

# Seasonal and tidal abundance of crab larvae in a tropical mangrove system, Gulf of Nicoya, Costa Rica

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**ABSTRACT:** Crab larvae were collected from a platform moored in the mouth of a mangrove estero (= tidal creek) in the Gulf of Nicoya on the Pacific coast of Costa Rica, Central America. Eight observation periods encompassed both spring and neap tides and covered all seasons of the year. During each observation period, samples were collected every 2 h over 5 consecutive tidal cycles. Samples were collected from a depth of 1 m with a gasoline-powered impeller pump; total volume of each sample was 10 to 12 m<sup>3</sup>. The gross taxonomic composition of the observed larval assemblage was similar to that seen in temperate estuaries along the Atlantic coast of North America. Larvae of *Uca* spp., Grapsidae, Xanthidae and commensal crabs such as *Pinnotheres* spp. were the most common. However, abundance of individual taxa was greater than that seen in temperate estuaries with common forms in excess of 1000 larvae m<sup>-3</sup>. In contrast to temperate estuaries, spawning occurred year-round, but individual taxa showed distinct seasonality. As in temperate estuaries, spawning in the estero was also influenced by lunar cycles and larvae of several taxa showed tidally rhythmic changes in abundance. Zoea I of *Uca* spp., Grapsidae, Xanthidae, *Pinnotheres* spp. and *Petrolisthes* spp. were significantly more abundant during ebb tides suggesting that these larvae were spawned in the creek and exported to the open Gulf. Advanced zoea and megalopae appeared to take advantage of nocturnal flood tides to be recruited back into the estuary. Export of early stages did not occur in all taxa. Abundance of early zoeal stages of *Pinnixa* spp. was not affected by tidal phase suggesting that early stages were not exported from the estero.

## INTRODUCTION

While many estuarine invertebrates have evolved behavioral mechanisms that enhance retention of larvae in the estuary, others export their larvae into coastal waters where further development occurs (Epifanio 1988). Larvae of retained species appear to regulate their vertical position in the water column, thus taking advantage of tidal and subtidal motion for upstream transport (Carriker 1951, Bousfield 1955, Wood & Hargis 1971, Sandifer 1975, Cronin & Forward 1979, 1982, Boicourt 1982, Seliger et al. 1982). Results of extensive laboratory studies have provided detailed understanding of the behavioral foundations of these adaptations. For example, studies have shown that crab larvae may alter their vertical position in response to light intensity (Forward 1974, Sulkin 1975), salinity (Latz & Forward 1977, O'Connor & Epifanio 1985), pressure (Knight-Jones & Qasim 1966, Naylor & Isaac 1973, Sulkin 1975, Wheeler & Epifanio 1978, Sulkin & van Heukelem

1982), gravity (Sulkin 1973, Latz & Forward 1977, Sulkin et al. 1980), and temperature (Ott & Forward 1976, Sulkin et al. 1980). Vertical movements in response to these environmental parameters may enhance retention of larvae in the estuary (Epifanio et al. 1989). Semilunar and lunar cycles of larval release may also affect dispersal and settlement rates of larvae (Christy 1978, Zucker 1978, Saigusa & Hidaka 1978, Bergin 1981, Saigusa 1981, Paula 1989) and may also result in landward transport of megalopae by spring tide currents (Christy 1978, 1982, 1986, DeCoursey 1981).

In exported species of crab larvae, recruitment to parental populations appears to be by immigration of megalopae and juvenile stages (Sandifer 1975, Dittel & Epifanio 1982, Epifanio et al. 1984). Recent evidence suggests that this may be accomplished by a combination of tidally rhythmic vertical migration (Epifanio et al. 1984, Epifanio et al. 1989) and wind-driven physical transport from the adjacent continental shelf into the estuary (Goodrich et al. 1989, Little & Epifanio 1990).

Despite the extensive literature on recruitment and dispersal patterns of estuarine crabs, little is known about the patterns of larval abundance in tropical estuaries. There have been a few studies of the general abundance of zooplankton in tropical embayments (Youngbluth 1980, Robertson et al. 1988), but there is limited information on the seasonal occurrence of larvae or on related physical factors that affect distribution in tropical systems (Epifanio & Dittel 1984). In this paper we present the results of an investigation of the seasonal and tidal abundance of crab larvae in a tropical mangrove system.

### STUDY SITE

The Gulf of Nicoya is an embayment located on the Pacific coast of Costa Rica at 10°N, 85°W (Fig. 1). The upper gulf, north of Isla San Lucas, is relatively shallow and is bounded by mangrove swamps along the east-

Morales narrows as it extends farther up the mangrove forest, and wide mud flats occur adjacent to its mouth. There is limited freshwater flow into the estero during the dry season, and water from the estero floods the mangrove forest on each rising tide.

