

LARVAL DRIFT AND POPULATION STRUCTURE OF THE PELAGIC PHASE OF *PLEURONCODES PLANIPES* (STIMPSON) (CRUSTACEA: GALATHEIDAE) OFF THE SOUTHWEST COAST OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

Reproductive areas, larval and postlarval drift, and population structure of the red crab *Pleuroncodes planipes* (Stimpson) are described using samples obtained off the southwest coast of Baja California in May, June, August, and November 1986, July 1988, and September 1993. The highest abundance of larval and postlarval stages were found in May. Based on the ages of the most abundant postlarval stages, the most intense reproductive period was probably in January and February. The larval production recorded June to November indicated sporadic reproduction. We confirmed that the nearshore regions located near Bahía Magdalena 24° N and Punta Eugenia 28° N are the primary nursery areas. Seasonal hatching areas were in the vicinity of upwelling regions. Major production of larval stages starts in the south. At the end of the reproduction season, the highest abundance is in the north suggesting this species has a seasonal reproduction cline keyed to the normal upwelling cycle along the west coast of Baja California. From the hatching areas, a larval drift caused by offshore surface transport, in turn caused by the upwelling, was seen. A one-celled cross-shelf circulation is proposed to explain the offshore larval drift at the west coast of Baja California. This process could play an important role in the recruitment of postlarval stages to the adult epipelagic population. Two size groups of adults were found in the water column. Both groups were found simultaneously only inshore and during the seasonal reproductive months (spring). The group of largest size found inshore are individuals of the benthic phase that may have migrated into the pelagic zone for reproduction. Using data of this study and the current available information, a conceptual model of the life history of *P. planipes* along the west coast of Baja California is proposed.

Distribution of the planktonic organisms is influenced mainly by the drift caused by ocean currents and advection events (McConaugha, 1992). For the red crab *Pleuroncodes planipes* (Stimpson, 1860), the dispersion process begins at hatching. The larval phase is about 130 days (five zoeal stages) (Boyd and Johnson, 1963) and postlarval (2 to 6 mm CL) about 4 or 6 months. Larval and postlarval stages can be potentially transported by surface Ekman transport (tens of kilometers) and cold-water filaments (hundreds of kilometers) perpendicular to the coastline. However, this offshore larval drift could be turned off by eddies (Hewitt, 1981; Poulain et al., 1987) or could be weakened by onshore advection caused by an El Niño event (Brodeur et al., 1985). A pelagic population composed of juveniles and adults is regularly found offshore. The individuals reach sexual maturity in about 1 yr (16 mm standard carapace length). The pelagic phase finishes when adults assume a benthic life (about 2 yrs old and about 32 mm standard carapace length) (Boyd, 1967; Longhurst, 1966). Several studies claim that pelagic and benthic phases do not have a clear separation (Blackburn and Thorne, 1974; Alvaríño, 1976; Blackburn, 1977). In this work, we have evidence that vertical distribution of both phases could overlap at least during the reproductive season. The pelagic larvae and adults of *P. planipes* seem to

play an important role in its distribution and the maintenance of genetic variation within the species. The year to year fluctuations in population size display an adaptation of its life cycle to regional oceanography.

Off western Baja California, anticyclonic wind-stress curl dominates the offshore portions of the California Current region. Close to the coast, the wind-stress curl tends to be cyclonic (Bakun and Nelson, 1991). Thus, Ekman divergence dominates at the ocean surface near the coast, and Ekman convergence dominates the offshore region. Strong upwelling usually occurs from March to June driven by prevailing northerly winds. A positive upwelling index is usually recorded throughout the year along Baja California (Bakun and Nelson, 1977). Cold water filaments accompanied by energetic jets with speeds often greater than 50 cm s^{-1} are a regular oceanographic feature of regions where seasonal coastal upwelling is a dominant process (Brink, 1992). Offshore Ekman transport could cause a complex larval drift pattern influenced by eddies, plumes, and jet streams (Power, 1986; McConaughy, 1992). Vertical profiles of the survey made during 1986 along the west coast of Baja California were shown by Gómez and Sánchez (1995). In May, the isotherms $< 15^\circ \text{C}$ were found deeper offshore than inshore, where they were found near the surface. We observed isotherms sloping generally upward toward the coast over the continental shelf. This indicated upwelling processes which could cause larval drift of the red crabs. In August and November, the water column was stratified showing a weak mixing. These data suggest that strong offshore transport is enhanced during the first 6 mo of the year.

The Galatheididae family includes about 230 species (Boyd, 1967; Zeldis, 1985). Five known species, (*Pleuroncodes monodon* (Milne Edwards), *Cervimunida johni* Porter, *Munida gregaria* (Fabricius), *M. rugosa* White, and *P. planipes*), exhibit the phenomena of mass occurrences of local sustained populations, mostly in highly eutrophic regions along Eastern current systems (Longhurst, 1967, 1969; Rowe et al., 1985). The highest abundance of *P. planipes* has been found near Bahía Magdalena (24°N), although its range is from California, USA to Nicaragua, and includes the Gulf of California (Boyd, 1967; Aurióles, 1992). Because of its high abundance, several studies have examined aspects of the general biology of *P. planipes* in the California Current System; vertical distribution (Alvaríño, 1976; Blackburn and Thorne, 1974), larval development (Boyd, 1960; Boyd and Johnson, 1963), ecological importance (Longhurst et al., 1967; Blackburn, 1969, 1977; Walsh et al., 1974; Morales and Arvizu, 1976; Rowe et al., 1985; Maeda et al., 1993), fishery potential (Longhurst, 1969; Kato, 1974), and as a biogeographic indicator (Glynn, 1961; Boyd, 1967; Longhurst, 1966; Alvaríño, 1976; Brinton, 1979; McLain and Thomas, 1983; Smith, 1985). Most of these studies have been made on adults (Aurióles, 1992; Aurióles et al., 1994; Guzmán and Aurióles, 1992). However, ecological studies relating larval drift to the upwelling regime and circulation of water have had less attention (Gómez and Sánchez, 1995).

