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Source: *Journal of Crustacean Biology*, Vol. 16, No. 3 (Aug., 1996), pp. 529-534

Published by: [The Crustacean Society](#)

Stable URL: <http://www.jstor.org/stable/1548743>

Accessed: 27/10/2010 18:38

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CONTRIBUTIONS TO THE ECOLOGY OF *PARANEBALIA BELIZENSIS* FROM THE WATERS OFF CENTRAL BELIZE, CENTRAL AMERICA

Richard F. Modlin

ABSTRACT

Characteristics that define the habitat of the leptostracan *Paranebalia belizensis* Modlin, inhabiting the waters of Twin Cays, a group of Belizian mangrove-covered islands, are described. A primary component of the habitat of this species appears to be *Halimeda opuntia*. The complex structure of this macroalga creates a filter that traps waterborne detrital particles; thus it collects the food of leptostracans. It also functions as a refuge from predation because its natural defenses discourage herbivory. From field observations and collections made within the habitat, information on the spatial and temporal distribution, population structure, and fecundity of *P. belizensis* is presented. Females and juveniles predominate the population. Males are rare and primarily occur in immature stages. Mature males were collected only in spring, when population size was largest. Reproduction is highest in early spring and continues throughout the year. Fecundity is not correlated with the total length of a female. Factors affecting the lack of ecological information on the leptostracans are discussed.

The ecology of this ancient group of crustaceans is poorly known. Fossils of Leptostraca date to the Paleozoic (Rolfe, 1981; Dahl, 1984; Bergström *et al.*, 1987) and are hypothesized to represent the ancestral form of modern Crustacea in the order Malacostraca. Over the years a plethora of articles have appeared debating this issue (Claus, 1887; Manton, 1977; Rolfe, 1981; Briggs, 1983; Schram, 1986; Dahl, 1987), but none have alluded to the ecology of this curious crustacean taxon.

Except for the limited habitat characterizations presented with descriptions of new species, studies that deal specifically with leptostracan ecology are rare (Citarella, 1965; Macquart-Moulin and Castelbon, 1983; Vader, 1973; Rainer and Unsworth, 1991) and limited to species of *Nebalia*. None are available for North American *Nebalia* spp. or *Paranebalia* spp. This paper presents data obtained from collections and field observations on the spatial and temporal distribution, population structure, and fecundity of *Paranebalia belizensis* Modlin, a recently described leptostracan from the waters of Twin Cays, Belize, Central America (Modlin, 1991).

Study Area.—Twin Cays archipelago is located about 16 km southeast of Dangriga Town, Belize, Central America, and 2.0 km west of Carrie Bow Cay on the Caribbean barrier reef system at 16°04'N, 88°50'W

(Fig. 1). This archipelago is composed of four mangrove-covered islands, with the two largest separated by a north-south channel. A complete description of the study areas can be found in Rützler and Feller (1987/1988) and Modlin (1990, 1993).

MATERIALS AND METHODS

Semiquantitative samples of the Twin Cays population of *P. belizensis* were obtained during visits to the Coral Reef Field Station of the Smithsonian Institution in Belize, Central America. In situ collections and observations were made during December 1988, July 1989, May 1990, February 1992, and June 1994 with the aid of snorkeling gear. Samples were collected by laying a 0.2-m² frame made from PVC tubing over the site to be sampled. The open end of a large cotton sample bag (≈55.0 l) was then placed over the frame. All flora and fauna within the quadrat were removed from the sediments or prop roots by hand and immediately pushed into the sample bag. The bag was quickly closed and secured with a drawstring. Panels of nylon netting (mesh size ≈ 0.2 mm²) sewn into the bottom allowed water to flow from the sample bag when it was raised above the surface.