### MATERIAL AND METHODS

Crab larvae were collected in 1987 from a platform moored in the mouth of Estero Morales in the deepest portion of the main channel, ca 5 m. During each observation period, samples were collected every 2 h over 5 consecutive tidal cycles. Observation periods encompassed both spring and neap tides and covered all seasons (Table 1). Samples were taken from a depth of 1 m using a gasoline-powered impeller pump with its outflow filtered through a 280 µm mesh plankton net. Each sample was the result of 0.5 h pumping that

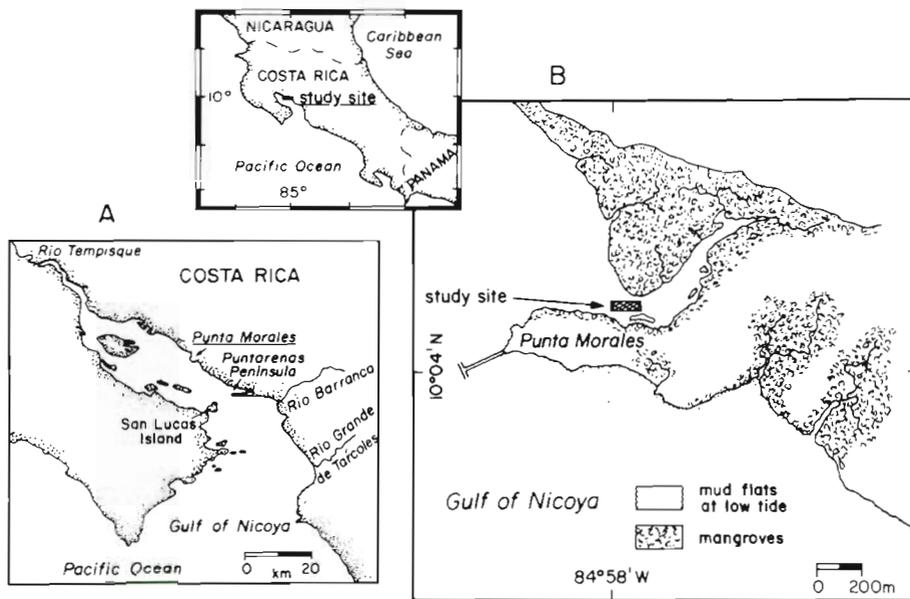


Fig. 1. Location of study site in the Gulf of Nicoya, Pacific coast of Costa Rica. (A) Gulf of Nicoya; (B) Estero Morales. (Modified from Vargas 1987)

ern and western shores. Depth in the upper gulf is generally less than 20 m, while in the lower gulf depths are greater than 200 m. Mean tidal range at Puntarenas is 2.3 m, and similar tidal ranges are found throughout the upper gulf (Voorhis et al. 1983). Seasonal variation in the chemical and physical characteristics of the gulf is controlled by a rainy season from May to November and a dry season from December through April (Epifanio et al. 1983, Voorhis et al. 1983).

The study site, Estero Morales, is a tidal creek on the eastern shore of the upper gulf (Fig. 1). The estero is bordered by mangrove swamps and is characterized by a main channel ca 200 m wide at its mouth. Estero

Table 1. Physical parameters in surface waters in Punta Morales, Gulf of Nicoya, Costa Rica. Data are grouped by tide and seasonally; values are means

Date (1987)	Temperature (°C)		Salinity (ppt)	
	Ebb	Flood	Ebb	Flood
27–30 Jan	28.3	28.2	30.6	30.4
9–11 Feb	28.4	28.5	30.9	30.6
6–8 May	29.7	29.8	33.0	32.8
14–16 May	29.9	29.8	32.5	32.5
11–13 Aug	30.0	30.0	28.5	28.6
18–21 Aug	32.9	32.8	26.7	26.2
5–7 Nov	29.4	30.0	24.0	24.2

allowed the filtration of 10 to 12 m<sup>3</sup> of water. The pump outflow was calibrated before each sampling period. Temperature and salinity at 1 m were measured simultaneously with each larval collection using a portable conductivity-salinity-temperature meter (YSI).

Samples were preserved immediately in 4 % formaldehyde and transferred to 70 % ethanol no later than 1 wk after collection. Samples were split using a Folsom splitter (Dittel & Epifanio 1982), and one randomly chosen subsample was analyzed for each collection. Larvae were categorized by zoeal and megalopal stages and identified to family or genus. Identification was done using available keys and original descriptions (Hyman 1920, Lebour 1928, Costlow & Bookout 1966, Costlow & Fagetti 1967, Hasmi 1968, Knight 1968, Gore 1972, Sandifer 1972, Martin et al. 1985, Fielder & Greenwood 1986).