Our objectives were to determine the season and areas of reproduction of *P. planipes*, the environment in which the most important production is found, and the distribution and abundance patterns as an effect of the larval drift from the center of distribution found along the southwest coast of Baja California. We also wanted to determine the population structure of the pelagic adult swarms where postlarvae are recruited. Previous works published in Russian summarize available literature on the life cycle of *P. planipes* (Kashkina and Kashkin, 1993a, 1993b). Results obtained during the present study along

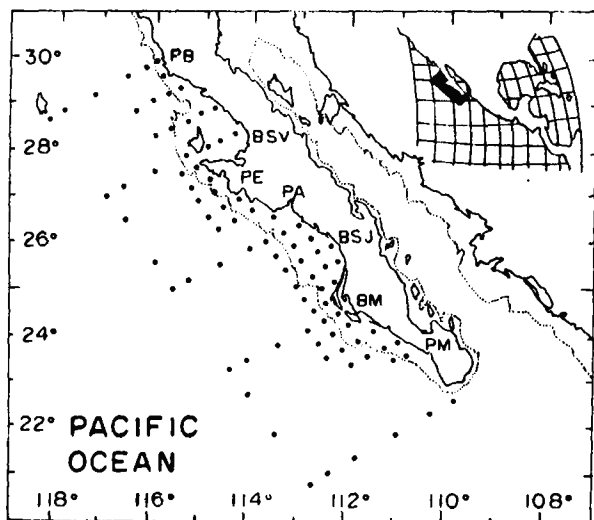


Figure 1. Stations sampled along the west coast of Baja California. PB = Punta Baja; BSV = Bahía Sebastián Vizcaíno; PE = Punta Eugenia; PA = Punta Abreojos; BSJ = Bahía San Juanico; BM = Bahía Magdalena; PM = Punta Marquez. Dotted line shows 200 m isobath.

with the current literature information were coalesced into a conceptual model of the life cycle of *P. planipes* along the western coast of Baja California.

MATERIALS AND METHODS

The larval and postlarval stages of *P. planipes* were collected during six oceanographic cruises made along the west coast of Baja California (21 - 29° N) during May (61 stations), June (28 stations), August (23 stations), and November of 1986 (58 stations), July 1988 (37 stations), and September 1993 (20 stations) (Fig. 1). Samples were obtained using paired Bongo nets, with mesh of 333 μ m and 505 μ m, sampling from 210 m as described by Kramer et al. (1972).

The larval stages collected in the 505 μ m net were identified and counted (minimum total length of zoea stage I is 2.6 mm). Samples were analyzed in their entirety. The zooplanktonic biomass was measured using the wet displaced volume method and normalized to ml 1000 m^3 using a calibrated flowmeter according to Kramer et al. (1972). We have followed Boyd (1960) in designating the five larval stages of *P. planipes*. Zoael stages I, II, and III were grouped as early larval stages and zoeas IV and V as later larval stages. The morphology of the postlarval stages (first juveniles) of the red crab *P. planipes* were easily identified because they resemble miniature adults. The smaller post-zoea stage have the pleopodal exopods armed with long plumose setae (caparace length: 2.5-3.0 mm), while those of the first postlarvae are non-setose and rudimentary (caparace length: 3.4-4.1 mm) (Brinton, 1979). Zoael stages I-III did not show significant day-night differences in abundance ($P > 0.01$), therefore both day and night samples were used to determine abundance of these stages. Zoael IV-V and postlarval stages showed significant day-night differences in abundance showing greater abundance during the night ($P < 0.01$) (Fig. 2). These stages were

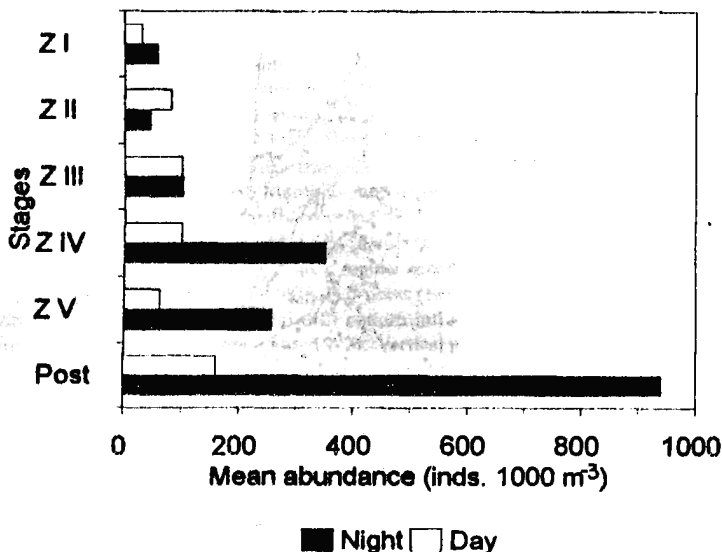


Figure 2. Night/day mean abundance (inds. 1000 m⁻³) of larval and postlarval stages of *Pleuroncodes planipes*. Combined data of abundance for all stations for May, June, August, and November 1986 caught with oblique bongo tows.

analyzed using only samples collected at night. For analysis, all larval and postlarval stage data were scaled to the number of individuals in 1000 m³ of filtered water (Kramer et al., 1972).

As an indicator of offshore Ekman transport, the monthly averages of the upwelling index (metric tons sec⁻¹ 100 m⁻¹ of coastline) for 1986 were obtained from the Pacific Fisheries Environmental Group, National Marine Fisheries Service, Pacific Grove, CA, for the areas near Punta Eugenia (27° N, 116° W) and Bahia Magdalena (24° N, 113° W). The study area was divided into three latitudinal regions, based on the coastal topography (points and bays), and offshore and inshore regions, separated by the 200 m isobath (continental slope), to analyze the geographical variations in the abundance of planktonic stages of the red crab.

Adults were identified by sex. Wet weight was determined with a balance (± 0.1 g). Caparace length (CL) of juveniles and adults, measured from the tip of the rostrum to the posterior midpoint of the caparace, was determined using an ocular micrometer (Blackburn, 1977). Several authors, Aurióles (1992) and Guzmán and Aurióles (1992), have measured the standard caparace length (SCL) from the base of subrostral spines of the rostrum to the posterior midpoint of the caparace. Comparing size measured both ways was possible by use of a linear correlation between SCL and CL made using 82 individuals with a sex ratio of about 1:1.

