Reintjes and King 1953; Randall 1967; Dragovich 1970).

Squilla empusa larvae are large crustacean larvae, attaining 17.5 mm long. The larvae undergo nine pelagic stages before settling to the bottom as postlarvae (Morgan and Provenzano 1979). Brooks (1878) found stomatopod larvae he assumed were those of *S. empusa* present in Chesapeake Bay from early July to the middle of August in the greatest abundance, but he discontinued the study before the larvae had completed their metamorphosis. No other data on larvae of this species have been added to the literature since.

Due to the paucity of ecological information on the larvae of this prevalent crustacean, an investigation was undertaken to determine their seasonal occurrence, distribution, and abundance in Chesapeake Bay. The abundance and duration of the larvae as part of the plankton may be important factors in the ecology of the bay, since the larvae not only serve as food for a variety of organisms, including commercially important fishes, but are also rapacious predators themselves, thriving on other members of the planktonic community.

In recent years the effects of temperature and salinity on the larval development of decapod crustaceans have been studied, but no studies have been made on the temperature and salinity tolerance for the larvae of any species within the Order Stomatopoda. Temperature and salinity are critical factors affecting the survival of marine and estuarine organisms, especially during the sensitive developmental stages upon which the success of the species relies. Thus, a qualitative determination of the temperature and salinity tol-

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erance of *S. empusa* is presented and a comparison of the laboratory result with the observed distributions is made.

METHODS

Research Applied to National Needs (RANN) Survey

The sampling area extended from lat. 37°40′ N, just north of the Rappahannock River, to the bay mouth, an area covering 1,300 km of the lower Chesapeake Bay (Figure 1). The survey area was divided into eight subareas designated A through H. A, D, and G were situated in the western portion and B, F, and H in the eastern section of the bay. These divisions were based on salinity differences in the bay, while areas C and E were separated because they represented channel areas.

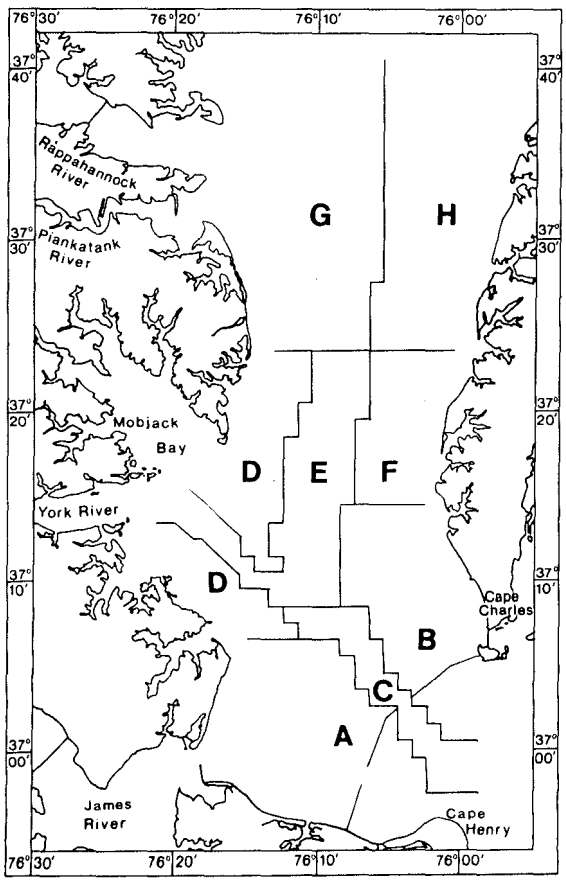

FIGURE 1.—Subareas (A-H) of RANN survey, August 1971 to July 1973, in lower Chesapeake Bay, Va.

The study area, consisting of 688 stations set 1.8 km apart, was sampled from August 1971 to July 1973. Three to five stations were randomly selected from each subarea to be sampled each month.

The plankton samples collected during the RANN survey were taken with a bongo sampler, having a mouth diameter of 18.7 cm (8 in) and equipped with 202 μm mesh nets. Stepped oblique tows were taken for varying lengths of time at each station, depending on station depth. A submersible pump was used at depth intervals of 2 m to gather hydrographic data. The temperature and salinities taken at each interval from each station were then averaged. All tows were taken during daylight. The stomatopod larvae were sorted from the general catch by the Virginia Institute of Marine Science staff and staged by the author.

