BULLETIN OF MARINE SCIENCE, 43(1): 77–87, 1988

ASPECTS OF THE POPULATION BIOLOGY OF THE MARINE ISOPOD *EXCORALLANA TRICORNIS OCCIDENTALIS* RICHARDSON, 1905 (CRUSTACEA: ISOPODA: CORALLANIDAE) AT CANO ISLAND, PACIFIC COSTA RICA

Hector M. Guzman, Vilma L. Obando, Richard C. Brusca and Paul M. Delaney

ABSTRACT

Diel and seasonal aspects of occurrence, density, size and sex ratios of the marine isopod *Excorallana tricornis occidentalis* from Cano Island, Costa Rica, were studied during 1984 and 1985. Surface and vertical plankton tows were taken over 24-hour periods. 2,916 individuals were collected; 42% were juveniles, 39% females and 17% males. Only one ovigerous female was collected (5.5 mm in length). Females probably remain hidden in the substrate while brooding embryos and mancas. Highest densities were found in November and January 1984, but differences in monthly densities were not statistically significant. *E. tricornis occidentalis* is a member of the demersal zooplankton community. Significant differences in isopod densities between sampled hours indicate that it has a nocturnal migratory behavior; in both surface and vertical tows it is found in the water column only between 1800 and 0600 h, with greatest emergence after midnight (between 2400 and 0300 h). This species is probably a nocturnal predator that feeds at night in the water column. Mean length for males was 5.17 mm, for females 4.76 mm, and for juveniles 2.48 mm; mean length for all 2,916 individuals was 3.91 mm. There were significant differences in isopod lengths between sampled years, months and hours. Adults predominated in most months. The largest percentages of juveniles occurred in July and November, indicating probable Spring and Fall recruitment bursts. Same-sex pairwise comparisons of mean body lengths showed *E. tricornis occidentalis* to be significantly smaller than its Atlantic con-specific *Excorallana tricornis tricornis*, and another Atlantic congener, *E. oculata*.

There are 20 known species/subspecies of *Excorallana*, all but one restricted to the New World. *Excorallana oculata* is a trans-Atlantic species, occurring in both the Caribbean and West Africa (this is the first published record of a member of this genus outside the New World). Only five described species occur in the eastern Pacific, three of which have probable analogs in the western Atlantic (Delaney, 1984). Most *Excorallana* species live in tropical latitudes, and in the Pacific are not found north of Point Conception, California, or south of Guayaquil, Ecuador. *E. meridionalis* is the only Pacific species known to occur south of the equator.

Excorallana tricornis occidentalis is an eastern Pacific subspecies, whose cognate (*E. tricornis tricornis*) occurs in the Caribbean and Gulf of Mexico. The Pacific subspecies is restricted to the Cortez, Mexican and Panamanian zoogeographic provinces of the Panamic Zoogeographic Region. Prior to this study, *E. tricornis occidentalis* had been reported only from Mexico and Panama, from the intertidal zone to 138 m in rocky habitats, sandy beaches and mangrove environments (Delaney, 1984). Brusca and Iverson (1985) predicted its occurrence in Costa Rican waters.

Parasitic, scavenging and free-living habits have been reported for corallanid isopods. *Excorallana tricornis occidentalis* has been reported as a commensal in sponges (Richardson, 1905; Delaney, 1984), in mangrove habitats (Monod, 1969),

