THE PELAGIC PHASE OF *PLEURONCODES PLANIPES* STIMPSON (CRUSTACEA, GALATHEIDAE) IN THE CALIFORNIA CURRENT

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INTRODUCTION

The planktonic habit may be prolonged into or recur in the adults of two species of Galatheidae. Harrison Matthews (1932) uses the terms "lobster-krill" or "whale feed" in reference to these: *Munida gregaria* (Fabricus) of southern South America and of New Zealand, and *Pleuroncodes planipes* Stimpson the red or pelagic crab of California and Mexico. Both occur at times as conspicuous concentrations of apparently adult crabs on which baleen whales are known to browse (Harrison Matthews, 1932); in addition, the studies of McHugh (1952) and Alverson (1963) on the tuna *Thunnus alalunga, Katsuwonus pelamis* and *Thunnus albacares* have shown that *Pleuroncodes* is a significant food item during their summer migration into the California Current; for *Thunnus* the pelagic crab may form up to 85% by volume of all stomach contents from certain areas during this period.

In addition to the normal methods of nutrition of galatheids (Nicol, 1932) both species of pelagic crabs are able to graze on phytoplankton by filtration; recorded by Matthews (1932), Beklemishev (1960) and Boyd (1963), this ability has been confirmed by studies at this laboratory which will be reported elsewhere.

The filtration mechanism is based on the highly setose second maxilliped which in post-larval *Munida* is very highly developed and distinguishes the *Grimothea* stage, in *Pleuroncodes* no such post-larval stage occurs and pelagic and benthic individuals are apparently indistinguishable from one another.

By its ability to graze, at least at times, on the phytoplankton, thus forming a rather direct link between primary production and commercially important predatory fish, *Pleuroncodes* merits study and it is the purpose of this paper to present a synthesis of the presently available data concerning its distribution in the California Current system. It is hoped that this may contribute to an understanding of the late summer "local banks" fishery for tuna in which the pelagic crab forms the dominant item of forage.

This study is based upon data from the regular pattern of stations of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) which are now available for a period of a decade and a half. Designed primarily to investigate the biology of the clupeid stocks of the California Current, these investigations included at every station a standard haul to 140 meters with a 1-meter zooplankton net; details of the sampling procedure and of the location of stations are described elsewhere (e.g. Ahlstrom, 1948; CalCOFI, 1963).

The data consist of records of the numbers of pelagic crabs removed in the laboratory from each zooplankton sample before voluming, and these numbers were extracted for the present study from the original data sheets. The actual specimens had neither been measured nor were subsequently retained except during 8 months of 1960 when the whole catch of pelagic crabs was measured by Boyd (1963) who recorded a range in standard carapace length of from 7 to 20 mm; it has been assumed here that the CalCOFI data to be discussed refer only to subadult and adult crabs within this size range.

A zooplankton net is not an ideal collecting instrument for pelagic crabs since a degree of avoidance certainly occurs, and for this reason the data have been used, as far as possible, non-numerically; because the number of individuals per haul is generally rather small and because the hauls are standardized, the data have not been transformed to numbers per standard volume.

There is no evidence to suggest that crabs in the pelagic phase migrate diurnally so that a population would descend during part of the day below the 140-meter level normally sampled, and although the data of Boyd (1963) and from recent work of this laboratory off Baja California suggest that diurnal migration may occur, it probably consists primarily of a withdrawal from only the upper tens of meters of water during daylight hours.

The present study was restricted, for practical considerations, to the years 1955–1962 inclusive, thus covering the end of the long and stable cool period which extended from the late 1940's to 1957 (Reid, 1960) and the years 1958–1959, when altered circulation in the California Current brought warmer conditions and an influx of southern organisms; also covered is the period of return to the more usual conditions which have subsequently persisted until the present.

GENERAL DISTRIBUTION IN THE INSHORE AREA

The CalCOFI stations fall into two groups: those inshore of station 70 on each line, which were worked at monthly intervals and extend (Figure 1) about 150 miles seawards between Point Conception and Cabo San Lucas; and those further offshore which

[1] Contribution from Scripps Institution of Oceanography.

were worked much less frequently and extend a further 150 miles seawards. These are referred to as the inshore and offshore areas, respectively.

In a consideration of the overall distribution of pelagic crabs within the inshore area, account must be taken of the change in distribution of many species in this area in 1958–1959 compared with the previous decade; these changes and the physical phenomena associated with them were discussed at the Rancho Santa Fe symposium (Sette and Isaacs, 1960) and subsequently Radovich (1961), Glynn (1961), and Boyd (1963) presented observational data which indicated that *Pleuroncodes planipes* was one of the species involved.

For the present purposes, therefore, two 3-year periods were considered separately and the percentage frequency occurrence of *Pleuroncodes* at each station was calculated for each period. These data are presented in Figure 1 for the periods 1955–1957 and 1958–1960 inclusive, and despite the considerable differences in the latitudinal distribution between the two periods certain common features appear. In particular, there appears to be a correspondence between the distribution of crabs and the general distribution of upwelled water derived from coastal upwellings.

Coastal upwelling is known to occur, mainly in the first half of the year, at a number of points along the coasts of southern and Baja California (Reid et al., 1958), and examination of the charts of surface isotherms from CalCOFI cruises shows that it occurs most strongly at Cabo Colnett, Punta San Eugenio and Cabo San Lazaro (e.g., CalCOFI, 1963), and within the bights which lie to the south of these capes. It has been shown (Sverdrup et al., 1942) that

