ECOLOGICAL STUDIES OF THE PUERULUS LARVAL STAGE OF THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS*[1]

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ABSTRACT

Ecological and related behavioral studies of the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*, involved the development and use of artificial and natural seaweed habitat traps, special paired neuston nets, and underwater night-lights for collecting and observing pueruli in nature. The results obtained indicate that pueruli first enter the coastal waters off San Diego, Calif., during May, and continue to appear regularly through September, but with no apparent relationship to lunar or temperature cycles.

Pueruli exhibit a strong attraction to floating habitat traps containing the surfgrass *Phyllospadix torreyi* and to bright lights at night. The results also suggest that the puerulus is a surface-swimming, pelagic form which may actively seek out specific nearshore areas for settlement, and thereby serve the important function of returning larval stages to areas suitable for demersal life of the young juveniles.

Previous studies of the California spiny lobster, *Panulirus interruptus* (Randall), and other spiny lobster species have concentrated primarily on either the adult or phyllosoma larval stages, leaving the biology of the intermediate, yet very important, puerulus and juvenile stages relatively unknown. This is particularly true for *P. interruptus*. Prior to the present study, essentially nothing was known about the ecological requirements or behavior of the puerulus or early juvenile stages, which together represent a period of 2-3 yr in the life history of this species. This is an unfortunate situation for an animal as heavily exploited by a commercial fishery as the California spiny lobster because, as Thorson (1950) has indicated, the abundance of any adult population is primarily dependent on the recruitment, survival, and growth of its larval and juvenile stages. Consequently, attempts to improve fishery yields through a better understanding of adult behavior and population ecology alone provide only a partial and temporary solution to the problem.

Increasing fishing pressure on the steadily declining stocks of *P. interruptus* and other spiny lobster species urges more than an academic interest in the ecological requirements of their puerulus and juvenile stages. On the basis of this information, for example, it may be possible to protect their natural habitats or to develop supplementary artificial habitats for them in nature. Techniques for culturing these stages under artificial conditions, as a means of supplementing natural stocks, must also be given serious consideration for the following reasons.

Evidence concerning *P. interruptus* (Johnson 1956, 1960, 1971) and other palinurid species (see, for example, Chittleborough and Thomas 1969) suggests that a majority of the phyllosoma and puerulus larvae may be lost from the population due to their long larval life (5-10 mo), during which they may be swept hundreds of kilometers offshore. Because of their small size, the surviving postpuerulus and early juvenile stages probably experience much higher predation mortality rates than do the adults (Winget 1968). In addition, evidence from limited studies of other spiny lobster species, including *P. argus*, *P. longipes cygnus*, and *Jasus edwardsii*, suggests that the nursery grounds of their postpuerulus and early juvenile stages are located in protected bays or estuaries (Sheard 1949; Lewis et al. 1952; Witham et al. 1964, 1968; Sweat 1968; C. B. Kensler, pers. commun.). If such estuarine nursery grounds are required by the early benthic stages of *P. interruptus*, reduction of this type of natural habitat as the result of commercial developments and water pollution may create a "weak link" in the life history of this species, at least within part of its geographical range.

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Aquaculture of *P. interruptus* or other palinurid lobsters, starting with the egg, has been attempted by several investigators as a means of bypassing what appears to be an inefficient recruitment process in nature. Yet all attempts to culture the phyllosoma larval stages from the egg through to the puerulus stage have been unsuccessful (for example, see Dexter 1972). This approach does not appear to be feasible at the present time, particularly on a mass culture basis, due to the long duration (5-10 mo in nature) and the poorly understood requirements of the delicate phyllosoma larval stages. In contrast, the succeeding puerulus and juvenile stages of spiny lobsters respond well to laboratory culture (Kensler 1967; Witham et al. 1968; Serfling and Ford in press a, b). Thus, if the puerulus stage of *P. Interruptus* proves to be abundant and relatively easy to collect in large numbers, particularly in certain offshore waters where these individuals might otherwise be swept away from coastal nursery grounds, it may be advantageous to supplement natural stocks by collecting pueruli and holding them in mass culture under controlled, optimal conditions through at least the early juvenile stages. These pueruli could either be reared directly to a marketable size under artificial conditions, or returned to the ocean, after passing the potentially critical early juvenile stages, for final growth and maturation. This approach to spiny lobster culture has also been proposed for *P. argus* by Ingle and Witham (1969).

The lack of ecological information on the puerulus stage of any spiny lobster species is due largely to the fact that investigators usually have been unable to collect more than a few individuals, despite extensive sampling in areas where they might be expected to occur. Consequently, the central question precluding further research has concerned the mode of life of the puerulus stage, i.e., whether it is primarily a benthic or pelagic form.

Evidence presented in the literature thus far supports about equally each side of the issue. Investigators who have failed to collect more than a few isolated pueruli, even after years of extensive sampling by conventional methods (Lewis et al. 1952; Johnson 1956, 1960, 1971; Harada 1957; Saisho 1966; Sims and Ingle 1966; Lazarus 1967), have concluded that the puerulus stage of their respective species is either primarily benthic, or concentrated in unknown pelagic areas. On the other hand, Gurney (1942), Sheard (1949), George and Cawthorn (1962), Chittleborough and Thomas (1969), and Chittleborough (1970) were able to collect small numbers of individuals in net hauls far out to sea, and thus suggested that the puerulus is a free-swimming stage.

Harada (1957) and Johnson (1960) reported collecting a few pueruli which were attracted to bright lights over shallow water at night, but both authors apparently believed they were lured from the bottom. Yet Lindberg (1955) reported that University of Hawaii personnel collected several pueruli of a *Panulirus* species which were attracted to surface night-lights in water several hundred meters deep, thereby eliminating the possibility that they were attracted from the bottom. Witham et al. (1968), Sweat (1968), Phillips (1972), and we have successfully attracted large numbers of pueruli to artificial habitat traps floating at the surface, thereby offering the first strong evidence that the puerulus is primarily a pelagic, surface-dwelling form.

Preliminary observations made originally by J. C. Van Olst (pers. commun.) in the spring of 1968, demonstrated that puerulus larvae of *P. interruptus* occurring in local coastal waters could be attracted to bright lights suspended underwater near the surface at night. This discovery prompted the following investigation into several aspects of puerulus behavior and ecology. The specific objectives of this study were: 1) to determine the mode of life of the puerulus stage of this species, e.g., whether it is primarily benthic or pelagic; and, having done so, 2) to develop and apply suitable field sampling techniques to study the general dynamics of puerulus recruitment with regard to seasonal, lunar, and daily periodicity, area of settlement, specific habitat preferences, and migratory behavior; and 3) to estimate the general abundance and possibility of collecting large numbers of this stage for use in aquaculture. Closely related studies were also conducted concurrently to investigate the habitat preferences and the natural growth rates of the early juvenile stages in nature, as well as the growth and survival of the juvenile stages at elevated temperatures in recirculating culture systems (Serfling 1972; Serfling and Ford in press a, b).

MATERIALS AND METHODS

The failure of standard sampling methods used by previous investigators to collect the puerulus stage prompted the development of novel equipment and techniques. These included underwater night-lights of high intensity, floating artificial and natural seaweed habitat traps, and a special paired neuston net, which are described in the following sections.

Underwater Night-Lights

Most of the night-light observations and collections were made from an adjustable ladder platform near the end of the Scripps Institution pier, at the position shown in Figure 1, under a variety of environmental conditions. A standard motion picture projection lamp of either 500 or 1,000 W was waterproofed at the electrical connection with silicone sealant. The light was mounted on a pole and lowered 30-50 cm below the surface. This unit illuminated a spherical area 5-8 m in diameter, depending on water turbidity. When suspended in this way it provided much greater illumination than when suspended just above the surface. Pueruli attracted to the light were removed with a dip net and maintained alive for further studies.