Larval concentrations were transformed to log (x + 1) to normalize distributions and to decorrelate the mean and variance. A Model I multifactor analysis of variance (ANOVA;  $\alpha = 0.05$ ) was used to test the effect of time of day, tidal stage, time of year, and lunar cycle (neap/spring tides) on the abundance of crab larvae. The F-ratio for each main effect was calculated as the mean square (MS) for that factor divided by the error mean square. Third and fourth order interactions were not analyzed because interpretation at those levels is difficult. For several taxa (Majidae, Leucosiidae and

*Callinectes*) 4-way ANOVA could not be used because zero-value cells occurred. Instead, 4 one-way ANOVAs were used.

## RESULTS

### Physical data

During the investigation, temperatures ranged from ca 28 to 33 °C, while salinities in the main channel varied from 24 to 33 ‰ (Table 2). Ebb tide salinities sometimes exceeded flood tide salinities; this suggests that evaporation and mangrove transpiration were high in the region upstream from our study site. Monthly precipitation during the rainy season ranged from 100 to 340 mm with peaks in July and September,

Table 2. Lunar and seasonal characterization of 1987 observation periods in Punta Morales, Gulf of Nicoya, Costa Rica

Observation period	Lunar phase	Annual season
26–28 Jan	Spring	Dry
9–11 Feb	Neap	Dry
6–8 May	Neap	Transition
14–16 May	Spring	Transition
11–13 Aug	Spring	Rainy
19–21 Aug	Neap	Rainy
5–7 Nov	Spring	Transition
30 Nov–2 Dec	Neap	Dry

Table 3. Overall composition, abundance and % abundance of all taxa and % frequency of occurrence of brachyuran crab larvae in Punta Morales, Gulf of Nicoya, 1987. --: the particular stage is not present in that taxon

Taxon	ZI	ZII	ZIII	ZIV	ZV	Meg.	Juv.	Total	%	% Freq.
Ocypodidae										
<i>Uca</i> spp.	352 006	1 756	399	190	192	9 056	0	363 599	43.0	99
Unidentified	4 432	0	0	4	0	0	12	4 448	0.5	11
Grapsidae	241 661	79	22	29	--	944	0	242 735	28.7	87
Pinnotheridae										
<i>Pinnotheres</i> spp.	95 019	6 697	4 949	4 024	1 139	1 312	594	113 734	13.5	99
<i>Pinnixa</i> spp.	3 422	288	93	44	76	1 399	774	6 096	0.7	74
Xanthidae	72 427	2 544	791	204	--	2 622	33	78 621	9.3	99
Porcellanidae										
<i>Petrolisthes</i> spp.	16 462	85	--	--	--	463	407	17 417	2.1	88
Paguridae	6	0	0	0	0	0	1 110	1 116	0.1	27
Portunidae										
<i>Callinectes</i> spp.	320	0	0	0	0	4	0	324	< 0.1	16
Majidae	289	7	--	--	--	23	0	319	< 0.1	28
Leucosiidae	297	7	1	7	0	0	0	312	< 0.1	21
Raninidae	0	0	0	0	0	29	0	29	< 0.1	4
Hippidae										
<i>Emerita</i> spp.	4	0	0	0	0	0	0	4	< 0.1	< 1
Other	16 473	5	8	4	0	24	32	16 546	1.9	48
Total	802 818	11 468	6 263	4 506	1 407	15 876	2 964	845 302		
% of total	95	1.4	0.7	0.5	0.2	1.9	0.4			

while dry season precipitation ranged from 0 mm in February to 40 mm in April (data from the Instituto Meteorológico de Costa Rica).

### Species composition

Both anomuran and brachyuran crabs were included in the analysis, and ca  $8.5 \times 10^5$  larvae and early juve-

Table 4. Average density (ind.  $m^{-3}$ ) of larval stages of each taxon in Punta Morales, January-December, 1987

