

AN ECOLOGICAL INTERPRETATION OF LOW TEMPERATURE RESPONSES IN *PENAEUS* *AZTECUS* AND *P. SETIFERUS* POSTLARVAE¹

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ABSTRACT

Postlarvae of two species of penaeid shrimp, *Penaeus aztecus* and *P. setiferus*, were exposed to varying temperatures under controlled conditions. *P. aztecus* regularly burrowed into the silty clay substrate as the temperature fell to 12-17°C, and emerged as the temperature rose to 18-21.5°C. Under identical conditions, *P. setiferus* showed neither type of activity.

Burrowing in response to low temperature is interpreted as a behavioral mechanism having survival value in the northwestern Gulf of Mexico for *P. aztecus*, which is known to reach estuarine areas early in the year, when bay waters are often cold. Such a mechanism would be less useful to *P. setiferus*, which usually arrives at bays during the summer.

The temperatures which stimulated burrowing of the postlarvae of *P. aztecus* in the laboratory are comparable with natural water temperatures off the Texas and Louisiana coasts during the winter. Furthermore, the temperature range which stimulated emergence of this organism from the substrate in the laboratory is quite similar to that associated with the appearance of most postlarvae of *P. aztecus* at bays. These findings support the hypothesis that most postlarvae of this shrimp species hibernate in the burrowed condition for at least a portion of the winter in the northwest Gulf of Mexico.

INTRODUCTION

It is well known that burrowing is a part of the normal behavior of adult penaeid shrimp. Commercial fishing efforts for *Penaeus aztecus* and *P. duorarum* in the Gulf of Mexico and the South Atlantic coast of the United States are largely nocturnal because of the diurnal burrowing habit of these species (Springer & Bullis, 1954). Fuss (1964) and Fuss & Ogren (1966), studying *P. duorarum* under field conditions, provided more definite evidence of a strong correlation between burrowing and daylight. Their filmed underwater observations indicated that burrowing gave protection from the predatory attacks of fishes. They also found that low water temperatures induced burrowing. Eldred *et al.* (1961) also suggested that burrowed shrimp are protected from extremely low water temperatures. Burrowing has not been reported for postlarval penaeid shrimp.

Previous work in this laboratory demonstrated marked effects of

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temperature on the growth of postlarval *P. aztecus* (Zein-Eldin & Aldrich, 1965). Animals held for one month at 11°C and 15-35‰ salinity showed excellent survival, but negligible growth, feeding, or other gross activity. Field observations by other workers indicated that young specimens of *P. aztecus* might be exposed regularly to winter and early spring temperatures in the coastal or near-coastal waters of the northwestern Gulf of Mexico (Baxter, 1963; Baxter & Renfro, 1966; St. Amant *et al.*, 1963). These observations suggested the need for a comparative study of the behavior of young shrimp at reduced temperatures. It seemed particularly pertinent to determine their ability to burrow when exposed to low temperatures, a response which might have survival significance in the natural environment as these decapods make the transition from a marine to an estuarine habitat.

MATERIALS AND METHODS

Postlarval specimens of *P. aztecus* and *P. setiferus* were collected from water about one meter deep near the beach at Galveston, Texas. Collecting gear consisted of a hand-drawn, 1-meter beam trawl suitable for retaining macroplankton (Baxter, 1963). All collections were made during July-August (of 1965), because at that season it is possible to find postlarvae of both species together in transit from offshore spawning grounds to estuarine nursery areas. Although most *P. aztecus* postlarvae appear at the bay entrance during March-April, we chose to test animals taken in July-August so that all shrimp came from comparable natural conditions. During collection, the water temperature ranged from 29 to 32°C, and salinity from 31 to 34‰. The animals were maintained in the laboratory at about 25°C and 25‰ for one to eight days before use in experiments. During this period, aeration was provided, and live larvae of brine shrimp (*Artemia salina*) were supplied as food.