Seaweed Habitat Traps

Pueruli placed in aquaria quickly settled and remained hidden in a variety of intertidal rock and plant substrates, but showed a preference for the surf grass *Phyllospadix torreyi.* They would continue to cling to any of these substrates, even when removed from the water. In an attempt to take advantage of this behavior, a variety of containers (Figure 2) for holding *Phyllospadix* and various species of red algae were floated under the lighted end of the Scripps Institution pier at the positions shown in Figure 1. The pier lights (three 200 W incandescent flood lamps mounted approximately 15 m above the water) apparently attracted pueruli to the pier, and the seaweed habitat traps provided convenient refuges in which they settled. The traps were retrieved and examined for pueruli every 4-6 days, providing a standard sampling system which could be operated continuously. The same types of habitat traps were also maintained on buoyed lines at several coastal locations in water 3-30 m deep, as discussed in a later section.

A variety of natural and artificial seaweed habitat trap designs, shown in Figure 2, were tested initially to develop a type most suitable for attracting pueruli. Included in the evaluation were several models of the "Witham" habitat design used by Witham et al. (1968) for collecting *P. argus* pueruli (Figure 2C). This trap was constructed of a synthetic fibrous material labeled "Conservation Web #200," manufactured by Minnesota Manufacturing and Mining Company.[3] The traps we developed and tested consisted of wood frames which contained either synthetic materials, e.g., burlap, foam rubber, nylon mop, and plastic screen and netting, or fresh natural seaweeds, held within either plastic cage sides (Figure 2A, B), or within net bags or wire screen (Figure 2D, E).

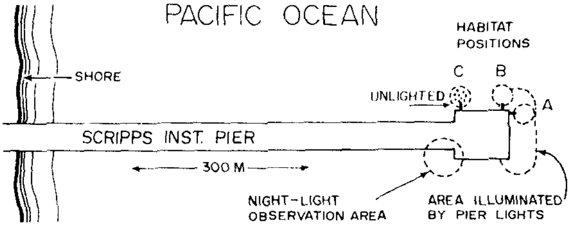

FIGURE 1.—Standard positions of puerulus habitat traps placed on the Scripps Institution pier, and the position from which night-light observations and collections of pueruli were made.

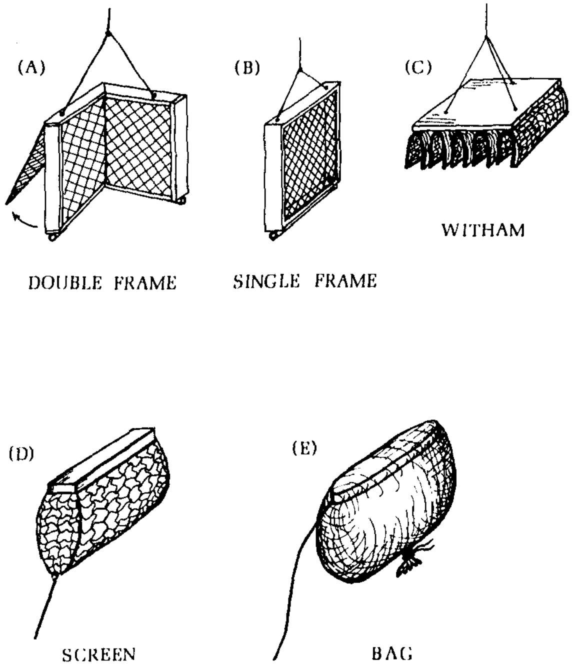

FIGURE 2.—Floating habitat trap designs employed in sampling puerulus larvae of *Panulirus interruptus.*

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

Suspension of the Habitat Traps

The strong surf and current conditions prevailing around the pier pilings required the development of a special system for suspending the habitat traps, as shown in Figure 3. This system allowed the trap to rise and fall during the tidal cycle, which has a vertical range of approximately 2.5 m, and in response to wave motion, thereby always remaining at the surface. The counterweight maintained a taut line and counteracted drag on the habitat trap caused by currents. No bottom anchor was necessary, thus eliminating problems of retrieval and fouling on kelp, and allowing the traps to be raised and lowered easily for examination. The traps also were held away from the pier pilings by the pole extension in order to prevent damage and entanglement.

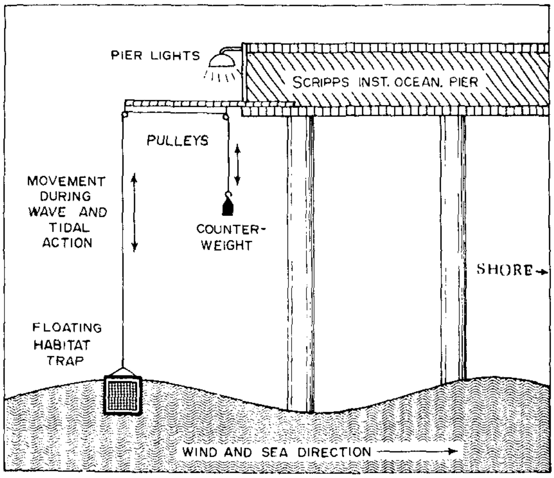

FIGURE 3.–The method employed in suspending habitat traps from the Scripps Institution pier.

Paired Neuston Nets

The results of night-lighting operations, discussed in a later section, suggested that the puerulus stage of *P. interruptus* swims within a few centimeters of the ocean surface. Thus, plankton or other nets towed below or near the surface probably would fail to catch this stage. Even surface tows made with a net breaking the surface might not be successful if it were trailed directly behind a vessel, because the "snow plow" action of the vessel might effectively push surface organisms away from the path of the net. Thus, paired neuston nets which could be mounted laterally on a small boat were developed to allow unobstructed surface water sampling, as shown in Figure 4. The presumed rarity of the puerulus stage required that these nets be of relatively large mesh size (5.0 mm) to allow reasonably fast towing speeds with a small boat (approximately 3 knots) and the filtration of large volumes of water. The short length and lateral position of the nets allowed their cod ends to be removed and emptied periodically without hauling the entire net from the water. The nets were towed with approximately 30% of the frontal area above water to ensure continual filtration of the top few centimeters of surface water, even during periods of low surface waves. The average frontal net area maintained submerged was approximately 0.7 square meter per net. Only rough estimates were made of the volumes and surface areas of water filtered during initial trials conducted during this study, as these were primarily concerned with evaluation of the sampler and with qualitative rather than quantitative results. The estimates of the water volume and surface area sampled were based on average boat speed and duration of the tow.

RESULTS

Night-Light Observations

Night-light observations were first conducted briefly in May 1968, and then resumed for a 2-mo period in September 1968. Night-light observations were also conducted again in the spring and summer of 1969, primarily to supplement information from the habitat traps also maintained during this period. The results of these observations, together with pertinent environmental data, are summarized in Table 1. During calm evenings in September 1968, pueruli were collected from the Scripps Institution pier at an average rate of approximately 4 per hour, with the highest rate reaching 12 pueruli collected within 90 min (8 per hour). No pueruli appeared during night-lighting conducted in October 1968, and further attempts were curtailed due to the onset of rough winter surf conditions which made the operation difficult. Night-lighting activities also were conducted at other San Diego localities during the period September-October 1968. These were: Quivira Basin in outer Mission Bay, Shelter Island in outer San Diego Bay, and the Imperial Beach pier. No pueruli were observed at any of these

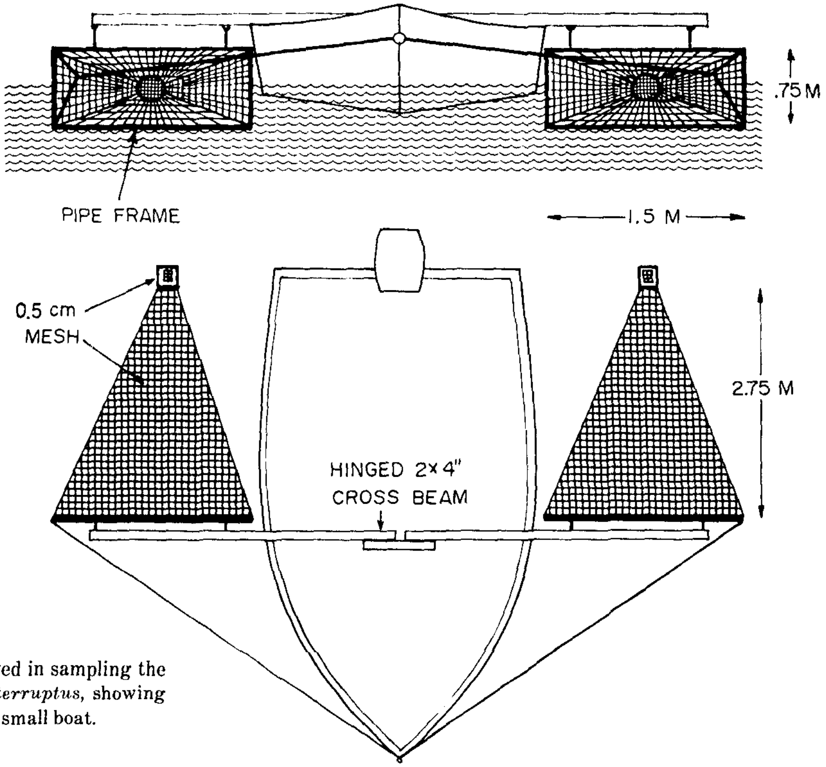

FIGURE 4.—Paired neuston nets employed in sampling the puerulus larval stage of *Panulirus interruptus*, showing the method used to deploy them from a small boat.

