TUDelft
Bibliotheek
Prometheusplein 1
Postbus 98
2600 MG DELFT

Telefoon: 015 - 2784636
Fax: 015 - 2785673
Email: Helpdesk.doc@Library.TUDelft.NL

Datum: 14-apr-05

Bonnummer: 878459

Aan: VLAAMS INSTITUUT VOOR DE ZEE
VISMIJN
PAKHUIZEN 45-52
B-8400 OOSTENDE
BELGIE

Tav:

Aantal kopieën: 7

Uw referentie(s): 1833157 1833157

Artikelomschrijving bij aanvraagnummer: 878459

Artikel: Differences in the crab fauna of the mangrove areas at the
Auteur: McIvor, C.; T.J. Smith
Tijdschrift: ESTUARIES
Jaar: 1995 **Vol.** 18 **Aflevering:**
Pagina(s): 591-597 **Plaatsnr.:** 8022

Estuaries Vol. 18, No. 4, p. 591–597 December 1995

Differences in the Crab Fauna of Mangrove Areas at a Southwest Florida and a Northeast Australia Location: Implications for Leaf Litter Processing

CAROLE C. MCIVOR[1, 2]
Florida Cooperative Fish and Wildlife Research Unit
117 Newins-Ziegler Hall, University of Florida
Gainesville, Florida, 32611

T. J. SMITH III[3]
Rookery Bay National Estuarine Research Reserve
Florida Department of Environmental Protection
10 Shell Island Road, Naples, Florida 33962

ABSTRACT: Existing paradigms suggest that mangrove leaf litter is processed primarily via the detrital pathway in forests in the Caribbean biogeographic realm whereas herbivorous crabs are relatively more important litter processors in the Indo-West Pacific. To test this hypothesis, we used pitfall traps to collect intertidal crabs to characterize the crab fauna in a mangrove estuary in southwest Florida. We also tethered mangrove leaves to determine if herbivorous crabs are major leaf consumers there. We compared the results with previously published data collected in an analogous manner from forests in northeastern Australia. The crab fauna in Rookery Bay, Florida, is dominated by carnivorous xanthid and deposit-feeding ocypodid crabs whereas that of the Murray River in northeastern Australia is dominated by herbivorous grapsid crabs. No leaves tethered at five sites in the forests in Southwest Florida were taken by crabs. This contrasts greatly with reported values of leaf removal by crabs in Australian forests of 28–79% of the leaves reaching the forest floor. These differences in the faunal assemblages and in the fate of marked or tethered leaves provide preliminary support for the hypothesis that leaf litter is in fact processed in fundamentally different ways in the two biogeographic realms.

Introduction

In the early 1970s, W. E. Odum published his pioneering dissertation work on mangrove food webs. Odum concluded that the food web in riverine mangrove forests of the North River on the southwest coast of Florida was largely driven by the consumption of decaying mangrove leaf litter. Further, he concluded that much of the leaf litter reaching the forest floor is exported to adjacent subtidal waters where it, too, enters a detrital food web (Odum 1971; Odum and Heald 1972). Through sometimes overzealous extrapolation by others in the field, Odum's work (1971) has taken on the status of a paradigm of the structure of mangrove food webs in general.

Recent work by Robertson and colleagues at the Australian Institute of Marine Science in Queensland, Australia, has documented the importance of sesarmid crabs (Grapsidae) in burying and consuming leaf litter within Australian mangrove forests (Robertson 1986; Robertson and Daniel 1989; Micheli 1993). Knowledge of the feeding activities of these herbivorous crabs resulted in a revision of earlier estimates (Boto and Bunt 1981) of carbon export from Australian mangrove forests. Leaf-burial by crabs results in the retention of 28% of estimated leaf fall in low- and mid-intertidal forests dominated by *Rhizophora* spp., and 71–79% of leaf fall in high intertidal forests of mixed species composition (Robertson 1986; Robertson and Daniel 1989). Based on these observations and calculations, Robertson hypothesized that food webs in

---

[1] Corresponding author.

[2] Present address: National Biological Service, Arizona Cooperative Fish and Wildlife Research Unit, 104 Biological Sciences East, University of Arizona, Tucson, Arizona 85721.

[3] Present Address: National Biological Service, South Florida/Caribbean Field Unit, OE-148, Florida International University Miami, Florida 33199.

