Local distribution and abundance of swimming crabs (*Callinectes* spp. and *Arenaeus cribrarius*) on a tropical arid beach

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Abstract–Distribution, abundance, and several population features were studied in Ensenada de La Vela (Venezuela) between 1993 and 1998 as a first step in the assessment of local fisheries of swimming crabs. *Arenaeus cribrarius* was the most abundant species at the marine foreshore. *Callinectes danae* prevailed at the estuarine location. *Callinectes bocourti* was the most abundant species at the offshore. Abundances of *A. cribrarius* and *C. danae* fluctuated widely and randomly. Ovigerous females were almost absent. Adults of several species were smaller than previously reported. This study suggests that fisheries based on these swimming crabs probably will be restricted to an artisanal level because abundances appear too low to support industrial exploitation.

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Swimming crabs of the family Portunidae are common in coastal habitats in tropical, subtropical, and temperate regions. Species of the genus *Callinectes* are widely distributed in the neotropics and subtropics (Norse, 1977; Williams, 1984) where they are a key resource in local fisheries (Ferrer-Montaño, 1997; Fischer, 1978; Oesterling and Petrocci, 1995) and are important in trophic relations of fish and organisms of sandy and sandy-mud bottoms (Arnold, 1984; Lin, 1991), and in seagrass meadows (Orth and van Montfrans, 1987; Wilson et al., 1987). Several species of portunids have been thoroughly studied (e.g. *C. sapidus*), and many aspects of their biology, ecology, biogeography, and fisheries (including types of fisheries and the commercial exploitation of these species as "soft-shell" crabs) have been addressed, (Taissoun, 1969, 1973a, 1973b; Norse, 1977, 1978; Norse and Estevez, 1977; Perry and Van Engel, 1979; Williams, 1984; Smith et al., 1990). However, some species remain poorly known. Knowledge about species of *Callinectes* is mainly restricted to temperate regions, in spite of their commercial importance in the Caribbean. Furthermore, although several features of the speckled swimming crab, *Arenaeus cribrarius,* have been studied in Brazil, such as relative growth and some ecological aspects of populations (Avila and Branco, 1996; Pinheiro et al., 1996, 1997; Pinheiro and Fransozo, 1993, 1998, 1999), and elsewhere, such as its role in the trophic web in a sandy beach in South Carolina and its larval development (Stuck and Truesdale, 1988; DeLancey, 1989), as far as we know there are no published accounts of its abundance in the southern Caribbean.

Several studies of portunids have been conducted on Venezuelan coasts (Taissoun, 1969, 1973a, 1973b; Rodríguez, 1980; Scelzo and Varela, 1988; Carmona-Suárez and Conde, 1996), including species that are commercially important at an industrial level and as a mainstay for artisanal and subsistence fisheries in many coastal villages (Ferrer-Montaño, 1997; Conde and Rodríguez, 1999). A few studies with emphasis on biogeographical, taxonomic, and morphometric features of the family have been conducted in Lake Maracaibo, a polyhaline system (Taissoun 1969, 1972, 1973a, 1973b; Schubart et al., 2001). Seven species of *Callinectes* and the speckled swimming crab, *A. cribrarius,* have been listed for the State of Falcón (Carmona-Suárez and Conde, 1996), which is characterized by protracted desolate coasts, sandy and sand-mud beaches (Carmona and Conde, 1989), and an abnormally arid climate (Lahey, 1973). Lake Maracaibo, which is roughly 240 km west of Ensenada de La Vela, has the largest crab and crabmeat industry in Venezuela. Most of it is exported to the United States, where it accumulated a total value of US$ 6.2 million in 1992 (Oesterling and Petrocci, 1995). The main crab species captured in this area is *C. sapidus*. Crabs have also been harvested near Punto Fijo and Coro, the latter just 10 km from Ensenada de La Vela. In this locality, *C. bocourti* is harvested by artisanal fishermen (senior author, personal obs.). In spite of this, nothing is known about the abundance, microdistribution, and population traits of swimming crabs on these arid beaches. Our study is thus important both ecologically and as a preliminary assessment of stock levels and their potential for sustainable exploitation. Also, few studies address the guild structure of portunid crabs in the Caribbean Basin (Taissoun, 1969, 1973a; Moncada and Gómez 1980; Buchanan and Stoner 1988), in spite of their importance to fisheries.

The purpose of our study was to widen our knowledge of the population biology of *A. cribrarius* and various species of *Callinectes* in the Southern Caribbean. We quantified the distribution and population aspects of several species of *Callinectes* and *A. cribarius* on a sandy beach and in a small estuary located on an arid shoreline in Falcón, western Venezuela. We present data on the distribution and abundance of a guild of portunids, their physical correlates, and some population characteristics of the dominant species in marine and estuarine habitats.

Materials and methods

Sampling area

Ensenada de La Vela (11°27′N, 69°34′W) is a small cove located on the central coast of the State of Falcón in western Venezuela next to Istmo de Médanos, a narrow low-lying isthmus that links Península de Paraguaná to the mainland (Fig. 1). Ensenada de La Vela lies at the center of a region that extends from eastern Panamá to the Paria Peninsula in eastern Venezuela that has been regarded as abnormally dry (Lahey, 1973). In Falcon's western coastal strip and in the Península de Paraguaná, rainfall is scarce and seasonal with peaks during October–December, when nearly 50–60% of the precipitation occurs. The average yearly rainfall on the peninsula is 400 to 600 mm (Goddard and Picard, 1976), although in some localities the environment is harsher with a mean of 256.8 mm (Conde and Díaz, 1992b). The mean air temperature is 27.7°C, and the average wind speed is 10 kph and seasonal (Goddard and Picard, 1976). No mangroves, coral reefs, or seagrass beds appear at Ensenada de La Vela.

Sampling procedures

All samplings were carried out outside the fishing areas used by local fishermen. Our study was conducted in three stages. During the first and second stages, crabs were sampled at two major biotopes, where three open-water marine stations at the foreshore and one enclosed estuarine station were set. Station 1 was located on the eastern corner of Ensenada de La Vela, the most protected area, where the surf action is extremely weak. Station 2 was also located in the marine front, but next to the inlet of a natural estuarine impoundment where a nearby basin drains. Station 3 was established in this estuarine area, which is not freely connected to the ocean because its exchange mouth is blocked by a sandbar for most of the year. Station 4 was also set at the oceanic front, but in a zone exposed to rugged surf, next to an area that has the strongest wave action in Venezuela. Marine stations were characterized by sandy bottoms, low-transparency waters, and low-lying coastal profiles, whereas the estuarine station was mainly composed of muddy substrate, and had little water movement. Most of the bottom was devoid of vegetation and was interspersed with scarce flat rocky patches. As a whole, some 300 m of shoreline were trawled during each sampling.