Cape Henry Survey

Using the Old Dominion University RV *Linwood Holton*, larval specimens of *S. empusa* were collected weekly at Cape Henry where a population of adults exists. By using a ½ m plankton net (153 μm mesh), 10 min stepped oblique tows were accomplished as the ship circled the collection site at idle speed. The volume of water filtered through the net was calculated from the duration of the tow and the area of the net because the flowmeters employed yielded wildly erratic readings. The volume of water filtered for a 10-min tow was calculated to be 47.6 m^3. Surface and bottom water temperatures and salinities were recorded for each tow, using an inductive salinometer with a 45.7 m cable.

Upon collection each plankton sample was placed in a 1.9 l (½-gal) jar and filled with seawater. Samples containing large amounts of biomass were split into two such jars to facilitate the survival of the stomatopod larvae until they could be separated from the sample. As many larvae as possible were extracted from the samples aboard the ship and the task was completed in the laboratory. These larvae were placed in 1.9 l jars filled with seawater and were grouped according to size so that cannibalism would be minimal. The jars were aerated until the samples reached the laboratory, whereupon the larvae were placed in compartmentalized plastic trays, one per compartment. Each compartment measured 4.5 × 5 × 4 cm. Medium used for rearing the larvae was

made from Instant Ocean Synthetic Sea Salts[2] (Aquarium Systems, Inc., Eastlake, Ohio) and tapwater.

Larvae representing all nine developmental stages of *S. empusa* were reared in 16 combinations of temperature and salinity, each having a similar composition of larval stages. The experimental temperatures used were 10°, 15°, 20°, and 25° C, and salinities were 10, 15, 25, and 35‰, chosen because they represent the range of conditions the larvae might be expected to encounter in the lower Chesapeake Bay. The salinities of 20 and 30‰ were omitted from the experimental regime because insufficient numbers of larvae were obtained to determine their tolerances to all intermediate salinities as well as to the more extreme salinities. Thirty-six larvae were subjected to each temperature-salinity combination. Because the larvae were not hatched in the laboratory under the temperature-salinity combination at which they would be reared, some larvae were subjected to changes as great as 5° C and 10‰ per day until the experimental value was attained. No light cycle was used in the experiment, the larvae being maintained in total darkness except for 10-min periods when the larvae were given fresh food and water.

Each larva was reared in 25 ml of water and given freshwater and approximately 30 *Artemia salina* nauplii/ml daily. Great increases in size from the first to the last stage necessitated adjustments in food size and quantity. At about the fifth stage of development food was switched from *A. salina* nauplii to decapod zoeae or *A. salina* larvae grown on a yeast or algal culture. While changing the culture medium, observations were recorded on the progress of each larva regarding the frequency of molting, duration of larval development, survival, and the stage of development.

Percent survival and molting frequency are often used as measures of success of larvae under different temperature-salinity regimes, but were not meaningful in this experiment because the larvae were captured at different stages of development and different places in the molt cycle. Therefore, the length of survival and number of molts were used as the standards of success. The temperature and salinity combinations which promoted the greatest number of molts and the longest periods of survival among the larvae were considered to be most conducive to the larval development of *S. empusa*, because the larvae were not only surviving best but were also maturing fastest. The mean number of ecdyses and days of survival were calculated for each larva and then collective means were figured for each temperature-salinity combination. In this way a general indication of success of populations under varying temperature and salinity conditions could be determined.

RESULTS

Seasonal Occurrence

The RANN survey extended from 16 August 1971 until 25 July 1973, and *S. empusa* larvae were found in the Chesapeake Bay only from late July to mid-September or late October (Figure 2). During these months in 1971 the RANN study sampled on 16-19 August, 21-23 September, and 26-29 October, while in 1972 samples were taken on 24-27 July, 15, 17, 18, 21 August, 12-14 September, and 16, 18, 24 October. In 1973, sampling was conducted on 23-25 July.