TABLE 1.—Results of night-light sampling for pueruli at the Scripps Institution pier and other San Diego localities.

Date	Number collected	Location	Time of sampling	Moon phase	Water temp. (°C)	Sampling period (min)	Suitability of conditions[1]
1968:							
May 15	0	Mission Bay	2000-2130	Full	16.0	45	Good
May 20	1	Scripps	2000-2130	Last Quarter	15.7	50	Fair
May 25	0	Mission Bay	1930-2030	New	16.4	60	Good
Aug. 28	9	Scripps	2130-2250	First Quarter	18.6	60	Good
Sept. 4	0	Imperial Beach	2030-2200	Full	20.7	80	Good
Sept. 7	4	Scripps	2200-2330	Full	20.0	40	Fair
Sept. 10	12	Scripps	2100-2230	Full—Last Quarter	20.5	90	Excellent
Sept. 16	3	Scripps	2000-2045	Last Quarter	20.7	40	Good
Sept. 26	4	Scripps	2000-2100	New—First Quarter	19.5	40	Fair
Oct. 2	0	Scripps	2230-2330	First Quarter—Full	18.3	50	Good
Oct. 10	0	Shelter Id.	2130-2250	Full—Last Quarter	18.5	80	Good
Oct. 20	0	Scripps	2200-2300	New	17.3	40	Good
Oct. 30	0	Scripps	2330-2430	First Quarter	16.8	30	Fair
1969:							
Apr. 5	0	Scripps	2030-2130	Full—Last Quarter	14.8	15	Poor
Apr. 20	0	Scripps	2130-2250	New—First Quarter	15.5	50	Good
May 7	0	Scripps	2030-2130	Last Quarter	15.9	20	Poor
May 15	0	Scripps	2130-2230	New	16.2	60	Good
May 23	6	Scripps	2145-2345	First Quarter	17.3	90	Good
June 4	3	Scripps	2200-2300	Last Quarter	18.1	30	Fair
July 10	14	Scripps	2100-2330	Last Quarter—New	20.5	90	Excellent
Aug. 7	6	Scripps	2130-2250	Last Quarter	21.5	70	Good
Sept. 12	4	Scripps	2210-2250	New	18.5	60	Fair
Sept. 22	0	Scripps	2030-2120	Full	18.0	20	Fair
Oct. 11	0	Scripps	2100-2230	New	18.0	50	Good
Oct. 20	0	Scripps	2000-2130	First Quarter	17.2	30	Fair

[1] The suitability of conditions for collecting pueruli was determined subjectively from general observations of current direction and velocity, wave height, and water clarity during the collecting period.

localities and work there was discontinued. Night-lighting observations during 1969 at the Scripps Institution pier provided a more complete picture of the apparent seasonal occurrence of pueruli, which first appeared in late May and were not observed after 4 September 1969.

These initial night-light studies allowed several interesting new observations on puerulus behavior. Previous investigators who reported that pueruli were occasionally attracted to night-lights (Harada 1957; Johnson 1960) presumed that the pueruli were lured off the bottom from rocky habitats where they had settled. However, this apparently was not the situation at the Scripps Institution pier for the following reasons.

The natural bottom substrate adjacent to the Scripps Institution pier for a radius of at least 500 m is entirely surf-washed sand. There is a small intertidal and subtidal rocky area approximately 500 m to the north, and an extensive rocky shoreline begins approximately 2 km to the south. While the pier pilings might afford a suitable habitat, we observed no pueruli or juveniles in several careful daytime and nighttime examination of the pilings, using scuba, during periods when there was active puerulus settlement in the habitat traps. In addition, direct observations of the free-swimming pueruli indicated that many individuals approached the light from a direction opposite that of the pilings. Perhaps most significant was the observation that the pueruli were seen swimming in only the top few centimeters of water; no individuals were ever seen approaching the light from a greater depth.

This opportunity to observe the free-swimming puerulus stage of *P. interruptus* thus demonstrated that, at least under these conditions, it is a surface-dwelling organism which occurs only in the top few centimeters of water. Consequently, the inconsistency or failure of standard plankton net tows to collect pueruli of this and other species probably is not due to the presumed benthic habits of this stage, but rather to improper sampling techniques. Only nets extending above the surface, and streamed parallel to the vessel's course with an unobstructed path, appear to be suitable. The likelihood of net avoidance accounting for previous failures seems minimal, as the pueruli of this species are relatively slow moving and easily captured in a hand held dip net, at least near a night-light.

Puerulus swimming speed in nature was measured by timing the passage of an individual between two lines suspended from a 2 m long, horizontally oriented pole, as it approached the underwater light. The mean swimming speed of six different pueruli under these conditions was 8 cm/s (range 6 to 9 cm/s). Individuals appeared to maintain this speed continuously, unless disturbed. In response to disturbance, they would spread their antennae and legs, sink slowly 5-20 cm, and then resume normal surface cruising with antennae held together and legs withdrawn. Illustrations of these swimming and sinking postures are shown in Figure 5.

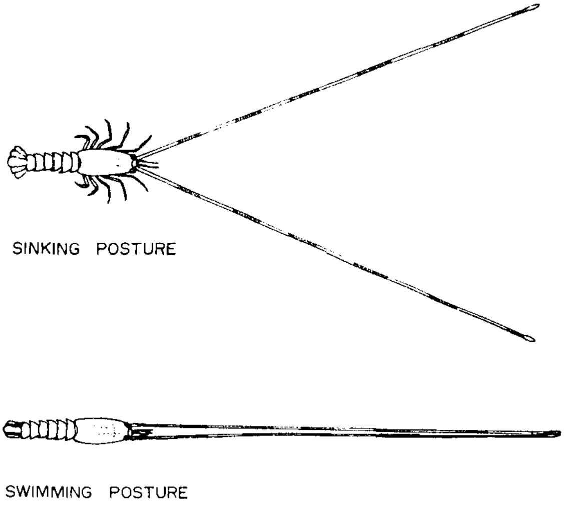

FIGURE 5.–Sinking and swimming postures of the puerulus larval stage of *Panulirus interruptus* as observed under a night-light.

Puerulus Pigmentation in Relation to Date of Settlement

Newly settled pueruli, or those collected during night-lighting, were always completely transparent. Pueruli held in open and closed system aquaria provided with *Phyllospadix* or other intertidal flora and fauna almost immediately began acquiring pigmentation, and this continued at a rapid rate. At temperatures of 18-20°C, pueruli would change from complete transparency to nearly complete pigmentation within 9-10 days, and would then moult into the first postpuerulus stage.

This occurred consistently among over 50 individuals we held in aquaria and observed systematically. Thus, the degree of pigmentation provided a reliable method of determining, within 1-2 days, the date of settlement. This technique provided a more accurate means of evaluating possible correlations between puerulus recruitment and changing environmental factors than by merely recording the date on which the habitat trap was examined, as done by Witham et al. (1968) and Sweat (1968). In his later study, Parker (1972) provided a more detailed description of the pigmentation and transformation of the puerulus and postpuerulus stages of *P. interruptus*.