Bagged samples were returned to the field station and each emptied into a bucket of fresh sea water. When all large material was vigorously rinsed and removed, the water was poured through a 0.2-mm mesh nylon dip net. To remove fine particulates and silt, the bucket was refilled with fresh sea water and the dip net residue resuspended, gently stirred, and again filtered. This procedure continued until the sea water, when mixed with dip-net residue, remained clear. The sample was again concentrated, emptied into a sample jar or plastic bag, stained with phloxine-B to ease sorting, and fixed in a 5.0–7.0% formaldehyde-sea-water solution for a period of 2–3 weeks. Leptostracans were

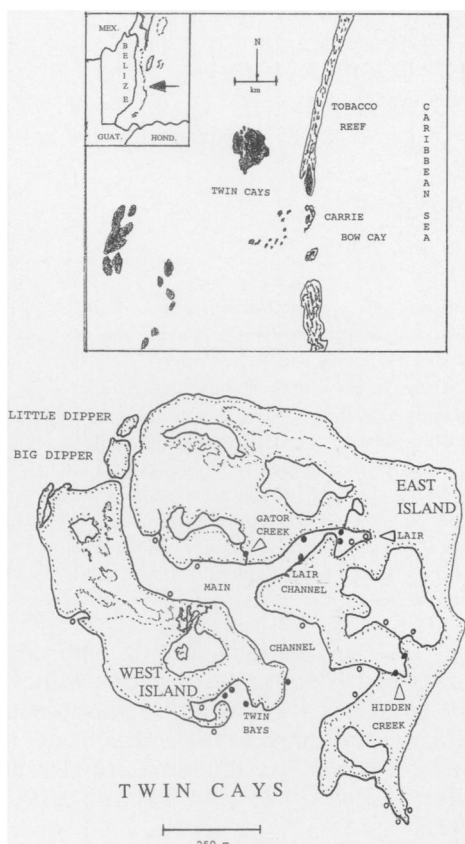


Fig. 1. Location of Twin Cays along the Belizean coral reef system (upper) and sampling sites, indicated by black dots and open circles, surveyed at Twin Cays, Belize (lower), during the 1988–1994 study period. Black dots are sampling sites where specimens of *Paranebalia belizensis* were collected; open circles are sites where no *Paranebalia* were collected. Arrow in inset indicates approximate position of the study area along the Belizean coast.

sorted by life stage, sexed, sized, counted, and preserved in 70% ethyl alcohol.

Total length was measured along the midline of the specimen from the articulation of the rostrum to the posterior margin of the eighth pleonite; caudal furcae were not included. Because some specimens were flexed or folded and damaged during straightening, total length was also determined from a linear regression relationship between total length (TL) and carapace length (CL), $TL = 1.5CL - 0.05$, $r = 0.98$, $N = 88$, where r is the correlation coefficient and N the number of measurements. Carapace length was measured along its dorsum from the articulation of the rostrum to its posterior margin. Total length of ovigerous females was determined before the larvae were scraped from the brood pouch.

Salinity and temperature at the sampling sites were measured at irregular intervals. Salinities were obtained in situ with a hydrometer and periodically verified with a Reichert Scientific Instruments refractom-

eter. Ambient water temperature was measured with a standard mercury thermometer.

All statistical analyses were done using the ABSTAT Statistical Software package (Anderson-Bell, Parker, Colorado, U.S.A.). None of the data were transformed.

Description of Collecting Sites.—Locations of the collecting sites are shown in Fig. 1.

Twin Bays, a shallow, average depth (d) = 1.0 m, pair of protected indentations along southern shore of West Island. Shoreline completely canopied by branches of the red mangrove *Rhizophora mangle* Linnaeus and dissected underwater by a tangle of prop roots. Highly localized, dense growths of *Halimeda opuntia* (Linnaeus) Lamouroux hang from the prop roots. These are lightly covered with fine detritus and harbor a rich community of hydroids, anemones, and sabellid worms. Heavily silted and calcified clumps of *H. opuntia* and *H. incrassata* (Ellis and Solander) Lamouroux are sparsely distributed along the bottom near the bank. Additional description of Twin Bays can be found in Modlin (1990).

Main Channel samples were collected on and near an unshaded calcareous bank located on West Island ($d < 0.3$ m). Very dense growths of *H. incrassata* cover the top of the bank, cascade over the precipice to a depth of 1.2 m, and merge with the turtle grass community, *Thalassia testudinum* Bank ex König. This algal community harbors few anemones and sabellids, but contains many young damselfish (Pomacentridae).