For the behavioral studies, we used a small Plexiglass tank (240 mm long, 90 mm high, and 30 mm wide) containing approximately 50 ml of substrate collected from Galveston Bay and 300 ml of sea water. The substrate and water were about 10 and 60 mm deep, respectively. The water temperature was reduced by circulating cold water through 6-mm-diameter glass tubing which was partially immersed in the experimental tank (Fig. 1). Water for the cooling system was refrigerated and continuously recirculated by a cooler (A. Daigger & Co.). Rate of cooling in the tank was controlled by varying the amount of glass tubing that was immersed in the sea water. A 210-watt heating tape, placed under the tank and connected to a variable transformer, was used to control temperature differentials between water and substrate. Water and substrate temperatures were measured and recorded continuously with a Yellow Springs Instrument Tele-thermometer (Model 47) and recorder (Model

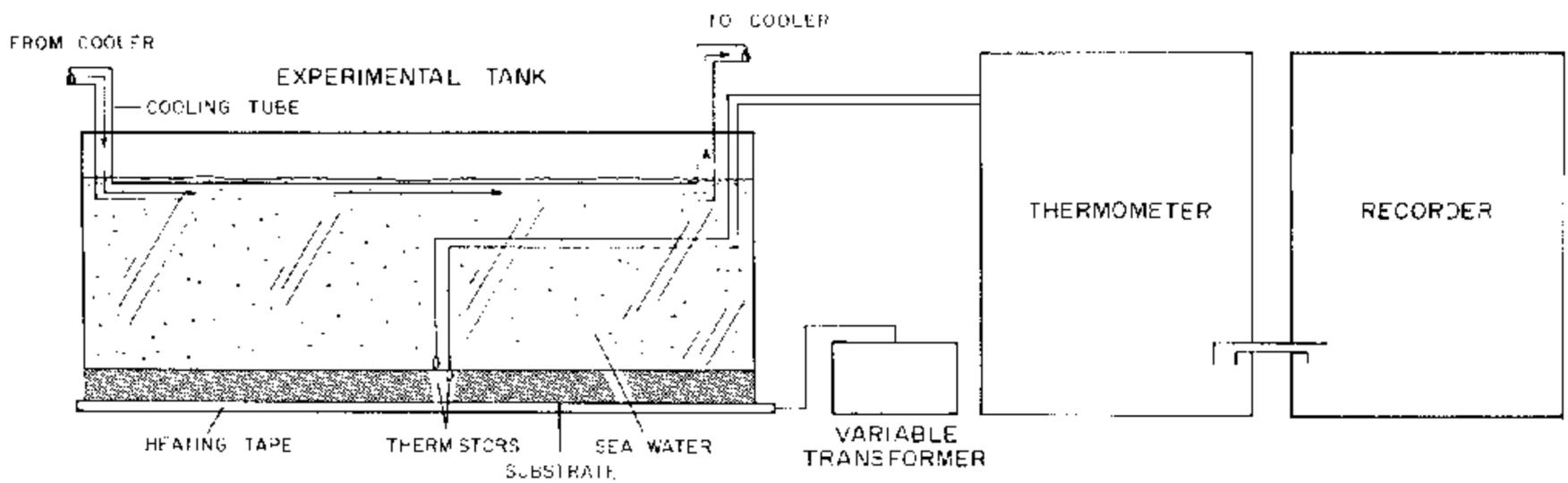


FIGURE 1. Experimental apparatus for the study of behavior of postlarval shrimp at reduced temperatures.

80). Thermistors attached to these instruments were located just above and below the water-substrate interface.

Preliminary observations suggested that rapid cooling rates and coarse texture of the substrate inhibited burrowing by postlarvae, whereas illumination stimulated such activity. Since one of our primary objectives was to determine and compare the burrowing abilities of *P. aztecus* and *P. setiferus*, we set up standardized test conditions which would neither stimulate nor interfere with postlarval burrowing. Cooling rates were reduced to 0.19°C per minute or less, and light was reduced to the level provided by two 40-watt, red, incandescent bulbs 150 mm behind the tank. A natural silty clay found to be suitable for burrowing was regularly used as the experimental substrate.

The substrate was collected from a natural bay shore by means of 25-ml pipettes with rubber bulbs attached to the pointed ends. A slurry of bay water and the upper layer (1-2 mm) of silty deposit was drawn into the pipette where the water was 50-75 mm deep. The material collected was 75 per cent clay, 22 per cent silt, and 3 per cent sand. (On one occasion, a *P. aztecus* postlarva which had burrowed into the substrate was taken in this process.)