Laboratory observations indicated that once the puerulus settled in a suitable substrate, its transformation into a postpuerulus proceeded without delay. However, a few individuals which were held in containers without fresh *Phyllospadix*, algae, or rocks containing epifauna, remained as transparent pueruli for 2-3 wk until death, suggesting strongly that the presence of such suitable habitat features is necessary to induce transformation to the postpuerulus stage.

After settlement, pueruli became photonegative and were never again seen swimming. In order to test the related question of whether or not a settled puerulus might desert a habitat trap upon its removal from the water, and thus produce unreliable trap catch data, one seaweed frame habitat trap and one Witham trap containing known numbers of pueruli were returned to the water for 5-10 min on two different occasions, and then retrieved. No individuals left either the Witham or seaweed traps. This, and the laboratory observations described above, indicate that the number of individuals found in a habitat trap probably is a reliable estimate of the number that settled there.

Comparison of Habitat Trap Types

Habitat traps were mounted either singly or in groups of two or three from one main support bar in order that at least six different types could be tested simultaneously from the three available Scripps Institution pier positions (position A, B, or C, as shown in Figure 1). The exact pier position and combinations of traps were alternated from time to time, as indicated in Table 2, in order to compensate for possible variations in unknown factors influencing puerulus settlement, such as current direction, eddies near the pilings, and differences in daytime or nighttime light intensities. The results of comparative habitat trap design studies conducted during the summer of 1969 are summarized in Table 2. These results indicate that all habitat traps containing natural seaweed proved markedly superior to the Witham artificial habitat trap for this species (Figure 2C).

Only 5 pueruli were collected by two Witham habitat traps ($\bar{x}$ = 2.5 per trap), while 97 pueruli were collected by four seaweed habitats ($\bar{x}$ = 24.2

TABLE 2.—Results of a comparison of the catch effectiveness of habitat traps suspended off the Scripps Institution pier. The catches of pueruli per trap are also recorded in terms of the specific location of the trap at the pier (a, b, or c). Positions A and B were lighted, while position C was unlighted, as shown in Figure 1. For descriptions of the habitat trap designs, see Figure 2 and text.

Date traps examined 1969	Duration of sampling period (days)	Number of pueruli collected in habitat traps						
		Seaweed habitat traps				Witham habitat traps		Total collected
		Double frame	Single frame	Bag	Screen	#1	#2	
June 14	6	—[1]	2 a	—	—	0 a	—	2
20	6	—	—	—	—	—	—	—
27	7	—	—	—	—	0 a	—	0
July 2	4	0	7 a	—	—	1 a	—	8
5	3	3 b	1 a	—	—	0 a	—	4
9	4	3 b	1 a	—	—	0 a	—	4
13	4	2 b	1 a	—	—	0 a	—	3
17	4	3 b	0 a	—	—	0 a	—	3
23	6	3 b	1 a	—	—	1 b	—	5
28	5	1 b	1 a	—	—	0 b	—	2
Aug. 4	6	23 b	2 a	—	—	1 b	—	26
6	2	2 b	1 a	—	—	0 b	—	3
10	4	1 a	4 b	0 c	0 c	0 c	0 b	5
16	6	3 a	8 b	1 c	0 c	0 c	0 b	12
27	11	2 a	12 b	1 c	1 c	0 c	1 b	17
Sept. 4	8	1 a	1 b	0 c	0 c	0 c	1 b	3
12	8	0 c	0 c	2 b	1 b	0 c	0 b	3
19	7	0 c	1 c	1 b	0 b	0 c	0 b	2
27	8	0 c	0 c	0 b	0 b	0 c	0 b	0
Oct. 3	6	0 c	0 c	0 b	0 b	0 c	0 b	0
Total		47	43	5	2	3	2	102

[1] Habitat trap not in position at this time.

per trap), when all were in continuous use during the same 90-day time period from June through September 1969 (Table 2). Comparison of these catch figures by a chi-square test for equality indicates that the mean catch of the seaweed traps was significantly higher than that of the Witham traps ($P < 0.05$). The Witham habitat trap was not effective, either when new or moderately fouled with a variety of sessile organisms, yet the natural seaweed habitat traps appeared to catch well regardless of the condition of the plant material. Variations in the abundance of pueruli throughout the summer and differences in settlement in the different habitat positions, as discussed in subsequent sections, did not allow specific comparisons to be made between results of the habitat trap designs listed in Table 2. Yet general comparisons indicate that there were no major differences in catch between these trap designs that are not attributable to the environmental causes discussed in subsequent sections below. However, the nylon bag habitat trap (Figure 2E) proved to be the best in terms of cost, ease of use, and durability. It also appeared to catch as well as the other types, although tests were begun too late in the final puerulus settlement season during which we sampled to verify this. Thus, the bag trap design is recommended for future studies of this nature, and was used by Parker (1972) in a later study.

Habitat Trap Success in Relation to Position on the Pier

A comparison of the catch results of the "double" and "single" frame seaweed habitat traps, as shown in Table 2, indicates that more pueruli were consistently collected from the B than the A position on the Scripps Institution pier (Figure 1), when either type of trap was placed there. A combined total of 65 larvae was collected in the B position, versus only 24 in the A position by these two traps during the same 82-day period from 2 July to 19 September. A comparison of these catch figures by a chi-square test for equality indicates that the catch at position B was significantly greater than at position A ($P < 0.05$). No explanation for this difference is apparent at the present time, but it seems to indicate that there may be subtle environmental effects which influence puerulus settlement in habitat traps to a greater extent than do variations in trap design.

Significance of Nocturnal Illumination of Traps in the Attraction of Pueruli

The strongly positive phototactic response exhibited by the puerulus stage during night-lighting observations suggested that nocturnal illumination may play an important role in the successful operation of habitat traps. To evaluate this, additional traps were maintained in an unlighted area of the Scripps Institution pier (area C in Figure 1).

The results, summarized in Table 3, indicate that during the period from 10 August to 29 September 1969, when each trap design was maintained at both the lighted (positions A and B) and nonlighted (position C) pier locations, all traps caught more larvae in the lighted positions. A total of 38 larvae were collected over 132 "trap-days" (1 trap in place for a 24-h period = 1 trap-day) in the lighted position, versus only 4 per 132 trap-days in the nonlighted position. Comparison of these total catch values by means of a chi-square test for equality indicates that the value for the lighted positions was significantly greater than for the unlighted one ($P < 0.05$). This suggests that noc-

TABLE 3.—A comparison of the number of pueruli caught in lighted and nonlighted habitat traps. For detailed descriptions of trap types, and lighted and nonlighted pier positions, see text and Figures 1 and 2.

	Lighted (positions A and B)			Nonlighted (position C)		
Type of habitat trap	No. individuals collected per trap	Sampling period (days)[1]	Catch per 20 trap-days	No. individuals collected per trap	Sampling period (days)[1]	Catch per 20 trap-days
Double frame	7	29	4.8	0	15	0
Single frame	25	29	17.2	1	15	1.32
Bag	3	15	4.0	2	29	1.38
Screen	1	15	1.32	1	29	0.68
Witham "a"	—[2]	—	—	0	44	0
Witham "b"	2	44	0.48	—	—	—
Mean catch per 20 trap-days			5.4			0.68

[1] Number of trap days during the period of 10 August to 29 September only (see Table 1).
[2] Habitat trap not in place.

turnal illumination plays a major role in the successful use of these habitat traps for pueruli of *P. interruptus*. The fact that no pueruli were caught in the unlighted habitat traps maintained offshore, as discussed in the next section, provides additional strong support for this conclusion.