The Lair, a shallow ($d = 0.5$ m), eutrophic pond in the middle of East Island with shoreline completely shaded. Within the Lair, sparse clumps of highly calcified and silted *H. opuntia* grow from, and on sediments beneath, prop roots. The primary collecting site was near the entrance to the Lair ($d = 2.0$ m). Here thick, lush growths of *H. opuntia* extend to a depth of 1.5 m, and are inhabited by an abundance of hydroids, anemones, and sabellid worms.

Lair Channel's northern shore and southern shore ($d = 1.0$ m) are similar, but because of the sun's movement and direction the northern shore receives sunlight longer during the day than the southern shore. Both shorelines are sparsely covered by red mangrove trees. *Halimeda opuntia* grows luxuriously from the prop roots along the northern shore and more sparsely along the southern shore.

Gator Creek ($d < 1.0$ m) a completely canopied tidal outfall drains an isolated pond in the northern half of East Island. Growth of *Halimeda opuntia* is limited to a few clumps suspended from prop roots hanging in midstream.

Hidden Creek ($d = 0.8$ m) is partially canopied and drains a large inland pond located at the southern half of East Island. *Halimeda opuntia* hangs in lush clumps from prop roots in exposed sections. The Hidden Creek sites are most similar to those found in the Lair.

Salinity averaged 35.3‰, range 33.0–36.5‰, at the collecting sites. Temperature averaged 28.2°C, range 27.0–29.0°C.

RESULTS

Surveys conducted between 1985 and 1987 in and around the islands of Twin Cays Archipelago indicated that an impor-

Table 1. Abundance (number/m²) of *Paranebalia belizensis* at the collecting sites sampled in the Twin Cays archipelago, Belize, in 1988, 1989, 1990, 1992, and 1994. TB = Twin Bays; MC = Main Channel; LL = Lair; LN = Lair channel northern shore; LS = Lair Channel southern shore; GC = Gator Creek; and HC = Hidden Creek. The number of samples collected () follows abundance.

Month/Year	Stations						
	TB	MC	LL	LN	LS	GC	HC
Dec 1988	387 (3)	153 (3)	600 (5)	120 (1)	200 (1)	480 (1)	—
Jul 1989	1,505 (2)	405 (2)	2,497 (3)	—	590 (1)	—	—
May 1990	—	420 (1)	8,487 (4)	—	—	—	—
Feb 1992	—	—	2,795 (2)	—	—	—	—
Jun 1994	—	—	940 (1)	—	—	—	1,310 (1)

tant component of the habitat of *Paranebalia belizensis* was the macroalga *Halimeda*, primarily *H. opuntia*. The association of *P. belizensis* with other taxa of macroalgae was extremely rare. During this early survey only a single specimen was collected when other aggregates of algae were sampled. A lone female was taken in December 1988 from a bed of *Caulerpa racemosa* (Forskål) J. Agardh that grew in Twin Bays. Consequently, sampling for this project concentrated on algal beds dominated by *Halimeda*.

Paranebalia belizensis was most abundant at more protected collecting sites (Fig. 1) and in less silted stands of *Halimeda*. Greatest concentrations were found in the Lair, Twin Bays, Gator Creek, and Hidden Creek (Table 1). Abundance was an order of magnitude lower at open channel sites. Although samples were not collected in all months of the year, those obtained in the

Lair suggested that abundance was greatest in spring and lowest in winter (Table 1).

The structure of the population of *P. belizensis* in the Lair is shown in Table 2. Males were most apparent in May and least so in December. They averaged 8.1% of the total population during the period sampled. Females constituted an average of 43.0% total Lair population and juveniles, 48.9%. Females were most numerous in June and juveniles in December. Females were in lowest abundance in December.