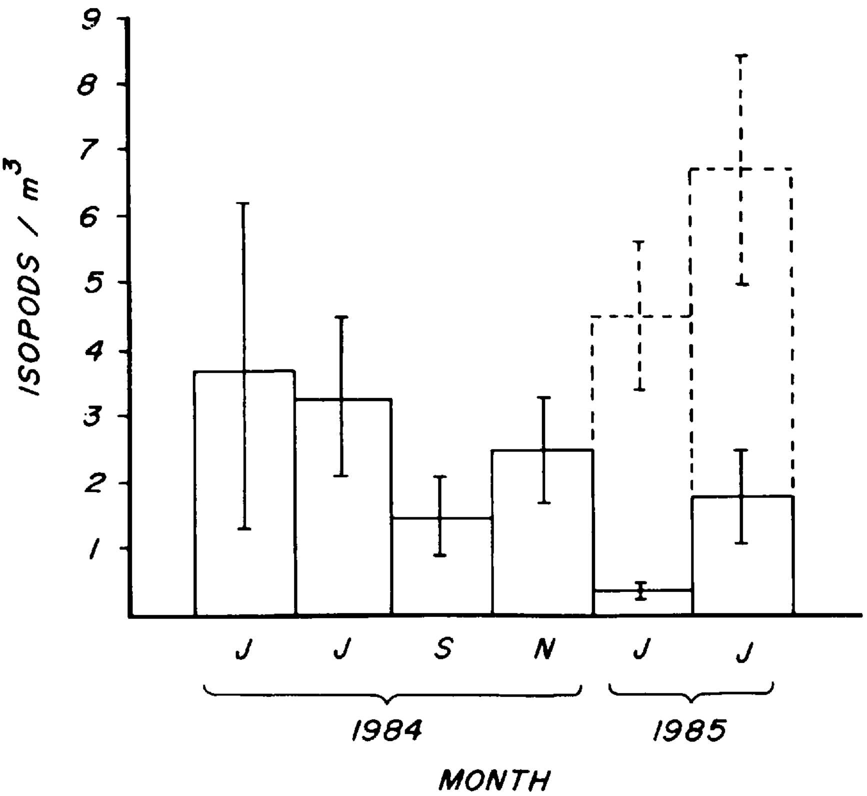


Figure 1. Mean densities (and standard deviations—solid bars) of *E. tricornis occidentalis* from surface tows in sampled months. Solid lines are data from 6-h interval samples (1984; 1985); dashed lines include data from 3-h interval samples (1985 only).

associated with hydrozoans on andesitic rocks (Delaney, 1984), and as a fish "parasite" from the body surface and nostrils of sea bass *Mycteroperca jordani* and jack *Caranx caninus* (Bowman, 1977). The present study describes the population composition, benthos-water column migratory behavior, and seasonal abundance of *E. tricornis occidentalis* at Cano Island, Costa Rica, and makes size comparisons of this species to seven other *Excorallana* species. This study is the first quantitative investigation of the population biology or ecology of a species in the family Corallanidae.

Methods

Cano Island (8°43'N, 83°52'W) is located approximately 15 km west of Pacific Costa Rica, north of the Osa Peninsula, Puntarenas Province. Coral reefs occur at 0.5–25 m depth around the island, particularly on the north and east sides. Seasonal samples were collected between January 1984 and July 1985 at a permanent station located approximately 500 m off the north coast of the island, directly opposite the house, in water 20–25 m deep. Four horizontal surface net tows were taken at 6-h intervals (0600, 1200, 1800, 2400) during January, July, September and November, 1984; and eight horizontal surface net tows were taken at 3-h intervals (0300, 0600, 0900, 1200, 1500, 1800, 2100, 2400) during January and July, 1985. Vertical tows were also made at the same time intervals, from 18 m to the surface.

All surface tows were made for 10-min periods, at an approximate speed of 2 knots, using a 280 μm plankton net with a 0.5-m diameter opening. The amount of water filtered was calculated as the product of distance traveled and size of the net opening, giving a final filtrate volume estimate of

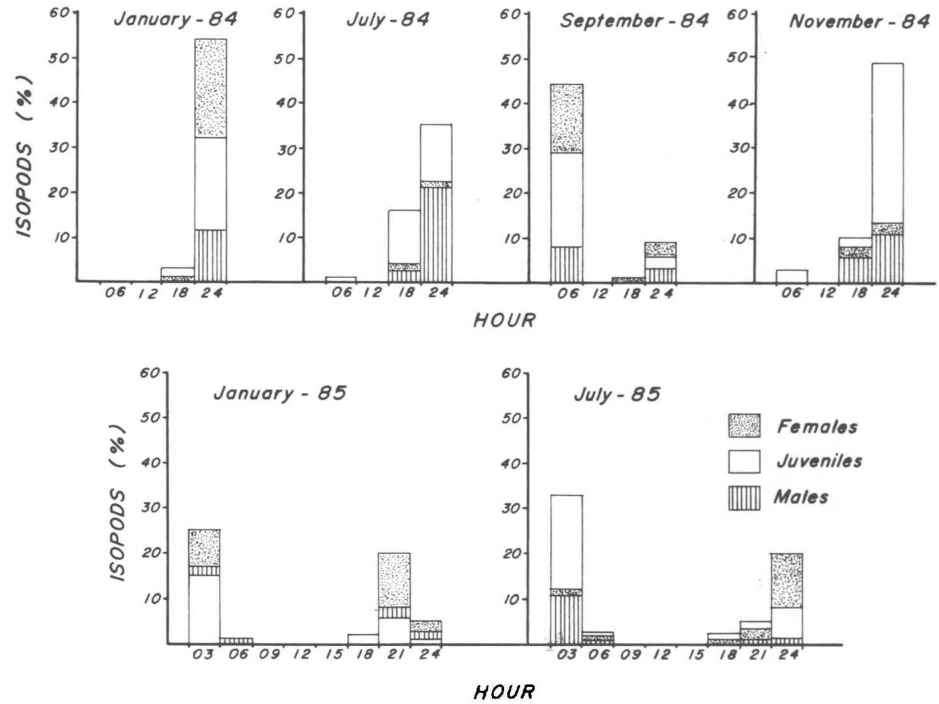


Figure 2. Distribution (by sex) of *E. tricornis occidentalis* per hour for each sampled month at Cano Island, 1984–1985.

123.5 m^3. All density calculations are based on these quantitative surface tow data. Samples were fixed for 72 h with 4% neutral formaldehyde, then transferred to 70% ethanol. All individual *E. tricornis occidentalis* captured were examined.