0160-8347/95/04591-07$01.50/0

Indo-West Pacific and Caribbean mangrove forests may differ significantly due to the role of herbivorous crabs in the former (Robertson 1987). To test this hypothesis, we quantified the composition and relative abundance of the crab fauna, and tethered mangrove leaves on the forest floor of a southwest Florida estuary, to determine if herbivorous crabs are a major component of the crab fauna, and if crabs actively consume newly fallen leaves in this location. We compared these data with analogous data available from a mangrove forest in northeastern Australia (Frusher et al. 1994).

Methods

STUDY SITES

Rookery Bay National Estuarine Research Reserve, Naples, Florida, USA (25°62′N, 80°25′W) is situated at the northernmost extent of the extensive complex of mangroves of the Ten Thousand Islands. Rookery Bay is a marine-dominated estuary with relatively little, and markedly seasonal, freshwater inflow. Tides are mixed semidiurnal and average 1.2 m. Mangrove forests cover approximately 3,500 ha of the 54,000 ha watershed. Salinity measured within the crab traps (see below) ranged from 24‰ at the downstream site to 21‰ in mid-bay to 2‰ at the upstream site (values from high intertidal zone). Porewater salinity in the forests of the Murray River, northeast Australia (18°17′S, 147°04′E), ranged from 30.2‰ near the mouth to 1.3‰ at the headwater region during the time of sampling (Frusher et al. 1994). Tides are semidiurnal, and average 2.4 m.

CRAB SAMPLING

We chose to sample intertidal crabs using pitfall traps (Smith et al. 1991). Accurate estimation of crab densities in vegetated intertidal locations is extremely difficult. Methods other than pitfall trapping include visual censusing (Warner 1969), counting burrows (Micheli et al. 1991), and removal by digging within quadrats designed to prevent escape from the defined area (Campbell 1977). None of the methods is without bias, and for our goals—obtaining relative abundance data—the pitfall trap is an appropriate choice. Importantly, use of this method in Florida allowed convenient comparisons with the Australian crab data collected with pitfall traps.

We installed pitfall traps at a representative site in each of three estuarine zones in Rookery Bay: near the mouth; at mid-estuary; and mid-way along Henderson Creek, the origin of most of the surface freshwater entering the estuary. At each site, we placed four replicate traps (15 cm wide × 20 cm deep) flush with the substrate at each of three intertidal elevations. Fiberglass mesh covered trap bottoms to permit water drainage on low tide.

Because of the lack of tide gauges at all locations, we defined elevations in part on the basis of vegetation associations. Low intertidal sites were within 2–3 m of permanent subtidal waters and were dominated by *Rhizophora mangle*. Mid-intertidal elevations occurred at the interface between the predominantly low intertidal *Rhizophora* and the two species characteristic of basin forests, *Avicennia germinans* and *Laguncularia racemosa*. At high intertidal sites, *Rhizophora* was absent and *Avicennia* and *Laguncularia* were both common. Whereas low- and mid-intertidal sites were well drained, high intertidal sites had 2–5 cm of standing water at low tide. Traps were cleared once daily on four successive days in September 1991 following the high spring tide of the previous night, resulting in a sampling effort of 144 trap nights. (Sampling three locations along the salinity gradient × 12 traps location^{-1} × four nights of trapping = 144 trap nights). Crabs were placed on ice and frozen pending identification and enumeration.

Five sites had previously been chosen for crab sampling from the mouth to the extent of tidal influence in the Murray River, Australia, a distance of 17 km. At each site, two trapping grids were established in both low and high intertidal zones. Each grid was 2 m on a side and contained five traps, one at each corner and one in the center. As in Rookery Bay, trapping was conducted over four successive nights, resulting in a total sampling effort of 400 trap nights in the Murray River. Mangrove species at the low intertidal site near the mouth included *Avicennia marina* and *Aegiceras corniculatum*. *Bruguiera parviflora*, *Rhizophora apiculata*, and *Excoecaria agallocha* dominated in the high intertidal zone. Mangrove species at the upper end of the estuary included *Barringtonia racemosa* and *Sonneratia casaolaris*. The same two species dominated both low and high intertidal zones at that location (Frusher et al. 1994). (For the present study, we include all Australian sites for purposes of comparing composition of the crab fauna with respect to feeding guilds but use only those sites at the two ends of the estuarine gradient for statistical comparisons of intertidal distribution with those of Rookery Bay.)