Prior to expulsion from the brood pouch, the total length of the manca stage of *P. belizensis* is 0.7 mm. Stage I juveniles measure 0.8 mm. Overall, juvenile size averaged 1.1 mm, range 0.8–1.7 mm. Males were easily separated at 1.5 mm total length by their inflated antennular flagellum. Males averaged 1.9 mm, range 1.5–2.3 mm. The smallest individuals distinguished as females were 1.8 mm in total length. Females averaged 2.9 mm, range 1.8–4.2 mm. Average total length of males and females was greatest in December, 2.1 mm and 3.4 mm, respectively. Smallest sizes were observed in June; males averaged 1.8 mm and females, 2.4 mm.

Antennal flagella of mature males of *P. belizensis* were heavily covered with setae; they looked like bottle brushes. Although very rare in collections, mature males were taken at all collecting sites. They were most numerous in the Lair (Fig. 1), but occurred there only in February and May. Mature males comprised 10.90% of the males collected at the Lair site in February and 5.28% in May (Table 2). Their abundance in February was 30 individuals/m² and 50/m² in May. By contrast, ovigerous females occurred in all Lair samples. Their greatest abundance, 160/m², was in June.

Table 2. Composition of the population of *Paranebalia belizensis* in the Lair collecting site at Twin Cays, Belize, in the months sampled. % Pop = % of population; % Mature = % of males that are mature; and % Ovig = % of females carrying developing larvae.

	Feb	May	Jun	Jul	Dec
Males					
% Pop	9.86	11.16	7.45	7.93	3.90
% Mature	10.90	5.28	0.00	0.00	0.00
Females					
% Pop	58.24	43.98	62.79	59.00	20.57
% Mature	8.30	4.29	5.08	3.42	18.96
Juveniles					
% Pop	31.89	44.86	29.79	33.06	75.53
Male to female ratios					
	1:6	1:4	1:8	1:7	1:5

Although the total length of mature and immature males overlap, mature males were larger than immature males. Mature males averaged 1.92 mm (standard error of the mean, $SE = \pm 0.03$), while immature males averaged 1.82 mm ($SE = \pm 0.02$). A Student's t -value of 2.43235 with 114 degrees of freedom indicated this difference to be significant ($P < 0.05$). Ovigerous females averaged 3.02 mm (range, 2.80–4.03 mm); these were always the largest females.

Fecundity of *P. belizensis* correlated poorly with total length. Data points to construct a least squares regression between the number of brood-pouch larvae and the total length of 130 ovigerous females were highly scattered ($r = 0.18$). The average-sized ovigerous female should carry an average of 5.0 larvae, but the range of larvae carried by this sized female varied from 2–16. This variability in brood-pouch larval number appeared characteristic of ovigerous females between 2.9–3.6 mm. A brood pouch that contained 16 larvae was observed only once. Total length of this specimen was 3.2 mm. Conversely, the two largest ovigerous females collected, both 4.03 mm, carried fewer larvae; one supported 4 larvae, the other 8.

DISCUSSION

The paucity in leptostracan ecological information appears to result from past taxonomic confusion and the sporadic nature of their appearance in collections. These notions fueled the presumption that the Order Leptostraca was composed of rather few cosmopolitan species that did not occur in sufficient numbers to support ecological studies. Professor Erik Dahl (personal communication) and Hessler (1984) found it difficult to comprehend how a group of crustaceans that lack free-swimming larval stages have the ability to become as cosmopolitan as past literature suggests.

Leptostracans brood their larvae in pouches and release them at an advanced juvenile stage. This adaptation restricts their dispersal, localizes distribution, and, under proper environmental conditions, may generate new morphological types and new species. However, the original characteristics being used to define species lacked the reliable subtlety necessary to recognize a new species. Taxonomic confusion existed be-

cause the original characteristics varied with age and life stage of individuals rather than with the species (Claus, 1887; Thiele, 1904, 1905; Dahl, 1985). Even though leptostracans conserve many primitive features, Dahl (1985) found a group of definitive diagnostic characters that allowed him to provincialize the European Shelf leptostracans. Kazmi and Tirmizi (1989), Dahl (1990), and Modlin (1991) have successfully applied the Dahl (1985) model to identify and, if necessary, describe newly found leptostracans.