Body length was obtained by measuring along the central axis of the animal, from the anterior margin of the cephalon to the posterior edge of the pleotelson. Males were recognized by the presence of appendix masculinae (on the second pair of pleopods) or by horns on the cephalon. Although horns positively identify males in this species, absence of horns does not necessarily indicate a female and hornless animals must be examined for appendix masculinae, and/or oostegites to positively confirm the sex. Gravid females are easily recognized by the presence of embryos in the oostegial marsupium. Individuals 3.0 mm or smaller were considered juveniles due to absence of externally visible sexual characters.

All collections of *E. tricornis occidentalis* examined during this study were deposited in the Zoology Museum at the University of Costa Rica (U.C.R. #1215). Other *Excorallana* species were measured in the same manner using specimens borrowed from the National Museum of Natural History (Smithsonian Institution) and the Zoologisk Museum, Copenhagen (syntype series of *E. tricornis tricornis*), or size data were taken from the published literature.

RESULTS

A total of 2,916 *E. tricornis occidentalis* (1,423 in 1984, 1,493 in 1985) was captured and examined. No significant differences in isopod density were noted between months or years. However, clear trends in density occurred. In 1984, the density per m^3 of isopods (surface tow data) decreased from January to September and then increased in November (Fig. 1). 1985 data from surface tows taken every 6 h showed an overall decrease in density compared to 1984. However, 1985 data including surface tows taken every 3 h showed a marked increase in density over 1984 (Fig. 1).

There were significant differences in isopod density at different sampling hours

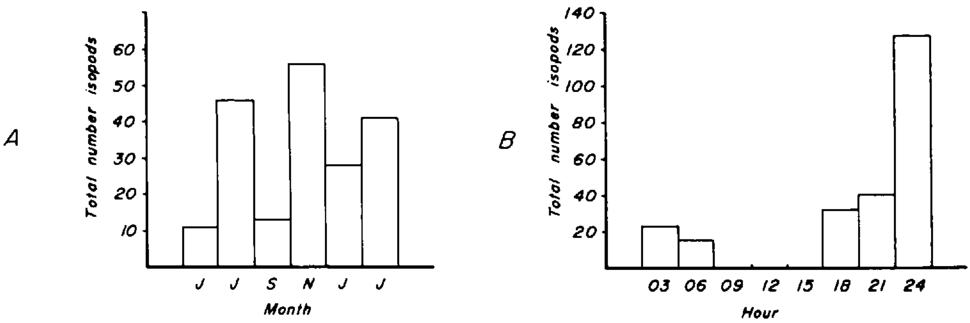


Figure 3. Total numbers of *E. tricornis occidentalis* per month (A) and per hour (B) collected in vertical tows at Cano Island, 1984–1985.

in each sampled month ($P < 0.05$, one-way ANOVA). The distribution of *E. tricornis occidentalis,* based on surface tow data, was almost entirely limited to 1800–2400 in January and July (1984), with the largest number of isopods found at 2400 (Fig. 2). During September (1984) isopods were distributed mainly from 2400–0600, with the largest number of isopods occurring at 0600. During November (1984) the distribution was similar to that of January and July, although a few juveniles (2.9% of total 24-h sample) were collected at 0600 (most juveniles occurred at 1800 and 2400) (10% and 48.8% of total sample) (Fig. 2).