During the first stage of sampling, trawling and environmental measurements were conducted monthly at each station from January 1993 to December 1994. Field campaigns included both rainy and dry seasons. Crabs were collected using a 7-meter long and 1.5-m tall hand seine (locally known as a "chinchorro"), with a mesh diameter of 1.0 cm. The hand seine was trawled perpendicular to the coast by two persons walking alongside the net in a 20-m long strip, parallel to the coast, at a depth ranging from 1 to 1.5 m. We repeated this process four times consecutively at approximately the same site. This is the procedure that local fishermen use to capture shrimp and fish to optimize fishing effort. Because waves break and depth does not exceed 1.5 m at our sampling sites, these sites were unsuitable for the other types of fishing gear used in other studies for capture of swimming crabs, such as crab pots, trot lines, otter trawls, and dip nets, among others (Sholar, 1979; van Montfrans et al., 1986; Prager et al., 1990; Ryer et al., 1990; Hsueh et al., 1992). Our method was also used by Carmona-Suárez and Conde (1996) to inventory brachyuran crabs in the State of Falcón, Venezuela. After each trawl at a given station, captured crabs were put in a bucket until sampling at that specific site was completed. When all four trawls were completed and the data were recorded, crabs were returned alive to the same place.

Because the behavior of some swimming crabs has been hypothesized to follow daily cycles of burrowing in the substratum during the day and of emerging at night (Warner, 1977; Fischer, 1978), we conducted a second stage of samplings from September 1997 to February 1998 at the same sites. We sampled during the day and the night of the same day or on consecutive days to determine if there were any systematic differences in the composition of the guild, in the abundance, size, and sex ratios of crabs, and to detect potential biases introduced by the sample design used in stage 1. The gear and sampling design for stage 2 was the same used during stage 1, but we were unable to collect crabs at the estuarine station because of a discharge of untreated domestic sewage at the beginning of 1997.

The purpose of the third sampling stage was to assess if guild composition and other characteristics were influenced by depth or by distance from the coast. Three new stations (inshore, midshore, and offshore) were sampled simultaneously in August 1998 and from June to July 1999, from the foreshore oceanward at intervals of 50 m (Fig. 1). The depth at the inshore station was ~1.5 m, and the depths at the mid- and offshore stations were ~2.5–3 m. During this stage, two crab pots with fish bait (as described by Oesterling, 1984) were deployed at each station for approximately 12 hours during the day, and for the same amount of time during the night, except in August 1998, when pots were deployed for 6 hours during the day and

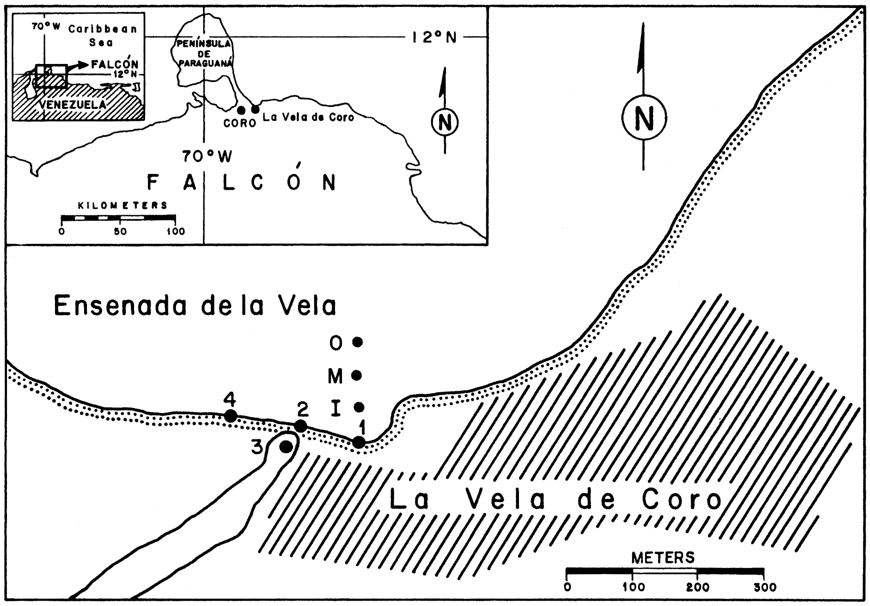

Figure 1

Map of sampling sites at Ensenada de La Vela, State of Falcón, Venezuela. Stations 1 to 4: = foreshore sampling sites (stages 1 + 2); I = inshore sampling site, M = midshore sampling site, O = offshore sampling site (stage 3).

other 6 hours during the night. This process was carried out for three to four consecutive days. No monthly or seasonal samples were taken at these three offshore stations.

Crab identification and characterization

Crabs from each stage were sorted to species, their sex was determined, and each crab was measured immediately after capture. Carapace length was measured with a 0.5-mm-precision Vernier caliper. This measurement was selected instead of carapace width because lateral spines can be abraded, making this measure of body size unreliable. This measurement method has also been used by Moncada and Gómez (1980) and Williams (1984). Animals were identified by using a key compiled from the information and keys in Taissoun (1969, 1973b), Fischer (1978), Rodríguez (1980), and Williams (1984). Juvenile females are identified by a triangular pleon and adults by a semicircular pleon. Adult males have an abdomen detached from the sternum; juveniles do not.

Environmental variables and data analysis

At each station, from January 1993 to December 1994, surface water temperature and salinity were measured with a 0.5°C precision mercury thermometer and a temperature-compensated hand refractometer, respectively. Dissolved oxygen was determined from November 1993 up to December 1994 with a YSI® dissolved oxygen meter. During the second and third sampling stages (1997–98 and 1999) only salinity values were recorded. Rainfall data were retrieved from the raw records of the meteorological station belonging to the Ministry of the Environment and Natural Resources (Venezuela), located at Coro Airport, about 10 km west of the sampling sites.

Population dynamics were analyzed only for the most abundant species that appeared regularly during each sample. Dissimilarities in body size between species were compared by using a two-tailed Student's *t*-test of the differences between two means. Sets of continuous variables were checked for normality with the Kolmogorov-Smirnov goodness-of-fit test. Homogeneity of variances of groups of data to be compared by *t*-tests was checked with Bartlett's test (StatSoft, 1992; Sokal and Rohlf, 1995). In those cases where normality or homoscedasticity were not met, data were log-transformed. Multiple comparisons were performed with the Tukey-Kramer method. The degree of association between crab abundance and environmental variables was assessed with the product-moment correlation coefficient. To compare abundance distributions between stations and diel samplings, R×C tables were analyzed with the *G*-test of independence. No extrinsic hypothesis were considered.