RESULTS

Environmental Conditions.—Along the west coast of Baja California there is a strong seasonal signal in the distribution of sea surface temperature (SST). Seasonal variability

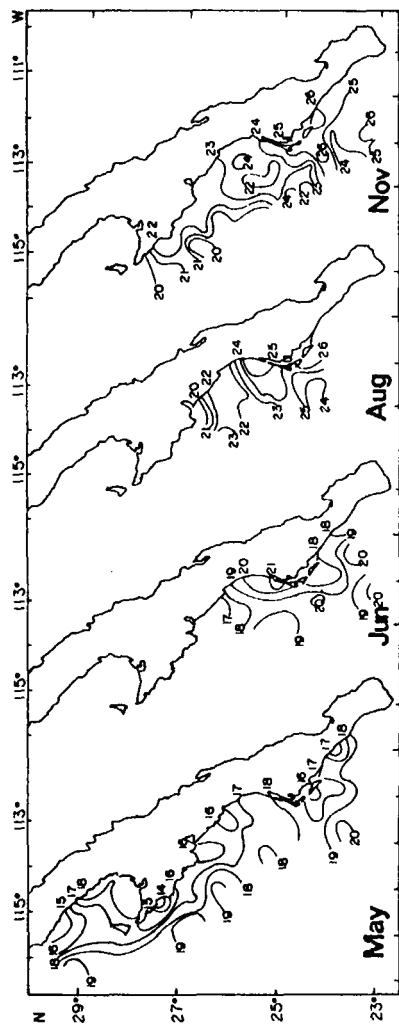


Figure 3. Sea surface temperature distribution along the west coast of Baja California during 1986 in May, June, August, and November.

Table 1. Seasonal variation of zooplanktonic biomass ($\text{ml } 1000 \text{ m}^{-3}$) along the west coast of Baja California.

	1986				1988	1993
	May	June	August	November	July	September
Sample size	61	28	23	57	29	13
Average	273.9	239.0	209.5	63.9	306.3	121.5
Standard deviation	473.2	305.7	326.7	110.7	454.3	82.9
Minimum	15.6	15.0	6.7	0.2	35.2	37.2
Maximum	2220.0	1021.0	1316.1	727.9	1840.0	281.0

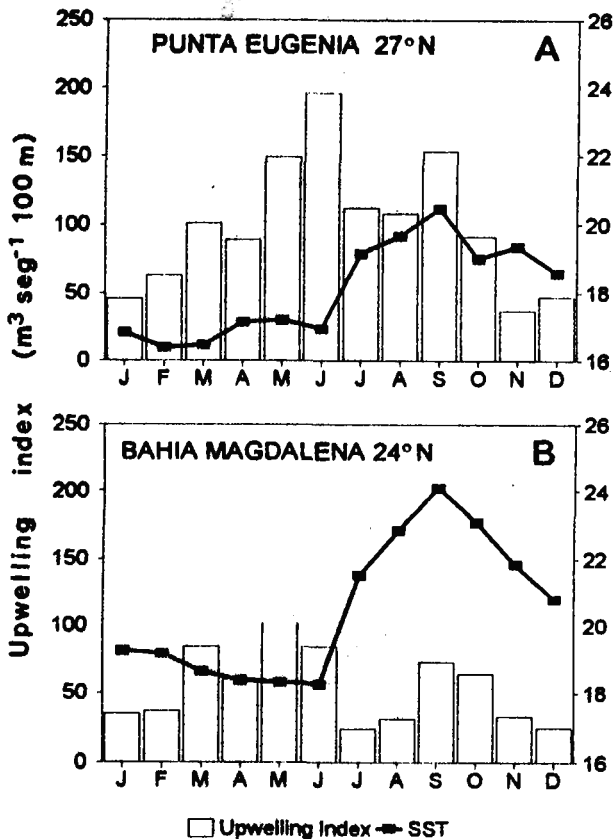


Figure 4. Monthly upwelling indices and mean SST during 1986 at Punta Eugenia (27° N , 116° W) (A), and Bahia Magdalena (24° N , 113° W) (B). Data obtained from Pacific Fisheries Environmental Group, National Marine Fisheries Service, Pacific Grove, CA.

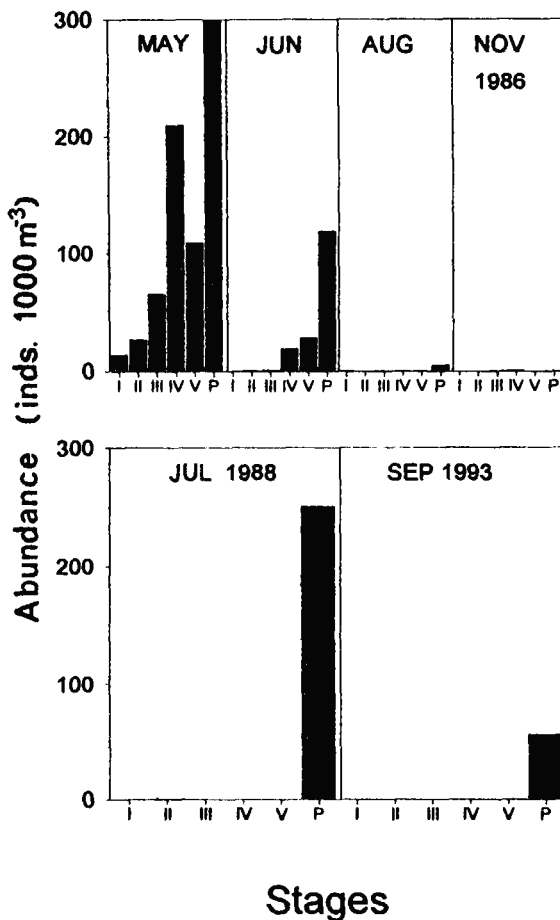


Figure 5. Total abundance (ind. 1000 m⁻³) of the planktonic stages of *Pleuroncodes planipes* during May, June, August, November 1986, July 1988, and September 1993.

was described using data obtained during four oceanographic surveys made during 1986. During May, when local upwelling is strongest, the water along the coast is much colder than the water further offshore (Fig. 3). During June, the SST ranged between 17 and 20.5° C, showing a small latitudinal gradient from 20° C in the south to 17° C in the north. However, there remained areas with a low SST near Bahía Magdalena (Fig. 3). From August to November, the northward moving core of equatorial water may underlie

