Development of Spiny Lobster (*Panulirus argus*) Phyllosoma Larvae in the Plankton near Bermuda

MARY W. FARMER[1], JACK A. WARD[2] and BRIAN E. LUCKHURST[2]
[1]*Williams — Mystic Maritime Studies Program*
Mystic Seaport Museum
Mystic, Connecticut 06355
[2]*Bermuda Division of Fisheries*
Department of Agriculture & Fisheries
P.O. Box CR52
Crawl, Bermuda
CRBX

ABSTRACT

Durante el estudio de dos años sobre la disperción de la etapa "phyllosoma" y el reclutamiento de la etapa puerulus, se encontró que la etapa número 1 de "phyllosoma" se encontraba en las aguas cercanas a la costa durante el tiempo comprendido entre junio y agosto. Las etapas II a la V ocurrieron simulta aneamente con la etapa I; las etapas VI a la XI aparecieron en secuencia a través del invierno. El reclutamiento de los puerulus tuvo su auge en agosto y septiembre aunque ocurrió durante la mayor parte del año. El tiempo transcurrido entre el período de mayor auge en concentraciones de la etapa I y aquel de mayor auge en reclutamiento, conjuntamente con las tasas calculadas de desarrollo en el plancton, sugiere una duración de etapa planctónica de aproximadamente un año para las larvas "phyllosoma" de *Panulirus* en el Mar de los Sargasos.

INTRODUCTION

The length of time spent in the plankton by *Panulirus argus* phyllosoma larvae has been estimated "tentatively" as more than six months (Lewis, 1951). Although a more certain knowledge of this time period is needed for any estimation of the dispersal patterns (Scheltema, 1971), and although dispersal patterns could aid in fisheries management decisions (Richards and Pothoff, 1980), little has since been learned about development rates of *P. argus* in the plankton (Lyons, 1981).

One difficulty with estimating duration of phyllosoma stages from the plankton is the extended spawning period for populations in the Caribbean (reviewed by Lyons, 1981). Year-round spawning, with peak activity at various times of the year, has been documented for Jamaica (Munro, 1974), Puerto Rico (Mattox, 1952), and the Bahamas (Smith, 1951; Kanciruk and Herrnkind, 1976). On the other hand, spawning occurs primarily during spring and summer in Florida (Lyons, 1981) and in Bermuda (Creaser, 1950; Sutcliffe, 1952).

If a population that demonstrates one or two spawning seasons lies downstream of populations that spawn year round, it is difficult to track development in the plankton or to attribute settlement patterns to recruitment from local populations. Most stages are present year-round, and modal increases in stage or size with time is not observed in this situation (Sims and Ingle, 1967; Richards and Pothoff, 1980). If a population with restricted spawning times is relatively isolated from populations that spawn year-round, however, tracking