To describe portunid guild composition, several diversity indices were used: Simpson's, Shannon-Weaver, and Hill's numbers (N1 and N2) (Ludwig and Reynolds, 1988). Simpson's index gives the probability that two individuals drawn from a population belong to the same species. The Shannon-Weaver index measures the average degree of uncertainty in predicting to what species an individual chosen at random would belong. Hill's numbers N1 and N2, whose units are number of species, show how many common and very common species appear in a guild or community and lessen the weight of rare species.

Results

Rainfall patterns

In 1993 and 1994, mean annual rainfall at Coro was 228.4 and 58.7 mm, respectively. Precipitation, which was below the historical yearly average (403.5 mm; 1921–87), was distributed irregularly. Wet and dry seasons did not show any evident pattern (Fig. 2). In 1993, rains peaked in April and May, and secondary peaks occurred in July and November, whereas in 1994, precipitation reached a maximum during July–August and there was a lesser amount in January. During the latter year, four months were entirely deprived of rain (Fig. 2).

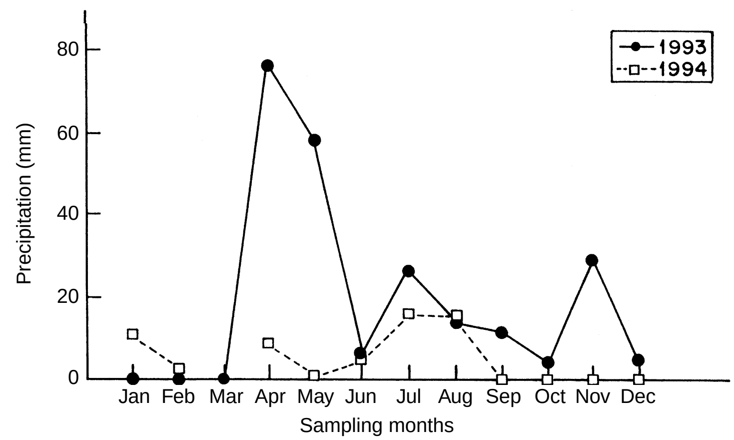

Figure 2

Rainfall in Coro (Falcón, Venezuela) during 1993 and 1994.

Physicochemical variables

Water temperature means and ranges from two-year monthly measurements at the estuarine and three foreshore stations are shown in Figure 3A. Temperature did not differ significantly among marine sites. However, mean water temperature was higher in the estuarine site (Table 1), with an average of 29°C, and so was the range, 25–34°C (Fig. 3A).

Mean salinity and its range varied slightly between marine stations (Fig. 3). The highest value was reached at station 1 and the lowest at stations 1 and 2. Salinity was significantly lower in the estuarine site (Table 1), but its range was much wider than at any other site (Fig. 3). Salinity varied very little over time at the marine stations, with the exceptions of the beginning of 1993, when salinity dropped to nearly 30‰, and November–December 1994 and the onset of 1994, when the water reached hypersaline levels (Fig. 3). Salinity at the estuarine site varied widely through time, peaking in February 1993, January 1994, and August 1994. Minima were registered in September 1993 and July 1994 (Fig. 3).

Mean dissolved oxygen was highest at station 2 and lowest at the estuarine site, where similarly the lowest absolute value observed throughout the study was recorded (Fig. 3). At the marine stations, dissolved oxygen had a smaller range than at the estuarine site, whereas the range was shifted to lower values. Oxygen increased steadily from the end of 1993 until the end of 1994, when concentrations plunged at stations 3 and 4, and less abruptly at station 1. At station 2, the oxygen concentration increased to a maximum value at the end of the year (Fig. 3). However, no significant differences in dissolved oxygen were found between stations (Table 1).

Table 1

One-way ANOVA and Tukey honest significant difference test between three foreshore (stations 1, 2, and 4) and the estuarine station (station 3) in Ensenada de La Vela (1993–94). M = mean.

Temperature: df = 84; *F* = 4.576; *P*=0.005*

Stations	1 M=27.418	2 M=27.60	3 M=28.968	4 M=27.532
1		0.982	0.010*	0.995
2	0.982		0.029*	0.999
3	0.010*	0.029*		0.020*
4	0.995	0.999	0.020*	

Salinity: df = 87; *F* = 47.153; *P*=0.001*

Stations	1 M=37.409	2 M=36.56	3 M=19.522	4 M=36.391
1		0.966	0.0001*	0.942
2	0.966		0.0001*	0.100
3	0.0001*	0.0001*		0.0001*
4	0.942	0.100	0.0001*	

Dissolved oxygen: df = 52; *F* = 1.296; *P*=0.286 not significant

Stations	1 M=7.814	2 M=8.143	3 M=7.021	4 M=7.736
1		0.943	0.535	0.999
2	0.943		0.236	0.899
3	0.535	0.236		0.619
4	0.999	0.899	0.619	

Distribution, abundance and diversity

Surf zone A total of 478 swimming crabs were collected during the first stage of our study in the surf and at the estuarine pond (Table 2). Overall, *A. cribrarius* and *C. danae* dominated. They were followed by *C. bocourti, C. sapidus, C. exasperatus, C. maracaiboensis*, and *C. larvatus*. At the marine biotope, where five species of portunids were caught throughout our study, *A. cribrarius* was the prevailing species, with shares of 77.5%, 73.7% and 86.5%, at stations 1, 2, and 4, respectively. The second most abundant species