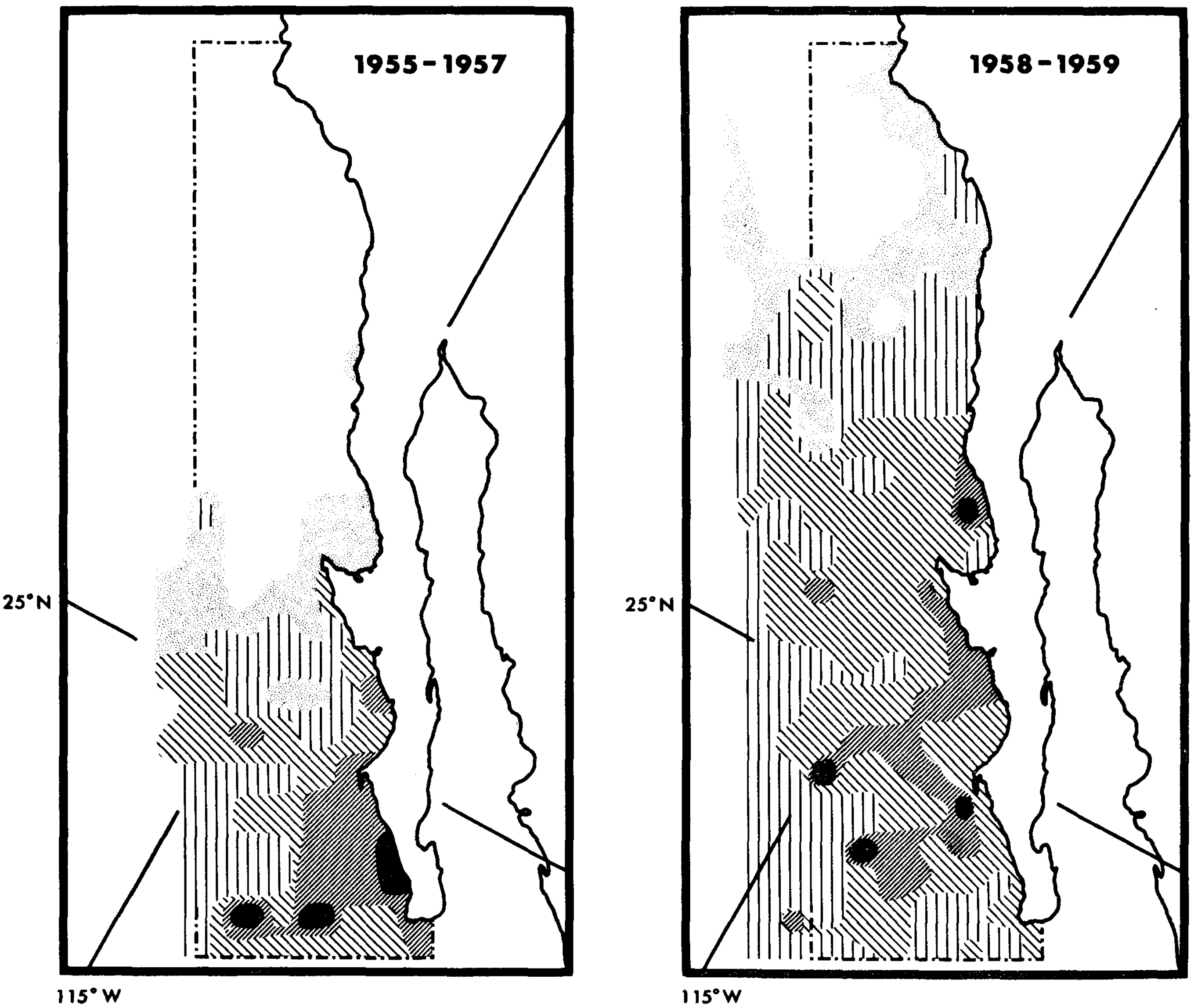


FIGURE 1. The percentage frequency of occurrence of adult *Pleuroncodes* at each of the CalCOFI inshore stations, data combined for the periods stated; the intensity of the shading is proportional to the percentage frequencies of occurrence, at the following intervals: 1–10%, 11–25%, 51–75%, 76–100% occurrence.

the water upwelled at the coast in the California Current drifts southward away from the coast as discrete tongues of cold surface water, and such tongues have been observed from Baja California coastal upwellings during the 1964 Scripps tuna oceanography studies (Scripps Institution of Oceanography, 1965). These studies have shown that biota, particularly phytoplankton, are more abundant in the upwelled water than elsewhere off this coast; examination of the charts of areal zooplankton abundance from the CalCOFI cruises (e.g., Thrailkill, 1956) confirm this statement.

Figure 1 shows that the highest frequencies of occurrence of *Pleuroncodes* during both periods studied appear to conform to the same pattern; that is, the highest frequencies are coincident with those areas expected to be most often occupied by recently upwelled water; during the 1964 cruises referred to above, the distribution of pelagic crabs could be related quite closely to tongues of upwelled water (Blackburn, pers. comm.), thus confirming the general pattern revealed in Figure 1.

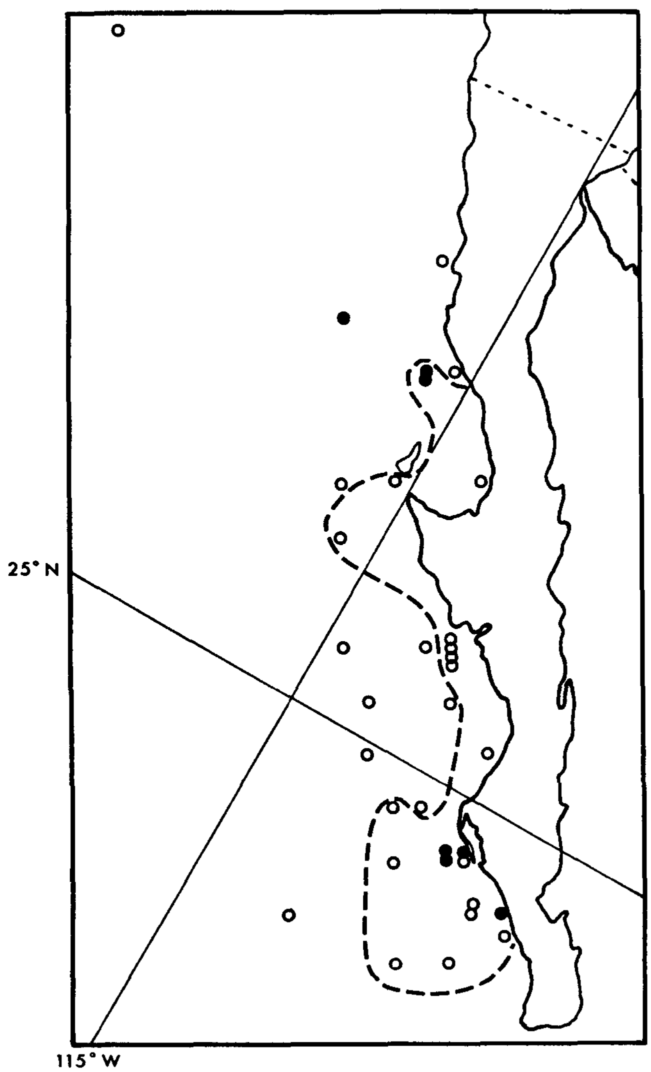


FIGURE 2. Distribution of all occurrences of more than 50 *Pleuroncodes* per haul; the line encloses all stations in the first half of the year showing that these tend to be closer inshore. Closed symbols, stations at which more than 100 crabs taken per haul.

Pelagic *Pleuroncodes* are very patchily distributed and are occasionally encountered in very dense and extensive concentrations at or near the surface; it has been assumed that all CalCOFI hauls containing more than 50 crabs indicate the existence of such a concentration, since such numbers were taken in only 36 of the total of about 1500 zooplankton hauls studied; obvious concentrations tended to be avoided during sampling, so these data are minimal. The distribution of these 36 stations are shown in Figure 2 from which can be seen that these are situated mainly within the influence of upwelled water originating near the major capes of Baja California; thus, in this situation not only are pelagic crabs more frequently encountered as isolated individuals than elsewhere, but also as dense surface shoals.

DISTRIBUTION IN OFFSHORE AND OCEANIC AREAS

Within the CalCOFI offshore area less than 500 stations were worked during the 8-year period and at only 52 of these were pelagic crabs taken in the zooplankton tows; the temporal distribution is shown in Table 1 and the distribution spatially in Figure 3. Occurrences were restricted, in the main, to an area off Punta San Eugenio and to the years 1958–1960.

The between-years variation is very much clearer in these data than is the within-year variation which, if

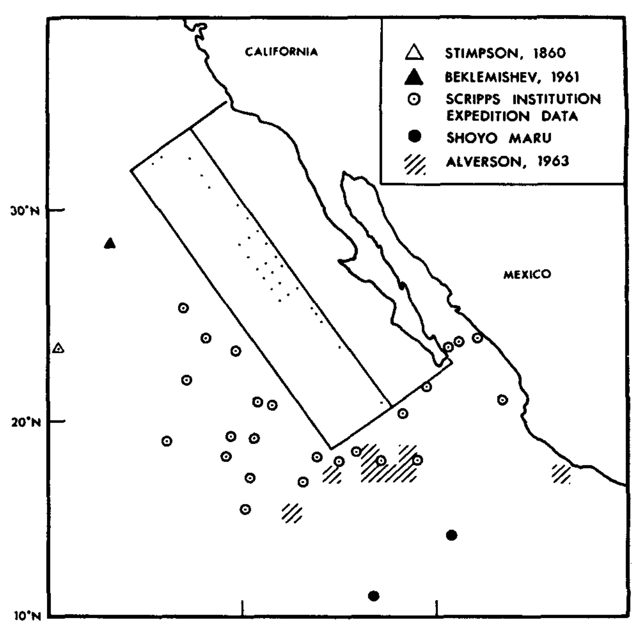


FIGURE 3. Distribution of *Pleuroncodes* in the offshore and oceanic area; the stations within the CalCOFI offshore area (indicated by a rectangle) at which the species occurred within the years 1955–1960 are shown by dots. The SIO expedition data includes the following cruises: Tethys, MidPac, Tuna Spawning, TO-58-1, TO-60-2 and La Pared.

it can be demonstrated, consists of a tendency for records to occur during the first 6 months of the year; this is difficult to determine with certainty because of the relatively low sampling intensity after July in each year. More than 50% of the occurrences were, in fact, restricted to the period January–June of 1959, a period during which particularly active northward movement of pelagic individuals was taking place within the inshore area.