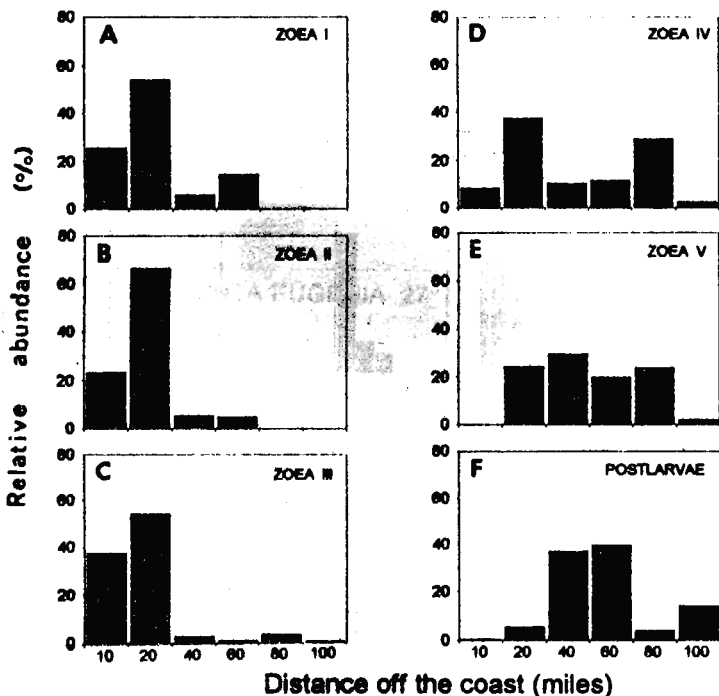


Figure 6. Relative abundance (% of total population at all stations) of the planktonic stages of *Pleuroncodes planipes* as a function of distance from coast (A-F).

a coastal undercurrent bringing tropical surface water up from the south with a recorded SST up to 26° C. An isotherm of 20° C was found in the sampled area in the north close to Bahia San Ignacio (27° N) during August and at Punta Eugenia (28° N) in November. The SST's were higher inshore than offshore, the reverse of the distribution in May and June (Fig. 3). The winds were calm and upwelling was in a relaxed state.

The monthly average upwelling indices for 1986 (metric tons sec⁻¹ 100 m⁻¹ of coast line) indicated the most intense upwellings recorded were in May, June, and September (>150) at Punta Eugenia (27° N), and in March, May, and June (> 82) at Bahia Magdalena (24° N). Positive upwelling indices were found throughout the year. The SST was lower in the first 6 mo of the year and increased in the second half of the year for both regions (Fig. 4A, B).

Seasonal Variations in Zooplankton Biomass.—Zooplanktonic biomass had its highest mean value in May, decreasing progressively during the rest of 1986. Lower zooplanktonic biomass was also found in September 1993, in a close relationship with the increase of SST. The highest mean biomass was recorded during July 1988 (Table 1). There was

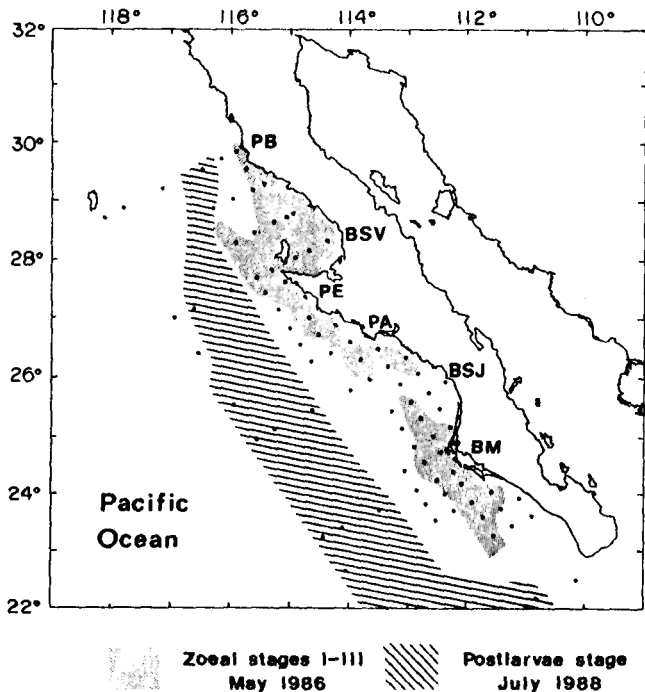


Figure 7. Inshore hatching areas, indicated by early zoeal stages (I-III) during May 1986 and offshore breeding areas, indicated by postlarvae stages, during the most extensive oceanographic survey in July 1988.

a notable decrease of biological production during the end of summer and start of autumn. Gómez and Sánchez (1995) found the highest concentrations ($> 1000 \text{ ml } 1000 \text{ m}^{-3}$) inshore, near Punta Eugenia, Punta Abrejos, and Bahía Magdalena in May, south of Bahía Magdalena in June, and close to Punta Abrejos in August. During November, zooplanktonic biomass below $500 \text{ ml } 1000 \text{ m}^{-3}$ was found along the west coast of Baja California. These high density centers coincided with lower SSTs and where mixing layers were found.

Seasonal Variation in Larval and Postlarvae Abundance.—During May, June, and August 1986, postlarvae were the most abundant of all stages. From the five zoeal stages, zoeas IV and V were the most abundant zoeal stages during May. In June, the abundance of postlarvae and later stages IV and V decreased. The densities of early larval stages decreased to $< 1 \text{ ind. } 1000 \text{ m}^{-3}$. In August and November, the abundance of all planktonic stages was $< 5 \text{ ind. } 1000 \text{ m}^{-3}$. In July 1988 and September 1993, only postlarval stages were found (Fig. 5).

Table 2. Mean and range of standard carapace length (mm) of *Pleuroncodes planipes* showing a latitudinal cline of size along the west coast of Baja California, Mexico. Punta Eugenia area (27° to 30° N), Bahía San Juanico (25° to 27° N), and Bahía Magdalena, (23° to 25° N). Size range is shown in parenthesis.