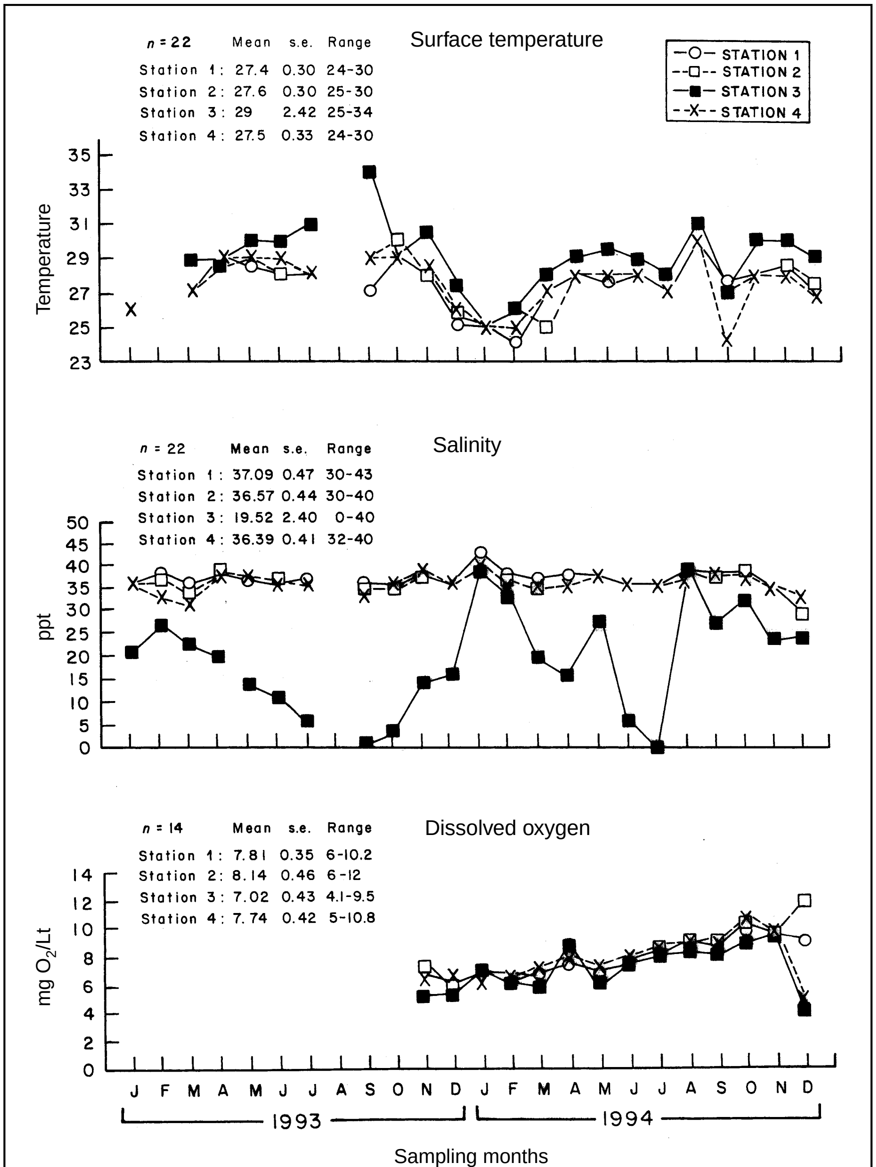

Figure 3

Surface temperature, salinity, and dissolved oxygen at the foreshore and estuarine stations in Ensenada de La Vela (Falcón, Venezuela).

at the marine stations was *C. danae* (Table 2). The highest number of species, six, was recorded at the estuarine site, where *C. danae* clearly dominated with a relative abundance of 75.2%, followed by *C. bocourti* (14.1%), *C. exasperatus* (4.5%), *C. sapidus* (2.5%), *C. maracaiboensis* (2.0%) and *C. larvatus* (1.5%). *Arenaeus cribrarius* was absent from the estuarine site. Overall, the highest diversity (Shannon-Weaver index) was registered at the estuarine station, followed by station 2, station 1, and finally station 4, the most exposed tract. Hill's diversity number 1 (N1), which indicates abundant species, was also highest at the estuarine station 3, followed by stations 2, 1, and 4 (Table 2). In a comparison of the two main biotopes (all three marine stations vs. the estuarine station) for the most frequent species (*A. cribrarius* and *C. danae*), their abundance was dependent on salinity (G=306; df=1, P<0.005). However, their abundance was independent of wave exposure, when only the stations in the marine biotope were considered (G=5.624; df=2, 0.05 >P>0.1).

Offshore A total of 173 swimming crabs were caught with crab pots. Abundance was highest at the seaward-most station, followed by the inshore and midshore stations (Table 3). The average number of individuals per pot at each site followed a similar sequence (offshore: 5.9 individuals/pot; inshore: 1.75 ind/pot; midshore: 1.5 ind/pot). Differences in abundance between offshore and inshore and between offshore and midshore stations were

Table 2

Overall abundance (no. of crabs) and diversity indexes for swimming crabs at seaside in Ensenada de La Vela (Venezuela).

		Station 1	Station 2	Station 3	Station 4	Totals (%)
A. cribrarius		86	70	0	64	220 (46)
C. danae		19	22	149	7	197 (41.2)
C. bocourti		0	2	28	1	31 (6.5)
C. maracaiboensis		0	0	4	0	4 (0.8)
C. sapidus		6	1	5	1	13 (2.7)
C. exasperatus		0	0	9	1	10 (2.1)
C. larvatus		0	0	3	0	3 (0.6)
Number of specimens		111	95	198	74	478
Number of species		3	4	6	5	
Simpson (λ')		0.6292	0.5928	0.5876	0.7542	
Shannon-Weaver (H')		0.6580	0.6930	0.8660	0.5230	
Hill's numbers	N1	1.9300	2.0000	2.3780	1.6870	
	N2	1.5894	1.6868	1.7018	1.3260	

Table 3

Overall abundance (no. of crabs) and diversity indexes for swimming crabs captured with crab pots in Ensenada de La Vela (Venezuela).

		Inshore	Midshore	Offshore	Totals
C. bocourti		30	30	69	129
C. maracaiboensis		2	4	13	19
C. danae		3	1	8	12
C. ornatus		6	3	2	11
C. sp. (unidentified)		0	2	0	2
Number of specimens		41	40	92	
Number of species		4	5	4	
Simpson (λ')		0.5537	0.5705	0.5860	
Shannon-Weaver (H')		0.8485	0.8823	0.7879	
Hill's numbers	N1	2.3361	2.4164	2.1987	
	N2	1.8062	1.7528	1.7065	

significant, whereas the difference between inshore and midshore was not. Overall, four species were caught, but *C. bocourti* prevailed at all the stations with at least 73.2% of the total quantity (Table 3). Frequency of crabs by species varied significantly with the distance of the station to the shore (G=17.024, 0.05 >P>0.01, df=8). *C. bocourti* maintained a constant presence through the three stations, ranging from 73.2 to 75.0% of total crabs at each station, the abundance of *C. maracaiboensis* increased seaward, and the abundance of *C. ornatus* decreased. *Callinectes danae* did not show any trend.

In this set of samples, taken at a distance from the shoreline, the highest diversity (Shannon-Weaver index) was registered at the midshore station, closely followed by the inshore station and the offshore station. Hill's diversity number 1 (N1), which indicates abundant species, was also highest at the midshore station, followed by inshore and offshore stations (Table 3).

Temporal variability

Because data for *C. bocourti*, *C. sapidus*, *C. exasperatus*, *C. maracaiboensis* and *C. larvatus* were too scarce to allow useful analysis, temporal variability of the abundance at the surf and at the estuarine pond was examined only for *A. cribrarius*, *C. danae*, and for total crabs. Temporal variability of the abundances of these species are shown in Figure 4. Abundances fluctuated widely and randomly throughout our study. The density of *A. cribrarius* peaked in April, July, and October 1993, as well as in February and October 1994 (Fig. 4). In the estuarine site, *C. danae* abundance peaked in May and October 1993, as well as in February, April, August, and November 1994 (Fig. 4). In the marine sites, *C. danae* abundance was considerably lower and maxima occurred in June, September, and October 1993, and in May and October 1994 (Fig. 4). No significant correlations were found between abundances of these two species and rainfall, water temperature, salinity, and dissolved oxygen (Table 4). However, when total crabs were regressed against rainfall at the estuarine site and oxygen at the foreshore, correlations were significant (Table 4). The negative correlation of this latter factor reached almost significant levels for both species at the marine ecotope.

