ON THE DISPERSAL OF LOBSTER LARVAE INTO THE EAST PACIFIC BARRIER (DECAPODA, PALINURIDEA)

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ABSTRACT

The seaward drift of phyllosoma larvae of lobsters occurring along the coast and adjacent islands of the eastern tropical Pacific Ocean was studied from plankton collections made jointly by the Scripps Institution of Oceanography, Tuna Oceanography Research Program, and the National Marine Fisheries Service, La Jolla, Calif.

Numerous samples taken with trawl and plankton nets were made across the Equatorial current system in two areas: lat. 15°N-5°S, long. 115°-125°W, and lat. 5°N-15°S, long. 95°-115°W. Many late developmental stages of *Panulirus penicillatus* and *P. gracilis* and a few *Scyllarides astori* were found, all apparently having drifted mainly with the South Equatorial Current over a distance of 1,800 to 2,000 or more nautical miles from their likely origin, the Galapagos Islands or the coast of Central America. A few larvae were found in the North Equatorial Countercurrent. This is at times a possible route for return to the adult habitat, but it is doubtful that any of the larvae that have drifted to the most western survey area will be returned by countercurrents in time for metamorphosis or that they can successfully negotiate the remainder of the expanse of the East Pacific Barrier to reach the mid-Pacific islands.

The present report is essentially a follow-up of a previous survey in which a large plankton collection made by the multiship eastern tropical pacific (EASTROPAC) Project in 1967-68 was used in part to ascertain the systematics and geographic distribution of the pelagic phyllosoma larvae of all of the spiny lobsters (Palinuridae) and slipper lobsters (Scyllaridae) known to inhabit the west coast and offshore islands of Central America, Colombia, and Ecuador (Johnson, 1971). In that survey an extensive area was covered along the coast and seaward both north and south of the Equator to about long. 126°W. It therefore forms the basic groundwork drawn upon in the present report dealing with the phyllosoma larvae taken during a more restricted offshore survey within the same area by the Scripps Tuna Oceanography Research Program (STOR) in cooperation with the National Marine Fisheries Service at La Jolla, Calif., and Honolulu, Hawaii. This offshore "skipjack survey" was designed and initiated in 1970 to study the migrations of young skipjack tuna, *Katsuwonus pelamis*, in the eastern tropical Pacific Ocean (Williams, 1971, 1972). A comprehensive review of the current system and water masses so important to pelagic larvae of the area is given by Wyrtki (1967).

From Point Conception southward to the Gulf of Guayaquil, Ecuador a total of four species of palinurid and two species of scyllarid lobsters occur. In the present survey only the larvae of *Panulirus penicillatus* (Olivier, 1811), *P. gracilis* (Streets, 1871), *P. inflatus* (Bouvier, 1895), and *Scyllarides astori* Holthuis, 1960 were found as expatriate larvae from the coast or coastal islands. *Panulirus interruptus* (Randall, 1840) occurs off the coast of southern and Baja California, too far north for its larvae to be expected to enter into the current system covered here except as rare stragglers in the North Equatorial Current. *Evibacus princeps* Smith, 1869 (the second scyllarid) although common to the eastern tropical Pacific, apparently has a larval period too short to be carried far from the coast (Johnson, 1971). The larvae of *P. gracilis* and *P. inflatus* are difficult to separate specifically if the fourth pereiopods have been lost. However, adults of only *P. gracilis* occur in the southern range including the Galapagos Islands and all but two larvae could be referred to that species. The larvae of *Jasus frontalis* (H. Milne Edwards, 1837) and *Scyllarus delfini* (Bouvier, 1909), the two lobsters found in the Juan Fernandez Islands off Chile, were not found in the equatorial currents or in the Peru Current to lat. 24°S during the EASTROPAC survey and none were taken in the present survey.