STATISTICAL DESIGN

The statistical design for Rookery Bay is a repeated measures MANOVA with trap being the unit of replication. The dependent variables are the abundances of the observed crab taxa. The two factors are estuarine location and tidal elevation: the repeated component is day. The design for the Murray River, Australia, was originally run as a

TABLE 1. Composition of the Rookery Bay (A) and Murray River (B) crab faunas captured in pitfall traps. Total numbers caught are the sum of all captures for a species summed over longitudinal gradient locations and intertidal elevations.

Species	Total Caught
(A) Rookery Bay, Florida, USA	
Family Xanthidae	
Eurytium limosum	372
Panopeus herbstii complex	35
Family Ocypodidae	
Uca rapax	157
Uca juveniles	18
Family Grapsidae	
Sesarma curacaoense	14
Aratus pisonii	4
Total	600
Trap Nights	144
Crabs per Trap	4.17
(B) Murray River, Queensland, Australia	
Family Xanthidae	
Atriplex tridentata	5
Family Ocypodidae	
Uca coarctata	5
Family Grapsidae	
Sesarma messa	157
Sesarma brevipes	93
Sesarma brevicristatum	16
Sesarma semperi-longicristatum	12
Sesarma borneenis	1
Sesarma juveniles	15
Neosarmatium crassum	3
Clistoesloma merguiense	1
Total	308
Trap Nights	400
Crabs per Trap	0.77

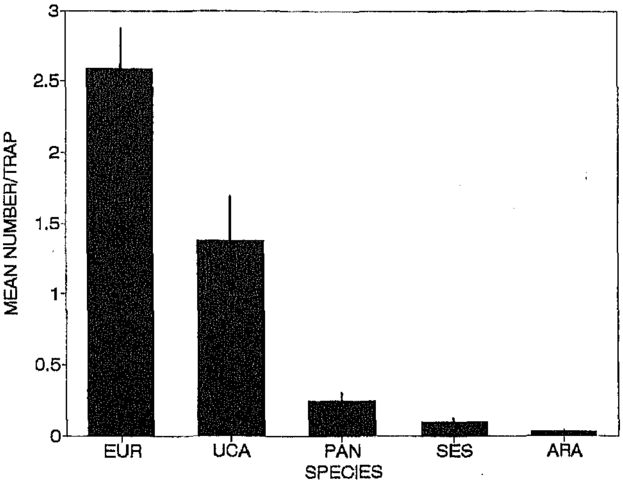

Fig. 1. Mean crab abundance by species summed across estuarine and intertidal locations. Error bars are 1 SE. Crabs taken in four successive days of pitfall trapping in Rookery Bay, Florida, USA. EUR = *Eurytium limosum*, UCA = *Uca rapax* plus *Uca* juveniles, PAN = *Panopeus herbstii* complex, SES = *Sesarma curacaoense*, ARA = *Aratus pisonii*.

three-factor ANOVA using crab species (four dominant species caught), site (five levels), and intertidal zone (high versus low) as the factors. The total number of a species caught per grid (set of five traps) was the dependent variable (Frusher et al. 1994). For purposes of the present comparison between the two estuaries, it was necessary to drop the variable "grid" from the Australian dataset and consider all 10 traps at a given set of estuarine and intertidal locations as the units of replication. The between estaury comparison of mean number of crabs per trap as a function of intertidal location was thus run as a repeated measures MANOVA in a manner analogous to the within estuary comparisons for Rookery Bay.

LEAF CONSUMPTION

Senescent leaves were picked from *Rhizophora* trees and individually tethered with a 1 m length of braided nylon line to plastic-coated, numbered lead fishing weights placed on the forest floor. Two groups of 10 leaves were placed at random sites at five locations in Rookery Bay: in low- and mid-intertidal forests downstream, and in mid-estuary; and on one overwash isle in mid-bay. Leaves were checked daily for signs of herbivory for two consecutive days. Rates of leaf herbivory were compared to published Australian data (Robertson 1986; Robertson and Daniel 1989).