Diel variations

Surf zone A total of 196 crabs were caught with hand seines at the foreshore during September 1997–February 1998 samplings: 82 crabs at night and 114 during the day (Table 5). Six species appeared in the diurnal samples (*A. cribrarius, C. danae, C. bocourti, C. larvatus, C. maracaiboensis* and *C. sapidus*), one of which (*C. sapidus*) did

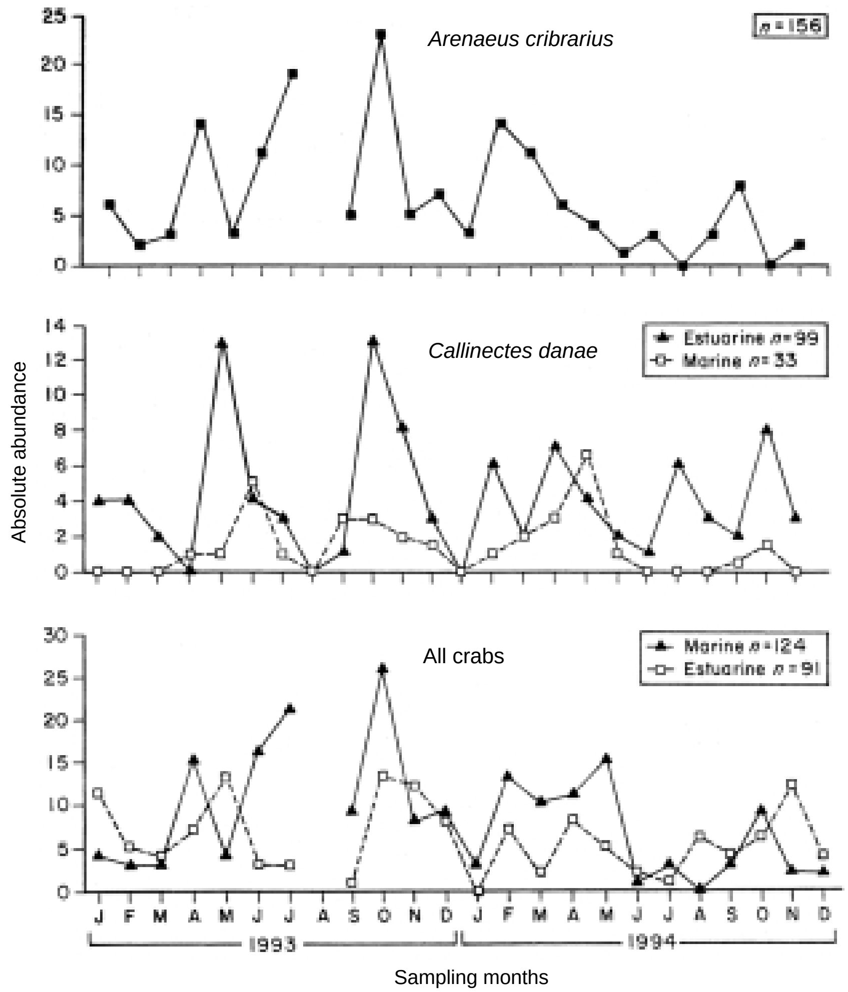

Figure 4

Abundance of *Arenaeus cribrarius*, *Callinectes danae*, and total captured crabs in Ensenada de La Vela (Falcón, Venezuela).

not appear at night. *Arenaeus cribrarius* was the dominant species followed by *C. danae*, during both diurnal and nocturnal samplings, whereas *C. maracaiboensis*, *C. bocourti*, *C. larvatus*, and *C. sapidus* were present in very low numbers. Guild composition did not differ significantly between day and night (G=1.630; 0.90>P>0.50; df=5), nor did the average number of individuals per trawl (0.86 vs. 0.62; t=1.702; 0.10>P>0.05; df=262). In both dominant species, *A. cribrarius* and *C. danae*, the average size of crabs caught during daylight hours (Table 5) did not differ significantly from those collected at night, nor did the size frequency distributions (G=3.820; df=4; 0.50>P>0.10). Sex ratios of these two species did not show significant diel differences either (G=0.030; 0.90>P>0.50; df=1; G=2.750; 0.50>P>0.10; df=1, respectively).

Offshore A total of 64 crab pots were deployed, 32 during each period. Four species were caught during both day and night (*C. bocourti*, *C. maracaiboensis*, *C. ornatus*, and *C. danae*). A total of 89 crabs were caught during the day and 84 at night (Table 6). *Callinectes bocourti* comprised 73.8% and 75.3% of the abundance during the day and night, respectively, followed by *C. maracaiboensis* (15.5% and 6.7%). No differences in guild composition or sex ratios were found between day and night samples at each of the sites (Table 6). Crab species did not show differences in carapace length between day and night captures (*C. bocourti*, t=0.704, P>0.05, df=155; *C. maracaiboensis*, t=1.355, P>0.05, df=13; *C. ornatus*, t=0.881, P>0.05, df=9; *C. danae*, t=1.811, P>0.05, df=10). Kolmogorov-Smirnov tests run for normality of carapace length distribution for species at the offshore station compared between day and night samples, were statistically nonsignificant.

Sex ratios and ovigerous females

At the foreshore, all the species had male-biased overall sex ratios (Table 7), although only *A. cribrarius*, *C. danae* and *C. sapidus* deviated significantly from the normal Mendelian ratio. Sex ratios for *C. bocourti* and *C. exasperatus* did not differ significantly from equality, possibly because of low sampling numbers for these species. In the estuarine site, none of the sex ratios deviated significantly from an even proportion, although *C. danae* did show a slight bias toward males (Table 7).

No berried females appeared at the foreshore nor at offshore stations. Only two ovigerous females were caught during our study; both were *C. danae* and were collected at the estuarine site in March 1994 (CL [carapace length]: 32.4 mm), and in May 1994 (CL: 43.25 mm).