The duration of the phyllosoma larval period as derived from studies of different species in

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Manuscript accepted December 1973.
FISHERY BULLETIN: VOL. 72, NO. 3, 1974.

nature indicate about 8 to 11 mo for palinurids (Johnson, 1960; Lazarus, 1967; Chittleborough and Thomas, 1969). In some scyllarids shorter periods are indicated (Saisho, 1962; Robertson, 1968), but in others, including *Scyllarides astori*, a length comparable to that of palinurids is suggested by the wide dispersal of the larvae.

These long drifting periods provide ample time for far and wide dispersal. Coincident with this, the number of larvae caught in a plankton tow is always small especially for the later stages and this precludes close statistical analysis for short surveys. But the presence of even small numbers of larvae when scattered over a large area or period of time are significant in indicating major outlines of the type of drift and dispersal by currents from adult spawning areas.

PROCEDURE

In view of the scarcity of larvae and the presence of only later developmental stages VI-XI (the final phyllosoma stage) in far offshore waters, the collections most generally useful were those from nets filtering large quantities of water: a 15 × 15 m mid-water trawl with a section of 3-mm bar mesh and towed obliquely in steps from 100 to 0 m or from 30 to 0 m for about 1 h 30 min; and a Blackburn micronekton net 5.8 m long constructed of nylon with mesh apertures of about 5.5 × 2.5 mm, and cod end of no. 56 XXX grit gauze. This net attached to a 5 × 5 foot (1.52 × 1.52 m) frame was towed about 60 min obliquely from 200 to 0 m. Samples were also analyzed from tows taken with a 5-m long "neuston" net constructed of nylon with mesh apertures of about 0.65 mm, and cod end of no. 56 grit gauze. This net was attached to a 1-m ring bent to form a narrow opening and buoyed to tow at the immediate surface for 15 min. For *David Starr Jordan* cruise 65, analyses were also made of all samples taken with a similar net attached to a regular 1-m ring towed obliquely from 200 to 0 m for 20-25 min simultaneously with the neuston net.

RESULTS

David Starr Jordan Cruise 57 and *Townsend Cromwell* Cruise 51 5 Nov.-21 Dec. 1970

In Figure 1 is shown the station pattern

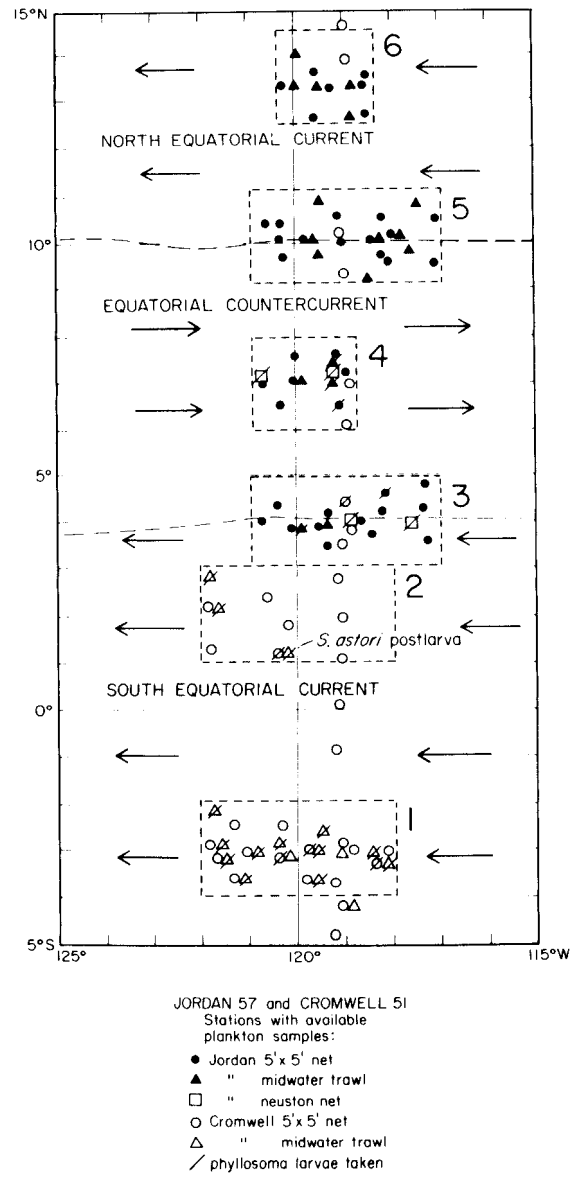

FIGURE 1.—RV *Townsend Cromwell* cruise 51 and RV *David Starr Jordan* cruise 57 station pattern in unit areas 1-6. Neuston net tows are shown only where larvae were taken.