Results

ROOKERY BAY: OVERALL PATTERNS OF CRAB NUMBERS AND BIOMASS

Six hundred individuals of five species were caught during 144 trap nights (Table 1a). The pitfall traps were effective for nonswimming, nonarboreal crabs that foraged within the intertidal zone. No swimming crabs (e.g., portunids) were captured despite their occurrence within the forest (Sheridan 1992; McIvor unpublished data). Similarly, the arboreal crab, *Aratus pisonii*, was rare in pitfall traps despite its observed abundance on mangrove trees in all forest types sampled. Data on that species are, therefore, not included in subsequent analyses. Pitfall traps appeared highly effective for four other intertidal crab taxa (Fig. 1). A xanthid, the white-clawed mud crab, *Eurytium limosum*, was the most abundant species, constituting 60% of the catch. *Uca rapax*, one of the fiddler crabs (an ocypodid), made up 32% of the samples. Another xanthid, *Panopeus* spp. (formerly *herbstii*, likely a mixture of recently defined species *obesus* and *simpsoni*, Williams 1983), constituted 5.7% of the catch. The least common species of those considered adequately sampled was a sesarmid, *Sesarma curacaoense*. This species made up only 2.6% of the catch. When ranked by biomass, *Eurytium* again

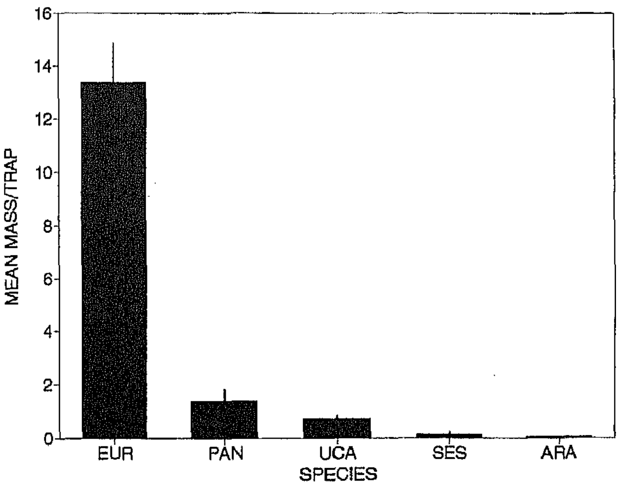

Fig. 2. Mean crab biomass (wet grams) by species summed across estuarine and intertidal locations. Error bars are 1 SE. Crabs taken in 4 successive days of pitfall trapping in Rookery Bay, FL, USA. Species abbreviations as in Fig. 1.

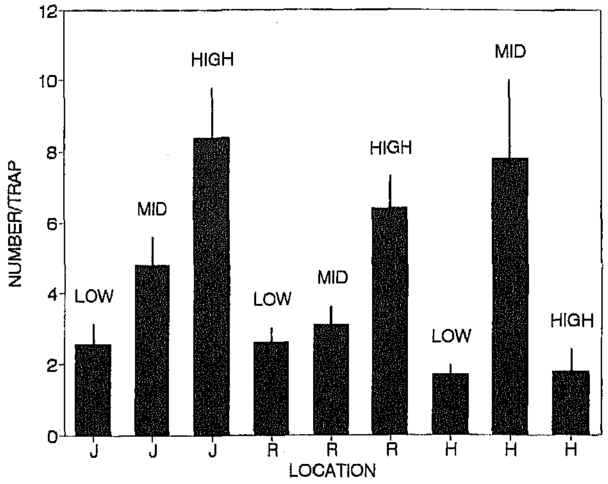

Fig. 3. Mean crab number trap^{-1} by estuarine and intertidal locations. Error bars are 1 SE. Crabs taken in four successive days of pitfall trapping in Rookery Bay, Florida, USA. J = Johnson Island near the mouth; R = Rookery Bay in mid-estuary; H = Henderson Creek, the most upstream location. The intertidal elevation is given above each bar.

dominated the assemblage. Because of its considerably greater size, *Panopeus* spp. displaced *Uca rapax* as the subdominant (Fig. 2).

ROOKERY BAY: CRAB DISTRIBUTION ACROSS ESTUARINE GRADIENTS

Mean total crab abundance per trap was 4.17 (Table 1a). Except for the mid-intertidal traps on Henderson Creek, mean crab abundance per trap decreased slightly on days 3 and 4 as crabs were removed from the habitat. Recruitment of very small *Uca* juveniles, possibly from the plankton, to the mid-intertidal traps at the upstream site resulted in a net increase in catch there on days 3 and 4.