Taxon	January	May	August	November
Ocypodidae				
<i>Uca</i> spp.	8.0	229.1	284.8	66.2
Unidentified	0.0	0.0	0.0	14.6
Pinnotheridae				
<i>Pinnotheres</i> spp.	6.4	25.5	26.6	26.6
<i>Pinnixa</i> spp.	5.9	1.8	3.5	1.2
Xanthidae	25.9	28.0	40.1	29.8
Grapsidae	2.6	40.4	124.6	22.2
Porcellanidae				
<i>Petrolisthes</i> spp.	7.8	7.6	9.9	5.5
Portunidae				
<i>Callinectes</i> spp.	0.4	0.0	1.1	1.4
Paguridae	2.8	0.7	0.7	0.8
Leucosiidae	0.6	0.5	0.8	0.5
Majidae	0.5	0.3	0.3	0.4
Other	0.0	0.0	0.1	0.0
Raninidae	0.4	0.2	0.1	0.0
Hippidae				
<i>Emerita</i> spp.	0.0	0.4	0.0	0.0

niles were collected during the study period. These were categorized in 10 families (comprising over 98 % of the total catch) and in a small group of unidentified brachyurans. Definition beyond family was often difficult, but 6 groups were further identified to genus.

Ocypodid larvae (*Uca* spp.) dominated the samples, comprising 43.0 % of the total catch (Table 3). Grapsids ranked second in abundance (28.7 %), followed by pinnotherids (13.5 %), xanthids (9.3 %) and porcellanids (2.1 %). Leucosiids, majids, raninids, and portunids were collected during most of the year, but were never found in large quantities. Altogether these taxa represented less than 1 % of the total catch.

When tabulated for all taxa, Zoea I were the most abundant stage, representing 95 % of all individuals collected (Table 3). Zoea Stages II to V were 2 orders of magnitude less abundant in most taxa, but the megalopa stage was often more abundant than the intermediate or advanced zoeal stages. Only in *Pinnotheres* spp. were zoea Stages III to V as abundant as the megalopa.

### Seasonal abundance

Zoeal abundance in 3 families (Leucosiidae, Portunidae, and Majidae) was so low that seasonal analysis was not performed. However, the more common taxa showed rather clear patterns of seasonal abundance (Table 4). Analysis of variance showed significant effects of season on abundance of zoea Stage I of ocypodids, grapsids, and *Pinnotheres* spp. (Table 5). For *Uca* spp., mean abundance increased from 8.0 zoeae  $m^{-3}$  during January/February (dry season) to

Table 5. Percent of total annual catch of Zoea I and megalopa for each taxon during the study period in Punta Morales, Gulf of Nicoya, Costa Rica

Taxon	January		May		August		November	
	Z I	Meg.	Z I	Meg.	Z I	Meg.	Z I	Meg.
Ocypodidae								
<i>Uca</i> spp.	1.0	31.0	40.0	13.0	48.0	24.0	11.0	32.0
Grapsidae	1.0	1.0	20.0	2.0	68.0	94.0	11.0	3.0
Xanthidae	20.0	34.0	22.0	7.0	31.0	45.0	27.0	14.0
Pinnotheridae								
<i>Pinnotheres</i> spp.	5.0	78.0	32.0	14.5	23.0	3.5	40.0	4.0
<i>Pinnixa</i> spp.	55.0	97.5	13.5	2.5	17.5	0.0	14.0	0.0
Porcellanidae								
<i>Petrolisthes</i> spp.	26.0	58.0	24.0	1.0	31.0	31.0	19.0	10.0
Majidae	74.0	65.0	12.5	0.0	7.0	0.0	6.5	35.0
Leucosiidae	46.0	0.0	18.5	0.0	8.5	0.0	17.0	0.0
Raninidae	0.0	90.0	0.0	7.0	0.0	3.0	0.0	0.0
Portunidae								
<i>Callinectes</i> spp.	25.0	0.0	0.0	0.0	10.0	0.0	64.5	100.0

more than 200 m<sup>-3</sup> as the rainy season began in May. By mid-rainy season (August), mean abundance had risen to nearly 300 m<sup>-3</sup>. Abundance fell to less than 70 m<sup>-3</sup> with the transition to dry season in November. A

similar pattern was observed in grapsid crabs with less than 3 zoeae m<sup>-3</sup> during dry season and nearly 125 m<sup>-3</sup> in mid-rainy season. A slight variation was seen in *Pinnotheres* spp. where mean densities increased from

Table 6. Results of 4-way ANOVA comparing the effects of tidal stage, time of day, lunar cycle and time of year on the abundance of larval stages and early juveniles of the various taxa collected during the study period. The analysis was performed on log-transformed densities. E: ebb, F: flood; N: night-time, D: day-time; s: spring tides, n: neap tides; NS:  $p > 0.05$ , \*  $p < 0.05$ . Interactions are indicated with abbreviations corresponding to each factor. >: significantly greater at  $\alpha = 0.05$ . One-way ANOVA was performed for Leucosiidae, Portunidae and Majidae