where net tows, positive or negative for phyllosoma larvae, were taken by the trawl or the 5 × 5 foot net. The stations occupied fall into more or less distinct unit areas as designed for the tuna study to correlate with the prevailing major elements of the Equatorial Current System.

The number and stages of larvae caught in the various nets are given in Table 1 for each of

the unit areas. Because of the scarcity of specimens, no attempt is made to give figures based on unit volume of water filtered.

In unit area 1, 52% of 27 tows (other than with the neuston or 1-m net) yielded a total of 87 larvae in this 8° square area in the South Equatorial Current. Nine neuston net tows caught no larvae.

The three stations below 4°S were negative and approach or fall into a large expanse of water that yielded no larvae during the EASTROPAC cruises (Johnson, 1971, Chart 12).

Unit area 2 also in the South Equatorial Current was less well sampled, but 36% of 11 tows with the trawl and 5 × 5 foot net yielded a total of 35 phyllosoma larvae and one scyllarid postlarva (nesto). The five neuston tows were negative.

The large number of larvae caught by the trawl in unit areas 1 and 2 when compared with the more northern unit areas is striking in indicating the tendency of the South Equatorial Current to retain its load of phyllosoma larvae in their long drift from the adult area.

In unit area 3 overlapping into the North Equatorial Countercurrent, which was well developed at the time (Williams, 1971), 20% of 15 tows with the trawl and 5 × 5 foot net were successful but yielded only seven larvae in these nets. However five additional larvae were caught in 2 of 11 neuston tows.

Unit area 4 comprises only a 2° square area within the North Equatorial Countercurrent. Here two of three trawls and one of nine 5 × 5 foot net tows yielded 3 and 1 larvae respectively while the neuston net caught a total of 10 larvae in two of eight tows. The successful neuston tows in this area and in unit area 3 were taken during evening or nighttime tows.

Unit areas 5 and 6 provided no phyllosomas although both areas were comparatively well sampled.

The relatively large number of larvae taken during these two cruises compared with the following cruises reflects more intensive sampling, especially with the trawl, but a seasonality in release of larvae in the adult area may also have contributed.

David Starr Jordan Cruise 60 6 Mar.-11 Apr. 1971

The stations occupied for plankton were more scattered and very few larvae were caught,

TABLE 1.—*David Starr Jordan* cruise 57 and *Townsend Cromwell* cruise 51. Types of gear, total number of tows taken (the successful number of which is shown in parenthesis) and the number of larval species caught with different gear in unit areas 1-6.

Unit areas No. of tows Successful no. in parentheses	Species taken and type of gear	Phyllosoma stages VII	VIII	IX	X	XI	Total larvae in unit area
1	*P. gracilis*, 5′ × 5′		1				
5′ × 5′, 14 (3)	*P. gracilis*, trawl	1	11	18	2		
Trawl, 13 (11)	*P. penicillatus*, trawl			7	16	16	
Neuston, 9 (0)	*S. astori*, trawl	1	1	3	4	6	87
2	*P. gracilis*, 5′ × 5′	1	1				
5′ × 5′, 8 (1)	*P. gracilis*, trawl	2		1	1		
Trawl, 3 (3)	*P. penicillatus*, trawl	1	10	11	6		
Neuston, 5 (0)	*S. astori*, 5′ × 5′		1				
	S. astori, trawl			1			35 + 1 nesto
3	*P. gracilis*, 5′ × 5′	1	2				
5′ × 5′, 13 (2)	*P. gracilis*, trawl	1		1	1		
Trawl, 2 (1)	*P. gracilis*, neuston	1	3	1			
Neuston, 11 (2)	*P. penicillatus*, trawl		1				12
4	*P. gracilis*, 5′ × 5′	1					
5′ × 5′, 9 (1)	*P. gracilis*, trawl			1			
Trawl, 3 (2)	*P. gracilis*, neuston	1	4	5			
Neuston, 8 (2)	*P. penicillatus*, trawl			1	1		14
5							
5′ × 5′, 13 (0)	none						
Trawl, 8 (0)							
Neuston, 11 (0)							0
6							
5′ × 5′, 8 (0)	none						
Trawl, 5 (0)							
Neuston, 8 (0)							0