Mean crab abundance increased with tidal elevation in the lower and mid-estuary but was highest in the mid-intertidal zone at the upstream location (Fig. 3). This difference in patterns of total crab abundance at different sites resulted in a significant interaction term between the factors estuarine and intertidal location in the MANOVA analysis (Table 2a). Omission of juvenile *Uca* (<5 mm) from the data being analyzed did not change the outcome. Repetition of the analysis on a subset of the data, omitting the upstream site, allowed a comparison of the relative importance of the two gradients of interest by removing the significant interaction term (Table 2b). Estuarine location was only marginally significant, whereas intertidal location was highly significant and explained 66% of the variation in total crab abundance at these two sites.

Individual species showed distinctive patterns of distribution. Briefly, *Eurytium* abundance was greatest in the lower and mid-estuarine locations, and increased with tidal elevation at both locations. *Uca rapax* was far more abundant at the Henderson Creek location and was most commonly found in mid and upper intertidal zones. *Panopeus* was captured almost exclusively in the lower intertidal traps in this study. This genus is primarily an inhabitant of the shallow subtidal portions of the estuary (Warner 1969). *Sesarma*, nowhere abundant, was captured in mid-intertidal zone in the lower and mid-estuary locations but primarily in the low intertidal zone at the Henderson Creek site. (Distributions of *Uca* and *Sesarma* lead us to conclude that the Henderson Creek site was, on average, higher in the intertidal zone than the other two sites.)

MURRAY RIVER: OVERALL PATTERNS OF CRAB NUMBERS

Pitfall traps revealed a species-rich intertidal crab fauna in the Murray River. Five species of sesarmid crabs, two additional species of grapsid crabs, and two species of crabs from other families

TABLE 2. MANOVA results for total abundance of four crab species combined in Rookery Bay.

	A. All Sites Combined		B. Omitting Most Upstream Site	
Effect	F ratio	Probability	F ratio	Probability
Estuarine location	$2.89_{2,27}$	<0.073	$3.93_{1,18}$	<0.063
Intertidal elevation	$14.86_{2,27}$	<0.0001	$23.23_{2,18}$	<0.0001
Interaction	$12.20_{4,27}$	<0.0001	$1.12_{2,18}$	>0.3477

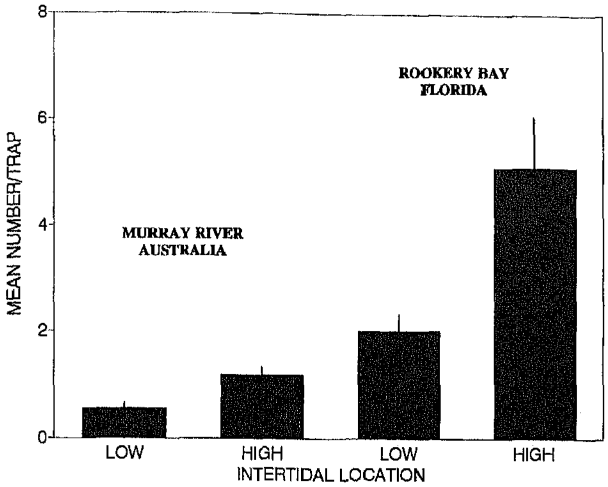

Fig. 4. Mean crab number trap^{-1} by intertidal location (low, high) in the two mangrove estuaries. The error bars are 1 SE. (Only data from locations near the two ends of the estuarine gradient were used.)

were captured in 400 trap nights for a mean of 0.77 crabs trap^{-1} (Table 1b).

MURRAY RIVER: CRAB DISTRIBUTION ACROSS ESTUARINE GRADIENTS

Four species of sesarmids made up 90.2% of the crab fauna (Table 1b). Crabs showed distinct zonation patterns both across the intertidal zone and along the longitudinal estuarine gradient (Frusher et al. 1994).

COMPARISON OF NORTH AMERICAN AND AUSTRALIAN DATA

Whereas carnivorous xanthids and deposit-feeding ocypodids dominated the assemblage at Rookery Bay, herbivorous grapsid crabs of the subfamily Sesarminae dominated the intertidal crab fauna in the Murray River, Australia. Overall crab abundance also differed significantly between the two estuaries (MANOVA, $F = 4.12$, $p \leq 0.048$, $df = 1$). Pitfall traps contained on average approximately 4 times as many crabs at the Rookery Bay site (Fig. 4). In both estuaries crab abundance was greater in the high intertidal zone than in the low intertidal zone (MANOVA, $F = 6.92$, $p \leq 0.002$, $df = 1$) (Fig. 4).