The monthly sampling program used by the RANN program left the larval occurrence of *S. empusa* somewhat unclear. In both years of the survey, larvae were found on the first day of sampling in July, 24 July 1972 and 23 July 1973; since a month elapsed between the June and July samplings, however, the earliest appearance of the

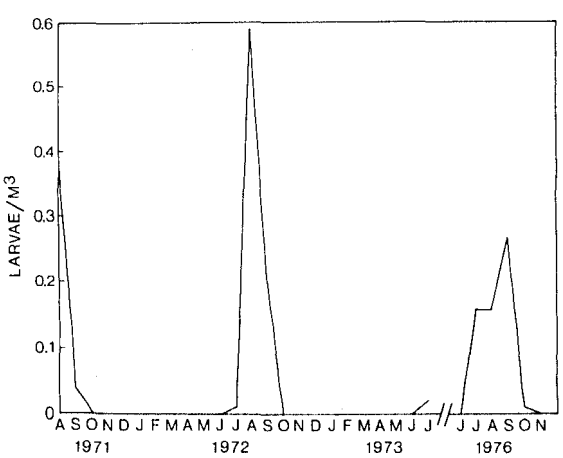

FIGURE 2.—Larval abundance of *Squilla empusa* collected from the lower Chesapeake Bay from August 1971 to July 1973 and from June to November 1976.

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

larvae could have gone undetected. The same problem occurred in defining the time of disappearance, for larvae were abundant on 14 September 1971 and 1972 but the next sampling was not conducted until 26 October 1971 and 16 October 1972. Only one Stage I larva was found in October 1971.

The Cape Henry data helped to determine more closely the planktonic duration of the larvae since a weekly sampling program was followed when weather permitted. In agreement with the RANN survey, the first larvae appeared in late July. Larvae were present on 28 July but none were found on 20 July. Larvae were found until 6 October; none were collected on 13 October. From the RANN and Cape Henry surveys it is apparent that the planktonic occurrence of *S. empusa* extends from the last week of July until the first week of October, a period of almost 11 wk or about 2½ mo.

Only Stages I-IV and IX were collected by the RANN survey (Figure 3). Bearing this in mind, the RANN data showed the month of maximum abundance to be August, with 0.37 larva/m^3 collected in 1971 and 0.59 larva/m^3 in 1972; September, July, and October trailed in order of decreasing abundance (Figure 2). The Cape Henry data, on the other hand, showed a peak abundance in September with 0.27 larva/m^3 in 1976 followed by August, July, and October.

All nine stages were collected during the Cape Henry sampling program (Figure 4). In July, when the larvae first began to appear, Stages I and II were the only stages collected in abundance and they were more numerous than in any following month. Several specimens of Stages V and VIII were also captured. All larval stages were present in August with younger larvae generally being predominant over older larvae. By early September the larvae had reached their peak abundance. Although some of the younger larval stages had begun to decline, they were still predominant. The latest larval stages, VIII and IX, were becoming increasingly abundant until October when only Stage IX larvae were obtained.

The abundance of larvae caught from each subarea during the RANN survey indicates that larvae were more prevalent in the eastern and channel areas of the bay than in the western portion

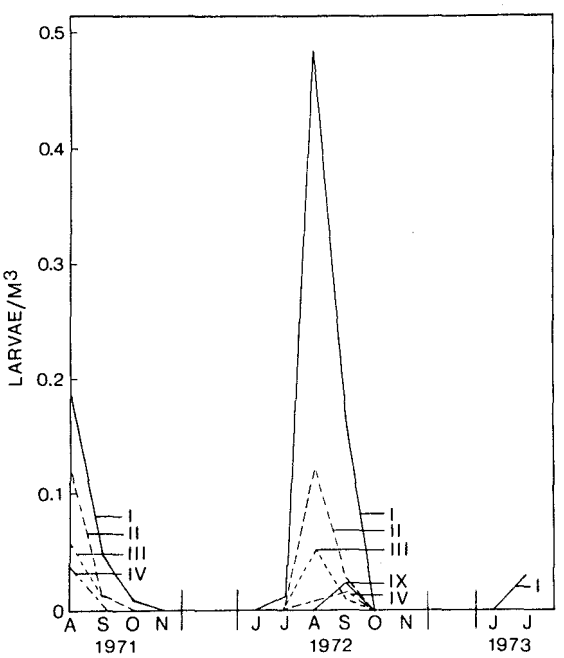

FIGURE 3.—Abundance of larval stages (I-IX) of *Squilla empusa* collected from the lower Chesapeake Bay from August 1971 to July 1973. Larval stages described in Morgan and Provenzano (1979).