Habitat Traps Maintained Offshore

Unlighted habitat traps of the "bag" and "screen" designs were anchored in water 3- to 15-m deep in the San Diego area off Point Loma, La Jolla, and off the northeast shore of Catalina Island, Calif., at the positions shown in Figure 6a, b. This was done to monitor the recruitment of pueruli at other locations along the San Diego coastline, and on the leeward side of a large offshore island, as well as to determine the importance of lights in attracting pueruli by comparing these unlighted traps with those placed under the Scripps Institution pier lights. The traps placed offshore were checked and refilled with fresh *Phyllospadix* and red algae every 10-15 days during August and September 1969. Many were lost, apparently because of entanglement with kelp and boat propellers. However, the large number maintained successfully failed to collect any pueruli, despite the fact that puerulus settlement at the Scripps Institution pier was relatively high during this same period. The four traps maintained at Catalina Island were situated directly above a shallow rocky area, approximately 2-6 m in depth, where we had observed many small first year juvenile lobsters the previous winter. We presumed that the presence of these young juveniles indicated that this was an area of high puerulus recruitment. Thus, failure of the unlighted traps to collect pueruli at this location was particularly surprising.

The failure of these offshore habitat traps may have been due not only to the lack of nocturnal illumination, but also to the presence of large quantities of *Phyllospadix* and algal flotsam in the areas where they were maintained. The probability of a puerulus settling in a seaweed habitat trap under such conditions would be small, considering the large volume of seemingly equally suitable patches of floating surfgrass and algae present in these areas. In contrast, relatively few masses of plant flotsam of this kind were observed in the area around the Scripps Institution pier.

In an attempt to evaluate this, many clumps of floating *Phyllospadix* were collected and examined for pueruli while deploying and checking the offshore habitat traps. No pueruli were found in this manner, but only a relatively small percentage of this material was examined relative to that present, thus leaving the question open to further investigation.

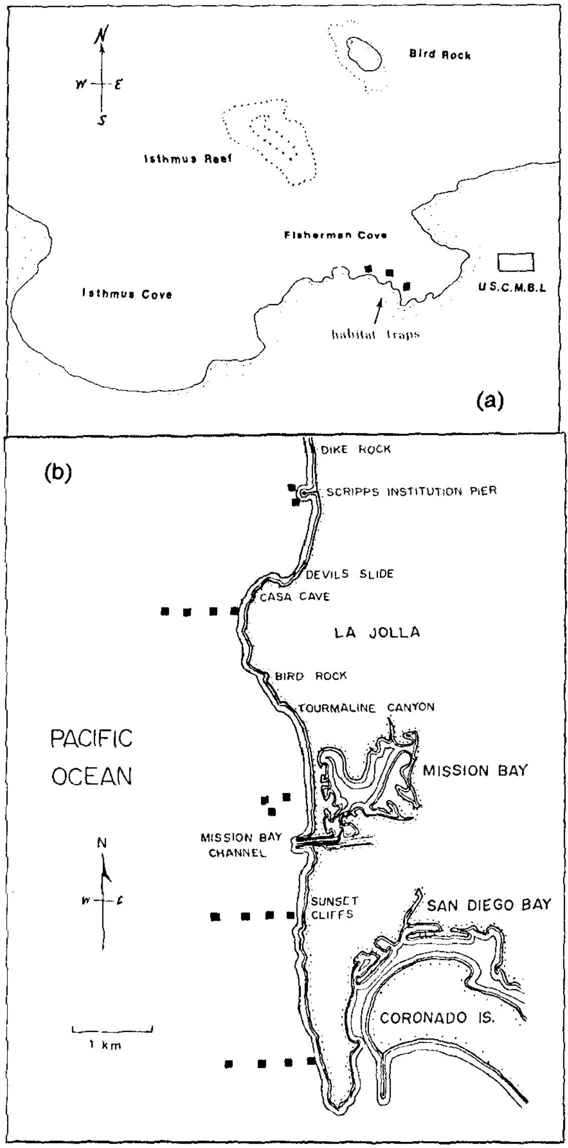

FIGURE 6.—Locations of sampling areas off northeastern Catalina Island (a) and San Diego (b) for puerulus and early juvenile *Panulirus interruptus*.

Neuston Net Sampling

Semiquantitative sampling with the paired neuston nets was initiated late in the study, during the period 3 September to 12 October 1969 (Table 4). The results of the habitat trap collections (Table 2) suggest that these towing operations were conducted during a period of very low puerulus abundance, yet two pueruli were collected during two separate towing efforts. Unfortunately, it was not possible to complete the development of these nets and begin sampling operations during the summer period of peak puerulus abundance.

TABLE 4.–Results of puerulus sampling with paired neuston nets.

Date 1969	Time	Surface area sampled (m²)[1]	Water volume sampled (m³)[1]	San Diego sampling localities	Number collected
3 Sept.	1400-1500	800	400	Mission Bay	0
10 Sept.	2000-2100	800	400	Mission Bay Channel	0
10 Sept.	2130-2230	800	400	Mission Bay Channel	1
20 Sept.	1800-1840	500	250	Off Pacific Beach	0
20 Sept.	1900-1930	300	150	Off Pacific Beach	1
7 Oct.	2000-2100	800	400	Off Pacific Beach	0
12 Oct.	1200-1330	1,000	500	Mission Bay Channel	0

[1]Estimated from average boat speed and duration of tow.

Concurrent studies of the distribution and abundance of the phyllosoma larval stage of *P. interruptus* in the same inshore areas, using standard 1 m and larger conical nets in surface and oblique towing patterns, failed to catch any pueruli (W. E. Hazen and J. H. Rutherford, pers. commun.). In addition, considering that Johnson (1956, 1960) obtained only a few pueruli during 7 yr of extensive sampling with surface and oblique hauls of a 1-m conical net, our preliminary results suggest that use of this neuston net system probably is a more effective sampling technique and should be thoroughly evaluated in future studies. These results also strengthen the argument that the puerulus is pelagic, occurs at the surface, and is a temporary member of the neuston community.

Relationship of Puerulus Settlement to Environmental Factors

Efforts to relate the influx of pueruli in major environmental factors, such as temperature, salinity, and lunar phase, were complicated by lack of information concerning other unmeasured or unknown variables which may have subtle effects on the settlement of pueruli in the habitat traps. These may include specific wave characteristics, current velocity and direction, and water turbidity. Therefore, the apparent low abundance of pueruli during some periods might be due to their failure to settle in the habitat traps, rather than their absence from coastal waters. Variations in surface salinity levels of water masses along the open coast when our sampling was conducted were very slight. Consequently, the influence of this factor probably was negligible and showed no obvious relationship to puerulus settlement, based on data available for the area of the Scripps Institution pier. Variations in wave heights and surf conditions occurring at the Scripps Institution pier during the summer also were relatively small. The range in height of swells recorded at the pier was 0.3-0.9 m (1-3 feet), and showed no obvious pattern in relation to puerulus settlement. However, the following general relationships between puerulus settlement and environmental conditions seem apparent.

Seasonal Periodicity

The results of night-lighting during 1969 (Table 1), and habitat trap sampling conducted in 1969 (Table 2) are presented together in Figure 7. These data indicate that the pueruli of *P. interruptus* began to appear in nearshore San Diego waters during late May, and occurred there continuously until mid-September, apparently reaching their greatest abundance during the first week of August. The habitat traps could not be maintained during rough winter surf conditions, and occasional night-light efforts during the winter were unsuccessful, so we were not able to establish conclusively that pueruli are absent from nearshore waters between October and May. However, evidence presented by Johnson (1960) on the seasonal periodicity of the later phyllosoma stages of *P. interruptus*, which are abundant only during the period from January to June, suggests that there would be no major influx of pueruli during the winter months, although a small number of individuals might be present throughout the year.