FATE OF TETHERED LEAVES

No leaves were taken down crab burrows in Rookery Bay. Only two of the 100 tethered leaves showed signs of herbivory: the herbivore was the coffee bean snail, *Melampus coffeus*.

Discussion

Bias of pitfall traps for crabs, though uninvestigated, is likely a function of species-specific behavior. *Eurytium limosum* are highly active predators of invertebrates within the intertidal zone (Kneib and Weeks 1990). Wilson (personal communication) observed these crabs respond to the vibrations of clicking fiddler crab claws by running toward the source of sound. It is possible that the vibrations of crabs captive in the pitfall traps attracted *Eurytium* to the traps. Such a scenario could cause an overestimation of the relative abundance of *Eurytium,* and an underestimation of the abundance of any crabs that became prey for *Eurytium* in the traps. Whereas we cannot completely discount the overestimation of *Eurytium,* we do not believe predation was a major problem in the traps. If predation were very prevalent in traps with *Eurytium* or *Panopeus,* we would expect to find parts of crabs, particularly legs. This was not the case: detached legs were almost always matched with an individual crab for estimation of biomass. Furthermore, many crabs were moribund or debilitated when cleared from the traps, likely a result of drowning: many intertidal crabs have gills modified for aerial existence and drown when they cannot periodically climb out of the water.

The pattern of increasing crab abundance with increasing tidal elevation observed in both southwest Florida and northeast Australia (Fig. 4) has also been observed in Malaysia (Sasekumar 1974). This pattern may be a function of a greater risk of predation from fish and swimming crabs (portunids) in the more frequently flooded low intertidal zone. The pattern could also result from longer feeding times afforded by shorter inundation periods in higher intertidal forests. In summer, Wilson (1989) found that predation risk for four species of crabs in fringing mangrove forests in south Florida was less in the canopy and on prop roots than on the forest floor, and less on low tide than on high tide, suggesting that the primary predators were nektonic.

The greater diversity of the intertidal crab fauna found in a northeastern Australian site compared to a site in southwest Florida (Table 1) is in agreement with previously described patterns of high diversity of mangrove crabs in the Indo-West Pacific (MacNae 1968). Such a pattern is consistent with the species-area hypothesis (Abele and Walters 1979; Connor and McCoy 1979): mangroves occupy far greater area in northeastern Australia and southeast Asia than in Florida and the Caribbean (Saenger et al. 1983).

The marked difference in average abundance of crabs in the two biogeographic areas (Table 1 and Fig. 4) was unanticipated, and begs explanation. A hypothesis, yet untested, is that greater predation from nekton in the Australian forests keeps crab numbers lower than in analogous habitats in Florida. Australian forests experience considerably greater depths of tidal inundation than do the forests of the Caribbean realm: mean tidal range in northeast Queensland is 2.6 m (Smith 1987) compared to 1.2 m in Rookery Bay. Deeper water permits access to the forest by large predaceous fishes (Morton 1990; Robertson and Duke 1990). It is reasonable to expect that shallower water depths in the forest, characteristic of the forests of Rookery Bay and other south Florida and Caribbean forests, preclude some larger predaceous fishes from foraging in these habitats.

The markedly different composition of the two crab faunas in terms of trophic guilds (Table 1, relative abundance of family Grapsidae) is the most striking result of our research. At least in Rookery Bay, the sesarmid crab fauna appears to be poorly developed with the result that there is little if any consumption of freshly fallen leaf litter. (*Melampus coffeus,* the coffee bean snail, has been previously identified as a mangrove leaf detritivore [Smith et al. 1989; Proffitt et al. 1993], though it's relative importance compared to herbivorous crabs is unknown.) Whereas the mangrove tree crab, *Aratus pisonii,* consumes some green leaf material in the canopy (Beever et al. 1979), this species is more omnivorous than herbivorous (McIvor unpublished stable isotope data; Wilson personal communication). *Sesarma curacaoense,* apparently more common near Flamingo in south Florida (Wilson 1989) than at our sites in Rookery Bay, almost certainly consumes mangrove leaf litter (Wilson personal communication) in addition to detritus (Abele 1973). Two congeners that occur in East Coast salt marshes, *Sesarma reticulatum* and *Sesarma cinereum,* consume live and dead plant material (*Spartina alternaflora*), and plant detritus respectively (Seiple and Salmon 1982). (These two species are uncommon at Rookery Bay: none were collected in our pitfall traps.)