Beyond the CalCOFI station pattern there are records of the occurrence of pelagic crabs from expedition results, although here the station density is even lower than in the CalCOFI offshore area; the known records from such sources are set out in Figure 3, which shows that these extend to about 1,000 miles offshore to the south-west of Baja California. There are several records from as far south as the Islas Tres Marias, but to the south of these islands only a single record exists, from the stomach contents of a single yellowfin tuna (Alverson, 1963). Records within the Gulf of California, where a population is known to exist (e.g., Boyd, 1963), are not shown in Figure 3.

It can be deduced from the data of Alverson (1963) that the relative frequency of occurrence of *Pleuroncodes* in the oceanic area is much less than closer to the coast; he recorded frequencies of occurrence of 88.2% in the inshore area compared to only 32.3% around the Revilla Gigedo Islands and even smaller frequencies south of the Gulf and off the Mexican west coast. Blackburn (MS) indicates lower volumes of *Pleuroncodes* per micronekton net haul in the oceanic area as compared with closer to Baja California.

Much further to the west, in the region of the Hawaiian Islands, there have been many investigations of the distribution of zooplankton and micronekton (e.g., King & Iverson, 1962) but apparently there are no records of the occurrence in the Central Pacific Ocean of pelagic *Pleuroncodes;* the question of the status and fate of the stocks in the oceanic areas of the Eastern Pacific will be discussed later.

VARIATION WITHIN YEARS, INSHORE AREA

The data are not entirely adequate for an analysis of seasonal variation of the distribution because the sampling frequency in the second half of the year was considerably lower than during the first half, particularly in the southern part of the inshore area. For example, no stations were worked in November south of Cabo Colnett from 1955–1960, and none during December from 1956–1960.

Within these limitations, the data indicate that pelagic crabs may be encountered in any month in the inshore area and that their occurrence follows no very clear seasonal cycle; this can be seen in the data from the years 1955 and 1958 (chosen because of relatively complete sampling coverage) presented in Figures 4a and 4b. It is possible (Figure 5) that, as in the offshore area, lower frequencies of occurrence may be found in the period August to December in some years, but the evidence is inconclusive.

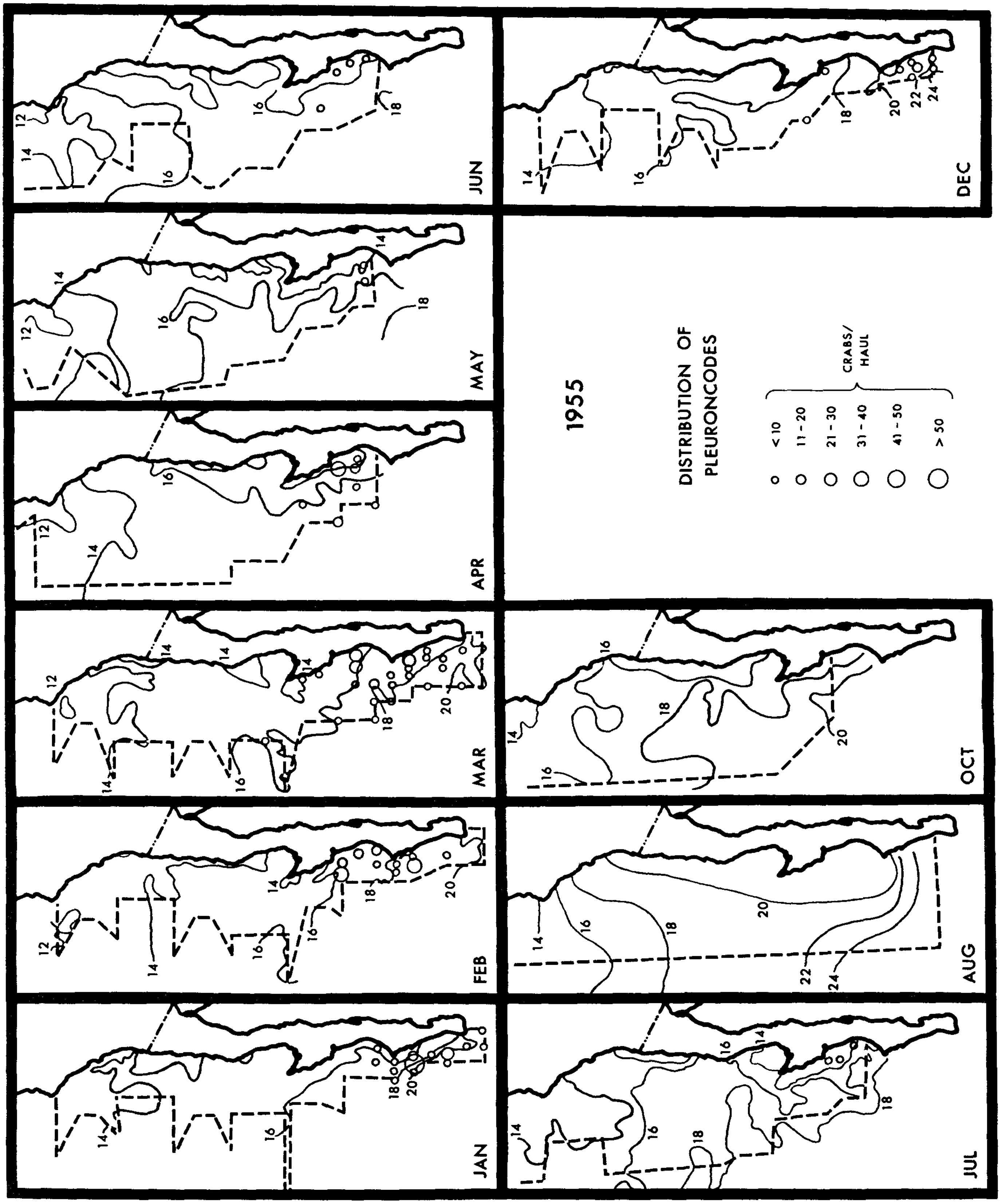
That a seasonal cycle of occurrence should be difficult to demonstrate is perhaps not surprising in view of the marked eurythermy of *Pleuroncodes.* Table 2, which summarizes all records of the benthic phase of the species for which there are also environmental data, shows that temperatures down to 9.0° C. are tolerated, while Table 3 indicates that temperatures up to 28.0° C. are tolerated in the pelagic phase. The demonstration in Figure 4, therefore, that the distribution of pelagic crabs was apparently unaffected by the passage of the 16–24 °C. isotherms through the area in which the crabs occurred is not surprising, and suggests that some factor other than temperature must be the direct determinant of distribution patterns and cycles.