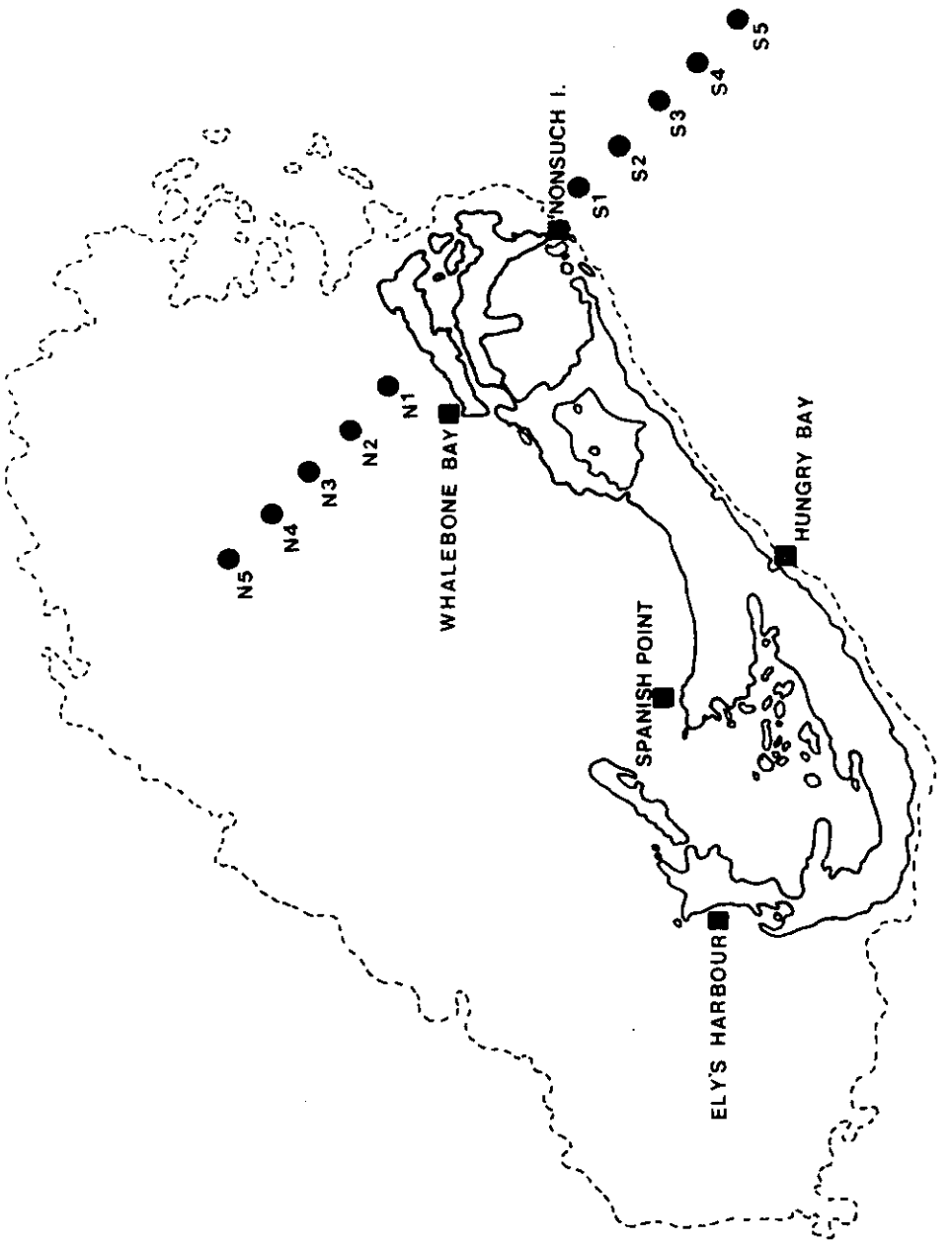

Figure 1. Sampling program conducted by the Bermuda Division of Fisheries. Plankton tows are done monthly at stations (circles) along the offshore transect. Pueruli are collected weekly from the artificial habitats (squares).

of the phyllosoma larvae were probably *P. argus*. (Note: Ratio of *P. argus* to *P. guttatus* females in traps on the outer reef was 20:1 (Sutcliffe, 1953). Personal observations by two of the authors, Ward and Luckhurst, suggest that *P. guttatus* is still much less abundant than *P. argus*. Both species are fished regularly.)

When staging, a specimen was designated as "intermediate" if the sizes of the characteristics being measured (*e.g.*, antennal length, thorax length) fell between ranges that represented two distinct stages as defined by Lewis (1951), or if the sizes of two or more characteristics represented one stage and the remaining characteristics represented another stage. Stages are artificial designations and are not presumed to represent instars (Lewis, 1951; Baisre *et al.*, 1964). "Intermediate" is likewise an artificial designation, not presumed to represent any unusual development pattern.