One to 16 hours before each experiment, five specimens of *P. aztecus* and five of *P. setiferus* were introduced into the tank, and the light level was reduced to the experimental level. Shrimp behavior during this pre-experimental control period was taken as representing the type of activity exhibited by a given group of animals under experimental conditions in the absence of varying temperature. Burrowing did not occur during these periods. Throughout the experiments one of us monitored and controlled the temperature changes in the tank and recorded the observations of another person, who continually watched the shrimp. Our earlier runs were terminated when shrimp had either burrowed or lost equilibrium (lying on their dorsal or lateral surfaces). In later experiments, we also

TABLE 1
RESPONSES OF THE POSTLARVAE OF TWO SPECIES OF SHRIMP
TO LABORATORY TEMPERATURE CHANGES

Temperature regime	Species	Number tested	Response to temperature decrease		Response to temperature increase	
			Number that burrowed	Per cent of total tested	Number that emerged	Per cent of total that burrowed
Decrease only	<i>Penaeus aztecus</i>	20	18	90	—	—
	<i>P. setiferus</i>	20	0	0	—	—
Decrease-increase	<i>P. aztecus</i>	30	29	97	29	100
	<i>P. setiferus</i>	30	0	0	—	—

made observations as the experimental tank and animals were returned to room temperature.

RESULTS

As experimental water temperatures were reduced from the initial (ambient) levels (24-27°C), several successive stages of shrimp behavior became apparent. The first stage, occurring in both species of shrimp at 16-21°C, was one of increased activity, during which the postlarvae swam about the tank continuously and rapidly. A further reduction of temperatures to 15-17°C caused an almost complete cessation of activity; the shrimp rested quietly on the substrate most of the time. A third and most marked stage of low-temperature behavior, usually taking place between 12 and 17°C, was regularly observed only in *P. aztecus* postlarvae. At that temperature range, these animals burrowed into the substrate. This was accomplished by means of abdominal undulations accompanied by movements of pereopods and pleopods, as described for burrowing of adult penaeids by Dall (1958), Egusa & Yamamoto (1961), and Fuss (1964). In both species, further reduction of temperature to 10-12°C resulted in loss of equilibrium in those individuals which had not burrowed into the substrate.

Our most striking findings were (1) burrowing by postlarval specimens of *P. aztecus*, and (2) the inability of postlarval specimens of *P. setiferus* to burrow. Ninety-four per cent of the 50 *P. aztecus* postlarvae tested burrowed in response to reduced temperature, while none of 50 *P. setiferus* showed this type of activity (Table 1).

A size difference between these species of shrimp is characteristic for postlarvae collected along beaches in this area. The *P. aztecus* were 8.5-13