For the entire study period the percentage of juveniles collected was 42%,

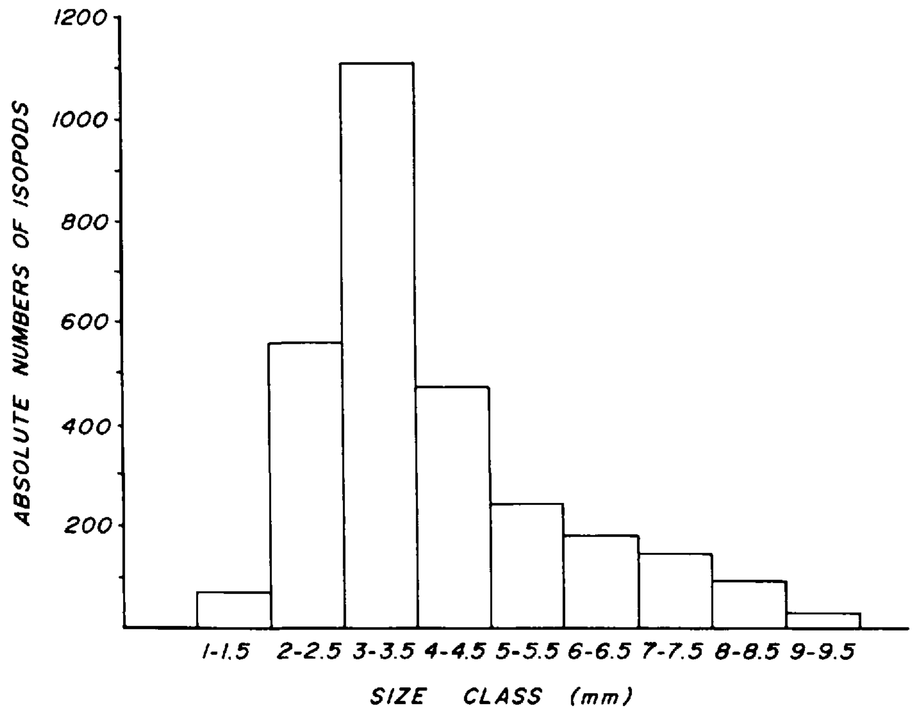


Figure 4. Absolute numbers and size classes of *E. tricornis occidentalis* from Cano Island (all samples combined).

Table 1. F-ratio statistics of isopod length versus sampled hours, months and years at Cano Island, Costa Rica

Source	df	Sum of squares	Mean square	F ratio	Significant difference in isopod size F prob.
		Between years			
Between	1	2,576.57	2,576.57	9.235	0.0024*
Within	2,925	815,062.93	278.99		
Total	2,926	818,629.50			
		Between months			
Between	5	94,583.18	18,916.68	76.32	0.0000*
Within	2,921	724,046.32	247.87		
Total	2,926	818,629.50			
		Between hours			
Between	7	44,531.37	6,361.62	23.99	0.0000*
Within	2,919	774,098.13	265.19		
Total	2,926	818,629.50			

* Indicates significance ($P < 0.01$)

females 39.8% and males 17.8%. Figure 2 shows the percentages of males, females and juveniles found at different hours for each sampled month. No relationship was found between sex and mean lengths versus sampling hour or month ($R = -0.6435$, Pearson's correlation test). 1985 distribution data were similar to 1984, although the increased sampling frequency (increased from every 6 h to every 3 h) allowed discrimination of some interesting trends (Fig. 2). In January most individuals were collected from 2100–0300, with most juveniles and adults occurring at 0300 (16.2% and 38.4% of the total 24-h sample, respectively). At 1800 a few juveniles were found (1.5% of total sample), while at 0300, 2100 and 2400 the population was dominated by adults. In July 1985, individuals also occurred from 1800–0600, with highest numbers appearing at 2400 and 0300. Juveniles predominated at 0300 and adults predominated at all other times.

As with surface tows, significant differences in numbers of isopods captured in vertical tows (to 18 m depth) occurred between hours ($P < 0.05$, one-way ANOVA), but not between months ($P > 0.05$, one-way ANOVA). However, both vertical tows and surface tows captured the most isopods in July and November 1984, and January 1985 (Fig. 3a). The vertical tow data were similar to the surface tow data, as both indicated that *E. tricornis occidentalis* was distributed in the

Table 2. Comparison of sex ratios for seven species of corallanid isopods

Species, location, source	N	Sex ratio (male/female)
Excorallana tricornis occidentalis (Cano Island, Costa Rica; this study)	2,916	0.436 (42% juveniles)
Excorallana tricornis tricornis (West Indies, syntype series; this study)	305	0.471
Excorallana tricornis tricornis (Gulf of Mexico; Menzies and Kruczynski, 1983)	58	2.846
Excorallana mexicana (same as above)	54	8.091
Excorallana antillensis (same as above)	54	1.041
Alcirona krebsii (same as above)	45	0.818
Lanocira rapax (same as above)	47	0.887
Excorallana oculata (West Africa; this study)	46	0.587

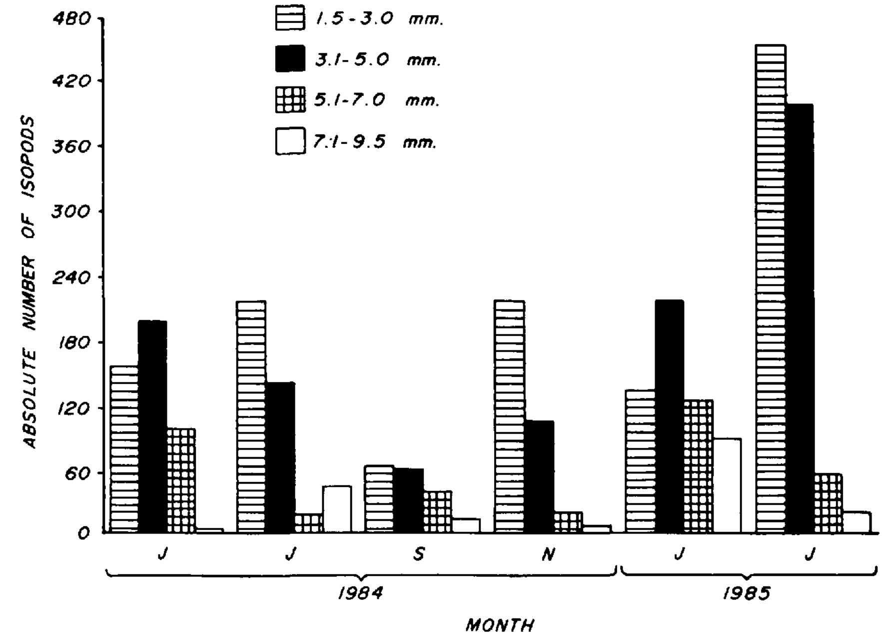


Figure 5. Absolute number of isopods, in four size classes, captured during each sampled month.

water column between 1800 and 0600, with largest numbers occurring near 2400 (Fig. 3b).