To what extent Rookery Bay is typical of south Florida and the Caribbean with regard to a poorly developed herbivorous crab fauna is not known. However, patterns of relative abundance of semiterrestrial crabs on mangrove-dominated isles off Belize (as determined in preliminary studies) are strikingly similar to those at Rookery Bay, that is, dominance by *Eurytium limosum* and several species of *Uca,* lesser numbers of individuals of the leaf-eating genera *Goniopsis* and *Ucides,* and no sesarmids (Smith and Ruetzler unpublished data). Wilson (personal communication) reports that *Sesarma curacaoense* is a secretive, shy crab that spends much of its time in hiding. Abele (1973) reports that the same species is "sluggish." Because of these behavioral traits, the species may be underrepresented in pitfall traps. However, the fact that none of our tethered leaves were taken by herbivorous crabs suggests to us that at least in Rookery Bay, the species, whatever its true abundance, is not common.

In other parts of the Caribbean, herbivorous crabs may be more common. Wiebe and Saucerman (unpublished data) reported that *Ucides cordatus* (Gecarcinidae) and *Goniopsis cruentata* (Grapsidae) removed 98% of baited leaves from a high intertidal forest in Jamaica. Rates of leaf removal in Belizean forests on mangrove-dominated islands are spatially variable and appear to be related to quality of leaf litter and to the relative occurrence of leaf-eating crabs (*Ucides, Goniopsis*) (McKee and Feller 1992). Certainly, other sites in this biogeographic realm need to be surveyed to test the generality of our results. Nonetheless, the observed differences in the faunal assemblages and in the fate of marked or tethered leaves provides preliminary support for Robertson's (1987) hypothesis that leaf litter is processed in fundamentally different ways in the two biogeographic realms.

ACKNOWLEDGMENTS

We wish to thank the Rookery Bay National Estuarine Research Reserve (RBNERR) for on-site logistic support. We thank R. Cowles and K. Kuss for field assistance, and many unpaid volunteers of the educational program at the RBNERR for help in sorting and enumerating samples. We thank M. Shirley for assistance with taxonomy, and A. Foster and V. Meretsky for statistical advice. We appreciate the contributions of the physical plant personnel of the Southeastern Science Center of the National Biological Service in Gainesville, Florida: they generously refurbished a boat for the project. We thank the Department of Fisheries and Aquatic Sciences at the University of Florida for computer support. The comments of two anonymous reviewers substantially improved the quality of this manuscript. This project was funded by National Oceanic and Atmospheric Administration grant NA-89-AA-D-CZ049 from the Marine and Estuarine Management Division to the senior author. This contribution is dedicated to the memory of W. E. Odum who supported and encouraged our research in tidal wetlands.

LITERATURE CITED

ABELE, L. G. 1973. Taxonomy, distribution and ecology of the genus *Sesarma* (Crustacea, Decapoda, Grapsidae) in eastern North America, with special reference to Florida. *American Midland Naturalist* 90:375–386.

ABELE, L. G. AND K. WALTERS. 1979. Marine benthic diversity: A critique and alternative explanation. *Journal of Biogeography* 6:115–126.

BEEVER, J. W., III, D. SIMBERLOFF, AND L. L. KING. 1979. Herbivory and predation by the mangrove tree crab *Aratus pisonii. Oecologia* (*Berl.*) 43:317–328.

BOTO, K. AND J. S. BUNT. 1981. Tidal export of particulate organic matter from a northern Australian mangrove system. *Estuarine and Coastal Shelf Science* 13:247–255.

CAMPBELL, G. R. 1977. A comparative study of the distribution, physiology, morphology, and behaviour of five Sesarminae species occurring along the Ross River Estuary, Townsville. MS Thesis, James Cook University, Townsville, Queensland, Australia.

CONNOR, E. AND E. MCCOY. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113:791–832.