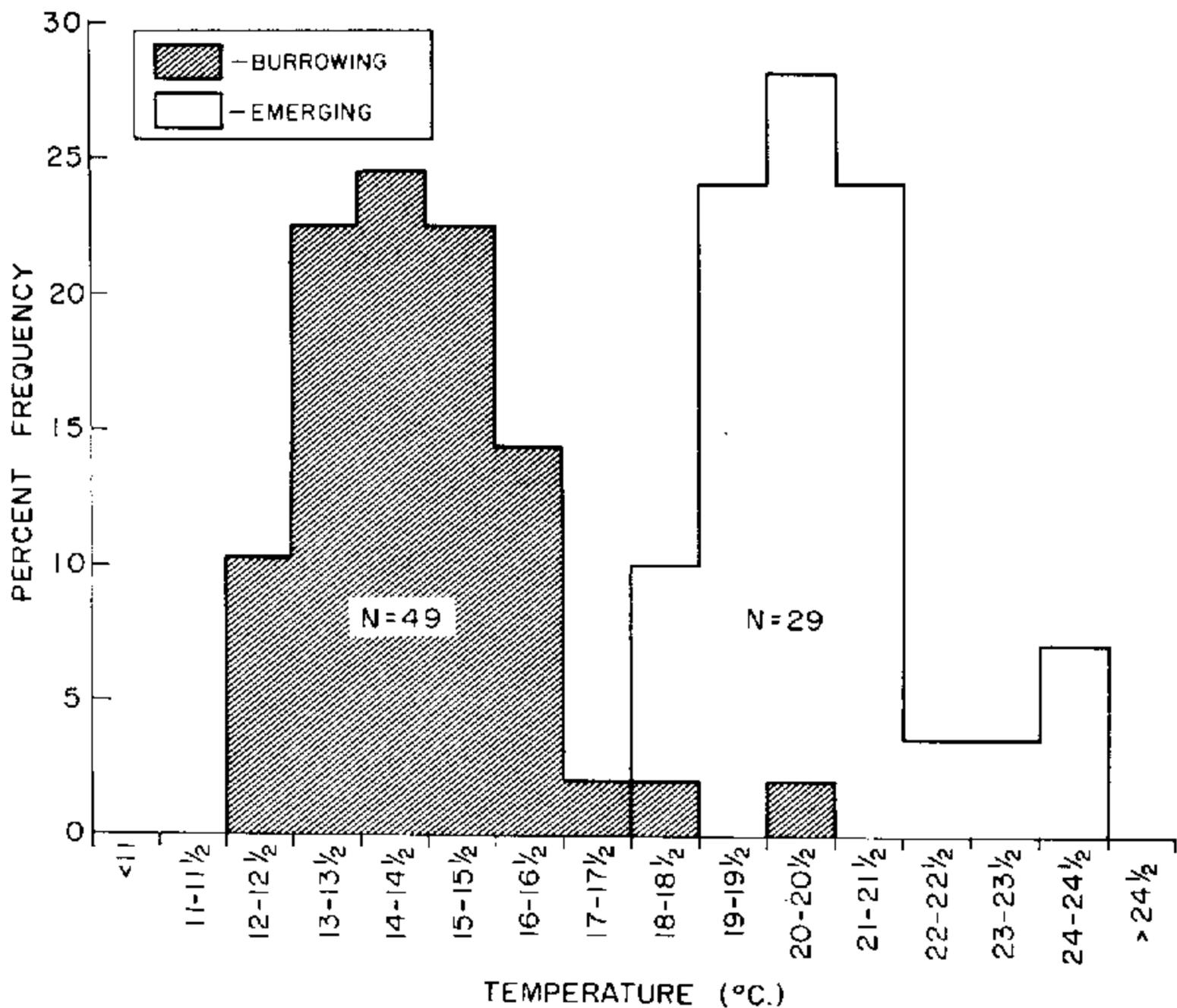


FIGURE 2. Per cent frequency distribution of burrowing and emerging of *P. aztecus* postlarvae at various temperatures. Shrimp which had not burrowed occasionally disturbed the buried animals, causing emergence followed by reburrowing in two instances. Hence, 49 instances of burrowing were observed among 47 shrimp.

mm in length, whereas the *P. setiferus* were only 6-8 mm long. The possibility that the postlarvae of *P. setiferus* were unable to burrow because of their smaller size led us to examine this possibility experimentally. Because larger postlarvae of this species were not readily obtainable alive from the field and are difficult to identify without injury, we used 10 specimens (11-17 mm in length) from a laboratory study of growth. Although the size advantage was now reversed in favor of *P. setiferus*, only one shrimp of this group burrowed when exposed to a temperature regime and substrate in which *P. aztecus* burrowed.

Several experiments were conducted to determine the effect of temperature differences between water and substrate on the incidence of postlarval burrowing. The tested differences (0.3°, 1.0°, and 1.2°C) had no significant influence on burrowing incidence of *P. aztecus*.

When sufficient experimental data had been collected to suggest that burrowing was a regular characteristic of the postlarval behavior of *P.*

aztecus, we conducted additional experiments, extending our observations to include an additional period during which experimental temperature was allowed to rise toward ambient levels (Table 1). This procedure provided data on the temperature range at which 29 postlarval specimens of *P. aztecus* burrowed and emerged. All of the animals which had burrowed emerged as the temperature reached 18-24.5°C. A frequency distribution of the temperatures at which postlarvae of this species burrowed and emerged shows that the two processes occur at markedly different temperature ranges (Fig. 2). Ninety-four per cent of the burrowing took place when temperatures were reduced to 12-16.5°C, while 86 per cent of the emerging occurred when temperatures rose to 18-21.5°C.