hence the data on larval distribution, species, and stages taken are entered directly on the chart (Figure 2). The successful tows indicate at least a presence of larvae in all of the major currents traversed. The North Equatorial Current at this time showed a few stage VII *P. penicillatus* with Clipperton Island a likely source of origin.

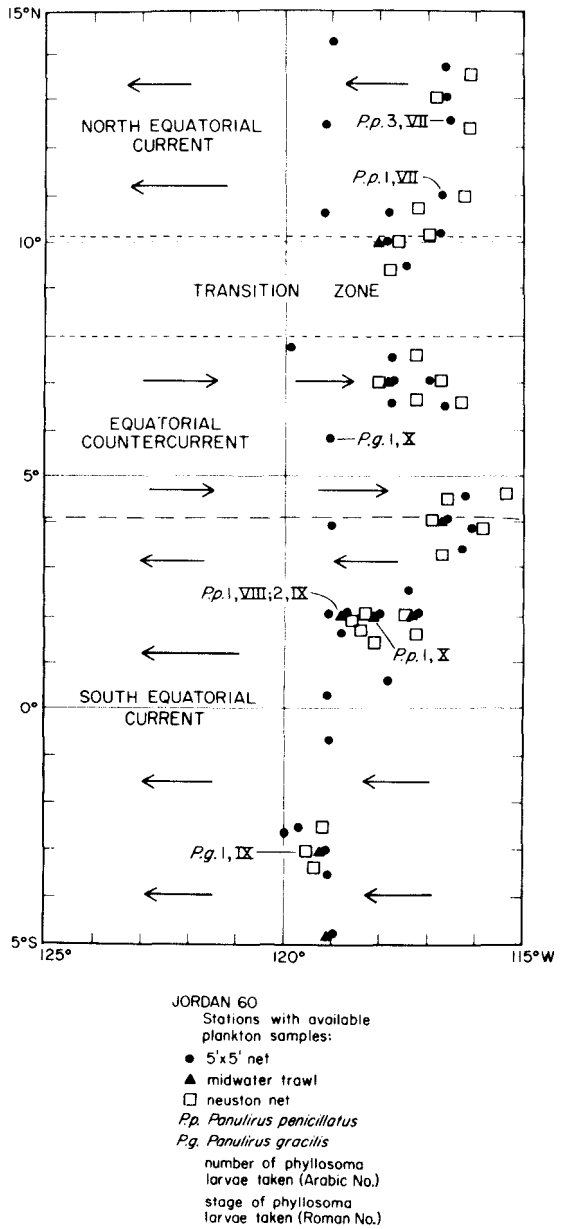

FIGURE 2.—RV *David Starr Jordan* cruise 60 station pattern with number and stage (Roman numeral) of phyllosoma larvae taken at station indicated.

David Starr Jordan Cruise 65 24 Aug.-30 Sept. 1971

As shown in Figure 3, this cruise covered an area much nearer the Galapagos Islands, from which most of the phyllosomas taken probably originated. It also extended less to the north and farther to the south. The data will again be presented here by unit areas (2° squares).

Unit 1 falls below lat. 11°S and yielded no larvae in a total of eight tows (Table 2). It is probable that the area is within the influence of the northern boundary of the western extension of the Peru Current which as already mentioned had few or no phyllosomas during the EASTROPAC cruises.