Body size

Table 8 shows the carapace length (mm) of the most abundant crab species at the foreshore and estuarine stations in Ensenada de La Vela. *Callinectes danae* from the foreshore stations were larger than those from the estuarine site (t=3.799, P<0.05, df=185). The mean cephalothorax length in this species from the foreshore stations was 29.75 mm, whereas in the estuarine zone, crabs averaged 25.16 mm. The average size of adult females from the estuarine station did not differ significantly from those at the foreshore stations. Adult males from the foreshore stations, however, were significantily larger than those from the estuarine site. Male and females sizes did not differ significantly in the foreshore stations, whereas at the estuarine site females were significantly larger (Table 8). Average carapace length of *A. cribrarius* (n=216) was 20.10 (range: 9.48–56.55; SE: 0.496). Juvenile females were significantly larger than juvenile males (t=5.02; P<0.001; df=148). Body size characteristics of *C. bocourti* are shown in Table 8. No differences in size between adult *C. bocourti* males and females from the estuarine site were found (t=0.187; P>0.5; df=14). All Kolmogorov-Smirnov tests run for normality of carapace length distribution for species that were compared at the foreshore and estuarine stations, were statistically nonsignificant.

Discussion

Of the nine species of *Callinectes* that have been reported for the tropical Western Atlantic (Williams, 1984), seven appeared at the foreshore of Ensenada de La Vela during our study. The species with the widest distributions were *C. danae* and *C. sapidus*, which were the only ones to appear at all the stations by the sea margin. *Callinectes maracaiboensis* and *C. larvatus* had the most restricted distribution, occurring only in the estuarine site, and *C. exasperatus* was present only in the estuary and at one of the marine stations. At the marine foreshore stations, *A. cribrarius* was the dominant species, with a share of 78% of the total catch in this ecotope, whereas *C. danae* (19%) was the second most abundant species. Meanwhile, in the estuarine site, where *A. cribrarius* was absent, *C. danae* was the prevailing species, followed by *C. bocourti*. Overall, the highest diversity was registered at the estuarine station, whereas at the foreshore the highest diversity was recorded in the

Table 4

Correlations between crab abundances and rainfall, salinity, temperature, and dissolved oxygen variables. ns = not significant.

		Rainfall			Salinity			Temperature			Oxygen		
Species	Biotope	*r*	*n*	Significance	r	*n*	Significance	*r*	*n*	Significance	*r*	*n*	Significance
Total crabs	Marine	0.1389	25	ns	−0.0634	34	ns	0.0634	33	ns	−0.4538	25	0.05>*P*>0.01
	Estuarine	0.4028	25	0.05>*P*>0.01	0.0408	34	ns	0.0774	33	ns	0.0620	25	ns
Callinectes danae	Marine	−0.0904	25	ns	0.0107	34	ns	0.1786	33	ns	−0.3155	25	ns
	Estuarine	0.1336	25	ns	0.0231	34	ns	0.2278	33	ns	0.1653	25	ns
Arenaeus cribrarius	Marine	−0.0904	25	ns	−0.0624	34	ns	0.0321	33	ns	−0.3389	25	ns
	Estuarine	Absent											

Table 5

Body size (carapace length in mm) and species abundance during diel observations at the foreshore of Ensenada de La Vela (1997–98). Percentages are given in parentheses in "Abundance" column.

Species	Period	Abundance	Mean body size	SE
A. cribrarius	day	91 (79.8)	19.14	0.94
	night	59 (72.0)	19.38	1.24
C. danae	day	17 (14.9)	21.92	1.89
	night	16 (19.5)	23.09	2.45
C. bocourti	day	1 (0.9)	21.3	—
	night	2 (2.4)	33.83	11.4
C. maracaiboensis	day	2 (1.8)	47.45	9.10
	night	4 (4.9)	37.28	6.05
C. larvatus	day	2 (1.8)	30.55	2.25
	night	1 (1.2)	15.65	—
C. sapidus	day	1 (0.9)	38.4	—
	night	0	—	—
Total	day	114		
	night	82		

Table 6

Distribution of species abundance (no. of crabs found) at the offshore stations during diel samplings and comparisons of sex ratios (all sites pooled).

		C. bocourti	*C. maracaiboensis*	*C. danae*	*C. ornatus*	*C.* sp.[1]	Totals	*G* (df=4)	Significance
Inshore	night	12	2	1	1	0	16	5.238	0.50>*P*>0.10
	day	18	0	2	5	0	25		
Midshore	night	18	3	0	2	2	25	4.226	0.50>*P*>0.10
	day	12	1	1	1	0	15		
Offshore	night	32	8	1	2	0	43	8.506	0.10>*P*>0.05
	day	37	5	7	0	0	49		
Total	night	62	13	2	5	2	84	7.940	0.10>*P*>0.05
	day	67	6	10	6	0	89		
Overall totals		129	19	12	11	2	173		

Sex ratios	*G*	Significance
C. bocourti	0.01	0.975>*P*>0.9
C. maracaiboensis	0.642	0.5>*P*>0.1
C. danae	0.07	0.9>*P*>0.5
C. ornatus	2.864	0.1>*P*>0.05

[1] Unidentified species.

most protected marine stations (2 and 1) followed by station 4, which is located at the most exposed tract. The values of Hill's diversity number 1 (N1) demonstrated a similar pattern and indicated that the number of abundant species was close to two at stations 2 and 3, slightly above this value at the estuarine station, and below at the most exposed station. Offshore guild composition was substantially different from that at the sea margin, as shown by pot samplings. Although several species were common to the three biotopes, each habitat had a distinctive dominant species: *Arenaeus cribrarius* at the surf zone (stations 1, 2, and 4), *C. danae* (station 3) in the estuarine pond, and *C. bocourti* offshore. Because different sampling gears were used at the sea border and offshore because of practical reasons, comparisons should be regarded as qualitative. However, artisanal fishermen do harvest *C. bocourti* when using beach seines in the areas next to our crab pot stations (senior author, personal obs.).

Inshore-offshore zonations of species at Ensenada de La Vela diverged from the gradients compiled by Norse and Fox-Norse (1979) for other areas in the Caribbean. In many localities, *C. bocourti, C. sapidus,* and *C. maracaiboensis* (the so-called *bocourti* group) are known to inhabit the waters by the seaside, whereas C. *marginatus* and *C. ornatus* are found at the seawardmost zone, and *C. danae* occupies the intermediate area. However, our patterns of

Table 7

Sex ratios for portunids captured in Ensenada de La Vela (1993–94).

	Male:female	Ratio	*G*	df	Significance
Marine stations					
A. cribrarius	155:61	2.5:1	21.607	1	$P<0.005$
C. danae	34:11	3.1:1	6.272	1	$0.01>P>0.025$
C. bocourti	0:1	0:1	—	—	—
C. sapidus	7:0	7:0	5.232	1	$0.01>P>0.025$
C. exasperatus	1:0	1:0	—	—	—
Estuarine station					
C. danae	79:63	1.3:1	0.900	1	$0.5>P>0.1$
C. bocourti	13:15	0.9:1	0.070	1	$0.9>P>0.5$
C. sapidus	2:3	0.7:1	0.088	1	$0.9>P> 0.5$
C. exasperatus	7:2	3.5:1	1.405	1	$0.5>P>0.1$
C. larvatus	2:1	2:1	—	—	—
C. maracaiboensis	2:2	1:1	—	—	—

Table 8

Carapace length (mm) for the most abundant species at the foreshore and estuarine stations in Ensenada de La Vela (Venezuela), and comparison of carapace sizes. ns = not significant.