Puerulus Stage

Witham habitats (Witham *et al.*, 1968; Little and Milano, 1980) were placed at five nearshore locations within the reef system in August of 1983 (Figure 1). An additional five habitats were installed July 1986; Nonsuch Island and Hungry Bay collectors were discontinued in April 1985. Data in this paper are from Whalebone, Ely, and Spanish Point collectors. Complete pueruli data are reported elsewhere in this issue (Ward, this issue). Sampling was begun on August 15th at twice weekly intervals. From October 1983 through January 1986 sampling was conducted at weekly intervals. Pueruli were relocated to mangrove or sea grass habitats more than 1 km downstream of collector stations and therefore would not likely be recollected.

RESULTS

Phyllosoma Larvae

A total of 5,757 *Panulirus* form B phyllosoma larvae were collected during the two-year study. Eighty-seven percent of all specimens were stage I. Stages I and II together accounted for 92 percent of the specimens, and both stages were collected at all five stations (Figure 3). Later stages were collected at the offshore stations but not at station S1, which was closest to land (Figures 1 and 3). Only two specimens of stage XI were collected, both at the offshore station S5 (Figure 3).

Larval concentrations ranged from 0 in May 1985 and January 1986 to 992 larvae per 1,000 cubic meters in July 1984, with an overall mean concentration of 97 larvae per 1,000 cubic meters (Figure 4B). The highest concentration of stage I occurred in July in both years (965 and 759 larvae per 1,000 cubic meters in 1984 and 1985, respectively) and tapered off to 11.6 and 9.9 larvae per 1,000 cubic meters, respectively. These peak concentrations of stage I and, to a lesser extent, of stage II accounted for the peaks in the annual pattern of larval abundance (Figure 4B). Highest concentrations were seen June—September, when water temperatures were ≥ 24.0° C (Figure 4A). Lowest larval concentrations did not necessarily correspond to lowest temperatures (Figure 4), and larvae were collected over the entire temperature range of 19.2—27.4° C, an 8.2° C difference.

Percentages of each phyllosoma stage caught during each month of the year in this study and in the pilot study in August 1983 are shown in Figure 5. Stages I—V occurred simultaneously from July until early October. Stages VI through XI dominated the larval samples sequentially from October through June.

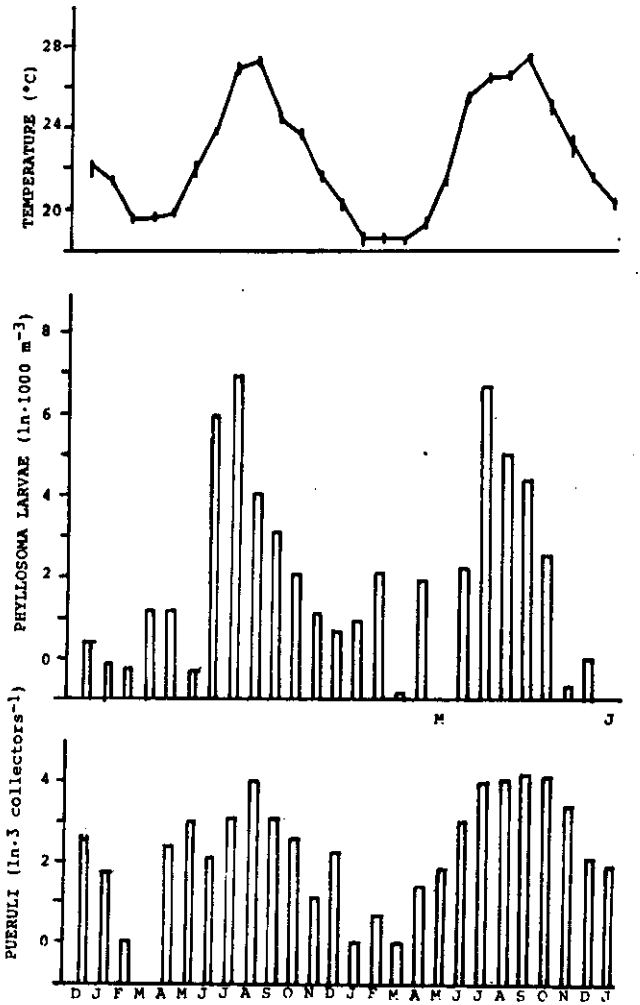

Figure 4. Temperature, larvae, and post larvae data from stations S1 — S5 and three post-larval collectors from December 1983 to January 1986. No phyllosoma larvae data are available for November 1985. A. Mean and range of surface water temperature for all stations at each sampling time. B. Concentration of phyllosoma larvae (in number 1000 m^{-3}) averaged for all stations at each sampling time. C. Number of pueruli collected from three artificial habitats over a one month period, for each month of the study.