In unit 2 within the South Equatorial Current, a total of 16 tows with the various nets yielded 19 larvae, mainly by the trawl.

Units 3 and 4 although within the South Equatorial Current had only two and four larvae respectively in a total of 18 mixed tows.

Unit 5 directly west of the Galapagos was the most productive of larvae where five of eight neuston hauls yielded a total of 33 specimens.

Unit 6, still within the South Equatorial Current, was less productive of larvae although three of eight neuston net tows took five larvae.

A total of 35 tows taken with the 1-m net simultaneously with the neuston net during the cruise yielded no larvae whatever (see Discussion).

David Starr Jordan Cruise 77 8 Jan.-17 Feb. 1973

Figure 4 depicts the station pattern across the current system. As in cruise 60 there were so few phyllosoma larvae that it will suffice to record the data relative to these directly on the chart. There were a few scattered palinurid larvae in the North Equatorial Current. The nearest likely source of these being Clipperton Island. A few also occurred in the northern part of the South Equatorial Current. That these probably came from the Galapagos Islands is indicated by the accompanying larvae of *Scyllarides astori*, the adult of which is relatively rare except in that area.

Of special interest however is the occurrence of a single, late stage *Parribacus* sp. phyllosoma in this group of stations. No adult species of this genus has been reported from the west

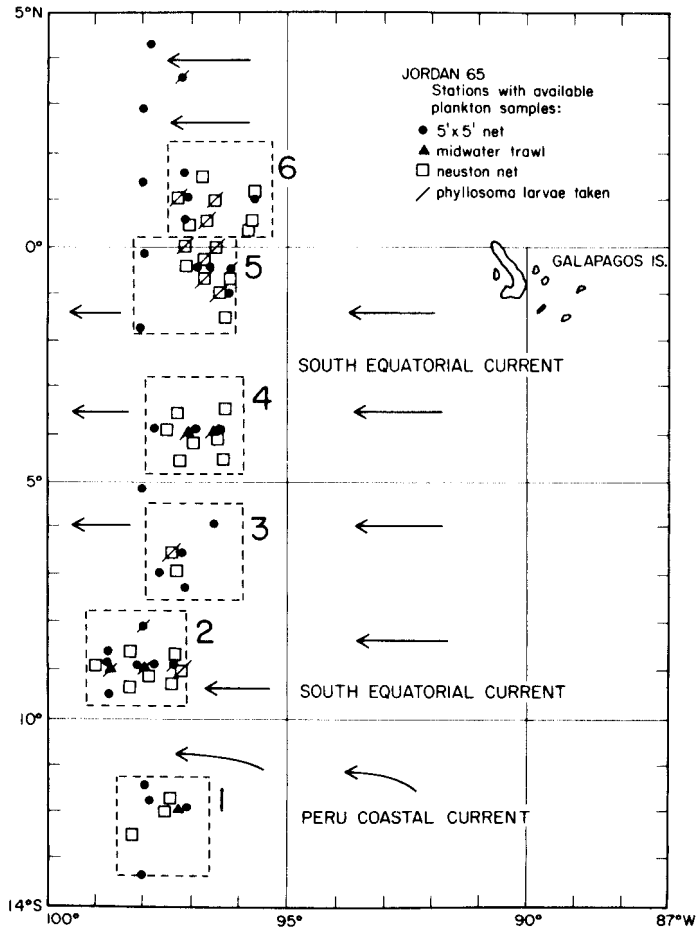

FIGURE 3.—RV *David Starr Jordan* cruise 65 station pattern in unit areas 1-6; 1-m net tow also made at neuston stations.

coast of the Americas. Hence one is forced to conclude that it most likely had drifted from islands to the southwest where the genus is known to occur. It should be mentioned here also that a late larva of this genus was taken at lat. 14°13.6'S, long. 126°00'W near the southern limit of the most distant offshore stations of EASTROPAC. Nothing is known regarding the duration of the entire floating period of this genus.