Relationship to Water Temperature

A comparison between surface water temperatures and puerulus trap catches obtained at the Scripps Institution pier indicates that the

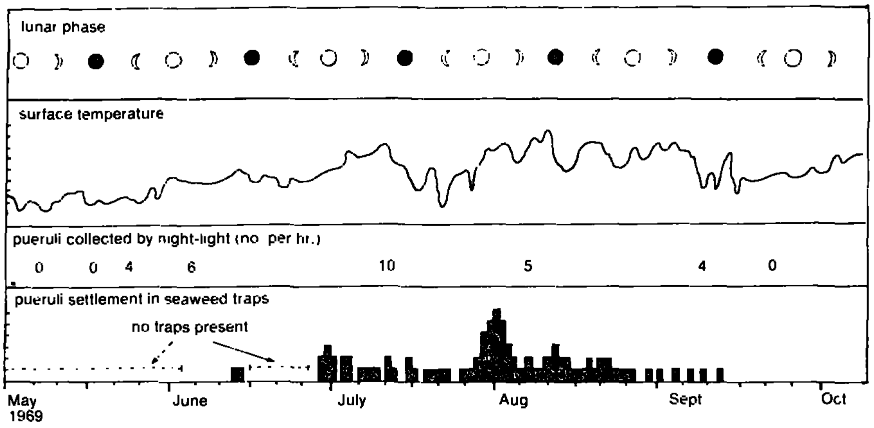

FIGURE 7.—Relationship of puerulus settlement to lunar, temperature, and seasonal cycles. The habitat trap catches are presented as catch per unit effort, and represent the total combined catch of two seaweed traps (primarily the single and double frame designs, Figure 2) maintained in the lighted pier positions (a and b). The date of original settlement for each puerulus was estimated within 1 to 2 days by its degree of pigmentation. Temperature data are from Scripps Institution pier records.

prevailing influx of pueruli corresponds with the seasonal period of highest temperatures, as shown in Figure 7. The peaks of puerulus settlement occurring during the first weeks of July and August also appear to correspond with periods of rising water temperatures. However, another possible interpretation of the settlement patterns shown in Figure 7 is that the low abundance of pueruli observed during the period of 10-25 July may have been caused by an influx of cold water originating from local submarine canyon upwelling, which occurs periodically. Such a cold upwelling water mass would not be expected to contain any pueruli if the surface-swimming habits attributed to this stage are correct, and could effectively prevent pueruli in warmer water masses from entering the pier area we sampled.

Lunar Perdicity

Studies by Witham et al. (1968) and Sweat (1968) of *P. argus* pueruli in Florida and by Phillips (1972) of *P. longipes cygnus* pueruli in Australia determined that puerulus settlement was highest during the new moon phase and did not occur at all during full moon periods. The abundance of *P. interruptus* pueruli, on the other hand, did not show any evident relationship to lunar phases. On two occasions during the first parts of July and August, there were apparent peaks in puerulus abundance during the full moon phase, as shown by the habitat trap results in Figure 7. Night-light and habitat trap collections and their relationship to lunar phases are summarized in Table 5. These data indicate that there were no lunar periods when pueruli of *P. interruptus* were not present and did not settle, and thus that they apparently do not respond to lunar cues, or at least not in the same manner as do species studied elsewhere.

Witham et al. (1968), Sweat (1968), and Phillips (1972) were unable to determine whether the absence of pueruli from their habitat traps during full moon periods was due to their absence from the area or their avoidance of the traps. The fact that pueruli of *P. interruptus* were present and settled in our habitat traps directly under the bright lights of the Scripps Institution pier in-

TABLE 5.—The relationship between lunar phases and puerulus abundance, as determined by habitat trap and night-light results. Total catches, given in detailed form in Tables 1 and 2, are presented below as catch per unit effort.

Lunar phase (eight equal divisions)		Habitat trap (mean catch/hour)[1]	Night-light (mean catch/hour)[2]
Full moon	(1)	5.0	3.0
	(2)	2.5	4.0
Last quarter	(3)	1.7	4.0
	(4)	1.7	10.0
New moon	(5)	2.0	1.0
	(6)	1.5	3.0
First quarter	(7)	1.8	6.5
	(8)	1.0	0.0

[1] Based on catches of the single and double frame traps only.
[2] Periods of poor conditions (i.e., unsuitable for observing pueruli) were excluded from calculation of the mean.

dicates that, at least for this species, illumination is not an inhibitory factor. In fact, it may serve as a stimulus for settlement.

In this regard it is important to note that persistent stratus overcast in the southern California coastal zone during the summer months results from upwelled water coursing southward from Point Conception. Thus, normal background illumination from the moon and stars generally is eliminated, although sky glow is present near major coastal cities. Consequently, at our sampling site the prevailing overcast and nocturnal illumination from the Scripps Institution pier lights could have masked any lunar effect, resulting in what we observed, puerulus settlement in traps during all moon phases.

Duration of the Puerulus Stage

Essentially nothing is known about the duration of the puerulus stage of any spiny lobster species. Sheard (1949) suggested that the puerulus of the western Australian spiny lobster, *P. longipes cygnus*, lasts for 2-3 wk, but offered no supporting evidence.

April was consistently the period of greatest abundance for the last phyllosoma stage (stage 11) of *P. interruptus*, based on evidence obtained by Johnson (1960) in extensive sampling during the period 1949-1957, as summarized in Figures 8 and 9. Most of the late stage phyllosoma larvae he collected were taken at stations 160-320 km (100-200 miles) offshore (Figure 9). Our data indicate that the greatest abundance of pueruli in coastal waters during 1969 was in early August, approximately 3½ mo after this peak in the abundance of stage 11 phyllosomes. Assuming that the duration of the eleventh phyllosoma stage extends for a period of 1 mo, and that shoreward migration is accomplished by the puerulus, rather than by the last phyllosoma larval stage (see subsequent discussion), then this suggests that the puerulus stage of *P. interruptus* may have an average duration of approximately 2½ mo. This timing is represented diagrammatically in Figure 8. Thus, a period of 2-3 mo appears to be a reasonable estimate for the average duration of the puerulus stage.

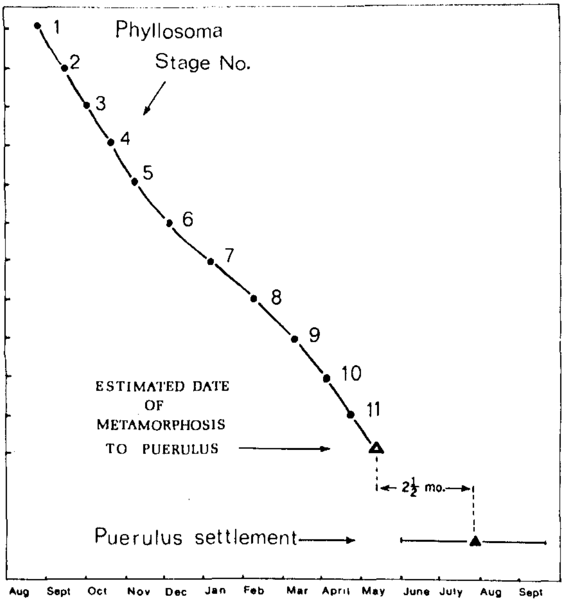

FIGURE 8.–Comparison of seasonal occurrence and dates of greatest abundance of the phyllosoma and puerulus larval stages. Data on the phyllosoma stages are from Johnson (1960).

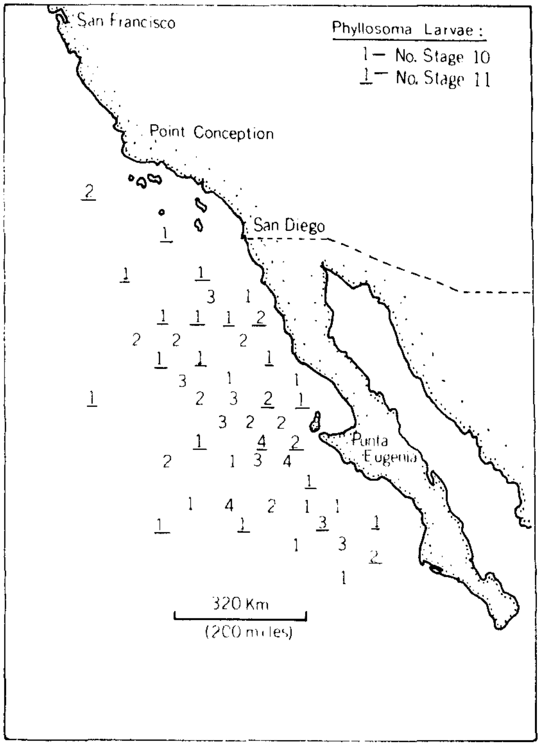

FIGURE 9.–Offshore distribution of the late stage phyllosoma larvae (stages 10 and 11) of *Panulirus interruptus* during the period from 1949 to 1955, as reported by Johnson (1960).