DISCUSSION

These results provide the first definite evidence of burrowing behavior in postlarval penaeid shrimp. The consistency with which reduced temperature elicited this type of activity in postlarval *P. aztecus* suggests that burrowing is a normal response of this animal to cold.

The absence of the burrowing response to low temperature in *P. setiferus* led us to compare the seasonal abundance and distribution of this species with that of *P. aztecus*. As reviewed by Williams (1965), in both *P. aztecus* and *P. setiferus* spawning and larval development occur at sea. The postlarvae then move to estuarine areas where they rapidly grow to subadult size (about 80-125 mm long) before migrating offshore to attain adulthood and spawn. There is a marked difference in the season at which postlarvae of the two species reach the bays. *P. setiferus* arrives at Galveston Bay during the summer, when water temperatures are consistently warm (about 25-32°C). Most individuals of *P. aztecus*, on the other hand, appear in March or April (Baxter, 1963), when bays are not only cool (averaging 15-25°C), but also subject to the drastic temperature reductions (often to 12°C) caused by atmospheric cold fronts (E. J. Pullen, in preparation). Thus, most postlarvae of *P. aztecus* are exposed to considerably lower and more changeable estuarine temperatures than those encountered by *P. setiferus*.

Although no definite evidence of postlarval burrowing has been reported from field investigations, the observations of St. Amant *et al.* (1963) are pertinent. In regard to *P. aztecus* postlarvae, they stated (p. 19): "The effect of cold water temperature or sudden drops in temperature is not altogether clear. Although the larvae may disappear completely from samples, we failed to note dead larvae in the sample after cold spells" (The temperature referred to was 11-12°C.) In view of our laboratory experiments, it now seems reasonable to suggest that burrowing, in response to reduced temperature, could have a significant effect on the availability of postlarvae to nets when water temperature is low, causing a temporary

disappearance of these animals from samples. The ability to burrow in response to low temperature may have special survival significance for *P. aztecus* during this period of their natural history. Burrowing can serve both to attenuate rates of temperature change to which the animal is exposed and to protect it from predatory attack when temperatures are low enough to slow avoidance or escape movements (Fuss & Ogren, in press). On the other hand, a burrowing response to low temperature would have no obvious adaptive significance for *P. setiferus* because the seasonal characteristics of this species' life cycle are such that most postlarvae do not encounter cold temperatures in the northwestern Gulf of Mexico.

Burrowing may play a similar role of importance to *P. aztecus* postlarvae even before they move into estuarine nursery areas. D. L. Harrington found temperatures of 11°C at 4 fathoms to 17°C at 25 fathoms off Galveston in January and February, 1963 (in preparation). Levels for June through September ranged from 20 to 31°C. His data for 1964 indicate a similar pattern. It is clear that winter offshore temperatures are commonly within or below the range which we have experimentally shown to stimulate burrowing by *P. aztecus* postlarvae.

In this connection, it is interesting to consider the relationship between natural water temperatures and the arrival of these organisms in bays. In regard to *P. aztecus*, St. Amant *et al.* (1963) stated: "Maximal postlarval densities apparently do not appear in Louisiana until water temperatures remain above 20°C" (p. 18). A similar course of events can be determined for Galveston Bay, Texas, from the field data of Baxter & Renfro (1966). They took simultaneous water temperatures and macroplankton samples semiweekly for 4 years at the entrance to Galveston Bay. A total of 376 samples yielded 32,093 *P. aztecus* postlarvae. More than half of the shrimp (58.1 per cent) were taken at temperatures of 18-22°C, a range which included only 17.5 per cent of the 376 temperatures recorded (Fig. 3). This nonrandom distribution suggests a marked relation between temperature and the occurrence of postlarvae. The pattern is quite similar to that shown above for temperature and the emergence of burrowed shrimp from the substrate.