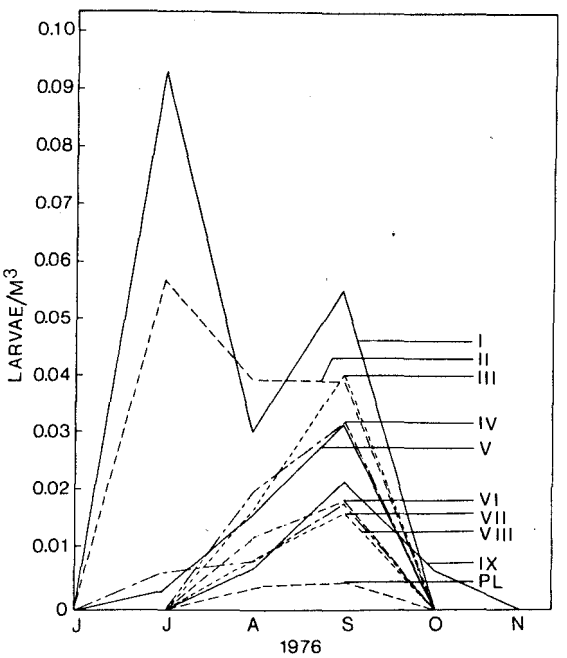

FIGURE 4.—Abundance of larval stages (I-IX) and postlarva (PL) of *Squilla empusa* collected at Cape Henry, lower Chesapeake Bay, from June to October 1976. Larval stages described in Morgan and Provenzano (1979).

TABLE 1.—Larval abundance of *Squilla empusa* with mean temperatures and salinities for each subarea (Figure 1) of the lower Chesapeake Bay for August and September 1971 and 1972.

	Lower			Middle			Upper	
	West A	Channel B	East C	West D	Channel E	East F	West G	East H
1971:								
Larvae/m³	0.13	0.36	0.19	0.12	0.28	0.28	0.05	0.47
Mean salinity	24.8	25.5	26.0	20.1	22.4	22.9	17.7	20.8
Mean temperature, °C	24.5	24.3	23.7	25.5	25.1	24.4	24.9	24.7
1972:								
Larvae/m³	0.43	0.44	0.41	0.04	0.70	0.89	0.02	0.08
Mean salinity	20.5	21.0	23.0	17.3	19.4	19.4	15.3	15.8
Mean temperature, °C	23.4	23.4	23.1	24.3	23.9	23.5	24.2	23.9
1971 and 1972:								
Larvae/m³	0.30	0.40	0.33	0.08	0.49	0.75	0.03	0.28
Mean salinity	22.7	23.2	24.5	18.7	20.9	21.1	16.5	18.3
Mean temperature, °C	23.9	23.9	23.4	24.9	24.5	24.0	24.6	24.3

(Table 1). Larvae were also more abundant in the lower regions of the sampling area than in the upper (subareas G and H).

Squilla empusa larvae occur in the Chesapeake Bay when the mean temperatures are the highest of the year. The first larvae were encountered in July for both 1972 and 1973 when mean temperatures were 25.2° and 24.5° C. The larvae were most abundant in August when the mean temperatures were 24.9° and 24.2° C in 1971 and 1972. The mean temperatures declined in September along with the abundance of larvae until larvae were rarely found or not found in October when temperatures were 19.7° and 19.4° C in 1971 and 1972. The mean salinity during the seasonal occurrence of the larvae in 1971 and 1973 fluctuated between 21.5 and 23.1‰, while in 1972 it was much lower as a result of Tropical Storm Agnes. In July 1972 the mean salinity was 16.5‰ and it increased to 21.2‰ in October when larvae no longer occurred in the plankton.

Temperature and Salinity Tolerance

Although none of the 576 larvae reared at the 16 different temperature and salinity combinations was reared through the entire pelagic development to metamorphosis, larvae survived well and molted frequently at 2 of the test combinations. At 20° C-25‰ and 25° C-25‰, 47% of the larvae molted three or more times, 24% underwent at least five ecdyses, and 3% molted seven times over a 6-wk period. Metamorphosis to postlarva occurred 34 times and was not a problem in the rearing process.