During winter (but not summer) months several "intermediate" stages as defined in the Methods section were observed, the most numerous being intermediate between VII and VIII. This stage was included in the data as stage VII, and the proportion it represented is stippled in Figure 5.

Puerulus Stage

No pueruli were collected in our plankton tows. The post-pelagic puerulus stage settled onto collectors virtually throughout the year, with a seasonal peak in August—September (Figure 4C).

DISCUSSION

Enough phyllosoma larvae were collected year-round within 5 nautical miles of Bermuda to detect a progression of stages of development. This pattern suggests that local larvae dominate the phyllosoma samples found near Bermuda and that these samples represent a Sargasso Sea mixture from Bermuda and other sources. Both temperature effects and the presence of larvae from other sources will influence the development pattern and hence estimation of time spent in the plankton by *P. argus*.

Temperature and Development Pattern

A relationship between temperature and growth is not unexpected and was noted for stage VI in *P. cygnus* (Chittleborough and Thomas, 1969; Ritz, 1972). Oceanic surface temperature at Bermuda varied annually over a range of 8° C (Figure 4C). Stages I—V occurred simultaneously during the warm months only. This simultaneous appearance may suggest rapid development of Bermuda larvae during this time (June—September). Stages VI through XI sequentially dominate the samples during the remaining months of the year, suggesting a slower development rate. Occurrence of intermediate stages in winter, particularly between stages VII and VIII, which accounted for the highest proportion of phyllosoma larvae in December (Figure 4), also indicated slower growth at colder temperatures.

In the Gulf of Mexico and Yucatan Straits, Austin (1972) found no phyllosoma larvae in waters cooler than 24° C. Although phyllosoma larvae have been found at cooler temperatures in the North Atlantic (Sims, 1968) and near Bermuda (present study), no stages smaller than stage VI have been found at these temperatures. Surface temperature for anywhere in the Sargasso Sea and Gulf Stream deviated from that at Bermuda by about 3—4° C for any month during the study (Oceanographic Monthly Summaries, 1983-1985) so that latitudinal variation was much less than the annual variation at Bermuda. Larvae in these waters will therefore be subjected to temperature regimes quite similar to that of Bermuda. It seems that early stages will be spent in warm water and that only the later stages will be subject to cooler temperatures.

Panulirus larvae undergo vertical migration (Buesa Mas, 1970) and will be subject to vertical variations in temperature. Phyllosoma larvae were found to a depth of 50 m in the Gulf of Mexico (Austin, 1972); it seems unlikely that these larvae migrate beneath the thermocline. A seasonal thermocline exists in the Sargasso Sea, and from July through early October the vertical temperature structure of the top 50 m ranges from 24 to about 27° C (Schroeder and Stommel, 1969). With the breakup of the seasonal thermocline, the 3° C temperature range extends down to 100 m and by February it extends to 400 m,

mean uneven development of Bermudian phyllosoma larvae. If peak settlement is the direct result of an earlier peak in stage I larvae, then Bermuda spiny lobsters appear to spend 12 to 14 month of their life cycle in the plankton. This 12 to 14 month period is consistent with the pattern of dominant stages discussed earlier. That pattern suggested a development period of approximately one year for phyllosoma larvae.

We conclude from these observations that planktonic development of *P. argus* takes approximately one year in the Sargasso Sea. From our data it is not possible to distinguish the effects of unequal growth rates of Bermudian larvae from the effects of input of larvae from other sources on the development pattern. Biochemical-genetic comparisons of population structures of larvae and Bermudian lobsters would be required to answer this question.

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