Saisho (1962) included *Parribacus antarcticus* in his generalization stating that the free-swimming life of scyllarids is shorter than for palinurids. This was based on laboratory studies of only the first three larval stages. However, if the present observations of the two late, but not yet the last, stage is characteristic of the genus they suggest that, like *Scyllarides astori*, the free-swimming life is not abbreviated.

DISCUSSION

This survey is of special interest in substantiating the earlier findings of the EASTROPAC survey relative to the far offshore drift of planktonic stages of lobster larvae in the Equatorial Current System. As in the earlier survey, only species known to occur in the east tropical area were found with one exception (*Parribacus* sp.) referred to above.

Assuming that the Galapagos Islands are the main source of the larvae encountered, it is evident that the westward transport with the South Equatorial Current involves at least a distance of about 1,800 nautical miles. In *Townsend Cromwell* cruise 51 larvae of each of the prevailing species *Panulirus penicillatus*, *P. gracilis*, and *S. astori* were netted in trawl tows at the western-most stations at long. 121°32'-121°54'W between lat. 02°45'N and

TABLE 2.—*David Starr Jordan* cruise 65. Types of gear, total number of tows taken (the successful number of which is shown in parenthesis) and the number of larval species caught with different gear in unit areas 1-6.

Unit areas No. of tows Successful no. in parentheses	Species taken and type of gear	Phyllosoma stages VI	VII	VIII	IX	X	Total larvae in unit area
1 5′ × 5′, 4 (0) Trawl, 1 (0) Neuston, 3 (0)	none						0
2 5′ × 5′, 7 (1) Trawl, 2 (2) Neuston, 7 (1)	*P. gracilis*, neuston *P. penicillatus*, 5′ × 5′ *P. penicillatus*, trawl *S. astori*, trawl		1 5 1	1 1 5 1	 1 3		19
3 5′ × 5′, 4 (0) Neuston, 2 (1)	*P. gracilis*, neuston		2				2
4 5′ × 5′, 3 (0) Trawl, 2 (2) Neuston, 7 (0)	*P. gracilis*, trawl			4			4
5 5′ × 5′, 6 (1) Neuston, 8 (5)	*P. gracilis*, neuston *P. penicillatus*, 5′ × 5′	6	14 1	10	2	1	34
6 5′ × 5′, 4 (0) Neuston, 8 (3)	*P. gracilis*, neuston	2		2	1		5
North of unit 6 Isolated Stn. 229	*P. gracilis*, 5′ × 5′			1			1

02°57′S. During the EASTROPAC survey only *P. penicillatus* was found at the western-most stations at about long. 126°W near the equator, a distance of about 2,000 nautical miles. These *P. penicillatus* larvae might conceivably have drifted eastward from the oceanic islands of the south Pacific where the adult is known to occur. But no other species common to the mid-Pacific islands has ever been found in any part of the eastern tropical Pacific survey areas except for the two specimens of *Parribacus* sp. mentioned previously. Obviously one sees here the working of the East Pacific Barrier towards maintaining a specific separation of west American and Indo-Pacific lobster faunas. *Panulirus penicillatus*, which occurs all the way through the Pacific and Indian Oceans to the Red Sea, is unique among lobsters in having successfully overcome this barrier to become established on offshore islands, but appears to have found additional barriers that prevent establishment on the coast of the mainland. George (1969) interprets this as a failure to compete successfully with the east Pacific mainland species that have evolved there by natural selection. The absence of *P. penicillatus* in the coastal environment may result largely from elimination of the larvae by an admixture of inimical coastal water as they approach the coast. This supposition is suggested by the fact that no larvae of this species have thus far been found at stations near the coast despite their capability of wide dispersal offshore.

Other crustacea with relatively shorter planktonic lives appear also to have migrated eastward across the East Pacific Barrier (Chace, 1962; Garth, 1966).

The countercurrents within the Equatorial Current System provide possible routes for return of east Pacific species that have either fortuitously or through instinctive behavior shifted into countercurrents, possibly through habits of diurnal migrations, and that have not drifted westward to a point of no return determined by requirements inherent in their life cycle.