Two additional points relating to collections of *P. aztecus* postlarvae made at temperatures outside the "laboratory emergence" range (Fig. 3) strengthen this comparison of laboratory and field data. First, the only sizable collection of shrimp made at a water temperature below 19°C yielded 1,682 specimens, taken at 16°C on April 4, 1962. It is noteworthy that this temperature represented an unusually low departure from the existing general trend. Temperatures for the two weeks preceding this collection ranged from 19 to 24°C, and those for the following two-week period were between 20 and 25°C. Secondly, most postlarvae collected at

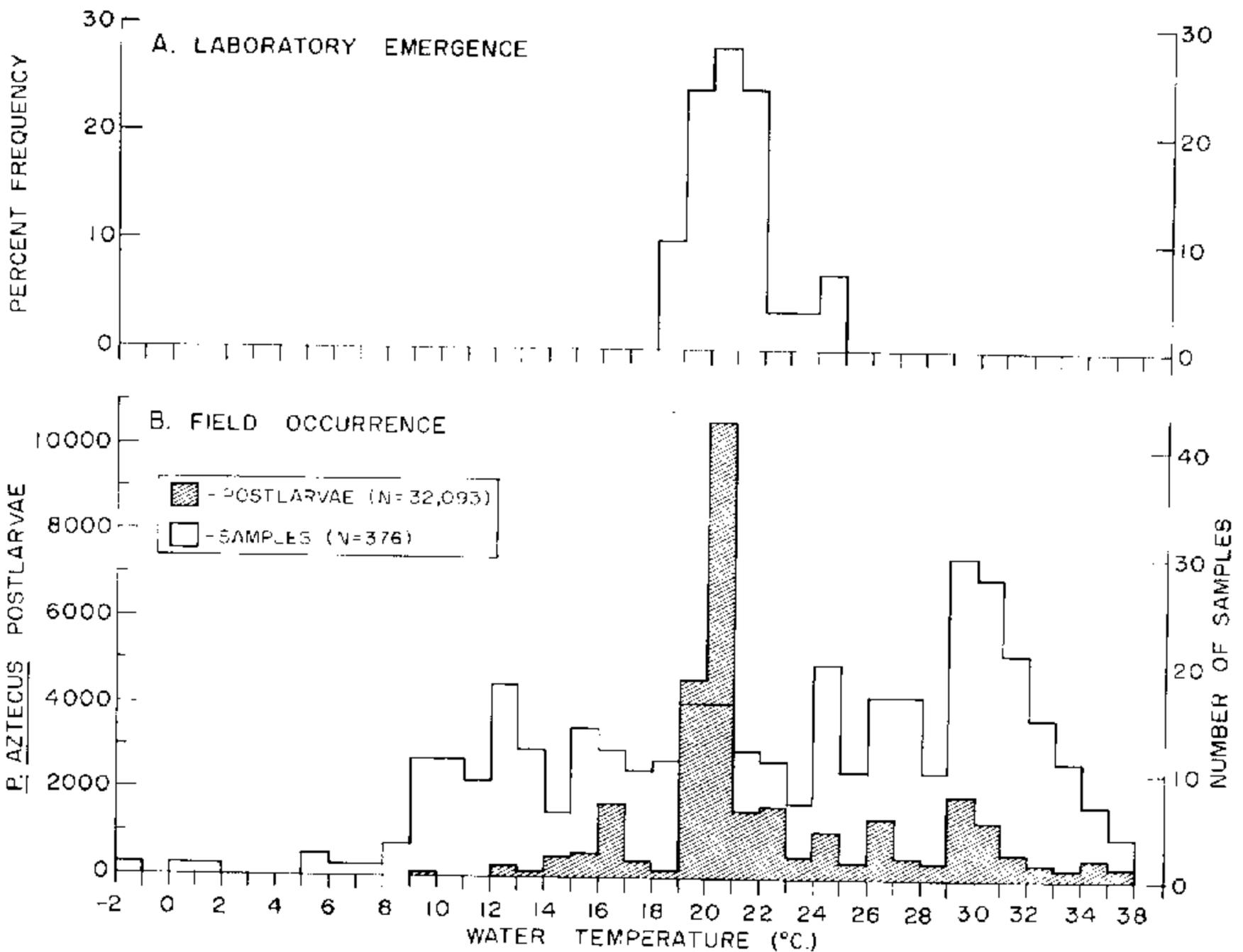


FIGURE 3. Temperatures associated with emergence of postlarvae of *P. aztecus*: A, Per cent frequency of postlarval emergence from substrate at various temperatures (laboratory results from Fig. 2); B, Frequency distribution of postlarvae collected at different temperatures at the entrance of Galveston Bay, 1960-63 (data from Baxter & Renfro, 1966).