DISCUSSION

Mode of Life of the Puerulus Stage

Johnson (1960) and Lindberg (1955) speculated that the puerulus of *P. interruptus* is a benthic form, largely because it occurs so infrequently in standard net tows. However, the results of this study strongly suggest that it is a pelagic form, and in particular a member of the surface-dwelling neuston. Several lines of evidence support this conclusion. Our observations of many free-swimming pueruli which were attracted to night-lights revealed that the pueruli always swam in the top few centimeters of surface water, and no individuals were ever observed moving toward the light from deeper water. Pueruli were readily collected in habitat traps floating at the surface. However, the occurrence of pueruli at greater depths cannot be ruled out on the basis of habitat trap evidence alone because the traps were not maintained at greater depths. Although preliminary and very limited, our surface sampling with neuston nets yielded a much higher catch per unit effort than did standard near-surface and oblique tow sampling methods employed by previous investigators.

The puerulus stage of *P. interruptus* also has specialized physical characteristics which suggest that it is adapted to a pelagic existence. These include: 1) heavily setose pleopods and a streamlined body for efficient, forward swimming; 2) a transparent body completely devoid of pigmentation; and 3) extremely long, delicate antennae which appear unsuitable for a benthic existence because they quickly break off upon settlement. In addition, at the time the puerulus moults into the first postpuerulus stage, it loses the setose pleopods and acquires stronger antennae, an expanded cephalothorax, and walking ability typical of later demersal stages. In fact, pueruli we collected and held in aquaria were never observed walking upon the substrate, instead only clinging to algae or crevices in rocks and shells. A more detailed description of this transformation process from puerulus to postpuerulus was developed in a subsequent study by Parker (1972).

Both Witham et al. (1968) and Phillips (1972) reported that, in comparative tests between habitat traps maintained on the surface and traps anchored 1-4 m below the surface, all but a few pueruli of *P. argus* and *P. longipes cygnus* were collected in those at the surface. Phillips collected only 1 out of 38 pueruli in traps at 4-m depth, and Witham collected 12 from one trap anchored on the bottom in water 1 m deep, as compared to an average of 27 pueruli in surface traps located nearby.

Sweat (1968) utilized a multiple plankton net array for studying the depth preference of *P. argus* pueruli in the Florida Keys area. This system consisted of three conical plankton nets mounted from a bridge across a shallow channel connecting Florida Bay with the Atlantic Ocean. The nets were suspended at the surface, at mid-depth (1 m), and on the bottom (2.3 m), and were operated for 2-h periods within the new moon phase during evening flood tides. The largest proportion of the pueruli were collected by the mid-depth net (116 at the surface, 418 at 1 m, 61 at 2.3 m depth). However, this may have been due to the particular conditions in the channel, including its shallow depth, water turbulence, and the possibility that the pueruli were in the process of settlement at the time of sampling.

In general, these observations by Sweat (1968), Witham et al. (1968), and Phillips (1972) agree with ours on *P. interruptus*. The pueruli of these species seem to be restricted primarily to the ocean surface, at least just prior to settlement.

The Functional Significance of the Puerulus Stage

On the basis of morphology and our observations of its behavior, the puerulus stage of *P. interruptus* appears to be well adapted for directed, forward swimming, as shown in Figure 5, rather than for the passive, pelagic existence apparently exhibited by all phyllosoma larval stages of spiny lobsters. What, then, is the purpose of this directed swimming? A possible answer is suggested by considering the early life history of the scyllarid lobster, *Scyllarus americanus*, which also has a phyllosoma larval stage but no transitional puerulus stage, moulting instead directly into a nonswimming, benthic juvenile (Robertson 1968). Some other scyllarid species have a transitional form called a puerulus or, more properly, a nesto stage. The phyllosoma larval period of *S. americanus* is quite short (4-5 wk), thereby allowing the larvae a much greater chance of remaining near the shallow coastal areas suitable for later demersal life. In contrast, the phyllosomes of palinurid lobsters and other species of scyllarids may be carried several hundred kilometers out to sea during their typical 5-10 mo larval existence. Obviously, the larvae must return not only to the coastal area, but also to very shallow nearshore zones if they are to transform and become established as demersal juveniles.

Previous investigators (Lindberg 1955; Johnson 1956, 1960, 1971; Saisho 1966; Sims and Ingle 1966; Lazarus 1967; Chittleborough and Thomas 1969; Chittleborough 1970) have postulated for several species that this recruitment in nearshore waters takes place during the phyllosoma stage, possibly through the action of countercurrents, upwelling, and eddies. Several studies, particularly those of Johnson (1960) and Chittleborough (1970), have shown clearly that large numbers of late stage phyllosoma larvae do remain well within the coastal areas in which the earlier larval stages occur. Evidence presented by Johnson (1960) also has shown that hydrography plays a major role in retaining a supply of late stage phyllosomes, and presumably pueruli, within reasonable distances from the coast. The presence, within one net haul, of several different phyllosome stages that must have been produced months apart, and the presence of late stage phyllosomes at the same locality, is good evidence that mixing processes and retaining eddies prevent wholesale flushing of these larvae from the coastal area. However, the late stage phyllosomes seem to be concentrated primarily in areas 50-250 km offshore, and the specific mechanism of onshore movement and recruitment has not been demonstrated.

If there were major active or passive movements of late stage phyllosomes toward shore, then one would expect to find relatively large numbers of them in shallow, inshore waters as well, or at least a trend in this direction. Most of the sampling reported by Johnson (1956, 1960) was conducted in waters 8 or more kilometers (≥ 5 miles) offshore. However, studies of the distribution and abundance of phyllosoma larvae of *P. interruptus* in San Diego waters much closer inshore by W. E. Hazen and J. H. Rutherford (pers. commun.) during the summer months of 1969-1970, employing surface and oblique net tows, failed to collect any individuals older than stage 2. This suggests that the later stages occur either many kilometers offshore, as observed by Johnson (1956, 1960), or are concentrated in unknown areas.

For lack of evidence to the contrary, it has also been suggested that these phyllosoma larvae occurring far offshore are lost to the population and must perish. For similar reasons, Lindberg (1955) and Johnson (1960) have speculated that when these phyllosomes moult into the puerulus stage, the puerulus quickly settles to the bottom while still in deep water. Presumably, some of these are then able to migrate onshore to the shallow coastal nursery areas as benthic puerulus or postpuerulus forms.

However, in light of our behavioral observations on both pueruli and juveniles, another more likely explanation is that the puerulus stage may have evolved specifically for this purpose of recruitment. These observations suggest to us that the puerulus is a transitional, pelagic stage specifically adapted for directional swimming, and that it is capable of returning by active means to nearshore nursery areas suitable for settlement, thereby fulfilling the key role in recruitment. During this process, the surface-swimming and associated positive phototactic behavior of the puerulus stage probably aid it in locating the shallow nearshore areas which our related observations suggest are required as nursery grounds for the early juvenile stages.

Exactly how important a role the puerulus stage plays in the recruitment of the demersal population probably depends on three factors: 1) the degree of "assistance" contributed previously by the late phyllosoma stages which may move actively, e.g., by vertical migrations, into shoreward-directed currents or eddies; 2) how effective the puerulus is in travelling over long distances, with regard to both swimming speed and endurance; and 3) how well the puerulus can navigate, considering the fact that aimless wandering or swimming away from the coast would markedly reduce its probability of survival.

It seems reasonable to expect that the puerulus can swim nearly continuously, as other nektonic crustaceans, such as euphausiids, apparently do. If so, our estimate of an 8 cm/sec average swimming speed for the puerulus indicates it has the potential to travel approximately 7 km (4.3 miles) per day, or about 500 km (350 miles) during the period of 80 days estimated as the approximate average duration of this stage. Thus, the 160-320 km (100-200 mile) distance from shore at which Johnson (1960) found most late stage *P. interruptus* phyllosomes (Figure 9) could be within the basic swimming capabilities of the puerulus stage, even if part of the time was spent swimming against surface currents or in an inactive state.