To evaluate how effective these return routes may be needs further study based on plankton collections designed to elucidate the vertical distribution of the larvae and the diurnal migrations that they undergo in relation to light, etc., and to the depths of prevailing countercurrents in relation to adjacent currents. In this connection it is

useful to examine the results of certain neuston and 1-m net tows, especially those taken during *David Starr Jordan* cruise 65 where 28.5% of 35 neuston tows yielded one or more larvae, and two tows contained eight and nine larvae respectively. All but two of the neuston tows that were positive for larvae were taken during dusk or darkness. The 1-m net tows taken simultaneously from 200 to 0 m yielded no larvae in either the nighttime or daytime tows. This discrepancy is rather surprising and the cause is not clear. But it may indicate that larvae are so scarce and widely dispersed vertically at depth that the 1-m net does not filter enough water to be effective at depth and its passage through the immediate surface layer is very brief, whereas the neuston net, although filtering less water, caught larvae because of their active concentration in a very narrow horizon at the very surface during conditions of reduced light. Other observations in the field (Chittleborough and Thomas, 1969) and in laboratory experiments (Ritz, 1972) demonstrate this behavioral response of phyllosoma leading to a migration into surface layers at night.

In *David Starr Jordan* cruises 57 and 60 the trawl and neuston tows show that larvae do get into the North Equatorial Countercurrent (Figures 1 and 2). This is an expected correlation with the physical studies of the countercurrent which indicate that some variable transverse circulation does occur across the current such that water is drawn in at the surface along the southern boundary and a loss occurs across the northern boundary (Wyrtki, 1967). The Equatorial Undercurrent at the Equator is another possible route for return to the Galapagos and surrounding area.

Williams (1972), in presenting a hypothetical model of an eastward passive migration of skipjack tuna from the central Pacific spawning area in recruitment of the fisheries in the eastern Pacific, has reviewed hydrographic details relative especially to the position, speed, and seasonal interruptions of the North Equatorial Countercurrent. The seasonal fluctuations of this current could aid or retard the passive migration of tuna larvae and juveniles from the spawning grounds depending upon the degree of coordination with the season of spawning. Much of this transport mechanism might apply also to the return of the long-lived lobster larvae. But it is not known if there is a significant seasonality in the release of the larvae in the adult habitat that might fortuitously correlate with the North Equatorial Countercurrent and thus enhance the likelihood of return of larvae that have drifted to the west. Data from EASTROPAC suggest a very long breeding season for the tropical species as judged by the persistent occurrence of early larval stages (III-IV) in