temperatures of 25°C and above were taken during the summer and early fall. Cook & Murphy (1966) have shown that, after being spawned in the laboratory, young specimens of *P. aztecus* require from 2 to 3 weeks to reach the postlarval stage of development at 24 to 30°C. Thus, postlarvae arriving at bays in the summer and fall could never have been exposed to temperatures capable of inducing burrowing. For this reason, summer and fall collections could logically be excluded from field data to be examined for evidence relating to the hypothesis that postlarval *P. aztecus* burrow in response to winter temperatures. In any case, the agreement between laboratory and field results is sufficient to support this hypothesis. Thus it is possible that postlarvae of *P. aztecus* burrow into the substrate for part of the winter before entering the bays in early spring.

Further support for this interpretation may be derived by considering seasonal changes in the size of *P. aztecus* postlarvae in relation to the influence of temperature on growth. Baxter & Renfro (1966) showed

that specimens of *P. aztecus* were larger in the spring than those collected at other seasons. The modal lengths were 12-13 mm for shrimp arriving at the bay during March-April, but only 10 mm for those taken in June through September. Zein-Eldin & Aldrich (1965) and Zein-Eldin & Griffith (1966) found that temperatures of 11-15°C greatly reduced postlarval growth, but permitted survival. Growth was only 0.0-0.6 mm per month at 11-15°C as compared with 9-23 mm per month at 20-30°C. Recalling Harrington's offshore water temperature data (given above), we infer that the growth rate of postlarval shrimp is less in winter than in summer and fall. This line of reasoning leads us to interpret the large size of *P. aztecus* postlarvae in the spring as the possible result of an extended period of slow growth offshore. If these animals were spawned in January or February, they should be smaller, not larger, than the fast-growing, summer-fall group on arriving at bays in the spring. On the basis of available evidence it seems reasonable to suggest that *P. aztecus* postlarvae reaching the bays in spring were spawned late in the preceding year.

The presence of *P. aztecus* postlarvae in the substrate offshore during December-February remains to be demonstrated. Final proof of postlarval hibernation in this species, and the importance of the burrowing mechanism to such a process, will await such evidence. The present work, however, characterizes *P. aztecus* postlarvae as having a rather specialized behavioral mechanism which seems well suited to protect this organism during the periods of torpidity induced by low temperature. Furthermore, the temperature range shown to elicit the burrowing response in the laboratory is commonly found during winter along the Texas-Louisiana coasts, where this species flourishes. Likewise, emergence of postlarvae in the laboratory was induced by a temperature range remarkably similar to that observed in nature when *P. aztecus* postlarvae enter bays during March or April.

Thus, laboratory evidence suggests that seasonal patterns of temperature distribution are adequate to induce burrowing by *P. aztecus* postlarvae during the winter and emergence in early spring, a sequence of events that fits in well with existing information regarding the seasonal occurrence of postlarval specimens of *P. aztecus*. We conclude that burrowing is a normal part of postlarval behavior in this species and represents an ecological mechanism through which it survives cold periods until temperatures more favorable for activity, feeding, and growth prevail.

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the potential significance of our experimental results. We are indebted to C. R. Mock for analyses of substrates.

SUMARIO

UNA INTERPRETACION ECOLOGICA DE LAS RESPUESTAS A LAS BAJAS TEMPERATURAS EN LAS POSTLARVAS DE *Penaeus aztecus* Y *P. setiferus*

Se presenta la primera evidencia reportada sobre la habilidad de las postlarvas de los camarones peneidos de enterrarse en un substrato.

Las postlarvas de *P. aztecus* se enterraron respondiendo a una reducción experimental de las temperaturas (usualmente dentro de una variación de 12°-17°C) y emergieron de 18°-21.5°C.

En los mismos experimentos, postlarvas de *P. setiferus* no se enterraron en respuesta a temperaturas bajas.

Se discute esta diferencia de conducta entre las especies en relación a sus respectivos patrones estacionales de abundancia de postlarvas. Se sugiere que el enterrarse es un mecanismo por medio del cual las postlarvas de *P. aztecus* sobreviven lejos de la costa por lo menos durante una parte del invierno y en las áreas estuarinas al principio de la primavera.

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