Latitudinal area	Mean		Range		Mean		Range	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
	1986							
	May		June		August		November	
Punta Eugenia	27.45	(23.1-32.8)						
Bahía San Juanico	32.18	(20.7-45.0)	28.90	(22.0-34.4)	21.23	(16.0-32.8)	20.14	(10.6-30.5)
Bahía Magdalena	20.26	(10.0-38.9)	22.41	(10.4-34.0)	22.27	(16.0-34.0)	18.79	(16.0-22.0)
	1989*				1990*			
	February		July		March		September	
Punta Eugenia			25.90	(17.0-27.0)	27.65	(20.0-48.0)	31.85	(25.0-33.0)
Bahía San Juanico	23.45	(19.0-32.0)	25.95	(16.5-31.0)	24.75	(18.0-33.0)	26.53	(22.3-36.3)
Bahía Magdalena	23.85	(15.0-39.0)	25.40	(15.0-29.0)	24.02	(14.0-33.0)	26.13	(20.0-35.0)

*Data obtained from Guzmán (1995) via bottom net trawls.

Inshore-Offshore Distribution.—We found a clear ontogenetic inshore-offshore distribution pattern. Early larval stages were found mainly inshore (< 20 mi) with the lowest abundance found between 40 and 60 mi. These are seldom found further offshore than 80 mi (Fig. 6A-C). Later larval stages were abundant in both regions (Fig. 6D-E). Postlarval stages were mainly offshore, peaking just offshore of the shelf-break (40 to 60 mi) (Fig. 6F). An example of these distribution patterns is shown with the inshore hatching areas indicated by early zoeae stages located between Punta Baja to Bahía San Juanico and near Bahía Magdalena during May 1986, and the distribution of postlarvae stages found in our most extensive oceanographic survey of July 1988 (Fig. 7).

Population Structure of the Adult Pelagic Phase.—In 1986, adults were most abundant in May and June, decreasing during warmer months (August, November) (Fig. 8A-D). In May, a bimodal distribution of CL was found, indicating two populations (Fig. 8A). One ranged from 10 to 30 mm and the second > 30 mm. Both groups had an approximate 1:1 sexual ratio. Individuals of the oldest group were found inshore south of Bahía San Juanico (25° N). Standard carapace length (mm) of *P. planipes* along three latitudinal regions (Punta Eugenia area 27° to 30° N, Bahía San Juanico 25° to 27° N, and Bahía Magdalena, 23° to 25° N) showed a latitudinal cline. During 1986, red crabs were collected with a bongo net in the water column (this study). During 1989 and 1990, these were collected with a bottom net sampling benthic population (Guzmán, 1995) (Table 2). Data showed the biggest individuals were found northward except August 1986 and February 1990 when no significant latitudinal differences were found ($P > 0.01$).

Size-Weight of the Pelagic Phase.—This relationship is described by a potential weight-length equation $W = a(CL)^b$ (where a and b are constants of the potential regression) obtained from all surveys for each sex. An allometric growth was found. For males $W = 3.42 \times 10^{-4}(CL)^{2.883}$ and $r = 0.94$; and for females $W = 4.74 \times 10^{-4}(CL)^{2.763}$ and $r = 0.92$

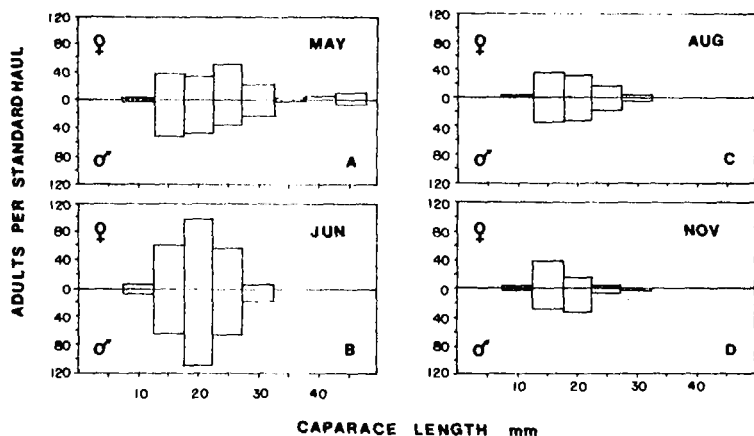


Figure 8. Population structure and length-frequency of the pelagic phase of *Pleuroncodes planipes* during May (A), June (B), August (C), and November (D) 1986.

Using this equation, we calculated the wet weight by sex as a function of size. Curves of biomass indicated June 1986 was the month with the highest pelagic phase biomass. This production decreased during the warmer months (Fig. 9A-D). During May 1986, the group of 10 to 30 mm CL contributed more biomass than the second group (> 30 mm) (Fig. 9A).

The linear regression ($n = 82$) to convert CL (including rostrum) to SCL (not including rostrum) is: $CL = 7.09 + 1.002 SCL$ and $r = 0.94$

DISCUSSION

Reproduction of *P. planipes* along the west coast of Baja California has a clear seasonality keyed to the regional oceanography. Despite a wide year-to-year seasonal variability in the duration and intensity of reproduction (Boyd, 1960; Boyd and Johnson, 1963; Longhurst, 1968; Kato, 1974; Alvaríño, 1976), it occurs during the first half of the year. Peak postlarval abundance in 1986 occurred during May (54 % of total abundance). The smaller proportion of early zoeal stages compared with more developed stages suggests the sampling period did not include the time of the most intense reproductive activity of the species. Based on mean age calculated from data, published by Boyd and Johnson (1963), the high postlarval abundance found in May 1986 was hatched in January and February. The lower abundances of larvae found during second half of year (June to November 1986) and the absence of zoeal stages during July 1988 and September 1993 have been interpreted as a result of sporadic reproduction or from high mortality rates.

Based on these biological criteria, a conceptual model of the life cycle of *P. planipes* is described separating two different temporal environments: the reproductive period (cool season) (Fig. 10A) and the non-reproductive period (warm season) (Fig. 10B).

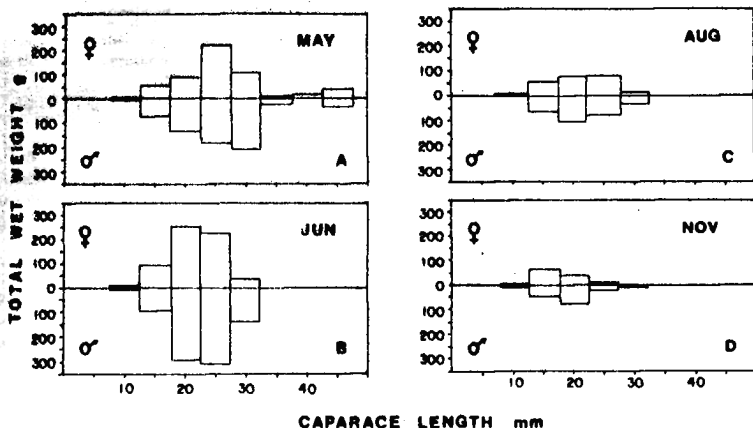


Figure 9. Total wet biomass (g) of the pelagic phase of *Pleuroncodes planipes* during May (A), June (B), August (C), and November (D) 1986.