The current patterns off the southern California and Baja California coasts are complex, and have been studied extensively (see, for example, Johnson 1956, 1960; Wyllie 1966). During the summer months the California Current system has a generally southward trend, but displays retaining eddies and a net northward onshore drift in the northern range of *P. interruptus* larval distribution near the southern California coast and adjacent Channel Islands. There is a net southerly or offshore drift for water masses off most of Baja California. Even the apparent swimming capabilities of the puerulus stage probably would not allow it to move against these strong, offshore surface currents, particularly because an object in the surface waters would be vectored at a 45° angle, or westwardly, to the wind and current forces.

As a specific example of this problem, review of mean geostrophic flow at the surface off California and Baja California for the months of June-September during the typical period 1950-1964 (Wyllie 1966) reveals that there was a net surface transport southward from Point Conception to Cabo San Lucas offshore from approximately 80-320 km (50-200 miles). Northward flow near shore during these summer periods occurred only in the Southern California Bight (San Diego to Ventura), while net offshore transport apparently occurred from Bahia San Quintin south to Cabo San Lucas as a precursor to the California Current Extension.

Thus, it appears very likely that a majority of the late stage phyllosoma and puerulus larvae in the surface layers in this region, more than about 40-95 km (25-60 miles) offshore, depending on variations in the current system, were swept seaward by geostrophic flows which averaged greater than 46 cm/sec (0.9 knots) during this typical 15-yr interval. Such individuals undoubtedly are lost to the population. On the other hand, individuals present closer to shore, or in retaining eddies near the Southern California Channel Islands and the shallow Bahia Sebastián Vizcaino-Isla Cedros area (Johnson 1960), are within distances and ocean surface conditions which would allow their nearshore recruitment by directed swimming of the puerulus stage.

The Significance of *Phyllospadix* in the Settlement of the Puerulus Stage

The strong preference by the puerulus stage for the habitat traps containing *Phyllospadix torreyi*, as compared to generally similar synthetic material in the Witham traps, seems particularly significant in view of the fact that both Serfling (1972) and Parker (1972) discovered numerous early juvenile stages primarily in areas which had thick growths of this surfgrass. Comparative evaluations of habitat traps filled with *Phyllospadix* and other substrates, such as giant kelp (*Macrocystis pyrifera*) fronds and holdfasts, the eelgrass (*Zostera marina*), and *Mytilus* clumps, might prove useful as a means of improving collection success with the traps.

Preference tests involving various substrates typical of different nearshore habitats might also suggest other areas of natural puerulus settlement. In this regard, however, substrate preference tests of the puerulus and postpuerulus stages conducted in the laboratory by Parker (1972) suggest that these stages favor *Phyllospadix* over *Macrocystis*, *Zostera*, several species of red algae, sand, and rock.

Evaluation of the Natural Seaweed and Artificial Habitat Traps

In comparative tests conducted by Witham et al. (1968), their Witham habitat trap proved somewhat more successful than two other seemingly poor refuges, a tire and a shingle (102 versus 77 and 57 pueruli collected, respectively, over a 10-mo period). Phillips (1972), studying *P. longipes cygnus* in Australia, found that his artificial seaweed habitat trap design collected more pueruli than a modified Witham trap, but only by a factor of approximately two. In contrast, the results of our comparative evaluations (Table 2) indicate that the average number of pueruli caught by the two lighted natural seaweed habitat traps (single and double seaweed frame) was 47 per trap, while on lighted Witham artificial substrate trap caught only 5 pueruli over the same time period and at the same location. This suggests that the natural seaweed trap design was approximately nine times more effective than the Witham trap. Secondly, the lighted habitat traps, regardless of the design, caught more pueruli than did nonlighted ones at the Scripps Institution pier during the same time period (33 and 7 pueruli respectively), suggested that a lighted trap was approximately four to five times more effective than an unlighted one. Thus, the system developed in this study, utilizing a combination of both nocturnal illumination and natural seaweed, clearly is much more effective in collecting pueruli of *P. in-*

terruptus than the nonlighted artificial habitat system utilized by Witham et al. (1968).

This suggests that natural seaweed habitat traps filled with native flora characteristic of juvenile habitats, in combination with nocturnal illumination, could prove to be a more successful means of sampling the pueruli of other spiny lobster species as well. If so, use of this modified sampling technique might indicate that the abundances of *P. argus* pueruli in Florida and those of *P. longipes cygnus* in Australia actually are much greater than previously estimated by Witham et al. (1968), Sweat (1968), and Phillips (1972).

Implications for Aquaculture and Fishery Management

If the small numbers of pueruli captured during this study are representative of puerulus availability throughout the geographic range of *P. interruptus*, large-scale collecting of this stage for purposes of aquaculture and restocking is not feasible and probably could not be justified. However, other locations, particularly those closer to the center of adult and larval concentrations, such as the Bahia Sebastián Vizcaino-Isla Cedros area off Baja California (Figure 9), should be investigated as potential sites for such large-scale collecting operations, as well as for purposes of locating the primary areas of puerulus settlement.

It also seems reasonable that the habitat trap collecting system developed in this study, if standardized and employed on a wider geographic scale, could prove useful for monitoring fluctuations in year class recruitment of pueruli, and thereby provide a means of predicting fluctuations in the size of the demersal population in following years. For example, an extension of our study by Parker (1972) during the years 1970-71 indicates that puerulus settlement at the Scripps Institution pier was much less than we observed during the same months in 1969. If this reduced recruitment was representative of a wider geographic area, then the size of the adult population available to the commercial fishery within the succeeding 5-8 yr might be expected to show corresponding changes.

SUMMARY

Basic ecological and behavioral information was obtained about the recruitment process, habitat preferences, and general abundance of the puerulus larval stage of *Panulirus interruptus*.

Pueruli of *P. interruptus* exhibit a strong positive phototactic response, and could be lured to a bright underwater night-light from the surface water surrounding the Scripps Institution of Oceanography pier.

Direct observations of free swimming pueruli by this method demonstrated that this stage is typically pelagic rather than benthic, and swims at the surface in a continuous and directed manner. Estimates of swimming speed were obtained.

The surface swimming behavior of this stage indicates that it probably can be properly sampled quantitatively only by large nets towed horizontally at the surface. This may explain why few pueruli have been taken by other conventional sampling methods. Paired neuston nets were developed specifically for this purpose and pueruli seemed to be sampled effectively in this manner during preliminary evaluations.

Puerulus larvae also were collected effectively in floating habitat traps containing the surfgrass, *Phyllospadix torreyi*. A variety of natural seaweed habitat trap designs were tested, and all appeared to be about equally effective in collecting pueruli; however, a nylon bag habitat trap proved best in terms of cost and durability. All natural seaweed habitat traps were markedly superior in collecting pueruli compared to the Witham habitat trap design, formed of synthetic fibrous material.

Habitat traps maintained under the lighted end of Scripps Institution pier collected many more pueruli than those not subject to such artificial illumination. The failure of habitat traps placed offshore to collect any pueruli may have been due to the availability of abundant seaweed flotsam in the areas where they were maintained, as well as lack of artificial illumination. Both the presence of intertidal plants (particularly *Phyllospadix*) and nocturnal illumination appear to play significant roles in the settlement of puerulus larvae in habitat traps.

The results of night-lighting and habitat trap sampling indicate that off San Diego, Calif., the seasonal influx and settlement of puerulus larvae is continuous, beginning in May and ending in September.

Estimates based on a comparison of the peak periods of abundance for pueruli and the preceding final phyllosoma larval stage suggest that the puerulus stage of *P. interruptus* has a duration of approximately 2½ mo. This is followed by settlement in shallow water and transformation to a benthic, postpuerulus form.

Based on observations of its surface swimming behavior and capabilities, preference for plant covered substrates, settlement behavior, and morphology, the puerulus appears to be a transitional, pelagic stage specifically adapted for directional swimming, whose function is to return from offshore by active means to nearshore areas suitable for settlement. Thus, it probably occupies the key role in recruitment.

The seemingly low abundance of pueruli in the southern California areas sampled suggests that it would not be practical or beneficial to attempt large collections there for purposes of aquaculture and restocking. However, other locations, including those closer to the center of the geographical range, should be investigated as potential large scale collecting sites.

Employed in a standardized manner, the habitat trap system developed in this study could prove useful in locating primary areas of puerulus settlement and in monitoring fluctuations in year class recruitment.

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