In general, larvae fared best at higher temperatures and salinities (20°, 25° C, 25, 35‰) and were least successful at the lower temperatures and salinities (10°, 15° C, 10, 15‰). Excluding larvae reared at 10° C, the longest survival and greatest number of molts occurred at salinities of 25‰ followed by 35, 15, and 10‰ in order of decreasing length of survival and number of molts (Figures 5, 6). Length of survival at 25°, 20°, and 15° C was similar but at 25° and 20° C the mean number of molts was much higher. At 10° C larvae

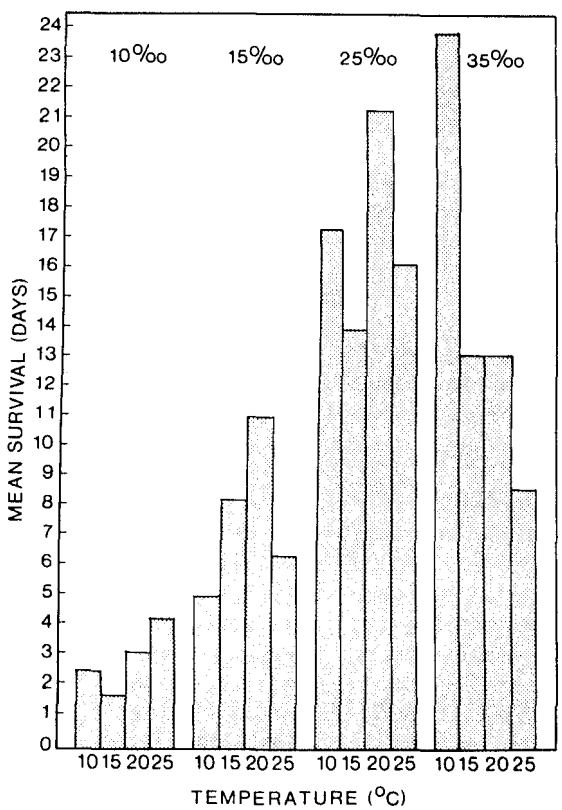

FIGURE 5.—Average survival, in days, for all larval stages of *Squilla empusa*, grouped by 16 temperature-salinity combinations according to salinity.

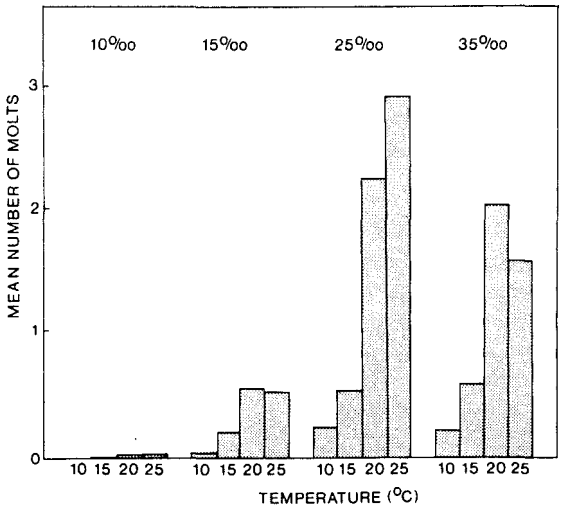

FIGURE 6.—Average number of ecdyses for all larval stages of *Squilla empusa* grouped by 16 temperature-salinity combinations according to salinity.

molted rarely and did not survive long at the lower salinities. At higher salinities molting occurred slightly more often and larvae at 10° C-35‰ were able to endure the longest of any of the combinations. Some of these larvae persisted for as long as 47 d, but usually without molting. Since these larvae did not appear to feed and moved only slightly, the low temperature only seemed to delay their deaths.

DISCUSSION

The information provided by the RANN survey only loosely delimited the seasonal occurrence of *S. empusa* larvae in Chesapeake Bay because of infrequent sampling. A weekly sampling program would have been beyond the scope of the investigation considering that the purpose of the RANN study was to survey the entire zooplankton community of the lower Chesapeake Bay over a 2-yr period. Supplemental data taken at Cape Henry combined with the RANN data indicate that the seasonal occurrence of *S. empusa* larvae extends from late July to early October, a period of about 11 wk. Observations made by Brooks (1878) concerning the planktonic duration of *S. empusa* larvae are in agreement with the current study, but the time of occurrence was slightly earlier in the previous study. Larvae were present in the plankton from early July through August when Brooks discontinued the study. Eleven weeks is a fairly short planktonic duration for stomatopod larvae. The temperate species *Oratosquilla oratoria*, common in Japan, has a 5-mo duration (Senta 1967), and *Pterygosquilla armata schizodontia* was discovered to remain in the plankton for up to 9 mo (Pyne 1972).