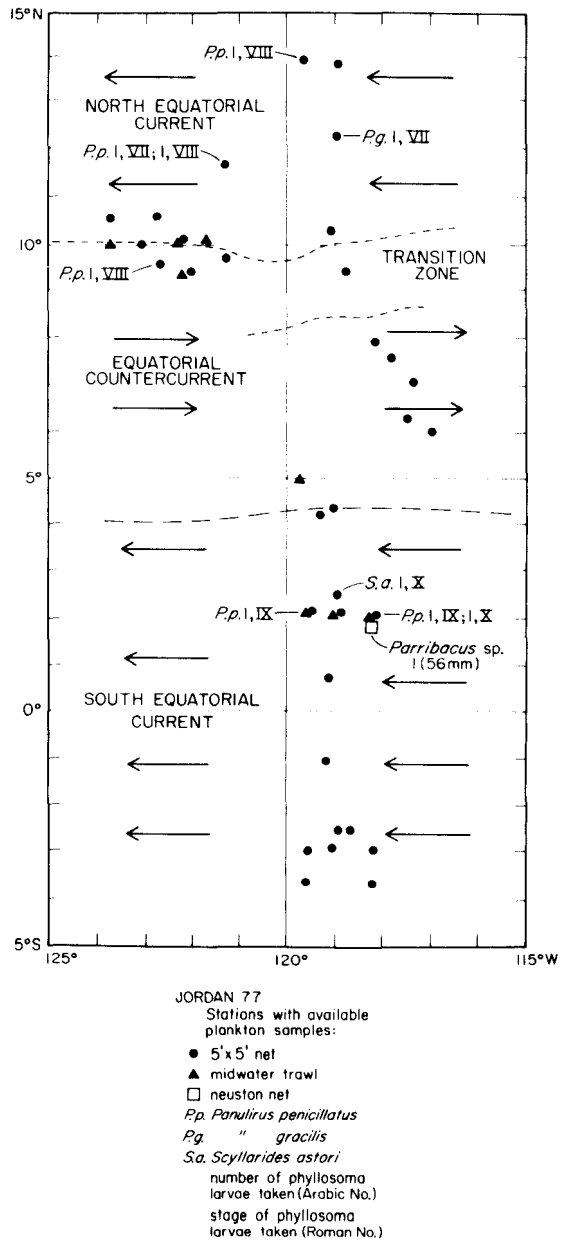

FIGURE 4.—RV *David Starr Jordan* cruise 77 station pattern with number and stage (Roman numeral) of phyllosoma larvae taken at station indicated. Neuston net tow is shown where larva was taken.

the more coastal waters. Larvae that have shifted into the countercurrents from the South Equatorial Current in the eastern part of its course may well be returned in time for metamorphosis near the coast or at offshore islands. It seems probable, however, that safe return from the area of the more westward stations surveyed is doubtful in view of the great distance covered and the expected attrition through predation, etc. Assuming, as before, that the larvae occurring below about lat. 10°N near long. 120°W, originated in the Galapagos Islands area and allowing an average of 20 nautical miles per day westward flow of the South Equatorial Current it would require 3 mo sustained drift to cover the 1,800 nautical miles involved. If shifted promptly at this point into the North Equatorial Countercurrent with an average speed of 15 nautical miles per day another 4 mo of sustained transport would be required to reach an adult area suitable for metamorphosis. It should be noted, however, that only larval stages VII to XI (final stage) were taken at the more distant stations on all skipjack cruises except *David Starr Jordan* cruise 65, the one nearest to the Galapagos Islands. This would indicate that even the youngest larvae taken near long. 120°W were probably older than 3 mo and the likelihood of much additional delay in returning by way of countercurrents militate against a safe return unless metamorphosis can be delayed pending encountering conditions favorable to metamorphosis and assumption of the benthic habit. Recruitment must depend mainly on larvae that have been retained relatively near the coast by coastwise currents, eddies, and backwashes.

None of the east Pacific larvae taken in the far offshore areas show any tendency to gigantism such as was believed to occur in some Crustacea when settlement has been postponed (Bruce, 1970).

To what extent metamorphosis of the phyllosoma larvae to the postlarval stage may take place in the far offshore waters is not known. No palinurid postlarvae were found in any of the cruises. However, a single specimen of *Scyllarides astori* postlarva (known as a nesto) was taken in a trawl at lat. 01°17'N, long. 120°06'W during *Townsend Cromwell* cruise 51 (Johnson, in press).

The chances of the larvae continuing to float successfully westward all the way to the mid–Pacific islands is unlikely and the absence of the species, except for *P. penicillatus*, in these islands substantiates this supposition and clearly manifests the East Pacific Barrier functioning against westward migration of the east Pacific species.

ACKNOWLEDGMENTS

The plankton collections and field data were kindly supplied to me by the coordinators of the Skipjack Cruises, involving the Institute of Marine Resources at Scripps Institution of Oceanography (SIO) and the National Marine Fisheries Service (NMFS), Southwest Fisheries Center, La Jolla, Calif. The laboratory work was supported by the Marine Life Research Program, the SIO part of the California Cooperative Oceanic Fisheries Investigation sponsored by the Research Committee of the State of California. Thanks are extended to Mizuki Tsuchiya of SIO for discussions pertaining to the hydrography and to Mary Farrel of NMFS for aid in sorting some of the samples.

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