Mean body length for all individuals collected was 3.91 mm ±1.67 (N = 2,916). The largest size classes for *E. tricornis occidentalis*, ranked in order of importance, were 3–3.5 mm, 2–2.5 mm and 4–4.5 mm (Fig. 4). Mean size for males was 5.17 mm (SD = ±0.07), for females 4.76 mm (SD = ±0.91), and for juveniles 2.48 mm (SD = ±0.38).

Length differences in *E. tricornis occidentalis* were highly significant ($P < 0.01$, one-way ANOVA) between years, months and hours (Table 1, Fig. 5). Figure 6 shows the mean length for each sampled month. The mean length ranged from 3.1–4.8 mm, and during most months it exceeded 3.5 mm, indicating a predominance of adult isopods in these periods. The largest mean length occurred in January 1985 and the smallest in November 1984. The distribution of mean lengths versus sampling hours shows the largest mean length at 2100, the smallest at 1800 and relatively similar values at 0300, 0600 and 2400 (Fig. 7). Sex ratios for samples of seven corallanid species are shown in Table 2. These samples vary greatly in size, as well as being derived from different authors or sources. No clear pattern is evident except for a strong similarity between the ratios of *E. tricornis occidentalis* and the syntype series of *E. tricornis tricornis* (0.436 and 0.471). The presence of only one ovigerous female in our collections may have biased the sex ratio calculations for *E. tricornis occidentalis.*

Mean body lengths for eight species of *Excorallana* are shown in Table 3. Corallanid isopods are uncommon in most museum collections, and available sample sizes were small. This may bias the computed values. The largest sample analyzed was that of *E. tricornis occidentalis* from the present study, which had the lowest mean body length of all species analyzed even if the large proportion of juveniles from this study is discounted. In comparison to the syntype series of

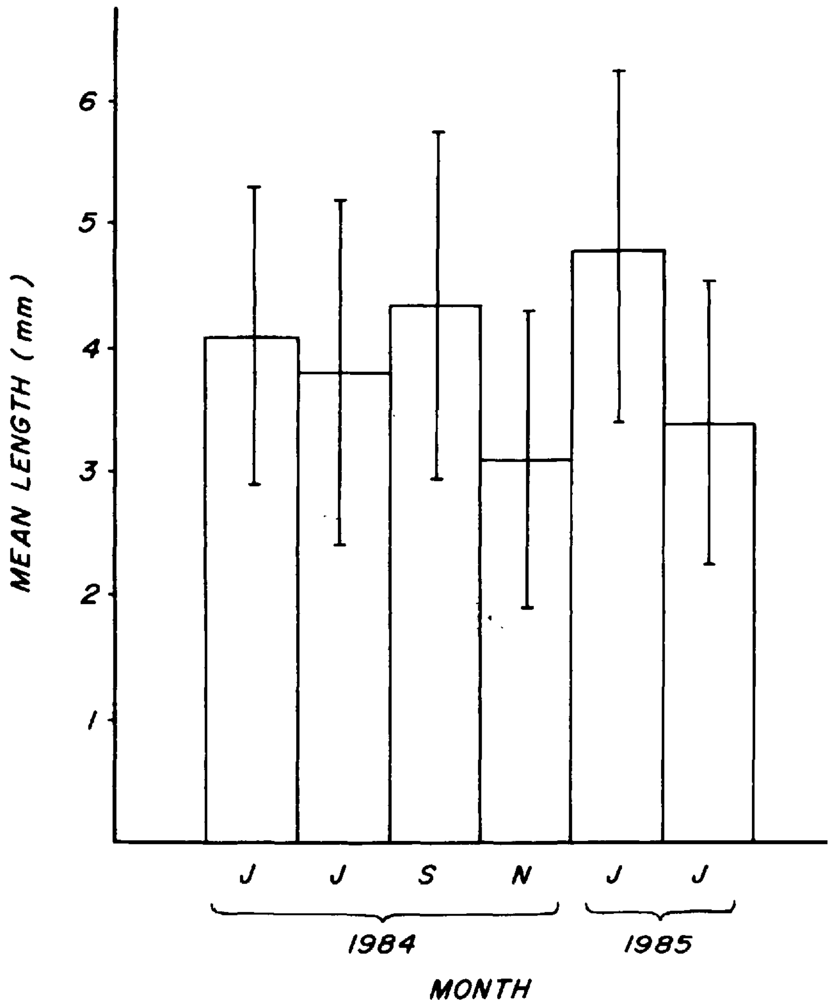
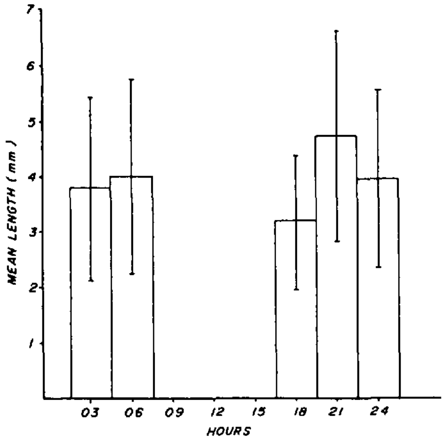