Taxon	Stage	Tide (T)	Diel (D)	Month (M)	Lunar (L)	Interaction
Ocypodidae						
<i>Uca</i> spp.	I	E > F	NS	*	s > n	T × L, D/M
	II	NS	NS	*	s > n	L × M
	III	NS	N > D	NS	NS	L × M
	IV	F > E	NS	*	n > s	T × L, D × L
	V	F > E	NS	NS	n > s	T × L, D × L
	Meg.	F > E	N > D	*	s > n	T × D, L × M
Grapsidae						
	I	E > F	N > D	*	s > n	T × D, T × L, L × M
	II	NS	NS	NS	NS	NS
	III	NS	NS	NS	NS	NS
	IV	F > E	NS	NS	NS	NS
	Meg.	NS	N > D	*	NS	D × M, T × L, L × M
Pinnotheridae						
<i>Pinnotheres</i> spp.	I	E > F	NS	*	s > n	L × M
	II	NS	N > D	*	n > s	D × M, D × L, L × M
	III	NS	N > D	NS	n > s	D × L
	IV	F > E	N > D	*	n > s	D × L
	V	F > E	N > D	*	NS	NS
	Meg.	F > E	N > D	*	s > n	T × D, D × L, D × M, L × M
	Juv.	F > E	N > D	NS	NS	L × M
<i>Pinnixa</i> spp.						
	I	NS	D > N	*	n > s	D × M
	II	NS	NS	NS	n > s	NS
	III	NS	NS	NS	NS	L × M
	IV	F > E	N > D	NS	NS	L × M
	V	NS	NS	NS	NS	NS
	Meg.	F > E	N > D	*	S > N	D × L, D × M, L × M
	Juv.	F > E	N > D	*	NS	T × D, L × M
Porcellanidae						
<i>Petrolisthes</i> spp.	I	E > F	N > D	*	n > s	T × D
	II	F > E	N > D	*	NS	L × M
	Meg.	F > E	N > D	*	NS	T × D, D × L, L × M, D × M
	Juv.	F > E	N > D	*	s > n	L × M, D × L
Xanthidae						
	I	E > F	NS	NS	NS	T × D, L × M
	II	F > E	NS	*	NS	NS
	III	F > E	N > D	NS	n > s	L × M
	IV	F > E	NS	NS	n > s	L × M
	Meg.	F > E	N > D	*	NS	T × D, L × M
Paguridae						
	I	NS	NS	NS	NS	NS
	Juv.	F > E	N > D	*		T × D, T × L, D × L, T × M, D × M, L × M
Leucosiidae						
	I	NS	NS	NS	NS	
	II	NS	NS	NS	NS	
	IV	NS	NS	NS	*	
Portunidae						
<i>Callinectes</i> spp.	I	NS	NS	*	s > n	
Majidae						
	I	NS	NS	NS	NS	

$6 \text{ m}^{-3}$  in mid-dry season to maximum densities of  $25 \text{ m}^{-3}$  or more during the rest of the year. In contrast *Pinnixa* spp. showed maximum abundance in mid-dry season and again in mid-rainy season, with minima during the 2 transition periods.

Analysis of variance showed no significant effect of season on abundance of zoea Stage I in the Xanthidae (Table 6), and the abundance of all stages was relatively high throughout the year.

Megalopae did not show the same pattern of seasonal abundance as zoea Stage I in any of the common taxa (Table 5). For example megalopae of *Uca* spp. were most abundant during January and November, even though zoea Stage I were much more abundant in May and August. This lack of correspondence suggests that mortality rate for zoeae may vary with season.

#### Diel and tidal variations in densities

Zoea Stage I of grapsids, xanthids, ocyropods (*Uca* spp.), porcellanids (*Petrolisthes* spp.), and some pinnotherids (*Pinnotheres* spp.) were significantly more abundant during ebb than flood tides, suggesting that these larvae were released in the estero and exported to the open gulf (Table 6). In Fig. 2 we show a time series of bihourly abundance of zoea Stage I of *Uca* spp. as an example of this pattern of abundance.