The role apparently played by upwelled water in determining the distribution of the pelagic phase suggests that the occurrence of the upwelling phenomenon itself may be correlated with the occurrence of pelagic crabs, and this hypothesis was tested in an area to the south of Punta San Eugenio. The occurrence of coastal upwelling can be determined most simply by the presence of surface isotherms running parallel to the coast, indicating an offshore tempera-

TABLE 1

OCCURRENCES OF PELAGIC CRABS IN CalCOFI OFFSHORE AREA (STATIONS WEST OF .80 ON LINES SOUTH OF 110); FOR EACH YEAR COLUMN A = NUMBER OF POSITIVE OCCURRENCES, B = NUMBER OF STATIONS WORKED

	1955		1956		1957		1958		1959		1960		1961		1962		1955–1960 % occurrence
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
January	--	3	--	1	--	--	--	3	7	16	4	13	--	13	1	16	26.7
February	--	4	--	--	--	3	--	4	1	4	2	6	--	--	--	--	14.3
March	--	4	--	3	--	1	--	4	3	6	1	6	--	--	--	--	16.7
April	--	1	--	5	--	12	--	17	6	16	2	12	1	18	4	20	12.9
May	--	6	--	6	--	6	2	12	3	12	--	4	--	--	--	--	10.9
June	--	6	--	6	--	12	--	--	6	4	1	4	--	--	--	--	21.9
July	--	6	--	5	2	11	1	6	3	12	--	9	--	20	--	14	7.2
August	--	--	--	--	--	--	--	--	--	12	--	--	--	--	--	--	(+)
September	--	--	--	--	--	--	--	--	--	4	--	--	--	--	--	--	(+)
October	--	4	--	--	--	10	3	11	--	8	--	--	--	20	--	18	4.2
November	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
December	--	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	(+)
% occurrence	0.0		0.0		3.6		10.5		31.7		18.5		1.4		7.3		


1955
DISTRIBUTION OF PLEURONCODES
< 10
11 - 20
21 - 30
31 - 40
41 - 50
> 50
CRABS/ HAUL
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
OCT
DEC

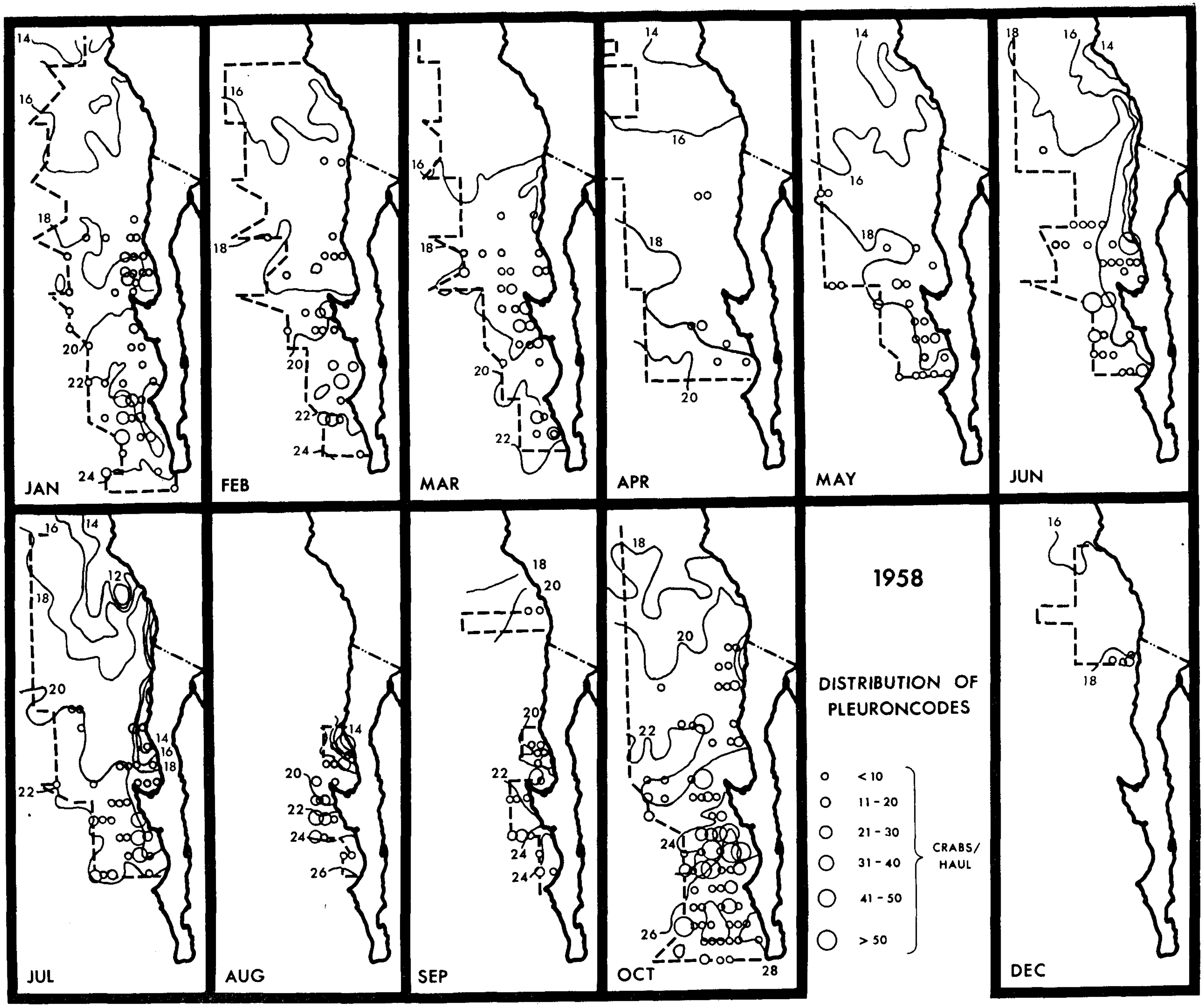


FIGURE 4. The distribution of *Pleuroncodes planipes* and certain surface isotherms monthly during the years 1955 and 1958. The region enclosed by the dotted line is that sampled during each cruise.

ture gradient; the temperature differences between two stations (127.34 and 127.40) off Punta San Eugenio was determined and from it was derived a monthly index of the intensity of upwelling at this cape.

These indices were then compared with the occurrence of red crabs in the upwelled water by reference to the numbers of occurrences and relative abundances per month at a small grid of seven stations to the southeast of the cape in the direction presumed to be taken normally by recently upwelled water. This investigation showed the regularity of the seasonal upwelling cycle from April until about July or August and also that the annual variation of frequency and abundance of crabs to have been far greater than any seasonal variation. The regression between upwelling and frequency and abundance of pelagic crabs indicates a zero correlation.

VARIATION IN THE DISTRIBUTION BETWEEN YEARS

Observational data which showed that *Pleuroncodes* was included in those species which extended their range to the north during the period 1958–1959 has been presented by Berner (1960), Radovich (1961), Glynn (1961), and Boyd (1963); these data are summarized below:

December 1957—*Pleuroncodes* present off La Jolla.
April 1958—Present off Monterey.