Figure 6. Mean monthly lengths (mm) (and standard deviations—solid bars) for *E. tricornis occidentalis* at Cano Island, 1984–1985 (surface tow data).

the Atlantic subspecies *E. tricornis tricornis* (N = 305), individuals of the Cano Island population of *E. tricornis occidentalis* were smaller. The former ranged from 4.0–9.0 mm in length, the largest size class being 6.0–6.9 mm (Fig. 8). *E. tricornis occidentalis* ranged from 1.0–9.5 mm in length, the largest size class being 3.0–3.5 (Fig. 4). Whether these differences are artifacts of sample size, geographic or seasonal variability, capture-gear selectivity, or represent true species differences will be uncertain until additional large samples are obtained and analyzed.

Statistical pairwise comparisons of mean specimen length for each sex were made between *E. tricornis occidentalis* (Cano Island, Costa Rica), *E. tricornis tricornis* (syntype series, West Indies) and *E. oculata* (West Africa), using the F-statistic to evaluate sample variances (Table 4). Each sex of *E. tricornis occidentalis* was significantly smaller ($P < 0.01$, F-statistic) than the same sex in the other two species compared (Table 4).



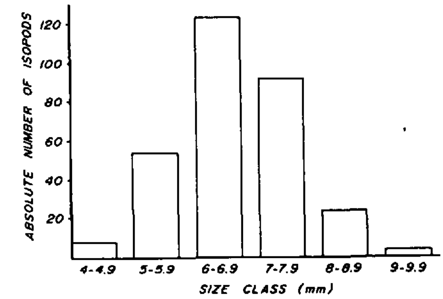


Figure 7. Mean length distributions (and standard deviations—solid bars), per sampled hour, for *E. tricornis occidentalis* at Cano Island, 1984–1985 (all data combined).

Figure 8. Frequency histogram of body lengths for *Excorallana tricornis tricornis* (syntype series from the West Indies, Zoologisk Museum, Copenhagen).

Discussion

Data from this study indicate that *E. tricornis occidentalis* is abundant and breeds year round at Cano Island, although definite peaks in the appearance of juveniles appear in the spring and fall. Largest mean body size and greatest proportion of adults occurred in January and September; largest percentages of juveniles occurred in the subsequent sample periods, in July and November, indicating probable spring and fall recruitment bursts. Only a single gravid female was captured during the course of this study (September 1984, 2400). Gravid females of *Excorallana tricornis occidentalis* were collected in bottom samples during March, April and August in the Gulf of California (Delaney, 1984). Two

Table 3. Mean body length for nine species of *Excorallana*

Species-Location	N	Mean length (mm)	Variance
Excorallana tricornis occidentalis (Cano Island, Costa Rica)	2,916	3.91	2.7889
Excorallana tricornis tricornis (West Indies, syntype series)	305	6.69	0.8477
Excorallana tricornis occidentalis (Gulf of California, types and others)	20	6.81	2.0687
Excorallana oculata (West Africa)	46	9.74	4.3858
Excorallana meridionalis (Chile, Carvacho and Yanz, 1971)	10	8.20	2.760
Excorallana bruscai (Gulf of California, type series)	24	8.14	1.2998
Excorallana houstoni (Gulf of California and Galapagos Islands, types)	7	5.90	3.7627
Excorallana sexticornis (Florida, types)	10	6.92	0.4203
Excorallana quadricornis (Virgin Islands and Brazil, types and others)	18	8.80	3.5275

Table 4. Same-sex pairwise comparisons of mean body length for three *Excorallana* species, using the F-statistic

Species, location, number		Male	Female
1. *Excorallana tricornis tricornis* (West Indies; syntype series)			
	mean length (mm) =	6.58	6.76
	N =	99	206
	variance =	0.7001	0.9085
2. *Excorallana tricornis occidenatlis* (Cano Island, Costa Rica)			
	mean length (mm) =	5.17	4.76
	N =	496	1,137
	variance =	0.0049	0.8281
3. *Excorallana oculata* (West Africa)			
	mean length (mm) =	11.29	8.83
	N =	17	29
	variance =	2.389	3.307