Later zoeal stages and megalopae of these taxa were more common during flood tides (Table 6). Superimposed on this tidal frequency was a diel and lunar pattern in abundance. Some stages in these taxa were

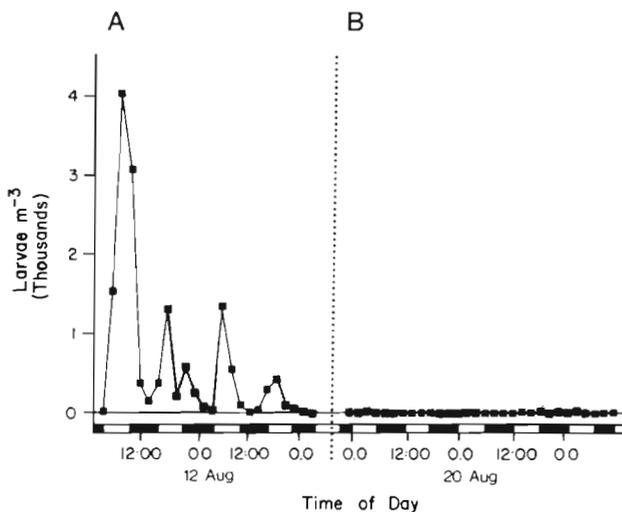


Fig. 2. *Uca* spp. Bihourly abundance of zoea Stage I in Estero Morales, Costa Rica over 5 consecutive tidal cycles. Dark areas on X-axis indicate flood phase. Light areas on X-axis indicate ebb phase. Shaded areas delineate periods of darkness. This pattern of abundance is typical of species that export zoea Stage I. (A) Spring tide period, 11 to 13 August 1987; (B) neap tide period, 19 to 21 August 1987

significantly more abundant during nocturnal spring tides. In addition, there was a significant interaction between time of day and tidal stage and between time of day and lunar cycle of the megalopal stage. Megalopae in all of these families were significantly more abundant during nocturnal spring floods. In Fig. 3 we show a time series of bihourly abundance of the megalopa stage of *Uca* spp. as an example of this pattern of abundance.

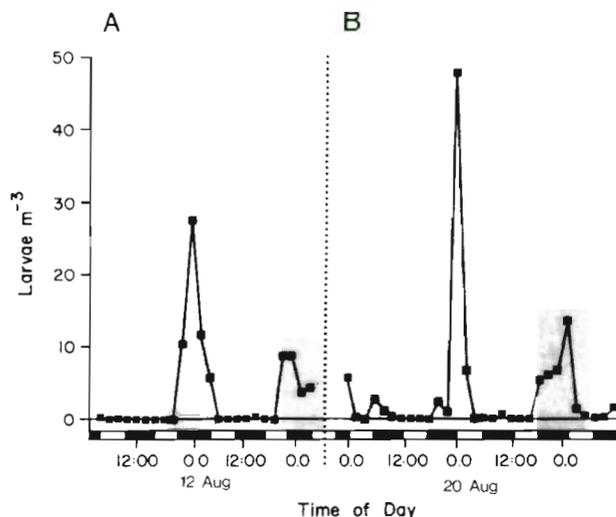


Fig. 3. *Uca* spp. Bihourly abundance of megalopae in Estero Morales, Costa Rica over 5 consecutive tidal cycles. Dark areas on X-axis indicate flood phase. Light areas on X-axis indicate ebb phase. Shaded areas delineate periods of darkness. This pattern of abundance is typical of species that depend on upstream transport of megalopae for recruitment. (A) Spring tide period, 11 to 13 August 1987; (B) neap tide period, 19 to 21 August 1987

Another pattern of larval abundance was observed in *Pinnixa* spp. (Pinnotheridae) where there was no significant effect of tidal phase (Table 6). In Fig. 4 we show a time series of bihourly abundance of zoea Stage I of *Pinnixa* spp. as an example of this pattern.

## DISCUSSION

### Composition and seasonal abundance

While the assemblage of crab larvae observed at Estero Morales showed little taxonomic affinity with assemblages in temperate estuaries further north along the Pacific coast (Gunderson et al. 1990), the relative abundance of common families collected in the estero was strikingly similar to the summer distribution reported in warm temperate estuaries along the Atlantic coast of North America. At Estero Morales, as well as in these Atlantic estuaries, larval collections are dominated by ocyropods (*Uca* spp.), pinnotherids,