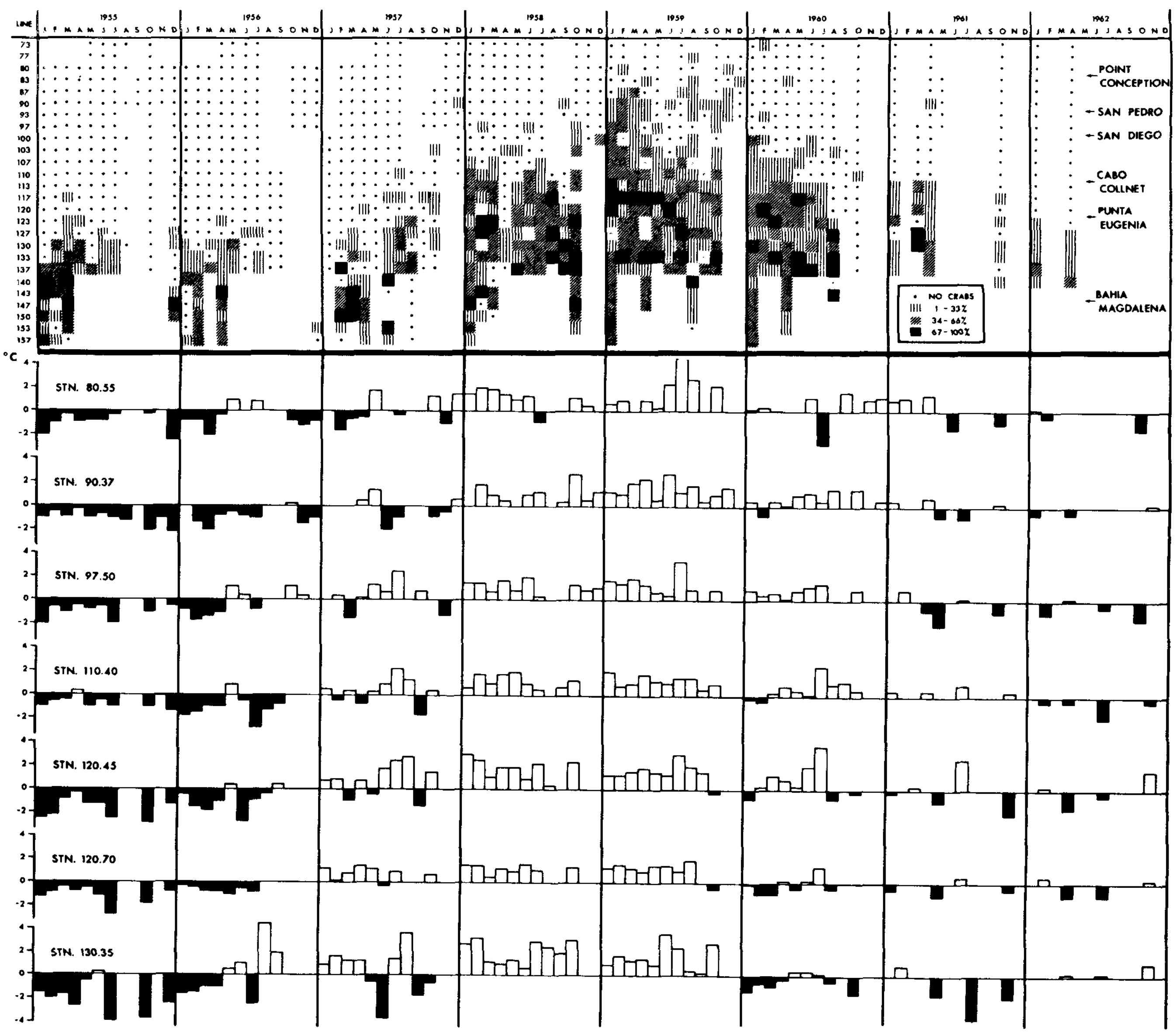


FIGURE 5. Monthly percentage frequency of occurrence of *Pleuroncodes* by station lines during the period 1955–1960 to show the northern range extension of the species during the warm years. The lower section of the figure indicates the temperature regime in terms of variation from the 6-year mean of stations selected as representative of conditions in the California Current between Cape San Lucas and Point Conception.

During 1958—Multiple beach strandings at San Diego, La Jolla and San Pedro.

January 1959—Present off San Pedro.

March 1959—Beach stranding at San Pedro.

December 1959—Massive numbers present off Santa Cruz, Anacapa, Santa Barbara Islands and Monterey.

January 1960—Beach stranding at Monterey and Santa Catalina.

It is now possible with the CalCOFI data to trace this range extension to the north rather more closely; in Figure 5 are summarized the frequency of occurrence data for the CalCOFI inshore area arranged by station lines running approximately normal to the coast and representing a latitudinal series at 26 intervals, each of 40 miles, extending from Cabo San Lucas in the south to Monterey in the north. For each station line a percentage frequency of occurrence of *Pleuroncodes* is given for each month, ranked in four categories.

The CalCOFI data show that a northward movement began some months before the first casual observation was made of their presence off La Jolla from a sport fishing boat; this movement started in the area between Punta San Eugenio and Cabo Colnett in June and July of 1957 and by October some individuals were recorded just to the south of Ensenada. The correspondence is very good between the arrival time off San Diego indicated by these data and from the observation tabulated above, though the CalCOFI data shows that they reached a little further to the north, to San Pedro, in the same month.

During 1958 the northern limit of the main population remained at about the latitude of San Diego, except for a single observation off Monterey in April and for two other April records at stations 80.120 and 80.130 about 300 miles seaward from Point Conception; Figure 5 indicates that while the main population did not extend much to the north of San Diego during 1958 there was an isolated population (perhaps the same as that recorded off San Pedro at the end of the previous year) which reached the latitudes of Monterey and Point Conception during the year.

In late 1958 further northward movement began and by the beginning of 1959 there was a continuous distribution southwards from the latitude of San Pedro for the first time; the population center, where frequencies of occurrence of 67–100% were recorded, shifted from its normal site off Bahia Magdalena to the region of Cabo Colnett. During 1959 the first massive stranding occurred at San Pedro and in the first months of 1960 the CalCOFI data show the range extension to have been complete and beach strandings were again noted at Monterey.

From early 1960 no further records of beach strandings or of casual sightings at sea off the coast of California are known and the CalCOFI data indicate that the range began shrinking during the first half of the year; by the end of 1961 both the northern limit and the area of greatest frequency had returned southward to approximately the same latitude as in mid-1957; a single crab taken off San Pedro (station 90.28) in April 1961 is the only anomaly during this return to earlier conditions.

Although Figure 5 shows that the northern movement very closely followed the timing of the change

TABLE 2

SUMMARY OF BENTHIC RECORDS OF *PLEURONCODES PLANIPES*; DATA FROM BOYD (MS.), PARKER (1963), PERKINS, BUREAU OF COMMERCIAL FISHERIES (PERS. COMM.). N = NUMBER OF STATIONS

	Depth (m)	T° (C)	O_2(ml/l)	N
Boyd	75–300	10.0–14.0	<0.5	15
Parker	64–366	9.0–14.0	0.5–2.0	8
Perkins	73–201	12.0–14.6	--	8

TABLE 3

FREQUENCY DISTRIBUTION OF TEMPERATURE AT 10 M AT STATIONS AT WHICH PELAGIC CRABS OCCURRED, 1955–1962 (DATA ARRANGED BY QUARTER YEARS, NUMBERED I–IV)