Species compared	F-statistic Male	F-statistic Female	Significant differences ($P < 0.01$)
1 vs. 2	142.88	1.097	Yes
1 vs. 3	3.412	3.640	Yes
2 vs. 3	487.55	3.994	Yes

explanations may account for the lack of gravid females in the Cano Island collections. Either the sampling regime was not done with adequate periodicity to determine when gravid females occur, or gravid females do not leave the substratum to enter the water column. The data clearly do not support the former explanation. Hence, the hypothesis that gravid females remain in the substratum while brooding embryos seems the more likely. Such behavior has been suggested for other isopods. Johnson (1976) described this behavior for *Cirolana harfordi* in California, and Kensley (1983) noted that in 42% of the reef crest isopod species at Carrie Bow Cay, Belize (including *E. tricornis tricornis*), females remained hidden within the reef crest habitat during brooding. The large percentage of juveniles (42% overall) in the Cano Island samples has not been reported for any other species of Corallanidae. This may be because other studies have not collected with a fine-mesh plankton net (280 μm), or perhaps were not as discriminating in sexing individuals (Menzies and Kruczynski, 1983).

Excorallana tricornis occidentalis has a strong diel migratory cycle. Individuals were found in the water column only from evening (1800) to early morning hours (0600), peaking at 2400–0300. Judging by collections made in other areas, individuals migrate to the benthos during the day, particularly to coral habitats or rocky substrata. Sampling in both deeper and shallower zones would be informative, as this region is under the influence of a permanent superficial thermocline at about 20 m depth, with a temperature gradient of about 4°C/10 m (Wyrtki, 1966). This thermocline is weaker during the dry season (December through February), and can be at 10–15 m during this period. The thermocline could be a barrier limiting the vertical migration of *E. tricornis occidentalis.* The densities of *E. tricornis occidentalis* found in November and January suggest a possible seasonal effect related to the beginning of the dry season and perhaps to the breakup of the thermocline and subsequent water mixing at this time (Wyrtki, 1966).

The nocturnal migration exhibited by *E. tricornis occidentalis* may represent a resource-partitioning behavior. Menzies and Kruczynski (1983) suggested that partitioning of species by depth among inner and middle continental shelf assem-

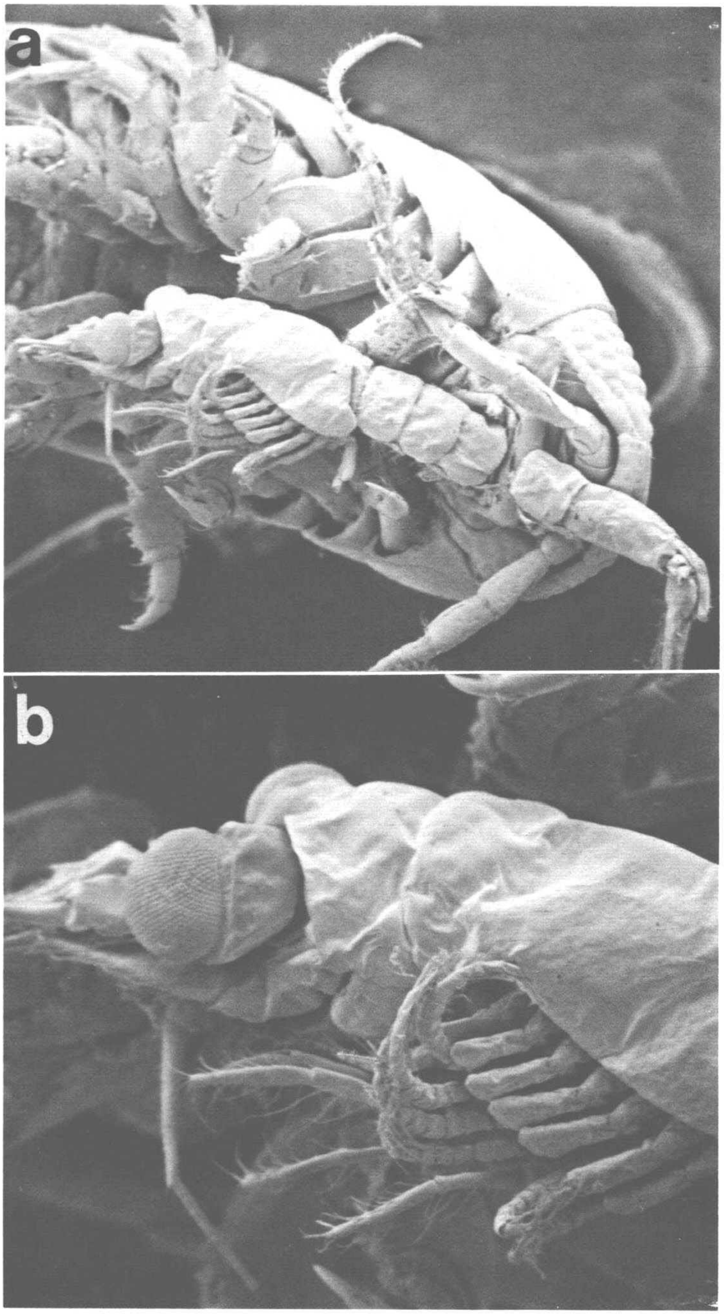


Figure 9. Scanning electron micrographs of *E. tricornis occidentalis* from Cano Island: (a) ventral view showing a mysid crustacean in the grasp of the isopod, 30×. (b) detail of mysid, 50×.