Leptostracans are rare when collections are not specifically made in their natural habitats. Recent literature suggests that leptostracans frequent benthic locations rich in organic detritus and sulfides, and poor in dissolved oxygen (Gamô and Takizawa, 1986; Kazmi and Tirmizi, 1989; Modlin, 1991; Rainer and Unsworth, 1991). Some of these can be unusual, e.g., marine caves (Bowman *et al.*, 1985) and deep-sea hydrothermal vents (Hessler, 1984). Leptostracans seem able to tolerate conditions found in such environments (Thiele, 1926/27).

The microcosm of *P. belizensis*, because of its mangrove swamp location, is organically rich. The odors emitted during collection indicate that the habitat is rich in sulfides. These conditions suggest low dissolved-oxygen concentrations.

Paranebalia belizensis appears to have a specific habitat. It prefers to occupy algal beds dominated by *H. opuntia*, that hang from prop roots or escarpments. *Halimeda opuntia* is distinctly segmented by articulating joints into overlapping frondlike branches (Taylor, 1960; Littler *et al.*, 1989). Unlike species of *Caulerpa* and other macroalgae, its thallus provides many interstices to trap detrital particles and a refuge for individuals of *P. belizensis*. The luxuriant arborescent growth of *H. opuntia* produces a large three-dimensional podlike mass that prevents leptostacans and other inhabitants from being flushed by strong currents. In addition, the plant synthesizes halimeda-toxin that repels herbivores and secretes a calcareous shell around older fronds making them unpalatable (Norris and Fenical, 1982; Littler *et al.*, 1983; Paul and Fenical, 1983; Padilla, 1989). Hendler and Littman (1986) considered *Halimeda* spp. to act as refuge-substrata that enhance survival be-

cause of their defense against herbivory. Nami (1988) found that *H. opuntia* shelters a greater faunal abundance and diversity than any other species of *Halimeda*. Within the Twin Cays archipelago lush growths of this alga were found in the Lair, Twin Bays, and Hidden Creek (Fig. 1); these were the locations where *P. belizensis* was in greatest abundance (Table 1).

Halimeda incrassata, the other abundant species of the Halimedaceae did not exhibit the arborescent growth of *H. opuntia*. It grows closer to the substrate and produces a thick, carpetlike covering. This species was dominant at sampling stations in the Main Channel, and along the northern and southern shores of the Lair Channel (Fig. 1).

Data obtained on the Lair population of *P. belizensis* indicated that its abundance peaked in spring, decreased through summer and autumn, and was lowest in winter (Table 2). Numbers observed in June 1994 are probably not representative of absolute population size in this month, because the quantity used to calculate density came from only a single sample. However, the composition of life stages in this sample was similar to that observed in July (Table 2). Female abundance was considerably greater than that of the males, but both decreased from spring to winter. Lowest population numbers were observed in winter. The population in winter was composed primarily of juveniles (Table 2). The samples used to describe annual change in the population of *P. belizensis* seem reasonable. Modlin (1991) found that the size of the population of the mangrove mysid *Mysidium columbiae* (Zimmer) at Twin Cay cycled similarly throughout the year.

Ovigerous females of *P. belizensis* were collected on each sampling trip (Table 2). This suggests that this species breeds continuously throughout the year. Peak reproduction occurs in spring (May) and is lowest in winter (December). The predominance of juveniles in December suggests that the previous year's adult cohort dies off and the juveniles give rise to the reproductive population in the following spring. This appears to be the typical reproductive strategy of small tropical crustaceans (Goodbody, 1965; Modlin, 1991). Although males appear available, albeit few in num-

ber (Table 2), the lack of mature individuals during most of the year seems to present a problem to this life-cycle scenario.