T°C	1955				1956				1957				1958				1959				1960				1961				1962				Σ 1955–1962				
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	I–IV
11																						1											--	1	--	--	1
12	1														1						2	2				4				1			3	7	--	--	11
13		2	1			2												1			4	4			3	1							7	10	1	--	18
14	4	2	1		1	2	1								3		1	5			9	3			1	5				1			16	18	--	--	39
15	4	2	1		2	6				3			1	2	1		20	6	1	1	27	10	1		5	4				1			59	34	4	1	98
16	10	2			5	4				2	1		17	4	2		45	36	3	1	35	38	5		8	3			2	6			122	99	11	1	224
17	11	3		2	4	2				5	1	1	17	23	2	2	53	54	2	1	20	22	1		3	3		1		3			108	115	6	7	236
18	5				4	3			5	13			13	20	4	3	39	34	7	2	7	7	1		2	2		1	4	3			59	82	12	6	179
19	6			1	4	3			9	4	2	4	10	8	15		16		9	9	16	4	6	1				1	1				62	19	32	14	129
20	4				6	1	1		4	1		1	7		13	4	17		13	11	7	1	5	1				1	1				46	3	32	17	99
21	1			4		1			2	3	6		8		11	10	10		32	5	8		5	2				1	2				31	3	54	11	111
22				1	1				2	2	6	2	12		7	9	12		18	5	2		1	2				1					28	2	32	20	83
23											2		4		4	3	8		5	4	1			1									13	--	11	8	32
24								1					2		2	3	11		4	3													13	--	6	4	26
25								1			2				2	8			7	9													--	--	11	18	29
26															1	12			4	2													--	--	5	14	19
27															1	12			1														--	--	2	12	14
28																7																	--	--	--	7	7

in the temperature regime, there are reasons to doubt a causative relationship even though this was implied by Radovich (1961); the area off Baja California to which the species was previously restricted was occupied throughout the period of northern range extension by apparently non-migratory crabs, and it is in any case doubtful if temperatures higher than those shown by Table 3 to be tolerated by pelagic crabs would have been encountered in the normal southern range of the species. Further, there is other evidence to show that organisms with little or no mobility were also involved at this time in the general northern movement of southern forms (Berner and Reid, 1961; Radovich, 1961).

Some mechanism beyond simply an ameliorating temperature regime is therefore required to explain these migrations, and this is to be found in the changes in the advective transport of surface waters which occurred in the California Current at this time (e.g., Sette and Isaacs, 1961). Although the 200 m flow is to the northward along Baja California and southern California throughout the year (Reid et al., 1958), the transport of adult pelagic crabs is presumably mainly in the mixed layer which flows predominately towards the south; there are four features of the California Current system (Reid et al., 1958, 1961) which *prima facie* seem to be relevant to the distribution of pelagic crabs: the Davidson Current, a northward coastal flow in winter which is effective only to the north of Point Conception; the great eddy south of Point Conception which leads to onshore flow throughout most of the year near Ensenada at around 32°N. and consequently to flow north and south from this point along the coast, reaching south to the region of Bahia Sebastian Vizcaino; the countercurrent which develops in winter along the coast of Baja California from Cabo San Lucas north to Punta San Eugenio where it meets the southerly flow from Ensenada; finally, the overall southward drift of the main current offshore of the above features.

In particular, the normally year-round coastal flow to the south between Ensenada and Punta San Eugenio as a consequence of the Point Conception gyre is probably of great significance in preventing the northward transport of southern species by the coastal countercurrents.

Examination of the charts of geostrophic flow for this area in the mimeographed CalCOFI data reports indicates that throughout 1955 and 1956 the situation was as described above; however, in the second half of 1957 a different pattern appeared; in July, for the first time, the whole coast from Bahia Sebastian Vizcaino north to San Diego was occupied by very disturbed flow containing a series of eddies which appear to have been capable of some transport towards the north, a situation already invoked by Johnson (1960) to explain the northward movement of phyllosoma larvae at this time; again, in October and December 1957 and in January 1958 the eddy extended unusually far south and close to the coast so that northward coastal flow effectively bridged the gap in northward flow from Punta San Eugenio. These data indicate that the correspondence between the start of range extension of pelagic crabs and the appearance of conditions of flow which could transport them northwards from Punta San Eugenio is very good; the flow to the north in the permanent eddy and in the winter countercurrent north of Point Conception are sufficient explanation of transport further to the north once the latitude of San Diego is reached.

During early 1958 there is little evidence of coastal flow to the north except that connected with the permanent eddy, but in October, in the month in which it has been suggested above that northward movement of crabs began again, possibilities of such transport recurred; the permanent gyre extended very far to the south, at least to 29° 30′ N. and was very close inshore at its southern end so that it produced coastal northern transport again from Bahia Sebastian Vizcaino; such transport was then continuous from this latitude to beyond Point Conception, where Davidson Current conditions were in effect. This situation coincided with the first reports of mass strandings at San Pedro.

Once again, in 1959 the same pattern was repeated: from June to September the permanent eddy extended further south than usual and the northward turn of the onshore flow occurred close to the coast, thus placing the beginning of northward flow farther south than usual; additionally, as in July 1957, the appearance of active eddies as far down as Bahia Sebastian Vizcaino gave further possibilities of northern transport. These eddies were contemporaneous with an active countercurrent south of Punta San Eugenio in August, and with Davidson Current conditions in the north from July until January 1960, in which month the final strandings of *Pleuroncodes* occurred in Monterey.

During April 1960, for the first time since the start of this series of observations in 1955, the eddy was so reduced as to be absent from the charts of geostrophic flow which thus showed an uninterrupted southward drift along the whole coast, including the bight to the south of Point Conception, from the latitude of Monterey south to Baja California del Sur; this pattern was repeated in July of the same year and suggests a mechanism which could flush the area north of Bahia Sebastian Vizcaino once more clear of *Pleuroncodes*—a flushing which certainly occurred during this period.

During the rest of 1961 and throughout 1962 the conditions returned to normal and it has been shown already that in these years *Pleuroncodes* was scarcely recorded north of the gap in the coastal countercurrent.

The two oceanic records in April 1958 referred to above may be explained, perhaps, by the same mechanisms as that suggested by Berner and Reid (1961) for occurrence of *Doliolum denticulatum* in the same area at the same time—by the southwesterly flow of a tongue of inshore water from an upwelling on the California coast to the north of Point Conception; it is likely that examination of the zooplankton from these stations would show the presence of a number of southern organisms.

While the oceanographic data are not complete and their correlation with the distribution of *Pleuroncodes* not devoid of subjectivity the correspondence certainly suggests that the circulation as indicated by charts of geostrophic flow is sufficient explanation of the major between-years variation in the distribution of *Pleuroncodes* during this period.

ECOLOGY OF THE PELAGIC PHASE

In the foregoing discussions *Pleuroncodes* has been considered as if it were a normal planktonic species, but it is also a very abundant member of the benthic community at 75–300 m along the continental edge of the west of Baja California, within the Gulf of California and on the west coast of Mexico south to the Islas Tres Marias (Boyd, 1963; Parker, 1963; Perkins, pers. comm.); the known distribution of the benthic phase is shown in Figure 6. If individuals have the capacity to alternate from benthic to pelagic phase and vice versa, a mechanism exists which could explain the irregularity of occurrence of the pelagic phase in the plankton record through the individuals settling on, or leaving, the deposits.