	Marine stations					Estuarine station			
Callinectes danae	*n*	Mean	Range	SE	*Callinectes danae*	*n*	Mean	Range	SE
Juvenile females	8	24.6	14.92–32.7	2.099	Juvenile females	37	22.6	11.28–35.6	1.069
Adult females	3	39.6	36.58–42.0	1.619	Adult females	26	39.8	31.45–47.4	0.832
Juvenile males	14	19.5	8.5–32.4	2	Juvenile males	43	15.8	7.62–27.4	0.691
Adult males	20	39.1	7.42–56.7	2.869	Adult males	36	23.7	10.4–48.4	1.897
	Marine stations only					Estuarine station only			
Arenaeus cribrarius	*n*	Mean	Range	SE	*Callinectes bocourti*	*n*	Mean	Range	SE
Juvenile females	61	22	11.3–36.94	0.831	Juvenile females	7	23.1	11.8–34.4	3.251
Adult females	--------- No adult females ---------				Adult females	10	41	34–45.1	1.126
Juvenile males	89	17.6	10.25–28.64	0.459	Juvenile males	4	19.6	16.6–23	1.314
Adult males	66	21.8	9.48–56.55	1.213	Adult males	6	41.8	24.4–56.5	5.035

		t	df	Significance
C. danae (all crabs)	foreshore/estuarine	3.799	185	$P<0.05$
C. danae (adult females)	foreshore/estuarine	0.065	27	ns
C. danae (adult males)	foreshore/estuarine	4.653	54	$P<0.001$
C. danae (foreshore stations)	females/males	0.766	43	ns
C. danae (estuarine station)	females/males	6.297	140	$P<0.001$

abundance for *Callinectes* species are similar to another Caribbean locality (Buchanan and Stoner, 1988): Laguna Joyuda (Puerto Rico). All the *Callinectes* spp. recorded in this coastal estuarine lagoon were also present in the estuarine station of Ensenada de La Vela. *Callinectes danae* was the dominant species in both sites, whereas *C. exasperatus* and *C. larvatus* were present in low numbers. *Callinectes maracaiboensis* was very scarce at Ensenada de La Vela, but it was not reported at all in Laguna Joyuda (Buchanan and Stoner, 1988), although Buchanan and Stoner cautioned that specimens of this species might have been misclassified and listed as *C. bocourti*. On the other hand, the high abundance of *A. cribrarius* at the marine front of Ensenada de La Vela differed from that of other studies in the Caribbean and Gulf of Mexico, where this species has been reported in low numbers. For instance, in the SW Gulf of Mexico *A. cribrarius* was less than 1% of the total portunid community (García-Montes et al., 1988). In Laguna de Términos (Mexico), a polyhaline coastal lagoon, four species of *Callinectes* were found in a population survey conducted during a whole year, but no individuals of *Arenaeus* were reported (Román-Contreras, 1986). In the same lagoon, Sánchez and Raz-Guzmán (1997) caught a single individual of *A. cribrarius* out of 986 specimens collected over a 17-year span. The differences probably are probably due to the polyhaline conditions at these settings, thus restricting the viability of *A. cribrarius*. However, in temperate sandy beaches, this species can be very common. On Bogue Banks, in North Carolina, *Arenaeus cribrarius* ranked as the most important brachyuran in a high-wave-energy sandy beach (Leber, 1982). In the surf zone at Folly Beach, South Carolina, *A. cribrarius* was one of the dominant brachyuran crabs during the summer and also a key predator of benthic organisms (DeLancey, 1989). *A. cribrarius* is considered to be well-adapted to marine and slightly hypersaline salinity regimes and to habitats with heavy surf and sand scouring in shallow coastal waters (Fischer, 1978; Williams, 1984). This fact was evident in our study, in which *A. cribrarius* was abundant and clearly constrained to a narrow strip in the surf zone.

Our results suggest the importance of salinity as an excluding axis in the distribution of some species of swimming crabs in the surf and estuarine pond of Ensenada de La Vela. In our study, *A. cribrarius* was present in salinities from 30‰ to 43‰, thus exceeding the upper limits of tolerance commonly reported for this species. The restricted distribution of this species is probably a consequence of its stenohalinity (27.5–36.5‰) (Gunter, 1950; Norse, 1978; Williams, 1984; Pinheiro, 1991; Avila and Branco, 1996), although very occasionally it may show up in estuaries (Williams, 1965) and can tolerate experimental salinities down to 17.25‰ (Norse, 1978). This range indicates that *A. cribrarius* prefers marine or near-marine environments, thus explaining its absence in station 3 (estuarine). In spite of being considered to be well adapted to heavy surf in shallow coastal waters (Fischer, 1978; Williams, 1984), *A. cribrarius* appeared to be abundant in all three foreshore stations, independent of water movement, and was most abundant in the more protected stations 1 and 2. Because the salinity did not show any major differences between foreshore and offshore habitats, other factors are at stake in determining the zonation observed for the other species. One of the main elements to consider is substrate composition (Norse and Fox-Norse, 1979; Pinheiro et al., 1997). Pinheiro et al. (1997) stated that distributional patterns of portunids in Fortaleza Bay (Brazil) are driven mainly by the granulometric composition of the sediments. Substrates at the foreshore and estuarine pond differed from offshore bottoms: at the foreshore the sediment was mainly sand; at the estuarine station a muddy bottom prevailed. At the offshore stations, silt was the main substrate. Hence, this difference could influence the distribution of swimming crabs in Ensenada de La Vela.

Callinectes danae was found in both biotopes at the foreshore but was more abundant at the estuarine site. In the marine stations of the surf zone, *C. danae* appeared more frequently in the most protected areas. The appearance and persistence of this species in both environments probably stems from its euryhalinity. In several Caribbean locations, *C. danae* has been observed dwelling in polyhaline environments (Taissoun, 1969; Norse, 1978; Buchanan and Stoner, 1988). Based on this evidence, it is not surprising to find *C. danae* in the entire range of salinities in Ensenada de La Vela, although it is important to underline that at the estuarine station it appeared when salinity was below the minimum (11‰) reported by Norse (1978). Also, several of the portunid species in the surf zone in Ensenada de La Vela were found in higher salinities than those reported by Norse (1978) in several localities in Jamaica, except *C. maracaiboensis* and *C. larvatus*. The absence of *C. ornatus* at the foreshore stations may be due to reasons other than the sampling method, because the same method was used by Carmona-Suárez and Conde (1996), where specimens of *C. ornatus* were frequently captured at different sites in the State of Falcón, Venezuela, including Ensenada de La Vela.