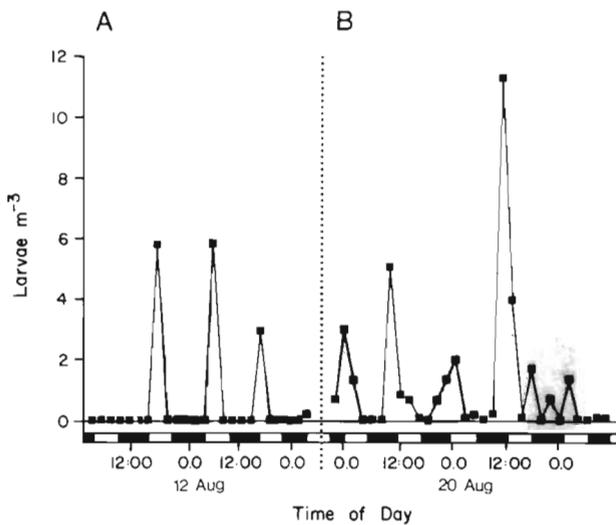


Fig. 4. *Pinnixa* spp. Bihourly abundance of zoea Stage I in Estero Morales, Costa Rica over 5 consecutive tidal cycles. Dark areas on X-axis indicate flood phase. Light areas on X-axis indicate ebb phase. Shaded areas delineate periods of darkness. This pattern of abundance is typical of species that do not show lunar, tidal, or diel rhythms. (A) Spring tide period, 11 to 13 August 1987; (B) neap tide period, 19 to 21 August 1987

xanthids, and grapsids (Sandifer 1973, 1975, Dittel & Epifanio 1982, DeLancey 1987). In Estero Morales these families comprised over 97 % of the larvae collected.

Crab larvae were common in Estero Morales throughout the year, but there were distinct seasonal patterns of abundance in the more common taxa. Ocypodids and grapsids showed maximum reproductive activity during the rainy season, while reproduction in xanthids appeared to be continuous throughout the year. However, xanthids were not identified beyond family, so it is possible that individual species may have shown seasonal spawning as well.

The 2 genera of Pinnotheridae collected in the study showed different patterns of seasonal abundance. Most stages of *Pinnotheres* spp. were significantly more abundant during the rainy season, and in contrast to all other genera, intermediate zoeal stages were relatively common in the estero. The presence of all larval stages, as well as juveniles, in the plankton suggests that *Pinnotheres* spp. reproduces in this region and that larvae are retained in the system. Similarly, larvae of temperate species of the genera *Pinnotheres* and *Pinnixa* have been found predominantly in near-bottom waters (Sandifer 1973, Goy 1976, Dittel & Epifanio 1982) where non-tidal circulation is upstream thus preventing expulsion from the estuary. Zoeal stages of *Pinnixa* spp. showed peaks in mid-dry and mid-rainy season, suggesting that more than one species was included in the collections.

In several common taxa there was considerable sea-

sonal variation in zoeal abundance, while megalopal abundance remained relatively constant (Table 6). The apparent decoupling of zoeal and megalopal abundance in the common taxa may also be related to our inability to define individual species, but there is also the suggestion of differing zoeal mortality rates in different seasons. These could be caused by seasonal changes in abundance of food and predators or by rainfall-related changes in the circulation of the upper gulf.

Majid, raninid, and leucosiid larvae occurred during most of the year but never in great abundance. This reflects the lack of spawning populations of these families in the upper gulf (Maurer et al. 1984). Portunid zoeae were also rare in Estero Morales in spite of large adult populations of *Callinectes arcuatus* in the upper gulf (Dittel et al. 1985). This is explained by the fact that *C. arcuatus* migrates to the lower gulf to spawn (DeVries et al. 1983) and that zoea larvae are apparently retained in that area (Epifanio & Dittel 1984). *C. arcuatus* megalopae were also rare in Estero Morales, suggesting that metamorphosis occurs in the lower gulf and that recruitment to adult populations is effected by juvenile migration.

#### Tidal, lunar, and diel variations

Responses to tidal, lunar, and diel cycles varied both within and among taxa, but 2 general categories emerged. Responses of larvae in the most common taxa fell into the first category where we usually observed a greater abundance of zoea Stage I during ebb than flood tides. This tidal effect was sometimes complicated by significant interactions with either diel or lunar phase, but the overall pattern of abundance suggests that spawning in this group occurred within the estero and that the early zoeae were exported from the estero. Some taxa, e.g. grapsids, *Uca* spp., and *Pinnotheres* spp., also showed greater abundance during spring tidal phases. Presumably this would result in augmented exportation, as the tidal prism (intertidal volume) is greater during spring than neap phases.

In this first group, intermediate and advanced zoeal stages, as well as megalopae, were generally more abundant during flood than ebb phases (with the exception of the grapsids). Presumably this resulted in a net import of these stages into the estero. With the megalopae of *Uca* spp. and *Pinnotheres* spp., abundance was also greater during spring than neap phases. Again, this would result in augmented transport of the larvae.

Larvae of *Pinnixa* spp. fell into a second category. Zoeae of *Pinnixa* spp. were significantly more abundant during daytime and during neap tides, but abun-

dance of early zoeal stages was not affected by tidal phase. This lack of tidal response by *Pinnixa* suggests that early zoeae are not exported from the estero. However, the relative abundance of advanced zoeal stages in the estero was no greater for *Pinnixa* than for the exported species discussed above. Furthermore, *Pinnixa* megalopae were significantly more abundant during flood tides, suggesting that megalopae are recruited into the estero from the adjacent gulf.