blages of isopods from the Gulf of Mexico may occur, including five corallanids—*E. tricornis tricornis, E. mexicana, E. antillensis, Alcirona krebsii* and *Lanocira rapax*. Aside from a possible correlation to the onset of the dry season, no relationships between isopod distribution and any physical parameters were noted.

Many species of *Excorallana* have been recorded as "temporary parasites" or micropredators of fishes (see Delaney, 1984 for review). Other corallanid species, such as *Tachaeae,* are known as micropredators of freshwater shrimps. One of the specimens of *E. tricornis occidentalis* from Cano Island was found to have an unidentified mysid crustacean in its grasp. Figure 9 shows a ventral view of the isopod possibly preying on the smaller mysid; the isopod's large piercing mandibles, maxillules and maxillae are clamped down through the fourth abdominal somite of the mysid.

The migratory activity exhibited by *E. tricornis occidentalis* at Cano Island may be related to predation by these isopods on fishes and planktonic invertebrates. Stepien and Brusca (1985) recently presented experimental evidence of nocturnal emergence of another flabelliferan isopod (*Cirolana diminuta*), a member of the California demersal zooplankton community, for purposes of predation. As these authors point out, the prevalence of nocturnal migration in nearshore ecosystems implies that the disadvantages of migrating into the water column at night (such as being preyed upon by nocturnal fishes) must be outweighed by the advantages. Possible advantages may include feeding, reproduction, molting, dispersal and niche diversification.

ACKNOWLEDGMENTS

We take this opportunity to thank A. Leon for drawing the figures used herein, and T. D. Stebbins for criticizing an early draft of this paper. Specimens were kindly loaned to P. M. Delaney by Dr. T. E. Bowman (Smithsonian Institution, Washington, D.C.) and Dr. T. Wolff (Zoologisk Museum, Copenhagen). This research was supported by a grant from the Vicerrectoria de Investigacion, University of Costa Rica (808-83-135) to H. M. Guzman, as well as grants from the National Science Foundation to R. C Brusca (BSR 8514093) and P. W. Glynn (OCE 8415615).

LITERATURE CITED

Bowman, T. E. 1977. Isopod crustaceans (except Anthuridae) collected on the Presidential Cruise of 1938. Proc. Biol. Soc. Wash. 89: 653–666.

Brusca, R. C. and E. W. Iverson. 1985. A guide to the marine isopod Crustacea of Pacific Costa Rica. Rev. Biol. Trop. 33(Supplement 1): 1–77.

Delaney, P. M. 1984. Isopods of the genus *Excorallana* Stebbing, 1904 from the Gulf of California, Mexico (Crustacea, Isopoda, Corallanidae). Bull. Mar. Sci. 34: 1–20.

Johnson, W. S. 1976. Biology and population dynamics of the intertidal isopod *Cirolana harfordi.* Mar. Biol. 36: 343–350.

Kensley, B. 1983. The role of isopod crustaceans in the reef crest community at Carrie Bow Cay, Belize. Mar. Ecol. 5:2 29–44.

Menzies, R. J. and W. L. Kruczynski. 1983. Isopod Crustacea (exclusive of Epicaridea). Mem. Hourglass Cruises 6(1): 1–126. Florida Dept. of Natural Resources, St. Petersburg, Florida.

Monod, T. 1969. Sur trois crustaces isopodes marins de la region Guyane-Amazone. Cah. O.R.S.T.O.M. Ser. Oceanogr. 7: 47–68.

Richardson, H. R. 1905. A monograph of the isopods of North America. U.S. Nat. Mus. Bull. 54: 1–727.

Stepien, C. and R. C. Brusca. 1985. Nocturnal attacks on nearshore fishes in southern California by crustacean zooplankton. Mar. Ecol. Prog. Ser. 25: 91–105.

Wyrtki, K. 1966. Oceanography of the eastern equatorial Pacific. Oceanogr. Mar. Biol. Ann. Rev. 4: 33–68.

DATE ACCEPTED: October 6, 1987.

ADDRESSES: *(H.M.G. and V.L.O.) Escuela de Biologia, Universidad de Costa Rica, San Pedro, Costa Rica.* PRESENT ADDRESSES: *(H.M.G.) Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Panama); (P.M.D.) Crustacea Laboratory, Invertebrate Zoology Section, Los Angeles County Museum of Natural History, Los Angeles, California 90007; (R.C.B.) Department of Marine Invertebrates, Natural History Museum, P.O. Box 1390, San Diego, California 92112.*