Based on the difference in the abundance and degree of setation observed between mature and immature male crustaceans in other orders of Malacostraca, e.g., the male lobe of mysidaceans (Johansson, 1992), those males of *P. belizensis* that have heavily setated antennular flagella are hypothesized to be mature. Mature males of this species were taken only in February and May, the months when male abundance was greatest (Table 2). Similarly, Rainer and Unsworth (1991) rarely collected males of the unnamed *Nebalia* that they were studying and took only one mature male during the period of their study. The reproductive biology and reproductive strategy of leptostracans is not known. Mature males may be only fortuitous in collections because they are so few in number or, for some reason, short-lived. Mature males, however, are assumed to be present throughout the year, because larvae in all stages of development were observed on each sampling trip.

ACKNOWLEDGEMENTS

I extend my appreciation to Dr. Frank Ferrari for his assistance while we were in the field and Dr. Marian L. Lewis who critically read the manuscript. Adrienne Froelich and Wendy Cook provided much needed help in the laboratory. Support for the project was provided by the Smithsonian Institution's Caribbean Coral Reef Ecosystem Program (CCRE), which is partially supported by the Exxon Corporation, and the Research Center of the University of Alabama in Huntsville through its Mini-Grant Program. This is contribution number 471 from the CCRE, Smithsonian Institution.

LITERATURE CITED

- Bergström, J., D. E. G. Briggs, E. Dahl, W. D. I. Rolfe, and W. Stürmer. 1987. *Nahecaris stuerzi*, a phyllocarid crustacean from the Lower Devonian Hunstrück Slate.—*Paläontologische Zeitschrift* 61: 273–298.
- Bowman, T. E., J. Yager, and T. M. Iliffe. 1985. *Speonebalia cannoni*, n. gen., n. sp., from the Caicos Islands, the first hypogean leptostracan (Nebaliacea: Nebaliidae).—*Proceedings of the Biological Society of Washington* 98: 439–446.
- Briggs, D. E. G. 1983. Affinities and early evolution of the Crustacea: the evidence of the Cambrian fossils.—In: F. R. Schram, ed., *Crustacean Issues* 1: 1–22. A. A. Balkema, Rotterdam, The Netherlands.
- Citarella, G. 1965. Sur une espèce indicatrice de pollution des eaux marines.—*Revue des Travaux de l'Institut des Pêches Maritimes* 29: 179–182.
- Claus, C. 1887. Über den Organismus der Nebaliden und die systematische Stellung der Leptostraken.—