Although Brooks (1878) found the *S. empusa* larvae in great abundance, sometimes collecting 200 or 300 in a single evening from the mouth of the James River, both the RANN data and the Cape Henry data showed that the larvae were never abundant. Because only five of the nine larval stages were collected during the RANN survey the abundance values are inordinately low. Apparently, the larger larvae are able to avoid the small bongo plankton nets. Great quantities of Stage I larvae were captured throughout the larval season but far fewer numbers of Stage II were caught and fewer still Stage III larvae were caught and so on until Stages V-VIII were not collected at all. The large decreases seem to be too great to be accounted for by mortality alone.

It is possible that the large, quick-moving (pers. obs.) stomatopod larvae could avoid the small mouth of the net which was easily detectable since sampling was conducted during daylight (Fleminger and Clutter 1965; McGowan and Fraundorf 1966; Murphy and Clutter 1972). Olney (1978) also used data collected during the RANN survey and found evidence of avoidance in other large, agile zooplankters, particularly mysids and fish larvae. A ½ m net and night sampling were used during the Cape Henry survey and the elusive stages missed by the bongo sampler were captured. Although all nine stages were collected, peak abundance was still slightly lower than the RANN values. The lower value may have resulted from the use of a smaller mesh net, from not employing a flowmeter to obtain better filtration estimates, or from yearly fluctuations in the population; but, the abundance figures determined by the RANN and Cape Henry surveys are low for an organism that has been considered to be abundant in Chesapeake Bay (Brooks 1878; Cowles 1930; Wass 1972).

The RANN data showed the month of maximum abundance to be August, but the Cape Henry data demonstrated a peak abundance in early September. Again, this discrepancy may be attributed to normal yearly variation, but it probably resulted from the RANN program having sampled only the younger element of the population.

Larvae reared in the laboratory survived longest and molted the greatest number of times at 20° C-25‰ and 25° C-25‰ which corresponds to the temperatures and salinities found in the bay where the larvae were most abundant. The mean temperature of the bay from July through September, the season of larval occurrence of *S. empusa*, ranged from 19.7 ° to 25.2° C while the mean salinity was recorded from 21.5 to 23.1‰ in 1971 and 1973.

The greater abundance of larvae in the eastern and channel subareas of the bay is likely a result of the higher salinities. In Chesapeake Bay salinities are higher on the eastern side than on the western side due to the earth's rotation (Coriolis force) and the differences are enhanced by the larger inflow of freshwater from rivers on the western side (Pritchard 1952). The lower salinities of the upper reaches of the sampling area are also probably responsible for the lesser larval abundances in subareas G and H.

In 1972, Tropical Storm Agnes produced the most extensive flooding and greatest freshwater runoff in Chesapeake Bay in many decades, if not centuries, causing the distribution and abundance of most estuarine organisms to be seriously disrupted (Andrews 1973). The mean salinity of the lower Chesapeake was reduced to 16.5‰ in July only to increase to 19.4‰ in October. Although the larvae were more abundant in 1972 than in 1971, the reduced salinity resulted in a distribution compressed into the more southern subareas where the salinity was greater. Few larvae were captured in subareas D, G, and H where salinities ranged from 15.3 to 17.3‰, which would be expected considering the poor development of larvae reared at 15‰ during the temperature and salinity experiment. Grant et al. (1976) found other zooplankters in the lower Chesapeake Bay to be as abundant in 1972 as in 1971 and their distributions were also compressed in 1972.

Of the *S. empusa* larvae reared at the most favorable temperature and salinity combinations for survival and growth, 3% of the larvae were reared through eight of the nine larval stages in 6 wk, indicating that the length of the pelagic larval development would be slightly longer than 6 wk. However, the appearance of the postlarvae in the bay 1 mo after the initial appearance of the larvae indicates a substantially briefer period of larval development, provided that all larvae originated within the bay. The development of the larvae reared in the laboratory may have been extended as a result of dietary insufficiencies and an overall more stressful environment. Furthermore, the few specimens of stages V and VIII collected early in the 1976 larval season may have drifted into the bay from more southerly populations where eggs may have hatched earlier and been transported by currents into Chesapeake Bay. Nevertheless, since all larval stages and the postlarva were collected in Chesapeake Bay throughout their seasonal occurrence, it appears that the populations of *S. empusa* in the bay is self-sustaining. In addition, the temperature and salinity tolerances of the larvae correspond to those of the adults, which may occur in salinities as low as 16‰, but are most abundant in waters >25‰ (Cowles 1930; Gunter 1950; Parker 1956; Lee and McFarland 1962).

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