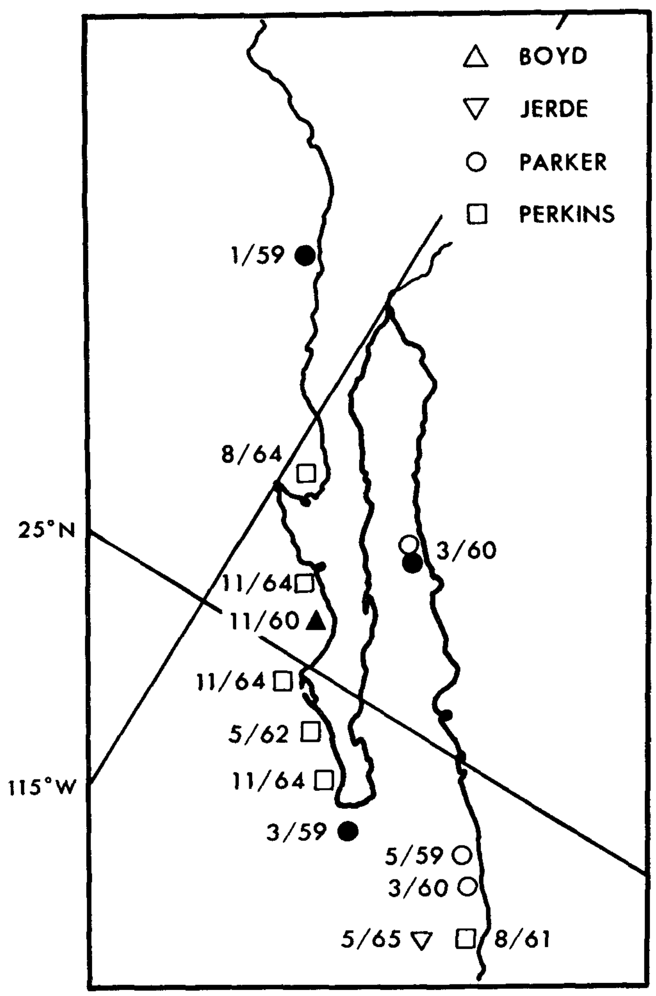


FIGURE 6. Distribution of the benthic records of *Pleuroncodes;* closed circles indicate the use of gear, such as a grab, in which there can have been no possibility of the crabs entering the gear in midwater.

The evidence to support this hypothesis is rather slight, however, and comprises mainly the demonstration by Boyd (1963) that the benthic stock in the area south of Punta San Eugenio examined by him overlapped in length frequency distribution with the pelagic stocks; only at the deepest station at which red crabs were taken by him was the modal length of the stock larger than had been recorded for individuals in the pelagic phase, so that by this criterion only at the deepest station was the population composed of individuals which must have finally settled into the benthic environment. Additionally, the hypothesis of alternation between the two phases is supported by the lack of morphological differentiation between pelagic and benthic individuals: benthic crabs retain the natatory setae fringing the appendages, and pelagic crabs retain the generalized form of the second maxilliped necessary for benthic existence, and only achieved in *Munida gregaria* after the pelagic *Grimothea* stage settles finally into the benthos.

While this is not, of course, direct evidence that alternation between the two phases occurs, it implies that such alternation is not impossible on morphological grounds, and that the pelagic phase is in some way comparable with the *Grimothea* of *Munida* thus being a post-larval extension or recurrence of the planktonic habit of the larvae, which in *Munida gregaria* is variable in duration, and hence in size attained, within rather wide limits (Harrison Matthews, 1932). It is postulated that in *Pleuroncodes planipes* the pelagic phase is comparable with the *Grimothea* stage, and that the lack of morphological specialization enables an individual, when the environment permits, to alternate between pelagic and benthic phases.

It is critical to a discussion of the ecology of the pelagic phase that its duration in the life of an individual should be established. Boyd (1963) inferred from his data on size distribution of benthic and pelagic stocks that the former contains individuals older than 2 years, while the pelagic individuals measured by him were only from 6 to 18 months old. From these data he inferred that it is only at carapace length of 25–28 mm, or about 2 years old, that the pelagic phase is finally abandoned.

A pelagic existence lasting 2 years renders it unlikely that an individual would be maintained throughout this period within the inshore area without being flushed seawards on the southwesterly flow of the California Current, and this could perhaps only be avoided if a considerable part of the period was spent temporarily in the benthic community. The distribution of pelagic crabs in the offshore and oceanic area (Figure 3) indicates that some flushing of individuals from coastal areas does occur.

Although relatively few individuals from the offshore and oceanic areas are available for study these suggest that such populations are mainly of small individuals less than 1 year old. Thus, samples taken in July 1957 by the IATTC/STOR Tuna Spawning Survey around the Revilla Gigedo Islands showed a unimodal population having a modal length of 6 mm, while at Clarion Island the same population was present, but mixed with a second population, comprising less than 10% of the total, having a modal length between 10–12 mm. At Morgan Bank and at the Alijos Rocks the larger of these two size-groups was dominant and included more than 90% of the individuals.

Similarly, during the April 1965 La Pared expedition of SIO, the population of pelagic crabs found in the region of the Revilla Gigedo Islands and further to the southwest were unimodal at 12–13 mm and contained no individuals larger than 17 mm. Small numbers of pelagic crabs taken from tuna stomachs at Clipperton Island by the *Shoyo Maru* were similar to these in size, as were those illustrated by Beklemishev (1960) as being typical of the population he investigated in the oceanic area north of the Revilla Gigedo Islands. Finally, Blackburn (pers. comm.) found that the inshore stocks off Baja California during August 1964 comprised individuals larger than these, except in the single case of a population at the extreme southwest of the station pattern, outside Morgan Bank, which was isolated from those further inshore and consisted only of small individuals similar in size to those listed above.

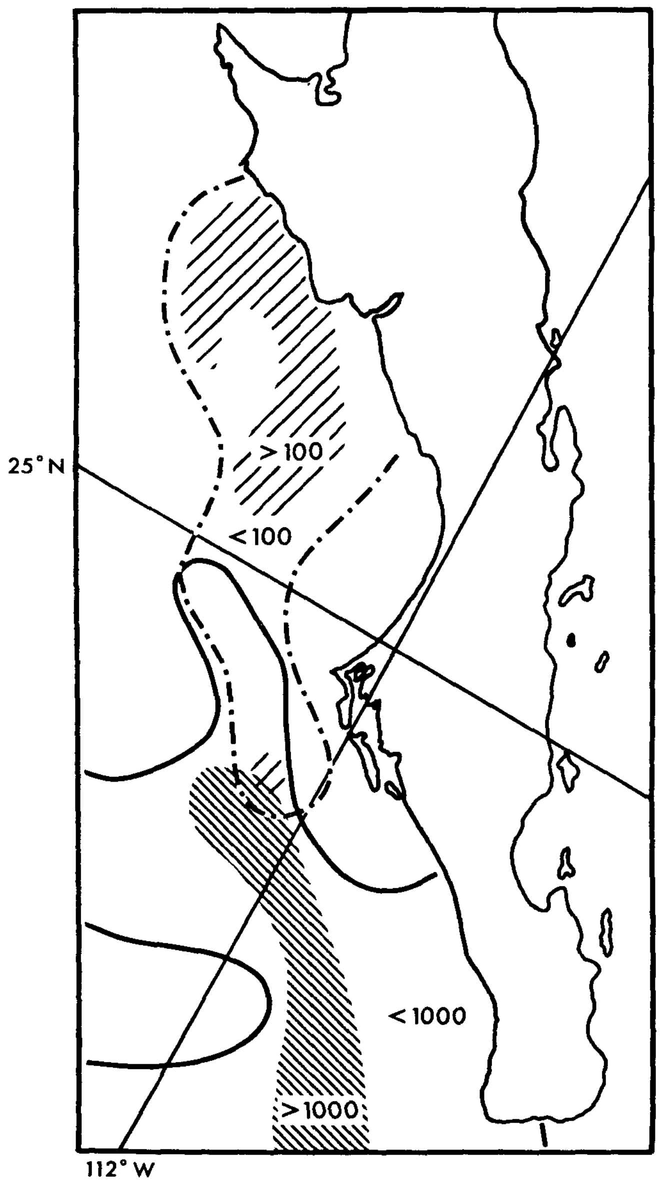


FIGURE 7. The distribution of larval (light shading) and postlarval (dark shading) *Pleuroncodes* during June, 1964.