### Comparisons with other estuaries

As in temperate species of *Uca*, zoea Stage I in Estero Morales was more abundant during spring ebb tides, whereas intermediate stages were more abundant during neap flood tides and megalopae during nocturnal spring flood tides. However, no diel pattern of abundance was observed for *Uca* zoea Stage I. This is in contrast to temperate estuaries where nocturnal hatching has been observed. Nocturnal hatching has been hypothesized to reduce predation on ovigerous adult females (DeCoursey 1979, Seiple 1979) and newly hatched zoeae (Christy 1982). It would appear that this would be selectively advantageous in tropical estuaries as well, so it is not clear why no evidence of the trait was seen in our data.

But overall, the species of *Uca* in Estero Morales appear to have evolved behavioral adaptations similar to those in temperate forms. These adaptations result in transport of Stage I larvae away from adult habitat and into open water where subsequent zoeal development occurs. Transport of megalopae to adult habitat appears dependent on flood tidal currents.

Just as for temperate grapsid crabs, our results show semilunar and tidal rhythms in the abundance of newly hatched zoeae (Saigusa & Hidaka 1978, Seiple 1979, Christy & Stancyk 1982, DeVries & Forward 1989), but grapsid megalopae appeared more influenced by time of day than by tidal movements. While the nocturnal abundance of grapsid megalopae may be important in avoiding predation, it would appear of little value in upstream transport of the megalopae.

As in temperate estuaries (Cronin & Forward 1982, Lambert & Epifanio 1982), xanthid larvae in Estero Morales showed clear tidal rhythms in abundance. Zoeal Stage I larvae were more abundant during ebb tides, while intermediate and advanced zoeae and megalopae were more abundant during flood tides. Other authors have reported an additional lunar rhythm in the abundance of the newly hatched zoeae of intertidal xanthids, but no such rhythm in subtidal species (Christy 1986, Salmon et al. 1986). Because we were unable to identify xanthid larvae beyond the level of family, we would have been unable to distinguish

these 2 patterns, even if they existed in Estero Morales.

Our results for porcellanid larvae are consistent with those reported by Christy (1986) for *Petrolisthes armatus* on the Pacific Coast of Panama. As in the present study, no synchronization of larval release related to lunar phase was observed in *P. armatus*. In contrast to Zoeae I, megalopae of *Petrolisthes* spp. in Punta Morales appeared to be influenced by tidal, diel and lunar phase. Ontogenetic variations in behavioral responses indicate that selective pressures may differ in the various stages. It is possible that in porcellanid crabs, megalopae require nocturnal flood tides of maximum amplitude to colonize suitable habitats whereas early stages depend on nocturnal ebb tides to be transported seaward.

### CONCLUSIONS

The gross taxonomic composition of the larval assemblage found in Estero Morales was similar to that seen in temperate estuaries along the Atlantic coast of North America. While our taxonomic analysis extended only to the level of genus, results of adult surveys on the Pacific coast of Central America indicate that species richness in Estero Morales exceeds that reported in temperate estuaries (Maurer et al. 1984). Additionally, the abundance of individual taxa was greater than that seen in temperate estuaries with common taxa exceeding 1000 larvae  $m^{-3}$ .

In contrast to temperate estuaries, spawning occurred year-round, but individual taxa showed distinct seasonality. As in temperate estuaries, spawning in Estero Morales was also influenced by lunar cycles. In addition, the larvae of several taxa showed tidally rhythmic changes in abundance just as reported for temperate systems. Early stages of many taxa were influenced by tidal movements and lunar cycles that would enable them to be transported seaward whereas later zoeal stages and megalopae appeared to take advantage of nocturnal flood tides to be recruited back into the estuary. But export of early stages did not occur in all crab taxa, and larvae of *Pinnotheres* spp. may be retained in the mangrove system throughout zoeal and megalopal development just as they are retained in the upper regions of temperate estuaries (Sandifer 1975).

The similarities between the larval assemblage in Estero Morales and the assemblages in the temperate estuaries along the Atlantic coast of North America are quite remarkable in light of spatial separation by many degrees of latitude and by the Isthmus of Panama. This pattern of similarity goes beyond taxonomic affinity and extends to apparent behavioral responses to lunar, diel, and tidal cycles. This suggests a set of selection factors that transcends latitude, but is common to estuarine environments.

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