Frusher, S. D., R. L. Giddins, and T. J. Smith, III. 1994. Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary: Effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. *Estuaries* 17:647–654.

Kneib, T. T. and C. A. Weeks. 1990. Intertidal distribution and feeding habits of the mud crab, *Eurytium limosum*. *Estuaries* 13: 462–468.

MacNae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Advances in Marine Biology* 6:73–270.

McKee, K. L. and C. Feller. 1992. Factors influencing rates of mangrove leaf litter removal by crabs in Belize. *Bulletin of the Ecological Society of America* 73:269 (Abstract).

Micheli, F. 1993. Feeding ecology of mangrove crabs in North Eastern Australia: Mangrove litter consumption by *Sesarma messa* and *Sesarma smithi*. *Journal of Experimental Marine Biology and Ecology* 171:165–186.

Micheli, F., F. Gherdi, and M. Vanni. 1991. Feeding and burrowing ecology of two East African mangrove crabs. *Marine Biology* 111:247–254.

Morton, R. M. 1990. Community structure, density, and standing crop of fishes in a subtropical Australian mangrove area. *Marine Biology* 105:385–394.

Odum, W. E. 1971. Pathways of energy flow in a south Florida estuary. Sea Grant Technical Bulletin No. 7. University of Miami Sea Grant Program (Living Resources), Miami, Florida.

Odum, W. E. and E. J. Heald. 1972. Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science* 22: 671–737.

Proffitt, C. E., K. M. Johns, C. B. Cochrane, D. J. Devlin, T. A. Reynolds, D. L. Payne, S. Jeppesen, D. W. Peel, and D. D. Linden. 1993. Field and laboratory experiments on the consumption of mangrove leaf litter by the macrodetritivore *Melampus coffeus* L. (Gastropoda: Pulmonata). *Florida Scientist* 56: 211–222.

Robertson, A. I. 1986. Leaf-burying crabs: Their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *Journal of Experimental Marine Biology and Ecology* 102:237–248.

Robertson, A. I. 1987. The determination of trophic relationships in mangrove-dominated systems: Areas of darkness, p. 292–304. *In:* C. D. Field and A. J. Dartnall (eds.), Mangrove Ecosystems of Asia and the Pacific: Status, Exploitation and Management. Australian Institute of Marine Science and the Australian Committee for Mangrove Research, Townsville, Australia.

Robertson, A. I. and P. A. Daniel. 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* 78:191–198.

Robertson, A. I. and N. C. Duke. 1990. Mangrove fish-communities in tropical Queensland, Australia: Spatial and temporal patterns in densities, biomass, and community structure. *Marine Biology* 104:369–379.

Saenger, P., E. J. Hegerl, and J. D. S. Davie. 1983. Global status of mangrove ecosystems. *The Environmentalist* Vol. 3 (Supplement 3):1–88.

Sasekumar, A. 1974. Distribution of macrofauna on a Malayan mangrove shore. *Journal of Animal Ecology* 43:51–69.

Seiple, W. and M. Salmon. 1982. Comparative social behavior of two grapsid crabs, *Sesarma reticulatum* (Say) and *S. cinereum* (Bosc). *Journal of Experimental Marine Biology and Ecology* 62:1–24.

Sheridan, P. F. 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. *Bulletin of Marine Science* 50:21–39.

Smith, T. J., III. 1987. Physical determinants of inter-estuary variation in mangrove species richness around the tropical coastline of Australia. *Journal of Biogeography* 14:9–19.

Smith, T. J., III, K. G. Boto, S. D. Frusher, and R. L. Giddins. 1991. Keystone species and mangrove forest dynamics: The influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science* 33:419–432.

Smith, T. J., III, H. T. Chan, C. C. McIvor, and M. B. Robblee. 1989. Comparisons of seed predation in tropical, tidal forests on three continents. *Ecology* 70:146–151.

Warner, G. F. 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. *Journal of Animal Ecology* 38: 379–389.

Williams, A. B. 1983. The mud crab, *Panopeus herbstii*, S. L. Partition into six species (Decapoda: Xanthidae). *Fishery Bulletin* 81:863–882.

Wilson, K. A. 1989. Ecology of mangrove crabs: Predation, physical factors and refuges. *Bulletin of Marine Science* 44:263–373.

Received for consideration, February 15, 1994
Accepted for publication, May 8, 1995