Reproductive Environment (cool period).—During the first 6 mo of a year, lower SSTs are dominant along Baja California. There is a gradual increase in the upwelling index from January reaching its highest intensity in late spring and early summer (Figs. 3,4).

Hatching areas, indicated by early zoeal stages (97 % of all larval stages I and II) and ovigerous females, were found inshore close to Punta Eugenia and Bahia Magdalena in May. These results confirm that these areas are the most important centers of hatching (Boyd, 1960; Longhurst, 1968) and are year-to-year, important primary breeding, hatching, and nursery areas for the species. Both areas showed upwelling characteristics having inshore-offshore SST gradients (12 to 15° C) (Figs. 3,4). It is believed that such capes are often associated with areas of enhanced upwelling or upwelling plumes associated with intense cyclonic wind-stress curl (Kosro and Huyer, 1986, Bakun and Nelson 1991; Brink, 1992).

Distribution patterns of each stage of development indicated a larval drift offshore. During active upwelling events (May and June), early larval stages of *P. planipes* consistently occupied the inner shelf region while the highest abundance of postlarvae were found in the outer shelf and slope regions. Bakun (1973, 1985), Nelson (1977), Huyer (1983), and Lynn and Simpson (1987) reported the most intense offshore Ekman transport occurs during March and May at Punta Eugenia and Bahia Magdalena. During this period, surface current parallels the coast with only a slight offshore component reaching a maximum strength of about 15 cm s⁻¹ (Bakun and Nelson, 1977). Our data of monthly upwelling indices demonstrated the strongest offshore Ekman transport occurred during March to June. This information and inshore hatching areas support the idea that upwellings are responsible for larval drift offshore. However, these cold filaments show the boundary between upwelling water and resident water to be very irregular with eddies and plumes of near-shore waters moving offshore. Kosro and Huyer (1986) and Brink

(1992) reported plumes of cold water, some measuring hundreds of kilometers in length and with a net offshore transport, in northern California. Drogue trajectories in the California Current system during 1985 and 1986 showed a complex offshore flow pattern (Poulain et al., 1987).

Detailed studies of cross-shelf circulation at the southern part of Baja California have not been made. Nevertheless, a cross-shelf circulation model based on a one-celled structure during the active upwelling phase upwelling reported by Huyer (1983) at the Oregon shelf, with the offshore flow in the surface Ekman layer and the onshore return flow in the geostrophic interior, could explain our results where larval and postlarval stages of *P. planipes* occupy inshore-offshore habitats. It is not known whether the structure and dynamics observed off Oregon are typical of the upwelling zone along the entire coast, though some of the same features have been observed off Baja California (Huyer, 1983). Peterson et al. (1979) proposed a cross-shelf circulation based on a two-celled model to explain the maintenance mechanism of zonation for several neritic copepod species in the Oregon upwelling system during active upwelling. However, a cross-shelf circulation model (one-celled) could be supported by results obtained off northern Baja California by Barton and Argote (1980). They observed strong vertical shear in the along-shore flow, with strong (50 cm sec^{-1}) southward and offshore flow at the surface, and a weak (5 cm sec^{-1}) southward flow at the bottom over the midshelf, all supporting the inshore-offshore transport during early summer.

In the present study, early larval stages showed no day/night abundance difference suggesting a narrow vertical distribution. Older larvae and postlarvae stages showed significant abundance differences indicating a wide vertical distribution. These stages could simply have avoided the net. Our results supported the ontogenic vertical distribution proposed by Alvaríño (1976) in which younger individuals are distributed near the surface and older animals deeper. Although early larval stages are found near the surface where offshore advection is a dominant feature, these zoeal stages apparently are able to be below the Ekman layer (ca. 0 - 20 m) and to avoid the offshore transport. This last is supported because they are seldom found further offshore than 20 mi. They are about 6 to 18 d old (Boyd and Johnson, 1963), which is enough time for them to drift between 43 and 129 mi in a straight line in a mean surface current velocity of 15 cm^{-1} . This cross-shelf circulation has been reported to be a maintenance mechanism of zonation for the euphausiid neritic species *Nyctiphanes simplex* along the west coast of Baja California (Lavaníegos, 1994; Gómez, 1995). When the upwelling reached its maximum offshore transport, late zoeal and postlarvae could be found within the Ekman layer mainly at night. It is possible the epipelagic adults drifted offshore by surface Ekman transport (Fig. 10A).

The peak of reproduction of *P. planipes* (February to March) occurs a little before the months of maximum offshore transport (May to June). The highest offshore surface transport occurs at the end of the seasonal reproduction, when most of the late larvae and postlarval stages are moved by a strong cross-shelf transport (May to early June) to the offshore adult epipelagic shoals. This explains the ontogenic inshore-offshore distribution found. This could be a reproductive strategy keyed to the regional oceanography which favored larval survival displaying a relatively low larval drift for its early stages. During an El Niño event, changes in the hydrographic conditions associated with onshore surface drift and reduced summer upwelling could explain inshore distribution of several offshore ichthyoplankton species (McLain and Thomas, 1983; Brodeur et al., 1985; Smith,

1985). This year-to-year variation of offshore transport could vary the offshore recruitment of postlarvae. However, El Niño 1986-1987 was weak and its influence on the community structure of the euphausiids in the southern part of Baja California was small (Gómez et al., 1995).