The inference apparently to be drawn from these data is that beyond the inshore area the flushed-out individuals appear to be derived not from the subadult and adult stocks of the inshore area which Boyd (1963) showed to have modal lengths up to 20 mm, but rather from the larval forms generated by this inshore stock.

There is only a single survey of the distribution of larvae and postlarvae (Cruise TO-64-1 of June, 1964) and this shows clearly the flushing-out of these forms (Figure 7) which are distributed in a linear manner from an origin to the south of Punta San Eugenio so that progressively older individuals were found progressively farther to the south along the main line of flow of the California Current; the numbers of individuals per standard volume did not diminish along the series and there was no indication that the megalops taken in the far south-west were random stragglers, so that the data was consistent with the major part of the population of larval forms being drifted offshore in the direction of the Revilla Gigedo Islands.

Johnson (1960) shows how a planktonic population of crustacean larvae can maintain itself in the California Current for periods of the order of 6 months and then settle effectively enough to maintain an adult population along the coast; it can be surmised that over a similar period (which is probably adequate to attain capability of first settlement to the benthos) a proportion of the larvae of *Pleuroncodes planipes* would similarly be maintained in the eddy system of the California Current without being swept out to sea. These might then commence alternation between the benthic and pelagic phase over the continental edge within their first 2 years of life.

It can be seen from Figure 3 that all the records of occurrence in the oceanic area are within the extension of the California Current, and none are within the Equatorial Counter Current to the south; this distribution carries the implication that there is no likely transport in the mixed layer which could return these individuals to the coast; however, a clear possibility exists of a simple descent to only about 200 meters to achieve return transport on the north-westerly flowing undercurrent.

This possibility is demonstrated, for example, by Reid (1965) who shows that the Pacific Intermediate Water moves north-eastwards towards the coast over much of the area occupied by offshore and oceanic pelagic crabs; the temperature tolerances of *Pleuroncodes* (Table 3) and the depth of benthic records indicate that prolonged residence at depths from 100 to 300 m, which would be required for such transport, are well within the capacity of the species.

Although most of the data on the distribution of pelagic crabs within the oceanic area come from normal oblique zooplankton hauls, integrated for depth, or from surface observations (e.g., Beklemishev, 1960), the only data which contain a depth element indicate that the highest densities of crabs were at depths suggestive of such return transport. During the La Pared cruise referred to above no crabs were observed at the surface west of about 113° longitude, but between 115 and 120° at the latitude of Clarion Island many crabs were taken in subsurface opening-closing net tows (Jerde, Berger, pers. comm.); their vertical distribution showed that they were distributed in the depth range 50–300 m even at night and that some of the largest concentrations (of more than 200 crabs per haul) occurred between 100–150 m, while down to 150–300 m concentrations of up to 60 crabs per haul occurred.

It is therefore postulated that a larva hatched in the inshore area off Baja California may either remain within the coastal eddies for the duration of its larval period and be recruited directly to the stock of pelagic sub-adults within the inshore area, or it may be flushed into the offshore areas while still a megalopa and be recruited to the offshore stocks of pelagic sub-adults. In the latter case while there appears to be a mechanism for purposeful return to the inshore areas, and although the data on the size structure of the population suggests that reproduction does not occur in the oceanic areas, these postulates cannot be directly proved.

Mass mortalities of pelagic *Pleuroncodes* by coastal strandings are well known (e.g., Stimpson, 1860; Matthews, 1932; Glynn, 1961; Boyd, 1963) as are massing of crabs in surface windrows at sea (Shimada in Boyd, 1963) and such observations suggest that at times pelagic *Pleuroncodes* may find themselves in inimical oceanographic situations; Boyd (1963) assumed that oceanic individuals in the California Current extension were in this state and were therefore expatriates contributing nothing further to the maintenance of the species.

This view and that expressed in the previous postulate are perhaps not entirely conflicting, for it is very likely that mortality during the offshore excursion is extremely high, and it may be presumed that the farther to the south-west a population of sub-adults is carried the greater will be the attrition by pelagic fish and other causes of mortality. (It is also very likely that even if the postulate of return migration on the undercurrent is shown to be correct, it will be found that there is a point of no return beyond which the crabs will be, as Boyd suggested for all oceanic individuals, expatriates of no further significance to the species as a whole.

It is now appropriate to consider the relative roles of the pelagic and benthic phase in the biology of the species in the inshore area; even here the proportion of the pelagic stock which at any time has the possibility of changing to the benthic phase is probably rather small, due to the narrow continental shelf to the west of Baja California, since most of the individuals are over depths greater than those at which the benthic phase has been found. Thus, it follows that individual residence times in the pelagic phase must be of the order of weeks or months, rather than days, if indeed such pelagic individuals have previously settled temporarily into the benthos.

During the northern movement of 1958–1960 already discussed the plankton record indicates that for limited periods pelagic crabs disappeared from the CalCOFI samples (as, for instance, during June and July 1959) and this, together with the record of Parker (1963) of benthic crabs off Ensenada during this year and the observations of Sund and Quast (Boyd, 1963) of the occurrence of *Pleuroncodes* in the stomach contents of many species of demersal fish off San Diego, including some with very slight swimming powers (e.g., *Pimelometopon pulchrum* and *Scorpaena guttata*) and which may be presumed to have taken the crabs on, or very close to, the bottom; this again suggests that the disappearance from the plankton record may well be due to settlement into the benthic community.

The sequence of events during the recession from the northern extension of the range again suggests a residence time in the pelagic phase of some weeks or months, and also that the benthic individuals re-entered the pelagic phase and were swept to the south again during this period.

SUMMARY

1. This survey of the ecology of the pelagic phase of *Pleuroncodes planipes* in the California Current indicates that this phase is comparable with the *Grimothea* stage of *Munida gregaria* in that it is an extension or recurrence of the larval habit, but differs from the *Grimothea* state in that no morphological differentiation is involved between the pelagic and benthic phases.

2. It is demonstrated that the distribution of the pelagic phase is restricted to water of the range 9–28° C., and that the bulk of the pelagic population occurs within 100 miles of the coast of Baja California, and that about 75% of the occurrences were in situations with 10 meter temperatures in the range 16–21° C.; the areas in which highest overall frequencies of occurrence and in which the very dense shoals occurred are those in which the influence of water derived from coastal upwelling and hence bearing high standing crops of biota is most likely to be felt.

3. Lower frequencies of occurrences are demonstrated in oceanic areas to the south-west of Baja California, and it is shown that these populations have their origin as larval forms generated over the continental shelf of Baja California and subsequently flushed out of this area on the offshore trend of the California Current. It is shown how a proportion of these could be returned to the coastal areas on the undercurrent formed by the Pacific Intermediate

Water below the California Current and its extension to the south-west.

4. Seasonal variation of occurrence of pelagic individuals in the coastal areas is rather slight, consisting only of a tendency for higher frequencies of occurrence in the first half of the year; however, the annual variation is very striking and a very extensive movement towards the north can be demonstrated during the years 1958–1960, culminating in occurrences to the north of Point Conception. This movement can be explained by reference to the changed patterns of transport in the oceanographic regime during this period, the patterns of geostrophic flow corresponding very well to what is required to explain the observed movements of crabs.

5. The relation between the benthic and pelagic phases appears to be complex, and it is suggested that during the first two years of life an individual may either be retained within the coastal eddies and alternate between benthic and pelagic environments, or it may be flushed out to the south-west with the possibility of returning subsequently to the coastal areas on the undercurrent within the first year or so of life; individuals older than this have not been found far offshore and are supposed either to have succumbed or to have returned to the coastal area. After the end of the second year of life the benthic habit appears to be finally adopted and no individuals older than this have been taken in the pelagic phase.

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