Total abundance of all swimming crabs both at the surf zone and at the estuarine station fluctuated widely and randomly through the year. This pattern also emerged when only the temporal abundance variations of the dominant species, *A. cribrarius* and *C. danae*, were examined. No significant correlations were found between abundances of these two species and rainfall, dissolved oxygen, water temperature, or salinity fluctuations. However, the inverse correlation of dissolved oxygen and abundance reached almost significant levels for both species at the marine foreshore and indeed was significant for the total abundance of crabs in the surf. Additionally, there was a positive correlation between rainfall and total abundance of crabs in the estuarine zone, possibly due to the increment of organic material washed into this environment from adjacent terrestrial areas. Although bibliographic evidence supports the adaptation of portunids to low levels of dissolved oxygen in their environment (DeFur et al., 1990; Rantin et al., 1996; Mangum, 1997), and the relation between respiration rates and salinity in two *Callinectes* species (Rosas et al., 1989), nothing supports the idea that the increase of swimming crab densities is due to the decrease in dissolved oxygen. It might be possible that augmenting food resources would increase populations of fishes and invertebrates or planktonic blooms, which in turn would require a higher oxygen demand in the area, subsequently provoking drops in oxygen and causing mortalities of high-oxygen-demanding invertebrates. In any event, these results suggest that fluctuations in oxygen levels might be a key element in regulating portunid populations at Ensenada de La Vela and merit further research efforts.

Berried females were remarkably scarce during our study. Only two, both belonging to *C. danae*, were caught throughout the first period at the estuarine site, and none were caught during day and night samplings in the surf zone nor offshore. Nonetheless, scarcity of ovigerous females of swimming crabs in these coasts is not exceptional. During a 2-year survey of crustaceans along 700 km of Falcón's shoreline, Carmona-Suárez and Conde (1996) caught very few berried females of several of the littoral portunid species. They caught only one berried female of *A. cribrarius* and no ovigerous females of *C. sapidus*, *C. larvatus*, *C. ornatus*, or *C. danae*. However, in estuarine areas, substantial numbers of berried females of *C. bocourti*, *C. maracaiboensis*, and *C. exasperatus* were caught in the tidal zone. The scarcity or sheer absence of egg-bearing females in some species of swimming crabs might be the result of habitat partitioning by sex. Differential distributions by sex have been reported for *C. sapidus* (Williams, 1965; Perry, 1975; Archambault et al., 1990), *C. maracaiboensis* (Norse, 1977), and *C. bocourti* (Taissoun, 1969; Norse, 1978). However, for the dominant species in the surf, *A. cribrarius*, ovigerous females do not seem to be segregated into deeper waters. In southern Brazil, ovigerous females of this species appeared in shallow waters close to the coast (Pinheiro et al., 1996). Similarly, many ovigerous females were collected in very shallow water, at the surf's edge in North Carolina (Williams, 1984). Likewise, for *C. bocourti* and *C. maracaiboensis* egg-bearing females have also been reported in marine shallow waters (Norse, 1977). Furthermore, adult females of most species inhabiting the surf zone at Ensenada de La Vela were observed in this area year-round. Thus, alternative explanations should be considered, such as lack of estuarine habitats or sustained harsh environmental conditions that do not allow energy to be invested in reproduction. For instance, a highly seasonal reproductive pattern, with periods without berried females, has been observed in populations of the mangrove tree crab, *Aratus pisonii*, living in hypersaline lagoons in this area (Conde, 1989); this pattern contrasts with the pattern for populations inhabiting other localities, where these crabs reproduce continuously throughout the year (Conde and Díaz, 1989a; Díaz and Conde, 1989). Also, undergrown or stunted specimens of various species of crustaceans have been reported in this area (Conde and Díaz 1989b, 1992a, 1992b; Carmona, 1992; Carmona-Suárez and Conde, 1996). Thus, it is possible that this arid coast lacks the necessary resources for these crabs to reproduce, except in a few estuarine spots. This hypothesis is also supported by the fact that the body size of several species of swimming crabs collected in our study was smaller than that reported in other locations (Fischer, 1978; Williams, 1984).

The only river near the Ensenada de La Vela is the Coro River, which lies approximately 2 km westwards. Because of current direction (east–west), it cannot influence estuarine conditions to the sampled area. The small estuary in the Ensenada de la Vela could be a possible local nutrient supplier. But its influence is restricted to a few days during the end of each year, when the estuary opens to the sea. The setup of an untreated sewage discharge in the small estuarine basin at the beginning of 1997 could in fact have a long-term impact, but it is possible that various species of swimming crabs may not be affected negatively, because of their capacity to live in polluted areas. Such is the case with *C. bocourti* (Taissoun, 1972; Williams, 1974), and *C. sapidus*, the main species in the Lake Maracaibo crab industry (Oesterling and Petrocci, 1995), where contamination due to several sources (i.e. sewage and oil) has reached high levels (Rodríguez, 2000).

Because trawl studies have shown greater abundances of blue crabs (*C. sapidus*) and, in general, other decapods at night (Wilson et al., 1990), we ran a series of day and night samplings at the marine front over a six-month period and later also undertook diel offshore pot sampling on several occasions. Although Fischer (1978) has stated that *A. cribrarius* burrows into the bottom during the day and emerges at night, we collected *A. cribrarius* in the same range of abundances and sizes during both day and night samplings. Similar results were achieved by DeLancey (1989) in South Carolina, where no significant differences were obtained from samples collected at day and night. Wilson et al. (1990) ascribed the lack of differences in day and night abundances of *C. sapidus* to the use of more effective sampling devices than previously employed. In our study, no major differences were observed in diversity, abundance, body size, or sex ratios for most species, even though two kinds of collecting gears were used; thus, it is feasible to consider that if daily cycles exist in the species, they do not have a significant impact on daily density variations. In turn, these findings may have practical consequences for the decisions regarding sampling schemes to assess fisheries in this area.

The exploitation of swimming crabs at Ensenada de La Vela must be considered only at the artisanal level because of the low abundance of all species treated in our work and their wide and random density fluctuations. In fact, local fisheries are currently limited to the artisanal capture of portunids by hanging nets or hand-driven trawling nets. The most captured species by fishermen is *C. bocourti* (senior author, personal obs.), but *C. danae* is also a promising staple to be harvested because it appears in all three major biotopes (marine inshore, offshore, and estuarine). *Arenaeus cribrarius*, a species commercially exploited in Brazil (Pinheiro and Franzoso, 1998) and regarded to have an excellent flavor (Fischer, 1978), may also be considered a target species because of its great abundance, although its small size may make it less desirable commercially.

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