Larval production is supported by both pelagic and benthic populations. The relative contribution has not been estimated. During the cold season (December to April), the benthic red crab including individuals between 18 and 30 mm SCL (25.1 to 37.2 mm CL) had an offshore-inshore movement showing a high abundance close to the coast (depths between 50 - 100 m) coinciding with seasonal reproduction (Aurioles, 1992). Benthic individuals apparently start their inshore-offshore movement in spring (Fig. 10A). During the reproduction season, part of this population may make daily vertical migrations, which was suggested by the > 30 mm group found in the water column during May 1986. Vertical migration of *P. planipes* is a process in which part of the benthic population could migrate close the surface during day or night looking for food (Boyd, 1967; Blackburn and Thorne, 1974; Blackburn, 1977) or to hatch their eggs. Similar reproduction strategy near the coast has been found in other galatheid crustaceans like *Munida gregaria* (Zeldis, 1985) in the subantarctic island of New Zealand and other pelagic crustacean decapods like *Euphyllax dovil* of the tropical Pacific coast (Norse and Fox-Norse, 1977).

Dense adult surface swarms have been found inshore during the first half of the year at coastal upwelling regions (Aurioles et al., 1994; personal observations) that have a high primary and secondary production (Roesler and Chelton, 1987). Our observations during May showed that the highest zooplanktonic biomass was found near Punta Eugenia and Bahía Magdalena, coinciding with upwelling regions and the possible red crab hatching areas. High zooplankton production recorded in the upwelling region represents high food availability, both for larvae and adults. Longhurst et al. (1967), Blackburn (1969), Arvizu et al. (1974), and Smayda (1975) reported pelagic adults of *P. planipes* frequently had massive concentrations in regions with good feeding.

Pelagic and benthic populations have a clear separation between them (Boyd, 1967). However, during the settlement process the time they spend between phases is not yet known. The results of this study showed, at least during the reproductive season, pelagic and benthic individuals could be mixed in the water column. However, the fact that individuals > 32 mm CL were found only inshore in Bahía San Juanico makes it unclear if a mixing between different sizes is a general feature for the species. This has not been found in other regions, particularly in the reproduction areas of Punta Eugenia and Bahía Magdalena. Longhurst (1966) and Alvarifo (1976) have reported the possibility of alternations between pelagic and benthic phases in the life of the same individual. During the reproduction season, an annual mass stranding of pelagic red crabs *P. planipes* occurs in Bahía Magdalena. This population was predominantly composed of animals between 13 to 20 mm SCL with a female-biased sexual ratio suggesting red crabs debilitated by reproductive activity (Aurioles et al., 1994). Our results did not show a bias in the sexual ratio probably because our samples were caught in the water column and were in better condition. A small part of the stranded individuals reported by Aurioles et al. (1994) were between 20 and 27 mm SCL overlapping with the size of the benthic population. Likewise, Blackburn and Thorne (1974) and Blackburn (1977), by means of acoustic records, found two groups of sizes, 18 to 27 mm and 28 to 35 mm (CL). The second group included individuals presumably from the benthic phase. These works support the hy-

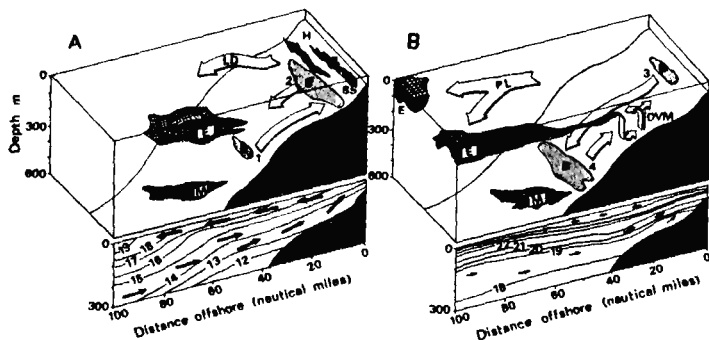


Figure 10. Conceptual model of the inshore-offshore movements during the life cycle of *Pleuroncodes planipes* along the west coast of Baja California. (A) reproductive season (cool period, Jan-May) and (B) non-reproductive season (warm period, June to November). H = Hatching area, SS = Surface swarms (adults), LD = Offshore larval drift, PD = Offshore postlarval drift, EP = Epipelagic population (0 to 200 m), MP = Mesopelagic population (475 to 600 m) (Alvaríño, 1976), BP = Benthic population, DVM = Diel vertical migration. Benthic population: 1 = Offshore-inshore movement (Dec-Apr), 2 = Start of inshore-offshore movement (May), 3 = Inshore-Offshore movement (Jun-Nov), 4 = Start of offshore-inshore movement (Dec) (Aurióles, 1992).

pothesis that during the reproductive season organisms of both size groups could be found in the water column in the same coastal regions.

Non-Reproductive Environment (warm period).—During the second half of year, a high increase in the SST dominates the southwest coast of Baja California (Figs. 3,4). During July to November, a stratification of the water column is a dominant feature. A northward moving core of equatorial water may underlie a coastal undercurrent bringing tropical surface water up from the south, and the along shore component of mean monthly geostrophic velocity is positive (southward flow) (Hickey, 1979 p. 215). The inshore-offshore transport was at a minimum.

During June, August, and November, surface flow from southern regions to higher latitudes causes the decreasing or the relaxation of the upwelling. The surface current changes direction and slows to less than 5 cm s^{-1} (Reid et al., 1958; Gómez and Vélez, 1982). During these months, the inshore-offshore ontogenic distribution of *P. planipes* was less evident.

Although *P. planipes* is considered a eurythermic species (Boyd, 1967, Aurióles, 1992), its early larval stages were found in a narrow range of SST at inshore regions featuring low SST's (14.5 to 18.5°C) during the first half of the year. If we consider that vertical distribution of red crab larvae is in the mixing layer (Boyd, 1960; Longhurst, 1968) this range could be cooler. Sea temperatures ranged from 12 to 18.5°C in the mixing layer where zoeas I and II were collected (Gómez and Sánchez, 1995). Of the small part of the red crab population reproducing when the SST increased (19 to 24°C) (June to November), the lower abundance of larval stages suggests that the probability of survival was considerably lower. Results obtained by Boyd and Johnson (1963) support this idea. The

mortality rate of the larval phase was low at lower temperatures under laboratory conditions. Stratification of the water column was found over all the study area causing a low rate of reproduction of the red crab and probably a low rate of survival of early larval stages. This same relation was determined with larval stages in other galatheids like *P. monodon* (Fagetti and Campodonico, 1971) and *Galathea rostrata* (Gore, 1979). A possible reproductive strategy of adults using favorable habitat, which is indicated by distribution and abundance of the planktonic stages and ovigerous females, has been proposed before (Longhurst, 1968; Aurióles, 1992; Gómez and Sánchez, 1995).