- Arbeiten aus dem zoologischen Institute der Universität Wien und der zoologischen Station in Triest 8: 1–148.
- Dahl, E. 1984. The subclass Phyllocarida (Crustacea) and the status of some early fossils: a neontologist's view.—*Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 145: 61–76.
- . 1985. Crustacea Leptostraca, principles of taxonomy and a revision of European shelf species.—*Sarsia* 70: 135–165.
- . 1987. Malacostraca maltreated—the case of the Phyllocarida.—*Journal of Crustacean Biology* 7: 721–726.
- . 1990. Records of *Nebalia* (Crustacea Leptostraca) from the southern hemisphere—a critical review.—*Bulletin of the British Museum of Natural History (Zoology)* 56: 73–91.
- Gamô, S., and Y. Takizawa. 1986. On *Paranebalia longipes* (Willemoes-Suhm, 1975) (Crustacea, Leptostraca, Nebaliacea) from Sagami Bay.—*Bulletin of the Biogeographic Society of Japan* 41: 31–36.
- Goodbody, I. 1965. Continuous breeding in populations of two tropical crustaceans, *Mysidium columbiae* (Zimmer) and *Emerita portoricensis* Schmidt.—*Ecology* 46: 195–197.
- Hendler, G., and B. S. Littman. 1986. The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars.—*Coral Reefs* 5: 31–42.
- Hessler, R. R. 1984. *Dahlella caldariensis*, new genus, new species: a leptostracan (Crustacea, Malacostraca) from deep-sea hydrothermal vents.—*Journal of Crustacean Biology* 4: 655–664.
- Johansson, K. U. I. 1992. The olfactory system of malacostracan crustaceans.—*Doctoral dissertation, Department of Zoology, University of Lund, Lund, Sweden*. Pp. 1–20.
- Kazmi, Q. B., and N. M. Tirmizi. 1989. A new species of *Nebalia* from Pakistan (Leptostraca).—*Crustaceana* 56: 293–298.
- Littler, M. M., P. R. Taylor, and D. S. Littler. 1983. Algal resistance to herbivory on a Caribbean barrier reef.—*Coral Reefs* 2: 111–118.
- Littler, D. S., M. M. Littler, K. E. Bucher, and J. N. Norris. 1989. Marine plants of the Caribbean.—*Smithsonian Institution Press, Washington, D.C.* Pp. 1–263.
- Macquart-Moulin, C., and C. Castelbon. 1983. Périodicité circadienne spontanée chez jeunes *Nebalia bipes* (Fabricius) (Crustacé: Phyllocarida). Induction et synchronisation initiale du rythme endogé d'activité.—*Journal of Experimental Marine Biology and Ecology* 70: 1–20.
- Manton, S. M. 1977. The Arthropoda. Habits, functional morphology and evolution.—*Clarendon Press, Oxford, England*. Pp. i–xx, 1–527.
- Modlin, R. F. 1990. Observations on the aggregative behavior of *Mysidium columbiae*, the mangrove mysid.—*Pubblicazioni della Stazione Zoologica di Napoli, Marine Ecology* 11: 263–275.
- . 1991. *Paranebalia belizensis*, a new species from shallow water off Belize, Central America (Crustacea: Malacostraca: Leptostraca).—*Proceedings of the Biological Society of Washington* 104: 603–612.
- . 1993. Population parameters, life cycle, and feeding of *Mysidium columbiae* (Zimmer) in the water surrounding a Belizian mangrove cay.—*Pubblicazioni della Stazione Zoologica di Napoli, Marine Ecology* 14: 23–34.
- Naim, Odile. 1988. Distributional patterns of mobile fauna associated with *Halimeda* on the Tiahura coral-reef complex (Moorea, French Polynesia).—*Coral Reefs* 6: 237–250.
- Norris, J. N., and W. Fenical. 1982. Chemical defense in tropical marine algae.—*In*: K. Rützler and I. G. Macintyre, eds., *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities*. Pp. 417–428. *Smithsonian Institution Press, Washington, D.C.*
- Padilla, D. K. 1989. Algal structural defenses: form and calcification in resistance to tropical limpets.—*Ecology* 70: 835–842.
- Paul, V. J., and W. Fenical. 1983. Isolation of halimedaerial: chemical defense adaptation in the calcareous reef-building alga *Halimeda*.—*Science* 221: 747–749.
- Rainer, S. F., and P. Unsworth. 1991. Ecology and production of *Nebalia* sp. (Crustacea: Leptostraca) in a shallow-water seagrass community.—*Australian Journal of Marine and Freshwater Research* 42: 53–68.
- Rölfe, W. D. I. 1981. Phyllocarida and the origin of the Malacostraca.—*Geobios* 14: 17–27.
- Rützler, K., and C. Feller. 1987/88. Mangrove swamp communities.—*Oceanus* 30(4): 16–24.
- Schram, F. R. 1986. Crustacea.—*Oxford University Press, New York, New York*. Pp. i–xiv, 1–606.
- Taylor, W. R. 1960. Marine algae of the eastern tropical and subtropical coast of the Americas.—*University of Michigan Press, Ann Arbor, Michigan*. Pp. 1–870.
- Thiele, J. 1904. Die Leptostraken.—*Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1889–1899*, 8: 1–26.
- . 1905. Über die Leptostraken der Deutschen Südpolar-Expedition 1901–1903.—*Deutschen Südpolar-Expedition 9 (Zoology)* 8: 61–68.
- . 1926/27. Leptostaca.—*In*: W. Kükenthal and T. Krumbach, eds., *Handbuch der Zoologie* 3: 567–592.
- Vader, W. 1973. *Nebalia typhlops* in western Norway (Crustacea Leptostraca).—*Sarsia* 53: 25–28.

RECEIVED: 14 August 1995.

ACCEPTED: 14 February 1996.

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