During late May to June, dense postlarvae swarms (>1000 org/1000 m^3) are usually found far off the coast (> 40 mi) that presumably recruit to the offshore epipelagic population about 4 to 6 mo after their hatching (Fig. 10B). During this period, the biomass decreases drastically. However, small postlarvae may be able to filter phytoplankton and feed on small zooplankton (Morales and Arvizu, 1976; personal observations). The California current carries out the juveniles (< 15 mm CL) far out to the south-west, to 130° W. In the open ocean, an area of pelagic red crab reproduction occurs as indicated by ovigerous females (Boyd, 1967; Longhurst and Seibert, 1971).

During late spring, the adult benthic red crabs begin to migrate from inshore reproductive areas to the offshore shelf break (100 - 200 m), or possible deeper waters, in late summer. The return "offshore-inshore" movement could start during late autumn (Aurióles, 1992; Guzmán and Aurióles, 1992). This coincides with the unimodal frequency distribution we found during the warm months.

Adult pelagic populations have wide daily vertical migrations having a epipelagic (0 - 225 m) and a mesopelagic (475 - 600 m) population (Alvaríño, 1976). However, the settlement of these in the benthic phase is not well known. Recent observation during October 1994 via a SIMRAD EY-200 working at 200 kHz showed daily vertical migration of dense swarms of red crabs (sampled via Isaacs-Kidd trawls) from the bottom close to the shelf break in the water column dispersing vertically during night time and returning to the bottom early in the morning (C. Robinson, ICMYL, UNAM pers. comm., 1995). This suggests the shelf-break could be the first settlement area explored by epipelagic swarms. Future observations could determine if settlement process occurs regularly in this area. Recruitment of *P. monodon* on the continental shelf off Chile appears to be associated with late summer development of the giant sulfur bacteria *Thioploca* spp., when the oceanographic regime in the area shifts to a relaxation of the upwelling regime (Gallardo et al., 1994).

Latitudinal Cline.—A latitudinal distribution pattern of larval and postlarval stages of the red crab was detected (Gómez and Sánchez, 1995). Early stages were more abundant in the north (Punta Eugenia) and postlarvae were more abundant in the south (Bahía Magdalena) in the first half of the year, suggesting a cline in the temporal reproductive activity of this species along the west coast of Baja California. A similar latitudinal cline was observed from the standard carapace lengths of adults collected in the water column and at the bottom. This showed a latitudinal cline from larval and postlarval stages where the largest larvae were found to the north (Table 2). Similar trends have been reported previously for pelagic and benthic adults (Arvizu 1976; Guzmán, 1995; Guzmán and Aurióles, 1992). Our data support the idea that a cline exists during the seasonal reproduction. The peak of reproduction starts off southern Baja California (Bahía Magdalena) and finishes northward (Punta Eugenia). There is a close relationship with reproduction and the seasonal counter current found during July to November, when a northward mov-

ing core of equatorial water may underlie a coastal undercurrent bringing tropical surface water up from the south. This latitudinal cline could be explained because Punta Eugenia and Bahía Magdalena have seasonally different oceanographic dynamics. The retention of *P. planipes* during its long pelagic existence over the continental shelf was considered by Longhurst (1966) to be made possibly by eddy flow inshore of the southerly drift of the California Current. This could be true for the population at Punta Eugenia, where a semi-permanent eddy has been reported (Hickey, 1979; Poulain et al., 1987), and can act as a mechanism of maintenance for larval stages, which could be trapped in the central eddy of the bay until the end of larval development (Hewitt, 1981; Lavaniegos, 1994). This eddy develops mainly in summer and fall (Hickey, 1979). Probably part of the juveniles and adults do not migrate to deeper water and reach their biggest sizes close to the coast. No evidence exists that similar current mechanisms occur in the most important area of reproduction located in Bahía Magdalena. Thus, the offshore transport and subsequent recruitment to offshore epipelagic population could explain why relatively smaller individuals are found in the water column in the south compared with northern regions. Apparently, inshore-offshore movements reported by Auriolos (1992) are more clearly observed along southern Baja California.

CONCLUSIONS

We propose that the space-time variations of seasonal distribution and abundance of the planktonic stages of the red crab along the west coast of Baja California are a consequence of two important processes. First, the season and hatching areas showed a reproductive cline associated with regional oceanography. The most intensive reproduction starts along the southern part of the peninsula of Baja California (Bahía Magdalena). At the end of the reproductive season, reproduction is most intense in the northern area (Punta Eugenia). Second, a larval drift from the hatching areas caused by offshore Ekman transport of the coastal upwelling is an important mechanism for the recruitment of postlarvae into the epipelagic adult population.

From about 230 described species in the family Galatheidae, only two species, *P. planipes* and *Munida gregaria*, are ever pelagic as adults (Boyd, 1967; Longhurst, 1966; Zeldis, 1985). For the rest of the species of the family, after at least a short time, the small postlarvae alternate between plankton and the benthos before assuming an exclusively benthic life (Boyd, 1967; Longhurst, 1967; Zeldis, 1985; Gallardo et al., 1994). Advection phenomena such as offshore transport, moving pelagic fish larvae away from their favorable habitats, was considered one of the most important factors in larval mortality (Bakun and Parrish, 1982; Bakun, 1985; Power, 1986). Dense offshore postlarvae swarms suggest that offshore transport is a favorable factor for survival of *P. planipes* and it plays an important role in the recruitment of postlarvae to the offshore pelagic aggregations. The spatial separation of the different life stages (planktonic, pelagic, and benthic) of these species may decrease the intraspecific competition for food and prevent strong cannibalistic behavior. Zeldis (1985) proposed a density-dependent regulation of the settlement to the bottom of pelagic cohorts caused by the benthic cohorts in *Munida gregaria* as a combination of cannibalism and non-lethal agonistic behavior. For the lack of benthic crabs, the settlement of pelagic animals to the bottom occurred early. In the red crab, the separation of both populations probably is regulated in a similar way and the epipelagic and benthic populations have only been found mixed during the reproductive season. The

particular life cycle of the red crabs, where its different larval stages remain spatially segregated, could explain how *P. planipes* is able to develop high concentrations within the southern Baja California upwelling system.

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